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The Downtonian ostracoderm *Sclerodus* Agassiz (Osteostraci: Tremataspididae)

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Synopsis

Various aspects of the morphology of the osteostracan *Sclerodus* Agassiz are described and discussed in the light of new specimens in an attempt to reconcile four different morphological interpretations. It is concluded that *Sclerodus* has normal osteostracan sensory fields, that the lateral line system may be represented as a series of pits, and that the margin of the cephalothoracic shield is penetrated by four fenestrae which may possibly have served a stabilizing hydrodynamic function. Relationships of *Sclerodus* are discussed with a review of osteostracan classification leading to discussion of computer-generated trees. A phylogeny is favoured which treats ateleaspids as a paraphyletic group and tremataspids as a monophyletic derived group.

Introduction

Sclerodus pustuliferus Agassiz is a small and rather unusual osteostracan restricted to the Downtonian of the Anglo-Welsh basin. Remains of *Sclerodus* are very common in the Ludlow Bone Bed and immediately overlying rocks, where it is easily recognized by its distinctive ornament of small, closely-packed hemispherical tubercles. However, the abundance of its remains is matched by our ignorance of its morphology. Only the dorsal half of the cephalic armour is known, and even here knowledge is incomplete. There are very few reasonably intact specimens and regrettably one of the best (Stensiö 1932: pl. 52, fig. 2) has now been lost. The fragments most commonly found are pieces of the main part of the shield and portions of the so-called 'cornua'. Each 'cornu' bears a marginal row of elongate tubercles, so that fragments of them were initially confused with jaws and teeth. More complete material enabled Lankester (1870) to confirm a suggestion made by Harley (*in* Murchison 1867) that *Sclerodus pustuliferus* is, in fact, an osteostracan and to provide the first restoration (Lankester 1870: fig. 31). Since that time three further restorations have been attempted (Stensiö 1932, Denison 1951*a*, Janvier 1975). No two of these agree on interpretation of structures which are obvious in other osteostracans, such as the presence or absence of cornua, pectoral sinuses or one or more lateral sensory fields.

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These discrepancies, combined with the fact that *Sclerodus* shows some interesting specializations along the rim of the cephalothoracic shield, make this monotypic genus an interesting subject for study. The main motivation derives from sporadic collecting in the Ludlow Bone Bed at Forge Bridge, Downton Castle estate, Shropshire by Dr W. Graham-Smith of Boars Hill, Oxfordshire. Dr Graham-Smith has collected many fragments of *Sclerodus*, some of which show unusual and previously undescribed pits surrounding the orbits. One specimen, BMNH P.58694, described and illustrated here (Fig. 5, p. 11), was particularly helpful in the reinterpretation of existing material. I am grateful to Dr Graham-Smith for the donation of several specimens. It has allowed me to redescribe and update our knowledge of *Sclerodus* and to offer comments on some of the more unusual aspects of this genus.

Historical review

Sclerodus pustuliferus was first described by Agassiz (*in* Murchison 1839: 606; pl. 4) from figures, sent to him by Murchison, of four fragmentary specimens. On the basis of these figures Agassiz likened the fragments to the grinding teeth of the 'bradyodont' *Psammodus*, and because of the rough pustulated surface he coined the name *Sclerodus* (rough-tooth) *pustuliferus*. On the same occasion Agassiz described seven further specimens as jaws and teeth under the names *Plectrodus mirabilis* and *Plectrodus pleiopristis*.

M'Coy (1853) reinterpreted nearly all the specimens figured by Murchison (1839: pl. 4), including those referred to species of the genera *Sclerodus* and *Plectrodus*, as being the remains of the crustacean *Pterygotus*. Additionally, he could see no reason to recognize separate species and united them all under the name *Pterygotus pustuliferus* (= *Plectrodus mirabilis* + *P. pleiopristis* + *Sclerodus pustuliferus*). It should be noted that M'Coy (1853: 13) apparently did not see the original material referred to those species because it had by then been 'lost' (see below).

Murchison (1853) replied testily, saying that he, and Messrs Salter and J. Sowerby, who had prepared the drawings sent to Agassiz, disagreed with the crustacean interpretation and maintained the identity of these remains as fish jaws and teeth. Egerton (1857) followed by describing more material from Ludlow as jaws of *Plectrodus mirabilis*. Thus, while authors disagreed over whether there were one or more species, almost all agreed that they were fishes and not crustaceans. This was confirmed by Harley (1861: 544, footnote) who had sectioned specimens and found them to be made of bone and dentine. Harley further suggested that they were the posterior spines (cornua) of cephalaspid fishes rather than fish jaws and teeth. Murchison, while acknowledging Harley's opinions (1867: pl. 35, legend), remained convinced that they were jaws and ankylosed teeth (1867: 241).

Lankester (1870: 58) supported Harley's view by describing tolerably complete head shields based on new material collected by Dr Grindrod and Mr Lightbody from the Downton Castle Sandstone of Ludford Lane, Ludlow. Lankester regarded *Plectrodus mirabilis* and *P. pleiopristis* as junior synonyms of *S. pustuliferus* and considered *Sclerodus* as a subgenus of *Auchenaspis* Egerton. He named this subgenus *Eukeraspis*, but he gave no reason why he dropped the name *Sclerodus*. *Eukeraspis* was associated with *Thyestes* (*Auchenaspis*) because Lankester believed that in both the shield was composed of a semicircular cephalic porton and an abdominal portion formed by separate paired plates. The abdominal portion was unknown for *Eukeraspis*, but Lankester predicted its presence, adding (1870: 59) '. . . this is a question which inquiry with the hammer may soon decide . . .'. Such inquiry has failed to find the abdominal division, but from Lankester's time *Sclerodus* has been closely associated with *Auchenaspis* (*Thyestes*). Nevertheless, Lankester (1870: fig. 31) did provide the first restoration of the cephalic shield.

Woodward (1891) agreed with Lankester over the restoration, association with *Thyestes*, and renaming *Eukeraspis*. But Woodward considered *Eukeraspis* to form a distinct genus (syn. *Sclerodus*, *Plectrodus*).

Thus, to this point in the confused history of *Sclerodus* there had been debate about whether the Ludlow Bone Bed material represented one, two or three species; whether it belonged to fishes or to crustaceans; whether it represented jaws and teeth or part of the cephalic shield;

and finally, whether the generic name should be changed to *Eukeraspis*. By the turn of the century the consensus seemed to be that there was one species, that it was a cephalaspid fish closely related to *Thyestes* and that the original material described by Agassiz represented the denticulated cornua and should go under the name of *Eukeraspis*.

Woodward (1917) considerably clarified the situation by following through his earlier suspicion (1891: 195) and a suggestion by Priem (1910: 5) that *Plectrodus mirabilis* and *P. pleiopristis* represented the dentigerous jaws of ischnacanthid acanthodians. This is the current status of *Plectrodus* (Denison 1979: 41). Thus, *Sclerodus pustuliferus* remains the only cephalaspid material described by Agassiz in Murchison's *The Silurian System*. The change of generic name to *Eukeraspis* is unnecessary (see also Stensiö 1932: 175, footnote).

Subsequent work on *Sclerodus* is chiefly that of Stensiö (1932), who has provided the most complete description, Denison (1951*a*, *b*) and Janvier (1975). These authors differ in their interpretations of the 'cornua' and sensory fields and their ideas are discussed in the relevant descriptive sections below. A summary of the differing ideas of the morphology is provided in Fig. 1.

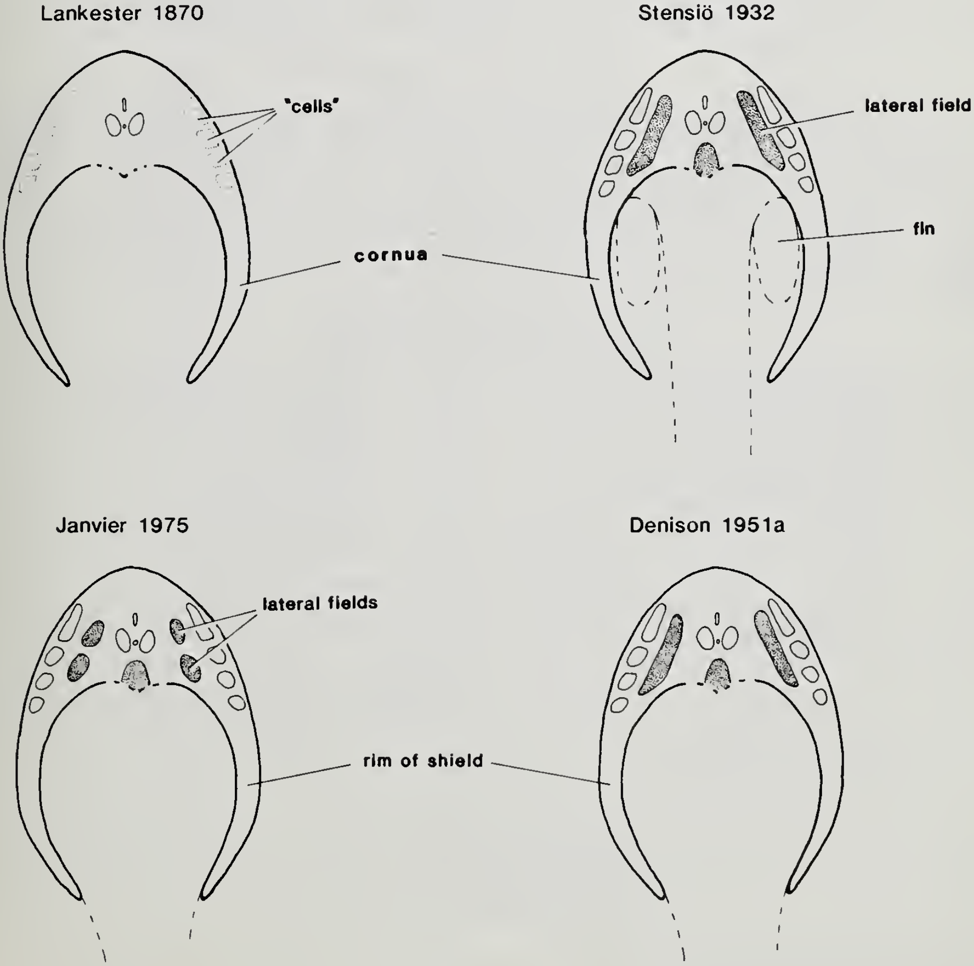


Fig. 1 *Sclerodus pustuliferus* Agassiz. Four morphological interpretations.

As described above, the early history of the study of *Sclerodus* was somewhat tangled. Unfortunately, the history of the original material is equally problematical. When Agassiz described *Sclerodus* and *Plectrodus* he did so from drawings. Murchison (1853), in his reply to M'Coy (see above), records that he had given the specimens, collected and mounted on cards by Rev. R. W. Evans, to the Geological Society of London. But he also records that the specimens could no longer be found (see also Murchison 1867: 133, footnote). So, sometime between 1839 and 1853 some of the specimens illustrated in plate 4 of *The Silurian System* had gone astray. It appears (Jeannet 1928) that some of the material was incorporated in the Musée d'Histoire Naturelle de Neuchâtel and later into the Institut de Géologie de l'Université de Neuchâtel where Agassiz taught, 1832–1846. It is possible that Agassiz, who visited England in 1840, or Joseph Dinkel, Agassiz' artist based at the Geological Society for several years, took some specimens to Neuchâtel with the intention of describing them more fully. But by then Agassiz was preoccupied with his glacial studies; in any event the descriptions were not forthcoming.

Woodward (1917: 74) found three of the original specimens in Neuchâtel in 1898 while Jeannet (1928: 106) records five of the original 11 specimens referred to *Sclerodus* and *Plectrodus*. There is only one of the four original specimens of *Sclerodus pustuliferus* and this is listed as number 3 and represents that illustrated in Murchison's *The Silurian System* (1839: pl. 4, figs 60–62). This was quite correctly chosen as the lectotype by Stensiö (1932).

Material and methods

The material studied belongs to the British Museum (Natural History) (BMNH); the British Geological Survey, Keyworth (BGS); and the Department of Geology, University of Birmingham (BU). The specimens are referred to by register number prefixed by their respective institutional abbreviations. Most of the material is from the Ludlow Bone Bed and was studied directly. Rubber latex casts were helpful in the study of the material from the Downton Castle Sandstone. Histological sections were made from isolated fragments found in the Ludlow Bone Bed.

Abbreviations used in figures

a.p	grooves housing anterior and posterior semicircular canals
a.pit	anterior pit
c.f	circumnasal fossa
d	canal leading to dorsal sensory field
d.a	groove for dorsal aorta
d.s.f	dorsal sensory field
h.v	groove for lateral head vein (jugular vein)
i.c.a	foramen for internal carotid artery
l.s.f	lateral sensory field
m.f	marginal fenestra
m.pit	middle pit
n.c	foramina for nerves
n.d	nasohypophysial duct
n.o	nasohypophysial opening
o	orbit
o.a	foramen for occipital artery
oes	groove for oesophagus
orn	ornament
o.r	olfactory recess
p.d	pineal duct
p.f	prebranchial fossa
p.o	pineal opening
p.pit	posterior pit
prof	foramen for profundus nerve
v.c	vestibular chamber
v.s	superficial vein issuing from head vein
IV, V_2, VII, IX	cranial nerves
1–4 s.e.l.	canals leading to lateral sensory fields (see p. 12)

Systematic description

Family **TREMATASPIDIDAE** Woodward, 1891

Genus ***SCLERODUS*** Agassiz, 1839

1839 *Sclerodus* Agassiz (in Murchison): 606.
1870 *Auchenaspis* Egerton (in part); Lankester: 58 (subgenus *Eukeraspis*).
1887 *Eukeraspis* Lankester; Zittel: 150.
1891 *Eukeraspis* Lankester (in part); Woodward: 193 (not *Plectrodus*).

DIAGNOSIS (emended). Tremataspids in which the circumnasal fossa is deep and elliptical, with a smooth floor: cephalothoracic shield perforated along lateral margin by four fenestrations, the largest lying anteriorly; thereafter each decreasing in size posteriorly: sensory lines absent, but perhaps represented by three pairs of pits lying close to the orbit and circumnasal fossa: abdominal region of the shield ossified along lateral margin only, leaving central part naked or perhaps covered with scales: ornament developed as regular hemispherical tubercles which are particularly large over the swellings immediately in front of and behind the pineal recess: margin of shield bearing a regular row of enlarged tubercles: histology of exoskeleton very simple, represented only by basal layer and overlying spongy bone with no circumareal canals.

TYPE AND ONLY SPECIES. *Sclerodus pustuliferus* Agassiz.

Sclerodus pustuliferus Agassiz

1839	*Sclerodus pustuliferus* Agassiz (in Murchison): 606; pl. 4, figs 27–32, 60–62.
1854	*Sclerodus pustuliferus* Agassiz; Murchison: pl. 35, figs 9–12.
1870	*Auchenaspis* (*Eukeraspis*) *pustulifera* (Agassiz); Lankester: 58, figs 31, 32; pl. 31, figs 9–14.
1932	*Sclerodus pustuliferus* Agassiz; Stensiö: 177, fig. 62; pl. 52, figs 1, 2; pl. 53, figs 1–5; pl. 56, fig. 1.
1951*a*	*Sclerodus pustuliferus* Agassiz; Denison: 185.
1975	*Sclerodus pustuliferus* Agassiz; Janvier: figs 2B, 5.

DIAGNOSIS. As for genus; the only species.

LECTOTYPE. Fragment of cornu: Institut de Géologie, l'Université de Neuchâtel number 3. Ludlow Bone Bed, Downtonian; Ludlow, Shropshire. Selected Stensiö (1932: 177).

MATERIAL. Fifty-five specimens were examined in this study, as detailed in Appendix, p. 27. The material comes from the Ludlow Bone Bed, Downton Castle Sandstone and Temeside Shales/Lower Red Downton Sandstone of Shropshire, Herefordshire and Staffordshire.

DESCRIPTION. The general shape of the shield is seen in BMNH P.9756, on which the restoration in Fig. 2 is based. The cephalic portion is strongly vaulted at the level of the orbits but the rim of the shield and so-called cornua are shallow.

There are few specimens which show the cephalic portion attached to the so-called cornua; more usually broken cephalic shields and isolated 'cornua' are found. One complete specimen (BMNH P.9756, Fig. 2) shows a total length of 45·5 mm, of which the cephalic portion is 21 mm long. Using the proportion of cephalic to 'cornu' length of this specimen one can estimate that the largest specimen (BGS GSM 5150) must have been about 85 mm in total length (snout to posterior level of 'cornua'). The greatest width occurs two-thirds of the way back and the outline of the head plus 'cornua' resembles that of *Dartmuthia* or *Tremataspis.*

The orbits are placed close together and this means that the pineal area is confined to a narrow longitudinal strip. No dermal pineal plate has been found and the extreme narrowness of the space left between the orbits may imply its absence. The pineal opening lies slightly below the surface where it opens at the end of a short duct within the skeleton (Figs 3, 5B, C). The duct is slightly asymmetrical which no doubt reflects the asymmetry of the underlying habenular recess as described by Janvier (1977) for *Belonaspis puella* (Wängsjö).

The anterior and posterior borders of the orbital area are raised into prominent ridges which bear ornament tubercles larger than those covering most of the shield. The anterior ridge runs into a crest surrounding the nasohypophysial opening, while the posterior ridge is continuous with a shallow ridge defining the dorsal sensory field (Fig. 3). The nasohypophysial opening is contained within the floor of a deep, well-defined depression—the circumnasal fossa (Stensiö 1932: fossa circumnasalis, Stensiö 1927; antorbital fossa, Lankester 1870). The nasohypophysial opening is slit-like and immediately surrounded by a narrow ridge of bone. The form of the circumnasal fossa is very similar to that seen in thyestidians (*sensu* Janvier 1981*b*) and especially to *Tremataspis* (Janvier 1985*b*: fig. 34A).

The nasohypophysial opening is an elongate slit similar to that seen in thyestidians. But it should be noted that a similarly-shaped opening is also seen in more plesiomorphic kiaeraspidians (Janvier 1981*b*). Such a shape implies that the hypophysial and nasal divisions are of

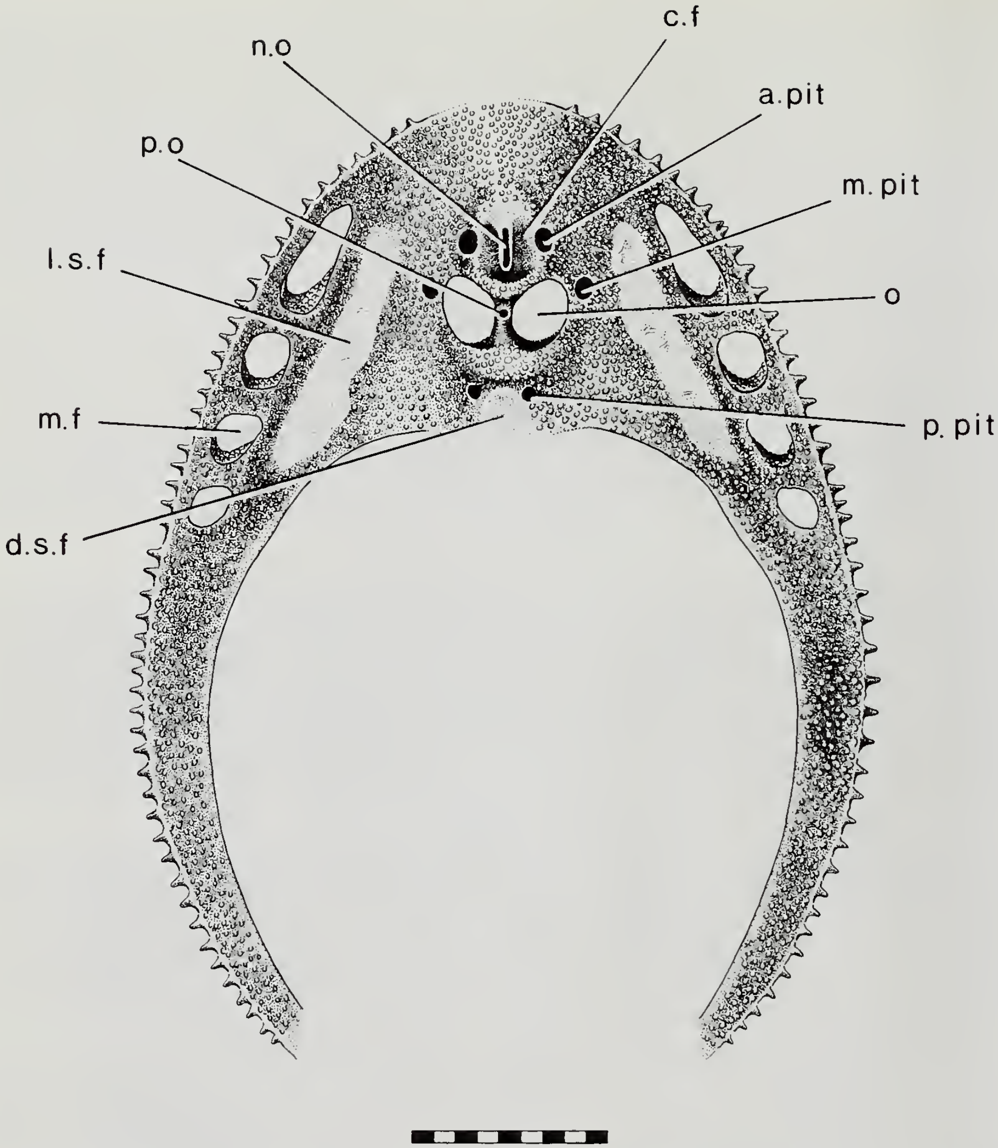


Fig. 2 *Sclerodus pustuliferus* Agassiz. Restoration of the cephalothoracic shield. Proportions based on BMNH P.9756. Scale bar in mm intervals.

equal size, in contrast to some other osteostracans where there is marked inequality between these openings (Janvier 1985*a*: fig. 59).

Several specimens show parts of the endocranial cavity, orbits and vestibular chambers, but all are poorly preserved so that only isolated details can be described. For the most part these details agree with those described for other osteostracans. The olfactory sac was housed within a deep recess (Fig. 5D) which forms the undersurface of the ridge between the orbits and the circumnasal fossa. More posteriorly, the grooves housing the anterior and posterior semicircular canals, flanked by a groove for a large jugular vein, can be seen in BGS GSM 5150 (Fig. 4A).

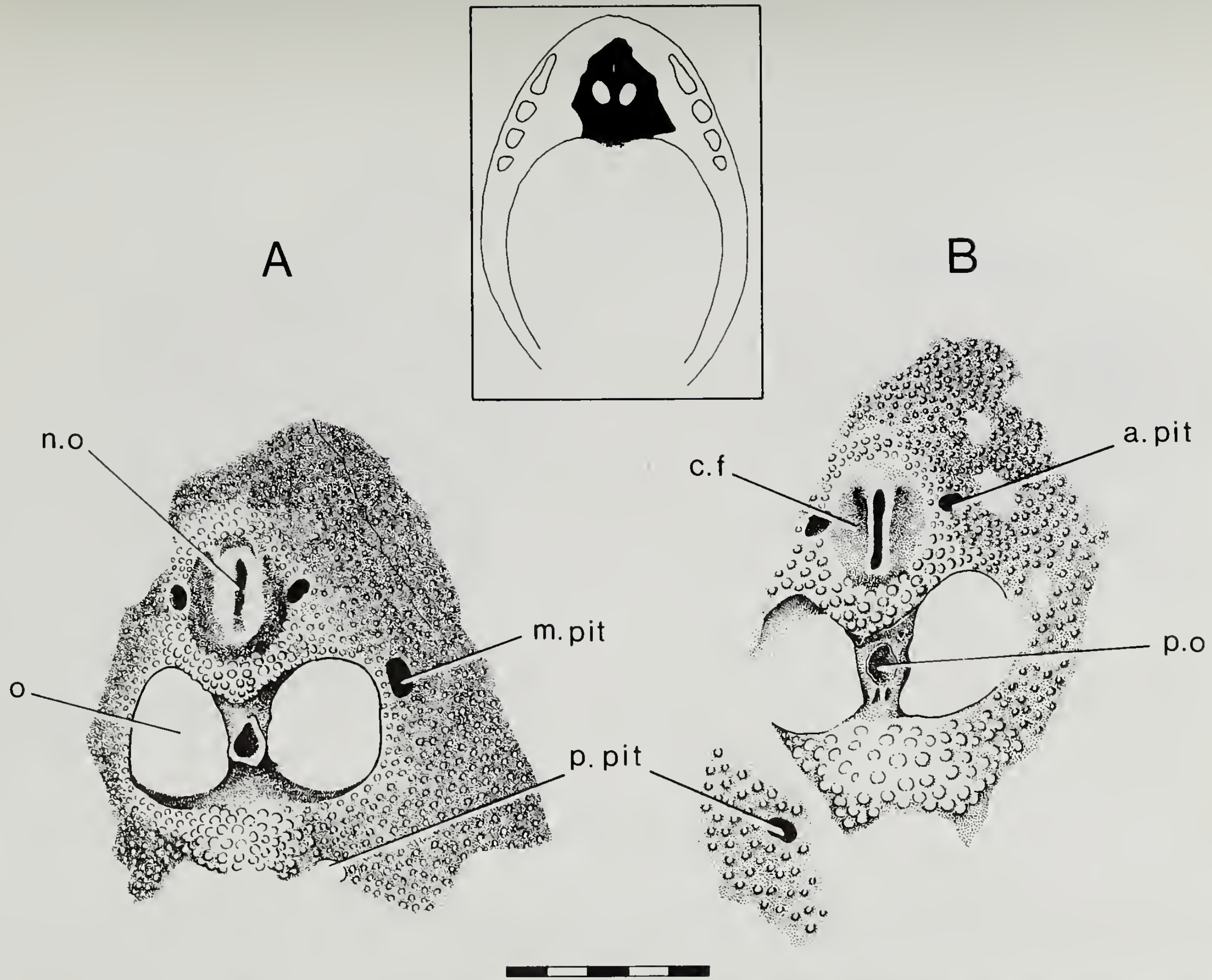
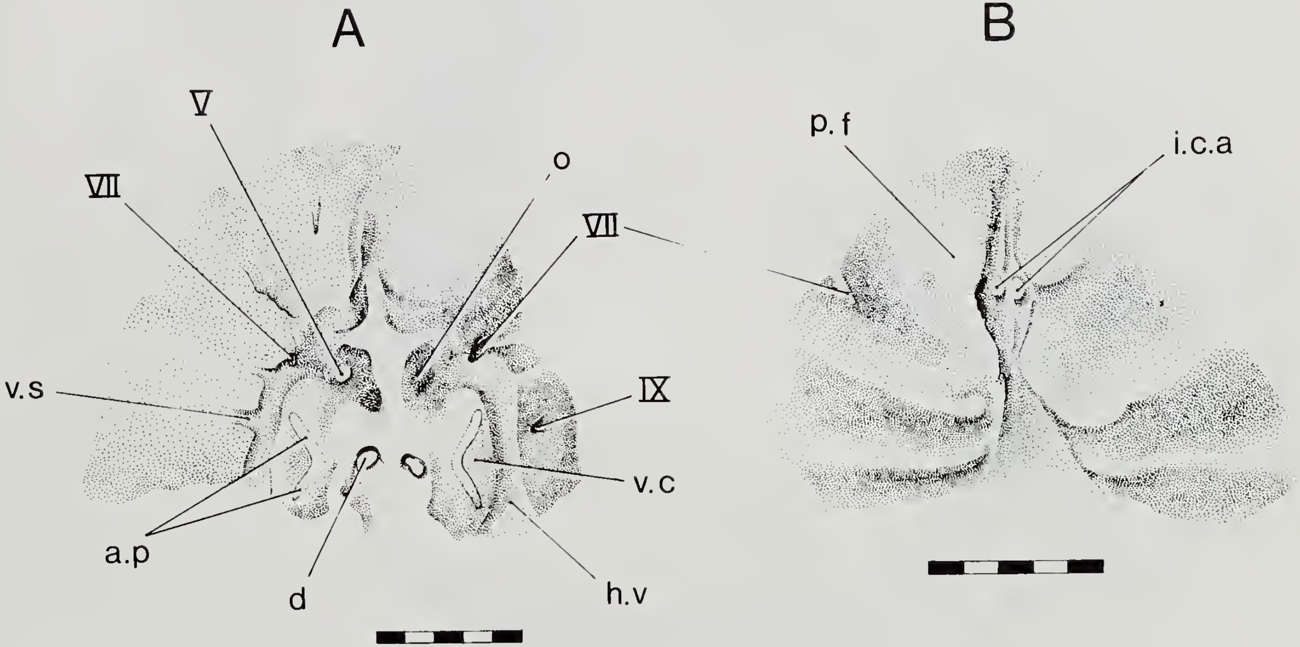


Fig. 3 *Sclerodus pustuliferus* Agassiz. Drawings of two specimens showing details of circumnasal fossa, pineal and orbital areas. A, BMNH P.27099. B, BMNH 35999. Scale bar in mm intervals.


A
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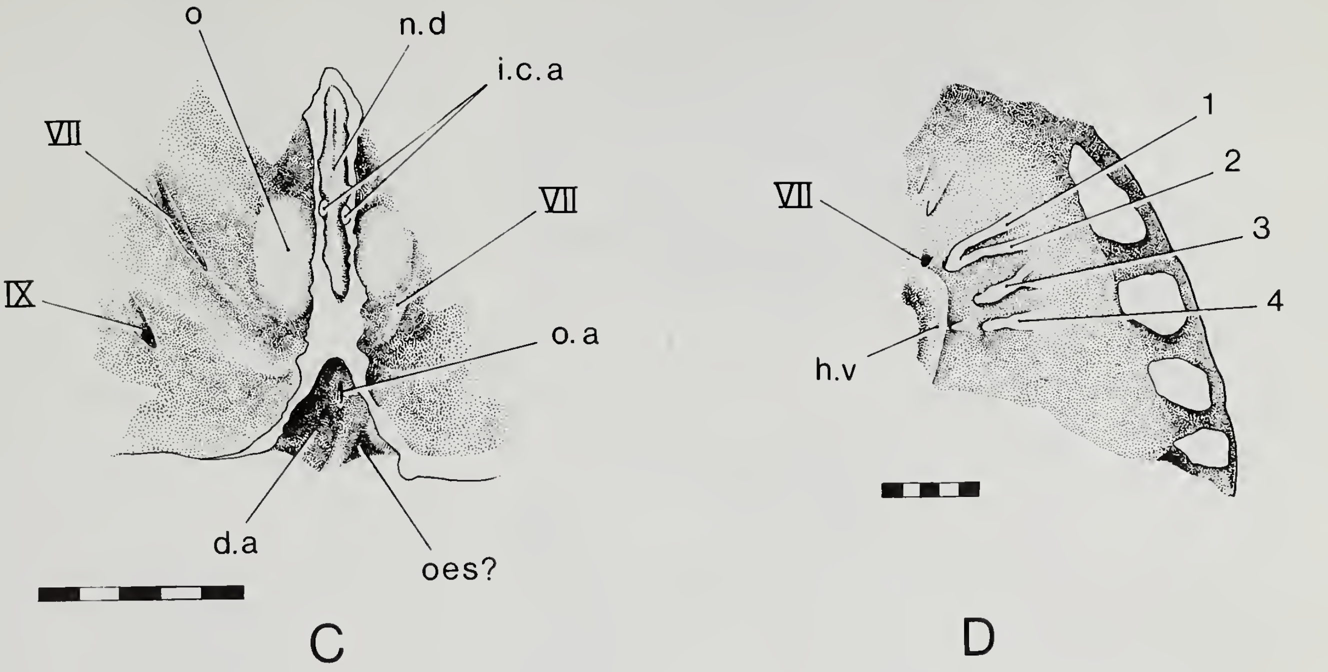

Fig. 4 *Sclerodus pustuliferus* Agassiz. Camera lucida drawings to show internal structures of cephalic shield as preserved in four specimens. A, BGS GSM 5150: dorsal view of brain cavity, floor of orbits and vestibular region. B, BGS GSM 21469: dorsal view of brain cavity and roof of oralobranchial chamber showing interbranchial ridges. C, BMNH P.9756: ventral view of central part of oralobranchial chamber showing orbital floor as swellings and ventral aspect of matrix-filled nasohypophysial duct; entire specimen illustrated by Stensiö (1932: pl. 53, fig. 5). D, BGS GSM 5149: dorsal view of right half of cephalic shield to show canals leading to lateral sensory field. Scale bars in mm intervals.

On the ventral surface the matrix infilling of the brain cavity suggests that the hypophysial duct is very long, reaching well back below the orbits and notched at the level of the anterior ends of the orbits by the entry of the internal carotid arteries (Figs 4B, C). The entry of the carotid arteries is asymmetrical, a fact which Janvier (1981*b*: 39) attributes to the constriction in this area caused by the proximity of the anterior cardinal veins. The material of *Sclerodus* is not good enough to comment on this suggestion. The floor of the orbit can be seen in BMNH P.9756 (Fig. 4C). Here it can be seen that the orbits of either side come into very close proximity with each other and may even meet, as in *Tremataspis* and *Oeselaspis* (Janvier 1985*b*: fig. 20). But there does not appear to be any medial recess of the posteroventral myodome (*sensu* Janvier 1981*a*; myodome of Stensiö 1927: fig. 28) such as is developed in most osteostracans (Janvier 1985*a*).

The posterior wall of the orbit is perforated by at least two foramina which lie close together and may be confluent (Fig. 5C). They are very unequal in size, the more dorsal being the smaller. They probably gave exit to the trochlearis above and the profundus below. The oculomotor may have entered the orbit through a small foramen lying near the floor and the medial wall. The floor and part of the rear wall of the orbit is perforated by a large foramen (Fig. 5C: V_2). I assume this is the trigeminal foramen through which V_2 and possibly VI passed. It probably also marks the place where the head vein entered the orbit, since there is no separate lateral foramen as in *Norselaspis* (Janvier 1981*b*: fig. 14A) or *Belonaspis* (Janvier 1977: fig. 7A). The path taken by the facial nerve marks the ventral surface of the orbit as a ridge (Fig. 4C) running anterolateraly immediately beneath the floor of the orbit.

Beneath the occipital region there is a triangular depression which pierces the postbranchial wall. It is best seen in BMNH P.9756 (Fig. 4C) and was labelled by Stensiö (1932: pl. 53, fig. 5) as the aortic groove. This is almost certainly correct, but the depression is of more complicated shape than implied by Stensiö. The depression (Fig. 4C) shows a deep groove which swings to the right as it passes posteriorly. This is typical for osteostracans and carried the dorsal aorta. The position of the issuing occipital artery may be indicated on the specimen illustrated (Fig. 4C, o.a). On the left side there is a shallower, shorter groove which appears to swing to the left. There are at least two interpretations of this groove: it could have housed the base of the subclavian artery (Janvier 1981*b*), or perhaps accommodated the oesophagus (Janvier 1984).

The orientation of the gill chambers is of the 'oligobranchiate' type as defined by Stensiö (1958). Only three branchial chambers are obvious on the specimens available (Fig. 4B) but there may well have been more, crowded posteriorly.

Sensory canal system. The sensory lines of *Sclerodus* are thought to have lain entirely superficial to the exoskeleton (Denison 1951*b*: 214) or to have been absent altogether (Stensiö 1932: 179). Certainly, no pit lines, grooves or pores mark the surface, a fact which Stensiö related to the absence of the superficial layer of the dermal skeleton. There are, however, other structures which may reasonably be interpreted as evidence of the sensory line system.

In specimens showing the orbital and nasohypophysial region there are often cup-shaped pits visible (Figs 3, 5, 6). Three pairs are consistently present (Fig. 3). The anterior is found at the level of the nasohypophysial opening and lies on or just outside the rim delimiting the circumnasal fossa. The middle pit lies close to the orbital margin, roughly level with the middle of the orbit. The posterior pit lies just behind the postorbital swelling close to the edge of the dorsal sensory field. One or more of these pits may be seen in several specimens (BMNH 35999, 45949b, P.9756, P.27099, P.48704, P.58694, BGS GSM 5151 and BU 1992). These pits seem to have been overlooked by earlier investigators, since one or more are present in specimens used by Stensiö and Lankester. It is possible that those authors considered the pits to be preservational artifacts, as many specimens show breaks in the exoskeleton. Two more recently discovered specimens (BMNH P.48704 and especially P.58694), which show the pits particularly clearly, demonstrate that they are not artifacts. In both specimens the rim of the pits is perfectly regular and the smooth lining is pierced by one or more minute foramina (Fig. 5). The undersurface of the left anterior pit of BMNH P.58694 (Fig. 5D) shows that the foramina pierce the base of a longitudinal groove upon the visceral surface.

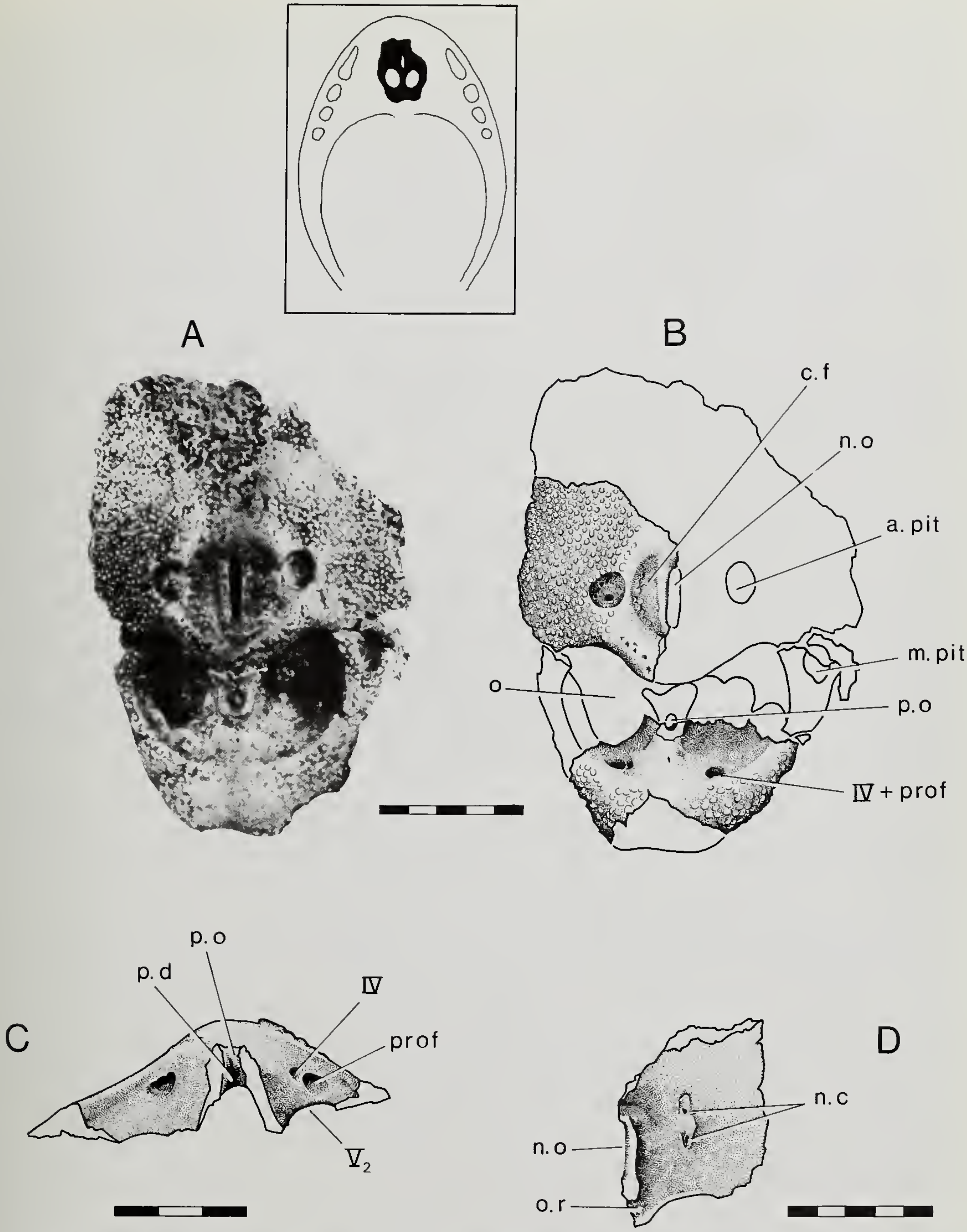

Fig. 5 *Sclerodus pustuliferus* Agassiz. BMNH P.58694, a specimen showing circumnasal fossa, orbits and pits: since its discovery the specimen has unfortunately been broken. A, specimen as originally collected—dorsal view, anterior towards top. B, drawing of remaining parts of specimen. C, anterior view of posterior wall of orbits. D, undersurface of fragment showing edge of naso-hypophysial opening and foramina piercing the floor of the anterior pit. Scale bars in mm intervals; note larger scale of C.

From the best preserved specimens it can be seen that each pit is ovoid to nearly circular in outline. The anterior and middle pits are of equal size and their longest diameter is about 75% as long as the nasohypophysial opening. The posterior pit is slightly smaller, being less than half the length of the nasophypophysial opening. In BMNH 45949b there is a further pit-like depression (Fig. 6A) located midway between the median line and the margin of the shield and at the transverse level of the posterior pit. This has been observed only on a single specimen, on one side only, and the borders of the pit are rather irregular; it thus may well be an artifact of preservation and it is not included in the restoration (Fig. 2).

Dr Janvier (personal communication) suggested that these pits may be the location of very large tubercles which have become lost during preservation. Longitudinal rows of enlarged dentine-capped tubercles are known in cladistically more derived thyestidians and, furthermore, Denison (1951*b*: fig. 35b) records that in *Thyestes verrucosus* Eichwald each tubercle is underlain by a deep cavity. This idea is attractive and it would certainly be good evidence for associating *Sclerodus* with thyestidians. However, I consider that the pits are real surface structures for three reasons. No specimen of *Sclerodus* shows any sign of tubercles other than the small general surface tubercles; the rim of each pit is perfectly smooth and it tips into the cavity without break; and the floor is perfectly smooth and pierced by foramina.

Functional interpretation of these pits is hampered by the rarity of comparable structures in other fishes. No other osteostracan appears to have such pits, but comparison raises two possibilities. These pits may be an unusual development of the lateral sensory fields or they may be parts of the cephalic lateral line system. The first possibility seems unlikely because lateral fields, with their canal innervation, are present as in other osteostracans (see below). Also, the pits are wholly contained within the exoskeleton and therefore unlike sensory fields, vacuities passing completely through the exoskeleton and filled with small tesserae. The second possibility is more plausible. The floor of a pit (Fig. 5D) is pierced by a foramen of a size suggesting that nerves supplying neuromasts passed through. Furthermore, the pits are disposed in positions that, in thyestidians (*sensu* Janvier 1981*b*), would lie along the infraorbital line which lies close to the orbital margin and turns medially anterior to the nasohypophysial opening. I am therefore inclined to the view that these pits represent an unusual development of the sensory line system of *Sclerodus*.

Sensory fields and related s.e.l. (sinus expansion of the labyrinth) canals. There have been three different interpretations of the sensory fields of *Sclerodus* (Fig. 1). Lankester (1870: fig. 31) recognized only the dorsal field which he described as the postorbital valley. Stensiö (1932: fig. 62) identified both dorsal and lateral sensory fields, while Janvier (1975: fig. 5 *11*) restored a dorsal plus subdivided lateral fields.

This investigation agrees with Stensiö's results and suggests that *Sclerodus* possessed the usual osteostracan complement of single paired lateral fields plus a median dorsal field (Fig. 2). In no specimen are they clearly seen. The dorsal field is particularly poorly known. The anterior end is seen in BU 1992 where the margin is described by a low semicircular ridge and may (BMNH P.27099) be notched by the posterior sensory pit (Fig. 3A). The posterior limit of the dorsal sensory field remains unknown. Two specimens (BGS GSM 5150, and that figured by Stensiö, 1932: pl. 52, fig. 2) show paired canals leading from the vestibular region to the dorsal field area. Stensiö (1927: fig. 27A, *des*) has restored these canals for *Kiaeraspis* and Janvier (1977: fig. 9A, *c.c.s.d.*) for *Belonaspis puella*, and there is nothing to suggest conditions in *Sclerodus* were any different.

Evidence for the presence of lateral sensory fields is provided by breaks in the exoskeleton and traces of the canals (s.e.l. canals) which lead to them. The canals may be seen most clearly in BGS GSM 5149 (Fig. 4D) among available material and they were also recorded by Stensiö (1932: pl. 52, fig. 2). The partial counterpart of the specimen illustrated by Stensiö is BMNH 45949b and is also illustrated by the author (1932: pl. 52, fig. 1); it can be seen that by superimposing the two illustrations the s.e.l. canals run to just within the inner margin of the space labelled as the lateral sensory field.

The pattern of the canals is different in the two specimens. In the specimen illustrated by

Stensiö the first canal is double and branches close to the lateral field; this is very similar to the pattern in thyestidians, kiaeraspidians and benneviaspidians (*sensu* Janvier 1981*b*). But in BGS GSM 5149 (Fig. 4D) the branching of the first canal occurs midway between the level of the orbit and the lateral field area, a condition which Janvier (1985*a*) ranks as plesiomorphic for osteostracans. Since only two specimens of *Sclerodus* show evidence of the s.e.l. canals it is unwise to speculate on the significance of one or the other pattern, particularly since variation is known within other thyestidian taxa (Denison 1951*a*). It is, however, worth remarking that the facial nerve appears to run in front of the first canal. Stensiö illustrates five main canals and by comparing the relationship between the canals and the lateral fenestrations it appears that the posterior two are not seen in BGS GSM 5149, probably as a preservational defect. It also appears as though the s.e.l. canals radiate regularly from the otic region: that is, they are not branched into two distinct groups as they are in *Oeselapis* and *Tremataspis* where there are two separate sensory areas.

A number of other specimens (BMNH 45949b, P.9756, P.41095, BU 1992) show evidence of the lateral sensory field as depressions or irregularly-shaped vacuities in the exoskeleton (Fig. 7A). These specimens show that the sensory field stretched from the level of the first marginal fenestration to the third. The lateral border is quite distinct but the inner margin is somewhat irregular. The size and extent of the lateral field is similar to that seen in *Dartmuthia*, *Saaremaspis* and *Thyestes*.

The 'cornua'. Lankester (1870) and Stensiö (1932) both considered that the shield of *Sclerodus* continued posterolaterally on either side as long cornua. Stensiö believed that the 'cornu' bordered a pectoral fenestra containing a fin. A countertheory (Denison 1951*a*, Janvier 1975) suggests that the so-called 'cornu' is really only the lateral margin of the cephalothoracic shield, that there were no pectoral fenestrae containing fins and that the area between the 'cornua' was occupied by an unarmoured abdomen.

A number of observations suggest to me that the latter theory is correct. The 'cornu' is highly asymmetrical in cross section such that the ventral surface is flat, or nearly so, the dorsal and mesial surfaces are concave and the mesial edge is considerably deeper than the lateral edge. The cross-sectional shape looks like the sectioned edge of the cephalic shield. The lateral edge bears a single row of well-developed tubercles. The dorsal and ventral surfaces bear regular small tubercles. But tubercles are absent from the mesial surface which is instead perfectly smooth. These observations contrast with the cross-sectional aspect of true cornua as seen in most cornuate osteostracans. There, the shape is roughly symmetrical and is flattened, the surfaces are all convex to a greater or less degree, and the ornament continues on to the mesial surface and is usually developed as a series of enlarged tubercles.

The medial wall of the 'cornu' sweeps anteromedially to merge with the postbranchial wall. If a pectoral fin were present there should be some sign of insertion as seen in *Boreaspis* (Janvier 1977) or *Benneviaspis* (Janvier 1985*a*). But in two specimens (BMNH P.45315, BGS GSM 5149) showing this area clearly the bone is perfectly smooth.

One final observation is that the 'cornua' of *Sclerodus* are solid structures (Stensiö 1932: pl. 56, fig. 1). Large cornua, such as are seen in cephalaspids and scolenaspids, are penetrated by several large canals thought to have contained various blood vessels (Wängsjö 1952: fig. 17).

Thus, as restored, I believe that the area of the body between the 'cornua' was naked and suggest that the exoskeleton was coextensive with the endoskeleton. In both *Tremataspis* and *Oeselaspis* the endoskeleton of the cephalic portion curves posterolaterally to line the edge of the shield: the development of the endoskeleton is particularly extensive in *Didymaspis* (Janvier 1985*b*: fig. 19).

Lateral fenestrations. The lateral margin of the cephalic shield is marked with fenestrations. Lankester (1870: 58) considered that these fenestrations were cells within the exoskeleton and were therefore roofed and floored by bone. Stensiö (1927: 240) originally interpreted them as remnants of a much subdivided lateral sensory field, but subsequently changed his mind. Stensiö (1932) and Denison (1951*a*) considered they were true holes passing through the shield

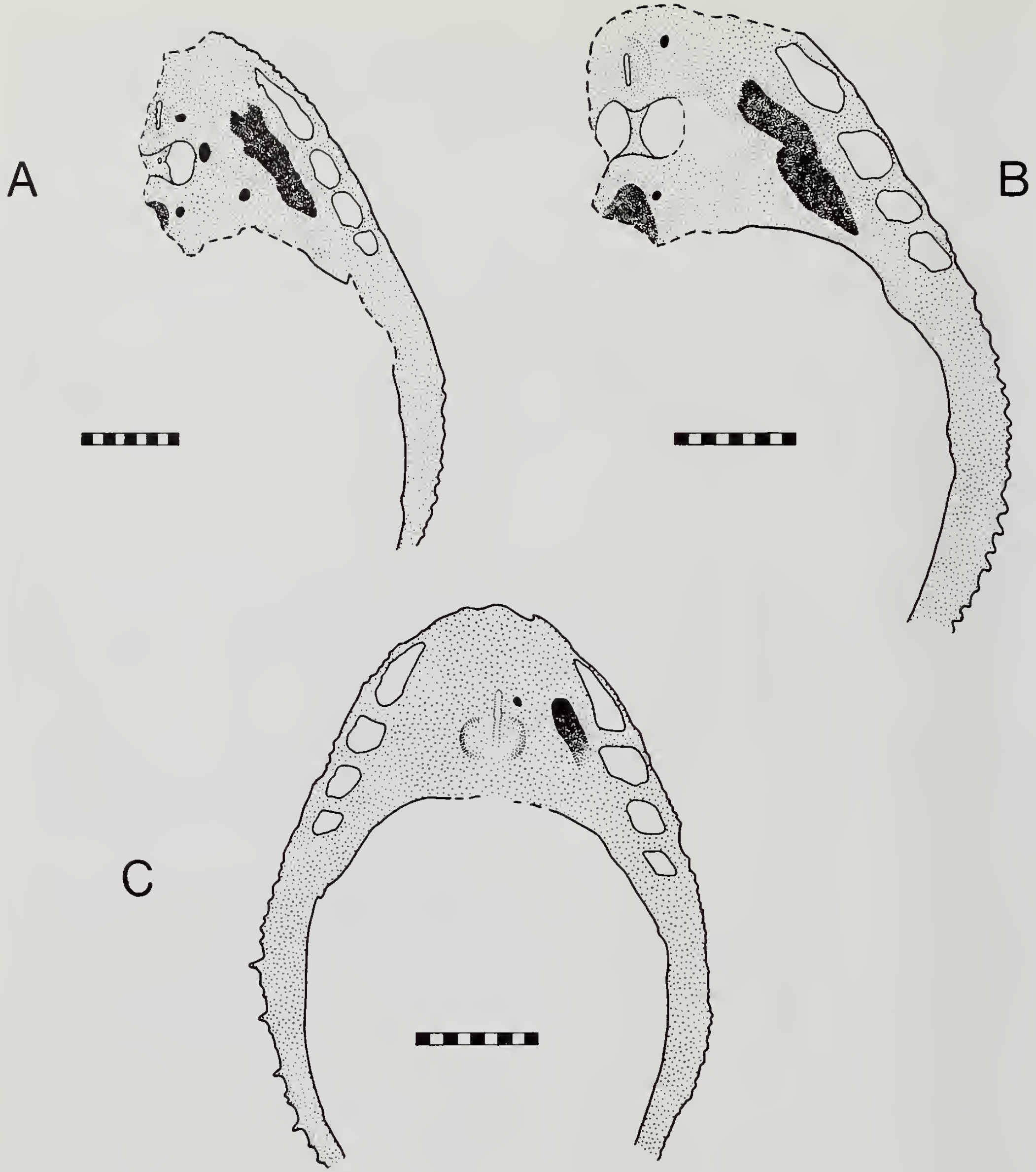

Fig. 6 *Sclerodus pustuliferus* Agassiz. Outline drawings of three specimens to show relative sizes and positions of nasohypophysial opening, dorsal and lateral sensory fields, pits and marginal fenestrations. A, BMNH 45949b, latex cast. B, BU 1992, latex cast. C, BMNH P.9756. Sensory fields–heavy stipple: area of shield–light stipple: sensory pits–black. Scale bars in mm intervals.

from top to bottom. Examination of specimens used in this study suggests this interpretation to be correct.

Fenestrae are seen clearly in many specimens, and where the lateral margin of the shield is complete it is obvious that there are four such fenestrae (BU 1992, BGS GSM 89283, GSM 21469, GSM 5149, GSM 5150, BMNH P.9752, P.9756, P.9757, P.9758, P.49015, 45949b).

Lankester (1870: fig. 31) showed six fenestrations, but none of the specimens used by him or any of the specimens used here show so many; the anterior two he showed are not present in any specimen. The most anterior fenestra is located at the transverse level of the naso-hypophysial opening and is elongate. The second, third and fourth become progressively smaller and more equidimensional (Figs. 2, 4D, 6, 7). The apparent regularity prompted an attempt to express the area of the posterior three fenestrae relative to the first (most anterior), which is always the largest in the series. The results obtained were very variable and this is probably because different specimens have been broken at different horizontal levels through the thickness of the shield. As an average of eight of the best preserved specimens, the area of the second fenestra is 75% of the first, the area of the third 56% and the fourth 46% of the first.

That the fenestrae passed right through the shield is not immediately obvious from the specimens available. The majority are preserved in dorsal view, in which it can be clearly seen that the ornament tips into the posterior walls of at least the anterior three fenestrae. Unfortunately the few specimens showing the ventral aspect are broken so it is not clear that the fenestrae reappear on the ventral surface. However, in these specimens the matrix infilling of the fenestrae stands well proud, implying considerable depth (P.49015, P.9756). The most direct evidence is provided by BMNH P.3247 (Fig. 7B). In this specimen the anterior end is broken through the last fenestra and it shows the walls of the fenestra passing without interruption from one surface to the other.

The posterior wall of each fenestration slopes anteroventrally and it appears that the slope is greatest within the anteriormost fenestra and becomes progressively more upright in more posterior fenestrae until the rear wall of the fourth fenestra is nearly vertical. Distortions of individual specimens preclude any attempt to measure precise angles. The anterior wall of each fenestra passes nearly vertically or only slightly anteroventrally through the shield. Several specimens (BMNH 45949b, P.9758, P.49015) show that the posterior wall of each fenestra, except perhaps the last, is ornamented with fine tubercles, considerably smaller than those covering the adjacent part of the shield. In BMNH 45949b (Fig. 7A) there is a clear line of division between the fine tuberculations lining the fenestra and the shield surface, suggesting that there may have been a small separate plate forming the rear wall of the fenestra, but this observation could not be confirmed on any other specimen. Despite this uncertainty the existence of an ornamented lining reinforces the view that they are true fenestrations rather than depressions or 'cells' within the structure of the bone.

The regularity of these fenestrae suggests that they were functionally important but it is difficult to be certain what this function may have been. There are no other osteostracans with such fenestrae, nor indeed are there many other animals showing such structures. The most obvious modern analogues are the marginal lunules in some clypeasteroid echinoids (sand dollars), the structure, evolution and possible functions of which have been discussed by Smith & Ghiold (1982). It is not possible to stretch comparison between lunulate echinoids and *Sclerodus* too far. There are quite considerable differences: unlike the fenestrations of *Sclerodus* the lunules of sand dollars are of roughly equal size, and in life they are partly filled with a thick epidermis containing spines and pedicellariae. Smith & Ghiold (1982) review the various hypotheses of echinoid lunule function. They are careful to point out that there may be a difference between the function of the anal lunule and the marginal lunules, which would be more comparable to those in *Sclerodus*. For the marginal lunules some seven hypotheses have been suggested (Smith & Ghiold 1982: 244–246). From their discussion those suggesting involvement with food gathering may be ignored. The most likely hypotheses for *Sclerodus* are hydrodynamic and, perhaps, assistance in burial, because these functions simply rely on lunule space and no associated epidermal structures. Furthermore the definite anteroposterior gradient in fenestra size (not seen incidentally in sand dollars) might suggest a hydrodynamic function.

Experiments on sand dollar tests have been carried out in wind tunnels and flume tanks (Telford 1981, 1983). It must be emphasized that these experiments treat the sand dollar simply as a geometrical shape, a fact which critics of hydrodynamic theories are quick to point out. But, accepting these parameters, the results indicate that the overall shape of a flat undersurface

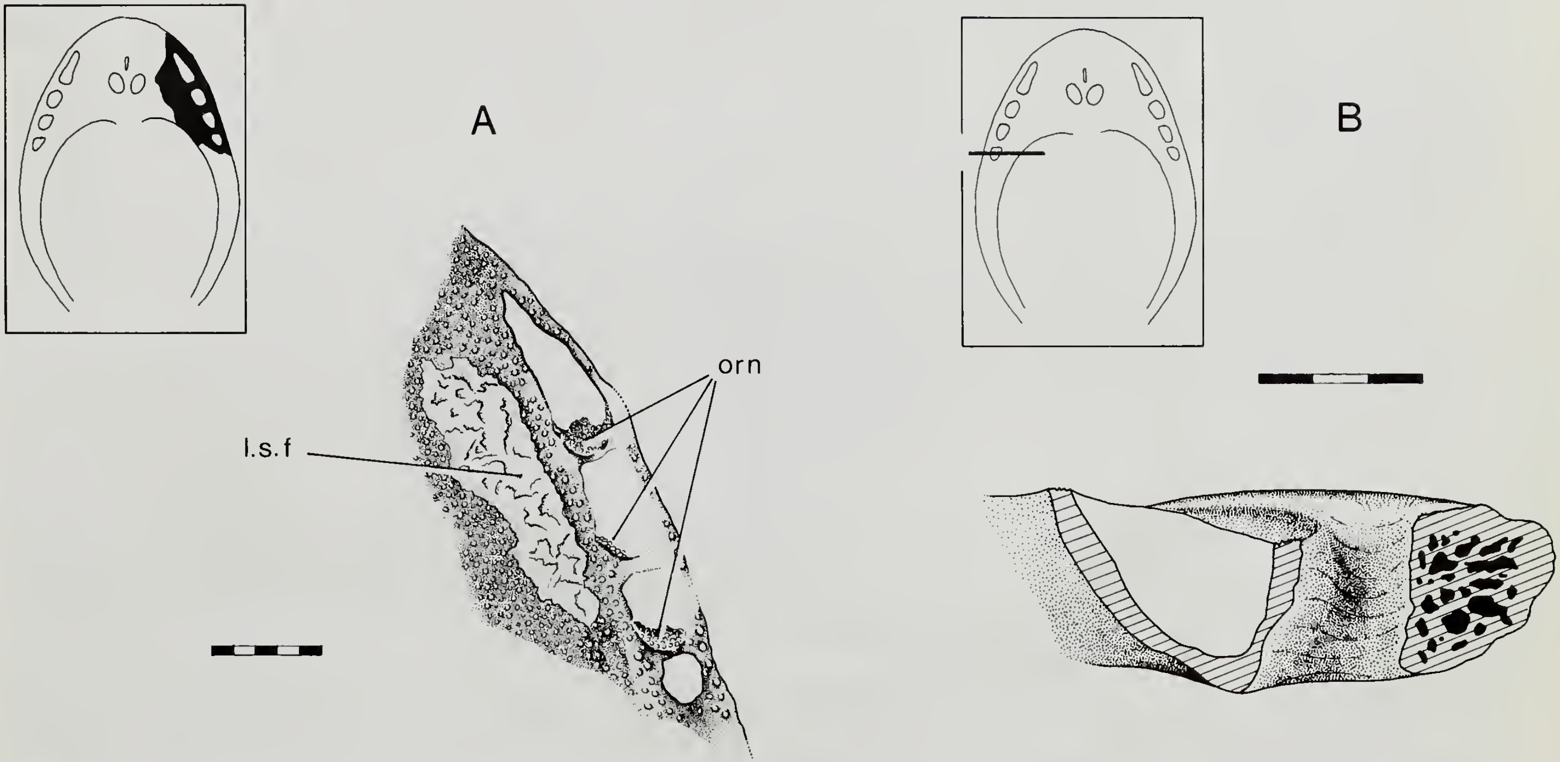

Fig. 7 *Sclerodus pustuliferus* Agassiz. A, drawing of latex cast of the edge of BMNH 45949b (Fig. 6A) to show lateral fenestrations with ornamented rear wall in at least the anterior three. B, BMNH P.3247, anterior view of broken 'cornu' showing rear wall of posteriormost fenestration. Scale bars in mm intervals.

and convex upper surface creates lift in a water current which is counteracted by the lunules. Some experiments (Telford 1983) suggest that the critical velocity (the water speed at which the sand dollar is lifted) might be increased by some 30%, implying that lunules could have a significant stabilizing effect; calculations made by Telford (1981: 619) suggest that moderate-sized sand dollars (7cm diameter) may well experience critical velocities in many modern shallow water environments.

There is little point in trying to perform similar experiments on a *Sclerodus* model since the shield is only part of the animal. But it is possible that the fenestrae provided some similar stabilizing function appropriate to a fish presumed to have lived in littoral waters and presumably subject to varying water speeds. The sectioned shape of *Sclerodus* is certainly that which would create lift if left uncompensated.

Relationships of *Sclerodus*

In this paper *Sclerodus* is placed in the family Tremataspididae. This requires some explanation in view of the very different hypotheses of relationships of *Trematapsis* and allies (Westoll 1945; Denison 1951*a*; Halstead 1982, 1985; Halstead Tarlo 1967; Janvier 1981*a*, 1985*a*, *b*, *c*) and the fact that *Sclerodus* is often placed in its own monotypic family.

The assignment of *Sclerodus* to a distinct family (Sclerodidae Berg 1940, Sclerodontidae Fowler 1947) is no more than a recognition of its uniqueness, which cannot be denied, but does not imply much about relationship. Stensiö (1932: 176) suggested it to be closely related to *Thyestes* and *Didymaspis* because the facial nerve (called V_2 by Stensiö) runs anterior to the first s.e.l. canal. This character is now known to be more widely distributed (*Procephalaspis*, *Witaaspis*, *Oeselaspis*, *Tremataspis*) but may still be significant, depending on whether one rates these taxa as constituting a monophyletic (Janvier 1981*b*), polyphyletic (Denison 1951*a*) or paraphyletic group (Halstead Tarlo 1967).

Denison (1951*a*: fig. 31) regarded tremataspids (*Didymaspis*, *Tremataspis*, *Saaremaspis*, *Dartmuthia*) as an ancestral group from which at least four different lineages of osteostracans evolved. Denison (1951*a*: 180) acknowledged that his group Tremataspidae was not necessarily a natural assemblage but that it only emphasised '. . . the convergence towards a central ancestral type'. He arrived at his conception of the ancestral type by determining polarity of several different character transformations using stratigraphical occurrence as the arbiter. Thus, he observed that the majority of Ludlovian osteostracans have small lateral fields, relatively few s.e.l. canals and a short prepineal region; the converse conditions would be derived. He admitted that the stratigraphical occurrence did not resolve whether the primitive osteostracan shield was long or short, or whether paired fins were primitively present or absent. But he decided that because *Tremataspis* showed the primitive condition of lateral fields, s.e.l. canals and prepineal length, then a long shield and absence of paired fins must also be primitive.

Denison's is the most clearly reasoned advocacy of the stratigraphical argument and the primitiveness of tremataspids, a view shared by Westoll (1945, 1985) and Halstead Tarlo (1967). *Sclerodus* shares many of these 'primitive' features such as a long carapace, short prepineal region, no paired fins or cornua and relatively short lateral sensory fields. But *Sclerodus* cannot be classified with tremataspids purely on the basis of 'primitive' features, since on these terms it would only mean that *Sclerodus* looked something like the ancestral osteostracan.

Janvier (1985*a*, *b*, *c*) has criticized this stratigraphical approach to character phylogeny in osteostracans by pointing out that forms such as *Ateleaspis*, with paired fins and large lateral fields, and *Procephalaspis*, with cornua and paired fins, occur contemporaneously with or even earlier than *Tremataspis*.

Halstead (1985) introduced another line of argument by claiming that *Tremataspis* shows a primitive geometry of the cephalic shield since, in gross outline, it resembles a cyathaspid heterostracan. If this doubtful reasoning is to mean anything then, presumably, its import lies in character distribution. Thus, if it could be shown that the *Tremataspis*/*Cyathaspis*-shaped shield was widely distributed amongst primitive members of the jawless fish groups then there might be some justification in assuming it to be a generalized feature. However, irrespective of which proposed phylogeny of jawless fishes one accepts (Forey 1984: fig. 3) the 'primitive' nature of the *Tremataspis/Cyathaspis* geometry cannot be justified on grounds of commonality.

If stratigraphy and commonality fail us then we are left with congruence of character distribution as the overriding criterion of choice: this has been the line of argument adopted by Janvier (1981*a*, *b*; 1985*a*, *c*). He concludes, like Stensiö, that *Tremataspis* and traditionally-accepted related genera are derived osteostracans. Janvier's approach is cladistic classification and he has attempted to determine plesiomorphic and apomorphic states, and then to check these against congruence. Janvier (1985*a*) suggests that non-cornuate genera such as *Ateleaspis* and *Aceraspis* are primitive because they exhibit micromery on the undersurface of the head, broad-based pectoral fins not flanked by cornua, and two dorsal fins. These features are generalized, based on outgroup comparison. Using this assumption Janvier's phylogeny of osteostracans (1985*a*: fig. 69) rates tremataspids as derived cornuate forms which have secondarily lost pectoral fins, reduced the number of s.e.l. canals and developed an elongate carapace. Furthermore, Janvier considers that the sister-group of tremataspids is *Thyestes*, with forms such as *Witaaspis*, *Auchenaspis salteri* and *Procephalaspis* as progressively more plesiomorphic forms. He refers to this entire assemblage as thyestidians.

Janvier's thyestidians include tremataspids as well as forms which Denison (1951*a*: fig. 31) regards as ancestral to the Ateleaspidae (non-cornuate osteostracans with paired fins) and Cephalaspidae (including benneviaspidians). Janvier's classification with respect to tremataspids agrees with Stensiö (1958), and is almost the antithesis of that of Denison (and also Halstead Tarlo 1967). In reaction to some recent criticism (Westoll 1985, Halstead 1985) Janvier (1985*c*: fig. 36) translated Denison's (1951*a*) tree into a cladogram and detailed some 14 incongruous character distributions which result.

I was interested to see what might happen if some of the data presented by Janvier (1985*a*, *c*) were subjected to cladistic computer analysis using PAUP (Phylogenetic Analysis using Parsimony) version 2.2, a program prepared by Dr David Swofford, which is designed to select the most parsimonious tree or trees which can be rooted to follow the fate of different character transformations. I chose to look at 16 taxa with respect to 27 characters. Some of them were higher taxa (cephalaspidians, kiaeraspidians, scolenaspidians, benneviaspidians, tremataspids *sensu stricto*), and it was therefore assumed that these groups are monophyletic. This may, of course, be disputed but Janvier (1985*a*) has discussed the arguments and I find his reasoning sound. More importantly, the advocates of competing theories also accept these groups (Denison 1951*a*, Halstead Tarlo 1967). Groups about which there is argument include the Ateleaspidae (*Ateleaspis*, *Aceraspis*, *Hirella*, *Hemiteleaspis* and *Hemicyclaspis*) and osteostracans traditionally associated with *Tremataspis* (*Auchenaspis*[1], *Witaaspis*, *Thyestes*, *Didymaspis*). Denison (1951*a*) and Ritchie (1967: 79) regarded the Ateleaspidae as monophyletic and derived from *Witaaspis* or the tremataspid *Saaremaspis*. Janvier, however, regards ateleaspid genera as primitive osteostracans forming a paraphyletic assemblage, with some being more nearly related to cornuate osteostracans than to other ateleaspids. In other words, for this analysis I have chosen to designate separate genera in those areas where classifications are substantially different.

Another problem area is character designation. As Janvier (1985*a*) implies in his classification there are several well-defined groups of osteostracans, but there is a problem of identifying characters to link groups other than those which are general to osteostracans. Thus, there may be polychotomies within osteostracan classification simply because there are no identifiable characters to resolve the issue further. This is a problem distinct from conflicting character distribution. The final difficulty stems from the uncertainty of distinguishing polarity of character state transformations. This is, of course, the source of most disagreements between conflicting classifications (see above) and is particularly difficult to resolve in an extinct group such as osteostracans.

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[1] For many years *Auchenaspis* and *Thyestes* have been regarded as synonyms (Woodward 1891: 195). Janvier (1985*a*: 122), however, retains *Auchenaspis salteri* Egerton and *Auchenaspis egertoni* Lankester as distinct from *Thyestes verrucosus* Eichwald. Janvier recognizes several synapomorphies of *Thyestes verrucosus* and Tremataspididae not present in species of *Auchenaspis*.

The most obvious features which can be compared amongst osteostracans are size, shape and complexity of the dorsal and lateral sensory fields, the canals leading to them and their relationship to cranial nerves. Additionally, there is variation in the development of the cornua and the trunk shield. Understandably, classifications have used these features. But since non-osteostracans do not have sensory fields or related canals, and the cornua are not easily compared with the skeletal outgrowths in other groups (e.g. spinals of placoderms or the cornual plates of pteraspidiform heterostracans), the polarity of many features associated with these structures is not resolvable by outgroup comparison.

The computer program built the 'tree', paying no regard to the entered polarity even though the data had been scored, in large part, in agreement with Janvier's assessment of primitive (0) or derived (1). The derived characters used in the program were:

1. Pectoral fins present, as evinced by sinus and/or area of attachment. Presence of pectoral fins in *Didymaspis* after Janvier (1985*a*).
2. Dorsal field separated from pineal plate. Converse condition—pineal plate contacting dorsal field—regarded as plesiomorphic within osteostracans. There are some intragroup exceptions where, for instance, nearly all members show one condition (e.g. benneviaspidians show pineal contacting the dorsal field) with one species (*Benneviaspis holtedahli* Stensiö) showing the derived condition.
3. Tesserae on undersurface of oralobranchial chamber. The plesiomorphic condition is micromery where there is a shagreen of minute scales exemplified in, for instance, *Ateleaspis*. Like Janvier (1984, 1985*a*) I feel confident about the polarity of this character since micromery (covering of small, equal-sized and regular-shaped units) is widespread amongst agnathan groups and primitive gnathostomes. The tesserate condition is, on the other hand, regarded as derived and is exemplified by *Saaremaspis* (Janvier 1985*b*: fig. 16) or *Hemicyclaspis murchisoni* (Egerton) (Stensiö 1932: pl. 7, fig. 3). Here the covering of the oralobranchial chamber is made up of *irregularly*-sized and *irregularly*-shaped units.
4. Pineal plate equidimensional or longer than broad. There are some intragroup exceptions which must be regarded as secondary reversals. For example, tremataspids generally show the derived condition but *Timanaspis* is exceptional.
5. Pineal plate absent. There are some intragroup exceptions; for instance, amongst cephalaspidians, which generally have a well-developed plate, this has been secondarily lost in *Hildenaspis* and *Mimetaspis*.
6. Orthobranchiate condition.
7. Pattern of branching of the first canal leading to the lateral sensory field. There are three conditions (Janvier 1985*a*: 107) but the polarity of transformation is by no means clear. For this reason the character is scored quite arbitrarily here: 0 = branching near lateral field, 1 = branching midway between eye and lateral field, 2 = branching near orbit.
8. Abdomen with scale-covered ventrolateral crest.
9. Cornual process. The development of the cornual process is regarded as a derived condition. There are problems with identifying a cornual process in kiaeraspidians but I follow Janvier (1981*b*) in believing the cornual process to be primitive for that group.
10. Long abdominal division of cephalothoracic shield (more than two segments incorporated into the shield).
11. Facial nerve running alongside or in front of first canal to the lateral sensory field.
12. Abdominal part of shield closed ventrally (may be secondarily reduced in extent in some, e.g. *Nectaspis*).
13. Branchial nerves penetrating gill chamber laterally. The condition of this character is only known sporadically throughout osteostracans.
14. Extrabranchial divisions large.
15. Opening of endolymphatic duct lying outside dorsal sensory field. The converse condition is considered plesiomorphic because it is more widely distributed amongst osteostracans. Some benneviaspidians and also *Didymaspis* have openings on the edge of the sensory field; these are considered to show the plesiomorphic condition.

16. Lateral sensory fields not extending greatly beyond level of nasohypophysial opening.
17. Lateral sensory fields reaching posteriorly well beyond level of dorsal sensory field.
18. Lateral sensory fields posteriorly expanded.
19. Supraoral fields with denticles. Condition is only known sporadically throughout osteostracans.
20. Anterior dorsal fin or fin scale absent. This character is regarded as unquestionably derived. Most primitive members of agnathan groups have two dorsal fins.
21. Solid rim to the shield.
22. Infraorbital line stopping short of lateral sensory field.
23. Posteroventral 'myodome' absent. See Janvier (1985*a*: 77) for discussion.
24. Infraorbital line running close to circumnasal fossa.
25. Paired fins constricted at base or separated from trunk scales.
26. Horizontal perforated lamina within the sensory canals of the middle layer of exoskeleton.
27. Enameloid layer.

The data matrix, as given in Table 1, includes the characters used by advocates of opposing hypotheses. The difference is that Janvier would choose *Ateleaspis* as the root of the tree whereas Denison, Westoll and Halstead would favour tremataspids. So the computer program was run twice using a different root. On each occasion there were 60 equally parsimonious trees, this being a reflection of the relatively poor quality of the data (approximately 30% homoplasy, and some possible dichotomies unsupported by characters—see below). The consensus trees (the common element of the 60 most parsimonious trees) are shown in Fig. 8 where the root is fixed at *Ateleaspis* on the left and tremataspids on the right.

The first observation is that the computer-generated tree, based on parsimony and using tremataspids as ancestor, is not at all like the tree advocated by Halstead Tarlo (1967) as illustrated in Fig. 9. Halstead Tarlo's tree is less highly resolved and, potentially, there may be considerably more dissimilarity between the two solutions presented in this figure: the major areas of difference may, however, be briefly mentioned. Halstead Tarlo's tree ranks cephalaspidians, kiaeraspidians and benneviaspidians as a trichotomy and as the most derived osteostracans. The consensus tree ranks these as successively more plesiomorphic sister-groups

Table 1 Character data matrix for 16 osteostracan taxa. For explanation of characters see text. A, *Ateleaspis*; B, *Aceraspis*; C, *Hirella*; D, *Hemiteleaspis*; E, cephalaspidians; F, kiaeraspidians; G, scolenaspidians; H, benneviaspidians; I, tremataspids; J, *Procephalaspis*; K, *Auchenaspis salteri*; L, *A. egertoni*; M, *Witaaspis*; N, *Thyestes*; O, *Didymaspis*; P, *Hemicyclaspis*.

	Characters																										
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
A	1	0	0	0	0	0	?	1	0	0	?	0	0	0	0	?	0	0	0	0	0	0	?	0	0	0	0
B	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	0	0	0
C	1	0	1	0	0	?	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	1	0	0
D	1	0	1	0	?	0	?	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	?	0	1	0	0
E	1	0	1	0	0	0	2	1	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0
F	1	1	1	0	?	1	0	1	1	1	0	1	1	1	0	0	0	0	0	?	1	1	1	0	1	0	0
G	1	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0
H	1	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0	0	1	0	?	1	1	0	0	1	0	0
I	0	1	1	1	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	1	1	1	1	1	0	1	1
J	1	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	0	0	0	?	1	1	1	1	1	?	0
K	1	0	1	0	0	0	0	1	1	0	1	1	0	?	0	1	0	0	0	?	1	1	?	1	1	?	0
L	1	0	1	0	0	0	0	1	1	1	1	1	0	1	0	1	0	0	0	1	1	1	?	1	1	?	0
M	1	1	1	1	0	0	0	1	0	1	1	1	0	?	1	1	0	0	0	?	1	1	?	1	1	?	1
N	1	1	1	1	0	0	0	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1
O	1	1	1	0	1	?	0	?	?	1	1	1	0	?	0	1	0	0	0	?	1	1	?	0	?	?	0
P	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	1	0	0

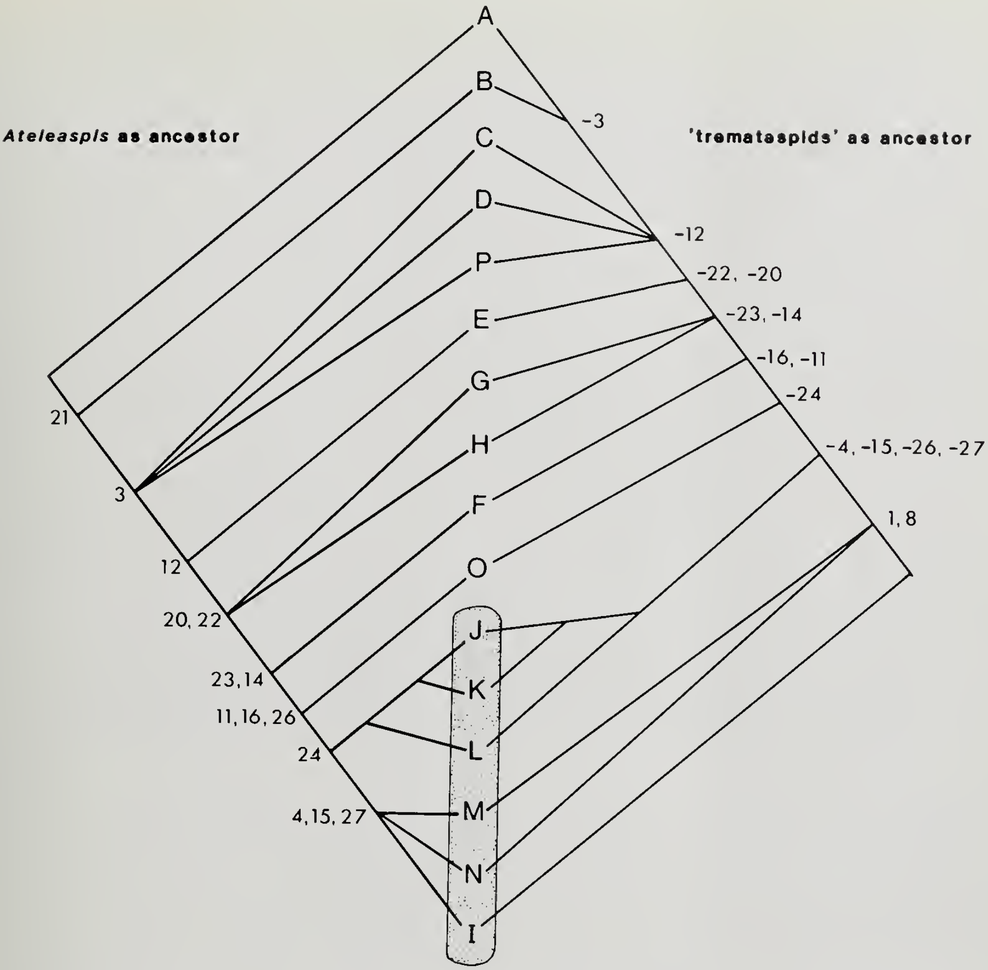

Fig. 8 Consensus tree produced from the 60 most parsimonious alternative solutions. Topography of the trees is identical. Left–the root placed at *Ateleaspis.* Right–the root placed at tremataspids. Only those characters treated as synapomorphies are shown. Taxa A–P as in Table 1. Numbers refer to characters detailed in text. Particular taxa under consideration are enclosed within stippled area.

to the Ateleaspidae. *Thyestes* occupies a very different position, being a derived taxon and the sister-group to cephalaspidians + kiaeraspidians + benneviaspidians in the Halstead Tarlo tree, while in the consensus tree it is the sister-group to all other osteostracans with the exception of tremataspids. Thus, whatever else the Halstead Tarlo tree might contain, it does not approach a parsimonious solution given the data used here (Fig. 9).

In Fig. 8 only the characters used once (synapomorphies) are applied to the diagrams. Those against the 'tremataspids as ancestor' tree are largely indicated as negative features, but this is a consequence of the way in which the characters were coded in the first place. Perusing this list we may note that some characters (11, 15, 16, 24, 26) are only found in osteostracans and it is therefore difficult to establish polarity. But one prediction of fixing the root at tremataspids is the deduction that the primitive osteostracan developed a complex horizontal lamina within the exoskeleton which was subsequently lost by most osteostracans. The alternative assumption

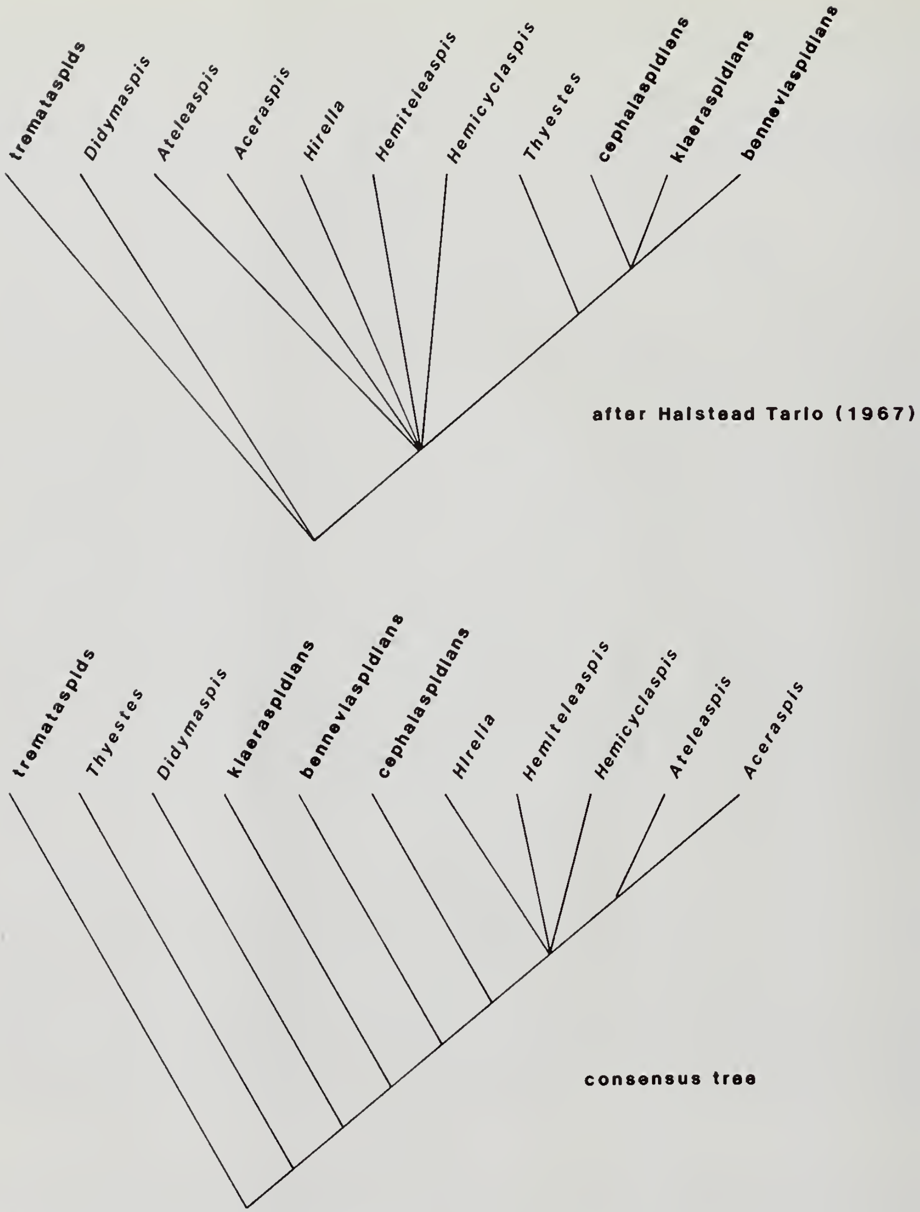

Fig. 9 Tree of osteostracan taxa produced by Halstead Tarlo (1967) compared with computer consensus tree rooted at tremataspids.

(*Ateleaspis* as ancestor) rates this character as an acquisition within a small group of osteostracans and so appears a more plausible alternative.

My main reasons for preferring the '*Ateleaspis* tree' centre on the behaviour of characters 3, 12 and 20. I believe that micromery is a primitive condition and that the tesserate (3) condition is derived. The micromeric undersurface of *Ateleaspis* and *Aceraspis* may be associated with the very small trunk scales in these forms which is probably also a plesiomorphic feature (Janvier 1985*a*: 106). I also believe that the ventral enclosure of the abdominal region (12) is a derived condition. And, finally, I consider that the presence of two dorsal fins (20) is a plesiomorphic feature, this being found in lampreys, some placoderms and the more primitive acanthodians. Many osteostracans have enlarged dorsal scales in place of one or both dorsal fins. Janvier (1984) uses the presence of such scales as a character. For instance, in the solution given in Fig. 10, Janvier would suggest that a character linking *Hemicyclaspis* and cladistically more derived taxa would be the presence of a modified scale in place of the anterior dorsal fin. This is perfectly acceptable and would be one way of resolving what is otherwise a trichotomy between some ateleaspidian genera (Fig. 8). It should also be noted that the presence of paired fins is here regarded as plesiomorphic for osteostracans, based on a higher level phylogeny which ranks gnathostomes and osteostracans as sister-groups (Janvier 1981*c*, Forey 1984).

In Fig. 10 one of the '*Ateleaspis* trees' is given in full and all characters (except no. 7—branching of s.e.l. canals) are included. It can be seen that the node linking *Hemicyclaspis* and cladistically more derived osteostracans is not supported by any characters, and that linking *Hemiteleaspis* and more derived osteostracans is only supported by character 7 which is very difficult to evaluate. These areas of uncertainty give rise to many of the alternative trees and are probably better depicted as a polychotomy incorporating *Hemiteleaspis*, *Hemicyclaspis*, *Hirella* and cladistically more derived taxa. The inclusion of additional characters (e.g. inferred modification of the anterior dorsal fin) may partially resolve this polychotomy.

Another area in which alternative trees varied concerns benneviaspidians, scolenaspidians and cladistically more derived osteostracans. The solution shown in Fig. 10 suggests benneviaspidians and scolenaspidians to be sister-groups, based on the common possession of posteriorly-expanded lateral sensory fields (18). The alternative solution ranks benneviaspidians as the sister-group to cladistically more derived forms, with scolenaspidians as the plesiomorphic sister-group. This is the solution preferred by Janvier (1985*a*), who bases it on the fact that in benneviaspidians and cladistically more derived forms the first s.e.l. canal branches near the lateral sensory field. The trichotomy shown in the consensus tree (Fig. 8) is therefore the result of conflicting character distributions which may only be resolved by discovering more characters.

Character 7—the branching pattern of the first s.e.l. canal—was entered as a multistate character, but the resulting transformations implied by the computer tree were very ambiguous. The primitive condition was fixed with reference to the condition in *Aceraspis* (see also Janvier 1985*a*), in which the canal branches midway between the eye and the lateral sensory field. A transformation of this presumed general condition in *Hemiteleaspis* and cladistically more derived forms shows branching very near the orbit (best exemplified in cephalaspidians). An even more restricted grouping—scolenaspidians, benneviaspidians and their sister-group—show transformation to a canal which branches near to the lateral field. Scolenaspidians show a reversal to 'primitive' conditions.

None of the conditions of the branching pattern is coextensive with any of the groups specified in Fig. 10. This character might therefore need re-examination in the light of the classification proposed here. In view of the fact that it is sometimes difficult to be certain whether the canal branches midway between the eye and the lateral field or whether it is nearer one than the other, and of the fact that there may be variation within a single species (p. 13), this character is not considered further even though it has traditionally been used in classifications of osteostracans.

Characters 5, 6, 13, 17 are treated as parallelisms. The behaviour of character 6 (orthobranchiate condition) is perhaps interesting. This is a character, used by Stensiö (1958), which might suggest that kiaeraspidians and benneviaspidians are sister-groups (see alternative in Janvier 1981*b*: fig. 43), but none of the computer-generated trees suggested this grouping.

The last area of uncertainty within the computer-generated tree concerns tremataspids, *Witaaspis* and *Thyestes*. The solution shown here (Fig. 10) ranks tremataspids and *Witaaspis* as sister-groups based on the secondary loss of the cornual processes (9). The alternative solution places tremataspids and *Thyestes* as sister-groups because of the common possession of a denticulated supraoral field (11). Neither character is clear cut: it is sometimes very difficult to be certain whether cornual processes are short or absent altogether, and the condition of the

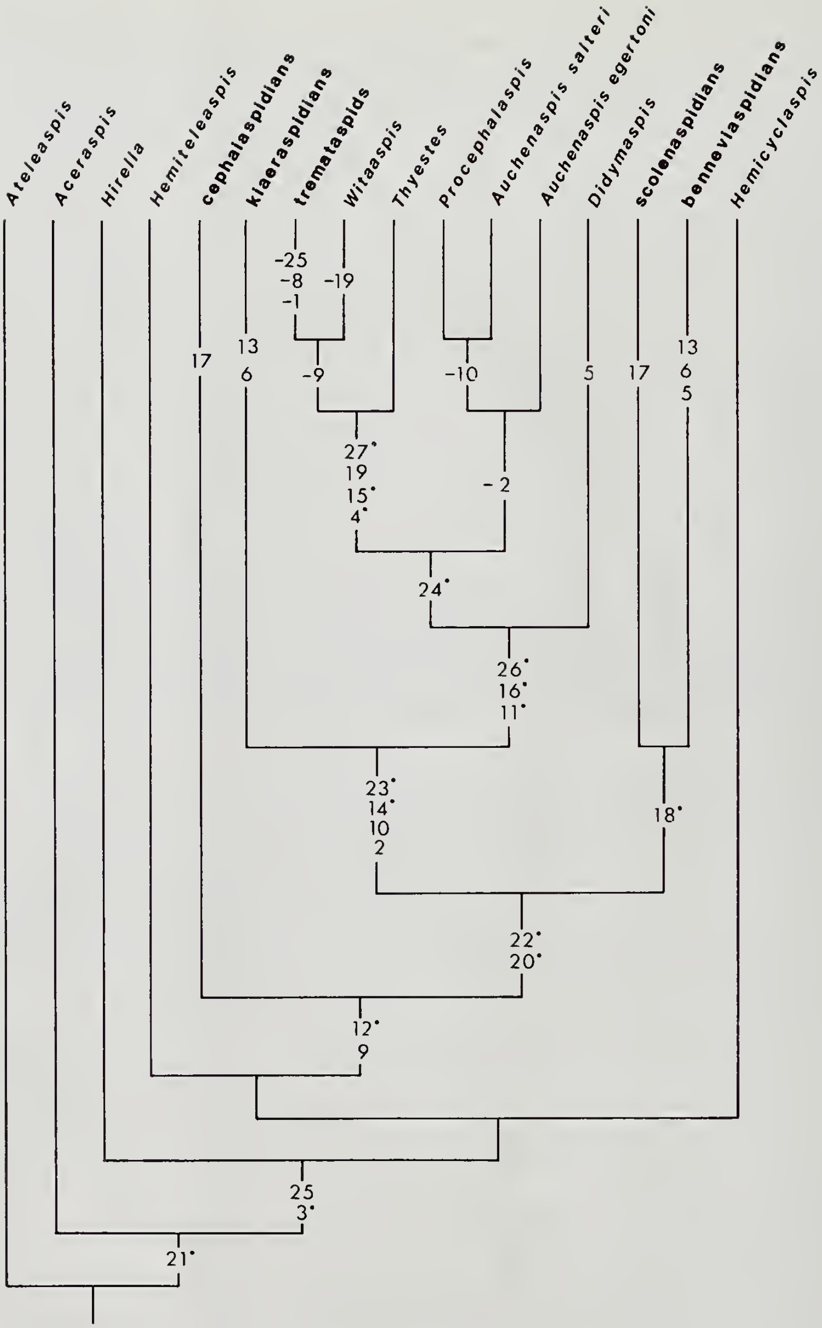

Fig. 10 One of the 60 most parsimonious trees rooted at *Ateleaspis* with all characters and character transformations shown. Synapomorphies designated with 'prime dot'. Other characters are parallelisms or reversals (minus signs). Character 7 omitted. See text for list and discussion of characters.

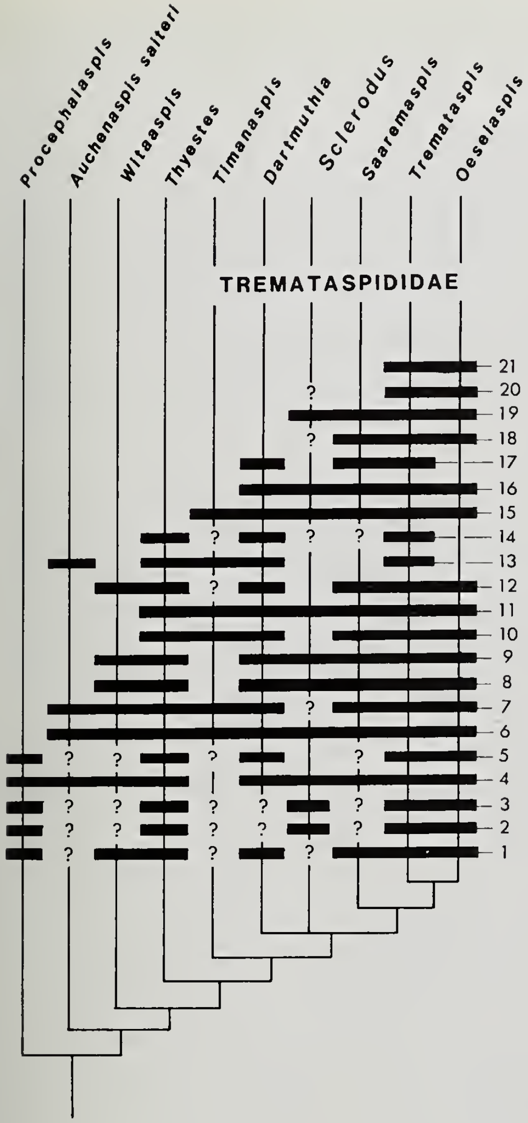

Fig. 11 Systematic position of *Sclerodus* inserted in a phylogeny of thyestidians produced by Janvier (1985*c*: fig. 40) with synapomorphies specified by that author—his numbering is used here. The synapomorphies are as follows: 1–infraorbital sensory canal running close to orbit and circumnasal fossa, 2–canal for facial nerve not running in orbit, 3–medial recess of posteroventral myodome absent, 4–pineal plate narrow or short, 5–horizontal lamina developed within exoskeleton, 6–abdominal division long or very long, 7–openings of endolymphatic ducts outside dorsal sensory field, 8–pineal plate very short, 9–dorsal sensory field separated from pineal recess, 10–nasohypophysial opening short or very short, 11–abdominal division very long, 12–superficial enameloid layer developed, 13–longitudinal rows of enlarged tubercles developed, 14–supraoral field triangular with denticles, 15–absence of paired fins, 16–circumnasal fossa deep and elliptical, 17–'cosmine' forming a continuous layer, 18–dorsal sensory field very short, 19–circumnasal fossa very short, 20–dorsal sensory field extremely short, 21–lateral sensory field divided into two parts. See text for discussion.

supraoral field is poorly known in many osteostracans. Janvier (1985*c*: fig. 40) prefers the second solution; he suggests that, in addition to the denticulated supraoral field, *Thyestes* and tremataspids show a slightly longer abdominal division and a shorter nasohypophysial opening. I find these characters difficult to evaluate, but they could be one way of resolving a trichotomy shown in the consensus tree. The important conclusion to be drawn is that, despite the differences between the computer-generated tree and Janvier's classification (1985*a*: fig. 69), both firmly support thyestidians as a group.

The implication for discussion about the interrelationships of *Sclerodus* is that I feel entitled to regard Tremataspididae as a monophyletic taxon to which additional taxa can be added in pectinate fashion as specified by Janvier (1985*a*, *c*); see Fig. 11. There are, as Janvier freely admits, some problems with this classification; the greatest is perhaps incomplete knowledge of morphology in certain forms. But given these constraints, *Sclerodus*, which is particularly poorly known, can be placed within the Tremataspididae as the sister-group of *Dartmuthia*, or of *Saaremaspis*, *Tremataspis* and *Oeselaspis*. These conflicting solutions are shown as a trichotomy in Fig. 11.

With respect to the cladogram of thyestidians produced by Janvier (Fig. 11), *Sclerodus* agrees in showing the synapomorphies numbered 2, 3, 9, 15, 16. Characters numbered 4 and 8 refer to the shape of the pineal plate, or the pineal recess when the plate has never been found (as in *Sclerodus*). These two characters are really differing degrees of development of the same feature and *Sclerodus* would appear to match that specified under character 8 most closely, exemplified by *Witaaspis* and *Thyestes*. Character 1—medial course of the infraorbital line—depends on interpretation of the pits within the shield (see p. 12). Characters numbered 6 and 11 refer to progressive lengthening of the abdominal shield which is also seen in kiaeraspidians. *Sclerodus* certainly shows a long abdominal division but this is only developed laterally.

Characters 7, 18, 20 refer to the size and shape of the dorsal sensory field, while character 14 concerns the supraoral field. These structures are unknown or too poorly known in *Sclerodus* to assess their status. Character 13 (longitudinal rows of enlarged tubercles), absent in *Sclerodus* (see p. 13), must be considered as a reversal. Character 21 (divided lateral sensory fields) is known to be absent; but the status of this character as a synapomorphy must be questioned since it is present in kiaeraspidians.

Characters 5, 12, 17 refer to details of histology, an aspect in which *Sclerodus* appears unique in several respects. There is one further feature of *Sclerodus* which recalls conditions in thyestidians. The lateral head vein (Fig. 4A) runs well outside the vestibular chamber and makes a broad medial sweep at the level of the orbit. This feature has not been considered in the above discussion on osteostracan classification because this part of the anatomy remains poorly known in most species.

Conclusions

The comparative information available for *Sclerodus* suggests that it is a member of the Tremataspididae, which is here accepted as a monophyletic group.

The Appendix (opposite) lists the stratigraphical occurrence of the *Sclerodus* specimens used in this study. In addition to this *Sclerodus* has been reported from the Ludlow Bone Bed of Brook House, Llangibby, Gwent; Downton Castle Sandstone of Beech Hill Farm, Usk, Monmouth; also Turners Hill (Temeside Beds), south Staffordshire (Ball 1951). Thus, *Sclerodus* is restricted to the Downtonian of the Anglo-Welsh depositional basin. It is also apparent that, even allowing for collecting bias at long-known and well-collected sites such as the Ludlow Bone Bed exposure at Ludford Lane, Ludlow, Shropshire, the majority of the specimens are found in the Ludlow Bone Bed and in the lower part of the Downton Castle Sandstone. Very few have been found in the overlying Lower Red Downton Group or its equivalent, the Temeside Shale. Even the listing of the specimens from Wallop Hall as coming from the Temeside Shale may have to be revised, to place them in the Downton Castle Sandstone (Dr J. B. Richardson, personal communication). This, and the evidence of the associated fauna and sedimentological features, indicate that *Sclerodus* was a marine fish becoming rare with the onset of brackish water conditions (Allen & Tarlo 1963).

The vertebrates most commonly associated with *Sclerodus* are acanthodians, *Cyathaspis banski* and thelodonts. In terms of Turner's (1973) thelodont faunas *Sclerodus* would be part of the upper part of the *Thelodus parvidens* fauna. Osteostracan congeners are *Auchenaspis* (*Thyestes*) and *Hemicyclaspis*, which are found in all but the lowermost levels of the Downton Castle Sandstone, and *Didymaspis* which appears in the overlying Lower Red Downton Group. Thus, *Sclerodus* is the earliest osteostracan to appear in the Anglo-Wesh basin and is one of the truly marine osteostracans. It appears to be the ecological equivalent of the Wenlock and Ludlovian thyestidians from Estonia which Märss & Einasto (1978) suggest occupied shallow lagoonal waters shoreward of sand-belt facies. Janvier (1985*c*: 211) suggested that *Tremataspis* and other derived tremataspids inhabiting these Baltic waters may have been burrowing forms.

These osteostracans have rather convex ventral surfaces such that the cross-sectional profile would be elliptical. I do not think that *Sclerodus* showed such a convexity; rather it is possible that it was able to submerge itself beneath the loose surface sand, and that the marginal fenestrae may have helped in this activity.

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I would like to thank Drs Colin Patterson, British Museum (Natural History), and Philippe Janvier, Institut de Paléontologie du Muséum National d'Histoire Naturelle, for encouragement and reading the manuscript, and Dr L. B. Halstead, Reading University, for bringing to my attention the fact that Dr W. Graham-Smith had recovered some interesting fragments of *Sclerodus*. My especial thanks are due to Dr Graham-Smith for donating his material. Dr C. J. Humphries and Mr A. Paterson, British Museum (Natural History), both provided considerable assistance with manipulation of the computer program: their help is gratefully acknowledged. Finally, I would like to thank Dr A. B. Smith, British Museum (Natural History), for his discussions of echinoid hydrodynamics and for his understanding following the inadvertent sacrifice of one specimen of a sand dollar.

Appendix

Material examined in the course of this study is listed below. The specimens are of very different quality and a mere listing of numbers might be misleading, so they are divided into three categories denoting different parts. Within each category the specimens are arranged stratigraphically, beginning with Ludlow Bone Bed, then overlying Downton Castle Sandstone, then Temeside Shale/Lower Red Downton or presumed equivalent.

Cephalic shields including details of orbit, nasohypophysial opening, brain etc.:
Ludlow Bone Bed, Ludford Lane, Ludlow, Shropshire—BMNH P.48704, BGS GSM 89284 (Lankester 1870: pl. 13, figs 10, 10a) and counterpart GSM 5151.
Ludlow Bone Bed, Forge Bridge, Downton Castle estate, Shropshire—BMNH P.58694.
Downton Castle Sandstone, Ludford Lane, Ludlow, Shropshire—BMNH 45949b (Lankester 1870: pl. 13, fig. 14; Stensiö 1932: pl. 52, fig. 1), 45949e, P.9756 (Stensiö 1932: pl. 53, fig. 5), BGS GSM 5150 (Lankester 1870: pl. 13, fig. 12), GSM 89283.
Downton Castle Sandstone, Kington, Hereford & Worcester—BMNH P.9752, P.31857, BGS GSM 89285, BU 1992.
Downton Castle Sandstone, Onibury (Norton), Shropshire—BMNH 35999, P.27099, BGS GSM 5149, 21469, 21470.
Temeside Shales, Wallop Hall, Shropshire—BMNH P.49015.

Portions of cephalic shields only showing marginal fenestrae:
Downton Castle Sandstone, Ludford Lane, Ludlow, Shropshire—BMNH 45949f, 45962, P.9757, P.9758.
Downton Castle Sandstone, Kington, Hereford & Worcester—BMNH P.5044, P.25403, BGS GSM 57541, GSM 89298.
Downton Castle Sandstone, Onibury (Norton), Shropshire—BGS GSM 89296.
Downton Castle Sandstone, Shobdon, Hereford & Worcester—BMNH P.25401.
Downton Castle Sandstone, Presteigne, Powys—BMNH P.31745.

'Cornua':
Ludlow Bone Bed, Ludford Lane, Ludlow, Shropshire—BMNH 45970b, c, P.3247 (Stensiö 1932: pl. 53, fig. 1), P.7360, P.25204, P.32255.
Ludlow Bone Bed, Clun, Shropshire—BMNH P.39559, P.39562, P.39572–6, P.49016.
Ludlow Bone Bed, Rushall, Woolhope, Hereford & Worcester—BMNH P.53119.
Downton Castle Bone Bed, Lucton, Hereford & Worcester—BMNH P.8927.
Downton Castle Sandstone, Ludford Lane, Ludlow, Shropshire—BMNH 45949 (Lankester 1870: pl. 13, fig. 11), 45949c, d, 45973 (Stensiö 1932: pl. 56, fig. 1), P.9897 (Stensiö 1932: pl. 53, fig. 3), P.25203 (Stensiö 1932: pl. 53, fig. 2).
Downton Castle Sandstone, Kington, Hereford & Worcester—BMNH P.25402, BGS GSM 5152.
Downton Castle Sandstone, Downton Bridge, Shropshire—BMNH 45970, 45970a.
Downton Castle Sandstone, Onibury (Norton), Shropshire—BMNH P.9897 (Stensiö 1932: pl. 53, fig. 3).
Temeside Shales, Wallop Hall, Shropshire—BMNH P.48954.
Temeside Shales, Baggeridge Colliery, south Staffordshire—P.17383–4.

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P. M. P. Zaborski

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Lower Turonian (Cretaceous) ammonites from south-east Nigeria

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Contents

Synopsis

Within most of Nigeria's Benue Trough uppermost Cenomanian and Lower Turonian strata are dominated by vascoceratid ammonite faunas of Tethyan affinities. Such assemblages range as far south as the Ezillo region in south-east Nigeria where *Nigericeras*, *Paravascoceras*, *Fagesia*, *Thomasites* and *Wrighto-*

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ceras occur. Barely 60 km south, however, at Lokpanta, the Lower Turonian contains faunas more easily correlated with those of the western interior of the United States and north-west Europe. The basal Turonian here is mainly characterized by *Watinoceras* spp., while the upper part of the Lower Turonian contains *Pachydesmoceras*, *Mammites nodosoides* (Schlüter), *Kamerunoceras*, *Fagesia*, *Neoptychites*, *Herrickiceras*? and *Hoplitoides latefundatus* sp. nov. This last form appears to provide an evolutionary link between *Wrightoceras* and typical *Hoplitoides*. The absence of the vascoceratid-rich faunas at Lokpanta is probably because of palaeoenvironmental factors.

Introduction

Uppermost Cenomanian and Turonian sediments are among the most widely distributed and richly fossiliferous parts of the Cretaceous system in Nigeria. During the early phases of systematic palaeontological work in Nigeria diverse collections of ammonites were attributed to the Lower Turonian (Reyment 1954, 1954*a*, 1955, 1957, Barber 1957). In recent years,

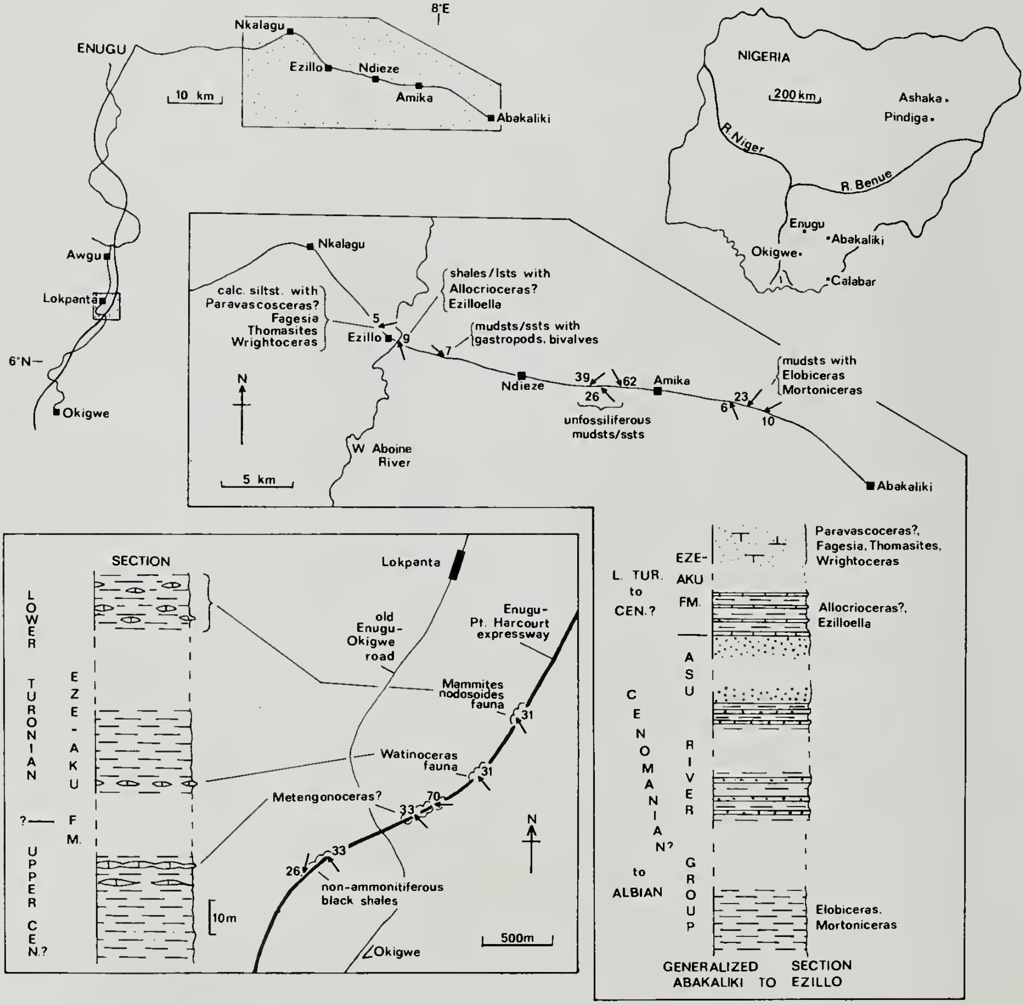


Fig. 1 Maps showing fossil localities and sections described in the text.

however, much of this material has been reassigned to the Upper Cenomanian and Middle Turonian. As a consequence, the faunal character of the Lower Turonian and its correlation within and outside Nigeria are in need of clarification. Material from the Lower Turonian of south-eastern Nigeria described here makes a considerable contribution to this.

The present faunas come from two areas (see Fig. 1). On the western outskirts of Ezillo (Eze-ilo), adjacent to the Enugu–Abakaliki highway, a disused pit exposes gently-dipping, micaceous, calcite-cemented siltstones yielding *Thomasites gongilensis* (Woods), *T. koulabicus* (Kler), *Wrightoceras wallsi* Reyment, *W.* cf. *munieri* (Pervinquière), *Fagesia* sp. and *Paravascoceras*? sp. Immediately south of Lokpanta three cuttings are present in a distance of less than 1 km on the Enugu–Port Harcourt expressway. In the most northerly of these cuttings 10–12 m of black, weathering sandy yellow, shales with large calcareous nodules contain an ammonite fauna of *Pachydesmoceras denisonianum* (Stoliczka), *Kamerunoceras puebloense* (Cobban & Scott), *Mammites nodosoides* (Schlüter), *Neoptychites cephalotus* (Courtiller), *Fagesia levis* Renz, *Hoplitoides latefundatus* sp. nov. and *Herrickiceras*? sp. Although ammonites occur here in their hundreds, larger specimens are, almost without exception, so badly crushed as to be unidentifiable. It is therefore usually the juvenile and middle whorls alone that are suitable for description. Directly south, a second cutting displays about 25 m of the closely similar underlying shales. In the lower 5 m of this sequence there are bands of dark grey, weathering sandy yellow, calcareous nodules whose surfaces are studded with the impressions of *Watinoceras* aff. *amudariense* (Arkhanguelsky), *W.* sp., *Kamerunoceras* cf. *eschii* (Solger), *Mammites*? sp. and *Neoptychites cephalotus*. Only tiny ammonites are preserved complete, the larger forms being recognized by fragments. The most southerly cutting exposes over 40 m of shales, silty in places, which include thin calcareous horizons formed from coalesced nodules. These beds are less fossiliferous but from their upper part have yielded several poorly preserved impressions of *Metengonoceras*? (Fig. 9, p. 39). The regional dip in these cuttings averages a little over 30° north-west, but rises abruptly to 70° west at the northern end of the last-described exposure. This fact suggests the proximity of faulting, and indeed minor faults can be observed within these cuttings.

The shales, silts and calcareous beds of late Cenomanian? to early Turonian age in most parts of southern Nigeria are conventionally referred to as the Eze-Aku Formation. This lithostratigraphic unit, formalized by Simpson (1954), is, however, not readily distinguishable from superjacent beds and is recognized primarily on the basis of its age. Though this is contrary to accepted stratigraphical practice, it is outside the scope of the present work to adopt other than a traditional approach here. A fuller discussion can be found in Petters & Ekweozor (1982).

Systematic descriptions

Repositories. Register numbers prefixed by the letter C are of specimens in the Department of Palaeontology, British Museum (Natural History), London. Those prefixed by the abbreviation UIN are of specimens in the Department of Geology, University of Ilorin, Nigeria.

Dimensions (in mm). D, diameter; Wb, whorl breadth; Wh, whorl height; U, umbilical diameter. Figures in parentheses are dimensions as a percentage of the total diameter. N = number of ribs in last whorl.

Superfamily **DESMOCERATACEAE** Zittel, 1895

Family **DESMOCERATIDAE** Zittel, 1895

Subfamily **PUZOSIINAE** Spath, 1922

Genus ***PACHYDESMOCERAS*** Spath, 1922

TYPE SPECIES. *Ammonites denisonianus* Stoliczka, 1895; by original designation.

Pachydesmoceras denisonianum (Stoliczka, 1865)
Figs 2–4

1865 *Ammonites denisonianus* Stoliczka: 133 (*pars*); pl. 66, fig. 2 (only); pl. 66a (*non* pl. 65, fig. 4; pl. 66, fig. 1).
1898 *Puzosia Denisoniana* (Stoliczka) Kossmat: 121; pl. 14, figs 5a, 5b; pl. 15, figs 5a, 5b.
1898 *Desmoceras Kamerunense* von Koenen: 55; pl. 7, figs 1–3.
1899 *Puzosia alimanestianui* Popovici-Hatzeg: 14; pl. 1.
1904 *Puzosia Denisoniana* (Stoliczka); Solger: 103; pl. 3, figs 1a, 1b; text-fig. 5.
?1904 *Puzosia Denisoni* (Stoliczka); Douvillé: 237; pl. 29, figs 1–4; pl. 30, figs 1a, 1b.
1907 *Desmoceras* (*Puzosia*) *Denisonianum* (Stoliczka) Boule, Lemoine & Thévenin: 21; pl. 5, figs 3–5.
?1912 *Puzosia denisoniana* (Stoliczka); Zimmermann: 542; pl. 26.
1914 *Puzosia denisoniana* (Stoliczka); Yabe: 72; pl. 7
1922 *Pachydesmoceras denisonianum* (Stoliczka) Spath: 127
1954 *Pachydesmoceras denisonianum* (Stoliczka); Matsumoto: 100 (with synonymy).
1955 *Pachydesmoceras kamerunense* (von Koenen); Reyment: 19.
1958 *Pachydesmoceras denisonianum* (Stoliczka); Reyment: 54.
1961 *Pachydesmoceras denisoni* (Stoliczka); Collignon: 39; pl. 8, figs 1a, 1b.
1965*a* *Pachydesmoceras denisoni* (Stoliczka); Collignon: 22; pl. 422, fig. 1752.

MATERIAL AND OCCURRENCE. Fourteen specimens (C.83511, C.85290–2, C.90292–301) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria.

DIMENSIONS.	D	Wb	Wh	U
C.90298	36	12·5 (35)	17 (47)	9 (25)
C.90297	50	15 (30)	22 (44)	13 (26)
C.90294	60	23 (38)	28 (47)	17 (28)
C.90292	65	25 (38)	29 (47)	18 (28)
C.90293	71	27 (38)	35 (49)	19 (27)

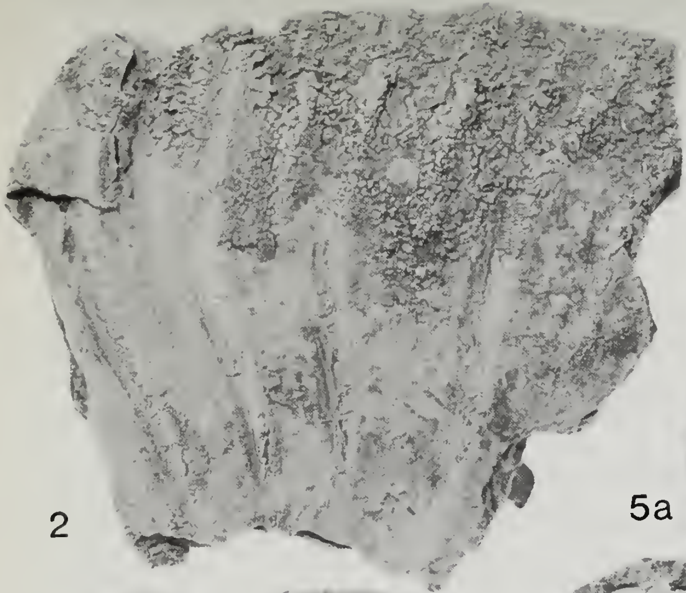
DESCRIPTION. The shell is moderately evolute, moderately compressed and has a broadly rounded venter. The earliest whorls are smooth but at diameters of 15–20 mm faint, narrow ribs appear in the ventral area. These ribs gradually extend to the umbilical shoulder, there being about eight in each whorl. At diameters of 40–50 mm minor ribs appear, confined to the outer part of the flank and the venter. They gradually strengthen and in the middle stages may outnumber the major ribs by as many as ten to one. In the later stages the major ribs dominate and at diameters in excess of 150 mm there are only one or two minor ribs intervening.

REMARKS. This material is exactly comparable with that described from Cameroun by Solger (1904: 103; pl. 3, figs 1a, 1b; text-fig. 5) as *Pachydesmoceras denisonianum* (Stoliczka). Reyment (1955: 17) at first included Solger's specimens in *P. kamerunense* (von Koenen), differentiating it from *P. denisonianum* on the basis of minor ribbing details and degree of inflation. Later, however, Reyment (1958: 54) referred them back to the latter species. There do not seem to be any significant differences between the Nigerian/Camerounian material and *P. denisonianum* and they are treated here as conspecific. *Puzosia alimanestianui* Popovici-Hatzeg (1899: 14; pl. 1) is another probable synonym. The inner whorls in the holotype of *P. hourcqi* Collignon (1961: 42; pl. 11, fig. 1) are poorly preserved but its later ornament resembles that in the present material and it may also be conspecific.

P. denisonianum and indistinguishable forms have a long stratigraphical range, at least from Cenomanian to Coniacian. *P. pachydiscoides* Matsumoto (1954: 101; pl. 9, figs 2a, 2b) is said to

Figs 2–4 *Pachydesmoceras denisonianum* (Stoliczka). Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 2, C.85290, × 1. Fig. 3, C.90301, × 1. Fig. 4a, b, C.90297, × 1.

Figs 5–6 *Kamerunoceras* cf. *eschii* (Solger). Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria. Fig. 5a, b, C.90370, × 1·5. Fig. 6, C.90371, × 1. Both latex casts.



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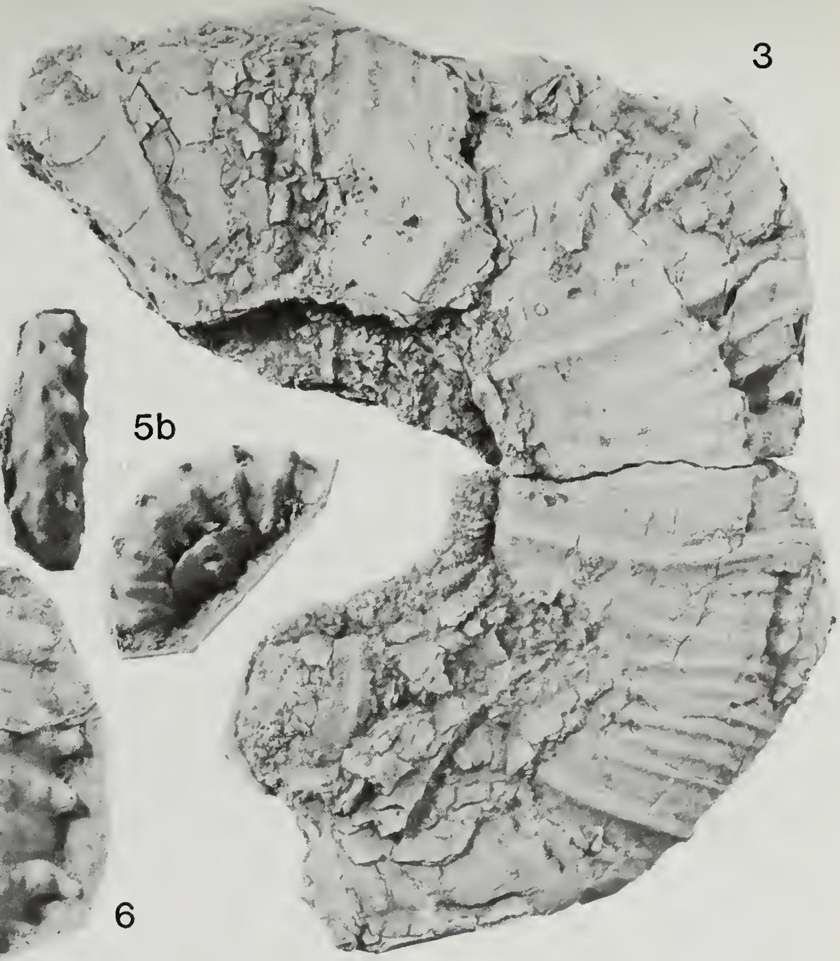

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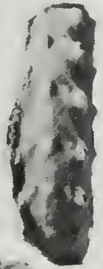
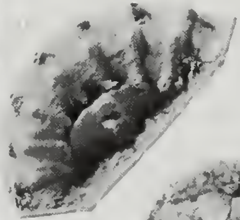
4a

4b



5a



5b

6

have higher whorls and more projected ribs than *P. denisonanum*. *P. maroccanum* Collignon (1966: 26; pl. 12, fig. 4) has broader whorls and develops strong ribbing earlier. In *P.*(?) *linderi* (Grossouvre 1894: 188; pl. 24, fig. 4; Collignon 1961: 41; pl. 10, figs 1, 1a; 1965: 8; pl. 379, fig. 1640) all ribs are of equal strength in the earlier whorls. *P. radaodyi* Collignon (1964: 58; pl. 333, fig. 1498) and *P. rarecostatum* Collignon (1961: 40; pl. 9, figs 1, 1a) both have stronger major ribbing which dominates the ornament even in the middle growth stages.

Superfamily **ACANTHOCERATACEAE** Grossouvre, 1894

Family **ACANTHOCERATIDAE** Grossouvre, 1894

Subfamily **EUOMPHALOCERATINAE** Cooper, 1978

Genus ***KAMERUNOCERAS*** Reyment, 1954*a*

TYPE SPECIES. *Acanthoceras eschii* Solger, 1904; by original destination.

Kamerunoceras* cf. *eschii (Solger, 1904)
Figs 5–6

cf. 1904 *Acanthoceras eschii* Solger: 124; pl. 4, figs 1–4.
non 1954*a* *Kamerunoceras eschii* (Solger) Reyment: 251; pl. 3, fig. 5; pl. 5, figs 3, 6; text-figs 2a, 2b (= *Kamerunoceras seitzi* (Riedel)).
non 1955 *Kamerunoceras eschii* (Solger); Reyment: 59 (= *Kamerunoceras seitzi* (Riedel)).
cf. 1958 *Kamerunoceras eschii* (Solger); Reyment: 55; pl. 1, figs 1a, 1b; pl. 2, figs 1a, 1b.
cf. 1979 *Kamerunoceras eschii* (Solger); Kennedy & Wright: 1166, 1175–1176; pl. 1, figs 4–9.

MATERIAL AND OCCURRENCE. Two specimens (C.90370–1) from the Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria.

DESCRIPTION. The smaller of these two specimens (C.90370, Fig. 5a, b) has a diameter of about 25 mm. It is evolute, its whorl breadth and whorl height being approximately equal. There are 16–17 ribs per whorl which are prominent only on the flanks where each bears bullate umbilical and inner ventrolateral tubercles. The ribs are effaced upon the venter where the ornament consists of clavate outer ventrolateral and siphonal tubercles, the latter situated a little adoral of the former. There are no minor ribs. The larger specimen (C.90371, Fig. 6) has a whorl breadth of some 20 mm. Again ribbing dominates the flank ornament while tubercles are more prominent upon the venter. There are strong, moderately spinose inner ventrolateral and weaker outer ventrolateral tubercles fusing to form a bituberculate structure. Along the median line are strong, rounded siphonal tubercles. Rib spacing is irregular. Minor ribs are absent.

REMARKS. Of the multitude of species referred to *Kamerunoceras* (see list in Kennedy & Wright, 1979), the present material is closest to the type species *K. eschii* (Solger 1904: 124; pl. 4, figs 1–4; Reyment 1958: 55; pl. 1, fig. 1; pl. 2, fig. 1; Kennedy & Wright 1979: 1175–1176; pl. 1, figs 4–9). Unfortunately, this is a poorly understood form, known only from the imperfectly preserved type specimen from southern Cameroun. It agrees, however, in its rather broad whorls, prominent flank ribs and comparatively massive ventrolateral tuberculation.

Kamerunoceras puebloense (Cobban & Scott, 1972)
Figs 7–8

1972 *Kanabiceras puebloense* Cobban & Scott: 73; pl. 15, figs 8, 9; pl. 37, figs 1–8; pl. 38, fig. 1.
1979 *Kamerunoceras puebloense* (Cobban & Scott) Kennedy & Wright: 1170.

MATERIAL AND OCCURRENCE. Four specimens (C.83518, C.90342–4) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Two further specimens (C.85299–300) from the same horizon and locality may also belong here.

DESCRIPTION. The shell is evolute with pentagonal whorl sections, which are a little higher than broad in the early stages, but slightly broader than high later on. Between diameters of 15 and

25 mm there are numerous ribs of markedly uneven development. These are projected forwards on the flank, backwards over the ventrolateral shoulder and form distinct chevrons over the venter. Major ribs bear prominent and spinose umbilical, inner and outer ventrolateral tubercles and more subdued but still well-defined siphonal tubercles. There are numerous intercalated ribs lacking umbilical tubercles but sometimes bearing subdued ventrolateral and siphonal tubercles; others show virtually no tubercle development at all. The venter is crossed by deep, chevron-shaped constrictions. At diameters of 50–70 mm the ribbing becomes more rectiradiate and regular, constrictions disappear and the major ribs come to dominate the ornament. Each bears highly spinose umbilical, inner and outer ventrolateral tubercles and a slightly lower siphonal tubercle. Intercalated ribs, dying out in the mid-flank region, generally alternate with the major ribs. They usually show exactly the same style and strength of ventral tuberculation as do the latter though the inner ventrolateral tubercles may be effaced. At these diameters there occur only a very few additional weak, fold-like ribs lacking tubercles altogether.

REMARKS. Cobban & Scott (1972: 73) first described *Kamerunoceras puebloense* from the Lower Turonian (*Mammites nodosoides* Zone) of Colorado. They referred it to *Kanabiceras* Reeside, a genus shown by Kennedy *et al.* (1981: 55) and Wright & Kennedy (1981: 54–55) to be a synonym of *Euomphaloceras* Spath. In fact, as pointed out by Wright & Kennedy (1981: 56), this species combines juvenile ornamentation similar to that in late members of *Euomphaloceras* with the evolute coiling and adult ornament characteristic of *Kamerunoceras.* Thus the early constriction-bearing whorls with their much multiplied, chevron-forming ventral ribs and tubercles resemble those in the late Cenomanian *Euomphaloceras euomphalum* (Sharpe) (see Kennedy 1971: 91; pl. 43, fig. 1; pl. 59, figs 1–5; Wright & Kennedy 1981: pl. 11, figs 1–8) and *E. septemseriatum* (Cragin) (see, for example, Cobban & Scott 1972: pl. 12, figs 5–27; Wright & Kennedy 1981: pl. 12, figs 1–8; pl. 13, figs 1–6; pl. 14, figs 5–9). Conversely, the evolute coiling and adult whorls with their lesser secondary ornament and more rectiradiate ribbing show closer similarities to *Kamerunoceras* (see Kennedy & Wright 1979 for a review of this genus). Since this material is clearly trending towards *Kamerunoceras* it is included therein, following the suggestions of Cooper (1978: 110), Kennedy & Wright (1979: 1170) and Wright & Kennedy (1981: 56). Although *K. puebloense* forms a clear link between its genus and the presumably ancestral *Euomphaloceras*, the more typical *Kamerunoceras*, *K.* cf. *eschii*, occurs below it at Lokpanta. As in Nigeria, *K. puebloense* is found in the upper part of the Lower Turonian in Colorado, though a similar form has been described from the very late Cenomanian of southern England (Wright & Kennedy 1981: 56; pl. 14, figs 3, 11).

The later whorls of *K. schindewolfi* (Collignon 1965: 31; pl. 389, fig. 1665) resemble those in the present material in their spinose tubercles and persistent minor ribbing. There are, however, mid-lateral tubercles in *K. schindewolfi.*

Subfamily **MAMMITINAE** Hyatt, 1900

Genus ***WATINOCERAS*** Warren, 1930

TYPE SPECIES. *Watinoceras reesidei* Warren, 1930 (= *Acanthoceras amudariense* Arkhanguelsky, 1916); by monotypy.

Watinoceras aff. ***amudariense*** (Arkhanguelsky, 1916)
Figs 10–12

MATERIAL AND OCCURRENCE. Three specimens (C.90366–8) from the Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria.

DIMENSIONS.	D	Wb	Wh	U	N
C.90367	13	4·5 (35)	5·6 (43)	3·8 (29)	37
C.90366	9	—	3·8 (42)	3·1 (34)	42

DESCRIPTION. The material at hand is of small size, the largest specimen having a diameter of only 13 mm. The shell is moderately evolute, compressed, with flattened flanks and, at first, a rounded venter, the whorl section becoming more pentagonal in shape later. The whorls are smooth up to diameters of 3–4 mm, when ribs appear, at first confined to the outer part of the flank and the venter. The whorls thereafter bear dense, rounded ribs mostly arising in pairs at the umbilical shoulder but sometimes bifurcating some distance down the flank. Intercalated ribs also occur. The ribs are projected over the venter but are interrupted by a narrow ventral sulcus. There are weak ventrolateral tubercles but umbilical tubercles become noticeable only at the largest diameters seen. One specimen (C.90368, Fig. 12), 11 mm in diameter, shows somewhat coarser ribs than the other two on its outer whorl. They form prominent chevrons upon the venter where they are again interrupted by a narrow sulcus.

REMARKS. Owing to their extremely small size, it is not possible to assign these specimens definite specific status. They most closely resemble the inner whorls of *Watinoceras amudariense* (Arkhanguelsky 1916: 48; pl. 7, figs 8–13; Wright & Kennedy 1981: 51; pl. 10, figs 6, 14; text-figs 19N, 19Q (with synonymy)), of which *W. reesidei* Warren (1930: 67; pl. 3, fig. 2; pl. 4, figs 9–12; see also, for example, Cobban & Gryc 1961: 186; pl. 38, figs 46–49) is the main synonym. The Nigerian material has a similar rib density and style of ornament, and such range as it shows in these features falls within that exhibited by figured specimens of this species. Thus the most coarsely ribbed Nigerian variant (C.90368) is similar to the example figured by Arkhanguelsky (1916: pl. 7, fig. 9). The main difference shown by the present material is its rather smaller umbilical diameter, 29–34% of the overall diameter against a consistent figure of about 40% in *W. amudariense*. In this respect the former is closer to specimens from Tarfaya figured by Collignon (1966: pl. 19, figs 14, 15) as *W.* sp. aff. *reesidei* Warren.

Watinoceras sp.
Figs 13–17

MATERIAL AND OCCURRENCE. Seven specimens (C.90361–5a, b, C.90369) from the Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria.

DIMENSIONS.	D	Wb	Wh	U	N
C.90365a	9	3·3 (37)	3·3 (37)	2·8 (31)	33
C.90365b	9·5	—	4·3 (45)	2·6 (27)	25
C.90369	12·5	6·5 (52)	4·5 (36)	3·6 (29)	27
C.90363	14	—	6 (43)	4 (29)	26

DESCRIPTION. This material is again of small size, the largest specimen having a diameter of 14 mm. The shell is moderately evolute. Its whorl height and whorl breadth are approximately equal at a diameter of about 9 mm but the latter increases much more rapidly so that the whorls develop a markedly depressed, pentagonal shape later on. The shell is smooth until

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Figs 7–8 *Kamerunoceras puebloense* (Cobban & Scott). Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 7a, b, C.90342, × 1. Fig. 8a–c, C.90344, × 1.

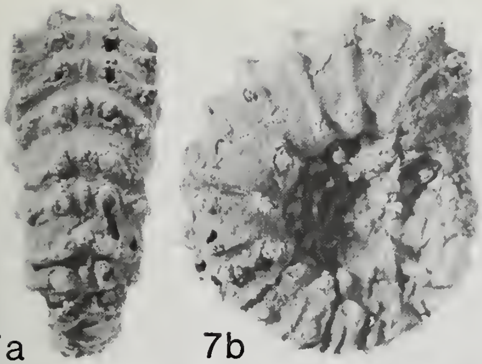
Fig. 9 *Metengonoceras*? sp. Eze-Aku Formation (Upper Cenomanian?), Lokpanta, south-east Nigeria. C.90373, × 1. This specimen shows pseudoceratitic sutures.

Figs 10–12 *Watinoceras* aff. *amudariense* (Arkhanguelsky). Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria. Fig. 10a, b, C.90367, × 1·5. Fig. 11, C.90366, × 1·5. Fig. 12, C.90368, × 1·5. All latex casts.

Figs 13–17 *Watinoceras* sp. Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria. Fig. 13a, b, C.90369, × 1·5. Fig. 14a, b, C.90362, × 1·5. Fig. 15a, b, C.90365a, × 2. Fig. 16, C.90365b, × 1·5. Fig. 17a, b, C.90363, × 1·5. All latex casts.

Figs 18–20 *Mammites nodosoides* (Schlüter). Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 18a, b, C.90336, × 1. Fig. 19a, b, C.90337, × 1. Fig. 20a, b, C.90341, × 1·5. See also Fig. 22a, b.

Fig. 21a, b *Mammites*? sp. Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria. C.90360, × 1·5. Latex cast.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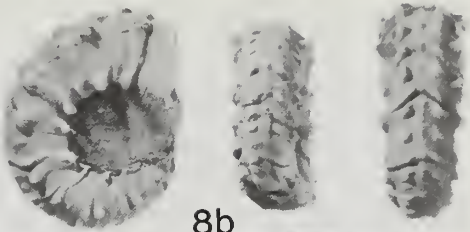
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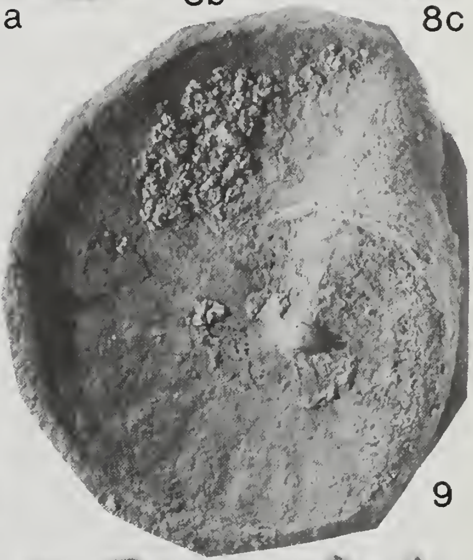
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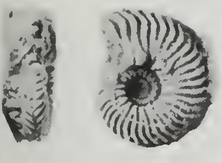

10a 10b


11


12

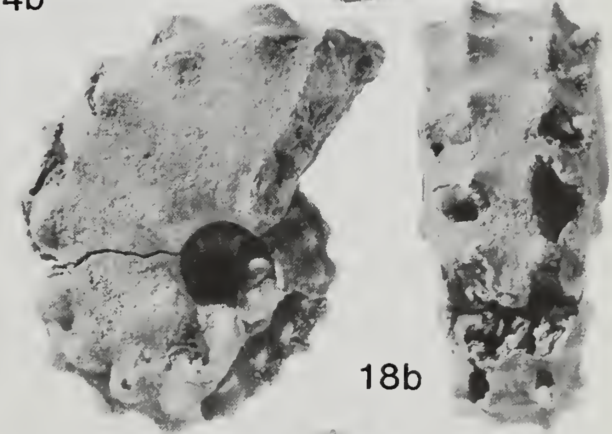

13a 13b

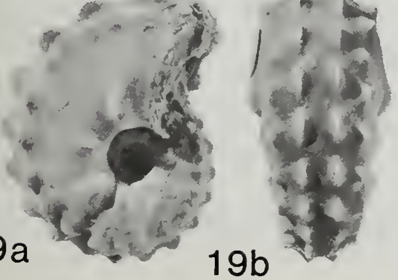

14a 14b

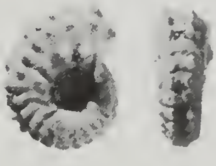

15a 15b

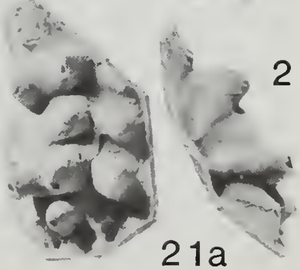

16


17a 17b


18a 18b


19a 19b


20a 20b


21a 21b

diameters as large as 4 mm, when fairly dense, rounded ribs appear. Prominent tubercles arise at a very early ontogenetic stage, the outer ventrolateral tubercles developing first, followed by the inner ventrolateral and umbilical tubercles. By a diameter of 10 mm all the tubercle rows are prominent and spinose. As growth proceeds rib density is reduced, the ribs themselves becoming higher and sharper. They mostly arise in pairs from the umbilical tubercles, though some intercalatories are also present. The ribs are projected forwards over the ventrolateral shoulders but are interrupted along the median line by an increasingly broad ventral sulcus.

REMARKS. The main characteristics of this form are its great whorl breadth and strong ornament. No previously described *Watinoceras* shows such a depressed whorl section at comparable diameters. *W. devonense* Wright & Kennedy (1981: 52; pl. 10, figs 7, 10, 12?, 13, 16) and *W. coloradoense praecursor* Wright & Kennedy (1981: 52; pl. 10, figs 4, 8, 9, 11, 15, 17, 18; text-figs 19G, 19K) show a rather similar style of ventral ribbing but are more compressed and the described material is of much larger size, precluding detailed comparison. The closely related genus *Benueites* Reyment, 1954 generally shows a less regular ornament than *Watinoceras*. The inner whorls of one species, *B. trinidadensis* Renz, however, may exhibit a similar style of ribbing and tuberculation to the present material (see Renz 1982: pl. 28, figs 14a, 14b) but they are again much more compressed. The Nigerian specimens may well represent a new species but without knowledge of their outer whorls this matter cannot be decided and it would be premature to describe them as such. Their initial whorls are similar to those in the contemporaneous material referred above to *Watinoceras* aff. *amudariense*. The latter, however, retains its fine ribbing and compressed whorls later into ontogeny. Reyment (1971), impressed by the fact that *Benueites* is frequently to be found represented by finely and coarsely ornamented forms lying side by side, considered that a novel form of ornamental dimorphism characterized the genus. Cooper (1978) doubted this view, as did Renz (1982: 91) who noted that the more coarsely ribbed members in Venezuela occupy a lower stratigraphical position. Cooper (1978: 120–122) himself proposed that *Watinoceras amudariense* was the microconch of *W. coloradoense* (Henderson), a large, coarsely decorated form (see, for example, Cobban & Scott 1972: 76; pl. 27, figs 11–19; pl. 28, figs 1–3, 5–9; text-figs 35–37; Wright & Kennedy 1981: 53, text-figs 18C–F). This suggestion was in turn doubted by Renz (1982: 93), and by Wright & Kennedy (1981: text-fig. 18G) who figured a large, densely ribbed *Watinoceras* which they suggested might represent the macroconch of *W. amudariense*. The nature of any dimorphism shown in *Watinoceras* therefore remains uncertain. It is of interest, however, to note the likeness of the earliest whorls in the two Nigerian forms described here, but whether this similarity has any special significance is difficult to ascertain, especially without the knowledge of their adult whorls.

Genus ***MAMMITES*** Laube & Bruder, 1887

TYPE SPECIES. *Ammonites nodosoides* Schlüter, 1871; by monotypy.

Mammites nodosoides (Schlüter, 1871)
Figs 18–20, 22

1829 *Ammonites nodosoides* Schlotheim [MS]; von Buch: 424 (nom. nud.).
1871 *Ammonites nodosoides* Schlüter: 19; pl. 8, figs 1–4.
1887 *Mammites nodosoides* Schlotheim sp. Laube & Bruder: 229; pl. 25, figs 1a, 1b.
1903 *Schlutericeras nodosoides* (Schlüter) Hyatt: 111.
1907 *Mammites nodosoides* (Schlotheim); Pervinquière: 309; pl. 18, figs 1a, 1b.
1907 *Mammites nodosoides* var. *afra* Pervinquière: 310; pl. 18, figs 2, 3; text-fig. 18.
1972 *Mammites nodosoides* (Schlotheim); Cobban & Scott: 78 (with synonymy).
1981 *Mammites nodosoides* (Schlüter); Wright & Kennedy: 75; pl. 17, fig. 3; pl. 19, fig. 3; pl. 20, fig. 4; pl. 22, fig. 4; pl. 23, figs 1–3; pl. 24, figs 2, 3; text-figs 19B, 23, 24 (with synonymy).
1982 *Mammites nodosoides* (Schlotheim); Renz: 89; pl. 27, figs 1–10.

MATERIAL AND OCCURRENCE. Seventy-two specimens (C.83517, C.85293–8, C.90327–41, UIN 486.1–50) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria.

REMARKS. This important species occurs abundantly in the upper part of the Lower Turonian at Lokpanta. Variation in the material is slight. The development of the outer ventrolateral tubercles is a little inconsistent. In the later stages they become highly clavate and sometimes fuse with the inner ventrolateral tubercles. Whorl height is greater than whorl breadth in the early and middle stages, but in the largest specimens collected the whorls become rather less compressed and here may resemble those in *Mammites wingi* Morrow (see Cobban & Scott 1972: 79; pl. 26, figs 1–4, 9, 10; pls 31–33; text-fig. 38; Wright & Kennedy 1981: 79; pl. 25, fig. 2; pl. 26, fig. 1; text-figs 25, 27). The inner whorls of *M. wingi* differ, however, in their more delicate ornament while rib density is greater in the adult stages.

***Mammites*? sp.**

Fig. 21a, b

MATERIAL AND OCCURRENCE. A single specimen (C.90360) from the Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria.

REMARKS. This small fragment, probably referable to the genus *Mammites*, shows a rather depressed whorl section. There are broad, rounded ribs, convex on the flanks and bent forwards over the venter, carrying strong umbilical and pointed inner and outer ventrolateral tubercles. Intercalated ribs, bearing outer ventrolateral tubercles alone, are present upon the venter.

Such meagre material is impossible to identify to species level, and even the generic assignment is questionable. It does, however, resemble the inner whorls of the basal Turonian *Mammites dixeyi* Reyment (1955: 50; pl. 9, fig. 4; pl. 10, fig. 3; pl. 11, figs 2a, 2b; text-figs 20, 21) from Nigeria. A *Mammites* from Trinidad (Reyment 1972: 365; fig. 8, 4a, 4b), probably of a somewhat younger age, is also similar, as is *M. nodosoidesappelatus* Etayo-Serna (1979: 85; pl. 13, fig. 1) from Colombia.

Family **VASCOCERATIDAE** Douvillé, 1912

(*nom. correct. & transl.* Spath, 1925; *ex* Vascoceratinés)

Subfamily **VASCOCERATINAE** Douvillé, 1912

Genus ***FAGESIA*** Pervinquière, 1907

TYPE SPECIES. *Olcostephanus superstes* Kossmat, 1897; by original designation.

Fagesia levis Renz, 1982

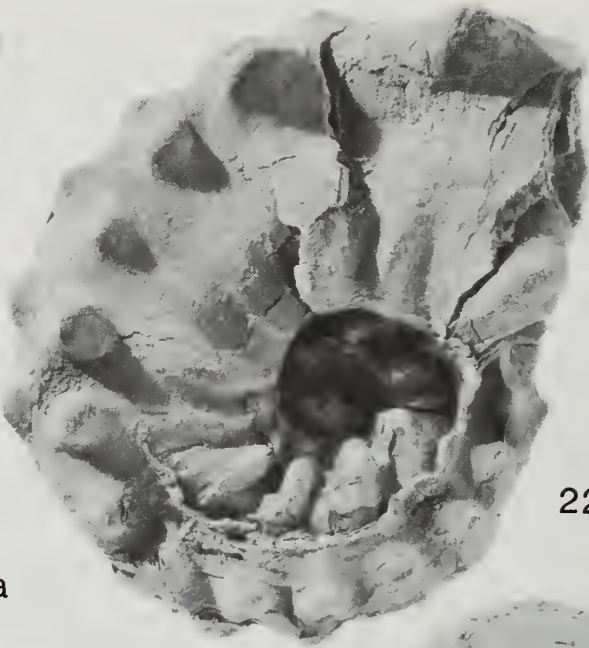
Figs 23–4, 27–8

1982 *Fagesia levis* Renz: 78; pl. 22, figs 20a, 20b; pl. 23, figs 1–3; text-figs 53, 59a–c.

MATERIAL AND OCCURRENCE. Twenty-nine specimens (C.85281–3, C.90319–20, UIN 487.1–24) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. A further six specimens (C.90321–6) from the same horizon and locality probably also belong here (Figs 25–6).

DESCRIPTION. Six small specimens (C.90321–6) show what are probably the juvenile whorls of this species. The shell at this stage is evolute and the whorls only slightly depressed with a rounded venter. There are strong, rounded ribs mostly springing in pairs from rather spinose umbilical turbercles and bending forwards over the venter. Intercalated ribs also occur. The ribs fade early in ontogeny and between diameters of about 45 and 60 mm they practically disappear, being represented thereafter by faint, broad folds, convex over the venter. The shell now becomes globular and evolute with 10–11 strong, rounded tubercles at the umbilical shoulder in each whorl. At diameters around 100 mm these tubercles become broader, flatter and less distinct and finally fade out altogether. The maximum diameter attained is about 200 mm. The suture is typical of the genus with highly elongated, much incised elements.


22a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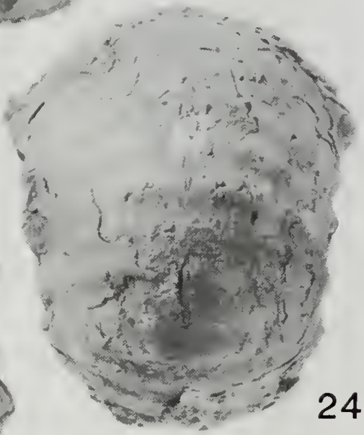
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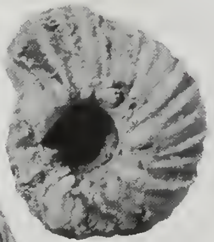
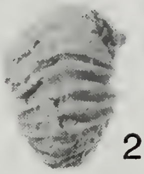
23


25a


25b


26

REMARKS. The inner whorls in *Fagesia* characteristically show strong ribs arising in twos or threes from umbilical tubercles. The ornament is generally lost later in ontogeny, the stage at which this occurs being a major factor in distinguishing between species. *F. superstes* (Kossmat 1897: 26; pl. 6, fig. 1; Pervinquière 1907: 322; pl. 20, figs 1–4) shows persistently strong ribbing and umbilical tuberculation, while *F. thevestensis* (Peron 1896: 23; pl. 7, figs 2, 3; Pervinquière 1907: 325; pl. 20, figs 5, 6) and the similar *F. boucheroni* (Coquand) (see Kennedy & Wright 1979*a*: 669, text-figs 1A, 1B) lose their ribbing a little earlier. *F. peroni* Pervinquière (1907: 329; pl. 20, figs 7, 8), on the other hand, loses first its ribbing, then its tuberculation, at a very early ontogenetic stage. The present material is intermediate between *F. peroni* and *F. thevestensis* in these respects. It conforms closely with the globular, evolute, early Turonian *F. levis* Renz (1982: 78; pl. 22, fig. 20; pl. 23, figs 1–3; text-figs 53, 59a–c) from Venezuela. Ontogenetic development in this species is very similar to that in the Nigerian specimens, though juvenile *F. levis* (see Renz 1982: pl. 23, figs 3a, 3b) are rather less densely ribbed than the presumed early whorls in the present Nigerian material (Figs 25–6). At this growth stage the latter is closer to the Colombian *F. zanelli* Etayo-Serna (1979: 89; pl. 13, fig. 11; pl. 14, fig. 5). In this form, however, the ribbing is said to strengthen during ontogeny with prominent narrow ribs persisting up to diameters of at least 50 mm (see Etayo-Serna 1979: pl. 14, fig. 5). Venezuelan specimens occurring with *F. levis* and referred to *F.* aff. *superstes* by Renz (1982: 78; pl. 22, figs 19a, 19b; pl. 23, figs 4a, 4b) differ only in having slightly stronger, more persistent ribbing. The Nigerian material includes forms such as these (Fig. 24); they are probably variants of *F. levis*.

F. bomba (Eck 1909: 179; pl. 17, figs 1, 2), the similar *F. involuta* Barber (1957: 27; pl. 9, fig. 3; pl. 29, figs 6, 7) and *F. simplex* Barber (1957: 27; pl. 8, fig. 1; pl. 29, figs 4, 5) all lose their ribbing early, but the first two species are markedly more involute than the present material, while *F. simplex* has a much simpler suture pattern. *F. lenticularis* Freund & Raab (1969: 36–42; pl. 6, figs 3–7; pl. 7, figs 1–3; pl. 8, figs 1, 2; text-figs 7h–k, 8a–i, 9a–c) and its varieties have a peculiar, eccentric mode of coiling. *F. rudra* (Stoliczka 1865: 122; pl. 60, fig. 1; Kennedy & Wright 1979*a*: 666; pl. 82, figs 1, 2) lacks umbilical tubercles. *F. pachydiscoides* Spath (see Wright & Kennedy 1981: 97, text-fig. 37) is more compressed. In addition, its umbilical tubercles persist to a very late stage, as is the case in *F. catinus* (Mantell) (see Wright & Kennedy, 1981: 88; pl. 26, fig. 2; text-figs 31–36, for review and synonymy) where they increase in strength during ontogeny. The ribbing also persists longer in *F. catinus* (see Powell 1963: 320; pl. 33, fig. 2; pl. 34, figs 1–5).

Genus *NEOPTYCHITES* Kossmat, 1895

TYPE SPECIES. *Ammonites telinga* Stoliczka, 1865 (= *A. cephalotus* Courtiller, 1860); by original designation.

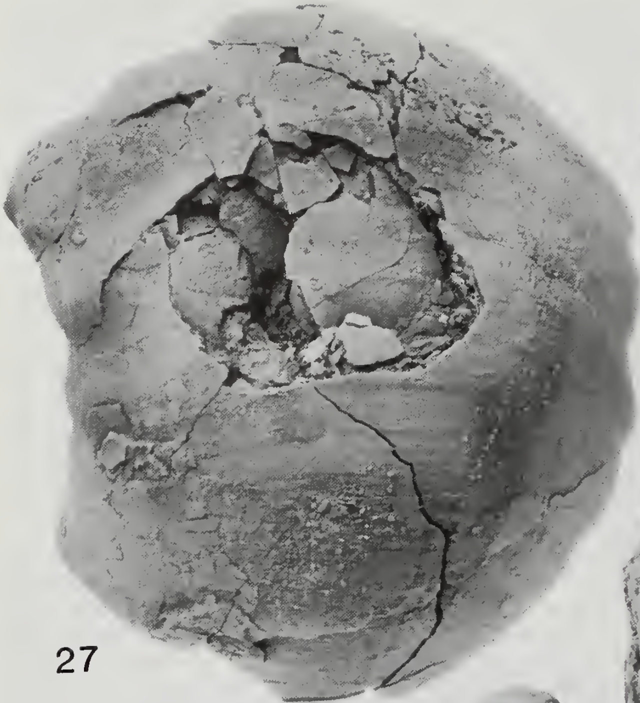
Neoptychites cephalotus (Courtiller, 1860)
Figs 31–2

1860 *Ammonites cephalotus* Courtiller: 248; pl. 2, figs 1–4.
1865 *Ammonites xetra* Stoliczka: 124; pl. 61, figs 1, 2.
1865 *Ammonites telinga* Stoliczka: 125; pl. 62, figs 1, 2.
1895 *Neoptychites xetra* (Stoliczka) Kossmat: 72.
1895 *Neoptychites telinga* (Stoliczka) Kossmat: 71; pl. 7, fig. 1.

Fig. 22a, b *Mammites nodosoides* (Schlüter). Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. C.90327, × 1. See also Figs 18–20.

Figs 23–24 *Fagesia levis* Renz. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 23, C.90319, × 1. Lateral view of specimen shown in Fig. 27. Fig. 24, C.90320, × 1. A variant with abnormally persistent ribbing. See also Figs 25–26(?), 27–28.

Figs 25–26 *Fagesia levis* Renz?. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. The presumed early whorls. Fig. 25a, b, C.90321, × 1. Fig. 26, C.90322, × 1.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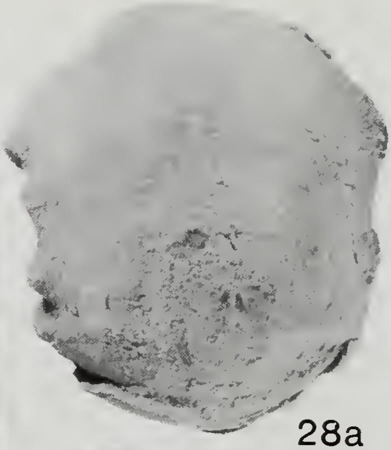
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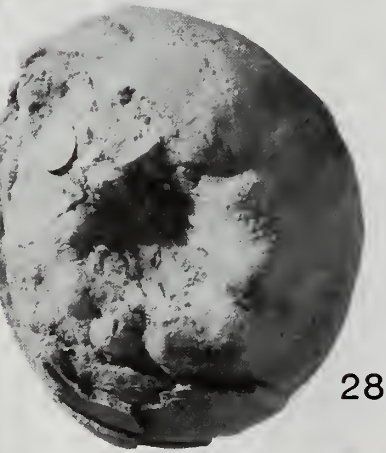
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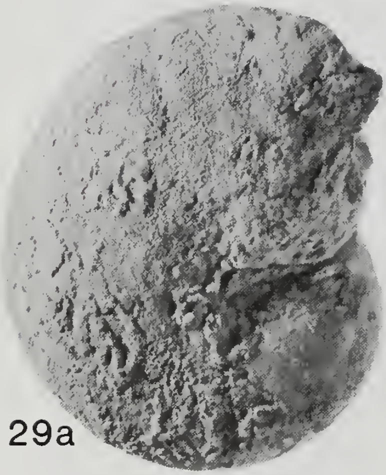
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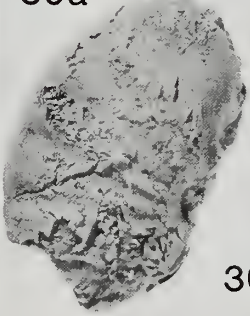
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30b

Figs 27–28 *Fagesia levis* Renz. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 27, C.90319, × 1. Ventral view of specimen shown in Fig. 23. Fig. 28a, b, C.85282, × 1. See also Figs 23–24, 25–26(?).

Fig. 29a, b *Thomasites gongilensis* (Woods). Eze-Aku Formation (uppermost Cenomanian or lowermost Turonian), Ezillo, south-east Nigeria. C.90354, × 1. See also Figs 34–35.

Fig. 30a, b *Herrickiceras*? sp. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. C.85287, × 1.

1907 *Neoptychites cephalotus* (Courtiller) Pervinquière: 393; pl. 27, figs 1–4; text-fig. 152.
1907 *Neoptychites gourguechoni* Pervinquière: 400; pl. 27, figs 8, 9; text-figs 155, 156.
1979*a* *Neoptychites cephalotus* (Courtiller); Kennedy & Wright: 670; pl. 82, figs 3–5; pl. 83, figs 1–3; pl. 84, fig. 3; pl. 85, figs 1–5; pl. 86, figs 5, 6; text-fig. 2 (with synonymy).
?1979 *Franciscoites suarezi* Etayo-Serna: 87; pl. 13, fig. 2; text-figs 8X, Y, ü.
1982 *Neoptychites* aff. *crassus* Solger; Renz: 88; pl. 26, figs 16a, 16b.
1982 *Neoptychites* aff. *telingaeformis discrepans* Solger; Renz: 88; pl. 26, figs 17a, 17b.
?1982 *Neoptychites transitorius* Renz: 87; pl. 26, figs 15, 18; text-figs 65d, 66A, 66a–d.

MATERIAL AND OCCURRENCE. At least five specimens, four (C.83512, C.85289, C.90317–8) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria; the other (C.90359) from a slightly lower (basal Turonian) horizon at Lokpanta.

REMARKS. This material is identical with *Neoptychites cephalotus* (Courtiller). The smallest specimen (C.90359), with a diameter of 21 mm, is moderately compressed, shows a sharply rounded venter and has the characteristic collared constrictions of the juveniles in this species (see, for example, Solger 1904: pl. 3, fig. 4; Pervinquière 1907: pl. 37, figs 3a, 3b; Riedel 1932: pl. 26, fig. 5; Reyment 1972: fig. 7, 1–3; Renz 1982: pl. 26, figs 17a, 17b; Cobban & Hook 1983: pl. 3, figs 9–11). *Franciscoites suarezi* Etayo-Serna (1979: 87; pl. 13, fig. 2), known only from juveniles, is also very similar and seems to be a synonym. The largest Nigerian specimen (C.85289) has a diameter of some 200 mm. It is adult and shows the distinctive constricted aperture of this species. Its whorls are smooth and triangular, the venter being narrowly rounded and raised up slightly along the median line on the early part of the body chamber.

Kennedy & Wright (1979*a*: 670–680) have discussed the genus *Neoptychites* at length. They treated *N. xetriformis* Pervinquière as a distinct species but noted its association with *N. cephalotus* in the Touraine area of France and raised the possibility of the two being dimorphs. Cobban & Hook (1983: 14–15), working with large collections from New Mexico, considered *N. xetriformis* to be a synonym of *N. cephalotus*. They regarded the latter species as highly variable, including both small, stout, ribbed forms of *N. xetriformis* character, as well as larger, slender, more weakly ornamented individuals having the form of *N. cephalotus*. They, too, suggested dimorphism but were disturbed by the lack of a clearly bimodal size pattern within the population. The Nigerian material is too sparse to contribute greatly to this problem and a conservative approach is followed here. It may be relevant, however, that along with the material from the *Mammites nodosoides* Zone at Lokpanta there comes a rather poorly preserved specimen (C.85288) of 90 mm diameter which shows broad whorls, a rounded venter and distinct, broad ribs. This individual is close to *N. xetriformis*, adding to the evidence for its coexistence with *N. cephalotus*.

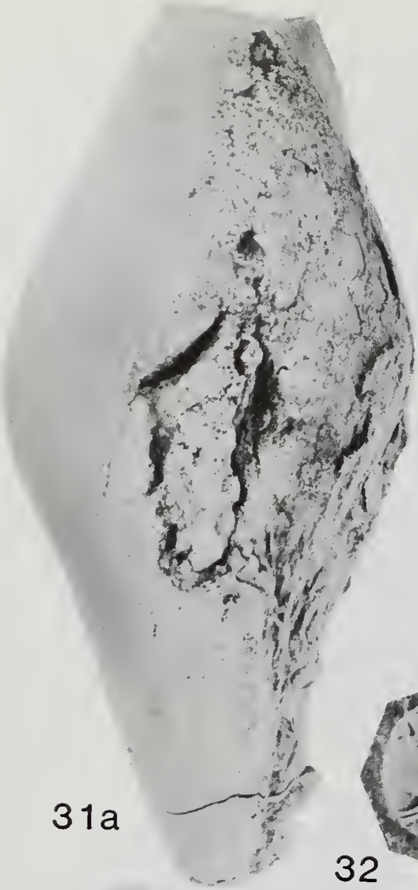
Kennedy & Wright (1979*a*: 680–681) showed that in France *Neoptychites* occurs some way up in the Turonian, above beds with *Mammites* of the *nodosoides* group. They regarded it as being approximately contemporaneous elsewhere in the world except for the western interior of the United States (Colorado) where it appears in the basal Turonian Zone of *Watinoceras coloradoense* (see Cobban & Scott 1972; Kauffman *et al.* 1978). The Nigerian material confirms this early occurrence of the genus, it being found below beds with *Mammites nodosoides*.

Subfamily **PSEUDOTISSOTIINAE** Hyatt, 1903

Genus ***THOMASITES*** Pervinquière, 1907

TYPE SPECIES. *Pachydiscus rollandi* Peron, 1889; by original designation.

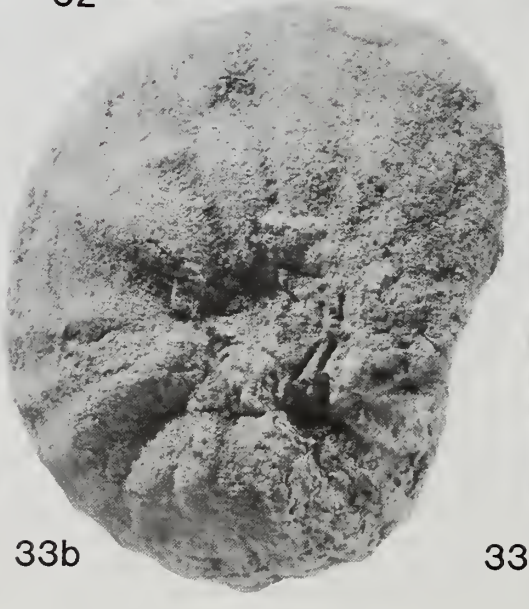
REMARKS. The close similarity between *Thomasites* and *Gombeoceras* Reyment has been remarked upon by several authors. Basse (1940: 457) included *Vascoceras gongilense* Woods, the type species of *Gombeoceras*, under synonymy in *Thomasites*. Reyment (1954: 151), in proposing the genus *Gombeoceras*, differentiated it from *Thomasites* by its more evolute shell, less triangular whorls, weaker umbilical tuberculation and non-constricted aperture. Freund & Raab (1969: 42–43), however, considered the morphological range in *Thomasites* to be wide enough to include *Gombeoceras*. They noted that the Nigerian material of *Gombeoceras* figured


31a


31b


32


33a


33b


33c

by Reyment (1954, 1954*a*, 1955) and Barber (1957) consisted entirely of phragmocones, the nature of the adult aperture being unknown. In fact, an undescribed, entire, adult specimen of *G. gongilense* (C.47561) from the Numan area of north-east Nigeria does indeed show the moderately constricted aperture characteristic of adult *Thomasites rollandi* (see Pervinquière 1907: pl. 22, figs 4a, 4b). The Nigerian specimen has a diameter of 130 mm; in *T. rollandi* the constricted aperture appears at diameters of 110–130 mm (Pervinquière 1907: 343). Reyment (1979) sought to maintain the separate status of *Gombeoceras*, stressing that *Thomasites* lacks a median or ventrolateral keel at any ontogenetic stage. Wright & Kennedy (1981: 99), however, pointed out that the siphonal ornament is highly variable in both *Thomasites* and *Gombeoceras*, and they could find no character to distinguish between the two. In view of their clear similarity, this latter view is followed here, *Gombeoceras* being treated as a synonym of *Thomasites*.

Thomasites gongilensis (Woods, 1911)
Figs 29, 34–5

1911 *Vascoceras gongilense* Woods: 282; pl. 21, fig. 7; pl. 22, fig. 1.
1954 *Gombeoceras gongilense* (Woods) Reyment: 151; pl. 2, fig. 1; pl. 3, fig. 6; text-fig. 1.
1954*a* *Gombeoceras subtenue* Reyment: 261; pl. 4, fig. 4; text-fig. 3f.
1955 *Gombeoceras gongilense* (Woods); Reyment: 63; pl. 14, fig. 5; pl. 21, fig. 4.
1957 *Gombeoceras gongilense* (Woods); Barber: 79; pl. 17, figs 1–6; pl. 18, figs 1–4; pl. 19, figs 1–6; pl. 20, fig. 3; pl. 37, figs 1–20.
1965 *Gombeoceras gongilense* (Woods); Reyment: pl. 2, fig. 3; pl. 3, figs 16, 19.
1976 *Gombeoceras gongilensis* (Woods); Offodile: 69; pl. 12, fig. 3.
1976 *Gombeoceras compressum* Barber; Offodile: 69; pl. 12, fig. 4.
1976 *Gombeoceras gongilense* (Woods); Offodile & Reyment: 58, text-figs 31, 32.
1976 *Gombeoceras compressum* Barber; Offodile & Reyment: 59, text-fig. 33.
1981 *Thomasites gongilensis* (Woods) Wright & Kennedy: 100; pl. 24, fig. 1; pl. 25, fig. 1.

MATERIAL AND OCCURRENCE. Two specimens (C.90353–4) from the Eze-Aku Formation (uppermost Cenomanian or lowermost Turonian), Ezillo, south-east Nigeria. A further specimen (C.90355) from the same horizon and locality may also belong here.

REMARKS. Barber (1957) demonstrated very clearly the wide degree of variation shown by populations of *Thomasites gongilensis* in north-east Nigeria. He suspected, but was unable to prove, that this variability was partly stratigraphical and geographical as well as individual in nature. He therefore separated his diverse morphotypes into a number of subspecies. Reyment (*in* Offodile & Reyment 1976: 53), however, preferred to regard these forms as separate species. In as much as they occur side by side or within a few metres of section in both the middle Benue Valley and north-eastern regions of Nigeria (Barber 1957, Offodile & Reyment 1976, Wozny & Kogbe 1983) and that they tend to grade into one another, it is probably more correct to regard them as mere varieties of *T. gongilensis*. Wright & Kennedy (1981: 100) suspected that a similar situation might prove to exist amongst the Tunisian populations of *Thomasites* described by Pervinquière (1907); all these forms may be varieties of *T. rollandi* (Peron).

Two varieties of *T. gongilensis* have been identified from Ezillo. The first (C.90354, Fig. 29a, b) is compressed, involute and with flattened flanks and a rounded venter. There are feeble ribs on the outer parts of the flank and venter; the latter also bears weak ventrolateral and siphonal tubercles. In all these respects, as in suture pattern, this specimen conforms closely with the variety *T. gongilensis* var. *compressus* (see Barber 1957: 41; pl. 19, figs 2a, 2b, 5a, 5b; pl. 33, figs 15, 16), the most compressed and one of the most feebly ornamented varieties of this species. The Tunisian form named *T. meslei* by Pervinquière (1907: 345; pl. 22, figs 8, 9) is very

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Figs 31–32 *Neoptychites cephalotus* (Courtiller). Fig. 31a, b, C.85289, × 0·65. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 32, C.90359, × 1. Eze-Aku Formation (basal Turonian), Lokpanta, south-east Nigeria; latex cast.

Fig. 33a–c *Thomasites koulabicus* (Kler). Eze-Aku Formation (uppermost Cenomanian or lowermost Turonian), Ezillo, south-east Nigeria. C.90352, × 1.

close to *T. gongilensis* var. *compressus*. Wright & Kennedy (1981: 100) noted the morphological overlap between the Tunisian and Nigerian populations of *Thomasites* but because the former was poorly preserved were unable to decide whether *T. gongilensis* should be brought into synonymy under *T. rollandi*.

The second specimen (C.90353, Fig. 34a, b) is moderately evolute and moderately compressed, though slightly crushed laterally. Its venter is broadly rounded at first but shows a low siphonal ridge later in ontogeny. There are low, rounded ribs upon the inner two-thirds of the flanks. The ventral ornament is weak at first but at its adoral end the specimen shows strong ventrolateral tubercles and clavate swellings upon the siphonal ridge. Two varieties of *T. gongilensis* resemble this specimen in their later whorls. *T. gongilensis* var. *inflatus* (Barber 1957: 43; pl. 18, figs 3, 4; pl. 33, figs 18–20) shows weakened ornament and a broad keel in its later stages but is more inflated. Rather closer is *T. gongilensis* var. *tectiformis* (Barber 1957: 41; pl. 17, figs 1–4; pl. 19, fig. 6; pl. 33, figs 4–6; Fig. 35) which, while displaying angular ventrolateral shoulders in its early whorls, develops a more rounded whorl section towards adulthood, when its ornament weakens though the keel persists.

A third Ezillo specimen (C.90355) has the overall dimensions of *T. gongilensis* var. *costatus* (Barber 1957: 41; pl. 18, fig. 1; pl. 19, figs 1, 3; pl. 37, figs 9, 10) but is too poorly preserved for certain identification.

In Nigeria, *Thomasites* has previously been reported from only one locality south of the Benue River, a section in the Konshisha River near Oturkpo (Reyment 1955: 63, 98; Fig. 46, p. 58). The present records, therefore, considerably extend its southerly geographical range.

Thomasites koulabicus (Kler, 1909)

Fig. 33a–c

1909 *Pseudotissotia koulabica* Kler: 157; pl. 6, figs 1–3; pl. 7, figs 1, 2; pl. 8, figs 1, 2.
1954*a* *Gombeoceras koulabicum* (Kler) Reyment: 261.
1958 *Thomasites koulabicus* (Kler) Tsagareli, Glazunova, Luppov & Mikhailov (*in* Orlov): 124; pl. 61, figs 3a, 3b; text-fig. 99b.
1966 *Koulabiceras koulabicum* (Kler) Atabekyan: 77.
1969 *Gombeoceras* (*Ferganites*) *koulabicum* (Kler); Stankievich & Pojarkova: 94; pl. 2, figs 3a, 3b; pl. 3, figs 1a, 1b.
?1969 *Gombeoceras* (*Ferganites*) *kanicum* Stankievich & Pojarkova: 95; pl. 3, figs 2a, 2b.
1969 *Gombeoceras* (*Ferganites*) *kleri* (Luppov MS) Stankievich & Pojarkova: 96; pl. 4, figs 1–3.
1981 *Thomasites koulabicus* (Kler); Wright & Kennedy: 100.

MATERIAL AND OCCURRENCE. A single specimen (C.90352) from the Eze-Aku Formation (uppermost Cenomanian or lowermost Turonian), Ezillo, south-east Nigeria.

DESCRIPTION. This specimen is moderately evolute. At first its whorls are rather inflated and the venter arched, but the body chamber becomes compressed with flatter flanks and a broadly rounded venter. The ornament of the phragmocone is very coarse; massive umbilical bullae give off pairs of strong, rounded ribs, while additional intercalated ribs arise some distance down the flanks. There are prominent ventrolateral tubercles, and clavate siphonal tubercles which tend to fuse so producing an intermittent keel. Upon the body chamber the ornament weakens, the ribs becoming flatter and lower, though the umbilical tubercles remain prominent.

REMARKS. As Tsargareli *et al.* (*in* Orlov 1958: 124) and Wright & Kennedy (1981: 99) have pointed out, *Pseudotissotia koulabica* Kler (1909: 157; pls 6–8), previously unknown outside Soviet Central Asia, is a *Thomasites*. It represents the most coarsely ornamented member of the genus yet known. Reyment (1954*a*: 261) and Barber (1957: 39, 45) were of the opinion that the morphological range of *T. gongilensis* overlaps that of *T. koulabicus*. Wright & Kennedy (1981: 99–100) preferred to maintain the two as distinct species. Since the ornament in *T. koulabicus* is consistently stronger than that in even the most coarsely decorated variety of *T. gongilensis*, *T. gongilensis* var. *crassicostatus* (Barber 1957: 45; pl. 18, figs 2a, 2b; pl. 33, figs 7, 8), and since the adult body chamber appears to undergo wholesale compression at adulthood (see Figs 33a, c; Kler 1909: pl. 8, fig. 1; Stankievich & Pojarkova 1969: pl. 3, figs 1a, 1b) rather than merely showing a constricted aperture like that in *T. gongilensis*, Wright & Kennedy's view is followed here. The size at which compression of the body chamber takes place in *T. koulabicus* is, however, variable. In the present material it takes place at an overall diameter of some 85 mm (phragmocone diameter 55 mm) when the ornament becomes effaced, indicating adulthood. In specimens figured by Kler (1909: pl. 7, figs 1, 2; pl. 8, fig. 1) these characters do not appear until phragmocone diameters of 90–95 mm and certain specimens (see Kler 1909: 157–158) reach overall diameters of nearly 150 mm. Perhaps this size difference reflects dimorphism.

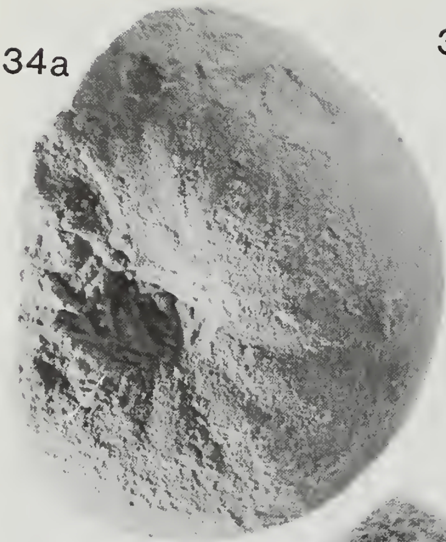
The genus *Koulabiceras* Atabekyan, 1966 (type species *Pseudotissotia koulabica* Kler) is a subjective synonym of *Thomasites. Gombeoceras* (*Ferganites*) Stankievich & Pojarkova (1969: 94) shares this type species and is therefore an objective synonym of *Koulabiceras*. Stankievich & Pojarkova (1969) referred the following species to *G.* (*Ferganites*): *G.* (*F.*) *koulabicum* (Kler), *G.* (*F.*) *kleri* Stankievich & Pojarkova (1969: 96; pl. 4, figs 1–3) and *G.* (*F.*) *kanicum* Stankievich & Pojarkova (1969: 95; pl. 3, figs 2a, 2b). The last of these has rather broad whorls, especially in its later growth stages. All three are nevertheless similar and, bearing in mind the wide degree of variation shown by species of *Thomasites*, all three probably belong in *T. koulabicus* (see also Wright & Kennedy 1981: 100). Stankievich & Pojarkova (1969: 91–93; pl. 1, figs 2, 3; pl. 2, figs 1, 2) described several additional *Thomasites* from the Soviet Union as *T.* cf. *globosotuberculatus* Pervinquière, *T.* cf. *jordani* Pervinquière and *T.*(?) *inflatus* sp. nov. These show a consistently strong ornament which is only rarely approached by the Tunisian material described by Pervinquière (1907). All the central Asiatic forms come from a similar stratigraphical horizon (Stankievich & Pojarkova 1969: 87–88) and one might speculate that, just as in the cases of the Tunisian and north-east Nigerian populations of *Thomasites*, they represent a complex of variants all belonging to the single coarsely ornamented species *T. koulabicus*.

Genus ***WRIGHTOCERAS*** Reyment, 1954

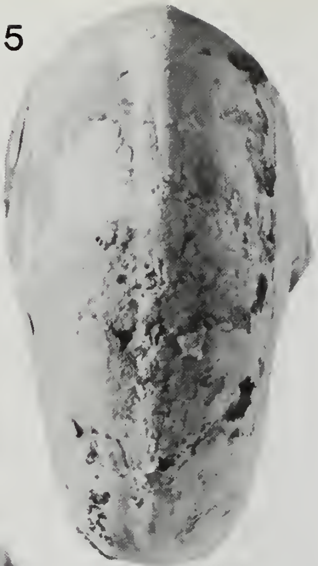
TYPE SPECIES. *Bauchioceras* (*Wrightoceras*) *wallsi* Reyment, 1954; by original designation.

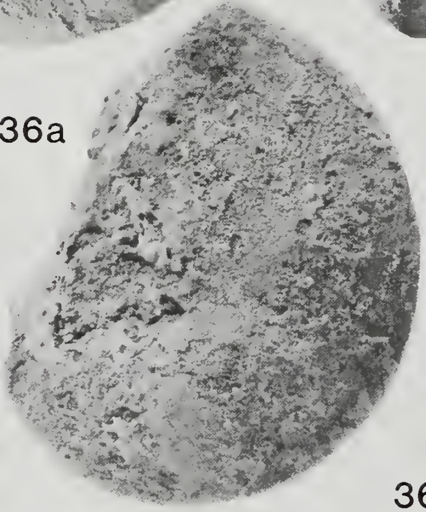
REMARKS. Members of this genus were first described from the Lower Turonian of Tunisia as *Hoplitoides munieri* Pervinquière (1907: 217; pl. 10, figs 1, 2) and *H. mirabilis* Pervinquière (1907: 218; pl. 10, fig. 3). Pervinquière (1907: 215–216) was aware that these forms were untypical of *Hoplitoides* von Koenen in that they exhibit tabulate venters not in the juvenile stages alone but throughout ontogeny. Rather than refer them to a new genus, however, he preferred to emend the diagnosis of *Hoplitoides* (see Solger 1904) and recognized within it two groups, those with tabulate venters throughout growth and those with narrowly rounded or sharpened venters in their later stages. He regarded the former group as ancestral to the latter. Kummel & Decker (1954) described similar, broad-ventered material from northern Mexico as '*Hoplitoides*' cf. '*H.*' *munieri* Pervinquière but indicated that it did not truly belong in this genus and should be included in a new taxon (see also Benavides-Cáceres 1956: 476). Reyment (1954), working primarily with material from northern Nigeria, proposed *Wrightoceras*, originally as a subgenus of *Bauchioceras* Reyment, 1954, in which he included *B.* (*W.*) *wallsi* as type species along with *Hoplitoides munieri* and *H. mirabilis*. Later, Reyment (1955) treated both *Bauchioceras* and *Wrightoceras* as subgenera of *Pseudotissotia* Peron, *Wrightoceras* being distinguished mainly by its lack of a siphonal keel. Barber (1957) followed this procedure. Kennedy, Cooper & Wright (1979) re-examined *Ammonites gallienni* d'Orbigny, the type species of *Pseudotissotia*, and suggested that *Bauchioceras* be treated as a strict synonym of *Pseudotissotia. Wrightoceras*, however, was maintained as a separate genus altogether since it shows at most a feeble siphonal keel in the juvenile stages only and possesses comparatively weak, impersistent ornament.

At present, the following can be referred to *Wrightoceras*: *W. wallsi* Reyment, *W. munieri* (Pervinquière), of which *W. mirabilis* (Pervinquière) may be a synonym, *W. inca* (Benavides-Cáceres), *W. llarenai* (Karrenberg), *W. submunieri* Wiedmann and *W. reymenti* Collignon & Roman. *Pseudotissotia gagnieri* Faraud (1951: 149; pl. 5, fig. 1) may also belong here but develops an untypical rounded venter. The Colombian genus *Imlayiceras* Leanza, 1967 (type species *Imlayiceras washbournei* Leanza 1967: 198; pl. 4, figs 1–4; pl. 6, figs 1, 4–6) differs from *Wrightoceras* only in the reported presence of faint constrictions on the early whorls. The later


34a


34b

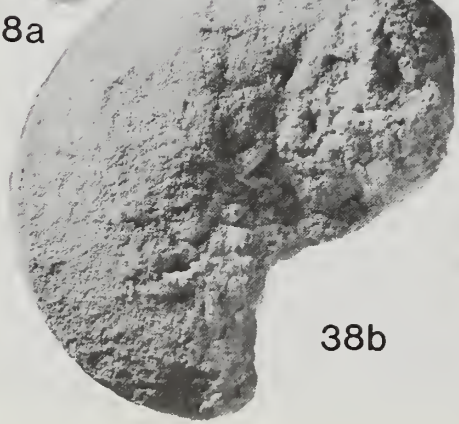

35

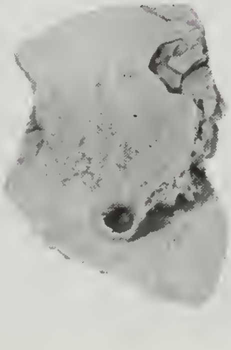

36a


36b


37


38a


38b


39a


39b

stages in the two genera are, however, indistinguishable and the Colombian material is perhaps better included in *Wrightoceras* also.

The relative stratigraphical positions of *Wrightoceras* and *Hoplitoides* are discussed below (p. 53).

Wrightoceras wallsi Rement, 1954
Figs 36–7

1954 *Bauchioceras* (*Wrightoceras*) *wallsi* Reyment: 160; pl. 2, fig. 4; pl. 3, figs 3, 3a.
1955 *Pseudotissotia* (*Wrightoceras*) *wallsi* (Reyment) Reyment: 71; pl. 24, fig. 1; text-figs 32a, 32c, 32d.
1957 *Pseudotissotia* (*Wrightoceras*) *wallsi* (Reyment); Barber: 53; pl. 24, figs 1, 2; pl. 34, figs 5, 13.
1965 *Pseudotissotia* (*Wrightoceras*) *wallsi* (Reyment); Reyment: pl. 4, figs 14–17.

MATERIAL AND OCCURRENCE. Two specimens (C.90349–50) from the Eze-Aku Formation (Lower Turonian), Ezillo, south-east Nigeria.

REMARKS. Barber (1957: 51) found populations of *Wrightoceras wallsi* to show a variable degree of compression. The two present specimens represent relatively slim variants and tend towards the material referred below to *W.* cf. *munieri* (Pervinquière). The smaller of the two (C.90349, Fig. 36a, b), with a diameter of 70 mm, has at first a slightly concave venter bordered by ventrolateral keels, becoming more tabulate later. It is exactly comparable with an individual of *W. wallsi* (C.47617, Fig. 37) from Kanawa near Gombe in north-east Nigeria at an equivalent size. The larger of the two specimens (C.90350) has a diameter of 240 mm and, apart from having a slightly more rounded adult venter, is very close to the large form from Deba-Habe near Gombe (C.47421) figured by Reyment (1955: pl. 24, fig. 1).

Material from northern Mexico described by Kummel & Decker (1954: 317; pl. 33, figs 1, 2; text-figs 7, 10) as '*Hoplitoides*' cf. '*H.*' *munieri* Pervinquière has a rather broader and more sulcate venter than Pervinquière's species, as these authors pointed out. It is close to *W. wallsi* but shows weak ribs on the flanks which sometimes cross the venter.

Wrightoceras cf. ***munieri*** (Pervinquière, 1907)
Figs 38, 40

cf. 1907 *Hoplitoides munieri* Pervinquière: 217; pl. 10, figs 1, 2.
cf. 1907 *Hoplitoides mirabilis* Pervinquière: 218; pl. 10, fig. 3.
cf. 1969 *Hoplitoides* cf. *H. mirabilis* Pervinquière; Freund & Raab 65; pl. 10, figs 1, 2; text-figs 13i–l.
cf. 1982 *Hoplitoides munieri* Pervinquière; Renz: 100; pl. 31, figs 3, 4, 6, 11.
cf. 1982 *Hoplitoides* cf. *munieri* Pervinquière; Renz: 100; pl. 31, fig. 5.

MATERIAL AND OCCURRENCE. Four specimens (C.90345–8) from the Eze-Aku Formation (Lower Turonian), Ezillo, south-east Nigeria.

DESCRIPTION. These forms are compressed, involute and smooth at all observed growth stages. The early whorls are a little inflated in the mid-flank region and have a moderately broad, sulcate venter up to a diameter of about 60 mm. The flanks later become more flattened and the venter tabulate. At diameters in excess of 70 mm the ventrolateral shoulders become rounded. The suture is not displayed.

Figs 34–35 *Thomasites gongilensis* (Woods). Fig. 34a, b, C.90353, × 1. Eze-Aku Formation (uppermost Cenomanian or lowermost Turonian), Ezillo, south-east Nigeria. Fig. 35, C.47555, × 1. Dukul Formation (uppermost Cenomanian or lowermost Turonian), near Numan, north-east Nigeria. See also Fig. 29a, b.

Figs 36–37 *Wrightoceras wallsi* Reyment. Fig. 36a, b, C.90349, × 1. Eze-Aku Formation (Lower Turonian), Ezillo, south-east Nigeria. Fig. 37, C.47617, × 1. Pindiga Formation (Lower Turonian), Kanawa, north-east Nigeria.

Fig. 38a, b *Wrightoceras* cf. *munieri* (Pervinquière). Eze-Aku Formation (Lower Turonian), Ezillo, south-east Nigeria. C.90347, × 1. See also Fig. 40.

Fig. 39a, b *Hoplitoides latefundatus* sp. nov. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Paratype C.85284, × 1. See also Figs 41–44.

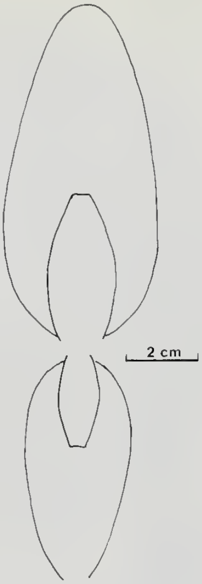


Fig. 40 Whorl section in *Wrightoceras* cf. *munieri* (Pervinquière). Based on specimen C.90345. See also Fig. 38a, b.

REMARKS. These specimens differ from the material referred above to *Wrightoceras wallsi* in their rather narrower venters which tend to become more distinctly rounded on the later whorls. The differences are, however, more of degree than kind and the two forms tend to grade into one another in the Ezillo population. The closest previously described species is *W. munieri* (Pervinquière) which is distinguished from its contemporary *W. mirabilis* (Pervinquière) on sutural grounds alone. These two have virtually identical gross morphologies and, as suggested by Reyment (1954: 157), Benavides-Cáceres (1956: 476) and Barber (1957: 53), they may be synonyms. Comparable material occurs in the Lower Turonian of the Negev, the *Hoplitoides* cf. *mirabilis* of Freund & Raab (1969: 65; pl. 10, figs 1, 2), and in Venezuela, the *H. munieri* and *H.* cf. *munieri* of Renz (1982: 100; pl. 31, figs 3–6, 11). Poorly preserved specimens from northern Mexico described by Böse (1920: 225; pl. 19, figs 1–3) also seem to be closely related.

Wrightoceras inca (Benavides-Cáceres 1956: 475; pl. 63, figs 6–11) is another similar form, said to be distinguished from *W. munieri* by faint, falciform ribs on the inner whorls. *W. submunieri* Wiedmann (see Wiedmann 1975: figs 6A–C; 1979: pl. 8, fig. 1; Wiedmann & Kauffman 1978: pl. 8, fig. 2) has a broader venter, more inflated inner flanks and strong ribbing on the early whorls; it resembles *W. llarenai* (Karrenberg 1935: 143; pl. 31, fig. 14; pl. 33, fig. 14). *W.*(?) *gagnieri* (Faraud 1951: 149; pl. 5, fig. 1) develops a rounded venter with flank ribbing terminating in ventrolateral tubercles. *W. reymenti* Collignon & Roman (*in* Amard *et al.* 1981: 57; pl. 9, figs 7a, 7b) has a very wide umbilicus, highly inflated whorls and a very broad, tabulate venter.

Family **COILOPOCERATIDAE** Hyatt, 1903

Genus ***HOPLITOIDES*** von Koenen, 1898

TYPE SPECIES. *Hoplitoides latesellatus* von Koenen, 1898 (= *Neoptychites ingens* von Koenen, 1897); by original designation.

REMARKS. The genus *Hoplitoides* includes involute, slender ammonites in which the venter is sulcate or flattened in the initial whorls and becomes sharp or narrowly rounded later on. The early whorls may be ribbed, with ventrolateral tubercles and umbilical bullae developed in some species. The suture possesses a very wide lateral lobe. The taxonomic history and occurrence of *Hoplitoides* has been reviewed by Cobban & Hook (1980: 5–6). Pervinquière (1907: 216) suggested that its ancestors were to be found amongst forms now included in

Wrightoceras which retain broad venters until adulthood. Reyment (1954: 157–158) at first doubted this view but subsequently (Reyment 1954*a*: 261; 1955: text-fig. 31) indicated just such a scheme, deriving *Hoplitoides* from *Wrightoceras.* Cobban & Hook (1980: 6) alternatively suggested that the ancestral form may have been *Choffaticeras* Pervinquière. The Nigerian material described here suggests that *Hoplitoides* was indeed derived from *Wrightoceras*, by way of forms such as those referred above to *W.* cf. *munieri.* These show a very broadly rounded venter in their adult stages but the juvenile whorls are close to those in slender *W. wallsi.* Certain forms belonging in this group show a suture pattern intermediate between those characteristic of *Wrightoceras* and *Hoplitoides* (see Pervinquière 1907: text-fig. 84; Freund & Raab 1969: text-figs 13j, 13l). As Pervinquière (1907: 218–219) noted, such types differ from the relatively simple pattern typical of *Wrightoceras* not in their basic construction, but in the accentuation of their subdivisions.

The Nigerian material of *W.* cf. *munieri* seems to be of very early Turonian age (see pp. 58–9). The upper part of the Lower Turonian at Lokpanta yields apparently more advanced transitional forms described below as *Hoplitoides latefundatus* sp. nov. These retain truncated venters until relatively large diameters of 65–75 mm but show a suture pattern like that in other *Hoplitoides* with a deep, wide lateral lobe even at a very early growth stage. The main occurrence of *Hoplitoides* in Nigeria is at Wadatta near Makurdi, where a thin limestone contains *H. ingens* (von Koenen), *H. gibbosulus* (von Koenen), *H.* cf. *wohltmanni* (von Koenen), *H. koeneni* Solger and *H. crassicostatus* Reyment. Reyment (1955) originally assigned this fauna an early Turonian age but later (Reyment 1978: 2) revised this to early Middle Turonian.

In the western interior of the United States *Hoplitoides* occurs only in New Mexico. The earliest recorded forms come from the lower part of the Zone of *Collignoniceras woollgari* (Mantell) of early Middle Turonian age. This material includes specimens comparable to *H. wohltmanni* (see Cobban & Hook 1979: 19; pl. 4, figs 3, 4; text-figs 10, 11; 1980: 7; pl. 1, figs 3, 4; text-figs 4, 5; 1981) but retaining truncated venters to a large diameter, and others close to *H. koeneni* (see Cobban & Hook 1979: 19; pl. 4, figs 1, 2; 1980: 6; pl. 1, figs 1, 2; pl. 3, figs 4, 5), again showing persistent truncation of the venter. *H. sandovalensis* Cobban & Hook (1980: 8; pl. 2; pl. 3, figs 6–8, 12–16; pl. 4; pl. 11, fig. 1; pl. 18, figs 4–6; text-figs 6, 7), a species developing a sharp venter at a very early ontogenetic stage, appears in the overlying Zone of *Prionocyclus hyatti* (Stanton).

Elsewhere in the world, specimens close to *Wrightoceras munieri* (see Freund & Raab 1969: 65; pl. 10, figs 1, 2) occur in 'Zone 6' in Israel, towards the top of these authors' Lower Turonian. In Venezuela similar forms (Renz 1982: pl. 31, figs 3, 5) are amongst the earliest Turonian ammonites known, occurring in Renz' (1982: 72–73) 'Assemblage 1' and 'Assemblage 2' of early Turonian age. *Wrightoceras* characterizes the basal Turonian of the Algerian Sahara, *Hoplitoides* occurring some distance above (Amard *et al.* 1981: 43–45) and these genera have a similar stratigraphical distribution in Brazil (Bengtson 1983: 44–47). Wiedmann (1960, 1979) describes three Spanish sections containing *Wrightoceras* and *Hoplitoides.* In two of these, at Puentedai and Picofrentes (see Wiedmann 1979: 191–193, text-fig. 15; 207–210, text-fig. 24), the former appears below the latter. At the third, Las Fuentes, however, *Hoplitoides* is listed as occurring, rather incongruously, very close to the bottom of the Turonian (Wiedmann 1979: 205).

This last record notwithstanding, the available evidence indicates that *Wrightoceras* appears very early in the Turonian. *Hoplitoides*, on the other hand, is a younger genus, being most common in the Middle Turonian. Indeed, Kennedy & Wright (1984: 288, 290) found no convincing evidence for its occurrence any earlier. The Nigerian Lower Turonian, however, contains the first members of this genus, as may also be the case in Venezuela.

Hoplitoides latefundatus sp. nov.

Figs 39, 41–4

Compare:

1979 *Hoplitoides* cf. *H. wohltmanni* (von Koenen); Cobban & Hook: 20; pl. 4, figs 3, 4; text-figs 10, 11.

1980 *Hoplitoides* cf. *H. wohltmanni* (von Koenen); Cobban & Hook: 7; pl. 1, figs 3, 4; text-figs 4, 5.

1981 *Hoplitoides wohltmanni* (von Koenen); Cobban & Hook: 30; pl. 5.
1982 *Hoplitoides mirabilis* Pervinquière; Renz: 99; pl. 30, figs 6, 7; pl. 31, fig. 10.

HOLOTYPE. C.90302 (Fig. 42a, b), from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria.

PARATYPES. At least fourteen specimens (C.83515, C.85284–5, C.90303–13) from the same horizon and locality as the holotype.

NAME. From the unusually persistent truncation of the venter.

DIAGNOSIS. A smooth *Hoplitoides* retaining a truncated venter until relatively large diameters of 65–75 mm. Venter thereafter sharply rounded.

DESCRIPTION. The juvenile whorls are compressed and almost invariably smooth, though rare specimens display faint, broad, prorsiradiate ribs until diameters as large as 45 mm. The juvenile venter is narrow and markedly sulcate until diameters of up to 60 mm, thereafter becoming tabulate and finally, at diameters of 65–75 mm, sharply rounded. The flanks at this stage are usually smooth, though very weak, fold-like ribs may be present in some specimens. The sutures are displayed only in a juvenile specimen (C.85284) of 25 mm diameter; the lateral lobe is broad and deep, the first lateral saddle elongate and rather deeply incised.

Along with this material a mass of large, smooth, involute ammonites were collected. These are all badly crushed and cannot be adequately described. Almost certainly, many represent the outer whorls of this species, indicating maximum diameters in excess of 200 mm.

REMARKS. This material resembles certain previously-described *Hoplitoides* in its lack of pronounced ornament at any growth stage. *H. ingens* (von Koenen) includes one variety, *H. ingens* var. *laevis* Solger (1904: 145; pl. 5, fig. 9), which is virtually smooth and *H. wohltmanni* (von Koenen 1897: pl. 1, fig. 2; pl. 2, figs 3, 9; 1898: 11; pl. 2, figs 1, 4, 7; Solger 1904: 133; pl. 5, fig. 7) possesses at most only a feeble decoration on its inner whorls. Both of these species, however, lose their truncated venters much earlier in ontogeny, at diameters around 20 mm in *H. ingens* (see Solger 1904: 141, 144, 145) and 30 mm in *H. wohltmanni* (see Solger 1904: 136). The material from the early Middle Turonian of New Mexico described as *H.* cf. *H. wohltmanni* by Cobban & Hook (1979, 1980), on the other hand, retains a truncated venter until diameters of at least 65 mm, much longer than in *H. wohltmanni*, as these authors remarked. It closely resembles the present specimens and, though a little younger, it may be conspecific. Another large *Hoplitoides* from New Mexico (Cobban & Hook 1981) does not develop a rounded venter until a diameter of nearly 70 mm and also seems to be closely related. Specimens from Venezuela referred by Renz (1982: 99; pl. 30, figs 6, 7; pl. 31, fig. 10) to *Hoplitoides mirabilis* Pervinquière are further smooth examples showing a comparable ontogenetic development. Pervinquière's species differs in retaining its truncated venter into adulthood and, as indicated above, is better placed in *Wrightoceras*. Egyptian material described by Douvillé (1928: 30; pl. 6, figs 2a, 2b) shows a broad venter at diameters of 60 mm or more and may be related to *H. latefundatus*.

H. gibbosulus (von Koenen) and its varieties (see Solger 1904: pl. 4, fig. 10; text-figs 44–48; Reyment 1955: pl. 17, fig. 8; pl. 18, fig. 1; pl. 19, fig. 4; pl. 21, fig. 3; pl. 22, fig. 2) and *H. crassicostatus* Reyment (1955: pl. 17, figs 3, 4) differ in being strongly ornamented species. *H. koeneni* Solger (1904: pl. 4, figs 8, 9; Reyment 1955: pl. 17, fig. 7; pl. 22, fig. 4) possesses strong ribs on its inner whorls. *H. lacabagnae* Etayo-Serna (1979: 91; pl. 13, fig. 9) and the similar *H. lagiraldae* Etayo-Serna (1979: 92, pl. 13, fig. 14) differ from *H. latefundatus* in that both show pronounced sickle-shaped ribs; in this ornament they resemble the '*H.* aff. *mirabilis* ribbed variety' of Renz (1982: 91; pl. 13, figs 7–9). *H. hernanmojicae* Etayo-Serna (1979: 90; pl. 13, figs 4, 8) is a poorly defined species, but is known to lose its truncated venter early in ontogeny.

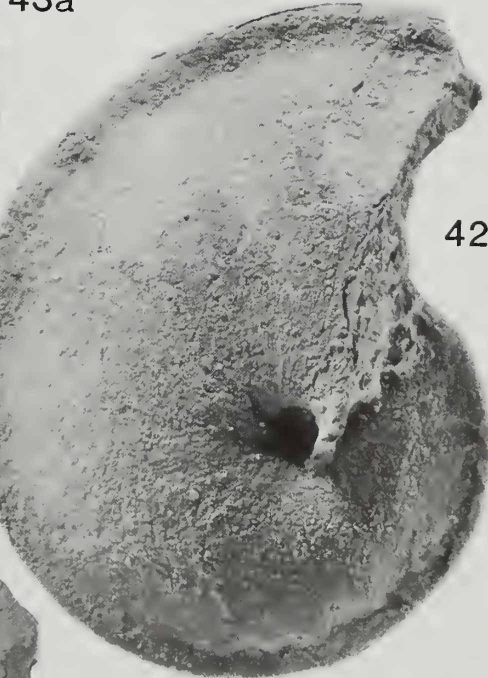
Figs 41–44 *Hoplitoides latefundatus* sp. nov. Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria. Fig. 41a, b, paratype C.90304, × 1. Fig. 42a, b, **holotype** C.90302, × 1. Fig. 43a, b, paratype C.90303, × 1. Fig. 44a, b, paratype C.90309, × 1. See also Fig. 39a, b.


41a

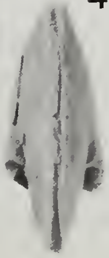

41b

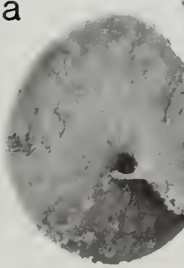

42a


43a


42b


43b


44a


44b

Genus *HERRICKICERAS* Cobban & Hook, 1980

TYPE SPECIES. *Placenticeras costatum* Herrick & Johnson, 1900; by monotypy.

Herrickiceras? sp.
Fig. 30a, b

MATERIAL AND OCCURRENCE. A single specimen (C.85287) from the Eze-Aku Formation (Lower Turonian, *Mammites nodosoides* Zone), Lokpanta, south-east Nigeria.

REMARKS. Cobban & Hook (1980: 22) proposed the genus *Herrickiceras* for the single species *Placenticeras costatum* Herrick & Johnson (1900: 214; pl. 28, figs 2, 3; Cobban & Hook 1980: 22; pl. 19, figs 10–18; text-fig. 16) from the Middle Turonian of New Mexico. It is characterized by a highly involute, compressed shell with a fairly broad, sulcate, bicarinate venter. There are sinuous ribs which are best developed on the outer part of the flank where they are projected forwards and expanded into clavate ventrolateral tubercles. The Nigerian material, admittedly meagre, shows all these features and may be best referred here. It occurs in the upper part of the Lower Turonian. *Herrickiceras* is otherwise known only from the Rio Puerco Valley area of New Mexico where it occupies a higher stratigraphical position, above the basal Middle Turonian *Collignoniceras woollgari woollgari* Subzone of the western interior.

Stratigraphical conclusions

Owing to the wealth of their ammonite faunas, the Nigerian and Camerounian Turonian have been the subject of considerable biostratigraphic attention (see Fig. 45). Reyment (1954) proposed their first comprehensive, three-fold, subdivision into:

	REYMENT (1954, 1955)	REYMENT (1956, 1965)	BARBER (1957)
UPPER TURONIAN	Youngest Beds	Zone of Romaniceras uchauxiense	Zone of Romaniceras uchauxiense
LOWER TURONIAN	Intermediate Beds	Zone of Hoplitoides ingens (=Zone of Kamerunoceras eschii)	Zone of Kamerunoceras eschii
	Oldest Beds	Zone of Pseudotissotia (Wrightoceras) wallsi (=Zone of Pachyvascoceras costatum)	Zone of Pseudotissotia (Bauchioceras) nigeriensis Zone of Paravascoceras costatum Zone of Vascoceras bulbosum

	PRESENT WORK	
	N.E. NIGERIA	LOKPANTA AREA
LOWER TURONIAN	Zone of Pseudotissotia nigeriensis (upper extent uncertain)	Zone of Mammites nodosoides beds with Watinoceras
UPPER CENOMANIAN	Zone of Paravascoceras costatum Zone of Vascoceras bulbosum	

Fig. 45 Table showing previous and present proposals for a biostratigraphic subdivision of the Turonian stage in Nigeria and Cameroun. The present work deals only with the Lower Turonian.

1. 'The Oldest Beds', containing the rich vascoceratid faunas characteristic of north-east Nigeria (later described in detail by Barber, 1957) but also represented in less abundance at Ezillo in south-east Nigeria;
2. 'The Intermediate Beds', with *Hoplitoides*, *Mammites*, *Kamerunoceras*, *Benueites*, *Choffaticeras* and *Neoptychites*; and
3. 'The Youngest Beds', with *Hoplitoides* and '*Romaniceras*', occurring in south-west Cameroun only.

Reyment (1955) retained this scheme with little modification though *Watinoceras* was added to the fauna of the 'Intermediate Beds'. Not recognizing a Middle Turonian substage, he regarded the 'Oldest Beds' and 'Intermediate Beds' as Lower Turonian and the 'Youngest Beds' as Upper Turonian. Barber (1957) was able to establish a more detailed zonation of the 'Oldest Beds' at Pindiga in north-east Nigeria, identifying a basal Zone of *Vascoceras bulbosum* (Reyment), a middle Zone of *Paravascoceras costatum* (Reyment) and an upper Zone of *Pseudotissotia* (*Bauchioceras*) *nigeriensis* (Woods). Wozny & Kogbe (1983) found a similar zonation to be applicable at Ashaka Quarry, some 100 km north of Pindiga. In later schemes, Reyment (1956, 1965) termed his 'Oldest Beds' the 'Zone of *Pachyvascoceras costatum* Reyment' (subsequently the 'Zone of *Pseudotissotia* (*Wrightoceras*) *wallsi*'), his 'Intermediate Beds' the 'Zone of *Kamerunoceras eschii*' (subsequently the 'Zone of *Hoplitoides ingens*') and his 'Youngest beds' the 'Zone of *Romaniceras uchauxiense* Collignon', remarking on the ill-defined nature of this last subdivision.

Recent work has shown that the fossiliferous beds in north-east Nigeria described by Barber (1957) are not, in fact, Turonian throughout, but are Upper Cenomanian in their lower part. Barber (1957: 61) himself suspected this, having made a special note of the occurrence of *Metengonoceras dumbli* (Cragin) in the lowest limestone bed exposed at Pindiga. This species is confined to the Cenomanian elsewhere (see, for example, Cobban & Scott 1972; Kennedy, Juignet & Hancock 1981). At Ashaka Quarry both *M. dumbli* and *Euomphaloceras septemseriatum* (Cragin), a reliable late Cenomanian guide fossil, occur in the zone of *Vascoceras bulbosum* in the lower part of the limestone–shale sequence exposed there (Wozny & Kogbe 1983). *E. septemseriatum* is also known from the middle Benue Valley region of Nigeria where it occurs directly below beds with *Paravascoceras*, *Vascoceras*, *Thomasites*, *Pseudotissotia*, *Wrightoceras* and *Neoptychites* (Offodile & Reyment 1976). Though the Upper Cenomanian is, therefore, undoubtedly present in central and north-east Nigeria, the location of its boundary with the Turonian is problematical. The overwhelmingly Tethyan nature of the vascoceratid faunas occurring here precludes ready comparison with the Boreal faunas of areas such as north-west Europe and the western interior of the United States where comprehensive zonal schemes are available and the position of the boundary can be fixed. *Thomasites gongilensis*, however, occurs occasionally in the Upper Cenomanian of the Sergipe Basin, Brazil (Bengtson 1983), and Wright & Kennedy (1981) also recovered examples from the uppermost Cenomanian of southern England. Since this species abounds in the Zone of *Paravascoceras costatum* in north-east Nigeria, Hancock & Kennedy (1981) suggested that the Cenomanian–Turonian boundary might best be placed at the base of the zone of *Pseudotissotia nigeriensis*, thus leaving only this last part of the sequence within the Turonian. As far as southern Nigeria is concerned, Reyment (1978) removed his 'Intermediate Beds' or 'Zone of *Hoplitoides ingens*' fauna from the Lower Turonian, preferring to regard it as early Middle Turonian in age. As a result, only the small fauna from Ezillo listed by Reyment (1955: 98) was assigned to the Lower Turonian. Being composed almost entirely of indigenous species, this fauna defies easy correlation. The extent and faunal character of the Lower Turonian in Nigeria has, therefore, become something of a problem. The present material is thus of great value in reassessing this part of the Nigerian Cretaceous and in suggesting correlation outside the country.

In the western interior of the United States and southern England two zones can be recognized in the Lower Turonian (see Cobban & Scott 1972, Kauffman *et al.* 1978, Cooper 1978, Wright & Kennedy 1981): a basal Zone of *Watinoceras coloradoense*, characterized above all by species of *Watinoceras*; and an upper Zone of *Mammites nodosoides* from which comes the bulk of the described European Lower Turonian ammonites. A similar subdivision seems to be possible in the Lokpanta area of Nigeria (Fig. 45, p. 56). Here, beds dominated by *Watinoceras* spp. can probably be correlated with the zone of *W. coloradoense*. Lying above are beds clearly corresponding with the zone of *M. nodosoides*. They contain the nominal species, *Fagesia* and *Kamerunoceras puebloense*, all characteristic of this zone in the United States western interior (see Cobban & Scott 1972). Below the Turonian beds at Lokpanta, shales have yielded a possible *Metengonoceras* which would indicate the presence of Upper Cenomanian sediments. If confirmed, this occurrence would form an interesting geographical link between beds of this age in north-east Nigeria, the middle Benue Valley and the Calabar region in the extreme south-east of Nigeria (see above, Zaborski 1985).

The fauna from Ezillo described here is more difficult to date precisely. It contains both *Thomasites* and *Wrightoceras*, though the latter occurs a little above the former in north-east Nigeria (Barber 1957, Wozny & Kogbe 1983). Since the entire Ezillo fauna was collected loose from a section several metres thick, however, it is possible that these genera are stratigraphically separated here also. Clearly the affinities of the Ezillo population are with the vascoceratid forms occurring as much as 600 km north in Nigeria, having virtually nothing in common with those at Lokpanta, barely 60 km distant (see Fig. 46). In north-east Nigeria *Thomasites gongilensis* occurs with *Paravascoceras*, another Ezillo faunal element, in beds which, according to Hancock & Kennedy (1981), lie very close to, and possibly just below, the Cenomanian–Turonian boundary. *Wrightoceras wallsi*, on the other hand, is confined to the upper part of the fossiliferous sequences at Pindiga and Ashaka and is of early Turonian age. The ammonite-bearing siltstone at Ezillo described here is underlain by a sequence of shales and oyster-rich limestones exposed on the eastern fringe of Ezillo town in the Western Aboine River (Fig. 1, p. 32). From here Reyment (1955: 65) recorded *Ezilloella ezilloensis* Reyment, a species probably occurring alongside *Euomphaloceras septemseriatum* in the Upper Cenomanian of the middle Benue Valley (Offdile & Reyment 1976). In addition, Offodile & Reyment (1976: 43) reported a possible specimen of *Allocrioceras annulatum* (Shumard) from the Western

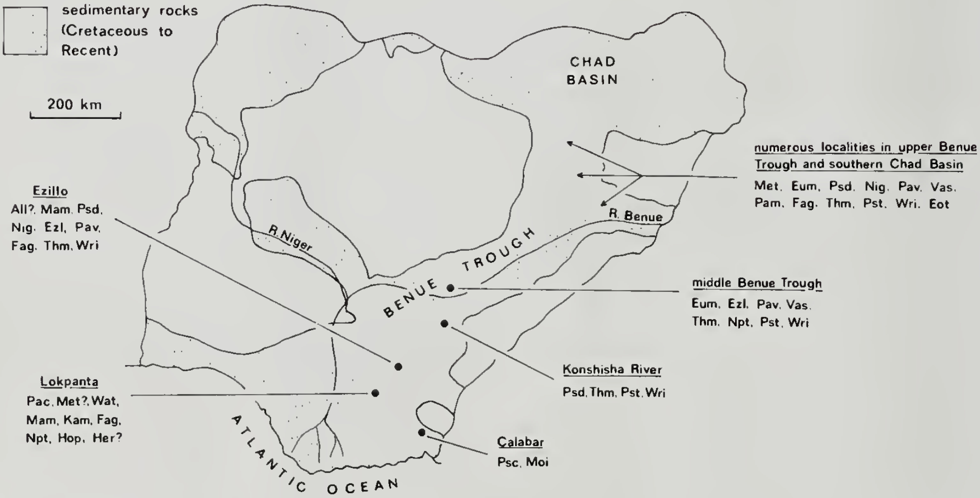


Fig. 46 Map of Nigeria showing distribution of late Cenomanian and early Turonian ammonite genera. All, *Allocrioceras*; Pac, *Pachydesmoceras*; Met, *Metengonoceras*; Psc, *Pseudocalycoceras*; Eum, *Euomphaloceras*; Kam, *Kamerunoceras*; Moi, *Metoicoceras*; Wat, *Watinoceras*; Mam, *Mammites*; Psd, *Pseudaspidoceras*; Nig, *Nigericeras*; Ezl, *Ezilloella*; Pav, *Paravascoceras*; Vas, *Vascoceras*; Pam, *Paramammites*, Fag, *Fagesia*; Thm, *Thomasites*; Npt, *Neoptychites*; Pst, *Pseudotissotia*; Wri, *Wrightoceras*; Eot, *Eotissotia*; Hop, *Hoplitoides*; Her, *Herrickiceras*. Data from Reyment (1954, 1954*a*, 1955), Barber (1957), Offodile & Reyment (1976), Wozny & Kogbe (1983), Zaborski (1985) and original.

Aboine River, another late Cenomanian species of the western interior and elsewhere (Cobban & Scott 1972, Wright & Kennedy 1981: 112). The present Ezillo fauna may therefore be regarded as occurring very close to the Cenomanian–Turonian boundary but almost certainly extending some distance above it. Its direct correlation with the Lokpanta assemblages is, however, not yet possible. Although the fragment of *Mammites*? described from the *Watinoceras*-bearing beds at Lokpanta bears some similarity to *M. dixeyi*, an Ezillo species, there is no useful correspondence between the faunas in these two areas. Only the relatively cosmopolitan genus *Fagesia* otherwise occurs in common.

In the Sergipe Basin, Brazil, *Wrightoceras*, *Thomasites* and *Paravascoceras* occur within a fauna regarded by Bengtson (1983) as basal Turonian ('Turonian 1'). Since, however, *Euomphaloceras septemseriatum* is present also, Bengtson (1983: 43–44) admitted the possibility that the base of the Turonian might be better placed at the bottom of the succeeding ('Turonian 2') faunal assemblage. This part of the Brazilian Turonian contains *Watinoceras amudariense*, *W.* spp., *Neoptychites cephalotus* and *Pachydesmoceras* among others, with *Fagesia* spp. present in the middle part and *Mammites nodosoides* extending throughout its middle and upper parts. This sequence appears to correlate with both the *Watinoceras* and *M. nodosoides*-bearing beds at Lokpanta, although the presence of *Coilopoceras*, *Hoplitoides ingens* and *H. gibbosulus* suggests that the Brazilian beds extend somewhat higher. On the Brazilian evidence, the Ezillo fauna could represent an horizon immediately below the *Watinoceras*-bearing beds at Lokpanta, its absence there being explained by non-exposure of the relevant beds. Alternatively, since uppermost Cenomanian and basal Turonian faunas appear to be present at both Ezillo and Lokpanta, palaeoenvironmental factors would be responsible.

During the late Cenomanian and early Turonian, the Benue Valley and north-eastern part of Nigeria were occupied by an arm of the Tethys extending across the Sahara (see review in Reyment 1980). By late Cenomanian times this epeiric seaway had already flooded the whole of this area. Ammonites such as *Metengonoceras dumbli* and *Euomphaloceras septemseriatum* seem to have been introduced from the widening Atlantic Ocean in the south, the former penetrating as far as Damergou in southern Niger (Schneegans 1943, Greigert & Pougnet 1967: 128). The vascoceratids seem to have been introduced from the north. This vast, shallow seaway, in which similar environmental conditions prevailed over great distances, was overwhelmingly populated by vascoceratid ammonites which have few counterparts in southern Nigeria. The area around Ezillo seems to have been close to the southern limit of this faunal province during the late Cenomanian and early Turonian. The most southerly part of Nigeria was, at this time, probably an area of deeper water, subject to greater influence from open oceanic circulation. Its ammonite faunas show their closest affinities with those of the western interior of the United States. Lower Turonian biofacies show similar variations in Iberia, where mammitids dominate the northern part of Spain, vascoceratids characterizing contemporaneous beds to the south (see Wiedmann 1979: text-fig. 6). Similarly, according to Young & Powell (1978), the Tethyan faunas of Mexico and trans-Pecos Texas are absent from central and northern Texas as a result of environmental factors.

However, perhaps the situation most closely similar to that in Nigeria occurs in Morocco (see Wiedmann *et al.* 1982, Einsele & Wiedmann 1982). The Lower Turonian of the Atlas–Meseta Basin in the north of the country is represented by a limestone facies containing familiar Tethyan genera such as *Vascoceras*, *Paravascoceras*, *Nigericeras* and *Thomasites*. In the west-coastal Tarfaya Basin, on the other hand, a series of laminated bituminous marls with limestone bands and nodules accumulated during the late Cenomanian to early Coniacian. This area lacks both the Turonian vascoceratids and the late Cenomanian *Neolobites*, a widely distributed genus in Tethyan faunas. Instead, the Upper Cenomanian and Turonian are dominated by forms of boreal affinities including *Metoicoceras*, *Watinoceras*, *Mammites*, *Benueites* and *Collignoniceras* (see Collignon 1966). Einsele & Wiedmann (1982) interpreted these faunal differences environmentally, believing the 'black shale' facies of the Tarfaya Basin to have formed in deeper, cooler waters subject to upwelling from the Atlantic Ocean. There is an obvious parallel between the Lower Turonian of Morocco and of Nigeria in both lithofacies and biofacies, but how far the comparison can be taken is, as yet, uncertain. Petters (1978) accounted for Cretaceous black shales in the Benue Trough by envisaging a high influx of organic matter into a relatively shallow seaway.

During the later part of the Turonian the sea retreated from the interior of Nigeria (Reyment 1980) and beds of this age are less easy to identify. Offodile & Reyment (1976), however, recorded Middle Turonian bivalves along with *Collignoniceras*, a diagnostic Middle Turonian ammonite (see Kauffman *et al.* 1978, Cobban & Hook 1979, Kennedy, Wright & Hancock 1980), from Nkalagu in south-east Nigeria. In addition, Reyment (1978) came to regard his 'Zone of *Hoplitoides ingens*' fauna from Wadatta as early Middle Turonian. This fauna is dominated by *Hoplitoides* and *Benueites*, which occur with *Mammites*, *Kamerunoceras* and *Coilopoceras*. Beds of similar age in western Cameroun also contain *Watinoceras*, *Neoptychites* and *Choffaticeras*. In Venezuela, Renz (1982) suggested *Benueites* to be characteristic of the Middle and Upper Turonian and the genus also occupies a relatively high position in the Turonian of the Tarfaya Basin (Collignon 1966). *Hoplitoides* is confined to the Middle Turonian of the western interior, into which *Watinoceras* persists (Cobban & Hook 1979, 1980). *Hoplitoides* does appear somewhat earlier in Nigeria but these are apparently transitional forms with persistently broad venters. Kennedy & Wright (1984) doubted that *Coilopoceras* occurs anywhere earlier than the Middle Turonian. It is probable, therefore, that Reyment (1978) is correct in his Middle Turonian dating of the Wadatta fauna. *Coilopoceras* (= *Glebosoceras* Reyment, 1954) has been recorded from several localities in Nigeria south of the Benue River by Reyment (1954, 1955, 1957) and from the top of the Odukpani Formation near Calabar (Zaborski 1985). In view of Kennedy & Wright's (1984) findings concerning the age of this genus, it is probable that it occurs in Nigeria somewhat higher than the Lower Turonian position previously suggested. Since diagnostic genera of the Upper Turonian such as *Prionocyclus* and *Subprionocyclus* (see Kauffman *et al.* 1978, Wright & Kennedy 1981, Hancock & Kennedy 1981) are unproven in Nigeria, it is not yet possible to identify this substage here with any certainty. Offodile & Reyment (1976: 46) believed the Upper Turonian to be absent in the Nkalagu region, Coniacian beds directly overlying the Middle Turonian.

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S. G. Molyneux

Geology Vol 41 No 3 30 July 1987

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The Arenig Series in South Wales

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Synopsis

This paper completes the first detailed description of the Arenig Series in south Wales, the fullest development of the Series in Britain. The fossil faunas are richer in species, and more differentiated stratigraphically, than has been supposed. The British Arenig is comparable in development to that in Scandinavia and North America, and affords the fullest section yet known at the edge of the Ordovician Gondwanan continent. The sequence is best developed in south Wales, between Carmarthen and St David's. Based on the stratigraphy of this area we propose three stages, in ascending order the Moridunian, Whitlandian and Fennian, which can be correlated internationally, although only the Fennian includes enough cosmopolitan graptolites to place the correlation unequivocally. The threefold division is recognizable throughout Wales, and has refined the correlation considerably. Important stratigraphical conclusions are:

(i) The type Arenig section at Arennig Fawr certainly includes the Moridunian; Whitlandian and earlier Fennian equivalents are not yet proven there. The base of the Moridunian may be as old as the *Tetragraptus approximatus* Biozone of the Pacific graptolite province.

(ii) Conversely, on Anglesey only the later Arenig is present.

(iii) There is a full Arenig succession on the western Llŷn Peninsula.

(iv) The Shelve Inlier is consistently developed in shallow-water facies compared with elsewhere in Wales, and may be somewhat incomplete at the base.

(v) The 'Tetragraptus Beds' (now Penmaen Dewi Formation) of the coastal sections at St David's, which have been referred to the late Arenig *Didymograptus hirundo* Biozone, are demonstrated to be of mid-Arenig (Whitlandian) age; Fennian has only been proved on Ramsey Island.

(vi) The Abercastle Formation, and part of what have been referred to as the Brunel Beds, which have been assumed to be of early Arenig age like the Ogof Hên Formation, are Whitlandian in age.

In the Carmarthen–Whitland area the Arenig succession is thick—a cumulative thickness of more than 1300 m—compared with its equivalents on the coast at St David's. Refinement of the biostratigraphy has led to the recognition of several new formations for the Whitlandian and Fennian rocks, which are described here: Blaencediw Formation, Colomendy Formation, Cwmfelin Boeth Formation, Pontyfenni Formation and Llanfallteg Formation in ascending order. A new map of the Whitland area records the outcrop of these formations, and their correlation throughout south Wales is discussed. The Afon Ffinnant Formation, an eastward equivalent of the Blaencediw Formation, is also proposed.

The fauna of the Whitlandian includes two new species, and the remainder, originally described by Salter and by Hicks, are here given their correct stratigraphical placing. The Fennian, however, includes a major new addition to the British trilobite fauna, with some twenty new species, many of them cyclopygids. This is the earliest known occurrence of the cyclopygid biofacies in Britain, and includes a suite of genera otherwise mostly known from younger rocks. Large-eyed pelagic forms are accompanied by a characteristic group of blind or nearly blind species, which we term the atheloptic assemblage. The combination of pelagic and atheloptic trilobites typified 'oceanic' sites with sediment accumulation probably below 300 m.

The following new taxa are described: the subfamily Pricyclopyginae; the genera *Circulocrania*, *Furcalithus*, *Gymnostomix*; the subgenus *Bohemilla* (*Fenniops*); and the following species: *Segmentagnostus whitlandensis*, *Shumardia* (*S.*) *gadwensis*, *S.* (*Conophrys*) *crossi*, *Bohemilla* (*Fenniops*) *sabulon*, *Degamella evansi*, *Microparia* (*M.*) *porrecta*, *M.* (*M.*) *teretis*, *Novakella copei*, *Sagavia glans*, *Pricyclopyge dolabra*, *Circulocrania orbissima*, *Bergamia rushtoni*, *Furcalithus radix*, *Stapeleyella abyfrons*, *Dionide levigena*, *Ampyx linleyoides*, *Dindymene saron* and *Colpocoryphe taylorum*; also the subspecies *Cyclopyge grandis brevirhachis* and *Pricylopyge binodosa eurycephala*.

Seven trilobite assemblage biozones are proposed for use in local correlation; some are traceable throughout Wales and England. From the base of the Arenig these are: *Merlinia selwynii* and *M. rhyakos* (Moridunian); *Furcalithus radix* and *Gymnostomix gibbsii* (Whitlandian); *Stapeleyella abyfrons*, *Bergamia rushtoni* and *Dionide levigena* (Fennian). Of these, only the last-named seem to correspond with the *hirundo* Biozone as recognized in the Lake District and north Wales. This attests to the disproportionate extent of the old *extensus* Biozone.

A good, continuous fossiliferous section between the Arenig and Llanvirn is described from the Llanfallteg railway cutting, which may be a candidate for a stratotype for the base of the Llanvirn, and the distribution of fossils through this section is documented. In this confacial section the Llanvirn boundary is marked by the appearance of abundant 'tuning fork' graptolites, but many species of both graptolites and trilobites cross the boundary. The name *D. artus* Biozone is proposed as a replacement for the *D. 'bifidus'* Biozone of the early Llanvirn.

Introduction

The Arenig Series has been relatively neglected in its type development in Britain compared with the Llandeilo, Caradoc or Ashgill. This is partly because the Arenig rocks have been regarded as poorly fossiliferous—there are few of the prolific localities which yielded classic faunas to the nineteenth century monographers—and because the twofold division into *Didymograptus extensus* and *D. hirundo* Biozones obscured their stratigraphical diversity. After studying fossiliferous and stratigraphically differentiated Arenig faunas in Spitsbergen and elsewhere we realised that either the Welsh Arenig Series must be incompletely developed, or its true stratigraphical sequence had not been recognized. In this work we show that the latter is the case. The Arenig in the type area of north Wales is indeed incomplete; it apparently comprises only the lower one-third of the Series. The fullest sequence has proved to be in south Wales, outcropping over a stretch of country running from Carmarthen to the coast at St David's. We studied the lower part of the sequence in the Carmarthen area, the results of which were published by Fortey & Owens (1978).

The present work completes the account of the trilobite and graptolite faunas through the mid- and late Arenig of south Wales, and summarizes the biostratigraphy of the Arenig Series throughout Wales. Faunas of articulate brachiopods have been recovered from the *M. selwynii*, *F. radix* and *S. abyfrons* Biozones, and will be described elsewhere, and a first account of the acritarch flora is given by Molyneux (1987). A preliminary note on the chordates, by R. P. S. Jefferies, is appended to the present paper.

We can now recognize seven broadly conceived biozones within the Series, and a major threefold division applicable throughout Britain, which we propose as stages. A preliminary account of the major divisions was given by Fortey (*in* Whittington *et al.* 1984). The Welsh Arenig is now known to be comparable in development to that of Scandinavia, China and North America. The number of trilobite species known has been trebled as a result of recognizing the true extent of the Series; the late Arenig fauna is almost entirely new, and the stratigraphical placing of the middle Arenig faunas has previously been incorrect. It remains true that, although rich in species, the fossils are relatively sparse—the specimens figured here are the product of nearly ten years' collecting. Nonetheless, it would not have been possible to unravel the complexities of the Arenig of south Wales without the help of the trilobite faunas. If this work has a general relevance, it is that macrofossils can still prove indispensible in solving broad-scale geological problems in areas of structural complexity.

Historical survey

The term 'Arenig' was introduced by Sedgwick (1852) for strata cropping out in the Arennig Fawr district, Gwynedd. Its first application in south Wales was by Hicks & Salter (1867) in the St David's district, Arenig strata there having previously being regarded (e.g. by Murchison (1839), and on Old Series one-inch Geological Survey maps) as Upper Cambrian, Llandeilo or

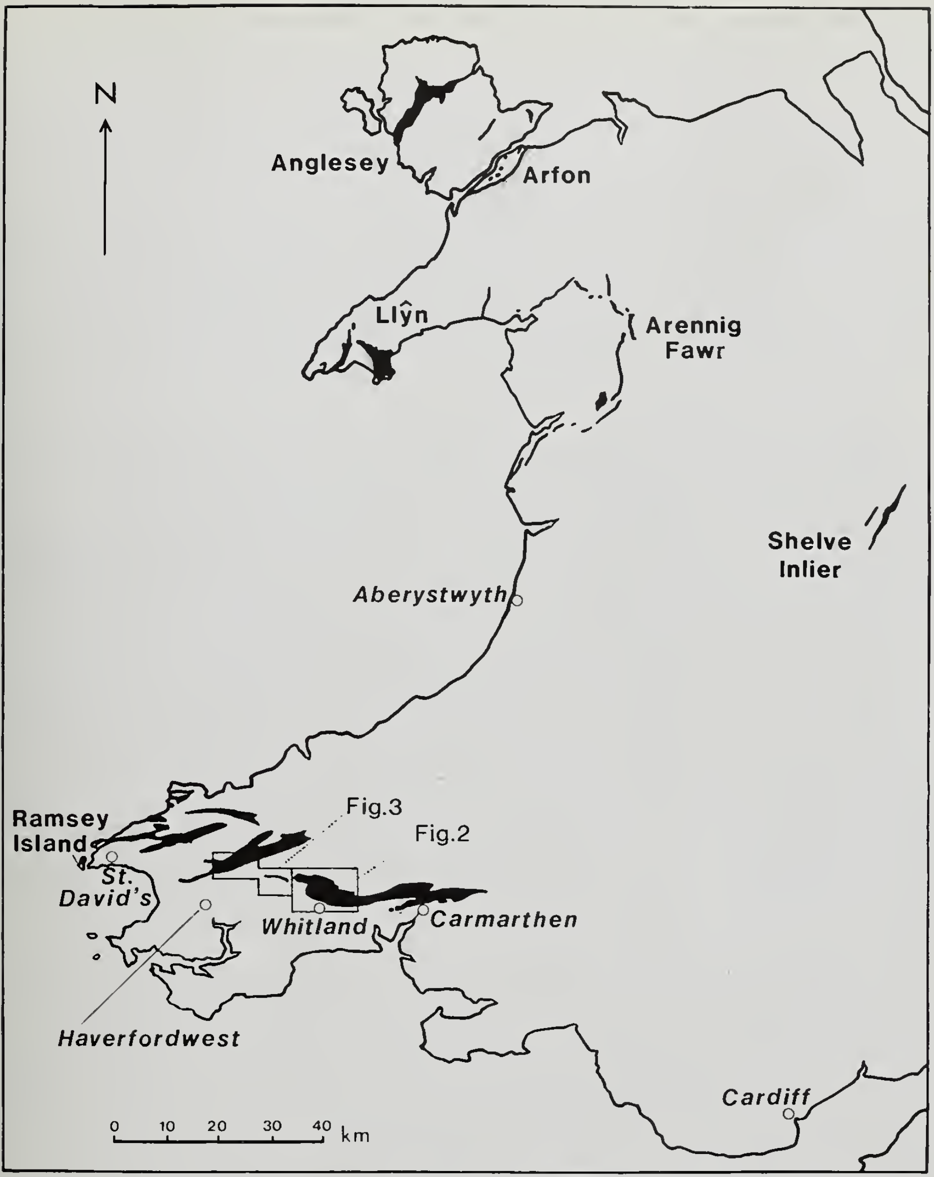


Fig. 1 Outcrops of Arenig age in Wales and the Welsh Borderland referred to in the text.

Caradoc. Subsequently, some strata, since shown to be of Arenig age (see Whittard 1960), were considered to belong to the Tremadoc (the Ogof Hên Formation: Hicks & Salter (1867), Hicks (1873); the Carmarthen Formation: Crosfield & Skeat (1896).) True Tremadoc strata have, however, recently been found in the Llangynog area near Carmarthen (Cope *et al.* 1978).

Arenig strata in south Wales were described in the last century by Hicks (1873, 1875) in the St David's area, by Roberts (1893) in the Whitland area, where he termed them '*Tetragraptus*-beds' (which name, or its variant '*Tetragraptus* Shales' came to be widely applied to the Arenig in south Wales in the ensuing years) and by Crosfield & Skeat (1896) in the Carmarthen area.

Roberts' work was taken up by a local amateur, D. C. Evans, whose description (1906) of the Whitland–St Clears area forms the basis of the current paper. In the words of O. T. Jones *in* Stephens (1941) 'It was recognised as a first-rate, masterly, piece of work that no one could pick to pieces'. In the same year Cantrill & Thomas (1906) described a small area around Llangynog. At the beginning of the present century the entire Arenig outcrop from the Whitland area in the west to Llanarthney in the east was mapped on the scale of 6 in : 1 mile by the Geological Survey, and was described in three memoirs (Strahan *et al.* 1907, 1909, 1914). For the Whitland area the Survey mappers drew much upon Evans' work.

Over the following years interest in the St David's–Haverfordwest area was renewed, and Arenig and contiguous strata were described in a series of papers, including those of Pringle (1911), Thomas & Jones (1912), Cox & Jones (1914), Thomas & Cox (1924), Cox *et al.* (1930), Cox (1930), Pringle (1930), and Williams (1934). In these, several local stratigraphical terms, especially for more arenaceous developments in the Arenig, e.g. Abercastle Beds, Porth Gain Beds, Brunel Beds, were proposed. After this period, apart from brief mention in W. D. Evans' (1945) paper on the Prescelly Hills, the Arenig of south Wales attracted little attention until Bates (1969) described the early Arenig Ogof Hên Formation on Ramsey Island. More recently Fortey & Owens (1978) revised the early Arenig stratigraphy of the Carmarthen area, and Cope (1980) described similar strata in the Llangynog area a short distance to the west.

The first zonation of the British Arenig was by Elles (1904), and was based upon graptolites from various sections in Wales (Afon Seiont, Caernarfon, Menai Straits, Llŷn, Arennig Fawr, St David's, and Haverfordwest–Carmarthen). She defined two new zones, *Didymograptus extensus* and *D. hirundo*, and included Lapworth's (1880) *D. bifidus* zone. The last-named was incorporated in the Arenig because Elles at that time did not accept Hicks' (1881) Llanvirn Series. Elles & Wood (1914) added a *Dichograptus* Zone below *extensus* in the Skiddaw Slates, but this has not been generally recognized, and Bulman (1958) could find no stratigraphical evidence for its existence. Later, Elles (1933) subdivided the *extensus* zone into four subzones, based upon the Skiddaw Slates succession, which in ascending order are: Upper Subzone of *Tetragraptus* (reclined), *Didymograptus deflexus*, *D. nitidus* and *Isograptus gibberulus*. Of these, the first-named has not been subsequently recognized (see Jackson 1962). The other three are now commonly accorded the status of zones (e.g. Skevington 1976; Cooper & Fortey 1982), which practice is followed here. A basal Arenig zone, the *T. approximatus* Zone, has been widely recognized throughout the world, but was not until recently (Stone & Rushton 1983) identified in the British Isles, where it has been found in the Girvan succession.

General reviews of the trilobites were given by Stubblefield (1939) and Thomas *et al.* (1984), and the total fauna of the Arenig of Wales by Bates (1969). Individual elements of the fauna have been described over almost 150 years: trilobites by Murchison (1839), Salter *in* Murchison (1859), Salter (1866*a*, *b*, 1867), Hicks (1873, 1875), Crosfield & Skeat (1896), Reed (1931), Whittard (1955–67), Bates (1969), Fortey & Owens (1978); brachiopods by Murchison (1839), Davidson (1868, 1869), Bates (1969); graptolites by Hopkinson (1872, 1873), Hopkinson & Lapworth (1875), Bulman (1928, 1934), Fortey & Owens (1978), Jenkins (1982), Zalasziewicz (1984*b*); crinoids by Hicks (1873), Ramsbottom (1961), Bates (1968*b*), Donovan (1984); asteroid by Hicks (1873), Spencer (1918, 1950); parablastoid by Paul & Cope (1982); bivalves by Hicks (1873), Carter (1971); hyolithid by Hicks (1873). None of these works, however, give any hint of the diversity of the faunas which are described herein.

Geology and lithostratigraphy of the Whitland district

In our previous paper (Fortey & Owens 1978) we described the geology of the Carmarthen district, in which the early Arenig (Moridunian) is best developed. The Moridunian rocks and the underlying Tremadoc (Cope *et al.* 1978) are there brought to the surface in the centre of a large anticline. However, the higher parts of the Arenig Series are not well exposed (p. 97). Westwards, early Arenig rocks are again brought to the surface in the structurally complex Llangynog inlier, but the higher parts of the Series are apparently faulted out. Between this area and St Clears, only late Arenig (Fennian) rocks are exposed. Yet another anticline brings earlier Arenig rocks to the surface in the area immediately to the north of Whitland. It is here that the succession of middle and upper Arenig rocks is most fully exposed, and in which the faunas are generally well preserved. It proved to be the critical area for an understanding of the biostratigraphical divisions of the Arenig Series, and for this reason a detailed account of the geology of the area is given here. Our new geological maps (Figs 2, 3) show the distribution of Arenig rocks over a 30 km tract from east of Whitland to Treffgarne, north of Haverfordwest.

The original account of the geology of the Whitland district was by D. C. Evans (1906), and the general structure he deduced has been confirmed by subsequent mapping. However, he conflated two coarse units within the Arenig Series, which we now recognize as the Blaencediw and Cwmfelin Boeth Formations, and referred the whole succession to the 'Tetragraptus Beds' without further stratigraphical refinement. Cantrill & Thomas (*in* Strahan *et al.* 1909) largely followed Evans' interpretations, although they did separate two units of 'grits', and their fossil collections have proved most useful. Since then, the area has been virtually unstudied.

Structure

The best exposures are to be found in an area of high ground lying about 3 km north of Whitland. The country is relatively hilly compared with the green and fertile agricultural land flanking the wide Tâf valley around Whitland, because the anticline brings to the surface a series of coarse turbidites which take much of the high ground. Physiography closely follows the lithology and structure of the rocks. The coarse units are exposed in two main areas: (1) in the vicinity of Whitland Abbey, on either side of the Afon Gronw, and westwards past Pen-cil-post to Cwmfelin-Boeth, and (2) in a broad upland area running more or less east–west to the south of Llwyn-derw, and extending past the farms known as Blaenweneirch and Blaencediw. The latter comprise the oldest beds in the area (Blaencediw Formation); at the centre of the anticlinal area dips are generally low. This area of coarse-grained rocks has, however, been thrust over younger beds to the south of Blaenweneirch, where a tract of soft mudstones in the Pontyfenni Formation produces a broad depression. A second anticlinal area is centred on an east–west axis just to the north of Whitland Abbey. The coarse turbidites here are much younger than those to the north, but they were equated by Evans (1906). Because they are underlain by shales (Whitland Abbey Member herein) in the neighbourhood of Whitland Abbey, Evans (1906) erroneously concluded that these shales were the oldest beds in the area ('lowest shales'). The late Arenig mudstones of the Pontyfenni Formation appear everywhere to overlie normally the higher turbidite formation, and form a drape around the edge of the anticlinal structure.

Over much of the area there are small scale reverse faults, indicating movement from the north. Faulting of this kind appears to predominate in this area compared with the Carmarthen district, over which repeated strong folding was the norm. Repetition by reverse faults of this kind probably accounts for the broad area of outcrop of the upper turbidites along the eastern side of the Afon Gronw. Dips increase progressively both north and south from the centre of the anticline. The generally northward dips along the southern area of the map indicate that the contact with the Llanvirn there is likely to be inverted and/or a thrust contact. The northern limit of the structure, where there is faulting against the Llanvirn, is probably a major normal fault to the north of Blaencediw, although there are sections further to the west where there is continuous passage between the Arenig and Llanvirn. Finally, there are a number of important north–south faults; the course of the Nant Colomendy clearly follows one of these, and boulders of vein quartz are common in the stream bed.

Distortion of fossils is generally slight, even in the soft mudstones, except at certain horizons in the Llanfallteg Formation. None of the argillaceous units is cleaved in this area, although correlative rocks in the Haverfordwest district can be strongly cleaved.

Lithostratigraphy

The elucidation of the stratigraphy of this district has entailed the discrimination of a number of lithostratigraphic units, which appear on the maps. With the exceptions of the Rhyd Henllan

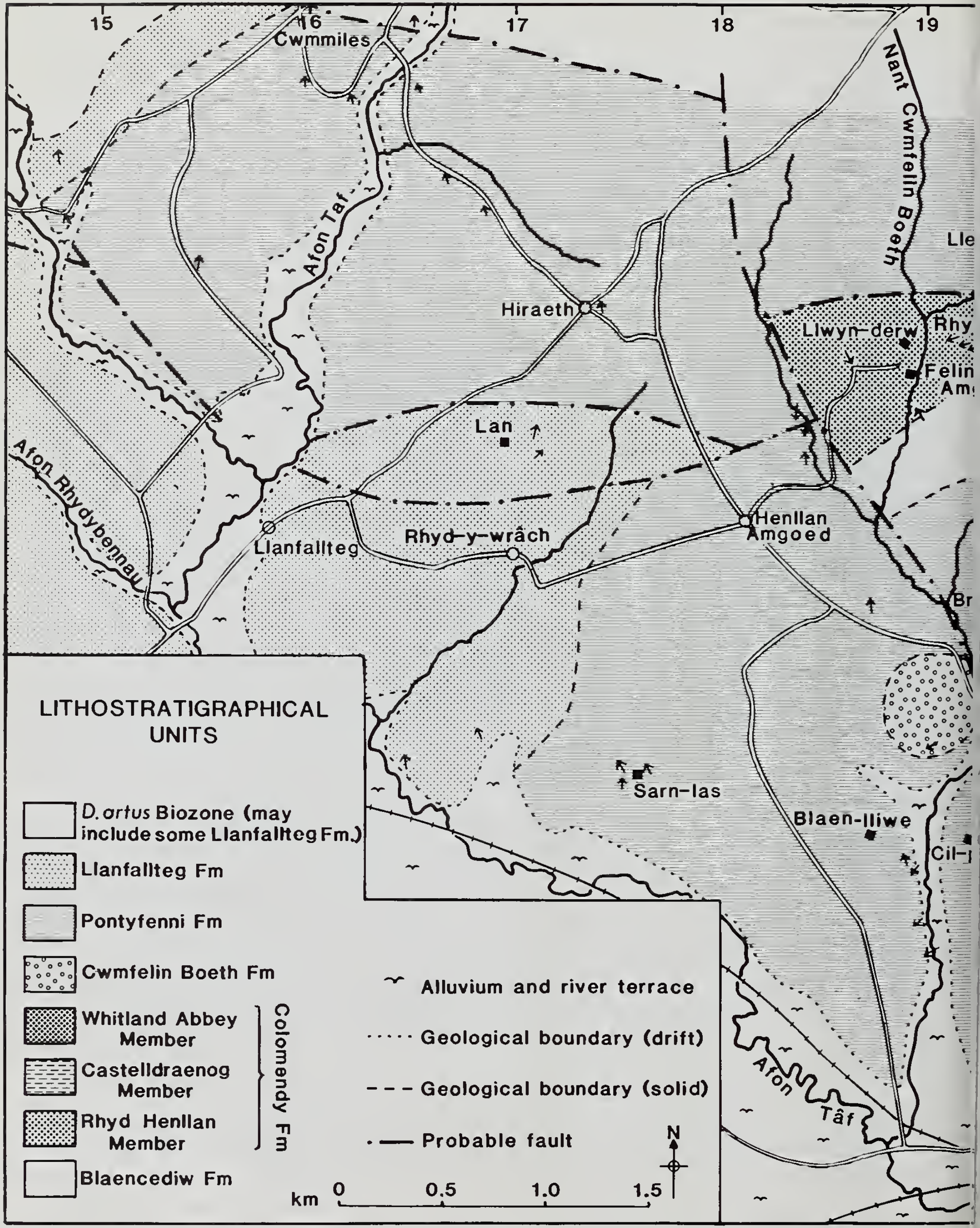
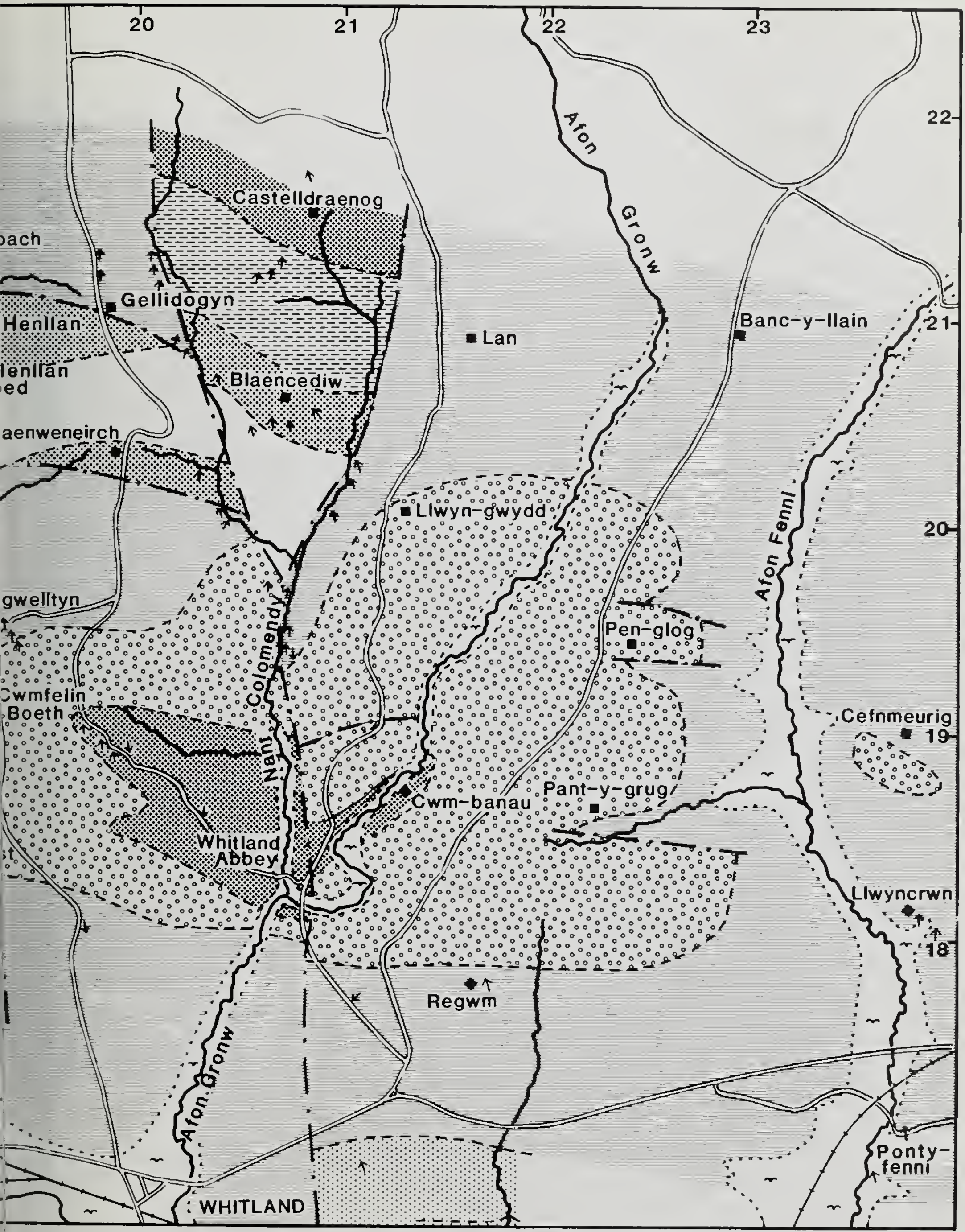


Fig. 2 Geological map of the Whitland area, based on the



authors' mapping and Geological Survey six-inch sheets.

Member and Cwmfelin Boeth Formation they can be traced for considerable distances across country, in some cases right to the coast. In no case is the exposure of any unit complete; thickness estimates are invariably the minimum that we can be sure about, and especially in the case of the poorly exposed late Arenig the real thickness may be considerably more than these minimum estimates. The stratigraphical column is summarized in Fig. 4.

Blaencediw Formation. This is exposed in the centre of the anticline in the area around Blaencediw and Blaenweneirch; it exceeds 80 m in thickness. The Blaencediw Formation forms the local base of the Arenig in the area, but we know from the fossils that it is younger than the Carmarthen Formation exposed to the east, and it is of Whitlandian age. Older beds are not seen, and it is possible that equivalents of the Carmarthen Formation were lacking in this area as they may be further to the west, in the area north of Haverfordwest. The type development of the Formation is in the old quarry (locality 31), 0·3 km NW of Blaencediw farm.

The Blaencediw Formation consists of closely set, poorly graded turbidites and channelled mass flow deposits occasionally reaching $\frac{1}{2}$m or so in thickness, separated by gritty shales or silts, with sporadic seams of black shale. Dendroid graptolites are particularly abundant at some horizons, and the type locality of this Formation yielded the well-preserved specimens of *Callograptus* species figured by Bulman (1928) (his 'Blaenweneirch' locality). When fresh the turbidites are black, and characteristically include clear, subrounded quartz clasts, which show 'wave' extinction in thin section. Pebbles of fine-grained igneous rocks and the occasional shale, fine sandstone or albitic felspar clasts have also been noted. These are considered to have been derived from a Precambrian source. When weathered, the siltier interbeds take on a yellow, buff, to almost white colour (possibly this appearance led to earlier descriptions of the beds as 'ashes'). The coarse beds often yield good moulds of single valves of brachiopods, and a rich brachiopod fauna has been obtained from several localities.

The grits have been quarried in a number of places. At the eastern edge of the outcrop a new quarry (locality 30) was opened in 1976 in the side of the track leading to Blaencediw farm. There are old quarries on the western side of the Nant-Cediw near Blaenweneirch. The Blaencediw Formation forms the high ground south of Felin Henllan Amgoed, and there are several old quarries here. The best fossil collecting is probably in the large quarry at the top of the hill (locality 39), which is reached by following the track over the hillside beyond Rhyd-henllan.

The middle Arenig (Whitlandian) age of the Blaencediw Formation is proved by the occurrence of the trilobite *Ogyginus hybridus* and a characteristic assemblage of articulate brachiopod species. An abundance of dendroid graptolites, including *Callograptus* and *Dendrograptus*, is also typical of the Whitlandian across south Wales, although particular species may have longer ranges, and are difficult to characterize.

The Blaencediw Formation probably represents relatively immature sediments, possibly derived from an uplifted area in the Haverfordwest district. We presume that the articulate brachiopods were derived from shallow water, and their disarticulated valves were emplaced along with the turbidites and mass flow deposits. Large inarticulate brachiopods, including a *Lingulella* as much as 5 cm long, are found between the turbidites, as are the dendroid graptolites, and these presumably inhabited the offshore environment.

From fossil evidence, the Blaencediw Formation is considered the equivalent of the Afon Ffinnant Formation of the Carmarthen district, which overlies the Carmarthen Formation there. Because the exposure is continuous in the east, while we cannot see the base of the Blaencediw Formation in the type area, we have chosen to make the formal definition of the base of the Whitlandian in the area east of Carmarthen, rather than in the Whitland district.

Colomendy Formation. The Colomendy Formation includes a considerable thickness of mudstones and shales comprising the rest of the mid-Arenig. In the Whitland area it can be divided into three members which are distinguished below.

RHYD-HENLLAN MEMBER. This overlies the Blaencediw Formation and is exposed to either side of the main outcrop of the latter. It is probably about 150 m thick. Passage between the two formations is poorly exposed in the east side of the Nant Cediw valley, and on the valley side

Fig. 3 G

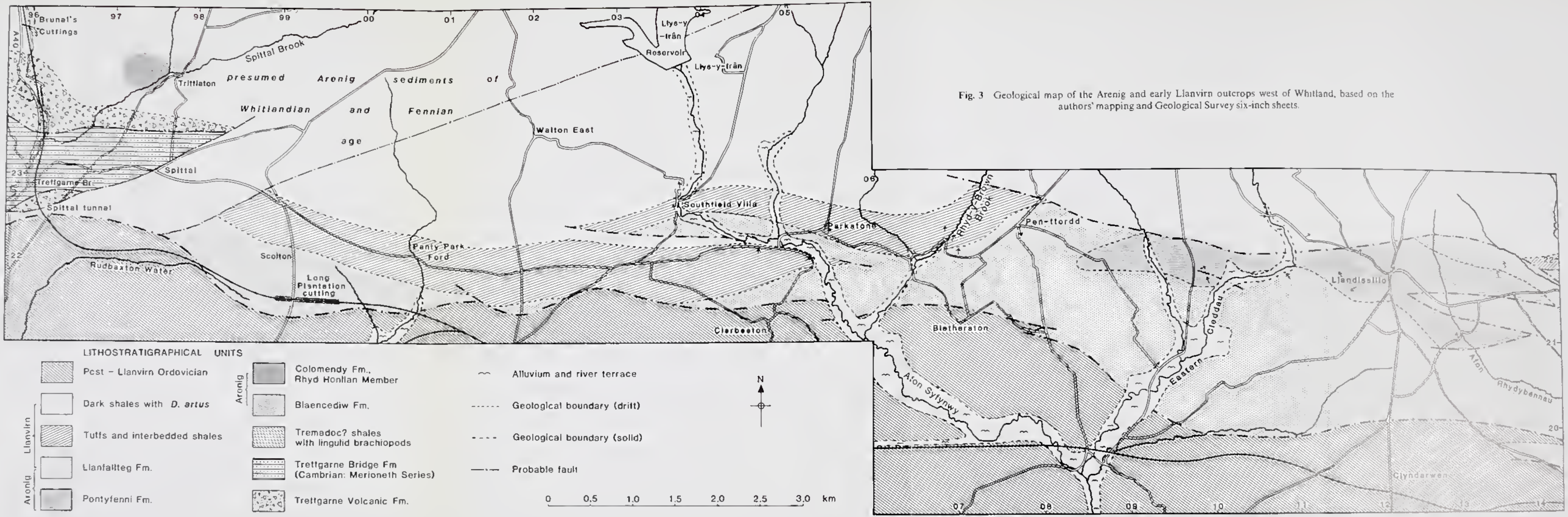


Fig. 3 Geological map of the Arenig and early Llanvirn outcrops west of Whitland, based on the authors' mapping and Geological Survey six-inch sheets.

south of Felin-Henllan-Amgoed. The Rhyd-Henllan Member consists of sandy or silty shales, which characteristically break out in large, flaggy slabs a centimetre or two thick. Their appearance is very like that of much of the Mytton Flags of Shropshire. By comparison with most of the Arenig rocks fossils are not hard to find, and certain bedding planes are covered with pygidia of *Ogyginus hybridus* (Salter). Poorly preserved specimens of the trinucleid *Gymnostomix gibbsii* are frequent, and there are occasional specimens of articulate brachiopods of Blaencediw type, and the asaphid trilobite *Bohemopyge scutatrix* (Salter).

The best (and type) exposure of the Member is in the lane leading to Felin Henllan Amgoed, a locality known to Salter, and in the banks of the lane leading downhill from Llywn-derw farm towards Rhyd-Henllan, where a good continuous section is seen. Elsewhere, exposures are confined to small scrapings in the sides of tracks, as on the hillside east of Rhyd-Henllan and near Blaenweneirch, or in the stream beds of the Nant Colomendy or Nant-Cediw. The fauna is typical of the Middle Arenig (Whitlandian).

CASTELLDRAENOG MEMBER. This is about 150 m thick, and consists of a series of highly fissile steel-grey shales. It is the only part of the Arenig Series in the Whitland district in which the rocks can be split to give completely flat bedding surfaces which are often slightly lustrous (a 'slaty' appearance, although there is no cleavage). Very weathered surfaces are often coloured yellow with a fluffy deposit of alum. This lithology is identical with that of the Arenig in Pwlluog, Whitesand Bay (part of the Penmaen Dewi Formation of Hughes *et al.*, 1982). There is no doubt that the Castelldraenog Member is also the temporal equivalent of this part of the Penmaen Dewi Formation, but for reasons explained later (p. 96) it is probable that the latter includes much else besides; hence we consider it preferable to introduce a local member name in the Whitland district.

The Castelldraenog Member is exposed extensively around the only outcrop area to the south of Castelldraenog Farm. The type locality is by the footpath leading down to the Nant-Cediw from Blaencediw and Castelldraenog farms. The member is also exposed along the Nant Colomendy and its small tributaries. Dips are generally low, and the beds form small bluffs among the trees.

Fossils are very rare; we have only recovered some fragments of the same dendroid graptolites which are abundant at certain horizons in Pwlluog, and *Tetragraptus* sp. However, the stratigraphical position is not in doubt because characteristic Whitlandian trilobites, including *Bohemopyge scutatrix*, occur below in the Rhyd Henllan Member and above in the Whitland Abbey Member. Even on the coast, where exposure of the Penmaen Dewi Formation is complete and accessible, fossil horizons are scarce, and more searching is required to find the appropriate horizons inland.

WHITLAND ABBEY MEMBER. This is extensively exposed around the ruin of Whitland Abbey, and in the lanes and streams around Castelldraenog farm. The gradation from the fissile shales of the Castelldraenog Member can be seen along the lane running from Blaencediw to Castelldraenog. The member is at least 200 m thick, and consists of a monotonous series of mudstones, often poorly fissile compared with the underlying member. When unweathered the mudstones are sooty black, but they are rarely encountered in this condition, usually weathering to a blotchy, rusty colour, and breaking into crumbling fragments.

In the centre of the southern part of the anticline, the mudstones can be examined in an old quarry opposite the Abbey ruins, and in the lane running from the Abbey to Pass-by, and in the dingle to either side of this lane. They are exposed again along the track on the west side of the Gronw about $\frac{1}{2}$ km north of the Abbey Farm. Here the shales and mudstones can be seen dipping under the Cwmfelin Boeth turbidites, a fact which led Evans (1906), who confused the Cwmfelin Boeth and Blaencediw formations, to regard the Whitland Abbey Member as the oldest beds in the area ('lowest shales'). The Whitland Abbey shales are exposed in the northern outcrop around Castelldraenog farm, in the farmyard and the lane leading down to the farm, and in the small dingle behind the farm. The mudstones are also extensively exposed in the stream bed of the upper reaches of the Nant Colomendy, and in the banks of the valley.

Fossils are very difficult to collect, but the occurrence of *Bohemopyge scutatrix*, *Cyclopyge*

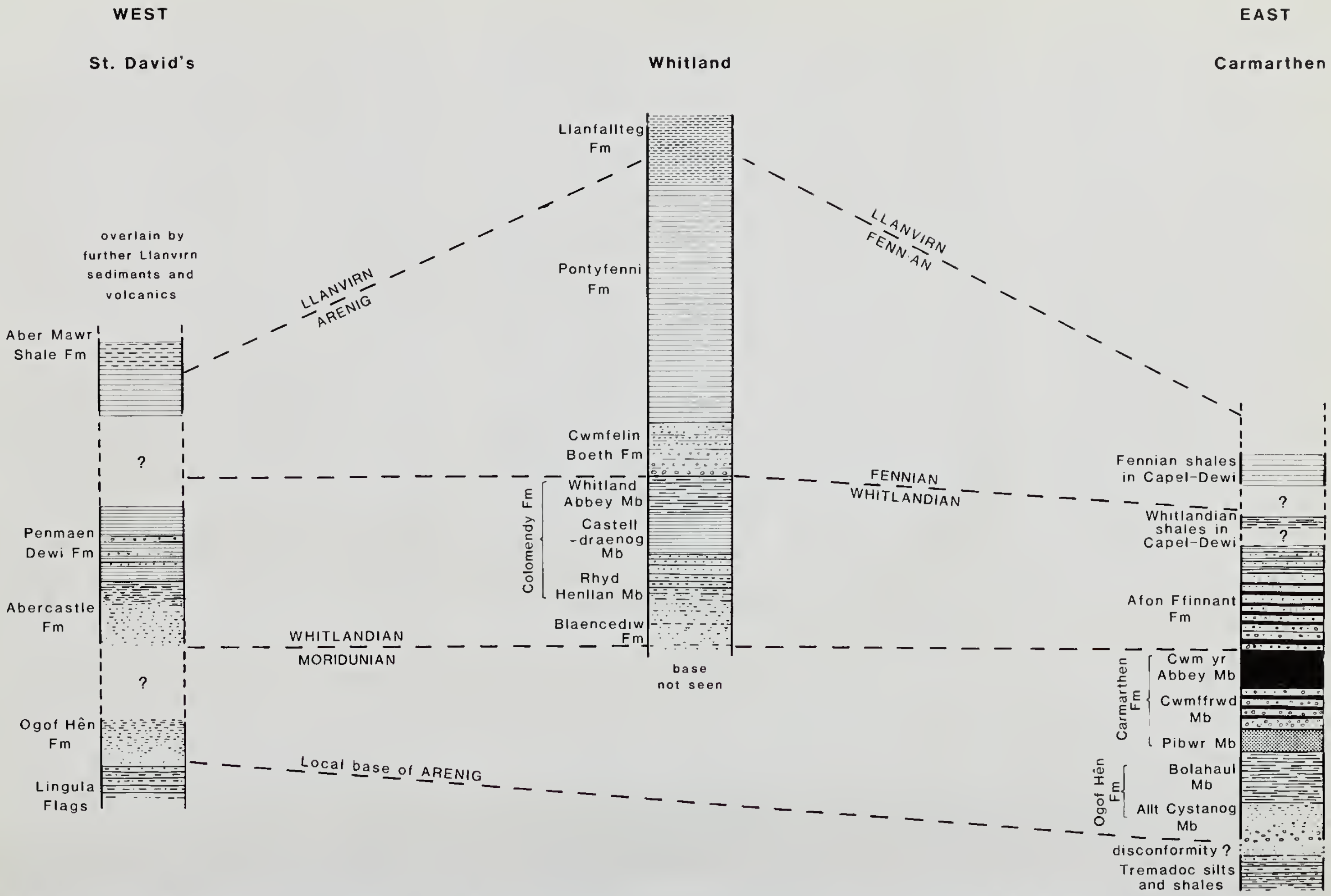


Fig. 4 Arenig lithostratigraphy and suggested correlations of formations from west to east in south Wales. For description of lithologies see text, and Fortey & Owens (1978) for Carmarthen and Ogof Hên formations.

grandis grandis and *Gymnostomix gibbsii* in the Abbey exposures show that the age is Whitlandian. A small, deflexed *Didymograptus* species has been collected at several localities.

Cwmfelin Boeth Formation. The base of the Cwmfelin Boeth Formation has been taken at the first coarse turbidite above the Whitland Abbey Member, and this is also taken as the base of the Fennian Stage. It is exposed by the track along the western side of the Gronw Valley (locality 22), 1 km NNE of The Manor at Whitland Abbey. The Formation probably exceeds 100 m in thickness, but it is hard to be more precise because we are uncertain about how much fault repetition there may be, and it is clear that the turbidites thicken and thin locally. A thick series of such beds is present behind Whitland Abbey Farm and Manor, where they form a conspicuous feature, described by D. C. Evans as a 'peculiar tump'. Over much of the outcrop single turbidite beds are about 1 m or less in thickness, and, unlike the Blaencediw Formation, they are usually well graded, with rounded clasts of rhyolite and rhyolitic tuffs, and mudstone flakes and plagioclase crystals. Unfossiliferous black shales a few cm thick serve to separate the turbidites.

The Cwmfelin Boeth Formation is exposed around a broad area of outcrop in the southern anticline, where it takes the high ground between outcrops of the Whitland Abbey Member and the Pontyfenni Formation. It appears at intervals on the valley sides of the Afon Gronw; on the western side there are several old quarries in the woods, and $\frac{1}{2}$km south of Whitland Abbey Farm. The Formation is exposed at several points along the road running along the ridge north of Regwm to Pen-glog. West of the Nant Colomendy the Formation is exposed in an old quarry on the hillside south-west of Aberdeuddwr, and near the abandoned farm of Pen-cil-post. The best exposures are in the neighbourhood of Cwmfelin Boeth, in a quarry adjacent to the Henllan Amgoed road (locality 35), in several quarries on the hill to the west, and in a small stream south of Bryngwelltyn farm where the upward passage into the Pontyfenni Formation can be examined.

Fossils are numerous in the upper part of the Formation within the turbidites, and they are probably derived from a relatively shallow source. Brachiopods are accompanied by the trilobite *Asaphellus*, the only horizon from which this genus has been recovered in this area.

Pontyfenni Formation. With the disappearance of the Cwmfelin Boeth turbidites the succession continues upwards into a considerable thickness of black mudstones and shales of the Pontyfenni Formation. The base may be formally defined above the last thick turbidite bed in the stream section (locality 37), near Cwmfelin Boeth, mentioned above. The whole thickness of the Pontyfenni Formation is nowhere exposed, but it occupies a very broad area of outcrop surrounding the anticlinal area and extending eastwards to Carmarthen and westwards to Llandissilio and beyond. We can only prove about 100 m of section, but the total thickness must be several times this figure: 300 m would probably be a conservative estimate. Parts of the succession are undoubtedly repeated by numerous faults and small folds, and there is local inversion near the southern limit of its area of outcrop. Because of the poor exposure, no attempt has been made to subdivide the formation on lithological grounds, although it certainly contains two successive faunas.

The Pontyfenni Formation consists of shales and blocky mudstones. When fresh these are dark, sooty grey to black in colour, and the mudstones are poorly fissile, breaking conchoidally rather than along the bedding. In the weathered condition the mudstones become almost white, producing a blotchy and crumbly rock from which it is difficult to extract fossils. A weathering pattern of concentric rings is typically developed, and exposed surfaces are often dark chocolate brown or purplish, rather than vermilion like the mudstones of the succeeding Llanfallteg Formation. Fossils are generally sparse, but when obtained are often remarkably well preserved, sometimes in full or partial relief (e.g. Figs 57, 101). The lower part of the Pontyfenni Formation includes shales which are more fissile than the typical mudstones, with silty and micaceous partings and numerous graptolites on some bedding planes. A common feature of many of the Pontyfenni outcrops is the presence of black, siliceous nodules, usually no bigger than a walnut, but occasionally 30 cm across. These split with the greatest difficulty, but may contain very well preserved fossils.

Unlike some of the Whitlandian units, the Pontyfenni Formation is remarkably uniform lithologically—it can be traced from Carmarthen with some breaks to the St David's area. In the Whitland area the best (and type) exposure is at Pontyfenni on the old course of the A40 east of Whitland. Beyond the eastern edge of the map (Fig. 2) it is again well exposed in a cutting by the main road just west of Banc-y-felin, and at several places, including the railway cutting, near Pwll-trap. It is exposed on both sides of the Afon Fenni: in an old quarry (locality 24) in the lane leading to Llwyn-crwn farm, and in the farmyard, about 1·5 km north of Pontyfenni; also on the western side in the streams and trackways running down from the high ground near Pen-glog and Pant-y-grug farms. In the area to the north of Whitland Abbey, an important fossiliferous outcrop is in the lane running from Pen-y-parc to Pass-by, which is in the lower part of the Formation not far above the last turbidite. Outcrops of Pontyfenni Formation in close proximity to some of the older formations prove the north–south faults marked on the map (Fig. 2). Below Gelli-diogyn farm, for example, a track running down to the stream has several exposures, while the track on the opposite side of the valley displays the Castelldraenog shales. Similarly, the courses of the Nant Colomendy and the stream west of the road from Henllan Amgoed to Llwyn Derw follow the outcrop of the soft Pontyfenni mudstones, which are exposed in the stream bed, passing to either side of the Whitlandian outcrop with its coarse grits. Outcrops are sporadic over the main outcrop area to the west of the Gronw. There are several small exposures on the western bank of the Nant Cwmfelin Boeth, and quite an extensive quarry behind Sarn-lâs farm. In the north of the area the Pontyfenni Formation is exposed at several places along the road to Cwmmiles, in a quarry below the village, and along the disused railway track. The same railway cutting exposes the upper part of the Formation to the north of Llanfallteg.

Pontyfenni Formation mudstones again reach the surface in what we suppose is a subsidiary anticline in the neighbourhood of Llandissilio (Fig. 3). Exposure is poor, but typical mudstones are seen about 1 km SW of Llandissilio in the lane side (locality 53) where the road crosses the Afon Rhydybennau, and west of Llandissilio in an old quarry (locality 54) 500 m SSW of Brechfa on the B4313.

The fauna of the Pontyfenni Formation is rich, but nowhere are trilobites common. In small outcrops one is most likely to find one of the characteristic cyclopygids. Small, lentil-shaped ostracodes are also typical. On faunal grounds we can divide the Pontyfenni Formation into two, but there is no question of lithological division with the poor outcrop available.

Llanfallteg Formation. The highest mudstones of the Pontyfenni Formation grade upwards into the Llanfallteg Formation, the highest lithostratigraphic unit described in this paper, which includes within it the Arenig–Llanvirn boundary. The contact with the Pontyfenni Formation is nowhere well exposed, but high Pontyfenni mudstones of typical lithology, with occasional biserial graptolites, underlie the Llanfallteg Formation in the type section along the Llanfallteg railway cutting (Fig. 8). This is much the best exposure of the Formation, where at least 60 m of section are exposed, but the complete thickness of the Formation must be somewhat greater, and certainly exceeds 100 m.

The Llanfallteg Formation consists of light grey mudstones and shales, much lighter in colour than those of the Pontyfenni Formation. They weather white or yellowish, but do not become as crumbly as the weathered Pontyfenni beds. Weathered surfaces often develop a characteristic vermilion staining. Much of the Llanfallteg Formation is more highly fissile than the underlying mudstones, but the shales are very soft and trilobites and other fossils take on any distortion to which the rocks have been subjected. Partial stipes of *Acrograptus acutidens* are probably the commonest fossils on weathered pieces of Llanfallteg shales. The siliceous nodules found in the Pontyfenni Formation are uncommon in the uppermost Arenig.

It is important to emphasize that there is no lithological change at all across the Arenig–Llanvirn boundary. The junction is well exposed in the small quarry at the southern end of the Llanfallteg railway section. As discussed below, the recognition of the Llanvirn boundary is governed by the sudden appearance of many 'tuning-fork' graptolites in the section (which are absent below), but this invasion is not reflected in any lithological change. For this reason there is no possibility of dividing the Llanvirn portion of the Llanfallteg Formation into a separate member.

Similar shales and mudstones continue up into the Llanvirn for some tens of metres—all are highly fossiliferous. Shales of this horizon are well exposed around Rhyd-y-wrâch as well as in the Llanfallteg section. The beds become more blocky and less fossiliferous higher in the Llanvirn, and there is apparently a gradual transition into the typical black, micaceous fissile shales, mapped as *bifidus* beds by the British Geological Survey, that occupy a broad outcrop to the north and south of the Whitland area.

The Llanfallteg Formation is an easily recognizable unit which takes up a broad stretch of ground in the neighbourhood of the type locality, where dips are low, and is repeated by minor folds and faults. We have not yet proved it in the Carmarthen area. Westwards it extends as far as the Scolton railway cutting, near Haverfordwest (locality 55), which has yielded a number of the earliest Llanvirn specimens figured in this paper.

Biostratigraphy

Elles' (1904, 1933) graptolite zonation is difficult to apply to much of the Arenig in south Wales, chiefly because the lowest two-thirds is in essentially non-graptolitic facies. Thus the correlation of our new stages (Fig. 11, p. 100) with the graptolite zones is tentative, but it may be possible to refine it in due course through Dr A. W. A. Rushton's current work on the Skiddaw Slates Group.

In the Arenig of south Wales, a more precise and satisfactory biozonation can be achieved using trilobites, and we here propose seven assemblages biozones. It is likely that it will eventually prove possible to create a finer biozonation, for some of our biozones are broadly based. As with much of the later Ordovician, trinucleids have proved to be some of the most sensitive biozonal indices, and we have used these for four of our biozones. Because appropriate trinucleids are lacking in the Moridunian and the later Fennian, we have resorted to asaphids in the former and a dionidid in the latter. The seven biozones are now described in ascending order.

Merlinia selwynii Biozone

This is well developed in the Ogof Hên Formation and in the lower Carmarthen Formation (Pibwr Member) and well seen at localities 1, 5 and 63. The eponymous asaphid occurs throughout most of the biozone, but is absent from the basal part, which instead has *Merlinia murchisoniae*; the two species overlap in range in the Henllan Ash and in the Pibwr Member. Other typical trilobites include *Myttonia fearnsidesi*, *Ampyx cetsarum*, *Neseuretus ramseyensis* and *N. murchisoni*. Of brachiopods, *Paralenorthis alata* and *Monorthis menapiae* are typical.

Merlinia rhyakos Biozone

To date, this biozone has only been proved in the Carmarthen area, where it occurs in the upper part of the Carmarthen Formation (Cwmffrŵd and Cwm yr Abbey members) and the lowest 40 m of the succeeding Afon Ffinnant Formation. Here, in an olenid biofacies, it is accompanied by *Bienvillia praecalva* in the lower part and by *Hypermecaspis venerabilis* and *Porterfieldia punctata* in the upper. Its base is defined in Allt Pen-y-Coed, locality 5E of Fortey & Owens 1978, and the lower part is well seen in this section; the upper part is well displayed in Nant y glasdwr (Fortey & Owens 1978 localities 3A, B) and in Cwm yr Abbey (Fortey & Owens 1978, locality 16).

Furcalithus radix Biozone

The base of this biozone is drawn at locality 16J, Cwm yr Abbey. It appears to incorporate only a small thickness of strata, with the fauna restricted to *Furcalithus radix*, *Ogyginus hybridus* and *Azygograptus eivionicus*. It has only been identified with certainty at Cwm yr

Abbey and Afon Ffinnant, but is probably represented in the arenaceous facies of the Blaencediw and Abercastle formations further west, and in a locality near Mathry (R. Kennedy, personal communication).

Gymnostomix gibbsii Biozone

A suitable section to define the base of this biozone precisely has not been found, but it presumably lies within the lower half of the Afon Ffinnant and Penmaen Dewi formations, and close to the junction of the Blaencediw and Colomendy formations. It includes a considerable thickness of strata, and is one of the most readily recognized in the field by the presence of the distinctive *Gymnostomix gibbsii*, which is usually associated with *Ogyginus hybridus*. The fauna of the biozone is restricted, and also includes *Cnemidopyge salteri*, *Shumardia* (*S.*) *gadwensis* and *Bohemopyge scutatrix*; the most diverse and abundant fauna has been collected at Pwlluog, Whitesand Bay. *Azygograptus hicksii* is locally abundant in the Afon Ffinnant and Penmaen Dewi formations, and dendroid graptolites (especially *Callograptus*) are frequent in the Blaencediw Formation and in the lower part of the Penmaen Dewi Formation.

Stapeleyella abyfrons Biozone

The characteristic fauna of this biozone, dominated by *Stapeleyella abyfrons* and *Segmentagnostus whitlandensis* is found at several localities in the basal Pontyfenni Formation, immediately overlying the Cwmfelin Boeth Formation, for example at Pen-y-parc (locality 38). The turbidites of the latter, which intervene between this fauna and that of the top of the *G. gibbsii* Biozone, are arbitrarily included in the *Stapeleyella abyfrons* Biozone.

Bergamia rushtoni Biozone

We estimate that some two-thirds of the Pontyfenni Formation is included in this biozone; in our present state of knowledge it is not possible to give a finer biozonation, although the presence of different trinucleids (e.g. *Stapeleyella* aff. *abyfrons*) in the lower part suggests that this may eventually be possible. The type development is at Pontyfenni (locality 23), but because of the nature of the exposures it is not possible to define its base satisfactorily. Included in this biozone are the diverse cyclopygid and atheloptic trilobite assemblages of the Pontyfenni Formation which includes over half those described herein; for many groups it is their first known appearance in the geological record. Graptolites include *D. hirundo*, *D. uniformis lepidus*, *Tetragraptus reclinatus* and *Pseudotrigonograptus ensiformis*. Their presence makes this biozone widely correlateable outside Britain.

Dionide levigena Biozone

This incorporates the Arenig part of the Llanfallteg Formation, and its type development is on the Llanfallteg railway cutting (locality 52). Passage downwards into strata containing a *B. rushtoni* Biozone fauna can nowhere be observed. Many of the trilobites, including the trinucleid *Stapeleyella inconstans*, pass upwards into the Llanvirn. The same applies to the graptolites; biserials such as '*Glyptograptus*' *austrodentatus*, '*G.*' *dentatus* and *Acrograptus acutidens* cross the boundary, which is marked by the influx of abundant pendent didymograptids.

Stages in the British Arenig

Moridunian Stage

Nowhere is there exposed a continuous passage between the Tremadoc and Arenig, and a suitable international stratotype for the base of the Arenig is lacking; the formal base of the Moridunian has still to be defined. It will be necessary to resort to artificial excavations to expose a section which will bear comparison with those outside Britain. There are two possible sites in Wales for such an excavation: around the type area of Arennig Fawr in north Wales,

Table 1 Stratigraphical distribution of trilobites and graptolites in the Arenig and basal Llanvirn in south Wales. Key to biozones: 1—*selwynii*; 2—*rhyakos*; 3—*radix*; 4—*gibbsii*; 5—*abyfrons*; 6—*rushtoni*; 7—*levigena*; 8—*artus*.

		Moridunian		Whitlandian		Fennian			Lower Llanvirn
TRILOBITES	page	1	2	3	4	5	6	7	8
Merlinia murchisoniae†	–	+	–	–	–	–	–	–	–
Ampyx cetsarum†	–	+	–	–	–	–	–	–	–
Neseuretus ramseyensis	238	+	–	–	–	–	–	–	–
Merlinia selwynii†	–	+	–	–	–	–	–	–	–
Myttonia cf. *fearnsidesi*†	–	+	–	–	–	–	–	–	–
Neseuretus murchisoni	239	+	–	–	–	–	–	–	–
Bienvillia praecalva†	–	+	+	–	–	–	–	–	–
Merlinia rhyakos†	–	–	+	–	–	–	–	–	–
Hypermecaspis venerabilis†	–	–	+	–	–	–	–	–	–
Cyclopyge? sp.†	–	–	+	–	–	–	–	–	–
Porterfieldia punctata†	–	–	+	+	–	–	–	–	–
Furcalithus radix	208	–	–	+	–	–	–	–	–
Bergamia sp. A	207	–	–	+	–	–	–	–	–
Ogyginus hybridus	143	–	–	+	+	–	–	–	–
O. sp. indet.	148	–	–	–	+	–	–	–	–
Segmentagnostus hirundo	116	–	–	–	+	–	–	–	–
Shumardia (*S.*) *gadwensis*	121	–	–	–	+	–	–	–	–
Leioshumardia sp. A	126	–	–	–	+	–	–	–	–
Microparia (*M.*) *boia*	172	–	–	–	+	–	–	–	–
Bohemopyge scutatrix	136	–	–	–	+	–	–	–	–
Cnemidopyge salteri	228	–	–	–	+	–	–	–	–
Furcalithus sedgwicki	209	–	–	–	+	–	–	–	–
Gymnostomix gibbsii	216	–	–	–	+	–	–	–	–
Cyclopyge grandis grandis	151	–	–	–	+	+	–	–	–
Segmentagnostus whitlandensis	116	–	–	–	–	+	–	–	–
Asaphellus whittardi	132	–	–	–	–	+	–	–	–
Stapeleyella abyfrons	213	–	–	–	–	+	–	–	–
Dionidella? sp. indet. 1	222	–	–	–	–	+	–	–	–
Arthrorhachis sp. indet.	114	–	–	–	–	?	+	–	–
Dindymene saron	235	–	–	–	–	+	+	–	–
Shumardia (*S.*) sp. A	123	–	–	–	–	+	?	–	–
Placoparia (*P.*) *cambriensis*	232	–	–	–	–	+	+	+	+
Ellipsotaphrus monophthalmus	189	–	–	–	–	+	+	+	+
Stapeleyella aff. *abyfrons*	215	–	–	–	–	–	?	–	–
Leiagnostus cf. *erraticus*	112	–	–	–	–	–	+	–	–
Shumardia (*Conophrys*) *crossi*	123	–	–	–	–	–	+	–	–
Girvanopyge sp. indet.	127	–	–	–	–	–	+	–	–
Bohemilla (*Fenniops*) *sabulon*	129	–	–	–	–	–	+	–	–
Cyclopyge grandis brevirhachis	154	–	–	–	–	–	+	–	–
Cyclopyge cf. *umbonata*	156	–	–	–	–	–	+	–	–
Degamella evansi	157	–	–	–	–	–	+	–	–
Microparia (*M.*) *broeggeri*	164	–	–	–	–	–	+	–	–
M? sp. indet. 1	173	–	–	–	–	–	+	–	–
M. (*Heterocyclopyge*) sp. indet.	174	–	–	–	–	–	+	–	–
Prospectatrix cf. *superciliata*	176	–	–	–	–	–	+	–	–
Sagavia glans	177	–	–	–	–	–	+	–	–
Pricyclopyge binodosa eurycephala	181	–	–	–	–	–	+	–	–
P. dolabra	184	–	–	–	–	–	+	–	–
Circulocrania orbissima	187	–	–	–	–	–	+	–	–
Psilacella cf. *doveri*	190	–	–	–	–	–	+	–	–

Table 1 *Continued*

		Moridunian		Whitlandian		Fennian			Lower Llanvirn
TRILOBITES	page	1	2	3	4	5	6	7	8
Barrandia sp. indet.	193	–	–	–	–	–	+	–	–
Illaenopsis harrisoni	194	–	–	–	–	–	+	–	–
Bergamia rushtoni	205	–	–	–	–	–	+	–	–
Ampyx linleyoides	223	–	–	–	–	–	+	–	–
Ectillaenus ?bergaminus	202	–	–	–	–	–	+	–	–
Dionidella? sp. indet. 2	223	–	–	–	–	–	+	–	–
Colpocoryphe taylorum	241	–	–	–	–	–	+	–	–
Ormathops nicholsoni	244	–	–	–	–	–	+	–	–
Corrugatagnostus cf. *refragor*	113	–	–	–	–	–	+	+	–
Segmentagnostus scoltonensis	118	–	–	–	–	–	+	+	+
Microparia (*M.*) *porrecta*	168	–	–	–	–	–	+	+	+
Selenopeltis buchi macrophthalma	250	–	–	–	–	–	+	+	+
Dionide levigena	220	–	–	–	–	–	–	+	+
Placoparina sp.	231	–	–	–	–	–	–	–	+
Dindymene didymograpti?	237	–	–	–	–	–	–	+	–
Microparia (*M.*) *teretis*	170	–	–	–	–	–	–	+	+
Novakella copei	174	–	–	–	–	–	–	+	+
Pricyclopyge binodosa binodosa	(181)	–	–	–	–	–	–	+	+
Barrandia homfrayi	191	–	–	–	–	–	–	+	+
Stapeleyella inconstans	212	–	–	–	–	–	–	+	+
Ampyx linleyensis	226	–	–	–	–	–	–	+	+
Seleneceme acuticaudata	230	–	–	–	–	–	–	+	+
Ectillaenus perovalis	119	–	–	–	–	–	–	+	+
Ormathops llanvirnensis	247	–	–	–	–	–	–	+	+
Cyclopyge kossleri	155	–	–	–	–	–	–	–	+
Gastropolus obtusicaudatus	161	–	–	–	–	–	–	–	+
Microparia (*M.*) aff. *broeggeri*	168	–	–	–	–	–	–	–	+
Selenopeltis buchi buchi	249	–	–	–	–	–	–	–	+
Dionide turnbulli	219	–	–	–	–	–	–	–	+
GRAPTOLITES									
Phyllograptus cf. *densus*†	–	+	–	–	–	–	–	–	–
P. cf. *angustifolius*†	–	+	–	–	–	–	–	–	–
Azygograptus eivionicus	276	–	–	+	?	–	–	–	–
A. hicksii	275	–	–	–	+	–	–	–	–
Tetragraptus (*T.*) *serra*	(251)	–	–	–	+	–	–	–	–
Didymograptus (*Expansograptus*) *goldschmidti*	272	–	–	–	+	+	+	–	–
D. (*Expansograptus*) *sparsus*	267	–	–	–	–	+	+	–	–
Tetragraptus (*T.*) *reclinatus reclinatus*	252	–	–	–	–	+	+	–	–
T. (*T.*) *reclinatus abbreviatus*	253	–	–	–	–	–	+	–	–
T. (*T.*) *bigsbyi askerensis*	252	–	–	–	–	–	+	–	–
D. (*Expansograptus?*) *uniformis lepidus*	270	–	–	–	–	–	+	–	–
D. (*Didymograptellus*) sp.	260	–	–	–	–	–	+	–	–
Pseudotrigonograptus ensiformis	278	–	–	–	–	–	+	–	–
*Pseudisograptus stellus**	–	–	–	–	–	–	+	–	–
Isograptus caduceus subsp.*	–	–	–	–	–	–	+	–	–
D. (*Expansograptus*) *hirundo*	260	–	–	–	–	–	+	?	–
'*Glyptograptus*' *dentatus*	282	–	–	–	–	–	+	+	+

Table 1 *Continued*

		Moridunian		Whitlandian		Fennian			Lower Llanvirn
GRAPTOLITES	page	1	2	3	4	5	6	7	8
Glossograptus acanthus	281	–	–	–	–	–	–	+	+
'Glyptograptus' austrodentatus	284	–	–	–	–	–	–	+	+
Acrograptus acutidens	278	–	–	–	–	–	–	+	+
A? sp. a	280	–	–	–	–	–	–	–	+
Didymograptus (*D.*) *artus*	258	–	–	–	–	–	–	–	+
D. (*D.*) *spinulosus*	255	–	–	–	–	–	–	–	+

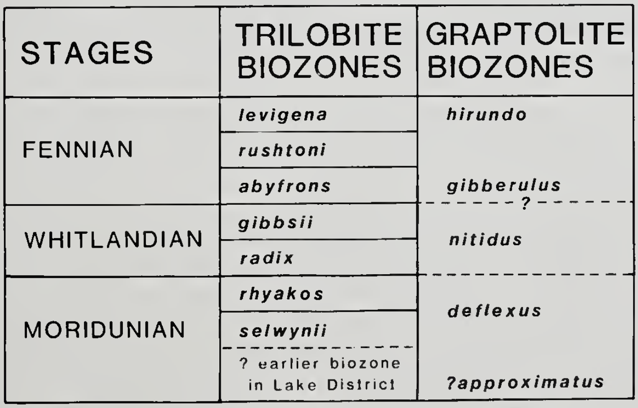
† Trilobites and graptolites marked with a dagger were described by Fortey & Owens (1978).
* Graptolites marked with an asterisk were described by Jenkins (1982).

and in the Carmarthen–Llangynog area of south Wales. Both, however, have attendant problems. At Arennig the position of the boundary coincides with the site of emplacement of an intrusion (Zalasiewicz 1984*a*), but this complication probably does not apply in the Carnedd Iago area, a short distance to the north. In the Llangynog district exposure is poor, and the area is structurally complex (Owens *et al.* 1982: fig. 1). We are currently investigating the possibilities of the few available sites in Wales, and recent discoveries in the Lake District are promising.

The Moridunian incorporates the *Merlinia selwynii* and *M. rhyakos* biozones (Figs 4, 5). Its most complete development is to be found in the Carmarthen area, although the best section for the lowest part is the type section of the Ogof Hên Formation on Ramsey Island (locality 63). The overlying Carmarthen Formation crops out only in the Carmarthen area, the only district in Wales where the upper part of the Stage has been proved. Faunally, the stage is characterized by the trilobites *Merlinia*, *Neseuretus*, *Myttonia* and *Ampyx* and by the brachiopods *Paralenorthis* and *Monorthis*. The oldest beds are of particular interest because they have yielded some of the earliest crinoids (*Ramseyocrinus cambrensis*), parablastoids (*Blastoidocrinus antecedens*) and asteroids (*Petraster ramseyensis*), as well as those of various groups of bivalves, currently being investigated by Dr J. C. W. Cope.

Whitlandian Stage

The standard section for the base of the stage is below the bridge in Cwm yr Abbey (SN 5002 1985) in a continuous stream exposure of the Afon Ffinnant Formation, 40 m above the base. It coincides with the *Merlinia rhyakos–Furcalithus radix* Biozone boundary. The fauna below the



STAGES	TRILOBITE BIOZONES	GRAPTOLITE BIOZONES
FENNIAN	*levigena*	*hirundo*
	rushtoni	
	abyfrons	*gibberulus*
		?
WHITLANDIAN	*gibbsii*	*nitidus*
	radix	
MORIDUNIAN	*rhyakos*	*deflexus*
	selwynii	
	? earlier biozone in Lake District	*?approximatus*

Fig. 5 Summary of stages and biozones in the British Arenig.

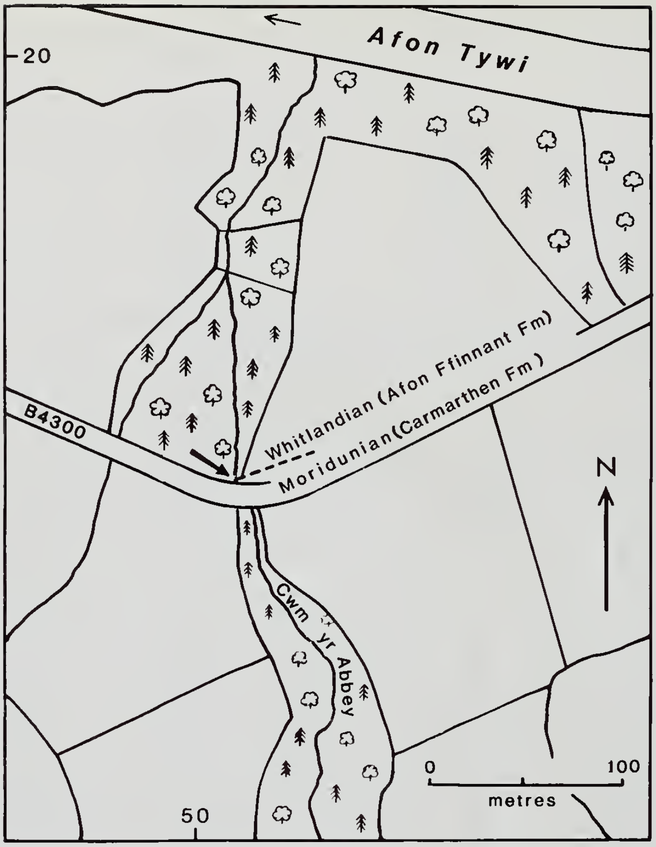


Fig. 6 Map showing proposed stratotype for the base of the Whitlandian Stage at Cwm yr Abbey, east of Carmarthen (see Fortey & Owens 1978: 231, fig. 3).

boundary includes *M. rhyakos* and abundant *Porterfieldia punctata* and that above it *Ogyginus hybridus*, *F. radix* and orthoconic nautiloids.

The higher part of the Whitlandian, which incorporates the *Gymnostomix gibbsii* Biozone, is represented in the Carmarthen area by the upper part of the Afon Ffinnant Formation which contains abundant *G. gibbsii* and *O. hybridus*, but the most complete and fossiliferous section is at Pwlluog, Whitesand Bay, in the Penmaen Dewi Formation. The trilobite fauna of this stage in its type development is characterized by the trinucleid genera *Furcalithus* and *Gymnostomix*, which are restricted to it, the asaphids *Ogyginus hybridus* and *Bohemopyge scutatrix* and the shumardiid *Shumardia gadwensis*. The graptolite fauna is small, and is dominated by *Azygograptus*.

Fennian Stage

The base is defined in the lane exposure opposite the bridge leading to Cwm-banau, north of Whitland (SN 2123 1862), at the base of the Cwmfelin Boeth Formation. Strata on either side of the boundary have yielded few fossils in the immediate vicinity, but the Whitland Abbey Member of the Colomendy Formation has yielded a typical *G. gibbsii* Biozone fauna at nearby Whitland Abbey. The Cwmfelin Boeth Formation carries a distinctive (allochthonous) fauna of articulate brachiopods, *Asaphellus* and *Cyclopyge grandis grandis*. Apart from the turbidites of the Cwmfelin Boeth Formation, much of the stage in its type development in the Whitland area is represented by sediments of offshore origin which carry a mixed graptolite–trilobite fauna.

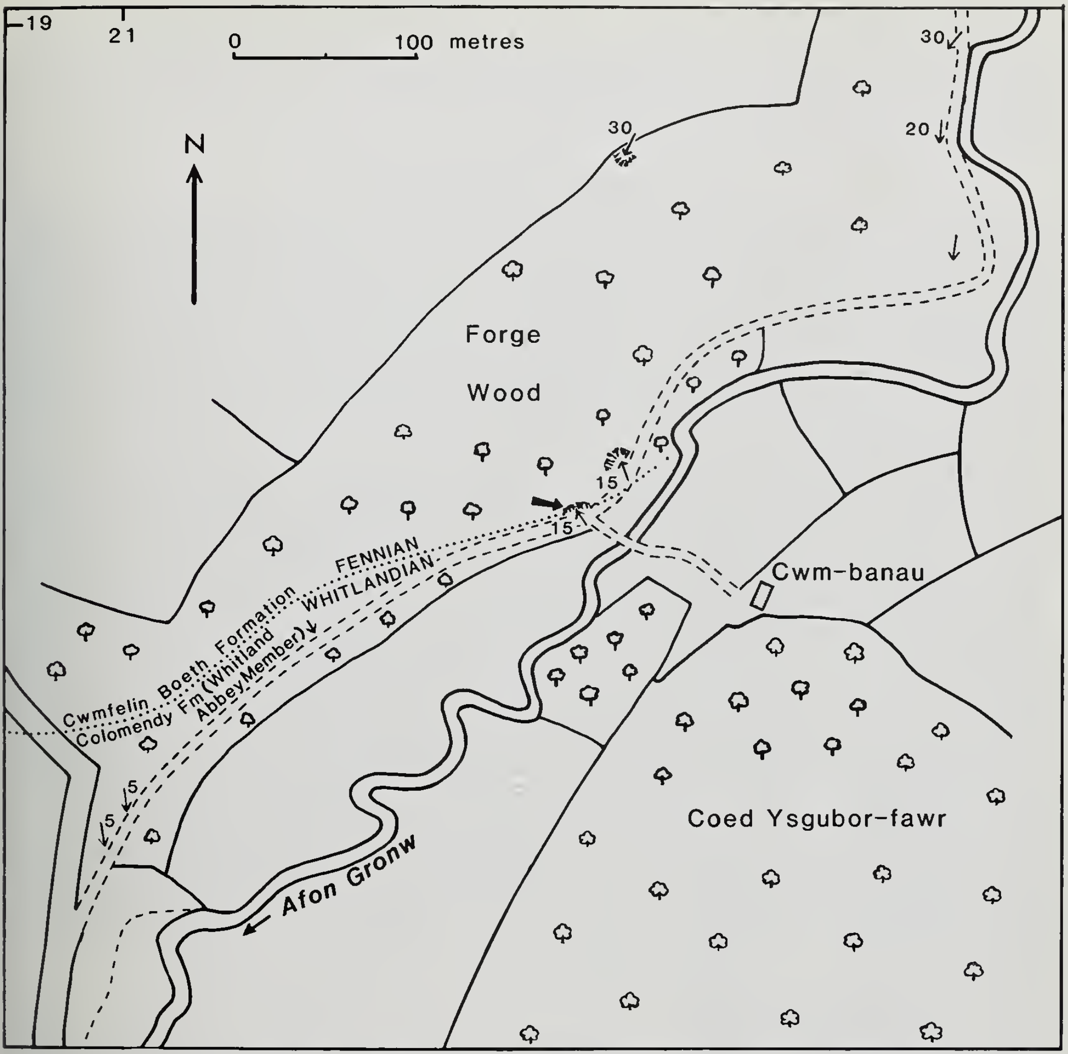


Fig. 7 Map showing proposed stratotype for the base of the Fennian Stage, northeast of Whitland Abbey (see Fig. 2).

The trilobites are dominated by cyclopygids, especially *Pricyclopyge*, and by the atheloptic assemblage of blind or small-eyed benthonic forms described below. The trinucleids *Bergamia* and *Stapeleyella* are typical of the stage, although both extend upwards into the Llanvirn.

The Fennian includes at least part of the *I. gibberulus* and all the *Didymograptus hirundo* graptolite biozones (see Fig. 11, p. 100). Jackson (1962) recognized the *D. hirundo* Biozone in the Lake District more from the abundance of biserial graptoloids than from the presence of the eponymous species. As Jenkins (1982) has observed, the ranges of *D. hirundo* and *I. gibberulus* overlap, and both can be found below the range of biserials. On Jackson's criterion, only the highest part of the Fennian (*Dionide levigena* Biozone) in the Llanfallteg Formation of south Wales would conform to his usage of the *Didymograptus hirundo* Biozone. The range of *D. hirundo* certainly extends down into the *Bergamia rushtoni* trilobite Biozone, and it is this fauna which includes identical trilobite species to those at Randel Crag in the Lake District. It is likely that the *Dionide levigena* and *B. rushtoni* Biozones together are equivalent to all the *Didymograptus hirundo* and at least part of the *I. gibberulus* Biozones, and in Jackson's (1962) usage the zonal boundaries would approximately coincide. Further refinement of detailed graptolite taxonomy from the Lake District, as opposed to the gross aspect of the fauna, will help to place these correlations on a firmer basis.

The Arenig–Llanvirn boundary

The base of the Llanvirn Series defines the top of the Fennian. The type locality of the Llanvirn is on the coast at Abereiddi Bay, north of St David's, SW Dyfed (Hicks 1881, Hughes *et al.* 1982, Whittington & Rickards *in* Whittington *et al.* 1984) where the boundary between the Arenig and Llanvirn is placed with some question between the Penmaen Dewi Formation and the Aber Mawr Shale Formation. The problem here is that the boundary interval is not well exposed and lacks fossils, and prolonged search in temporary sections apparently close to the Llanvirn boundary as Caer-Rhŷs Farm (at SM 7954 3031 and SM 7957 3050) in 1974 and 1977 failed to provide any.

The early Llanvirn has a rich fauna, and has traditionally been distinguished regionally from the underlying Arenig by the appearance of tuning-fork graptolites. The best section for the boundary interval that we have been able to find is at Llanfallteg, near Whitland (locality 52), where the exposure is continuous, fossiliferous, and with little distortion (Fortey & Owens *in* Rushton *et al.* 1979). Here, the boundary lies within the Llanfallteg Formation, and there is every indication that sedimentation was continuous. As might be expected in such circumstances there is no sharp faunal break at the Llanvirn boundary (Fig. 9), which has to be arbitrarily taken at the appearance of the first tuning-fork graptolites. Many other species appear for the first time lower in the section, and continue upwards into the Llanvirn. This kind of gradation is to be expected in a truly continuous succession and we do not regard it as a disadvantage. It would have been possible to take a lower horizon as the base of the Llanvirn, e.g. at the appearance of the first abundant biserial graptolite fauna, but this would have placed it at or near the base of the Llanfallteg Formation, and at a lithological change, which seems inadvisable especially as it also takes the boundary away from the horizon traditionally used.

We know of one other Welsh section in which there is continuous exposure across the Arenig–Llanvirn boundary, that on the Afon Seiont, Caernarfon (Elles 1904). Fossils are rarer here, and because it is much more distant from the type area of the Llanvirn, we do not consider that the section is appropriate as a potential stratotype for the Arenig–Llanvirn boundary.

Name of basal Llanvirn biozone

The earliest biozone of the British Llanvirn has been termed the *Didymograptus bifidus* Biozone. *D. bifidus* (Hall) is a species from the Quebec Group, and it occurs in rocks of Arenig, not Llanvirn, age. It has recently been shown (e.g. Cooper & Fortey 1982, Jenkins 1983) that Hall's *D. bifidus* is not conspecific with the British Llanvirn forms identified with *D. bifidus* by Elles & Wood (1901). Obviously a new name is needed for the British early Llanvirn Biozone; on recent stratigraphical columns it has tended to appear as the *D.* '*bifidus*' Biozone. Jenkins (*in* Hughes *et al.* 1982) utilized '*Glyptograptus*' *dentatus* for this purpose. This is not an apposite choice, because we show here (p. 282) that the range of '*G.*' *dentatus* extends well down into the Arenig. We suggest that the Biozone of *Didymograptus artus* is a suitable replacement. *D. artus* is widely recorded from this horizon, and is probably one of the more distinctive species in the variable plexus of Llanvirn pendent didymograptids.

Are stages necessary?

Chlupáč, Flügel & Jaeger (1981) have presented a case that the 'series' of the British Ordovician are not greatly different in duration from stages in other parts of the geological column, and that the division of the British 'series' into stages (in the Caradoc, for example) represents an

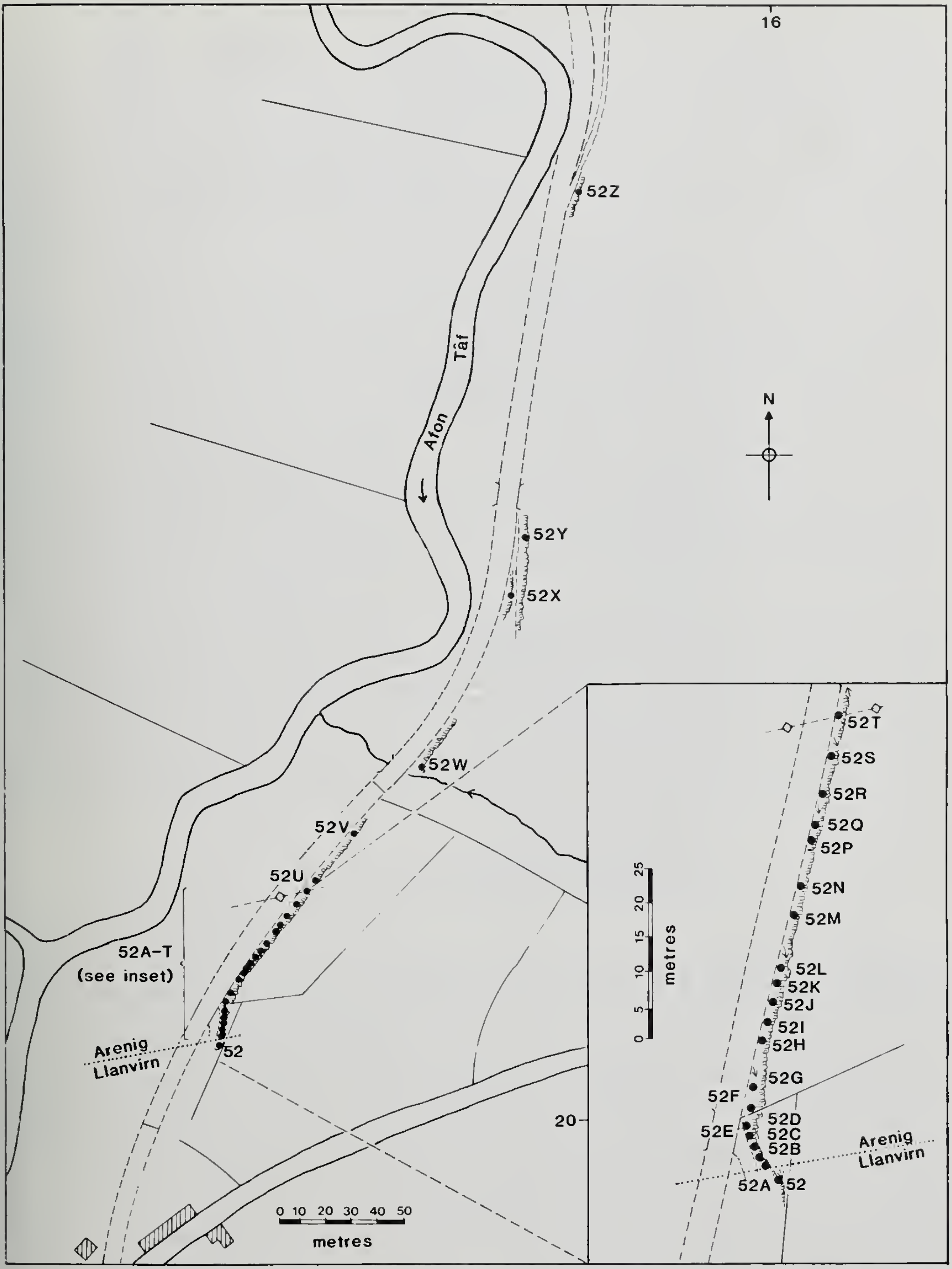


Fig. 8 Map of Llanfallteg railway cutting (disused), showing position of localities spanning the Arenig–Llanvirn boundary.

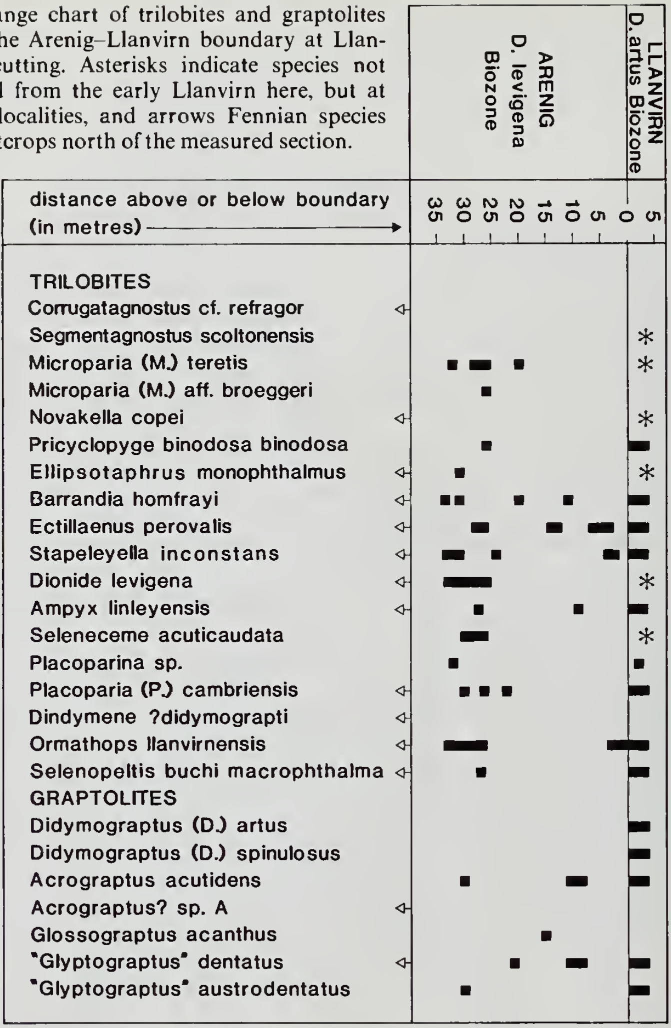


Fig. 9 Range chart of trilobites and graptolites across the Arenig–Llanvirn boundary at Llanfallteg cutting. Asterisks indicate species not recorded from the early Llanvirn here, but at nearby localities, and arrows Fennian species from outcrops north of the measured section.

unnecessarily fine subdivision, which was not considered useful in the international stratigraphical arena. We need to justify the introduction of stages within the Arenig Series here.

1. If the Ordovician (including Tremadoc) is taken as lasting between 65 (Harland *et al.* 1982) and 78 m.y. (McKerrow *et al.* 1985), we may estimate the duration of our proposed stages as follows. We assume that the Ordovician series are equal in duration, except that the Llanvirn and Llandeilo taken together are regarded as no longer than any other series. The Llandeilo has long been recognized as comparatively short, and our assumption is justified by the numbers of graptolitic divisions which can be recognized within a series. We regard the Harland *et al.* estimated duration of 10 m.y. for the Llandeilo, which consists of only one biozone, as improbable. On our estimation the Arenig would have lasted between 13 m.y. and 15 m.y., according to which radiometric age estimate is followed. Our three stages, if about equal in duration, would each have the order of magnitude of 4 to 5 m.y. Stages in the Jurassic are about 6 m.y. on average. There is thus little difference in estimated duration between our Arenig stages and those of the Jurassic, which are often accepted as exemplifying what a stage should be. The stage divisions of the Caradoc would still be considerably more finely drawn

(less than 2 m.y. if the chronology of Harland *et al.* is followed) and the criticisms of Chlupáč *et al.* (1981) might be more persuasive at this stratigraphical level.

2. Stage names exist in Scandinavia (and Estonia) for the Arenig interval. Why not apply these names to the British series? First, as we discuss below, the criteria for correlation with the Scandinavian succession are few and uncertain. Second, Britain probably lay at the edge of the Gondwanan continent (Cocks & Fortey 1982), well removed and at a latitude different from the Scandinavian craton. Faunal provinciality was at a maximum in the Arenig. In the words of Chlupáč *et al.* (1981: 78) 'separate and different sets of stages for a single system are deemed acceptable for distinct palaeobiogeographic regions as long as sufficiently precise interregional correlations cannot be achieved.' The British regional stages should form the standard for the Gondwanan sector.

3. Stages defined on graptolitic rocks are based on the sequence of faunas in Victoria, Australia (Thomas 1960). They have been widely applied in North America and New Zealand, and are of correlative value in China, arctic U.S.S.R., South America and elsewhere (Cooper & Fortey 1982). Four stages (Bendigonian (part), Chewtonian, Castlemainian and Yapeenian) approximate to the Arenig Series, a division on about the same scale as that proposed here.

4. The threefold division used here has already proved its worth in refining our understanding of sedimentation and correlation of Arenig sequences within the British Isles. It approximates to the informal threefold division of the Arenig in the Pacific graptolite realm ('lower', 'middle' and 'upper') suggested by Cooper & Fortey (1982: 168). There are still many difficulties in the way of detailed correlation, not least the endemicity of the faunas, but this correspondence does at least permit informal discussion of worldwide events during the Arenig, with reference to the type development of the Series.

In summary, proposition of Arenig stages is justified because they are divisions broad enough to be commensurate with stages elsewhere in the geological column, and comparable with other subdivisions already usefully employed through the same time interval. Separate stage divisions for the type area are particularly applicable to the Arenig where correlation problems are at their most acute; our divisions may provide a standard for Gondwana. Finally, they have already proved useful nationally, and there is reason to suppose that they will correspond to a broad-scale, and practical, threefold division of the Arenig on the international scale.

Correlation in the British Isles

1. St David's–Haverfordwest

Cox (e.g. 1916: 283, 1930: 279) stressed the twofold division of the Arenig in Pembrokeshire into a lower arenaceous and an upper argillaceous division. It is now evident (see p. 94) that the arenaceous sediments in this area, as elsewhere, are not coeval, and the succession is therefore more complex than has been supposed.

Moridunian. The Ogof Hên Formation at its type development rests discomfortably upon 'Lingula Flags' (Ogof Velvet Formation of Kokelaar *et al.* 1985). The faunas from the earlier sandy/silty sediments are rich and well known (see Bates 1969), dominated by *Paralenorthis alata* (Sowerby), *Monorthis menapiae* (Davidson), *Merlinia murchisoniae* (Murchison) and *Neseuretus ramseyensis* Hicks, and are broadly equivalent to those of the Bolahaul Member at Carmarthen. The Ogof Hên Formation also crops out along the north side of the St David's anticline near Carnedd-lleithr and Llan-verran, and was formerly exposed near Tremaenhir, NW of Solva (Hicks 1873). Other arenaceous strata in the neighbourhood, formerly equated with the Ramsey Island succession, are now known to be of early Whitlandian age, and belong to the Abercastle Formation (see below). Later Moridunian strata have nowhere been proved in this area, unless the olenid recorded from the Roch borehole (Dr A. W. A. Rushton, verbal communication 1984) is conspecific with one of those from the Carmarthen Formation.

However, it is possible that some of the Arenig sequence exposed between Aber-mawr and Pwllderi on the west side of Pen Caer is of Moridunian age. Cox (1930: 281) described 200 feet of flaggy sandstones and micaceous sandy shales as 'Abercastle and Porth Gain Beds' which are apparently underlain by flags, quartzites and dark shales variously named the Cerrig Gwynion Quartzite, Trwyn Llwyd Quartizite, Aberbach Quartzites, Porth Duggan Flags and Porth Duggan shales. He noted (1930: 280) that they included lithological types peculiar to this region of Pembrokeshire in the Arenig. They occur in three fault-bounded outcrops, and some horizons have yielded *Callograptus* and lingulacean brachiopods, but no diagnostic fauna. Since the Abercastle Formation is of early Whitlandian age, a large proportion of these sediments may, by inference, be of Moridunian age; if they are, it seems that in this area comparatively shallow-water conditions persisted throughout the Moridunian. However, further work is needed before their age and correlation can be placed on a firmer footing.

Whitlandian. Cox (1916) divided the arenaceous sediments underlying the Tetragraptus Shales in the Abereiddi–Abercastle area into the Abercastle Beds below and the Porth Gain Beds above. The Abercastle Beds, a series of cleaved, sandy blue-grey mudstones, are exposed in the cores of anticlines at Abercastle and at Pwll Llong, about 1 km to the west. Nowhere is the base seen. In thin section the rocks show numerous phenocrysts of plagioclase felspar and rounded lava fragments derived from the erosion of a calc-alkaline magma similar to that of the Treffgarne Volcanic Formation. The Porth Gain Beds have a larger outcrop, being exposed at various points along the coast from Porth Egr in the west to Aber Yw, a short distance east of Abercastle. They comprise micaceous sandy mudstones overlain by a coarse felspathic grit. They can be observed to pass upwards into the Tetragraptus Shales near the jetty on the east side of Porth Gain (locality 59). In most outcrops, they are faulted at their base against Lingula Flags, although sandy mudstones like those at Porth Gain can be seen passing down into the Abercastle Beds at Abercastle (Cox 1916: 287). Cox (1916: 288) was of the opinion that these are almost certainly the correlatives of the sediments at Porth Gain, an opinion with which we concur.

We regard this succession as comprising the Abercastle Formation, and consider Cox's Porth Gain Beds to be a member at the top. The presence of *Ogyginus hybridus* (in the past usually referred to '*O. selwynii*') in the lower part of this formation indicates its Whitlandian age and its equivalence to the Blaencediw Formation of the Haverfordwest and Whitland areas; an orthid brachiopod which occurs in the Porth Gain Member at Porth Gain also occurs in the Blaencediw Formation and in the lower part of the Rhyd Henllan Member of the Colomendy Formation at Whitland. Although they have afforded no fossils, the siltstones and sandstones on the northern part of Trwynhwrddyn are lithologically like the Abercastle Formation, with which we here tentatively equate them, rather than with the Ogof Hên Formation as has been the practice in the past. The nature of the junction with the underlying Lingula Flags here is controversial; the presence of a thin conglomerate suggests an unconformable base for the Arenig, although the whole area of the boundary is much disturbed by faulting.

A further arenaceous division, the Brunel Beds, was described by Thomas & Cox (1924) from the Brunel cuttings on the east side of the Treffgarne Gorge. These overlie a succession of extrusive igneous rocks, the Treffgarne Volcanic Formation. At the northern end of the Brunel cuttings the Brunel Beds have yielded a fauna of dendroid and extensiform graptolites. Correlative strata in Triffleton Quarry a short distance to the east have yielded a richer fauna including *Ogyginus hybridus* which shows them to be equivalent to the Blaencediw Formation in which we here include them. Some of the rocks described as Brunel Beds by Williams (1934) from the east end of the St David's anticline may also be equivalent (but see above, under Moridunian). The succession at the southern end of the Brunel cuttings is apparently separated by a fault from those at the northern end, and the lowest sediments seen, at the extreme southern end, are cream-coloured shales lithologically somewhat resembling the Treffgarne Bridge Beds of Upper Cambrian (Merioneth Series) age. They have yielded a fauna of lingulacean brachiopods and occasional bivalves, the latter including *Glyptarca*, a genus not hitherto recognized from pre-Arenig strata and known from the Ogof Hên Formation on Ramsey Island (Dr J. C. W. Cope,

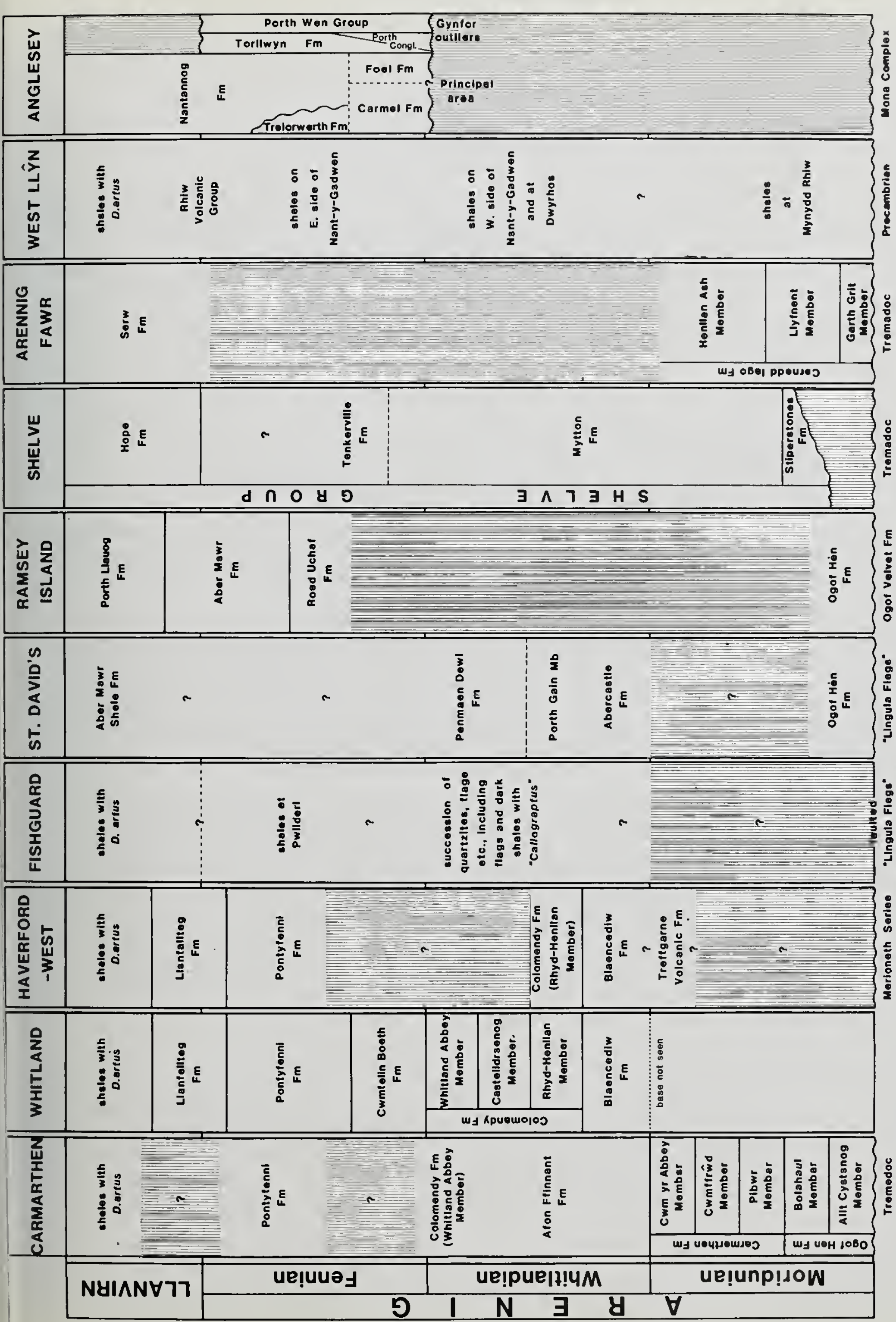


Fig. 10 Correlation of Arenig formations in England and Wales.

personal communication 1984). Their precise age remains equivocal, but has implications for that of the Treffgarne Volcanic Group, which may be of early Arenig or Tremadoc age. Its resemblance to the Tremadoc Rhobell Volcanic Group of Gwynedd favours the latter (Dr R. E. Bevins, personal communication 1984). Rounded lava fragments of Treffgarne type are common in the Blaencediw Formation at Triffleton. Sediments closely resembling the Rhyd Henllan Member of the Colomendy Formation overlie the Blaencediw Formation in the country adjacent to Triffleton Quarry, but have so far yielded no fauna.

The Tetragraptus Shales of the St David's peninsula were named the Penmaen Dewi Shale Formation by Jenkins in an unpublished Ph.D. thesis (University of Cambridge 1979) and by Hughes *et al.* (1982) in an excursion guide. The latter (1982: 54) inferred that the type section was at Pwlluog, Whitesand Bay. However, although they are most fossiliferous there, owing in part to favourable cleavage–bedding relationship, they are in faulted contact with the underlying (presumed) Abercastle Formation; this circumstance renders it an unsuitable section in which to define the base. We here define the base of the formation (whose name we here shorten to Penmaen Dewi) at the jetty on the east side of Porth Gain (loc. 59), where its passage downwards into the underlying Porth Gain Member of the Abercastle Formation is well exposed. The only richly fossiliferous section is at Pwlluog. Beds near the base, in Hicks' (1875) 'Lower Arenig', have yielded *Bergamia*? sp., *O.* cf. *hybridus*, an orthid brachiopod and dendroid graptolites, suggesting that this horizon is not far above the Abercastle Formation. Higher horizons, as for example at the north end of the section (Hicks' (1875) 'Middle Arenig'), have afforded *Gymnostomix gibbsii*, *Furcalithus sedgwicki*, *Bohemopyge scutatrix*, *Cyclopyge grandis grandis*, *Cnemidopyge salteri* and *Shumardia gadwensis*, the richest known assemblage of the *G. gibbsii* Biozone in south Wales. These faunas clearly show that the Penmaen Dewi Formation is equivalent to the Colomendy Formation at Whitland and most of the Afon Ffinnant Formation (see below) at Carmarthen.

Fennian. Because they tend to be well cleaved, most of the higher beds of the Penmaen Dewi Formation on the mainland have yielded no fossils, and their assumed Fennian age cannot be proved, only inferred on the assumption that the succession is complete. At Pwllderi, Pen Caer, shales lithologically like the Pontyfenni Formation are said to have yielded extensiform didymograptids (Cox 1930: 284), although we have not seen any material, and failed to collect any further. Similar shales in the Spittal district, Haverfordwest, are badly cleaved, and have yielded no diagnostic fauna.

On Ramsey Island, the Road Uchaf Formation (Kokelaar *et al.* 1985) has yielded a rich early Fennian graptolite fauna including *Isograptus caduceus* (Salter) sspp., *Pseudisograptus stellus* (Hopkinson) and numerous dendroids at Road Uchaf (Jenkins 1982), whilst the Arenig part of the overlying Aber Mawr Formation (of Kokelaar *et al.* 1985, not of Hughes *et al.* 1982), the pencil slates at Aber Mawr, lithologically like the Pontyfenni Formation, have yielded abundant extensiform didymograptids, *Degamella evansi* and *Ormathops nicholsoni*, indicative of the *Bergamia rushtoni* Biozone. Attenuated equivalents of the Arenig part of the Llanfallteg Formation have yielded no fossils on Ramsey Island (Aber Mawr), and nor have the equivalent strata on the mainland.

2. The Carmarthen area

The lower, more arenaceous part of the Bolahaul Member of the Ogof Hên Formation contains the earliest Moridunian fauna in the area, and with *Merlinia murchisoniae*, *Neseuretus ramseyensis* and *Paralenorthis alata* compares closely with the Ogof Hên fauna from Ramsey Island. The higher, more muddy part of the member has *M. murchisoniae*, *Neseuretus murchisoni* and *Ampyx cetsarum*, but very few articulate brachiopods. The succeeding Pibwr Member of the Carmarthen Formation is dominated by *Merlinia selwynii*, with rare *A. cetsarum*, *M. murchisoniae*, *Myttonia* cf. *fearnsidesi* and *Pseudophyllograptus* spp. These faunas are closely matched in the Henllan Ash (see below). The remainder of the Carmarthen Formation has a characteristic olenid fauna, not yet identified elsewhere. The Carmarthen Formation is conformably overlain by a thick sequence of alternating shales and turbidites comprising what we here name the Afon Ffinnant Formation. The base is defined at the base of the first turbidite below the bridge in Cwm yr Abbey (SN 5002 1983). The lowest beds are of Moridunian age, but the bulk of the formation belongs to the Whitlandian (*Furcalithus radix* and *Gymnostomix gibbsii* Biozones). *Ogyginus hybridus* occurs throughout, accompanied by *F. radix* at the base and by *G. gibbsii* for most of the rest of the sequence. The turbidites contain polydeformed clasts of Precambrian quartz and schist, indicating erosion of a Precambrian basement, presumably to the south. Probable higher Whitlandian strata with *Bohemopyge scutatrix* occur in Capel-Dewi stream (Survey locality Carm. 40NW Wλ7) in a fault-bounded outcrop. These Whitlandian faunas correspond closely with those of the Colomendy and Penmaen Dewi formations further west. Fennian faunas which include *Ormathops nicholsoni*, *Illaenopsis harrisoni* and *Pricyclopyge binodosa eurycephala* have also been recorded from Capel-Dewi stream, and evidently broadly correspond with the Pontyfenni Formation, and the presence of *Asaphellus whittardi* near the old adit (locality 20E) suggests early Fennian, by analogy with its occurrence in the Whitland district. Elsewhere in the Carmarthen district, proved Fennian strata occur only in isolated exposures in the neighbourhood of Bancyfelin (e.g. locality 21).

3. North Wales

The stratigraphy and graptolite fauna of the type Arenig area has been recently revised by Zalasiewicz (1984*a*), who employed Lynas' (1973) nomenclature from the neighbouring Migneint. He recognized three successive graptolite faunas, a lower one in the Llyfnant Member characterized by *Didymograptus* aff. *simulans*, a middle one in the Henllan Ash Member with *Azygograptus* cf. *eivionicus* and an upper one from the top of the Henllan Ash with *Didymograptus* cf. *praenuntius* and *Tetragraptus reclinatus*. He noted that these faunas offered no firm correlation with any of the *deflexus*, *nitidus* or *gibberulus* Biozones, but showed that there was no clear evidence for the *hirundo* Biozone, as previously claimed (e.g. by Fearnsides (1905), Lynas (1973)). Whittington (1966) described the limited trilobite fauna of the Henllan Ash; of this, *Merlinia murchisoniae*, *Neseuretus murchisoni* and *Ampyx cetsarum* occur also in the higher part of the Bolahaul Member in south Wales, whilst *M. murchisoniae* and *A. cetsarum* are common to the Pibwr Member. These indicate a Moridunian age for the Henllan Ash, and it is likely that most, if not all, of the Whitlandian and Fennian are absent from the type area.

Work in progress by A. Beckly has proved the presence of all three Arenig stages in the western Llŷn (Fig. 10, p. 95), and much of the Arenig is probably also present in the Bangor–Caernarfon area; Elles (1904) described the Afon Seiont sequence which apparently has representatives of the *gibberulus* and *hirundo* Biozones, and Jenkins (1982) demonstrated the presence of the *gibberulus* Biozone on the Menai Strait. Correlation of the largely arenaceous sequence on Anglesey (Bates 1972) with the rest of the Welsh Arenig is equivocal. Williams (1974: 12) noted the common occurrence of *Paralenorthis proava* in the Carmel Formation and the Henllan Ash, but Dr M. G. Bassett has examined specimens from the latter in the collections in the National Museum of Wales and considers them to be closer to *P. alata*, and not to belong to *P. proava*. This means that there are no species in common, for the trilobites, *Neseuretus monensis*, *Ogyginus*? sp. (*Ogygiocaris selwynii* of Bates 1968*a*), *Ampyx* sp. and *Annamitella* (= *Monella*) *perplexa* are all endemic. A 'late Arenig' age was implied for the succeeding Treiorwerth Formation by analogy of its brachiopod fauna with that of the Summerford Group, Newfoundland (Neuman & Bates 1978: 577). Assuming this to approximate to the Fennian, the Carmel Formation may by implication be Whitlandian, or could fall also within the Fennian. In the adjacent Bangor area Beckly has found new asaphid and *Neseuretus* species in arenaceous deposits underlying shales with *Azygograptus eivionicus*, which are of Whitlandian age. It seems that shallow-water onshore conditions prevailed in much of the Whitlandian and Fennian in the Bangor–Anglesey area, although the offshore mudstones with isograptids on the Menai Strait of *gibberulus* Biozone age suggests that the pattern is more complex, and is likely also to involve structural factors.

4. Shelve

Before our work in south Wales, the richest known Arenig shelly faunas from England and Wales originated from the Mytton and Tankerville Flags, and the trilobites, brachiopods and graptolites have been described by Whittard (1955–67), Williams (1974) and Strachan (1986) respectively. The basal transgressive Stiperstones Quartzite has yielded only *Neseuretus grandior*, which we consider to be a synonym of *N. ramseyensis* which occurs in the Ogof Hên Formation; this being the case, the two formations would appear to be approximately coeval. The lowest third of the Mytton Flags contains trinucleids, asaphids and calymenids. The two former are represented by endemic species, although related species of the same genera occur in the Henllan Ash and Ogof Hên and lower Carmarthen formations. Of the calymenids, *Neseuretus parvifrons* occurs also in the Henllan Ash, whilst *N. murchisoni* is common to that formation and the upper part of the Bolahaul Member in the Carmarthen district, which implies that this part of the Mytton Flags equates with the Moridunian. The presence of *Cyclopyge grandis grandis* about 300 m above the base of the Mytton Flags suggests a Whitlandian or early Fennian age, although the characteristic Whitlandian asaphid and trinucleid species are absent. The diverse trinucleid fauna from the top third of the Mytton Flags has no counterpart in Wales, but occurring as it does above the level with *C. grandis grandis* must be either late Whitlandian or early Fennian in age. The apparent presence of *N. parvifrons* with this fauna suggests that this species persisted longer at Shelve, perhaps because rather shallow water conditions continued. The fauna of the Tankerville Flags and Shelve Church Beds includes the trilobites *Asaphellus whittardi*, *Placoparia cambriensis*, *Pricyclopyge binodosa* and *Selenopeltis buchi macrophthalma* and the graptolite *Didymograptus* (*Expansograptus*) *hirundo*, which occur in the Fennian in south Wales. There is no indication at Shelve of the late Fennian fauna found in the Llanfallteg Formation; this fauna and its containing sediments apparently represent a regressive phase (see also p. 105), and the on-shelf position of the Shelve inlier might mean that it did not reach this area. It is likely, therefore, that the latest Arenig is absent from Shelve, and it is possible that there are also gaps within the Mytton Flags sequence, as might be expected in a relatively onshore shallow-water succession.

5. The Lake District

The Skiddaw Group, a series of flaggy sandstones, silty mudstones and slates, is generally rather poorly fossiliferous. The supposed Tremadoc age of certain beds at Barf has long been discounted (Molyneux & Rushton 1985: 123), but definitive late Tremadoc trilobites and acritarchs have recently been found in the River Calder section at the western edge of the outcrop. A late Lancefieldian graptolite fauna identified from the area north of Skiddaw (Rushton 1985*b*) suggests that it might be possible to find a continuous Tremadoc–Arenig passage in the Skiddaw Slates, but despite past claims to the contrary, *T. approximatus* has not been found (Stone & Rushton 1983). The Hope Beck Slates, hitherto thought unfossiliferous, have recently yielded *Didymograptus* cf. *vacillans* Tullberg (Molyneux & Rushton 1985), indicative of the *deflexus* Biozone, which is also the age of the succeeding lower part of the Loweswater Flags; the upper Loweswater Flags contain a *nitidus* Biozone fauna. The Hope Beck Slates and Loweswater Flags thus broadly equate with the Moridunian and Whitlandian stages, but have not afforded any of the characteristic trilobites. The report of '*Trinucleus gibbsii*' from the Ullswater inlier cannot be substantiated, firstly because the specimen(s) was apparently mislaid (Postlethwaite & Goodchild 1886: 468), and secondly because only the Llanvirn is represented there. Most, if not all, of the trilobites from the Skiddaw Slates appear to have originated from the *gibberulus* and *hirundo* Biozones, well represented in the Kirk Stile Slates. Here there occur cyclopygids and members of the Fennian atheloptic fauna (e.g. *Ormathops nicholsoni*, *Illaenopsis harrisoni* and *Selenopeltis*), also found in the Pontyfenni Formation in south Wales. It seems likely that offshore conditions persisted throughout much of the Arenig in the Lake District, and the rich isograptid fauna (Jenkins 1982) of the Kirk Stile Slates, a sure indicator of more oceanic conditions, occurs only in the Road Uchaf Formation, Ramsey Island in south Wales. The top of the Skiddaw Slate Group (or Eycott Group of Wadge, 1978) is of Llanvirn age, and the *artus* and *murchisoni* Biozones are present (Jackson 1978). Whether there is a continuous Arenig–Llanvirn passage is not yet known.

International correlation

The faunas of the Arenig Series in Wales are dominated by endemic forms, and international correlation is correspondingly difficult (Fortey *in* Whittington *et al.* 1984). Assuming that the position of Wales at the edge of an early Ordovician Gondwanan continent is correct, there are virtually no other known faunas occupying a similar palaeogeographical position with which a direct comparison is possible. The Welsh Arenig is in this sense unique: most of the comparable faunas are known from younger rocks in England or Bohemia; a number of the brachiopods are known from 'island' faunas, the stratigraphical positions of which are themselves in dispute. Almost all the trilobite genera are making their earliest appearance in the Welsh Arenig, but a few (e.g. *Microparia*, *Ormathops*) are known from even earlier occurrences in the Montagne Noire, southern France. Correlation is based on a few more widespread species, and the inferences are particularly indirect for the earlier part of the Series. In general, though, it is apparent that our complete biostratigraphical sequence shows that the type Arenig is comparable in development with other fully developed sequences of Arenig age in Scandinavia, Spitsbergen and the western United States.

Moridunian

The base of the Moridunian Stage (not yet formally defined) is also the base of the Arenig Series; its international correlation is difficult. The Moridunian of south Wales (Fortey & Owens 1978) includes a trilobite fauna with species endemic to Wales, and the occurrence in the Carmarthen Formation of *Pseudophyllograptus densus*, a long-ranging species in Scandinavia, is not diagnostic. The faunas from the Henllan Ash in the type area of Arennig Fawr (Whittington 1966, Zalasiewicz 1984*a*) are the same endemic suite as the Moridunian of south Wales, and the graptolites recorded by Zalasiewicz (1984*a*, *b*) are not stratigraphically unequivocal. Correlation of the early Moridunian in north Wales with the *deflexus* Biozone of the Lake District is based on the presence at Arennig Fawr of a didymograptid of *deflexus* type (Zalasiewicz 1984*a*), a typical morphology for that horizon in the Lake District (Jackson 1962), but since on a world scale graptolites of the same general type have a long range through the Arenig (Cooper & Fortey 1982) this is not entirely satisfactory. The earliest described Arenig graptolite fauna from the Lake District (Jackson 1979, who states it is 'slightly older than the *deflexus*' Biozone) may correlate with the *T. approximatus* Biozone of Scandinavia, because Jackson (1979: 29) records a distinctive species otherwise only known from that horizon in Scandinavia. Rushton (1985*b*) has recently described a late Lancefieldian graptolite from below, and in stratigraphical continuity with, Jackson's fauna, and so the evidence for a complete Tremadoc to early Arenig sequence in the Lake District appears to be increasing, notwithstanding that earlier reports of *T. approximatus* itself from the Lake District are unconfirmed or erroneous (Stone & Rushton 1983). In Sweden, *T. approximatus* occurs within the *phyllograptoides* Biozone, low in the Hunneberg Series (Törnquist 1904: 6); the base of the Moridunian may, therefore, eventually prove to equate with the base of the Hunnebergian if the former is defined within the Lake District sequence.

It is usually stated that equivalents of the *T. approximatus* Biozone are missing from Wales (Skevington 1969). The *T. approximatus* fauna is widespread in the 'Pacific' graptolite province, and has been suggested as a widely correlatable base for the Arenig Series (Skevington 1963, 1968). However, the possibility cannot be excluded that equivalents of at least part of the *T. approximatus* Biozone are present in the basal Arenig in Wales; the described graptolites are not sufficiently diagnostic to disprove this (Zalasiewicz 1984*a*). In addition, we note:

1. Faunas with *Merlinia selwynii* are underlain in south Wales by the Ogof Hên Formation with *M. murchisoniae*. It is accordingly possible that these basal beds are referable to an earlier stratigraphical horizon, and hence possibly as early as the range Biozone of *T. approximatus*.

2. Although there was a regression at the end of the Tremadoc, and the Arenig is transgressive at its base, there is little physical evidence for a break in the Arennig Fawr area (although

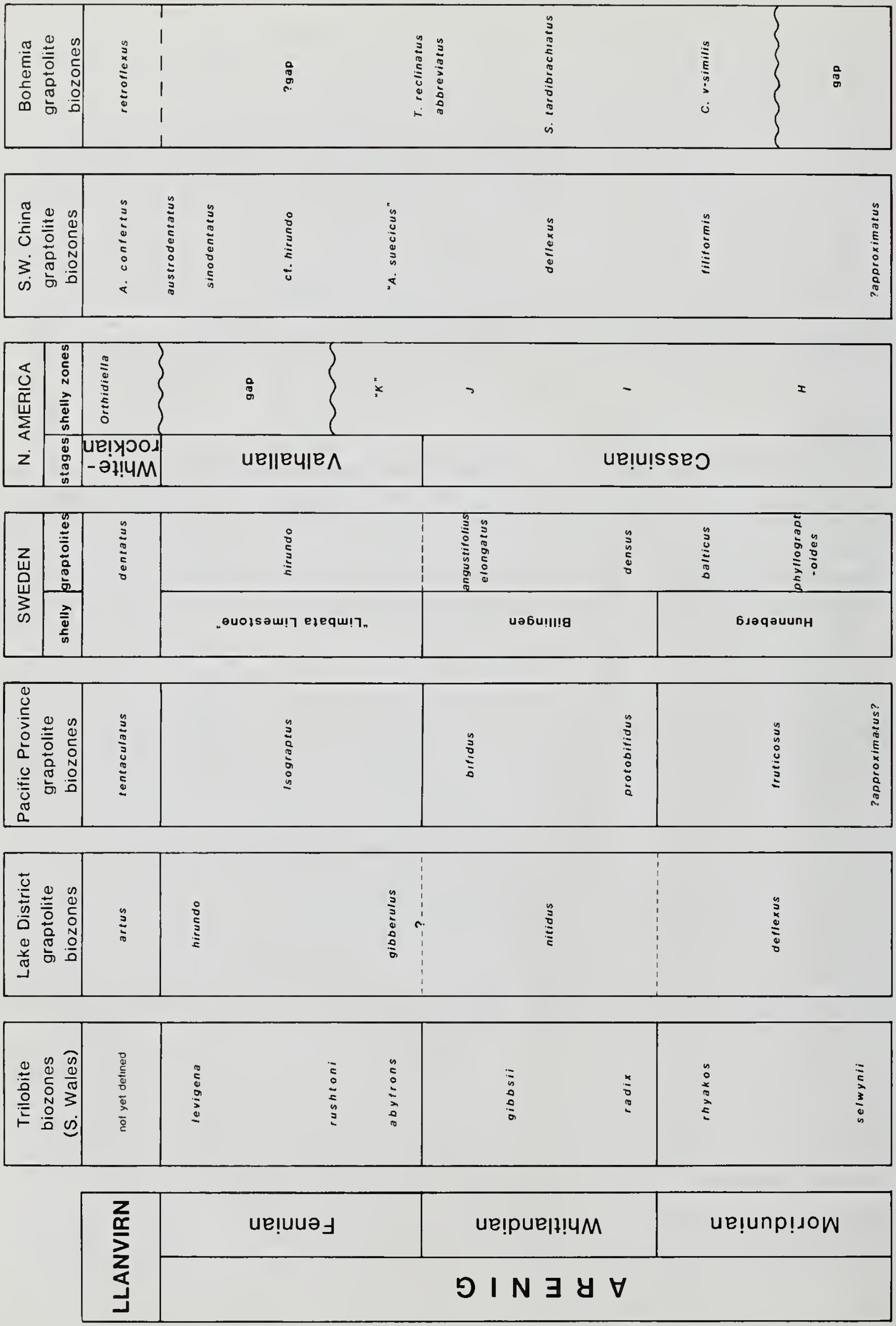


Fig. 11 International correlation of the type Arenig.

elsewhere in north and south Wales it is an unconformity), the boundary between the Tremadoc and Arenig being marked only by a thin, sandy seam.

3. The distribution of the *T. approximatus* plexus of species with H-shaped rhabdosomes may have been related to palaeolatitude and bathymetry. Its known stations are from sites which have been described as lying near the palaeoequator or at temperate latitudes in the earlier Ordovician: North America (Quebec, Newfoundland, Idaho, Nevada, British Columbia, Yukon, etc.), Australia, New Zealand, arctic Siberia, eastern China, cordilleran Argentina, Scotland and Scandinavia. It is possible that the *approximatus* group failed to penetrate very high latitudes near the Ordovician pole, and particularly more inshore facies, and this might explain its absence from the English Lake District, Bohemia, France, and other areas in boreal Gondwana. If this is the case its absence may be related to palaeolatitude and water temperature.

The higher part of the Moridunian (Biozone of *M. rhyakos*) presumably correlates approximately with some or all of the higher part of the Bendigonian Stage of Australia, and possibly with the *T. fruticosus* Biozone of North America (Cooper & Fortey 1982: fig. 2), but detailed correlation is impossible without graptolitic evidence.

Whitlandian

There is little evidence bearing on the international correlation of the Whitlandian, other than its intermediate position between the Moridunian and Fennian. It is broadly the equivalent of the *D. nitidus* Biozone of the Lake District. None of its characteristic trilobite fauna has been recorded outside Wales, although it is widespread and in places abundant there. Once again this is probably the result of the unique development of biofacies in Wales at this time, because some of the characteristic forms (*Ogyginus*, *Cnemidopyge*, *Cyclopyge*) are more widespread in the Llanvirn or later. Nor do the small numbers of graptolites so far recovered help much, because *Azygograptus hicksii* is unknown outside Wales, *Tetragraptus serra* has a long range, and *D.* (*Expansograptus*) *goldschmidti*, *sensu* Kraft is otherwise only known from the Klabava Formation of Bohemia. Based on the faunas below and above, we may suggest a general correlation with the Chewtonian (and probably early Castlemanian Ca1) of the Australian sequence, and the *D.* '*protobifidus*' and *D. bifidus* Biozones of North America, (?all) Billingenian of Sweden, and 'Middle Arenig' in the usage of Cooper & Fortey (1982: 168).

Fennian

The correlation of the later Arenig is somewhat easier than in the case of the Moridunian or Whitlandian because of the occurrence of more widespread, and stratigraphically reliable, graptolite species; it includes the equivalents of the *I. gibberulus* and *D. hirundo* Biozones. Isograptid species from Wales (Jenkins 1982) are all from Fennian localities; based on the work of Cooper (1973), these isograptids are the basis of correlation with the upper Castlemainian (Ca3) to Yapeenian of the Australian sequence, the *Isograptus* Biozone of North America (Berry 1960), and the 'upper Arenig' of the Pacific Province in general (Cooper & Fortey 1982: 168). Other graptolites confirm this. For example, *Pseudotrigonograptus* (quadriserial) has been recovered from the Pontyfenni Formation, and is known in many localities (Australia, New Zealand, U.S.A., Spitsbergen, Tamir, SE China) from Castlemainian (Ca2–3) and Yapeenian. So the general correlation of the Fennian is not in doubt. What is more difficult is the precise correlation of its limits, and of the biozones within it. Because the *D. levigena* and *B. rushtoni* trilobite biozones equate with all of the *hirundo* and at least part of the *gibberulus* graptolite biozones (see above), it is assumed that the early Fennian is the equivalent of the earliest part of the *Isograptus* Biozone with *I. victoriae victoriae* (Ca2 of the Australian sequence), and that the boundary between the Whitlandian and Fennian approximates to that between the informally-named 'Middle' and 'Upper' Arenig of the Pacific graptolite province (Cooper & Fortey 1982). This provisional conclusion may have to be modified when more graptolites are discovered.

The appearance of Llanvirn pendent didymograptids stratigraphically shortly after the appearance of true (diplograptid) biserials in the latest Arenig appears to be a widespread phenomenon; it happens in Scandinavia (Skevington 1965) and SE China (Mu *et al.* 1979), and so far as can be judged from the other graptolite species the appearance of these pendent didymograptids is coeval.

Bohemia

Bouček (1973), and, in several papers, Kraft (1971, 1972, 1973, 1974) have discussed the graptolites and correlation of the Arenig of Bohemia. The Klabava Formation there is divided into several biozones; the oldest of these, the *v-similis* Biozone, was correlated by Bouček with the *balticus* Biozone of Scandinavia and the *deflexus* Biozone of the Lake District. The grounds for this are obscure, other than the occurrence of numerous deflexed graptolites at this horizon. The species listed by Bouček (1973: 138) are *D.* (*Corymbograptus*) *v-similis*, *D.* (*C.*) *uniformis* and *D.* (*Expansograptus*) *densus*. Of these, the first and last named are so far endemic to Bohemia; *D. uniformis* is known otherwise from the Lake District, from the *D. nitidus* or *I. gibberulus* Biozones. We have identified *D. goldschmidti*, *sensu* Kraft 1977, from the Whitlandian and earliest Fennian in south Wales. What evidence there is from specific comparisons tends to suggest that the early part of the Klabava Formation is mid- to early late Arenig in our usage. The trilobites from the middle to upper part of the Klabava Formation ('Euloma Shales') include *Microparia broeggeri* and an *Illaenopsis*, which compare with the fauna from the Pontyfenni Formation in south Wales of late Arenig age. Bouček's youngest graptolite biozone (*T. reclinatus abbreviatus* Biozone) includes further endemic graptolites, but also '*Phyllograptus*' (presumably *Pseudophyllograptus*) *angustifolius*, *Azygograptus suecicus*, and *Tetragraptus pseudobigsbyi*, all of late Arenig age elsewhere. Bouček also mentions an unchanging dendroid fauna running throughout the Bohemian succession. It seems to us probable that the Arenig succession in Bohemia is incomplete.

Synoptic history of the Arenig in south Wales

The regression at the end of the Tremadoc brought shallow-water *Neseuretus* facies across the entire south Welsh region. Whether or not there was an unconformity on the Tremadoc beneath is not yet certain, but it is certain that a previously accepted view of uplift during Tremadoc times is incorrect, because rich Tremadoc faunas are present in the Llangynog area (Owens *et al.* 1982), and these are of a more oceanic character than those of Shropshire. The Tremadoc history further to the west will depend on a reassessment of the age of the so-called 'Lingula Flags' there. The subsequent transgression during the Moridunian was gradual, recorded in two upward-deepening successions at Carmarthen and St David's, in which flaser-bedded silts and sands with numerous trace fossils grade upwards into mudstones (Bates 1969, Fortey & Owens 1978). Locally, as at Llangynog, Precambrian rhyolitic islands were onlapped during the transgressive phase, and the fringing seas afforded suitable habitats for bivalves and echinoderms (Paul & Cope 1982) as well as more widespread trilobites and brachiopods. Basal beds in these areas may include coarse rhyolite-pebble conglomerates. The transgression proceeded from west to east, because it is probable that the earliest part of the Moridunian is absent in Shropshire. The shallow-water and presumably diachronous *Neseuretus* facies was succeeded by the raphiophorid biofacies (Fortey & Owens 1978) representing soft, muddy sea floor conditions which supported great numbers of *Merlinia selwynii*, rarer *Ampyx cetsarum*, and infaunal bivalves, but little else. Rocks deposited in this environment were thick and widespread around Carmarthen, but their westward equivalents are probably much thinner shales. Open ocean connections were sufficient for the appearance of a few graptolites (*Pseudophyllograptus*) at this time at one horizon, but a fully oceanic suite of species is not yet known.

In the later Moridunian a positive fault-bounded block (or blocks) was becoming established in the Haverfordwest area. This may have contributed to turbidites in the Carmarthen area.

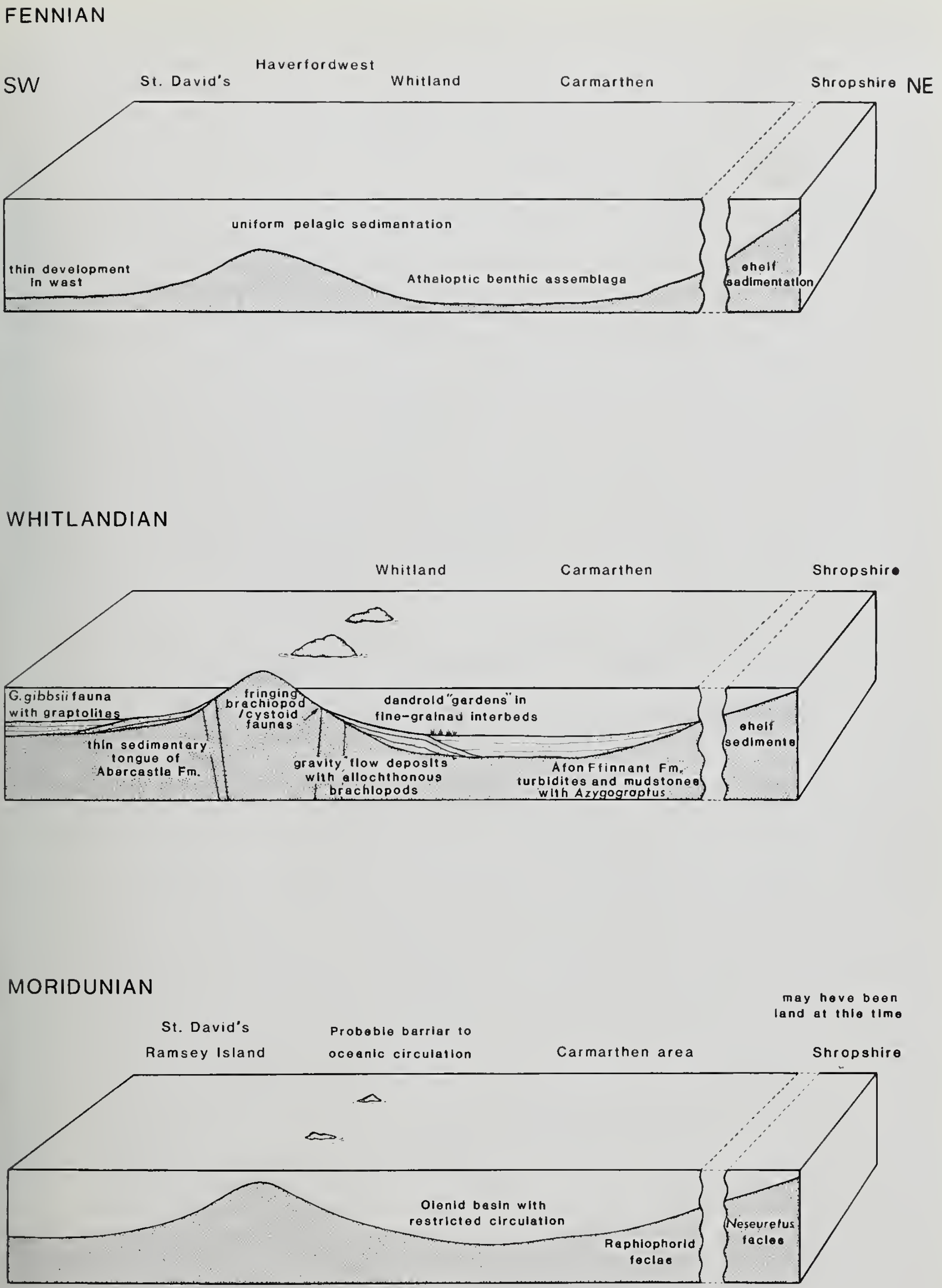


Fig. 12 East–west profiles from Shropshire across south Wales, to summarize distribution of sedimentary environments and associated faunas for the three stages of the Arenig.

The effect of this seaward barrier combined with the continuing transgression was to produce a stagnant basin with restricted oceanic circulation in the Carmarthen region. The low bottom-water oxygenation was well suited to the olenid trilobites (olenid biofacies), which gradually become the dominant element of the faunas in the upper part of the Carmarthen Formation (Cwmffrwd and Cwm yr Abbey Members). The westward equivalents of these deposits are not certainly identified. It is clear that the area of thick sediment fill lay to the east, and this may have been associated with an extensional basin.

The early Whitlandian is a dominantly clastic facies with fine silts, and volcaniclastic rocks including fragments much like the Treffgarne volcanics, forming a distinctive lithofacies extending from Abercastle on the coast to an area north of Haverfordwest. Similar rocks in the Whitland district contain clasts of Precambrian rhyolites and quartz. 'Island' faunas were extensively developed, with a rich fauna of articulate and inarticulate brachiopods, together with cystoids in the shallower sites, often now found as allochthonous material in mass flow deposits and turbidites which comprise the thick sequence of the Blaencediw Formation north of Whitland. The early Whitlandian marks the end of the restricted olenid basin in the east, with the complete disappearance of the characteristic trilobite family within a few metres of the base. During the Whitlandian, conditions suitable for flourishing 'gardens' of dendroid graptolites were widespread: they appear within the well-laminated siltstones separating allochthonous brachiopod-rich beds in the Haverfordwest area, at Blaeweneirch near Whitland, and at St David's; the last two localities furnished many of the specimens monographed by Bulman (1927–34). The eastward equivalents of the Blaencediw Formation are to be found in the Afon Ffinnant Formation—a thick sequence of turbidites and interbedded shales. Again, the main sediment fill appears to have been in the Carmarthen–Whitland area rather than to the west, where evidence of turbidites is confined to fine distal turbiditic horizons usually on the scale of a few mm, forming light-coloured stripes within the Penmaen Dewi Formation. The characteristic trilobite fauna with *Ogyginus*, *Bohemopyge*, *Shumardia gadwensis*, *Furcalithus sedgwicki* and *Gymnostomix gibbsii* spreads across all south Wales during the Whitlandian, but is nowhere abundant. Cyclopygids, especially *Cyclopyge grandis grandis*, appear in numbers for the first time in the south Welsh Arenig, and graptoloids, *Azygograptus*, *Expansograptus* and *Tetragraptus*, are locally numerous—the first suggestion of a more 'oceanic' character in the faunas.

The late Arenig, Fennian Stage, begins with a local turbiditic interval in the Whitland area (Cwmfelin Boeth Formation), which yields the youngest of the three faunas of articulate brachiopods (here allochthonous) in south Wales. Its equivalents to east and west have not been identified. But the succeeding Pontyfenni Formation represents the most uniform, and most oceanic, conditions over the whole area. Dark mudstones with siliceous nodules are characteristic, and this lithofacies with its accompanying fauna outcrops from east of Carmarthen to the extreme west of the area on Ramsey Island. The trilobite fauna is distinctive, a combination of large-eyed pelagic species dominated by the Cyclopygidae, with blind, or nearly blind, benthic forms which we have termed (p. 106) the atheloptic assemblage. We believe that this formation accumulated beneath a water depth of at least 200 m and probably more. Its oceanic character is indicated also by the occurrence of cosmopolitan graptolites of the genera *Pseudotrigonograptus* and *Isograptus* (Jenkins 1982) which do not penetrate into shallower shelf seas (Fortey 1984). The trilobite fauna is rich in species but sparse in numbers of individuals, although some compensation for this is the high proportion of articulated specimens, often moulted arrangements of parts, which attests to the quiet sea-floor conditions that pertained during the Fennian. Trilobites are accompanied by a varied fauna of carpoid chordates, including the genera *Cothurnocystis*, *Balanocystites*, *Anatifopsis*, *Guichenocarpos*, *Reticulocarpos* and *Lagynocystis* (see R. P. S. Jefferies herein, p. 285), many hyolithids, and rare, soft-bodied coelenterates. This peculiar facies has its earlier counterpart in the lower Arenig of the Montagne Noire, and appears in the Llanvirn of Bohemia and Shropshire, then (Fortey 1984) attaining a wider spread later in the Ordovician with the Llandeilo–Caradoc transgression. The Pontyfenni Formation is its only known occurrence in the late Arenig. Several of its characteristic species have been found also in the Lake District.

Upward passage into the Llanfallteg Formation is marked by a lithological change to grey-coloured, very soft and fissile shales, and with this change the atheloptic trilobite assemblage disappears, although the Cyclopygidae do not. We attribute the faunal change to a worldwide regression at the end of the Arenig, which reduced sea level enough to permit the establishment of a trilobite fauna including species with normally-developed eyes, of which *Barrandia* is the most numerous. There is no change in lithology, and no drastic faunal change, across the Arenig–Llanvirn boundary, which is best exposed along the Llanfallteg railway cutting. Pendent didymograptids do appear suddenly, however, and this is the criterion for recognition of the boundary, together with the first appearances of a few trilobite species. The Llanfallteg Formation is also widely developed, from east of Carmarthen to Aber Mawr on Ramsey Island. As usual, it is thinner to the west. Volcanic activity was prevalent in the early Llanvirn, as at Fishguard, and volcanogenic sediments may partly account for the lithological change near the Arenig–Llanvirn boundary. Shortly above our studied sections there are numerous tuffaceous ‘chinastone’ horizons. The ensuing Llanvirn transgression is accompanied by a reversion to deep-water sedimentation, with black shales, mudstones and turbidites which once more comprise the dominant lithology from Carmarthen to the coast.

In summary, the Arenig Series in south Wales records an upward-deepening and then ultimately regressive sequence much complicated by local uplift and turbidite emplacement. It includes the best-developed deeper water fauna on the edge of the Gondwanan continent at this time, in a marginal but ensialic basin. Sedimentation is particularly thick and complete in the Carmarthen–Whitland area, thinner near the coast. Although the east–west transect is now described, little is known about what happens to the north, where the stratigraphy of the Sealyham Group and the shales of the Maenclochog area have yet to provide the fossils crucial to unravelling the stratigraphy.

The cyclopygid biofacies and atheloptic trilobite assemblage

The Arenig of south Wales includes the earliest known development of the cyclopygid biofacies. The Cyclopygidae were a group of trilobites with hypertrophied eyes, wide axial development, and other morphological features consistent with a pelagic mode of life (Fortey 1974, 1985*b*). They were not, however, epipelagic like their homoeomorphs *Carolinites* and *Opipeuter*, both of which penetrated into inshore sediments in the earlier Ordovician around the palaeoequator. Cyclopygids are rare or absent in inshore facies, for example, the *Neseuretus* biofacies in the early Ordovician (Fortey & Morris 1982). This is shown by their rarity in the Mytton Flags in Shropshire compared with the contemporary rocks in south Wales. Diverse and numerous cyclopygids are associated with peripheral continental sites with free access to the open ocean. For the Arenig around Ordovician Gondwana the appropriate sites are really only described on its eastern margin in south and north Wales and the Lake District. There is also some evidence of a like development on the opposite side of Törnquist's Ocean (Tjernvik 1956, Cocks & Fortey 1982) where the cyclopygid biofacies is developed on Bornholm, and encountered in boreholes off the southern edge of the Scandinavian platform; it may be present this early at the eastern edge of Kazakhstania (Apollonov 1975). By the Llanvirn there was a general shoreward onstep of exterior biofacies accompanying the Llanvirn transgression, and this introduced the cyclopygid biofacies into Bohemia (Šárka Formation), Thuringia (Richter & Richter 1954), Bulgaria (Spassow 1958) and the Hope Shales, Shropshire (Whittard 1961*a*).

The cyclopygids were probably mesopelagic (Fortey 1985*b*; see also p. 180), occupying the depth zone of about 200–700 m and living about the upper part of the continental slope and within deep marginal basins with free access to the open ocean. They constituted a natural community, but one which was unrelated to the sea bottom conditions where the sediments in which they are found were accumulating. They can be found with more than one assemblage of benthic genera; this is shown in south Wales by the different associations with which they are found in the Pontyfenni Formation (with blind or small-eyed species) and in the Llanfallteg Formation (with normal-eyed trilobites including *Barrandia* and *Ectillaenus*). For this reason it is difficult to apply the term 'community' to the total assemblage, including the cyclopygids, as it is recovered in the field. We refer to the faunal associations in which cyclopygids are a dominant element by the broad term 'cyclopygid biofacies', recognizing that this includes a blend of the pelagic with the benthic elements, and as such is a superimposition of more than one community in the strict sense. It is important to emphasize that the recognition of the cyclopygid biofacies depends on the family being an important fraction of the total trilobite fauna—30% or more, as in the Pontyfenni Formation. The recovery of a single specimen in a large non-cyclopygid fauna does no more than suggest that it may be worthwhile searching for the cyclopygid biofacies in adjacent areas.

As well as the cyclopygids, the pelagic fauna certainly included the peculiar trilobite *Bohemilla*—a genus also making its first known appearance with the cyclopygid biofacies in south Wales—and the enigmatic *Girvanopyge* (= *Cremastoglottos*). The odontopleurid *Selenopeltis* is more difficult to interpret. It is found with the cyclopygid biofacies, but also extends (Bruton & Henry 1978) into areas in France and Spain where cyclopygids are rare or unknown. Nowhere is it common. It has large eyes, but otherwise its morphology is unlike that of a typical pelagic trilobite, being relatively broad and with a narrow axis. Its wide tolerance of facies changes might suggest that it alone was epipelagic or epiplanktonic, the alternative being that it was nektobenthic with a wide range of tolerance. It is interesting that Whittington & Hughes (1972) used *Selenopeltis* as an 'index fossil' of the high latitude *Selenopeltis* province, and if the animal indeed had epipelagic habits one would expect it to be a good indicator of temperature (and hence broadly latitudinal) constraints.

There is an interesting association, particularly in the Fennian, of the mesopelagic trilobite fauna with a benthic fauna of blind or nearly blind trilobites. These include *Ormathops nicholsoni, Illaenopsis harrisoni, Dindymene saron, Colpocoryphe taylorum, Ampyx linleyoides* and *Bergamia rushtoni*. This is evidently different from what Fortey & Owens (1978) termed the raphiophorid community, in which normal-eyed asaphids predominate, and which replaces the *Neseuretus* fauna in deepening-upward sequences. Equally it is distinct from the olenid biofacies—not one olenid has been found above the Whitlandian. If the olenid biofacies is a response to low oxygen tension (and relatively deep water) to which the olenids were specifically adapted, then this other benthic association is different. In support of normal oxygenation is the fact that the small-eyed fauna is associated with other benthic organisms—bivalves, carpoid chordates and hyolithids—none of which occurs in the Carmarthen Formation with the olenids. The associated lithologies are dark mudstones with siliceous nodules, and a similar lithology is also associated with Llanvirn occurrences of the cyclopygid biofacies. More than half the trilobites recovered are more or less articulated, often in moult arrangements, which testifies to relatively quiet bottom conditions. Certain beds show much evidence of burrowing by soft-bodied animals, and we presume that the sea bottom was an unconsolidated mud. We term this distinctive type of benthic trilobite association the **atheloptic** (Gr. 'shrunken-eyed') assemblage. It probably represents a genuine community, but without further documentation of its occurrence elsewhere we prefer the noncommital term 'assemblage' for the moment.

The depth at which the atheloptic assemblage lived can be estimated from two lines of reasoning. First, the geological occurrence is in an exterior site, well removed geographically from the shelf faunas of the Mytton Flags. Within the column it lies far above the transgressive base of the Arenig, and includes no elements of the *Neseuretus* community and none of the asaphids abundant in what we (Fortey & Owens 1978) termed the raphiophorid community; the only genus in common is *Ampyx*, a large genus containing groups of species that may be only distantly related (*A. linleyoides* from the Fennian is not closely related to *A. cetsarum* from the Moridunian). If the Arenig represents a deepening-upwards sequence in south Wales, as we propose, then the atheloptic assemblage lies at the deepest end of the gradient.

The second approach derives from the morphology of the trilobites themselves by comparison with modern analogues. Clarkson (1967) pointed out that crustaceans which are blind or with atrophied visual organs tend to be commoner below about 600 m water depth. In oceanic waters sunlight can penetrate at very low intensities to 600–650 m (Boxshall 1981: 152), but in more turbid epicontinental seas to less than half this depth. Since the cyclopygids may have occupied the depth zone of 200 m and below, it seems reasonable to infer a depth of 300 m or more for the atheloptic assemblage.

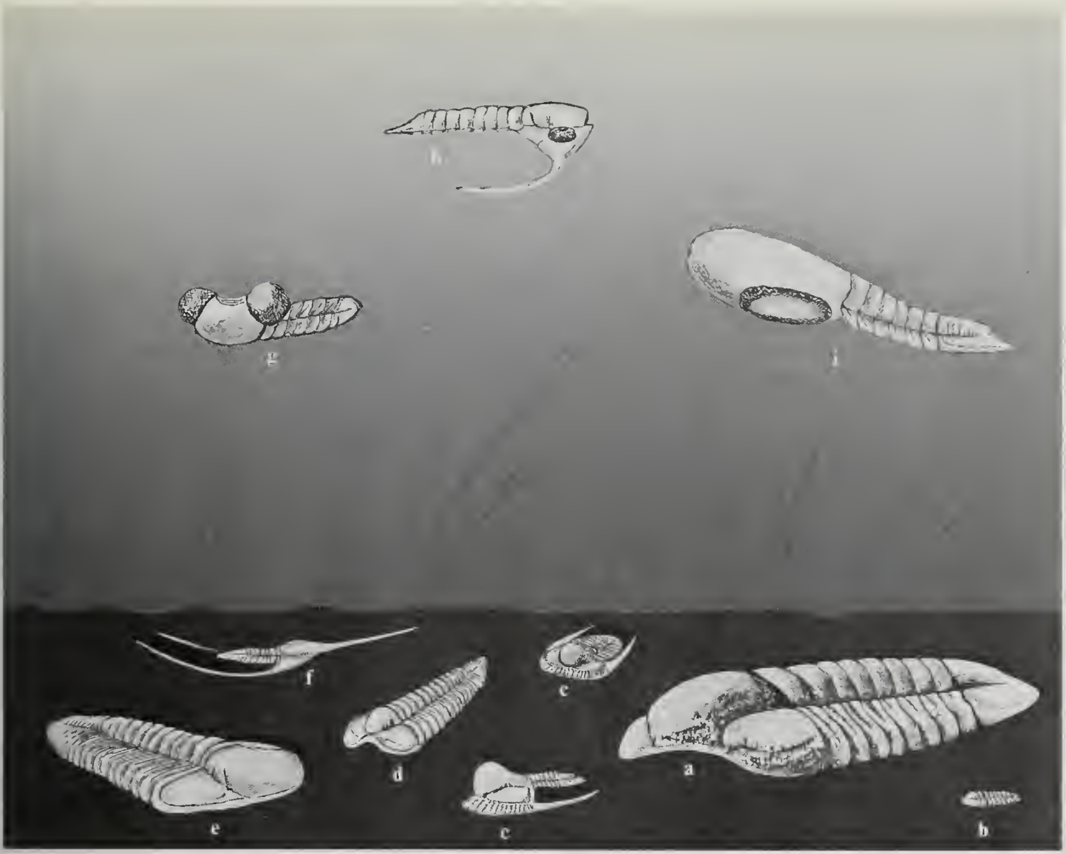


Fig. 13 Atheloptic assemblage of blind, or nearly blind, benthic trilobites (a–f), together with free-swimming, large-eyed mesopelagic forms (g–i). a, *Illaenopsis*; b, *Shumardia*; c, *Bergamia*; d, *Colpocoryphe taylorum*; e, *Ormathops nicholsoni*; f, *Ampyx*; g, *Pricyclopyge*; h, *Bohemilla* (*Fenniops*); i, *Degamella*.

The regression near the Arenig–Llanvirn boundary presumably reduced the water depth sufficiently for normal-eyed trilobites to thrive during the deposition of the Llanfallteg Formation. Since the cyclopygids are also numerous there the depth could not have been less than about 200 m. The change during the regression need not have been very great if the atheloptic assemblage lived just below, and the normal-eyed assemblage just above, the critical depth of light penetration. Because they were inhabitants of the water column well below the surface and somewhat insulated from the constraints of surface temperature conditions, the cyclopygids are not confined to the Gondwanan plate in the early Ordovician, as are the shallow shelf genera such as *Neseuretus*. They were capable of living in the appropriate sites at former temperate latitudes around Baltica and Kazakhstania, as indicated above. They did not penetrate into tropical latitudes at that time, however. One of us (RAF) has made an intensive search in the appropriate lithology in the Cow Head Group of western Newfoundland, which accumulated off the shelf of the North American continent during the early Ordovician. No fossils of cyclopygids were discovered. The oldest occurrences in North America are Middle Ordovician: the earliest of these is probably from the Normanskill Shale (*Niobe*? *huberi* Roy, 1929 is likely to be a *Degamella* sp.), while typical cyclopygid biofacies are known from the Ashgill of Quebec (Cooper & Kindle 1936) and the Whitehouse Formation in the Girvan district of Scotland. The early history of the group is associated with higher latitudes in the early Ordovician, and with a distribution mutually exclusive from that of the tropical pelagic genera *Carolinites* and *Opipeuter*.

The oldest known cyclopygid is *Prospectatrix* Fortey 1981, from the British Tremadoc, but it is a rare fossil, and its occurrence there is not equivalent to the cyclopygid biofacies of the later Ordovician. Cyclopygids are also known from the latest Tremadoc–earliest Arenig of the

Montagne Noire, southern France (Thoral 1935), and it is perhaps here that the earliest cyclopygid biofacies may be sought. The presence in the Montagne Noire of *Illaenopsis*—a characteristic trilobite of the atheloptic assemblage—and of the same genera of carpoid chordates as those from the Pontyfenni Formation indicates that the combination benthic and pelagic faunas typical of the cyclopygid biofacies may have been established before the end of the Tremadoc.

Raymond (1925), Weir (1959) and Kobayashi & Hamada (1971) emphasized supposed migrations of cyclopygids, basing their evidence on stratigraphical and geographical distributional data. We prefer to regard distribution as the result of the discovery of the appropriate biofacies, with the distribution of the trilobites themselves being effectively simultaneous within the biofacies belt. This is shown, for example, by the similarity or identity of species of the family from China (Zhou 1977), Kazakhstan (Koroleva 1982) and Bohemia (Marek 1961), almost at the extremes of its geographical range, and we suspect that critical revision will show that individual species may be dispersed far more widely than the present taxonomy allows. Discovery of the cyclopygid biofacies depends on the preservation of the appropriate former geographical site. In many areas the appropriate exterior site is simply not preserved: for example, there are relatively few places where sufficiently exterior Arenig sites have survived the effects of tectonism, and south Wales is one of the few. Transgressive periods introduced the cyclopygid biofacies onto peripheral shelf regions where it had a higher chance of preservation, as during the Llanvirn and in the later Ordovician (Fortey 1984).

Palaeogeographic affinities of the Arenig faunas

The position of Wales on the western edge of an early Ordovician Gondwana has been claimed on evidence derived both from faunas (e.g. Cocks & Fortey 1982) and from multidisciplinary studies (such as Ziegler *et al.* 1979). The Arenig faunas of south Wales confirm this from several aspects.

1. Inshore faunas with the trilobite *Neseuretus* are only found at the regressive intervals, e.g. in south Wales at the base of the Arenig, but the *Neseuretus* biofacies is found through most of the sequence in Shropshire, indicating its persistence in shallower clastic facies there. This fauna is to be regarded as one of the more reliable indicators of the former extent of Gondwana (Fortey & Morris 1982) and may be found over a wide area of Armorica, Iberia, northern Africa, South America, eastern Newfoundland, the Middle East, the Himalaya and ultimately Yunnan and other parts of China. Individual species of *Neseuretus* probably range widely over this area. Most of the records, however, are from Llanvirn or Llandeilo rocks. Wales is the one site peripheral enough to retain a record of this fauna in the earlier part of the Arenig. Wherever the appropriate transgressive facies occurs—in the Fennian of Anglesey, for example—so too does *Neseuretus*, accompanied by a restricted fauna of brachiopods. In south Wales the appropriate conditions are found at the base of the Arenig sequence (Fortey & Owens 1978) and do not reappear, for the only subsequent record we have of *Neseuretus* is as a rare occurrence in a siltstone of Whitlandian age.

2. The majority of our trilobite genera, even those occurring in more exterior biofacies, are also confined to Gondwanan occurrences, mostly in younger rocks elsewhere in the appropriate palaeoecological settings. The exception is the olenid biofacies, which includes genera of worldwide distribution and independent of 'provincial' or palaeogeographic boundaries (*Hypermecaspis*, *Bienvillia*, *Porterfieldia*). The olenid biofacies was peculiarly adapted to low-oxygen sea floor conditions, and can be found wherever the right conditions pertained. For the rest of the fauna, apart from the endemic trinucleids (which are largely confined to Britain), we list the following genera which are restricted to other Gondwanan occurrences: *Corrugatagnostus*, *Illaenopsis*, *Barrandia*, *Ectillaenus*, *Ormathops*, *Colpocoryphe*, *Dindymene*, *Merlinia*, *Ogyginus*, *Selenopeltis*, *Placoparia*, *Bohemilla*, *Girvanopyge* and *Bohemopyge*. The Cyclopygidae, including another ten genera, were also confined to peripheral Gondwana sites and along the poleward edge of Baltica until late in the Ordovician, when they appeared *en masse* in peripheral sites at the edge of the former North American continent.

3. We noted before (Fortey & Owens 1978: 45) that the deeper water facies also included genera which could be found in exterior facies at the edge of other palaeocontinents—in this case outside Gondwana. This is in contrast to the platform Gondwana faunas, such as those described recently by Henry (1980) and Hammann (1983), which consist entirely of Gondwanan endemic genera. Excluding the specialized olenid biofacies this list includes the following genera from the Arenig of south Wales: *Leiagnostus*, *Arthrorhachis*, *Segmentagnostus*, *Cnemidopyge*, *Shumardia*, *Leioshumardia*, *Asaphellus*, *Dionide*, *Ampyx*, *Seleneceme*. Of these *Ampyx*, *Shumardia* and *Arthrorhachis* are cosmopolitan. *Dionide*, *Seleneceme* and *Leioshumardia* are so far recorded from peripheral sites at the edge of Ordovician North America. The first-named is known from numerous stations in Britain, Bohemia, Armorica etc., while *Leioshumardia* has only previously been described from western Newfoundland (Whittington 1965). *Leiagnostus* and *Cnemidopyge* are known otherwise from Baltica. The fact that close comparisons can be made between species in marginal facies on different continents already by the Arenig—the time usually accepted as one of maximum 'provinciality'—demonstrates the possibility of faunal interchange between exterior facies in advance of major provincial merging.

4. Graptoloids include a number of forms that are confined to peri-Gondwanan graptolitic facies. *Azygograptus* in the Arenig is one such. It appears as the first graptolite in upward-deepening successions and may have been adapted to epiplanktonic life in less 'oceanic' sites. Other Gondwanan forms are: *Didymograptus* (*Expansograptus*) *uniformis lepidus*, *D.* (*E.*) *sparsus*, *D. hirundo* s.s. and *Acrograptus acutidens*, and probably the Llanvirn pendents. But other graptolites, like some of the exterior facies trilobites, appear to have been independent of palaeogeography. These belong to what Fortey (1984) termed the 'isograptid biofacies', a more exterior suite of species regarded as living at greater depth in the water column. Examples listed from south Wales include *Pseudotrigonograptus ensiformis*, '*Glyptograptus*' *austrodentatus*, '*G.*' *dentatus*, *Glossograptus acanthus*, *Tetragraptus serra*, *T. bigsbyi* and *Pseudisograptus* spp. These bridge the so-called 'Atlantic' and 'Pacific' graptolite provinces, and are correspondingly important for correlation purposes. They can be regarded either as precocious invaders signalling the broadly uniform worldwide graptolite faunas of the Caradoc, or as members of a continuously more uniform oceanic graptolite fauna, a view which we favour from the palaeogeographic and facies evidence.

The four lines of evidence are consistent with the inferred position for Wales during the Arenig. Most of the trilobite genera we have found in south Wales only became widespread over Gondwana in the Llanvirn or later, as the Llanvirn transgression moved shelfwards. A few genera (*Asaphellus*, *Prospectatrix*) had persisted from the Tremadoc. There were no genera in common with the cratonic, low latitude faunas of North America or Australia, and very few in common with Baltica, which we regard as having been at temperate latitudes. All the evidence we have is consistent with the view that Britain must have lain at high latitudes in the earlier Ordovician, while the facies distribution proves the marginal position of south Wales relative to that huge area of Gondwana over which Grès Armoricain clastic facies were accumulating.

Fossil localities

The localities referred to in the text, and on the maps (Figs 1, 2, 4–6) are listed below, and follow on from the list of Fortey & Owens (1978: 240) which gives details of localities 1–15 and 16A–G. Apart from locality 16, they are arranged geographically from east to west; old Geological Survey localities from which we did not collect are quoted in the text under their original survey designations.

16. Cwm yr Abbey (Afon Ffinnant Formation): 16H 50 m at 355° from the road bridge (SN 5002 1983); 16J 60 m at 355° from the road bridge (SN 5002 1985); 16K 85 m at 356° from the road bridge (SN 5002 1986); 16L 90 m at 337° from the road bridge (tributary to main stream) (SN 4449 1986).
17. Allt Cwm-arbont (Afon Ffinnant Formation): 17A 85 m at 108° from Arbont Cottage (SN 5251 1883); 17B 55 m at 73° from Arbont Cottage (SN 5238 1891).

18. Afon Ffinnant (Afon Ffinnant Formation): 18A 700 m at 174° from Pont ar Ffinnant (SN 5099 1942); 18B 642 m at 170° from Pont ar Ffinnant (SN 5100 1949); 18C 410 m at 156° from Pont ar Ffinnant (SN 5106 1973); 18D 160 m at 124° from Pont ar Ffinnant (SN 5103 2003); 18E 150 m at 124° from Pont ar Ffinnant (SN 5102 2003); 18F 50 m at 136° from Pont ar Ffinnant (SN 5093 2007).
19. Exposure on south side of B4300, 140 m west of Pont ar Ffinnant (SN 5078 2006) (Afon Ffinnant Formation)
20. Stream section at Capel-Dewi (Afon Ffinnant? (20F) and Pontyfenni formations (20 A–E)): 20A 137 m at 181° from road bridge (SN 4705 2120); 20B 176 m at 186° from road bridge (SN 4703 2017); 20C 178 m at 186° from road bridge (SN 4703 2017); 20D 188 m at 187° from road bridge (SN 4702 2016); 20E 195 m at 189° from road bridge (SN 4701 2015); 20F 205 m at 190° from road bridge (SN 4701 2014).
21. Road cutting north side of A40, 100 m at 148° from Castell-y-waun, 0·6 km SW of Bancyfelin (SN 3191 1756) (Pontyfenni Formation).
22. Stream exposure 447 m at 133° from Sabulon (SN 2490 1628) (Pontyfenni Formation, ?*B. rushtoni* Biozone).
23. Old quarry at Pontyfenni, on north side of old A40 (SN 2379 1690 to SN 2381 1693) (Pontyfenni Formation, *B. rushtoni* Biozone).
24. Old quarry 117 m at 112° from Llwyn-crwn (SN 2399 1795) (Pontyfenni Formation, *B. rushtoni* Biozone).
25. Stream exposure 190 m at 256° from Pant-y-grug (SN 2253 1842) (Pontyfenni Formation, *B. rushtoni* Biozone).
26. Temporary exposure in farmyard at Regwm (SN 2166 1767) (Pontyfenni Formation, *S. abyfrons* Biozone).
27. Old quarry 100 m west of Whitland Abbey (SN 2070 1817) (Colomendy Formation, Whitland Abbey Member, *G. gibbsii* Biozone).
28. Stream-bed in Allt y Clyn, 800 m at 327° from Whitland Abbey (SN 2040 1883) (Colomendy Formation, Whitland Abbey Member, *G. gibbsii* Biozone).
29. Stream-bed, Nant Colomendy, 350 m at 214° from Pant-gwyn (SN 2074 1949) (Pontyfenni Formation, ?*B. rushtoni* Biozone).
30. Trackside quarry 190 m at 256° from Blaencediw (SN 2056 2050) (Blaencediw Formation).
31. Old quarry 330 m at 288° from Blaencediw (SN 2043 2065) (Blaencediw Formation).
32. Exposures on west side of lane NE of Gellidiogyn (Pontyfenni Formation): 32A 140 m at 49° from Gellidiogyn (SN 2010 2119); 32B 160 m at 39° from Gellidiogyn (SN 2010 2123).
33. East side of valley, 370 m at 41° from Gellidiogyn (SN 2023 2138) (Colomendy Formation, Castelldraenog Member).
34. Exposures at Castelldraenog: 34A west side of farmyard, 70 m at 234° from Castelldraenog (SN 2080 2143) (Colomendy Formation, Whitland Abbey Member); 34B west side of track, 150 m at 3° from Castelldraenog (SN 2084 2160) (?Pontyfenni Formation).
35. Old quarry on west side of valley at Cwmfelin Boeth (SN 1908 1924) (Cwmfelin Boeth Formation).
36. Stream exposure 150 m at 140° from Bryngwelltyn, Cwmfelin Boeth (SN 1940 1940) (Cwmfelin Boeth Formation).
37. Stream exposure 100 m at 136° from Bryngwelltyn, Cwmfelin Boeth (SN 1937 1945) (Pontyfenni Formation, *S. abyfrons* Biozone).
38. Roadside section at Pen-y-parc (SN 1981 1951 to SN 1988 1954) (Pontyfenni Formation, *S. abyfrons* Biozone).
39. Old quarry on hillside 420 m at 89° from Felin-Henllan-Amgoed (SN 1931 1972) (Blaencediw Formation).
40. Exposure at Pant, 690 m at 152° from Blaen-lliwe (SN 1892 1779) (Pontyfenni Formation).
41. Lane cutting by old quarry 520 m at 154° from Blaen-lliwe (SN 1884 1795) (Pontyfenni Formation).
42. Exposure in hedge bank 190 m at 108° from Blaen-lliwe (SN 1879 1834) (Pontyfenni Formation).
43. Old quarry on hillside 430 m at 236° from chapel at Cwmfelin Boeth (SN 1887 1882) (Cwmfelin Boeth Formation).
44. Stream bed exposure immediately south of bridge at Rhyd-caer-Emlyn, Henllan Amgoed (SN 1847 2015) (Pontyfenni Formation).
45. Old quarry on east side of valley, 130 m at 166° from Felin-Henllan-Amgoed (SN 1892 2058) (Colomendy Formation, Rhyd Henllan Member).
46. Exposures in lane leading to Felin-Henllan-Amgoed (Colomendy Formation, Rhyd Henllan Member): 46A 50 m at 238° from Felin-Henllan-Amgoed (SN 1884 2066); 46B 90 m at 288° from Felin-Henllan-Amgoed (SN 1880 2072).

47. Laneside exposures north of Llwyn-derw (Colomendy Formation, Rhyd Henllan Member): 47A 40 m at 55° from Llwyn-derw (SN 1888 2084); 47B 90 m at 38° from Llwyn-derw (SN 1890 2088).
48. Laneside exposures immediately west of Sarn-lâs (Pontyfenni Formation): 48A 100 m at 302° from Sarn-lâs (SN 1735 1878); 48B 70 m at 248° from Sarn-lâs (SN 1738 1871).
49. Temporary exposure at Hendref, Henllan Amgoed (SN 1772 2042) (Pontyfenni Formation).
50. Exposure at Cefn-maen-llŵyd, Rhyd-y-wrâch (SN 1679 1976) (Llanfallteg Formation, *D. artus* Biozone).
51. Old roadside quarry 200 m at 212° from Cwmmiles (SN 1608 2224) (Pontyfenni Formation).
52. Old railway cutting north of Llanfallteg (Pontyfenni (52Z) and Llanfallteg (52, *D. artus* Biozone, 52A–Y, *D. levigena* Biozone) formations): 52 small quarry at south end of cutting (SN 1571 2013): basal 3 m of Llanvirn. 52A–S east side of track, south of core of anticline (SN 1571 2014 to SN 1575 2019), stratigraphically below the base of the Llanvirn as follows: 52A, 0–1·5 m; 52B, 1·5–3 m; 52C, 3–4 m; 52D, 5 m; 52E, 6 m; 52F, 7–9 m; 52G, 9–11 m; 52H, 11–13 m; 52I, 13–15 m; 52J, 15–17 m; 52K, 17–19 m; 52L, 19–21 m; 52M, 21–23 m; 52N, 23–25 m; 52P, 25–27 m; 52Q, 27–29 m; 52R, 29–31 m; 52S, 31–33 m. Positions shown on Fig. 8, p. 91. 52T, core of anticline, 33 m below base of Llanvirn (SN 1575 2020). 52U, immediately north of core of anticline, 31–33 m below base of Llanvirn (SN 1576 2021). 52V (SN 1579 2024), 52W (SN 1583 2028), 52X (SN 1587 2037), 52Y (SN 1588 2039): separated by structural complexities from southern part of section, and distance below Llanvirn boundary unknown. 52Z by entrance to narrow track leading from path of railway (SN 1591 2057).
53. Section on north side of road, 340 m at 124° from Brynaeron, Llandissilio (SN 1295 2101) (Pontyfenni Formation).
54. Old quarry 520 m at 154° from Brechfa, Llanycefn (SN 0994 2168) (Pontyfenni Formation).
55. Long Plantation railway cutting, Scolton (SM 9916 2152 to SM 9930 2153) (Llanfallteg Formation, *D. artus* Biozone).
56. Triffleton Quarry (SM 9774 2428) (Blaencediw Formation).
57. Brunel cuttings, east side of Treffgarne Gorge (SM 9602 2448 to SM 9603 2470) (Blaencediw Formation at north end; ?Tremadoc at south end).
58. Old quarry at Abercastle (SM 8531 3355) (Abercastle Formation).
59. Exposure on east side of Porth-gain (SM 8143 3262) (junction of Abercastle Formation (Porth Gain Member) and Penmaen Dewi Formation).
60. Small quarry 500 m at 356° Lleithyr, north of St David's (Ogof Hên Formation).
61. Exposures in Pwlluog, north end of Whitesand Bay (61A, B: southern inlet; 61C, E: northern inlet, beach level; 61D, F: northern inlet, cliff top; 61G: north side of Craig y Creigwr) (all Penmaen Dewi Formation) (61A SM 7328 2738, 61B SM 7322 2747, 61C SM 7320 2746, 61D SM 7322 2753, 61E SM 7312 2758, 61F SM 7317 2760, 61G SM 7302 2759).
62. Ramsey Island: Aber Mawr, beach level (SM 7005 2425) (Pontyfenni Formation equivalent).
63. Ramsey Island: Cliff top at Ogof Hên (SM 7080 2520) (Ogof Hên Formation).

Collections and repositories

The trilobites and graptolites described herein were largely collected by the authors over the ten year period from 1974 to 1983. They are supplemented by existing museum collections, especially those of the British Geological Survey, and by specimens kindly presented by numerous individuals, listed in the acknowledgements.

Figured and cited specimens are housed in the following institutions, except where stated otherwise: British Museum (Natural History) (register number prefixes I, Q, E, H and It), British Geological Survey, Keyworth (BGS and/or GSM), National Museum of Wales (NMW) and Sedgwick Museum, Cambridge (SM).

Systematic descriptions: Trilobites

by R. A. Fortey and R. M. Owens

Trilobites are described family by family in the same order as in the *Treatise on Invertebrate Paleontology* (Harrington *et al.* 1959), with the exception that the Nileidae are classified with the Cyclopygidae in the superfamily Cyclopygacea, as proposed by Fortey (1981). Terminology generally also follows the *Treatise* except that the glabella is understood to include the occipital ring. The use of the term **baccula** (-ae) for swellings at the base of the glabella follows Öpik (1967) and Fortey (1975). We use the term **axial shield** (Henningsmoen 1957) for moulted exoskeletons consisting of cranidium + thorax and pygidium.

Family **AGNOSTIDAE** Salter 1864

Genus ***LEIAGNOSTUS*** Jaekel 1909

TYPE SPECIES. *Leiagnostus erraticus* Jaekel 1909, by monotypy.

Leiagnostus cf. ***erraticus*** Jaekel 1909
(Figs 14a, b)

MATERIAL. Imperfect dorsal exoskeleton, BGS Pr557 + Pr581; pygidia: It.19560, NMW 84.17G.30.

STRATIGRAPHICAL RANGE. Upper Arenig, Fennian, zone of *Bergamia rushtoni*, Pontyfenni Formation.

LOCALITIES. Pontyfenni (loc. 23), and Cwmmiles (loc. 51).

DISCUSSION. So featureless an agnostid does not require description of the general morphology. One pygidium (Fig. 14b) shows details of the pygidial axial musculature. The axis appears to be subfusiform, with a terminal tubercle at about two-thirds pygidial length; the median tubercle is far forward and is flanked by two pairs of muscle impressions; two further pairs lie behind these. The articulating half ring is well shown on the large pygidium of Fig. 14a; it is short (sag.) with a narrow ring furrow, which is not deepened into pits at its lateral extremities. Using Öpik's (1967: 71–72) categories of articulating devices, that of *Leiagnostus* appears to be of the basic (peronopsid) kind. The articulating device of Metagnostidae (Geragnostidae of authors, see Fortey 1980) is of the glyptagnostid kind: for example, *Geragnostus* (Tjernvik 1956: pl. 1, fig. 10), *Arthrorhachis* (Fortey 1980: pl. 2, fig. 15) and *Galbagnostus* (Whittington 1965: pl. 4, fig. 7). Hence *Leiagnostus* is not likely to be an effaced metagnostid if this criterion is of phylogenetic importance. Effacement itself is highly polyphyletic in the Agnostida, and Howell's (1935) family Leiagnostidae based on this aspect of morphology is clearly unsatisfactory. That metagnostids did become almost as effaced as *Leiagnostus* is shown by highly effaced *Geragnostus* from Bohemia termed *Neptunagnostella* by Pek (1977); the articulating ring remains long (sag.)

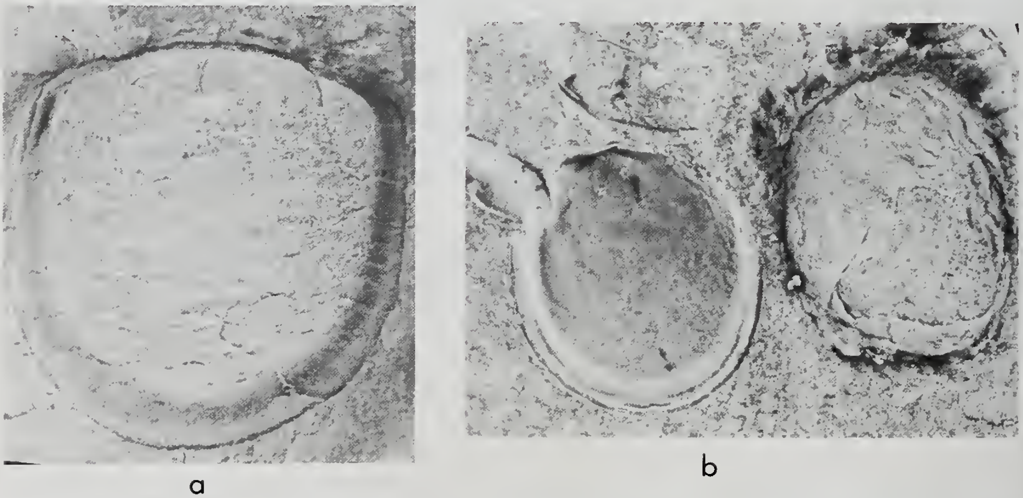


Fig. 14 *Leiagnostus* cf. *erraticus* Jaekel 1909. Pontyfenni Formation, late Arenig (Fennian), *Bergamia rushtoni* Biozone. a, large pygidium, loc. 23, × 8, It.19560; b, cephalon and pygidium, the latter showing muscle impressions on internal exoskeletal surface, loc. 23, × 8, GSM Pr581.

in these forms (Pek 1977: pl. 3, fig. 3). So on the strength of the articulating device we place *Leiagnostus* in the Agnostidae, following Öpik's (1967) classification. The pygidial musculature is not particularly helpful because indications of four pairs of impressions are to be found on both Agnostidae (e.g. Westergård 1946: pl. 16, fig. 16) and Metagnostidae (e.g. Pek 1977: pl. 3, fig. 4).

The type species of *Leiagnostus*, *L. erraticus* Jaekel, is known from the holotype, a complete enrolled specimen from *geschiebe* material probably originating from the uppermost Arenig or early Llanvirn of Sweden. This specimen was re-illustrated by Neben & Krueger (1971: pl. 11, figs 37–38). The cephalon lacks a border, which is wide on the pygidium, itself only about 3 mm long. Our large pygidium is twice this size, and differs from the type of *L. erraticus* in being almost parallel-sided with the maximum width behind the mid-length. A smaller pygidium from Wales (Fig. 14b), which is only a little larger than the type, resembles it in general proportions and in having an oval outline, so it is likely that small changes in pygidial outline accompanied continued growth. The pygidial tubercle does not show up on Jaekel's original; this may be because it is covered with cuticle in this region, and the tubercle may be mostly a thinning of the exoskeleton. The Welsh specimens are crushed, and largely show parietal surfaces on which the tubercle is visible, so this difference may be less than it seems, but caution dictates that we should qualify our determination. The development of the tubercle is variable in other species; in *L. bohemicus* from the Llanvirn of Bohemia it varies from a prominent bulge to a minute, faint pustule (Pek 1977: pl. 5, figs 1–5). It is in a more posterior position than in *L.* cf. *erraticus*—at a fifth to a quarter of pygidial length (excluding half ring), but at one seventh or less of pygidial length on the Fennian specimens. The same distinction applies to *L. franconicus* Sdzuy 1955 from the Tremadoc of Germany, and to *L.* cf. *turgidulus* from the Tremadoc of south Wales (Fortey & Owens, *in* Owens *et al.* 1982: pl. 1, fig. b). *L. turgidulus* Harrington & Leanza 1957 from the Tremadoc of Argentina lacks a defined mid-axial tubercle but the postaxial tubercle is clearly visible, indicating that the axis in this species extended much further backwards than on *L.* cf. *erraticus*. The pygidial border on *L. peltatus* Tjernvik 1956 from the early Arenig of Sweden is extremely narrow. *L. alimbeticus* Balashova 1961 is known from cephalic parts only, and cannot be properly evaluated in a genus in which pygidial details are essential in discriminating species. *L. foulonensis* Howell 1935 appears to show a cephalic border as well as a broad pygidial one, and is therefore excluded from *Leiagnostus*.

Family **METAGNOSTIDAE** Jaekel 1909

(= Geragnostidae Howell 1935; Trinodidae Howell 1935; Arthrorhachinae Raymond 1913).

Genus ***CORRUGATAGNOSTUS*** Kobayashi 1939*a*

TYPE SPECIES. *Agnostus morea* Salter 1864 (see Whittard 1955: 11).

Corrugatagnostus cf. ***refragor*** Pek 1969

(Figs 15a–c)

cf. 1969 *Corrugatagnostus refragor* Pek: 383; pl. 1, fig. 1.
cf. 1977 *Corrugatagnostus refragor* Pek; Pek: 29–30; pl. 7, figs 4, 5; text-fig. 9.

MATERIAL. Headshields, It.19561, It.19563; pygidium, It.19562.

STRATIGRAPHICAL RANGE. Upper Arenig, Fennian; biozones of *Bergamia rushtoni* and *Dionide levigena*.

LOCALITIES. Type locality of Pontyfenni Formation, and Llanfallteg Formation, type section.

DISCUSSION. This species is known from sparse and rather poorly preserved material which does not permit a full description. In its glabellar structure it is a typical *Corrugatagnostus*—essentially a metagnostid *en grand tenu* (Fortey 1980: text-fig. 4). The scrobiculae are, however, rather weakly developed by comparison with the type species (Whittard 1955: text-fig. 2; Pek 1977: 27–29; pl. 5, figs 6–8; pl. 6, figs 1–7; pl. 9, fig. 1; Pek & Prokop 1984) and with some

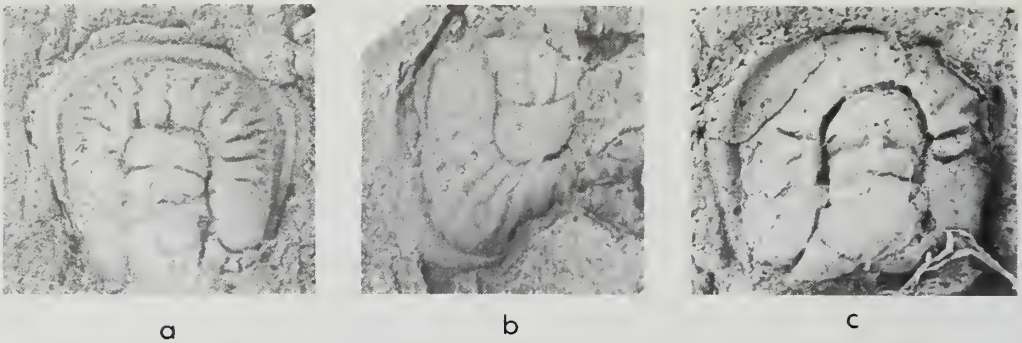


Fig. 15 *Corrugatagnostus* cf. *refragor* Pek 1977. Late Arenig (Fennian). a, latex cast from cephalic shield showing pattern of scrobiculae, Pontyfenni Formation, *B. rushtoni* Biozone, loc. 23, × 10, It.19561; b, latex cast from incomplete pygidium, Llanfallteg Formation, late Arenig, Biozone of *Dionide levigena*, type section, loc. 52, × 10, It.19562; c, latex cast from incomplete cephalon, Pontyfenni Formation, locality as Fig. 15b, × 12, It.19563.

others: *C. sol* Whittard 1955, *C. convergens* Weir 1959. *C. fortis* (Novák 1883; see Pek 1977: 31; pl. 7, figs 1, 2; pl. 8, fig. 7) is weakly scrobiculate, but with a strongly zonate cephalon, and with an anterior glabellar furrow which does not arch forwards medially. There are four species with scrobiculae weakly developed as in our species: *C. refragor* Pek 1969, *C. chekiangensis* Sheng 1964, *C. transitus* Lu 1975 and *C. jiangshanensis* Lu 1964 (see also Lu *et al.* 1976: pl. 9, fig. 3). Of these, *C. jiangshanensis* lacks the second transglabellar furrow, which indicates that it is a scrobiculate *Segmentagnostus* rather than a true *Corrugatagnostus*. The same probably applies to *C. chekiangensis* Sheng. *C. transitus* is known from a pygidium only, and this has more, but weaker, scrobiculae than in our species, and the terminal piece of the pygidium contracts in width from the preceding axial ring. *C. refragor* Pek is from the Llanvirn Šárka Formation of Bohemia, and is very close to our species; apart from similar density of scrobiculae, the anterior transglabellar furrow is arched gently forwards and the glabellar tubercle does not strongly protrude into the frontal glabellar lobe as it does on *C. morea*. Such differences as there are may well be because of preservation, the Bohemian species being well-preserved in relief. For example, the Fennian cephala are wider than long, where the type material of *C. refragor* has cephalic length almost equal to width, but if crushing 'opened out' the fixed cheeks this distinction may not be important. However, the cephalic border furrows are broader anterolaterally on the Welsh specimens, as if they were incipiently zonate. This difference is important enough for us to introduce the qualification into the determination.

Genus *ARTHRORHACHIS* Hawle & Corda 1847

TYPE SPECIES. *Arthrorhachis tarda* Hawle & Corda 1847, by monotypy.

REMARKS. We follow Fortey (1980: 25–29) in using the generic name *Arthrorhachis* for metagnostids lacking transglabellar furrows, and having a short pygidial axis with the terminal piece shorter than the postaxial field. These will have been referred to *Geragnostus* or *Trinodus* previously.

Arthrorhachis sp. indet.
(Figs 16a–d)

MATERIAL. Cephalic shields: It.18569, NMW 33.189.G23; pygidia: It.19566–7.

STRATIGRAPHICAL RANGE. Upper Arenig, Fennian, biozone of *Bergamia rushtoni* and probably also that of *Stapeleyella abyfrons*.

LOCALITIES. Pontyfenni Formation, type locality; and Llwyn-crwn, loc. 24; Pen-y-parc roadside section, loc. 38.

Fig. 16 *Arthrorhachis* sp. indet. Late Arenig (Fennian). a, imperfect cephalon and thoracic segment, *S. abyfrons* Biozone, loc. 38, × 4, It.19564; b, cephalon, *B. rushtoni* Biozone, loc. 24, × 4, NMW 33.189.G23; c, latex cast from thorax and pygidium, *B. rushtoni* Biozone, loc. 23, × 6, It.19566; d, latex cast from pygidium, loc. 23, × 6, It.19567.

Discussion. The Fennian species from south Wales is known by imperfectly preserved material, and adds little to our understanding of the genus as a whole. A full description of the morphology of *Arthrorhachis* has been provided by Kielan (1960) and Fortey (1980), and comparative remarks only are given here. The Fennian species differs from most other *Arthrorhachis* spp., including the type species, in that the pygidial axis has a terminal piece which is wider than the preceding axial ring; in this respect it is more like some (but not all) species of *Geragnostus*. This character alone serves to distinguish our species from the following *Arthrorhachis* from the early Ordovician: *A. saltaensis* (Harrington & Leanza 1957) from Argentina; *A. danica* (Poulsen 1965) (and its subspecies in Fortey, 1980), *A. erratica* (Jaekel 1909), *A. mobergi* (Tjernvik 1956), *A. elliptifrons* (Tjernvik 1956) and *A. lentiformis* (Angelin 1854) from Scandinavia and Spitsbergen; *A. hebetatus* (Dean 1973*b*) from Turkey; Howell's (1935; see also Capera *et al.* 1978) three species from the early Arenig of the Montagne Noire, southern France (*A. chinianensis*, *A. abruptus* and *A. corpulentus*, probably all variants of one species); and *A.* cf. *mobergi* (Tjernvik) Chang & Fan 1960 (also Lu *et al.* 1965: pl. 2, figs 13–14) from China. *Trinodus valmeyensis* Ross 1958, from the western United States, has an advanced glabellar tubercle and would now be referred to *Galbagnostus* Whittington.

The only early Ordovician species with the same pygidial axial structure is *A. hupehensis* Lu 1975 (especially his pl. 1, fig. 13) from the late Arenig (or earliest Llanvirn) of SW China, although Lu's pl. 14, fig. 14 shows a more usual *Arthrorhachis* pygidial axis. The Welsh and Chinese specimens are unlikely to be conspecific, because the pygidial border of the latter is consistently much wider—about one-sixth (sag.) pygidial length as compared with less than one-tenth.

One much later (Caradoc) species with a similar pygidial axial structure is *A. pragensis* Přibyl & Vaněk 1968 (see Pek, 1977: 24–25; pl. 1, figs 9, 10; Pek & Prokop 1984), but in this species the axis (excluding half ring) is much shorter than the postaxial field, where they are nearly equal on our specimens. Although the median pygidial tubercle is not well preserved on the Welsh pygidia, it is clearly a narrower, less tumid structure than that of *A. pragensis*.

The stratigraphically early cephalon from the *Stapeleyella abyfrons* Biozone has a wider border than those from the *Bergamia rushtoni* Biozone, but with so few specimens we can say nothing about the intraspecific variation. Cephalic features are generally similar throughout the genus.

In summary, it is probable that we have a new *Arthrorhachis* species in the Pontyfenni Formation, but the material is inadequate to name it as such; hence we place it under open nomenclature.

Genus *SEGMENTAGNOSTUS* Pek 1977

TYPE SPECIES. *Agnostus caducus* Barrande 1872, by original designation; Llandeilo, Bohemia (Whittard 1955, Pek 1977, Pek & Prokop 1984).

DIAGNOSIS. Metagnostids with one deep transglabellar furrow, shaped like an inverted 'v'; pygidium like that of *Geragnostus*.

DISCUSSION. This genus was discussed at length by Fortey (1980: 27), who noted that the glabellar structure differed fundamentally from that of *Arthrorhachis* and *Geragnostus* with regard to the incision of the transglabellar furrow relative to cephalic musculature. The inverted 'v' transglabellar furrow is regarded as the defining character; if a second pair of glabellar furrows is present at all they appear as small indentations in the sides of the glabella. Pek (1977) included *Agnostus frici* Holub 1908 within his concept of the genus, on which a second pair of furrows is strongly developed, essentially in the arrangement characteristic of *Corrugatagnostus*, and this species is probably better regarded as a non-scrobiculate member of that genus.

Fortey (1980) listed five species besides the type species assignable to *Segmentagnostus* as we understand it: from Britain, France and Argentina. To these may be added: *Geragnostus merus* Zhou (*in* Lu *et al.* 1976) from Jiangxi, China; that specimen of *Geragnostus sinensis* Sheng 1974 on his pl. 1, fig. 1b from Yunnan; and *Geragnostus scoltonensis* Whittard 1966, from Wales, and *S. stubblefieldi* Rushton & Hughes 1981 from the Great Paxton borehole. The distribution of the genus appears to be peri-Gondwanan, matching that of *Neseuretus*, for example, although *Segmentagnostus* is found in deeper water facies. However, the presence of a probable *Segmentagnostus* in western Newfoundland (Fortey 1982) suggests that the genus could yet prove to be more widespread in the appropriate facies.

Segmentagnostus hirundo (Hicks 1875)
(Fig. 17a)

1875 *Agnostus hirundo* Hicks: 176; pl. x, fig. 10.
1914 *Agnostus maccoyi* Salter; Thomas *in* Strahan *et al.*: 18.
1939*b* *Geragnostus* (*Micragnostus*) *hirundo* (Hicks) Kobayashi: 579.
1955 *Geragnostus hirundo* (Hicks); Whittard: 7–8 (*pars*); pl. 1, fig. 4, *non* figs 1–3.

HOLOTYPE. Pygidium, SM A15265, from the Whitlandian of 'Whitesands Bay' (presumably Pwlluog), St David's, Dyfed. The counterpart of this specimen is I.709 in the British Museum (Natural History).

STRATIGRAPHICAL RANGE. Whitlandian, *Bergamia gibbsii* Biozone.

OTHER OCCURRENCE. Rhyd Henllan Member of Colomendy Formation, loc. 47.

MATERIAL. Cephalic shield, It.19596; pygidium BGS Pr1850.

DISCUSSION. Whittard (1955) refigured the holotype, a poorly preserved pygidium. He believed the type material was of late Arenig age, which we now know to be incorrect, and we here assign Whittard's supposed *S. hirundo* from Shropshire to *S. scoltonensis* (see below). There is nothing to add to Whittard's description of the type specimen. We have collected an extremely poorly preserved cephalic shield (It.19596) from Pwlluog which shows that the species is probably correctly referred to *Segmentagnostus*. A well-preserved, incomplete pygidium from the Whitland area (Fig. 17a) gives a better idea of pygidial morphology than the type. The pygidial marginal spines are minute compared with *S. scoltonensis* as interpreted here (cf. Whittard 1955: pl. 1, fig. 2), but like that species the mid-part of the first axial ring is hardly defined, in this respect contrasting with *S. whitlandensis* sp. nov.

Segmentagnostus whitlandensis sp. nov.
(Figs 17d–g)

1914 *Agnostus hirundo* Salter; Thomas *in* Strahan *et al.*: 19.

HOLOTYPE. Cephalic shield, It.19569.

PARATYPES. Pygidia: It.19570–2; BGS Pr1756–8, Pr1766.

TYPE LOCALITY AND HORIZON. Loc. 38; Late Arenig, Fennian, Pontyfenni Formation, *Stapeleyella abyfrons* Biozone. Known only from the type locality.

NAME. After the Whitland district.

DIAGNOSIS. *Segmentagnostus* with granulate surface sculpture; median glabellar tubercle not immediately behind transglabellar furrow; terminal piece on pygidial axis equal to or exceeding length of postaxial field; first pygidial axial ring well-defined medially.

DESCRIPTION. Cephalon with maximum width near rear, this equal to sag. length. Glabella occupies two-thirds cephalic length, and two-fifths maximum width, expanding in width gently forwards to anterolateral corners. Axial furrows deep, somewhat wider posteriorly. Transglabellar furrow only slightly less deep, forming a deep inverted 'v' and dividing the glabella into two lobes, the frontal lobe slightly more than half the length of the posterior lobe. The median glabellar tubercle is prominent, and at a small distance behind the transglabellar furrow, almost opposite its outer ends. Posteromedially the glabella is extended into a median acumination between the basal lobes, which are of the inflated triangular form usual in metagnostids. Border defined by a very deep furrow which is widest anterolaterally; border comprises well under 10% cephalic length.

The best preserved pygidia include external moulds, showing the granulation which we presume covered the whole dorsal surface. The pygidial axis is of the usual *Segmentagnostus*

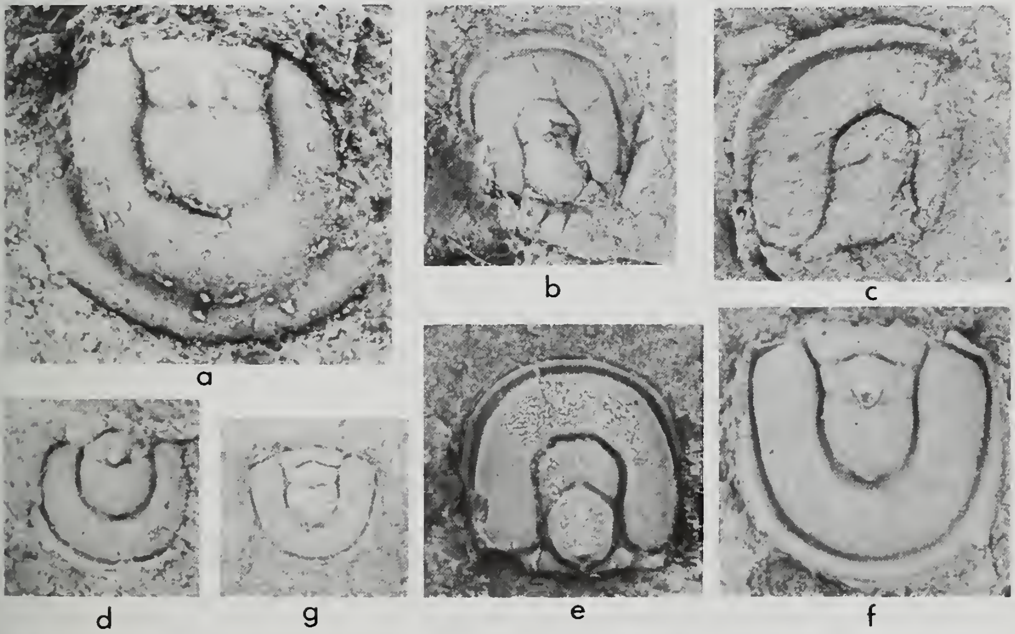


Fig. 17 a, *Segmentagnostus hirundo* (Hicks 1875). Late Arenig (Fennian); pygidium, Rhyd Henllan Member, loc. 47, Whitlandian, *gibbsii* Biozone, × 12, GSM Pr1850. b–c, *Segmentagnostus scoltonensis* (Whittard 1966); b, cephalon, Llanfallteg Formation, type section, Fennian *Dionide levigena* Biozone, × 15, It.19597; c, cast from incomplete cephalon, Pontyfenni Formation, loc. 23, *Bergamia rushtoni* Biozone, × 8, It.19598. d–g, *Segmentagnostus whitlandensis* sp. nov., late Arenig (Fennian, *Stapeleyella abyfrons* Biozone), Pontyfenni Formation, loc. 38. d, latex cast from external mould of incomplete pygidium showing granulation, × 12, It.19570; e, **holotype**, cephalon, internal mould showing tubercle behind transglabellar furrow, × 12, It.19569; f, latex cast from well-preserved pygidium, × 20, GSM Pr1758; g, pygidium, × 12, GSM Pr1766.

form, tapering past the two axial rings, and expanding gently around the terminal piece. The structure of the axial rings is generally the same as in *S. mccoyii* as described by Hughes (1969) except that the first axial ring is well defined medially; the prominent median tubercle is on the second ring only, and slightly impinges on the terminal piece. There is also a minute tubercle at the tip of the axis. Terminal piece long, equal to or exceeding in length the postaxial field. Borders relatively narrow, as on cephalic shield, with very small marginal spines.

DISCUSSION. There are two differences between the pygidia of this species and those of *S. hirundo* and *S. scoltonensis* which are not likely to be accountable as differences in size or preservation. The pygidial border on *scoltonensis* is almost twice as wide posterolaterally, and the first axial ring narrows markedly abaxially and is effaced, whereas on *S. whitlandensis* the median lobe is quite well defined there and only slightly narrower (sag.) than those on either side. The second distinction also applies to *S. mccoyii* (Salter) (see Hughes, 1969: pl. 1, fig. 3). The granulate surface is at present unique to *S. whitlandensis* among described *Segmentagnostus*, but preservation may not be adequate to record it on other species. *S. whitlandensis* differs from all other post-Arenig *Segmentagnostus*, including the type species (Whittard 1955: text-fig. 2a; Pek 1977: pl. 1, fig. 7) in having the glabellar tubercle distinctly posterior to the transglabellar furrow.

Segmentagnostus changes little throughout its long history: the earliest species *S. neumanni* (Harrington & Leanza 1957) from the Lower Tremadoc of Argentina is generally like the youngest, *S. merus* (Zhou 1976), from the Upper Ordovician of China. Harrington & Leanza (1957: 69) state that the glabellar tubercle on their species 'does not reach the transglabellar furrow' (but see their fig. 13, 10), and if this is so it is the only species besides *S. whitlandensis* with this character. *S. neumanni* differs from the Welsh species because the transglabellar furrow is a very weak 'inverted v', the posterior glabellar lobe is longer, and the pygidium carries long marginal spines.

Segmentagnostus scoltonensis (Whittard 1966)

(Figs 17b, c)

1955 *Geragnostus hirundo* (Hicks); Whittard: 7–8 (*pars*); pl. 1, figs 1–3, *non* fig. 4.
1966 *Geragnostus scoltonensis* Whittard: 266–267; pl. 46, figs 3–5.

HOLOTYPE. Distorted complete exoskeleton, SM A44493.

TYPE LOCALITY AND HORIZON. Llanfallteg Formation, early Llanvirn part, *D. artus* Biozone; Scolton Railway cutting, Dyfed.

OTHER OCCURRENCES. Llanfallteg Formation, latest Arenig part; Tankerville Flags of Shropshire (Upper Arenig); Pontyfenni Formation (Upper Arenig, *B. rushtoni* Biozone), loc. 23; ?Stapeley Volcanics, Llanvirn, Shropshire.

FIGURED MATERIAL. Cephalic shields: It.19597–8.

DISCUSSION. The holotype of this species is considerably elongated (sag.) by distortion (Whittard 1966: pl. 46, fig. 4) and its morphology is not easy to interpret. Our view of this species is therefore inevitably influenced by stratigraphical considerations. When Whittard (1955) described *S.* '*hirundo*' (Hicks) from the Tankerville Flags, he assumed that the type of that species from St David's was from the late Arenig ('*D. hirundo* Zone') also. We now know it to be much older (Whitlandian). On the other hand the type of *S. scoltonensis* is from the Llanfallteg Formation, and there are other similarities between the Llanfallteg Formation fauna and that of the Tankerville Flags in Shropshire. Whittard (1966) stressed the absence of a second pair of glabellar furrows (posterior to the transglabellar furrow) as the important specific character of *S. scoltonensis*, but the same is true of his (1955) so-called *hirundo* from the Tankerville Flags. These specimens also show the glabellar tubercle immediately behind the transglabellar furrow, which is an important difference from the *S. whitlandensis* cephalon figured here. Broad pygidial borders, compared with *S. mccoyii* (Salter) or *S. stubblefieldi* Rushton & Hughes 1981, are present on the type of *scoltonensis* and the *Segmentagnostus* from the Tankerville Flags. Hence we consider it likely that the Scolton and Tankerville specimens are conspecific, the name *scoltonensis* should be applied to them, and that the species ranges across the Arenig–Llanvirn boundary.

We figure here cephalic shields from the upper part of the Pontyfenni Formation, of similar age to the Tankerville *scoltonensis*, and from the succeeding *Dionide levigena* Biozone of the Llanfallteg Formation. Both show a slightly shorter frontal glabellar lobe when compared with Whittard's (1955: pl. 1, fig. 1) cephalic shield, but since this proportion shows a certain range of variation in *Segmentagnostus* (Hughes 1969: table 1), and is altered by distortion, this is not regarded as important. The larger cephalic shield (Fig. 17c) shows a faint indication of a second pair of glabellar furrows. Whittard (1966: pl. 46, fig. 5) also figured a cephalic shield from the Stapeley volcanics, which would imply a stratigraphical range into the later Llanvirn, although it is as well to be cautious about this until a pygidium is discovered from the later horizon.

S. scoltonensis is distinguished from *S. stubblefieldi* Rushton & Hughes 1981, from the Llanvirn of the Great Paxton Borehole, by the latter having a pygidial axis which tapers uniformly past the first two rings to an almost rectangular terminal piece; a prominent median ridge on the pygidial axis of *S. stubblefieldi* produces a distinct tripartition of the anterior axial ring. The type of *S. scoltonensis*, poorly preserved though it is, is clearly like the Tankerville specimens in these characters. *S. scoltonensis* is very like *S. hirundo* from the middle Arenig; if our attribution of the Tankerville specimens to the former is correct the marginal pygidial spines are more prominent on *S. scoltonensis*, and the first two pygidial axial rings account for a greater proportion (sag.) of the pygidial axis. More material of both species needs to be discovered to assess the limits of variation.

Family **SHUMARDIIDAE** Lake 1907

Genus ***SHUMARDIA*** Billings 1862

Type species. *Shumardia granulosa* Billings 1862, by monotypy.

Discussion. Several generic and subgeneric names have been proposed for *Shumardia*-like trilobites recently, and there is the question of whether the genus *Conophrys* Callaway (type species *C. salopiensis* Callaway 1877) should be revived. Fortey (1980) reviewed *Shumardia, sensu lato* and concluded that the described species did not unequivocally divide into two—*Shumardia* and *Conophrys*—in spite of the differences between their type species. Fortey & Rushton (1980) redescribed the shumardiid *Acanthopleurella* Groom, which is distinguished from *Shumardia* by having only four thoracic segments, two of which are macropleural, and in having a long (sag.) occipital ring, genal spines, and short, stubby pygidial axis. They also illustrated what is probably the best-preserved specimen of *Conophrys salopiensis* yet discovered. Fortey (1980) did not consider *Kweichowilla* Chang 1964 (type species *K. minuta* Chang 1964), and Přibyl & Vaněk (1980: 14) have recently proposed the subgenus *Shumardia* (*Shumardella*) with *S. bohemica* Marek 1964 as type species.

So there are now four possible supraspecific taxa to be considered: *Shumardia*, *Conophrys*, *Kweichowilla* and *Shumardella*. The type species of *Shumardia* was revised by Whittington (1965); we note that its glabella is well defined anteriorly, with large anterolateral lobes. Whittington considered that it lacks a macropleural thoracic segment, and the long (sag.) pygidium is without borders laterally. *Conophrys salopiensis* from Shropshire and Wales has been identified with the species *S. pusilla* (Sars) (Stubblefield 1926), but is a distinct form (P. Whitworth, personal communication 1972). The glabella is defined anteriorly, with rather small anterolateral lobes; genal spines are lacking (Fortey & Rushton 1980: fig. 17); the fourth thoracic segment is macropleural; the pygidium is transverse with the axis extending nearly to the border, which is narrow but distinct. *Kweichowilla* has not been formally diagnosed, although the type species has been illustrated three times (Chang *et al.* 1964; Lu & Zhang 1974: pl. 55, figs 2, 3; Yin & Li 1978: pl. 162, figs 10, 11). It is distinguished by its relatively huge, drop-like glabella lobes, which extend far back, and by the broad glabellar tongue which extends to the anterior cranidial margin. The pygidium attributed to *K. minuta* is elongate and subtriangular like that of the type species of *Shumardia*. The type species of *Shumardella* is known from the cranidium alone, a fragmentary pygidium figured by Marek (1964) being only doubtfully associated. On *S. bohemica* the furrows defining the anterolateral glabellar lobes are narrow, and the lobes do not bulge outwards in the manner of most shumardiids, so that the glabellar outline is nearly parabolic. The posterior borders on the fixed cheeks are relatively wide (exsag.) and not depressed below the rest of the cheek.

On the basis of the type species alone the four taxa appear easily definable, but as Fortey (1980) observed, when other species are taken into account the distinctions are less clear-cut. If the genera were phylogenetic units one might expect pygidial characters to be consistent with cephalic ones, but this is not so. For example, several species with *Shumardia*-like cranidia have transverse, *Conophrys*-like pygidia (*S. minaretta* Fortey 1980), others with *Kweichowilla*-like cranidia have transverse pygidia unlike the type species of that genus (e.g. *S. forbesi* Stait & Laurie 1983). The classification of such species as *S. curta* Stubblefield 1927 and *S. ctenata* Robison & Pantoja-Alor 1968, which have free pleural tips on the pygidium, is also unclear. There may be an argument for employing subdivisions within the large genus *Shumardia* as Dean (1973*a*) suggested, and a compromise may be to use subgeneric categories based on the type species; species for which no pygidium is known, or with ambiguous combinations of characters, may be referred to *Shumardia, sensu lato*.

Using this approach, the following diagnoses may be proposed, with some of the previously described *Shumardia* species listed in Fortey (1980) indicated with their subgeneric placing.

Shumardia (*Shumardia*): Glabella defined anteriorly inside cephalic margin; anterolateral glabellar lobes large, swollen, but not extending far back; macropleural thoracic segment lacking; pygidium elongate-triangular, axis not extending near margin, and well-defined borders lacking. *Shumardia granulosa* Billings 1862, *S. dicksoni* Moberg & Segerberg 1906, *S. lacrima* Koroleva 1964, *S. tarimuensis* Zhang 1983 and *S. gadwensis* sp. nov. (p. 121).

Shumardia (*Conophrys*): Glabella defined anteriorly inside cephalic margin; anterolateral glabellar lobes small to moderate sized, not greatly inflated; macropleural thoracic segment present (where thorax known); pygidium transversely oval or semicircular, axis extending to border; narrow pygidial borders present, or elevated marginal rim. *C. salopiensis* Callaway 1877, *C. pusilla* (Sars 1835), *C. nericiensis* Wiman 1905 (but with short pygidial axis), *C. oelandica* Moberg 1901, ?*C. bottnica* Wiman 1902, *C. changshanensis* Lu (*in* Lu *et al.* 1976), *C. keguqinensis* Xiang & Zhang 1984.

Shumardia (*Kweichowilla*): Glabella continued forward as broad tongue to cranidial margin, often more or less effaced; glabellar lobes extending backwards, large, drop-like; pygidium transverse, or triangular. *K. minuta* Chang 1964, *K. hongyaensis* Lu & Zhang 1974, *K. lacrimosa* Dean 1973*a*, *K. acuticaudata* Fortey 1980, *K. matchensis* Legg 1976, *S. sagittula* Whittington 1965, *K. forbesi* Stait & Laurie 1983.

Shumardia (*Shumardella*): Cranidium narrow (tr.), glabella parabolic to clavate, not reaching cranidial margin, with anterolateral lobes not greatly projecting, defined by narrow glabellar furrows. *S. bohemica* Marek 1964, *S. polonica* Kielan 1960, *S. scotica* Reed 1903, *S. extensa* Weir 1959, *S. tenacis* Zhou *in* Lu *et al.* 1976. These are all late Ordovician species; the earlier Ordovician *S. phalloides* Fortey 1980 is generally similar, but the glabella has a narrow tongue.

The genus *Eoshumardia* Hupé 1953 is only described from its type species from the Upper Cambrian, *Shumardia orientalis* Mansuy (1916: pl. 1, figs 28a–e). Mansuy's cranidium on fig. 28a shows a prominent occipital spine; the anterolateral glabellar lobes are well developed as in *Shumardia* (*Shumardia*); there may be bacculae in the axial furrows (but from the illustrations it is impossible to tell whether these structures may simply be uncleaned matrix); the posterior cranidial border is wide (exsag.). The pygidium assigned by Mansuy is somewhat elongate (sag.) in the manner of *Shumardia* (*Shumardia*), but with the axis long and narrow and extending almost to the margin. *Eoshumardia* is closest to *Shumardia (Shumardia*) of our usage, but its validity will depend on the redescription of the type species. The genus *Koldinioidia* Kobayashi

1931 has been used by Robison & Pantoja-Alor (1968) and Shergold (1975) to apply to shumardiids with tapering glabella, and glabellar lobes hardly defined. Zhou & Zhang (1984) have redescribed the type species (*K. typicalis*), which is not at all like the species subsequently assigned to *Koldinioidia*; the cranidium is similar to that of *Eoshumardia*. The pygidium figured by Zhou & Zhang is transverse, like that of *Conophrys*.

Subgenus ***SHUMARDIA*** Billings 1862

Shumardia **(*Shumardia*)** ***gadwensis*** sp. nov.

(Figs 18a–i, 20)

HOLOTYPE. Dorsal exoskeleton, It.19573.

PARATYPES. Dorsal exoskeletons: It.19574–5, It.19578; cranidia: It.19576–7, NMW 84.17G.35; pygidium: It.19579.

TYPE LOCALITY AND HORIZON. East side of Nant-y-Gadwen, Llanfaelrhys, Llŷn Peninsula; Middle Arenig (Whitlandian), Biozone of *Gymnostomix gibbsii*, unnamed mudstone formation.

NAME. After the type locality.

OTHER OCCURRENCES. Also known from the Whitlandian mudstones beside track of Dwyrhos Farm, west of Aberdaron, Llŷn Peninsula. In south Wales, *S. gadwensis* occurs in the Whitlandian of Pwlluog, north of Whitesand Bay, St David's, Dyfed, in the Penmaen Dewi Formation, Biozone of *Gymnostomix gibbsii*, and from slightly higher in the section just below the igneous intrusion (loc. 61G). From the Afon Ffinnant Formation, *S. gadwensis* has been recovered from the Cwm Arbont locality (Fortey & Owens 1978: fig. 3), near top of section, and from Afon Ffinnant loc. 16K.

DIAGNOSIS. *Shumardia* (*Shumardia*) with fixed cheeks of transverse width at posterior margin less than that of occipital ring. Pygidium with four axial rings, two deep pairs of pleural furrows, and without border. Exoskeletal surface not granulate.

DESCRIPTION. None of the material of this species is perfectly preserved, but we have several articulated specimens, and taken together the material is adequate to produce the reconstruction shown on Fig. 20, p. 125. It is a useful guide fossil for the Whitlandian, and the only representative of *Shumardia* (*Shumardia*) from undoubted Arenig rocks. For these reasons it seems advisable to name it. The entire specimens are either somewhat stretched or compressed and it is not possible to give a length/width ratio; however the cephalon, thorax and pygidium are about equal in length (sag.). Transverse convexity is considerable, and as usual in shumardiids this is because the cheeks and thoracic pleurae are sharply downturned laterally. On many specimens the lateral edges have collapsed, often in a somewhat lopsided fashion (Fig. 18a). On the least distorted specimens the cranidium is twice as wide as long. The width of the fixed cheek at its widest, at the posterior margin, is a little less than the transverse width of the occipital ring, but the cheeks appear relatively narrower when crushed. Glabella tapers only slightly forwards to drop-like glabellar lobes which are fairly prominent, slightly inflated, and protrude into the side axial furrows. The transverse width of the lobes is a little less than the width of the mid-part of the glabella between them. The front of the glabella is distinctly defined at an obtuse point well inside the margin. The preglabellar furrow is deep on all but the small cranidium in Fig. 18e (on which the front of the glabella can still be seen), which may be attributable to preservation as the occipital furrow is also faint on this specimen. Smaller specimens, including the complete exoskeleton in Fig. 18c, show a small occipital spine which we have not seen on larger cranidia; loss of this spine is presumed to be a feature of later ontogeny. Posterior border furrow deep adaxially, but fading rapidly laterally, as it curves a little forwards. No specimen shows details of the free cheeks. The holotype shows a small baccula on the left side of the glabella; no other specimen is well enough preserved to show this feature.

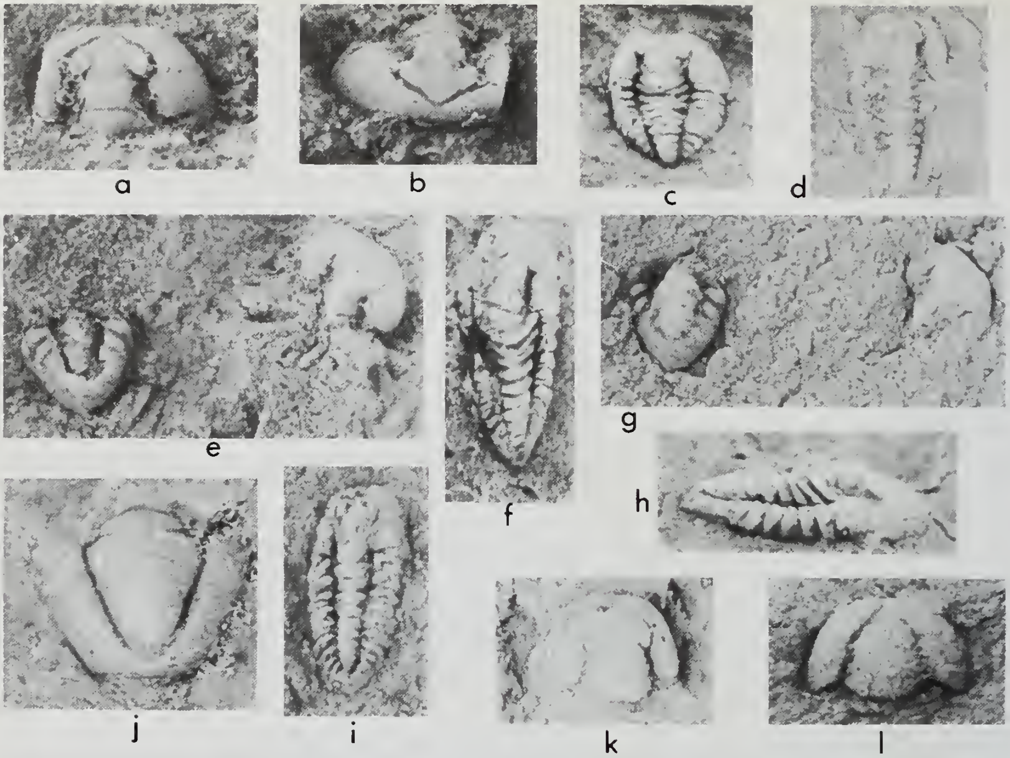


Fig. 18 a–i, *Shumardia* (*Shumardia*) *gadwensis* sp. nov. Middle Arenig (Whitlandian, *G. gibbsii* Biozone); a, b, cranidium, internal mould but well-preserved, with original relief preserved on right side, dorsal and anterior views, Afon Ffinnant Formation, loc. 17, × 12, It.19576; c, cast from **holotype**, somewhat compressed small dorsal exoskeleton, mudstones in Nant-y-Gadwen, Llŷn, north Wales, × 12, It.19573; d, poorly-preserved but not distorted dorsal exoskelton, showing thoracic segments, Penmaen Dewi Formation, near intrusion, north of Whitesand Bay, × 6, It.19575; e, g, pygidium (It.19579) and cranidium (It.19577) on same slab, internal mould and latex cast from counterpart showing undistorted proportions of pygidium; note occipital spine on small cranidium, loc. as Fig. 18a, × 15; f, h complete exoskeleton, slightly distorted by tectonic extension, dorsal and lateral views, locality as holotype, Fig. 18c, × 14, It.19574; i, small exoskeleton, internal mould, Dwyrhos Quarry, Llŷn, north Wales, × 20, It.19578. j–k, *Shumardia* (*Shumardia*) sp. A. Upper Arenig (Fennian); j, pygidium, Pontyfenni Formation, (*S. abyfrons* Biozone), loc. 38, × 14, It.19582; k, cranidium, same locality, × 12, It.19580. l, *Leioshumardia* sp. A; dorsal view, Middle Arenig, Whitlandian, Afon Ffinnant Formation, loc. 17, × 14, It.19583.

The smaller complete specimen apparently shows five thoracic segments. The larger (Fig. 18f) one is not well preserved but shows a ring-like structure behind the occipital ring which could be interpreted as evidence of a sixth segment. A poorly preserved but otherwise undistorted specimen from Whitesand Bay (Fig. 18d) shows six thoracic segments also, as does a small specimen (Fig. 18i) from Dwyrhos Quarry, Llŷn. None is macropleural. The axis tapers backwards after the third segment. Pleural furrows are short, not extending onto the downturned, faceted pleural tips.

Axial taper continues backwards on the pygidial axis: axial furrows enclose an angle of about 30°. Pygidium triangular, slightly wider than long, without border; axis extends to two-thirds pygidial length. There are certainly four axial rings; a faint fifth may be present on the flanks of the rounded terminal piece. There are two pairs of deep pleural furrows, which curve backwards but do not extend to the pygidial margin. The external mould (Fig. 18g) of the best-preserved specimen shows a much shorter third pair of pleural furrows and a suggestion of a fourth pair. Some of the material is well enough preserved to suggest that the exterior surface of the whole exoskeleton was probably smooth, and assuredly not granulate like *S.* (*S.*) *granulosa* Billings.

Discussion. Whittington (1965) has given a full description of the type species *Shumardia* (*Shumardia*) *granulosa* Billings 1862, from the Shumardia Limestone, Quebec. It is generally similar to *S. gadwensis*, particularly with regard to pygidial morphology. Whittington's pl. 16, fig. 12 clearly shows the bacculae adjacent to the base of the glabella which are also present on the holotype of *S. gadwensis*. There are several good specific differences: the glabella of *S. granulosa* is proportionately narrower, width of the occipital ring being less than that of the fixed cheeks; the anterior glabellar lobes are wider (tr.) and more inflated; the pygidium has a flattened postaxial border (this is not true of Whittington's pl. 16, figs 5–9, however); there is a granulate surface sculpture. *S. dicksoni* Moberg & Segerberg (1906: pl. 4, figs 17–22) is less similar to *S. gadwensis*; if the cranidium is correctly assigned the glabella has small anterolateral lobes, a rounded front, and a second pair of glabellar furrows; the pygidial axis is much shorter than that of *S. gadwensis*. *S. lacrima* Koroleva 1964, from the Middle Ordovician of Kazakhstan, has a cranidium very like that of *S. gadwensis*, although the fixed cheeks are narrower and the anterolateral glabellar lobes protrude further into the axial furrows. The pygidium is distinctive: it has five or six pairs of short pleural furrows.

S. (*S.*) *gadwensis*, *dicksoni* and *granulosa* together constitute the concept of *Shumardia* (*Shumardia*) advocated here.

Shumardia **(*Shumardia*)** sp. A

(Figs 18j, k)

Material. Cranidia: It.19580–1; pygidia: It.19582–3.

Stratigraphical range. Upper Arenig (Fennian), Biozone of *Stapeleyella abyfrons*; ?Biozone of *Bergamia rushtoni*.

Localities. Pontyfenni Formation, Pen-y-parc section (loc. 38); Gelli Diogyn (loc. 32a).

Discussion. There is a second species of *Shumardia* (*Shumardia*) from a higher stratigraphical level than *S.* (*S*). *gadwensis*. It appears to be another new species, but the material is far from sufficient to name it formally. The cranidium differs from that of *S. gadwensis* in having even narrower fixed cheeks and in having a depressed area in front of the glabella (like the type species, *S. granulosa*). The pygidium is highly effaced, and in this it differs from all other *Shumardia* (*Shumardia*) spp. Although the axis is long, only one ring is defined, and that incompletely. This is not an artefact of preservation, because both specimens show it, and the axial furrows are of usual depth.

Subgenus *CONOPHRYS* Callaway 1877

Type species. *Conophrys salopiensis* Callaway 1877; Shineton Shales, Shropshire.

Shumardia **(*Conophrys*)** ***crossi*** sp. nov.

(Figs 19a–h, 20)

Holotype. Exoskeleton with right side of cranidium damaged, It.19584.

Paratypes. Imperfect exoskeletons: It.19585–6, NMW 84.17G.36; cranidia: It.19587–8, BGS JP4883–4; pygidia: It.19589–90, NMW 84.17G.37–38.

Type locality and horizon. Loc. 23; Pontyfenni Formation type locality, Upper Arenig (Fennian), biozone of *Bergamia rushtoni*.

Name. For Mr F. Cross, who collected the holotype, and many other specimens figured in this work.

OTHER OCCURRENCES. *S.* (*C.*) *crossi* has only been found in the Pontyfenni Formation of south Wales, biozone of *Bergamia rushtoni*. It is known otherwise from west of Banc-y-felin, at Rushmoor (Survey loc. 38SW Eλ5), at Bron-y-Gaer (Survey loc. 38SW Eλ1), and at Sarn-lâs (loc. 48).

DIAGNOSIS. *Shumardia* (*Conophrys*) with broad (tr.) anterior glabellar lobe, which is hardly pointed and defined by faint preglabellar furrows; bacculae present in axial furrows. Six thoracic segments, no macropleural segment. Pygidial axis exceptionally broad for subgenus, occupying half pygidial width at first ring.

DESCRIPTION. The holotype (Figs 19a–c) is almost undistorted and shows the original convexity. Exoskeleton almost twice as long as wide. This specimen demonstrates that the glabella was turned down with the cephalic edge, but still terminates inside the margin. Other cranidia are all slightly crushed. That in Fig. 19h apparently shows the glabella continuing to the margin as a tongue in the manner of *Kweichowilla* (right side), but this is an artefact of preservation. Glabella occupies just under half cranidial width at occipital ring. Axial furrows are deep posteriorly but shallow abruptly around the anterior glabellar lobe, so that they appear effaced on the more poorly preserved material; the course of the preglabellar furrows can be discerned on internal moulds (Fig. 19d). There are distinct bacculae which constrict the base of the glabella a little. The anterolateral glabellar lobes protrude outwards, but not far beyond the level of the lateral margins of the occipital ring; the furrows defining them are narrow and do not extend more than one-third across the median glabellar lobe. On flattened cranidia the position of the anterolateral lobes is displaced relatively backwards because of the splaying out

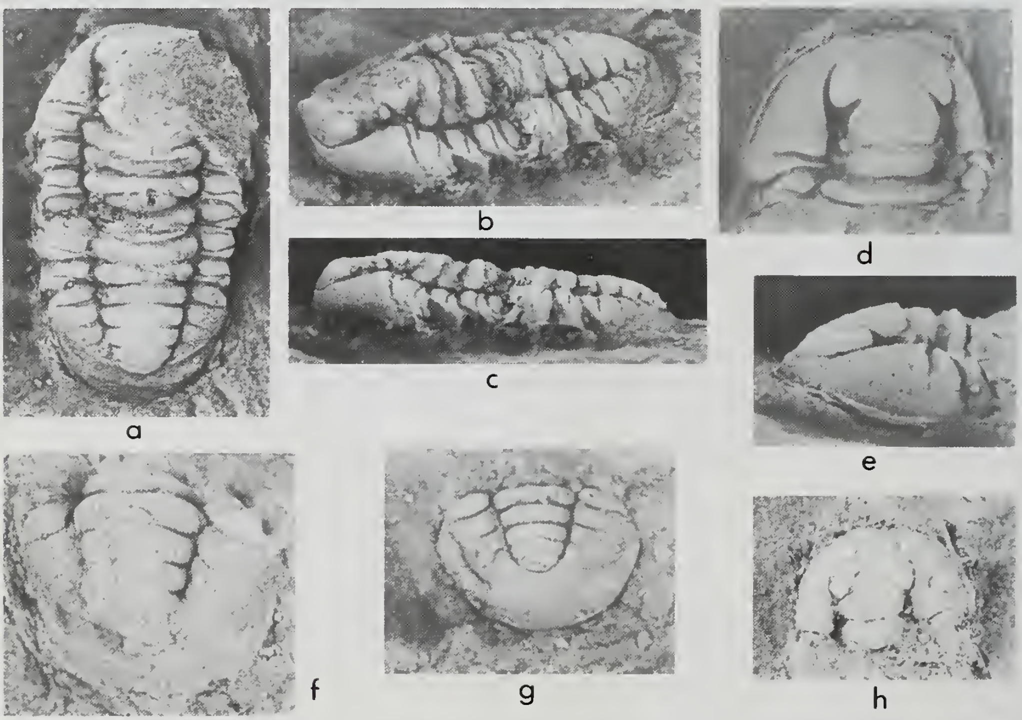


Fig. 19 *Shumardia* (*Conophrys*) *crossi* sp. nov. Upper Arenig, Fennian (*Bergamia rushtoni* Biozone), loc. 23. a–c, **holotype**, incomplete dorsal exoskeleton, dorsal, oblique and lateral views, × 8, It.19584; d, e, cranidium and one thoracic segment, dorsal and lateral views, × 9, It.19587; f, latex cast from natural mould of larger pygidium, × 10, It.19589; g, well-preserved pygidium, × 12, It.19590; h, crushed cranidium, × 8, It.19588.

of the cranidial margin. The front of the glabella is almost bluntly rounded about the mid-line, or with a faint suggestion of a point (Fig. 19d). Posterior border furrow deep, not reaching cranidial margin; border widens laterally.

Thorax with axis nearly three times as wide as thoracic pleurae; we have found no evidence of a macropleural segment. Structure of pleurae typically shumardiid, with depressed front margin fitting beneath preceding pleura, transverse pleural furrows near back of pleura, and deep, downturned facet. Axis hardly tapers backwards.

Pygidia in relief are two-thirds to three-quarters as long as wide (long (sag.) half-ring is excluded); flattened examples may appear a little longer as the postaxial field is extended. The axis is very wide (tr.)—half pygidial width at first ring—and transversely convex, with only gentle backward taper to a broadly rounded termination at about 0·7 of pygidial length (again half-ring excluded). Four axial rings are defined by furrows which are distinctly fainter medially (the fourth may be hard to discern); the first three rings are of equal length (sag.). The three pairs of pleural furrows are progressively shorter backwards, the third pair being very short. In the relief material the postaxial field slopes down to a narrow (sag.) flattened border, which becomes narrower away from the mid-line and does not extend to the anterolateral margins. This may be obliterated on crushed material. The holotype shows the extent of the doublure where it is impressed on the dorsal surface; wide on the mid-line, and narrowing rather abruptly to the second pair of pleural furrows.

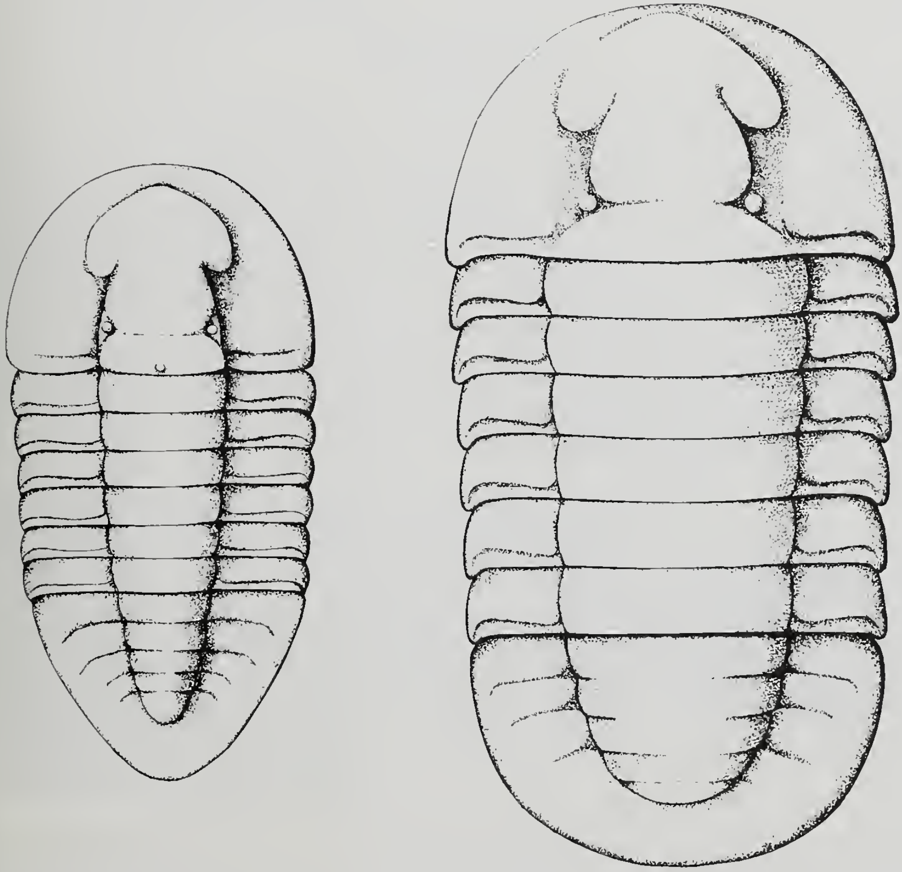


Fig. 20 Reconstructions of *Shumardia* (*Shumardia*) *gadwensis* sp. nov. (left) and *S. crossi* sp. nov. (right); × 18 approx.

Well-preserved material shows a distinctive surface sculpture of irregular anastomosing ridges; around the front margin of the cranidium there are close-set raised lines parallel to the margin. One pygidium (Fig. 19g) shows lines of small tubercles on the hind margin of the axial rings, and a similar sculpture was probably present on thoracic rings.

Discussion. *S.* (*C.*) *crossi* is a distinctive species of *Conophrys*; its wide pygidial axis distinguishes it from all others given in the generic discussion above. Indeed the relatively long pygidium, with a flattened border, is perhaps more like *Shumardia* (*Shumardia*), although it does not have the typical triangular pygidial outline, and the development of the anterolateral glabellar lobes is more like that of most *Conophrys* spp. Tremadoc species of *Conophrys* have a macropleural segment, for example the type species *C. salopiensis* (Fortey & Rushton 1980: figs 16, 17). Its loss in the Arenig may not be important. It is possible that the presence of bacculae may prove a more reliable character to distinguish *Shumardia* (*Shumardia*) which this species shares with *S.* (*S.*) *granulosa* and *S.* (*S.*) *gadwensis*, but there are many shumardiids described which are too imperfect to be sure of this detail. A *Conophrys* of similar age is *S.* (*C.*) *minaretta* Fortey from the Arenig of Spitsbergen (Fortey 1980: pl. 3, figs 1–10); it has an acute front of the glabella, wide cephalic axial furrows, and the pygidial axis, apart from having the usual, relatively narrow proportions of *Conophrys*, also has five axial rings.

Genus ***LEIOSHUMARDIA*** Whittington 1965

Type species. *Leioshumardia minima* Whittington 1965, by original designation.

Leioshumardia sp. A
(Fig. 18l)

Material. Cranidium, It.19583

Occurrence. Arbont, in mudstones with *Shumardia* (*Shumardia*) *gadwensis*, near top of local section. See Fortey & Owens, 1978: fig. 3, loc.17A.

Stratigraphical range. Middle Arenig (Whitlandian), biozone uncertain, possibly *G. gibbsii*.

Discussion. *Leioshumardia* has hitherto been known only from the type species, itself represented by two cranidia. Our single specimen is clearly a different species, but cannot be named formally. Its occurrence in south Wales is nonetheless of interest in showing how off-shelf genera may be widely distributed as early as the Arenig. We have already noted similar species of *Shumardia* (*Shumardia*) and *Hypermecaspis* in eastern North America and south Wales. The Welsh specimen differs from the type species in having a triangular, rather than barrel-shaped glabella, and a weakly defined occipital furrow. The glabella terminates at a point close to, but inside, the cranidial margin, as it does on *L. minima*. There is a superficial similarity between *L.* sp. A and *Clelandia*, especially *C. reliqua* Rushton & Tripp 1979. The sutures on *Clelandia* are not marginal as they are in *Leioshumardia*, and the structure of the cranidial posterior border is of the usual ptychoparioid type. On both characters the Arenig species is like *Leioshumardia* and unlike *Clelandia*.

Family **REMOPLEURIDIDAE** Hawle & Corda 1847

Genus ***GIRVANOPYGE*** Kobayashi 1960

1961*a* *Cremastoglottos* Whittard: 187
1976 *Gamops* Šnajdr: 232
1983 *Nanlingia* Wei & Zhou: 217.

Type species. *Lichapyge*? *problematica* Reed 1906, by original designation.

Discussion. The peculiar genus *Cremastoglottos* was described from the Hope Shales on the basis of cranidia only (Whittard 1961*a*). A year previously Kobayashi had proposed *Girvanopyge* for some pygidia from the Whitehouse Beds of Girvan figured by Reed (1906). There was no way of knowing that these pygidia belonged to the same genus of trilobites as the

Cremastoglottos cranidia until Marek (1977) described a complete specimen from Bohemia. The cranidium and pygidium are both so distinctive that there is no doubt that *Cremastoglottos* is a junior synonym of *Girvanopyge*. Fortey (1981) proposed that *Girvanopyge* (there called *Cremastoglottos*) was allied with the remopleuridids rather than the ellipsotaphrids, and this family placing is adopted here. Marek (1977) noted that the genus *Gamops* Šnajdr 1976 was congeneric with *Cremastoglottos*, with which we concur. Finally, Wei & Zhou (1983) described *Nanlingia* from pygidia only from a cyclopygid biofacies in east China, but without mentioning any of the foregoing. This is a *Girvanopyge* species, closely similar to the type species. An additional species ascribed to *Cremastoglottos* was proposed by Hörbinger & Vaněk (1983), who recognized *Lichapyge*? *problematica* Reed 1906 as a probable *Cremastoglottos*, but without mentioning Kobayashi's genus, of which they may have been unaware. Additionally, a specimen from Germany attributed to *Cyclopyge* by Jentsch & Stein (1961) may prove referable to *Girvanopyge*.

Now that the somewhat lengthy synonymy has been recognised it is clear that *Girvanopyge* is another widespread, circum-Gondwanan genus confined to the cyclopygid biofacies appropriate to its pelagic habits (Fortey 1981: 609). Like many of the cyclopygid genera, it ranges from Arenig to Ashgill with apparently little change.

SPECIES INCLUDED. *G. problematica* (Reed 1906), *G. occipitalis* (Whittard 1961*a*), *G.* aff. *occipitalis* (Marek 1977), *G. mrazeki* (Šnajdr 1976), *G. caudata* (Wei & Zhou 1983), *G. barrandei* (Hörbinger & Vaněk 1983) and *G.* sp. indet. (below).

Girvanopyge sp. indet.
(Figs 21a–c)

STRATIGRAPHICAL RANGE. Upper Arenig, Fennian, biozones of *Bergamia rushtoni* and *Dionide levigena*.

LOCALITIES. Pontyfenni Formation type locality, and Llwyn-crwn, loc. 24. Llanfallteg Formation, type section, 18 m below Arenig–Llanvirn boundary.

MATERIAL. Pygidia: It.19592–3, NMW 84.17G.120; incomplete cranidia: NMW 84.12G.41a, b, It.19594; thoracic segment: It.19595.

DISCUSSION. The poor material of this species is enough to show that it is a new species of *Girvanopyge*, but not adequate to name it. The cranidia are not complete, but clearly show the course of the axial furrow as interpreted by Fortey (1981), with a sharp outward bend in front of the occipital region. Of the two pygidia the smaller example (Fig. 21c) retains one spinose thoracic segment, as do several of the pygidia figured by previous authors (e.g. Wei & Zhou 1983: pl. 72, fig. 9). This specimen is from the Llanfallteg Formation; the posterior pygidial

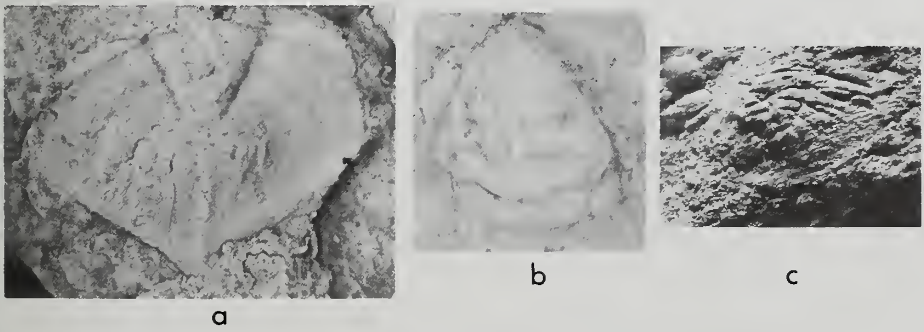


Fig. 21 *Girvanopyge* sp. indet. a, latex cast of pygidium showing median acumination, Upper Arenig, Fennian (*B. rushtoni* Biozone), loc. 24, × 3½, It.19592; b, incomplete, crushed cranidium, horizon as last, loc. 23, × 6, NMW 84.12G.41; c, flattened pygidium and one segment, oblique illumination, *D. levigena* Biozone, Llanfallteg Formation, loc. 52P, × 3, It.19595.

margin appears to be evenly rounded about the mid-line. Two stratigraphically earlier pygidia from the Pontyfenni Formation are better preserved and on these specimens the border is distinctly acuminate, a feature which distinguishes it from all the other *Girvanopyge* species listed above. There is some doubt whether the Pontyfenni and Llanfallteg specimens are conspecific, or whether the difference in the pygidial border is a reflection of a difference in preservation. However, both differ from other *Girvanopyge* spp. in having weakly-defined pleural and interpleural furrows which are only present adaxially; on all the later species the pleural and interpleural furrows are equally well developed, and are directed backwards almost to the pygidial margin. The short, triangular pygidial axis and postaxial ridge on *Girvanopyge* sp. indet. are still distinctive enough to place the generic assignment on a firm basis. A spinose thoracic segment from the Pontyfenni Formation is unlike that of any cyclopygid, and is probably one of the posterior segments of *Girvanopyge* sp. indet. (cf. Marek, 1977).

Family **BOHEMILLIDAE** Barrande 1872

Genus ***BOHEMILLA*** Barrande 1872

TYPE SPECIES. *Bohemilla stupenda* Barrande 1872.

Subgenus ***FENNIOPS*** nov.

TYPE SPECIES. *Bohemilla* (*Fenniops*) *sabulon* sp. nov.

DIAGNOSIS. Subgenus of *Bohemilla* with small palpebral lobes, symmetrically disposed about the 3P glabellar furrows; wide (tr.) frontal glabellar lobe, equal in width to occipital ring; postocular fixed cheeks wider (tr.) than in *Bohemilla* (*Bohemilla*).

NAME. After the Afon Fenni, near Whitland.

DISCUSSION. Species which have been attributed to *Bohemilla* fall into two morphological groups, one of which is recognized here as the new subgenus *Fenniops*. The type species of *Bohemilla* (*Bohemilla*), *B. stupenda* Barrande, has been revised by Whittard (1952) and Marek (1966). The front of the glabella contracts in width in front of the 2P glabellar furrows, coincident with the large palpebral lobes that lie alongside the forward part of the glabella; glabellar furrows are long (tr.), median glabellar lobe less than one-third glabellar width. The relict postocular fixed cheeks are very narrow (tr.), and widen forwards only slightly. Other *Bohemilla* species are very similar in cephalic construction: *B. scotica* Reed 1914, *B. pragensis* Marek 1966 and *B. tridens* Rushton & Hughes 1981. A second group of species ('Gen. indet.' of Whittard, 1952) has shorter palpebral lobes, and a broad frontal glabellar lobe gently rounded about the mid-line. The postocular fixed cheeks are relatively wide (tr.) behind the eyes in this group. This is the basis of the new subgenus *Fenniops*. As well as the type species, which is new, two species are included: *B. praecedens* Klouček 1916 and *B. klouceki* Marek 1966.

The structure of *Fenniops* is presumed to be the more primitive, because the wider fixed cheeks are more comparable with those of other ptychoparioid trilobites, and the occipital ring and glabellar furrows are not as specialized as they are in *Bohemilla* (*Bohemilla*). We believe subgeneric status for *Fenniops* is appropriate, because the *Bohemilla* and *Fenniops* morphologies have overlapping stratigraphical ranges, and do not intergrade. *Bohemilla* (*Bohemilla*) extends from the Llanvirn to the Ashgill, *Bohemilla* (*Fenniops*) from the Arenig to the Llandeilo. However, their shared peculiarities are such that they surely have a common ancestor, which subgeneric classification implies. The earlier members of both *B.* (*Bohemilla*) (Rushton & Hughes 1981: pl. 5, fig. 16) and *B.* (*Fenniops*) (Fig. 22d herein) have a cranidial anterior border, and short thoracic pleurae.

B. (*Fenniops*) *sabulon* is the oldest described bohemillid (although A. W. A. Rushton informs us that he has a still earlier example from the Late Tremadoc), and its glabellar structure is likely to be primitive for the group. It certainly lacks the peculiarities of *B.* (*B.*) *stupenda*, which had suggested to Fortey (1974) that *Bohemilla* might be related to *Opipeuter*, a view he subsequently rejected (Fortey 1981). Marek (1966), Fortey (1974) and Rushton & Hughes (1981) all accepted *Bohemilla* as a remopleuridacean. The glabella of *B.* (*Fenniops*) *sabulon* is consistent with this interpretation because it shows a bulge in width in front of the occipital ring, a typical remopleuridacean feature. The free cheek of *B.* (*Fenniops*) *klouceki* is very like that of some kainellids (e.g. *Pseudokainella keideli*; see Harrington & Leanza, 1957). On the other hand Fortey (1981) regarded the glabellar furrows of *Psilacella* and *Bohemilla* as homologous, and hence both ellipsotaphrines and *Bohemilla* as derived from a common ptychoparioid ancestor. We have suggested below (p. 187) a different interpretation of the glabellar furrows of ellipsotaphrines, one which would allow them to be included within the Cyclopygidae (from which they were excluded by Fortey, 1981). There is no feature of *Bohemilla* which indicates that it should be included within the Cyclopygacea. Deciding the affinities of these specialized pelagic trilobites is particularly difficult in the absence of stratigraphical and morphological intermediates connecting them with known groups, and much depends on the interpretation of features which may have been profoundly modified in response to this mode of life. However, this probably does not apply to the mid-glabellar bulge on *Bohemilla* (*Fenniops*) *sabulon*, and taken with the form of the free cheek, the spinose pygidium and the narrow anterior cranidial border, this tends to favour a remopleuridacean origin for *Bohemilla*. The early species also shows a small interocular cheek (Fig. 22g), a character present on many early *Apatokephalus*-like remopleuridids.

If *Bohemilla* is a remopleuridacean its origin is presumably independent of that of *Opipeuter* Fortey 1974 and *Girvanopyge* Kobayashi 1960 (= *Cremastoglottos* Whittard 1961*a*), two more extraordinary pelagic trilobites with supposed remopleuridacean origins (Fortey 1981). Pelagic morphology arose on five different occasions in the Ordovician; our view on how this may have happened is summarized in Fig. 62 (p. 188), a modification of Fortey, 1981: text-fig. 4.

Bohemilla* (*Fenniops*) *sabulon sp. nov.
(Figs 22a–g, 23)

HOLOTYPE. Cranidium, with three thoracic segments detached, It.15939. Fig. 22b, c.

PARATYPES. Cranidium and partial thorax, It.15940; cranidia: It.15942–5; incomplete exoskeleton NMW 84.12G.31.

TYPE LOCALITY. Type section of Pontyfenni Formation, loc. 23.

STRATIGRAPHICAL RANGE. Found only at the type locality; upper Arenig, Fennian, biozone of *Bergamia rushtoni*.

NAME. Sabulon is a farm near the type locality.

DIAGNOSIS. *Bohemilla* (*Fenniops*) with palpebral lobes about same length as occipital ring; distinct cranidial anterior border. Back margin of postocular fixed cheek subtends an angle of 40°–50° to sagittal line.

DESCRIPTION. Cranidia which are preserved in relief have a rather gentle transverse convexity; the fixed cheeks are disposed horizontally, while the palpebral lobes are elevated. Glabella excluding occipital ring of length equal to width between anterolateral corners; occipital ring about one-quarter length of preoccipital glabella. Course of axial furrows is sinuous: occipital ring tapers forwards, glabella then expands in width past 1P lobe to a maximum at 2P, tapers again past 3P lobe as far as 3P furrow, finally expanding in width once more towards the anterolateral corners of the glabella. The line connecting the anterolateral corner of the glabella with the posterolateral edge of the occipital ring is parallel to the sagittal line, and tangential to the median glabellar 'bulge'. The occipital furrow is narrow, curved rather evenly backwards, very slightly shallower medially. Glabellar furrows narrow, slit-like, extending one-third of the way across the glabellar. 1P curves a little forwards and inwards and has a hooked inner end; 2P is transverse. This makes the 1P lobe wider (exsag.) inwards, while the 2P lobe is widest at its outer end. The 3P furrow is only half as long as the other two, and slopes slightly backwards. Frontal lobe of the glabella, that area in front of the 3P glabellar furrows, is twice as wide (tr.) as long (sag.), and slopes down peripherally into a very narrow but sharply defined preglabellar

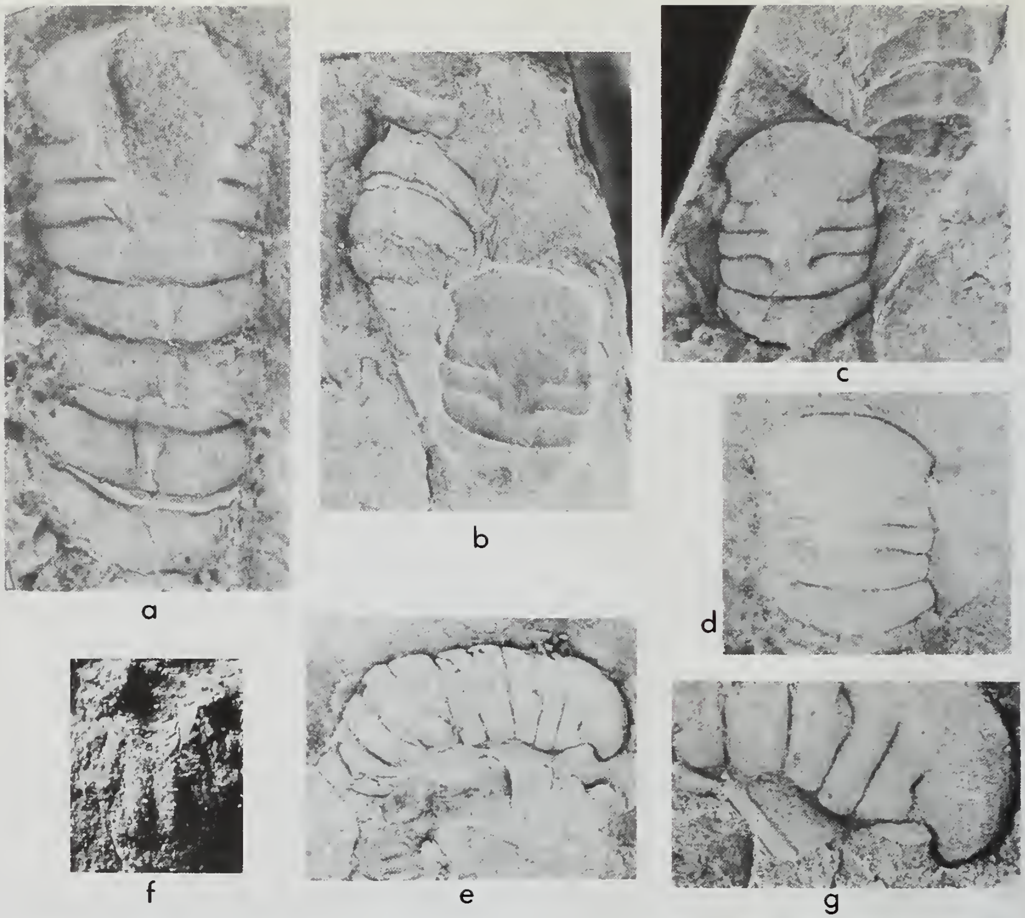


Fig. 22 *Bohemilla* (*Fenniops*) *sabulon* subgen. et sp. nov. Upper Arenig, Fennian, *Bergamia rushtoni* Biozone, loc. 23. a, incomplete cranidium and three thoracic segments, × 6, It.15940; b, c, **holotype** part and counterpart, showing thoracic pleurae, × 6, It.15939; d, cranidium, showing border well, It.15945, × 6; e, f, g, incomplete exoskeleton, NMW 84.12G.31; e, × 4; f, latex cast from pygidium under high contrast illumination, showing displaced seventh thoracic segment, × 12; g, detail of glabella, × 8.

furrow. The specimen shown in Fig. 22d has a slight median dimple. Anterior cranidial border narrow, rim-like, distinctly wider at mid-line. It just curves around the anterolateral corner of the glabella, narrowing into a 'gutter' running to the palpebral lobe. The occipital ring carries a sagittal ridge which extends into a tiny tubercle at the posterior margin; the specimen in Fig. 22d shows a pair of posterior tubercles developed in a position comparable with the occipital spines of *B.* (*Bohemilla*) *tridens* Rushton & Hughes 1981. Palpebral lobe gently curved, sited adjacent to the glabella and symmetrically disposed about the 3P glabellar furrow; a faint, narrow rim is defined, outlining a crescentic interocular area. The palpebral lobe has a length (exsag.) slightly less than that of the occipital ring. Flat, triangular postocular cheek with maximum transverse width between 0·3 and 0·45 of that of adjacent glabella. Posterior margin inclined forwards at an angle between 40° and 50° to sagittal line. Narrow, bevelled posterior border, defined by shallow furrow. Suture runs inwards and forwards from lateral tip of fixed cheek to palpebral lobe, in front of which it follows the 'gutter' to curve round the front margin of the cranidium. Cranidial surface probably minutely granulose. We have not found the free

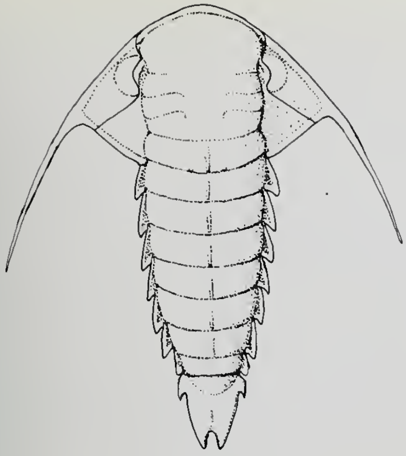


Fig. 23 Provisional reconstruction of *Bohemilla (Fenniops) sabulon* subgen. et sp. nov. It is based on the assumption that NMW 84.12G.31 shows the full complement of thoracic segments, and that the free cheek was like that of *B. (Fenniops) klouceki* and other bohemillids.

cheek. Thoracic segments had minute triangular pleurae (Fig. 22c) like those figured by Rushton & Hughes (1981) on *B. tridens*, with prominent articulating boss adjacent to the axial furrows. Structure of axial rings much like that of occipital ring, with sagittal ridge and faint indication of a pair of tubercles along posterior margin. The most complete specimen (Fig. 22e) shows seven thoracic segments, but the pygidium is detached from the thorax and it is possible that there were additional segments; if this were so it is likely that there would be traces of them on the same bedding plane, since the specimen is otherwise articulated. We have used the seven thoracic segments in our tentative reconstruction, Fig. 23. The pygidium, the first associated with a bohemillid, is not well preserved, but shows a short axis without rings, and clearly a pair of long posterior border spines; there was probably a second, shorter pair outside these but they are not so clearly shown. This suggests a pygidial structure comparable with a remopleuridid such as *Robergiella*.

DISCUSSION. The two species of *B. (Fenniops)* which require discussion are both from the Bohemian Ordovician: *B. (Fenniops) praecedens* Klouček from the Llanvirn and *B. (Fenniops) klouceki* Marek from the Llandeilo. Both have been revised by Marek (1966). Whittard (1952: pl. 33, figs 13–16) illustrated four cranidia under open nomenclature, which Marek subsequently referred to *B. (Fenniops) klouceki*. *B. (Fenniops) praecedens* is quite coarsely tuberculate, especially at the inner ends of the glabellar furrows. The glabella expands forwards such that the frontal lobe is the widest part. *B. (Fenniops) sabulon* is more similar to *B. (Fenniops) klouceki*. The median glabellar expansion is more developed on the latter, such that the width of the glabella behind the palpebral lobes exceeds that across the frontal glabellar lobe. The cranidial anterior border of *klouceki* has apparently become incorporated within the frontal glabellar lobe: Marek (1966: 150) records a 'shallow inframarginal furrow' which may correspond with the preglabellar furrow on *sabulon*. Three specimens figured by Marek (1966: pl. 1, fig. 7; pl. 2, figs 3, 8) show that the palpebral lobes on *klouceki* are slightly longer than the occipital ring, and hence larger than on *sabulon*. The 1p glabellar furrow on *klouceki* is much more hooked at its inner end. Two, perhaps three, of Whittard's cranidia show the 1p furrows united across the glabella. This may be an artefact of preservation, as his figs 13, 14 show obvious crushing, but if so it is puzzling that the 2p furrows are not so conjoined. In any case, the glabellar shape of Whittard's figs 13–15 is more like that of *klouceki* than like *sabulon*.

Family **ASAPHIDAE** Burmeister 1843

Fortey & Owens (1978: 260) discussed in detail the classification and differentiation of certain Arenig and related asaphids, and demonstrated a succession of *Merlinia* species in the Moridunian. Previously it had been assumed that most British Arenig asaphids belonged to '*Ogygia*' or

'*Ogygiocaris*' *selwynii*; this assumption dates from a statement by Thomas (*in* Strahan *et al.* 1907: 7) that 'specimens of *O. marginata* have since been submitted to Mr P. Lake, who compared them with Salter's types of *hybridus* from Henllan Amgoed. He is of the opinion that *O. marginata* and *A. hybridus* are identical, but that both must be referred to *O. selwynii* Salt.'. Whittard (1964: 232) upheld this synonymy. Such an assessment was perfectly reasonable, given the indifferent preservation of the types of *hybridus* and of much of the material from other localities (only recently has our collecting afforded well-preserved specimens). However, it has led to the erroneous correlation in particular of Arenig arenaceous deposits such as those described herein as the Ogof Hên, Abercastle and Blaencediw formations. The correct determination of the asaphids is critical to a proper understanding of the stratigraphy.

It is possible to identify three successive asaphid faunas in the Arenig of south Wales. *Merlinia* characterizes the Moridunian (see Fortey & Owens 1978), *Ogyginus* and *Bohemopyge* the Whitlandian and *Asaphellus* the Fennian. It should be noted that in other areas these genera are found outside these ranges. For instance *Merlinia major* (Salter 1866*a*) ranges throughout the Mytton Flags Formation in the Shelve inlier, which presumably incorporates strata of Moridunian, Whitlandian and Fennian age (see also p. 98). Elsewhere in Britain *Merlinia* has also been recorded from the Llanvirn of the Great Paxton borehole, Cambridgeshire (Rushton & Hughes 1981). *Ogyginus* is unknown from the British Fennian, but is common in the succeeding Llanvirn and Llandeilo (Whittard 1964, Hughes 1979), and *Asaphellus* occurs also in the Tremadoc.

Subfamily **ISOTELINAE** Angelin 1854

Genus ***ASAPHELLUS*** Callaway 1877

(Synonyms: *Asaphelloides* Kobayashi 1937; *Asaphoon* Hutchison & Ingham 1967; *Hemigyraspis* Raymond 1910; *Megalaspidella* Kobayashi 1937; *Plesiomegalaspis* Thoral 1946).

TYPE SPECIES. *Asaphus homfrayi* Salter 1866, by original designation.

DIAGNOSIS. Subisopygous asaphids with flat to slightly concave cephalic and pygidial borders. Glabella subparallel sided, or with slight constriction at level of eyes; axial furrows often effaced but frontal glabellar lobe always clearly demarcated from border. Eyes small to medium-sized at, or slightly in advance of, cephalic mid-length. Preocular facial sutures subparallel and close to glabella, curving strongly adaxially near cephalic margin to meet at mid-line at highly obtuse point; postocular sutures strongly divergent and distally curving strongly backwards and becoming slightly recurved before cutting posterior cephalic margin. Hypostoma with elongate (sag.) oval outline, medially rounded, slightly concave or with small point. Pygidial axis well defined; pleural fields smooth to moderately furrowed, and up to eight pairs of ribs. Inner margin of pygidial doublure subparallel to pygidial margin.

REMARKS. Arenig and Llanvirn asaphid species sharing the characters listed above have been placed in several different genera, in part because it has been fashionable to consider *Asaphellus* as a 'Tremadoc' genus and most of the others as 'Arenig'. We believe that such a division is artificial, and when compared one with the other, the features by which they have been discriminated (e.g. size and position of eye, degree of taper of glabella, whether the posterior margin of the hypostoma is weakly concave or slightly pointed, definition of pygidial pleural ribs) can hardly be considered of higher than specific rank. We therefore follow the similar arguments of Pillet *et al.* (*in* Courtessole *et al.* 1985: 39) in placing such species in *Asaphellus*, and regarding the other names (listed above) as subjective synonyms. *Asaphoon* was based upon four tiny specimens which we think are likely to be meraspides or small holaspides of *Asaphellus*.

Asaphellus whittardi (Bates 1969)

(Figs 24a–h)

1914 *Ogygia* sp.; Cantrill *in* Strahan *et al.*: 15.
1964 *Ogygiocaris murchisoniae* (Murchison); Whittard: 238 (*pars*); pl. 37, figs 12, 13; pl. 38, figs 1–4 [*non* pl. 38, figs 5–11, = *Merlinia murchisoniae*].
1969 *Megalaspidella*(?) *whittardi* Bates: 20, 22.
1978 *Megalaspidella whittardi* Bates; Fortey & Owens: 280.

HOLOTYPE. BGS GSM85363, internal mould of cranidium (Whittard 1964: pl. 38, fig. 3).

TYPE HORIZON AND LOCALITY. Fennian, *D. hirundo* Biozone, Tankerville Flags Formation; Bergam Quarry, Shelve inlier, Shropshire.

MATERIAL. Numerous specimens have been recovered from the type locality (see Whittard 1964: 240); in south Wales the following material is known. From Fennian, *S. abyfrons* Biozone, Cwmfelin Boeth Formation: BGS TCC928/929, incomplete cephalon with seven attached thoracic segments from Survey loc. Carm. 37SW Eλ6, Whitland Abbey; cranidia It.18910, It.18911, free cheek It.18912, pygidia It.18913–15, NMW 84.17G.1a, b, 2a, b, all from locality 36, Cwmfelin Boeth. From presumed early Fennian: cranidium It.18916, from locality 20E, Capel-Dewi.

DIAGNOSIS. *Asaphellus* with moderately inflated glabella, weakly laterally constricted with four pairs of weakly impressed furrows; thoracic and pygidial axes well defined, the latter with 10 rings; pygidial pleurae with 6–7 pairs of well-defined ribs; interpleural furrows weak and shallow; broad, concave pygidial border.

DESCRIPTION. Glabella, including occipital ring, ranges from about 0·8 times as wide as long on large specimens to 0·6 times on smaller ones. From the posterolateral corners it first widens slightly to achieve its greatest posterior width at about half the distance to the posterior end of the palpebral lobe. It then narrows as far as a point opposite the posterior end of the palpebral lobe and then widens again to achieve its greatest anterior width (tr.), which is about the same as its greatest posterior width, just anterior to 3P furrows. A small sagittal tubercle is present opposite 1P lobes. In sagittal profile it is almost flat, the frontal lobe curving down gently and merging insensibly with the weakly concave preglabellar area, which is 0·15 times length (sag.) of glabella on large specimens, 0·25 on smaller ones. In transverse profile it is gently and evenly curved. Four pairs of weakly impressed muscle areas: 1P originates close to the axial furrow opposite anterior end of palpebral lobe, and directed obliquely forwards; 2P subparallel, a short distance behind 1P; 3P and 4P close together and of similar length and depth, opposite posterior part of palpebral lobe and directed nearly transversely. Lateral parts of occipital furrow indicated by weak, transversely elongated depressions similar to 3P and 4P and directed weakly obliquely backwards. Axial furrow shallow, deepest at its posterior extremity and in the stretch opposite the palpebral lobe.

Palpebral lobe ranges from being 0·2–0·3 of length (sag.) of glabella plus occipital ring on small specimens to 0·12 on large ones, its outer margin elevated almost to height of sagittal region of glabella. Eye apparently narrow and crescentic. Preocular sutures more or less parallel, converging opposite frontal lobe of glabella in an even curve, meeting to form an obtuse point sagittally. Preocular section of fixed cheek markedly narrower than preglabellar area. Postocular suture defines a broad, subtriangular cheek. Pleuroccipital furrow wide and deep, defining narrow posterior border. Genal spine broad-based, with a broad, shallow median furrow which runs into a very weak lateral border furrow, which like preglabellar furrow is indicated only by a change of slope. Cephalic doublure broad, extending inwards almost as far as outer edge of eye, with fine, subparallel terrace lines (Fig. 24b; Whittard 1964: pl. 38, fig. 2). Reduced in breadth at hypostomal suture. Hypostoma unknown.

Thorax with eight segments, axis narrow, well defined and scarcely narrowing backwards. Pleurae with rather shallow, oblique pleural furrows which are terminated laterally beyond the fulcrum by the posterior edge of the facet. Ends of pleurae falcate. Whittard (1964: 240) noted a panderian protuberance, succeeded posteriorly by an apparent panderian opening, on each pleura (Whittard 1964: pl. 38, fig. 4).

Pygidium subparabolic. Axis long, narrow, well defined and tapering evenly backwards and terminating at the inner edge of the border. Ten rings present, separated by broad ring furrows that deepen laterally, producing the effect of paired furrows. Pleural areas gently convex with six or seven pairs of ribs with deep pleural furrows, the depth accentuated on internal moulds; ribs flat-topped, with weak interpleural furrows extending along their length. Both pleural and interpleural furrows terminate at inner edge of border. Border concave and broad, rising steeply

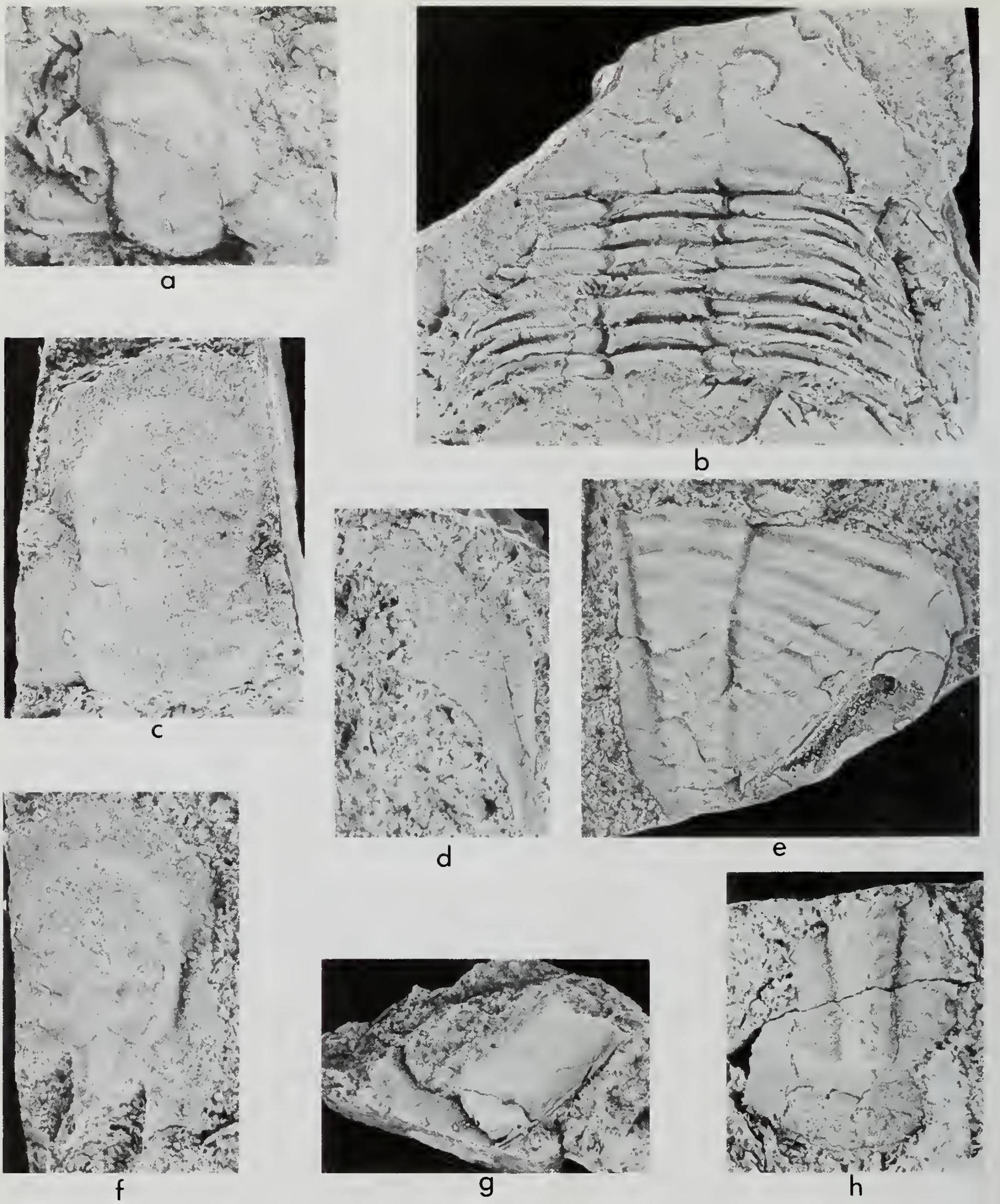


Fig. 24 *Asaphellus whittardi* (Bates 1969). Upper Arenig, Fennian Stage, *S. abyfrons* Biozone. a, cranidium, internal mould, × 2, It.18916, loc. 20E, Capel-Dewi; b, incomplete cephalon with seven attached thoracic segments, × 1·5, BGS TCC928, Cwmfelin Boeth Formation, Whitland Abbey. c–h, Cwmfelin Boeth Formation, loc. 36, Cwmfelin Boeth: c, cranidium, internal mould, × 1·25, It.18910; d, free cheek, latex cast of external mould, × 2, It.18912; e, incomplete pygidium, internal mould, × 1·5, It.18913; f, incomplete cranidium, internal mould, × 2, It.18911; g, incomplete pygidial doublure, internal mould, × 1·5, It.18914; h, incomplete pygidium, internal mould, × 2·5, It.18915.

up towards pleural lobes. Pygidial doublure broad, ventrally convex, well seen on a fragmentary specimen from Cwmfelin Boeth (Fig. 24g).

REMARKS. Whittard (1964: 238) conflated *A. whittardi* with the Moridunian species *Merlinia murchisoniae*, but Bates (1969: 20) demonstrated the distinctness of Whittard's Tankerville Flags material. We have identified this species in the basal Fennian in the Whitland and Carmarthen areas and the description above includes both these and the Shelve specimens. The presence of *A. whittardi* in the early Fennian implies that the Tankerville Flags may be of early Fennian age. It is one of the few Tankerville species so far identified in south Wales; others such as *Pricyclopyge binodosa eurycephala* are longer-ranging.

A. whittardi is distinctive among *Asaphellus* species in having well-defined pygidial axial rings and pleural furrows. In overall morphology it closely resembles *A. graffi* (Thoral 1946), type species of *Megalaspis* (*Plesiomegalaspis*) from the 'lower middle Arenig' of Cabrières, Montagne Noire, but the latter differs in having a less inflated glabella, the eye proportionately further from the lateral margin, a longer preglabellar area, a broader pygidial axis and ill-defined axial rings and pleural ribs (except in small specimens). Thoral recognized several varieties of *graffi* as well as other asaphid species from the same locality. The name *graffi* was applied to large specimens in which the pygidial pleural furrows are more or less effaced; 'varieties' such as *lata* and *major* we suspect to be intraspecific variants. *Plesiomegalaspis*? *convexilimbata* Thoral (1946: 72; pl. 9, fig. 3; pl. 13, fig. 2; pl. 15, fig. 6) and *P. angustirhachis* Thoral (1946: 71; pl. 16, fig. 2) are based upon smaller specimens with better-defined pleural ribs; *Megalaspis mucronata* Thoral (1946: 56; pl. 7, fig. 2) and *M. striatula* Thoral (1946: 58; pl. 7, figs 3(?), 5) are based on even smaller ones. These appear to us simply immature *A. graffi*; Gigout (1951: 282; pl. 2, figs 1–5) figured similar small specimens from the Arenig between Casablanca and Mazagan (El Jadida), Morocco, as *Plesiomegalaspis graffi*. In none of these are the pygidial axial rings and pleural ribs as well defined as in *A. whittardi*, but a pygidium figured by Thoral (1946: 89; pl. 15, fig. 2) as *Ogygiocaris*? *inflexicostata* is very similar, differing only in having a narrower border, relatively broader pleural areas and more (9) pygidial pleural ribs; if not conspecific it must be very closely related.

A new *Asaphellus* species discovered recently in sandstones of possible Whitlandian age in the Bangor area by A. Beckly (personal communication 1984) is clearly distinct from *A. whittardi*, although it generally resembles *A. graffi*. A further *Asaphellus* has been recovered from siltstones of controversial (Tremadoc or Arenig) age near Carmarthen (Cope *et al.* 1978: 196; Owens & Fortey 1982: 253). This specimen (NMW 78.1G.1) is also similar to *A. graffi*, but has a smaller eye and prominent terrace lines on the thoracic axis; the pygidium is unknown.

Asaphellus lugneensis Pillet, Courtessole & Vizcaino (*in* Courtessole *et al.* 1985: pl. 4, figs 1–12; pl. 5, figs 1–8) from the Arenig Grès du Foulon Formation, Montagne Noire, is also similar to *A. whittardi*, but is distinguished by its shorter (sag.) preglabellar field, more distinct lateral border furrow and more effaced pygidial axial rings and pleural ribs.

Subfamily **NIOBINAE** Jaanusson 1959

Genus ***BOHEMOPYGE*** Přibyl 1950

TYPE SPECIES. *Ogygia discreta* Barrande 1872, by monotypy.

DIAGNOSIS. Niobine asaphids which may attain a large size. Differing from *Niobella* in relatively narrow cephalic and pygidial axis, broader preglabellar field, and wider (tr.) postocular cheeks. Differing from *Gog* in having almost triangular to transverse pygidium with relatively well defined border, and without scalloped inner edge of pygidial doublure. Differing from *Niobina* in having a notched hypostoma.

DISCUSSION. *Bohemopyge* was hitherto known from *B. discreta* from the Llanvirn of Bohemia. It is one of a group of early Ordovician niobines differing from *Ogygiocaris* and *Ogygiocarella* in having a well-defined occipital ring. As the diagnosis indicates, it is very close to the Tremadoc genus *Niobina*, and the only important difference relates to the unforked hypostoma of the latter, a primitive character of general occurrence in early asaphids. The relatively complete development of interpleural furrows on *Niobina davidis* is scarcely a generic character. Jaanusson (*in* Harrington *et al.* 1959: O350) states that the pygidium of *Bohemopyge* lacks a border. This is a puzzling assertion, because the original of Barrande (1872: pl. 7, fig. 23) clearly shows one, as does the specimen of Novák & Perner (1918: pl. 3, figs 1, 2; re-illustrated by Horný & Bastl, 1970: pl. 5, fig. 6). Presumably the statement was based on Perner's drawing which does not well represent the border. The known material of *B. discreta* is all small; assigning *B. scutatrix* (Salter) to the genus means that some large trilobites are included, and some of the differences they show from *B. discreta* may be ontogenetic. Short genal spines are present on *B. discreta*, being absent from *B. scutatrix*, but it is possible that they were reduced later in ontogeny. In any case, the presence or absence of genal spines is not considered a generic character. When undistorted, large pygidia of *B. scutatrix* have a triangular outline, which is different from the posteriorly truncate to gently rounded outline of *Niobella*. The cephalon of *B. scutatrix* is very like that of the type species of *Gog*, *G. catillus* Fortey 1975 from the Arenig of Spitsbergen, but the pygidium of that genus has a distinctively scalloped dorsal surface along the paradoublural line which might indicate its closest relatives are to be found in *Ogygiocaris* rather than *Bohemopyge* or *Niobina*. Přibyl & Vaněk (1980) erected a genus *Araiocaris* based on *Ogygiocaris araiorhachis* Harrington & Leanza 1957 from the Arenig of Argentina. This form is also similar to *Bohemopyge*; it has more segments in the pygidial axis and the occipital structure may be more like that of *Ogygiocaris*. Přibyl & Vaněk considered differences from *Ogygiocaris* in their original discussion, but did not discriminate *Araiocaris* from *Bohemopyge* or any other asaphid.

There are thus five trilobite generic names within this closely-knit group, which is more than the morphological variation really allows: *Niobella*, *Niobina*, *Bohemopyge*, *Araiocaris* and *Gog*. For the moment we retain *Bohemopyge* as the closest match for the Welsh species, while recording that it may be possible to include *Bohemopyge* within an enlarged concept of *Niobina* if one allows the same kind of hypostomal variation within this genus as in *Niobe* and *Niobella*.

Bohemopyge scutatrix (Salter 1859)
(Figs 25–28)

1859 *Ogygia peltata* Salter *in* Murchison: 54 (nom. nud.).
1859 *Ogygia scutatrix* Salter *in* Murchison: 52; Fossils (9) 1.
1866*a* *Ogygia peltata* Salter; Salter: 135–136; pl. 17, figs 8–10.
non 1866*a* *Ogygia scutatrix* Salter; Salter: 133–134; pl. 17, figs 11–13.
1866*b* *Ogygia peltata* Salter; Salter *in* Ramsay; 313: pl. 12, fig. 8.
1867 *Ogygia peltata* Salter; Salter: 177–178; pl. 25*, figs 1–4.
1867 *Ogygia bullina* Salter: 178; pl. 25*, fig. 5.
1875 *Ogygia peltata* Salt.; Hicks: 176.
1928 *Ogygia selwyni* (Salter); Matley: 491.
1931 *Niobe* (*Niobe*) *peltata* (Salter) Reed: 446.
1946 *Ogygia scutatrix* Salter; Lake: 336.
1964 *Ogyginus peltatus* (Salter) Whittard: 246.
1984 *Gog peltata* (Salter); Fortey *in* Whittington *et al.*: 21.

NOMENCLATURE. This species has usually been referred to *Ogygia peltata* Salter, 1866. However, Lake (1946) pointed out that the single specimen figured by Salter in 1859 as *O. scutatrix*, which is from Whitesand Bay, Dyfed, is the same as that subsequently used by Salter (1866*a*: pl. 17, fig. 8) as the type of *O. peltata*. In his text Salter (1866*a*: 133) definitely excluded the originals of his pl. 17, figs 9, 10 from his '*peltata*' there, so there is little choice but to conclude that *O. peltata* is an objective synonym of *O. scutatrix*. Salter had evidently intended *peltata* to apply to the Arenig species from south Wales, and *scutatrix* to the Tremadoc species from north Wales, now known as *Niobina davidis* Lake, 1946. But we are obliged to follow the *Rules of Zoological Nomenclature* in using the name *scutatrix*.

HOLOTYPE. BGS GSM7618. Incomplete dorsal exoskeleton from the old slate quarry north of Whitesand Bay; Penmaen Dewi Formation, Whitlandian. Original of Salter, 1859. Fig. 25a.

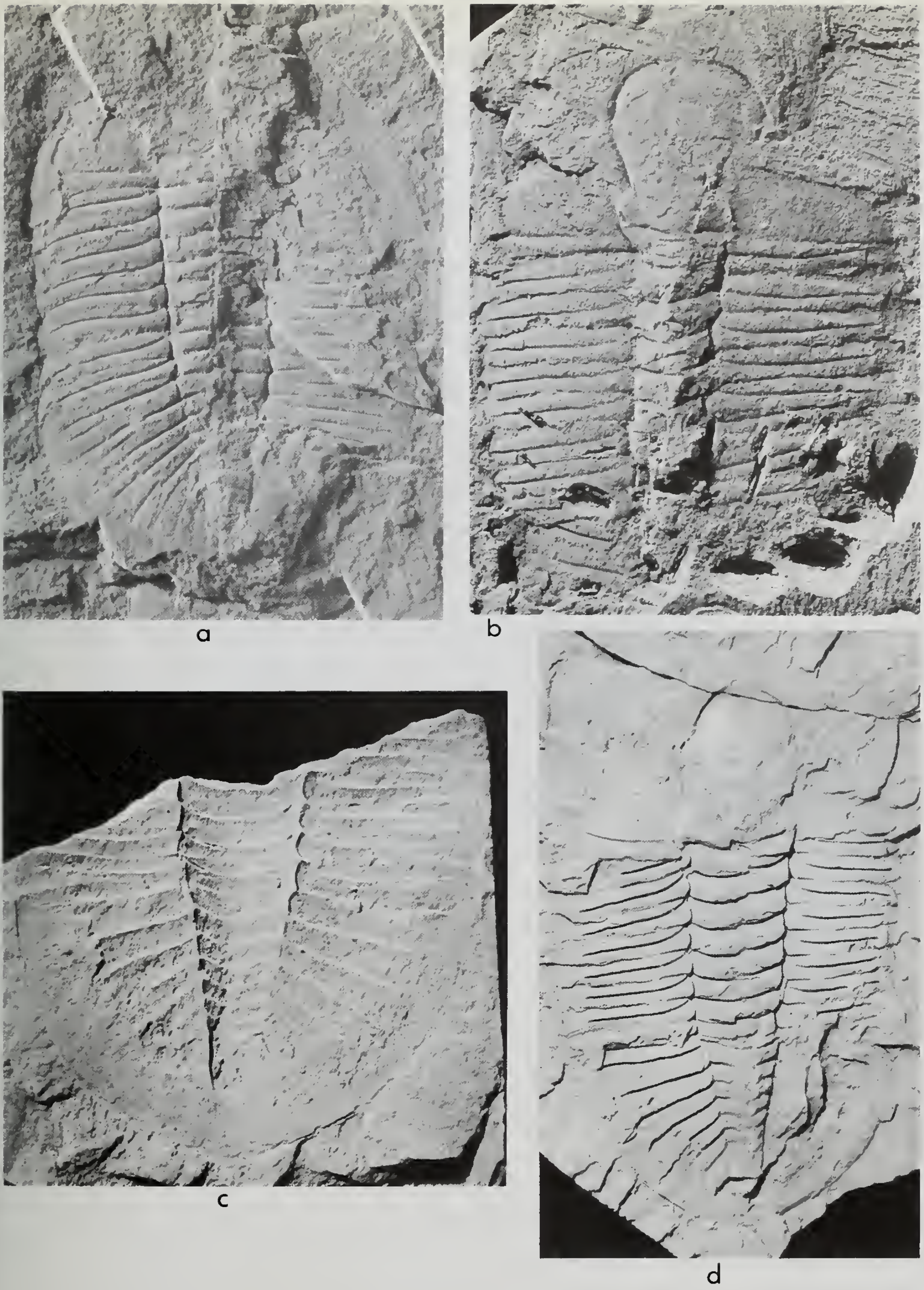


Fig. 25 *Bohemopyge scutatrix* (Salter 1859). Middle Arenig, Whitlandian (*G. gibbsii* Biozone), Penmaen Dewi Formation, slate quarry at Pwlluog, north of Whitesand Bay, St David's, Dyfed. a, holotype, imperfect dorsal exoskeleton, original of Salter, 1859, × 1, GSM 7618; b, small imperfect axial shield with dislocation of right side over thorax, type of *Ogygia bullina* Salter 1867, × 2, SM A16728; c, external mould of undistorted but flattened large pygidium and partial thorax, paradoublural line on left, × 2, SM A44344; d, small axial shield, flattened but otherwise undistorted, × 1, SM A44343a.

FIGURED MATERIAL. Dorsal exoskeletons and axial shields in varying degrees of completeness: BGS GSM7616; SM A16728–30, A33438, A44340, A44343–4; I.14284; NMW 27.110.G251; hypostoma: BGS GSM12873; cranidium: NMW 27.110.G253.

DIAGNOSIS. *Bohemopyge* with triangular pygidium on which interpleural furrows are present, but do not extend to axial furrows.

LOCALITIES. This is a widespread guide fossil to Whitlandian rocks. Most of the specimens in Museum collections derive from the type locality, north of Whitesand Bay in the Penmaen Dewi Formation. In south Wales, it has also been recovered from the Whitland Abbey Member of the Colomendy Formation (loc. 27, NMW 84.17G.39), from the Rhyd Henllan Member of the Colomendy Formation (loc. 47A, NMW 84.17G.40) and from the equivalent of the Whitland Abbey Member in the stream immediately west of Capel-Dewi, east of Carmarthen (loc. 20F). In north Wales, it is confined to the Llŷn Peninsula, where it has been recovered from two localities: mudstones in east side of Nant-y-Gadwen, and mudstones and shales in the track south of Dwyrhos Farm, Aberdaron.

STRATIGRAPHICAL RANGE. Whitlandian (M. Arenig), Zone of *Gymnostomix gibbsii*.

DESCRIPTION. Salter's specimens from north of Whitesand Bay are large, flattened examples, with the indifferent preservation usual from that locality. Relatively well preserved specimens from north Wales are mostly smaller, some in relief, and such differences as there are from the type material can be attributed to the style of preservation. Whole exoskeletons are about 1·7 times as long as wide, with the cephalon, thorax and pygidium of equal length (sag.). Convexity is low (sag., tr.), the whole axis gently convex with a gentle downward slope on the pleural regions. Cephalon 0·6 times as long as wide. Cranidium twice as wide at posterior margin as at palpebral lobes. Glabella (including occipital ring) up to twice as long as wide at mid-length, but often somewhat less. Glabellar shape is a little variable, which may be partly attributable to preservation. The least distorted example (Fig. 28b) is fusiform with a truncately rounded anterior lobe; axial furrows are subparallel, with a slight expansion in front of, and a slight taper before, the palpebral lobes. Axial furrows are well defined, except at the bacculae, where they almost disappear. Occipital ring invariably well defined by deep occipital furrow, which is somewhat backward-curved medially. Some examples (Fig. 27b) have a glabella which is more obviously truncate at the front. The holotype of *Ogygia bullina* Salter, 1867, has an apparently subcircular frontal glabellar lobe. This is a small, ill-preserved specimen, and the right fixed cheek (and the thoracic pleurae behind) has been displaced towards the axis, thereby obscuring the right posterior part of the glabella. It is this displacement which produces an apparently narrow axis and distorts the shape of the glabella. All other features are those of *scutatrix*, and we regard this specimen as an unusually preserved example of that species, and *bullina* as a subjective synonym of *scutatrix*. Glabellar furrows are obscure in available preservation but what can be seen on the best-preserved glabella (Fig. 28b) are of typical niobine pattern (compare Fortey 1975: pl. 2, fig. 1; Horný and Bastl 1970: pl. 5, fig. 6). Palpebral lobes close to glabella, anterior ends almost reaching axial furrow, small, only about one-sixth glabellar length. The transverse line connecting the anterior limits of the palpebral lobes is at cephalic mid-length. Sutures diverge at 80° to sag. line behind the eyes, and only curve backward at the outer one-third of the fixed cheeks to cut the posterior margin at a right angle. Anterior branches of facial sutures diverge at a lesser angle in front of the palpebral lobes (30°–40°) before curving round the anterior cranidial margin to meet on the mid-line in an obtuse point. The preglabellar field so defined is about one-sixth glabellar length, and is flat. The wide postocular cheeks are about the same width (tr.) as the occipital ring; posterior border widens (exsag.) laterally.

Salter originally (1859, 1866*a*) inferred a genal spine on the free cheek; later (1867) he portrayed a rounded genal angle, which we believe is correct. No specimens are well enough preserved to show the eye. Doublure (Fig. 28a) very wide beneath the free cheek and narrowing around the preglabellar furrow as is usual in niobines, carrying about twelve terrace lines parallel to its margin. Some specimens (Fig. 27a) show the trace of the median sutures. One

Fig. 26 *Bohemopyge scutatrix* (Salter 1859). Middle Arenig, Whitlandian (*G. gibbsii* Biozone), Penmaen Dewi Formation, slate quarry at Pwlluog, north of Whitesand Bay, St David's, Dyfed. a, large, imperfect axial shield showing doublure on pygidium, × 1, GSM 7616; b, hypostoma, × 1, GSM 12873.

quite well preserved hypostoma (Fig. 26b) is typical of niobines, being very like that of *Niobe emarginula* (Tjernvik 1956: pl. 4, fig. 15). The median notch is hardly developed, but it is certain that there was no median acumination as in *Niobina*. The apparently rather transverse attitude of the maculae may be an artefact of flattening.

Neither the hypostome nor the dorsal exoskeletal surface shows consistent evidence of sculpture. Niobines frequently have fine exoskeletal lines and ridges, and their apparent absence on most specimens may be a matter of their lack of preservation in argillaceous rocks. One of the north Wales relief specimens has indications of such fine ridges (Fig. 28d).

Thorax with axis only slightly tapering backwards, width less than that of pleurae. Salter abandoned a distinction between forms with relatively wide axis and those with a narrower axis

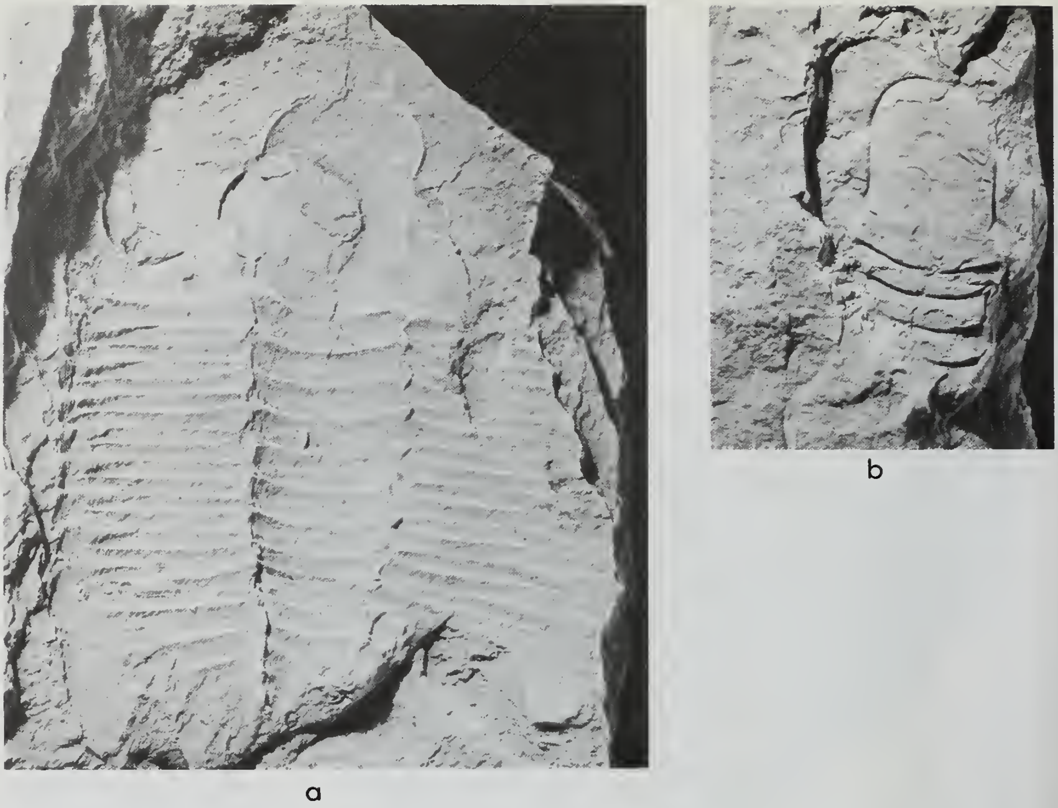


Fig. 27 *Bohemopyge scutatrix* (Salter 1859). Middle Arenig, Whitlandian (*G. gibbsii* Biozone), Penmaen Dewi Formation, slate quarry at Pwlluog, north of Whitesand Bay, St David's, Dyfed. a, external mould of imperfect dorsal exoskeleton, showing median suture and slightly truncate glabella, original of Salter 1867: pl. 25*, fig. 1 (as *Ogygia peltata*), × 2, SM A16729; b, glabella and part of thoracic axis, × 1, SM A33438.

(allegedly female and male), recognizing the variability in this character. The largest specimens have axial width more closely approaching pleural width. Deep pleural furrows almost bisect the pleurae and run nearly to their tips. Tips of pleurae of anterior segment are bluntly rounded; posterior segments acquire short but distinct spines.

Pygidium when undistorted always has a distinctly triangular outline, but a little transverse extension will destroy this (Fig. 28a). Pygidial length/width ratios fall in the range 0·51 to 0·75 for less distorted material; the smallest ratio belongs to the largest specimen. The narrow axis always occupies less than one-third, and on some specimens less than one-quarter anterior pygidial width, and continues gentle backwards thoracic taper to rounded tip at 0·8 of pygidial length. Eight axial rings are discernible, occasionally a faint ninth, and the less flattened material shows that the terminal piece was distinctly elevated above the border. Eight pairs of pleural furrows, with a short ninth pair adjacent to the terminal piece, deep and narrow and running to border. Interpleural furrows are much weaker, and correspond to the outer parts of the pleural furrows only; on some flattened specimens they may be almost obliterated. Transverse extension (Fig. 28a) tends to overdeepen them. Border not sharply defined, especially laterally, and may have been gently sloping behind the axis rather than horizontal. Doublure of slightly less width than that of pygidial axis, concave inner margin over which tips of pleural furrows pass, and with about 12 terrace lines. Axial half rings appear to increase in length progressively (sag.) forwards from pygidial half ring.

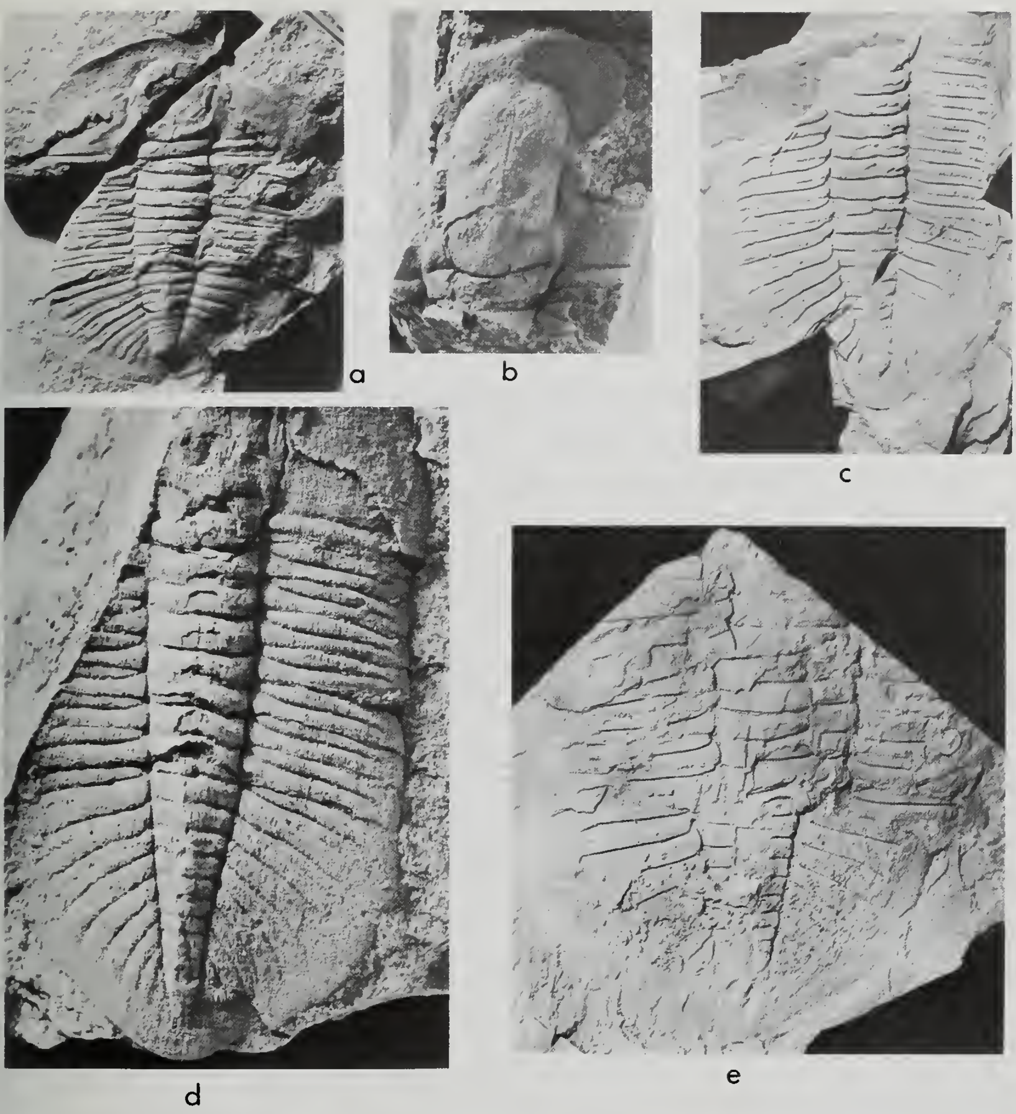


Fig. 28 *Bohemopyge scutatrix* (Salter 1859). Middle Arenig, Whitlandian. a, small exoskeleton in partial relief, slightly extended transversely, which exaggerates pygidial interpeural furrows and increases resemblance to *Niobina*, Nant-y-Gadwen, Llanfaelrhys, Aberdaron, Llŷn, north Wales, Whitlandian mudstones, probably *G. gibbsii* Biozone, × 1, NMW 27.110.G251; b, well-preserved incomplete cranidium in relief, same locality, × 2, NMW 27.110.G253; c, small incomplete dorsal exoskeleton, in relief, showing slightly acuminate pygidial margin, mudstones below Dwyrhos Farm, Aberdaron, Llŷn, probably *G. gibbsii* Biozone, × 2, I14284; d, incomplete axial shield, flattened but undistorted otherwise (compare Fig. 28c), *G. gibbsii* Biozone, Penmaen Dewi Formation, slate quarry at Pwlluog, north of Whitesand Bay, St David's, Dyfed, × 0·5, SM A44340; e, large pygidium retaining posteromedian acumination, but more transverse than Fig. 28d, same locality, original of Salter 1867: pl. 25*, fig. 4, × 0·5, SM A16730.

DISCUSSION. As discussed above, *B. scutatrix* is morphologically intermediate between *Niobina davidis* and *Bohemopyge discreta*. Apart from the difference in the hypostoma, which is pointed in *N. davidis*, the Tremadoc form has consistently longer interpleural furrows on the pygidium, which extend to the axial furrows. The pygidial doublure is also wider (Lake 1946: pl. 47, fig. 2). The type species of *Bohemopyge* apparently lacks pygidial interpleural furrows entirely (Barrande 1872: pl. 7, fig. 23) and is more transverse; the pygidial border widens backwards slightly but is not pointed medially. Cranidia of *B. scutatrix* and *B. discreta* are nearly identical; better-defined glabellar furrows on the latter (Horný & Bastl 1970: pl. 5, fig. 6) are probably because of the superior preservation of Bohemian material. The presence of genal spines on *B. discreta* is not necessarily of importance, because the known material is small, and asaphid genal spines often become shorter during ontogeny (e.g. Fortey 1980: 260).

Whittard (1964) placed *scutatrix* ('*peltata*') in *Ogyginus*. The cranidium, however, is so typically niobine, especially with regard to the good definition of the occipital ring and the sharply defined preglabellar field, that such an assignment is likely to be incorrect.

Subfamily **OGYGIOCARIDINAE** Raymond 1937

Genus ***OGYGINUS*** Raymond 1912

TYPE SPECIES. *Asaphus corndensis* Murchison 1839, by original designation.

DIAGNOSIS. Preocular suture intramarginal but may run very close to margin in some individuals (Hughes 1979: 126); glabella flask-shaped, widest (trans.) across frontal lobe; up to three pairs of weak muscle impressions; occipital ring ill-defined; anterior border narrow (sag.), flat or weakly convex; cephalic border furrow crosses onto preocular cheek only in early species, where it is weak, but typically terminates at the preocular facial suture; hypostome with entire posterior margin, which is acuminate; thoracic segments typically with Z-shaped or zetoidal axial furrows; pygidial axis up to 11 rings; pleural areas with 7–9 pairs of pleural ribs, pleural furrows typically deep and broad, interpleural furrows when present are weak.

REMARKS. Hughes (1979: 122) followed the diagnosis of Whittard (1964: 245), but we have found it necessary to modify it here in order to include Arenig species and to exclude those characters common to many other asaphids. Hughes (*op. cit.*) gave the stratigraphical range of the genus from the Lower Llanvirn to the upper part of the Lower Llandeilo and noted its occurrence in Wales, Shropshire and Brittany, regarding records from elsewhere as either very tentative or invalid.

Several Arenig species are attributable to *Ogyginus*; they are *O. hybridus* (Salter 1866*a*) and *O.* sp. indet. (see below) from south Wales, *O. armoricanus* (Tromelin & Lebesconte 1876) from the Grès Armoricain supérieur, Brittany (Henry 1971: 66, pl. 1, figs 1–11; 1980: 37, pl. 1, figs 4, 5, 7), *O. terranovicus* Dean (*in* Dean & Martin 1978: 15; pl. 5, figs 4–9; pl. 6, figs 1–7; pl. 7, figs 1–4) from the Wabana Group, Bell Island, eastern Newfoundland, *O. planus* (Thoral 1946: 86; pl. 11, fig. 6; pl. 15, fig. 7) from the 'lower middle Arenig', Montagne Noire, and *O. orbensis* Pillet, Courtessole & Vizcaino (*in* Courtessole *et al.* 1985: 44; pl. 6, figs 1–8) from the Grès de la Cluse de l'Orb and Grès du Foulon formations, Montagne Noire. The earliest of these are *O. planus*, *O. orbensis* and *O. hybridus*; Courtessole *et al.* (1985) gave the age of the two former as lower Arenig, but by analogy with the stratigraphical occurrence of *O. hybridus* in the Whitlandian, these species may also be of a similar age; this can only be resolved when the correlation between Wales and the Montagne Noire becomes better understood. The oldest *O. terranovicus* occur with graptolites indicating an horizon near the top of the *D. extensus* Biozone (Dean *in* Dean & Martin 1978: 3), suggesting equivalence to the later Whitlandian, whilst *O. armoricanus* is probably of a similar age (Henry 1980: 223). At Cwm yr Abbey, in the stratotype section for the base of the Whitlandian, *O. hybridus* occurs only a short distance above the youngest *Merlinia rhyakos* (Fortey & Owens 1978), and the ranges of the two species probably overlap in the basal few metres of the Whitlandian. The name *hybridus* is more apposite than Salter can ever have imagined, for this species has characters typical of both *Ogyginus* and *Merlinia*; of the latter, the presence of the cephalic border furrow on the preocular fixed cheek, the rather elongated hypostome and the weak pygidial pleural furrows may be noted in particular. *Ogyginus* characters include the flask-shaped glabella and the very narrow anterior border; assignment to *Ogyginus* is based upon the acquisition of the latter features. It seems likely that *Ogyginus* has its origins in *Merlinia*, and in addition it may be noted that some *M. rhyakos* (e.g. Fortey & Owens 1978: pl. 5, fig. 4) show a tendency towards developing zetoidal thoracic axial furrows, a feature that Whittard (1964: 245, 246) stressed as an important attribute of *Ogyginus*; also immature *M. selwynii* pygidia (Fortey & Owens 1978: pl. 8, fig. 4; pl. 9, fig. 4) are strikingly similar in shape and proportions to those of adult *O. hybridus*.

Ogyginus hybridus (Salter 1866*a*)
(Figs 29–32)

1866*a* *Asaphus*? (*Basilicus*) *hybridus* Salter: 153; pl. 23, figs 8, 9.
1906 *Ogygia marginata*, var.; Evans: 608.
1906 *Ogygia Selwynii* Salt.; Evans: 608.
1907 *Asaphus*? (*Basilicus*) *hybridus* Salter; Thomas *in* Strahan *et al.*: 7.
1907 *Ogygia marginata*? Crosfield & Skeat; Thomas *in* Strahan *et al.*: 15.
1914 *Ogygia selwyni* (Salter); Cantrill & Thomas *in* Strahan *et al.*: 14 (table).
1914 *Ogygia selwyni* (Salt.); Thomas *in* Strahan *et al.*: 18.
1914 *Asaphus* (*Basilicus*?) *hybridus* Salt. [*Ogygia selwyni* Salt.]; Thomas *in* Strahan *et al.*: 18.
1931 *Basilicus*? *hybridus* (Salter); Reed: 451.
1964 *Ogygiocaris selwyni* (Salter) Whittard: 232; pl. 35, fig. 10.
1982 *Ogyginus* cf. *hybridus* (Salter); Owens & Fortey: 251, 256, 257.

LECTOTYPE (selected Whittard 1964: 237). BGS GSd3151, internal mould of pygidium.

TYPE STRATUM AND LOCALITY. Salter (1866*a*: 154) stated this to be 'Llandeilo Flags?, Henllan Amgoed, Carmarthenshire', but in the plate caption (1866*a*: pl. 23, figs 8, 9) modified the horizon to 'Caradoc Shales'. Since only Arenig strata crop out in the environs of Hennlan Amgoed, it may safely be assumed that both these alternatives are incorrect. Thomas (*in* Strahan *et al.* 1914: 18) considered that exposures in the lane from Llwyn-derw to Felin Henllan Amgoed (loc. 46, Colomendy Formation, Rhyd Henllan Member) were probably those from which the type specimens of this species were obtained. The lithology of the matrix of Salter's specimens is certainly that of the Rhyd Henllan Member, but it is equally possible that they originated from other exposures in the vicinity of Llwyn-derw (e.g. locs 47A, B) which have also yielded the species. Thus while we are confident this is the general area from which the types originated, we would hesitate to regard Thomas' suggestion as definitive.

OCCURRENCE. Type stratum: locs 46A, B, 47A, B, Rhyd Henllan. Blaencediw Formation: loc. 39, Rhyd Henllan; loc. 56, Triffleton. Abercastle Formation: loc. 58, Abercastle. Afon Ffinnant Formation: locs 16H–L, Cwm yr Abbey; locs 17A, B, Cwm Arbont; locs 18A–F, Afon Ffinnant; loc. 19, Ffinnant road section.

DIAGNOSIS. *Ogyginus* with short length of cephalic border furrow on preocular fixed cheek, effaced on larger specimens; hypostome with small tongue on posterior margin; thoracic and pygidial pleural areas very broad, so that anterior width of pygidial axis is markedly less than distance between axial furrow and inner edge of facet; pygidial pleural ribs weakly defined, more accentuated on smaller specimens, where interpleural furrows are also present; dorsal exoskeleton smooth, terrace lines restricted to cephalic and pygidial margins and lateral parts of thoracic pleurae.

DESCRIPTION. This species may reach a large size, and a thorax plus pygidium from loc. 16L (Fig. 30b) has a sagittal length of almost 80 mm, and the complete specimen would have been perhaps 120 mm long. The glabella expands forwards so that the transverse distance across the frontal lobe is on average about 80% of the sagittal length; it is narrowest at mid-length, opposite the palpebral lobe. It is only weakly inflated both in sagittal and transverse profiles, and the axial furrows are only weakly defined, especially posterior of the palpebral lobe. Any degree of crushing renders the glabellar muscle areas difficult to see, as in much of our material.

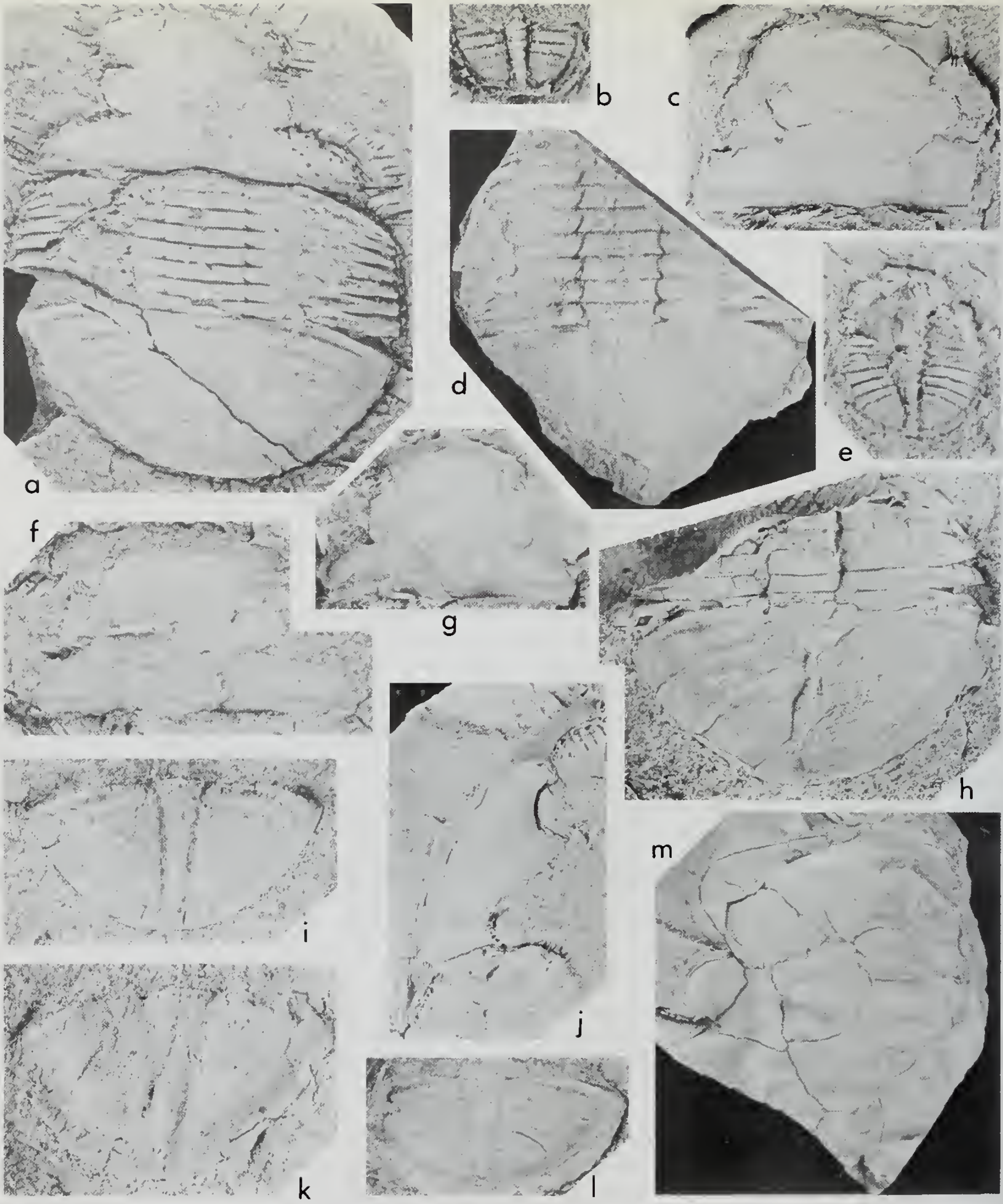


Fig. 29 *Ogyginus hybridus* (Salter 1866*a*). Middle Arenig; a, d, f, h, i, k from Whitlandian, Colomendy Formation, Rhyd Henllan Member, Henllan Amgoed, locs 46A (i), 46B (h), 47A (a, f, k), 47B (d); b, c, e, g, j, l, m from Whitlandian, Afon Ffinnant Formation; Cwm yr Abbey, loc. 16L (g); Afon Ffinnant, locs 18C (b, e, j, l, m) and 18E (c). a, axial shield, × 2, It.18917; b, meraspid pygidium, latex cast of external mould, × 20, It.18918; c, small cranidium, × 2·5, It.18919; d, incomplete thorax with elongated pygidium, × 1·5, It.18920; e, meraspid, latex cast from external mould, × 10, It.18921; f, cranidium showing weak furrow on preocular cheek, × 3, It.18922; g, small cranidium, × 5, NMW 84.10G.2; h, pygidium with parts of five thoracic segments, × 2, BGS HT518; i, small pygidium, latex cast from external mould, × 2, BGS Pr1846; j, free cheek, × 2, It.18923; k, pygidium, latex cast from external mould, × 2·5, It.18924; l, small pygidium, × 4, It.18925; m, incomplete large cranidium showing muscle impressions, × 2, It.18926.

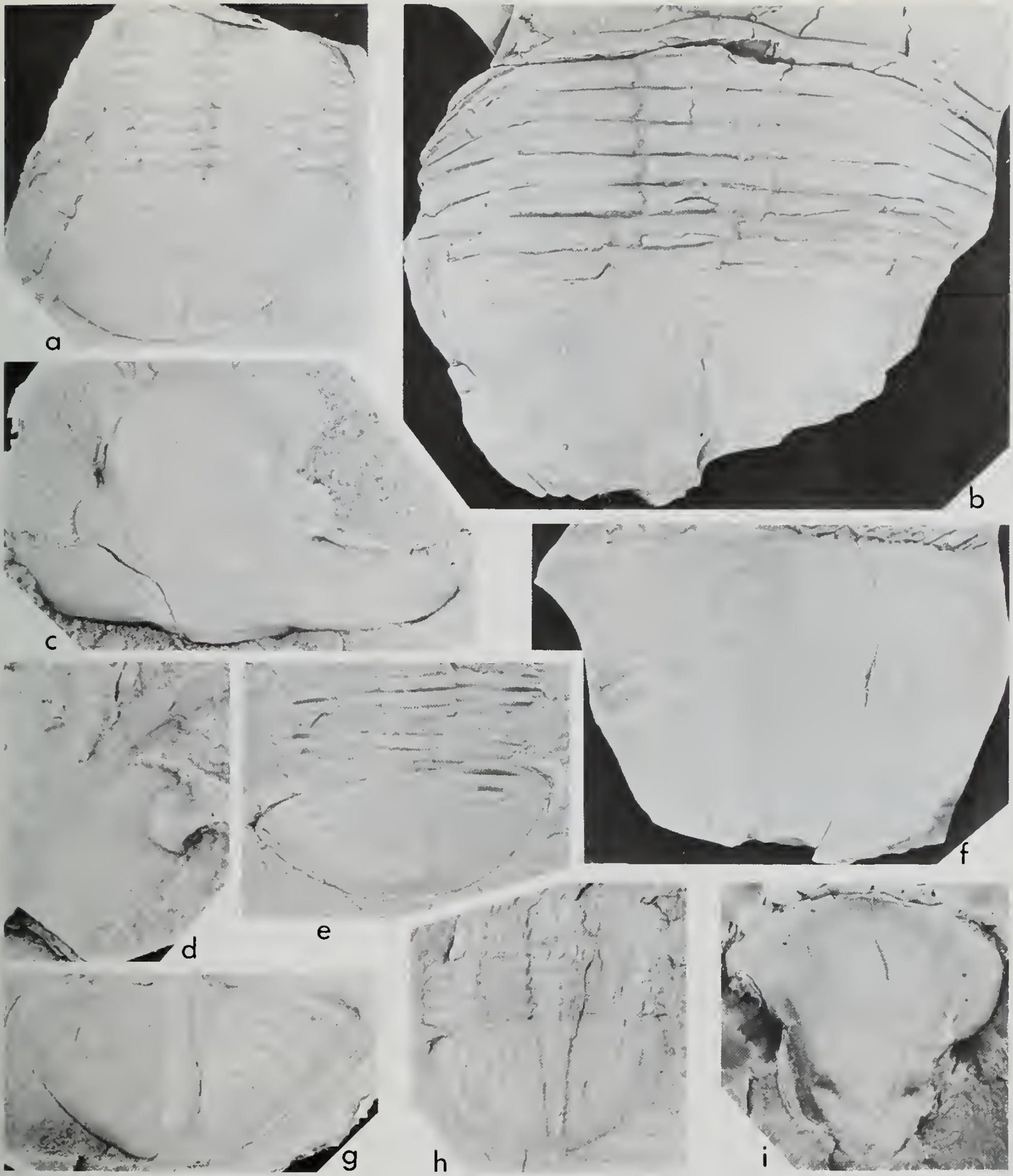


Fig. 30 *Ogyginus hybridus* (Salter 1866*a*). Middle Arenig, Whitlandian Stage, Afon Ffinnant Formation; a–d, f, g, i from Cwm yr Abbey, locs 16K (a, g) and 16L (others); e, h from Afon Ffinnant, loc. 18E. a, thorax and pygidium, latex cast from external mould, × 1·25, NMW 84.17G.1b; b, large thorax and pygidium, × 1, NMW 84.10G.6a; c, cranidium, latex cast from external mould, × 2·5, NMW 84.10G.1a; d, incomplete free cheek, × 2, NMW 84.10G.3a; e, disarticulated thorax with broad pygidium, × 2, It.18927; f, incomplete large pygidium, × 1, NMW 84.10G.7a; g, pygidium, latex cast from external mould, × 2, NMW 84.17G.180a; h, small thorax and pygidium, × 2·5, It.18928; i, hypostoma, × 2, NMW 84.10G.10.

They are proportionately deeper on large specimens (Fig. 29m) which show probably four pairs; none of our material shows the basal (1p) pair well, but transverse 2p is well seen in Fig. 29m. The same specimen shows a forwardly oblique 3p anterior to the palpebral lobe, and in front of this there is a suggestion of a weak 4p.

The palpebral lobe is placed at approximately mid-length and close to the axial furrow, although is proportionately further forward on large cranidia. On the latter, the postocular suture describes a more sharply backward oblique course than on smaller ones, and on crossing the pleuroccipital furrow it turns inwards (well seen on some free cheeks, e.g. Fig. 29j). The preocular suture runs close to, and diverges forwards slightly from, the frontal lobe of the glabella. Many specimens have a short, shallow length of the cephalic border furrow traversing the preocular fixed cheek (e.g. Fig. 29f), but this is absent from all specimens from locs 18C and 18E (e.g. Figs 29c, m) which however correspond in other details with specimens in which it is present.

The pleuroccipital furrow is broad and marked, terminated laterally at the genal angle. It delimits a narrow posterior border. Lateral border furrow broad and rather shallow, not well seen on our material. Genal spine short, broad-based. Doublure rather narrow, of similar width to the border, narrowing at hypostomal suture. Hypostome broadly triangular, very large specimens being as long (sag.) as wide (tr.), smaller ones 85–90% as wide as long. This is in contrast to those of *O. corndensis* which are wider than long, even in smaller specimens (e.g. Hughes 1979: 131, figs 58, 59) and also of smaller specimens of *O. armoricanus* which are as wide as long (e.g. Henry 1980: pl. 1, fig. 7a). *O. hybridus* also differs in having rather long (exsag.) anterior wings. Maculae prominent, lying in front of narrow, crescentic posterior body. Posterior margins acuminate, like *Merlina rhyakos* (Fortey & Owens 1978: pl. 5, figs 1, 2). Fine terrace lines laterally run subparallel to the margin, and are transverse on the sagittal part of the anterior body.

Thorax of typical *Ogyginus* type, with zetoidal axial furrows and spindle-shaped pleural furrows. Pleurae very broad, so that distance from axial furrow to the inner end of the fulcrum is always markedly greater than the transverse width of the axis. Pygidium with a long, narrow axis with up to 12 rings. These are defined by very shallow, transverse ring furrows which are deepest laterally and almost effaced sagittally. Axis weakly convex, and hardly elevated above adjacent pleural areas, and terminates at inner edge of doublure. Pleural areas gently convex and very broad, so that distance from axial furrow to inner edge of fulcrum is almost invariably in excess of transverse width of anterior end of axis, although in a few specimens (e.g. Fig. 29d) the values are almost equal. Seven to eight pairs of weakly-defined ribs, almost effaced on larger specimens where traces of only more anterior pleural furrows are discernible; interpleural furrows can be seen only on small specimens (Figs 29b, l). Abaxial parts of pleural areas slope down quite steeply (seen on specimens preserved in relief) to narrow pygidial border. Pygidial doublure narrow, about same width as border. Dorsal exoskeletons smooth, apart from terrace lines around margins of cephalon and pygidium and at lateral extremities anterior and posterior pleural bands of thoracic pleurae.

The collection from loc. 18C includes several meraspides, mostly pygidia which show well-defined axial ring furrows and deep, parallel pleural and interpleural furrows on the pleural areas. The only cephalon is ill-preserved, but an isolated free cheek (Fig. 31b) shows a proportionately longer genal spine and larger eye than on mature specimens.

REMARKS. Intrinsic factors such as the subtle differences upon which many asaphid species are defined, and extrinsic ones including type of sediment and distortion from different directions conspire to make the specimens described here as *Ogyginus hybridus* particularly intractable to interpret. The most obvious differences are seen in the pygidia. Some (e.g. Fig. 30e) are decidedly broader than are others (e.g. Fig. 30h). In an attempt to express this objectively we measured the anterior end of the pygidial axis and plotted this against the distance from the axial furrow to the inner end of the articulating facet; the result showed that two groups could just be differentiated (Fig. 32). Wider specimens are nearly all from the mudstones of the Afon Ffinnant Formation, less wide ones from silty horizons within it, or from similar lithologies in

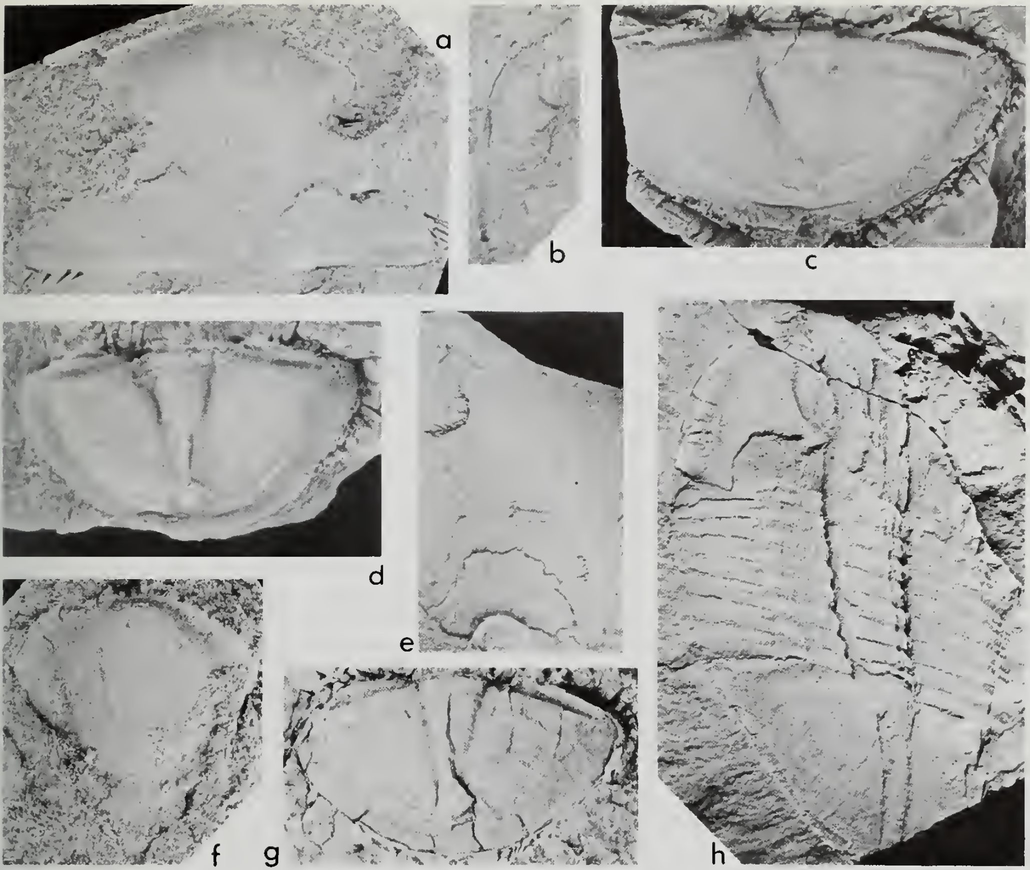


Fig. 31 *Ogyginus hybridus* (Salter 1866*a*). Middle Arenig, Whitlandian Stage, Afon Ffinnant Formation; a, c–f from Ffinnant road cutting, loc. 19; b from Afon Ffinnant, loc. 18C; g from Allt Cwm-arbont, loc. 17A; h from Penmaen Dewi Formation, probably lower part, Whitesand Bay. a, cranidium, × 2, It.18929; b, small free cheek with long genal spine, × 5, It.19004; c, d, pygidia, respectively × 3, It.18930, × 2, It.18931; e, free cheek, × 1·5, It.18932; f, hypostoma, × 3, It.18933; g, pygidium, × 2, It.18934; h, tectonically distorted complete specimen, note tiny genal spine on left side, × 2, SM A44355.

the Colomendy, Blaencediw and Abercastle formations, although wider forms do occur also in most of these. Comparatively few cephalic remains are known; on cranidia the only marked variation occurs within the Afon Ffinnant mudstones; specimens from locs 18C and 18E (Figs 29c, m) lack the border furrow on the preocular fixed cheek, whilst all others have it. Free cheeks mostly have a short, broad-based genal spine, but those from loc. 19 (Fig. 31e) have a proportionately longer one, whilst specimens from the Penmaen Dewi Formation (Fig. 31h) have a minute genal spine.

Unfortunately these cephalic and pygidial differences are not distributed in a consistent way throughout our samples, and it is not possible at this stage to suggest what, if any, taxonomic significance they might have, or whether they are a product of intraspecific variation, perhaps exacerbated by effects of preservation. We suspect, however, that there might be two subspecies; the types of *hybridus* (Whittard 1964: pl. 35, fig. 10) belong to the comparatively narrower morph.

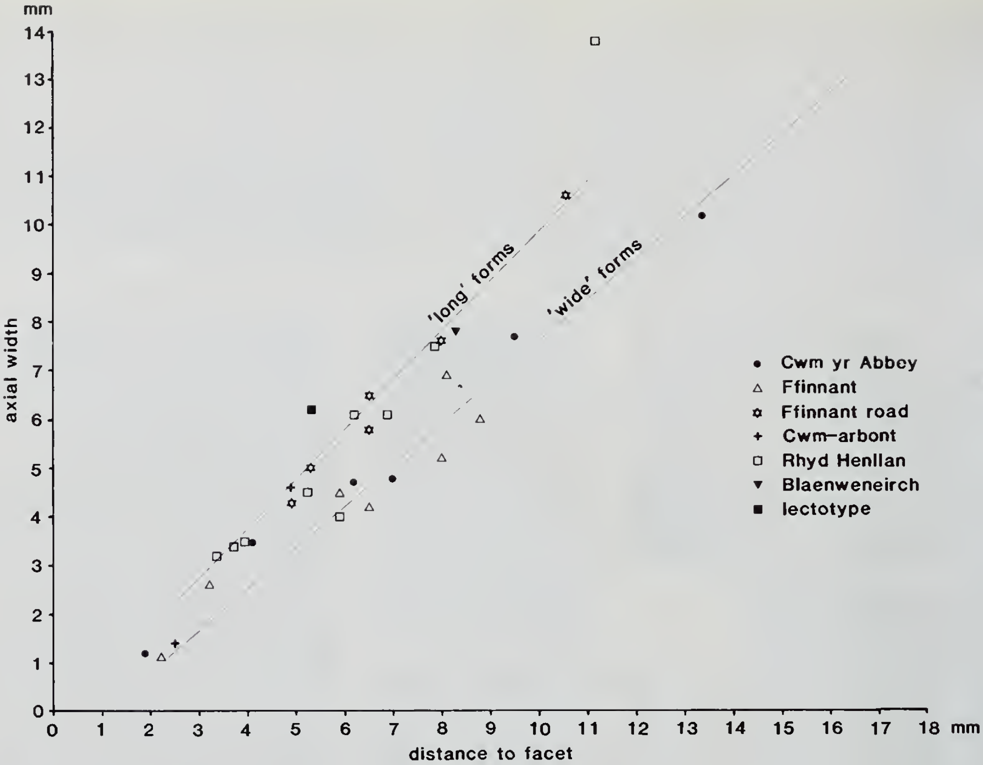


Fig. 32 Plot of anterior axial width against distance from axial furrow to inner end of articulating facet on pygidia of *Ogyginus hybridus* (Salter), to show distribution of 'wider' and 'longer' forms from various localities.

Thoral (1946: 86; pl. 11, fig. 6; pl. 15, fig. 7) described *Ogygiocaris*? *plana* from the 'lower middle Arenig' of Cabrières, Montagne Noire. His three syntypes are large specimens, each with the pygidium and part of the thorax preserved, and they compare exactly with our broader forms of *O. hybridus*, and there can be no doubt that they also belong to *Ogyginus*. Thoral had no cephalic material of *O. planus* but Pillet, Courtessole & Vizcaino (*in* Courtessole *et al.* 1985: 43) figured as *Ogygiocaris*? *plana* cranidia (1985: pl. 2, figs 1–3) and free cheeks (pl. 2, figs 4, 5) from different localities in the Montagne Noire in the upper part of the Grès et Schistes de La Maurerie and the Grès de la Cluse de l'Orb formations. The cranidia differ from *O. hybridus* in having a longer preglabellar field and the frontal lobe of the glabella being poorly defined; no specimen has a section of the cephalic border furrow on the preocular fixed cheek. On the assumption that these specimens are conspecific with Thoral's, *O. plana* is evidently distinct from, but clearly closely related to, *O. hybridus*. *O. orbensis* is distinguished from *O. hybridus* by a longer (sag.) preglabellar field, the preocular facial suture being close to the glabella, no cephalic border furrow on the preocular fixed cheek and a wider base to the genal spine. The pygidium is proportionately longer than in most *O. hybridus*.

Ogyginus sp. indet.
(Figs 33a, b)

MATERIAL. It.18935, cephalon with 7 thoracic segments from loc. 47B, Rhyd Henllan. NMW 33.189.G152, pygidium and 8 segments from 'Henllan Amgoed'. Both from Colomendy Formation, Rhyd Henllan Member.

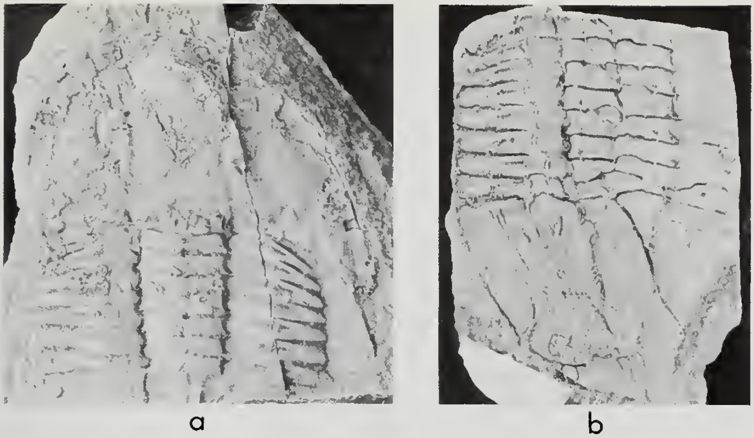


Fig. 33 *Ogyginus* sp. indet. Middle Arenig, Whitlandian Stage, Colomendy Formation, Rhyd Henllan Member. a, cephalon with seven thoracic segments, Rhyd Henllan, loc. 47B, × 1·5, It.18935; b, thorax and pygidium, Henllan Amgoed, × 0·8, NMW 33.189.G152.

Description. The cephalon is badly preserved, but shows a very long, broad-based genal spline that extends backwards as far as the sixth thoracic segment; the eye is forwardly placed, close to the glabella, which apparently has a weak constriction at mid length. The thoracic axial furrows have the characteristic zetoidal configuration of *Ogyginus*. The thoracic segments have the inner parts of the pleurae markedly narrower (tr.) than the axis. The pygidium is 0·6 times as long (sag.) as wide (tr.), with the axis tapering quite rapidly backwards; the pygidial doublure is rather broad. The anterior part of the glabella and the thoracic axial rings carry prominent terrace lines.

Remarks. The blade-like genal spine, narrow inner sections of the pleurae, broad pygidial doublure and presence of terrace lines on the axial regions readily distinguish these specimens from *O. hybridus*, which occurs at the same locality. A new species is evidently represented, but the present material is insufficient to name it.

Superfamily **CYCLOPYGACEA** Raymond 1925

We follow here the definition of Cyclopygacea given by Fortey (1981), and include the Nileidae in this superfamily as well as the Cyclopygidae.

Family **CYCLOPYGIDAE** Raymond 1925

Subfamily **CYCLOPYGINAE** Raymond 1925

Diagnosis. Cyclopygids with five to seven thoracic segments, no nodes on third axial ring. Cranidium with an arcuate to parabolic outline, in some genera extended into a 'nose' anteriorly; glabellar furrows variably expressed, with a maximum of three pairs in *Novakella*. Pygidium with or without border; axis usually wide and relatively short, and may be more or less effaced.

Genera included. *Cyclopyge* Hawle & Corda 1847; *Microparia* Hawle & Corda 1847; *Microparia* (*Heterocyclopyge*) Marek 1961; *Microparia* (*Quadratapyge*) Zhou 1977; *Aspidaeglina* Holub 1911; *Sagavia* Koroleva 1967; *Degamella* Marek 1961; *Novakella* Whittard 1961*a*; *Xenocyclopyge* Lu 1962; *Gastropolus* Whittard 1966.

Discussion. Since the *Treatise* (Harrington *et al.* 1959) the number of cyclopygid genera has trebled. The Arenig of south Wales includes the earliest known diverse cyclopygid assemblage, particularly rich in the Fennian, where they are accompanied by two other, morphologically

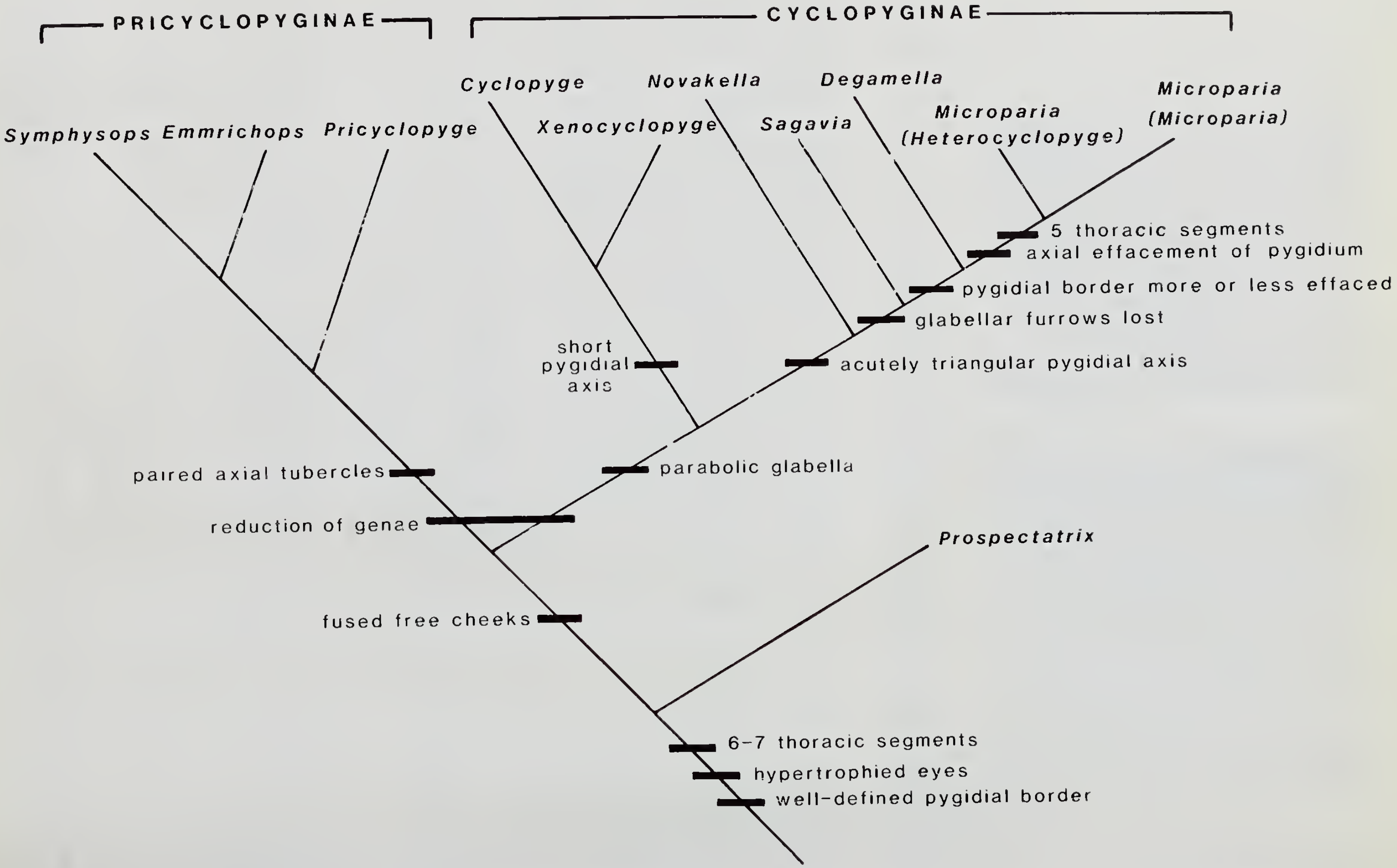


Fig. 34 Cladogram of relationships within the family Cyclopygidae as revised in this work. Autapomorphies of genera discussed in text.

convergent but unrelated, trilobites *Girvanopyge* and *Bohemilla*. It is clear that many of the cyclopygid genera—*Microparia*, *Cyclopyge*, *Degamella*, *Novakella*, *Gastropolus*—are extraordinarily conservative. Species from the Arenig of south Wales are very similar to ones from the Ashgill of Scotland, Bohemia and Kazakhstan. This may reflect the stability of the off-shelf habitat in which they lived, relatively free from the perturbations that influenced the shelf faunas. The genera appear to be quite well defined by the later Arenig, and presumably the earlier history of the family must be sought in the early Arenig and Tremadoc of such areas as the Montagne Noire. Kobayashi & Hamada (1971) made a start on recognizing subfamilies within the Cyclopygidae with the discrimination of the Ellipsotaphrinae (p. 187). Here we separate another monophyletic subfamily, the Pricyclopyginae, to include *Pricyclopyge*, *Symphysops* and ? *Emmrichops*. The remaining genera are accommodated within the Cyclopyginae. The subfamily includes cyclopygids with mostly elongate (sag.) cranidia with a parabolic outline and the maximum width at or near the posterior margin. Palpebral rims are narrow, gutter-like; anterior fusion of the eyes occurs in several genera. Thoracic segment number is constant within genera through the Arenig–Ashgill interval, but we know that primitively cyclopygids may have had seven segments, and loss of one or two segments presumably happened in the later Tremadoc or early Arenig. For example, *Cyclopyge azaisi* Thoral, 1935, from the ?latest Tremadoc of the Montagne Noire is essentially a *Degamella* with seven thoracic segments. The most primitive cyclopygid is *Prospectatrix* Fortey, 1981, from the Tremadoc of Britain, which also has seven segments. As is usual with primitive forms its assignment to a subfamily, when all are based on advanced characters, is difficult; because it lacks the thoracic structure of the Pricyclopyginae, it may be arbitrarily placed in the Cyclopyginae. A series of vincular notches have been recognized on the free cheeks of *Cyclopyge* and *Degamella* (Fig. 40b); this may prove to be a uniting character of Cyclopyginae, or it may be generally distributed in the family. The hypostome is known in *Cyclopyge*, *Microparia* and *Degamella*: it is wide (tr.) and short (sag.), and quite different from that cautiously assigned by Whittard (1961*a*) to *Pricyclopyge*.

Genus *CYCLOPYGE* Hawle & Corda 1847

TYPE SPECIES. *Egle rediviva* Barrande 1846.

DISCUSSION. Fortey & Owens (1978) redescribed *Aeglina grandis* Salter, 1859, and attributed it to *Microparia*. Since then, the discovery of new material has added more information. The assignment of *grandis* to *Microparia* was incorrect; well-preserved cranidia show the basal pair of glabellar furrows characteristic of *Cyclopyge*, together with a typical pygidial structure. We follow the diagnosis of Marek (1961) here.

Cyclopyge grandis grandis (Salter 1859)
(Figs 35a–f, 36)

Synonymy as in Fortey & Owens (1978: 256, 258) under *Microparia grandis* but their pl. 4, fig. 9 is excluded.

TYPE INFORMATION. See Fortey & Owens 1978: 258.

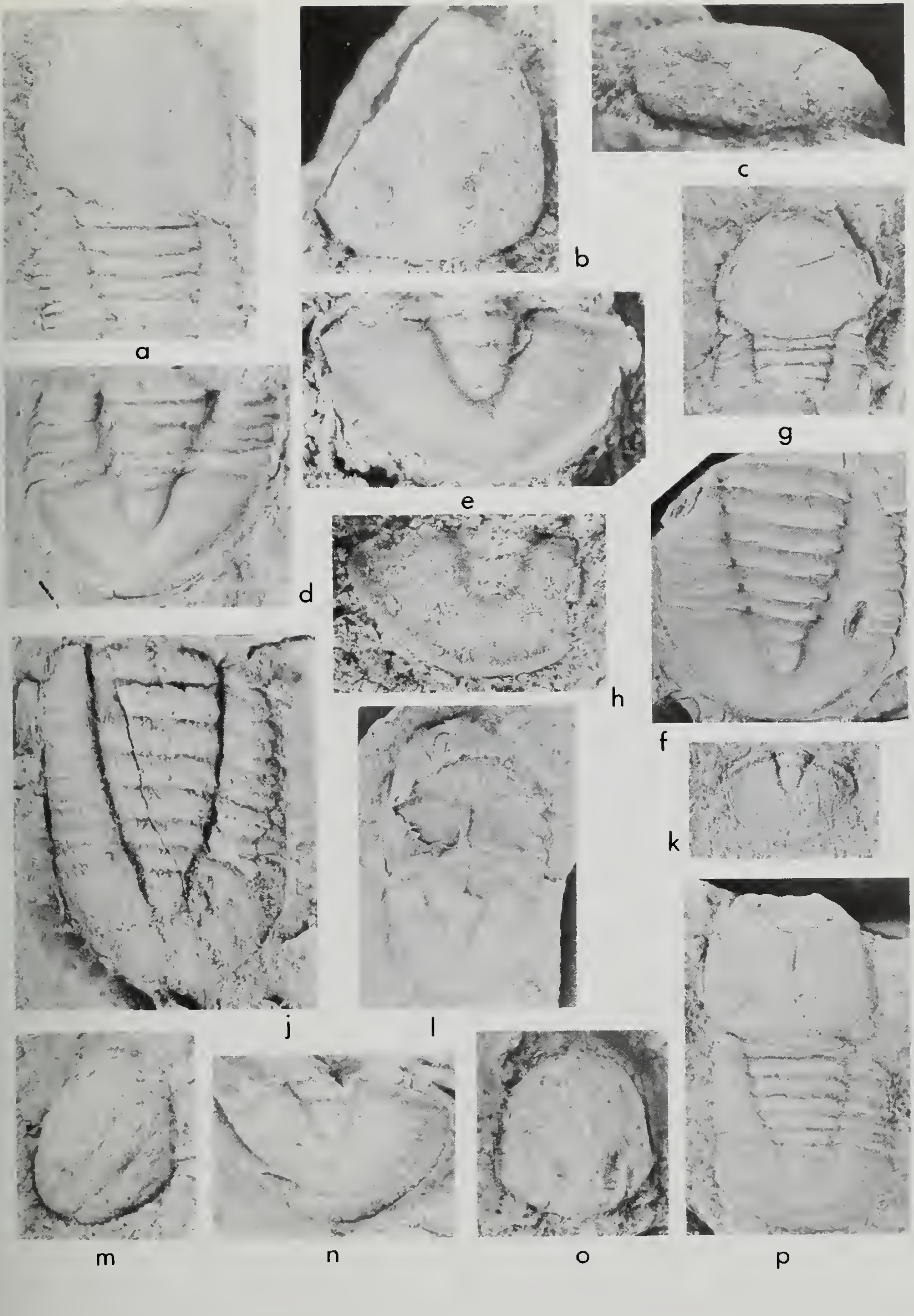
FIGURED MATERIAL. Axial shields: NMW 27.110.G259, G362, I.711; cranidium: It.19600; pygidium: It.19601.

STRATIGRAPHICAL OCCURRENCE. Middle to basal Upper Arenig (Whitlandian–lowest Fennian). Frequent in Penmaen Dewi Formation at Pwlluog; Whitland Abbey Formation, loc. 27; Cwmfelin Boeth Formation, in turbidites and interbedded shales, locs 36, 43; unnamed Arenig mudstones on east side of Nant-y-Gadwen, near Llanfaelrhys, Llŷn Peninsula, north Wales, and equivalent beds at Dwyrhos Farm, near Aberdaron; one pygidium from the Mytton Flags, Shropshire. The specimen assigned here by Fortey & Owens (1978: pl. 4, fig. 9) from the Carmarthen Formation is now referred to ?*Cyclopyge* sp. (see Table 1, p. 85).

DISCUSSION. When we first redescribed this species we based our interpretation on poorly preserved type and topotype material, and a well-preserved incomplete dorsal exoskeleton from the Carmarthen Formation (Fortey & Owens 1978: pl. 4, fig. 9) which we assumed was conspecific. This assumption was wrong. Well-preserved specimens from Whitlandian mudstones in north Wales compare exactly with the poor material from the type locality, but differ from the specimen from the Carmarthen Formation, which now has to be excluded from the species. The cranidia show the broadly truncate-oval form, long palpebral rims and spine-like relict fixed cheeks typical of *Cyclopyge*, as well as the basal pair of glabellar furrows, which are subdued on flattened material. A specimen in full relief from the Cwm-felin-Boeth Formation (Fig. 35b) also shows a sagittal ridge, running forwards from the glabellar furrows to the glabellar tubercle. Pygidia were correctly assigned previously; the new material includes well-preserved examples showing four or five pairs of extremely narrow furrows probably representing interpleural boundaries. These do not survive distortion or flattening. The border is narrow, and well defined along its length, with a concomitantly narrow doublure. The axis tapers evenly backwards, and one axial ring is invariably deeply defined; the second ring is only faintly indicated adjacent to the axial furrows, and rarely defined. Length of the axis exceeds the length of the postaxial field to the border furrow (see discussion of *Cyclopyge grandis brevirhachis* below).

This is possibly the oldest known species of *Cyclopyge*; both those attributed to this genus by Tjernvik (1956) from the early Ordovician of Sweden lack the typical glabellar structure, and were referred to *Heterocyclopyge* by Lu (1975: 175). A species from the Montagne Noire described by Pillet & Courtessole (1985) as *Incisopyge*? *theroni* is closely similar to *C. grandis grandis*, and is described as originating from the Lower Arenig; it is certainly better referred to *Cyclopyge*. The type species from the Caradoc of Bohemia was revised by Marek (1961: 19–21; *in* Horný & Bastl 1970: pl. 7, fig. 3), and is like *C. grandis grandis* in most features of the exoskeleton, again showing how conservative was cyclopygid morphology. It is best distinguished by its short pygidial axis; on Marek's reconstruction the terminal piece is shown as hardly longer than the one defined axial ring. There are also one or two pairs of pygidial pleural furrows. On the cranidium, the axial furrows on *C. rediviva* take a much sharper adaxial bend inside the relict postocular cheek. Other species of *Cyclopyge* differ from *C. grandis grandis* in pygidial details: pygidial axes are either shorter, as in *C. rediviva*, or if as long have more defined axial rings and furrowed pleural fields, as in *C. kossleri* (Klouček 1916). Several species (*C. rotundata* Lu 1975; see Han 1978) has the eyes fused into a single unit—a derived character in several cyclopygid genera. The eyes of *C. grandis* were separate. There is variation in the preservation of the raised circular areas (probably representing a thinning of the cuticle)

Fig. 35 a–f, *Cyclopyge grandis grandis* (Salter 1859). a, cranidium and thorax retaining some relief, Nant-y-Gadwen, Llanfaelrhys, Llŷn Peninsula, Whitlandian (probably *G. gibbsii* Biozone), × 5, NMW 27.110.G362; b, c, uncrushed internal mould of incomplete cranidium, dorsal and lateral views, showing basal pair of muscle impressions and sagittal ridge, Cwmfelin Boeth Formation, early late Arenig, Fennian, *S. abyfrons* Biozone, loc. 36, × 5, It.19600; d, three thoracic segments and pygidium, near original relief, locality as Fig. 35a, × 5, NMW 27.110.G259; e, entirely undistorted pygidium, horizon and locality as Fig. 35b, × 5, It.19601; f, thorax and pygidium from type locality, showing indication of second axial ring, Whitlandian (*G. gibbsii* Biozone), old quarry in Pwlluog, north of Whitesand Bay, St David's, Dyfed, × 4, I711. g–h, j–o, *Cyclopyge grandis brevirhachis* subsp. nov., Upper Arenig, Fennian. g, small cranidium and 3 thoracic segments, most transverse specimen, *B. rushtoni* Biozone, loc. 24, × 5, NMW 21.306.G32; h, mould of pygidium, full relief, stratigraphical and morphological intermediate between *C. grandis grandis* and *C. grandis brevirhachis*, *S. abyfrons* Biozone, loc. 36, Cwmfelin Boeth Formation, × 4, It.19603; j, thorax and pygidium, *B. rushtoni* Biozone, loc. 23, Pontyfenni Formation, × 5, It.19602; k, pygidium, horizon and locality as Fig. 35j, × 6, It.15906; l, **holotype** incomplete dorsal shield with free cheeks displaced backwards, *B. rushtoni* Biozone, loc. 24, × 4, It.15931; m, cranidium, cast of external mould, horizon and locality as holotype, × 5, It.18578; n, pygidium, horizon and locality as holotype, × 4, It.15904; o, cranidium, horizon and locality as holotype, × 5, It.19607. p, *Cyclopyge* cf. *C. umbonata* (Angelin). Axial shield, Upper Arenig, Fennian, Biozone of *B. rushtoni*, loc. 23, × 5, It.15908.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which lie behind the inner ends of the glabellar furrows, which are obliterated during any compression.

Cyclopyge grandis grandis is a useful guide fossil to the Whitlandian; the earliest Fennian specimens from the Cwmfelin Boeth Formation (Fig. 35e) cannot be distinguished from those from the earlier horizons. Later Fennian specimens all have the characters of *C. grandis brevirhachis*, which is discussed below. We noted previously that Whittard's (1961*a*) Cyclopygid C was to be referred to *C. grandis grandis*, and indeed provides one of the faunal links between the Mytton Flags and the Arenig of south Wales.

Cyclopyge grandis brevirhachis subsp. nov.
(Figs 35g–o, 36)

HOLOTYPE. Incomplete dorsal exoskeleton, It.15931.

PARATYPE MATERIAL. Thorax and pygidium, It.19602; pygidia, It.15904, It.15906, It.15907, NMW 84.17G.171; cranidia: It.18677–8, It.19607, NMW 21.306.G32, 84.17G.172; cranidium with free cheek, NMW 84.12G.29.

TYPE LOCALITY AND HORIZON. Pontyfenni Formation, loc. 24; Upper Arenig, Fennian, *B. rushtoni* Biozone.

STRATIGRAPHICAL RANGE. Upper Arenig, Fennian, *B. rushtoni* Biozone; locs 23, 24.

NAME. 'Short axis'.

DIAGNOSIS. A subspecies of *Cyclopyge grandis* with length of pygidial axis equal to or less than length of postaxial field, measured from the tip of the axis to the border furrow on the sagittal line.

DISCUSSION. This subspecies is established for populations of *Cyclopyge grandis* from the Pontyfenni Formation which differ from the the nominate form in having a relatively long pygidium, and hence the pygidial axis occupying a proportionately shorter fraction of the pygidial length. This can be expressed as the ratio of the length of the axis, measured from the furrow defining the half ring to the furrow defining the tip, to the postaxial field from the tip of the axis to the middle of the border furrow. The holotype of *C. grandis grandis* is poorly preserved and the tip of the axis and the border furrow are obscured, so that it is not possible to obtain a reliable measurement of this proportion. However, better preserved, flattened but otherwise almost undistorted pygidia are known from the type locality at Pwlluog, St David's (one of these is shown on Fig. 35f), and five of these have given ratios of between 1·20 and 1·33 with a mean of 1·28. From the good material in full or partial relief at Nant-y-Gadwen, Llŷn, we obtained ratios between 1·20 and 1·60 with a mean of 1·30. All available material of *C. g. brevirhachis* yields ratios 0·85–1·0, mean 0·95. Pygidia of *C. grandis grandis* are typically nearly semicircular if undistorted; width/length ratios of *C. g. brevirhachis* are in the range 1·6–1·8. This proportion is readily altered by distortion, however. On pygidia of *brevirhachis* the width of the terminal piece on the axis is equal to or less than its length; the terminal piece on *grandis grandis* is wider than long, but again axial or transverse distortion obscures this difference. Where the pygidial doublure can be observed on *C. grandis brevirhachis* it is wider than on *C. grandis grandis*, which has the merest strip underlying about half the border. If the proportions of the thorax and pygidium of *brevirhachis* from the type locality of the Pontyfenni Formation are not greatly altered, as seems likely, then its thorax is also proportionately longer than that of *C. grandis grandis*: width only slightly more than length, whereas undistorted *C. grandis grandis* have length about two-thirds width. We can find no differences between the two subspecies on the cranidia. Free cheek with border, as *C. grandis grandis* (Fortey & Owens 1978: pl. 4, fig. 8).

In an undistorted condition pygidia of the two subspecies can be distinguished quite easily but the differences can be obscured by distortion—particularly transverse extension, which reduces the measurable proportional distinctions. Specimens from the upper part of the range of *grandis grandis* in the basal Fennian Cwmfelin Boeth Formation are not different from those

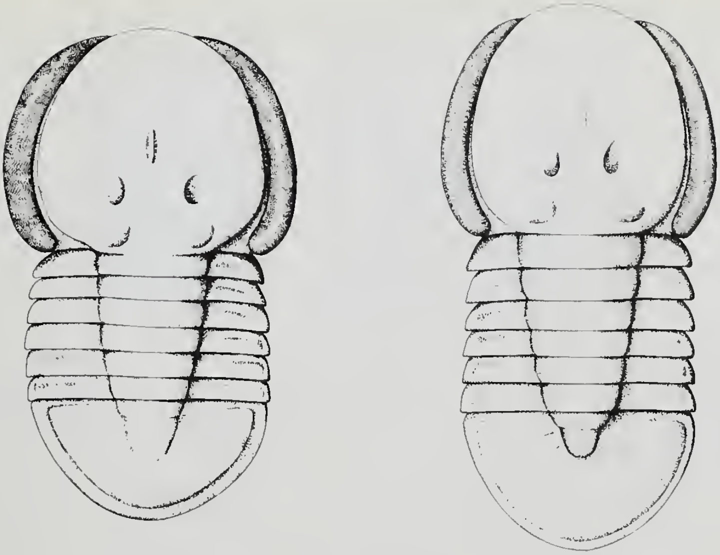


Fig. 36 Comparative reconstructions of (left) *C. grandis grandis* (Salter), to replace that in Fortey & Owens, 1978, and (right) *C. grandis brevirhachis* subsp. nov., both about × 3.

in the Whitlandian, although one specimen (Fig. 35h) has the axis hardly greater in length than the postaxial field, and might be regarded as transitional in this character.

The slender pygidial axis with elongate terminal piece is not known in other *Cyclopyge* species; in those with axes as short, the terminal piece is usually rather bluntly rounded. *Cyclopyge alia* and *C. festa* from Kazakhstan (Koroleva 1967) are species with short pygidial axes which are difficult to assess from the available illustrations; both are from the Upper Ordovician and are unlikely to be related to *C. grandis brevirhachis*. Both also appear to be similar to *C. marginata* Hawle & Corda (Marek 1961: pl. 1, figs 11, 12), which has a wider, blunt-tipped pygidial axis compared with the new subspecies.

Cyclopyge kossleri Klouček 1916
(Figs 37a, b)

1916 *Aeglina kossleri* Holub (in litt.); Klouček: 8.
1961 *Cyclopyge kossleri* (Klouček 1916) Marek: 25–26; pl. 1, figs 14–17; text-fig. 7.

Material. One incomplete dorsal shield, SM A44533.

Locality and horizon. Llanfallteg Formation, earliest Llanvirn, Scolton Railway Cutting.

Discussion. This is the first record of the species in Britain. It has been fully described from the Llanvirn Šárka Formation of Bohemia by Marek (1961). Type material is in full relief, whereas the specimen from the Llanfallteg Formation is slightly flattened, and the cranidium is also distorted. The latter, however, shows the characteristic pair of furrows which prove assignment to *Cyclopyge*. The pygidium of *C. kossleri* is distinctive: it has a long and well-segmented axis showing three axial rings and a small triangular terminal piece, and the pleural fields carry two pairs of furrows. It is, in fact, similar to transitory pygidia of other cyclopygids (e.g. *C. umbonata bohemica*; see Marek, 1961: pl. 2, fig. 5), but is too large to be such, and is associated with the full complement of thoracic segments. *C. kossleri* probably arose by neotenic displacement of immature characters into the adult. The specimen from south Wales clearly shows the same pygidial features, and the determination can be made with confidence.

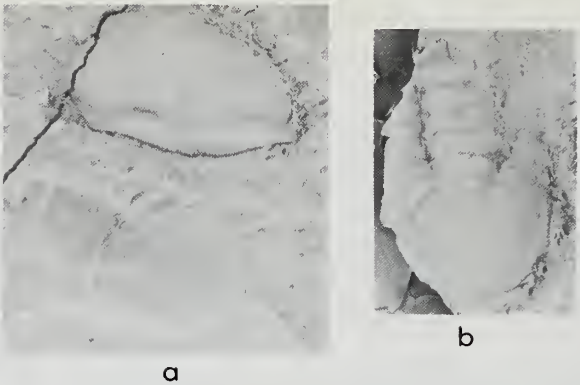


Fig. 37 *Cyclopyge kossleri* Klouček, 1916. Early Llanvirn, *D. artus* Biozone, Llanfallteg Formation, Scolton cutting, × 6, SM A44533. a, cranidium and external mould of incomplete thorax and pygidium; b, counterpart of latter.

***Cyclopyge* cf. *umbonata* (Angelin 1854)**
(Fig. 35p)

cf. 1854 *Corynexochus ? umbonatus* Angelin: 60; pl. 33, fig. 10.
cf. 1961 *Cyclopyge umbonata umbonata* (Angelin) Marek: pl. 1, fig. 10.
cf. 1971 *Cyclopyge umbonata* (Angelin 1854); Neben & Krueger: pl. 13, fig. 19.

MATERIAL. One nearly complete axial shield, It.15908.

LOCALITY AND HORIZON. Pontyfenni Formation, type locality at Pontyfenni; Upper Arenig, biozone of *Bergamia rushtoni.*

DISCUSSION. One articulated specimen from the late Arenig falls outside the range of variation of *C. grandis*, and in particular of *C. g. brevirhachis* from the same horizon. The pygidial border is very wide, about one-quarter total pygidial length; on *C. grandis, sensu lato,* there is some variation in this character, but it is never wider than one-sixth pygidial length, and usually one-eighth or less. The pygidial axis is also relatively wide, and bluntly rounded, when compared with that of *C. grandis.*

The pygidium of *C. umbonata*, Angelin's original specimen and presumably the holotype by monotypy, was illustrated by Marek (1961); its origination from the 'Orthoceras Limestone' of Sweden suggests it is not very different in age from the Welsh specimen (see Neben & Krueger 1973). Neben & Krueger (1971) attributed a cranidium, but from a glacial erratic. *C. umbonata* also has a wider pygidial border than other *Cyclopyge* spp., and is close to our specimen on most other characters. The identification has to be qualified, however. The Welsh specimen shows a faint second axial ring on the pygidium, whereas the type of *umbonata* has apparently one strong ring—more like *C. grandis* in this respect. The cranidium attributed by Neben & Krueger was probably longer than that of our specimen. It is impossible to assess the importance or otherwise of such small differences until more is known about variation in *C. umbonata* from the type area, hence our determination is qualified.

Another similar species is *C. stigmata* Poulsen 1965 from Bornholm, also from the later Arenig. However, Poulsen mentions a third pygidial axial ring, and the pygidial border narrows postaxially.

Genus ***DEGAMELLA*** Marek 1961

TYPE SPECIES. *Aeglina princeps* Barrande 1872, original designation.

DIAGNOSIS. Large cyclopygid trilobites having elongated cranidium, occupying as much as half total length, which is produced into an anterior 'nose'. Eyes of medium to large size with laterally-directed field of view. Three pairs of cephalic muscle impressions may or may not be visible, and never deeply incised as in *Novakella*. Thorax of six or seven segments without dorsal organs on third segment. Pygidium sub-semicircular; axis long, usually effaced posteriorly; border ill-defined; pygidial doublure wide.

DISCUSSION. Marek (1961: 45, footnote) and Whittard (1966: 287) stated that *Degamella* was likely to be a junior synonym of *Novakella* Whittard 1961*a*. Here we retain them as separate genera, and distinguish both from *Microparia* also at the generic level. The south Wales faunas show that the typical morphologies of *Degamella*, with extended glabella, and *Novakella*, with incised slit-like glabellar furrows, are already distinct in the Arenig, and indeed they continue with little change into the Ashgill of the Whitehouse Group, Scotland (J. K. Ingham, personal communication). Such long independent histories of two distinctive groups, each with several species, is stratigraphical evidence for two separate monophyletic taxa, for which generic status is appropriate. *Degamella* and *Novakella* share a number of characters which indicate that they are more closely related one to another than to *Microparia*: six thoracic segments; long cranidium; wide pygidial doublure. The morphology of *Microparia* was also established by the Arenig, with a similarly long subsequent history, and its generic status seems to be equally justified. Five thoracic segments appears to be a stable character in *Microparia*. *Microparia nudus* Whittard 1961*a*, from the Llanvirn of Shropshire, has six thoracic segments, and proportions more like those of *Degamella princeps* than typical *Microparia* species; hence we would refer it to *Degamella*, as defined here. We allow seven thoracic segments in *Degamella* because a specimen which has been attributed (possibly incorrectly) to *Aeglina azaizi* Thoral, 1935 (Fig. 38e) appears to be a typical *Degamella* except in that it retains the primitive segment number.

Degamella evansi sp. nov.
(Figs 38–40)

HOLOTYPE. Axial shield, It.15909.

PARATYPE MATERIAL. Axial shields, NMW 33.189.G133, It.15932, NMW 33.189.G3, 84.17G.41–3; exoskeleton with displaced cheeks, It.19707; free cheeks, It.15910–1, It.19610; cranidium, It.15912; hypostoma, It.19611; pygidia, It.19612, NMW 84.17G.44.

TYPE LOCALITY. Pontyfenni Formation, loc. 23; Fennian, *B. rushtoni* Biozone.

STRATIGRAPHICAL RANGE. Upper Arenig, Fennian, *B. rushtoni* Biozone, loc. 23; and Ramsey Island, Aber Mawr (? *B. rushtoni* Biozone), loc. 62.

NAME. After D. C. Evans, pioneer geologist of the Whitland District.

DIAGNOSIS. *Degamella* with cranidium longer (sag.) than width at posterior margin; eyes larger than in *D. princeps*. Narrow palpebral rims extend very far back; no posterolateral fixed cheeks defined. Pygidial doublure of equal width along its length.

DESCRIPTION. The species is known from three well-preserved axial shields, which are $2\frac{1}{2}$ times longer than wide, an elongate form characteristically associated with an actively swimming mode of life (Fortey 1985*b*). The cranidium accounts for half this length, and the length of the thorax is equal to, or slightly less than, that of the pygidium. The axial shields are somewhat flattened, but the cranidium illustrated in Fig. 40c is preserved in the 'nodular' fashion in which much of the original convexity survives; if this is so then the transverse vaulting is lower than it is in *D. princeps*. Convexity across thorax and pygidium is always low in *Degamella*.

Cranidium longer than wide, the 'nose' broadly rounded rather than acuminate; cranidium expands in width (tr.) slightly forwards to a maximum at about one-third cranidial length, tapering more rapidly forwards. There is no indication of glabellar furrows or 'muscle insertion areas', but the preservation is likely to be inadequate to preserve them. Palpebral gutters only just fall short of posterior margin; anteriorly they run outwards alongside the glabella as it expands in width, and shortly in front of this, at about half cranidial length, they become ventral enough to be concealed beneath the frontal glabellar lobe. Fused free cheeks are

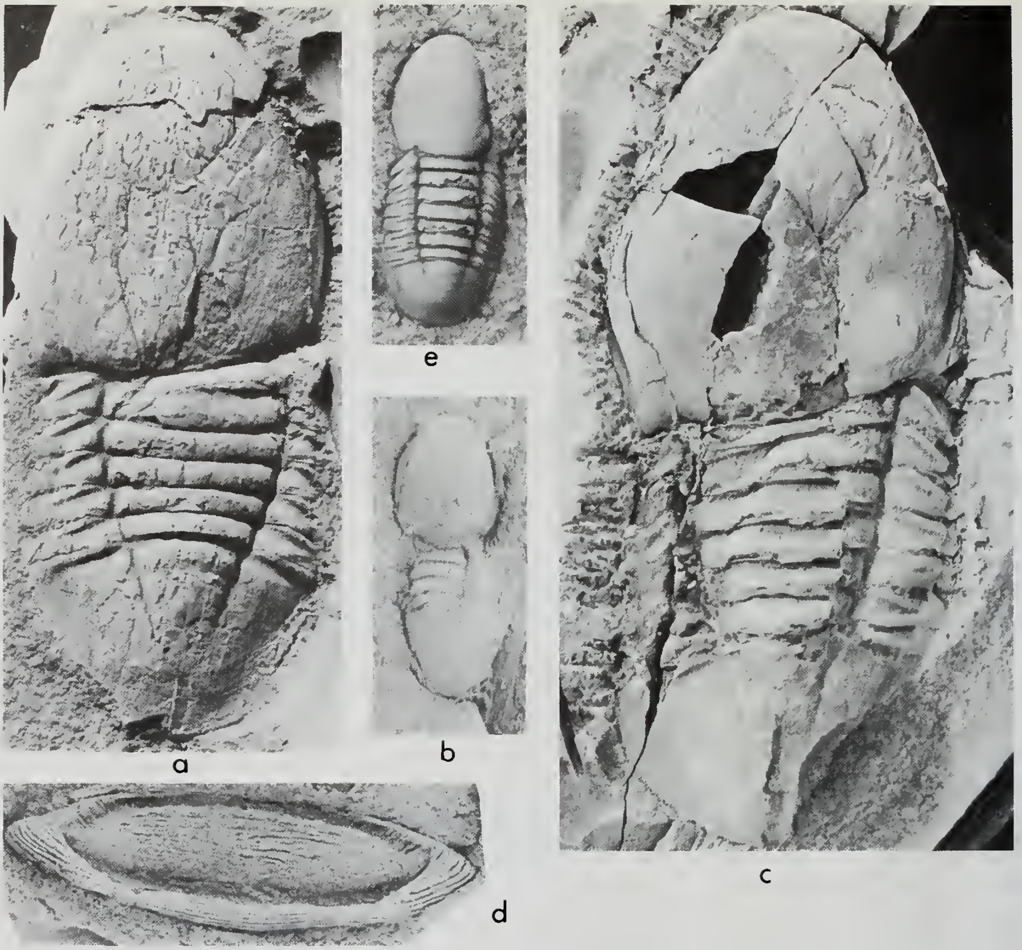


Fig. 38 a–d, *Degamella evansi* sp. nov. Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23. a, axial shield, sixth thoracic segment not clearly visible on this specimen which has cranidium slightly displaced relative to thorax, presumably during moulting, × 2, NMW 33.189.G133; b, latex cast from natural mould of small dorsal shield, only four thoracic segments visible (possibly indicating meraspide condition if not displaced), × 4, It.15932; c, **holotype**, large damaged axial shield, × 2, It.15909; d, latex cast from external mould of hypostoma, × 5, It.19611. e, *Degamella azaisi* (Thoral)?, latex cast from well-preserved shield for comparison with *D. evansi*, early Arenig, Montagne Noire, × 2, It.8158.

undoubtedly to be referred here, both on grounds of size and because they are closely similar to those of *D. princeps* (Marek 1961: text-fig. 18). They show the broad doublural platform which lay ventrally beneath the glabellar 'nose'; but the eyes are large, taking up virtually all the dorsal librigenal surface, except for a very narrow border, and they presumably occupied the entire area abutting the palpebral rims.

Hypostome (Fig. 38d) is extremely transverse, almost four times wider than long, densely covered with terrace ridges, and with a prominent posterior border but a less distinct anterior border. It is like that attributed to *Degamella* cf. *princeps* by Whittard (1966: pl. 49, fig. 12), and is reasonably assigned to *D. evansi*.

Six thoracic segments of usual cyclopygid form, with adaxial articulation on the first segment, and somewhat further from axis posteriorly. Axis occupies about two-thirds width at

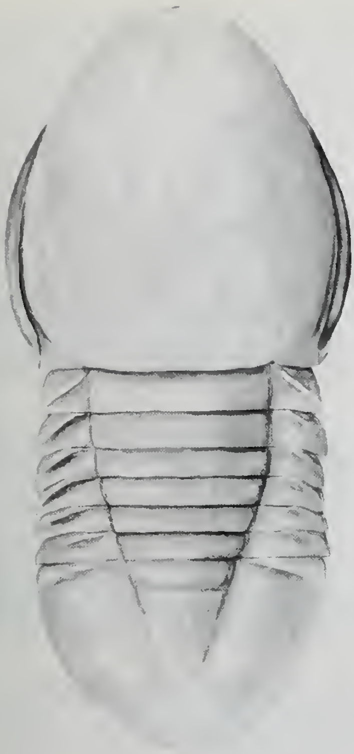


Fig. 39 Reconstruction of axial shield of *Degamella evansi* sp. nov., × 2 approx.

first segment, but less than half on sixth segment. Most of the axial taper occurs on the posterior three segments. Prominent articulating facets, steeply downsloping on first segment. The holotype shows the narrow thoracic doublure, which apparently narrows to almost nothing on the first segment. The half rings are raised, rim-like, and longer (sag.) anteriorly, indicating that the bulk of flexure during enrollment occurred on the anterior segment.

Pygidium five-eighths as long as wide, with pygidial axis occupying about three-eighths pygidial width at anterior margin. Axial furrows continue backward taper of posterior part of thorax, enclosing an angle of 30°–40°; tip of axis effaced, but it certainly extends to nearly two-thirds pygidial length. One ring furrow is defined, with traces of a second. Broad, but ill-defined, border hardly present postaxially. Wide doublure extends back beneath border, not narrowing conspicuously towards anterolateral edges, and carrying 8–10 terrace ridges which run slightly oblique to the posterior pygidial margin.

DISCUSSION. Considering the difference in age, this species is remarkably like the type species, *D. princeps princeps* (Barrande 1872: pl. 14, figs 3–8), from the Llandeilo Dobrotivá Formation of Bohemia (see Marek 1961: 46–48; pl. 4, figs 1–7; text-figs 17, 18; *in* Horný & Bastl 1970: pl. 7, fig. 8). Thorax and pygidium are identical. The cephalic impressions shown on Marek's (1961: text-fig. 17) reconstruction are visible only with exceptional preservation—many specimens from the Dobrotivá Formation do not show them—and the fact that none of the Arenig specimens preserve them is of no importance. The distinguishing characters of the new species are entirely cephalic: in *D. princeps princeps* the axial furrows curve adaxially away from the facial sutures as the posterior margin is approached, before becoming effaced, thereby defining a long (exsag.), triangular fixed cheek; on *D. evansi* the axial/palpebral furrow continues along the edge of the cranidium almost to the posterior margin. The eyes on *D. princeps* are remarkably small for a cyclopygid, and there is concomitantly a relatively large border on the free cheek; this is not the case in *D. evansi*, on which the eye occupies most of the available area as

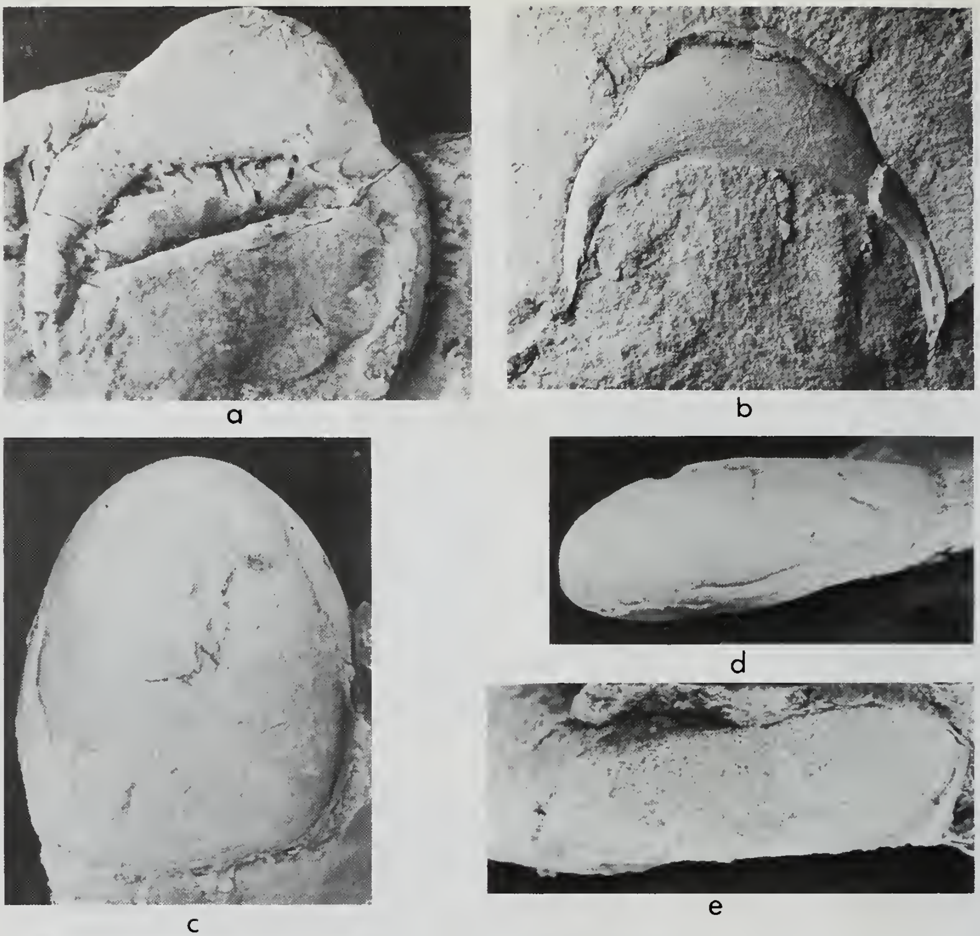


Fig. 40 *Degamella evansi* sp. nov. Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23. a, internal mould of conjoined free cheeks from ventral side, narrow, long eyes preserved at lateral edges, × 2·2, It.15910; b, external mould of conjoined free cheeks, vincular noches shown on right, × 3, It.19610; c, d, × 2, It.15912, dorsal and lateral views of cranidium; e, detail of eye showing its large size as compared with *D. princeps*, × 6, It.15911.

it does on other cyclopygids. The close similarity between *D. evansi* and *D. princeps* might imply that the smaller eye of the latter is in this case a derived character, the larger eye being primitive. The occurrence of the small-eyed form is itself surprising, because the family as a whole maximizes visual area.

Klouček (1916) distinguished the subspecies *Degamella princeps praecedens* from a stratigraphically earlier horizon than *D. princeps princeps*, in the Llanvirn Šárka Formation of Bohemia. The holotype, a fragmentary cephalon, was illustrated by Marek (1961: pl. 4, figs 8, 9), and considered by him to be unique. In the collections of the British Museum (Natural History) there is a nearly complete exoskeleton of a *Degamella* (I.15277), presented by Klouček, and stated to be from D1 of Šárka and therefore likely to represent the subspecies *praecedens*. This exhibits no differences from *D. princeps princeps*, and the specimen differs from *D. evansi* in the same characters; in view of this the status of the subspecies *praecedens* is regarded as doubtful. *D. gigantea* (Barrande 1872) from the Ashgill of Bohemia has even smaller eyes than *D. princeps*. *Degamella nuda* (Whittard 1961*a*) from the Llanvirn of Shropshire differs from *D.*

princeps and *D. evansi* in that the cranidium of the mature holaspis (1961*a*: pl. 24, fig. 5) is much less than half the total axial length. The pygidium is like that of *D. evansi* externally, but the doublure widens noticeably backwards; small cranidia of *D. nuda* are quite transverse. *D. nuda*, like *D. evansi*, has large eyes. Whittard identified a series of vincular notches in the cheek doublure of *D. nuda*, as did Marek (1961) on *D. princeps*, and Han (1978) on *Cyclopyge*. These notches may prove to be another character linking the subfamily Cyclopyginae as defined here.

If the large eyes of *D. evansi* and *D. nuda* are primitive it would confirm Marek's view that *Microparia* and *Degamella* are closely related.

Genus ***GASTROPOLUS*** Whittard 1966

1974 *Lisogoraspis* Apollonov: 76.

Type species. *Gastropolus brevicaudatum* Whittard 1966, see below.

Diagnosis. Cyclopygid trilobites with six thoracic segments, and cephalon more than twice as long (sag.) as the pygidium. Cranidium resembling that of *Microparia* but with large, triangular remnant fixigenal areas. Pygidium exceptionally transverse, with an elliptical outline; border and axis well defined.

Discussion. The genus *Gastropolus* was originally proposed by Whittard (1966) on the basis of two specimens of a distinctive pygidium, together with a pygidium with six thoracic segments attached, all from the Hope Shales (Llanvirn) of Shropshire; he was not able to associate cephalic parts. We are now able to diagnose the genus more completely because there is a complete, but poorly-preserved, specimen from the Lake District (Fig. 41a), which allows us to associate relatively well-preserved cranidia and pygidia from south Wales. Mr R. Kennedy has also kindly shown us an entire specimen he has collected from the Llanfallteg Formation. *Gastropolus* is a distinctive cyclopygid, especially because of its excessively wide pygidium, which is like that of no other trilobite. The cranidium is more typically cyclopygine, but the comparatively large remnant fixed cheeks form a pair of wide triangular areas at the posterior cephalic margin, which distinguishes the cranidium from those of *Microparia*, *Degamella* and *Sagavia*. Apollonov (1974) described *Lisogoraspis* from the Upper Ordovician of Kazakhstan, again from pygidia. These are similar in all respects to that of *Gastropolus*, and *Lisogoraspis* is accordingly listed as a subjective synonym of *Gastropolus*. Whittard proposed the species *G. brevicaudatum* as the type species but we regard it as being the same as the poorly known species *obtusicaudata* Hicks from Llanvirn quarry.

In its cranidial morphology *Gastropolus* is clearly a cyclopygine, related to *Microparia*, *Sagavia* and *Degamella*, which also have triangular fixigenal remnants, although not as wide (tr.). The presence of six thoracic segments, and a well-defined pygidial border and axis, incline us to classify it closer to *Degamella* and *Sagavia* than to *Microparia*. It is a homoeomorph of *Emmrichops*, another transverse cyclopygid, but which we regard as a probable pricyclopygine (below). *Microparia* itself includes one species, *M. porrecta* sp. nov., which has a pygidium as transverse as that of *Gastropolus*. Presumably there was a particular niche in the bathypelagic habitat to which these forms were adapted. Unlike other cyclopygids there is a poor 'fit' between cephalon and pygidium and it is not obvious whether *Gastropolus* was capable of enrollment. It is interesting that the hypostoma of *Degamella* is also remarkably wide (Fig. 38d). If that of *Gastropolus* were similar it is possible that the wide pygidium engaged with the wide hypostoma rather than the cephalic doublure during enrollment.

Gastropolus obtusicaudatus (Hicks 1875)
(Figs 41–43)

1875 *Aeglina obtusicaudata* Hicks: 185; pl. 10, fig. 3.
1885 Group A, no. 2; Postlethwaite: 74; pl. 3, fig. 16.
1886 *Aeglina obtusicaudata* Hicks; Postlethwaite & Goodchild: 463; pl. 8, fig. 16.
1961*a* *Cyclopyge obtusicaudata* Hicks; Whittard: 179.
1966 *Gastropolus brevicaudatum* Whittard: 294; pl. 50, figs 10–12.

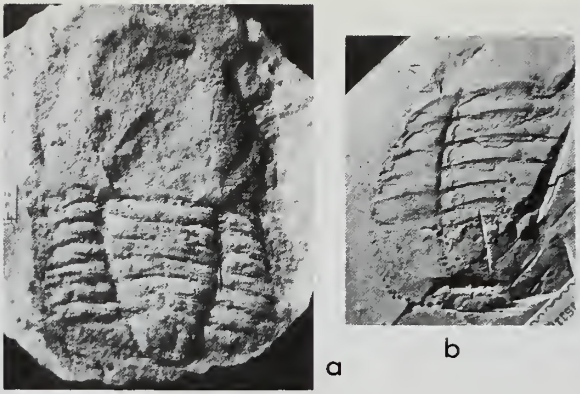


Fig. 41 *Gastropolus obtusicaudatus* (Hicks 1875). a, cast of poorly preserved axial shield, original of Postlethwaite 1885: pl. 3, fig. 16 (as drawn by Goodchild). Outerside, Lake District, × 1, SM A45444; b, holotype, thorax and pygidium in poor preservation, original of Hicks 1875: pl. 10, fig. 3, Llanvirn quarry, early Llanvirn, presumed to be *D. artus* Biozone, × 1, SM A45154.

HOLOTYPE. Thorax and pygidium, SM A45154, from the early Llanvirn of Llanvirn quarry.

MATERIAL. Pygidia: It.19615–6; cranidia: It.19613–4.

DIAGNOSIS. See that of genus.

STRATIGRAPHICAL RANGE. The species occurs in the Llanfallteg Formation, early Llanvirn part, in south Wales at Cefn-maen-llŵyd farmyard. Hope Shales, Shropshire, early Llanvirn; Skiddaw Slates at Outerside, probably also from the earliest Llanvirn.

DESCRIPTION. Entire exoskeleton slightly less than twice as long as wide, the cephalon accounting for half the total length. Cranidium wider than long, maximum width at posterior margin between 0·7 and 0·9 of sagittal length. The glabella has a nearly circular outline; the axial furrows converge inwards and backwards quite sharply, but fade out before reaching the posterior cranidial margin. The fixed cheeks so defined have a maximum width about three-quarters length (exsag.) and are slightly inflated. The sutural margins of the remnant fixed cheeks are gently convex-outwards. Palpebral rims are apparently lacking. Otherwise, the cranidium is almost featureless; there are faint indications of a few terrace lines on the frontal glabellar lobe. We presume that large eyes lay along the cephalic margin as in other cyclopygids. Thorax with six segments. Apart from being relatively wide (tr.) it is of usual cyclopygid construction, with the axis hardly tapering over the first three segments, thereafter tapering

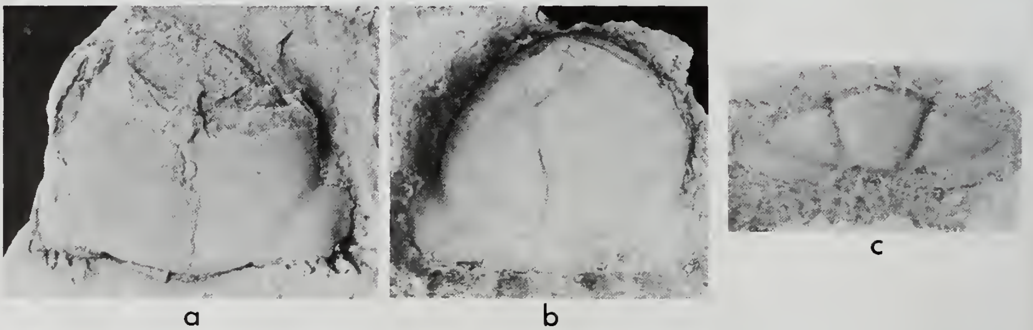


Fig. 42 *Gastropolus obtusicaudatus* (Hicks 1875). Early Llanvirn, *D. artus* Biozone, Llanfallteg Formation, loc. 50. a, large cranidium with partially damaged frontal glabellar lobe, × 2, It.19613; b, cranidium, × 3, It.19614; c, pygidium, × 3, It.19615.

gently backwards into the pygidial axis. On the sixth segment the width of the axis is only slightly greater than the width of the pleurae.

Pygidium three times as wide as long, with gently convex pleural fields, and a well-defined flat to gently convex border. Axis occupies one-third or less of pygidial width at anterior margin, and this width exceeds its length; posterior taper very gentle to broadly rounded tip at border furrow. Although the half-ring is prominent no axial rings are defined. Posterior border widest posterolaterally. Doublure coincident with border, carrying very sparse terrace ridges.

DISCUSSION. Although the Lake District specimen is not well preserved it is clearly identical to the species from the Llanfallteg Formation and from Shropshire. The latter was originally described with the specific name *brevicaudatum* Whittard. Whittard (1966) described the thorax of the articulated specimen from the Hope Shales as 'almost barrel-shaped'. We regard this observation as mistaken, because the barrel-like appearance of Whittard's pl. 50, fig. 10 is produced by partial breakage of the thoracic axis at its anterior end. Comparison of all this material with the type of *obtusicaudatus* Hicks is more difficult because of the imperfect preservation of the unique specimen from Llanvirn quarry. It is, however, certainly a *Gastropolus*, showing the six segments, transverse pygidium and short pygidial axis typical of the genus. The pygidial pleural fields are slightly less transversely extended but it is doubtful whether much importance can be attached to this in view of the degree of distortion often found in Llanvirn quarry specimens. Since almost all the species originally described by Hicks from Llanvirn quarry have also been recognized in the early Llanvirn of the Llanfallteg Formation it is likely that this applies to the *Gastropolus* as well. We have one fragment of a thorax and pygidium from Llanfallteg which appears to be more similar to Hicks' specimen. We therefore feel obliged to use the Hicks name for all these early Llanvirn *Gastropolus* specimens, and *G. brevicaudatum* Whittard accordingly becomes a subjective junior synonym of *obtusicaudatus* Hicks.

Gastropolus mirabilis (Apollonov) from the upper Ordovician of Kazakhstan is known from pygidia which appear to be indistinguishable from those of *G. obtusicaudatus*. Apollonov (1974: pl. 3, figs 10, 11) figured a cephalon as 'Cyclopygidae gen.' which is of the appropriate kind to belong with the *Gastropolus* pygidia, and which has even wider triangular fixed cheeks than *G. brevicaudatum*. His 'gen. et sp. indet 2' (1974: pl. 21, fig. 11) is a transitory pygidium with 3 thoracic segments which is likely to be that of *Gastropolus*.

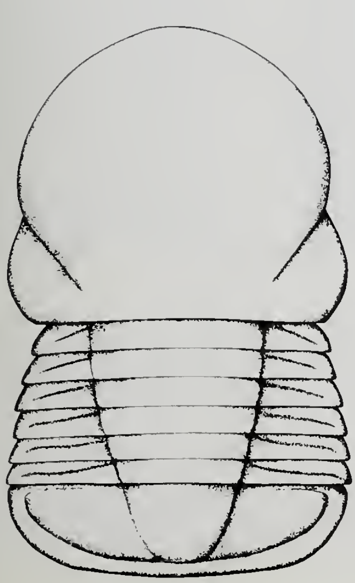


Fig. 43 Reconstruction of axial shield of *Gastropolus obtusicaudatus* (Hicks), × 3 approx.

Genus *MICROPARIA* Hawle & Corda 1847

Type species. *Microparia speciosa* Hawle & Corda 1847, by original designation.

Diagnosis. Middle-sized cyclopygids with five thoracic segments. Cranidium with parabolic outline, lacking incised glabellar furrows. Front of glabella never extended into a long 'nose', and cephalic doublure correspondingly short (sag.) Eyes extend almost whole length of cranidium and may become fused anteriorly. Pygidium usually with weakly-defined border best developed posterolaterally; doublure narrow to wide. Pygidial axis wide and short, not convex (tr.), either poorly defined, with up to one or two rings weakly indicated (subgenus *Microparia*), or clearly defined with three axial rings and a minute triangular terminal piece (subgenus *Heterocyclopyge*).

Discussion. Our concept of *Microparia* differs in some respects from that of Marek (1961). We exclude from the genus those large cyclopygids with six thoracic segments and a long glabellar 'nose' which are placed in *Degamella* or *Novakella* herein. On the other hand we include *Heterocyclopyge* Marek 1961, as a subgenus of *Microparia*. Marek originally discriminated *Heterocyclopyge* from *Microparia* on the basis of its 'almost subtetragonal' pygidium, with the pygidial axis distinctly defined. The close relationship between *Microparia* and *Heterocyclopyge* is demonstrated by *M. broeggeri* from south Wales, described below. In that species there is variation in the definition of the pygidial axis, which is posteriorly effaced in the majority of specimens, and typical of *Microparia*, but in others is defined almost to the tip (Fig. 44d); the pygidium is long (sag.) compared with many *Microparia* spp. Variation within *M. broeggeri* bridges the characters of *Microparia* and *Heterocyclopyge* rather well. The two morphologies appear to separate in the Llanvirn and later. It may be that *M. broeggeri* is one of the rare examples where an ancestral species can be identified. In any case it proves that *Microparia* and *Heterocyclopyge* are more closely related to one another than to *Degamella* or *Novakella*, and subgeneric status for *Heterocyclopyge* is used to express this relationship.

Zhou (1977) proposed a subgenus *Microparia* (*Quadratapyge*) for cyclopygids with five thoracic segments, well-defined, short pygidial axis, and very wide flattened border. This pygidial morphology is more different from that of *Microparia* (*Microparia*) than that of *Microparia* (*Heterocyclopyge*), and if further species of *Quadratapyge* can be recognized it may warrant full generic status.

Subgenus *MICROPARIA* Hawle & Corda 1847

Diagnosis. *Microparia* with pygidial axis only clearly defined anteriorly, if at all.

Microparia* (*Microparia*) *broeggeri (Holub 1912)
(Figs 44a–e, 45a–e, 48)

1912 *Aeglina bröggeri* Holub: 7; pl. 1, fig. 8.
1961 *Microparia* (*Microparia*) *bröggeri* (Holub) Marek: 45; pl. 3, fig. 16.

Type locality. Klabava Formation, Arenig, Bohemia.

Figured material. Axial shields: It.18551, It.18586, It.15933; pygidia: It.19617, It.15934–5; free cheek: It.19626.

Other material. It.18588–99, It.18617, It.15936, NMW 84.17G.45–52.

Stratigraphical range. Upper Arenig, Fennian. Widely distributed through the upper part of the Pontyfenni Formation, *Bergamia rushtoni* Biozone, Llwyn-crwn, Pontyfenni, etc.; north Wales, west side of Nant-y-Gadwen, Llŷn.

Description. Axial shields are approximately twice as long as wide; on the best preserved dorsal exoskeleton the cranidium accounts for 0·43 of total length, and the thorax 0·25 of total length, with the pygidium 0·32 of total length. In other specimens the cranidium can occupy 0·40 of the dorsal length; the thorax is invariably shorter than the pygidium. All specimens have suffered some degree of flattening; because *Microparia* spp. do not have much convexity,

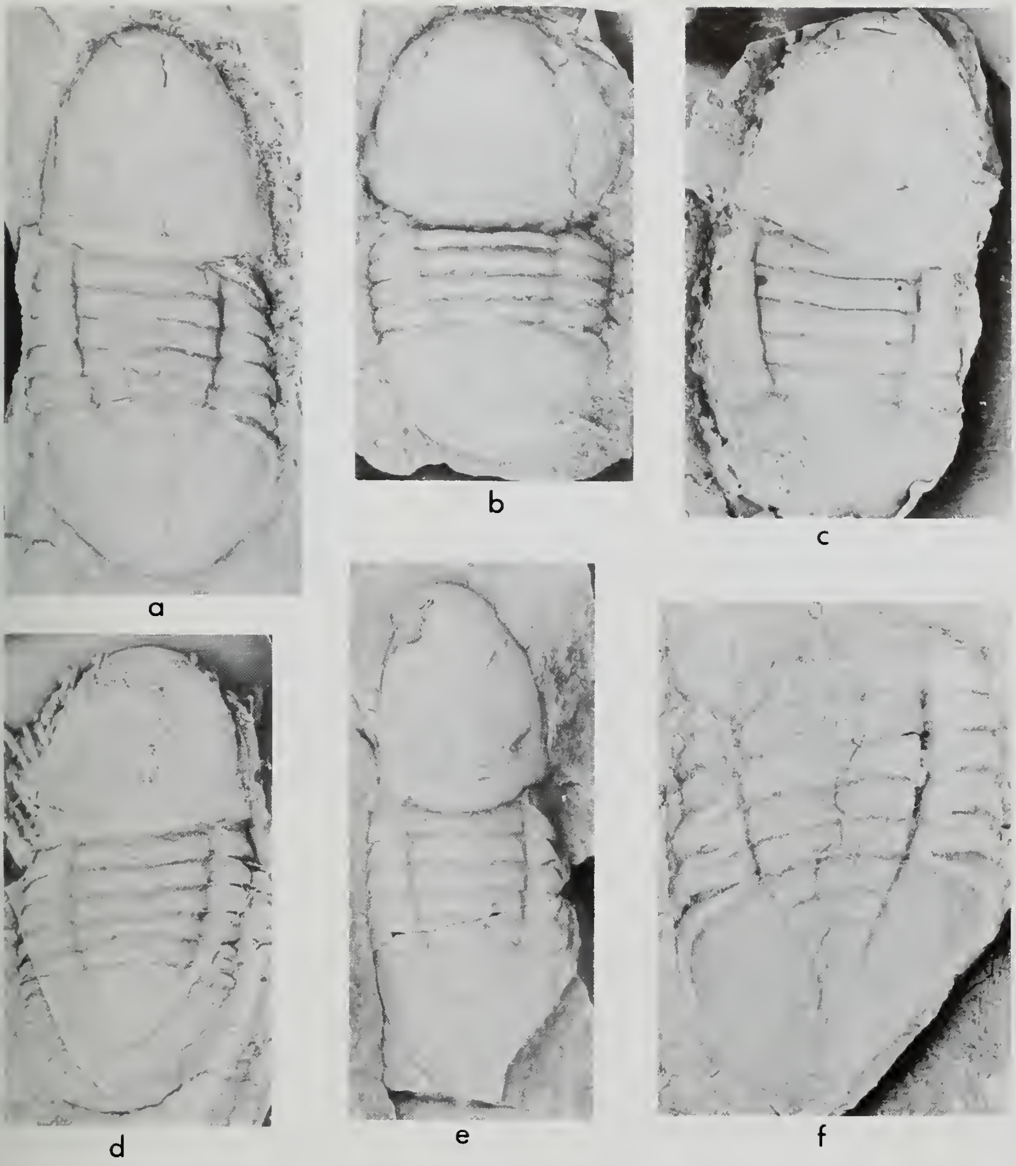


Fig. 44 a–e, *Microparia* (*Microparia*) *broeggeri* (Holub 1912). Upper Arenig, Fennian. a, axial shield, Pontyfenni Formation, *B. rushtoni* Biozone, loc. 24, × 3, It.18551; b, cast from dorsal exoskeleton, comparing with Holub's original, locality as Fig. 44a, fifth thoracic segment partly concealed beneath cephalon, × 3, It.18586; c, cast from axial shield in presumed moult arrangement, loc. 24, × 4, It.15934; d, cast from axial shield of slightly distorted specimen, *B. rushtoni* Biozone, loc. 23, × 4, It.15933; e, axial shield of largest specimen, with more elongate cranidium, × 3, It.19617; f, *M.* (*Microparia*) aff. *broeggeri*, stratigraphically young specimen with slightly better definition of pygidial axis, Llanfallteg Formation, loc. 52E, *Dionide levigena* Biozone, × 4, It.19624.

except at the front of the cranidium, it is thought that the proportions have not been altered. No doubt the free cheeks hung down almost vertically from the sides of the cranidium as they do in other species.

Cranidium with the broadly arcuate outline typical of the genus, and virtually featureless; widest posteriorly; length/width ratios somewhat variable, ranging between 1·3 and 0·75 with a mean of 1·0. Palpebral rims do not extend very far back; posterolaterally on the cranidium there are slightly inflated subtriangular areas presumably representing relict fixed cheeks. Free cheeks consisting of large oval eyes connected by united doublure, not closely approaching mid-line in front, with a small section of border posteriorly. Cephalic surface smooth except for fine lines close to, and parallel to, the margin of the cranidium. One specimen (Fig. 45b) shows the cephalic doublure with the hypostoma in place.

Thorax of five segments, parallel-sided or expanding in width slightly backwards; axial taper slight over first three segments, more rapid over posterior two. Half-rings about one-third sagittal length of axial rings. Pleurae bluntly spinose, point of articulation remaining quite close to axis. Dorsal surface of axial rings carry about six raised lines near posterior margins, which are also present on the posterior part of the pleurae.

Pygidium generally about two-thirds as long as wide, but highly variable (length/width ratio in range 0·60 to 0·83); outline broadly arcuate, larger examples showing tendency to become triangular (Fig. 45d). Pygidial axis occupies 0·44–0·48 of pygidial width at anterior margin, where it is defined by a prominent rim-like half-ring, tapering backwards quite rapidly, axial furrows enclosing an angle of about 60°. On most examples the axis becomes effaced posteriorly, but on the large specimen (Fig. 44a) it is traceable to beyond half pygidial length and almost to its tip. One axial ring is discernible on all but the most completely flattened specimens, of similar length (sag.) to the axial rings on the thorax, and defined either by a complete ring furrow or by a pair of depressions representing its outer ends. Faint indications of a second ring on many specimens. Narrow border, present only laterally, present as a rather poorly defined flattened area on most specimens, but can appear as a narrow, gently convex rim on some flattened material. Pygidial doublure widens backwards to a maximum on mid-line of about one-quarter pygidial length, and on exterior surface carries 7–10 terrace ridges, which can appear on dorsal surface of composite moulds. Apart from anterior furrow pleural fields are smooth, or with two or three pairs of obscure ridges indicating segmentation.

Discussion. The holotype and only known Bohemian specimen of *Microparia broeggeri* is lost, according to Marek (1961). We have to rely on Holub's (1912: pl. 1, fig. 8) figure to characterize the species. This does, however, clearly show features which can be matched on the numerous specimens from the Pontyfenni Formation: the pygidium slightly longer than the thorax with a deeply rounded outline; effaced pygidial axis with only the first ring defined by a pair of lateral impressions. Holub's figure also shows a slight increase in the transverse width of the thorax backwards, which can be matched on the specimen shown in Fig. 45c. Given the otherwise conservative morphology of *Microparia* these shared similarities are likely to be of specific significance, and Holub's name is accordingly used for our new material from south Wales. It is like the type species, *M. speciosa* (e.g Marek 1961: pl. 3, figs 5–10; *in* Horný & Bastl 1970: pl. 7, fig. 1; Kielan 1960: pl. 10, fig. 6), of Ashgill age, which is distinguished mainly by its relatively transverse pygidium, with a wider axis and relatively effaced pygidial axis.

The other Bohemian species revised by Marek (1961) include *M. brachycephala* (Klouček 1916), a species in which the maximum cranidial width exceeds the sagittal length in dorsal view, and the pygidial doublure is broader than in *M. broeggeri*, and *M. prantli* Marek 1961, which has thorax and pygidium equal in length, and the cranidium is produced into a distinct 'nose'. The closest species is probably *M. plasi* Marek 1961, from the Dobrativá Formation (Llandeilo), which is very similar to *M. broeggeri* in the relative lengths of cephalon, thorax and pygidium, degree of effacement, and width of pygidial doublure. Marek (1961: 44) notes the presence of three faint pairs of cephalic muscle impressions; their absence on the Arenig material from Wales could well be a matter of preservation. The distinguishing character is in the shape of the cranidium, which is widest not at the posterior margin, as in *M. broeggeri*, but

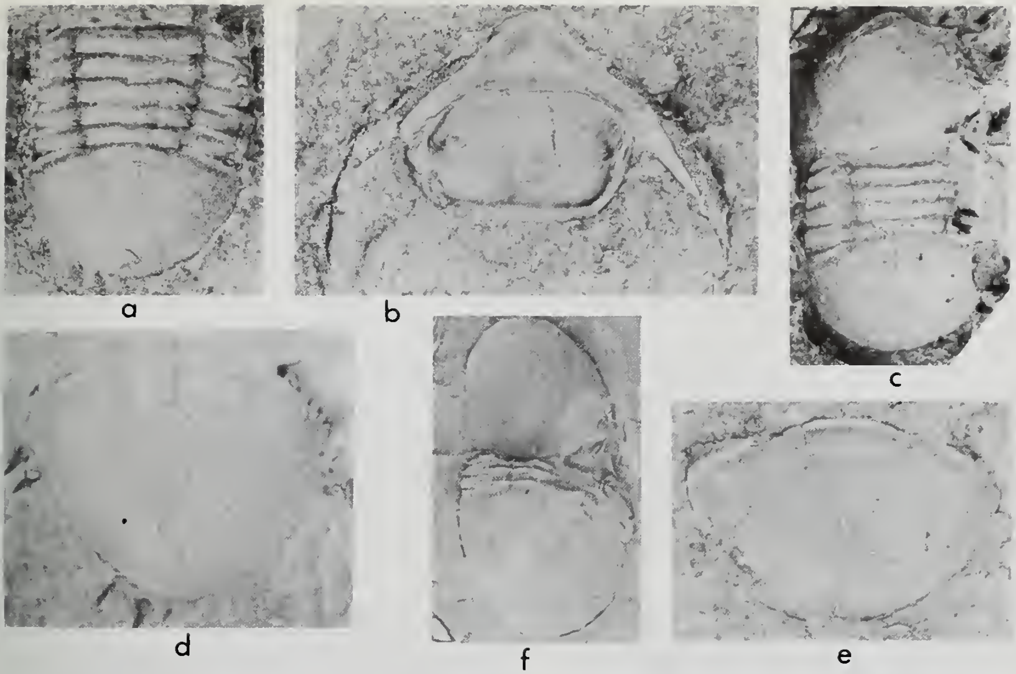


Fig. 45 a–e, *Microparia* (*Microparia*) *broeggeri* (Holub 1912). Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 24. a, small thorax and pygidium, most transverse specimen, × 6, It.19625; b, fused cheeks and hypostoma, × 3, It.19626; c, small specimen comparing with Holub's type specimen, × 4, It.15931; d, large pygidium showing tendency to elongate-triangular shape, × 3, It.15934; e, cast of pygidium, loc. 24, × 6, It.15935. f, *Microparia* (*Microparia*) *boia* (Hicks 1875). Middle Arenig, Whitlandian, *G. gibbsii* Biozone, Pwlluog, north of Whitesand Bay, St David's, Dyfed. Holotype, axial shield with cranidium displaced over thorax, × 4, SM A16731.

some distance in front, both palpebral lobes and axial furrows being bowed outwards, rather in the manner of *Pricyclopyge*.

Rushton & Hughes (1981) suggested that *M. plasi* might prove to be a junior synonym of *M.* (*Heterocyclopyge*) *shelvensis* Whittard 1961, from the Llanvirn of Shropshire, attributing the better definition of the pygidial axis and its rings on the holotype of that species to 'frontal compression' in the preservation. In our view this is not probable; the good definition of the pygidial axis is the critical character of *Heterocyclopyge* (see above), to which *shelvensis* should be referred. There are three specimens of *M.* (*H.*) *shelvensis* in the collections of the British Museum (Natural History) and the axial furrows are deep on all of them. The form described as *M.* cf. *shelvensis* from the Great Paxton borehole has an effaced pygidial axis, and also shows a forward expansion on the cranidium (Rushton & Hughes 1981: pl. 3, fig. 7), which in our view renders it indistinguishable from *Microparia* (*Microparia*) *plasi*, except perhaps for a slightly more rapid taper on the pygidial axis. Of Whittard's (1940: pl. 5, figs 6–8) original figured material all except the subsequently designated holotype of *M. shelvensis* are more like *M. plasi*.

Microparia (*Microparia*) *major* (Salter 1853) is a well-preserved, unique specimen of a thorax and pygidium from a probable late Llandeilo locality in Anglesey. It is virtually without a pygidial border, and has a very narrow doublure, and hence is quite different from *M.* (*M.*) *broeggeri*; it may prove to be a senior synonym of *M.* (*M.*) *lusca* Marek 1961.

As discussed above, the definition of the pygidial axis on *M.* (*M.*) *broeggeri* is somewhat variable, and the species forms a link between *Microparia* (*Microparia*) and *M.* (*Heterocyclopyge*). The stratigraphically youngest specimen we have recovered is from the

Llanfallteg Formation (Fig. 44f) and on this specimen the axis is visible almost to its tip. It is almost intermediate between *M. broeggeri* and *M. shelvensis*, although the weak development of the border is like the Arenig species. We refer to it as *M.* aff. *broeggeri*.

Microparia **(*Microparia*)** ***porrecta*** sp. nov.
(Figs 46a–d, 47)

Holotype. Pygidium, BGS Pr1940.

Paratypes. Cranidium with three thoracic segments It.19630; cranidium It.19631.

Type locality and horizon. 'Roadside 200 yd E by S of Llan, $\frac{3}{4}$ mile NE of Llanfallteg railway station' (Geol. Survey loc. Wλ9); Llanfallteg Formation, uppermost Arenig part.

Stratigraphical range. The paratypes are from the earliest Llanvirn part of the Llanfallteg Formation at Cefn-maen-Llwyd farmyard, and from the Upper Arenig (Fennian, Biozone of *Bergamia rushtoni*) of the type locality of the Pontyfenni Formation, loc. 23, respectively.

Diagnosis. *Microparia* with cranidium 1·5 times wider than long, and palpebral rims not extending far back; pygidium more than 2·5 times wider than long, axis not defined, and with broad doublure.

Name. 'Extended'.

Description. No complete specimen of this species is known, but the association of the very wide cranidia with the transverse pygidium is probable. We have nominated the pygidium as

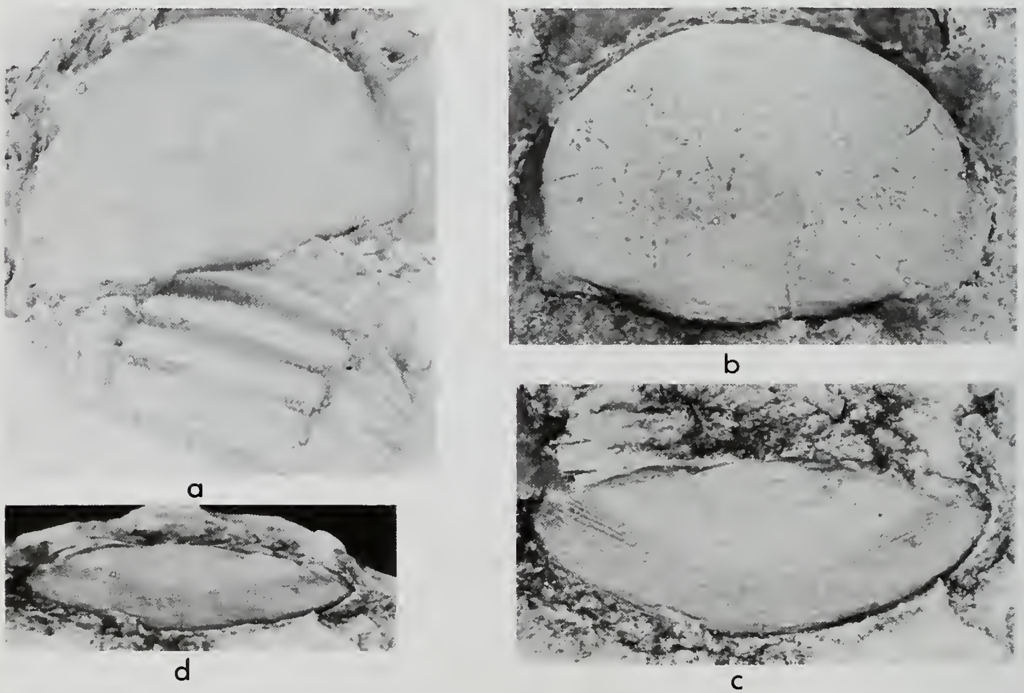


Fig. 46 *Microparia* (*Microparia*) *porrecta* sp. nov. a, cranidium and three thoracic segments, Llanfallteg Formation, early Llanvirn, *D. artus* Biozone, loc. 50, × 4, It.19630; b, cranidium, preserved with natural relief, Pontyfenni Formation, upper Arenig, Fennian, *B. rushtoni* Biozone, loc. 23, × 6, It.19631; c, d, pygidium with 2 thoracic segment tips, Llanfallteg Formation, latest Arenig, *D. levigena* Biozone, Geological Survey locality Wλ9 (Strahan *et al.* 1914: 20), **holotype** BGS Pr1940, dorsal, × 8, and posterior, × 6, views respectively.

holotype because it differs from that of any other cyclopygid. The cranidium is wider than any *Microparia* species but does not differ in structure. Maximum cranidial width is attained some distance in front of the posterior cranidial margin, this being one and a half times the sagittal length, or slightly more. The specimen from the Pontyfenni is preserved in relief, showing very gentle transverse convexity, but a steep downward slope around the edge of the forward cranidial margin. Palpebral rims are comparatively well defined anteriorly, where they are narrow and tucked beneath the frontal part of the median cephalic lobe; backwards they are wider but become fainter, being hardly discernable behind the point of maximum cranidial width. However, the pleuroccipital furrows are faintly indicated at the posterior cranidial margin, indicating that the glabella there occupies about three-fifths the maximum cranidial width.

Only the first three thoracic segments are preserved, but we have based the reconstruction (Fig. 47) on the assumption that there were five segments as in all *Microparia*. The axis is very wide; on the anterior segment the pleurae are only about one-third the axial width (tr.). Otherwise the thoracic structure is as conservative as in other cyclopygids. The first thoracic ring shows well the characteristic sagittal elongation of the first articulating half ring.

The transverse pygidium has a gently arcuate posterior outline, and wide, weak border only developed laterally. There is no trace of the axis, but some indication of its extent is given by the inward extension of the narrow (exsag.) facets, which show that it occupied about half the pygidial width. Doublure wide, occupying more than a third of the sagittal length, and slightly wider laterally, carrying 7–8 terrace lines.

Discussion. The cranidium from the Pontyfenni Formation is so like that from the Llanfallteg Formation that it is likely the one species ranges from the Fennian into the earliest Llanvirn. It is such a distinctive form that the possibility of its generic separation from *Microparia* was considered. However, it is best regarded as a *Microparia* in which transverse extension has reached an extreme development, while it retains the structures of the cranidium and pygidium seen on other members of the genus. It is a homoeomorph of *Emmrichops* and *Gastropolus*, but in our view is closely related to neither of these genera. The width of the cranidium and pygidium distinguishes *M. porrecta* from any other species of *Microparia*.

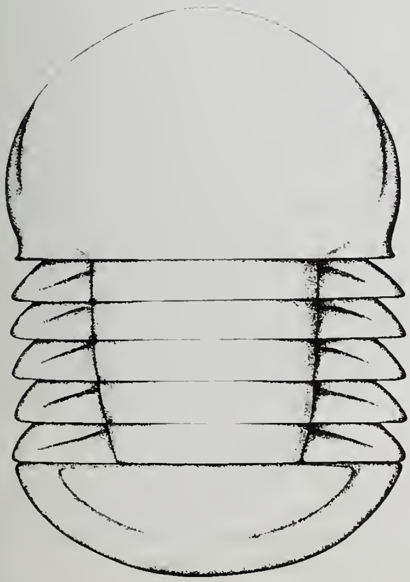


Fig. 47 Reconstruction of axial shield of *Microparia* (*Microparia*) *porrecta* sp. nov., × 3 approx.

Microparia (*Microparia*) *teretis* sp. nov.
(Figs 48, 49)

HOLOTYPE. Axial shield, BGS Pr1991.

PARATYPES. Incomplete dorsal exoskeleton SM A44523; cranidium It.19634; pygidia It.19632–3, NMW 84.17G.54–55; free cheek It.19706; thorax and pygidium NMW 84.17G.53.

TYPE LOCALITY AND HORIZON. Llanfallteg Formation, Rhyd-y-wrâch, near Llanfallteg; earliest Llanvirn.

STRATIGRAPHICAL RANGE. Llanfallteg Formation, spanning the Arenig–Llanvirn boundary. Type section, 20 m below boundary (52L); earliest Llanvirn of locs 50, 52; and Scolton railway cutting, loc. 55.

DIAGNOSIS. *Microparia* with broadly oval exoskeleton less than twice as long as wide; thorax and pygidium about equal in length, and cranidium not greatly longer. Cranidium broad (tr.) for genus, poorly defined palpebral rims. Pygidium almost twice as wide as long with relatively wide border which is distinctly defined laterally.

NAME. 'Smoothed off'.

DESCRIPTION. The holotype preserves what is probably the original convexity: low transversely, with a gently swollen cranidium, narrowly but steeply down-turned around its anterior edge. The exoskeleton is less elongate than *Microparia broeggeri*, width across the mid-part of the thorax more than half sagittal length. Cranidial outline is very broadly and gently rounded about mid-line, cranidial length only about two-thirds width (length/width ratio in the range 0·62–0·75). Maximum cranidial width achieved shortly in front of posterior cranidial margin. Otherwise dorsal cranidial surface is devoid of features; specimens do not show palpebral rims.

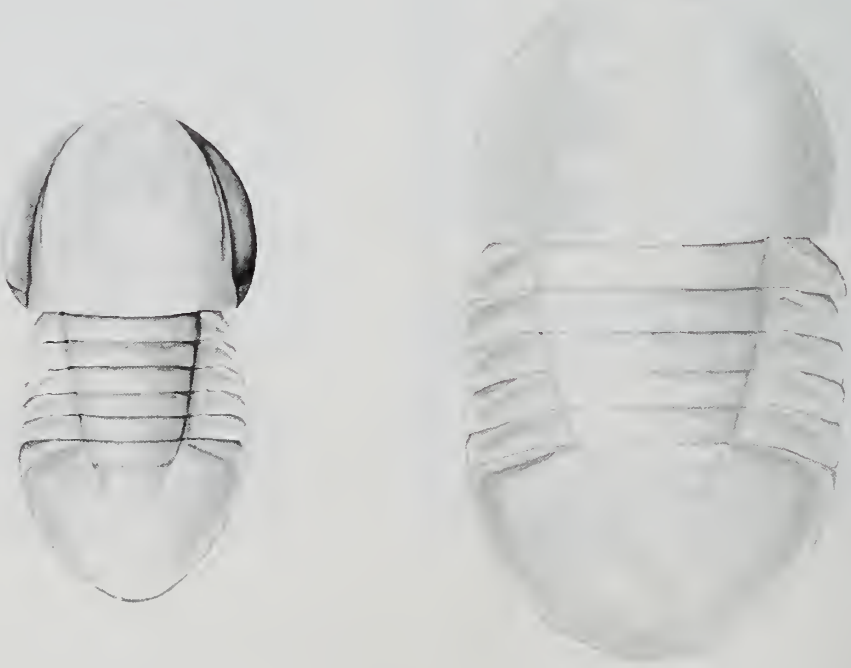


Fig. 48 Reconstructions of dorsal exoskeleton of *Microparia* (*Microparia*) *broeggeri* (Holub), left, and axial shield of *M.* (*Microparia*) *teretis* sp. nov., right, both × 3 approx.

We presume that a gently curved eye belongs here, which has a short postocular border like most *Microparia* spp. Facial sutures evenly curved except for a short sigmoidal curve at posterior margin. Glabellar tubercle at two-thirds cranidial length.

Thorax about two-thirds cephalic length. Broad axis about three-fifths cranidial width at first segment, with very gentle posterior taper. Pygidium of about the same length (sag.) as the

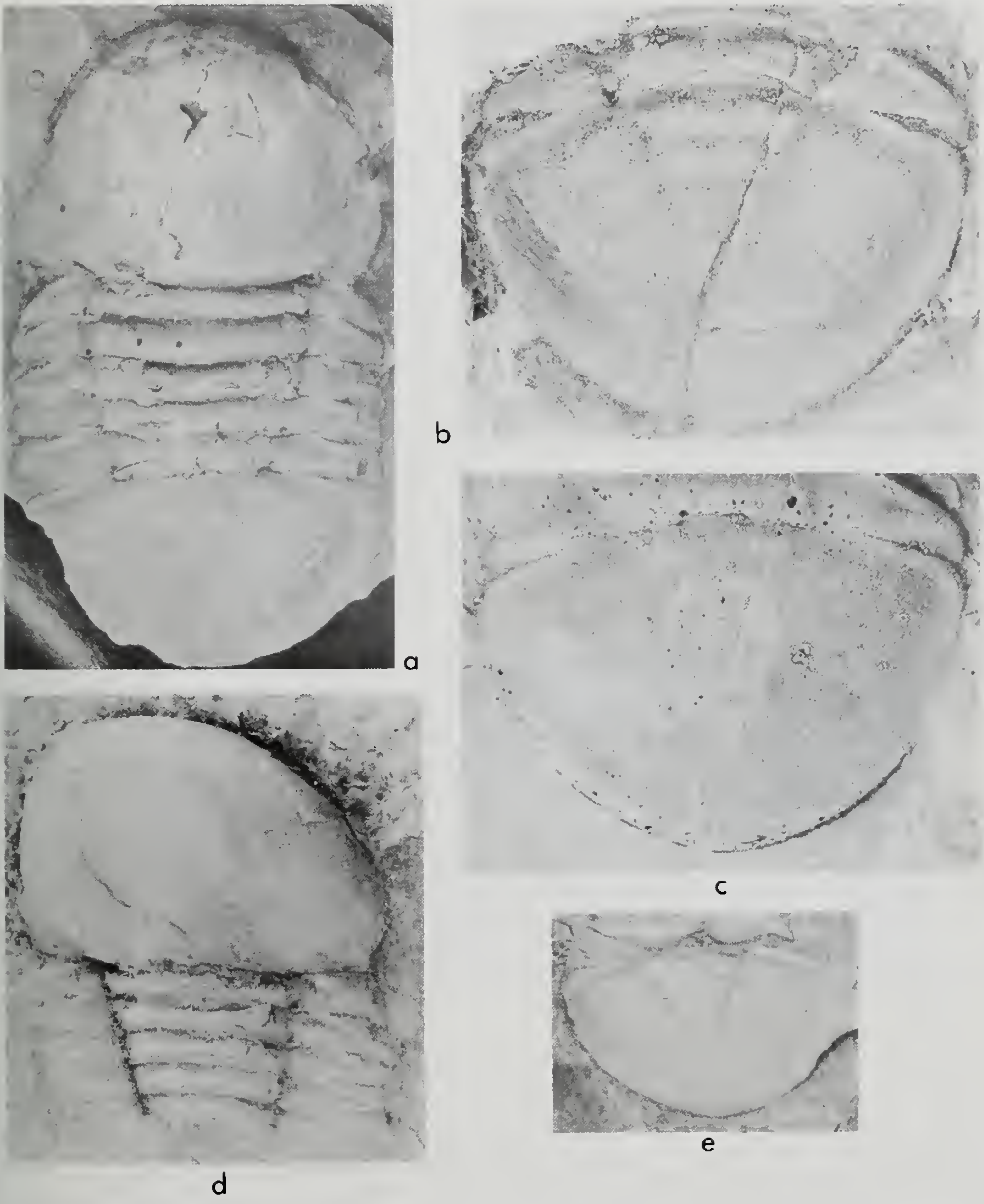


Fig. 49 *Microparia* (*Microparia*) *teretis* sp. nov. Llanfallteg Formation. a, holotype, axial shield, early Llanvirn, *D. artus* Biozone, loc. 50, × 3, BGS Pr1991; b, c, pygidium with one thoracic segment, internal mould and latex cast from counterpart external mould to show sculpture, loc. 50, × 6, It.19632; d, cranidium and thorax, slightly distorted, loc. 55, × 6, SM A44523; e, small pygidium, loc. 52E, latest Arenig, *D. levigena* Biozone, × 6, It.19633.

thorax, and almost twice as wide as long. Axis poorly defined, but rapidly tapering, as in most *Microparia* spp. Three axial segments are faintly indicated on the holotype. The border is relatively well defined and gently convex anterolaterally, wide, and widening backwards until it becomes obscure postaxially. Doublure also widens backwards to midline, at its widest about one-quarter of pygidial length.

Dorsal surface is almost without sculpture; there are a few terrace lines on the thoracic axial rings, and fine, subtransverse terrace ridges on the posterior part of the pygidium. The pygidial doublure carries about eight stronger terrace ridges.

Discussion. This *Microparia* is distinguished from most others, including the type species, by its very broad and gently rounded cranidium lacking distinct palpebral rims. Of the Bohemian species revised by Marek (1961) it is closest to the Llandeilo *M. brachycephala* (Klouček 1916), which is itself distinguished from the type species, *M. speciosa*, by a relatively broad cranidium. Marek's figures and measurements show that the length/width ratio of the cranidium of *M. brachycephala* is in only just less than 1, whereas the comparable ratio in *M. teretis* is less than 0·8. The pygidial doublure of *M. brachycephala* is wider, and the palpebral rims are better defined. *M. laevis* Whittard, 1961*a*, has an even wider cranidium than *M. teretis*, and the pygidial border is narrow and distinctly flattened. *M. porrecta* sp. nov. (p. 168) also has a wider cranidium, and the pygidium is altogether more transverse. *Pricyclopyge wattisoni* Hughes 1979, from the Lower Llandeilo of Builth, is very like *Microparia brachycephala*, and it would be difficult to refer it to any genus other than *Microparia* unless the six-segment thorax (Hughes 1979: fig. 5) could be proved to belong. The pygidium illustrated by Hughes (1979: fig. 8) is more transverse than that of large *M. teretis*, and with narrow lateral borders, but it resembles the smaller examples of our species more closely (Fig. 49e). Its axis is much narrower, however, and distinctly defined anteriorly.

It is interesting to note some resemblance between *M. teretis* and the small specimens (not the large holotype) of '*M.*' *nudus* Whittard, 1961*a*, here assigned to *Degamella*. The degree 5 meraspis (Whittard 1961*a*: pl. 24, fig. 9) has a very wide cranidium, like *M. teretis*. There is of course no question of our large specimens being meraspides. Even the small *nudus* specimens are distinguished by their wide pygidial doublures and gently tapering pygidial axes.

Microparia* (*Microparia*) *boia (Hicks 1875)
(Fig. 45f)

1875 *Aeglina Boia* Hicks: 185; pl. 10, figs 9, 9a.
1939*b* *Gallagnostoides boia* (Hicks) Kobayashi: 580.
1961*a* *Cyclopyge boia* (Hicks) Whittard: 179.

Holotype. Crushed and slightly distorted axial shield, SM A16731.

Type locality. Whitlandian of the old quarry north of Whitesand Bay, St David's.

Stratigraphical range. Only known from the type locality, Whitlandian, biozone of *Gymnostomix gibbsii.*

Other material. Axial shield, GSM 8689.

Discussion. This species is known from imperfect material from the type locality; attempts to recover it from the mudstone facies of the Whitlandian have not been successful. It is of some interest as the earliest *Microparia.* The holotype has the cranidium displaced backwards over the front of the thorax. Even so traces of three and possibly four thoracic segments can be seen. Kobayashi (1939*b*) presumably based his determination of the specimen as representing a new agnostid genus on Hicks' schematic figure. The species is generally like *M. broeggeri* (Holub) (p. 164), and Hicks' name would, of course, have priority over Holub's if it were conspecific. Several features suggest that this is not the case. There is no trace of the pygidial axial furrows on *M. boia*. Since the half-ring and anterior pygidial pleural furrows *are* discernible, one would expect the axial furrows to be preserved also if they had been defined. There appears to be no lateral pygidial border, and the doublure, clearly shown on the holotype, is narrower. Although *M. boia* is probably distinct from *M. broeggeri*, we cannot give a satisfactory diagnosis of the species on the basis of the material known at present.

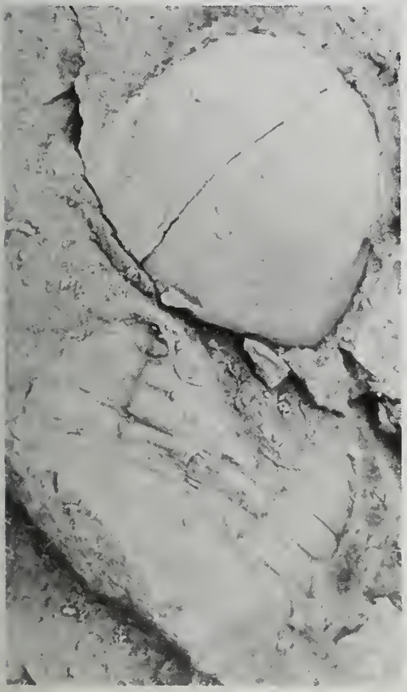
Microparia? sp. indet. 1
(Fig. 50)

MATERIAL. Incomplete axial shield It.19635, from the type locality of the Pontyfenni Formation, loc. 23.

STRATIGRAPHICAL RANGE. Fennian, Upper Arenig, biozone of *Bergamia rushtoni.*

DISCUSSION. This species is known from only one specimen, but is obviously distinct from *Microparia broeggeri* (Holub) from the same horizon. The cranidium is wider than long, and the front of the glabella is broadly rounded, almost semicircular, carrying a conspicuous sculpture of incised lines running parallel to the cranidial margin. The axial furrows take an inward bend at about cranidial mid-length, thereby defining a long (exsag.), narrow fixed cheek, but they fade out well before the posterior cranidial margin. The thorax shows five segments of usual *Microparia* type. The pygidium is incomplete, but what there is shows that the axis was probably not defined dorsally, and that there was a distinct border, at least laterally.

The broadly rounded frontal glabellar lobe, and the inward curve of the axial furrows, is very different from *M. broeggeri*, and indeed other *Microparia* species. *M. teretis* also has a wide cranidium, but it is featureless, without sculpture or distinct furrows. Later species of *Degamella* tend to have axial furrows which take an inward bend, and this is associated with smaller eyes than is usual for cyclopygids. However *Microparia* sp. indet. 1 is not related to *Degamella*, because it lacks a cranidial 'nose' and has five thoracic segments. It is certainly a new species, and may even be generically distinct from *Microparia*, but we have too little material to name it formally.



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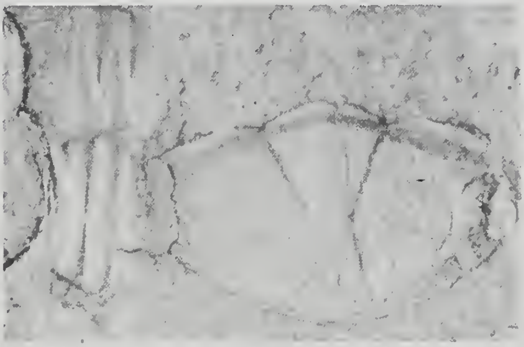

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Fig. 50 *Microparia*? sp. indet. 1. Pontyfenni Formation, Upper Arenig, Fennian, *Bergamia rushtoni* Biozone, loc. 23, imperfect axial shield, × 5, It.19635.

Fig. 51 *Microparia* (*Heterocyclopyge*?) sp. indet. Pontyfenni Formation, Fennian, *B. rushtoni* Biozone, loc. 23, × 6, BGS Pr579.

Subgenus *HETEROCYCLOPYGE* Marek 1961

Type species. *Cyclopyge pachycephala* Hawle & Corda 1847.

Diagnosis. *Microparia* species with a well-defined pygidial axis.

Microparia (*Heterocyclopyge*?) sp. indet.

(Fig. 51)

Material. Pygidium with three displaced thoracic segments, BGS Pr579.

Stratigraphical range. Pontyfenni Formation, loc. 23; Upper Arenig, Fennian, *B. rushtoni* Biozone.

Discussion. This single specimen cannot be formally named. The pygidium is at once distinguished from that of *Microparia* (*Microparia*) *broeggeri* (Holub) by its narrow axis and deep axial furrows, except at the tip. It is thus closest to *Heterocyclopyge* as defined here. However it also differs from *Microparia* (*Heterocyclopyge*) *pachycephala* (Hawle & Corda) and *M.* (*H.*) *shelvensis* Whittard in that the axial rings are not defined, so that even its inclusion in *Heterocyclopyge* is uncertain. The doublure appears to be narrow, and the border ill-defined. See *Circulocrania orbissima* gen. et sp. nov., pp. 186–7.

Genus *NOVAKELLA* Whittard 1961*a*

(= *Incisopyge* Pillet & Courtessole 1985: 213)

Type species. *Aeglina bergeroni* Novák, *in* Novák & Perner 1918, by original designation; authorship discussed in Whittard, 1961*a*: 170, 1966: 285.

Discussion. We recognize *Novakella* as a genus distinguished from *Degamella* by its deep, slit-like glabellar furrows, which are visible even on flattened material. Other dorsal furrows are also generally deep, for example axial rings and pleural furrows on the pygidium. On the type species the glabellar furrows are perhaps less incised than they are in *N. copei* sp. nov. or *N. incisa* Whittard, but they are quite clearly of the same form (Marek 1961: pl. 4, fig. 11). The genus *Incisopyge* Pillet & Courtessole 1985, with *N. incisa* as type species, is diagnosed in the same way as *Novakella* herein, of which it is considered a subjective synonym.

Novakella copei sp. nov.

(Figs 52a–d)

1885 *Aeglina* sp.; Postlethwaite: pl. 3, fig. 15.
1886 *Aeglina* sp.; Postlethwaite & Goodchild: 463: pl. 8, fig. 15.

Holotype. Axial shield It.15937.

Paratypes. Cranidium It.19637; pygidium It.19638; axial shield GSM 32833.

Type locality and horizon. Llanfallteg Formation, earliest Llanvirn of loc. 50.

Stratigraphical range. From the Llanfallteg Formation, the species occurs in the type section below the Llanvirn boundary, and at the type locality just above the boundary. A specimen from the Lake District recorded as 'Skiddaw' is presumably of Upper Arenig (Fennian) age there.

Name. For Dr J. C. W. Cope, who has assisted the authors in countless ways during the research for this paper.

Diagnosis. *Novakella* with relatively short, bluntly rounded cranidium; pygidium triangular, border ill-defined, with about four pairs of pleural furrows, and rapidly tapering axis.

Description. Exoskeleton twice as long as wide, the thorax and pygidium being subequal in length and each about 0·6 that of cranidium. Specimens are flattened, and characters such as the depth of furrows may have been affected by this, but flattening will not have affected the

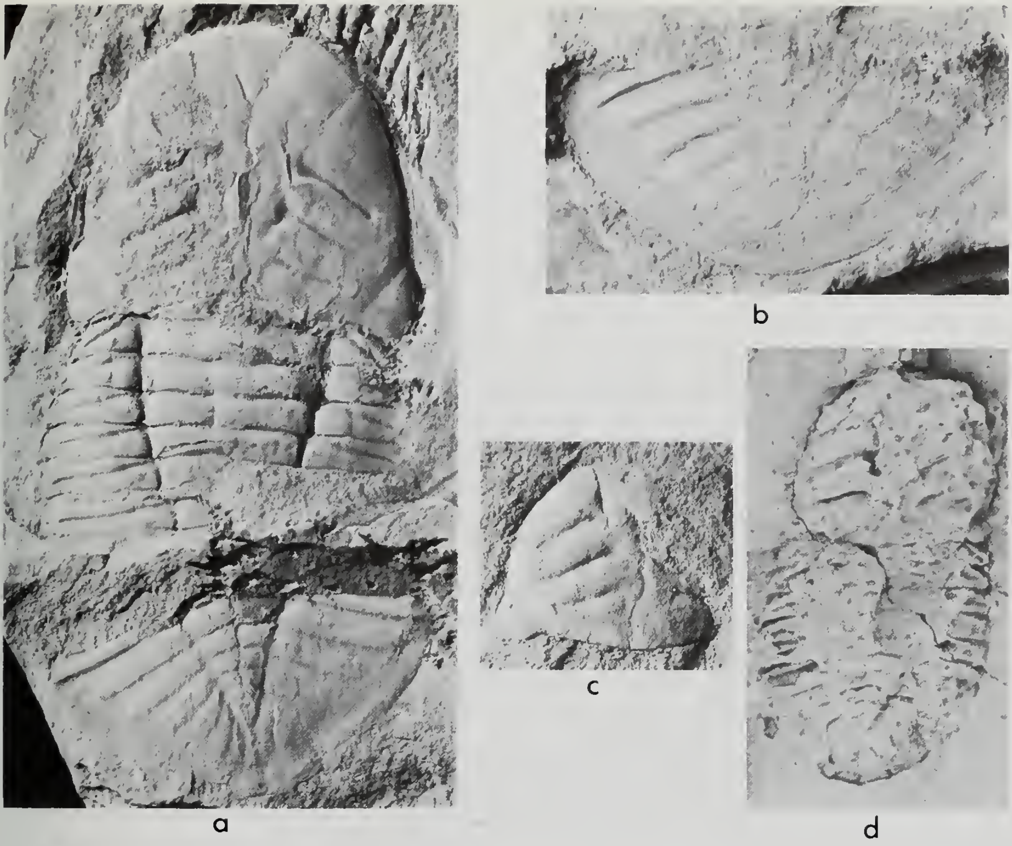


Fig. 52 *Novakella copei* sp. nov. a, **holotype**, axial shield, Llanfallteg Formation, loc. 50, early Llanvirn, *D. artus* Biozone, × 2, It.15937; b, pygidium showing doublure, locality as Fig. 52a, × 2, It.19638; c, latex cast from fragmentary cranidium, Llanfallteg Formation, loc. 52V, latest Arenig, Fennian, *Dionide levigena* Biozone, × 2, It.19637; d, small poorly preserved axial shield, Skiddaw Slates of 'Skiddaw', original of Postlethwaite 1885: pl. 3, fig. 15, × 4, GSM 32833.

broadly rounded outline of the front of the cranidium, which is almost semicircular. Maximum cranidial width is at its posterior margin and this just exceeds the sag. length. Axial furrows weakly defined posteriorly, such that the short, triangular postocular cheeks are hardly distinguishable from the glabella. Three pairs of glabellar furrows of usual form for *Novakella*, with 2P longest and 3P most forward-inclined. Narrow, gutter-like palpebral rims extend backwards as far as the outer ends of 2P. Free cheeks not known.

Six thoracic segments, pleurae widening progressively backwards. Articulation on first segment close to axial furrow and further removed therefrom on posterior segments. Pleural furrows distinctly defined, nearly reaching tips of pleurae. Pleural terminations are distinctly truncate.

Pygidium broadly triangular, almost twice as wide as long. At least in the flattened preservation the border is not conspicuously flattened, but may have been more so in full relief. Four pairs of rather broad pleural furrows are defined, with indications of a weak fifth pair. Axis sharply conical, axial furrows including an angle of 40°–45°, and extending to two-thirds pygidial length; five (a faint sixth) axial rings are defined, which become progressively shorter (sag.) posteriorly; small terminal piece forms an almost equilateral triangle. Surface apparently lacking any sculpture.

DISCUSSION. *Novakella* is a very rare genus, and the holotype of the new species is one of the best preserved specimens known. *N. copei* is easily distinguished from the type species, *N. bergeroni*, from the Llanvirn Šárka Formation of Bohemia and the Hope Shales, Shropshire (Marek 1961: 50–52; pl. 4, figs 10–15; Whittard 1961*a*: pl. 23, fig. 5), which has an extended glabellar 'nose' making the cranidium longer than wide, and a semicircular, rather effaced pygidium. *Novakella incisa* Whittard, 1961*a* (:170; pl. 23, fig. 6) is known from a single specimen from the Hope Shales; compared with the holotype of *N. copei* the glabella is less broadly rounded anteriorly and clearly defined posteriorly; the 3P glabellar furrows are more strongly forward-directed; the pygidium has a narrow, more gently tapering axis and six pairs of clearly-defined pleural furrows. However, it should be noted that Whittard's holotype is smaller than ours, and it is likely that the relative depth of the furrows, for example, is a function of size; our smaller cranidium is more like *N. incisa* in its cephalic furrows (Fig. 52c). The difference in cranidial outline, and the shape and width of the pygidial axis, may be better specific characters. A smaller specimen of *N. copei* from the Lake District supports this; it is poorly preserved, but it shows that the pygidial axis was like that of *copei* rather than *incisa* at this size, and the glabellar front is broadly rounded.

Genus ***PROSPECTATRIX*** Fortey 1981

TYPE SPECIES. *Cyclopyge genatenta* Stubblefield 1927, by original designation.

DIAGNOSIS. See Fortey 1981: 611.

Prospectatrix cf. ***superciliata*** (Dean 1973*b*)
(Fig. 53)

cf. 1973*b* *Pricyclopyge superciliata* Dean: 314–316; pl. 6, figs 2, 4, 6, 8, 9, 14.

TYPE LOCALITY AND HORIZON. Sobova Formation, Taurus Mountains, Turkey; late Arenig.

OCCURRENCE IN WALES. Pontyfenni Formation, Upper Arenig, Fennian, biozone of *Bergamia rushtoni*; from type locality of Pontyfenni Formation and Capel-Dewi, loc. 20E.

MATERIAL. Cephalon NMW 84.17G.56; free cheek NMW 85.7G.16.

DISCUSSION. A single specimen of a cephalon from the Pontyfenni Formation is preserved in partial relief, with the forward part of the median cephalic lobe partly filled by a siliceous nodule; it is the posterior boundary of this nodule which produces the appearance of a transglabellar furrow. As its irregularity shows, this is an artefact of preservation. *Prospectatrix* is the most primitive cyclopygid known, with long (exsag.) relict fixed cheeks. When redescribing the type species from the Tremadoc of Shropshire and Wales, Fortey (1981: 612) suggested that the species *superciliata* Dean might also be referred to the same genus, which is confirmed by the new specimen from Wales. The course of the axial furrow is shown on the right-hand side of the specimen, the eye having been partly pushed over the cranidial margin. The Welsh

Fig. 53 *Prospectatrix* cf. *superciliata* (Dean 1973). Cephalon. Apparent transglabellar furrow is an artefact of preservation, as forward part of glabella is preserved within a nodule; course of axial furrow shown on right with fixigena over which the eye has been displaced. Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23, × 6, NMW 84.17G.56.

specimen is very like the holotype figured by Dean (1973: pl. 6, figs 2, 6, 8) from the Sobova Formation. *P. superciliata* is distinguished from *P. genatenta* in having fixed cheeks only about half (tr.) as wide, and in the broadly rounded frontal glabellar lobe. The Welsh specimen could be considered conspecific with the Turkish species on these criteria. A small difference is that our cephalon shows a sculpture of fine lines around the front of the glabella, as in many other cyclopygids; because the Turkish material is exfoliated we cannot say whether the same kind of sculpture was present. Accordingly, we are obliged to qualify our determination of *P. superciliata*. Dean (1973: 343) gives the type locality of *P. superciliata* an early Arenig age assignment, and if this is correct there is a significant age difference between the Turkish and Welsh occurrences.

Genus ***SAGAVIA*** Koroleva 1967

Type species. *Sagavia felix* Koroleva 1967, by original designation.

Discussion. The type species of *Sagavia* has been reported from the upper Middle Ordovician of Kazakhstan (Koroleva 1967, 1982) and Uzbekistan (Abdullaev 1972); another species, *S. elongata*, was described by Petrunina (1975) from southern Tien Shan. *Sagavia* is distinguished from *Microparia* by its well-defined pygidial axis, and relatively broad and well-defined pygidial border; the cranidium is parallel-sided and subrectangular rather than broadly arcuate in outline. *Heterocyclopyge* Marek 1961 also has a well-defined pygidial axis, but in that genus the cranidium is *Microparia*-like and there is no distinct pygidial border. Two well-preserved cyclopygid exoskeletons (lacking free cheeks) from the Arenig of south Wales are immediately distinguishable from *Microparia* and *Degamella* species in the Fenni Formation by their wide and well-defined pygidial borders. This species differs from previously described *Sagavia* species in several details, however: the pygidial axis is not so clearly defined posteriorly, and the cranidium is elongate-arcuate in outline, more like that of *Degamella*. There are five thoracic segments, like *Sagavia*, while *Degamella* has six. With this combination of characters its generic assignment is difficult. Variation in the shape of the cephalic lobe is known *within* genera in the cyclopygids, as in *Pricyclopyge*, and it seems reasonable, therefore, to emphasize the broad pygidial border in the generic placing. On this interpretation, the structure of the pygidial axis is then presumably primitive, indicating a common ancestry of *Sagavia* and *Microparia* or *Degamella*.

Sagavia glans sp. nov.
(Figs 54a–c, 55)

Holotype. Well-preserved exoskeleton lacking free cheeks, BGS Pr574–5.

Paratypes. Dorsal exoskeleton It.19640; thorax and pygidium, It.19641; pygidium, It.19642.

Type locality and horizon. Pontyfenni Formation, type locality at Pontyfenni.

Stratigraphical range. Upper Arenig, Fennian.

Name. ‘A bullet or projectile’, referring to the shape of the cranidium.

Diagnosis. A *Sagavia* species with cranidial outline more deeply arcuate than other species of the genus; pygidial axis not defined posteriorly; pygidial border widening backwards.

Description. Like most of the specimens from the type locality of the Pontyfenni Formation the holotype has escaped much distortion, and other specimens have similar proportions. The elongate-oval outline of the exoskeleton was thus presumably original—the exoskeleton is three times as long as wide. Thorax slightly shorter than pygidium (sag.), which attains nearly three-quarters of cephalic length.

Cranidium 1·3 times as long as wide, widest at rear end, whole outline deeply arcuate. Palpebral rims narrow adjacent to anterior two-thirds of cranidium. Relict fixed cheeks form long, narrow (exsag.) triangular areas at base of glabella, poorly defined on inner edges. Glabella without muscle insertion areas—or preservation may be inadequate to show them—and

Fig. 54 *Sagavia glans* sp. nov. Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23. a, **holotype**, axial shield, × 3, BGS Pr574; b, c, slightly imperfect dorsal exoskeleton, × 4, and enlargement of thorax and pygidium taken from latex mould of counterpart to show sculpture of raised lines, × 7, It.19640.

smooth apart from scattered raised lines around front margin running parallel to cranidial outline. Free cheek consisting largely of eye which extends along much of the cranidial margin (Fig. 54b).

Thorax with five segments, parallel-sided, but with axis tapering backwards, so that the pleurae correspondingly increase in width; pleurae on the first segment are exceedingly short and nearly triangular, whereas at hind margin of fifth segment the axis only comprises half the thoracic width. As in other cyclopygids the articulating half ring on the first segment is relatively long (sag.) compared with the posterior segments. Transverse raised lines run across axial rings.

Pygidium $\frac{7}{8}$ as long as wide, with axis slightly more than one-third transverse width at anterior margin. Axis continues taper of posterior part of thorax (axial furrows enclosing about 40°). On the holotype, only the first ring is clearly defined, the second ring faintly so, and behind this the axis is hard to distinguish from the pleural fields. Internal mould of paratype (Fig. 54b) has better-defined axis (except tip) showing three axial rings. Border distinctly defined, almost flat, comprising one-fifth (sag.) of pygidial length, narrower anteriorly, and widest on midline. Dorsal surface sculpture of raised lines tending to form a network on pleural flanks, not extending over axis, and parallel to pygidial margin on border. Doublure extended beyond border furrow, carrying 8–10 terrace ridges. There are obscure indications of perhaps two pleural furrows.

DISCUSSION. The general problems of classifying this species have been discussed above. *Sagavia felix* Koroleva 1967, *S. modica* Koroleva 1967, *S. elongata* Petrunina 1975, *S. novakellaformis* Koroleva 1982 and *S. heterocyclopygeformis* Koroleva 1982 all have pygidial axes which are

Fig. 55 Reconstruction of *Sagavia glans* sp. nov., × 3 approx.

well-defined around their tips, and their pygidial borders are widest posterolaterally rather than postaxially; none appear to have the surface sculpture of raised lines noted on our species. The south Wales species is considerably older than the Russian ones, which come from the Caradoc or Ashgill.

Subfamily ***PRICYCLOPYGINAE*** nov.

Diagnosis. Cyclopygidae having six thoracic segments, the third axial ring carrying a pair of hollow bulbs. Cranidium round to ovoid, with maximum width some distance in front of posterior margin. Glabellar furrows feebly developed, up to two pairs of transverse impressions. Pygidium wide, triangular to transversely elliptical, with a deeply defined border. Pygidial axis convex (tr.) and well defined, not rapidly tapering, falling somewhat short of border.

Genera included. *Pricyclopyge* Richter & Richter 1954; *Symphysops* Raymond 1925; if the association of cephalon and pygidium of *Emmrichops* Marek, 1961, given by Hughes (1979) is correct this genus also probably belongs here (for further discussion see under *Gastropolus*, p. 161); *Circulocrania* n. gen. (p. 186) may also prove to be a pricyclopygine.

Discussion. This subfamily is erected to include cyclopygids with the apomorphic character of a pair of hollow nodes or bulbs on the third axial ring of the thorax. The structure and possible function of these is discussed further below. Whatever their function they are unusual structures which are unlikely to have evolved more than once, and they are regarded as good evidence for the common ancestry of cyclopygids having them. The thorax has been described in *Pricyclopyge* and *Symphysops*, and the bulbs are present on thoraces of all the known species. The pricyclopygines are also characterized by having a cranidium which expands in width forwards at first, so that the cranidial outline is rounded, or elongate-elliptical rather than parabolic as in cyclopygines. Palpebral rims on pricyclopygines are flatter and broader than on cyclopygines. The pygidial borders are characteristically rather flat, and distinctly defined by a deep border furrow which does not get shallower over the mid-line, as it does on many cyclopygines. The thorax is not known for either *Emmrichops* or *Circulocrania* n. gen., but a pygidium attributed to the former, and the cranidial outline of the latter, suggest that both may belong in this subfamily rather than Cyclopyginae. Like almost all other cyclopygids, *Pricyclopyge* and *Symphysops* show the trend towards anterior fusion of the eyes.

It seems unlikely that the specialized organs on the third thoracic segment could have arisen more than once in separate cyclopygid groups: hence *Symphysops* Raymond and *Amicus* Koroleva, both of which have these organs, are likely to belong to the same monophyletic group as *Pricyclopyge*. *Symphysops* has well-developed glabellar muscle impressions compared with *Pricyclopyge*, and the glabella produced forwards into a 'nose' of varying proportions, and the glabellar tubercle is advanced. The type species of *Amicus*, *A. montanus* Koroleva 1967, is closely similar to *Symphysops*, and it may prove to be a junior synonym of that genus. As discussed by Whittard (1961*a*), the poorly known *Aspidaeglina* Holub probably also belongs within this group.

Thoracic organs of *Pricyclopyge*. The third thoracic segment of *Pricyclopyge*, as mentioned above, includes on the axis a pair of bulbs or 'hollow nodes' (Whittard 1961*a*: 174). These hollow, inflated structures (Fig. 59a) appear to be formed entirely *within* the cuticle: internal moulds often show the lower surface of the structure, external moulds the exterior, convex surface, while some specimens show a convex mould of the hollow interior. Ruedemann (1934) made a comparison between these hollow nodes and the luminous organs of certain free-swimming crustacea. Since cyclopygids almost certainly had pelagic habits (Fortey 1985*b* and p. 105) this comparison is of considerable interest. Much new information is available about the luminous organs of living crustaceans (Herring, 1978, reviews the literature). Many such organs are internal structures and would be expected to leave little trace on the exoskeleton. But some, especially superficial photophores on decapod crustacea, appear to form similar hollow structures (Dennell 1940: fig. 30), sometimes with cuticular lenses on the exterior surfaces. True cuticle does not extend on the inner side of such structures, however, and the largest we can find, on *Sergestes* (or *Sergia*) *challengeri*, are not more than 170 μm long, whereas the structures on *Pricyclopyge* attain a length of 600 μm. Crustaceans often have many such organs, rather than a single pair.

In support of the photophore explanation is the suggestion that 'those species possessing photophores have larger eyes than those lacking these organs' (Dennell 1940: 376), which obviously applies to *Pricyclopyge* as compared with the typical trilobite. Herring (1978: 230) notes that 'cuticular (superficial) photophores are generally common in mesopelagic species, though absent in the bathypelagic realm'. *Pricyclopyge* is absent from inshore sediments, such as the Mytton Flags, or the Armorican–Iberian region during the Arenig, but is regularly found in deeper facies in Wales. During the Llanvirn transgression, as the deeper facies migrated shelfwards, *Pricyclopyge* appeared in the Hope Shales, or in the Synclinal d'Ancenis at the southern edge of the Armorican Massif (Henry 1980). It is reasonable to deduce mesopelagic habits from its occurrence.

The evidence for a cuticular photophore function for the hollow nodes on *Pricyclopyge* is incomplete and partly circumstantial, but is consistent with its inferred life habits deduced from other morphological features, and with field occurrence. If correct, it would imply that *Pricyclopyge* probably lived below 200 m and above 700 m in the water column. The majority of such photophores in living crustaceans are ventrally directed; if this were true for *Pricyclopyge* it would have swum on its back.

Genus *PRICYCLOPYGE* Richter & Richter 1954

Type species. *Aeglina prisca* Barrande, 1872, by original designation.

Discussion. The genus *Pricyclopyge* includes cyclopygids with six thoracic segments, the third segment carrying the peculiar pair of organs discussed in detail above. The median cephalic lobe is generally subcircular, and the front margin is gently rounded about the mid-line; the pygidium has a triangular outline, with well-defined borders and a relatively long axis.

Hörbinger & Vaněk (1985) distinguished a subgenus *Bicyclopyge* (type species *Aeglina binodosa* Salter) on the basis of lack of extended thoracic pleural spines on the posterior thoracic segments; we regard this character as significant only at the specific or subspecific level.

Pricyclopyge binodosa eurycephala subsp. nov.
(Figs 56, 57)

1985*a* *Pricyclopyge binodosa* (early form) Fortey: 23; fig. 5A.

HOLOTYPE. Perfectly preserved cephalon, It.15918.

PARATYPES. The series includes axial shields: It.15913–4, It.15928, It.18525, It.18531, It.18516, It.18527, NMW 84.17G.57–60, 84.12G.9a, 84.12G.20; cranidia and cephala: It.15924–6, It.15921, It.18518–9, It.18548, NMW 84.17G.61–63; pygidia (±thorax): It.15920, It.15927, It.18523; free cheeks: It.15915, It.18539, NMW 84.17G.64–66.

TYPE LOCALITY AND HORIZON. Pontyfenni Formation, type locality, loc. 23; Fennian (*B. rushtoni* Biozone).

STRATIGRAPHICAL RANGE. The subspecies is widespread through the Pontyfenni Formation, Upper Arenig, Fennian, biozone of *Bergamia rushtoni*: locs 20C–E, 21, 23, 25, 29, 32A, 37, 40, 44, 48, 53, 54. Stratigraphically early forms have been found in the *S. abyfrons* Biozone, loc. 38. Transitional material with *P. binodosa binodosa* occurs in the Llanfallteg Formation.

DIAGNOSIS. A stratigraphically early subspecies of *P. binodosa* with nearly circular cranidium in which maximum cranidial width is attained behind cranidial mid-length; entire cephalon with greatest width (tr.) further forward than in *P. binodosa binodosa*.

NAME. From the Greek—'wide head'.

DISCUSSION. A full description of *P. binodosa binodosa* has been given by Whittard (1961*a*), and because almost all the details are the same as in the present form, they need not be described here. Rushton & Hughes (1981) have also discussed *P. binodosa binodosa* and figured some small growth stages. It is a highly conservative form, ranging from the Arenig to the Llandeilo. Two subspecies have previously been distinguished from *P. binodosa binodosa*: *P. binodosa prisca* (Barrande 1872) and *P. b. longicephala* (Klouček 1916). The former was regarded as a synonym of *P. binodosa binodosa* (Salter 1859) by Marek (1961), who observed that the preservation of the cephalic muscle impressions was highly variable (features used by Whittard, 1961*a*, to discriminate *P. b. prisca*); spines on the sixth thoracic pleurae of *P. b. prisca* were 'preserved only rarely in several specimens' (Marek 1961: 32), and Marek regarded their apparent absence on all British specimens as a matter of preservation. Rushton & Hughes (1981: pl. 2, fig. 21) figured a beautifully preserved thorax of *P. binodosa binodosa* on which the non-spinose pleural terminations of the sixth thoracic segment are undeniable. Hence we concur with their view and that of Whittard (1966: 287) that *prisca* is a valid subspecies characterized by spinose posterior segment(s), while agreeing with Marek (1961) that any supposed cephalic differences between *prisca* and *binodosa* are probably the result of preservation—their cephala are identical. It remains a possibility that *both* subspecies *prisca* and *binodosa* are present in the Llanvirn of Bohemia (Hörbinger & Vaněk 1985). No specimen from the Arenig of south Wales has an extended sixth thoracic segment, and the preservation is adequate to be certain on this point in at least six specimens.

The differences between *P. binodosa binodosa* and *P. binodosa eurycephala* are on the cephalon only, and of course the same differences apply between *P. binodosa prisca* and *P. b. eurycephala*. On the cranidium of the new subspecies the axial furrows swing outwards rather sharply very shortly in front of the posterior cephalic margin. The angle enclosed by these furrows is typically in the range 65°–80° in the population of *P. binodosa eurycephala*, compared with 45°–65° in *P. b. binodosa*. This results in a more rapid attainment of maximum cranidial width, which was quantified in some detail by Fortey (1985*a*): the population from loc. 23 shows a normal distribution in this character, clearly distinct from *P. binodosa binodosa*.

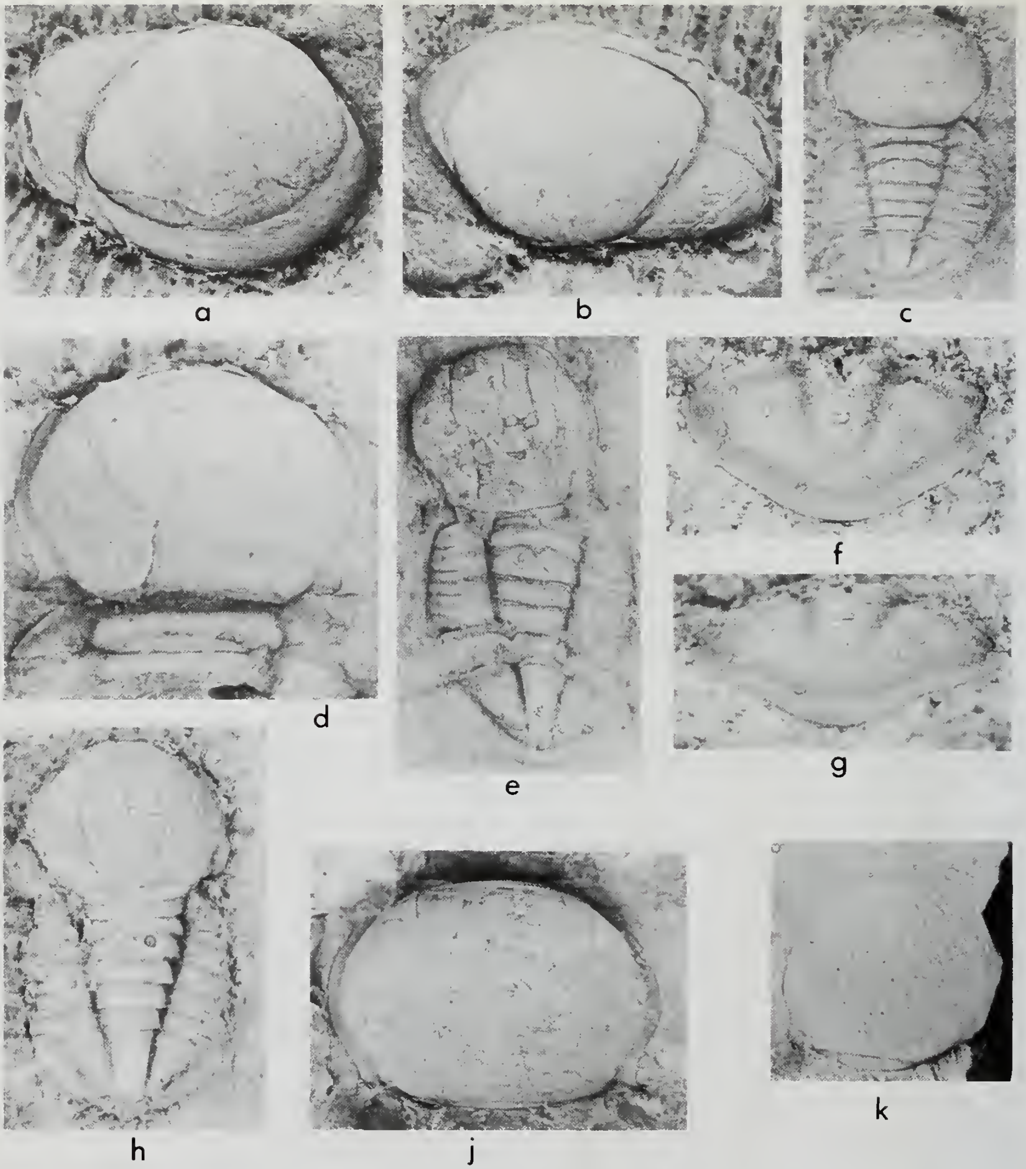


Fig. 56 *Pricyclopyge binodosa eurycephala* subsp. nov. Upper Arenig, Fennian. a, b, cranidium and left cheek in dorsal and anterior views, Pontyfenni Formation, *B. rushtoni* Biozone, loc. 23, × 4, It.15921; c, small axial shield showing cranidial sculpture, horizon and locality as Fig. 56a, × 3·5, It.15928; d, large flattened cranidium and front part of thorax, the former showing the glabellar tubercle, horizon and locality as Fig. 56a, × 4, It.18519; e, moult arrangement of axial shield, specimen showing exceptional subparallel posterior part of glabella, horizon and locality as Fig. 56a, × 3·5, It.15913; f, g, internal mould of pygidium in full relief, dorsal and posterior views, stratigraphically earliest example, *S. abyfrons* Biozone, Cwmfelin Boeth Formation, Geological Survey locality Carm. 37SW Eλ14, lane SW of Pass-by, × 6, BGS TCC959; h, axial shield, horizon and locality as Fig. 56a, × 4, It.15916; j, widest cranidium, horizon and locality as Fig. 56a, × 4, NMW 84.17G.61; k, stratigraphically early cranidium with very posterior maximum width of median cephalic lobe (crinkle cleavage does not distort the proportions), *S. abyfrons* Biozone, loc. 38, × 4, It.19644.

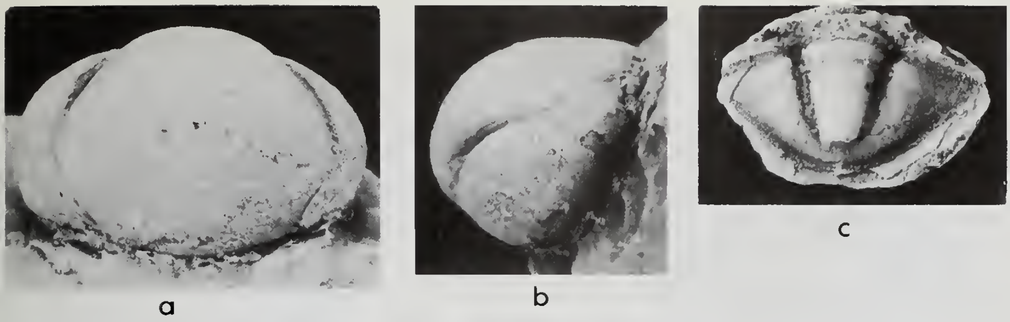


Fig. 57 *Pricyclopyge binodosa eurycephala* subsp. nov. Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23. a, b, **holotype**, perfectly preserved cephalon, dorsal and lateral views, × 6, It.15918; c, pygidium in full relief, × 3, It.19643.

There is a stratigraphical intergradation, but the two forms are distinct between the *rushtoni* Biozone and the Llanvirn. The maximum cranidial width of the median cephalic lobe in *P. binodosa eurycephala* is behind cranidial mid-length, as measured along the sagittal line. On *P. b. binodosa* maximum width is attained at, or in front of, cranidial mid-length. The glabellar tubercle, and the circular depressions to either side of it, are variably preserved, and no taxonomic importance is attached to their absence on certain specimens. Palpebral rims are always clearly defined. One specimen (Fig. 56e) shows the glabella only gently expanding in width at first near its posterior margin but still attaining maximum cranidial width behind cranidial mid-length. On the entire undistorted cephalon (Fig. 57a) maximum cephalic width of *P. b. eurycephala* is far forwards in comparison with the perfectly preserved cephala of *P. b. prisca* illustrated by Marek (1961: pl. 1, fig. 20; pl. 2, fig. 1), on which maximum width is near the back end of the cephalon in dorsal orientation. Specimens of this quality are rare, however. These subtle differences are worth taxonomic recognition, because they are of stratigraphical importance: *P. b. eurycephala* is apparently confined to the Fennian, where *Pricyclopyge* is one of the commoner fossils.

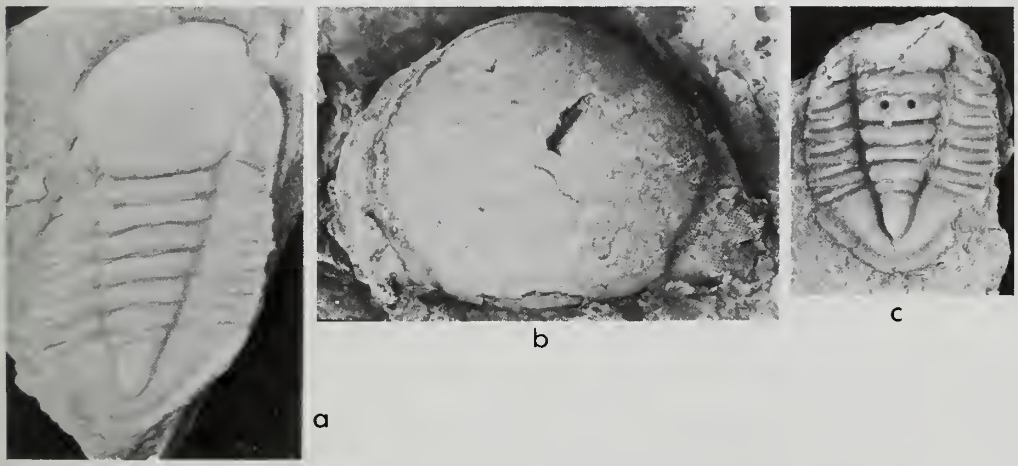


Fig. 58 *Pricyclopyge binodosa binodosa* (Salter 1859), for comparison with *P. binodosa eurycephala* subsp. nov. a, axial shield, slightly distorted, showing forward expansion of median glabellar lobe, Llanvirn above Llanfallteg Formation, St Clears, Dyfed, × 2, NMW 33.189.G49; b, transition cephalon between *P. binodosa binodosa* and *P. b. eurycephala* from Llanfallteg Formation, loc. 50, maximum width of median cephalic lobe at half cranidial length, × 3·5, It.19708; c, undistorted thorax and pygidium, Llanfallteg Formation, *D. levigena* Biozone, loc. 52K, × 3, It.19709.

The change between *P. binodosa eurycephala* and *P. binodosa binodosa* is probably entirely gradual (Fortey 1985*a* and Fig. 58b). In this connection it is interesting to note that *P. binodosa longicephala* shows the same changes taken further (Marek 1961: pl. 1, fig. 21); on this subspecies cranidial maximum width has become very anterior, while maximum cephalic width is at the posterior cephalic margin. All these changes are related to a change in the course of the axial furrows in front of the thorax, which gradually more and more come to continue (on the cephalon) the forward expansion in width of the thoracic axis, by reducing the sharp outward bend in the course of the axial furrows in the earlier subspecies. Rushton & Hughes (1981) showed that the glabellar expansion of small growth stages of *P. binodosa binodosa* was gradual, and unlike that of the adult. Hence the change from *eurycephala–binodosa/prisca–longicephala* seems to be an example of heterochrony. The same glabellar structure is also present on the primitive cyclopygid *Prospectatrix* (Fortey 1981), and on *Pricyclopyge superciliata* Dean 1973*b*, from Turkey.

Pricyclopyge wattisoni Hughes 1979, which has adaxially effaced pygidial borders, may perhaps be better referred to *Microparia. Pricyclopyge ? campestris* Koroleva 1967 is represented only by a poorly preserved exoskeleton, but this clearly shows gentle anterior divergence of the axial furrows on the cranidium in the manner of *P. binodosa longicephala. P. synophthalma* (Koušek 1916) has the eyes confluent anteriorly, which we have not observed on any Welsh specimen; *P. obscura* Marek 1961 is discussed below; *P. sichuanensis* Li 1978 has an extended sixth thoracic segment, and may prove to be a synonym of *P. bindosa prisca.*

Pricyclopyge dolabra sp. nov.

(Figs 59a–d)

Holotype. Nearly complete dorsal exoskeleton, It.19662.

Paratypes. Cephalon, BGS JP3525; cranidium, It.19660; pygidium, It.18517.

Type locality and horizon. Upper Arenig (Fennian, biozone of *Bergamia rushtoni*); Pontyfenni Formation, type locality.

Stratigraphical range. Fennian (biozone of *Bergamia rushtoni*) Pontyfenni Formation at type locality and Capel-Dewi (Geological Survey loc. Carm. 40NW Wλ9).

Diagnosis. *Pricyclopyge* with long cranidium, length equal to, or slightly exceeding, maximum transverse width of median cephalic lobe, which is posterior to cranidial mid-length. Glabellar tubercle at mid-length. Palpebral rims relatively narrow. Anterior glabellar tongue broad (tr.). Thoracic axis wide, weakly tapering. Pygidium longer than that of *P. binodosa.*

Name. 'A grubbing mattock', which the cranidium somewhat resembles.

Discussion. Most of the general features of this species are present on *Pricyclopyge binodosa eurycephala*, and do not require description. The holotype is a large specimen, $3\frac{1}{2}$ cm long, preserved in some relief. Specimens of *P. binodosa eurycephala* are up to 3 cm long, and have the same broadly rounded cranidium as smaller examples of the subspecies. *P. dolabra* has a relatively much longer cranidium, with a broadly truncate outline at the front. There are no intermediates between this species and *P. binodosa eurycephala*, and it is clearly a distinct species, although rare compared with the *binodosa* group. Like *P. binodosa eurycephala* in the Pontyfenni Formation the cranidium expands in width rather rapidly to a maximum behind glabellar mid-length; on the small cranidia this is attained further back than on the holotype. The lateral outline of the cranidium is a rather gentle outward-bowed curve; this is reflected also in the outline of the eye, which is gently curved, and apparently less bulbous than that of *P. b. eurycephala.* A median cephalic tubercle is preserved on one example at cranidial mid-length.

The thorax of the holotype only preserves five segments: the pygidium is a little displaced, and presumably the whole is a moulted exoskeleton. A sixth segment is likely to have been present, particularly in view of the discrepancy in width between the axis of the fifth segment

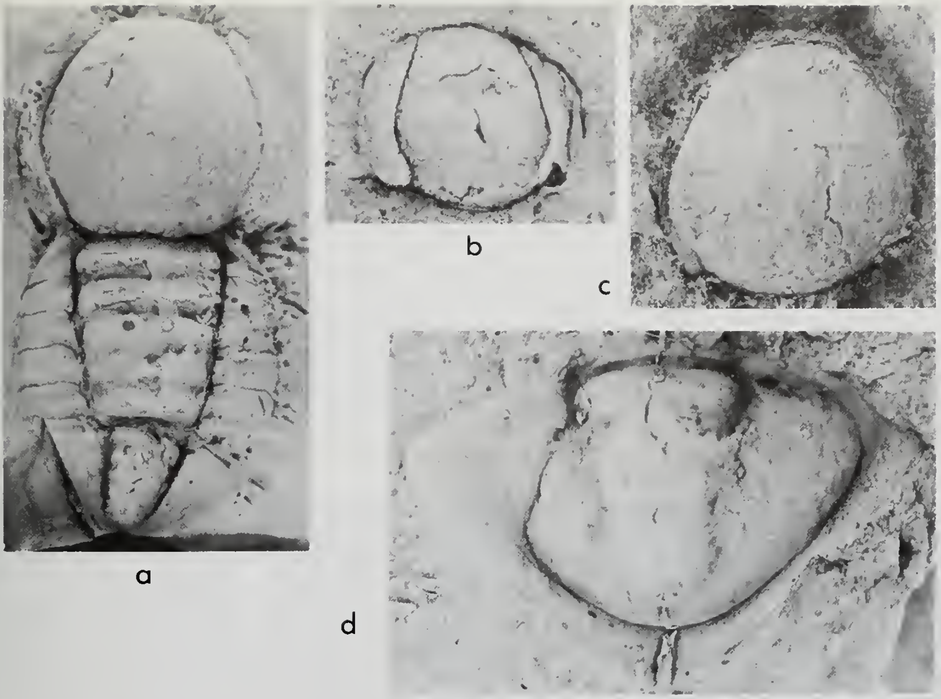


Fig. 59 *Pricyclopyge dolabra* sp. nov. Upper Arenig, Fennian, *B. rushtoni* Biozone. a, **holotype**, exoskeleton with pygidium a little displaced and eyes poorly preserved, loc. 23, × 2, It.19662; b, latex cast from cephalon, Capel-Dewi, × 6, GSM 3525; c, cranidium, locality as holotype, × 6, It.19660; d, cast from mould of pygidium, locality as holotype, × 6, It.18517.

and the anterior part of the pygidial axis, but whether or not this segment was macropleural is unknown. The very narrow (tr.) first thoracic pleurae are probably related to the large size of the holotype, and largest *P. binodosa eurycephala* are little different. However, the posterior taper of the thoracic axis on *P. dolabra* is much less, so that at the fifth segment the pleurae are only just over half as wide as the axis; on *P. binodosa eurycephala* on the largest individual the pleurae are two-thirds as wide as the axis here, and relatively even wider on smaller specimens.

The pygidium is incompletely preserved on the holotype, but shows a long, tumid axis with one ring defined, and three more indicated along the axial furrow. In view of the relatively wide proportions of the thoracic axis it seems reasonable to assign the pygidium shown in Fig. 59d to the species; it is generally more elongate, convex (tr.) and with narrower pleural regions than the pygidium of *P. binodosa eurycephala*. Pygidia of the latter are half as long as wide, or less, whereas the pygidium assigned to *P. dolabra* is two-thirds as long as wide.

P. dolabra is clearly distinct from the *P. binodosa* group on most characters. Marek (1961) described *P. obscura* from the Llanvirn Šárka Formation of Bohemia, a species in which the length of the cranidium exceeds the maximum width of the median cephalic lobe, and with narrow, gutter-like palpebral rims. *P. obscura* is known only from the cranidium, although specimens attributed to *P. binodosa* by Hörbinger & Vaněk (1985) may belong here. The cranidium has a broadly rounded anterior outline rather than a truncate one as in *P. dolabra*. Marek states that the maximum width of the median cephalic lobe is at half cranidial length, while it is always posterior to this in *P. dolabra*; less important is the pair of occipital muscle impressions on *P. obscura*, because such impressions vary widely with preservation in cyclopygids, and particularly *Pricyclopyge*.

Genus *CIRCULOCRANIA* nov.

Type species. *Circulocrania orbissima* sp. nov.

Diagnosis. Cranidium flat, nearly circular. Front margin downturned into a wide (tr.) but short tongue.

Name. 'Circular head'.

Discussion. This very odd cyclopygid was confused at first with flattened *Pricyclopyge binodosa eurycephala*, which similarly has a broad cranidium. However, it soon became clear that the lack of palpebral rims was an original feature: these are easily prepared on *Pricyclopyge*. Moreover, the flat surface of the cranidium was also original; whenever *Pricyclopyge* is flattened, it being a genus with a certain amount of transverse relief, the flattening is apparent as strong cracks on the surface (e.g. Fig. 56d). Furthermore, *Pricyclopyge* has a long anterior tongue which accommodated the dorsoventrally deep eyes. The holotype of *C. orbissima* (Figs 61a, c, d) is preserved in nearly full relief, with a short tongue, and has almost no other features. A few transverse raised lines are somewhat like those on *Pricyclopyge*, where they are forward-bowed in the occipital region. There is a median tubercle at about two-thirds cranidial length, with circular impressions to either side.

Circulocrania is without question a new cyclopygid, but we hesitated before naming it on the cranidium alone. Dr J. K. Ingham has informed us that a similar kind of circular cranidium occurs in the Whitehouse Formation (Ashgill) of Girvan, so it seems this is another long-ranging cyclopygid morphology. It is considered preferable to name formally what is, after all, a distinctive if featureless cranidium, rather than add it to our long list of undetermined cyclopygids. There are three candidates for its post-cephalic parts: cyclopygid thorax and pygidium 1 and 2 (Figs 60a, b), or possibly the pygidium and incomplete thorax described as *Microparia* (*Heterocyclopyge*?) sp. indet. (p. 174; Fig. 51). But there is no evidence to assign one or the other to the cranidium.

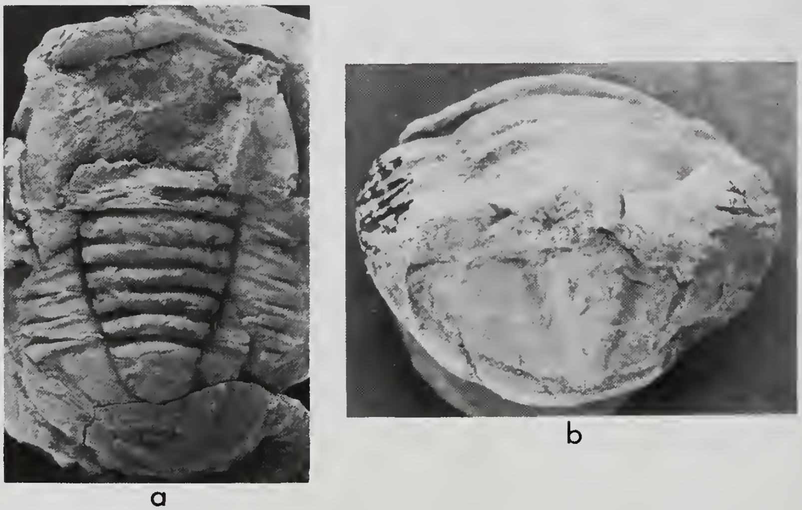


Fig. 60 Undetermined probable cyclopygid thoraces and pygidia, Upper Arenig, Fennian, *B. rushtoni* Biozone, loc. 23. a, × 3, It.19667; b, × 6, It.19668. (Not described, but see above).

Circulocrania orbissima sp. nov.
(Figs 61a–e)

HOLOTYPE. Cranidium, It.19663.

PARATYPES. Cranidia: It.19664–5, NMW 84.17G.167–8.

TYPE LOCALITY AND HORIZON. Upper Arenig, Fennian, biozone of *Bergamia rushtoni*. So far recovered only from Pontyfenni, loc. 23.

DIAGNOSIS. See genus.

NAME. 'Most circular'.

DESCRIPTION. The cranidium departs slightly from the circular, being a little wider than long. The posterior margin is gently backward-curved, the anterior margin deeply rounded about the midline and downturned. The holotype shows a faint sagittal ridge. The eyes presumably ran around the margin of the cranidium as far as the downturned tongue, but may have continued to be united anteriorly as in other cyclopygids.

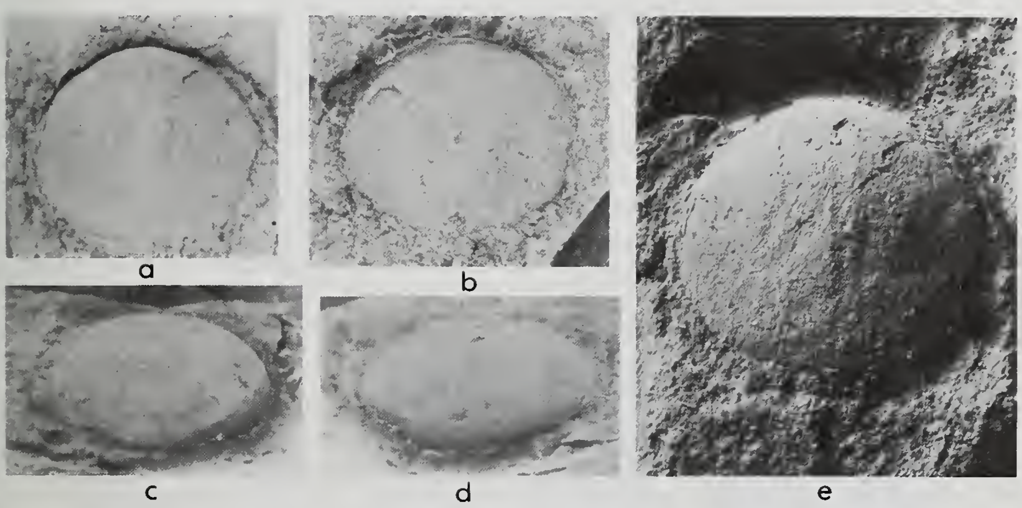


Fig. 61 *Circulocrania orbissima* gen. et sp. nov. Upper Arenig, Fennian, *B. rushtoni* Biozone. a, c, d, **holotype**, internal mould of cranidium, dorsal, oblique lateral and anterior views, × 3, It.19663; b, cranidium, × 3, It.19664; e, enlargement of latex cast from holotype in oblique light, to show posterior terrace lines and glabellar tubercle with faint circular impressions to either side, × 4, It.19663.

Subfamily *ELLIPSOTAPHRINAE* Kobayashi & Hamada 1971

Fortey (1981) pointed out the difficulty in reconciling ellipsotaphrine morphology with that of other cyclopygaceans, especially with regard to their deeply incised lateral glabellar furrows, and favoured a separate ptychoparioid origin for them, possibly in common with *Bohemilla* (see p. 129). On the other hand the structure of the rest of the exoskeleton, including the thorax, and the fact that the pygidium is almost identical to those of some species of *Cyclopyge*, argues for a common ancestry of ellipsotaphrines and other cyclopygids. The problem may be resolved if the ellipsotaphrines are paedomorphic, with the lateral glabellar furrows originating as larval features and finding expression in the adult. Such an explanation would be compatible also with the pygidial structure, which is like that of immature cyclopygids illustrated by Marek (1961). *Psilacella pulchra* Zhou 1977 has three pairs of glabellar furrows which are comparable with those of *Novakella*. *Ellipsotaphrus* itself is more of a problem, as it apparently shows an

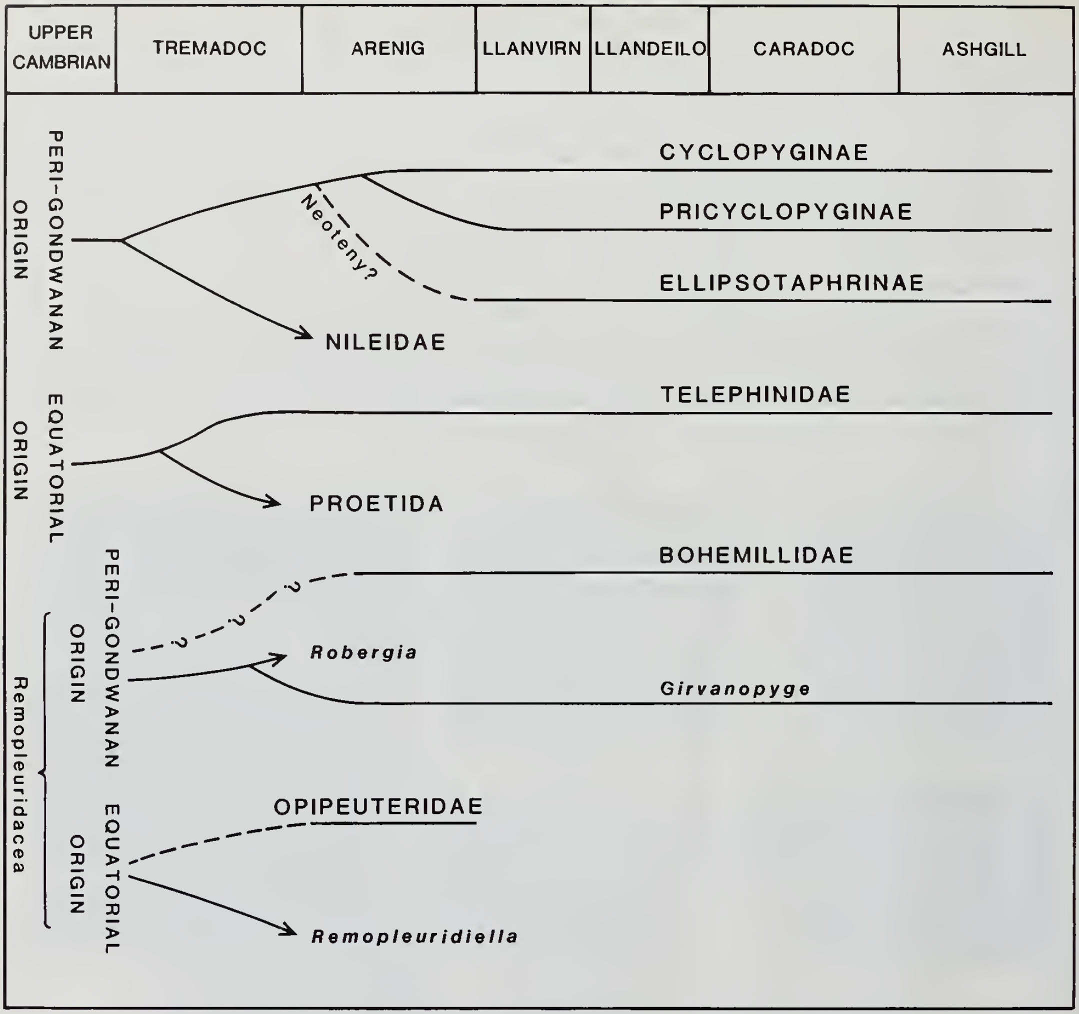


Fig. 62 Theory of relationships of Ordovician pelagic trilobites, showing polyphyletic derivation of pelagic morphology.

occipital ring, and the absence of a defined occipital ring is a derived character of the Cyclopygacea *sensu* Fortey, 1981. This problem might be resolved if the basal transglabellar furrow on *Ellipsotaphrus* is not truly occipital, that is, if it is homologous with the basal pair of glabellar furrows on other cyclopygaceans. Support for this is to be found in three species of *Ellipsotaphrus*, *E. infaustus* (Barrande 1852), *E. pumilio* Whittard 1952 and *E. zhongguoensis* Zhou 1977. On these there are distinct furrows near the posterolateral cranidial margins, which probably represent the pleuroccipital furrows. These are behind the first transglabellar furrow, and on *E. zhongguoensis* (Zhou 1977: pl. 69, fig. 4) extend adaxially behind it. This may be taken as evidence that the occipital segment is incorporated within the unfurrowed area behind the first transglabellar furrow, which would then, of course, no longer be occipital. Then the three sets of glabellar furrows would be homologous with those of other cyclopygaceans. The transglabellar first two furrows are still a considerable departure from usual cyclopygacean morphology. Similar furrows are developed in other trilobites with probable pelagic habits—in *Irvingella*, for example. This discussion well illustrates the problems of phylogenetic argument when the majority of the characters available are the result of specialized adaptation. We prefer the interpretation of *Ellipsotaphrus* as an aberrant cyclopygacean rather than a homoeomorph of the group, but the problem will not be completely solved until primitive ellisotaphrines are discovered.

Genus *ELLIPSOTAPHRUS* Whittard 1952

TYPE SPECIES. *Aeglina monophthalma* Klouček 1916, by original designation.

Ellipsotaphrus monophthalmus (Klouček 1916)
(Figs 63a–e)

1916 *Aeglina monophthalma* Klouček: 13; pl. 1, figs 4–6.
1940 *Phylacops monophthalmus* (Klouček) Whittard: 137; pl. 6, figs 1–3.
1952 *Ellipsotaphrus monophthalmus* (Klouček) Whittard: 312; pl. 32, figs 10–16.
1954 *Cyclopyge* (*Ellipsotaphrus*) *monophthalmus* (Klouček) Richter & Richter: 11–12.
1959 *Ellipsotaphrus monophthalmus* (Klouček); Richter & Richter, *in* Harrington *et al*: O363.
1961 *Ellipsotaphrus monophthalmus* (Klouček); Marek: 60–61; pl. 6, figs 13–17; text-fig. 24.
1961*a* *Ellipsotaphrus monophthalmus* (Klouček); Whittard: 169; pl. 23, figs 3, 4.
1970 *Ellipsotaphrus monophthalmus* (Klouček); Marek, *in* Horný & Bastl: pl. 7, fig. 6.
1983 *Ellipsotaphrus whittardi* Hörbinger & Vaněk: 304; pl. 1, figs 3, 4.

TYPE LOCALITY AND HORIZON. From the Dobrotivá Formation (Llandeilo) of Bohemia.

OCCURRENCE IN SOUTH WALES. Fennian, Upper Arenig, biozones of *Stapeleyella abyfrons* to *Dionide levigena*. Shales interbedded with Cwmfelin Boeth turbidites, loc. 36. Pontyfenni Formation loc. 23 (type locality), loc. 62, and Bancyfelin. Llanfallteg Formation type section, loc. 52, and early Llanvirn part of Llanfallteg Formation (Whittard 1952: pl. 32, fig. 16).

MATERIAL. Complete exoskeleton, It.19669; thorax and pygidium, It.19670; cranidia and cephala It.19671–2, NMW 84.17G.67–68, 85.1G.47; pygidium BGS HT335.

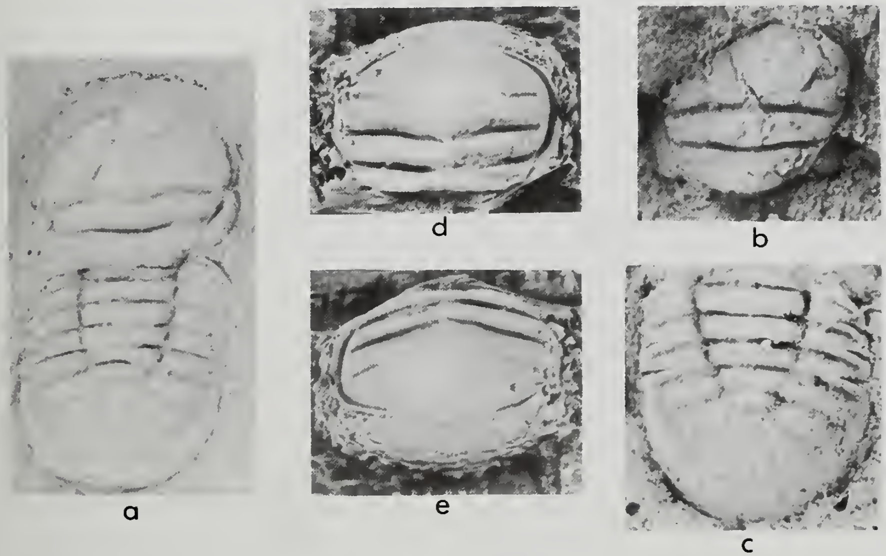


Fig. 63 *Ellipsotaphrus monophthalmus* (Klouček 1916). a, entire exoskeleton, Upper Arenig, Fennian, *D. levigena* Biozone, Llanfallteg Formation, loc. 52R, × 8, It.19669; b, cranidium, Pontyfenni Formation, *B. rushtoni* Biozone, loc. 23, × 11, It.19671; c, three thoracic segments and pygidium, Cwmfelin Boeth Formation, loc. 36, *S. abyfrons* Biozone, × 12, It.19670; d, e, cephalon, dorsal and anterior views, loc. 62, × 8, NMW 85.1G.47.

DISCUSSION. This species has been fully described by Marek (1961) and further description is unnecessary. The complete specimen from the Llanfallteg Formation (Fig. 63a) is one of the best specimens known. The type material of the species is very much younger than our material, but we can detect no differences between our specimens and a complete Bohemian specimen (Marek 1961: pl. 6, figs 15–17). *E. monophthalmus* is thus one of the longest-ranging trilobite species, and is further evidence of the conservatism of cyclopygids. One might have anticipated that the early forms would have had eyes separate, rather than fused, in line with other cyclopygids. The eye is not well preserved on the complete specimen, but seems to form a single unit, and a specimen (Fig. 63d, e) from Ramsey Island certainly has a united eye. The oldest specimen is from an early Fennian horizon, and is a partial thorax and pygidium. Without a cranidium it is not possible to be certain of its identity with *E. monophthalmus*, but the pygidium is so similar to that from the type locality that there is no good reason to qualify the determination.

Hörbinger & Vaněk (1983) have separated Whittard's (1961) material of *E. monophthalmus* as a distinct species, *E. whittardi*, based on the fact that the cranidium of Whittard (1961*a*: pl. 23, fig. 3) has a slight median accumination, and the second transglabellar furrow is straight rather than kinked backwards medially. In fact Whittard's other specimen (1961*a*: pl. 23, fig. 4), which they also assign to *whittardi*, has a median acumination no more developed than many specimens of *E. monophthalmus* (cf. Horný & Bastl 1970: pl. 7, fig. 6) from the type area. Nor is the supposed difference in the transglabellar furrow reliable, because it is much influenced by preservation: crushing or transverse extension both produce a straight, deep furrow. Our specimens from the Pontyfenni Formation have transverse glabellar furrows (and show an acuminate glabellar front) whereas the Llanfallteg complete specimen is in all respects a typical *monophthalmus*. Hence it seems likely to us that there is a single species in Britain and Bohemia, and we include *whittardi* in the synonymy of *monophthalmus*.

Genus ***PSILACELLA*** Whittard 1952

TYPE SPECIES. *Psilacella trirugata* Whittard 1952, by original designation.

Psilacella doveri (Etheridge 1876)
(Figs 64a, b)

1876 *Niobe doveri* Etheridge, *in* Ward: 110–111; pl. 12, fig. 2 (note that the names for figs 2 and 3 on the plate are transposed).
1885 *Niobe doveri* Etheridge; Postlethwaite: 71; pl. 2, fig. 13 (drawing by Goodchild).
1886 *Niobe doveri* Etheridge; Postlethwaite & Goodchild: 461; pl. 8, fig. 13.

HOLOTYPE. Incomplete dorsal exoskeleton, SM A40455.

TYPE LOCALITY AND HORIZON. Etheridge (1876) states that the specimen was recovered from the scree at Randel Crag in the Lake District; specimens from here are from Jackson's *gibberulus* Zone and probably equate with the Fennian in south Wales.

DISCUSSION. The holotype is a poor flattened exoskeleton. Nonetheless it does show the conspicuous lateral glabellar furrows which distinguish *Psilacella* from other cyclopygids. The cranidium is twice as long as Whittard's specimens of *P. trirugata* and the third pair of glabellar furrows are not discernible; this may be a specific difference, an ontogenetic difference, or the result of poor preservation. Six thoracic segments are apparently of usual cyclopygid form. The pygidium has two pairs of deep pleural furrows and the pygidial axis has four (possibly five) rings, and extends to the border, which is widest on the midline, and different from that of *P. trirugata* which has a border which becomes narrower and fainter posteriorly, and a short axis. *Psilacella* is otherwise known from China (Zhou 1977); *P. hunanensis* has two pairs of strong pygidial pleural furrows like *P. doveri*, but on other characters is more like the type species.

From south Wales we have one external mould of an incomplete pygidium (Fig. 64b) from the Pontyfenni Formation which is much smaller than that on the holotype of *P. doveri* and comparable with those of other described species. Like *P. pulchra* Zhou 1977, both pleural and

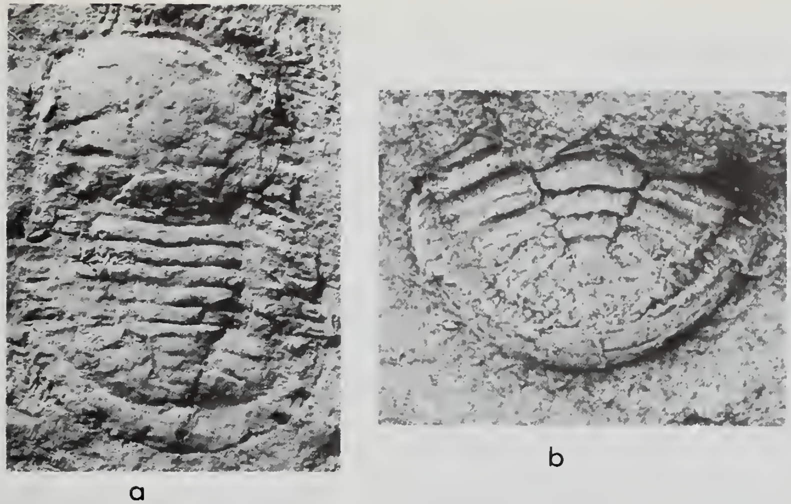


Fig. 64 a, *Psilacella doveri* (Etheridge 1876). Holotype, poorly preserved axial shield, Randel Crag, Lake District, late Arenig, '*gibberulus* Zone', × 2, SM A40455; b, *P.* cf. *doveri*, cast from pygidium (plus partial thoracic segment) of small example, Upper Arenig, Fennian, Pontyfenni Formation, loc. 32A, × 10, It.19673.

interpleural furrows are developed; the pygidial axis, probably with four rings, falls short of a moderately well defined convex border, shorter (sag.) on the midline than on the holotype of *P. doveri*. Like the type species there is a well-defined anterior segment. Whether this pygidium is that of *P. doveri* at a smaller stage of growth is uncertain, although it is certainly like that of *Psilacella*. Perhaps the difference in the relative lengths of the pygidial axis makes conspecificity unlikely. For this reason we record this pygidium as *Psilacella* cf. *doveri*.

Family **NILEIDAE** Angelin 1854

Genus ***BARRANDIA*** M'Coy 1849

TYPE SPECIES. *Barrandia cordai* M'Coy 1849, by monotypy.

DIAGNOSIS. See Whittard (1961*b*: 221–222) and Hughes (1979: 154).

Barrandia homfrayi Hicks 1875
(Figs 65a–d)

(For synonymy see Whittard (1961*b*: 222) and Hughes (1979: 156)).

HOLOTYPE. Imperfect dorsal exoskeleton, SM A15627, Llanvirn quarry.

OCCURRENCE IN SOUTH WALES. Earliest occurrence in south Wales is in the Llanfallteg Formation, type section, 20 m below Arenig–Llanvirn boundary. The species continues and is common into the Llanvirn part of the Llanfallteg Formation, at Rhyd-y-wrâch, Scolton and elsewhere, and continues into the dark 'bifidus' beds where it is widespread. We have recovered specimens from St Clear's and from Bifidus Shales exposed by the A 48 just east of Carmarthen.

MATERIAL. Figured: axial shield It.19674; cheeks and hypostoma It.19675; pygidia It.19676–7. Other material: It.19678–9, NMW 84.17G.69–75.

DISCUSSION. The type species of *Barrandia* has been fully described by Hughes (1979), and Whittard (1961*b*) gave an exhaustive account of *B. homfrayi* itself.

Fig. 65a shows what is evidently a degree 6 meraspis. It is relatively large: as in *Illaenopsis* the final complement of thoracic segments may be achieved at a much later stage in ontogeny

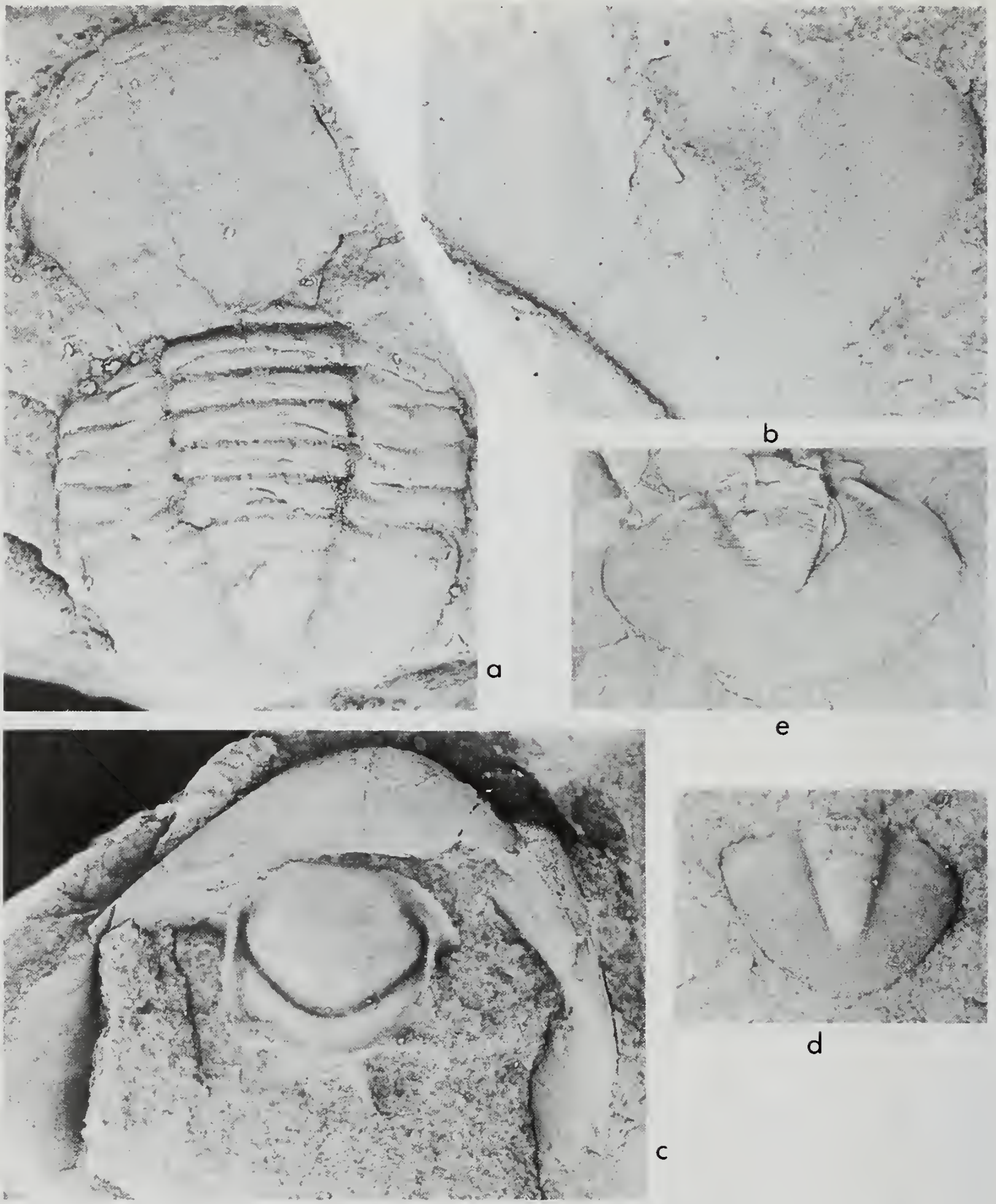


Fig. 65 a–d, *Barrandia homfrayi* Hicks 1875. Llanfallteg Formation. a, axial shield of large degree 6 meraspis moult arrangement showing pygidial segmentation, early Llanvirn, *D. artus* Biozone, loc. 50, × 6, It.19674; b, cast from external mould of pygidium to show details of fine surface sculpture, loc. 50, × 6, It.19676; c, fused free cheeks and hypostoma from ventral side, loc. 50, × 6, It.19675; d, small pygidium showing two axial rings, internal mould, loc. 50, × 6, It.19677. e, *Barrandia* sp. indet., pygidium, upper Arenig, Pontyfenni Formation, *B. rushtoni* Biozone, Banc-y-felin, compare sculpture with Fig. 65b, × 4, GSM HT338.

than in other trilobites. Hughes (1979) and Fortey (1975) noted the retention of 'parathoracic' segments in comparatively large nileid pygidia. In the specimen of *B. homfrayi* two segments are retained, and they are 'thoracic' even to the extent of showing articulating half-rings, yet they are equally clearly still a part of the pygidium. The retention or release of segments was of less functional importance in nileids than in some other families, and this may account for the variability in the number of segments (7–9) within the group. There may be seven or eight segments within *Nileus* itself. *B. bianularis* Whittard, 1961*b*, differs from *homfrayi* in having two pygidial axial rings, albeit rather weakly defined; other differences between *bianularis* and *homfrayi* cited by Whittard, such as a supposedly shorter pygidial axis, cannot be confirmed from measurements on a population of *homfrayi*. In view of the propensity of *Barrandia* to retain segments in the pygidium this axial distinction is not convincing, and it is possible that *bianularis* is merely an intraspecific variant. However, all the larger (pygidium 1 cm long or more) specimens in our collections from the Llanfallteg Formation are like typical *homfrayi*.

Barrandia sp. indet.
(Fig. 65e)

MATERIAL. Pygidium, BGS HT338–9.

OCCURRENCE. Pontyfenni Formation, Bancyfelin Railway cutting, Geol. Survey loc. Wλ3.

STRATIGRAPHICAL RANGE. Upper Arenig, Fennian, probably biozone of *Bergamia rushtoni*.

DISCUSSION. This single example of a pygidium is undoubtedly distinct from *B. homfrayi*, which it underlies stratigraphically. The outline of the pygidium is oval rather than sub-semicircular as it is in *B. homfrayi*, and with a width/length ratio of 1·5 it is more transverse than many specimens of *homfrayi*. The axis is much less than half pygidial length. The simplest distinction is the surface sculpture: the dorsal surface of *homfrayi* is covered with terrace ridges of the utmost fineness, which on the Fennian form are much stronger and only about half as dense. The closest comparison among described species is probably with *Barrandia* cf. *cordai* from the Llandeilo, figured by Hughes (1979: fig. 126), which also has a strong sculptural pattern, although denser than *Barrandia* sp. indet. Furthermore, the axis on Hughes' specimen is much longer (sag.). So the Arenig species is probably a new one, but it cannot be formally named on the basis of one specimen.

Genus ***ILLAENOPSIS*** Salter 1866*a*

TYPE SPECIES. *Illaenopsis thomsoni* Salter 1866*a*, by monotypy.

DISCUSSION. Whittard (1961*b*) redescribed the type species of *Illaenopsis*, and noted that Salter's genus was probably the senior synonym of *Eurymetopus* Postlethwaite & Goodchild 1886. The type species of the latter is *E. harrisoni* Postlethwaite & Goodchild 1886, and this is the species of which we have much new material from the Pontyfenni Formation. Like many of the species there its eyes are extremely reduced, the palpebral lobes being present as tiny flexures near the front of the cranidium. Whittard (1961*b*: 220) interpreted *I. thomsoni* thus: '. . . it may have been a blind trilobite like so many from the Hope Shales, or one in which the eyes had almost atrophied.' Examination of Whittard's material has convinced us that *I. thomsoni* had minute palpebral lobes like *I. harrisoni* (e.g. top right on his pl. 31, fig. 5). This being so, there are no significant differences between *Illaenopsis* and *Procephalops* Whittard 1967, the type species of which, *P. hopense*, was also collected from the Hope Shales. In fact, we consider that *P. hopense* is probably the same species as *I. thomsoni*, such small differences as there are being because of the smaller size of the former and because of preservational variation.

Whittard did not consider *Rokycania* Přibyl & Vaněk 1965, based on *Barrandeia* (sic) *primula* Holub 1912 from the Arenig Klabava Formation of Bohemia, when he erected *Procephalops*. The type of cephalon of *R. primula* (Horný & Bastl 1970: pl. 5, fig. 9) shows the advanced, tiny eyes, and well-defined anteriorly expanding glabella typical of *Illaenopsis*; a nearly complete specimen of *R. primula* as illustrated here (Fig. 66e). Hence we would regard *Rokycania* also as a synonym of *Illaenopsis*. Furthermore, Courtessole & Pillet (1976), apparently unaware of both *Rokycania* and *Procephalops*, erected another new generic name, *Pseudobarrandia*, on the same type species, *Barrandeia* (sic) *primula* (which they erroneously record as *prima*) as *Rokycania*. Thus *Pseudobarrandia* is an objective synonym of *Rokycania*, and joins the list of subjective synonyms of *Illaenopsis*.

To summarize, *Illaenopsis* is probably the senior synonym of no less than four other generic names, a remarkable number for so a rare trilobite: *Eurymetopus*, *Rokycania*, *Procephalops* and *Pseudobarrandia*. It is also very like two other genera, both from the Tremadoc: *Psilocephalinella* Kobayashi 1951 (senior synonym of *Borthaspis* Stubblefield 1951, with the same type species, *Psilocephalus innotatus* Salter 1866*a*) and *Borthaspidella* Rasetti 1954. Both have small eyes in a forward position; *Psilocephalinella* is somewhat more effaced than *Illaenopsis*, and with the palpebral lobes further from the glabella and slightly further back. *Borthaspidella* has a narrower glabella more abruptly expanding anteriorly, and wider, acute postocular fixed cheeks. These are perhaps rather subtle differences to be of generic significance.

Illaenopsis as understood here includes the following species: *I. thomsoni* Salter 1866*a*; *I. primula* (Holub 1912); *I. harrisoni* (Postlethwaite & Goodchild 1886); *I. griffei* (Courtessole & Pillet 1976). *I. stenorhachis* Harrington & Leanza 1957, which was used in the *Treatise* (Harrington *et al.* 1959) to illustrate the characteristics of the genus, has a narrow rhachis and wide frontal glabellar lobe, and should perhaps be referred to *Borthaspidella*, although its convex postocular sutures are like those of *Illaenopsis*.

Illaenopsis harrisoni (Postlethwaite & Goodchild 1886)

(Figs 66a–d, 67, 68, 69)

?1876 *Asaphus* sp.; Etheridge, *in* Ward: 111–112; pl. 12, fig. 1.
1885 sp. C no. 1; Postlethwaite: 77–78; pl. 3, fig. 21.
?1886 Unnamed trilobite; Postlethwaite & Goodchild: 456–457; pl. 6, fig. 1.
1886 *Eurymetopus cumbrianus* Postlethwaite & Goodchild: 459–460; pl. 7, fig. 10.
1886 *Eurymetopus harrisoni* Postlethwaite & Goodchild: 460–461; pl. 8, fig. 21.
1897 *Eurymetopus harrisoni* Postlethwaite & Goodchild; Postlethwaite: 13; and cover illustration.
1961*b* *Eurymetopus harrisoni* Postlethwaite & Goodchild; Whittard: 219–220.

HOLOTYPE. Incomplete dorsal exoskeleton, Fitz Park Museum, Keswick, C1. The only original specimen.

TYPE LOCALITY. Randel Crag, Lake District; upper part of the Skiddaw Slates.

FIGURED MATERIAL. Incomplete exoskeletons: I5331, It.19680–1; cranidia: It.19685, It.19688, It.19690; hypostoma: It.19684; free cheek: It.19682; pygidia: BGS Pr620, It.19689, It.19683, It.19686–7.

ADDITIONAL MATERIAL. NMW 84.12G.32, 84.17G.76–80.

OCCURRENCE IN SOUTH WALES. Upper Arenig, Fennian, Pontyfenni Formation at its type locality and at Llwyn-crwn, locs 23, 24, and loc. 20D; *B. rushtoni* Biozone.

DESCRIPTION. Postlethwaite & Goodchild (1886) named two species from two specimens from the Lake District—*Eurymetopus cumbrianus* and *E. harrisoni*—which we regard as belonging to a single taxon. Because the holotype of *harrisoni* is much the more complete and better preserved, we select this name to apply to the species.

I. harrisoni grew to a considerable size; it is much the largest Fennian trilobite, fragments from the Lake District and south Wales indicating a maximum length of about 20 cms. Changes in proportion occur throughout ontogeny; larger specimens from the Pontyfenni Formation are like the holotype, but we have a suite of specimens spanning a wide size range. Most of the available material is flattened, but a cranidium in full relief from the Pontyfenni Formation (Fig. 68a) shows considerable transverse convexity, with the cheeks sloping down from a convex glabella, and a steep forward slope on the frontal glabellar lobe. Entire exoskeletons are nearly twice as long as wide; if the small axial shield with imperfect thorax shown on Fig. 67a is undistorted it suggests that smaller specimens were exactly twice as long as wide.

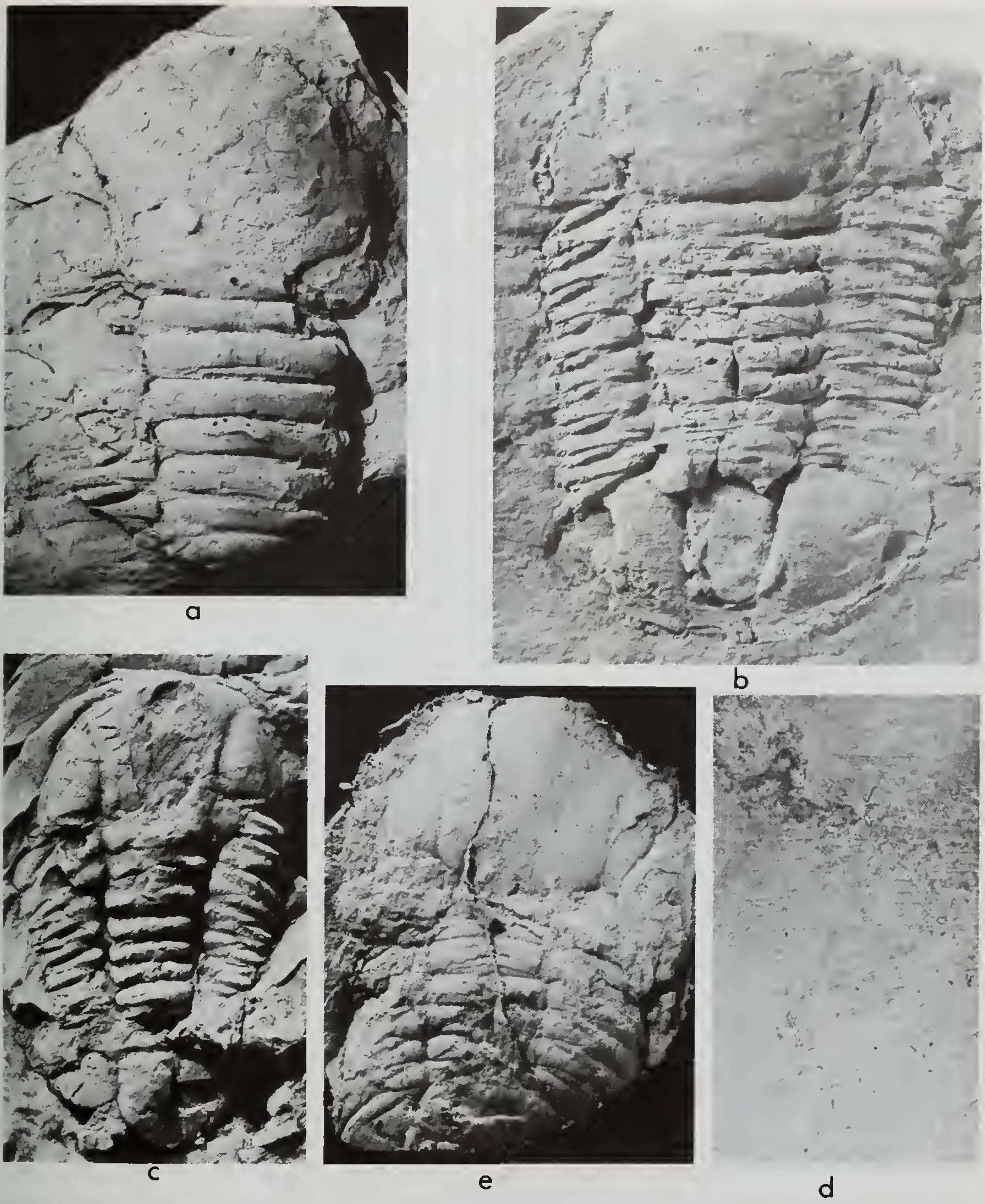


Fig. 66 a–d, *Illaenopsis harrisoni* (Postlethwaite & Goodchild 1886). Upper Arenig. a, poorly preserved, incomplete large axial shield, holotype of *Eurymetopus cumbrianus* Postlethwaite & Goodchild, late Arenig, Randel Crag, Bassenthwaite, Lake District, × 0·5, I5331; b, holotype, imperfect axial shield, Randel Crag, Bassenthwaite, Lake District, probably *I. gibberulus* Biozone, × 1, Fitz Park Museum, Keswick; c, imperfectly preserved axial shield with minute palpebral lobe at top right, Pontyfenni Formation, *B. rushtoni* Biozone, loc. 23, × 1, It.19680; d, detail of surface sculpture of fixed cheek, Pontyfenni Formation, *B. rushtoni* Biozone, loc. 24, about × 10, latex cast taken from It.19690. e, *I. primula* (Holub 1912), latex cast from a partly articulated axial shield from the Klabava Formation, × 1, Rokycany Museum, Bohemia.

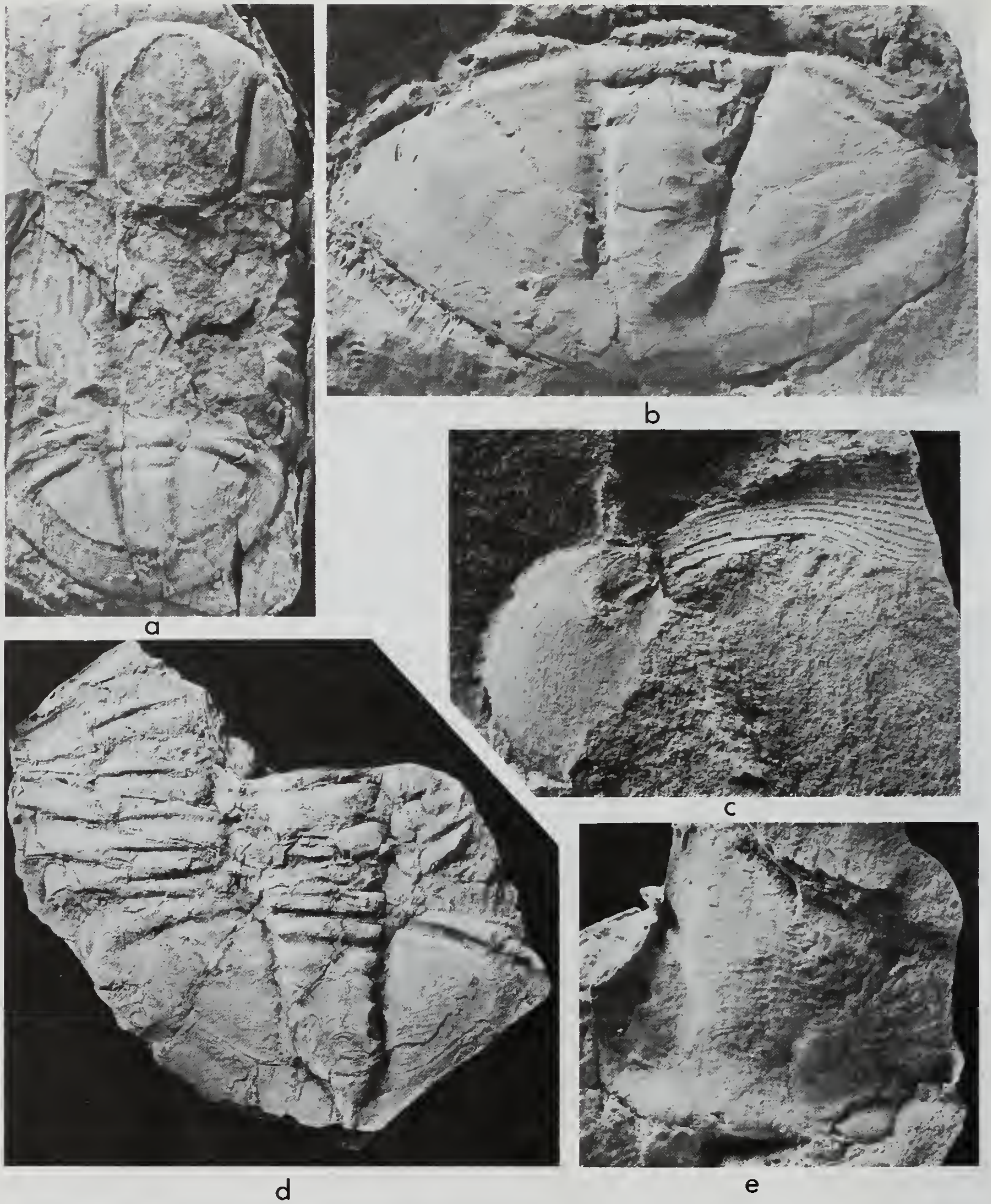


Fig. 67 *Illaenopsis harrisoni* (Postlethwaite & Goodchild 1886). Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation. a, axial shield with damaged axial area, loc. 23, × 1·5, It.19681; b, large pygidium showing sculpture, loc. 24, × 1, GSM Pr620; c, free cheek and doublure, loc. 24, note how fine lines on cheek turn into base of ocular region, × 3, It.19682; d, incomplete large thorax and pygidium, showing wide pleurae, loc. 24, × 1, It.19683; e, cast from incomplete hypostoma, loc. 24, × 2, It.19684.

The thorax accounts for about 40% of the length, and the length of the cephalon is slightly greater than the length of the pygidium.

The cranidium has its maximum width at the posterior margin, this exceeding the sagittal length. On small examples in relief the width/length ratio is about 1·25; large examples are more transverse with the same ratio up to 1·7. The glabella occupies half, or slightly less than half, the width at the occipital margin. Axial furrows are deep posteriorly, parallel on the smallest examples, diverging slightly forwards on cranidia of length about 1·5 cm, and more strongly so on larger specimens. Regardless of size, the axial furrows take a sharp outward bend at the level of the palpebral lobes, becoming shallower in the process. They do not quite reach the cranidial margin, but may appear to do so on some flattened specimens. Width of frontal glabellar lobe is 1·4–1·5 times width of glabella at posterior margin on cranidia 1 cm long or larger. No glabellar muscle impressions defined. Small specimen (Fig. 68a) shows a prominent median tubercle at glabellar mid-length. Internal moulds show the typical cyclopygacean articulating pits in the axial furrows at the posterior cranidial margin. Minute palpebral lobes are about one-tenth sagittal cranidial length, and only gently arcuate-outwards, hence easily overlooked on poorly preserved material. Postocular facial sutures are gently convex-outwards, meeting the posterior margin at a right angle, often rounded.

Free cheeks yoked together by doublure, as usual in advanced nileids. They probably hung down at a steep angle to create a broad upward arch about the mid-line, because on the flattened specimen they are twisted outwards relative to the doublure. Genal angle very broadly rounded, the profile of the cheek almost forming a semicircle. The small specimen with the cheek in place (Fig. 68e) shows that at this size there was certainly an eye. We have not found evidence of the visual surface on large specimens, and it is possible that it was lacking (note how the terrace ridges take an inward turn into the ocular area on Fig. 67c, an unusual feature). Doublure widens medially, with about fifteen very strong terrace ridges.

Hypostome is typically nileid, subsquare in outline, with the middle body weakly defined, tapering backwards, and maculae at its posterolateral edges. The posteromedian acumination is not prominent. Terrace lines are strong, as on doublure, transverse over middle body, but curving parallel to the lateral edges of the borders. The hypostoma is generally less transverse than that of *Nileus* itself, but very like that of *Poronileus* (Fortey 1975: pl. 15, fig. 7) except for the less prominent median acumination.

Eight thoracic segments of similar length (sag., exsag.) along the thorax, and with gentle axial taper; at third segment width of axis is 1·3–1·4 times the width of the pleura, but on very large specimens pleural width may equal or even exceed axial width. Articulation of usual nileid form: adaxial on first segment, and progessively removed from the axis posteriorly. Pleural furrows deep.

Pygidium twice as wide as long, axis at front occupying less than one-third pygidial width and tapering gently posteriorly to rounded tip at three-quarters pygidial length. One axial ring is usually defined across the axis, the secondly feebly so at most, and there are additional indications of three (?four) axial segments as faint depressions alongside the axial furrows. Apart from a prominent half-rib, the pleural fields are unfurrowed on larger pygidia. On relatively small ones, about 1 cm across, one pair of pleural and interpleural furrows are defined (Fig. 69). The largest example is more than 2 cm across, and is the largest transitory pygidium of any trilobite! It is relatively common for nileids to retain a single segment defined in the pygidium, but not normally to a diameter of 1 cm or more, and so this may be regarded as a neotenic feature associated with the relatively great size of *I. harrisoni*. A convex border is usually defined laterally, and never extends behind the axis. Doublure with inner outline closely following the posterior pygidial margin, its width at mid length (measured normal to the pygidial margin) being 0·5–0·6 of that of the pygidial axis anteriorly. It also carries terrace lines, but finer and denser than those on the cephalic doublure. An immature pygidium (Fig. 68d) is assigned to *I. harrisoni*, with a long, narrow axis and a few faint pleural furrows.

The whole exoskeletal surface except the thoracic axis is covered with a dense, fine surface sculpture of lines. These are not terrace ridges; they are more like finely incised grooves. On well-preserved surfaces (Fig. 66d) they are themselves interspersed with other lines of the

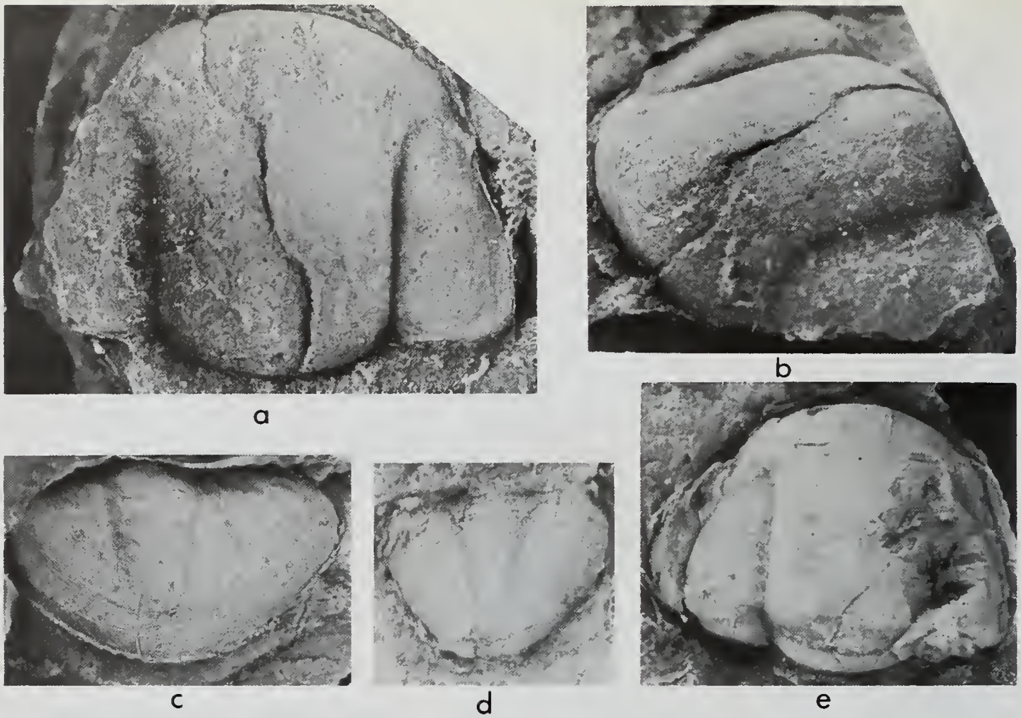


Fig. 68 *Illaenopsis harrisoni* (Postlethwaite & Goodchild 1886). Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23. a, b, well-preserved smaller cranidium, in relief, dorsal and oblique lateral views, × 6, It.19685; c, latex cast of smaller pygidium, × 4, It.19686; d, presumed transistory pygidium with indications of four segments, × 6, It.19687; e, small cephalon in relief in nodule, showing eye on left (the apparent occipital ring is an artefact produced by the first thoracic segment), × 6, It.19688.

utmost fineness. The lines are bowed forwards over the glabella and pygidial axis. On the free cheeks they run almost parallel with the margin except where curving inwards in the ocular region; on the pygidial pleural fields they are more or less transverse.

Discussion. This species is very close to *I. thomsoni* (Salter), as redescribed in Whittard (1961*b*), particularly incorporating *Procephalops hopense* Whittard, 1967, into that species, as we suggested above. The lectotype (Whittard 1961*b*: pl. 31, fig. 3) shows four clearly defined axial rings on the pygidium, which we cannot match on any specimen of *I. harrisoni*. We have observed the same feature on other specimens of *I. thomsoni* (e.g. BGS GSM292) from the Hope Shales, and the well-defined rings seem to be associated with a small amount of transverse extension; in any case they are not visible on other specimens (Whittard 1961*b*: pl. 31, fig. 4; 1966: pl. 50, fig. 7) which are little distorted. All the articulated specimens of *I. thomsoni* have wider thoracic pleurae, compared with *I. harrisoni* of similar size, such that the exoskeleton is more broadly oval, width only about two-thirds the length. Such wide thoracic pleurae can be matched on only the largest specimens of *I. harrisoni*. The holotype of *Procephalops hopense* is more elongate, but even here the axis is narrow, and there may have been a certain amount of axial extension on this specimen. The surface sculpture of *I. thomsoni* and *I. harrisoni* is similar. The most consistent difference relates to the width of the pygidial doublure, which is wider on *I. thomsoni*, two-thirds or more the maximum pygidial axial width. The facial sutures behind the palpebral lobes on *I. thomsoni* diverge outwards at a higher angle than they do on *I. harrisoni* cranidia in relief, but since flattening would presumably alter this angle little reliance can be

Fig. 69 *Illaenopsis harrisoni* (Postlethwaite & Goodchild 1886). Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23. Transistory pygidium, with one unreleased segment, × 3, It.19689. This species has the largest transitory pygidium of any trilobite.

placed on it; again, very large *I. harrisoni* cranidia are little different in this character. In general, specimens of *I. thomsoni* about 6 cm long most closely resemble those specimens of *I. harrisoni* which would have been perhaps 12 cm or more long, and there may be no more difference between the species than a different rate of ontogenetic development. This is supported by the fact that 'giant' transitory pygidia of *I. harrisoni* are known (Fig. 69) at a size when all *thomsoni* are mature. Undistorted material in relief of *I. thomsoni* is needed before the status of *I. harrisoni* can be clarified further.

I. primula (Holub 1912) (see Kraft 1972; Horný & Bastl 1970; Fig. 66e herein) from the Arenig of Bohemia is also similar to *I. harrisoni*, but the fixed cheeks are probably narrower, and the eye larger, such that the palpebral lobe is about one-sixth cephalic length. The articulated specimen (Fig. 66e) of *I. primula* apparently shows only seven thoracic segments, but the cranidium is slightly displaced, and there may have been eight as in other *Illaenopsis*. In any case this would not constitute a generic difference. *I. griffei* Courtessole & Pillet 1976, from the Upper Tremadoc of Montagne Noire also has larger palpebral lobes than *I. harrisoni*, and the glabella hardly expands outwards at the level of the eyes.

Family **ILLAENIDAE** Hawle & Corda 1847

We here accept the arguments of Lane & Thomas (1983) in not recognizing subfamilial groupings in the Illaenidae at this stage.

Genus *ECTILLAENUS* Salter 1867

TYPE SPECIES. *Illaenus perovalis* Murchison 1839, from the Llanvirn of the Shelve inlier, by original designation.

DIAGNOSIS. Illaenid with more or less straight cephalic axial furrows; eye tiny, or absent; postocular facial suture incurved at its posterior end; hypostoma triangulate with anterior margin nearly transverse, or curved gently forwards medially; anterior wings long and rather narrow; thorax of ten segments, axis well defined; pygidium approximately as long (sag.) as cephalon, doublure extending for *c.* 30%–50% of pygidial length (sag.)

REMARKS. The hypostoma of *Ectillaenus* (e.g. Šnajdr 1957: pl. 2, fig. 10; pl. 3, fig. 4; pl. 6, figs 2, 3; Rábano & Gutiérrez-Marco 1984: pl. 3, figs 3, 4) contrasts strongly with that of *Illaenus* (e.g. Whittington 1965: pl. 52, figs 7–13; Fortey 1980: pl. 10, fig. 11) in being proportionately shorter and wider, with much narrower anterior wings and in lacking an indentation on the anterior margin. In these respects it more closely resembles that of certain styginids—e.g. *Bumastus barriensis* Murchison 1839 (see Lane & Thomas, *in* Thomas 1978: pl. 2, figs 5, 11a, b).

Ectillaenus perovalis (Murchison 1839)
(Figs 70a–i)

1839 *Illaenus? perovalis* Murchison: 661; pl. 23, figs 7a, b.
1867 *Illaenus* (*Ectillaenus*) *perovalis* Murchison; Salter: 211; pl. 26, figs 5–8.
1875 *Illaenus Hughesii* Hicks: 184; pl. 9, fig. 7.

1909 *Illaenus perovalis* Murch.; Cantrill, *in* Strahan *et al.*: 33.
1914 *Illaenus perovalis* Murch.; Thomas, *in* Strahan *et al.*: 27, 28.
1961*b* *Ectillaenus perovalis* (Murchison) Whittard: 211; pl. 2, figs 6–13; pl. 30, figs 1, 2 (with further synonymy).
1961*b* *Ectillaenus hughesi* (Hicks) Whittard: 214; pl. 30, figs 3–7 (with further synonymy).
1984 *Ectillaenus perovalis* (Murchison); Rábano & Gutiérrez-Marco: 231.
1984 *Ectillaenus hughesi* (Hicks); Šnajdr: 21.

LECTOTYPE. Selected Whittard (1961*b*: 213). BGS GSM6844, complete internal mould from fine-grained tuff interbedded with Hope Shales, Hope Mill, Shelve inlier; figured Whittard 1961*b*: pl. 29, figs 6, 7 (specimen lost—Whittard 1961*b*: 213).

MATERIAL. Relatively common in Llanfallteg Formation at Llanfallteg; from *D. levigena* Biozone recorded from locs 52C, 52D, 52H, 52I, 52N, 52P, 52Q, 52W and 52X, and from *D. artus* Biozone recorded from loc. 52. Also found in Llanfallteg Formation, *D. artus* Biozone at loc. 50, Cefn-maen-llŵyd (It.18938–9, BGS Pr1996), and loc. 55, Scolton (NMW 84.17G.125), quarry 119 m SE of Cefn-farchen, south of Rhyd-y-wrâch, Pem. 24SE Eλ21 (BGS Pg96). Elsewhere in *D. artus* Biozone: old quarry at Dan-yr-Allt, 2·7 km SW of Bancyfelin, Carm. 45NW Eλ4 (BGS JP4953), Llanvirn quarry (type locality of *E. hughesii*) and in Hope Shales Formation, Shelve inlier (see Whittard 1961*b*: 213, 215).

DIAGNOSIS. *Ectillaenus* which lacks eyes. Cephalon with sculpture of closely-set terrace lines interspersed with rows of small puncta; entire pygidium with sculpture of puncta: small ones on pygidial axis, larger ones on pleural areas and the largest around posterior ends of axis. Pygidial doublure extending for almost 50% of pygidial length.

REMARKS. This species was described fully by Whittard (1961*b*: 211). He considered it to be separate from the contemporaneous *E. hughesii*, which he claimed is to be distinguished on proportions, on relative abundance and on the restriction of *E. perovalis* to few localities, with *E. hughesii* being ubiquitous in the lower part of the Hope Shales. The latter cannot be claimed in any way as biological differences, and there are no morphological features to back them up. In particular, the sculpture, which is clearly distinct in different *Ectillaenus* species, is identical in *perovalis* and *hughesii*. The only one of Whittard's criteria which could possibly have any validity is that of proportion. He claimed that length–breadth ratios could be used to distinguish the species, stating (1961*b*: 214), for instance, that in pygidia width : length ratios of 10 : 9 and 10 : 6 are typical for *E. perovalis* and *E. hughesii* respectively. However, on foregoing pages (1961*b*: 212, 213) he noted that in *perovalis* the uncrushed holotype (*sic*) has pygidial proportions of 10 : 7 whilst in partly crushed specimens they are 10 : 9. He thus seems to have placed greater stress on crushed specimens than on uncrushed ones in his arguments. Our specimens give pygidial ratios of between 10 : 5·5 and 10 : 7·5. All the material is to a greater or lesser degree crushed, but the least compressed specimens give ratios of between 10 : 6 and 10 : 7, which seem to represent the true proportional range. There can be no doubt that the wide range in ratios is to be accounted for by extrinsic agencies of crushing and compression. We thus consider that only one species is represented both in Shelve and in south Wales.

Whittard (1961*b*: 214) included the Bohemian species *E. benignensis* (Novák & Perner 1918) (Llandeilo, Dobrotivá Formation) and, with a mark of interrogation, *E. sarkaensis* (Novák & Perner 1918) (Llanvirn, Šárka Formation) in synonymy with *E. hughesi*, thereby extending the stratigraphical and geographical range of the latter considerably. Šnajdr (1984) has, however, conclusively demonstrated that *E. benignensis* is a distinct species, with distinct sculpture and a narrower pygidial doublure (see Šnajdr 1984: pl. 1, figs 4–6). *E. sarkaensis* (Šnajdr 1957: pl. 3, figs 1–7; pl. 5, fig. 11) seems also to be distinct, with a much narrower pygidial doublure and more effaced cephalon and pygidium.

Whittard (1961*b*) described two further species, *E. cunicularis* and *E. bergaminus* from the Shelve Church Beds and Tankerville Flags respectively. The former was based upon a cranidium and a distorted pygidium, and he claimed (1961*b*: 210) that it differed from *E. bergaminus* (based on well-preserved complete specimens and isolated exoskeletal parts) in having less dense terrace lines which are more regular, a narrower cranidium and shorter pygidium in which the axis is well defined and an equilateral triangle in outline (compared with a biconcave

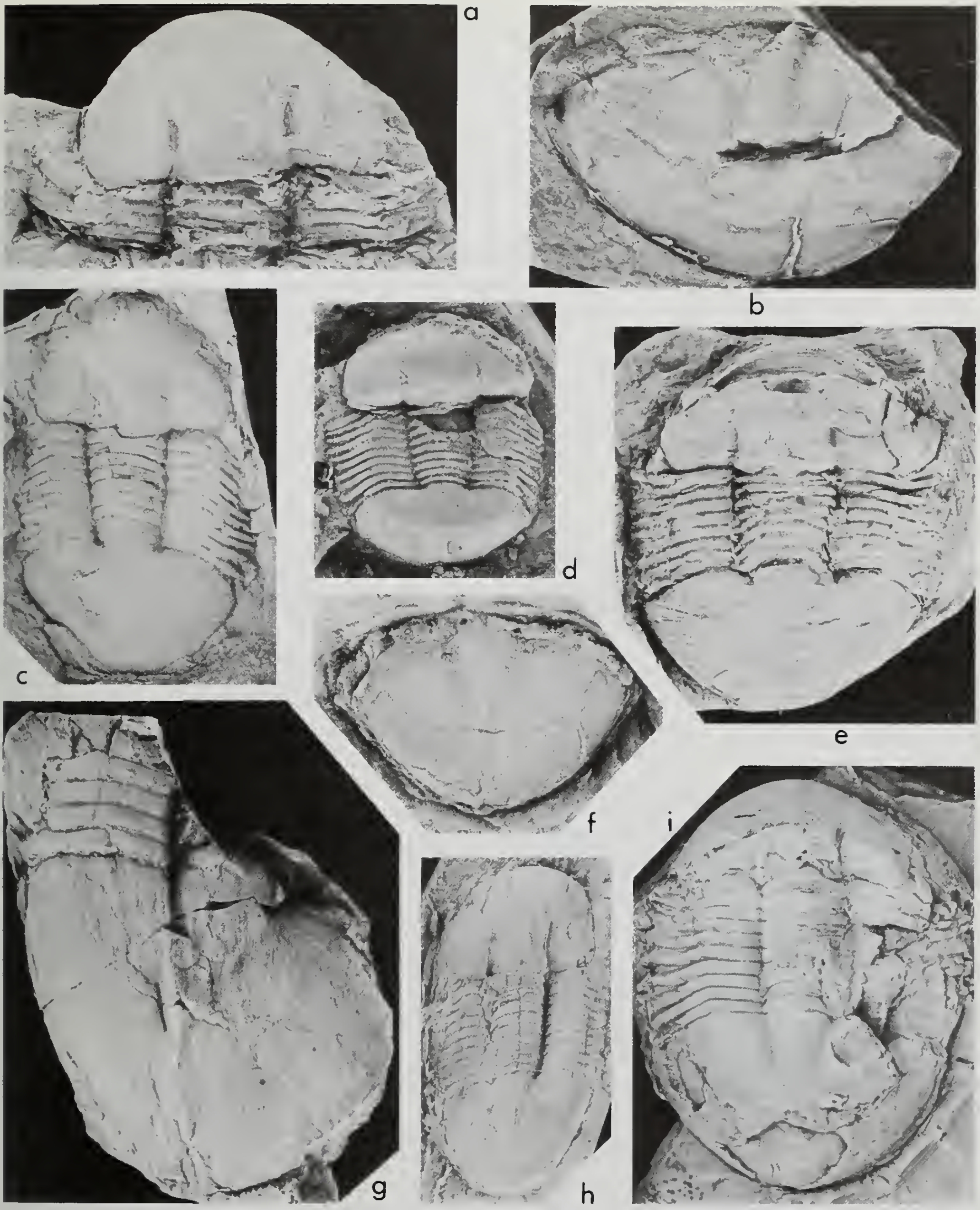


Fig. 70 *Ectillaenus perovalis* (Murchison 1839). Llanfallteg Formation, lower Llanvirn, *D. artus* Biozone (c–f) or upper Arenig, Fennian Stage, *D. levigena* Biozone (a, b, g–i). a, cephalon with three thoracic segments, loc. 52N, Llanfallteg, × 5, It.18936; b, pygidium showing doublure, loc. 52I, Llanfallteg, × 2·5, It.18937; c, axial shield, latex cast from external mould, loc. 50, Cefn-maen-llŵyd, × 2, It.18938; d, small axial shield, Cefn-farchen, × 4·5, BGS Pg96; e, complete specimen with cephalon damaged, to show rostral plate, Rhyd-y-wrâch, × 1·5, NMW 33.189.G127; f, pygidium showing form of axis and doublure, loc. 50, Cefn-maen-llŵyd, × 4, It.18939; g, large pygidium with part of thorax, showing sculpture, loc. 52I, Llanfallteg, × 1·5, It.18940; h, laterally compressed axial shield, latex cast from external mould, loc. 52P, Llanfallteg, × 1·5, It.18941; i, complete specimen, preserving original proportions and relief, loc. 52W, Llanfallteg, × 2, It.18942.

axis, frequently unenclosed posteriorly in *E. bergaminus*). The Shelve Church Beds are now known to be of Fennian age, not Lower Arenig as Whittard supposed. Thus these species are more or less contemporaneous. A further topotype almost complete *E. bergaminus* (NMW 72.5G.1a, b; Fig. 71a) has the pygidium partially exfoliated to expose a triangular, well-defined axis, and the cranidium has a sculpture of terrace lines like those on *E. cunicularis*. The paratype pygidium of *E. cunicularis* is a crushed and distorted external mould on which the axis seems to be accentuated. There seems little reason to retain *cunicularis* and *bergaminus* as separate species; we recommend that the latter name is used, since it is based upon more complete material. *E. bergaminus* differs from *E. perovalis* in having a minute eye (Whittard 1961*b*: pl. 28, fig. 11) and in having a sculpture of terrace lines with only subordinate puncta on the cranidium and pygidium, the puncta on the latter concentrated on the posterior part. Rare *Ectillaenus* in the Fennian in south Wales, probably belonging to *E. bergaminus*, are described below.

Ectillaenus giganteus (Burmeister 1843) from the Llanvirn and Llandeilo of Brittany and the Iberian peninsula broadly resembles *E. perovalis*, but is immediately distinguished in possessing an eye and a much shorter (sag.) pygidial doublure (cf. Rábano & Gutiérrez-Marco 1984: pl. 1, figs 1, 7 and specimens shown in Fig. 70, p. 201).

Ectillaenus ?bergaminus Whittard 1961*b*
(Figs 71b–d)

MATERIAL. Badly preserved complete specimen lacking free cheeks NMW 85.7G.1a, b, and cranidium It.18975, from Fennian, *B. rushtoni* Biozone, Capel-Dewi, locs 20D, E; pygidium It.18976 from same horizon, Pontyfenni, loc. 23.

REMARKS. None of the material is sufficiently well preserved to assign it to *E. bergaminus* with confidence, but such morphological details as can be seen suggest that in all probability it belongs to this species. These include the fine terrace lines on the cranidium and pygidium (those on the latter can only be detected in the external mould NMW 85.7G.1b in very low

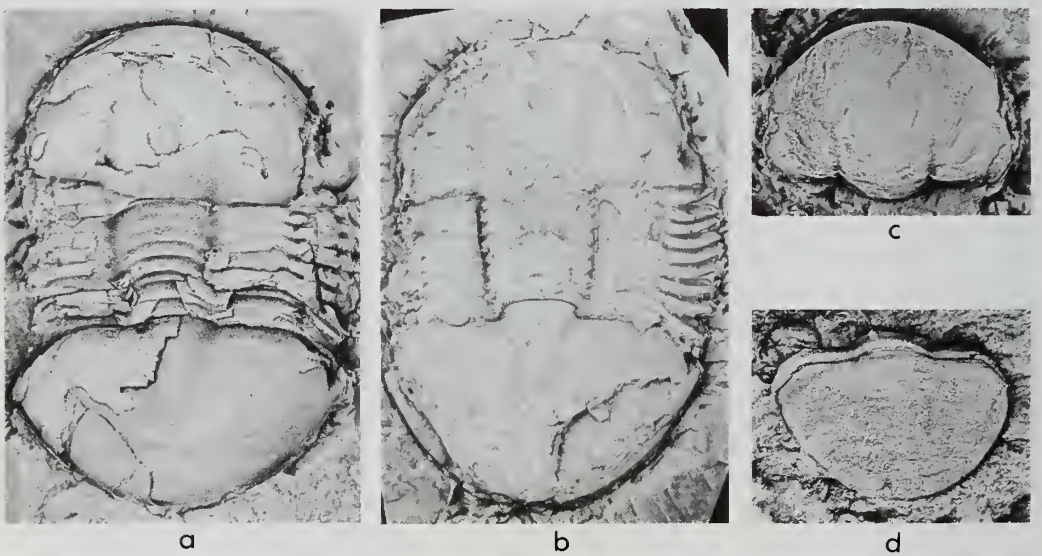


Fig. 71 a, *Ectillaenus bergaminus* Whittard 1961*b*. Axial shield, upper Arenig, Fennian Stage, Tankerville Flags, Bergam quarry, Shelve inlier, × 2, NMW 72.5G.1a. b–d, *E. ?bergaminus* Whittard 1961*b*. b, badly preserved axial shield, Fennian Stage, loc. 20E, Capel-Dewi, × 1·5, NMW 85.7G.1a; c, cranidium, loc. 20D, Capel-Dewi, × 5, It.18975; d, pygidium, latex cast from external mould, loc. 23, Pontyfenni, × 6·5, It.18976.

angle light) and those on the lateral parts of the thoracic pleurae (cf. Whittard 1961*b*: pl. 29, fig. 2; Fig. 71b–d). The small pygidium from Pontyfenni has the pygidial axis more or less effaced, and is possibly specifically distinct from the Capel-Dewi specimens.

Family **TRINUCLEIDAE** Hawle & Corda 1847

Comparatively few trinucleids have been reported from the Arenig, and most are from Wales and the Welsh borders, although *Hanchungolithus* species occur in SE Ireland and southern France (Hughes *et al.* 1975: 553). In recent years they have also been documented from China (Lu 1975 [several 'Llanvirn' species herein are really Upper Arenig, *Glyptograptus sinodentatus minor* Biozone age: Zhou Zhiyi, personal communication 1984]; Yin & Lee 1978). All these occurrences are in shelf facies in the peri-Gondwanan area, attesting to the probable origin and early radiation of the family in this region. Most known hitherto in the Welsh area are from the Mytton Flags Formation, Shelve inlier, from which Whittard (1955, 1966) described species of *Myttonia*, *Bergamia*, *Incaia*, *Lordshillia* and *Cochliorrhoe*. The last-named has subsequently been synonymized with *Bergamia*, and the *Incaia* species transferred to *Anebolithus* (Hughes *et al.* 1975: 560). Elsewhere, the old species *gibbsii* and *sedgwicki* from Pwlluog, Whitesand Bay were placed by Whittard (1955) in *Bergamia* (the latter with a mark of interrogation); Whittington (1966) described *Myttonia fearnsidesi* from the Henllan Ash and Fortey & Owens (1978) *M.* cf. *fearnsidesi* from the Carmarthen Formation.

The present study has revealed more trinucleids from the Whitlandian and Fennian, but no more from the Moridunian. Combining the information from these with that from already known material, it is now possible to reassess the early history of the Trinucleidae. Hughes *et al.* (1975: 583, fig. 120) gave concurrent ranges in the Arenig for *Hanchungolithus*, *Myttonia*, *Anebolithus*, *Lordshillia* and *Bergamia*, with only the latter extending into the upper half of the series (the presence of *Hanchungolithus* being inferred, for it is known also from the Llanvirn). Much of their information derived from the Mytton Flags species, but we are now able to offer greater stratigraphical precision.

Moridunian strata in south and north Wales have yielded only *Myttonia* (although *Hanchungolithus* has recently been reported from the Llŷn Peninsula: A. Beckly, personal communication 1984). We presume that the lower part of the Mytton Flags Formation with *Myttonia* and *Anebolithus* is of (?mid-) Moridunian age (see also p. 98). Whittard (1966: 303) stated, and indicated on his table 2 (1961*b*: 209) that *Myttonia multiplex* ranged throughout the Mytton Flags, although in describing this species (1966: 273) he quoted examples only from the lowest Mytton Flags, and we have not seen specimens in substantiation of his higher stratigraphical records. Aside from this somewhat ambiguous information, all other *Myttonia* records are from the Moridunian, of which stage the genus appears to be characteristic. The earliest Whitlandian is characterized by *Furcalithus* gen. nov. (p. 207), which in the mid-Whitlandian is joined by early *Bergamia* species, and the distinctive *Gymnostomix gibbsii*. The first *Stapeleyella* occur in the early Fennian. We assume that the higher Mytton Flags (the horizon 2000 ft above the base, of Whittard 1966) with *Bergamia*, *Lordshillia* and *Anebolithus* are of early Fennian age.

It is thus apparent that there is a succession of trinucleids throughout the Arenig, with three distinct kinds—*Myttonia*, *Anebolithus* and *Hanchungolithus*—already present by the mid-Moridunian. Hughes *et al.* (1975: 553) proposed that all other trinucleids are likely to be derived ultimately from the Hanchungolithinae which they regarded (1975: 585) as the 'ancestral trinucleid group'. We consider this unlikely, although we would admit that all presumably were derived from a single ancestral group in the Tremadoc. The morphology of *Hanchungolithus*, and of other members of the Hanchungolithinae as recognized by Hughes *et al.*, except *Myttonia*, is broadly similar to that of early marrolithines, in particular *Protolloydolithus*. Indeed, it is only necessary to add E_1 and F pits to *Hanchungolithus* to derive a *Protolloydolithus*-like form; so we would concur with the *Hanchungolithus*–*Protolloydolithus* link they proposed (Hughes *et al.* 1975: 583, fig. 20). We are less convinced, however, by their contention that *Myttonia* is a late hanchungolithine. In his numerical taxonomic study of trinucleids, Temple (1980: 227) placed *Myttonia* cf. *fearnsidesi* Whittington (of Fortey & Owens 1978) with the Trinucleinae, an association with which we agree, especially since *Furcalithus*, unknown to Hughes *et al.*, is morphologically and stratigraphically intermediate between *Myttonia* and *Bergamia*. Hughes *et al.* placed *Myttonia* in the Hanchungolithinae on account of such characters as the marginal girder and large number of irregular pits, but on the lower lamella of *M. fearnsidesi* Whittington (1966: 494) describes 'a broad, smooth, gently convex area about which the fringe is flexed, . . . suggestive of a weakly developed girder'. A similar feature is present in *M.* cf. *fearnsidesi* (e.g. Fortey & Owens 1978: pl. 11, figs 4, 6). If an 'incipient girder' such as this were to develop into a true girder, the fringe structure thereby produced would not be very different from that of *Furcalithus radix*, given further organization of the I series of pits. Despite the presence of a large number of irregular pits in *Myttonia*, these are fewer and much larger than in *Hanchungolithus*, but comparable in size and number to early trinucleines such as *F. radix*. We thus propose to transfer *Myttonia* to the Trinculeinae, even though it necessitates admitting into the subfamily a genus in which there is only rudimentary radial alignment of pits at best (see modified diagnosis below).

Hughes *et al.* (1975: 583, fig. 120) placed *Anebolithus* between *Myttonia* and *Lordshillia*, presumably lending weight to the possession of a marginal girder. Such a placement is to us untenable, since it seems that *Anebolithus* developed a very simple fringe early on, and is much more difficult to link with *Myttonia* than are *Furcalithus* or early *Bergamia*. It is likely that *Anebolithus* represents a small, independent Arenig–Llanvirn lineage upon which some *Bergamia* (e.g. *B. rushtoni* sp. nov. (p. 205); *B. artemis* Rushton & Hughes) with secondary simplification of the fringe, and reduction in the number of radii, converge morphologically. So far only two species of *Anebolithus* have been described, *A. simplicior* (Whittard) and *A.* sp. of Hughes (1971), the second represented by but one specimen. Whittard (1966) recorded *A. simplicior* from horizons 600 ft and 2000 ft above the base of the Mytton Flags. From the lower horizon there appears only to be a single specimen (Whittard 1955: pl. 3, fig. 7), most of the fringe of which is not preserved, and it may not be conspecific with *A. simplicior*. In fringe, genal, sculptural and pygidial characters the Whitlandian *Gymnostomix* gen. nov. (p. 215) closely resembles *Anebolithus simplicior*, and it is likely that the genera are closely related.

Furcalithus is apparently restricted to the lower part of the Whitlandian. The pits are essentially radially aligned, with two E arcs and three or four I arcs, with some remnant irregularity apparent in the latter. It appears as if a Whitlandian radiation from *Furcalithus* gave rise on the one hand to *Bergamia*, through reduction in number of I arcs and development of deep radial sulci and increased organization of the posterolateral I pits, and on the other to *Stapeleyella* with its characteristic interradii on the E arcs. The earliest *Stapeleyella*, *S. abyfrons*, has a highly irregular arrangement of adventitious pits, giving rise to an incipient 'Y' arrangement of interradial ridges. Meraspides of *S. inconstans* figured by Whittard (1955: pl. 4, figs 11, 12) have a fringe with a large number of long, narrow radial sulci very like that mature *Furcalithus*? sp. (Fig. 76) from the Whitlandian of Llŷn (although the latter lack inter-radii in the E series), adding further weight for an origin of *Stapeleyella* in the *Bergamia–Furcalithus* complex. We agree with Hughes *et al.* (1975: 560) that *Lordshillia*, presumably derived from *Bergamia* in the late Whitlandian–early Fennian, almost certainly gave rise to *Trinucleus*.

Subfamily **TRINUCLEINAE** Hawle & Corda 1847

DIAGNOSIS. Fringe with no F pits, other than posterior fossula. Pits essentially radially aligned except in *Myttonia*, which has incipient alignment only. Glabella with prominent pseudofrontal lobe with three pairs of lateral glabellar furrows. Pits on upper lamella generally regularly arranged. Usually no occipital spine.

REMARKS. The above diagnosis is essentially that of Hughes *et al.* (1975: 555), modified to include *Myttonia* (see also discussion above).

Genus ***BERGAMIA*** Whittard 1955

TYPE SPECIES. *Bergamia rhodesi* Whittard 1955, Fennian Stage, Tankerville Flags; Shelve inlier, Shropshire; by original designation.

DIAGNOSIS. See Hughes *et al.* (1975: 558).

Bergamia rushtoni sp. nov.
(Figs 72a–k)

1906 *Trinucleus* sp.; Evans: 612 (list).

HOLOTYPE. NMW 21.306.G4a, b, dorsal exoskeleton with associated, displaced lower lamella, from Fennian, Pontyfenni Formation; loc. 23, Pontyfenni.

PARATYPES. Numerous specimens from the type locality in BM(NH), NMW and BGS from the type locality; also from type horizon, loc. 20D, Capel-Dewi; BGS TCC759, a badly preserved cranidium from Rushmoor near Bancyfelin (Geol. Survey loc. Carm. 38SW Eλ5) probably also belongs to this species.

STRATIGRAPHICAL RANGE. Fennian, *B. rushtoni* Biozone.

DIAGNOSIS. Typically 15 or 16, rarely up to 18 radii per half-arc, in deep radial sulci in adult specimens, but sulci of E and I series separated in some immature ones; radii widely spaced in front of glabella, interradial areas considerably wider than radii, the latter becoming more crowded posterolaterally; E_1 and I_n complete; E_2 close to E_1, and commences normally at R2 or R3; I_1 begins at R6 or R7; auxiliary pits commonly absent, but may rarely be developed in one or two interradii; coarse reticulation on glabella and genal lobe.

NAME. For Dr A. W. A. Rushton, for the continued help he has given in this project.

DESCRIPTION. Fringe rather narrow and of constant width. Typically 15 or 16, and rarely up to 18 rows of pits per half-arc, in deep radial sulci in adult specimens (e.g. Fig. 72e), but E and I series separated in immature specimens (e.g. Fig. 72j). Radii widely separated in front of glabella, but become more crowded laterally; thus the interradial areas are about twice as wide as the sulci frontally, but are only as wide laterally. Most specimens have 15 or 16 radii per half-arc, in rare cases up to 18. E_1 complete, E_2 normally commencing at R2 or R3, but may be delayed until R9. Auxiliary pits rarely developed, and their position is random, for example e_{1-2} has been observed in iii and xiii. I_n complete, I_1 developed from R5–R7 up to R15. A typical fringe formula is: E_1 0–16, E_2 3–15, I_n 0–16, I_1 7–15.

Glabella with coarse reticulate sculpture and with swollen pseudofrontal lobe which overhangs the fringe sagittally to obscure its inner portion in dorsal view. Three pairs of lateral glabellar furrows of which 1P and 2P are both deep and of similar depth; 3P weak and small, forming small indentation on the flank of the pseudofrontal lobe. Axial furrow narrow and deep at anterior end of pseudofrontal lobe, but backwards broadens where the posterior part of the glabella narrows, whilst the inner flank of the cheek runs more or less exsagittally. Occipital ring narrow and upturned, differentiated from the glabella by a broad, shallow occipital furrow that deepens into small pit close behind the 1P furrow. Genal lobe with a coarse reticulate sculpture, coarsest on the inner posterior part, finer towards the leading edges. There is a suggestion of a faint, backwardly oblique eye ridge on some specimens (e.g. Fig. 72b), a character typically absent in *Bergamia*. Pleuroccipital furrow broad and deep, and behind it is a very narrow, upturned posterior cephalic border. Genal spine long and grooved, extending considerably further backwards than the pygidium.

Thorax of six segments, in general structure like those of other *Bergamia* species. The first four maintain an almost constant width (tr.), the fifth and sixth being progressively narrower (tr.).

Pygidium with three or four narrow axial rings, the axis extending backwards almost to the posterior margin where it impinges upon the downturned pygidial border. Pleural area with two weakly-defined ribs that extend to the well-marked inner edge of the border.

REMARKS. The type species, *B. rhodesi* Whittard (1955: 32; pl. 3, figs 8–13) differs from *B. rushtoni* in having only auxiliary pits (e_{1-2}) in RO, with E_1 and E_2 commencing at R1, a greater number of radii (18–19) and I_1 developed only in R1–R5, and a decidedly finer sculpture. *B. inquilina* (Whittard 1966: 278; pl. 48, figs 5–10) and *B. matura* (Whittard 1966: 280; pl. 48, figs 11, 12) (possibly conspecific, see Hughes *et al.* 1975: 558) are both similar to *B. rushtoni* in

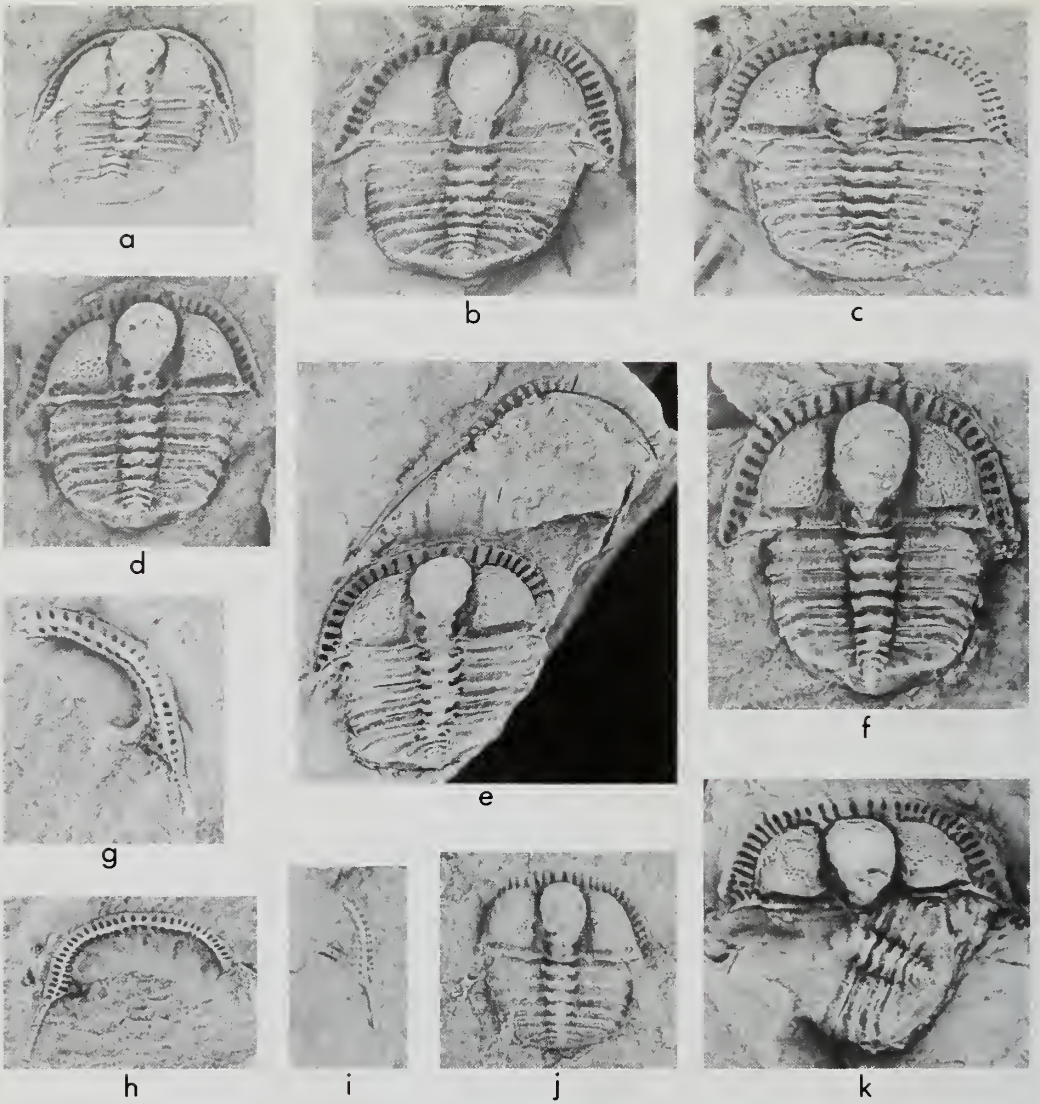


Fig. 72 *Bergamia rushtoni* sp. nov. Upper Arenig, Fennian, *B. rushtoni* Biozone; all except i from Pontyfenni Formation, loc. 23, Pontyfenni. a, small entire specimen, latex cast, × 5, It.18943; b, axial shield with well-developed radial sulci, and traces of ocular ridges, × 3·5, NMW 84.11G.1a; c, axial shield with radial sulci only developed laterally, × 4·5, It.18944; d, axial shield with some anterolateral pits of E and I series not in sulci, × 5, It.18945; e, **holotype**, axial shield with associated displaced lower lamella, × 3·5, NMW 21.306.G4a; f, large axial shield with well-developed radial sulci frontally, × 4, NMW 84.11G.2a; g, incomplete lower lamella, × 6, It.18946; h, ditto, × 7, It.18947; i, ditto, loc. 24, Llwyn-crwn, × 8, It.18948; j, small entire specimen, latex cast, × 4, NMW 77.9G.35a; k, disarranged axial shield with some pits of E and I series separated anterolaterally, × 4·5, NMW 84.11G.3a.

number of radii and distribution of pits in E_1, I_n and I_1, but there are small differences in E_2; in *B. inquilina* its development is irregular, and it commences at R3, R5, R7 or R8, extending to R14 or R15 (Whittard 1966: 279), and in *B. matura* ranges from R0 or R1 to R17 (Whittard 1966: 280). Both *B. inquilina* and *B. matura* have a comparatively large number of auxiliary pits in e_1 and e_2, and it is this feature more than any other that distinguishes them from *B. rushtoni*, in which auxiliary pits are but rarely developed (see above). It is likely that *B. rushtoni* has evolved from *B. inquilina*, *B. matura* or a similar form by the total or almost total loss of auxiliary pits, and a similar reduction has taken place in *B. rhodesi*. *B. inquilina* and *B. matura* are of late Whitlandian or earliest Fennian age, and thus occupy an appropriate stratigraphical position to have given rise to *B. rushtoni* in the Pontyfenni Formation and *B. rhodesi* in the Tankerville Flags. A further stage in the simplification of the fringe is seen in the Llanvirn species *B. artemis* Rushton & Hughes (1981: 630; pl. 2, figs 1–14, 16, 17) from the Great Paxton Borehole; here E_1 and E_2 (with 12–15 pits per half-arc) converge posterolaterally to form twin pits at about R10, and become a single arc in the last three radii. I_n is the only inner arc developed.

The dorsal exoskeleton of *B. rushtoni* shows a striking similarity to *Anebolithus simplicior* (Whittard) (Hughes *et al.* 1975: pl. 1, figs 17, 19), particularly in its cephalic sculpture and in the presence of deep radial sulci on the fringe. Without a lower lamella it might be easy to confuse the two, but they can be readily distinguished by the spacing of the sulci in front of the glabella. The interradial areas are narrower than the sulci in *A. simplicior* (Hughes *et al.* 1975: pl. 1, fig. 17), but much wider in *B. rushtoni* (e.g. Fig. 72e).

Bergamia sp. A
(Fig. 73)

MATERIAL. Incomplete external mould of cranidium, NMW 85.9G.1, from Whitlandian, Blaencediw Formation, Blaencediw Quarry (loc. 29).

DESCRIPTION. The pseudofrontal lobe appears to be rounded and somewhat swollen; traces of a reticulate sculpture can be seen on the genal lobes. A half-arc has 24 radii in deep, rather narrow radial sulci; three pits can be seen in one of these, but the position of the girder is unknown.

REMARKS. The disposition of pits in deep radial sulci suggests that this specimen is a *Bergamia*. A second similar fragmentary cephalon has been recovered from the same horizon at loc. 39, and specimens that are possibly conspecific have been found low in the section at Pwlluog (loc. 61A). The latter include a very badly preserved, cleaved cranidium which shows distinct radial sulci like the present specimen, and which clearly differentiate it from *G. gibbsii* and *F. sedgwicki* that occur higher in the section at Pwlluog.

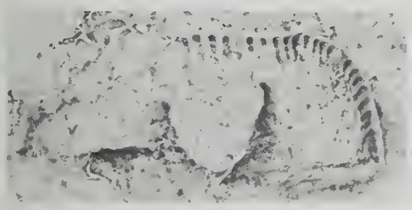


Fig. 73 *Bergamia* sp. A. Middle Arenig, Whitlandian, ?*F. radix* Biozone, Blaencediw Formation, loc. 31, Blaencediw. Incomplete cranidium, latex cast showing radial sulci and traces of reticulation on genal lobe, × 5, NMW 85.9G.1.

Genus ***FURCALITHUS*** nov.

TYPE SPECIES. *Furcalithus radix* sp. nov.

NAME. Latin *furca*, 'a pitchfork', which some radii with closely associated interradii in type species resemble, plus suffix *-lithus*.

DIAGNOSIS. Trinucleine with radial sulci only very weak, if present; E_1, E_2 complete; I_n, I_1 complete, I_2 complete or extending round most of fringe, I_3 may also be present; 4–?8 interradii present in I series. Pygidium with axis reaching, but not impinging on, narrow posterior border.

REMARKS. The general relationships between *Furcalithus* and other contemporaneous trinucleines are discussed above. Main differences from *Myttonia* are: presence of girder and radially aligned pits around entire fringe (apart from proterolateral corners); from contemporaneous *Bergamia* species, *Furcalithus* differs in the lack of deep sulci, presence of more I arcs, presence of interradii in the I series and a narrower pygidial border onto which the axis does not extend. However, the Llandeilo *Bergamia* species *B. prima* and *B. whittardi* (Hughes 1971: 140 and 146 respectively) have more pits in the I series than do earlier ones, and in this respect resemble *Furcalithus*. However, interradii are absent and the pygidium has the typically broad border of *Bergamia*; the similarity of the fringe is presumably the result of convergence.

Furcalithus radix sp. nov.

(Figs 74a–e, 75)

HOLOTYPE. It.18949, dorsal exoskeleton lacking lower lamella and genal spines.

TYPE LOCALITY AND HORIZON. Whitlandian Stage, *Furcalithus radix* Biozone; about 70 m above base of Afon Ffinnant Formation, Cwm yr Abbey, loc. 16K.

PARATYPES. It.18950, NMW 84.10G.9a, b–14a, b, all from basal 100 m of Afon Ffinnant Formation, Cwm yr Abbey, loc. 16L.

STRATIGRAPHICAL RANGE. Whitlandian, *F. radix* Biozone, basal 100 m of Afon Ffinnant Formation.

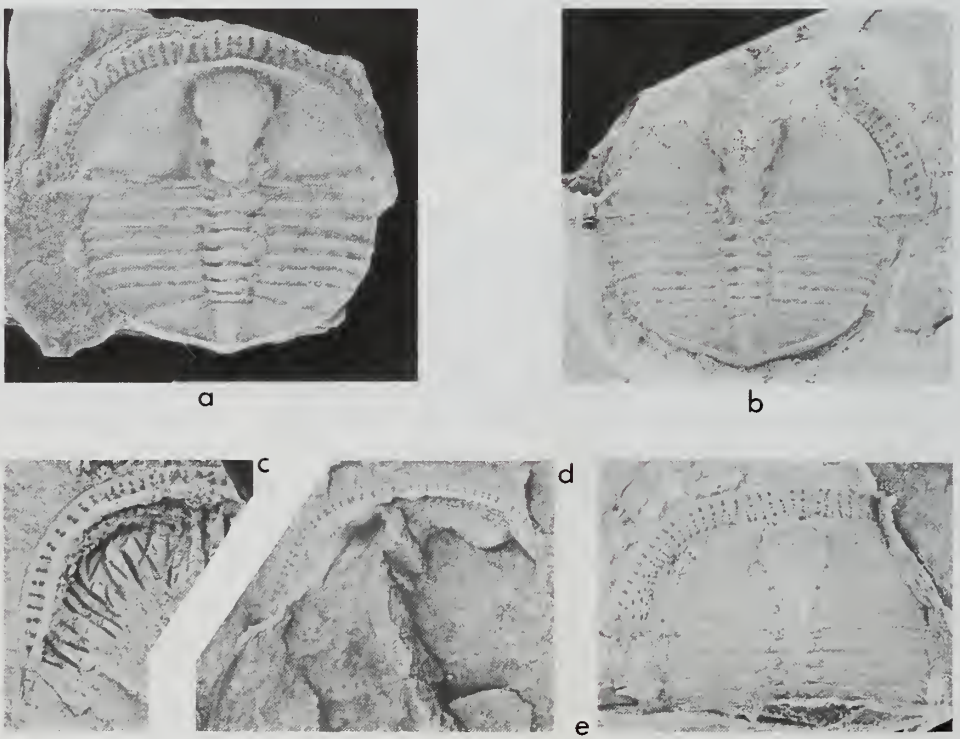


Fig. 74 *Furcalithus radix* gen. et sp. nov. Middle Arenig, Whitlandian Stage, *F. radix* Biozone, Afon Ffinnant Formation. a, **holotype**, axial shield, loc. 16K, Cwm yr Abbey, × 5, It.18949; b, incomplete axial shield, loc. 16L, Cwm yr Abbey, × 6, NMW 84.10G.11a; c, partial lower lamella, loc. 18E, Afon Ffinnant, × 5, It.18950; d, lower lamella with genal spine, locality as Fig. 74b, × 4, NMW 84.10G.12a; e, cranidium with five thoracic segments, locality as Fig. 74b, × 5, NMW 84.10G.13b.

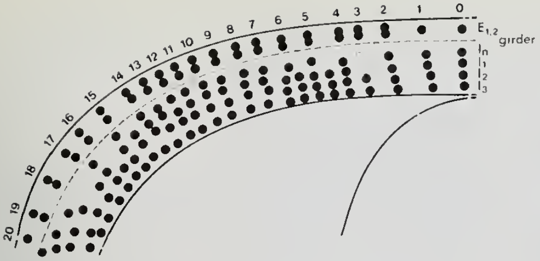


Fig. 75 Half-fringe of *Furcalithus radix* gen. et sp. nov., showing distribution of pits, based on Fig. 74e.

DIAGNOSIS. Radii per half-arc 20–22, E_1, E_2 complete, with paired pits, close together; I_n, I_{1-3} complete; four or five interradii in I series, typically at or near radii 4, 6, 14 and 17; weak flexure on genal lobe.

NAME. 'A root'; the earliest member of the *Furcalithus–Bergamia–Stapeleyella* stock.

DESCRIPTION. Glabella with deep 1P, 2P and 3P furrows. Glabellar node about half-way along glabella. Axial furrows broad and shallow, with anterior fossula represented by a weak linear feature. A short distance abaxially from 1P furrow, and slightly posterior to it, there is a small, shallow pit. There is a second similar pit a short distance behind the 1P furrow (well seen on Fig. 74b); this we interpret as the occipital pit, although some trinucleines possess two small pits in addition to the occipital pit close to the base of the glabella (Hughes *et al.* 1975: 541). Occipital furrow broad and shallow; occipital ring a narrow, backwardly-curving band, without spine. At posterior end of axial furrow is a weak, elongate alar lobe.

Genal lobe traversed by a weak flexure which near the genal angle is expressed as a narrow ridge which runs onto the posterior cephalic border. A small posterior fossula is situated just adaxial to this ridge in the posterior border furrow. The flexure has the appearance of being accentuated in front of the glabella, but this seems in large part to be a result of compression. The genal lobes and glabella have a fine reticulate sculpture, that of the leading edges of the former being somewhat finer. The axial furrows are devoid of such sculpture. Fringe strongly flexed at the girder, the position of which on the dorsal surface is indicated by a smooth band (see especially Fig. 74e); this is not a raised ridge, or 'list' (cf. Hughes *et al.* 1975: 550). Twenty to twenty-two radii per half-arc, not in sulci, although these appear to be present on internal moulds (Fig. 74a). E_1 and E_2 complete, close together. E_3 pits seen in radii 9, 16 and 17 on one specimen (Fig. 74e). I_n and I_{1-3} extend at least as far as radius 17 or 18, posterior to which the arrangement becomes more or less chaotic. On the best-preserved fringe (Fig. 74e) interradii 4, 6, 14 and 17 are well seen, but position of the interradii does not appear to be consistent, although there is insufficient material to be able to analyse this statistically. Certain interradii converge in an outwards direction with adjacent radii to produce a 'fork'. Thorax of six segments, of the normal trinucleine structure. Pygidium with narrow border, weakly reflexed on either side of the axis, which just impinges onto it. Six or seven axial rings, which become progressively more weakly defined backwards. Pleural fields with five pairs of ribs, more clearly identified on external rather than on internal moulds.

Furcalithus sedgwicki (Salter 1866*b*)
(Figs 76a–d)

1866*b* *Trinucleus Sedgwicki* Salter: 319; pl. 12, fig. 9.
1881 *Trinucleus Sedgwicki* Salter; Salter & Etheridge: 516; pl. 12, fig. 9 (copy of Salter, 1866).
non 1906 *Trinucleus sedgwickii* Salt.; Evans: 609 (list) [= *Stapeleyella abyfrons*].
non 1914 *Trinucleus sedgwicki* Salt.; Thomas, *in* Strahan *et al.*: 14 [= *Myttonia* cf. *fearnsidesi*].
1955 *Bergamia*? *sedgwicki* (Salter) Whittard: 33; pl. 4, figs 3, 4.
1960 ?*Bergamia sedgwicki* (Salter); Whittard: 182 (list).
1971 *Bergamia*? *sedgwicki* (Salter); Hughes: 145.
1975 *Bergamia*? *sedgwicki* (Salter); Hughes *et al.*: 558.
1980 *Trinucleus sedgwicki* Salter; Temple: 224.

Lectotype (here selected). GSM 49670, cephalon.

Type locality and horizon. Whitlandian Stage, *Gymnostomix gibbsii* Biozone; south side of St David's Head (presumably Pwlluog, vicinity of locs 61D and F), Dyfed.

Material. Cranidia and cephala from type stratum, Pwlluog, locs 61C–F.

Stratigraphical range. Whitlandian, *G. gibbsii* Biozone.

Diagnosis. Approximate distribution of pits as follows: 17–19 radii per half-arc, E_1, E_2 complete; I_n, I_1 0–16 or 17, I_2 (?)6–16; interradii in, il? ii–vi, xii–xv; i_2 at least xii, xiii, xiv. Glabella and genal lobes apparently smooth.

Description. The small amount of material available of this species is all indifferently preserved and variously distorted. The proportions of the glabellar and genal lobes are like *F. radix*. The fringe differs in that the individual pits are larger, there are fewer radii, a greater number of interradii, and no I_3 in the I series; there are fewer irregular pits on the posterolateral corners.

Remarks. Whittard (1955: 34) remarked on the difference in the I series of pits between *F. sedgwicki* and the type species of *Bergamia*, *B. rhodesi*, and only placed *sedgwicki* in *Bergamia* with considerable doubt. These same characters of the I series are very similar to those of *F. radix*, and are noted above.

Whittard (1955: 31) suggested that trinucleids from the Whitlandian of Dwyrhos, Aberdaron and Nant-y-Gadwen, Llŷn Peninsula, may belong to *Myttonia*, but noted that the external pits in the upper lamella appear to occur in sulci. We have obtained and examined further material

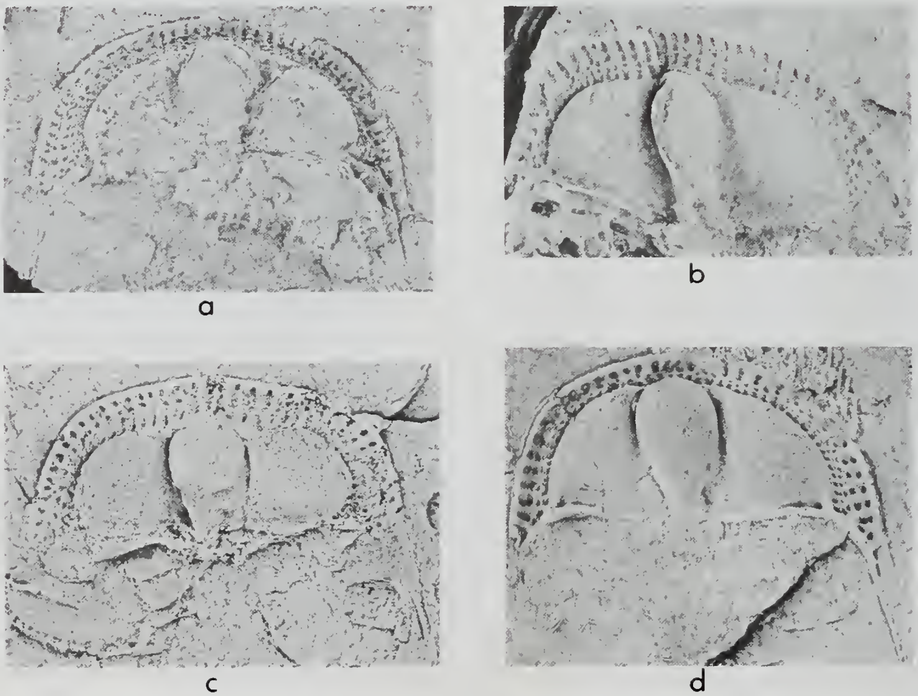


Fig. 76 *Furcalithus sedgwicki* (Salter 1866*b*). Middle Arenig, Whitlandian Stage, *G. gibbsii* Biozone, Penmaen Dewi Formation, Pwlluog, Whitesand Bay. a, cephalon, latex cast from external mould, × 3, In.38217; b, cranidium, × 4, BGS GSM49672 (original of Whittard 1955: pl. 4, fig. 4); c, cephalon, latex cast from external mould, loc. 61F, × 4, It.18953; d, **lectotype** cephalon, latex cast from external mould, × 3, BGS GSM49670 (original of Whittard 1955: pl. 4, fig. 3).

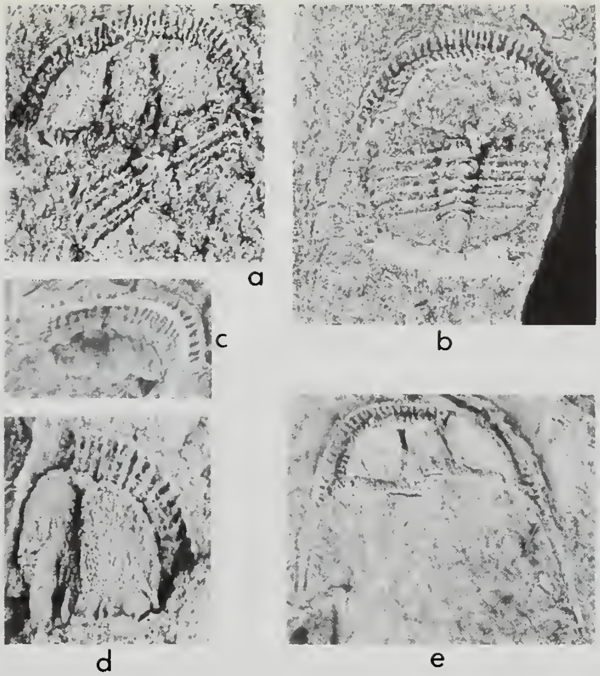


Fig. 77 *Furcalithus*? sp. Middle Arenig, Whilandian Stage, Llŷn Peninsula, Gwynedd; Dwyrhos, Aberdaron (a, b, e) or east side of Nant-y-Gadwen, Rhiw (c, d). a, small cranidium with associated thoracic segments, × 10, NMW 27.110.G276; b, complete specimen, cephalon damaged (note broad genal spine), × 4, I14282; c, incomplete lower lamella, × 4, It.18951; d, incomplete cranidium, latex cast from external mould, × 8, It.18952; e, cephalon, showing long, broad genal spines, × 4, NMW 27.110.G275.

(Figs 77a–e) from these localities. The general aspect of the fringe is not unlike *F. sedgwicki*, but we can confirm the presence of distinct radial sulci; the poor preservation of the available specimens means that it is not possible to be certain whether or not there are interradii in the I series. There are arguments for placing this material either in *Bergamia* (distinct radial sulci) or in *Furcalithus* (the probability of a large number of I arcs); because it bears closest resemblance to *F. sedgwicki*, we place it with question in *Furcalithus*, but definite assignment must await better material.

Genus ***STAPELEYELLA*** Whittard 1955

TYPE SPECIES. *Stapeleyella inconstans* Whittard, 1955; from Lower Llanvirn, *D. artus* Biozone, topmost Hope Shales Formation, Shelve inlier: by original designation.

DIAGNOSIS. E_{1-2} and sometimes E_3 present, and all generally complete; some pits of E_4 may be present. I_1, I_n complete, very close together frontally. Pits on upper lamella in radial sulci, many interradial ridges bifurcating external to E_1 to produce intercalated short sulci with E_2 or E_2 and E_3 and frontally E_4, typically forming a series of 'Y's, but arrangement may be highly irregular. Pygidium like *Bergamia*.

REMARKS. We have modified the diagnosis of *Stapeleyella* given by Hughes *et al.* (1975: 559) in order to accommodate *S. abyfrons* sp. nov. (see below). This extends the range of the genus at least as far back as the early Fennian. Its possible relationships with *Furcalithus* and *Bergamia* are discussed above.

Stapeleyella inconstans Whittard 1955
(Figs 78a–f)

1955 *Stapeleyella inconstans* Whittard: 36; pl. 4, figs 7–13; pl. 5, figs 1–6 (with earlier synonymy).
1975 *Stapeleyella inconstans* Whittard; Hughes *et al.*: 559; pl. 2, figs 29–31.
1980 *Stapeleyella inconstans* Whittard; Temple: 221.

Lectotype (selected Temple 1980: 221). GSM 92971, complete dorsal exoskeleton on slab with two individuals (figd Whittard 1955: pl. 4, fig. 7 (left hand specimen); Hughes *et al.* 1975: pl. 2, fig. 29 (upper specimen)).

Type locality and horizon. Topmost Hope Shales Formation, path W of Brithdir, 1·6 km ENE of Old Church Stoke, Powys (Shelve inlier).

Occurrence in south Wales. Arenig, highest Fennian Stage, Llanfallteg Formation, Llanfallteg (locs 52A–C, N, R, T–X). Llanvirn, *artus* Biozone, Llanfallteg (loc. 52), Llanilwyd, St Clears, Cefn-maen-llŵyd, Rhyd-y-wrâch (loc. 50), Llandissilio (loc. 53), Long Plantation railway cutting, Scolton (loc. 55), railway cutting WNW of Clarbeston Road station.

Diagnosis. *Stapeleyella* with E_1–E_3 normally complete, but E_3 sometimes absent from more anterior radii. E_4 may be developed laterally. Interradii with e_2 and e_3 (but only exceptionally with e_1), these pits normally persisting to interradii 9 or 10, occasionally extending as far as 16. Interradial ridges enclosing interradii give rise to characteristic 'Y's on anterior part of fringe. I_1, I_n normally complete, although in some only I_n present frontally. I_2 and I_3 may appear as early as third and eighth radii respectively, but can appear in more posterior radii. Sculpture reticulate, coarse on glabella, finer on genal lobes.

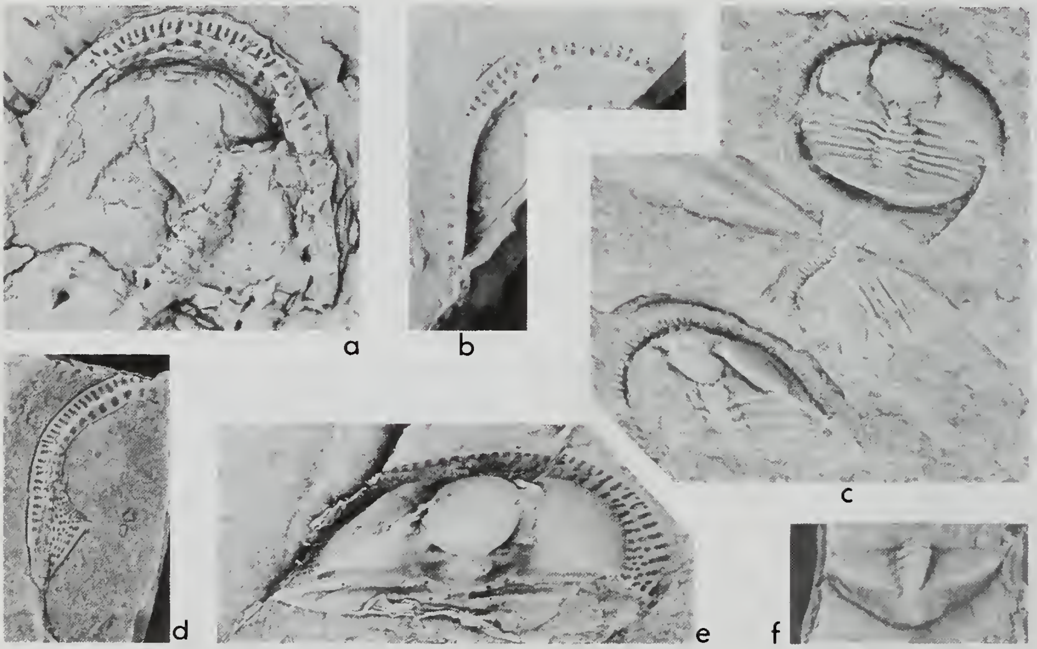


Fig. 78 *Stapeleyella inconstans* Whittard 1955. Llanfallteg Formation, Upper Arenig, Fennian Stage, *D. levigena* Biozone (a, f) or lower Llanvirn, *D. artus* Biozone (others). a, moult arrangement showing lower lamella, loc. 52U, Llanfallteg, × 3, It.18954; b, incomplete lower lamella, loc. 52, Llanfallteg, × 3, It.18955; c, group of specimens, loc. 55, Scolton, × 3·5, It.18956; d, incomplete lower lamella, Clôg-y-frân, Whitland (Geological Survey loc. 37SE Wλ1), × 2·5, BGS TCC866); e, cephalon with attached thoracic segments, latex cast from external mould, loc. 55, Scolton, × 5, It.18957; f, pygidium, loc. 52B, Llanfallteg, × 4, It.18958.

REMARKS. Whittard (1955: 36) described this species in detail, and noted the variable nature of details on the fringe. The material from south Wales falls within the range of variation described by Whittard, although in this material most specimens apparently have only I_n present anteriorly, whilst Whittard (1955: 37) noted that only occasionally I_2 (i.e. I_1 in current terminology) is delayed until the eighth radius, with the norm being the presence of complete I_n and I_1 arcs. However, I_1 and I_n tend to be very close together frontally, so any distortion, which is widespread in our samples, could easily make a close pair of pits appear as one. Nevertheless, several specimens (e.g. Fig. 78b) definitely have only I_n anteriorly. In the E series, most specimens have complete E_1–E_3 arcs, although some have only E_1 and E_2. Those with only E_1 and E_2 frontally occur in samples which include specimens with E_{1-3} frontally.

Our material is neither plentiful enough nor sufficiently well preserved for the identification of any successive changes in fringe morphology, if indeed such occur. *S. inconstans* is uncommon in the Arenig part of the Llanfallteg Formation, but becomes abundant in the basal Llanvirn, and slabs have been found at Scolton with large numbers of specimens.

Two further species from the Lower Llanvirn of England and Wales have been ascribed, one with question, to *Stapeleyella.* Whittard (1955: 40) distinguished *S. murchisoni* (Salter), possibly from the Arenig, but more likely from the Lower Llanvirn, of the Shelve inlier, from *S. inconstans* on:

> 'the more elongated glabella, on the sloping outer face of the cheek-lobe and on the absence of deep second and third glabellar furrows, of a pseudofrontal lobe, of a median tubercle, of a reticulated ornament on the glabella, and of a scrobiculate ornament on the cheek-lobes; the fringe is also more simple because the inner series of pits shows no more than two rows (?) and few auxiliary pits appear in the outer series'.

The type material of *S. murchisoni* is variously distorted, and we suspect that many of these 'differences' are due to the vagaries of preservation. However, the details of the fringe do seem to be distinct.

The type material of *S.? etheridgei* (Hicks) from the Lower Llanvirn of Llanvirn Quarry is badly preserved and distorted. It was placed by Whittard (1955: 34) in *Bergamia* with doubt, and transferred tentatively to *Stapeleyella* by Hughes *et al.* (1975: 560). Since *S.? etheridgei* occurs at exactly the same horizon as *S. inconstans* elsewhere in south Wales, it seems likely that it belongs to the same species. However, without extra better-preserved specimens from Llanvirn Quarry we regard it best for the time being to restrict the name *S.? etheridgei* to the type material.

Stapeleyella abyfrons sp. nov.
(Figs 79a–h)

1906 *Trinucleus Sedgwickii* Salt.; Evans: 609 (list).
1914 *Trinucleus* sp.; Thomas, *in* Strahan *et al.*: 19 (list).
1914 *Trinucleus gibbsi* Salt.; Thomas, *in* Strahan *et al.*: 19 (list).

HOLOTYPE. It.18962, dorsal exoskeleton lacking lower lamella.

TYPE LOCALITY AND HORIZON. Fennian, *S. abyfrons* Biozone, Pontyfenni Formation; Pen-y-parc (loc. 38).

PARATYPES. Numerous specimens (e.g. It.18959–61, It.18964–5, NMW 84.17G.140–159) from type locality, several specimens (It.18963, NMW 84.17G.161–3) from Regwm (loc. 26), and one specimen from entrance to former Llangan vicarage.

STRATIGRAPHICAL RANGE. Fennian, *S. abyfrons* Biozone.

DIAGNOSIS. Radii 16–17. E_{1-2} complete, with e_{1-2} or e_2 only in interradii o, iv, v or ix or close thereto, but distribution highly variable, and can occur up to 12th interradius. Resultant crudely 'Y'-shaped interradial ridges irregularly disposed, and fewer than in *S. inconstans.* I_n, I_1 complete. Some I_n pits laterally paired. Very fine reticulate sculpture on glabella and genal lobes.

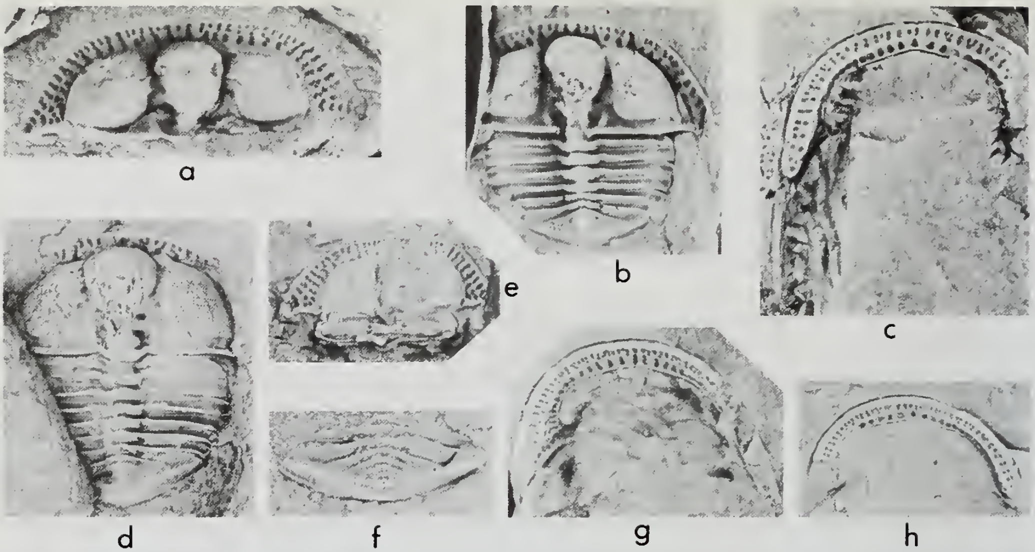


Fig. 79 *Stapeleyella abyfrons* sp. nov. Upper Arenig, Fennian Stage, Pontyfenni Formation, *S. abyfrons* Biozone; loc. 38, Pen-y-parc (except e). a, cranidium, × 6, It.18959; b, small complete specimen, latex cast from external mould showing bacculae, × 3·5, It.18960; c, lower lamella, × 3·5, It.18961; d, latex cast from **holotype**, external mould of almost complete axial shield, × 2, It.18962; e, small cranidium with attached thoracic segments, loc. 26, Regwm, × 8, It.18963; f, small pygidium, latex cast from external mould, × 10, BGS Pr1765; g, lower lamella, × 6, It.18964; h, lower lamella, × 6, It.18965.

Name. In reference to lack of ordered Y-shaped interradial ridges.

Description. Glabella clavate, with deep 1P and 2P furrows, and weak 3P on pseudofrontal lobe. Small occipital pit a short distance behind 1P furrow, running into axial furrow close to it. Occipital furrow very shallow medially, occipital ring rather narrow, without spine. Broad, shallow axial furrow narrows and deepens anteriorly in vicinity of pseudofrontal lobe. Prominent, small, ovate alar lobe at posterior end of axial furrow. Genal lobes evenly rounded; those and glabella with very fine reticulate sculpture.

Fringe narrow, with 16–17 radii, strongly flexed at girder. E_{1-2} complete. e_{1-2} or e_2 only in some interradii, concentrated towards the anterior; a typical distribution is in o, iv, v and ix, but there is considerable variation on this pattern. These give rise to a few irregularly disposed, commonly asymmetrical 'Y'-shaped interradial ridges. I_n, I_1 complete; some pits in I_n laterally paired, the components of each pair being very close together. Pits near posterolateral corner of fringe irregularly disposed. Pygidium and thorax like those of *S. inconstans* except that the pygidial border does not broaden so much towards the posterior and the pleural furrows are a little deeper.

Remarks. *S. abyfrons* is the earliest *Stapeleyella* so far recorded. The principal distinctive feature which differentiates it from *S. inconstans* is the comparative disorganization of the e pits to produce a small number of rather irregularly disposed, ill-formed 'Y'-shaped interradial sulci; there are fewer pits in both the E and I series. The presence of two arcs of E pits and two of I makes *S. abyfrons* intermediate in this feature between contemporaneous *Bergamia* with E_{1-2} and I_n and *S. inconstans.* The differentiation of *Stapeleyella* from *Bergamia* presumably took place in the Whitlandian, and the lower Llanvirn specimen that Hughes *et al.* (1975: 558; pl. 2, fig. 28) suggested was an 'intermediate' stage between *Bergamia* and *Stapeleyella* from north Wales is evidently not on this part of the phyletic lineage. It seems more likely to be a different *Stapeleyella* species.

Stapeleyella aff. *abyfrons* sp. nov.

(Figs 80a, b)

1909 *Trinucleus* sp.; Thomas, *in* Strahan *et al.*: 18.

MATERIAL. Disarranged dorsal exoskeleton, and several cephalic fragments.

HORIZON AND LOCALITY. Fennian, Pontyfenni Formation, ?*B. rushtoni* Biozone; cutting on A40, Castell-y-waun, west of Bancyfelin (loc. 21).

DESCRIPTION. Glabella and genal lobes with fine reticulate sculpture, occipital ring without spine. Sixteen radii per half-arc. E_1, E_2 complete, very close together anteriorly, more widely separated posteriorly. A few interradii with e_1 and e_2 present towards anterior. I_n and I_1, like the E series, very close together anteriorly, and more widely separated posteriorly. Both apparently complete; I_2 in fifteenth and possibly sixteenth radius.

REMARKS. The presence of interradii in the E series invites comparison with such species as *Bergamia rhodesi* Whittard, *B. matura* Whittard and *B. inquilina* (Whittard), although there are apparently fewer than in any of these species. Unlike those, there is an (apparently) complete I_1 (note that Whittard 1955, 1966 used a different I series terminology from that used here) and some I_2. The presence of incomplete E_1 and E_2, together with (apparently) complete I_n and I_1, immediately invites comparison with *Stapeleyella abyfrons*, although there are fewer radii, larger pits and greater regularity, with only a few interradii in the E series and no paired I_n. Although there are virtually no characteristic Y-shaped interradial ridges, we on balance prefer to associate these specimens with *Stapeleyella*, for other fringe characters are more similar to contemporaneous members of this genus than they are to those of *Bergamia*.

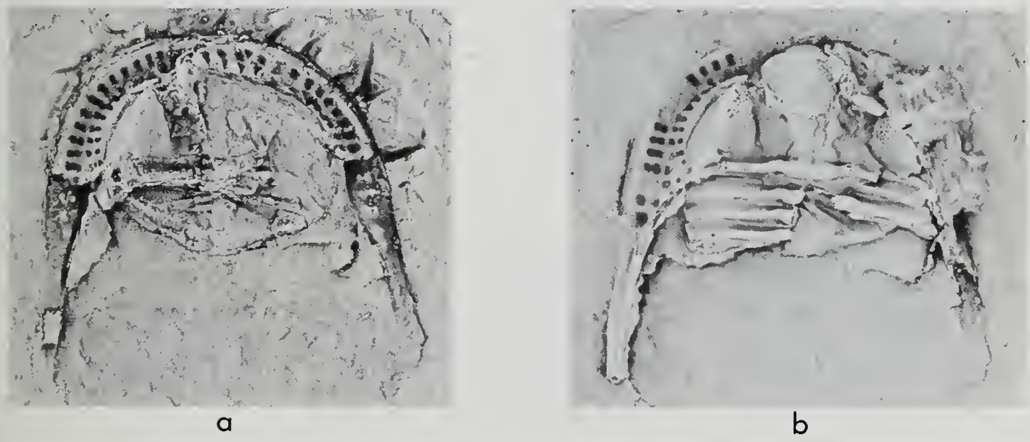


Fig. 80 *Stapeleyella* aff. *abyfrons* sp. nov. Upper Arenig, Fennian Stage, Pontyfenni Formation, ?*B. rushtoni* Biozone, loc. 21, Castell-y-waun. a, complete specimen, × 5, It.18966; b, latex cast from external mould of same specimen, × 5.

Genus *GYMNOSTOMIX* nov.

TYPE SPECIES. *Trinucleus gibbsii* (Salter *in* Murchison 1859).

NAME. Greek *γυμνός* bare, plus *στόνυξ*, a beam, in reference to the marginal girder.

DIAGNOSIS. Fringe narrow with marginal girder. I_n and I_1 complete, I_2 present anteriorly and anterolaterally, a few I_3 anterolaterally. Prominent crest on genal lobe, extending across anterior end of axial furrow and merging with front of glabella. Pygidium like *Bergamia*.

REMARKS. Whittard (1955: 34) placed the type species of *Gymnostomix* in *Bergamia*, and suggested that it might be the same as *B. rhodesi*. He listed a number of syntypes and gave a fringe formula which included both E and I arcs, but admitted that it might be unreliable because of poor preservation of the syntypes. He was clearly mistaken in identifying E and I arcs, for *G. gibbsii* has a marginal girder (well seen in Figs 81c, d), which feature immediately distinguishes it from *Bergamia*. Instead *G. gibbsii* shows a greater or lesser degree of resemblance to other trinucleid genera with a marginal girder, *Anebolithus*, *Incaia* and *Famatinolithus*. From all it is distinguished by the presence of prominent genal ridges; in addition it differs from *Anebolithus* (Hughes *et al.* 1975: pl. 1, figs 16–19) in possessing some pits in I_2 and I_3 and lacking deep radial sulci. *Famatinolithus* (Hughes *et al.* 1975: pl. 1, figs 13–15) differs in having a broad marginal rim, no genal prolongations and a preglabellar field. *Incaia* (Hughes & Wright 1970: pls 127, 128; Hughes *et al.* 1975: pl. 2, figs 20–22) has a similar fringe, but differs in having prominent lateral eye tubercles and a different pygidial structure. Immature *G. gibbsii* (Fig. 81g), however, have distinct eye ridges, in contrast with, for example, similar-sized *Stapeleyella inconstans* (Whittard 1955: pl. 4, fig. 9) and *Bergamia whittardi* (Hughes 1971: pl. 8, figs 4, 6).

Of the three genera discussed above, *Gymnostomix* shows closest resemblance to *Anebolithus*, the earliest representative of which occurs in the Moridunian, low in the Mytton Flags Formation, Shelve inlier, and it seems likely that its origins lie in this genus.

Gymnostomix gibbsii (Salter *in* Murchison 1859)
(Figs 81a–j)

1859 *Trinucleus Gibbsii* Salter, *in* Murchison: 53; Fossils (9), fig. 7.
1866*b* *Trinucleus Gibbsii* Salter; Salter: 319; pl. 12, fig. 10 [copy, Salter *in* Murchison, 1859].
1867 *Trinucleus Gibbsii* Salter; Murchison: 51; Fossils (10), fig. 7 [copy, Salter *in* Murchison, 1859].
1872 *Trinucleus Gibbsii* Salter; Murchison: 51; Fossils (10), fig. 7 [copy, Salter *in* Murchison, 1859].
1873 *Trinucleus Gibbsii* Salter; Salter: 22 [with figure].
1881 *Trinucleus Gibbsii* Salter; Salter & Etheridge: 380 (list), 516; pl. 12, fig. 10 [copy, Salter *in* Murchison, 1859].
non 1884 *Trinucleus Gibbsii* Salter; La Touche: 56; pl. 2, fig. 33 [= *Stapeleyella inconstans* Whittard 1955].
1906 *Trinucleus* sp.; Evans: 608 (list).
?*non* 1913 ?*Trinucleus Gibbsii* Salter; Postlethwaite: 14 (list).
non 1914 *Trinucleus gibbsi* Salter; Thomas, *in* Strahan *et al.*: 19 (list). [= *Stapeleyella abyfrons* sp. nov.].
non 1932 *Trinucleus gibbsi* Salter (= *T. etheridgei* Hicks); Matley: 262 [= *Bergamia*? sp. of Hughes *et al.* 1975: 558; see discussion of *S. abyfrons*].
1955 *Bergamia gibbsi* (Salter) Whittard: 33; pl. 4, figs 1, 2, 5.
1960 *Bergamia gibbsi* (Salter); Whittard: 182 (list).
1971 *Bergamia gibbsi* (Murchison); Hughes: 145.
1975 *Bergamia gibbsi* (Salter *in* Murchison); Hughes *et al.*: 558 (list).
1982 *Bergamia gibbsii* (Salter *in* Murchison); Owens & Fortey, *in* Bevins & Roach: 76 (list).
1982 *Bergamia gibbsii* (Salter *in* Murchison); Owens & Fortey: 257 (list).

LECTOTYPE (selected Temple 1980: 221). GSM 23037, external mould of cephalon and thorax.

TYPE LOCALITY AND HORIZON. Whitlandian, Penmaen Dewi Formation; old slate quarry south of St David's head (presumed to be our loc. 61F).

OTHER MATERIAL. Numerous specimens from Penmaen Dewi Formation, Pwlluog (loc. 61E, F); Colomendy Formation, Rhyd Henllan (locs 47A, B) and Whitland Abbey members (loc 27), and Afon Ffinnant Formation, loc. 18C.

Outside south Wales, *G. gibbsii* has been found in the Whitlandian of Parwyd, Llŷn Peninsula (A. Beckly, personal communication, February 1984). Postlethwaite's (1913) doubtful record from the Lake District seems to have been spurious, for no trinucleids are known from the Arenig part of the Skiddaw Slates Group; the only records appear to have been from the Llanvirn part in the Cross Fell inlier (Dr A. W. A. Rushton, personal communication, February 1984).

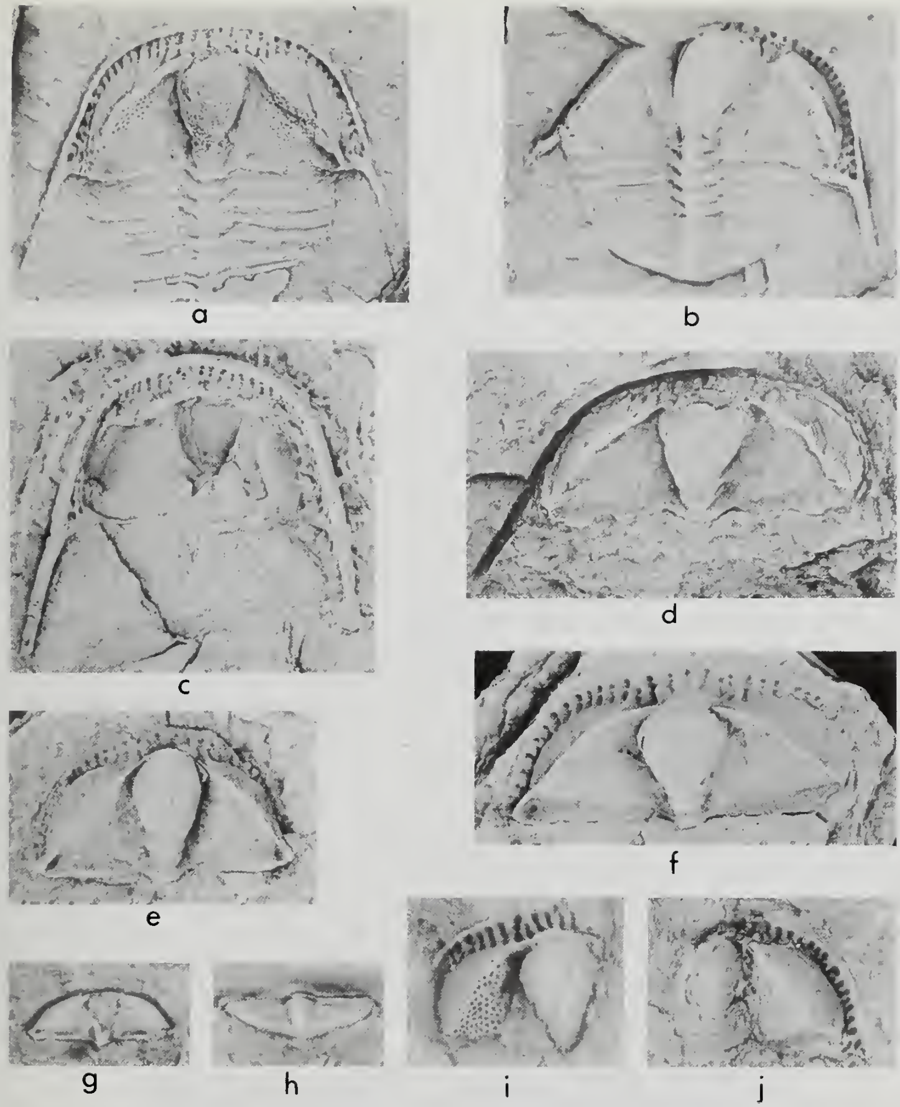


Fig. 81 *Gymnostomix gibbsii* (Salter *in* Murchison 1859). Middle Arenig, Whitlandian Stage, *G. gibbsii* Biozone, Penmaen Dewi Formation, Pwlluog, Whitesand Bay (a–f), or Afon Ffinnant Formation, loc. 18C, Afon Ffinnant (g–j). a, lectotype cephalon and thorax, latex cast from external mould, old slate quarry (probably loc. 61F), × 4, BGS GSM23037 (original of Whittard 1955: pl. 4, fig. 1); b, complete specimen, latex cast from external mould, × 3·5, BM(NH) 46404; c, latex cast of ventral side of cephalon, showing marginal girder, loc. 61F, × 3, It.18967; d, cephalon, internal mould showing marginal girder, × 4, I1370; e, cranidium, loc. 61F, × 5, It.18968; f, cranidium, × 4·5, BGS GSM23034 (original of Whittard 1955: pl. 4, fig. 2); g, meraspid cranidium with eye ridges, × 15, It.18969; h, pygidium, × 8, It.18970; i, incomplete cranidium, latex cast of external mould, × 10, It.18971; j, incomplete cranidium, × 10, It.18972.

STRATIGRAPHICAL RANGE. Whitlandian, middle and upper parts.

DIAGNOSIS. Fringe with I_n and I_1 complete, I_2 present anteriorly and anterolaterally, a few I_3 anterolaterally. Sculpture of coarse reticulate pattern on glabella and posterior genal lobes; finer on anterior part of genal lobes.

Description. Glabella clavate, expanding rapidly forwards. Deep 1P and 2P furrows, 3P probably present. Small glabellar node. Small, ovate, alar lobe at posterior end of axial furrow, occipital ring narrow, backwardly curving, and without spine. Genal lobe with prominent crest running from posterolateral corner to merge with front of glabella and enclosing anterior end of axial furrow. In the broad posterior border furrow, just inside the crest, there is a prominent posterior fossula. On glabella and genal lobe posterior to crest there is a coarse reticulate sculpture; the leading edge of the genal lobe, anterior to the ridge, has a very fine reticulate sculpture. This is commonly obscured when preservation is poor (Fig. 81a). A similar differentiation of genal lobe sculpture is seen in *Anebolithus simplicior* (e.g. Hughes *et al.* 1975: pl. 1, figs 17, 19). An immature cranidium (Fig. 81g) has prominent eye ridges, but no trace of these is present in the adult.

Fringe narrow with narrow, upturned margin and rather narrow marginal girder. Number of radii in range 18–21. I_n and I_1 complete in very shallow radial sulci (accentuated by certain directions of distortion). I_2 commonly present in anterior radii, typically between 2 and 6. Occasionally I_2 seen in posterior radii (e.g. Fig. 81a). I_3 rarely present in radii 2–4.

Thorax of typical trinucleine structure; pygidium similar to that of *Bergamia*, with broad margin which widens towards the sagittal line. Axis impinges onto margin, and contains 4–5 axial rings.

Remarks. *Gymnostomix gibbsii* is readily recognized and distinguished from other trinucleids by the presence of the distinctive genal ridges, which make it distinctive in the field and a valuable guide fossil for Whitlandian strata. Whittard (1955: 34) claimed that the ridges 'were probably caused by the compression of the lateral cheek-lobes over their leading edges' and stated that they were not present on all specimens, quoting GSM 49673 as substantiating this. We have examined this specimen, which is a slab containing in the region of thirty cranidia, nearly all of which clearly show the ridges. One specimen near the centre appears not to have them, but this is preserved in such a way that the anterior parts of the cheek lobes are compressed under the posterior parts. This would seem to be the only specimen upon which Whittard could have based his contention. We have found *G. gibbsii* in several different lithologies and kinds of preservation, and all specimens have the genal ridges. Moreover, no specimens of another trinucleid, *Furcalithus sedgwicki*, which occurs in association with *G. gibbsii* at the type locality, have any suggestion of such ridges, which might be expected if they were a preservational feature. We are thus in no doubt that the ridges are original. *Bergamia*? sp. of Bates (1968*a*: 184; pl. 13, figs 3, 4, 9, 13) from the '*bifidus*' Beds of Anglesey also has crests on the genal lobes, but they are more rounded than in *G. gibbsii*, meet the glabella further back and do not cross the axial furrow. Because of preservation, Bates was unable to detect the position of the girder. It is possible that this material represents a second *Gymnostomix* species, although on balance an assignment to *Bergamia* seems more appropriate.

Family **DIONIDIDAE** Gürich 1907

Šnajdr (1981) proposed two dionidid genera, *Dionidepyga* (type species *Dionide jubata* Raymond 1925) and *Dionideina* (type species *Dionide prima* Klouček 1916) which are of Llanvirn–Llandeilo and Llanvirn age respectively. Whilst he pointed out the difference one from the other, he compared neither with *Dionide*. Many of the characters listed for each genus (e.g. details of lateral glabellar furrows, presence of external girder) are common to both, and to *Dionide*, and cannot therefore be regarded as diagnostic. For *Dionidepyga* Šnajdr noted that the pits on the fringe were not differentiated as to size; however, one of the cranidia figured by him (1981: pl. 4, fig. 3) shows clearly large pits just inside the border, very similar to those seen, for example, in the type species of *Dionide*, *D. formosa* (Whittington 1952: pl. 1, figs 1–3) from the mid-Caradoc of Bohemia and in *D. magnifica* (Owen & Bruton 1980: pl. 6, figs 1, 3, 6, 7) from the late Caradoc of the Oslo district. Šnajdr's (1981: 281) statement that a median glabellar spine is present in *D. jubata* cannot be substantiated: all figured specimens have only a small median node. We can see no justification for retaining *Dionidepyga* as a separate genus, and here regard it as a junior subjective synonym of *Dionide*. Whilst many characters of *Dionideina* are similar to *Dionide*, it differs in having alar lobes, a broad band of large pits inside the cephalic border and a reduced number of pygidial axial rings (*c*. 10) and pleural ribs (8–9). This combination of characters suggests that *Dionideina* should probably be regarded as being distinct from *Dionide*. In possessing alar lobes it is similar to *Dionidella* Prantl & Přibyl 1949*a*, but differs from it in lacking well-defined 2p glabellar furrows, in having large pits close to the cephalic border and a contrasting structure of the pygidial pleural ribs (see Šnajdr 1981: pl. 1, fig. 1).

A further dionidid, *Dionide* (*Paradionide*) Chang & Fan 1960, type species *D*. (*P*.) *anmenensis* from the Lower Llanvirn of west Kansu, China, is distinctive in having a small, circular glabella, nine thoracic segments of similar length (sag., exsag.) and a very narrow axis. We agree with Owen & Bruton (1980: 21) in considering *Paradionide* a separate genus.

Four dionidids are present in the Arenig–early Llanvirn of south Wales. The two later species can be assigned to *Dionide*, but the two earlier ones are more difficult to assign, and are placed with question in *Dionidella* (see p. 221). It is possible that these species belong to an independent genus, but the material is insufficient for its discrimination.

Genus ***DIONIDE*** Barrande 1847

[= *Polytomurus* Hawle & Corda 1847, *Trigyrops* Kobayashi 1940, *Dionidepyga* Šnajdr 1981.]

TYPE SPECIES. *Dione formosa* Barrande 1846, from the Zahořany Formation (mid Caradoc) of Bohemia; by original designation.

Dionide turnbulli Whittington 1952

(Figs 82a, b)

1958 *Dionide turnbulli* Whittington; Whittard: 96; pl. 13, figs 1–8 (with earlier synonymy).

HOLOTYPE. SM A16715a, b; cephalon.

TYPE LOCALITY AND HORIZON. Llanvirn, *artus* Biozone, Llanfallteg Formation; Long Plantation Cutting, Scolton (loc. 55).

STRATIGRAPHICAL RANGE. Llanvirn, *artus* Biozone.

DIAGNOSIS. Genal lobes smooth and connected by a smooth 'preglabellar field' in front of glabella; strong genal caecum; fringe crossed by anostomosing ridges; single row of larger pits immediately inside cephalic border. Pygidium with *c*. 18 axial rings, pleural areas with *c*. 12 ribs with deep interpleural furrows.

OCCURRENCE. Outside the type locality recorded from Hope Shale and Stapeley Volcanic formations, Shelve inlier (see Whittard 1958: 98).

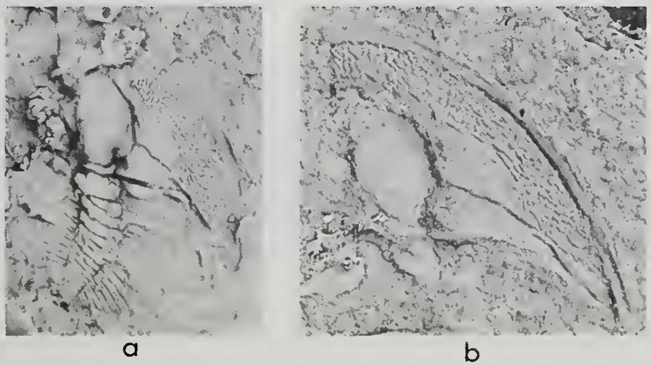


Fig. 82 *Dionide turnbulli* Whittington 1952. Lower Llanvirn, *D. artus* Biozone, Llanfallteg Formation. a, latex cast of incomplete axial shield, old quarry north of Clarbeston, × 4, It.18973; b, incomplete topotype cranidium, loc. 55, Scolton, × 9, It.18974.

REMARKS. This species has been adequately described by Whittington (1952: 8), with supplementary remarks by Whittard (1958: 96). Extra topotypic specimens are figured here for comparison with *D. levigena* sp. nov., described below.

Dionide levigena sp. nov.
(Figs 83a–e, 84)

HOLOTYPE. Complete specimen with anterior part of thorax telescoped beneath cephalon, NMW 85.26G.1.

TYPE LOCALITY AND HORIZON. Lower Llanvirn, *D. artus* Biozone, Llanfallteg Formation; Cefn-maen-llŵyd, loc. 50.

PARATYPES. Complete specimen with damaged cephalon, BGS TCC454, stream 320 m NW of Gelli, near Llangynog (Geol. Survey loc. Carm. 45NE Wλ4); partially complete dorsal exoskeletons (It.19006–7, NMW 84.17G.134, 136, 138), cephalon (NMW 84.17G.139), cranidia (It.19005, It.19008–9, NMW 84.17G.18, 19, 135), and lower lamella (NMW 84.17G.137) from *D. levigena* Biozone, Llanfallteg Formation, Llanfallteg, locs 52E, P–T, W.

DIAGNOSIS. Cephalon with narrow, well-defined border; genal lobes smooth, not connected by smooth preglabellar field in front of glabella; fringe with numerous small, equal-sized pits, no anastomosing ridges; pygidium transverse, with nine axial rings and eight unfurrowed pygidial pleural ribs.

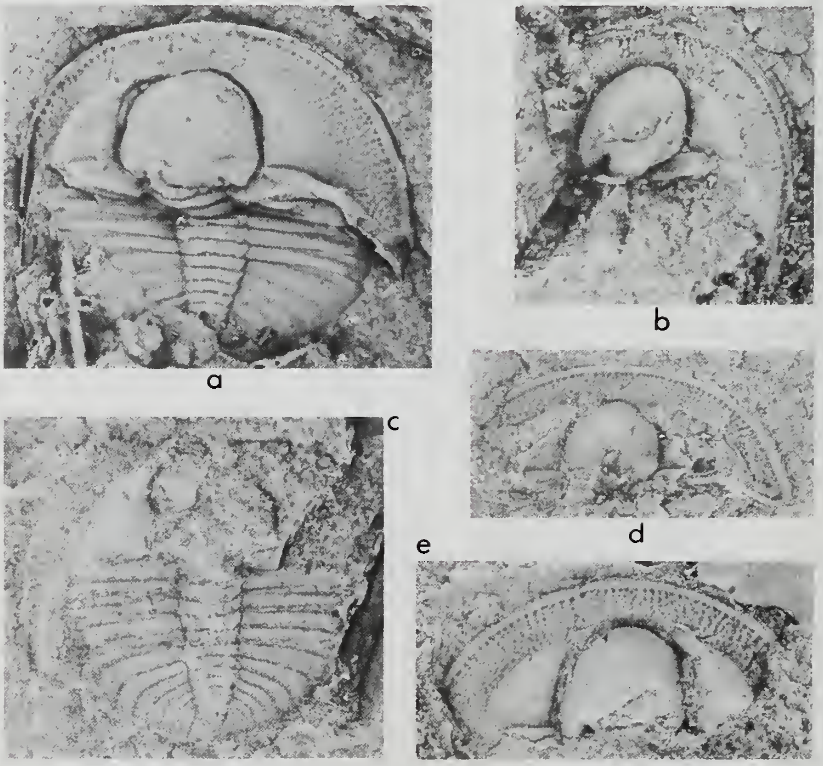


Fig. 83 *Dionide levigena* sp. nov. Llanfallteg Formation: a, c, Lower Llanvirn, *D. artus* Biozone; b, d, e, Upper Arenig, Fennian Stage, *D. levigena* Biozone. a, **holotype**, complete specimen with anterior part of thorax telescoped beneath cephalon, latex cast from external mould, Cefn-maen-llŵyd, loc. 50, × 6, NMW 85.26G.1; b, incomplete cephalon, loc. 52E, Llanfallteg, × 7, It.19005; c, complete specimen, cephalon damaged but showing pygidium well, stream 320 m NW of Gelli, near Llangynog (Geological Survey loc. Carm. 45NE Wλ4), × 6, BGS TCC454; d, incomplete cranidium showing median node on glabella, loc. 52W, Llanfallteg, × 10·5, It.19008; e, incomplete cranidium showing detail of pitted fringe, latex cast from external mould, loc. 52T, Llanfallteg, × 7, It.19009.

NAME. Latin: *levis*, 'smooth' and *gena*, 'cheek'; reference to the smooth genal lobes.

DESCRIPTION. Cephalon with narrow, well-defined border. Glabella plus occipital ring occupies about three-quarters cephalic length. Small median glabellar node present, no lateral furrows but short, deep basal furrows present. Occipital ring narrow (sag., exsag.), extending transversely as far as outer margin of basal glabellar furrow. Pleuroccipital furrow narrow but distinct, defining broad posterior cephalic border. Inner part of cheek smooth, weakly inflated. Fringe with numerous, small equal-sized pits which extend as far as frontal lobe of glabella. Anastomosing ridges absent. Genal angle prolonged into broad-based spine of unknown length.

Thorax presumed to be of six segments, as in other *Dionide* species, but in the holotype (Fig. 83a) it is telescoped beneath the cephalon, and only parts of five segments can be seen. The other complete specimen (Fig. 83c) has only four, so this is probably a large meraspid. Axis narrow (tr.), the axial furrows forming a zetoidal pattern, so that each ring is distinctly wider (tr.) anteriorly than posteriorly. Pleurae very broad, bluntly truncated distally and with shallow, narrow pleural furrows that extend for most of their length, adaxially lying close to the anterior margin of the pleura, abaxially about half-way along (exsag.).

Pygidium subparabolic, slender axis with nine narrow well-defined rings. Pleural areas with eight pairs of ribs with rather narrow, shallow pleural furrows that curve gently backwards adaxially; distally, all except the first turn more strongly posteriorly. No interpleural furrows.

REMARKS. This species is distinct from most other *Dionide* species in having smooth genal lobes and a rather short, transverse pygidium with comparatively small numbers of axial rings and pleural ribs without interpleural furrows. These characters invite comparison with the dionidid *Trinucleoides*, although the latter has a rather different glabella with a deep, pit-like 2P furrow and a prominent spine on the frontal lobe. The sum of characters of *D. levigena* is closer to *Dionide* than to *Trinucleoides*, so we prefer to classify it with the former, at least until further material becomes available.

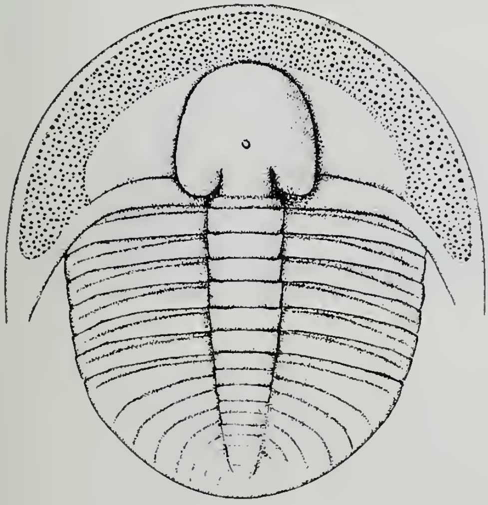


Fig. 84 Reconstruction of *Dionide levigena* sp. nov., × 6 approx.

Genus *DIONIDELLA* Prantl & Přibyl 1949*a*

TYPE SPECIES. *Dionidella incisa* Prantl & Přibyl 1949*a*; Llanvirn, Šárka Formation, Šárka, Prague; by original designation.

DIAGNOSIS. Cephalic anterior and lateral border furrows ill-defined, with cheeks and anterior and lateral cephalic borders pitted, except for small, smooth alar lobes; glabella with deep 1P furrows and small, pit-like 2P; thorax relatively longer and narrower than *Dionide*; pygidium with 11 axial rings and 10 pairs of pleural ribs, with posterior pleural bands terminating well short of the margin and the anterior pleural bands abaxially tapering to a point, extending close to margin.

REMARKS. Whittard (1958: 95) contended that acceptance of *Dionidella* as a distinct genus depended upon the 'unique arrangement of the glabellar furrows and on the preglabellar field'. The preglabellar field does not seem to us to be a significant feature, but the glabellar morphology and the disposal of the pygidial pleural ribs, together with the combination of characters listed above, can be regarded as diagnostic. Rare dionidids from the Pontyfenni Formation have cephala whose morphology approaches that of *D. incisa* more closely than any *Dionide* species, although they lack the deep, pit-like 2P. Because of this latter circumstance, we assign these specimens to *Dionidella* with question.

***Dionidella*?** sp. indet. 1

(Figs 85a, b)

1914 *Dionide* sp.; Thomas, *in* Strahan *et al.*: 19.

MATERIAL. Cranidium, BGS Pr1735–6 (counterparts).

HORIZON AND LOCALITY. Fennian, *S. abyfrons* Biozone, Pontyfenni Formation; Pen-y-parc, loc. 38.

DESCRIPTION. Cephalon sub-semicircular, without well-defined border, which is represented by only a slight change in slope. Glabella 0·6 of length (sag.) of cephalon, with small basal lobes, but these are not well seen on the specimen. Occipital ring much narrower (tr.) than glabella. Small, smooth triangular alar lobes extend forwards almost as far as basal glabellar lobes, their forward edges defined by low ridges. Anastomosing ridges with interspersed puncta radiate from glabella and extend up to cephalic margin. Posterior cephalic border broad and flat, narrowing slightly laterally, where the narrow posterior border furrow is deflected weakly backwards. It dies out before reaching the lateral margin, at position of lateral border furrow.

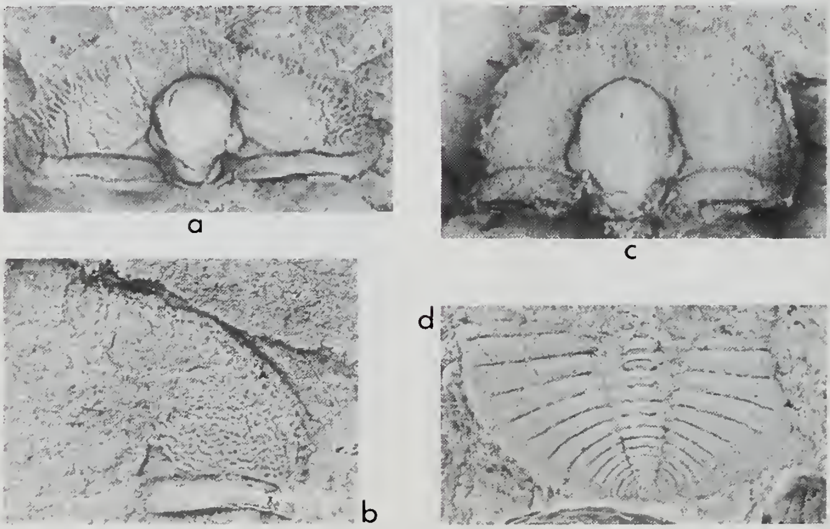


Fig. 85 a, b, *Dionidella*? sp. indet. 1. Upper Arenig, Fennian Stage, *S. abyfrons* Biozone, Pontyfenni Formation, loc. 38, Peny-y-parc. a, cranidium, × 11, BGS Pr1735; b, incomplete cranidium showing fine pits and anastomosing ridges, × 8, It.18977. c, d, *Dionidella*? sp. indet. 2. Upper Arenig, Fennian Stage, *B. rushtoni* Biozone. c, cranidium, loc. 23, Pontyfenni, × 6, It.18978; d, pygidium, latex cast from external mould, loc. 24, Llwyn-crwn, × 6, It.18979.

REMARKS. Apart from lacking 2P furrows, this cranidium differs from those of *D. incisa* in being proportionally shorter and wider, and in having prominent anastomosing ridges. So far as we are aware, this is the earliest recorded dionidid.

***Dionidella*? sp. indet. 2**
(Figs 85c, d)

MATERIAL. Cranidia: It.18978 from Pontyfenni, loc. 23 and NMW 84.17G.165a, b from Blaen-lliwe, loc. 42. Pygidium: It.18979 from Llwyn-crwn, loc. 24. All from Fennian, *B. rushtoni* Biozone, Pontyfenni Formation.

DESCRIPTION. Cranidium with semicircular outline, anterior and lateral borders defined only by a change in slope. Glabella 0·6 of length of cephalon (sag.), with basal lobes defined by shallow furrows. No alar lobes, and entire cheeks and preglabellar area covered by anastomosing ridges with interspersed puncta; these are weaker than in *D.*? sp. indet. 1. Pleuroccipital furrows markedly arched forwards, defining broad, smooth posterior cephalic border.

Pygidium of subparabolic outline with narrow axis extending for most of pygidial length and comprising 14 rings. Pleural areas with 14 pairs of ribs which do not extend to margin. Interpleural furrows only apparent in their short, distal abaxial parts. Marginal area of pygidium smooth.

REMARKS. We assume that the above material belongs to one species, since all occurrences are at approximately the same horizon. The principal difference from *D.*? sp. indet. 1 is in the cephalic outline (which may be in part the result of tectonic influences), the lack of alar lobes and weaker anastomosing ridges. The pygidium differs from that of *D. incisa* in having more axial rings and pleural ribs, and in not having the anterior pleural bands extending on to the pygidial border region.

Family **RAPHIOPHORIDAE** Angelin 1854

Genus *AMPYX* Dalman 1827

TYPE SPECIES. *Ampyx nasutus* Dalman 1827; see Whittington, 1950.

Ampyx linleyoides sp. nov.
(Figs 86a–e, 87d, 88a)

1906 *Ampyx* cf. *salteri*; Evans: 612.

HOLOTYPE. Exoskeleton lacking free cheeks, It.15946.

TYPE LOCALITY AND HORIZON. Pontyfenni Formation, loc. 23; Upper Arenig, Fennian, *B. rushtoni* Biozone.

STRATIGRAPHICAL RANGE. Upper Arenig, Fennian, *B. rushtoni* Biozone, also at loc. 53.

FIGURED PARATYPES. Axial shields: It.19694, NMW 84.17G.81–2; cranidium: It.19693; pygidium: NMW 84.17G.83.

OTHER PARATYPE MATERIAL. Axial shields: It.18579, NMW 33.189.G102; thorax and pygidium: It.19696; thorax: It.18553; pygidia: It.18559, NMW 84.17G.84.

DIAGNOSIS. *Ampyx* with stout, long frontal spine with T-shaped cross section. Pygidium with axial rings poorly defined; border not clearly marked from pleural fields; raised lines on posterior border curving up onto periphery of pleural fields. Punctate surface sculpture.

NAME. Distinct from *linleyensis*.

DISCUSSION. This species is extremely like *A. linleyensis* Whittard 1955, which he exhaustively described. Whittard described 'long' and 'wide' morphs of *linleyensis*; no taxonomic importance is attached to this, and the 'long' forms (such as in Fig. 86a) may include those which have undergone a small amount of tectonic extension. The holotype of *linleyoides* is undistorted.

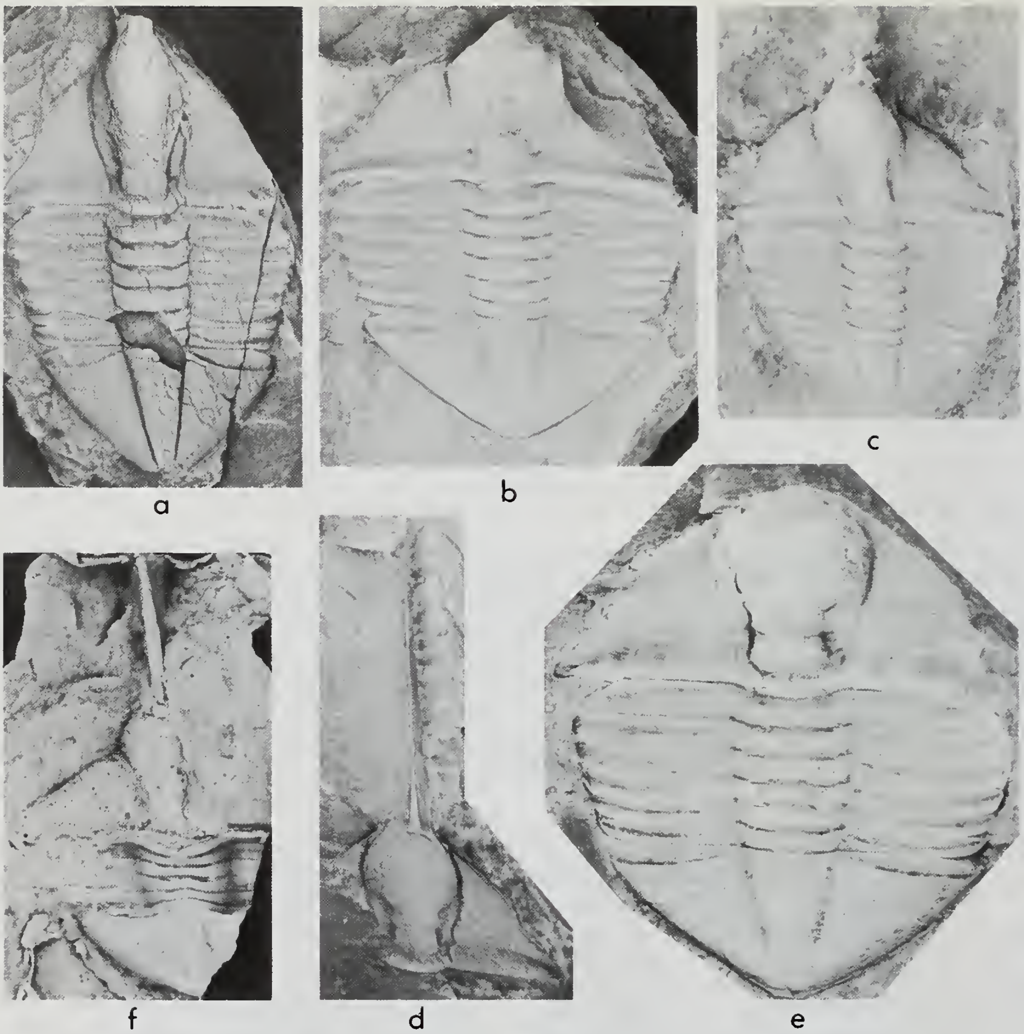


Fig. 86 a–e, *Ampyx linleyoides* sp. nov. Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23. a, axial shield slightly extended by distortion, × 2, NMW 84.17G.81; b, **holotype**, incomplete axial shield, × 3, It.15946; c, small axial shield, × 6, NMW 84.17G.82; d, cranidium preserving frontal spine showing carinate form, × 2·5, It.19693; e, axial shield, × 4, It.19694. f, *Ampyx* aff. *linleyoides*, same horizon and locality, cast from incomplete axial shield, × 4, It.19697.

This specimen, and others as well preserved, show fine-scale dorsal punctation, faint on the pygidium, which is not recorded on *linleyensis*, but Rushton & Hughes (1981) record this kind of sculpture on *A.* cf. *linleyensis* from the Great Paxton Borehole. The frontal spine is long on *A. linleyoides* and in flattened condition has a characteristic carinate appearance. Examination of *A. linleyensis* shows that the spine on this species had the shape in cross-section of an inverted T, and that the consequent dorsal carina can, on some specimens (Whittard 1955: pl. 2, fig. 1), continue onto the front of the glabella. The specimen shown in Fig. 86d shows that the same spine shape was likely in *A. linleyoides.* One small specimen in relief (Fig. 86f) shows a frontal spine which is square in cross section; this specimen apparently also has wider fixed cheeks than *linleyoides*, and we are cautious about referring it to the same species; it is recorded as *A.* aff. *linleyoides.*

The specific characters which permit recognition of *linleyoides* are on the pygidium. The pygidial border on *linleyensis* is extremely short and vertical, and clearly defined by an abrupt change in slope at the edge of the pleural fields. In *A. linleyoides* the border is not so defined, is wider, and carries some 8–10 raised lines which extend onto the lateral parts of the pleural fields. Flattening serves to exaggerate the differences; on *A. linleyensis* the border crushes down and the margin of the pleural fields may become a little elevated as a rim, while on *A. linleyoides* the border opens backwards to display the raised lines on the border clearly. We have examined more than thirty specimens of *linleyensis*, and of these only three show the raised lines extending onto the pygidial pleural fields. Other specific differences may be affected by preservation. The pygidial axis of *linleyensis* is more convex (tr.) posteriorly, standing well above the pleural fields; the tip of the pygidial axis on *linleyoides* is low and often effaced to such a degree that it is difficult to distinguish from the border. The expression of this difference obviously depends on the degree of flattening. The axis on *linleyensis* is narrower: its width at the anterior ring is half its length or even less, on undistorted material; on *linleyoides* we have width/length ratios between 0·6 and 0·7 in undistorted material, but measurement of axial length is difficult because of the posterior effacement. Most well-preserved pygidia of *linleyensis* have a distinctly concave-sided axis (Whittard 1955: pl. 2, figs 1–3); *linleyoides* has a straight-sided pygidial axis, even when it is distorted (Fig. 87d). On almost all specimens of *linleyensis* from the Stapeley Volcanics in Shropshire the axial rings on the pygidium are clearly-defined across the mid-part of the axis (the furrows are often kinked backwards medially). Six rings are clearly visible and up to fifteen have been observed. Definition of axial rings on *linleyoides* is poor; only two or three are clearly defined, the remainder up to a maximum of ten being very indistinct. This may have some connection with preservation in the dark mudstones of the Pontyfenni Formation, because *linleyensis* preserved in a similar lithology also appear to have less clearly defined axial rings (Fig. 87b), and we attach less importance to this than a comparison of the types alone would suggest. A crushed *linleyoides* pygidium on which the ring furrows are deepened is shown on Fig. 87d. Probably more useful is the greater backward curvature of the anterior pygidial pleural furrows on *linleyensis*. The transverse line connecting the most posterior parts of these furrows cuts the third or fourth axial ring on *linleyensis*, but on *linleyoides* it cuts the second ring or the furrow behind it. The pygidial differences have been discussed at length because they are rather subtle. The specimen of *linleyensis* most like *linleyoides* which we have been able to find is figured in Fig. 87c; although the axial ring development is like the Arenig form it can still be distinguished on the structure of the border and the pleural furrows. The two species are, however, very closely related.

A. linleyoides belongs to *Ampyx*, *sensu stricto*, as defined by Fortey (1975). Whittard (1955) distinguished *linleyensis* from other British species, and the same distinctions apply to *linleyoides*. As noted above, the species referred by Whittard (1955) to *Ampyx salteri* Hicks, from the Mytton Flags, is certainly not that species, which we here assign to *Cnemidopyge*. Whittard's *salteri* (Fig. 87a) is another *Ampyx*, but not the same as either *linleyensis* or *linleyoides*. Its pygidium is relatively small, less transverse, and without backward-concave pleural furrows; the frontal spine on the cranidium is short, and with a circular cross section. Several other *Ampyx* species require discrimination from *linleyoides*. The type species, *A. nasutus* (Whittington 1950: pl. 74, figs 3–9) is generally very similar in proportions; but it has a tubular frontal spine, more obviously concave facial sutures, and an emarginate pygidial border. Because of their bowed pygidial pleural furrows *A. nasutus*, *linleyensis* and *linleyoides* should be included within any restricted concept of *Ampyx*. Of the numerous raphiophorids from the Arenig of Spitsbergen only one, *A. spongiosus* Fortey 1975, resembles *A. linleyoides* in overall proportions and surface sculpture. *A. spongiosus* has a rather slender frontal spine with a circular cross section, and the anterior pleural furrows on the pygidium (Fortey 1975: pl. 22, fig. 9) are not curved as they are on *linleyoides*, *linleyensis* and *nasutus*. Fortey (1975) noted the resemblance between *A. spongiosus* and *A. volborthi* Schmidt (*sensu* Skjeseth, 1952), which has a pygidial pleural structure like that of *spongiosus*, but with a rather sharply downturned border like *linleyensis*. *Ampyx abnormis* Yi, 1957 (see Lu 1975: pl. 39, figs 5–11; pl. 40, figs 1–7) apparently ranges from the late Arenig to Llandeilo in China. Lu notes that the pygidial

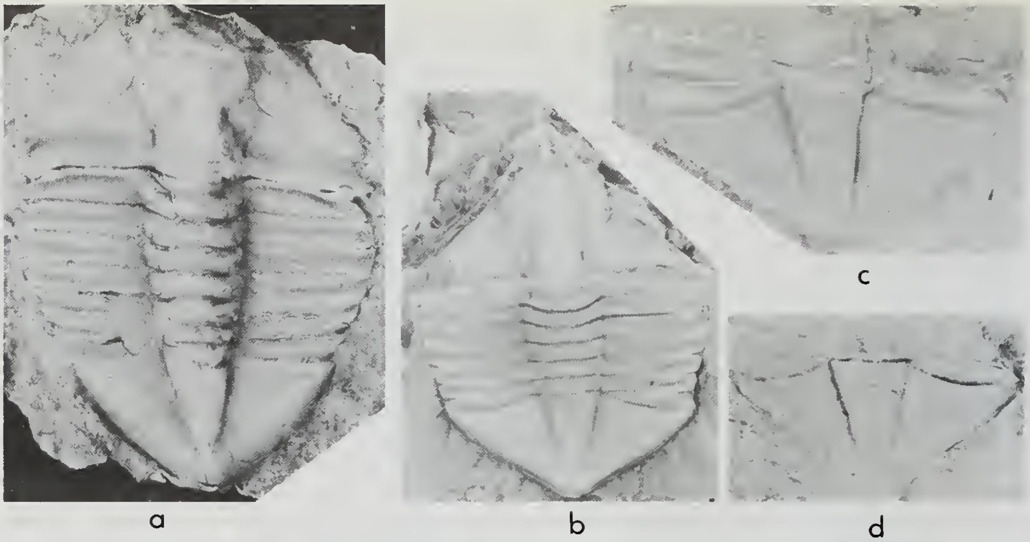


Fig. 87 a, *Ampyx* cf. *reyesi* Benedetto & Malanca 1975 (Whittard's *A.* '*salteri*'). Cast from external mould of axial shield for comparison with *A. linleyoides* sp. nov., 'Lowermost Mytton Flags, head of Mytton Batch', Shropshire, × 3, GSM 92940 (counterpart of Whittard, 1955: pl. 1, fig. 19). b, c, *Ampyx linleyensis* Whittard. b, axial shield preserved in mudstone for comparison with *A. linleyoides* in similar preservation, early Llanvirn, 300 m east by south of Wernddu, $\frac{1}{2}$ mile west of Llanllwch, Dyfed, × 4, GSM HT354; c, latest Arenig, Fennian, *D. levigena* Biozone, Llanfallteg Formation, loc. 52Q, × 3, It.19698. d, *Ampyx linleyoides* sp. nov. Flattened pygidium with overdeepened furrows, for comparison with *A. linleyensis*, Fennian (*B. rushtoni* Biozone), Pontyfenni Formation, loc. 23, × 4, NMW 84.17G.83.

structure is like that of *A. spongiosus* rather than *A. nasutus* (and *A. linleyoides*). Of the specimens from the Arenig horizon illustrated by Lu that on his pl. 39, figs 10, 11 has a slender, unfluted frontal spine, and other cranidia show a preglabellar field, and apparently do not have incised glabellar furrows. Another Arenig form from China, *A. yii* Lu, would now be referred to *Rhombampyx* Fortey, 1975.

Several South American species have also been described. One of these, *A. reyesi* Benedetto & Malanca 1975, from the 'upper Arenig or Lower Llanvirn' of Jujuy Province, Argentina, is similar to *A. linleyoides* in most respects, but like other species mentioned above the pygidial pleural furrows are nearly straight, and the frontal spine is described as having a circular cross section. Přibyl & Vaněk (1980) described *A. pallens* from the Llanvirn of Bolivia, but without reference to *reyesi*, which it so strongly resembles that it may well prove its junior synonym. In any case *A. reyesi*/*pallens* provides by far the closest comparison with Whittard's *Ampyx* ('*salteri*') from the Mytton Flags. Compare, for example, the pygidium of Fig. 87a with Přibyl & Vaněk, 1980: pl. 19, fig. 1. For this reason we have designated the Shropshire species *Ampyx* cf. *reyesi* (Fig. 90). Similarity of raphiophorids between Britain and South America is given further support by the resemblance between the *Ampyx*? sp. figured by Harrington & Leanza (1957: fig. 116.4) from Argentina and *A. linleyensis*.

Ampyx linleyensis Whittard 1955
(Figs 87b, c, 88c)

(For synonymy see Whittard 1955: 18).

HOLOTYPE. Axial shield, GSM 92943.

TYPE LOCALITY AND HORIZON. Stapeley Volcanic Group, Tasgar Quarry, Shelve district, Shropshire; Llanvirn, *D.* '*bifidus*' Zone.

OCCURRENCE IN SOUTH WALES. Llanfallteg Formation, type section at Llanfallteg Railway cutting from 20 m below Arenig–Llanvirn boundary to highest beds in Llanvirn exposed; and at Rhyd-y-wrâch farm and Scolton railway cutting. The species extends into the overlying black Llanvirn shales. Latest Arenig (*Dionide levigena* Biozone) to early Llanvirn.

FIGURED MATERIAL. It.19698, GSM HT354.

ADDITIONAL MATERIAL. NMW 33.189.G134, 33.189.G18, It.19699.

DISCUSSION. This species has been fully discussed under *A. linleyoides* sp. nov. above (pp. 224–5), which it resembles closely. Specimens from the Llanfallteg Formation have the characters of *linleyensis* whether they are above or below the Arenig/Llanvirn boundary. Rushton & Hughes (1981) have described *A.* cf. *linleyensis* from the Great Paxton borehole. These specimens are more like *linleyensis* than like *linleyoides*, and they could well be accommodated within the range of variation of the former. We have mentioned above the possible occurrence of *linleyensis* in Argentina.

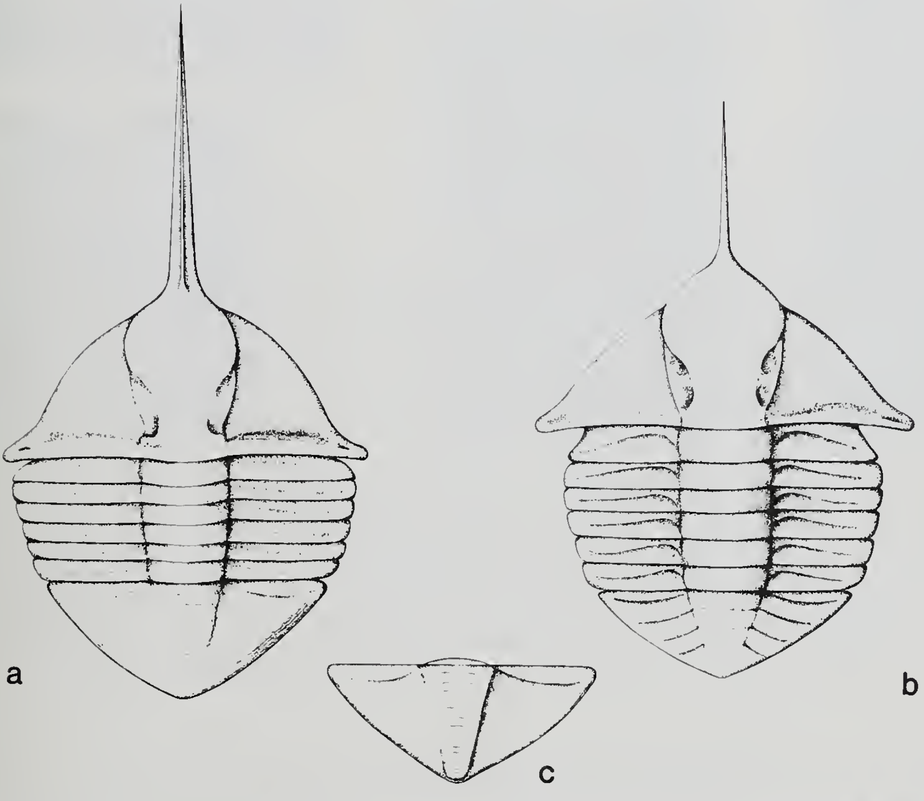


Fig. 88 Comparative reconstructions of axial shields of British Arenig raphiophorid species. a, *Ampyx linleyoides* sp. nov., Fennian, *B. rushtoni* Biozone; b, *Cnemidopyge salteri* Hicks, Whitlandian, *G. gibbsii* Biozone; c, pygidium of *A. linleyensis* Whittard, latest Fennian and early Llanvirn. All × 3 approx. See also Fig. 90.

Genus *CNEMIDOPYGE* Whittard 1955

TYPE SPECIES. *Trinucleus nudus* Murchison 1839, by original designation.

DIAGNOSIS. The diagnosis of Hughes (1969) is followed here, except that we admit species with the pygidium smaller than the cephalon.

Cnemidopyge salteri (Salter 1873)
(Figs 88b, 89a–c)

1873 *Ampyx Salteri* Hicks MS; Salter: 22.
1875 *Ampyx salteri* Hicks: 182; pl. X, figs 7, 8.
non 1884 *Ampyx salteri*; La Touche: 56; pl. 2, fig. 34.
non 1940 *Ampyx salteri* Hicks; Whittard: 161; pl. 5, fig. 8.
pars 1955 *Ampyx salteri* Hicks; Whittard: 15–18; pl. 1, fig. 15, *non* figs 16–21.
non 1966 *Ampyx* aff. *salteri* Hicks; Whittington: pl. 2, figs 1–3, 6.
1969 *Ampyx salteri* Hicks; Hughes: 63 (compared with *Cnemidopyge*).
pars 1978 *Ampyx salteri* Hicks; Fortey & Owens: 255; *non* fig. 8a.

LECTOTYPE (herein selected). Exoskeleton lacking free cheeks, original of Hicks, 1875: pl. 10, fig. 8; BM(NH) I352.

TYPE LOCALITY AND HORIZON. 'Middle' Arenig of Hicks (1875), Penmaen Dewi Formation, the old quarry in Pwlluog. It is associated here with *Bohemopyge scutatrix*, *Shumardia* (*Shumardia*) *gadwensis*, *Gymnostomix gibbsii* etc. Whitlandian (biozone of *Gymnostomix gibbsii*).

OTHER LOCALITIES. South of Dwyrhos Farm, Aberdaron, Llŷn Peninsula; Whitlandian mudstones.

FIGURED MATERIAL. Dorsal exoskeletons lacking free cheeks: I14278, In.48526.

ADDITIONAL MATERIAL. I730, I14279, SM A15592.

DIAGNOSIS. *Cnemidopyge* with relatively small and transverse pygidium having only three pairs of strong pleural furrows.

DESCRIPTION. Available material of this species is all imperfect—flattened from the type locality, or somewhat distorted from north Wales. Partly because of this it has been much confused with other raphiophorids, such as *Ampyx cetsarum*. Axial shields show that the thorax is about as long (sag.) as the glabella, and both are longer than the pygidium. The length of the latter is exaggerated in flattened material because the borders are opened out in this preservation; less distorted material (Fig. 89b) indicates that the pygidial borders were declined nearly vertically.

Cranidium with maximum width at posterior margin, this more than twice sag. length (excluding spine). Glabella is crushed on our material; it expands forwards rather more rapidly than is the case in many *Ampyx* species, for example to a maximum at about its mid-length, this being 0·8 of its sag. length. Although muscle insertions areas are obscured by crushing the larger specimens show clear evidence of two pairs of impressions within the glabella, which isolate a lateral glabella lobe, and which are consistent with the crushing of a cranidium of the kind illustrated by Hughes (1969: pl. 2, fig. 11). Frontal spine with circular cross section, slender, length not exceeding that of glabella. Occipital ring and border both well defined, border furrow a little convex-forwards. So far as can be judged the facial suture was also convex-forwards over much of its length, except where kinked backwards near genal angle. Free cheeks not known.

Thorax with six segments, maximum transverse width at back end of second, first segment slightly macropleural (exsag.). Thorax tapers backwards, as it does in small, but not in large, holaspides of *C. nuda*; axis hardly tapers. The notable thoracic feature is the strong, forward arching on the pleural furrows of the early segments, particularly the first; it is progressively less marked on the second to fourth segments. Hughes (1969) figures triangular extensions of the axial rings towards the crests of the arched furrows, and some indication of the same feature in a crushed condition is shown by Fig. 89b.

Pygidium transverse; as preserved flattened, its width is more than twice length, but with the borders turned downwards in original orientation it may have been three times as wide as long. Axis tapers gently to border (furrows enclose angle of about 30°); the back end of the axis is apparently not defined. Only three or four narrow (sag.) axial rings are defined. There are three pairs of deep pleural furrows, which slope gently backwards. Border wide, not medially emarginate. Apart from raised lines on pygidial border, surface sculpture is not preserved.

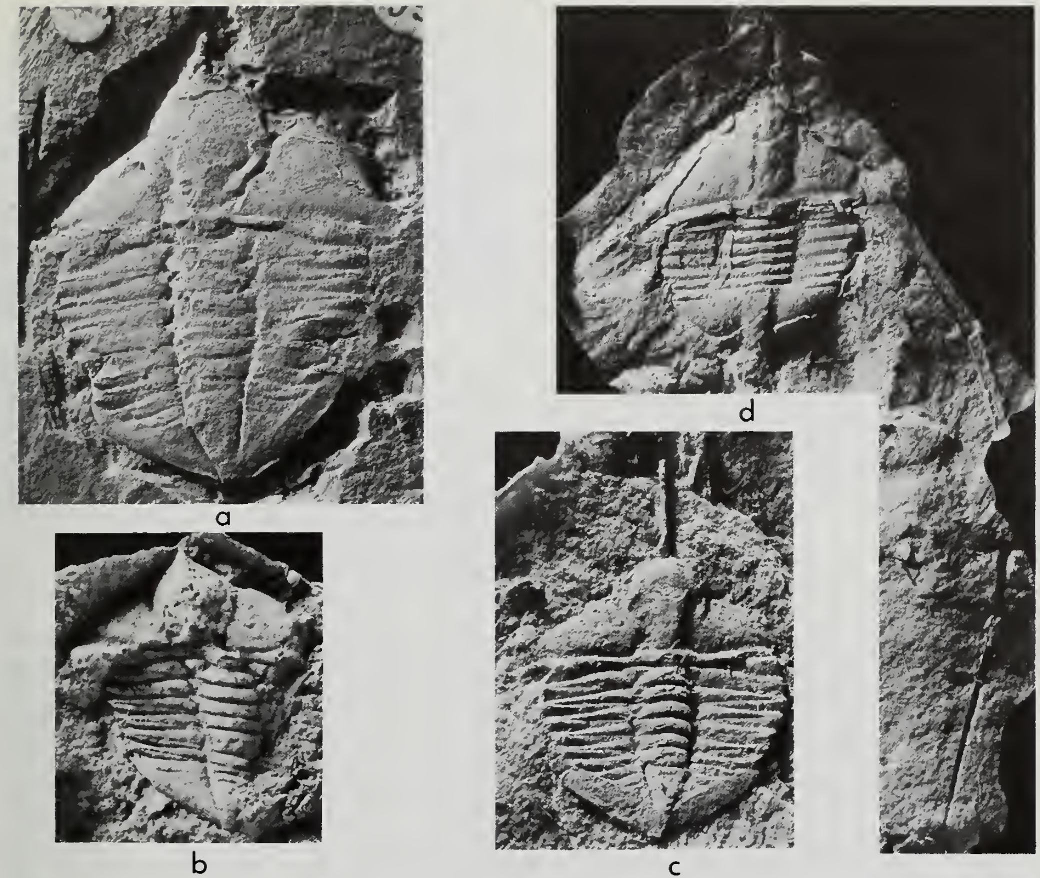


Fig. 89 a–c, *Cnemidopyge salteri* (Salter 1873). Middle Arenig, Whitlandian, *G. gibbsii* Biozone. a, **lectotype**, flattened axial shield, Penmaen Dewi Formation, old state quarry, Pwlluog, north of Whitesand Bay, St David's, Dyfed, × 2, I352 (original of Hicks, 1875: pl. 10, fig. 8); b, cast from slightly distorted axial shield but preserving natural convexity, Whitlandian mudstones on track below Dwyrhos Farm, Aberdaron, Llŷn Peninsula, north Wales, × 3, I14278; c, cast from axial shield, somewhat flattened but otherwise undistorted, horizon and locality as lectotype, × 3, In.48526. d, *Ampyx cetsarum* Fortey & Owens 1978, latex cast from entire specimen, Moridunian, lower part of *M. selwynii* Biozone, Ogof Hên Formation, Bolahaul Member, Llangynog, × 2, It.19700; this form has been confused with *Cnemidopyge salteri* in the past, but note distinctive pygidial structure.

Discussion. Hughes (1969) suggested that *Ampyx salteri* Hicks might be an early representative of the genus *Cnemidopyge.* Hughes cited the well-furrowed pygidium as evidence for this assignment; the strong forward arching on the anterior thoracic pleural furrows and the structure of the glabella are also consistent with the type species, *C. nuda.* Hughes revised the British species of *Cnemidopyge*, which are from the Llanvirn or later; all of them have larger pygidia with at least twice as many pleural furrows as in *C. salteri.* It was to be anticipated that the earlier species of the genus would have a smaller pygidium like those of other raphiophorids and we see no reason to exclude *salteri* from *Cnemidopyge* on the basis of this character alone.

Raphiophorids from the early Arenig (Moridunian) in Wales which have been compared with *C. salteri* are all referable to *Ampyx cetsarum* Fortey & Owens 1978. There is now no possibility of confusing the two: *A. cetsarum* has a gently-forward expanding glabella, a charac-

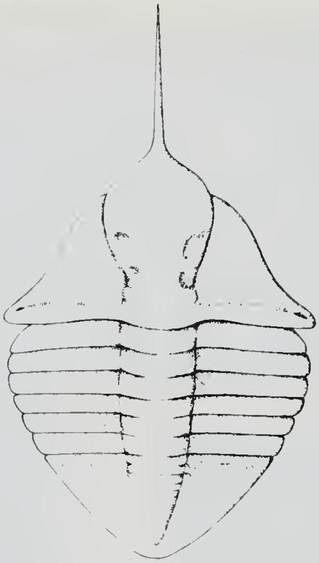


Fig. 90 Reconstruction of axial shield of *Ampyx* cf. *reyesi* Benedetto & Malanca 1975. Moridunian, Shelve Inlier, Shropshire. × 3 approx.

teristic occipital structure, and almost all furrows are suppressed on the pygidium. Our original material of this species was imperfect. Here (Fig. 89a) we illustrate a well-preserved, complete specimen, which was collected after our original work.

Whittard (1955) identified *C. salteri* from the Shelve Inlier, from specimens in the Mytton Flags. Fig. 87a shows a cast from the external mould of the best preserved of Whittard's specimens. On the basis of this identification, Fortey (1975) assigned *salteri* to *Ampyx*, *sensu stricto*. The Mytton form is, however, clearly different from *salteri*: it lacks the characteristic thoracic structure, the pygidium is relatively long (sag.) and the pygidial pleural furrows are not distinct. It is here referred to *Ampyx* cf. *reyesi* Benedetto & Malanca (Fig. 90). Fortey & Owens (1978: fig. 8a) used Whittard's concept as the basis for their reconstruction of *salteri*, which is now seen to be incorrect; a new version is presented here as Fig. 88b.

Family **ALSATASPIDIDAE** Turner 1940

Genus ***SELENECEME*** Clark 1924

TYPE SPECIES. *Seleneceme propinqua* Clark 1924, by monotypy.

DIAGNOSIS. See Whittard (1960: 117–118); comments in Fortey & Shergold (1984: 352).

Seleneceme acuticaudata (Hicks 1875)
(Fig. 91)

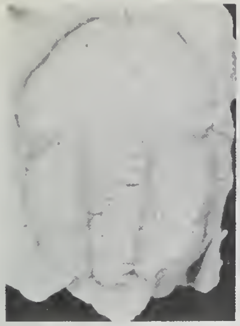
(For synonymy see Whittard 1960: 118).

HOLOTYPE. SM A15628, Llanvirn quarry.

OCCURRENCE IN SOUTH WALES. *S. acuticaudata* appears in the Llanfallteg Formation, 18 m below the Arenig/Llanvirn boundary, in the type section (loc. 52k), and persists into the early Llanvirn, ranging from the *Dionide levigena* to *D. artus* Biozones. It occurs in the Scolton railway cutting (loc. 55), Llanfallteg Formation, and widely in the *D. artus* Biozone.

FIGURED SPECIMEN. It.19701.

ADDITIONAL MATERIAL. NMW 33.89.G160, 84.17G.85–9.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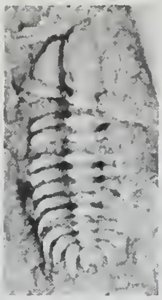
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Fig. 91 *Seleneceme acuticaudata* (Hicks 1875). Uppermost Arenig, Fennian Stage, *D. levigena* Biozone, loc. 52a, Llanfallteg, cranidium and partial thorax, × 3, It.19701.

Fig. 92 *Placoparina* sp. Latex cast from external mould, basal Llanvirn, loc. 52, Llanfallteg, × 7, NMW 85.67G.1b.

Discussion. This species has been fully described by Whittard (1960), and the present material adds nothing to his description; it is figured as a matter of record. The first occurrence of the species is below the Arenig/Llanvirn boundary and hence earlier than in Shropshire. The glabellar tubercle is very subdued on our material, but we regard this as a matter of preservation only.

Family **CHEIRURIDAE** Hawle & Corda 1847

Subfamily **ECCOPTOCHILINAE** Lane 1971

Genus ***PLACOPARINA*** Whittard 1940

Type species. *Cryphaeus Sedwickii* M'Coy 1849, from presumed Llandeilo; Builth Wells district, Powys. By original designation.

Placoparina sp.
(Fig. 92)

Material. A small, complete internal mould with counterpart external mould, NMW 85.67G.1a, b, from the basal Llanvirn, Llanfallteg Formation; loc. 52, Llanfallteg. A larger, badly preserved 'ghosted' complete specimen, NMW 84.17G.173, from same horizon, loc. 52V.

Remarks. The smaller, better preserved specimen is disarticulated behind the cephalon, the second and the seventh thoracic segments; the eighth thoracic segment is attached to the pygidium, and we interpret the specimen as a degree 7 meraspis. Although not well preserved, its general morphology is consistent with that of *Placoparina* (compare Whittard 1958: pl. 15, figs 6, 9). The larger specimen is less informative, but appears to possess the characteristic pleural spines on the pygidium. The specimens are not well enough preserved to tell whether they belong to *P. sedgwicki* (M'Coy).

Family **PLIOMERIDAE** Raymond 1913

Subfamily **PLACOPARIINAE** Hupé 1953

Genus ***PLACOPARIA*** Hawle & Corda 1847

Type species. *Trilobites zippei* Boeck 1828, from the Llandeilo, Dobrotivá Formation; Prague district, Czechoslovakia. By original designation.

Remarks. Three subgenera of *Placoparia* have been described: *Placoparia*, *Coplacoparia* Hammann 1971*a* and *Hawleia* Prantl & Šnajdr 1957. Of these *Placoparia* has been recognized in the Arenig of Britain, the Llanvirn of Britain, Brittany, Spain, Portugal and Bohemia and the Llandeilo of Bohemia; *Coplacoparia* from the Llandeilo of Spain and Brittany, and *Hawleia* from the Caradoc and Ashgill of Bohemia and Poland respectively. Hammann (1971*a*), Henry & Clarkson (1975) and Romano (1976) have studied in detail the evolution and distribution of

Placoparia species, recognizing in particular the progressive development of coaptative structures. The only species with known Arenig representatives is *P.* (*P.*) *cambriensis*, a few specimens of which Whittard (1958: 108, as *P. zippei*; 1966: 284, as *P. barrandei*) recorded from the Tankerville Flags and Shelve Church Beds in the Shelve inlier. We have identified further specimens from the Pontyfenni Formation in south Wales.

Subgenus ***PLACOPARIA*** Hawle & Corda 1847

Placoparia (***Placoparia***) ***cambriensis*** Hicks 1875
(Figs 93a–m)

1875 *Placoparia cambriensis* Hicks: 186; pl. 9, figs 1, 2.
1906 *Placoparia cambrensis* (sic) Hicks; Evans: 614, 617 (lists).
1909 *Cheirurus* sp.; Thomas, *in* Strahan *et al.*: 13.
1909 *Sao* sp.; Cantrill, *in* Strahan *et al.*: 33.
1958 *Placoparia zippei* (Boeck); Whittard: 104 *pars*; pl. 16, figs 6–10, text-fig. 6a, d–h [*non* fig. 6b, c, = *P. zippei*]. (With full synonymy).
1958 *Placoparia* sp.; Whittard: 108; pl. 16, fig. 11.
1966 *Placoparia barrandei* Prantl & Šnajdr; Whittard: 283.
1967 *Placoparia cambriensis* Hicks; Dean *in* Whittard: 309.
1971*a* *Placoparia* (*Placoparia*) *cambriensis* Hicks; Hammann: 57; pl. 1, figs 3–9; pl. 3, fig. 27; text-fig. 2.
1971*b* *Placoparia cambriensis* Hicks; Hammann: 266, 270.
1974 *Placoparia* (*Placoparia*) *cambriensis* Hicks; Hammann: 114; pl. 10, figs 172–174.
1975 *Placoparia* (*Placoparia*) *cambriensis* Hicks; Henry & Clarkson: 88; pl. 1, figs 1–4; pl. 3, figs 1–3; text-fig. 3A.
1976 *Placoparia* (*Placoparia*) *cambriensis cambriensis* Hicks; Romano: 15; pl. 1a, b.
1976 *Placoparia* (*Placoparia*) *cambriensis armoricensis* Romano: 15.
1980 *Placoparia* (*Placoparia*) *cambriensis* Hicks; Henry: 51; pl. 5, figs 1–3; pl. 6, fig. 4; text-fig. 16A.
1984 *Placoparia* (*Placoparia*) *cambriensis* Hicks; Rábano: 10; pl. 1, figs 1–15 (with further synonymy for Iberian material).

LECTOTYPE (selected Hammann 1971*a*: 58). BGS GSM35263, complete specimen from Llanvirn, *D. artus* Biozone; Llanvirn quarry, Abereiddi, Dyfed. Figured Hicks 1875: pl. 9, fig. 2; Whittard 1940: pl. 5, fig. 3; refigured here as Fig. 93m.

MATERIAL. From Fennian, Pontyfenni Formation, *B. rushtoni* Biozone: NMW 84.11G.5a, cephalon with two attached thoracic segments; It.18980, ill-preserved complete specimen; It.19010, NMW 84.12G.10a, b, ill-preserved enrolled specimens; NMW 84.11G.4a, pygidium; all from loc. 23, Pontyfenni. BGS Pr616, ill-preserved complete specimen from loc. 24, Llwyncrwn; BGS JP3533/34, incomplete cranidium from loc. 20A (Carm. 40NW Wλ5), Capel-Dewi. From *S. abyfrons* Biozone: BGS Pr1751, small incomplete cephalon and pygidium; BGS Pr1794, cranidium; NMW 84.17G.181, cephalon and part of thorax; all from loc. 38, Pen-y-parc. From Aber Mawr Formation, Pencil Slates: NMW 84.17G.182 enrolled specimen from loc. 62, Aber Mawr, Ramsey Island. From Tankerville Flags: BGS GSM92936, cranidium from Bergam quarry, Shelve inlier. From Shelve Church Beds: BGS GSM102436–7, cranidia from Wood House Gravels, Shelve inlier and BGS GSM92937, cranidium from Shelve. Numerous specimens, sometimes occurring in 'graveyards', from Fennian, *D. levigena* Biozone, Llanfallteg Formation: locs 52C, 52M, 52P–S, 52U, 52W, Llanfallteg. Also common in basal Llanvirn, *D. artus* Biozone, Llanfallteg Formation: loc. 50, Cefn-maen-llŵyd; loc. 52, Llanfallteg; loc. 55, Scolton.

Elsewhere in south Wales, the species has been recorded from the Llanvirn, *D. artus* Biozone: old quarry north of Clarbeston (SN 0465 2210), It.18981; stream section SW of Cefn-maen-llŵyd (Pem. 24SE Eλ12), BGS Pr2013; Bodau farmyard, Rhyd-y-wrâch (Pem. 24SE Eλ13), BGS Pr2018/19; St Clears area, NMW 33.189.G38, 33.189.G82, 33.189.G88; south of Castell-gorfod (Carm. 38NW Wλ8); stream section between Tŷ-rhos and Gors, SW of Llangynog (Carm. 45NE Wλ2), BGS JP3483/84.

In other parts of Britain, the species occurs commonly at the same horizon in the Hope Shales Formation (see Whittard 1958: 108) and occasionally in the Skiddaw Slates Group,

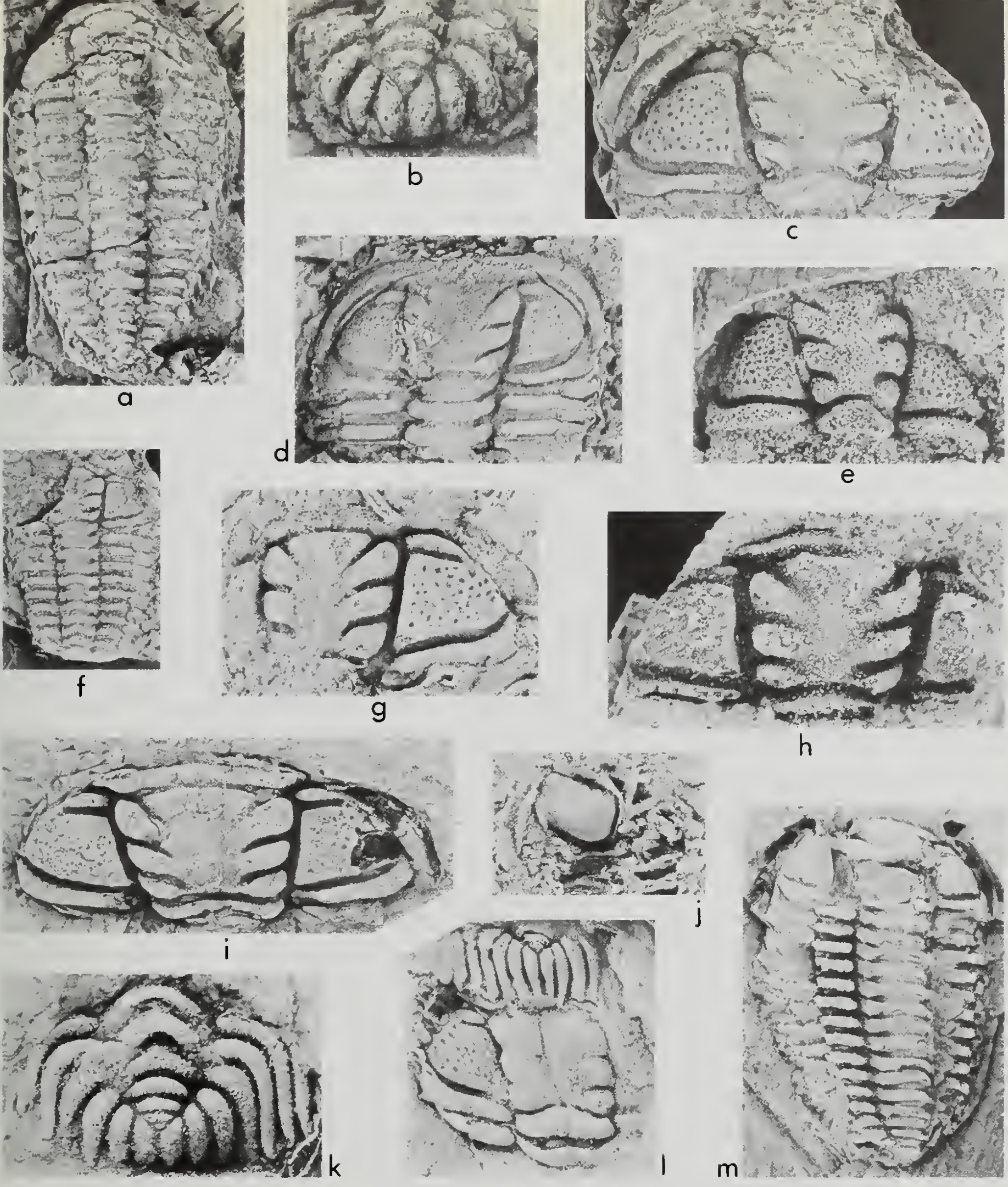


Fig. 93 *Placoparia* (*Placoparia*) *cambriensis* Hicks 1875. Upper Arenig, Fennian Stage, Pontyfenni Formation, *S. abyfrons* Biozone, loc. 38, Pen-y-parc (c, f); *B. rushtoni* Biozone, loc. 23, Pontyfenni (a, b, d); Fennian Stage, Tankerville Flags, Bergam Quarry, Shelve inlier (g) and Shelve Church Beds, cart track north of Wood House, Gravels, Shelve inlier (e, h); Fennian Stage, *D. levigena* Biozone, Llanfallteg Formation, loc. 52P, Llanfallteg (j); lower Llanvirn, *D. artus* Biozone, Llanfallteg Formation (i, k–m). a, axial shield, × 3, It.18980; b, small pygidium, × 10, NMW 84.11G.4a; c, cranidium with associated free cheek, × 4, BGS Pr1794; d, cephalon with two attached thoracic segments, × 3·5, NMW 84.11G.5; e, cranidium, latex cast from external mould, × 5, BGS GSM102437; f, small incomplete axial shield, × 6·5, BGS Pr1751; g, cranidium, latex cast from external mould, × 5, BGS GSM92936 (counterpart of original of Whittard, 1958: pl. 14, fig. 10); h, cranidium, × 6, BGS GSM102436; i, cranidium with associated free cheek, old quarry north of Clarbeston, × 3·5, It.18981; j, ventral side of anterior end of axial shield with hypostoma, × 5·5, It.18982; k, pygidium with two attached thoracic segments, latex cast from external mould, loc. 50, Cefn-maen-llŵyd, × 8, It.18983; l, enrolled specimen, latex cast from external mould showing cephalon and pygidium (the pygidial pleural spines have been elongated by distortion), stream 275 m south of Rhyd-y-wrâch (Geological Survey loc. Pem. 24SE Eλ12), × 5, BGS Pr2013; m, lectotype, complete axial shield, Llanvirn quarry, × 2, BGS GSM35263 (original of Hicks 1875: pl. 9, fig. 2).

where it has been reported from Outerside (SM A15622–3) and Whiteside (BGS GSM35239: syntype of *Ormathops nicholsoni*, see p. 244) in the Lake District, and at Ellergill (SM A15624) in the Cross Fell inlier.

The numerous foreign occurrences are listed by Hammann (1971*b*), Henry & Clarkson (1975), Romano (1976) and Henry (1980).

DIAGNOSIS. Glabella widens only slightly towards anterior; axial furrows straight; preglabellar furrow distinct, anteriorly convex; cheek with coarse pitted sculpture, with larger pits towards outer edge; pygidium with three or four axial rings and a terminal piece; pygidial spines short.

REMARKS. This species has been described by Hammann (1971*a*: 58), and the diagnosis above is based upon his (our translation from the original German). Because Whittard (1966: 284) considered the Shelve Church Beds to be of *extensus* Biozone age, the range of *P. cambriensis* has been assumed to extend down into the lower part of the Arenig. It is shown above (p. 98) that these are of likely Fennian age, and the known range of the species therefore extends no further back than the early Fennian. Whittard (1958: 108; pl. 16, fig. 11) figured a pygidium from the Shelve Church Beds as *Placoparia* sp., but noted that it showed no apparent differences from *P. cambriensis*; we here include it in that species.

Placoparia occurs infrequently in the lower two biozones of the Fennian in south Wales. The material is fragmentary and mostly not well preserved, but as far as can be seen corresponds in all essentials to *P. cambriensis* from the *D. levigena* Biozone and the Lower Llanvirn.

Romano (1976) recognized two subspecies of *P.* (*P.*) *cambriensis*, one (*cambriensis*) with four rings on the pygidial axis, the other (*armoricensis*) with three, the two of mutually exclusive distribution in the Llanvirn: the former in Britain, north Portugal and Bohemia, the latter in Brittany and Spain. Rábano (1984) identified *P.* (*P.*) *cambriensis* (at one locality in association with *P.* (*P.*) *c. armoricensis*) in the Montes de Toledo, Spain, and argued on morphological and distributional grounds that there was no basis for two subspecies. In the light of Rábano's data, we consider the pygidial difference to be more likely the result of individual variation, or of preservational differences, than of taxonomic significance.

Family **ENCRINURIDAE** Angelin 1854

Subfamily **DINDYMENINAE** Henningsmoen 1959

Genus ***DINDYMENE*** Hawle & Corda 1847

TYPE SPECIES. *Dindymene fridericiaugusti* Hawle & Corda 1847, Ashgill Králův Dvůr Formation; Prague district, Czechoslovakia. Subsequently designated by Barrande, 1852: 816.

DIAGNOSIS. Glabella inflated, clavate, expanding forwards; lateral glabellar furrows, when developed, short and shallow, being confined to vertical face of glabella adjacent to axial furrow; facial suture close to cephalic margin, running along border furrow; thorax of 10 or 11 segments; pygidium with 5–12 axial rings and two, or rarely three, pairs of pleural ribs.

REMARKS. The above diagnosis is modified from those of Henningsmoen (*in* Harrington *et al.* 1959: O448) and Kielan (1960: 146) to include *Cornovica* Whittard. The latter was proposed for the Llanvirn species *C. didymograpti* Whittard 1960, from the Hope Shales Formation, Shelve inlier, and Whittard laid stress upon the cephalic sculpture, the glabella not projecting beyond the cephalic border, the presence of glabellar furrows in addition to 1P and 11 rather than 10 thoracic segments as particulars which distinguish it from *Dindymene* species. The sculpture, however, is closely similar to that of certain *Dindymene* species (e.g. *D. longicaudata*—compare with Whittard 1960: pl. 17, figs 8–10 and Kielan 1960: pl. 30, fig. 2). The amount of glabellar projection is only a matter of degree, and can be affected by distortion; all Whittard's *Cornovica didymograpti* with the glabella well preserved (Whittard 1960: pl. 17, figs 8–10) are somewhat distorted, and their appearance is very similar to that of distorted *Dindymene hughesiae* (Ingham 1974: pl. 18, fig. 12). The only real differences, therefore, are the presence of 2P and 3P lateral glabellar furrows and 11 thoracic segments.

The bulk of described *Dindymene* species are of Ashgill age, and the genus has only scant representatives in the Caradoc and Llandeilo. The Llanvirn *Cornovica didymograpti* and the Arenig species described below are considerably earlier than most 'typical' *Dindymene*, and they might be expected to retain what are evidently primitive characters for the genus—2P and 3P glabellar furrows and 11 thoracic segments. The presence of three pairs of pleural ribs rather than the customary two in *Dindymene longicaudata* and an undescribed *Dindymene* from the Upper Whitehouse Beds, Girvan (Ingham 1974: 85) presumably bears testimony to earlier species with 11 thoracic segments. On the basis of these arguments we believe that *Cornovica* is best regarded as a subjective synonym of *Dindymene*.

Whittard (1960: 123) claimed that *Cornovica* occupied an intermediate position between *Dindymene* and the Llanvirn genus *Plasiaspis* Prantl & Přibyl, because the latter has 12 thoracic segments and deep lateral glabellar furrows. However, the structure of the glabella and anterior border area of *Plasiaspis* (see Horný & Bastl 1970: pl. 15, fig. 2) is quite different from those of both of the others, although its general morphology suggests that its placement in the Dindymeninae is correct. More recently Strusz (1980: 6) excluded both *Cornovica* and *Plasiaspis* from the Dindymeninae because, among other characters, both had a rostral plate; he claimed that the rostral and connective sutures are ankylosed in *Dindymene*, 'of levisellid pattern'. Kielan (1960: 143) stated that the ventral cephalic sutures are incompletely known, but were probably of levisellid type. We can find no reference to a description of the ventral cephalic morphology in *Dindymene*, but a specimen of *D. longicaudata* figured by Kielan (1960: pl. 28, fig. 5) has the front part of the glabella missing and exposing what appears to be a rostral plate, which compares closely with that of *Cornovica didymograpti* figured by Whittard (1960: pl. 17, figs 1, 2). We would thus dispute that the sutures are ankylosed in *Dindymene*, or at least in *D. longicaudata*. There is therefore no reason on this basis to exclude *Cornovica* or *Plasiaspis* from the Dindymeninae. Even if they are found to be ankylosed in some *Dindymene*, and such might be expected to occur in late members of the lineage, all other characteristics point to a close association—to the extent that we have synonymized *Cornovica* with *Dindymene*. Strusz' (1980: 6) claim that *Cornovica* and *Plasiaspis* are 'probably cybelinids' cannot therefore be upheld, nor do we see any reason to elevate the Dindymeninae to family status. *Prosopiscus* Salter (*in* Salter & Blandford 1865), included with question in the Dindymeninae by Henningsmoen (*in* Harrington *et al.* 1959: O449), has recently been shown by Fortey & Shergold (1984: 357) to have affinities with the Phacopina. Kielan (1960: 144) added the Ashgill genus *Eodindymene* Kielan, which is like *Dindymene* in all respects apart from having the facial suture crossing the cheek. We are doubtful if this one character warrants generic distinction, and suggest that separation at subgeneric level at the most would be more appropriate. *Dindymenella* Lu *et al.* 1976 has lateral glabella furrows slightly longer than in *Dindymene didymograpti*, but not as long as in *Plasiaspis*. The pygidial pleurae are broad (tr.) and in contact for most of their length. On the basis of the figured material (Lu *et al.* 1976: pl. 14, figs 9–11) we are uncertain whether *Dindymenella* is a dindymenine, or belongs to another encrinurid subfamily.

Dindymene saron sp. nov.
(Figs 94a–i, 95)

HOLOTYPE. It.18984, cephalon with eight thoracic segments.

TYPE LOCALITY AND HORIZON. Fennian Stage, *S. abyfrons* Biozone, Pontyfenni Formation; loc. 38, Pen-y-parc.

PARATYPES. From type locality: BGS Pr1755, It.18989, NMW 84.17G.160, thoraces with pygidia; It.18986, incomplete cranidium. From *B. rushtoni* Biozone; loc. 23, Pontyfenni: It.18985, It.18988, complete specimens; It.18991, cephalon and thorax; It.18990, cephalon with thoracic segments; It.18987, cephalon.

DIAGNOSIS. *Dindymene* with three pairs of short lateral glabellar furrows; small, prominent 1P lobe; glabella with sculpture of fine granules, cheeks reticulate with tiny granules; thorax of 11 segments with long pleural spines; pygidium with 5–6 axial rings and two pairs of long pleural spines.

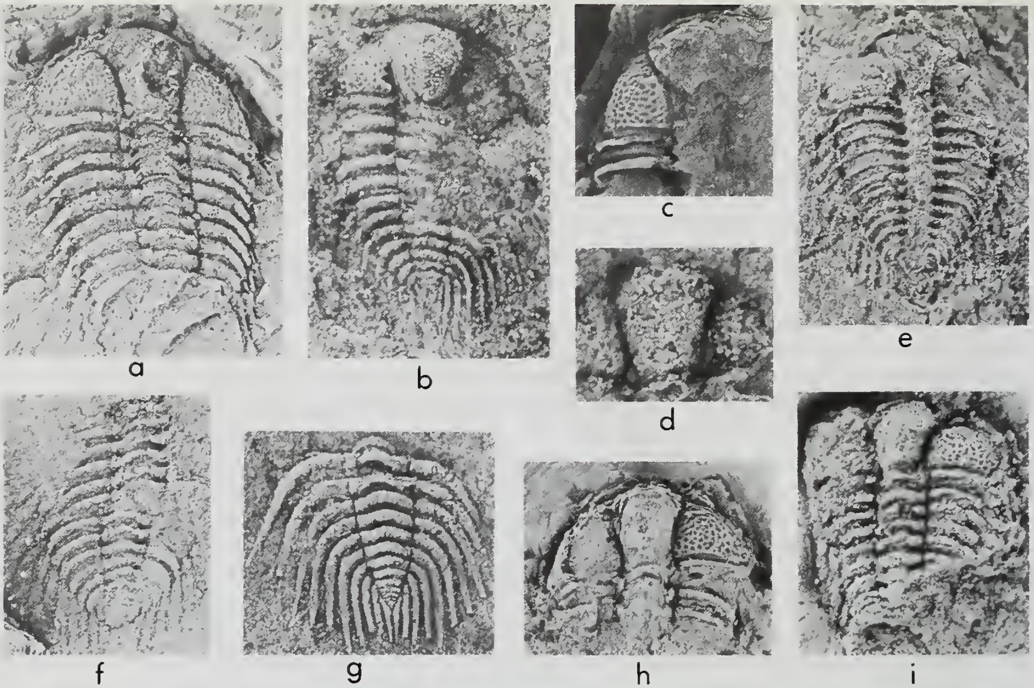


Fig. 94 *Dindymene saron* sp. nov. Upper Arenig, Fennian Stage, Pontyfenni Formation, *B. rushtoni* Biozone, loc. 23, Pontyfenni (b, d, e, h, i) or *S. abyfrons* Biozone, loc. 38, Pen-y-parc (a, c, f, g). a, **holotype**, cephalon with seven thoracic segments, × 5, It.18984; b, small axial shield, latex cast from external mould, × 10, It.18985; c, incomplete cephalon showing sculpture of cheek, × 5, It.18986; d, cranidium, latex cast from external mould, showing sculpture on glabella, × 12·5, It.18987; e, small axial shield, × 6, It.18988; f, thorax and pygidium, × 8, It.18989; g, small thorax and pygidium, latex cast from external mould, × 12·5, BGS Pr1755; h, cephalon with two thoracic segments, × 4·5, It.18990; i, small cephalon and thorax, × 11, It.18991.

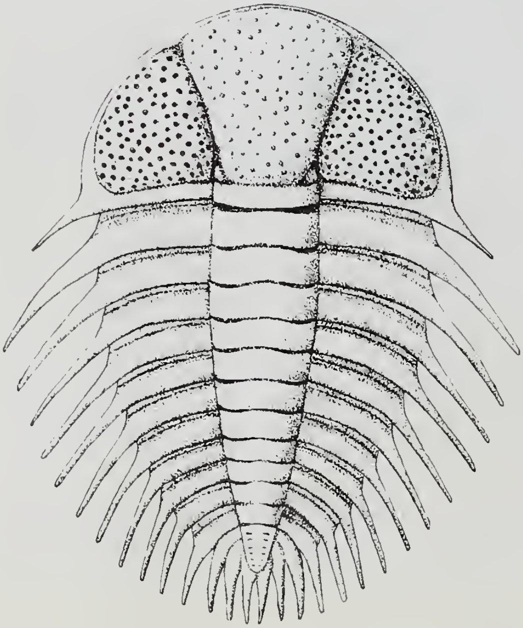


Fig. 95 Reconstruction of *Dindymene saron* sp. nov., × 8 approx. Facial suture not indicated (but see Whittard 1960: pl. 17, fig. 10).

Name. Greek *σάρον*, a broom, alluding to the long thoracic pleural spines.

Description. Glabella clavate, extending as far as, but not overhanging, anterior border, which seems to be defined by a shallow anterior border furrow (Fig. 94a); of three pairs of short lateral glabellar furrows, 1P deepest, which defines a small, ovate and rather prominent 1P lobe depressed below level of remainder of glabellar surface. Sculpture of fine, dense granules. Cheek coarsely reticulate; interspersed fine granules only seen in external moulds (Fig. 94d). Genal spine not well preserved in our material, but on the holotype appears to extend straight outwards and backwards from the genal angle. Facial suture not seen, but probably it ran outside the genal spine as on *D. didymograpti.*

Thorax of 11 segments, whose pleural ribs are extended into long spines. A small specimen (Fig. 94b) appears to have only 10 thoracic segments, and this is presumably a late meraspis; it appears to have a finely granulose sculpture on the pleurae.

On only one specimen (Fig. 94g) is the pygidial axis at all well preserved. It tapers backwards rapidly to a point, and has five rings and a tiny terminal piece. A larger specimen shows perhaps six axial rings. There are two pairs of long spinose pleurae, the anterior longer than the posterior pair.

Remarks. *D. saron* is the earliest known *Dindymene.* It differs from *D. didymograpti* (Whittard 1960) in details of the cephalic sculpture, particularly in the coarser reticulation of the cheek and the more numerous, finer granules on the glabella. The thoracic and pygidial pleural spines are much longer, and there are fewer (five or six as opposed to seven) axial rings.

Rare and ill-preserved specimens of a *Dindymene* have been found in the Fennian part of the Llanfallteg Formation at locs 52V and 52W, Llanfallteg; these are presumably referable to *D. didymograpti*, although it is possible that they belong to what appears to be another species that occurs in the *D.* '*bifidus*' Beds at Penarfynydd, Llŷn (Figs 96a, b). This has a reticulate sculpture on the cheek, with only occasional small granules; the glabella is apparently smooth, and has only sparse granules. There are 10 thoracic segments. This combination of features distinguishes it from both *D. didymograpti* and *D. saron*, suggesting the presence of a third early *Dindymene* in the Arenig–Llanvirn of Wales.

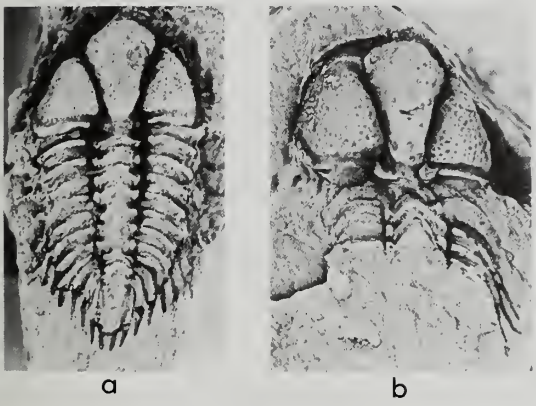


Fig. 96 *Dindymene* cf. *didymograpti* (Whittard 1960). Lower Llanvirn, *D. artus* Biozone, Penarfynydd, Rhiw, Llyn Peninsula, Gwynedd. a, complete axial shield, × 6·5, NMW 27.110.G795; b, cranidium with four thoracic segments, showing sculpture on cheek, × 4, NMW 27.110.G648.

Family **CALYMENIDAE** Milne Edwards 1840

Subfamily **REEDOCALYMENINAE** Hupé 1955

Genus ***NESEURETUS*** Hicks 1873

Type species. *Neseuretus ramseyensis* Hicks 1873, Moridunian, Ogof Hên Formation; Ramsey Island. Subsequently designated by Vogdes (1925: 106).

Remarks. We follow here the arguments of Whittard (1960), Whittington (1966) and Henry (1980) in placing *Neseuretus* in the Calymenidae, not the Homalonotidae, and accept Henry's (1980) and Hammann's (1983) assignment to the subfamily Reedocalymeninae.

Several *Neseuretus* species have been recovered from the British Arenig, and these have been described by Whittard (1960), Whittington (1966) and Bates (1968*a*, 1969), mostly from the lower part of the series, and are listed by Fortey & Morris (1982: 69, 70). Some of these are likely to be synonyms—for instance *N. brevisulcus* Whittard 1960 is distinguished from *N. parvifrons* (M'Coy 1851) principally upon the degree of development of the weak anterior border furrow, a feature that Whittington (1966: 503) noted was highly variable. The distinction seems to us to be accounted for by a combination of this variation and preservation; both species occur together in the lower third of the Mytton Flags. Bates (1969: 23) included *N. grandior* with question in the synonymy of *N. ramseyensis.* The differences between the two (only pygidia are known of the former) are 10 axial rings and 8–9 pleurae in the former, with corresponding figures of 8 or 9 and 7 or 8 in the latter. This hardly seems to us a specific difference, and we here include *grandior* in *ramseyensis.*

Cyclopyge (see above) and *Neseuretus* are the only trilobites having species common to the Mytton Flags and the Arenig of north and south Wales; thus *N. parvifrons* occurs also in the Henllan Ash and *N. murchisoni* (rarely) in that formation and in the Ogof Hên Formation, Bolahaul Member. Our (Fortey & Owens 1978: 233 and 237, fig. 6) records of *N. parvifrons* in south Wales were erroneous; the material is all referable to *N. murchisoni.* Specimens resembling *N. complanatus* occur rarely at loc. 19. It may be assumed that those parts of the Mytton Flags (the lower third) with *N. murchisoni* and *N. parvifrons* equate with the Moridunian. Records of *N. murchisoni* from higher in the Mytton Flags (upper third), on the basis of Whittard's 1960: pl. 29, fig. 12, do not belong to this species, and his figured specimen more closely resembles *N. parvifrons*, which he records (1966: 304) as occurring throughout the formation—in contradiction to his earlier (1960: 144) statement that it is apparently restricted to the lower third. It is possible that the higher records refer to forms like those on his 1960: pl. 20, fig. 12, and not to *parvifrons, sensu stricto.*

Hammann (1983: 57) has shown how Llanvirn–Llandeilo *Neseuretus* species in Spain favour particular facies, and the same apparently holds true for British Arenig species. Thus *Neseuretus ramseyensis* occurs in micaceous silty mudstones or in arenaceous sediments; *N. parvifrons* in micaceous silts of the Mytton Flags and sandy mudstones or muddy felspathic sandstones in the Henllan Ash; and *N. murchisoni* in the muddy sediments of the Bolahaul Member and within the Mytton Flags.

Neseuretus ramseyensis Hicks 1873
(Figs 97a–g)

1873 *Neseuretus ramseyensis* Hicks: 44–45; pl. 3, figs 7–10, 16–22.
1960 *Neseuretus grandior* Whittard: 141; pl. 20, figs 1, 2.
1960 *Neseuretus parvifrons* (Salter); Whittard: 145 *pars* (reference to *N.? elongatus* only).
1960 *Neseuretus murchisoni* (Salter); Whittard: 148 *pars*; pl. 21, figs 1, 2 only.
1969 *Neseuretus ramseyensis* Hicks; Bates: 23; pl. 8, figs 3, 4, 6–12; pl. 9, figs 1–3, 6 (With full synonymy).
?1975 *Neseuretus grandior* Whittard; Struve: 279, fig. 28.

Lectotype (selected Whittard 1960: expl. to pl. 21). BGS GSM10166, cranidium from Ogof Hên Formation, Ramsey Island.

Occurrence. At type locality; in lowermost, silty part of Bolahaul Member, Llangynog inlier and Star Cottage, Carmarthen (loc. 8, Fortey & Owens 1978); Stiperstones Quartzite, Shelve inlier.

Diagnosis. *Neseuretus* with narrow, upturned anterior border, distinct preglabellar furrow; lateral glabellar furrows weak on larger specimens; pygidium with 8–10 axial rings, 7–9 pleural ribs, axis not reaching posterior margin.

Remarks. Bates (1969: 23) redescribed this species, but noted that distortion makes accurate description difficult. The cephalon closely resembles that of *N. murchisoni*, and these species can really only be discriminated upon pygidial differences, *N. ramseyensis* typically having 8

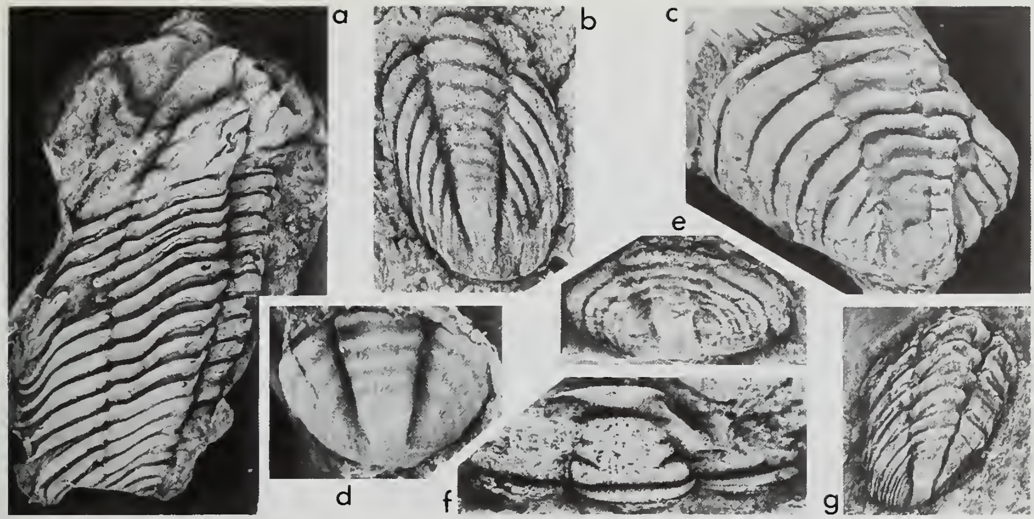


Fig. 97 *Neseuretus ramseyensis* Hicks 1873. Lower Arenig, Moridunian Stage, Ogof Hên Formation, Bay Ogof Hên, Ramsey Island (a, b, f, g), Bolahaul Member, Llangynog (c, d) and Star Cottage, Carmarthen (Fortey & Owens 1978: loc. 8B) (e). a, cephalon and thorax, latex cast from external mould, × 2·5, NMW 29.308.G240b; b, pygidium showing eight axial rings, × 3, NMW 29.308.G63; c, large pygidium, × 1·5, NMW 78.8G.41; d, small pygidium, relatively undistorted, latex cast from external mould, × 5·5, NMW 78.8G.42; e, small distorted pygidium (compare with Fig. 97d), × 4, NMW 75.45G.235a; f, small cranidium, × 6, NMW 27.110.G762; g, small pygidium with four attached thoracic segments, × 2, NMW 85.68G.1.

(sometimes 9) axial rings and 7 pairs of pleural ribs, compared with 5 and 4 in *N. murchisoni*. Much of the material of *N. ramseyensis* is of a comparatively large size, and it might be considered that the larger numbers of rings and ribs are a function of this. However, specimens of comparable size show the same differences, so the presence of two taxa, albeit closely related, seems to be real.

Struve (1975: 219, fig. 28) figured an incomplete external mould of a *Neseuretus* pygidium in an erratic quartzite pebble from Hessen, Germany, as *N. grandior* Whittard (= *N. ramseyensis*, see above). Although there is general resemblance to Whittard's specimens, we only include this specimen with question in *ramseyensis* because the pleural areas are proportionately much narrower (although this may be an artefact of preservation), and insufficient details can be discerned for a definitive identification. Nevertheless, its occurrence suggests the presence of shallow-water *Neseuretus*-bearing quartzites on the southern margin of Tornquist's Sea, be they of Arenig or later age.

Neseuretus murchisoni (Salter 1865)
(Figs 98a–e)

1960 *Neseuretus murchisoni* (Salter); Whittard *pars*: 148; pl. 20, figs 6–11, 13–15 [*non* fig. 12, = ?*N. parvifrons*]. (With full synonymy).
1966 *Neseuretus murchisoni* (Salter); Whittington: 503; pl. 4, figs 14, 15, 17–19.
1978 *Neseuretus parvifrons* (M'Coy); Fortey & Owens: 233, 237.

LECTOTYPE (selected Shirley 1931: 14). BGS GSM35256, cranidium from Mytton Flags; Lord's Hill, Snailbeach. Figured Shirley (1931: pl. 1, fig. 5) and Whittard (1960: pl. 20, fig. 6).

OCCURRENCE. In south Wales the species is recorded from mudstones of the Bolahaul Member, Ogof Hên Formation, locs 9 and 12 of Fortey & Owens (1978: 241), and from temporary exposures (1981) along Carmarthen bypass, south of Pensarn, Carmarthen. It occurs rarely in

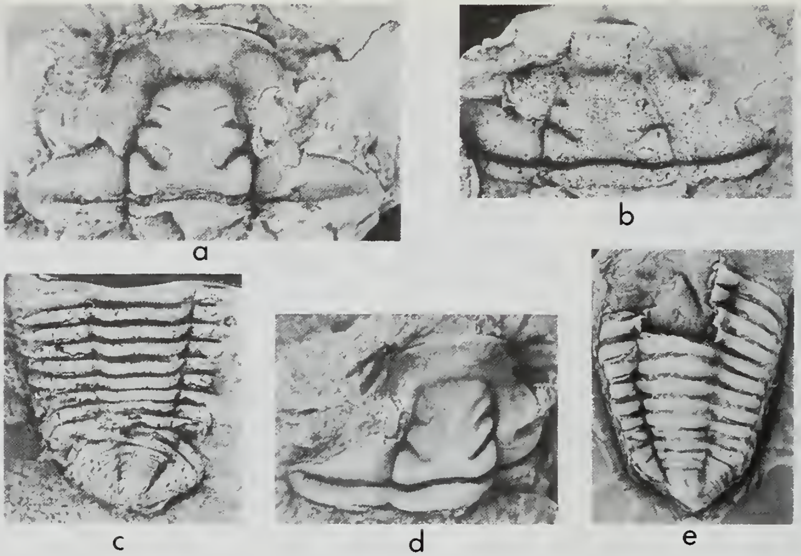


Fig. 98 *Neseuretus murchisoni* (Salter 1865). Lower Arenig, Moridunian Stage, Ogof Hên Formation, Bolahaul Member, temporary exposures (1981) on Carmarthen bypass, south of Pensarn (a, e), temporary exposure at water treatment plant, Penddaulwyn Fawr, Capel-Dewi (Fortey & Owens 1978: loc. 12) (d) and tipped material at Wennallt, Allt Cystanog, Carmarthen (Fortey & Owens 1978: loc. 9) (b, c). a, undistorted cranidium, preserving original relief, × 3·5, NMW 85.17G.1a; b, cranidium, latex cast from external mould, × 4, NMW 75.45G.230; c, thorax and pygidium, latex cast from external mould, × 3·5, NMW 75.45G.228; d, cranidium showing large palpebral lobe, × 4·5, NMW 76.3G.19; e, thorax and pygidium, × 2, NMW 85.17G.2a.

the Carnedd Iago Formation, Henllan Ash Member, Arennig Fawr district (Whittington 1966: 503), and commonly in the lowest one-third of the Mytton Flags, Shelve inlier.

DIAGNOSIS. Cranidium like *N. ramseyensis*; pygidium with axis anteriorly about one-third anterior breadth (tr.), and extending to posterior margin, composed of five rings and a terminal piece; four pairs of pleural ribs.

REMARKS. This species has been fully described by Whittard (1960: 148), and well-preserved specimens from the Bolahaul Member are illustrated here for comparison.

***Neseuretus* cf. *complanatus* Whittard 1960**
(Figs 99a–d)

MATERIAL. One incomplete cephalon and two incomplete pygidia from the Whitlandian, Afon Ffinnant Formation, loc. 19.

REMARKS. The cephalon resembles *N. complanatus* from the Mytton Flags in having a flat lateral profile (compare Fig. 99b with Whittard 1960: pl. 20, fig. 5), but we are uncertain whether this is at least in part produced by compression both in our specimen and in Whittard's. Otherwise it is closely comparable with that of *N. parvifrons* except that in the type of *complanatus* the palpebral lobe is apparently larger and in it and our specimen the glabella is proportionately longer and narrower.

Subfamily **COLPOCORYPHINAE** Hupé 1955

Genus ***COLPOCORYPHE*** Novák, *in* Novák & Perner 1918

TYPE SPECIES. *Calymene Arago* Rouault 1849 from the Llanvirn–Llandeilo of la Couyère, Ille-et-Villaine, Brittany, France. By original designation.

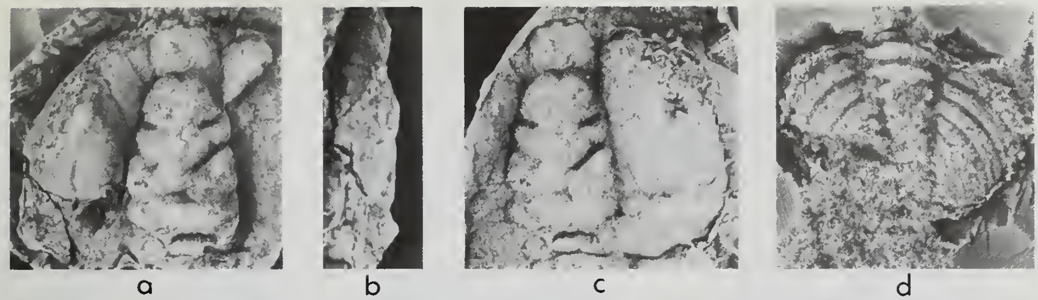


Fig. 99 *Neseuretus* cf. *complanatus* Whittard 1960. Middle Arenig, Whitlandian Stage, Afon Ffinnant Formation, loc. 19, Ffinnant road cutting. a–c, cranidium, internal mould, lateral view of same and latex cast from external mould, × 3, It.18992; d, incomplete pygidium, × 3, It.18993.

Colpocoryphe taylorum sp. nov.
(Figs 100a–h)

Holotype. NMW 84.11G.6a, complete specimen.

Paratypes. It.18994–5, cranidia; It.18996, NMW 77.9G.36, 84.12G.26, 28, 84.17G.128–133, thoraces with pygidia; NMW 84.12G.25a, b, 84.12G.27, pygidia. All loc. 23.

Type locality and horizon. Fennian Stage, *B. rushtoni* Biozone, Pontyfenni Formation; loc. 23, Pontyfenni.

Other material. A badly-preserved complete specimen from loc. 22, Sabulon, probably belongs to this species.

Diagnosis. *Colpocoryphe* with subquadrate glabella with truncated frontal lobe; palpebral lobe small, distant from axial furrow; pygidium with one incised pleural and interpleural furrow; axis with 12 rings.

Name. For Mr C. T. and Mrs I. Taylor, who presented the authors with a number of important specimens.

Description. Glabella subquadrate, frontal lobe truncated, more or less transverse. 1P furrow deep, running obliquely backwards at about 45° to exsagittal line drawn through its axial end. Abaxially there is a suggestion of a bifurcation. 2P a little over half way along glabella from posterior; it is somewhat shorter and shallower than 1P, and is directed backwards at a smaller angle. 3P short, weak, rather less than halfway from 2P to anterior margin of glabella, and directed slightly backwards, transverse or slightly forwards: this variation is probably due in part to degree of compression. One specimen shows a small 4P, a short distance in front of 3P, of similar depth and length, and directed slightly forwards. Occipital furrow approximately transverse, curved weakly forwards laterally. Occipital ring as wide as, or marginally wider (tr.) than glabella.

Axial furrow more or less straight for most of its length, curving inwards towards occipital furrow round 1P lobe. Preglabellar furrow shallower than axial, confluent with anterior border furrow. Inner part of fixed cheek broad; palpebral lobe situated distant from axial furrow with its margin slightly elevated above level of adjacent cheek. It is small, about an eighth of the sagittal length of the glabella on larger specimens. The only specimen with the fixed cheek preserved (Fig. 100c) shows a small eye, making this one of the few eyed species in the Fennian atheloptic assemblage. Pre- and postocular branches of facial suture both outwardly convex, the postocular branch being considerably longer than the preocular. Anterior cranidial border clearly defined and backwardly convex in dorsal view; lateral cephalic border hardly defined, being confluent with remainder of free cheek. Posterior border furrow deep and broad, defining abaxially widening posterior cephalic border.

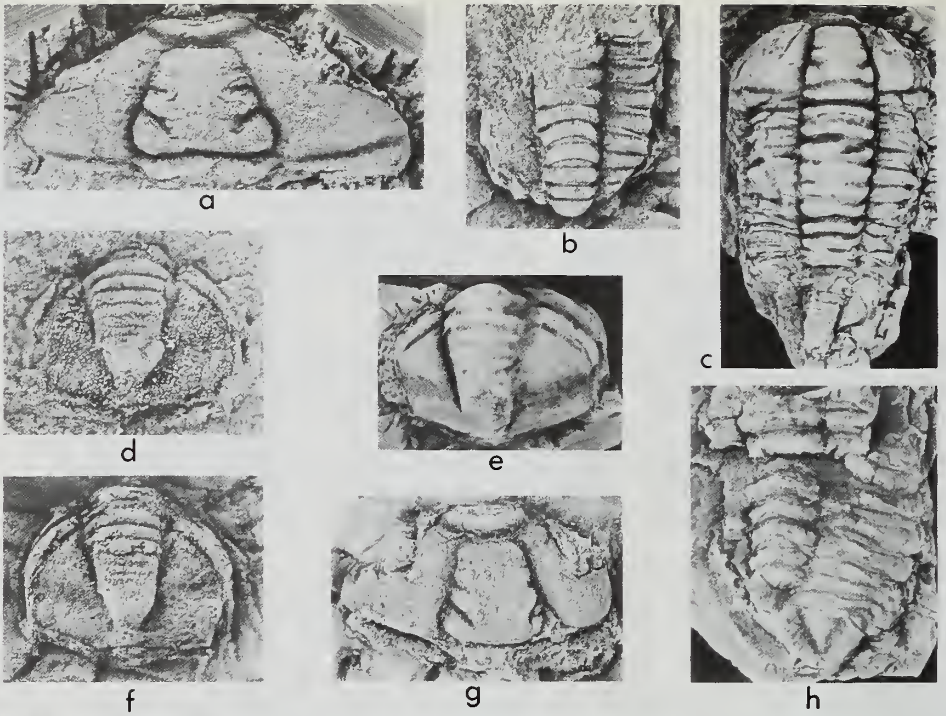


Fig. 100 *Colpocoryphe taylorum* sp. nov. Upper Arenig, Fennian Stage, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23, Pontyfenni. a, cranidium showing fine granulose sculpture and small palpebral lobe, × 4, It.18994; b, small thorax, × 10, NMW 77.9G.36; c, **holotype**, almost complete axial shield, × 2, NMW 84.11G.6a; d, f, small pygidium, latex cast from external mould showing granulose sculpture, and internal mould, × 10, NMW 84.12G.25a, b; e, large pygidium, × 3, NMW 84.12G.27; g, small cranidium, × 5, It.18995; h, thorax and pygidium, showing rounded lateral extremities of thoracic pleurae, × 3, It.18996.

Thorax of thirteen segments, which give a typically concave lateral profile which may be consistent with a burrowing mode of life for this species of the kind suggested by Hammann (1983: 29, text-fig. 11). Pleurae with narrow anterior and broad posterior bands, and flexed steeply downwards at fulcrum.

Pygidium with distinct border furrow typical for *Colpocoryphe*, which tends to be less pronounced on smaller specimens than on larger ones. Pleural area with one pleural and one interpleural furrow, but otherwise smooth. Axis broad, with 11–12 rings which become progressively narrower (sag.) and less well defined towards posterior. It tapers backwards only slightly as far as a position opposite border furrow, after which it tapers rapidly to a blunt end which merges insensibly with posterior border before reaching posterior margin.

Sculpture on cranidium and pygidium of numerous, very fine granules.

Remarks. The most distinctive feature of this species is the small palpebral lobe, situated distant from the axial furrow. This, together with the subquadrate glabella, immediately distinguishes it from the other Arenig species *C. thorali* Dean and *C. maynardensis* Courtessole, Pillet & Vizciano, both from the Montagne Noire. Both have a much larger eye which is situated close to the axial furrow, as well as more furrows in the pleural fields (see e.g. Dean 1966: pl. 11, figs 1, 2, 10; pl. 12, figs 1, 4, 6–9, 11; Courtessole *et al.* 1983: pl. 3, figs 5, 7, 8; pl. 4, figs 2, 3, 6, 10, 11, 13, 14, 16, 18; pl. 5, figs 3, 6, 7). Courtessole *et al.* (1983: 17, 22) considered two species, with concurrent stratigraphical ranges, to be represented within Dean's (1966) material of *C. thorali*. Some they retained in *Colpocoryphe* as a new species, *C. deani*, with the remainder placed in *Salterocoryphe thorali*. They did not make clear their precise reasons for this division, nor did they fully justify their transferrence of *thorali* to *Salterocoryphe*. On the basis of the illustrated material we follow Dean, and consider one species only to be present, and to belong to *Colpocoryphe* rather than the closely related *Salterocoryphe*; in particular it lacks the distinctively shaped glabella and ribbed pygidial border of the latter genus.

Of Llanvirn species, *C. thorali conjugens* Hammann from Spain has a larger eye, close to the axial furrow (e.g. Hammann 1983: pl. 12, figs 112a, b), but like this subspecies, *C. taylorum* has a subquadrate glabella and one pleural and one interpleural furrow on the pygidium (cf. Figs 100d, e, f and Hammann 1983: pl. 12, figs 111b, 113a), whilst the Llandeilo *C. rouaulti* Henry from Brittany (Henry 1970: pl. B) and Spain (Hammann 1983: pl. 13) has a proportionately longer, narrower glabella with a more rounded frontal margin, the eye closer to the axial furrow and only one pleural furrow on the pygidial pleural field. Compared with all other *Colpocoryphe* species, *C. taylorum* is the only one found in sediments of comparatively deep water origin, and to this may be related the much reduced eye.

Family **DALMANITIDAE** Vogdes 1890

Subfamily **ZELISZKELLINAE** Delo 1935

Genus ***ORMATHOPS*** Delo 1935

Type species. *Dalmanites atavus* Barrande 1872, from the Llanvirn Šárka Formation, Osek, near Rokycany, Bohemia. By original designation.

Diagnosis. Zeliszkelline with broad, flat anterior border; facial suture distant from anterior glabellar margin; 3p straight or sigmoidal; eye forwardly placed, ranging from being moderately large to being reduced to a few lenses, or may be absent; lenses, apart from those on upper horizontal row, are all the same size, and lens-packing is never entirely regular; deep palpebral furrow present in most species; small genal spine present in immature specimens. Pygidium triangular to subparabolic, axis with 7–10 rings, pleural areas with 4–6 pairs of ribs; hypostome with straight lateral margins, or slightly constricted at mid-length.

Occurrence. Arenig–Llanvirn of British Isles, Montagne Noire, France, Anti-Atlas, Morocco, and Bohemia.

Remarks. *Ormathops* is the earliest known member of the Phacopina and is the earliest trilobite with schizochroal eyes (Clarkson 1971). Unlike all other Phacopina, the eye lenses of *Ormathops* are the same size, and the packing arrangement is never entirely regular, as has been demonstrated by Clarkson (1971). The earliest *Ormathops* is *O. borni* Dean 1966 from the *D. extensus* Biozone of the Montagne Noire. Destombes (1972) recognized this species from a similar horizon in the Anti-Atlas, Morocco, but placed it in *Pterygometopus* because all of the lateral glabellar furrows are deeply incised, the eyes are large and because of the outline and configuration of the palpebral lobes, hypostome and pygidium. Now that more *Ormathops* species are known these characters cannot be used to exclude *O. borni* from the genus. In particular, Clarkson (1971) has shown that *O. borni* and the type species *O. atava* both have a distinctive kind of primitive schizochroal eye. The Moroccan *O. borni* has a consistently larger eye than does the material from the Montagne Noire, and it may be a different species. On the other hand, Clarkson (1971) described a wide variation in the size of the eye and number of lenses in *O. atava* which might be the result of intraspecific variation; the same may apply to *O. borni*.

O. atava, of Llanvirn age, has somewhat smaller eyes than does *O. borni*, but Fennian species from south Wales are either blind, as in the case of *O. nicholsoni*, or have the eye reduced to only a dozen or so lenses, as in *O. llanvirnensis*. Thus eye reduction or loss occurs in the earliest Phacopina, and anticipates the same sequence which is repeated in several different lineages of later taxa, especially in the late Devonian. In both the Fennian and the late Devonian, this eye reduction and loss is found in atheloptic assemblages.

There might be a temptation to separate off the reduced-eyed and blind *Ormathops* species as subgenera. We would caution against this, however, because it is likely to produce a facile artificial classification that might obscure true relationships. Eye reduction and loss probably occurred iteratively within *Ormathops*, with several short-lived independent lineages developing reduced eyes or eye loss as they invaded deeper-water offshore habitats.

Ormathops nicholsoni (Salter 1866)
(Figs 101a–m, 102)

1866 *Phacops Nicholsoni* Salter, *in* Harkness & Nicholson: 486 *pars*, figs c, d (lectotype only; other syntype probably *Placoparia*).
1875 *Phacops Nicholsoni* Salter; Hicks: 187.
1876 *Phacops Nicholsoni* Salter; Ward: 106.
1881 *Phacops Nicholsoni* Salter; Etheridge: 113.
1885 *Phacops nicholsoni* Salter; Postlethwaite: pl. i, figs 2–4.
1886 *Phacops nicholsoni* Salter; Postlethwaite & Goodchild: 457; pl. 1, fig. 2.
1905 *Phacops Nicholsoni* Salter; Reed: 176.
1935 *Phacops nicholsoni* Salter; Delo: 403.
1940 ?*Calyptaulax nicholsoni* (Salter) Delo: 9, 12.
1958 *Ormathops nicholsoni* (Salter) Struve: 183, 187.
1960 *Ormathops nicholsoni* (Salter); Whittard: 128 *pars*; pl. 16, fig. 6 [*non* fig. 7, = *O. llanvirnensis*].
1966 *Ormathops nicholsoni* (Salter); Dean: 297.
1971 *Ormathops nicholsoni* (Salter); Clarkson: 52.

LECTOTYPE. From Salter's two syntypes, Whittard (1960: 129) selected a moult arrangement of cephalon and thorax plus pygidium (Tullie House Museum, Carlisle) from the Skiddaw Slates Group (probably Fennian) of Whiteside, Cumbria. However, Goodchild (*in* Postlethwaite 1885, plate explanations) stated that his figure 2, which is the same specimen, was 'drawn from the original type specimen figured by Mr Salter'; selection of the lectotype therefore dates from Goodchild, not Whittard.

MATERIAL. Besides the lectotype, Salter (*in* Harkness & Nicholson 1866: 486) mentioned a further specimen, now BGS GSM35239, an ill-preserved incomplete thorax and pygidium from Whiteside. On examination, we consider that this specimen is referable to *Placoparia cambriensis* and not to *O. nicholsoni.* Another ill-preserved Lake District specimen labelled *nicholsoni*, GSM 35240 from Skiddaw, is also more likely to be a *Placoparia.* In south Wales abundant well-preserved specimens have been collected from the Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, at Pontyfenni, loc. 23, and a few also from Capel-Dewi, loc. 20D, and the Aber Mawr Formation at Aber Mawr, Ramsey Island, loc. 62.

DIAGNOSIS. *Ormathops* with preocular suture close to anterolateral corner of glabella; without eyes, but with deep palpebral furrow on anterior end of cheek; 3P furrow deep, sigmoidal; pygidium broadly triangulate with 9 axial rings and 6 pairs of pleural ribs with deep, narrow interpleural furrows; sculpture of fine pits on cheek, and very fine puncta on glabella and cephalic border; hypostoma with straight, backwardly converging lateral margins.

DESCRIPTION. Glabella expanding rapidly forwards in front of 2P lobe so that width (tr.) across basal lobes is 50%–60% of that across frontal lobe. 1P–3P furrows all of similar depth, and all extend for about the same distance inwards, extending more than halfway towards sagittal line. 1P furrow directed slightly backwards, and deepens and widens adaxially, and bifurcates distally into two short branches, the posterior of which runs approximately exsagittally. 2P furrow more or less transverse; 2P lobe slightly longer (exsag.) than 1P; 3P furrow sigmoidally curved, and directed strongly obliquely backwards. Occipital furrow arched weakly forwards sagittally, and of approximately equal depth along its length (tr.). Occipital ring widens a little sagittally, and has a small median node.

Cheek weakly convex. Short, prominent palpebral furrow present in a forward position, running parallel to the margin, its adaxial end opposite 3P furrow, close to axial furrow. It is proportionately further back in small specimens (e.g. Fig. 101i). A short, raised palpebral lobe is present in front of palpebral furrow, but the eye is apparently absent. We have failed to detect any lenses, but such are easily seen on material of *O. llanvirnensis* in which the preservation is similar, or in some cases worse. Facial suture runs obliquely across cephalic margin from a

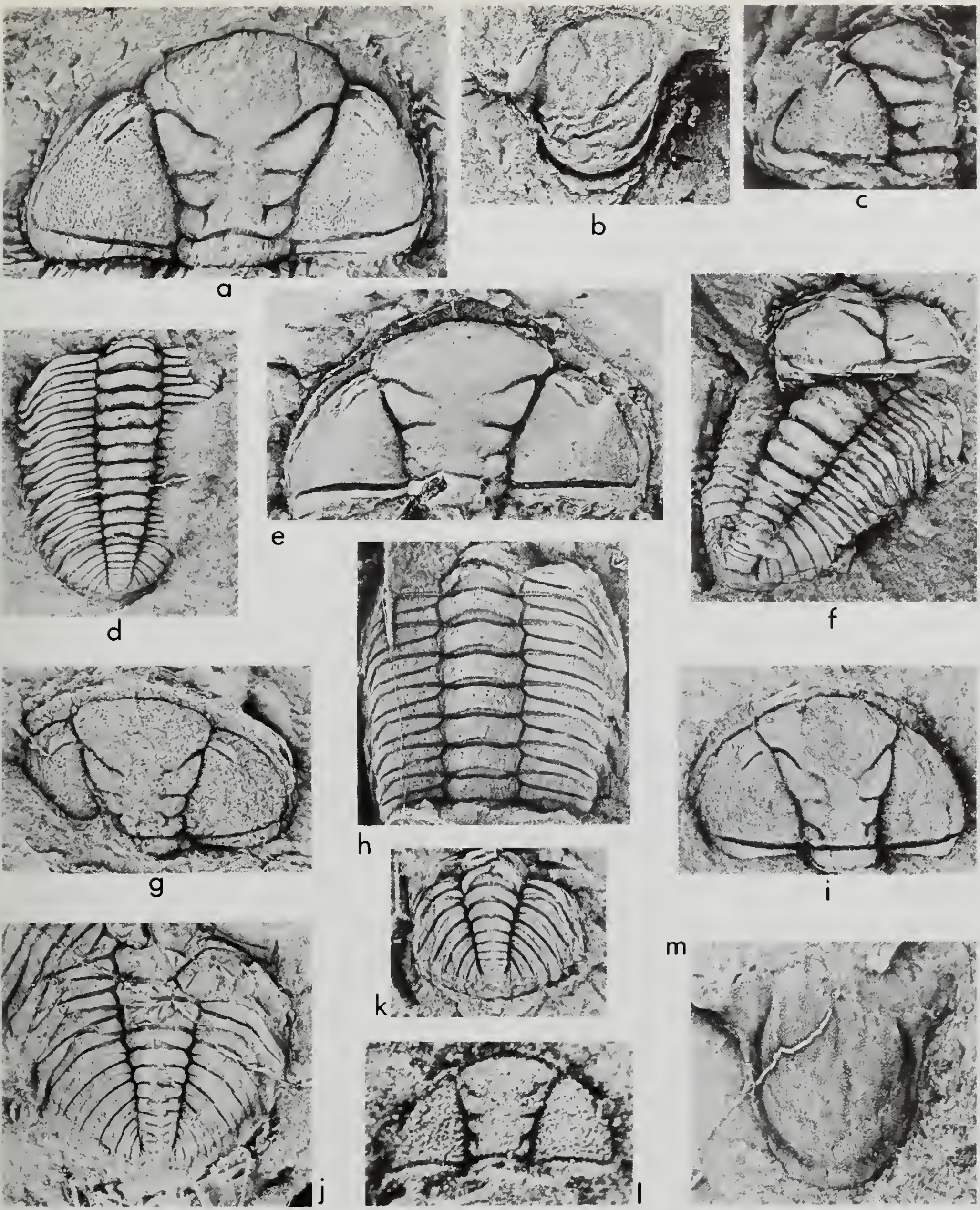


Fig. 101 *Ormathops nicholsoni* (Salter 1866). Upper Arenig, Fennian Stage, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23, Pontyfenni. a, large cephalon, showing sculpture on cheek and glabella, × 3, NMW 84.11G.7a; b, hypostoma showing anterior wings, × 7, It.18997; c, small incomplete cranidium lacking free cheek, × 6, NMW 84.12G.17a; d, thorax and pygidium, latex cast from external mould, × 4, NMW 84.11G.8b; e, cephalon, × 5, NMW 84.11G.9a; f, moult arrangement of reversed cephalon and thorax and pygidium, × 2, It.18998; g, small cephalon, latex cast from external mould, × 5·5, NMW 84.11G.10; h, thorax, latex cast from external mould, showing rows of small pits on pleurae, × 10, NMW 84.11G.11b; i, small cephalon, latex cast from external mould, showing ocular ridge distant from border furrow, × 5·5, NMW 84.11G.12b; j, pygidium with associated thoracic segments, latex cast from external mould, × 3, NMW 85.69G.1b; k, small pygidium, × 4, It.18999; l, immature cephalon, latex cast from external mould, × 15, It.19000; m, hypostome, latex cast from external mould showing granulose sculpture, × 6, It.19001.

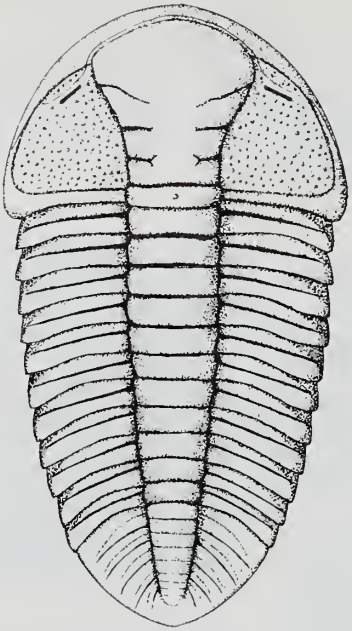


Fig. 102 Reconstruction of *Ormathops nicholsoni* (Salter 1866), × 2·5 approx.

position a short distance in front of genal angle to cross onto cheek a short distance behind palpebral furrow; after running along the front of the palpebral lobe, it runs close to the anterolateral corner of the glabella, and then around the frontal lobe. One small specimen (Fig. 101c) apparently lacks the free cheek, which suggests that in immature individuals, at least, the suture might have been functional. Anterior and lateral borders flat, widest opposite the palpebral lobe. Genal angle rounded, but a short spine present in small specimens (Fig. 101l). Posterior border widens markedly towards genal angle.

Glabella with sculpture of fine pits and tiny granules; cheek with coarser pits interspersed with fine ones; anterior, lateral and cephalic borders with fine granules.

Hypostoma with anterior margin arched gently forwards. Anterior wings transverse, elongate and narrow. Lateral margins weakly convergent, posterior gently rounded. Lateral and posterior border furrows define narrow borders of approximately equal width. Anteriorly lateral border furrow widens and becomes shallower at base of anterior wing. Median body gently convex, without lobes. Whole surface finely pitted.

Thorax of eleven segments. The axis widens slightly as far as the third or fourth axial rings, behind which it tapers very gently backwards. Pleurae with deep, oblique pleural furrows which extend close to the ends of the pleurae, which are bluntly rounded. One specimen (Fig. 101h) has a series of small pits on each anterior pleural band. That these are a primary and not a preservational feature is indicated by their regular disposition, although their presence on one specimen only is difficult to explain.

Pygidium of broadly triangulate outline. Axis tapers very gently backwards, with nine clearly defined rings and bluntly terminating: it is about 0·9 of pygidial length. Six pairs of pleural ribs with narrow, shallow interpleural furrows running more or less parallel with deeper pleural furrows. Both extend close to margin. Narrow border area of pygidium smooth. Thorax and pygidium both have sculpture of fine granules.

REMARKS. Whittard (1960: 129; pl. 16, fig. 7) included in this species a cephalon from the Hope Shales. The shallow 3p furrow and lack of a deep palpebral furrow preclude inclusion of this specimen in *O. nicholsoni*, and show that it belongs to *O. llanvirnensis*. Šnajdr (1984) has shown why *O. barroisi* (Klouček) from the Llanvirn of Bohemia cannot be included within the synonymy of *O. nicholsoni*, as Whittard (1960: 129) had claimed. Examination of a specimen in the British Museum (Natural History), It.19015, allows us to substantiate Šnajdr's contention, and we note in particular the effaced 2P and 3P furrows and very short, shallow palpebral furrow as characters which distinguish *O. barroisi* from *O. nicholsoni*.

Ormathops llanvirnensis (Hicks 1875)
(Figs 103a–g)

1875 *Phacops llanvirnensis* Hicks: 187; pl. 9, figs 3, 4.
1905 *Phacops llanvirnensis* Hicks; Reed: 176.
1906 *Phacops llanvirnensis* Hicks; Evans: 616–617.
1907 *Phacops llanvirnensis* Hicks; Cantrill, *in* Strahan *et al.*: 16.
1909 *Phacops llanvirnensis* Hicks; Thomas, *in* Strahan *et al.*: 30.
1914 *Placoparia* (sic) *llanvirnensis* Hicks; Thomas, *in* Strahan *et al.*: 28.
1918 *Phacops llanvirnensis* Hicks; Perner, *in* Novák & Perner: 16, 42.
1940 *Phacops llanvirensis* (sic) Hicks; Delo: 12.
1958 *Ormathops*? *llanvirnensis* (Hicks) Struve: 183.
1958 '*Phacops*' *llanvirnensis* Hicks: Struve: 184.
1960 *Ormathops nicholsoni* (Salter); Whittard: 128 *pars*; pl. 16, fig. 7 [*non* fig. 6, = *O. nicholsoni*].
1960 *Ormathops llanvirnensis* (Hicks); Whittard: 130; pl. 16, figs 8, 9.
1971 *Ormathops llanvirnensis* (Hicks); Clarkson: 52.

LECTOTYPE. Here selected: SM A45155, complete internal mould; figured Hicks 1875: pl. 9, fig. 4 and Whittard 1960: pl. 16, fig. 9.

TYPE LOCALITY AND HORIZON. Llanvirn, *D. artus* Biozone; Llanvirn Quarry, Dyfed.

MATERIAL. Hicks' other syntype, BGS GSM35238, is from the type locality, from which several further badly preserved specimens have been found. The species occurs sporadically in the Fennian, *D. levigena* Biozone, Llanfallteg Formation at Llanfallteg, locs 52A, B, P–S (It.19002–3; NMW 33.189.G15), and more frequently in the early Llanvirn Llanfallteg Formation at Llanfallteg, loc. 52 (NMW 84.17G.185); Long Plantation Cutting, Scolton, loc. 55 (NMW 84.17G.186); in Cefn-farchen farmyard, Llanfallteg (BGS Pr2029/30, Pr2031); at Cefn-maen-llwyd, Rhyd-y-wrâch, loc. 50 (NMW 84.17G.187); the Whitland district (NMW 33.189.G115); Castell-gorfod mill, north of St Clears (NMW 33.189.G150); and in *D.* '*bifidus*' shales, Afon Breinant, *c.* 2 km east of Llandeilo (BGS TCC414, TCC432).

DIAGNOSIS. *Ormathops* with preocular suture a little distant from anterolateral corner of glabella; with tiny eye of *c.* 12–15 lenses on a narrow lozenge of cheek defined by suture running in front of shallow palpebral furrow; 3P furrow shallow, sigmoidal; pygidium subparabolic with 8–9 axial rings and 6 pairs of pleural ribs with deep, narrow interpleural furrows; sculpture like *O. nicholsoni*.

DESCRIPTION. This species is very similar in general morphology to *O. nicholsoni*. Its glabella can be distinguished in being proportionately narrower (tr.) across 1P lobes, in expanding more rapidly forwards from a point further backwards and in having 3P furrow much shallower than 1P and 2P. The palpebral furrow is much shallower, and cannot be detected on badly preserved specimens. This is in constrast to *O. nicholsoni* where it can almost always be seen, even, for example, in the badly preserved lectotype (Whittard: 1960; pl. 16, fig. 6). There is a tiny eye composed of 12–15 lenses.

The pygidium is subparabolic and has a proportionately narrower axis, and wider pleural areas with deeper pleural furrows.

REMARKS. Although often quoted, *O. llanvirnensis* has been known only from badly preserved material from Llanvirn quarry, and Whittard (1960: 130) was uncertain whether it was synonymous with *O. nicholsoni*. Better material from old collections in the BGS and National Museum of Wales, apparently unknown to Whittard, as well as further material collected by us, now allows better understanding of this species, which can certainly be distinguished from *O. nicholsoni* as well as from other *Ormathops*. *O. alata* Whittard (1960: 131; pl. 16, fig. 10), based upon a

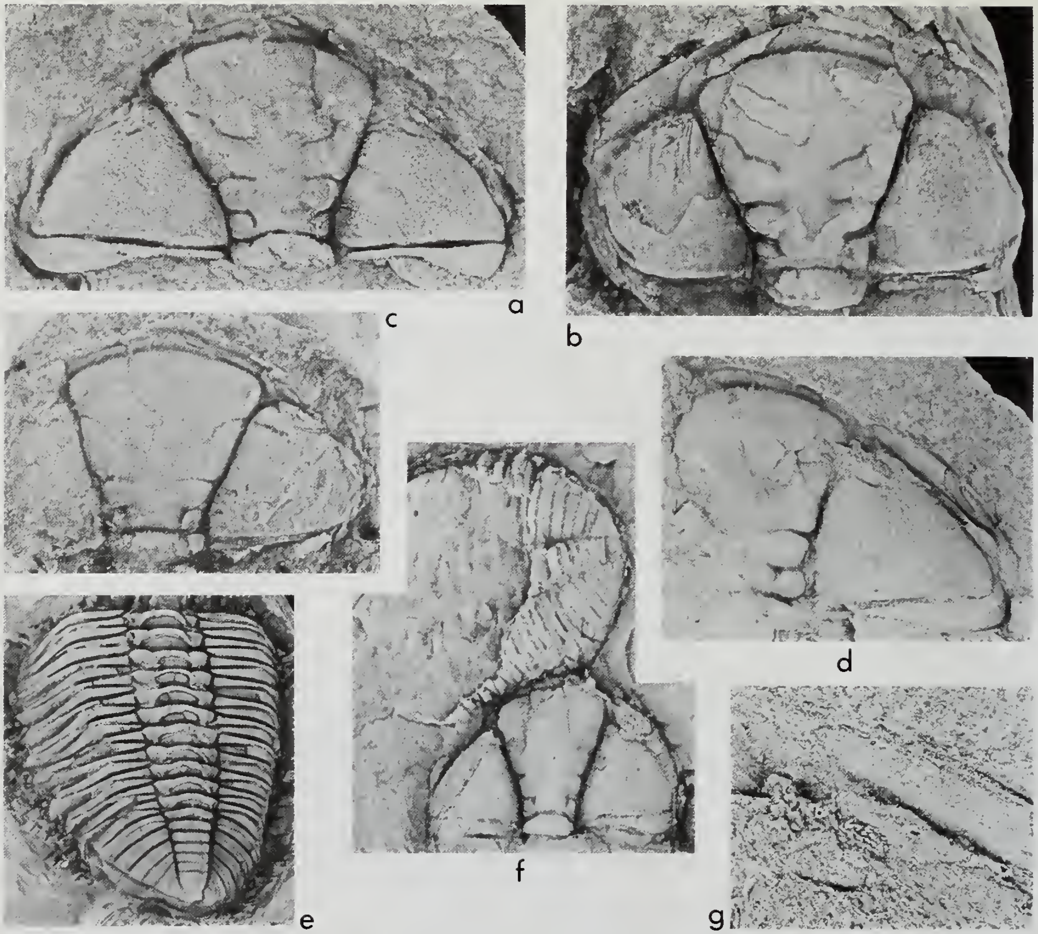


Fig. 103 *Ormathops llanvirnensis* (Hicks 1875). Llanfallteg Formation, uppermost Arenig, Fennian Stage, *D. levigena* Biozone (b, f) or basal Llanvirn, *D. artus* Biozone (others). a, well-preserved cephalon showing sculpture, latex cast from external mould, Whitland, × 3·5, NMW 33.189.G115; b, cephalon preserving original relief, and showing course of suture in front of glabella, loc. 52P, × 4, It.19002; c, incomplete cephalon, Cefn-farchen (Geological Survey loc. Pem. 24SE Eλ15), × 3, BGS Pr2031; d, incomplete cephalon, locality as Fig. 103c, latex cast from external mould showing eye, × 3, and g, detail of eye of same specimen showing lenses, × 8, BGS Pr2030; e, thorax and pygidium, Castell-gorfod mill, north of St Clears, × 1·5, NMW 33.189.G150; f, moult arrangement of displaced cephalon, thorax and pygidium, loc. 52T, Llanfallteg, × 3, It.19003.

single small cephalon from the Hope Shales, seems to be distinct from both *O. llanvirnensis* and *O. nicholsoni*; from the latter it can be distinguished in lacking a palpebral furrow and in having a straight 3P furrow, and from the former in having a deep, straight 3P furrow. It cannot be excluded, however, that *O. alata* may be simply an immature *O. llanvirnensis*; we lack comparative material of a similar size.

Family **ODONTOPLEURIDAE** Burmeister 1843

Genus ***SELENOPELTIS*** Hawle & Corda 1847

Type species. *Odontopleura buchii* Barrande 1846, by monotypy.

Diagnosis. See Bruton, *in* Bruton & Henry (1978: 894).

Selenopeltis buchi buchi (Barrande 1846)
(Fig. 104)

(For synonymy see Whittard 1961*b*: 197–198).

LECTOTYPE (selected Van Ingen 1901). National Museum, Prague, IT 700, ČD 714; original of Barrande (1852: pl. 37, fig. 25) and refigured Přibyl & Vaněk (1973: pl. 1, fig. 1).

TYPE LOCALITY AND HORIZON. Letná Formation, Caradoc; Bohemia.

OCCURRENCE IN WALES. Early Llanvirn Llanfallteg Formation (*D. artus* Biozone); Rhyd-y-wrâch, loc. 50.

FIGURED MATERIAL. Thorax and pygidium, It.19703.

DISCUSSION. The taxonomy of *S. buchi* has received a great deal of attention (Whittard 1961*b*; Dean 1964; Bruton 1968; Přibyl & Vaněk 1973; Bruton & Henry 1978) and we have nothing new to add here. We follow Bruton (*in* Bruton & Henry 1978) in using the familiar name *buchi* rather than *inermis* Beyrich as recommended by Whittard (1961*b*). But we regard *macrophthalma* Klouček as a subspecies of *buchi* rather than a separate species, because 'the only reliable criterion' (Bruton & Henry 1978: 896) for distinguishing the two is a difference in surface sculpture. The pygidial pleural fields of *buchi buchi* are coarsely tuberculate, while fine granulation is generally distributed over the exoskeleton of *macrophthalma*. The lectotype of *inermis* (Přibyl & Vaněk 1973: pl. 3, fig. 2) has coarsely rugose pygidial pleural fields and this may provide a criterion for recognizing this taxon.

A fine thorax and pygidium from the earliest Llanvirn of south Wales has coarse tubercles on the axial rings and on the pygidial pleural fields; it is the typical subspecies *buchi* in Bruton's sense. The lectotype of *buchi* does not show any details on the axis, but does show tuberculate free cheeks, which is the sculptural type associated with *buchi* on other examples. The figure of the fine specimen in Horný & Bastl (1970: pl. 19, fig. 1), as the subspecies *buchi*, was reproduced by Přibyl & Vaněk (1973) as the subspecies *inermis*; in sculptural type it is certainly like *buchi*, *sensu* Bruton (*in* Bruton & Henry 1978) and Whittard (1961*b*). The thoracic axis, however, is not tuberculate as it is on the Welsh material.

Fig. 104 *Selenopeltis buchi buchi* (Barrande 1846). Early Llanvirn, *D. artus* Biozone, Llanfallteg Formation, loc. 50, Cefn-maen-llwyd, cast of external mould (base of cranidium, thorax and pygidium showing tuberculation), × 3, It.19703.

Selenopeltis buchi macrophthalma (Klouček 1916)
(Fig. 105)

(For synonymy see Bruton 1968: 65. Also Bruton, *in* Bruton & Henry 1978: 895–896; pl. 1, figs 2, 3, 5, 7).

LECTOTYPE (selected Prantl & Přibyl, 1949*b*, as 'holotype'). National Museum, Prague, L 843; figured Bruton (1968: pl. 11, fig. 13). Šárka Formation, Llanvirn, Bohemia.

OCCURRENCE IN WALES. The earliest occurrence of *S. buchi macrophthalma* is in the late Arenig (Fennian, biozone of *Bergamia rushtoni*), type locality of the Pontyfenni Formation; it is also recorded from the latest Arenig (biozone of *Dionide levigena*) and the earliest Llanvirn (*D. artus* Biozone) of the Llanfallteg Formation, type section, and at Scolton. Whittard (1961*b*) records two Llanvirn occurrences in Dyfed, at Abergwili and St Clear's.

MATERIAL. More or less complete exoskeletons: It.19704, It.19710, NMW 84.12G.24; cranidium and pygidium: It.19705; also It.19547a, b, NMW 84.17G.90.

DISCUSSION. As noted above, the difference between *buchi buchi* and *buchi macrophthalma* is a sculptural one, and most reliably determined on the pygidium. A series of specimens from the Pontyfenni Formation shows the fine granulation typical of the subspecies *macrophthalma*, and there is no difference between these specimens and one from the early Llanvirn. Whittard (1961*b*) also drew attention to the more rapid backward curvature of the pygidial pleural ribs on *buchi buchi* compared with *buchi macrophthalma*; in effect the ribs on *macrophthalma* run out horizontally for a short distance before commencing their backward curve. Whether this subtle difference is consistent is difficult to say on the basis of a few specimens, but it does apply to the material we have collected (compare Fig. 104 with Fig. 105). Whittard reported *macrophthalma* from the Shelve Church Beds, which we would regard as probably equivalent in age to the Pontyfenni specimens.

There may prove to be a gradualistic series *macrophthalma–buchi–inermis*, but it will require a great deal of material to demonstrate it. At the moment the evidence supports the appearance

Fig. 105 *Selenopeltis buchi macrophthalma* (Klouček 1916). Upper Arenig, Fennian, *B. rushtoni* Biozone, loc. 23, Pontyfenni, cast from incomplete dorsal exoskeleton, × 2, It.19704; note lack of tuberculate sculpture and gently curved pygidial pleural ribs.

of the tuberculate *buchi* subspecies at the Arenig/Llanvirn boundary, which is of considerable stratigraphical interest.

No cranidium from south Wales shows evidence of the occipital spines which are found on *Selenopeltis gallica* Bruton and *binodosa* Dean.

Systematic descriptions: Graptoloids

by R. A. Fortey

We have not attempted to describe the dendroid graptolites in this work. Some of these were described by Bulman (1927) but there are many more species which would repay the attention of a systematist. As far as the graptoloids are concerned, Jenkins (1982) has more recently described the isograptids from Wales and this work does not require repetition here. Terminology follows that of Bulman (1970) with modifications introduced by Cooper & Fortey (1982). Frequent use is made of the stipe expansion diagrams employed by Cooper & Fortey, and thecal spacing is computed according to the method of Howe (1983), as well as the usual 'th in 10 mm'.

Stipe characters such as width, thecal inclination and overlap are customarily used in the definition of dichograptid species. Fortey (1983) showed that these are not truly independent characters, and that their interrelationships could be described geometrically. The characters used here are shown on Fig. 106. For partially flattened rhabdosomes the most accurately measured characters are: W, the stipe width; d, the thecal spacing; θ, thecal inclination and ϕ, the apertural angle. These effectively define the thecal length and width, as well as thecal overlap, for reasons of geometry alone. Stipe width, reflecting continued thecal growth, is clearly variable within single species. Thecal spacing tends to vary within at most 3–4 thecae per 10 mm on distal stipes.

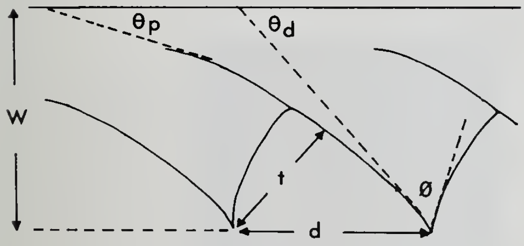


Fig. 106 Parameters used in the description of dichograptid stipes, modified from Fortey (1983). Thecal inclination can be divided into proximal, θp, and distal, θd; thecal spacing (d) is measured between apertural denticles, and a 5d measurement between th 10 and th 15 is also used as a standard; the usual thecal spacing of authors is the number of 'd in 10 mm' in the distal stipes.

Order **GRAPTOLOIDEA** Lapworth 1875

Family **DICHOGRAPTIDAE** Lapworth 1873

Subfamily **DICHOGRAPTINAE** Lapworth 1873

Genus ***TETRAGRAPTUS*** Salter 1863

Type species. *Fucoides serra* Brongniart 1828. The type specimen was located and type species redescribed by Cooper & Fortey (1982). *T. serra* occurs in the Penmaen Dewi Formation (Whitlandian) of Pwlluog, and is recorded on the range chart (p. 86).

Subgenus ***TETRAGRAPTUS*** Salter 1865

Diagnosis. See Cooper & Fortey, 1982: 190. The subgenus *Tetragraptus* (*Tetragraptus*) is used for those tetragraptids with reclined stipes, and development like that of *T.* (*Tetragraptus*) *serra*.

Tetragraptus* (*Tetragraptus*) *bigsbyi askerensis Monsen 1937
(Figs 107a, b)

1937 *Tetragraptus bigsbyi* var. *askerensis* Monsen: 172–173; pl. 4, figs 15, 16; pl. 5, fig. 35; pl. 13, figs 5, 6; pl. 19, figs 4, 6, 9.

Holotype. Palaeontological Museum, Oslo, K 0679; from the Lower Didymograptus Shale, *Phyllograptus angustifolius elongatus* Biozone (late Arenig); Slemmestad, Norway.

Diagnosis. See Monsen, 1937: 172.

Occurrence in south Wales. Upper Arenig, Fennian, *Bergamia rushtoni* Biozone at loc. 24, Llwyn-crwn.

Material. Q5798; NMW 33.189.G205.

Discussion. The lectotype of *T. bigsbyi bigsbyi* (Hall 1865) was figured by Skevington (1965), who discriminated this species from other reclined tetragraptids by its very steeply recurved stipes, producing a deeply U-shaped profile. The type is from a possible late mid-Arenig horizon at Lévis, Quebec (Skevington 1965: 5). Elsewhere *T. bigsbyi bigsbyi* is recorded from the early Arenig (Cooper 1979; Cooper & Fortey 1982) to the uppermost Arenig (Skevington 1965). Monsen (1937) distinguished several 'varieties' which are available for subspecific names. The stipes of the type and other fully grown specimens of *T. bigsbyi bigsbyi* are at least 2·5 mm, and usually more than 3 mm, wide at th 7–8. Monsen (1937) described 'var.' *askerensis* from the late Arenig of Norway, with narrower stipes; there is no doubt that these include mature specimens, because her pl. 9, figs 4, 6, 9 are actually larger than most specimens of *T. bigsbyi bigsbyi*. Stipe width is not usually a good specific character, but it may vary at population level from one closely related taxon to another. Monsen's population includes at least twelve specimens. These may prove to be population variants of *T. bigsbyi bigsbyi*, or may represent a separate subspecific group. Because two specimens from south Wales also have stipes less than 2 mm wide, and are of the same age as Monsen's *askerensis*, the latter explanation is tentatively adopted here, and the name *askerensis* is used as a subspecies.

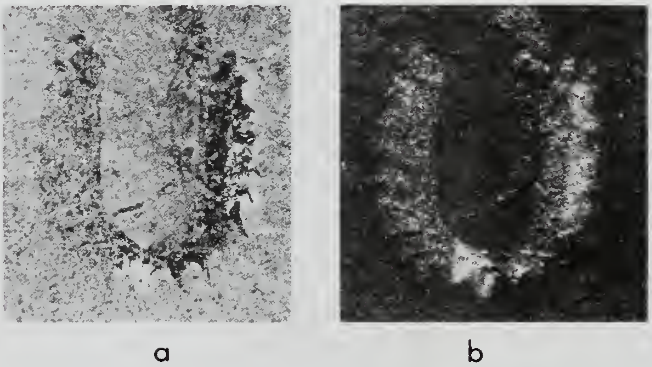


Fig. 107 *Tetragraptus* (*Tetragraptus*) *bigsbyi askerensis* Monsen 1937. Upper Arenig, Fennian, *B. rushtoni* Biozone, loc. 24. a–b, stipe pair, flattened, × 5, Q5798; a beneath alcohol, b in reflected light.

Tetragraptus* (*Tetragraptus*) *reclinatus reclinatus Elles & Wood 1902
(Fig. 108)

1902 *Tetragraptus reclinatus* Elles & Wood: 67, fig. 41; pl. 6, figs 5a–e.
1909 *Tetragraptus serra* (Brongniart); Cantrill, *in* Strahan *et al.*: 20.
1982 *Tetragraptus* (*Tetragraptus*) *reclinatus reclinatus* Elles & Wood; Cooper & Fortey: 203–205, figs 24, 25.

Lectotype. Q18, selected Cooper & Fortey (1982). This is the original of Elles & Wood, 1902: pl. 6, fig. 5c (and not fig. 5e as stated by Cooper & Fortey 1982).

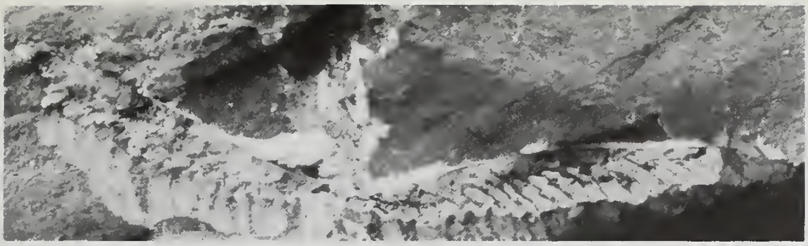


Fig. 108 *Tetragraptus* (*Tetragraptus*) *reclinatus reclinatus* Elles & Wood 1902. Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23, specimen preserved in partial relief, under alcohol × 3, Q5799.

TYPE LOCALITY AND HORIZON. Randel Crag, Lake District, probably *gibberulus* Biozone.

OCCURRENCE IN SOUTH WALES. Upper Arenig, Fennian, *Bergamia rushtoni* Biozone, Pontyfenni Formation, at loc. 23.

MATERIAL. Q5799.

DISCUSSION. The species was discussed in detail by Cooper & Fortey (1982) and further comment is not required here. Specimens from the Pontyfenni Formation are mostly too poor for subspecific determination, but the specimen figured preserves true stipe profiles, showing the gentle reclination characteristic of the species. Maximum stipe width on this specimen is 2·5 mm, slightly wider than the lectotype (Cooper & Fortey 1982: 209), but still narrower than *T. serra*. *T. reclinatus toernquisti* Monsen is narrower than *T. reclinatus reclinatus*, and the south Wales specimen is accordingly placed in the latter subspecies.

Tetragraptus (*Tetragraptus*) *reclinatus abbreviatus* Bouček 1956
(Fig. 109)

1956 *Tetragraptus* (*Tetragraptus*) *reclinatus abbreviatus* Bouček: 26; pl. 1, figs 2, 3; text-fig. 8a–d.
1973 *Tetragraptus reclinatus abbreviatus* Bouček; Bouček: 22–23; pl. 2, figs 5–7; text-fig. 3a–d.
1977 *Tetragraptus* cf. *pseudobigsbyi* Skevington; Kraft: 12–13 *pars*; pl. 5, fig. 2; pl. 6, figs 1, 2, 4 [*non* pl. 6, fig. 3].
1982 *Tetragraptus reclinatus abbreviatus* Bouček; Cooper & Fortey: 206–207, fig. 27.

HOLOTYPE. National Museum, Prague, L7607.

TYPE LOCALITY AND HORIZON. Klabava Formation, Rokycany, Bohemia; upper Arenig, *Tetragraptus reclinatus abbreviatus* Biozone.

OCCURRENCE IN SOUTH WALES. Upper Arenig, Fennian, *Bergamia rushtoni* Biozone. Pontyfenni Formation, loc. 23.

MATERIAL. Q5801.

DISCUSSION. This subspecies was described from quite good, although flattened, material by Bouček, 1973. Kraft (1973) regarded the taxon as inadequately characterized and referred Bouček's material to *T.* cf. *pseudobigsbyi* Skevington, 1965, figuring additional Bohemian specimens. Cooper & Fortey (1982) recognized both *T. pseudobigsbyi* and *T. reclinatus abbreviatus*

Fig. 109 *Tetragraptus* (*Tetragraptus*) *reclinatus abbreviatus* Bouček 1956. Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23, × 6, Q5801.

from Spitsbergen. The most important difference between these taxa is the deeply excavated thecal apertures of *T. reclinatus abbreviatus*, which cut back for a third or more of the total stipe width, and the ventrally projecting part of the sicula in this species, which forms a large 'tooth' on a line with the tips of th 1^1 and th 1^2. On *T. pseudobigsbyi*, as in *T. serra* and *T. reclinatus reclinatus*, the sicula lip is relatively inconspicuous compared with those of the first two thecae, and the apertural excavations are a quarter or less of the stipe width. These differences do seem worth recognizing taxonomically. The material recorded by Skevington (1965) as *T.* cf. *pseudobigsbyi* (late Arenig, Sweden) is like *T. reclinatus abbreviatus* in thecal characters. Whether any of Monsen's (1937) 'varieties' of *T. bigsbyi* are relevant for comparison is not yet known. It may prove that the subspecies *askerensis*—which is separated here—is the senior name for *abbreviatus*, because its proximal end characters (e.g. Monsen 1937: pl. 19, fig. 9) are apparently similar. None of the specimens illustrated by Bouček (1973) or Kraft (1977), however, have the deeply recurved stipes usually taken to characterize *T. bigsbyi.*

Genus ***DIDYMOGRAPTUS*** M'Coy 1851

Cooper & Fortey (1982) divided the old form genus *Didymograptus* into a number of subgenera, and attempted to define each one as a monophyletic group. This is the procedure which we follow here. It is not without attendant difficulties, because the definition of phylogenetically based subgenera requires a knowledge of proximal end structure of the type species of each. These subgenera arose by the elevation by various authors of Elles & Wood's (1901) informal subdivisions based on gross rhabdosomal form, and there is no certainty that developmental details will be known for the nominated type species, or even that they will have well-preserved proximal ends.

Subgenus ***DIDYMOGRAPTUS*** M'Coy 1851

TYPE SPECIES. *Graptolithus murchisoni* Beck 1839.

DIAGNOSIS. Subgenus of *Didymograptus* with pendent stipes. Proximal end shows a long and narrow sicula with low origin of th 1^1.

DISCUSSION. Cooper & Fortey (1982) distinguished two subgenera of pendent *Didymograptus: Didymograptus* s.s. and *Didymograptellus*, type species *D. bifidus* (Hall). On the latter they demonstrated isograptid development, which is primitive for the graptoloids as a whole. Th 1^1 has an origin high on the sicula, and the two grow downwards side by side before beginning further thecal budding, which is typically isograptid. Where it is known, most Arenig pendent *Didymograptus* have such development, and are to be referred to *Didymograptus* (*Didymograptellus*). Another type of proximal end development, termed the *artus* type—to replace the so-called *bifidus* type of Bulman, 1936 (see Cooper & Fortey 1982: 172; 1983: 206)—has the th 1^1 dicalycal. At the time of publication of Cooper & Fortey (1982) proximal end descriptions of Llanvirn pendents suggested that the *artus* type may have been the rule for these, and this was incorporated into the diagnosis of *Didymograptus* (*Didymograptus*). Since that time Jenkins (1983) has described *D. pluto* partly from relief material of Llanvirn age; this species has isograptid development like that previously described in *D. minutus*. Strachan & Khashogji (1984) have redescribed the type slab from Builth with *D. murchisoni* on which the concept of *Didymograptus* (*Didymograptus*) has to be founded. Cooper & Fortey (1982) noted that this slab does not include specimens good enough to be sure of development type and used indirect evidence to infer that *artus* development was likely. However, Strachan & Khashogji (1984) have since figured a specimen from Shelve, claimed to be conspecific with *murchisoni*, with an isograptid arch and hence an isograptid development. Unequivocal *artus* development is known from other Llanvirn pendents (summary in Cooper & Fortey 1983).

It is clear from the foregoing that both a form of isograptid development and *artus* development occur in Llanvirn pendent didymograptids, and that it is often impossible, from flattened material, to be sure which pertains. For the definition of *Didymograptus* (*Didymograptus*) it is therefore preferable to have some character which will distinguish it from *Didymograptus*

(*Didymograptellus*) without recourse to finer details of branching which are not visible from the types of established species. Even the identification of *D. murchisoni* from Shelve (by Strachan & Khashogji, 1984) or Abereiddi Bay (by Jenkins, 1982) is itself an inference. Jenkins claims *artus* development type for *murchisoni*, while Strachan & Khashogji claim isograptid development type for the same species. However, a character present on type *murchisoni* and other Llanvirn pendents is a low metasicular origin of th 1^1. We here diagnose *Didymograptus* (*Didymograptus*) to emphasize this character. The typical sicula is as shown by Jenkins (1983: text-fig. 2) or Fig. 112 herein: a long, narrow cone enclosing an angle of only 10°–15°. The side-by-side arrangement of the sicula and th 1^1 in *Didymograptus* (*Didymograptellus*) produces a broader cone projecting above the stipes and enclosing an angle of about 30°. This difference can be made out on many flattened specimens; it therefore affords a practicable way of discriminating *Didymograptus* (*Didymograptus*) from *Didymograptus* (*Didymograptellus*).

Didymograptus* (*Didymograptus*) *spinulosus Perner 1895
(Figs 110, 111, 112a)

1895 *Didymograptus spinulosus* Perner: 22; pl. 5, figs 9, 10.
?1895 *Didymograptus bifidus* var. *incertus* Perner: 23; pl. 5, figs 5, 6, 8; pl. 6, fig. 2.
?1901 *Didymograptus stabilis* Elles & Wood: 49; pl. 4, fig. 2.
1932 *Didymograptus spinulosus* Perner; Bouček: text-fig. 3A.
1973 *Didymograptus spinulosus* Perner; Bouček: 88–90; pl. 13, figs 1–4; text-fig. 27.
?1973 *Didymograptus incertus* Perner; Bouček: 91–93; pl. 13, fig. 5; text-fig. 28.
1973 *Didymograptus* cf. *acutus* Ekström; Skevington: 45–46; pl. 8, fig. 2.
1983 *Didymograptus pluto* Jenkins: 642–647, text-figs 2–4 (? part only).

HOLOTYPE. National Museum, Prague NM-L 7564. The only original specimen, according to Bouček (1973: 89).

TYPE HORIZON AND LOCALITY. Lower Llanvirn, Šárka Formation, *Corymbograptus retroflexus* Biozone; village of Osek, Bohemia.

OCCURRENCE IN SOUTH WALES. Llanfallteg Formation, early Llanvirn part; loc. 52, Llanfallteg railway cutting, loc. 50, Cefn-maen-llwyd and loc. 55, Scolton.

MATERIAL. Q5161, Q5163, and distal stipe fragments.

DISCUSSION. Cooper & Fortey (1982) and Jenkins (1983) emphasized the importance of proximal end structure in interpreting pendent didymograptids, which are probably the most difficult group of dichograptids to determine specifically. Variation within populations is also important; the opposite extremes in approach to variation are illustrated by the work of Jenkins (1983), who treated all specimens from one horizon as part of a single species, and that of Mu *et al.* (1979), who adopted a typological approach. It is clear, however, that the number of named species must be excessive, given the few specific characters available.

The earliest abundant pendent didymograptids in south Wales appear within the Llanfallteg Formation at what we have taken as the Arenig–Llanvirn boundary. A well-preserved proximal end (Fig. 112a) shows what is interpreted as an isograptid arch; it appears to be identical to that figured by Jenkins (1983: text-fig. 2)—that is, it shows isograptid development type. The low origin of th 1^1 and the narrow sicula 2 mm in length are clearly shown on this specimen, which conforms to *Didymograptus* (*Didymograptus*) as diagnosed herein. Stipe width at th 1 is 0·5–0·6 mm; the stipe expansion curve (Fig. 111) shows rapid proximal expansion over the first ten thecae or so, while the curve flattens distally so that there is little or no distal increase, at a final width of 1·4–1·8 mm. Thecal spacing distally is 14–16 thecae in a 10 mm section of stipe. Distal stipes are parallel to slightly divergent, and no taxonomic importance is attached to final stipe attitude.

The description just given precisely matches that of the holotype of *D. pluto* Jenkins 1983, from the Great Paxton borehole. This specimen is the right-hand one photographed by Skevington (1973: pl. 8, fig. 2); the specimen number referred to by Jenkins (1983: 643) is BGS By8204. This, in the Geological Survey catalogue, is a bivalve, *Redonia*, and this quoted

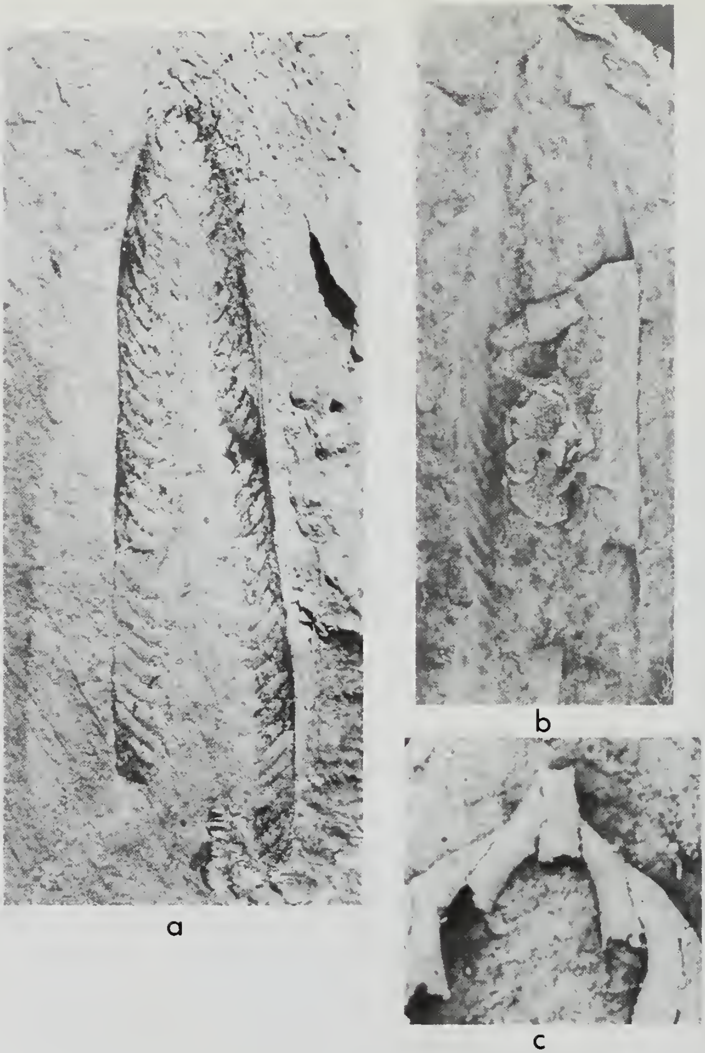


Fig. 110 *Didymograptus (Didymograptus) spinulosus* Perner 1895. a, early Llanvirn, *D. artus* Biozone, Llanfallteg Formation, loc. 55, whole rhabdosome, × 4, Q5163; b, Lower Llanvirn, cast of holotype, *C. retroflexus* Biozone, Šárka Formation, Osek, Bohemia, × 4, Nat. Mus. Prague NM–L 7564 (cast supplied by Dr R. Prokop); c, as last, latex cast of proximal end (showing probable isograptid development in obverse view, sicula incomplete), × 15, Nat. Mus. Prague NM–L 7562, specimen figured by Bouček (1973: pl. 13, fig. 1).

number is clearly an error for By8205—which is the specimen number for Skevington's figured slab. Fig. 111 shows the identical stipe expansion diagrams for one of the fully grown specimens from the Llanfallteg Formation and the holotype of *D. pluto*. However, the description also matches the type specimen of *D. spinulosus* Perner 1895 from the early Llanvirn *Corymbograptus retroflexus* Biozone of Bohemia; the stipe expansion diagrams completely overlap. Furthermore, Bouček (1973: pl. 13, fig. 1, lower left; Fig. 110c herein) has figured a specimen in relief which shows a good isograptid arch in obverse view, and another (*ibid.*, fig. 4) which shows a narrow sicula. On the basis of comparison with these specimens we are obliged to refer the Llanfallteg material, and *D. pluto*, to the senior species *D. spinulosus* Perner, a form

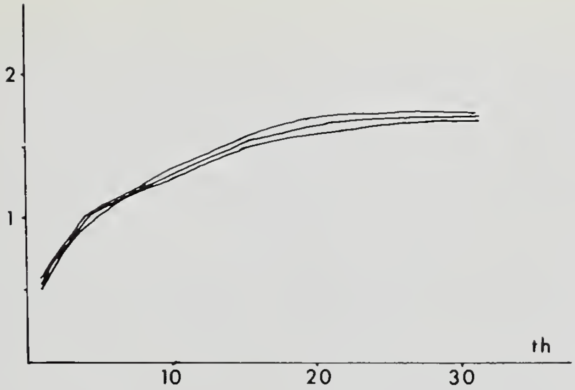


Fig. 111 Stipe expansion diagram for the type of *D. spinulosus* Perner 1895, the type of *D. pluto* Jenkins 1983, and the specimen of *D. spinulosus* shown on Fig. 110a, showing coincidence of growth curves.

which was not considered by Jenkins when he listed comparisons with *D. pluto*. Given the other similarities of British and Bohemian faunas, both among graptolites and trilobites, it is not surprising to find that there are similarities among the pendent didymograptids.

Although the type-for-type comparisons are straightforward, there are problems when whole populations are considered. Jenkins (1983: 645) included an extremely wide range of variation in *D. pluto*, reflecting 'successive populations of one slowly evolving species'. This included not only variation in distal stipe width, which is common in dichograptoids, but also very wide ranges in thecal spacing, sicula length, and so on. The variation was sufficient to encompass perhaps the majority of other described pendents. Probably the most surprising aspect of such variation was the inclusion within the same species of forms with distally uniform stipes like the holotype, and those with more-or-less slow, continuous increase in stipe width throughout the rhabdosome (e.g. Jenkins 1983: text-fig. 3k, u). This difference was originally used by Elles & Wood (1901: 37, 45) to discriminate 'species groups' within the pendent didymograptids. In my experience the shape of the stipe expansion is constant within a dichograptid species, even when distal characters, especially stipe width, are variable. Stipe growth patterns are discernible on most specimens, other than those gerontomorphic ones in which the proximal end has become enveloped within a covering of periderm. A continuous increase in stipe width is supposedly characteristic of the Llanvirn forms referred by Elles & Wood to *D. bifidus* Hall, which are now known (Cooper & Fortey 1982) to be unrelated to Hall's species which is of Arenig age and has a different proximal end development. Perner (1895) named several other species from the same horizon as *D. spinulosus*: *D. oligotheca*, *D. barrandei*, *D. bifidus incertus*. If *D. spinulosus* were as variable as Jenkins' description of *D.* '*pluto*', some, if not all, of these 'species' would be included together, and the choice of *D. spinulosus* as a name would become arbitrary. Bouček (1973: fig. 28b) figured what appears to be *artus* development on *D. incertus* (to which he gave specific recognition), and if this is substantiated it will be different enough from *spinulosus* to exclude it from consideration. Several British species, such as *D. stabilis* Elles & Wood, and some of the Llanvirn *D.* '*bifidus*', would possibly be included within *D. spinulosus*, even allowing moderate intraspecific variation, although the proximal structure of the specimens used by Elles & Wood is not clear.

The nomenclatorial situation is highly complicated, and best resolved in the context of a review of the pendent didymograptids as a whole, which is beyond the scope of this work. As long as we adhere to the *Rules of Zoological Nomenclature* the Bohemian species of Perner, 1895, revised by Bouček (1973), cannot be ignored. They have the advantage that they antedate the subsequent proliferation of names. It seems likely that the proximal end structure with low sicular origin of th 1^1 and isograptid development is widespread in Llanvirn pendents (see also

Strachan & Khashogji 1984), although how many 'species' it applies to is not resolved. If Jenkins' (1983) wide degree of intraspecific variation is accepted, *spinulosus* will acquire several synonyms. However, such characters as the shape of the stipe expansion diagram may prove important in discrimination of species, and multivariate statistical treatment of pendents may help in the recognition of species with overlapping ranges of variation. For example, the range of 11 to 25 distal thecae in 10 mm shown by Jenkins (1983: text-fig. 1) is extraordinarily large for a single species, but could be produced by overlap of two or more normal curves of lesser span. In any case, we cannot apply any name other than *D. spinulosus* Perner to these early Llanvirn pendents from the Llanfallteg Formation.

Didymograptus* (*Didymograptus*) *artus Elles & Wood 1901
(Figs 112b–d, 113)

1901 *Didymograptus* (*Didymograptus*) *artus* Elles & Wood: 48–49, fig. 30; pl. 4, figs 6a–d.
1931 *Didymograptus artus* Elles & Wood; Bulman: 31, text-fig. 9.
1932 *Didymograptus artus* Elles & Wood; Bouček: 128, text-fig. 3d–f.
1947 *Didymograptus artus* Elles & Wood (*pars*); Ruedemann: 326–327; pl. 54, figs 3–7, 9 [*non* figs 8, 10].
1967 *Didymograptus artus* Elles & Wood; Skwarko: 171–190; pls 21–23.
1973 *Didymograptus artus* Elles & Wood; Bouček: 85–87, fig. 26e–g; pl. 15, fig. 7.
1976 *Didymograptus artus* Elles & Wood; Legg: 28; pl. 9, figs 1–6.
1979 *Didymograptus* cf. *artus* Elles & Wood; Mu *et al.*: 64; pl. 21, fig. 2.

HOLOTYPE. SM A17772, as specified by Elles & Wood (1901: 49).

TYPE LOCALITY AND HORIZON. Early Llanvirn; Thornship Beck, Shap, Cumbria.

OCCURRENCE IN SOUTH WALES. Llanfallteg Formation, the first pendent to appear at the Arenig–Llanvirn boundary. On type section, loc. 52, and at loc. 50, Cefn-maen-llwyd. Elles & Wood figured the species from Ramsey Island, and if some of the *D. 'bifidus'* prove to be intraspecific variants, it occurs also at Llanvirn quarry.

DIAGNOSIS. *Didymograptus* (*Didymograptus*) with th 1^1 dicalycal; sicula slender, 1·3–1·6 mm long; stipes 0·4–0·6 mm wide at th 1, expanding gradually to a width of 1·2–1·6 mm at about th 20 and almost constant thereafter. Thecal spacing typically dense, 18 in 10 mm distally or more, although specimens with 15–17 per 10 mm may prove to belong in the species. Distal stipe characters: θ 40°–55°, ϕ acute, 30°–45°.

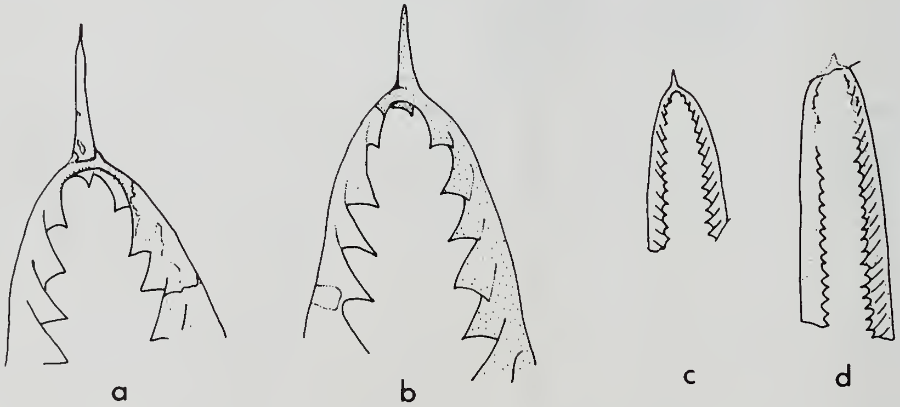


Fig. 112 a, *Didymograptus* (*Didymograptus*) *spinulosus* Perner 1895, early Llanvirn, *D. artus* Biozone, Llanfallteg Formation, loc. 52, 18 m above first appearance of pendent graptoloids, proximal end showing isograptid arch, × 10, Q5161. b–d, *Didymograptus* (*Didymograptus*) *artus* Elles & Wood 1901, early Llanvirn, *D. artus* Biozone; b, loc. 52, basal bed of Llanvirn, proximal end, × 10, Q5165; c, loc. 50, × 3, Q5166; d, loc. 52, × 3, Q5164.

MATERIAL. Q5162, Q5164–6, NMW 84.17G.91–3. Specimens with looser thecal spacing, Q6167–8.

DISCUSSION. Material from the type locality is not well preserved, and none we have examined shows the proximal end characters. However, the very dense thecal spacing is unusual enough to make it probable that Skwarko (1967) was correct in identifying his perfectly preserved specimens with *D. artus*, and which has th 1^1 dicalycal. A proximal end from the Llanfallteg Formation (Fig. 112b) also shows a dicalycal th 1^1, and the length of the sicula and narrow proximal stipe width compare with the type of *D. artus* and with Skwarko's specimens. Distal stipes such as Q5164 show the dense distal thecal spacing (18–20 in 10 mm) which Elles & Wood considered diagnostic of the species. Such specimens can be referred to *D. artus* confidently. Specimens from the Llanfallteg Formation have the stipes distally slightly divergent. The sicula size is smaller than on *D.* (*D.*) *spinulosus*, well under 2 mm on our specimens, but there are not enough specimens to be certain there was no intraspecific variation. However, other descriptions of *D. artus* agree on the small size of the sicula; the smallest measurement given is 1·2 mm by Bulman (1931).

As was discussed for *D.* (*D.*) *spinulosus* above, problems become apparent when larger populations are considered. For example, specimens from the Llanfallteg Formation, loc. 50, have thecal spacing as low as 15 per 10 mm in distal stipes (Q5137). These may well prove to be part of the population of *D. artus*—but proximal end preservation is not good enough to show the mode of development. Legg (1976) included specimens from Western Australia with thecal spacing of 16–17 per 10 mm within a population of *D. artus*; similar specimens from the Lake District were figured by Skevington (1970: figs 83, f). Such variation opens up the possibility that former south Welsh records of *D. stabilis* (as at Lampeter Velfrey, Cantrill *in* Strahan *et al.* 1914: 26), and *D.* cf. *bifidus*, refer to population variants of *D. artus*. Further there are (?distorted) specimens from the type locality at Thornship Beck (e.g. H2739) with the dense thecal spacing of *D. artus*, but distal stipe width reaching more than 2 mm—like *D.* '*bifidus*' from Llanvirn Quarry. The range of variation within *D. artus* obviously needs further clarification, and may even extend to include some of the British '*bifidus*' although presumably not those with larger siculae. In the mean time, it does seem to be correct to refer those narrower specimens with dense thecal spacing, a small sicula, and dicalycal th 1^1 to *D. artus*, *sensu stricto*. Slightly more slender forms from China have been referred to *D. changningensis* Ni (*in* Mu *et al.*, 1979).

Because it is a widespread species *D. artus* is regarded as the most suitable zonal index to replace *D.* '*bifidus*' (*non* Hall) as the nominate species for the basal biozone of the Llanvirn.

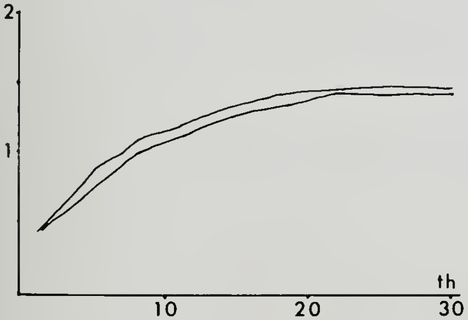


Fig. 113 Stipe expansion diagram for two typical examples of *D. artus* from south Wales.

Subgenus ***DIDYMOGRAPTELLUS*** Cooper & Fortey 1982

TYPE SPECIES. *Graptolithus bifidus* Hall 1865, by original designation.

DIAGNOSIS. Subgenus of *Didymograptus* with pendent habit; th 1^1 originates high on sicula, and the two grow together to form a pair. Development of isograptid type.

Didymograptus (*Didymograptellus*) sp.
(Fig. 114)

Occurrence. Fennian, *Bergamia rushtoni* Biozone, Pontyfenni Formation; loc. 23, Pontyfenni.

Material. One specimen, Q5170.

Discussion. This incomplete specimen is worth noting as a rare example of a pendent didymograptid from below the Llanvirn in Wales. It is not possible to determine it on the basis of so little material, and because the proximal part is not well preserved. It does, however, apparently show a high origin of th 1^1 and is therefore to be assigned to *Didymograptellus*. The sicula is only about 1 mm long, but may not be preserved distally; stipes expand to 1 mm in width; three thecae in 2 mm at the distal end indicate a probable mature thecal spacing of 14–15 in 10 mm, which is like *D. bifidus* (Hall). Stipe width is more like that of *D. protobifidoides* Bouček 1973. Small, distorted pendent didymograptids from Aber Mawr, Ramsey Island (loc. 62), are also late Arenig, but are not specifically determinable.

Fig. 114 *Didymograptus* (*Didymograptellus*) sp. Upper Arenig (Fennian), *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23, × 10, Q5170.

Subgenus *EXPANSOGRAPTUS* Bouček & Přibyl 1953

[= *Extensograptus* Bouček & Přibyl 1953*a*: 267 (presumably a mis-spelling, repeated in error by Bulman, 1970: V104).]

Type species. *Graptolithus extensus* Hall 1865.

Didymograptus (*Expansograptus*) *hirundo* Salter 1863
(Figs 115, 116, 117, 120c)

1863 *Didymograptus hirundo* Salter: 137, fig. 13f.
1870 *Didymograptus patulus* Hall; Nicholson: 339–341; pl. 7, fig. 1 [*non* text-fig. 1].
1898 *Didymograptus patulus* Hall; Elles: 504–506, figs 22–23.
1901 *Didymograptus hirundo* Salter; Elles & Wood: 15–17; pl. 1, figs 5b, c [?*non* fig. 5a].
?1934 *Didymograptus hirundo* Salter; Hsü: 26; pl. 1, figs 8a–d.
1936 *Didymograptus hirundo* Salter; Bulman (*pars*): text-fig. 25e [?*non* fig. 25f].
1937 *Didymograptus hirundo* Salter; Monsen: 120–121; pl. 15, figs 8, 12.

?*non* 1947 *Didymograptus hirundo* Salter; Ruedemann: 334–335; pl. 55, figs 45, 47; pl. 56, fig. 26.
1951 *Didymograptus hirundo* Salter; Gigout: 277; pl. 2, fig. 6.
1953 *Didymograptus hirundo* Salter; Spjeldnaes (*pars*): 178, text-fig. 2c, ?d [*non* fig. 2e].
1974 *Expansograptus hirundo* (Salter) Tsai; 76–77; pl. 6, figs 10–14.
1985*a* *Didymograptus hirundo* Salter; Rushton: 197–198.

LECTOTYPE. BGS GSM6803. Salter's original listing indicates that he had two collections with *D. hirundo* to hand, and these specimens are therefore syntypes. Elles & Wood's (1901: 17) identification of Salter's 'type specimen' is therefore regarded as a lectotype designation.

TYPE LOCALITY AND HORIZON. Skiddaw Slates, Ellen Gill, Lake District (a locality not to be confused with the better-known Ellergill). At or near the type locality (Rushton 1985*a*) there is a graptolite fauna which may indicate the *I. gibberulus* Biozone. Biserial graptolites are lacking. Elsewhere in the Lake District *D. hirundo* appears earlier than the biserial graptolites, and it is the abundance of these, rather than the presence of *D. hirundo* itself, which is the feature of the *D. hirundo* Biozone in the usage of Jackson (1962).

OCCURRENCE IN SOUTH WALES. Fennian, *B. rushtoni* Biozone, Pontyfenni Formation; Llwyn-crwn, loc. 24, apparently below the appearance of biserial graptolites; and at Pontyfenni (loc. 23) along with the earliest examples of biserial graptolites. True *D. hirundo* also occurs in the Tankerville Flags in Shropshire.

MATERIAL. Q5148–9, NMW 84.17G.94–5.

DIAGNOSIS. *Didymograptus* (*Expansograptus*) reaching large size, stipes slightly reclined. Initial thecal growth rapid, stipe width increasing quickly from 1·5 mm over first five thecae, but stipes continue to widen gradually distally to at least th 70, and a maximum width of 3·3–3·6 mm. Thecal apertures thus describe a distinct arch beneath the sicula. Thecal spacing of 11–12 thecae in 10 mm distally (th 10–th 15 repeat distance about 4·5 mm). Thecae curved, distal inclination 50°–60° to dorsal wall, thecal apertures strongly flared, cutting back to about a quarter of stipe width distally.

DESCRIPTION. The description modifies that of Elles & Wood (1901). Rushton (1985*a*) illustrated the type and other material from the type locality. Specimens from south Wales and the Lake District are without doubt conspecific, and *D. hirundo* is perhaps one of the more distinctive species in the monotonous *Expansograptus* group. As Elles & Wood noted, it can grow exceptionally large—some rhabdosomes exceeded 60 cm across. There is a small declined part at the proximal end corresponding to about three thecae on either stipe, then distally the stipes become slightly reclined, and straight; the reclination accounts for no more than 15°, usually 5°, as measured from a horizontal line drawn normal to the long axis of the sicula. This slight reclination appears to be characteristic and consistent for the species. Elles & Wood give an 'exceptionally long' sicula length exceeding 3 mm. This appears to have been based on specimens from Nant-y-Gadwen, Llŷn, or Lake District specimens which are not usual. The type, and others here placed in *D. hirundo*, have a sicula which is 2·3–2·6 mm long (as does the original of Elles & Wood 1901: text-fig. 9b). Th 1^1 originates high on the sicula; isograptid development cannot be proved from any of our material. Subsequent thecal growth is shown by the stipe expansion diagrams (Fig. 116). Increase in stipe width is very rapid beneath the declined part of the rhabdosome, gradually decreasing in magnitude distally, but the stipes *do* continue to increase in width for a considerable length, and this is highly characteristic of the species, being unusual among extensiforms. This increase continues at least as far as th 70, and probably very gradually to th 100 in some cases. The shape of the stipe expansion curve is typical of the species, but the ultimate stipe width is variable. At th 30 we have widths varying between 2·75 and 3·0 mm (mean 2·9 mm); the greatest stipe width we have recorded is 3·75 mm, but Elles & Wood mention stipes as wide as 4 mm. The narrowest dimension in the mature (about th 100) stipe we have seen is 3·0 mm. Ultimate stipe width is not an important specific character; wider stipes are associated with continued thecal growth, and hence, for geometrical reasons (Fortey 1983) with thecae with slightly higher distal inclinations.

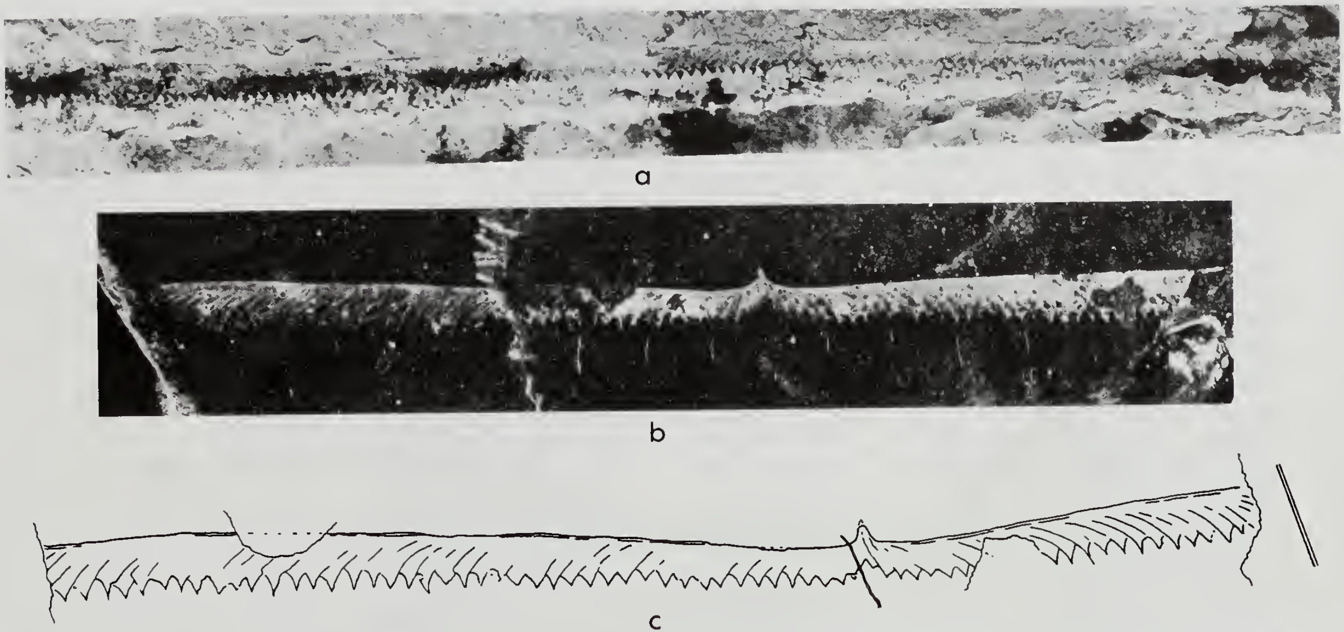


Fig. 115 *Didymograptus* (*Expansograptus*) *hirundo* Salter 1863. a, Upper Arenig, Fennian (*B. rushtoni* Biozone), Pontyfenni Formation, loc. 24, large rhabdosome from south Wales, Q5148, × 1·5; b, Skiddaw Slates, probably *I. gibberulus* Biozone, Randel Crag, Cumbria, × 2, Fitz Park Museum, Keswick, Harrison Coll. c, Ellen Gill, about 5 km north-east of Bassenthwaite, Cumbria, probably *I. gibberulus* Biozone, lectotype, GSM6803, × 2·8, refigured from Rushton (1985a: fig. 1).

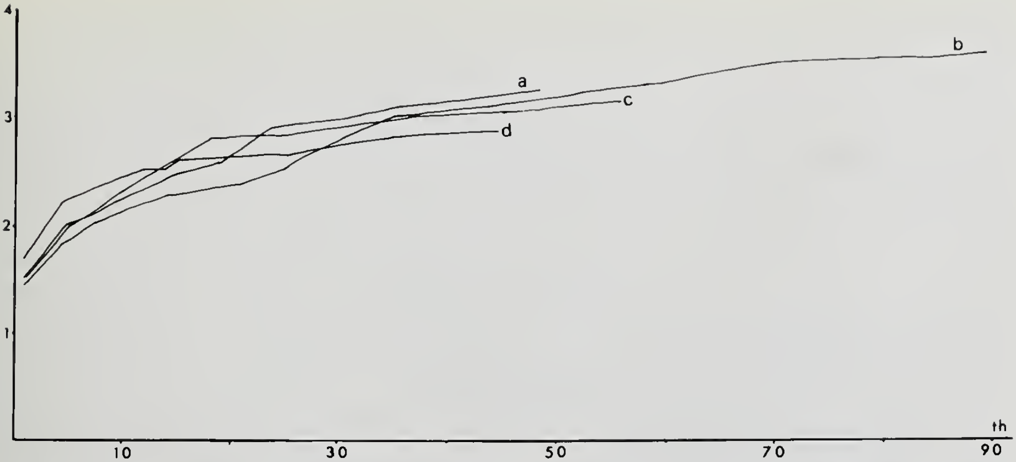


Fig. 116 Stipe expansion diagram for *Didymograptus* (*Expansograptus*) *hirundo* Salter, showing rapid proximal increase and distal slow but regular increase in stipe width. c is lectotype; b, large specimen from south Wales, Fig. 115a; a, d, two other Lake District specimens.

Thecae are highly curved, with initial θ 20°–30°, apertural θ 50°–60° (?70°) according to the stage of growth reached; as always with curved thecae, they are conical, with distal t less than 1 mm; l, exclusive of common canal, up to 4 mm. The flared apertures are concave, and cut back to about a quarter of the stipe width in the distal part of the stipe, proportionately more proximally. For thecal spacing, our measurements differ from those of Elles & Wood, who quote 9–10 thecae in 10 mm. All the specimens we would attribute to *D. hirundo* have between 11 and 12 thecae included within 10 mm in the mature part of the stipe; in fact this spacing pertains from about th 7 to the end of the stipe. In terms of thecal repeat distance, five thecae th 10–th 15 is taken as standard, and 5d on all our specimens lies between 4·4 and 4·6 mm.

Discussion. There are a number of specimens attributed to *D.* (*Expansograptus*) *hirundo* by Elles & Wood (1901: pl. 1, fig. 5a) and Bulman (1936) in which the sicula and proximal thecae appear to have continued to grow to effectively fill in the arch between the first three thecae, making the ventral margin of the stipe perfectly straight throughout the rhabdosome. Specimens apparently of this kind from China were described as *D. abnormis* by Hsü (1934). In other characters they are like *hirundo*, and they consistently occur together at the same horizon. It is possible that such specimens are aberrant individuals of *D. hirundo*, although this cannot be certainly demonstrated, and in the synonymy they are excluded with caution from the species.

In south Wales we have recovered *D. hirundo* from the upper part of the Fennian, *B. rushtoni* Biozone; in the Lake District it first occurs in the equivalent *I. gibberulus* Biozone, as noted above, but extends into Jackson's (1962) *D. hirundo* Biozone with abundant biserials. In Shrop-

Fig. 117 *Didymograptus* (*Expansograptus*) *hirundo* Salter. See Fig. 115a. Detail of flattened proximal end, showing high inclination of ventral walls of thecae to either side of sicula, × 10, Q5148.

shire it occurs in the Tankerville Flags, in the probable equivalent of the *B. rushtoni* Biozone. *D. hirundo* is therefore distributed through the upper two trilobite biozones of the Fennian; it does not extend into the Llanvirn. In spite of the confusion over its extended distribution compared with the biozone that carries its name, it is a stratigraphically useful species. Outside Britain what is probably the true *hirundo* occurs in the biozone of *Phyllograptus angustifolius elongatus* in Norway, and also in Morocco. Hsü (1934) figured *D. hirundo* and Mu *et al.* (1979) described *D.* cf. *hirundo* from south-west China; the proximal details are too obscure to be sure whether this material is conspecific or not.

Didymograptus* (*Expansograptus*) *nitidus (Hall 1858)
(Figs 118, 119, 120d)

1858 *Graptolithus nitidus* Hall: 129.
1865 *Graptolithus nitidus* Hall (*pars*): 69–71; pl. 1, figs 1–7, 9 [*non* fig. 8].
1868 *Didymograptus nitidus* (Hall) Nicholson (*pars*): 135.
?1892 *Didymograptus nitidus* (Hall); Barrois: 91–92.
1901 *Didymograptus nitidus* (Hall); Elles & Wood: 10–11, figs 5a–d; pl. 1, figs 2b, c [?*non* fig. 2a]. (Gives earlier British synonymy.)
1904 *Didymograptus nitidus* (Hall); Ruedemann: 671–674, figs 66–70; pl. 13, figs 1–5; pl. 14, figs 5, 6.
non 1912 *Didymograptus nitidus* (Hall); Hoeck: pl. 13, figs 8, 9.
1928 *Didymograptus nitidus* (Hall); Matley: 491 (listed).
1947 *Didymograptus nitidus* (Hall); Ruedemann: 339–340; pl. 55, figs 11–13 [?*non* fig. 14].
1960 *Didymograptus nitidus* (Hall); D. E. Thomas: 28; pl. 4, figs 40, 42. (Gives earlier Australian references.)
non 1960 *Didymograptus nitidus* (Hall); Berry: pl. 8, fig. 11.
1963 *Didymograptus nitidus* (Hall); Ross & Berry (*pars*): 88–89 [*non* pl. 5, figs 2, 4].
non 1976 *Didymograptus nitidus* (Hall); Braithwaite: 44–48; pl. 9, figs 8, 12, 14–23; pl. 18, figs 1–8; pl. 19, figs 1–6 [= *Xiphograptus* sp.].
?1979 *Didymograptus nitidus* (Hall); Mu *et al*: 98; pl. 34, figs 11, 12 (high horizon, insufficient description). (Earlier Chinese references listed.)
1982 *Didymograptus nitidus* (Hall); Cooper & Fortey: fig. 40f, g.

LECTOTYPE (here selected). Original of Hall (1865: pl. 1, fig. 7); GSC 914b, figured here as Fig. 118a.

TYPE LOCALITY AND HORIZON. Quebec Group shales at Point Lévis, Quebec. Raymond (1914: 524, 529) records the species from the lower part of the *Didymograptus bifidus* Biozone, at

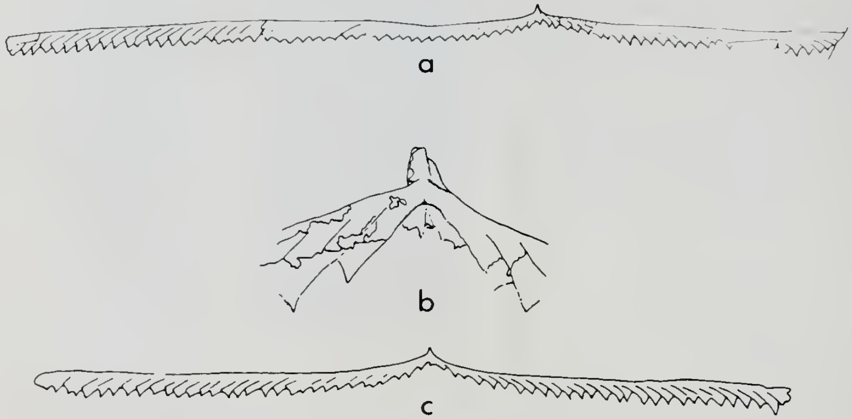


Fig. 118 *Didymograptus* (*Expansograptus*) *nitidus* (Hall 1858). Arenig, Quebec Group, Point Lévis. a, **lectotype**, GSC 914b, × 2; b, detail of proximal end showing isograptid arch, and relatively high angle between ventral walls of th 1^1 and th 1^2, × 10, GSC 914d (Hall 1865: pl. 1, fig. 6); c, × 2, GSC 914e. Figs 118b and c after Cooper & Fortey 1982: fig. 40, with magnification corrected.

Begin's Hill Quarry. O. M. B. Bulman recollected at this site; in an unpublished manuscript I have seen he records the species also from the underlying *Phyllograptus typus* Biozone. Both these occurrences belong within the Middle Arenig, probably in the Chewtonian–Castlemainian 1 interval of the Australian stratigraphic standard.

OTHER MATERIAL. Four other specimens in Hall's type series, GSC 914.

DIAGNOSIS. *Didymograptus* (*Expansograptus*) with stipes declined proximally (in range 135°–155°) and distal stipes horizontal to very slightly declined. Isograptid development; ventral walls of th 1^1 and th 1^2 include a high angle; sicula 1·3–1·5 mm long, stipe width at th 1 0·7–0·8 mm. Stipe expansion rather steady until about th 20 and very little thereafter, to maximum between 1·5 and 1·75 mm. Distal thecae moderately flared at apertures and with tiny denticles, but interthecal septum inclined at 20°–35° to dorsal wall; distal thecal spacing 11–12 in 10 mm (th 10–15 distance in range 3·8–4·2 mm); ϕ always less than 90° and usually about 60°, so that apertures cut back about one-third of total stipe width distally.

DISCUSSION. Hall described the general features of this species, and the essential characters in the diagnosis require no further comment. Most of the original periderm has disappeared from the types. Although not present in south Wales, the species is present in north Wales associated with a Whitlandian trilobite fauna, and in the Lake District. Hall's types are a small population, but there are enough examples to suggest that previous views of *D. nitidus* have been too inclusive. A shallow-deflexed shape, with declined proximal end and more horizontal distal stipes, is regarded as a necessary character of the species, because such stipe characters seem to be fairly constant in other *Expansograptus* spp. Hence this would exclude such supposed *nitidus* as that in Berry (1960: pl. 8, fig. 11) with evenly declined stipes; there are other named species with this habit. About six thecae to either side of the sicula are involved in the declined portion of the rhabdosome (even in that specimen with distally declined stipes the dorsal stipe wall is concave), which projects only some 2–3 mm above the distal parts. Isograptid development was noted by Elles & Wood (1901: fig. 5d) in material from the type locality, and by Cooper & Fortey (1982: fig. 40g, reproduced as Fig. 118b herein) on a proximal end on GSC 914d which preserves the original relief. In all respects except the declined proximal part *nitidus* seems to be a typical *Expansograptus*. Note that Cooper & Fortey (1982: fig. 40f) recorded a magnification of × 3 on one of Hall's original specimens; this should have been × 2, and a correct reproduction is shown in Fig. 118 herein.

The sicula is 0·4 mm wide at its aperture, and somewhat curved away from th 1^1 (as it is also in *D. extensus*). In profile this appears as a 'tooth' about 0·3 mm long, projecting between th 1^1 and th 1^2. Free ventral walls of these thecae enclose an angle of 80°–100° and are 0·6–0·7 mm long. No specimens show the origin of th 1^1 perfectly, but it is clear that the origin of the first theca lies high on the sicula and that the sicula and first theca grow side by side as a pair for at least 1 mm.

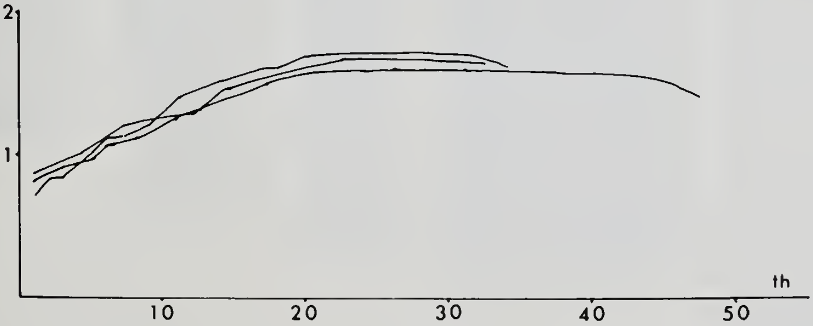
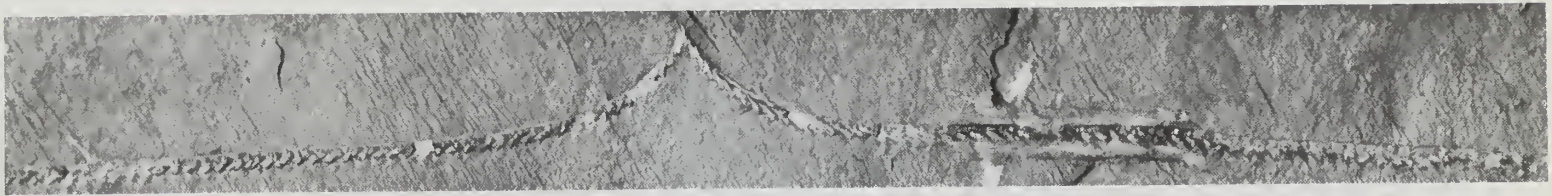
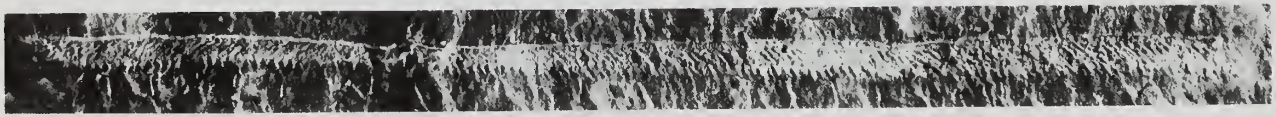
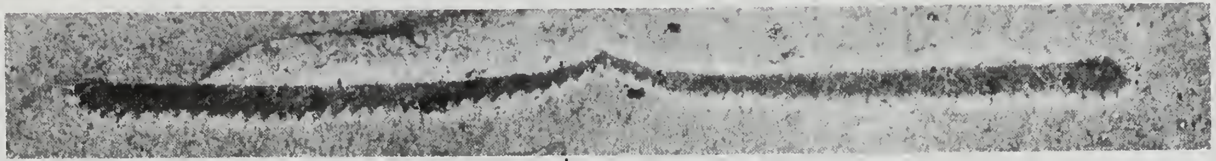


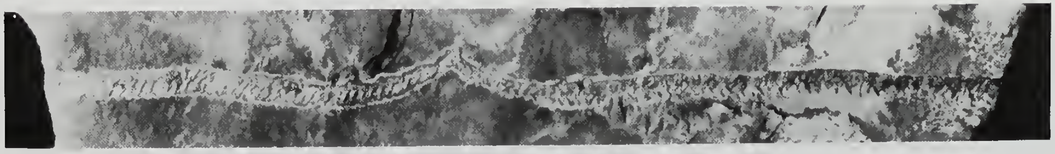
Fig. 119 Stipe expansion diagrams for three specimens of *D.* (*Expansograptus*) *nitidus* (Hall) from the type series.


a


b


c


d


e

Cooper & Fortey (1982) revised *D. extensus* (Hall), and stated that this species should not include specimens with a declined proximal end, such as most of those assigned to *D. extensus* from the English Lake District. Apart from this, *D. extensus* has an almost linear, gently sloping stipe expansion diagram from a narrower proximal end than *D. nitidus*. The proximal end structure is similar enough, however, to show that *nitidus* and *extensus* should both be referred to the same subgenus, *Expansograptus*. *D. uniformis* Elles & Wood may have had a proximal end development comparable to that of *D. nitidus*, but there are twice as many thecae involved in the steeply declined part of the rhabdosome, which projects up to 6 mm above the distal stipes, which themselves are narrower than in *nitidus*. Evans (1906) listed *D. nitidus* from Fennian localities in south Wales. This may have been based on general stipe form, because we cannot find any specimens which are referable to this species by comparison with the type material. The most similar material is probably what we refer to here as *D. uniformis lepidus* Ni, which is discussed in more detail below (p. 270); this species is at once distinguished from *D. nitidus* by its dense thecal spacing. The development, and virgellar spine, on the material from Utah identified as *D. nitidus* by Braithwaite (1976) shows that it belongs with *Xiphograptus* Cooper & Fortey rather than with *Expansograptus*, and it cannot be conspecific with Hall's species.

Taking a view of *D. nitidus* based on the type material, it does seem to be confined to the middle part of the Arenig in North America, Britain and Australia. Reported occurrences from the late Arenig have not been substantiated. An evolutionary 'series' *extensus* → *nitidus* → *hirundo* has been quoted, but *D. extensus*, *sensu stricto*, is an unlikely ancestor of *nitidus* because of differences in the proximal end structure. *D. hirundo* and *D. nitidus* are more alike—for example in the arch beneath the proximal end, and in the form of the distal thecae—and it is possible to derive *hirundo* from *nitidus* by continued growth of both thecae and stipes.

***Didymograptus* (*Expansograptus*) *sparsus* Hopkinson 1875**

(Figs 121a, b, 122–3)

1875 *Didymograptus sparsus* Hopkinson, *in* Hopkinson & Lapworth: 643; pl. 33, figs 2a–d.
1875 *Didymograptus pennatulus* Hall; Hopkinson, *in* Hopkinson & Lapworth: 643–644; pl. 33, fig. 3a–d.
1901 *Didymograptus sparsus* Hopkinson; Elles & Wood: 17–18, fig. 10; pl. 1, figs 6a, b.
?1909 *Didymograptus* cf. *sparsus* Hopkinson; Cantrill, *in* Strahan *et al.*: 20.

LECTOTYPE. Specimen with proximal end, on type slab, SM A16947. Selected Elles & Wood, 1901: explanation of plate 1.

TYPE LOCALITY AND HORIZON. Upper Arenig, Fennian, probably *Bergamia rushtoni* Biozone; Road Uchaf, Ramsey Island.

OTHER OCCURRENCES. ?South Wales, Llwyn-crwn, loc. 24; *B. rushtoni* Biozone (stipe fragments only; may be end variant of *D.* cf. *goldschmidti*). Lake District, Outerside; at Arenig/Llanvirn boundary.

MATERIAL. On type slab, also SM A16948, at least 5 proximal ends and numerous distal fragments; numerous specimens on slabs SM A16946, A16951, A16958; Fitz Park Museum, Keswick, Harrison Coll., for Outerside specimen.

Fig. 120 Arenig *Didymograptus* (*Expansograptus*) species. a, *Didymograptus* (*Expansograptus*?) *uniformis uniformis* Elles & Wood 1901, holotype, late Arenig, Bassenthwaite Sand Beds, Cumbria, × 2, Q8; b, *Didymograptus* (*Expansograptus*?) *uniformis* cf. *lepidus* Ni 1979, Upper Arenig, Fennian, *B. rushtoni* Biozone, loc. 23, × 5, Q5180: differs from typical *lepidus* in its more declined stipes; c, *D.* (*Expansograptus*) *hirundo*, Upper Arenig, Lake District, × 1·5, Fitz Park Museum, Keswick, Harrison Coll.; d, *D.* (*Expansograptus*) *nitidus* (Hall 1865), type loc. of Hall, Lévis, Quebec, × 3, GSC 514e; e, *D.* (*Expansograptus*) *uniformis lepidus* Ni 1979, Upper Arenig, Fennian, *B. rushtoni* Biozone, loc. 23, × 2, Q5092.

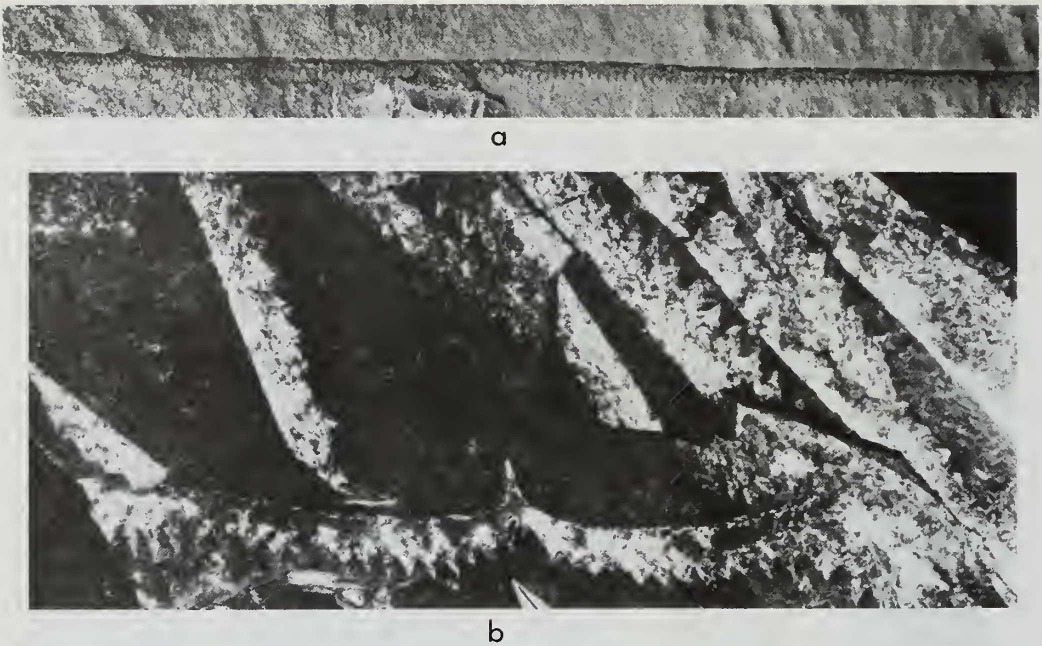


Fig. 121 *Didymograptus* (*Expansograptus*) *sparsus* Hopkinson 1875. a, near Arenig/Llanvirn boundary, Outerside, Cumbria, large undistorted specimen, × 1, Fitz Park Museum, Keswick, Harrison Coll.; b, Rhoad Uchaf, Ramsey Island, Dyfed, Fennian, probably *B. rushtoni* Biozone, slab with distorted material, × 3, SM A16951: pointer at centre bottom indicates inferred direction of extension. (Specimen at bottom is that used by Hopkinson (1875: pl. 33, fig. 3a) as illustrative of *D. pennatulus*; all such specimens are here regarded as tectonically altered *D. sparsus*).

DIAGNOSIS. Large *Expansograptus*, proximal part declined, but only for two or three thecae, thereafter horizontal. Sicula large, stipes exceed 2 mm width at th 1 and achieve maximum width of about 2·8 mm (range of variation probably considerable) at about th 10, which then remains constant. Thecae very widely spaced, between 8 and 9 per 10 mm in mature part of stipe (th 10–th 15 5·5 mm); apertures very flared, and deeply cut back to more than one-third stipe width, t = 1 mm, $\phi = 20°–30°$.

DISCUSSION. The slab including the type specimen has obviously suffered a certain measure of distortion. The type specimen lies at a low oblique angle to the direction of maximum extension, and the stipes have been slightly thinned as a result and the thecal spacing increased. Many of the other stipes on the type slab are close to the direction of extension: the very low thecal spacing recorded by Elles & Wood (1901) of 7 in 10 mm seems to be based on such specimens; on others preserved more or less normal to the long axis of the strain ellipsoid spacing is reduced to 10 or 11 in 10 mm. We regard almost all the specimens on the type slab as belonging to the single species *sparsus*, and include also a specimen from the same horizon figured by Hopkinson (1875: pl. 33, fig. 3a) as *D. pennatulus* Hall (which is one of the tectonically compressed specimens). The only exception (Hopkinson 1875: pl. 33, fig. 3e) is a very broad stipe that may belong to *D. hirundo*.

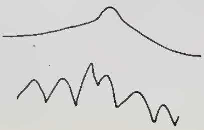


Fig. 122 *Didymograptus* (*Expansograptus*) *sparsus* Hopkinson. Proximal end of specimen shown in Fig. 121a, flattened but otherwise not distorted, to show small sicula 'tooth' and low angle between ventral walls of th 1^1 and th 1^2, apex of sicula resorbed, × 5.

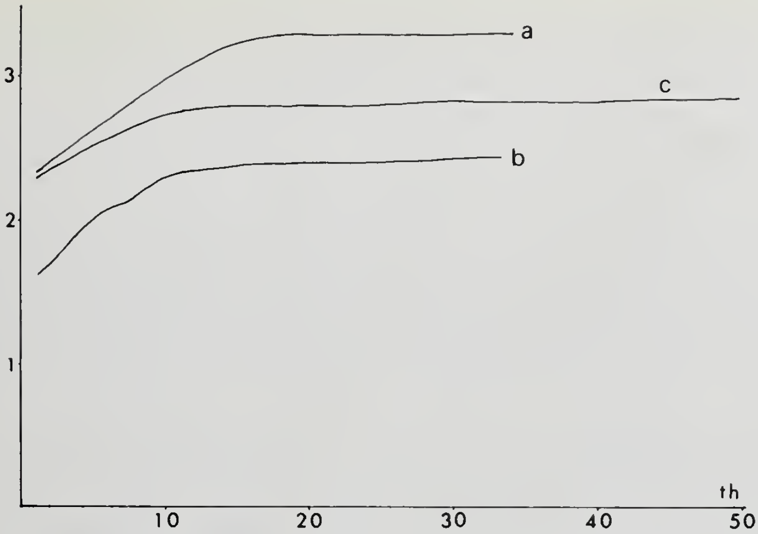


Fig. 123 Stipe expansion diagrams for *D.* (*Expansograptus*) *sparsus* Hopkinson; a, wide stipe (called *pennatulus* by Hopkinson) from type locality; b, from holotype, tectonically extended (Elles & Wood 1901: pl. 1, fig. 6a); c, undistorted specimen Fig. 121a herein, lying about midway between these two extremes.

Knowledge of *D. sparsus* in an undistorted condition has derived from a specimen from the Lake District, figured here as Fig. 121a. The specimen has a final stipe width of 2·8 mm, and its stipe expansion diagram lies between the wider and narrower specimens on the type slab (Fig. 123). The distal thecal spacing is between 8 and 9 thecae in 10 mm, which is still low for an *Expansograptus*. It is not possible to be sure exactly how much distortion accounts for the variation in distal stipe width on the type slab. Extreme values are 2·2 mm parallel to extension and just over 4 mm normal to it. The type specimen, 2·5 mm wide, is nearly parallel to extension, and certainly thinned by tectonism. On the other hand some specimens nearly parallel to extension are 3 mm wide, and were originally wider. There was presumably a good deal of variation in final stipe width (as in other extensiforms), embracing the values 2·6 to 3·3 mm and maybe more. Taking the extreme values produced by distortion on the type slabs the formula

$$\text{original width} = \sqrt{\text{compressed width} \times \text{extended width}}$$

gives values close to that of the Outerside specimen. The important specific character is not the stipe width, but the widely-spaced thecae with their flared apertures, and the wide initial stipe width with relatively low stipe expansion (Fig. 123). The species certainly grew very large: the Lake District specimen has one stipe 12 cm long without a termination.

The proximal end of the holotype was figured by Elles & Wood; the sicula exceeds 3 mm in length, but has possibly been tectonically altered. However, all the type series show a similarly large sicula regardless of distortion type. Not much can be inferred about mode of development from the type series, but the proximal end profile is much like that of *D. nitidus* (Fig. 118b). The Lake District specimen (Fig. 122) is not much better; the top of the sicula has been resorbed to form a low hump. The free ventral walls of th 1^1 and th 1^2 are as long as 1·6 mm and enclose a small acute angle. The asymmetrical sicular aperture forms a 'tooth' about 0·5 mm long. Stipe width at th 1 about 2 mm; smaller values on the type slab are because of distortion.

Didymograptus (*Expansograptus*) *patulus* (Hall) has similarly flared thecae, but (Cooper & Fortey 1982: fig. 44) narrower proximal stipe width and hence a steeper proximal growth gradient, and more closely spaced thecae. *D.* (*E.*) *sparsus* is one of the more distinctive *Expansograptus*, but it is not yet recorded outside the United Kingdom.

Didymograptus **(*Expansograptus*?)** ***uniformis uniformis*** Elles & Wood 1901
(Fig. 120a)

1901 *Didymograptus uniformis* Elles & Wood: 12–13, text-fig. 6; pl. 1, fig. 4.

HOLOTYPE. Well-preserved complete rhabdosome, Q8. The only original specimen.

TYPE LOCALITY AND HORIZON. The holotype bears a label recording its occurrence in the Bassenthwaite Sand Beds; this is a late Arenig (probably *gibberulus* to *hirundo* Biozone) horizon.

DIAGNOSIS. Deflexed *Expansograptus*? with distal stipes almost horizontal; deflexed portion of rhabdosome protrudes about 6 mm above distal stipes, and involves some 10–12 thecae on either side of the sicula. Development not known, acute angle between ventral walls of th 1^1 and th 1^2. Gradual increase in stipe width from 0·8 mm at th 1 to 1·1 mm at th 10; subsequent increase extremely gentle, to a maximum of 1·4 mm. Distal stipes appear nearly uniform, with 11–12 thecae in 10 mm (th 10–th 15 4·5 mm), θ about 30°, t = 0·5 mm, $\phi = 60°$.

DISCUSSION. The type specimen of *uniformis* is the only one available, and our concept of the form must perforce be based upon it. Fortunately, it is well preserved. It is, however, difficult to be certain that there is no distortion, for example, with regard to the rather acutely declined proximal end. The fact that the two stipes are identical suggests that distortion is not serious, and a fragmentary stipe lying at right angles to the holotype has similar thecal proportions, although without a proximal end there is no way of being sure that it belongs to *uniformis*. We also have specimens with similarly declined proximal ends from south Wales referred to the subspecies *lepidus* (below). There is little to add to Elles & Wood's description apart from a photograph of the type specimen. The sicula is not clearly shown and does not exceed 1·5 mm, but Elles & Wood's text-fig. 6 shows 1·6 mm and it is conceivable that the specimen was more complete when first drawn. There is an apparent contradiction between their diagnosis and description, the former stating that the maximum stipe width is 1·6 mm, the latter that it is 1·3 mm. The maximum width is in fact 1·45 mm measured to the tip of a small denticle visible on some distal thecae. There is, of course, no way of knowing what intraspecific variation there may have been within *D. uniformis uniformis*; for example, it is not likely that the very slight declination of the distal stipes is of specific significance, and if it is like other dichograptids the distal stipe width would be somewhat variable. The closest species is *D. nitidus* (Hall), redescribed herein, from which it differs in having about twice as many thecae involved in the prominent declined part of the rhabdosome, thinner distal stipes (not regarded as important), and a slow rate of stipe expansion that soon levels off. Elles & Wood also described *D.* cf. *uniformis* (1901: pl. 1, fig. 3) from a slab from Raulnay in the Lake District. This slab includes some 8 specimens with proximal ends, showing structure like that of *D. nitidus*, but similar to *uniformis* in stipe width; the general habit, such as the projection of the declined part above the distal stipes, is like *D. nitidus*. The population is apparently an intermediate between *uniformis* and *nitidus*, but the development is like the latter. Populations from the Pontyfenni Formation in south Wales differ from *uniformis uniformis* consistently in a single character only, and these are described below as a different subspecies. As mentioned below, both may be related to Llanvirn species attributed to *Corymbograptus* rather than to *Expansograptus*. The straight-sided inverted V of the proximal end distinguishes the *uniformis* group from the early Arenig *Corymbograptus* of *v-fractus* type.

Didymograptus **(*Expansograptus*?)** ***uniformis lepidus*** Ni 1979
(Figs 120e, 124a–c, 125)

1906 *Didymograptus nitidus* (Hall); Evans: 611.
1906 *Didymograptus extensus* (?); Evans: 612.
1909 *Didymograptus* cf. *uniformis* Elles & Wood; Cantrill, *in* Strahan *et al.*: 12, 20.
1951 *Didymograptus simulans* Elles & Wood; Gigout: 277–278, text-fig. 57.
1979 *Didymograptus lepidus* Ni, *in* Mu *et al.*: 99; pl. 34, figs 16, 17; pl. 35, figs 1–5.

TYPE MATERIAL. In Nanjing Institute of Palaeontology. Late Arenig of south-west China, *Didymograptus nexus* Biozone (equivalent to '*Glyptograptus*' *sinodentatus* Biozone).

OCCURRENCE IN SOUTH WALES. *Bergamia rushtoni* Biozone; loc. 21, Castell-y-waun; loc. 23, Pontyfenni; and Survey locality Carm. 37SE Wλ4, Nant-yr-allwyn.

MATERIAL. NMW 84.12G.5–7, 84.12G.18, 84.12G.21, 84.12G.36, 84.17G.96–100; Q5092–103, Q5182–5.

DIAGNOSIS. Subspecies of *D. uniformis* differing from the type in its closely spaced thecae, 14–16 (?17) in 10 mm in mature parts of stipe (th 10–15: 3·0 to 3·6 mm). Proximal end declined, but proportions variable, involving 6–15 thecae to either side of sicula; distal stipes very gently declined or horizontal. Sicula 1·2–1·4 mm long, development uncertain; acute angle between ventral walls of th 1^1 and th 1^2. Gentle increase in stipe width through first 20 thecae or so, distally uniform, but final stipe width varies between 1·20 mm and 1·6 mm on different specimens. On distal stipes θ varies between 30° and 55°, ϕ between 45° and 60°.

DISCUSSION. The very close thecal spacing is exceptional in an extensiform, as noted by Ni (*in* Mu *et al.* 1979: 99). Ni also provided data on stipe width at various thecal numbers which is consistent with growth of our material (Fig. 125). Ni does not mention a stipe width greater than 1 mm, but her pl. 34, fig. 17 is 1·2 mm wide distally and hence within the range of variation of our material. The material figured by Ni has weakly declined proximal portions, projecting only about 2 mm above the distal stipes, like our specimen shown in Fig. 120e. However, the Welsh material does include specimens, such as NMW 84.12G.7, with steeply declined proximal ends perhaps 4 mm above the distal stipes, and hence much more like the type of *uniformis uniformis*. The initial angle of declination varies between 100° and 130°, the lower angles being on those specimens more like *uniformis uniformis*. This is a wider range than that given by Ni, but assuredly within a population from a single locality at Pontyfenni. Given the similarity of the material identified as *lepidus* with the type of *uniformis*, for example in the acute angle enclosed by the free ventral walls of th 1^1 and th 1^2, and in view of our lack of knowledge of intraspecific variation of *uniformis* at the type locality, it is appropriate to regard the Fennian form as a subspecies of *uniformis* distinguished by its dense thecal spacing, which is a consistent character. *D. uniformis lepidus* grew quite large: incomplete rhabdosomes with proximal ends show that whole colonies were more than 16 cm long.

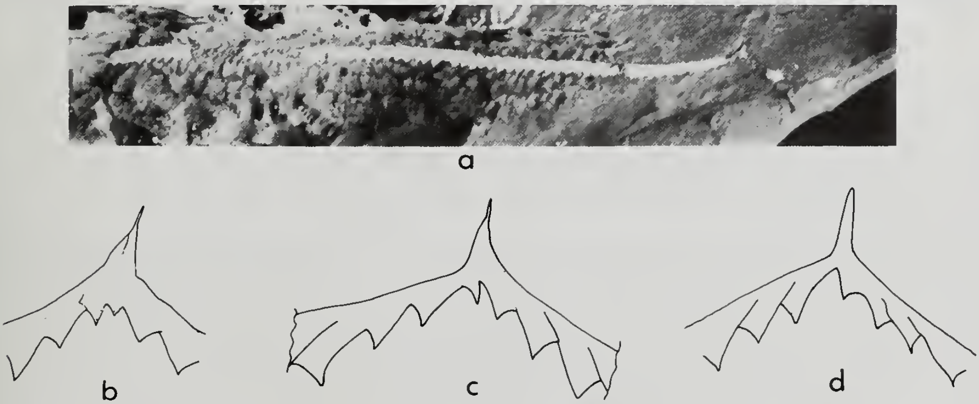


Fig. 124 a–c, *Didymograptus* (*Expansograptus*?) *uniformis lepidus* Ni 1979. Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23; a, stipes partly chloritized, × 2, Q5182; b, proximal end, × 10, from Q5092; c, showing sicula 'tooth', × 10, Q5099. d, *Didymograptus* (*Expansograptus*?) *simulans* Elles & Wood 1901, proximal end for comparison with *lepidus*, showing how distal part of sicula aligns itself with one stipe; type slab, Skiddaw Slates, Barf, Cumbria, probably *D. nitidus* Biozone, × 10, SM A17698.

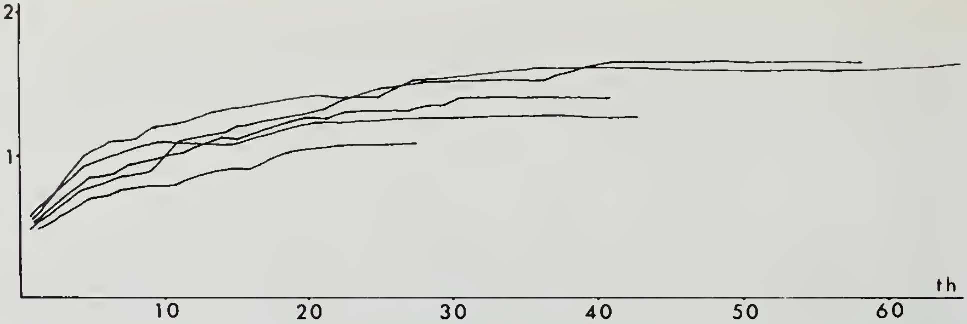


Fig. 125 Stipe expansion diagrams for population of *D.* (*Expansograptus*?) *uniformis lepidus* Ni 1979 from loc. 23, showing range in distal stipe width.

Despite some quite well preserved material the proximal end development is not clear. The sicula is about 1·3 mm long, narrow, with an oblique aperture that forms a very short 'tooth' in profile between the stipes (0·2 mm long). Th 1^1 begins high on the sicula; free ventral walls of th 1^1 and th 1^2 are 0·5–0·7 mm long, and enclose an acute angle (45°–70° on measured material). The possibility of *artus* development cannot be excluded. Proximally declined large specimens of this species resemble narrow-stiped versions of such Llanvirn *Corymbograptus* species as *C. retroflexus*, which is reported by Bouček (1973: 54) to have *artus* development. The stipe expansion diagrams show a good deal of distal variation in stipe width; as usual in dichograptids this is not an important character. Wider stipes are those associated with higher θ and lower ϕ (narrower stipes *vice versa*) for the geometrical reasons described by Fortey (1983). It seems possible that the wide specimens are the result of continued thecal growth in older colonies. Of our specimens, 80% have distal stipe widths 1·3–1·5 mm and thecal spacing is 15 in 10 mm.

We have two specimens (one shown in Fig. 120b) which have a longer declined proximal portion of the rhabdosome. These may be no more than population variants: they are named here as *D.* (*Expansograptus*?) *uniformis* cf. *lepidus*.

D. simulans Elles & Wood 1901 is superficially similar to *D. uniformis lepidus* in growth habit, but has a distinctively different proximal end structure (Fig. 124d).

Didymograptus* (*Expansograptus*) *goldschmidti Monsen 1937, *sensu* Kraft 1977
(Figs 126–7)

1937 *Didymograptus goldschmidti* Monsen: 117–118; pl. 1, figs 22, 39, 45.
1973 *Expansograptus extensus* (Hall 1865); Bouček: 37; pl. 6, fig. 5.
1977 *Expansograptus goldschmidti* (Monsen) Kraft: 15–16; pl. 8, figs 1–3.
?1979 *Didymograptus alatus* Chen; Mu *et al.*: 107–108; pl. 37, figs 2–4.
?1979 *Didymograptus patulentis* Chen; Mu *et al.*: 105–106; pl. 36, figs 5, 20, 21; pl. 37, fig. 1.

TYPE LOCALITY AND HORIZON. The holotype is K 0666, in the Palaeontological Museum, Oslo. From the biozone of *Phyllograptus densus*, Lower Didymograptus Shales; Ensjø, Norway.

OCCURRENCE IN SOUTH WALES. Rare in the later Whitlandian, biozone of *Gymnostomix gibbsii*; common in the Fennian, biozones of *Stapleyella abyfrons* and *Bergamia rushtoni*. Localities: 24, 25, 38, 40, 48 in Pontyfenni Fm.; 28, 34 in Whitland Abbey Member of Colomendy Fm.

MATERIAL. Q5150–2, Q5790–7; NMW 33.189.G204.1–2, 33.189.Gla, 33.189.G128, 33.189.G135, 84.17G.174–179.

DIAGNOSIS. See Kraft, 1977: 15.

DISCUSSION. A group of deflexed forms is included here, which have proved particularly difficult to determine specifically. These all have a small deflexed proximal portion involving 3–5 thecae

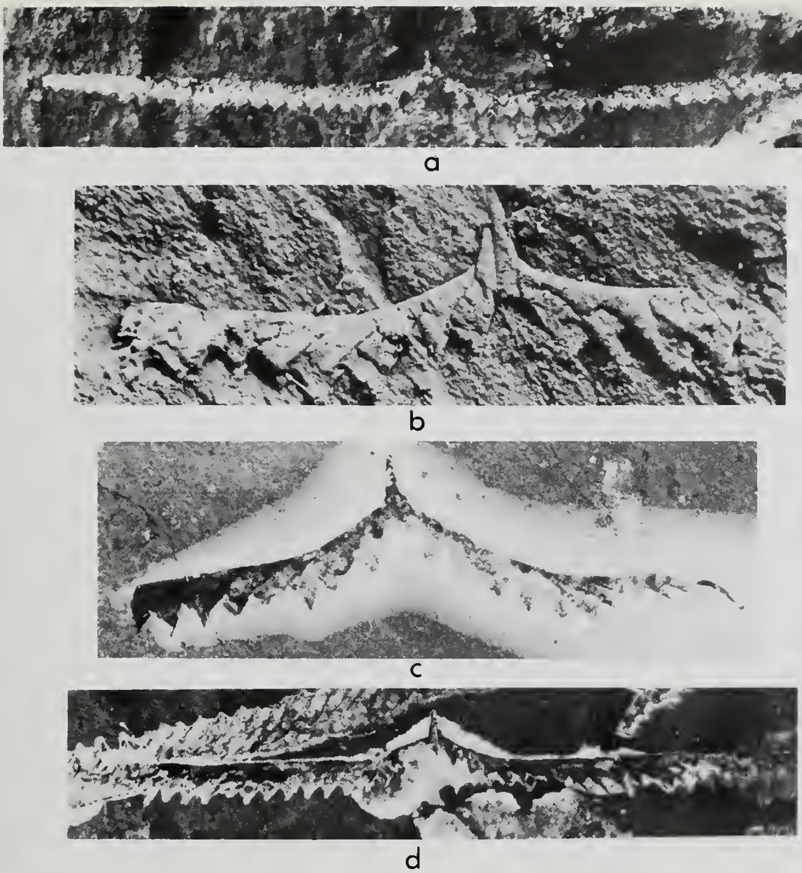


Fig. 126 *Didymograptus* (*Expansograptus*) *goldschmidti* Monsen 1937, *sensu* Kraft 1977. a, Upper Arenig, Fennian, *B. rushtoni* Biozone, loc. 24, thin-stripe morph, × 3, Q5790; b, probably *B. rushtoni* Biozone, loc. 40, latex cast from relief specimen showing isograptid development in obverse view, × 8, Q5791; c, same horizon, loc. 25, × 5, Q5792; d, *S. abyfrons* Biozone, loc. 38, × 3, Q5793.

to either side, distally nearly horizontal to slightly reclined. Sicula exceeds 2 mm in length (2·1–2·4 mm), forming a distinct tooth between th 1^1 and th 1^2, the ventral walls of which enclose an acute angle. Thecae are distinctly flared, trumpet-like, with the apertures cutting back to up to half the stipe width. Specimens in relief show that th 1^1 originates high on the sicula, and that there was isograptid development. There is a great deal of variation in other characters. The Whitlandian specimens are small (about 3 cm across); some Fennian specimens are also small, but others grew to at least three times that length. Some specimens (Fig. 127a) have distal apertural denticles (d) 1 mm apart (corresponding to spacing of 9–10 in 10 mm); others have thecal spacing of 12–13 in 10 mm. Stipe width at th 1 is 1·1–1·5 mm; distal stipe width is usually stable after about the fourth theca, and may be as little as 1·4 mm, but other specimens are up to 2·0 mm wide; stipe fragments from Pen-y-parc in the early Fennian probably belong here and are up to 2·5 mm wide. θ prox 20°–30°, distal 45°–60°; ϕ is acute, 60°–80°.

If this is a single species, it is a highly variable one. Those specimens with widely spaced thecae are like *D. sparsus*, but with narrower stipes. The large sicula and dependent proximal thecae distinguish the species from *D. nitidus* (Hall). Kraft (1977) figured some specimens from the Arenig of Bohemia which include some examples identical to our material except for a

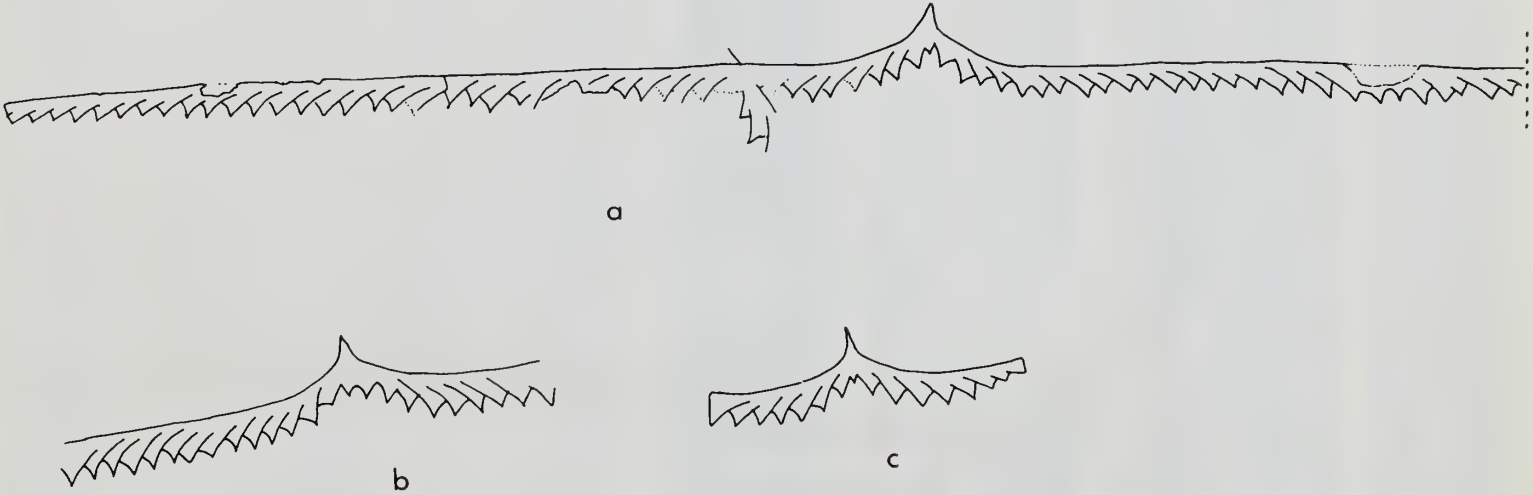


Fig. 127 *Didymograptus* (*Expansograptus*) *goldschmidti* Monsen 1937, *sensu* Kraft 1977. Upper Arenig, Fennian, *B. rushtoni* Biozone, loc. 24; a, large specimen (82 mm, stipe truncated at right), × 3, NMW 33.189.G128; b, thicker-stiped form, × 3, Q5151; c, with slightly reclined stipes, × 3, Q5152.

slightly less declined proximal part—which we know to be somewhat variable in *Expansograptus*. Kraft referred these to *D. goldschmidti* Monsen, and this identification is followed here. However, it is noted that Monsen (1937: 117) did not describe such acute thecal apertures, and she quotes a sicula length as long as 3 mm. For this reason the identification of *D. goldschmidti* is qualified, until a revision of the type material is available. A broader specimen was figured by Kraft as *Expansograptus* cf. *cinnereus* Monsen. Kraft's description of *goldschmidti* quotes 9–10 thecae per 10 mm, but if it is correct to assign specimens such as our Fig. 126a to the same species the total range would be 9–13.

Some of the variation in this species may be accounted for by continued growth of the rhabdosome, although this ought not to apply to thecal spacing. Some small specimens are also narrower; continued growth at the distal end of the stipes may have been accompanied also by small growth increments on proximal thecae. Large rhabdosomes clearly show a decline in stipe width at the distal, growing tip (Fig. 127a). However, since we have only found the larger specimens in the Fennian it is possible that there was also a phylogenetic change in the direction of large colonies, from small in the Whitlandian to large in the Fennian.

Some of the species from the later Arenig of China described in Mu *et al.* (1979) are probably conspecific with the present form, especially those referred to *Didymograptus patulentis* Chen (Mu *et al.* 1979: pl. 36, fig. 20; pl. 37, fig. 1) and *D. alatus* Chen. The former compares with the larger specimens from Llwyn-crwn, for example. There are nomenclatorial problems here also. *D. patulentis* was proposed to distinguish some late Arenig forms from *D. patulus* (Hall), under which name they had been described from Sweden by Törnquist (1901). Cooper & Fortey (1982) suggested that Törnquist's material might be referred to *Xiphograptus*, on the basis that Törnquist described a virgellar spine on one of his specimens. Examination of Törnquist's types in Lund University in 1985 failed to substantiate the presence of this spine, and it does not seem to be present on the Chinese material illustrated by Mu *et al.* (1979). *D. alatus* Chen (*in* Mu *et al.* 1979: pl. 37, figs 2–4) has slightly reclined stipes, like the south Wales specimen shown in Fig. 126a. Clearly the group of didymograptids having a small declined proximal part, large sicula, dependent th 1^1 and th 1^2, and flared thecae, requires comparative nomenclatorial revision, starting with the earliest named taxa. For this reason we employ Monsen's name here, while acknowledging that identical forms to the south Wales specimens occur in Bohemia and China.

Genus ***AZYGOGRAPTUS*** Nicholson & Lapworth, *in* Nicholson 1875

TYPE SPECIES. *A. lapworthi* Nicholson 1875, by monotypy.

DIAGNOSIS. See Bulman 1970: V116.

Azygograptus hicksii (Hopkinson 1875)
(Figs 128b, c)

1875 *Tetragraptus Hicksii* Hopkinson, *in* Hopkinson & Lapworth: 651; pl. 33, figs 12a–d.
1902 *Azygograptus Hicksii* (Hopkinson) Elles & Wood: 94–95, text-fig. 55; pl. 13, figs 2a–c.

LECTOTYPE. SM A17831. Selected from Hopkinson's syntypes by Elles & Wood (plate explanation) as 'type'; original of Hopkinson, *in* Hopkinson & Lapworth 1875: pl. 33, fig. 12c, d.

TYPE LOCALITY AND HORIZON. Penmaen Dewi Formation, Pwlluog, Whitesand Bay, near St David's, Dyfed; Whitlandian, *Gymnostomix gibbsii* Biozone.

OTHER OCCURRENCE. Afon Ffinnant Formation, on Afon Ffinnant, east of Carmarthen, isolated shale outcrop between locs 18C and 18D; Whitlandian, ?*G. gibbsii* Biozone.

MATERIAL. SM A17379–94; Q5172–3.

DIAGNOSIS. *Azygograptus* with more widely spaced thecae than any other species of the genus; distance between thecal apertures d = 1·6–2·8 mm. Stipe originates near base of sicula, which carries prominent spine on opposite side. Distal stipe width 0·9–1·5 mm.

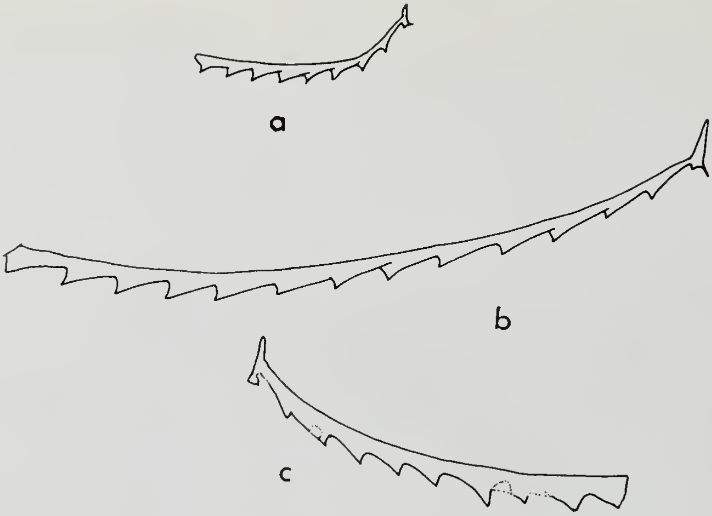


Fig. 128 Arenig *Azygograptus* species, all × 3. a, *A. eivionicus* Elles 1922, Afon Ffinnant Formation, Middle Arenig, Whitlandian, ?*F. radix* Biozone, loc. 18E, Q5175; b, *A. hicksii* (Hopkinson 1875), Penmaen Dewi Formation, Middle Arenig, Whitlandian, *C. gibbsii* Biozone, Pwlluog, north of Whitesand Bay, St David's, Dyfed, rhabdosome showing spine on sicula, SM A17393; c, *A. hicksii* (Hopkinson), same horizon and locality, SM A17392.

Discussion. Elles & Wood (1902) gave a good general description of this species, which is known from a type population of more than 20 specimens. It has wide stipes with very spaced thecae, and this alone distinguishes it from other *Azygograptus*. This feature does not seem likely to be the result of distortion; other species of trilobites and graptolites from near the type locality are not distorted, and the species occurs also in the Carmarthen district where there is a different tectonic setting. Sicula 1·5–2·1 mm long, th 1 probably originating quite low down on sicula and curving away from it at once, 0·2–0·3 mm above sicula aperture. Well-preserved proximal ends, such as on SM A17392–3 (two specimens; Fig. 128b, c) show a prominent spine curving away from the sicula on the opposite side to the stipe; this is regarded as a likely specific character, although it is not visible on poorly preserved specimens (or ones, like the type, which have been covered in Canada balsam). Width at th 1, 0·6–0·9 mm; attaining mature stipe width by th 3 to th 9 with little change therafter. The majority of specimens in the type population (Fig. 130) are 1·2–1·4 mm wide. Overall rhabdosome shape varies from nearly straight to quite strongly curved, and no taxonomic importance is attached to this.

A. hicksii is known from the later Whitlandian. *A. eivionicus* from the early Whitlandian, with thinner stipes and more crowded thecae, is distinguished below. A population attributed to *hicksii* from Afon Ffinnant, which is probably stratigraphically between the two, has intermediate characters (Fig. 130) with regard to stipe width and sicula size. It is likely that there is a temporal gradation between the two species. These Ffinnant specimens are referred to *A. hicksii* because they have the very loose thecal spacing noted in the type population.

Azygograptus eivionicus Elles 1922
(Figs 128a, 129)

1915 *Azygograptus lapworthi*; Nicholas: 113.
1922 *Azygograptus eivionicus* Elles: 299–301.
?1979 *Azygograptus eivionicus* Elles; Mu *et al.*: 110; pl. 38, figs 11, 12.

Holotype. Original of Elles 1922: fig. 1, which is referred to by her as 'type' on the figure explanation; SM A17372. Strachan (1971: 19) referred to Elles' originals as 'syntypes'.

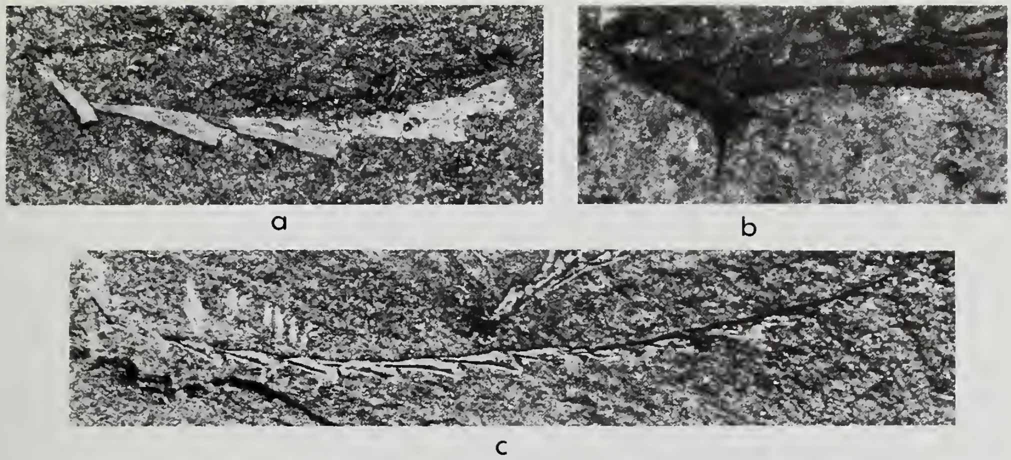


Fig. 129 *Azygograptus eivionicus* Elles 1922. Middle Arenig, Whitlandian, ?*F. radix* Biozone, Afon Ffinnant Formation, loc. 18E, pyritized material; a, b, small specimen with well-preserved proximal end, × 10 in reflected light, and sicula (under alcohol) showing sicula spine on anti-stipe side, × 20, Q5174; c, fully grown rhabdosome, × 5, Q5176.

Type locality and horizon. Nant, south of Llanengan, Llŷn Peninsula, north Wales; before late Arenig, but exact horizon unknown.

Occurrence in south Wales. Afon Ffinnant Formation, abundant at locs 18D and 18E, middle Arenig, Whitlandian, *F. radix* Biozone. Also Blaencediw Formation at loc. 31, Blaencediw.

Material. Q5174–9; NMW 84.17G.105–7.

Diagnosis. *Azygograptus* with stipes almost straight to strongly curved. Sicula 1·1–1·3 mm long with slender apertural process. Stipe originates at 0·2 mm from sicula aperture, and makes an acute angle with it. Stipe width at th 1 0·5–0·6 mm; distal stipe width 0·6–0·9 mm with a mean between 0·7 and 0·8 mm; distance between thecal apertures d = 1·3–1·5 mm.

Discussion. The salient features are given in the diagnosis. As noted above there is a gradation between this form and *A. hicksii*, which has wider stipes (Fig. 128) and more spaced thecae: it is like an *A. eivionicus* in which the thecae have become larger. Like *A. hicksii*, well-preserved *eivionicus* show a delicate sicula spine, which curves outwards almost at right angles to the long axis of the sicula. *A. lapworthi* Nicholson 1875 is best distinguished by the comparatively high origin of the stipe on the sicula, with which it subtends a right angle. *A. suecicus* Moberg 1892 from the late Arenig is altogether thinner and more gracile. Specimens from the Lake District referred to this species by Elles & Wood are probably more correctly assigned to *A. eivionicus*.

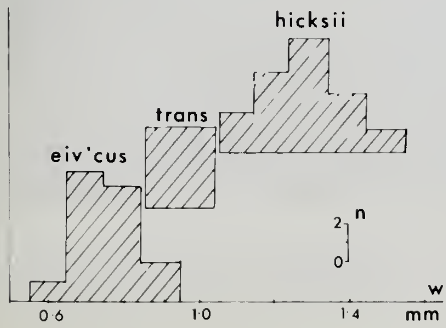


Fig. 130 Histograms of mature stipe width, w, for Whitlandian *Azygograptus* species; *A. hicksii* populations do not overlap with those of *A. eivionicus*, but a transitional population 'trans' has been found on Afon Ffinnant.

There they occur with a *D. nitidus* Biozone assemblage. Supposed *A. suecicus* from China described by Mu *et al.* (1979) also appear to compare more closely with *A. eivionicus*, which they record from the same horizon. There is a good deal of variation in the curvature of the stipes in the south Wales population: some specimens are hardly curved, others turn through a right angle.

The species' occurrence in the Afon Ffinnant Formation is as a monospecific 'graveyard'. It is the first graptoloid to appear in the succession there, and may have been capable of living shorewards from other graptoloid species.

Genus ***PSEUDOTRIGONOGRAPTUS*** Mu & Lee 1958

TYPE SPECIES. *Graptolithus ensiformis* Hall 1865; see Cooper & Fortey 1982: 247.

Pseudotrigonograptus ensiformis (Hall 1865)
(Fig. 135a)

(For synonymy see Rickards (1973) and additional comments in Cooper & Fortey (1982)).

TYPE LOCALITY AND HORIZON. Lévis, Quebec, from latest Arenig.

OCCURRENCE IN SOUTH WALES. Fennian, *Bergamia rushtoni* Biozone, Pontyfenni Formation; loc. 23, Pontyfenni.

MATERIAL. Q5104; NMW 84.17G.108–9.

DISCUSSION. This species was given a full description by Rickards (1973) and by Cooper & Fortey (1982), and further description is not necessary. The specimens from the Fennian are relatively well preserved, but in the usual mode for this genus, in which the apertures are not visible; the specimen breaks along the septum to give a straight-sided appearance (Fortey 1971). The specimen illustrated is the most complete we have discovered, exceeding $4\frac{1}{2}$ cm in length, but other fragments are from even larger individuals. The illustrated specimen is the 'narrow' form associated with the shorter diameter of the more or less rectangular cross section of the rhabdosome (Cooper & Fortey 1982: text-fig. 53d); in these the cross-sectional width is slightly less than 3 mm. Other specimens show the 'wide' section, with a transverse width of up to 4 mm. The fact that these specimens break with a 180° angle between opposite thecal series shows that the form of *Pseudotrigonograptus* here is the quadriserial scandent type, rather than the triserial type described from relief material from Spitsbergen by Fortey (1971), in which the angle between adjacent thecal series is 120°. Suggestions that the triserial and quadriserial forms might be placed in different genera (e.g. Cooper 1979) do not seem well advised, as virtually all other characters are closely similar, including the unique stipe construction.

P. ensiformis is an almost ubiquitous species in more 'oceanic' graptoloid biofacies and is one of the few distinctive species to span the so-called Atlantic and Pacific provinces in the late Arenig. It is present in black shale facies, but not cratonic graptolite facies, in North America, as in Texas, New York, British Columbia, Newfoundland and Quebec. It is distributed in Taimyr, parts of China, Australia (Victoria) and New Zealand. Its occurrence also in south Wales and the Lake District is therefore of considerable importance for correlation. The first appearance of the quadriserial form is in the later Arenig.

Subfamily **SIGMAGRAPTINAE** Cooper & Fortey 1982

Genus ***ACROGRAPTUS*** Tsai 1969

TYPE SPECIES. *Didymograptus affinis* Nicholson 1869, by original designation.

Acrograptus acutidens (Elles & Wood 1901)
(Figs 131–133)

1875 *Didymograptus affinis* Nicholson; Hopkinson, *in* Hopkinson & Lapworth: 645; pl. 33, figs 6b, c (?6a).

1901 *Didymograptus acutidens* Lapworth MS; Elles & Wood: 25–26, text-fig. 15a–c; pl. 2, figs 3a–d.

non 1904 *Didymograptus acutidens* Lapworth; Ruedemann: 683–684; pl. 13, fig. 15.
1909 *Didymograptus acutidens* Lapw.; Cantrill, *in* Strahan *et al.*: 30 (listed).
?1931 *Didymograptus acutidens* Lapworth MS, Elles & Wood; Bulman: 30–31; pl. 2, fig. 13.
1934 *Didymograptus acutidens* Lapworth MS em. Elles & Wood; Hsü: 33; pl. 2, fig. 3.
non 1947 *Didymograptus acutidens* Lapworth; Ruedemann: 324; pl. 55, fig. 1; pl. 56, fig. 18.
1971 *Didymograptus acutidens* Elles & Wood; Strachan: 14.

LECTOTYPE (selected Strachan 1971: 14). SM A16985; original of Elles & Wood 1901: pl. 2, fig. 3a.

TYPE LOCALITY AND HORIZON. Porth Hayog (= Porth Llauog), Ramsey Island; Llanvirn.

OCCURRENCE IN SOUTH WALES. *A. acutidens* is abundant in the Llanfallteg Formation, appearing in the uppermost Arenig (*Dionide levigena* Biozone) and continuing into the early Llanvirn. We have recovered it from all our Llanfallteg Formation localities.

DIAGNOSIS. Slender, gently declined (130°–150°) *Acrograptus*, with stipes that increase very gradually from 0·4–0·6 mm to a maximum of 1·5–2·0 mm. Thecal shape characteristic, with acute ϕ, and apertural margin usually making an angle of slightly less than 90° to dorsal stipe margin to give acutely toothed appearance. Distal thecal spacing variable with 10–13 (?14) thecae per 10 mm; th 10–15 4·3–4·5 mm; t = 0·5 mm, $\theta = 30^\circ$ or less.

MATERIAL. Q5156–60, Q5186; NMW 84.17G.110–115.

DISCUSSION. The species has a slender sicula 1·3–1·5 mm long, and very thin proximal parts of both stipes (Fig. 131b) which originate slightly asymmetrically to either side of the sicula; this suggests that *acutidens* is correctly referred to *Acrograptus*. Distal stipes abound in the Llanfallteg Formation, but proximal ends are rare. From the slow rate of distal stipe width increase it is likely that the species had stipes at least 15 cm long to attain maximum width. Elles & Wood (1901) gave a good general description of the species, to which a little can be added. All the

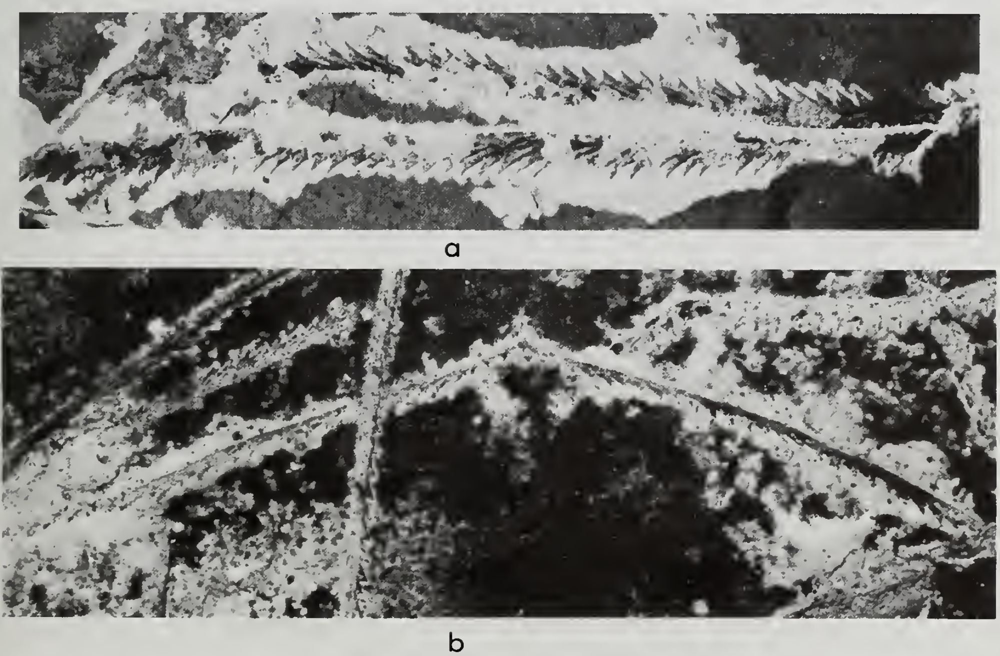


Fig. 131 *Acrograptus acutidens* (Elles & Wood 1901). Llanfallteg Formation, both × 3; a, two distal stipes, early Llanvirn, *D. artus* Biozone, loc. 50, Q5186; b, well-preserved proximal end showing slow increase in stipe width, same locality, Q5156.

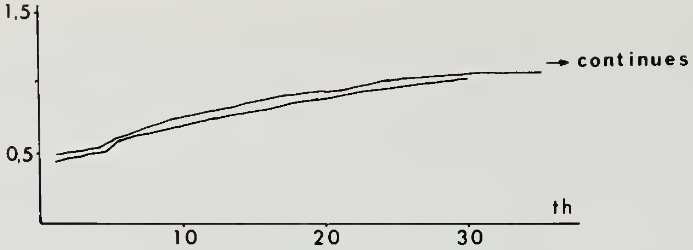


Fig. 132 Stipe expansion diagram for best-preserved *Acrograptus acutidens* (Elles & Wood).

material we have found indicates that a declined proximal part is characteristic of the species, and we would exclude such specimens as Ruedemann's (1947: pl. 55, fig. 1) from Deepkill with immediately horizontal stipes; these are from an earlier Arenig horizon, probably equivalent to the *D. nitidus* Biozone of Britain. Many distal stipes are flexed or bent, and it is probable that they were somewhat flexible. None of the proximal ends are well enough preserved for the development to be reliably discovered; a projecting portion of the sicula is characteristically sigmagraptine. The stipe expansion diagram (Fig. 132) is a gentle curve from a narrow origin; the stipes continue to expand in width distally, but at a very low rate, about 0·1 mm per 15–20 thecae. Proximal thecae are about 1 mm long, and nearly rectimarginate, with a short lip. Distal thecae have a distinctive appearance, as noted by Elles & Wood: Q5160 is in relief, and shows some details of this thecal structure. The common canal is 0·4 mm wide; thecae are as long as 1·7 mm, and inclined at a low angle of 20° proximally, and curving very gently to 30° at the aperture. The apertural margin is cut back steeply, often so that the angle between it and the dorsal wall of the stipe is slightly less than 90°; ϕ is therefore acute, as low as 30°. There is an apertural denticle. The stipe appearance then is characteristically sharp-toothed, as implied by the specific name. Note that other species can *acquire* this appearance with tectonic shortening, but there is no question of this with the material from the Whitland area, which is often well preserved. Distal thecal spacing appears to be very variable, usually 12–13 thecae in 10 mm, but examples of distal stipes have been found with spacing as low as 10 or as high as 14 per 10 mm. This is probably a consequence of small variations in θ at low inclinations, since thecal spacing $d = t \sin \theta$ (Fortey 1983), and for constant t and low θ any variation in $\sin \theta$ will produce a relatively large variation in d.

A. acutidens appears below the Llanvirn boundary, but is abundant in the early Llanvirn also. Cantrill & Thomas (*in* Strahan *et al.* 1909: 25) record the species in what they believed to be the top of the *D. 'bifidus'* shales. It is one of the few species distinctive enough to be recognized from distal stipe fragments.

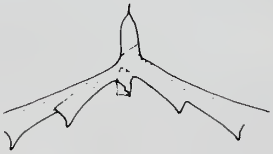


Fig. 133 Proximal end of *Acrograptus acutidens*, × 10, based on Q5156.

Acrograptus ? sp. a of Skevington, 1965
(Fig. 134)

1965 *Didymograptus* n. sp. a aff. *D. gracilis* Törnquist, 1890; Skevington: 21–22, fig. 24 (gives earlier synonymy).

1965 *Didymograptus* cf. n. sp. a aff. *D. gracilis* Törnquist; Skevington: 22.

Original locality and horizon. Halludden Borehole, Öland; at, or immediately below, Arenig/Llanvirn boundary (Skevington 1965: fig. 73).

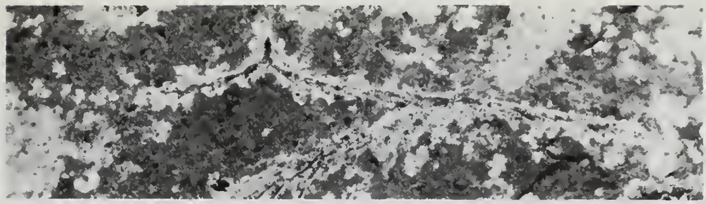


Fig. 134 *Acrograptus*? sp. a of Skevington, 1965. Llanfallteg Formation, latest Arenig, *D. levigena* Biozone, loc 52H, × 5, Q5172.

Occurrence in south Wales. Fennian, *Dionide levigena* Biozone, Llanfallteg Formation; loc. 52W.

Material. Q5172.

Discussion. Skevington (1965) named his 'nov. sp. a' for Holm's 'mutation' of *Didymograptus gracilis* Törnquist. He noted that true *gracilis* had an asymmetrical proximal end, which we would now regard as sigmagraptine (Cooper & Fortey 1982: fig. 66f). In 'sp. a' the origin of the thecae is almost symmetrical to either side of the sicula, the apertural lip of which projects as a minute tooth. From the Llanfallteg Formation—and from the same stratigraphical position as Skevington's examples—we have a gracile specimen with exactly the same proximal end. This is more complete than was the material from Öland, from which it differs only in having the sicula 0·1 mm longer, and the stipe width also being 0·1 mm wider. The sicula is 0·9 mm long and 0·25 mm wide at its base. The stipes are declined at about 140° initially but become more horizontal after th 2. Thecae have the very low inclination invariable in gracile species, ϕ is a high acute angle and there appears to be a minute apertural denticle. Distance between thecal apertures varies between 0·8 and 1·0 mm (equivalent to 10–12 thecae in 10 mm). Stipe width at th 1 is 0·3 mm, increasing to no more than 0·4 mm at th 17.

Extremely thin species such as this are easy to overlook. However, the difference in proximal end structure from other *Acrograptus* spp. indicates that this *A.*? sp. a is likely to prove a distinctive late Arenig form. Because of the difference from the typical sigmagraptine, it is included with question in *Acrograptus*. None of the *Acrograptus* species described by Bouček (1973) from Bohemia is as thin—the closest is apparently *A. lipoldi*, but this is reported to be 1·0 mm wide at 15 mm from the sicula, where our specimen is still less than 0·4 mm. It is tempting to name it as a new species but the scarcity of material makes this inadvisable at the moment. Accordingly, the open nomenclature coined by Skevington (1965) is used again here.

Family **GLOSSOGRAPTIDAE** Lapworth 1873

Genus ***GLOSSOGRAPTUS*** Emmons 1855

Type species. *G. ciliatus* Emmons, by monotypy (Emmons 1855: 108).

Diagnosis. See Bulman 1970: 122.

Glossograptus acanthus Elles & Wood 1908

(Fig. 135b)

1908 *Glossograptus acanthus* Elles & Wood: 314, figs 208a, b; pl. 33, figs 4a–c.
1935 *Glossograptus acanthus* Elles & Wood; Harris & Thomas: 302–303, fig. 3 (13–16).
1960 *Glossograptus acanthus* Elles & Wood; Berry: 70–71.
1960 *Glossograptus acanthus* Elles & Wood; Turner: 89; pl. 7, fig. 8.
1964 *Glossograptus acanthus* Elles & Wood; Obut & Sobolevskya: 71; pl. 15, figs 1, 2.
1971 *Glossograptus acanthus* Elles & Wood; Skevington & Archer: 76 (listed).
1974 *Glossograptus acanthus* Elles & Wood; Tsai: 105, text-fig. 38; pl. 11, figs 25a, b.
1979 *Glossograptus acanthus* Elles & Wood; Cooper: 81, text-fig. 65; pl. 15, fig. k.

HOLOTYPE. According to Strachan (1971: 27), Elles & Wood (1908) indicated their pl. 33, fig. 4a as type specimen, SM A17441.

TYPE LOCALITY AND HORIZON. 'Sruffaunduff, ½ mile W of Summit of Bencraff, Connemara', Republic of Ireland. Originally described by Elles & Wood as Arenig, the fauna from here has been re-evaluated (Dewey, Rickards & Skevington 1970: 30–31) as of early Llanvirn age.

DIAGNOSIS. See Elles & Wood, 1908: 314.

OCCURRENCE IN SOUTH WALES. Elles & Wood recorded the species from the early Llanvirn of St David's. Our new occurrence is from 15 m below the Arenig/Llanvirn boundary in the Llanfallteg section, latest Arenig, *Dionide levigena* Biozone.

MATERIAL. Q5171.

DISCUSSION. The species is represented in our collections by a well-preserved specimen from the latest Arenig. The specimen retains sufficient relief to see the monopleural arrangement of the thecal series, showing that it is a typical *Glossograptus*. There is nothing to add to the recent descriptions given in the synonymy. Our specimen has a maximum diameter of 6 mm; some seven pairs of apertural spines up to 2 mm long curve downwards in the proximal part; lengthwise distance between apertural spines in the mature part of the rhabdosome is 0·8–1·0 mm. The species is of considerable stratigraphical importance, being very widespread: Australia, New Zealand, Texas, Ireland, Kazakhstan, Taimyr, South America and Wales. It appears to be confined to the uppermost Arenig and early Llanvirn.

Family **DIPLOGRAPTIDAE** Lapworth 1873

Genus ***GLYPTOGRAPTUS*** Lapworth 1873

TYPE SPECIES. *Diplograptus tamariscus* Nicholson 1868; original designation of Lapworth (1873: table of classification).

DISCUSSION. The concept of *Glyptograptus* has to be based on the type species, *G. tamariscus*. *Glyptograptus* has been defined on the basis of its thecal form, as have other biserials; modern work would emphasize instead the mode of development at the proximal end. On this criterion it is doubtful whether either of the species described here would be referred to *Glyptograptus* s.s. '*G.*' *dentatus* has steeply upward curved proximal thecae, in this respect resembling the type species of *Undulograptus* Bouček (*U. paradoxus*, well illustrated from relief material by Bouček, 1973). '*G.*' *austrodentatus*, on the other hand, has proximal thecae with rather low inclination, and probably a different proximal structure. It may not be congeneric with '*G.*' *dentatus*. Such generic reassignments are now being carried out in the context of a revision of these genera as a whole (C. E. Mitchell, personal communication 1985), using isolated or relief material. Here the usual name of *Glyptograptus* is used in quotations to indicate the provisional classification.

'*Glyptograptus*' *dentatus* (Brongniart 1828)

(Figs 135d, e, g, j, 136)

(For synonymy see Bulman (1963: 673) and Skevington (1965: 55)).

NEOTYPE AND HORIZON. Geological Survey of Canada, 943, proposed Bulman 1963: 672, 675, text-fig. 4a; from what is probably the early Llanvirn (?*P. tentaculatus* Biozone), Point Lévis, Quebec.

OCCURRENCE IN SOUTH WALES. Widely recorded in the *Didymograptus artus* (*D.* '*bifidus*', auctt.) Biozone of the early Llanvirn, in which it is generally distributed. Here we add the common occurrence of the species in the uppermost Arenig biozone of *Dionide levigena* (throughout loc. 52) in the Llanfallteg Formation, and rare occurrence in the Fennian, biozone of *Bergamia rushtoni*; type locality of Pontyfenni Formation, loc. 23. The species ranges through the top two biozones of the Arenig and into the early Llanvirn.

MATERIAL. Q5105, Q5808–15.

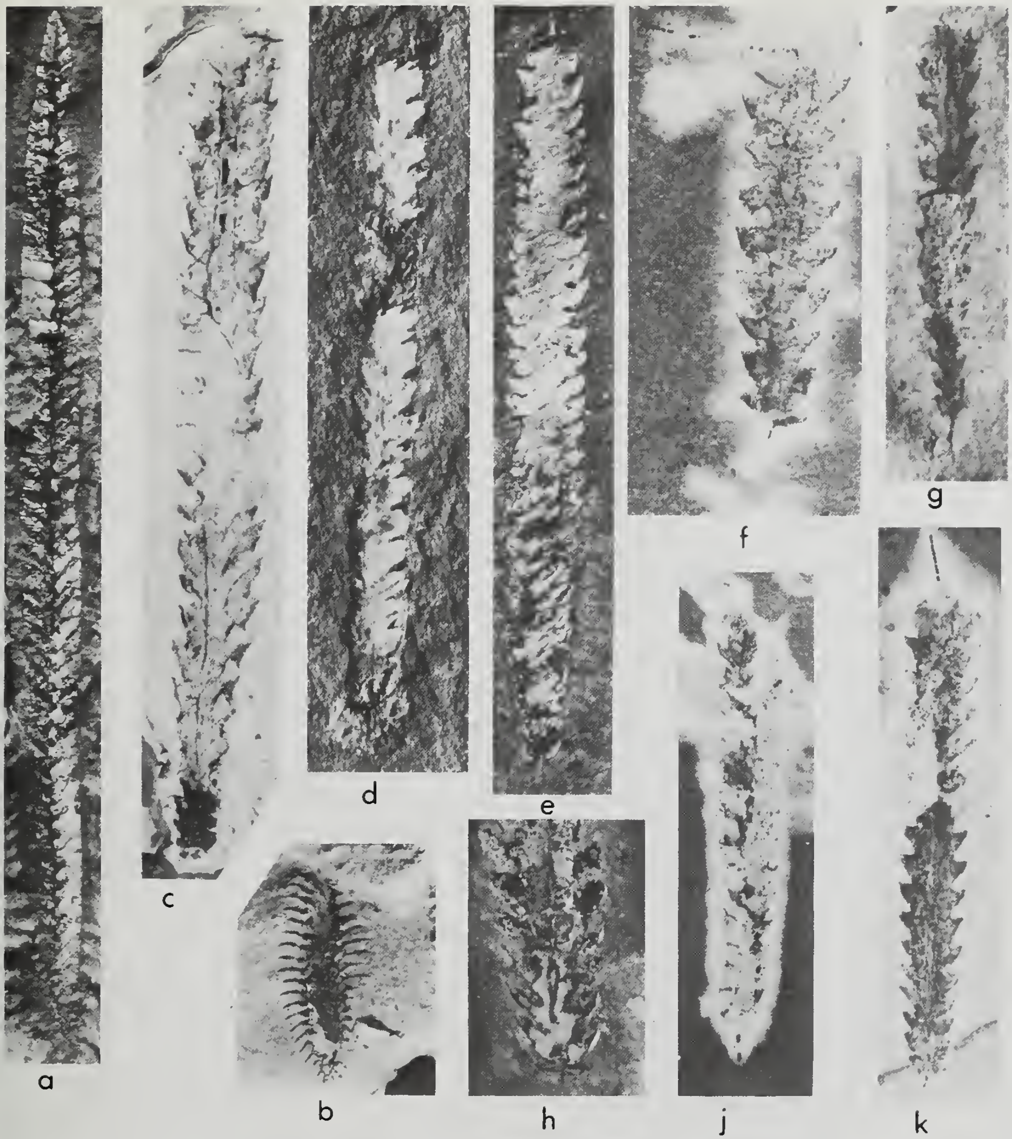


Fig. 135 Scandent graptoloids from the late Arenig to earliest Llanvirn of south Wales. a, *Pseudotrigonograptus ensiformis* (Hall 1865), Upper Arenig, Fennian, *B. rushtoni* Biozone, Pontyfenni Formation, loc. 23, × 3, Q5104. b, *Glossograptus acanthus* Elles & Wood 1908, latest Arenig, Fennian, *D. levigena* Biozone, Llanfallteg Formation, loc. 52J, × 2, Q5171. c, f, h, k, '*Glyptograptus*' *austrodentatus* Harris & Keble 1932, Llanfallteg Formation; c, large specimen widening slowly to more than 2 mm, late Arenig, *D. levigena* Biozone, loc. 52S, × 6, Q5802; f, well-preserved rhabdosome, early Llanvirn, *artus* Biozone, loc. 50, × 10, Q5803; h, detail of proximal part of wide morph in relief, showing median septum and th 1^1, late Arenig, *D. levigena* Biozone, loc. 52L, × 8, Q5804; k, well-preserved form, slowly increasing in width, locality and horizon as last, × 5, Q5805. d, e, g, j, '*Glyptograptus*' *dentatus* (Brongniart 1828); d, narrow morph from early horizon, Upper Arenig, Fennian, *B. rushtoni* Biozone, loc. 23, × 6, Q5808; e, wide morph from early horizon as Fig. 135d, × 5, Q5809; g, early Llanvirn, *D. artus* Biozone, loc. 50, × 6, Q5810; j, *D. levigena* Biozone, loc. 52P, × 5, Q5811.

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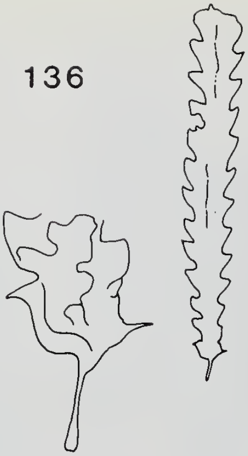

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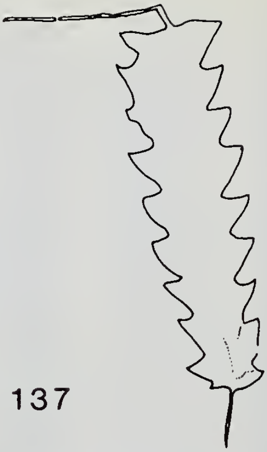


Fig. 136 '*Glyptograptus*' *dentatus* (Brongniart 1828). Well-preserved small rhabdosome, × 5, and detail of its proximal end, about × 20, early Llanvirn, *D. artus* Biozone, loc. 50, Llanfallteg Formation, Q5810.

Fig. 137 '*Glyptograptus*' *austrodentatus* Harris & Keble 1932. Typical specimen, Llanfallteg Formation, early Llanvirn, *D. artus* Biozone, loc. 50, × 10, Q5803.

DIAGNOSIS. See Bulman, 1963: 673–675.

DISCUSSION. Bulman (1963) revised *G. dentatus*, and further description of isolated material was given by Skevington (1965). Elles & Wood (1907: fig. 174; pl. 31, figs 4b–d) have already illustrated material from the Llanvirn part of the Llanfallteg Formation (misspelled 'Llanfanteg' on their p. 254). This is often well preserved, in full or partial relief. The species is distinguished from *G. austrodentatus* particularly by the sharp upward growth of th 1^1 and th 1^2, with a stout virgellar spine. Specimens conforming to Bulman's *sensu stricto* usage of *dentatus* are numerous in the latest Arenig and earliest Llanvirn. The earliest biserials in Wales, and probably as old as anywhere, are from the *Bergamia rushtoni* Biozone. These include (Fig. 135e) a specimen which has a maximum width of 2·5 mm, and which also tapers distally. Bulman cites 2·2 mm as a maximum for *G. dentatus*. Tectonic 'extension' is not usually evident in the Pontyfenni Formation and it is believed that the wide stipe was originally so. The same horizon has also yielded a narrow specimen which widens rather rapidly to 1·6–1·7 mm (Fig. 135d), a width which is retained throughout the rest of the rhabdosome. This form is intermediate between typical *dentatus* and what Bulman (1963) called *G. shelvensis* (with distal width 1·3–1·5 mm) from the Shelve Church Beds, Shropshire. We have other specimens (Fig. 135j) from beds as high as Llanvirn which are only slightly wider than *shelvensis*, and it seems possible that *shelvensis* may not prove distinct from *dentatus*. Here a broad view of the latter species is taken to include both wide and narrow morphs. In any case the choice of *G. dentatus* as a zonal fossil for the early Llanvirn (cf. Jenkins, *in* Hughes *et al.* 1982: 53) is inappropriate because it extends so far below the usual usage of that interval.

'*Glyptograptus*' *austrodentatus* Harris & Keble 1932
(Figs 135c, f, h, k, 137)

(For synonymy see Bulman (1963: 679) and Mu *et al.* (1979: 134)).

LECTOTYPE (selected Bulman 1963: 679). Geol. Surv. Victoria 31365.

TYPE LOCALITY AND HORIZON. Basal Darriwilian (equivalent to early Llanvirn); Victoria, Australia.

Occurrence in south Wales. Llanfallteg Formation, from latest Arenig (*Dionide levigena* Biozone) to early Llanvirn, throughout loc. 52; also locs 50, 55.

Material. Q5802–7; NMW 84.17G.116–7.

Diagnosis. See Bulman, 1963: 679, and comments below.

Discussion. This species is differentiated from *G. dentatus* primarily by its streptoblastic development, which results in a conspicuously truncated proximal end, and with the first pair of thecae not growing strongly upwards. This feature is shown well on specimens from south Wales in partial or full relief (Fig. 135h). The virgellar spine is more slender than on *G. dentatus*. Specimens such as that in Fig. 135f belong within the type population as described by Bulman (1963: text-fig. 6). Bulman described a number of 'varieties', which have no formal taxonomic status; Skevington (1965: 56–58) chose to elevate one of these to formal subspecific rank. Mu (*in* Mu *et al.* 1979) added one further subspecies and additionally proposed many new species, all from the *G. austrodentatus* Biozone. Legg (1976) described *G. situlus* from Western Australia, which also appears to have an *austrodentatus*-like proximal end. We have specimens from the Llanfallteg Formation (Fig. 135h) which widen rather rapidly to 2·2 mm. This exceeds the width allotted to any of Bulman's 'varieties', but is apparently the same as Mu's species *G. robustus* (Mu, *in* Mu *et al.* 1979: 135; pl. 47, figs 14, 16, 18) and possibly *G. austrodentatus major* Mu 1979. While it is interesting that such similar specimens occur in both Wales and China I am reluctant to use Mu's names for such specimens, because there is gradation between them and more 'typical' forms. Such wide forms tend to be flattened distally, and flattening too may have contributed to increase the transverse dimension; Mu's specimens are also clearly flattened. Skevington (1965: 58) mentions the occurrence of broad and narrow morphs of *G. austrodentatus*, but attaches no taxonomic importance to this feature. It seems probable that there was a good deal of intraspecific variation in *G. austrodentatus*, especially with regard to stipe width. Bulman (1963: 680) also noted a wide range of variation in distal thecal spacing, and measuring the distal 3 or 4 thecae and correcting for 'th in 10 mm' on the Llanfallteg specimens there is a range from 13 to 16 in 10 mm, with a mean between 14 and 15.

Whatever the final taxonomic status of the several 'varieties' of, and co-occurring 'species' with, *G. austrodentatus* it is significant for correlation that in China, Britain, and the Canning Basin, Western Australia (Legg 1978) *Glyptograptus* of *austrodentatus* type underlie pendent didymograptids, including *D. artus*.

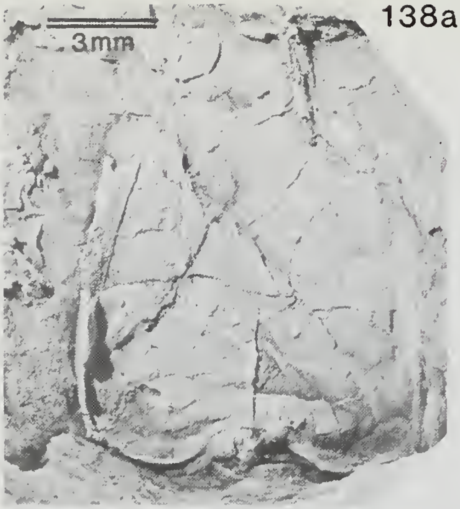
Acknowledgements

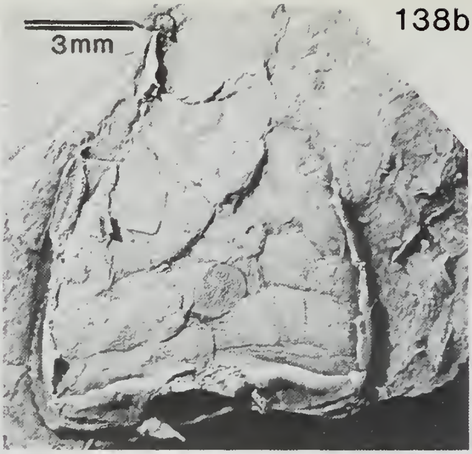
We could not have completed this work without the generous help of friends and colleagues in collecting specimens or providing us with information. We thank especially Dr J. C. W. Cope, Mr F. Cross, Mr E. K. Jones, Mr C. T. and Mrs I. Taylor and Dr R. P. S. Jefferies for giving us specimens they found for study. We also acknowledge the help of Dr R. E. Bevins, Dr R. A. Cooper, Dr C. J. Jenkins, Mr R. Kennedy, Dr M. G. Bassett, Mr S. F. Morris and Dr A. W. A. Rushton. Dr Rushton and Dr D. Price helped us greatly in locating specimens in the British Geological Survey and Sedgwick Museum, respectively. Dr W. Wimbledon and the Nature Conservancy Council are thanked for their help in exposing the Llanfallteg railway section. We record our debt to the photographic unit of the British Museum (Natural History) and Mrs Kathi Bryant for assistance with photography, and to Mrs Lin Norton for drafting diagrams. Miss Paula Westall, Mrs Edna Richards and Mrs Beryl Chant typed various parts of the manuscript.

The chordates—a preliminary note

by R. P. S. Jefferies

Eight genera, and eight or perhaps nine species, of primitive chordates are now known from the Upper Arenig of the Whitland area. This is remarkable, seeing that none at all was known from the Welsh Lower Ordovician until May 1979 when Dr R. M. Owens found a specimen of *Cothurnocystis* sp. (Figs 139a, b) in the Upper Arenig Pontyfenni Formation, in the disused





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139b

Fig. 138 a, b, *Mitrocystella* sp. a, dorsal and b, ventral aspect. Locality: Pontyfenni. *B. rushtoni* Biozone, Pontyfenni Formation, Upper Arenig. E63158a, b.

Fig. 139 a, b, *Cothurnocystis* sp. a, dorsal and b, ventral aspect. Note the gill slits as a prominent series of openings on the left side of the head. Locality: Llwyn-crwn. *B. rushtoni* Biozone, Pontyfenni Formation, Upper Arenig. NMW 84.17G.119a, b.

quarry at Llwyn-crwn. The purpose of this note is to record these zoologically important animals, in the hope that further search will discover more of them and thus allow this part of the fauna to be properly described.

All the chordates found are primitive forms which retain a calcite skeleton of echinoderm type ('calcichordates'). General accounts of these animals are given in Jefferies (1981*a*, 1986). To avoid confusion it must be mentioned that many workers regard them as echinoderms, notably

Ubaghs in the *Treatise of Invertebrate Paleontology* (1967), and sometimes they are referred to as carpoid echinoderms. There has recently been some published controversy on their affinities (Philip 1979, Chauvel 1981, Ubaghs 1981, Jefferies 1981*b*, Jollie 1982).

The calcichordates, in cladistic terms, are a paraphyletic group and so the word 'calcichordate' should only be used informally. They are co-extensive with the 'Stylophora' as used in the *Treatise* and can be divided into two major kinds—the 'Cornuta' and the 'Mitrata'. Both groupings are likewise paraphyletic and the names are placed in inverted commas for that reason. Satisfactory classification of the calcichordates, however, depends on placing them in the stem-groups of recent groups, as in the list below. The term 'stem-group', and also 'crown-group', have a precise meaning as explained in Jefferies (1979, 1986).

The cornutes are stem-group chordates. The mitrates, on the other hand, are primitive crown-group chordates since all known mitrates are primitive members of the extant chordate subphyla—whether stem-group acraniates, stem-group tunicates or stem-group vertebrates.

All calcichordates are divided anatomically into a head and a tail. The tail was almost certainly locomotory (Jefferies 1984) and served to pull the head rearwards across the sea floor, either in the sediment or on its surface according to the species. Cornutes had external gill slits, on the left side of the head only, and were primitively asymmetrical in other respects also. Mitrates are deduced to have had internal gill slits, on left and right sides of the head, and were fairly symmetrical in external outline, though with large asymmetries inside the head.

The forms are all found in the Pontyfenni Formation near Whitland and are as follows:

(1) **Cornutes**

(a) *Cothurnocystis* sp. Localities: Pen-y-parc, Llwyn-crwn, *S. abyfrons* to *B. rushtoni* Biozones. Fig. 139a, b. A new species. It is similar to *Cothurnocystis fellinensis* Ubaghs (1969) from the Lower Arenig of the Montagne Noire but lacks a median plate (y) dorsal to the tail insertion.

(b) *Reticulocarpos* sp. 1. Locality: Pen-y-parc, *S. abyfrons* Biozone. Fig. 141a, b. A new species, not identical with either of the two described forms, i.e. *Reticulocarpos hanusi* Jefferies & Prokop from the Llanvirn of Bohemia or *R. pissotensis* Chauvel & Nion from the Llandeilo of Normandy.

(c) *Reticulocarpos* ?sp. 2. Locality: Pontyfenni, *B. rushtoni* Biozone. Fig. 146. This is much smaller than R. sp. 1 and is either a juvenile of that species or belongs to a different species.

(2) **Mitrates**

(a) *Lagynocystis* sp. Locality: Pontyfenni, *B. rushtoni* Biozone. Fig. 145. A stem-group acraniate. Probably a new species since, unlike the only described species *L. pyramidalis* (Barrande) from the Llanvirn of Bohemia, it seems to lack dorsal spikes in the foretail and has only three spikes on the styloid.

(b) *Balanocystites* sp. Locality: Pontyfenni, *B. rushtoni* Biozone. Fig. 142a, b. A stem-group tunicate. It is characteristic of the genus that the two enlarged ventral plates (g on the right and j on the left) encroach only a short distance onto the dorsal surface.

(c) *Guichenocarpos* sp. Locality: Pontyfenni, *B. rushtoni* Biozone. Fig. 144. A stem-group tunicate. This genus resembles *Balanocystites* but differs in having a tall flange, U-shaped in plan with the U open anteriorly, on the dorsal surface.

(d) *Anatifopsis* sp. Locality: Pontyfenni, *B. rushtoni* Biozone. Fig. 143. A stem-group tunicate. This genus resembles *Balanocystites* but the ventral plates g and j extend further onto the dorsal surface. (*Anatifopsis* Barrande 1868 is identical with *Anatiferocystis* Chauvel 1941 and is often regarded as a crustacean.)

(e) *Mitrocystites* sp. Locality: Pen-y-parc, *S. abyfrons* Biozone. Fig. 140. A stem-group vertebrate. Only one specimen is known and it is too badly dissociated to be compared with particular described species.

(f) *Mitrocystella* sp. Locality: Pontyfenni, *B. rushtoni* Biozone. Fig. 138a, b. A stem-group vertebrate. This is a new species. It differs from *Mitrocystella incipiens* (Barrande), from the Llandeilo of Brittany and Bohemia, in its small size; and from *Mitrocystella barrandei* Jaekel, from the Llanvirn of Bohemia, in having cuesta-shaped ribs on the posterior part of the ventral

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141a

141b

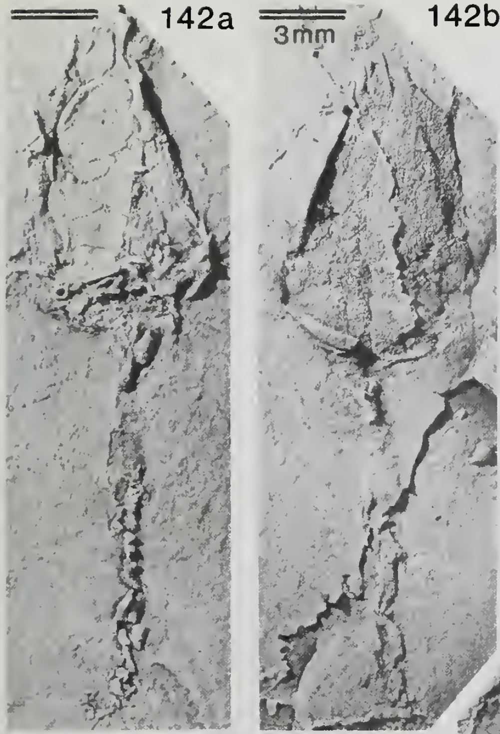
Fig. 140 *Mitrocystites* sp. Hind-tail ossicles are visible near the left of the picture and head plates elsewhere. Badly dissociated, but mainly ventral in aspect. Locality: Pen-y-parc. *S. abyfrons* Biozone, Pontyfenni Formation, Upper Arenig. E63146a, b.

Fig. 141 a, b, *Reticulocarpos* sp. 1. a, dorsal and b, ventral aspect. Locality: Pen-y-parc. *S. abyfrons* Biozone, Pontyfenni Formation, Upper Arenig. E29927.

surface instead of being smooth. It differs from both these species in having a concave dorsal surface.

A similar chordate fauna is known from other argillaceous occurrences in the earlier part of the Ordovician at the western edge of what is considered to have been a Gondwanan continent. Thus the present fauna is much like that of the Llanvirn Šárka Formation of Bohemia, as exposed at the famous localities of Šárka and Osek. At these localities, as near Whitland, the

142a 142b



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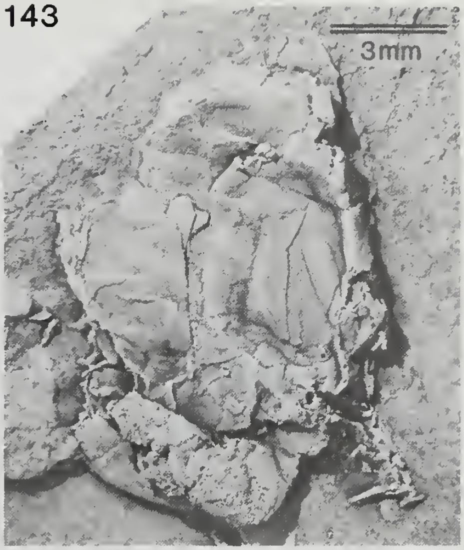

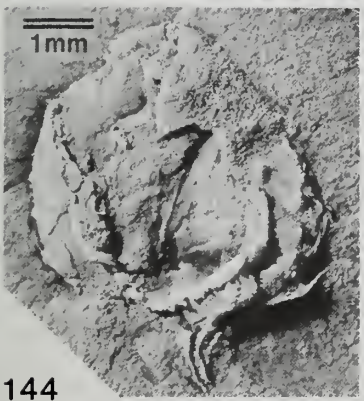

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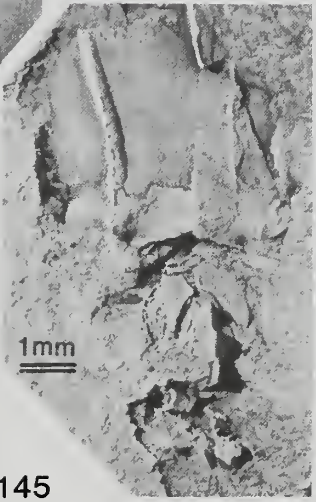

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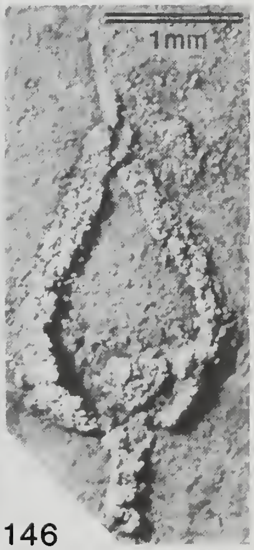

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Fig. 142 a, b, *Balanocystites* sp. a, dorsal and b, ventral aspect; bar = 3 mm. Locality: Pontyfenni. *B. rushtoni* Biozone, Pontyfenni Formation, Upper Arenig. NMW 78.8G.43a, b.

Fig. 143 *Anatifopsis* sp. Dorsal aspect. Locality: Pontyfenni. *B. rushtoni* Biozone, Pontyfenni Formation, Upper Arenig. E63160.

Fig. 144 *Guichenocarpos* sp. Dorsal aspect. Locality: Pontyfenni. *B. rushtoni* Biozone, Pontyfenni Formation, Upper Arenig. E63155.

Fig. 145 *Lagynocystis* sp. Dorsal aspect of foretail and posterior part of head. Locality: Pontyfenni. *B. rushtoni* Biozone, Pontyfenni Formation, Upper Arenig. E63159b.

Fig. 146 *Reticulocarpos* sp. ?2. Dorsal aspect. Locality: Pontyfenni. *B. rushtoni* Biozone, Pontyfenni Formation, Upper Arenig. E29928.

genera *Cothurnocystis*, *Reticulocarpos*, *Lagynocystis*, *Balanocystites*, *Guichenocarpos*, *Anatifopsis*, *Mitrocystites* and *Mitrocystella* occur, though some, or perhaps all, of the species are different. It can also be compared with the Traveusot Formation (Schistes à Calymènes) of the Llandeilo of Brittany in which most of the same genera recur, although *Mitrocystites* is rare there (Chauvel 1981) and *Cothurnocystis* and *Reticulocarpos* are absent. The Lower Arenig of the Montagne Noire also contains calcichordates (Ubaghs 1969, Thoral 1935), though the only genera known to be shared with the Whitland occurrence are *Cothurnocystis* and *Guichenocarpos* (*Anatifopsis escandei* Thoral 1935 is a *Guichenocarpos* according to my observations). It is unfortunate that the south Welsh chordates have never been found in siliceous nodules like those which contain the best-preserved specimens in Brittany, Bohemia and the Montagne Noire.

As to facies, it seems that advanced cornutes, such as *Reticulocarpos*, and most mitrates, preferred a soft muddy sea bottom in which sessile benthos was often rather rare.

The south Welsh occurrences show that chordates can be found in shaly Ordovician rocks if especially searched for. The paucity of known occurrences world-wide is probably not caused by original absence. Rather is it the case that palaeontologists have not been interested in these animals, despite their zoological significance, and therefore did not know them when they saw them.

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New taxonomic names and the page numbers of the principal references are in **bold** type.

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Appendix. Acritarchs and Chitinozoa from the Arenig Series of south-west Wales

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Contents

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Synopsis

Thirty-two samples were collected from the Arenig Series of south-west Wales to assess the occurrence and stratigraphical distribution of microfossils. All the samples yielded acritarchs and 6 also yielded chitinozoa. The microfossils are generally poorly preserved and rare, many taxa being represented by single specimens.

The species recorded from 14 samples are grouped into 7 assemblages (Microfossil Assemblages I–VII). Assemblages I–IV are of Moridunian (lower Arenig) age. Assemblage I occurs in the Allt Cystanog Member of the Ogof Hên Formation, assemblages II and III are present in the Cwmffrŵd Member of the Carmarthen Formation, and assemblage IV occurs in the Cwm yr Abbey Member of the same formation and at the base of the overlying Afon Ffinnant Formation. Assemblage V is of Whitlandian (middle Arenig) age, occurring in the Whitland Abbey Member of the Colomendy Formation. Assemblages VI and VII are both of Fennian (upper Arenig) age, and occur in the Pontyfenni Formation.

Biozones are not formally defined, but published and unpublished sources suggest that at least some of the microfossil assemblages from south Wales are comparable with those from Arenig rocks of northern England, north Wales and western Europe.

One new acritarch species *Stellechinatum papulessum* is described and one new combination *Stellechinatum uncinatum* (Downie) is proposed. Several acritarch and one chitinozoan species are described under open nomenclature.

Introduction

Fortey & Owens (1978, 1987) have demonstrated the presence of a complete and fossiliferous Arenig succession in south-west Wales, extending from east of Carmarthen to Ramsey Island

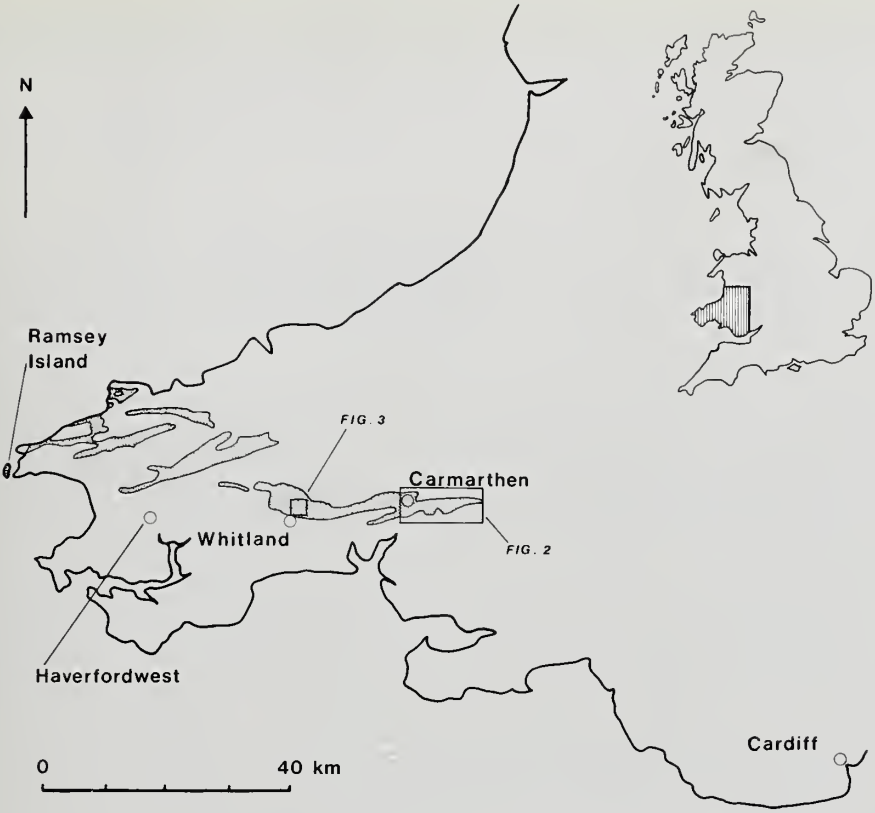


Fig. 1 Outcrop of Arenig rocks in south-west Wales (stippled).

(Fig. 1). Acritarchs and chitinozoa have been recorded from Arenig rocks in the Carmarthen–Whitland area; in this paper, their stratigraphical distribution is described.

Lower Arenig lithostratigraphy in the Carmarthen area is as follows (Fortey & Owens 1978, 1987):

		minimum thickness
Afon Ffinnant Formation		?
Carmarthen Formation	Cwm yr Abbey Member	45 m
	Cwmffrŵd Member	*c.* 70 m
	Pibwr Member	85 m
Ogof Hên Formation	Bolahaul Member	50 m
	Allt Cystanog Member	25 m

The Allt Cystanog Member of the Ogof Hên Formation comprises conglomerates, sandstones and siltstones. Its contact with the underlying Tremadoc rocks is nowhere exposed but it becomes finer upwards, passing through a transition into the micaceous mudstones and shales of the Bolahaul Member. The lowest 5 m of the Pibwr Member, comprising the lowest beds of the Carmarthen Formation, are transitional in character with the Bolahaul Member. Above that, the Pibwr Member comprises black, well-bedded mudstones. Above the Pibwr Member, the Carmarthen Formation is divided into the Cwmffrŵd Member, consisting of turbidites and shales, and the Cwm yr Abbey Member, comprising grey, poorly bedded mudstones. The latter are overlain by turbidites of the Afon Ffinnant Formation.

The Afon Ffinnant Formation is considered to be equivalent to the Blaencediw Formation of the Whitland area, where the middle and upper Arenig sequence is as follows (Fortey & Owens 1987):

		minimum thickness
Llanfallteg Formation (in part)		100 m
Pontyfenni Formation		300 m
Cwmfelin Boeth Formation		100 m
Colomendy Formation	Whitland Abbey Member	200 m
	Castelldraenog Member	*c.* 150 m
	Rhyd Henllan Member	*c.* 150 m
Blaencediw Formation		80 m

The Blaencediw Formation consists of poorly graded turbidites and channelled mass flow deposits, gritty shales and siltstones, and occasional black shales. Its base is not seen. The Colomendy Formation is divided into the sandy and silty shales of the Rhyd Henllan Member, the grey, fissile shales of the Castelldraenog Member and the black, poorly fissile shales of the Whitland Abbey Member. The latter are overlain by the well graded turbidites and black shales of the Cwmfelin Boeth Formation. The Pontyfenni Formation consists of black or dark grey shales and poorly fissile mudstones, passing upwards into the light grey mudstones and shales of the Llanfallteg Formation. The base of the Llanvirn Series lies within the latter.

Fortey & Owens (1987) define seven trilobite assemblage biozones in the Arenig Series of south-west Wales. The *Merlinia selwynii* Biozone is well developed in the Bolahaul and Pibwr Members. The *Merlinia rhyakos* Biozone occurs in the Cwmffrŵd and Cwm yr Abbey Members and in the lowest 40 m of the Afon Ffinnant Formation. The *Furcalithus radix* Biozone is restricted to the Afon Ffinnant Formation and probably also to the Blaencediw Formation. The base of the succeeding *Gymnostomix gibbsii* Biozone is presumed to lie within the lower half of the Afon Ffinnant Formation and close to the boundary of the Blaencediw and Colomendy Formations. The *Stapeleyella abyfrons* Biozone is represented by faunas from several localities in the basal Pontyfenni Formation but the base of the Biozone is arbitrarily taken at the base of the Cwmfelin Boeth Formation. The upper two-thirds of the Pontyfenni Formation is included in the *Bergamia rushtoni* Biozone and the Arenig part of the Llanfallteg Formation in the *Dionide levigena* Biozone. (See Fig. 4.)

On the basis of the trilobite faunas, three major divisions of the Series have been recognized. The base of the lower Arenig Moridunian Stage, incorporating the *M. selwynii* and *M. rhyakos* Biozones, has still to be defined. The base of the succeeding Whitlandian Stage is placed 40 m above the base of the Afon Ffinnant Formation and coincides with the base of the *F. radix* Biozone. The base of the upper Arenig Fennian Stage is defined at the base of the Cwmfelin Boeth Formation and is arbitrarily correlated with the base of the *S. abyfrons* Biozone. The base of the Llanvirn Series, defining the top of the Fennian, is taken at the first appearance of pendent didymograptids in the type section of the Llanfallteg Formation.

The Arenig rocks of south-west Wales were deposited at the edge of the Gondwanan continent (Fortey & Owens 1984). The Ogof Hên Formation comprises shallow water sediments, deposited during the initial phase of the Arenig transgression and containing the *Neseuretus* Community, an association of inshore trilobites (Fortey & Owens 1978). In the Pibwr Member, this association is replaced by the Raphiophorid Community, suggesting deeper water, which in turn is replaced in the Cwmffrŵd and Cwm yr Abbey Members by the Olenid Community, indicating deep, oxygen-deficient conditions. It is believed that the Carmarthen area was the site of a stagnant basin with restricted oceanic circulation, separated from the open ocean by a positive, fault-bounded block or blocks in the Haverfordwest district. The turbidites of the Afon Ffinnant and Blaencediw Formations mark the end of the restricted Olenid basin, the abundance of dendroid graptolites at certain horizons in the Blaencediw Formation suggesting quiet, shallow, oxygenated conditions. In the later Whitlandian, the trilobite and graptolite faunas provide evidence for an open oceanic environment. This environment persisted into the

Fennian, predominantly a time of mud deposition throughout south Wales with local turbidite sedimentation represented by the Cwmfelin Boeth Formation in the Whitland area. The faunal evidence suggests that the Pontyfenni Formation may have been deposited at a depth of 300 m or more, and the Llanfallteg Formation at shallower depth but probably more than 200 m. There is every indication that sedimentation was continuous throughout the Arenig and across the Arenig–Llanvirn boundary.

Palynology

Thirty-two samples have yielded acritarchs and six have also yielded chitinozoa. Abundance and diversity are generally low and preservation is poor; much of the material is heavily carbonized, opaque and brittle. Several specimens are distorted by the internal growth of crystals, probably of pyrite.

Sampling

Full details of sample localities (Figs 2, 3) are given on pp. 359–60.

Ogof Hên Formation. Five samples were collected from this formation, one (MPA 20074) from the top of the Allt Cystanog Member and four (MPA 20075–6, 20079–80) from the Bolahaul Member. All yielded microfossils.

Carmarthen Formation. Four samples (MPA 20077–8, 20086–7) were collected from the Cwmffrŵd Member and nine (MPA 20081–5, 20088–90, 20103) from the Cwm yr Abbey Member. All yielded acritarchs. No samples were collected from the Pibwr Member.

Afon Ffinnant Formation. Two samples (MPA 20104–5) from the base of this formation yielded acritarchs.

Colomendy Formation. Five samples (MPA 20094–8), all yielding acritarchs, were collected from the Whitland Abbey Member. No samples were collected from the Rhyd Henllan and Castell-draenog Members nor from the underlying Blaencediw Formation.

Pontyfenni Formation. Four samples (MPA 20099–102) were collected immediately above the base and three (MPA 20091–3) from about the middle of this formation. All yielded microfossils.

No samples from the Cwmfelin Boeth or Llanfallteg Formations were examined.

Biostratigraphy

The definition of acritarch biozones is unjustified because sampling and recording of species is incomplete, but the microfossils can be grouped into seven assemblages (I–VII). The stratigraphical position of these assemblages is shown in Fig. 4 and the occurrence of microfossil taxa in Fig. 5.

Microfossil Assemblage I. This is present in MPA 20074 and includes the acritarchs *Acanthodiacrodium* aff. *spinum* Rasul, ?*Coryphidium minutum* Cramer & Diez, *Micrhystridium* aff. *acuminosum* Cramer & Diez, *Polygonium* sp. A, ?*Uncinisphaera*? sp. D, *Veryhachium minutum* Downie, ?*Vogtlandia flosmaris* (Deunff) Dean & Martin and species of *Micrhystridium*, *Peteinosphaeridium* and *Stelliferidium*. One chitinozoan and several scolecodonts were recorded but have not been determined.

Microfossil Assemblage II. This occurs in MPA 20077 from the middle of the Cwmffrŵd Member in Nantycaws dingle (Owens & Fortey 1982; Fig. 2C herein) and is dominated by acanthomorphitic acritarchs. Species present include *Acanthodiacrodium* aff. *angustum* (Downie) Combaz, *Baltisphaerosum*? sp., *Cymatiogalea*? sp., ?*Polygonium* sp. A, *Stelliferidium* sp., *Uncinisphaera*? sp. D, *Uncinisphaera*? sp. E and the '*Veryhachium trispinosum*' group. The presence of *Uncinisphaera*? sp. E and '*V. trispinosum*' and the absence of *M.* aff. *acuminosum* distinguishes this assemblage from Microfossil Assemblage I.

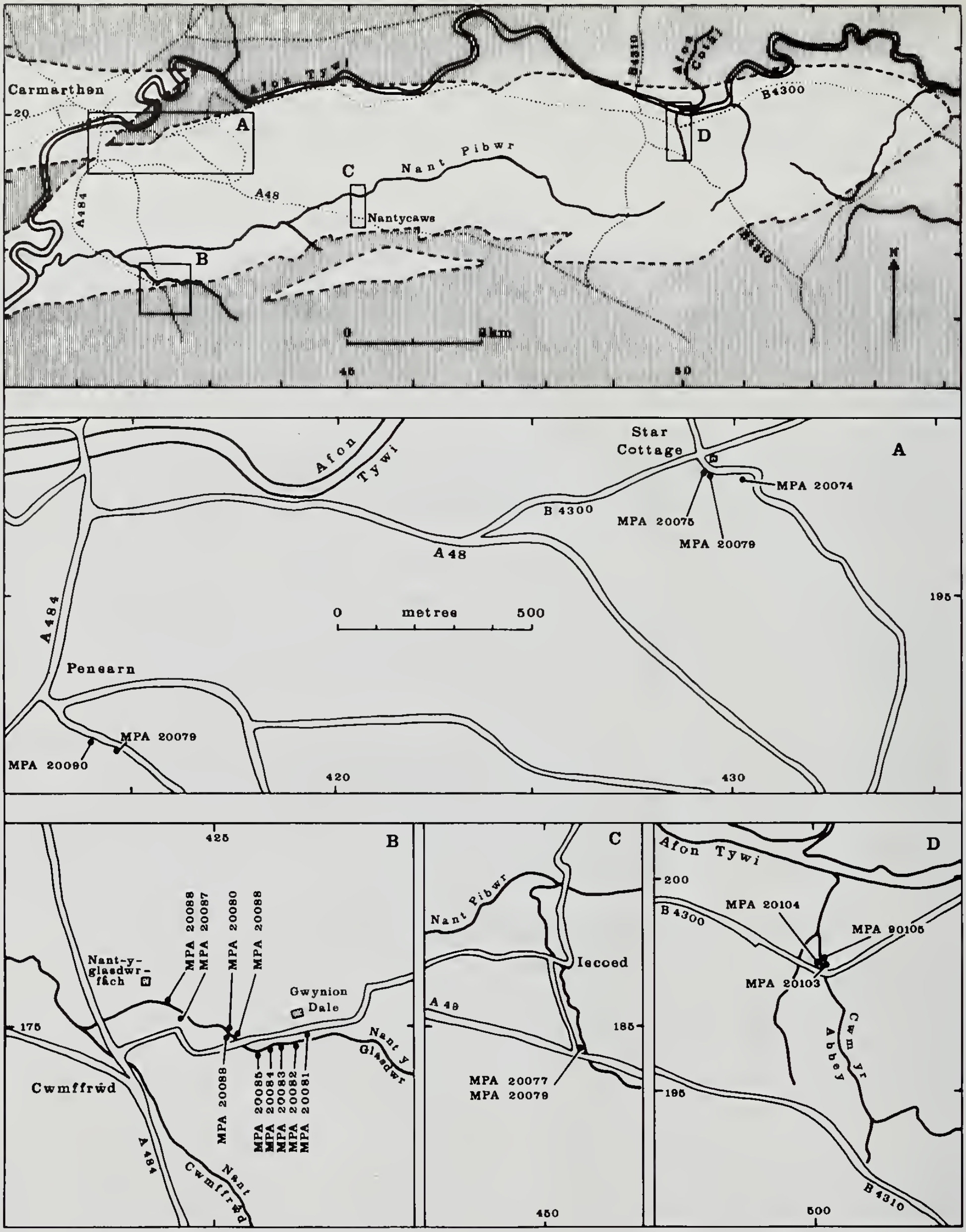


Fig. 2 Sample localities east of Carmarthen. Insets B–D drawn to same scale as A.

Microfossil Assemblage III. One sample (MPA 20087) from the top of the Cwmffrŵd Member in Nant y Glasdwr yielded a poor microflora in which a number of acritarch taxa are represented by single specimens. Species present include *Acanthodiacrodium* sp. A, *Barakella* sp. A, *Coryphidium*? sp. A, *Peteinosphaeridium* sp., *Stelliferidium* sp. and cf. *Uncinisphaera*? sp. D.

Microfossil Assemblage IV. This occurs in samples from the Cwm yr Abbey Member (MPA 20084, 20103) and the base of the Afon Ffinnant Formation (MPA 20104), comprising a rich

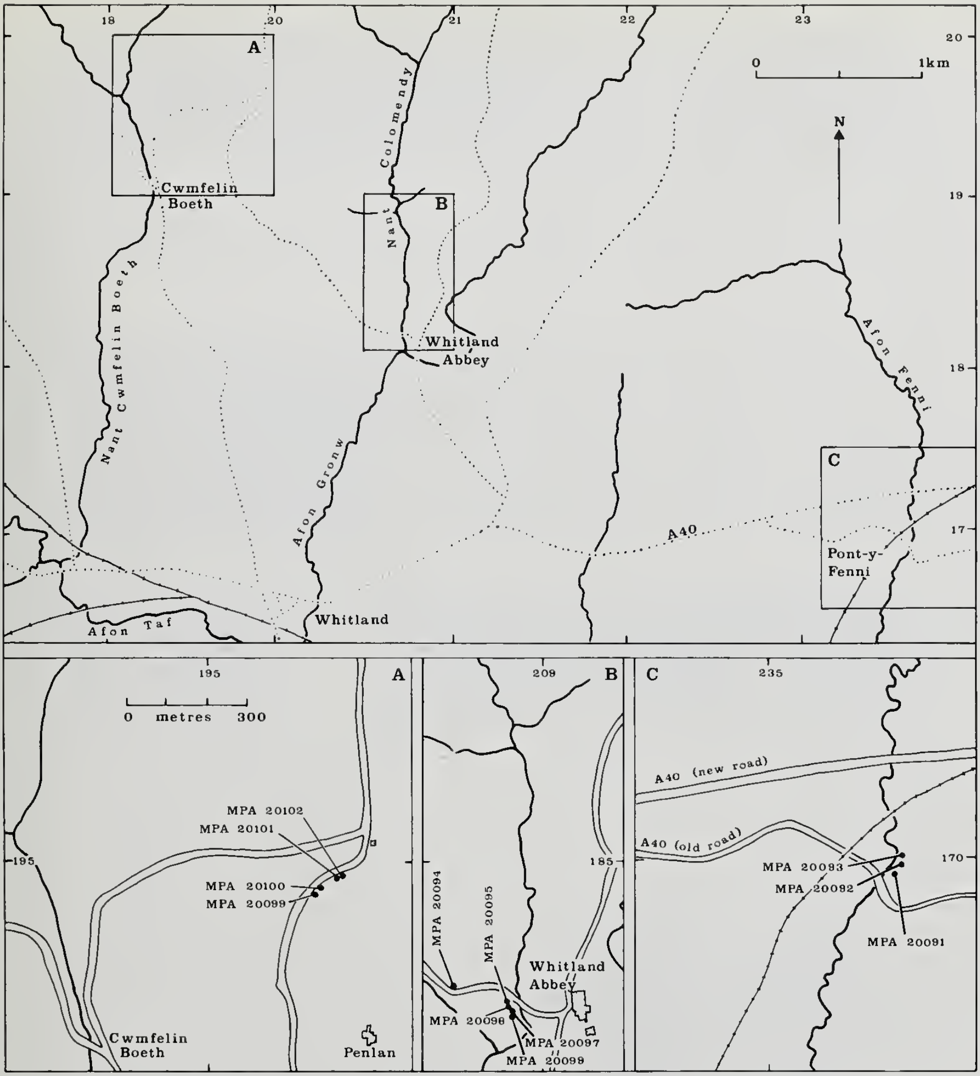


Fig. 3 Sample localities in the Whitland area. Insets B and C drawn to same scale as A.

and diverse assemblage that is dominated by acanthomorphitic acritarchs. *Micrhystridium* aff. *henryi* Paris & Deunff, *M.* cf. *inconspicuum aremoricanum* Paris & Deunff and *M.* aff. *nannacanthum* Deflandre distinguish this assemblage from others. Other important taxa are *Polygonium* sp. B, *Solisphaeridium* sp. B and *Uncinisphaera*? sp. F.

Microfossil Assemblage V. This is present in the Whitland Abbey Member (MPA 20098) and is distinguished by the dominance of small acanthomorphitic acritarchs, including *Micrhystridium* spp. A–D.

Microfossil Assemblage VI. This occurs immediately above the base of the Pontyfenni Formation (MPA 20099–102). It comprises a diverse microflora distinguished from other assemblages by the presence of *Coryphidium bohemicum* Vavrdova, ?*Frankea hamata* Burmann, *Orthosphaeridium* sp., *Stellechinatum unicinatum* (Downie) comb. nov., ?*Striatotheca mutua* Burmann,

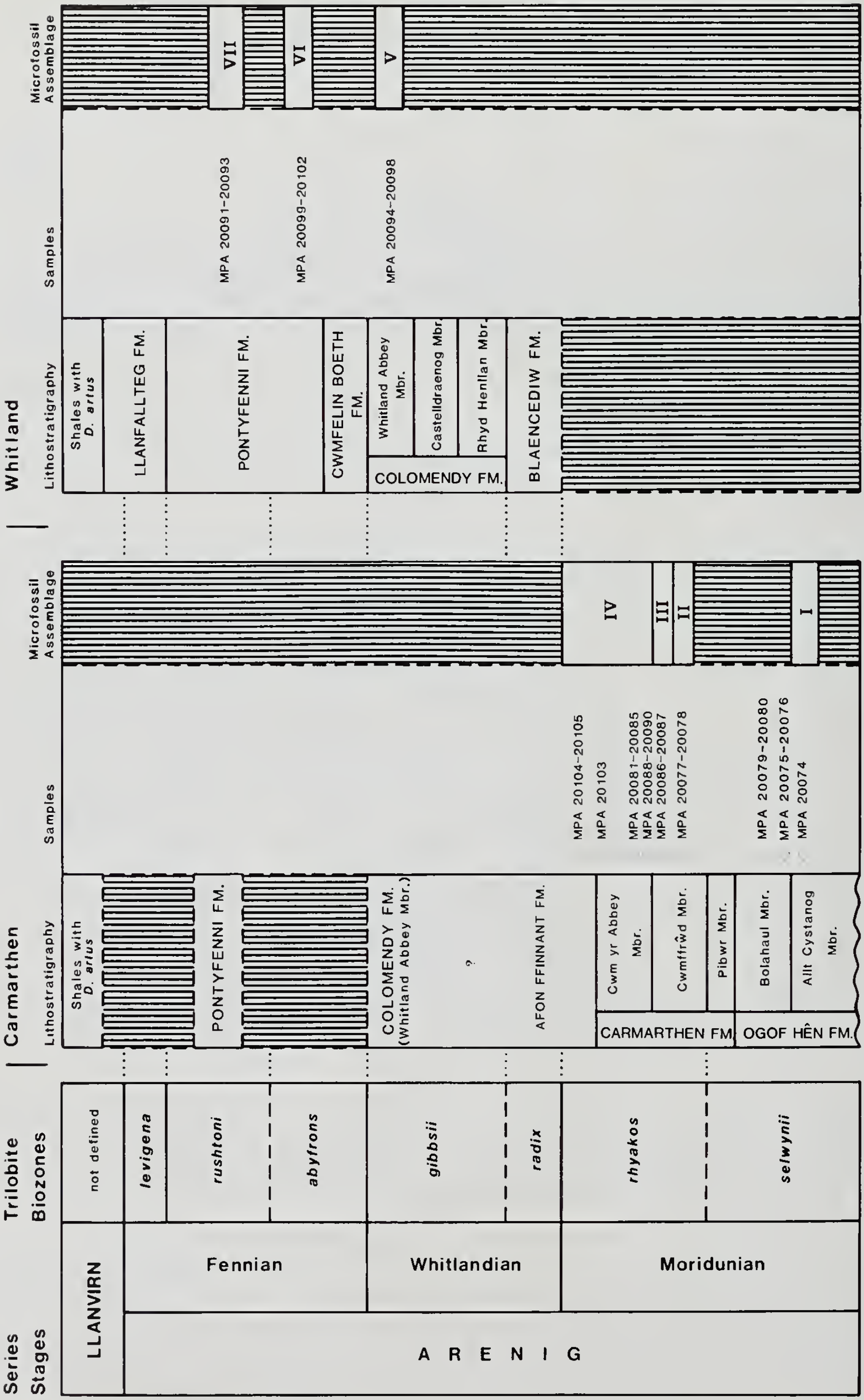


Fig. 4 The stratigraphical distribution of samples and microfossil assemblages in the Carmarthen and Whitland areas.

?*S. rarirrugulata* (Cramer, Kanes, Diez & Christopher) Eisenack, Cramer & Diez, and *Uncinisphaera*? spp. A and B. Rare chitinozoa and scolecodonts are present in MPA 20099.

Microfossil Assemblage VII. Three samples (MPA 20091–3) from the type section of the Pontyfenni Formation yielded diverse and abundant microfossils, including the acritarchs *Coryphidium bohemicum* Vavrdova, *Dasydorus cirritus*? Playford & Martin, *Orthosphaeridium ternatum* (Burmann) Eisenack, Cramer & Diez, *Solisphaeridium* sp. A, *Stellechinatum papulessum* sp. nov, *Stelliferidium* aff. *fimbrium* (Rasul) Rasul and *Uncinisphaera*? sp. C. This assemblage also has a more abundant and diverse chitinozoan fauna than any other, comprising *Belonechitina* spp., *Conochitina* cf. *chydaea* Jenkins, *Lagenochitina* sp. A and *L. cylindrica*? Eisenack.

Discussion

The samples from the Bolahaul Member yielded rare, small and simple acanthomorphitic acritarchs whose preservation is too poor for identification.

The '*Veryhachium trispinosum*' group may be a useful biostratigraphical marker in the Moridunian. In south-west Wales it appears in Microfossil Assemblage II from the Cwmffrŵd Member of the Carmarthen Formation, and in eastern Newfoundland its earliest recorded occurrence is approximately 500 m above the base of the Arenig (Dean & Martin 1978). However, Martin (1982) showed that it also occurred in the Tremadoc, which suggests that the taxonomy and biostratigraphy of forms placed in the group will have to be revised and clarified before its significance can be appreciated.

Reworked Cambrian and Tremadoc acritarchs, including *Cymatiogalea bellicosa* Deunff, *Timofeevia lancarae* (Cramer & Diez) Vanguestaine, *Vulcanisphaera britannica* Rasul and *V. turbata*? Martin, occur at the top of the Cwm yr Abbey Member in MPA 20103 and immediately above the base of the Pontyfenni Formation in MPA 20099.

Comparison with assemblages from other areas

Arenig acritarchs are known from other areas of England and Wales, principally through the unpublished work of Booth (1979). Samples collected in north Wales, from the Afon Seiont at Caernarfon, the Menai Straits Inlier and Garth Point at Bangor, are considered to be of Fennian age (Dr R. A. Fortey, personal communication). The acritarch floras contained a number of taxa not recorded from south-west Wales, but also included *Coryphidium bohemicum*, *Striatotheca rarirrugulata*, *Frankea hamata* and *Uncinisphaera*? sp. B, species that are present in Microfossil Assemblage VI. Booth also reported *C. bohemicum*, *S. rarirrugulata*, *Uncinisphaera*? sp., *Orthosphaeridium ternatum* and *Frankea sartbernardensis* (Martin) Burmann from Outerside in the Lake District, where Jackson (1978: 92) recorded graptolites of the *Didymograptus hirundo* Biozone. The Outerside assemblage is again similar to Microfossil Assemblage VI although *O. ternatum* has only been recorded from the higher part of the Pontyfenni Formation, in Microfossil Assemblage VII.

Acritarchs of inferred Arenig age have been described from elsewhere in north-west England. Turner & Wadge (1979) have published an account of 'mid' Arenig acritarchs from the south-western Lake District, recording *C. bohemicum*, *S. rarirrugulata* and *F. hamata*. This assemblage is best compared with Microfossil Assemblage VI and is probably of Fennian age. A similar assemblage was recorded by Molyneux (1979) from the Lady Port Banded 'Group' on the Isle of Man. Lister (*in* Arthurton & Wadge 1981: 6–11) has reported early Ordovician acritarchs from the Cross Fell Inlier where he recognized four assemblages, the older two being of probable late Arenig age. There is little similarity between Lister's assemblages and those from south-west Wales but many key taxa were described subsequent to Lister's investigations in the late 1960s. His material needs to be re-examined before any useful comparisons can be made.

Nothing has been published previously on acritarchs from rocks of known Moridunian or Whitlandian age in Britain, but assemblages from the Glen Dhoo Flags and Lonan Flags on the Isle of Man are of probable latest Tremadoc or earliest Arenig age (Molyneux 1979). Differences between these assemblages and those from the Moridunian of south-west Wales hinder detailed comparison, but the '*Veryhachium trispinosum*' group has not been recorded

	MPA 20093	MPA 20092	MPA 20091	MPA 20102	MPA 20101	MPA 20100	MPA 20099	MPA 20098	MPA 20104	MPA 20103	MPA 20084	MPA 20087	MPA 20077	MPA 20074
Belonechitina spp.			8											
Conochitina cf. *chydaea*			6											
Lagenochitina cylindrica?			1											
Lagenochitina sp. A	1	11	18											
?Adorfia prolongata	1		1											
Dasydorus cirritus?	5	11	2											
Orthosphaeridium ternatum	1		3											
Solisphaeridium sp. A			4											
Stellechinatum papulessum	8	2	3											
Stelliferidium aff. *fimbrium*		1	1											
Uncinisphaera? sp. C			9											
Coryphidium bohemicum		1	1	4		3								
Stellechinatum uncinatum	1				1		5							
'*Veryhachium trispinosum*' group	3	4	16				2	2	3	6	1		1	
Cymatiogalea bellicosa							1(r)							
?Frankea hamata				1										
Orthosphaeridium sp.					1									
?Striatotheca mutua							1							
?Striatotheca rarirrugulata				1										
Timofeevia lancarae							1(r)							
Uncinisphaera? sp. A							3							
Uncinisphaera? sp. B							7							
Vulcanisphaera britannica							1(r)							
Vulcanisphaera turbata?							1(r)			1(r)				
Nothooidium? spp.					1				1					
Micrhystridium sp. A								6						
Micrhystridium sp. B								8						
Micrhystridium sp. C								7						
Micrhystridium sp. D								2						
Micrh. aff. *henryi*									1	4				
Micrh. cf. *inconspicuum aremoricanum*									3	12	6			
Micrh. aff. *nannacanthum*										2	11			
Polygonium sp. B											6			
Solisphaeridium sp. B										4	2			
Striatotheca sp.										1				
Uncinisphaera? sp. F										4				
Acanthodiacrodium sp. A												1		
Barakella sp. A												1		
Coryphidium? sp. A												1		
Uncinisphaera? sp. D												?	7	?
Acanthodiacrodium aff. *angustum*													1	
Baltisphaerosum? sp.													1	
Cymatiogalea? sp.													3	
Uncinisphaera? sp. E													2	
Acanthodiacrodium aff. *spinum*														1
?Coryphidium minutum														1
Micrh. aff. *acuminosum*														3
Polygonium sp. A														2
?Vogtlandia flosmaris														1
Microfossil Assemblages	VII			VI				V	IV			III	II	I

Fig. 5 Distribution and abundance of acritarch and chitinozoa species: (r) indicates that the species is probably reworked from the Tremadoc or Cambrian.

from either the Manx assemblages or those from the Ogof Hên Formation. Furthermore, specimens of *Coryphidium* in the Glen Dhoo and Lonan Flags, referred previously to *C. bohemicum*, are probably not the same as Fennian specimens, having long, slender and flexible rather than short, conical and capitate processes.

Acritarchs of reported Arenig age are also known from Europe, north Africa, North America and Australia (Martin 1982). In a number of cases there is no independent evidence for an Arenig age, the age of the assemblages being inferred from their composition and comparisons with existing data. However, Rauscher (1973) has described acritarchs from the undivided *Didymograptus extensus* Biozone of the Montagne Noire, France, recording *Coryphidium bohe-*

micum, *Striatotheca rarirrugulata* and specimens of the '*V. trispinosum*' group. Comparison with south-west Wales suggests that the assemblage is probably of early Fennian age, implying that it is from the upper part of the *D. extensus* Biozone.

Vavrdova (1965, 1966, 1972, 1973, 1976) has described acritarchs from the Klabava Shales in the Rokycany district, 'U Starého hradu' ['at the old castle'] south-east of Klabava, Bohemia, where they occur in the *Tetragraptus* cf. *pseudobigsbyi* Biozone, a biostratigraphical unit that replaced the *T. reclinatus abbreviatus* Biozone (see Martin 1982: 35). The *Tetragraptus reclinatus abbreviatus* Biozone was regarded as being approximately equivalent to the *Isograptus gibberulus* Biosubzone of the British succession (Cooper & Fortey 1982: fig. 2), implying correlation with the Fennian. The acritarch assemblage 'U Starého hradu' includes *C. bohemicum* and the '*V. trispinosum*' group as well as a number of taxa not recorded from south-west Wales. Similarity between the two areas is apparently limited.

Arenig acritarchs from the upper part of the Bell Island Group and the overlying Wabana Group of Bell Island, eastern Newfoundland, have been recorded by Martin (*in* Dean & Martin 1978). Graptolites from approximately 20 m above the base of the Wabana Group are reported to indicate the upper part of the *D. extensus* Zone, implying a Fennian age. The acritarch assemblages have little in common with those from south-west Wales, containing thirty species of which six are recorded in this paper.

Acritarchs from equivalents of the Arenig Series in the Baltic region of the U.S.S.R. have been described by Timofeev (1959). The Baltic assemblages are unlike those from south-west Wales, where none of Timofeev's species have been recognized. The differences might arise from separation of the two areas across climatic zones in the Arenig, faunal evidence placing south-west Wales at high latitudes and the Baltic at temperate latitudes (Cocks & Fortey 1982).

No Arenig chitinozoa have hitherto been described from the British Isles, although Lister (*in* Arthurton & Wadge 1981) has reported chitinozoa from rocks of probable Arenig age in the Cross Fell Inlier. Post-Arenig chitinozoa have been described by Jenkins (1967) from the Hope Shales of Lower Llanvirn age in the Shelve Inlier of Shropshire. The specimens of *Conochitina* cf. *chydaea* and *Lagenochitina cylindrica*? that are present in Microfossil Assemblage VII resemble species recorded by Jenkins, but there is otherwise little in common with his Lower Llanvirn faunas. Many of the species that are characteristic of Llanvirn assemblages, notably species of *Siphonochitina*, are absent from the Pontyfenni Formation, as are other taxa such as *Cyathochitina campanulaeformis* and species of *Rhabdochitina* which range upwards from the Llanvirn. In contrast, the most common form in the Pontyfenni Formation, *Lagenochitina* sp. A, is apparently absent from the Hope Shales.

Arenig chitinozoa have been described from Quebec (Achab 1982), Spitsbergen (Bockelie 1980), Belgium (Martin 1969*a*), France (Rauscher 1968, 1973), north Africa (Benoit & Taugourdeau 1961), south-west Europe (Paris 1981), Australia (Combaz & Peniguel 1972) and Sweden (Grahn 1980). Further work, including scanning electron microscopy, is needed before comparisons can be made between these faunas and the chitinozoa from south-west Wales.

Very little comparison can be made with other areas, probably reflecting inadequate sampling for Arenig acritarchs and chitinozoa. Even this account is based on so few samples and such incomplete coverage that it should be regarded as preliminary. Martin (1982) notes that information from the Lower Arenig graptolite biozones of *Tetragraptus approximatus* and *Didymograptus deflexus* is sparse. It may be significant that many of the previously described assemblages are more similar to Microfossil Assemblage VI than any other, the earlier assemblages from south-west Wales occupying an interval that has not been sampled elsewhere.

Systematic descriptions: Acritarchs

Figured specimens are deposited in the Palaeontological Collections of the British Geological Survey, Keyworth, and are registered in the series MPK 4870–4978.

Figure explanations include the specimen's register number (e.g. MPK 4971), details of the sample and an England Finder co-ordinate (e.g. K34/0) to locate the specimen on the slide. The co-ordinates were obtained on a Zeiss photomicroscope bearing the number 66303.

Acritarch genera and species are described alphabetically.

Open nomenclature. The genus name followed by 'sp. A', &c., is used when the species seems to be new but cannot be formally described on the available material. I use 'sp.' alone to indicate the material cannot be assigned to an existing species owing to poor preservation, or because the potentially diagnostic characters carry low taxonomic weight, requiring population study (for which there is insufficient material) to diagnose a new species, as against a variety of an existing species (as with *Striatotheca* sp., p. 346).

The use of '?' in different positions follows the convention of the British Geological Survey *Notes for Authors* (Dhonau 1982: 22).

Genus *ACANTHODIACRODIUM* Timofeev, 1958

TYPE SPECIES. *Acanthodiacrodium dentiferum* Timofeev 1958.

Acanthodiacrodium aff. ***angustum*** (Downie 1958) Combaz 1967
Fig. 6A, B

aff. 1958 *Diornatosphaera angusta* Downie: 345–346; pl. 17, figs 7, 8; text-fig. 3e.
aff. 1962 *Lophodiacrodium angustum* (Downie) Deflandre & Deflandre-Rigaud: 194.
aff. 1967 *Acanthodiacrodium angustum* (Downie) Combaz: 15; pl. 3, figs 67–72.

MATERIAL. One specimen.

OCCURRENCE. Cwmffrŵd Member: MPA 20077.

DESCRIPTION. The vesicle is ellipsoidal and opaque but more or less intact. About 20 short, rounded, densely crowded cones are present at each pole on the long axis of the vesicle.

DIMENSIONS. Vesicle diameter 37 × 30 μm; cone length less than 1 μm.

REMARKS. This specimen resembles the Tremadoc species *Acanthodiacrodium angustum* and morphologically similar species such as *Lophodiacrodium filiforme* (Timofeev) Deflandre & Deflandre-Rigaud. Poor preservation does not allow a positive identification.

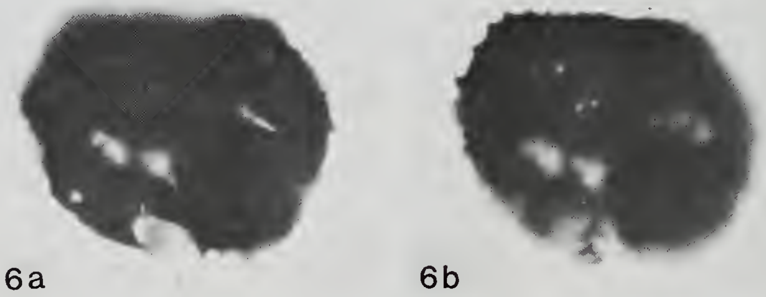


Fig. 6A, B *Acanthodiacrodium* aff. *angustum* (Downie 1958) Combaz 1967, high and low focus; MPK 4870, sample MPA 20077, Cwmffrŵd Member; slide 2, J20/1, × 1200.

Acanthodiacrodium aff. ***spinum*** Rasul 1979
Fig. 7A, B

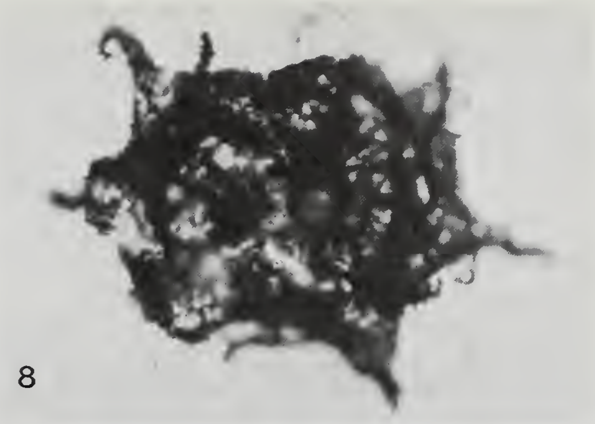
aff. 1979 *Acanthodiacrodium spinum* Rasul: 66–67; pl. 3, figs 1–7.

MATERIAL. One specimen.

OCCURRENCE. Allt Cystanog Member: MPA 20074.

DESCRIPTION. The specimen is opaque but otherwise has suffered little damage. The vesicle is ellipsoidal with a slight equatorial constriction. The processes are short, flexible and tapering, and have evexate or capitate distal terminations. They may be solid or hollow. Approximately 25–30 processes are present at each pole.


7a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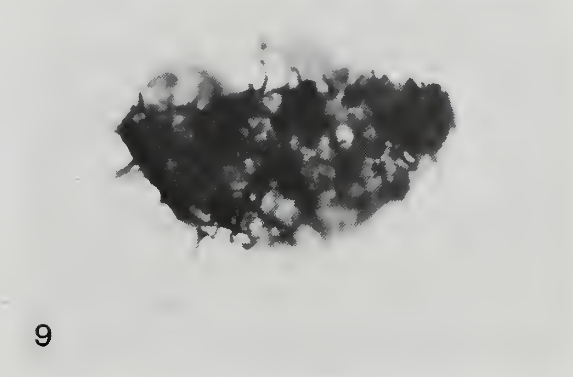
7b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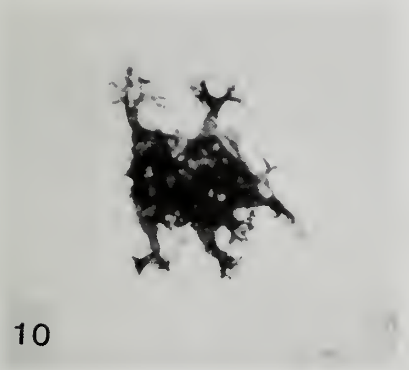
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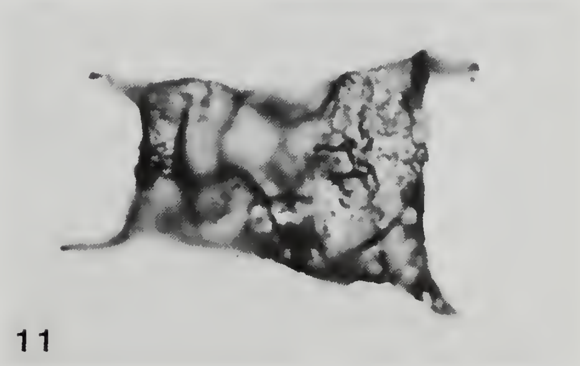
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Fig. 7A, B *Acanthodiacrodium* aff. *spinum* Rasul 1979, high and low focus; MPK 4871, sample MPA 20074, Allt Cystanog Member; slide 2, N63/1, × 1200.

Fig. 8 *Acanthodiacrodium* sp. A; MPK 4872, sample MPA 20087, Cwmffrŵd Member; slide 2, E24/0, × 1200.

Fig. 9 *Baltisphaerosum* ? sp.; MPK 4873, sample MPA 20077, Cwmffrŵd Member; slide 2, U24/2, × 1200.

Fig. 10 ?*Adorfia prolongata* Burmann 1970; MPK 4874, sample MPA 20093, Pontyfenni Formation; slide 1, P22/0, × 480. See Fig. 12.

Fig. 11 *Barakella* sp. A; MPK 4875, sample MPA 20087, Cwmffrŵd Member; slide 1, E30/3, × 1200. See Fig. 13.

Dimensions. Vesicle diameter 24 × 19 μm; process length 4 μm.

Remarks. The gross morphology and dimensions of this specimen resemble those of *Acanthodiacrodium spinum*, described by Rasul (1979) from the *Clonograptus tenellus* Zone and Brachiopod Beds of the Tremadocian Shineton Shales. *A. spinum*, however, has hollow, acuminate processes and a finely striate vesicle.

Acanthodiacrodium sp. A
Fig. 8

Material. One specimen.

Occurrence. Cwmffrŵd Member: MPA 20087.

Description. The specimen is dark brown to grey and more or less intact. The vesicle is roughly hexagonal, but is drawn out along one axis. The processes are concentrated at the poles of the long axis, seven at one pole and four at the other. The processes are stout, conical, and together with the vesicle are covered by robust, hollow cones or hairs with solid tips. The narrow equatorial zone may be striate, the rather indistinct striae being parallel to the long axis of the vesicle.

Dimensions. Vesicle diameter 40 × 33 μm; process length 12 μm.

Remarks. The robust ornament distinguishes this specimen from most other species of *Acanthodiacrodium*. *A. achrasi* Martin, 1972, is similar but is smaller and has a finer ornament.

Genus ***ADORFIA*** Burmann, 1970

Type species. *Adorfia firma* Burmann 1970.

? ***Adorfia prolongata*** Burmann 1970
Figs 10, 12

? 1970 *Adorfia prolongata* Burmann: 295; pl. 5, figs 1, 2, 5.
? 1978 *Adorfia prolongata* Burmann; Dean & Martin: 7; pl. 2, figs 6, 9; pl. 3, fig. 27.

Material. Two specimens.

Occurrence. Pontyfenni Formation: MPA 20091, MPA 20093.

Description (based on one specimen from MPA 20093). The vesicle is subpolygonal to quadrate in outline. The process bases coalesce in part to mask the vesicle outline. Process stems are stout and cylindrical or slightly tapered. The processes divide distally by dichotomy, with up to five orders of division. The terminal branches on each process are long and recurved, and are apparently capitate. Nine processes are present.

Dimensions. Vesicle diameter: 26 × 28 μm and 28 × 34 μm
Process length (overall): *c.* 20–25 μm
Process length (stem): *c.* 13–16 μm
Process width (base): 4–5 μm

Remarks. The specimen from MPA 20093 apparently has capitate process terminations, a character diagnostic of the genus *Adorfia* Burmann. The dimensions of the vesicle and processes

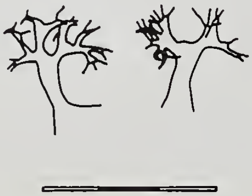


Fig. 12 ?*Adorfia prolongata* Burmann 1970, detail of processes; MPK 4874. Bar represents 30 μm. See Fig. 10.

are consistent with those of *A. prolongata*, and the number of processes on the specimen falls within the range of variation recorded by Martin (*in* Dean & Martin 1978). Poor preservation precludes positive identification of the specimen.

Genus ***BALTISPHAEROSUM*** Turner, 1984

TYPE SPECIES. *Baltisphaerosum christoferi* (Kjellstrom 1976) Turner 1984.

***Baltisphaerosum*?** sp.
Fig. 9

MATERIAL. One specimen.

OCCURRENCE. Cwmffrŵd Member: MPA 20077.

DESCRIPTION. The specimen is hemispherical with a smooth or finely granulate wall. Its shape suggests that it is one half of a spherical vesicle which has split equatorially. About 30 short, slender, hollow and evexate processes, which are plugged at the base and do not communicate with the interior of the vesicle, are present.

DIMENSIONS. Vesicle diameter 40 × 20 μm; process length 7 μm.

REMARKS. The shape of the specimen suggests excystment by means of an equatorial split. Simple, hollow, proximally plugged processes and this type of excystment are diagnostic of *Baltisphaerosum*. Assignment to *Baltisphaerosum* is tentative, however, because this taxon is poorly recorded in the Arenig of south-west Wales, and also because it is difficult to be certain that the splitting is not the result of accidental damage. The specimen has much shorter processes than other known species of *Baltisphaerosum*.

Genus ***BARAKELLA*** Cramer & Diez, 1977

TYPE SPECIES. *Barakella fortunata* Cramer & Diez 1977.

Barakella sp. A
Figs 11, 13

MATERIAL. One specimen.

OCCURRENCE. Cwmffrŵd Member: MPA 20087.

DESCRIPTION. The vesicle is rectangular and bears four processes, one at each corner. The processes are short and stout, with rounded distal terminations. The vesicle and processes are covered by short hairs or grana, and one of the two shorter sides of the vesicle has an area of short anastomosing hairs midway along its length.

DIMENSIONS. Vesicle diameter 36 × 24 μm; process length 8 μm.

REMARKS. The area of short anastomosing hairs is diagnostic of the genus but the ornament distinguishes this specimen from other species of *Barakella*.

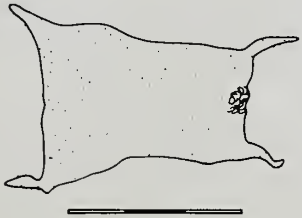


Fig. 13 *Barakella* sp. A, detail of surface ornament and the structure midway along one of the two shorter sides; MPK 4875. Bar represents 30 μm. See Fig. 11.

Genus *CORYPHIDIUM* Vavrdova, 1972

TYPE SPECIES. *Coryphidium bohemicum* Vavrdova 1972.

Coryphidium bohemicum Vavrdova 1972
Figs 14–18, ? 20

1972 *Coryphidium bohemicum* Vavrdova: 84–85; pl. 1, figs 1, 2; text-fig. 4.

MATERIAL. Nine specimens.

OCCURRENCE. Pontyfenni Formation: MPA 20092–20100, 20102.

DESCRIPTION. The vesicle is quadrate with straight or concave sides and broadly rounded corners. Striations on the vesicle wall are more or less parallel to the sides of the vesicle. There are about 30 processes, concentrated at the corners of the vesicle, which have short, stout, conical stems and apparently hollow capitate distal terminations; the conical stems may be solid or hollow.

DIMENSIONS. Vesicle diameter: range 18–26 μm; mean 21 μm.
Process length: range 1·5–2·5 μm; mean 2 μm.
Process width: less than 1 μm.

REMARKS. The vesicles of the specimens from the Pontyfenni Formation conform to the diagnosis of *Coryphidium bohemicum*, but the processes are slightly shorter than those originally described by Vavrdova (1972). The distal process terminations of the Pontyfenni specimens are unlike any of the examples illustrated by Vavrdova, but as the processes of *C. bohemicum* are reported in the diagnosis to be distally heteromorphic, capitate terminations are not necessarily inconsistent with the determination. Specimens with predominantly capitate terminations on short, stout, conical stems appear to be characteristic of the Fennian; Booth (1979) illustrates a number of examples from the Fennian of north Wales, and Turner & Wadge (1979) illustrate three poorly preserved specimens with apparently similar processes from rocks of probable Fennian age in the Lake District. The specimens from the Pontyfenni Formation have fewer processes than the type material.

?***Coryphidium minutum*** Cramer & Diez 1976
Fig. 19

?1976 *Coryphidium minutum* Cramer & Diez: 205; pl. 23, figs 7, 10; text-fig. 2: 7.

MATERIAL. One specimen.

OCCURRENCE. Allt Cystanog Member: MPA 20074.

DESCRIPTION. The specimen is split at one end but is otherwise undamaged. The vesicle is quadrate with more or less straight sides and broadly rounded corners. The vesicle wall is apparently smooth. The processes are more prominent at the corners of the vesicle but are not restricted to that position. They are relatively short, slender and bifid, and may be hollow. It is not clear whether the processes communicate with the interior of the vesicle. About 40 processes are present.

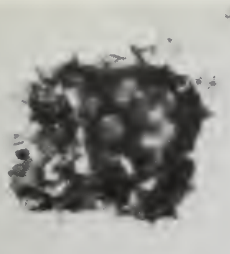
DIMENSIONS. Vesicle diameter 28 × 20 μm; process length 2·5 μm.

REMARKS. The specimen resembles *Coryphidium minutum* as illustrated by Cramer & Diez (1976) from rocks of alleged Upper Arenig age in Morocco. According to its diagnosis, *C. minutum* has slightly shorter processes with simple or capitate distal terminations.

Coryphidium? sp. A
Figs 21–22

MATERIAL. One specimen.

OCCURRENCE. Cwmffrŵd Member: MPA 20087.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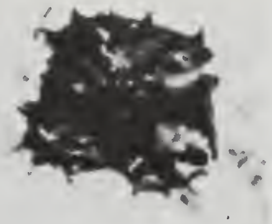
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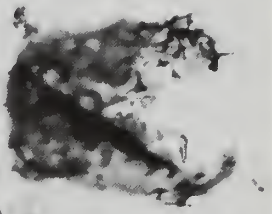
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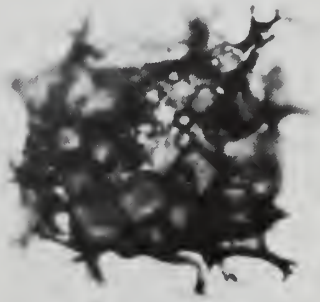
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Figs 14–18 *Coryphidium bohemicum* Vavrdova 1972. All Pontyfenni Formation; × 1200. Fig. 14, MPK 4876, sample MPA 20100; slide 1, W64/2. Fig. 15, MPK 4877, sample MPA 20102; slide 1, Q66/0. Fig. 16, MPK 4878, sample MPA 20102; slide 1, X74/4. Fig. 17, MPK 4879, sample MPA 20102; slide 1, M52/0. Fig. 18, MPK 4880, sample MPA 20092; slide 1, Q62/4.

Fig. 19 ?*Coryphidium minutum* Cramer & Diez 1976; MPK 4881, sample MPA 20074, Allt Cystanog Member; slide 1, J49/3, × 1200.

Fig. 20 *Coryphidium bohemicum*? Vavrdova 1972; MPK 4882, sample MPA 20093, Pontyfenni Formation; slide 1, P30/0, × 1200.

Fig. 21 *Coryphidium*? sp. A; MPK 4883, sample MPA 20087, Cwmffrŵd Member; slide 1, H37/0, × 1200. See Fig. 22.

Description. The vesicle is quadrate with straight sides and broadly rounded corners. The vesicle wall is apparently smooth. The processes, which are concentrated at the corners of the vesicle, are stout and have elaborate distal terminations that bifurcate to the second order. The terminal branches of the processes may be capitate. Sixteen processes are present. Excystment may be by means of a straight split that occurs along one side of the vesicle.

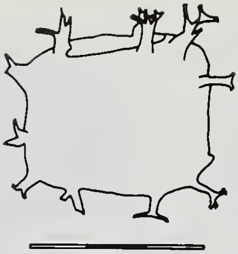


Fig. 22 *Coryphidium*? sp. A; MPK 4883. Bar represents 30 μm. See Fig. 21.

DIMENSIONS. Vesicle diameter: 32 × 25 μm.
Process length: 7 μm.
Process width: 1·5 μm.

REMARKS. The vesicle has been distorted by crystal growth in the internal cavity but otherwise preservation is fair. The shape of the vesicle and the concentration of processes at the corners are characteristic of *Coryphidium*, but the specimen has longer and more elaborately branching processes than known species of that genus. The specimen may also differ from *Coryphidium* in its excystment mechanism. The split along one side is interpreted as a means of excystment whereas in the type species, *C. bohemicum*, it is reported to be by means of a large opening of irregular shape, usually oval or polygonal (Vavrdova 1972; Martin *in* Dean & Martin 1978). The genus *Tetraniveum* Vavrdova, 1976, has a similar vesicle shape and process arrangement, but the processes are simple.

Genus ***CYMATIOGALEA*** Deunff, 1961

TYPE SPECIES. *Cymatiogalea margaritata* Deunff 1961.

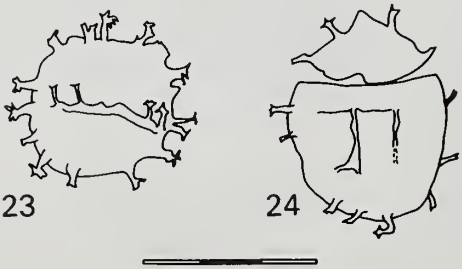
Cymatiogalea bellicosa Deunff 1961
Fig. 25A, B

1961 *Cymatiogalea bellicosa* Deunff: 42; pl. 1, fig. 13.
1961 *Cymatiogalea pudica* Deunff: 42; pl. 1, fig. 4.
1964 *Cymatiogalea bellicosa* Deunff; Deunff: 122; pl. 1, figs 10–12, 16, 19–20.

MATERIAL. One specimen.

OCCURRENCE. Pontyfenni Formation: MPA 20099.

DESCRIPTION. The vesicle is hemispherical, with a large polar opening (macropyle). The processes are stout and cylindrical, dividing distally into several short branches, all of which are of the first order, arising from a common point on the stem. The processes show some variation in length, the longer ones being situated opposite the macropyle while those nearer the opening are much shorter. The processes support a veil.



Figs 23, 24 *Cymatiogalea*? sp.; sample MPA 20077, Cwmffrŵd Member; bar represents 30 μm. Fig. 23, MPK 4885; slide 2, N24/0. See Fig. 26. Fig. 24, MPK 4886; slide 2, V25/4. See Fig. 27.

Dimensions. Vesicle diameter: 26 × 36 μm; process length 8 μm opposite macropyle, decreasing to 3 μm near macropyle.

Remarks. *Cymatiogalea bellicosa* is widespread in rocks of Tremadoc age. In Britain, it occurs in the lower part of the Shineton Shales, of early Tremadoc age, in Shropshire (Rasul 1974, 1979). Its presence in the Pontyfenni Formation indicates probable reworking.

***Cymatiogalea*? sp.**

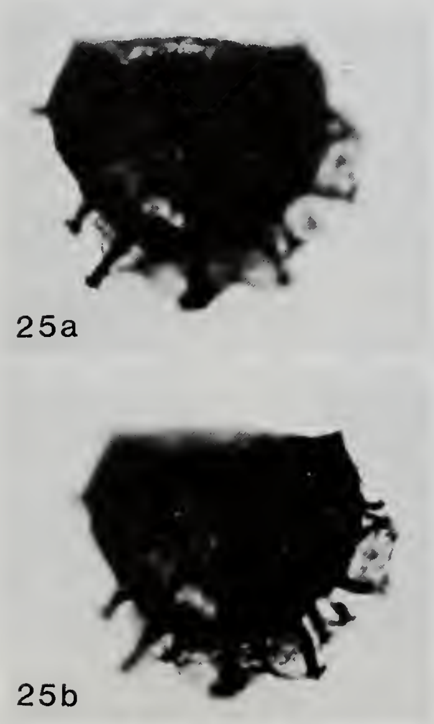
Figs 23–24, 26–27

Material. Three specimens.

Occurrence. Cwmffrŵd Member: MPA 20077.

Description. The vesicles are subspherical, and that of one specimen (Figs 24, 27) may be divided into polygonal fields; this specimen may also have a macropyle. The processes are short, hollow, and cylindrical, and are plugged at the base so that the process interiors do not communicate with the vesicle cavity. They are usually divided distally into four or five filaments, but on one specimen (Figs 23, 26) they have more elaborately branched distal terminations which divide to the second order.

Dimensions. Vesicle diameter: range 24–36 μm; mean 29 μm.
Process length: range 3–5 μm; mean 4 μm.



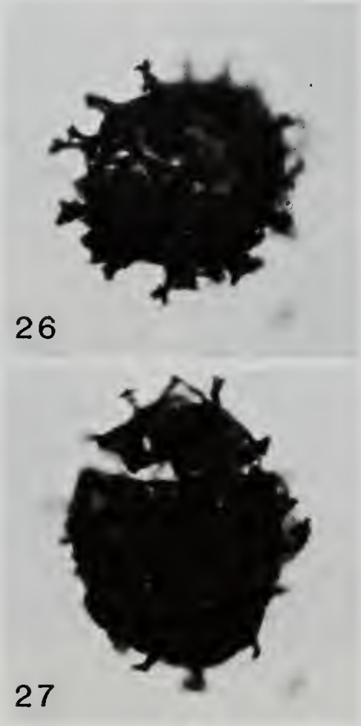


Fig. 25A, B *Cymatiogalea bellicosa* Deunff 1961; MPK 4884, sample MPA 20099, Pontyfenni Formation; slide 1, S34/3, × 1200.

Figs 26, 27 *Cymatiogalea*? sp.; × 1200. Fig. 26, MPK 4885. See Fig. 23. Fig. 27, MPK 4886. See Fig. 24.

REMARKS. Assignment of these three specimens to *Cymatiogalea* is based on the apparent presence of a macropyle and polygonal fields on one specimen. These characters are diagnostic of the genus according to the emended diagnosis given by Deunff *et al.* (1974). The determination is tentative because of poor preservation.

Genus ***DASYDORUS*** Playford & Martin, 1984

TYPE SPECIES. *Dasydorus cirritus* Playford & Martin 1984.

Dasydorus cirritus? Playford & Martin 1984
Figs 28–43

?1984 *Dasydorus cirritus* Playford & Martin: 198, fig. 6A–C.

MATERIAL. Eighteen specimens.

OCCURRENCE. Pontyfenni Formation: MPA 20091–3.

DESCRIPTION. The vesicle is subtriangular or egg-shaped. One end, usually the narrower, is smooth and is acutely rounded or is drawn out into a short apical protuberance. The rest of the vesicle is covered by numerous randomly distributed, short, stiff and evexate or capitate hairs. Excystment may have been by means of a longitudinal split, either alone or in combination with loss of the smooth apical region.

DIMENSIONS. Vesicle length: range 38–58 μm; mean 49 μm.
Vesicle width: range 32–48 μm; mean 37 μm.
Length of hairs: less than 2–2·5 μm.

REMARKS. The specimens are very similar to those described and figured by Playford & Martin (1984), but the smooth apex is more acutely rounded and in some cases is developed into a short protuberance. These albeit slight morphological differences, and the difference in preservation, disallow a confident identification until more is known about the morphology and occurrence of the species.

The excystment mechanism of *Dasydorus* is unknown but four specimens from the Pontyfenni Formation (Figs 33–36, 41–43) provide some evidence. Each shows a longitudinal split, accompanied on one specimen by loss of the smooth apical region. Given their state of preservation, it is difficult to eliminate incidental damage as its cause, but the consistent appearance of the split suggests that it may be a true excystment opening.

Playford & Martin (1984) note that the genus *Pirea* Vavrdova differs from *Dasydorus* by possessing a distinct apical process. The short apical protuberance on some of the Welsh specimens resembles this process, suggesting a possible relationship between the two genera.

Genus ***FRANKEA*** Burmann, 1970

TYPE SPECIES. *Frankea hamata* Burmann 1970.

?***Frankea hamata*** Burmann 1970
Fig. 44

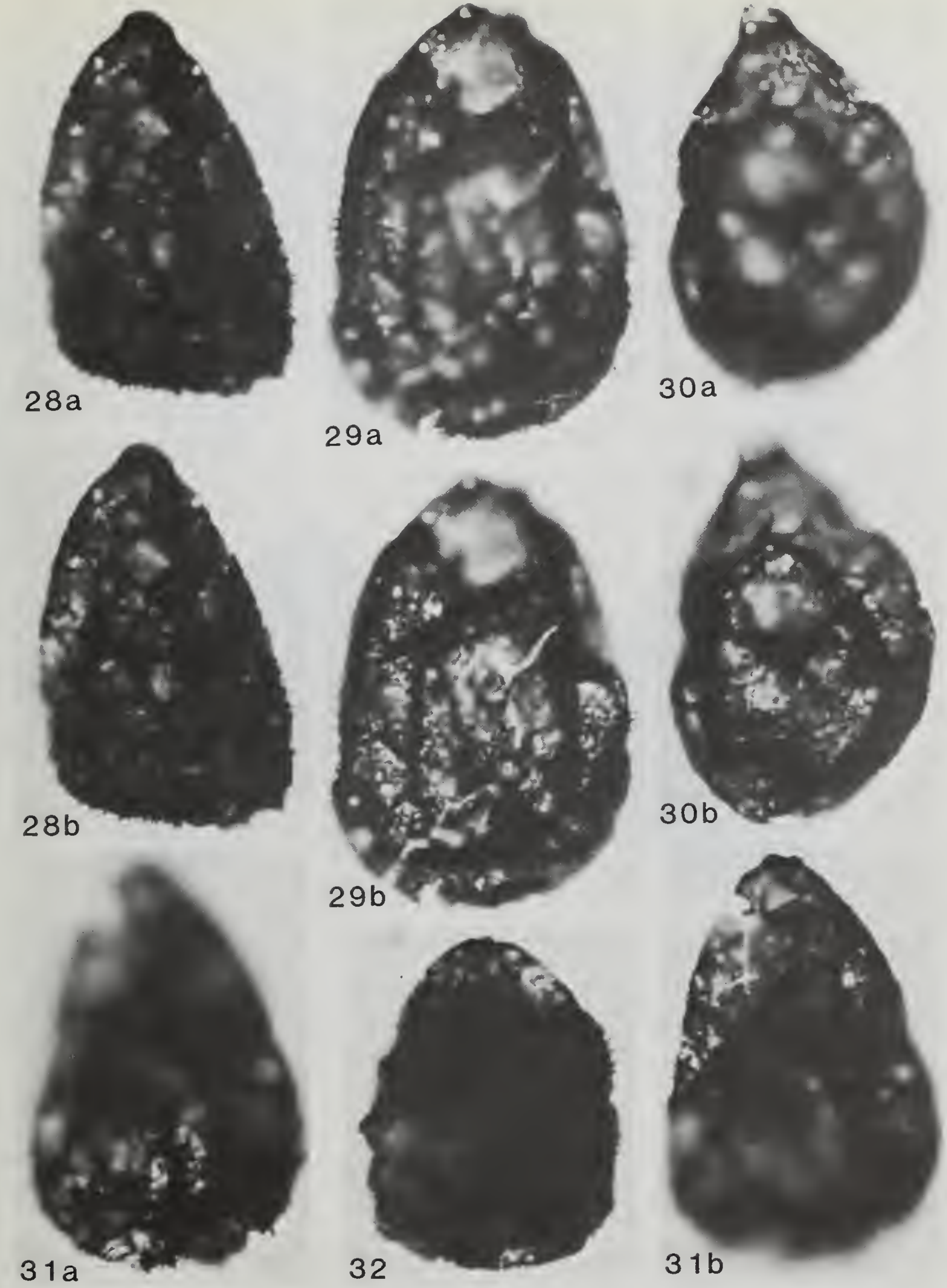
?1970 *Frankea hamata* Burmann: 290–291; pl. 2, figs 7, 9, 10.

MATERIAL. One damaged specimen.

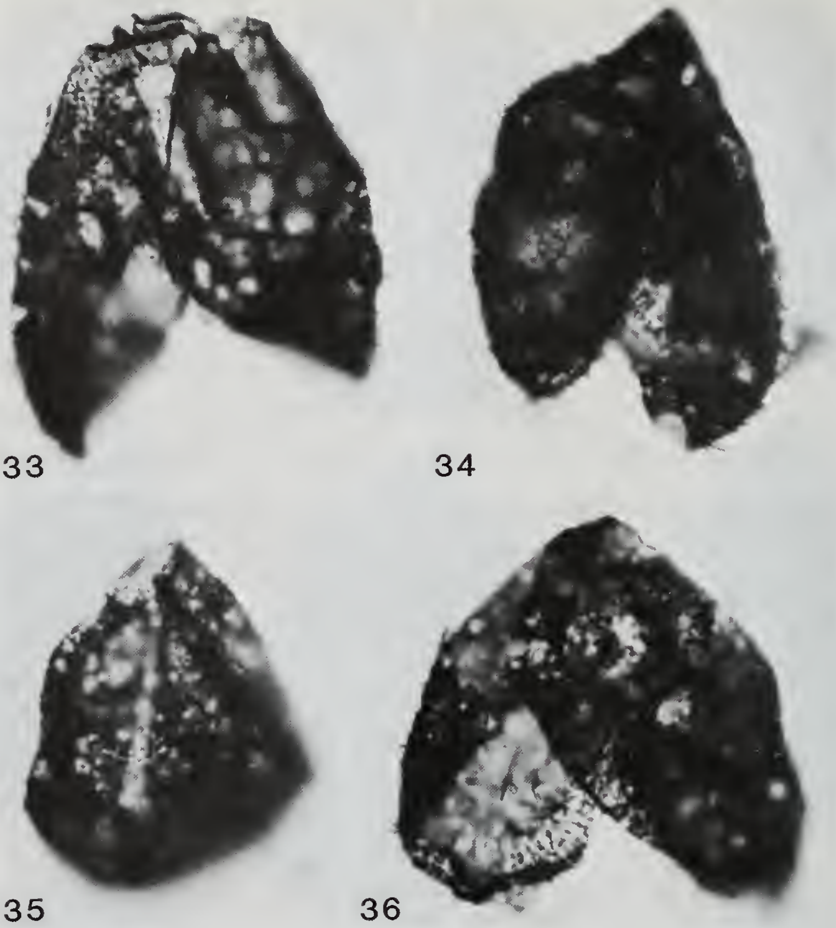
OCCURRENCE. Pontyfenni Formation: MPA 20102.

DESCRIPTION. The vesicle is broken but was probably triangular. Two processes are present, situated at two corners of the triangle; the third corner is broken. The processes are short and divide distally. One process divides into two long, recurved filaments.

DIMENSIONS. Vesicle diameter 24 × 20 μm; process length 4 μm.



Figs 28–32 *Dasydorus cirritus*? Playford & Martin 1984. All Pontyfenni Formation; × 1200. Fig. 28A, B, high and low focus; MPK 4915, sample MPA 20091; slide 1, J28/1. See Fig. 39. Fig. 29A, B, high and low focus; MPK 4916, sample MPA 20092; slide 2, Q34/0. See Fig. 37. Fig. 30A, B, specimen with protuberance resembling apical horn, high and low focus; MPK 4917, sample MPA 20093; slide 1, J31/4. See Fig. 40. Fig. 31A, B, high and low focus; MPK 4918, sample MPA 20092; slide 1, W36/0. Fig. 32, MPK 4919, sample MPA 20091; slide 1, D35/1. See Fig. 38.



Figs 33–36 Excystment mechanism of *Dasydorus cirritus*? Playford & Martin 1984. All sample MPA 20092, Pontyfenni Formation; × 1200. Fig. 33, specimen with longitudinal split; MPK 4920; slide 1, E24/0. Fig. 34, specimen with partial longitudinal split developing at the antapex; MPK 4921; slide 1, F56/2. See Fig. 41. Fig. 35, specimen with partial longitudinal split restricted to one side of the vesicle and also exhibiting loss of the apical region; MPK 4922; slide 1, K24/1. See Fig. 43. Fig. 36, specimen with partial longitudinal split developing at the antapex; MPK 4923; slide 2, K34/2. See Fig. 42.

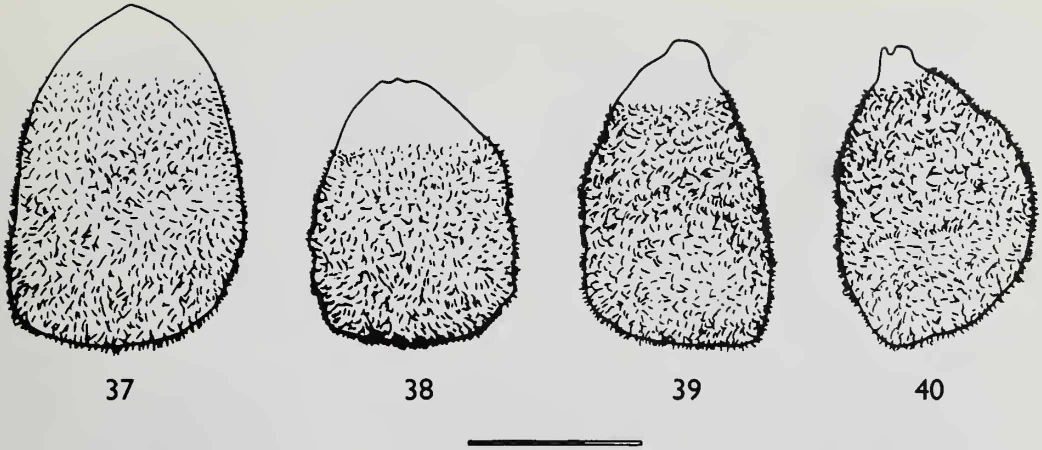
REMARKS. Identification of the specimen is tentative because of damage to the vesicle. Even so, the probable shape of the vesicle and the distal terminations of the processes are characteristic of *Frankea hamata*, and the determination is probably correct. The processes are shorter than those of the type specimen (Burmann 1970).

Genus ***MICRHYSTRIDIUM*** Deflandre, 1937

TYPE SPECIES. *Micrhystridium inconspicuum* Deflandre 1937.

Micrhystridium aff. ***acuminosum*** Cramer & Diez 1977
Figs 45–47, 70

aff. 1977 *Micrhystridium acuminosum* Cramer & Diez: 347; pl. 1, figs 3, 4, 10; text-fig. 3: 3.

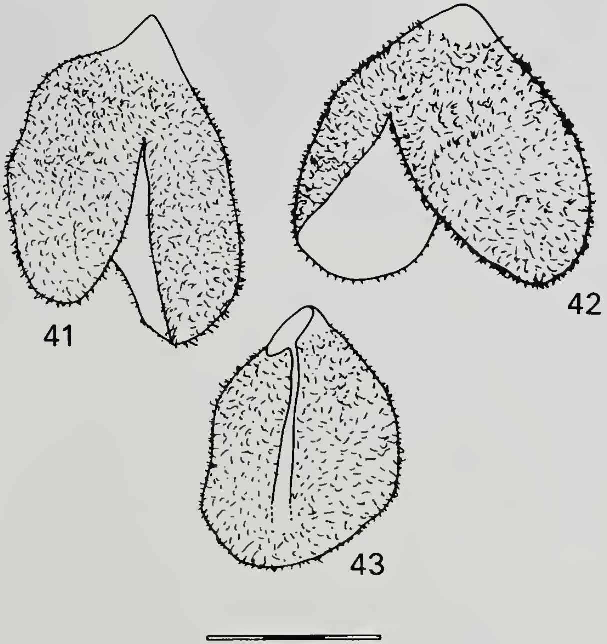


Figs 37–40 *Dasydorus cirritus*? Playford & Martin 1984. Bar represents 30 μm. Fig. 37, MPK 4916. See Fig. 29. Fig. 38, MPK 4919. See Fig. 32. Fig. 39, MPK 4915. See Fig. 28. Fig. 40, MPK 4917. See Fig. 30.

Material. Three specimens.

Occurrence. Allt Cystanog Member: MPA 20074.

Description. The vesicle is small and subspherical. The outline of the vesicle is partially masked by the process bases. The processes are numerous, relatively short and conical, extending distally into acuminate, needle-like tips.



Figs 41–43 Excystment mechanism of *Dasydorus cirritus*? Playford & Martin 1984. Bar represents 30 μm. Fig. 41, MPK 4921. See Fig. 34. Fig. 42, MPK 4923. See Fig. 36. Fig. 43, MPK 4922. See Fig. 35.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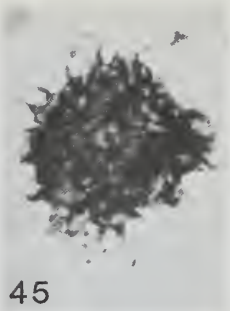
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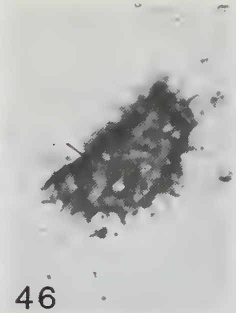
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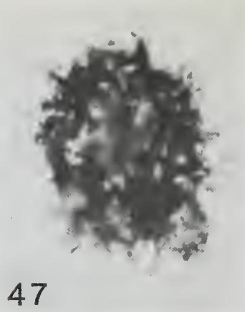
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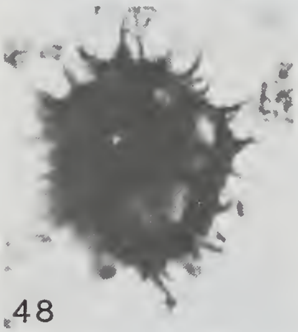
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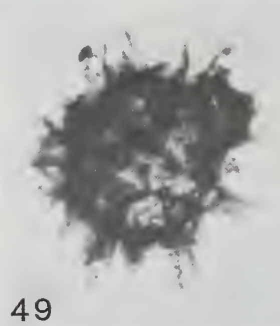
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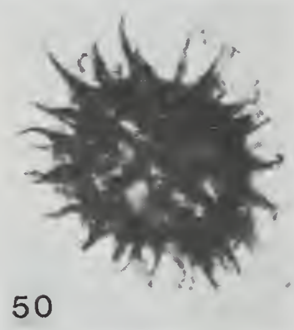
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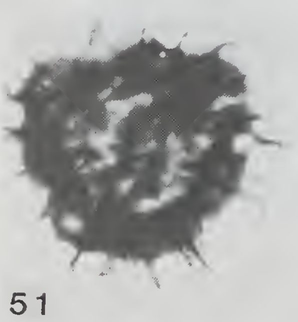
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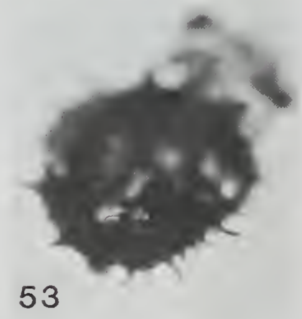
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Fig. 44 ?*Frankea hamata* Burmann 1970; MPK 4887, sample MPA 20102, Pontyfenni Formation; slide 1, R54/3, × 1200.

Figs 45–47 *Micrhystridium* aff. *acuminosum* Cramer & Diez 1977; sample MPA 20074, Allt Cystanog Member; × 1200. Fig. 45, MPK 4888; slide 2, H70/2. See Fig. 70. Fig. 46, MPK 4889; slide 1, S53/3. Fig. 47, MPK 4890; slide 1, H71/0.

Figs 48–50 *Micrhystridium* cf. *inconspicuum aremoricanum* Paris & Deunff 1970; × 1200. Fig. 48, MPK 4891, sample MPA 20103, Cwm yr Abbey Member; slide 2, L57/3. Fig. 49, MPK 4892, sample MPA 20103, Cwm yr Abbey Member; slide 2, D74/2. Fig. 50, MPK 4893, sample MPA 20104, Afon Ffinnant Formation; slide 2, L51/2. See Fig. 74.

Figs 51–53 *Micrhystridium* aff. *henryi* Paris & Deunff 1970; sample MPA 20103, Cwm yr Abbey Member; × 1200. Fig. 51, MPK 4894; slide 2, H74/2. Fig. 52, MPK 4895; slide 2, V70/1. See Fig. 73. Fig. 53, MPK 4896; slide 2, R53/1.

DIMENSIONS. Vesicle diameter range 10–22 μm, mean 18 μm; process length 3 μm.

REMARKS. The processes on each of the three specimens resemble those of *Micrhystridium acuminosum* and suggest an affinity with that species, although *M. acuminosum* has a larger vesicle and longer, stouter processes.

Micrhystridium aff. *henryi* Paris & Deunff 1970
Figs 51–53, 73

aff. 1970 *Micrhystridium henryi* Paris & Deunff: 31–32; pl. 2, figs 2, 10, 14, 15, 18; pl. 3, fig. 7.

MATERIAL. Five specimens.

OCCURRENCE. Cwm yr Abbey Member: MPA 20103. Afon Ffinnant Formation: MPA 20104.

DESCRIPTION. The vesicle is subspherical with about 30–40 processes. The sides of the vesicle between the process bases are straight or slightly curved; if curved they may be either concave or convex. The processes taper from narrow bases to acuminate distal terminations.

DIMENSIONS. Vesicle diameter range 20–26 μm, mean 23 μm; process length 4–5 μm.

REMARKS. The small, subspherical vesicles and numerous, relatively short processes suggest a relationship between these specimens and *Micrhystridium henryi. M. henryi* has shorter and more numerous processes, their bases coalescing to mask the outline of the vesicle. Specimens from the Fennian of north Wales, referred by Booth (1979) to *M. henryi*, are closer to this material from south-west Wales than to the type material, but have slightly shorter processes.

Micrhystridium cf. *inconspicuum aremoricanum* Paris & Deunff 1970
Figs 48–50, 74

cf. 1970 *Micrhystridium inconspicuum aremoricanum* Paris & Deunff: 32; pl. 2, fig. 20.

MATERIAL. Twenty-one specimens.

OCCURRENCE. Cwm yr Abbey Member: MPA 20084, MPA 20103. Afon Ffinnant Formation: MPA 20104.

DESCRIPTION. The vesicle is small and subspherical, bearing about 30 processes. The processes are simple, relatively short, acuminate and narrowly conical. Their bases tend to coalesce, masking the outline of the vesicle.

DIMENSIONS. Vesicle diameter range 14–24 μm, mean 19 μm; process length range 3·5–8 μm, mean 5 μm.

REMARKS. The material from south-west Wales is very similar to the type material of *Micrhystridium inconspicuum aremoricanum* and to specimens recorded by Booth (1979), but the processes of the specimens from south-west Wales are commonly about a quarter of the vesicle diameter in length, rarely a third or more. The original diagnosis states that the processes are about a third of the vesicle diameter, and Booth also records the length as being approximately a third. The difference is slight but may distinguish the present specimens from the type and Booth's material.

The type material of *M. inconspicuum aremoricanum* was recorded from the base of the Andouillé Formation north of Rennes (Paris 1981: 19), considered to be of Llanvirn age (Babin *et al.* 1974: 365). Booth's material came from the Fennian of north Wales and the Llanvirn of the Welsh Borderland and Lake District. In south-west Wales, *M.* cf. *inconspicuum aremoricanum* appears in the upper Moridunian, but has not been recorded from the Whitlandian or Fennian.

Micrhystridium aff. *nannacanthum* Deflandre 1945
Figs 54–57, 71

aff. 1942 *Micrhystridium nannacanthum* Deflandre: 476; fig. 13 (nomen nudum).
aff. 1945 *Micrhystridium nannacanthum* Deflandre: 66; pl. 3, figs 5–7.

MATERIAL. Thirteen specimens.

OCCURRENCE. Cwm yr Abbey Member: MPA 20084, MPA 20103.

DESCRIPTION. The vesicle is small and subspherical, bearing about 30 short, hair-like processes. The processes are slender, parallel-sided, possibly solid and are evexate or capitate.

DIMENSIONS. Vesicle diameter range 12–22 μm, mean 16 μm; process length less than 2 μm.

REMARKS. According to the diagnosis (Deflandre 1945), *Micrhystridium nannacanthum* has short spines that do not exceed 1 μm in length. The specimens from south-west Wales are distinct, in that they have slightly longer processes, some having distinctive rounded or capitate distal terminations. They also have larger vesicles than the type material. A specimen illustrated by Lister (1970: pl. 10, fig. 11) from the late Silurian of Shropshire also differs from the present material, having a smaller vesicle with shorter, stouter and fewer processes. Booth (1979) has recorded several specimens of ?*M. nannacanthum* from the Fennian of north Wales and the Llanvirn of the Lake District. His specimens resemble these from the Cwm yr Abbey Member but he notes that his have numerous, short, evenly distributed, conical spines which have either blunt or acuminate distal terminations. In south-west Wales, *M.* aff. *nannacanthum* has only been recorded from the upper Moridunian.

Micrhystridium sp. A

Figs 58–59, 66

MATERIAL. Six specimens.

OCCURRENCE. Whitland Abbey Member: MPA 20098.

DESCRIPTION. The vesicle is small and subspherical. Its outline is largely masked by the processes, the bases of which tend to coalesce. The processes are short, stout, cylindrical or slightly tapered, with either evexate or acuminate distal terminations. The sides of the vesicle, where visible between the process bases, are straight or concave. About 20 processes are present.

DIMENSIONS. Vesicle diameter range 10–16 μm, mean 12 μm; process length less than 2–2·5 μm.

REMARKS. *Micrhystridium* sp. A may be distinguished from *M.* aff. *nannacanthum* by its smaller size and longer, relatively stout processes and from *Micrhystridium* spp. B–D by its cylindrical rather than conical processes.

Micrhystridium sp. B

Figs 60–61, 67

MATERIAL. Six specimens.

OCCURRENCE. Whitland Abbey Member: MPA 20098.

DESCRIPTION. The vesicle is small and subspherical. Its outline is masked by the process bases, which tend to coalesce. The processes are numerous, short, conical and acuminate.

DIMENSIONS. Vesicle diameter range 9–15 μm, mean 12 μm; process length less than 2 μm.

REMARKS. It is difficult to determine the number of processes present on each specimen because of poor preservation, but there are probably more than thirty.

Micrhystridium sp. C

Figs 62–63, 68

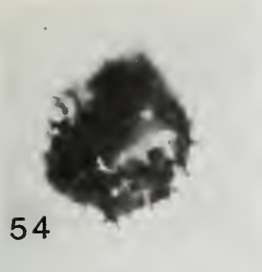
MATERIAL. Seven specimens.

OCCURRENCE. Whitland Abbey Member: MPA 20098.

DESCRIPTION. The vesicle is small and subspherical. The processes are numerous, slender, tapering and acuminate. Their bases tend to mask the outline of the vesicle, but where visible the sides are convex.

DIMENSIONS. Vesicle diameter range 8–16 μm, mean 13 μm; process length range 3–5 μm, mean 3·5 μm.

REMARKS. The exact number of processes is uncertain because of poor preservation, but is probably 25 or more. *Micrhystridium* sp. C may be distinguished from *Micrhystridium* sp. B by its longer processes.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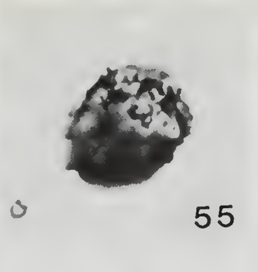
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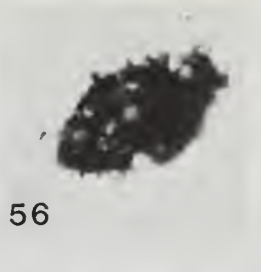
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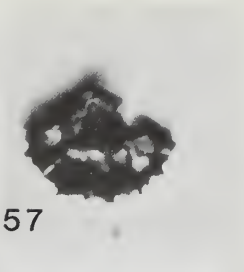
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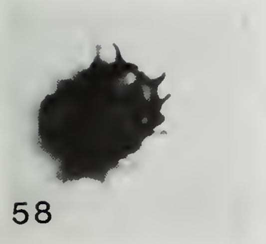
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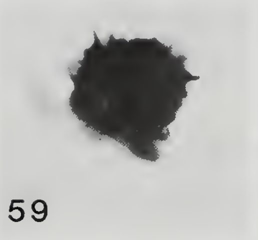
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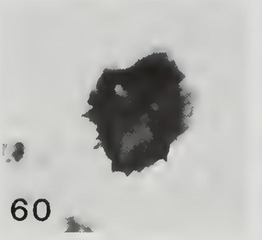
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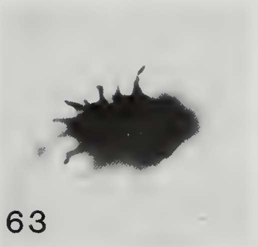
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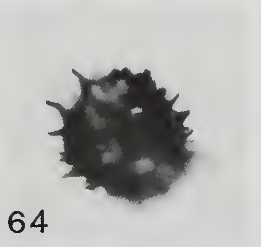
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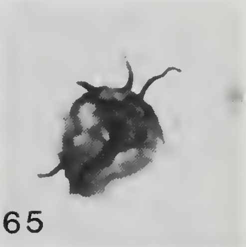
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Figs 54–57 *Micrhystridium* aff. *nannacanthum* Deflandre 1945; sample MPA 20084, Cwm yr Abbey Member; × 1200. Fig. 54, MPK 4897; slide 2, T55/3. See Fig. 71. Fig. 55, MPK 4898; slide 2, T64/2. Fig. 56, MPK 4899; slide 2, W54/0. Fig. 57, MPK 4900; slide 2, X66/4.

Figs 58, 59 *Micrhystridium* sp. A; sample MPA 20098, Whitland Abbey Member; × 1200. Fig. 58, MPK 4901; slide 1, W62/2. See Fig. 66. Fig. 59, MPK 4902; slide 1, B57/2.

Figs 60, 61 *Micrhystridium* sp. B; sample MPA 20098, Whitland Abbey Member; × 1200. Fig. 60, MPK 4903; slide 1, N60/4. See Fig. 67. Fig. 61, MPK 4904; slide 1, S52/2.

Figs 62, 63 *Micrhystridium* sp. C; sample MPA 20098, Whitland Abbey Member; × 1200. Fig. 62, MPK 4905; slide 1, S55/1. See Fig. 68. Fig. 63, MPK 4906; slide 1, R60/1.

Fig. 64 *Micrhystridium* sp. D; MPK 4907, sample MPA 20098, Whitland Abbey Member; slide 1, R53/2, × 1200. See Fig. 69.

Fig. 65 *Micrhystridium* sp.; MPK 4908, sample MPA 20098, Whitland Abbey Member; slide 1, P64/3, × 1200. See Fig. 72.

Micrhystridium sp. D

Figs 64, 69

MATERIAL. Two specimens.

OCCURRENCE. Whitland Abbey Member: MPA 20098.

DESCRIPTION. The vesicle is small and subspherical, its sides masked by the process bases which tend to coalesce. The processes are numerous, short, conical and acuminate.

DIMENSIONS. Vesicle diameter range 13–16 μm, mean 15 μm; process length range 2–3 μm, mean 2·5 μm.

REMARKS. The exact number of processes is uncertain owing to poor preservation, but one specimen has at least 40. *Micrhystridium* sp. D may be distinguished from *Micrhystridium* sp. B by its longer, more numerous processes, and from *Micrhystridium* sp. C by its shorter, more numerous processes.

Micrhystridium sp.
Figs 65, 72

MATERIAL. One specimen.

OCCURRENCE. Whitland Abbey Member: MPA 20098.

DESCRIPTION. The specimen has a small, subspherical vesicle with convex sides. Eight processes are present. They are long, slender, possibly solid and evexate, tapering slightly from narrow bases that have an angular contact with the vesicle wall. The vesicle diameter is 14 × 12 μm and process length is approximately 7 μm.

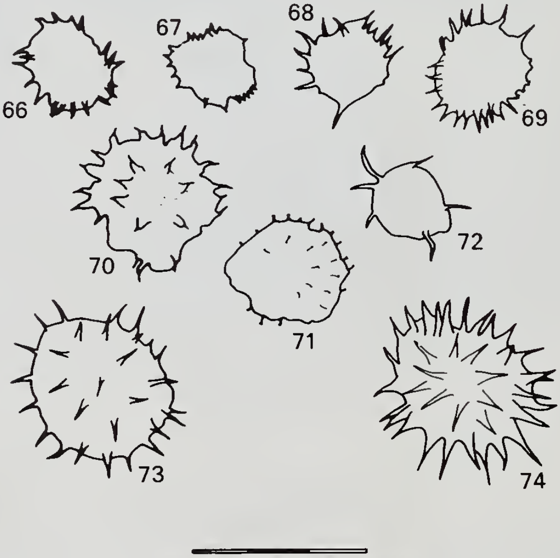
Genus *NOTHOOIDIUM* Loeblich & Tappan, 1976

TYPE SPECIES. *Nothooidium mordidum* (Cramer, Allam, Kanes & Diez 1974) Loeblich & Tappan 1976.

***Nothooidium*?** spp.
Figs 75–76

MATERIAL. Two specimens.

OCCURRENCE. Afon Ffinnant Formation: MPA 20104. Pontyfenni Formation: MPA 20101.



Figs 66–74 *Micrhystridium* spp., comparative illustrations of specimens recorded from the Arenig Series in south-west Wales. Bar represents 30 μm. Fig. 66, *Micrhystridium* sp. A; MPK 4901. See Fig. 58. Fig. 67, *Micrhystridium* sp. B; MPK 4903. See Fig. 60. Fig. 68, *Micrhystridium* sp. C; MPK 4905. See Fig. 62. Fig. 69, *Micrhystridium* sp. D; MPK 4907. See Fig. 64. Fig. 70, *Micrhystridium* aff. *acuminosum* Cramer & Diez 1977; MPK 4888. See Fig. 45. Fig. 71, *Micrhystridium* aff. *nannacanthum* Deflandre 1945; MPK 4897. See Fig. 54. Fig. 72, *Micrhystridium* sp.; MPK 4908. See Fig. 65. Fig. 73, *Micrhystridium* aff. *henryi* Paris & Deunff 1970; MPK 4895. See Fig. 52. Fig. 74, *Micrhystridium* cf. *inconspicuum aremoricanum* Paris & Deunff 1970; MPK 4893. See Fig. 50.

Descriptions. The specimen from the Afon Ffinnant Formation (Fig. 75) has an elongate, pear-shaped vesicle, one end of which is concave suggesting the presence of an opening. The ornament consists of grana and short, conical, evexate and possibly solid processes. The vesicle of this specimen is 48 μm long and 36 μm wide.

The specimen from the Pontyfenni Formation (Fig. 76) has a similar elongate, pear-shaped vesicle, one end of which is concave, and an ornament of cones and rods with evexate distal terminations. The vesicle of this specimen is 45 μm long and 40 μm wide.

Remarks. The two specimens are very similar and may represent the same species, although the processes on the specimen from the Pontyfenni Formation are longer and more slender than those on the Afon Ffinnant specimen. Determination of both specimens as *Nothooidium* is tentative because the poor preservation makes it difficult to demonstrate that the truncated ends of the vesicles are cyclopylomes. *N. mordidum* is smaller and has an ornament that consists of flat-crested verrucae. *Ooidium* sp. 2 of Cramer & Diez (1977: pl. 6, fig. 20) is very similar but is only illustrated and not described.

Genus ***ORTHOSPHAERIDIUM*** Eisenack, 1968

Type species. *Orthosphaeridium rectangulare* (Eisenack 1963) Eisenack 1968.

Orthosphaeridium ternatum (Burmann 1970) Eisenack, Cramer & Diez 1976

Fig. 77A, B

1970 *Baltisphaera ternata* Burmann: 306; pl. 7, fig. 1; pl. 9, fig. 4.
1976 *Orthosphaeridium ternatum* (Burmann) Eisenack, Cramer & Diez: 529.

Material. Four specimens.

Occurrence. Pontyfenni Formation: MPA 20091, MPA 20093.

Description. The vesicle is subspherical with three long, slender, acuminate processes which are arranged at *c.* 120° intervals around the circumference. They are constricted slightly towards the base. Both vesicle and processes bear an ornament of short hairs or cones.

Dimensions. Vesicle diameter range 48–60 μm, mean 52 μm; process length up to 76 μm.

Remarks. The specimens are poorly preserved but are readily determined as *Orthosphaeridium ternatum. O. procerum* (Burmann) Eisenack *et al.* 1976 has a more asymmetrical arrangement of processes.

Orthosphaeridium sp.

Fig. 79

Material. One specimen.

Occurrence. Pontyfenni Formation: MPA 20101.

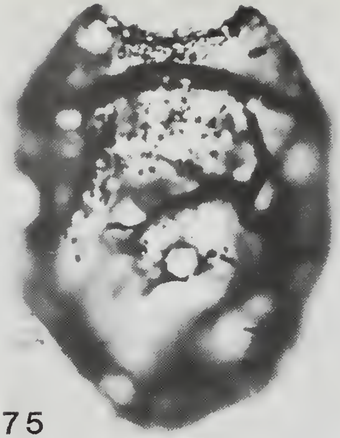
Description. The vesicle is subspherical with four processes, all broken. The process stems are stout and are constricted towards the base. Both vesicle and processes have an ornament of short, robust hairs.

Dimensions. Vesicle diameter 50 × 43 μm.

Remarks. This specimen resembles *Orthosphaeridium quadrinatum* (Burmann) Eisenack, Cramer & Diez 1976, but its poor preservation precludes a positive determination.

Genus ***POLYGONIUM*** Vavrdova, 1966

Type species. *Polygonium gracile* Vavrdova 1966.



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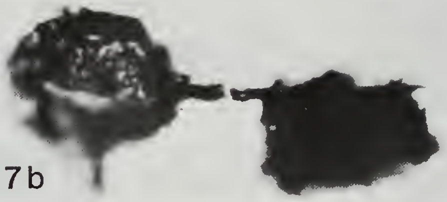

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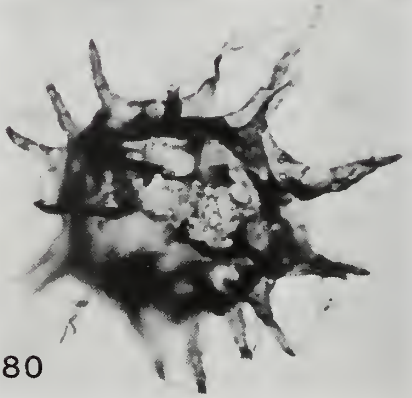


80

Polygonium sp. A
Figs 80–81

MATERIAL. Two specimens, plus several fragments.

OCCURRENCE. Allt Cystanog Member: MPA 20074.

DESCRIPTION. The outline of the vesicle is subpolygonal. The sides of the vesicle are straight or concave; occasionally they may be masked by the wide process bases. The processes are long, tapering and evexate. The proximal half of each process is relatively stout and thick-walled, while the distal half is thinner-walled and flexible. The difference between the two halves is quite distinct, the change taking place abruptly. The distal half of the process may break away leaving a straight or V-shaped distal edge. About 25 processes are present on one specimen.

DIMENSIONS. Vesicle diameter range 26–30 μm, mean 28 μm; process length *c.* 18 μm.

REMARKS. The description is based on one specimen from the Allt Cystanog Member (MPA 20074); a number of fragments in the same sample have similar features. One specimen may also be present in the Cwmffrŵd Member (MPA 20077) but the preservation is too poor to be certain.

Polygonium sp. B
Fig. 78

MATERIAL. Six specimens.

OCCURRENCE. Cwm yr Abbey Member: MPA 20084.

DESCRIPTION. The vesicle is large and subspherical with a polygonal outline. The sides of the vesicle are straight or concave; occasionally they may be masked by the broad process bases. The processes are long, stout, flexible, tapering and acuminate; about 20 are present.

DIMENSIONS. Vesicle diameter range 24–36 μm, mean 31 μm; process length range 14–16 μm, mean 15 μm.

REMARKS. Most specimens are broken and their preservation is poor. The size and polygonal outline of the vesicle and the relatively long, stout processes are distinctive.

Genus ***SOLISPHAERIDIUM*** Staplin, Jansonius & Pocock, 1965

TYPE SPECIES. *Solisphaeridium stimuliferum* (Deflandre 1938) Staplin, Jansonius & Pocock 1965.

Solisphaeridium sp. A
Figs 82–83, 86

MATERIAL. Four specimens.

OCCURRENCE. Pontyfenni Formation: MPA 20091.

DESCRIPTION. The vesicle is subspherical with convex sides. The processes are long, slender, smooth, evexate, moderately flexible, solid and slightly tapering. They number more than 40 on each specimen.

Figs 75, 76 *Nothooidium* sp.; × 1200, Fig. 75, MPK 4909, sample MPA 20104, Afon Ffinnant Formation; slide 2, G54/0. Fig. 76, MPK 4910, sample MPA 20101, Pontyfenni Formation; slide 1, G28/0.

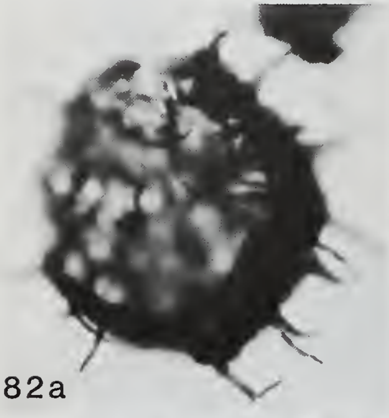
Fig. 77A, B *Orthosphaeridium ternatum* (Burmann 1970) Eisenack, Cramer & Diez 1976; A × 1200, B × 480; MPK 4911, sample MPA 20091, Pontyfenni Formation; slide 1, X41/0.

Fig. 78 *Polygonium* sp. B; MPK 4912, sample MPA 20084, Cwm yr Abbey Member; slide 2, Y30/4, × 1200.

Fig. 79 *Orthosphaeridium* sp.; MPK 4913, sample MPA 20101, Pontyfenni Formation; slide 1, S26/2, × 1200.

Fig. 80 *Polygonium* sp. A; MPK 4914, sample MPA 20074, Allt Cystanog Member; slide 2, U42/4, × 1200. See Fig. 81.

Fig. 81 *Polygonium* sp. A; MPK 4914. See Fig. 80. Bar represents 30 μm.



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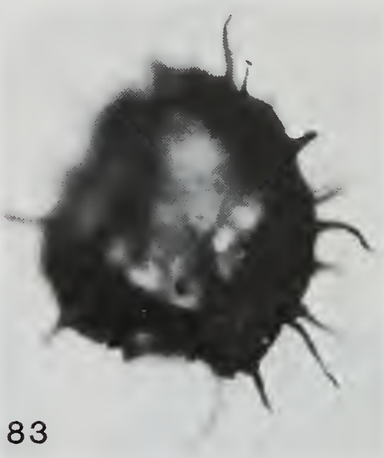

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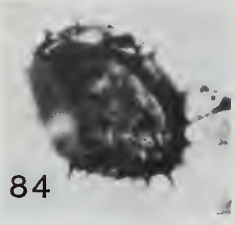

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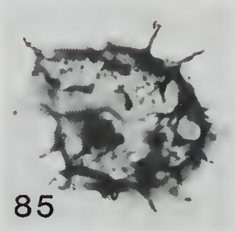

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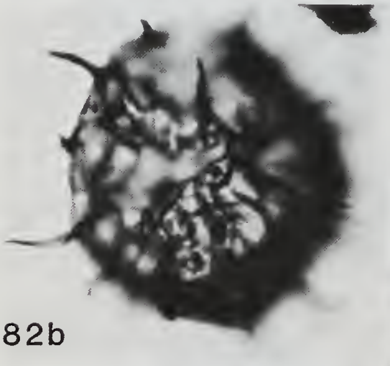

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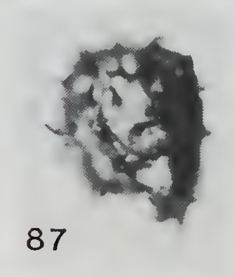

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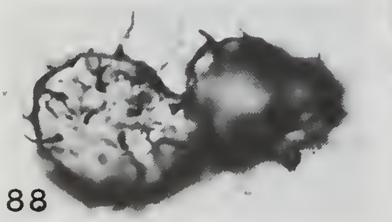

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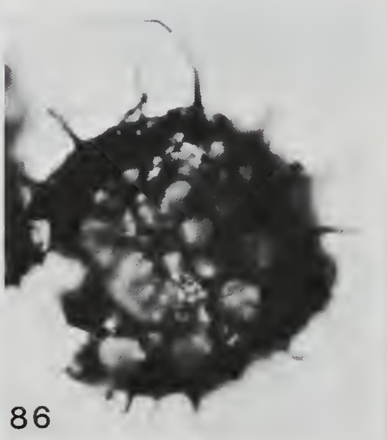

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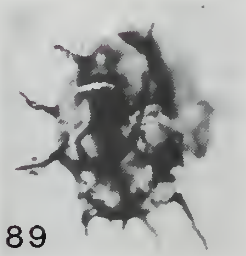


89

Figs 82, 83, 86 *Solisphaeridium* sp. A; sample MPA 20091, Pontyfenni Formation; × 1200. Fig. 82A, B, high and low focus; MPK 4924; slide 1, U27/1. Fig. 83, MPK 4925; slide 1, P43/4. Fig. 86, MPK 4928; slide 1, Q28/3.

Figs 84, 85, 87–89 *Solisphaeridium* sp. B; Cwm yr Abbey Member; × 1200. Figs 84, 85, 87, sample MPA 20103. Fig. 84, MPK 4926; slide 2, N58/2. Fig. 85, MPK 4927; slide 2, Q53/3. Fig. 87, MPK 4929; slide 2, Q75/3. Figs 88, 89, sample MPA 20084. Fig. 88, MPK 4930; slide 2, X59/4. Fig. 89, MPK 4931, slide 2, X51/4.

DIMENSIONS. Vesicle diameter range 34–43 μm, mean 37 μm; process length range 11–20 μm, mean 14 μm.

REMARKS. Superficially, the specimens resemble two species of *Solisphaeridium* described by Cramer & Diez (1977) from the Upper Arenig of Morocco. *S. solare* has a smaller vesicle and relatively long, stout processes, while *S. solidispinosum* is distinguished by its numerous, acuminate, conical processes.

Solisphaeridium sp. B

Figs 84–85, 87–89

MATERIAL. Six specimens.

OCCURRENCE. Cwm yr Abbey Member: MPA 20084, MPA 20103.

DESCRIPTION. The vesicle is subspherical and has a granulate wall. The sides of the vesicle between the process bases are convex, rarely concave. Numerous short, slender, tapering, acuminate and possibly solid processes are present.

DIMENSIONS. Vesicle diameter range 17–24 μm, mean 21 μm; process length range 2–8 μm, mean 5 μm.

REMARKS. The short processes and the nature of the ornament on the vesicle distinguish these specimens from the type and other species of *Solisphaeridium*. The specimens from MPA 20084 have about 15–20 processes, their lengths being more or less equal to a third of the vesicle diameter. Those from MPA 20103 differ slightly, in that they have more than 30 processes with an average length of less than a fifth of the vesicle diameter. Since relatively few specimens have been recorded and their preservation is poor, these differences are not used to separate the specimens from the two samples.

The specimens bear a strong resemblance to *Baltisphaeridium cinctum* (Timofeev) Rauscher (*in* Rauscher 1973: 71; pl. 2, figs 7a–b) but have smaller vesicles.

Genus ***STELLECHINATUM*** Turner, 1984

TYPE SPECIES. *Stellechinatum celestum* (Martin 1969*b*) Turner 1984.

Stellechinatum papulessum sp. nov.

Figs 90–92

DIAGNOSIS. A species of *Stellechinatum* with eight to ten processes, which are wide and conical at the base but cylindrical distally. The processes, and possibly the vesicle, bear an ornament of very small grana.

HOLOTYPE. MPK 4932 (Figs 90–1): MPA 20091, Pontyfenni Formation.

OTHER MATERIAL. Twelve specimens, paratypes.

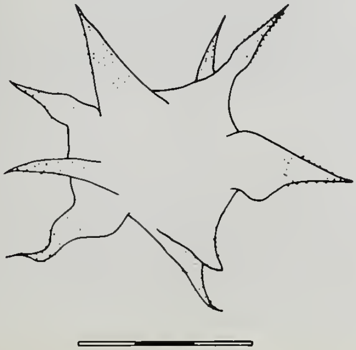


Fig. 90 *Stellechinatum papulessum* sp. nov., **holotype**; MPK 4932, sample MPA 20091, Pontyfenni Formation; slide 1, O39/3. Bar represents 30 μm. See Fig. 91.

OCCURRENCE. Pontyfenni Formation: MPA 20091–3.

NAME. 'Small pimple or pustule', referring to the fine ornament.

DESCRIPTION. The outline of the vesicle is variable. On some specimens, the sides of the vesicle are masked by the wide, coalescing process bases; on others, the sides of the vesicle are clearly visible, resulting in a polygonal outline. The processes are wide and conical at the base, becoming more cylindrical distally. They taper to an evexate distal termination. A slight constriction is rarely present at the base of the distal, cylindrical part of the process. The average process length is just over half of the vesicle diameter.

DIMENSIONS. Vesicle diameter: range 24–36 μm; mean 29 μm.
Process length: range 14–21 μm; mean 17 μm.
Process width (at base): range 6–11 μm; mean 9 μm.

REMARKS. Several specimens are distorted by the growth of crystals within the vesicle cavity.

The type species, *Stellechinatum celestum* (Martin) Turner, has a similar outline, similar vesicle dimensions and approximately the same number of processes with wide bases. It is distinguished from *S. papulessum* sp. nov. by its relatively long, acuminate processes and its ornament of slender spines on the processes and vesicle. *S. helosum* Turner 1984 has comparable vesicle dimensions and a similar ornament but has longer and more numerous acuminate processes with narrower bases. *S. brachyscolum* Turner 1984 has more numerous processes with an ornament of long spines. *Goniosphaeridium splendens* (Paris & Deunff) Turner 1984 has a similar gross morphology, but has a smooth wall and more numerous processes.

Stellechinatum uncinatum (Downie 1958) comb. nov.
Figs 93–94

1958 *Hystrichosphaeridium longispinosum* var. *uncinatum* Downie: 337; text-fig. 2a.
1965 *Baltisphaeridium longispinosum* var. *uncinatum* (Downie) Downie & Sarjeant: 92.
1965 *Baltisphaeridium uncinatum* (Downie) Martin: 425–426; text-fig. 1.
1970 *Micrhystridium uncinatum* (Downie) Cramer: 107–108; pl. 6, figs 97–98, 101; text-fig. 29d (*pars*).
non 1971 *Goniosphaeridium uncinatum* (Martin) Kjellström: 27–28; fig. 18 [*err. cit. pro Goniosphaeridium uncinatum* (Downie) Kjellström].

MATERIAL. Seven specimens.

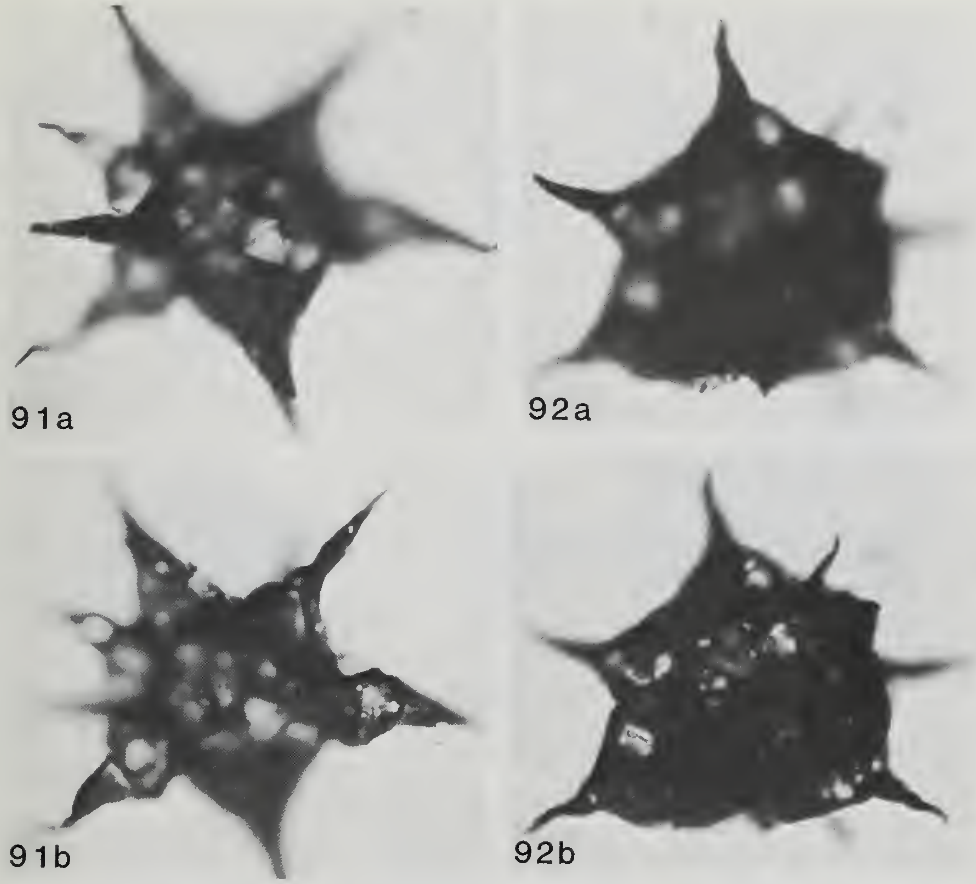
OCCURRENCE. Pontyfenni Formation: MPA 20099, MPA 20101, MPA 20093.

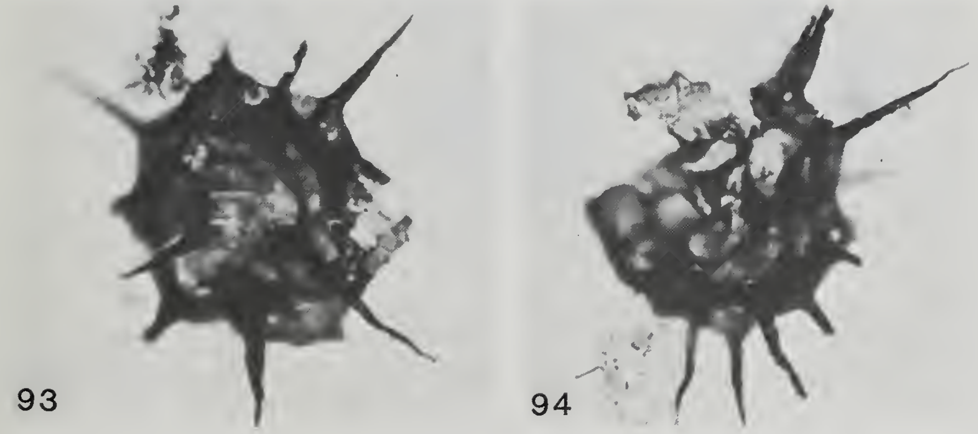
DESCRIPTION. The vesicle is polygonal or subpolygonal in outline, with more or less straight sides. There are about 15 processes, which are slender, tapering, acuminate and may be solid. They have relatively narrow bases, bear an ornament of short spines, and are just over half the vesicle diameter in average length.

DIMENSIONS. Vesicle diameter: range 22–32 μm; mean 29 μm.
Process length: range 15–18 μm; mean 17 μm.
Process width (at base): 2·5–3 μm.

REMARKS. The holotype of *Hystrichosphaeridium longispinosum* var. *uncinatum* Downie (1958: fig. 2a) has a polygonal vesicle with several tapering, acuminate processes, the latter bearing short lateral hairs. The species is morphologically comparable with the genus *Stellechinatum* Turner and is here recombined with it.

Turner (1984) describes *Stellechinatum* as having wide process bases. In contrast, on the holotype of *S. uncinatum* (Downie) comb. nov. they are relatively narrow. Other species of *Stellechinatum*, notably *S. brachyscolum* Turner 1984 and *S. helosum* Turner 1984, have process bases of variable width, the narrower bases being comparable with those of *S. uncinatum* (Downie) comb. nov. *S. helosum* is distinguished from *S. uncinatum* (Downie) comb. nov. by its ornament of grana rather than of spines on the processes. *S. brachyscolum* has more processes than *S. uncinatum*, their conical bases coalescing to form the vesicle outline.





Figs 91–92 *Stellechinatum papulessum* sp. nov.; sample MPA 20091, Pontyfenni Formation; × 1200. Fig. 91A, B, **holotype**, high and low focus; MPK 4932; slide 1, O39/3. See Fig. 90. Fig. 92A, B, high and low focus; MPK 4933; slide 1, N41/1.

Figs 93–94 *Stellechinatum uncinatum* (Downie 1958) comb. nov.; sample MPA 20099, Pontyfenni Formation; × 1200. Fig. 93, MPK 4934; slide 1, R30/2. Fig. 94, MPK 4977; slide 1, M35/3.

Three of the specimens illustrated by Cramer (1970: pl. 6, figs 97–98, 101) are unlike *S. uncinatum* (Downie) comb. nov., two having subspherical vesicles and relatively long processes, the third fewer processes that, together with the vesicle, are covered by an ornament of relatively coarse spines. Only the text-figure (Cramer 1970: text-fig. 29d) bears some resemblance to the holotype and to the material illustrated herein. The specimen illustrated by Kjellström (1971: fig. 18), from the Middle Ordovician of Gotland, has more numerous processes with broad, conical bases and is comparable with *Stellechinatum brachyscolum* from the Caradoc of England.

Genus ***STELLIFERIDIUM*** Deunff, Gorka & Rauscher, 1974

TYPE SPECIES. *Stelliferidium striatulum* (Vavrdova 1966) Deunff, Gorka & Rauscher 1974.

Stelliferidium aff. ***fimbrium*** (Rasul 1974) Rasul 1979
Figs 95, 97

aff. 1974 *Priscogalea fimbria* Rasul: 47; pl. 3, figs 1–2.
aff. 1979 *Stelliferidium fimbrium* (Rasul) Rasul: 69.

MATERIAL. Two specimens.

OCCURRENCE. Pontyfenni Formation: MPA 20091–2.

DESCRIPTION. The vesicle is subspherical and granulate, and has a large polar opening (macropyle). About 20–25 processes are present; they are hollow and cylindrical but it is not clear if they communicate with the vesicle cavity. Distally, they divide into three or four long, recurved branches that lie at a tangent to the surface of the vesicle. Striations radiate from the base of each process across the surface of the vesicle.

DIMENSIONS. Vesicle diameter range 26–28 μm, mean 27 μm; process length range 5–8 μm.

REMARKS. The specimens resemble the Tremadoc species *Stelliferidium fimbrium* (Rasul) Rasul but are smaller and may have more robust distal terminations.

Genus ***STRIATOTHECA*** Burmann, 1970

TYPE SPECIES. *Striatotheca principalis* Burmann 1970.

? ***Striatotheca mutua*** Burmann 1970
Fig. 96A, B

?1970 *Striatotheca mutua* Burmann: 301; pl. 11, fig. 2.
?1978 *Striatotheca mutua* Burmann: Dean & Martin; 9; pl. 2, figs 12, 13; pl. 3, fig. 18.

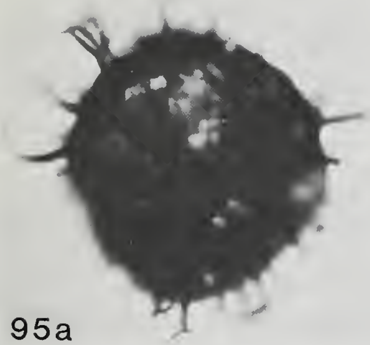
MATERIAL. One specimen.

OCCURRENCE. Pontyfenni Formation: MPA 20099.

DESCRIPTION. The vesicle is elongate and pentagonal in outline. Two processes are present but the total number may have been five or six; they are relatively short, conical and evexate. Striations extend from the base of each process and are more or less parallel to the five sides of the vesicle.

DIMENSIONS. Vesicle diameter 38 × 26 μm; process length 18 μm.

REMARKS. The holotype (Burmann 1970: pl. 11, fig. 2) has a more or less rectangular outline with three processes at each pole on the long axis. The diagnosis also refers to the vesicle as being four-sided. The processes on the holotype are longer than those on the present specimen from the Pontyfenni Formation. Martin (*in* Dean & Martin 1978) describes the vesicle of *S. mutua* as being polyhedral, and although she remarks that the outline is quadrangular, one specimen (Dean & Martin 1978: pl. 3, fig. 18) may be interpreted as having five or six sides. Martin's specimens have dimensions similar to that from the Pontyfenni Formation, although the latter has relatively shorter processes.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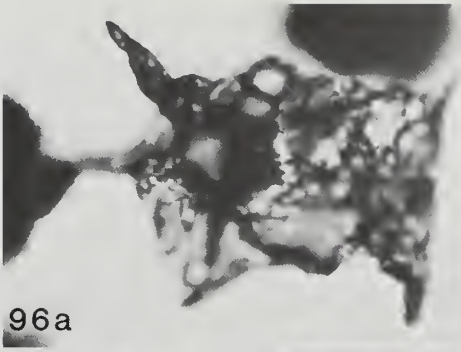
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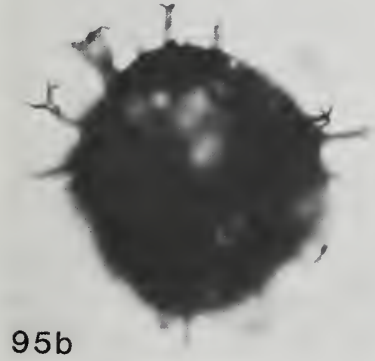
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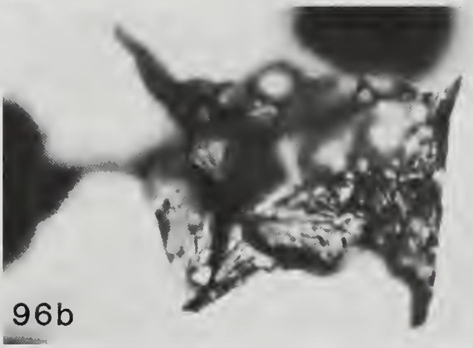
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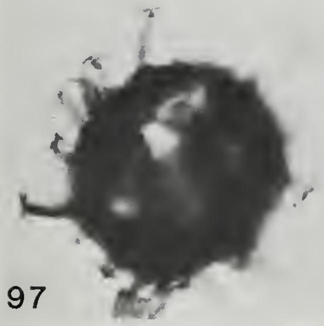
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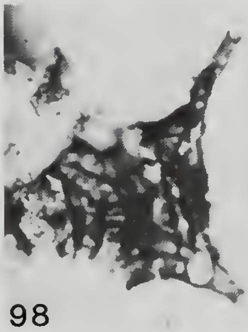
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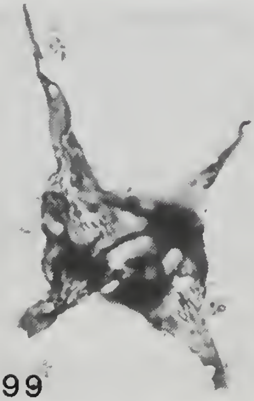
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Figs 95, 97 *Stelliferidium* aff. *fimbrium* (Rasul 1974) Rasul 1979; Pontyfenni Formation; × 1200. Fig. 95A, B, high and low focus; MPK 4978, sample MPA 20092; slide 1, L34/3. Fig. 97, MPK 4936, sample MPA 20091; slide 1, V62/0.

Fig. 96A, B ?*Striatotheca mutua* Burmann 1970, high and low focus; MPK 4935, sample MPA 20099, Pontyfenni Formation; slide 1, M31/4, × 1200.

Fig. 98 ?*Striatotheca rarirrugulata* (Cramer, Kanes, Diez & Christopher 1974) Eisenack, Cramer & Diez 1976; MPK 4937, sample MPA 20102, Pontyfenni Formation; slide 1, Q70/4, × 1200.

Fig. 99 *Striatotheca* sp.; MPK 4938, sample MPA 20103, Cwm yr Abbey Member; slide 2, H67/0, × 1200.

? *Striatotheca rarirrugulata*
(Cramer, Kanes, Diez & Christopher 1974) Eisenack, Cramer & Diez 1976

Fig. 98

?1974 *Rugulidium rarirrugulatum* Cramer, Kanes, Diez & Christopher: 61; pl. 25, figs 19, 21, 23; pl. 26, fig. 24.

?1976 *Striatotheca rarirrugulata* (Cramer, Kanes, Diez & Christopher) Eisenack, Cramer & Diez: 775–776.

MATERIAL. One damaged specimen.

OCCURRENCE. Pontyfenni Formation: MPA 20102.

DESCRIPTION. The vesicle is four-sided, broken and striate; there are 4–6 widely spaced striations across its width. Two processes, both broken, are present at two of the corners of the vesicle.

DIMENSIONS. Vesicle diameter 21 × 20 μm; process length more than 11 μm.

REMARKS. Although the specimen is too badly damaged for a positive identification, its size, shape and the nature of its striate ornament suggest it is most probably a specimen of *S. rarirrugulata*.

Striatotheca sp.

Fig. 99

MATERIAL. One specimen.

OCCURRENCE. Cwm yr Abbey Member: MPA 20103.

DESCRIPTION. The vesicle is four sided, folded and closely and relatively coarsely striate; there are about two striations per μm across the width of the vesicle. Four processes, at the corners of the vesicle and lying in the same plane, are long and conical, tapering to an acuminate tip from a broad base. The striations extend a little way onto the base of each process but the process stems are smooth.

DIMENSIONS. Vesicle diameter: 22 × 14 μm.
Process length: 25 μm.
Process width (at base): 4 μm.

REMARKS. The specimen is distinguished from other species of *Striatotheca* by the combination of small size and relatively long, broad-based processes. *Striatotheca frequens* Burmann, 1970, and *S. principalis* Burmann, 1970, are both larger and have relatively short processes. *S. principalis parva* Burmann, 1970, is of similar size but also has relatively short processes.

Genus ***TIMOFEEVIA*** Vanguestaine, 1978

TYPE SPECIES. *Timofeevia lancarae* (Cramer & Diez 1972) Vanguestaine 1978.

Timofeevia lancarae (Cramer & Diez 1972) Vanguestaine 1978

Fig. 127

1972 *Multiplicisphaeridium lancarae* Cramer & Diez: 42; pl. 1, figs 1–4, 6, 8; text-fig. 1.

1978 *Timofeevia lancarae* (Cramer & Diez) Vanguestaine: 272.

MATERIAL. One specimen.

OCCURRENCE. Pontyfenni Formation: MPA 20099.

DESCRIPTION. The vesicle is subspherical and its surface is divided into a number of polygonal fields by dark folds or protuberances. Twenty-five processes are visible, situated at the angles of the polygonal fields. They have hollow, cylindrical stems and divide distally to the fourth order. The terminal branches are fine filaments which, in some cases, link adjacent processes.

Dimensions. Vesicle diameter 32 × 28 μm; process length 12 μm.

Remarks. The elaborate distal process terminations of *Timofeevia lancarae* are diagnostic. The species has been recorded from the early Middle Cambrian to earliest Tremadoc (?) in Spain (Cramer & Diez 1972; Fombella 1978), and from the Middle and Upper Cambrian of Random Island, eastern Newfoundland (Martin & Dean 1981). Its presence in the Pontyfenni Formation is probably on account of reworking from rocks of Cambrian or, less likely, Tremadoc age.

Genus *UNCINISPHAERA* Wicander, 1974

Type species. *Uncinisphaera lappa* Wicander 1974.

Remarks. A number of species recorded from the Arenig succession of south-west Wales have similar features and are tentatively referred to the genus *Uncinisphaera* Wicander, 1974. The diagnostic characteristics of *Uncinisphaera* are a granulate wall, spherical vesicle and ornamented processes: at least two of these features are present on each of the taxa considered here. It is possible that all the species described herein are related to each other, but unlikely that they are closely related to the Devonian species *Uncinisphaera lappa* Wicander 1974 and *U. acantha* Wicander & Wood 1981. *Uncinisphaera* is distinguished from *Stellechinatum* by its spherical or subspherical rather than polygonal vesicle.

Uncinisphaera ? sp. A

Figs 100–101, 119–120

Material. Three specimens.

Occurrence. Pontyfenni Formation: MPA 20099.

Description. The vesicle is large, subspherical and, although poorly preserved, appears to have a granulate wall. There are about 40–50 slender, acuminate, moderately flexible and slightly tapering processes. They are relatively short, their average length being about one quarter of the vesicle diameter, possibly solid and bear an ornament of short lateral hairs.

Dimensions. Vesicle diameter range 33–48 μm, mean 40 μm; process length range 9–12 μm.

Remarks. The apparently granulate wall and ornamented processes would justify assignment *Uncinisphaera*, but the determination is tentative because of poor preservation.

U. lappa is smaller and has fewer, stouter, more conical processes. *U. acantha* is smaller and has fewer, relatively long processes. For comparisons with other taxa see the remarks under the following species of *Uncinisphaera*.

Uncinisphaera ? sp. B

Figs 102, 104, 121–122

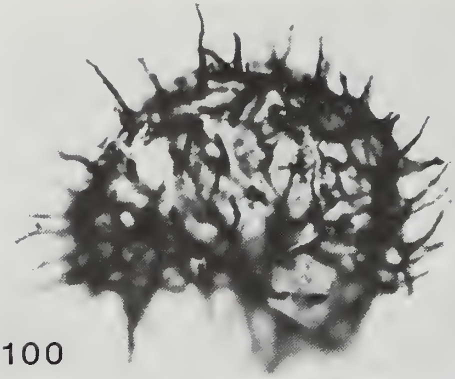
Material. Seven specimens.

Occurrence. Pontyfenni Formation: MPA 20099.

Description. The vesicle is large and subspherical, with convex or concave sides between the process bases. There are about 50 relatively short, stiff or slightly flexible and evexate processes, which bear an ornament of short hairs; they average about one-ninth of the vesicle diameter in length.

Dimensions. Vesicle diameter range 46–66 μm, mean 54 μm; process length range 5–10 μm, mean 6 μm.

Remarks. *Uncinisphaera* ? sp. B is distinguished from *Uncinisphaera* ? sp. A by its larger size and shorter processes. The two taxa occur together in the Pontyfenni Formation, but no gradation occurs between them.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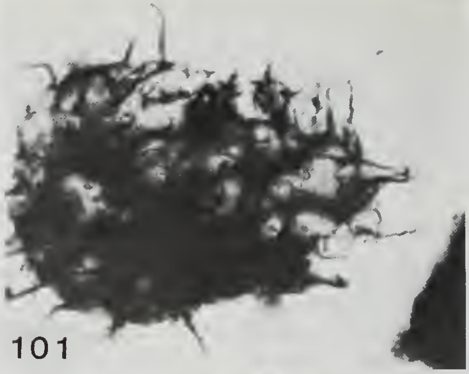
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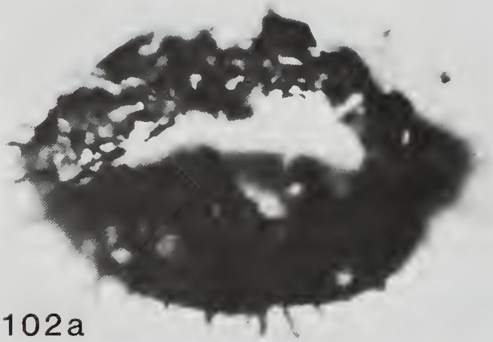
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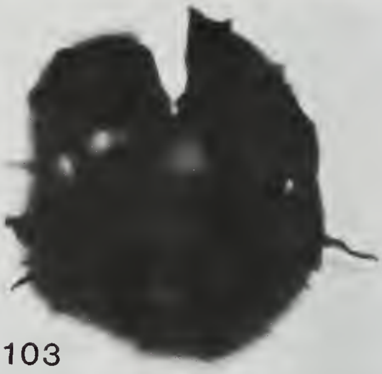
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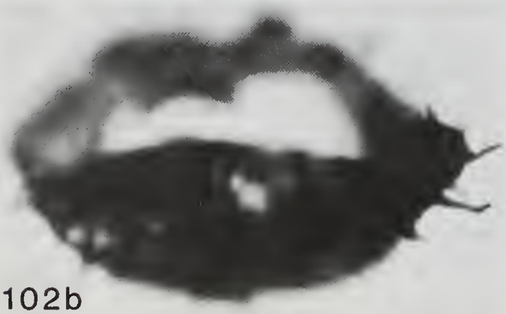
102b


105a


104


105b

Uncinisphaera ? sp. C
Figs 103, 105, 123

MATERIAL. Nine specimens.

OCCURRENCE. Pontyfenni Formation: MPA 20091.

DESCRIPTION. The vesicle is subspherical with straight or convex sides. There are about 20 slender, simple, stiff, tapering and evexate processes, with an ornament of fine hairs or grana. One specimen apparently has an equatorial split.

DIMENSIONS. Vesicle diameter range 34–46 μm, mean 41 μm; process length range 4–10 μm, mean 8 μm.

REMARKS. *Uncinisphaera* ? sp. A has longer processes and a more prominent ornament. *Uncinisphaera* ? sp. B is larger and also has a more prominent ornament on the processes. *U. lappa* and *U. acantha* have smaller vesicles. For other comparisons see the remarks under *Uncinisphaera* ? sp. D.

Uncinisphaera ? sp. D
Figs 106–109, 124

MATERIAL. Nine specimens.

OCCURRENCE. Cwmffrŵd Member: MPA 20077, MPA 20087(?). Allt Cystanog Member: MPA 20074(?).

DESCRIPTION. The vesicle is large and subspherical with convex sides. The few, short, slender processes are relatively stiff, tapering and evexate. The number of processes is variable, between seven and seventeen; the lower number may reflect poor preservation.

DIMENSIONS. Vesicle diameter range 39–44 μm, mean 41 μm; process length range 5–8 μm, mean 6 μm.

REMARKS. *Uncinisphaera* ? sp. D is very similar to *Uncinisphaera* ? sp. C, but may be distinguished by its fewer, shorter processes. The differences are very slight, however, and it is possible that the two forms are conspecific. One specimen from the Allt Cystanog Member has shorter processes than the specimens of *Uncinisphaera* ? sp. D from the Cwmffrŵd Member, but is otherwise similar. The presence of the species in the upper part of the Cwmffrŵd Member (MPA 20087) is questionable because it is based on the occurrence of a few, poorly preserved specimens.

Uncinisphaera ? sp. E
Figs 110–111, 125

MATERIAL. Two specimens.

OCCURRENCE. Cwmffrŵd Member: MPA 20077.

DESCRIPTION. The vesicle is subspherical to subpolygonal. The processes are relatively short, conical and acuminate, and bear short lateral hairs. About 30 processes, about one third of the vesicle diameter in length, are present.

DIMENSIONS. Vesicle diameter range 30–32 μm, mean 30·5 μm; process length 8–10 μm.

REMARKS. *Uncinisphaera* ? sp. A is larger and has more numerous and more slender processes.

Figs 100, 101 *Uncinisphaera*? sp. A; sample MPA 20099, Pontyfenni Formation; × 1200. Fig. 100, MPK 4939; slide 1, M31/2. See Fig. 119. Fig. 101, MPK 4940; slide 1, N38/0. See Fig. 120.

Figs 102, 104 *Uncinisphaera*? sp. B; sample MPA 20099, Pontyfenni Formation; × 1200. Fig. 102A, B, MPK 4941; slide 1, M24/0. See Fig. 122. Fig. 104, MPK 4943, slide 1, R27/0. See Fig. 121.

Figs 103, 105 *Uncinisphaera*? sp. C; sample MPA 20091, Pontyfenni Formation; × 1200. Fig. 103, MPK 4942; slide 1, X42/1. Fig. 105A, B (B phase contrast), MPK 4944; slide 1, Q43/0. See Fig. 123.


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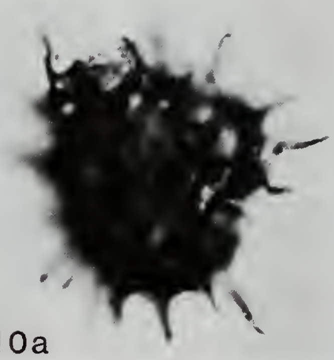
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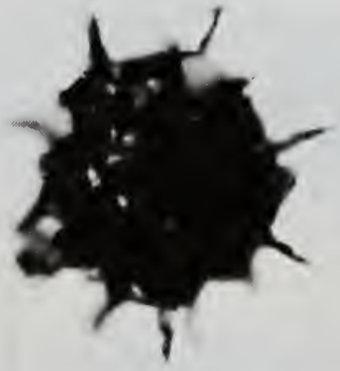
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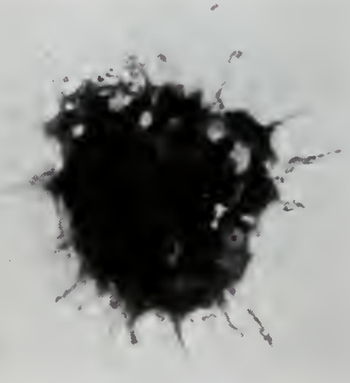
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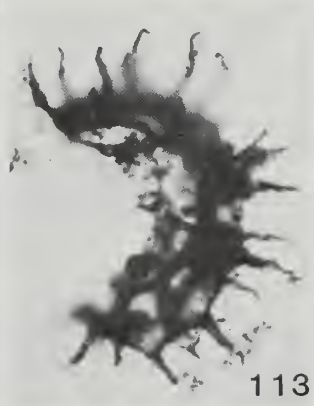
Figs 106–108 *Uncinisphaera*? sp. D; sample MPA 20077, Cwmffrŵd Member; × 1200. Fig. 106, MPK 4945; slide 2, M32/1. See Fig. 124. Fig. 107, MPK 4946; slide 2, R38/3. Fig. 108, MPK 4947; slide 2, L25/1.

Fig. 109 cf. *Uncinisphaera*? sp. D; MPK 4948, sample MPA 20074, Allt Cystanog Member; slide 1, F22/0, × 1200.

Figs 110–111 *Uncinisphaera*? sp. E; sample MPA 20077, Cwmffrŵd Member; × 1200. Fig. 110A, B (B phase contrast), MPK 4949; slide 2, J42/0. See Fig. 125. Fig. 111, MPK 4950; slide 2, P29/1.


112a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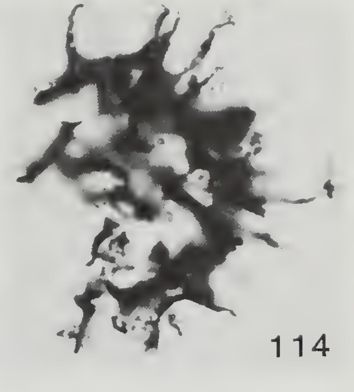
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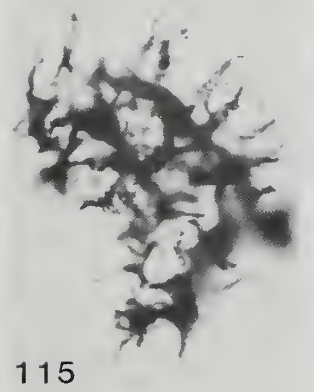
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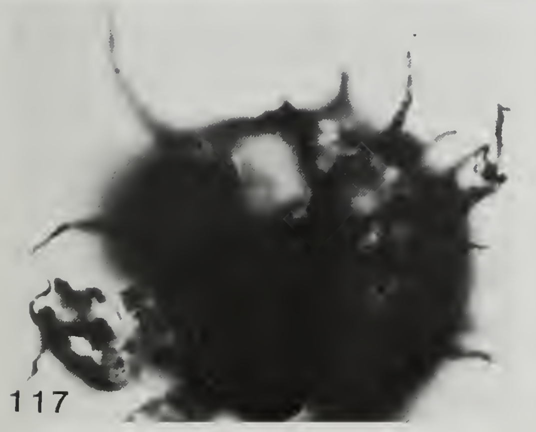
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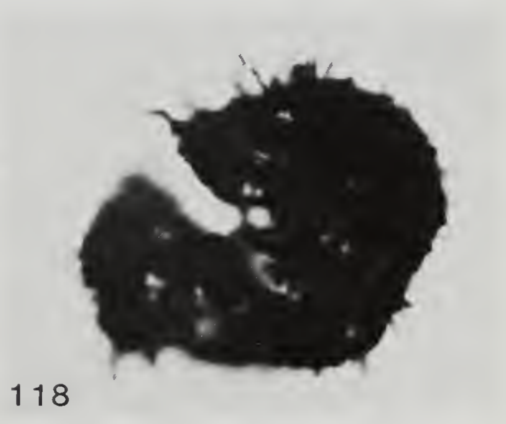
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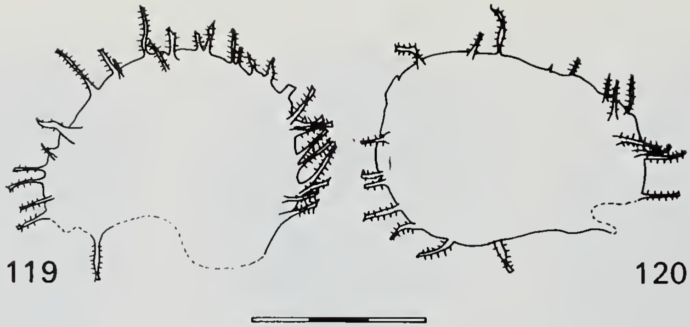
Figs 112–115 *Uncinisphaera*? sp. F; sample MPA 20103, Cwm yr Abbey Member; × 1200. Fig. 112A, B, high and low focus, MPK 4951; slide 2, G21/2. See Fig. 126. Fig. 113, MPK 4952; slide 2, J56/0. Fig. 114, MPK 4953; slide 2, J58/4. Fig. 115, MPK 4954; slide 2, S64/0.

Figs 116–118 *Uncinisphaera*? spp.; Cwm yr Abbey Member; × 1200. Fig. 116, MPK 4955, sample MPA 20084; slide 2, K44/0. Fig. 117, MPK 4956, sample MPA 20103; slide 1, E33/0. Fig. 118, MPK 4957, sample MPA 20084; slide 2, G35/3.



Figs 119–120 *Uncinisphaera*? sp. A. Bar represents 30 μm. Fig. 119, MPK 4939. See Fig. 100. Fig. 120, MPK 4940. See Fig. 101.

Uncinisphaera ? sp. F
Figs 112–115, 126

Material. Four specimens.

Occurrence. Cwm yr Abbey Member: MPA 20103.

Description. The vesicle is subspherical and its sides are either masked by the process bases or concave. About 30 conical, relatively short, acuminate and granulate processes, with an average length of one quarter of the vesicle diameter, are present.

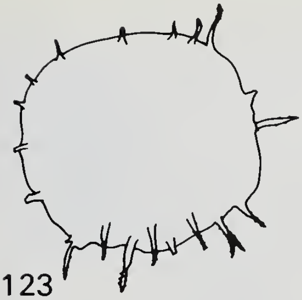
Dimensions. Vesicle diameter range 28–35 μm, mean 33 μm; process length *c.* 8 μm.

Remarks. Preservation is generally poor and three out of the four specimens are broken. The species may be readily distinguished by its broad conical processes which tend to mask the vesicle sides.

Uncinisphaera ? spp.
Figs 116–118

Remarks. Three poorly preserved specimens from the Cwm yr Abbey Member are included in the genus.

Figs 121–122 *Uncinisphaera*? sp. B. Bar represents 30 μm. Fig. 121, MPK 4943. See Fig. 104. Fig. 122, MPK 4941. See Fig. 102.



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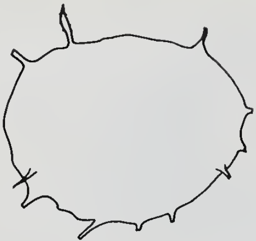

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Fig. 123 *Uncinisphaera*? sp. C; MPK 4944. Bar represents 30 μm. See Fig. 105.
Fig. 124 *Uncinisphaera*? sp. D; MPK 4945. Bar represents 30 μm. See Fig. 106.

Two specimens from MPA 20084 have subspherical vesicles with straight or convex sides. The processes, numbering 30–40, are relatively short, slender and moderately flexible, and bear a sparse ornament of fine hairs. The vesicle diameters are 38 × 39 μm (Fig. 116) and 48 × 37 μm (Fig. 118), and the average process length is 6 μm. The specimens may represent the same species but this cannot be confirmed because of their poor preservation.

One specimen (Fig. 117), from MPA 20103, has a large subspherical vesicle with straight or convex sides and a granulate surface. The processes, of which there are at least 21, are long, stout and moderately flexible, and are covered in relatively long hairs; their distal terminations are evexate or consist of two short, recurved hairs. The vesicle diameter is about 50 μm, and process length 16 μm.

Genus ***VERYHACHIUM*** Deunff 1954 *ex* Downie 1959

TYPE SPECIES. *Veryhachium trisulcum* (Deunff 1951) Deunff 1959 *ex* Downie 1959.

'***Veryhachium trispinosum***' group

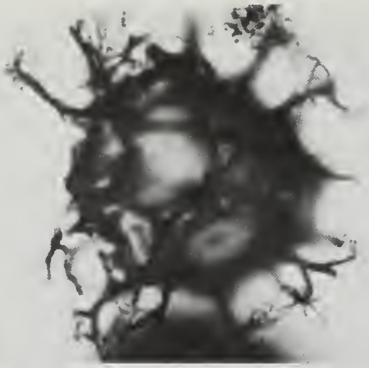
Figs 129, 131, 133

REMARKS. Three-spined species of *Veryhachium* are recorded from the Cwmffrŵd Member of the Carmarthen Formation and throughout the succeeding part of the Arenig Series (Fig. 5, p. 318). They are most common in the Fennian.

125

126

Fig. 125 *Uncinisphaera*? sp. E; MPK 4949. Bar represents 30 μm. See Fig. 110.
Fig. 126 *Uncinisphaera*? sp. F; MPK 4951. Bar represents 30 μm. See Fig. 112.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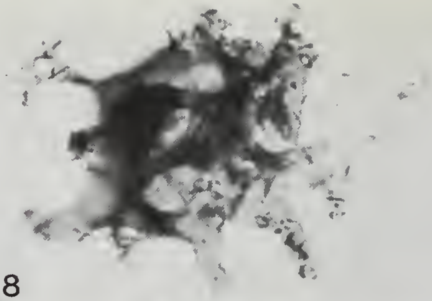
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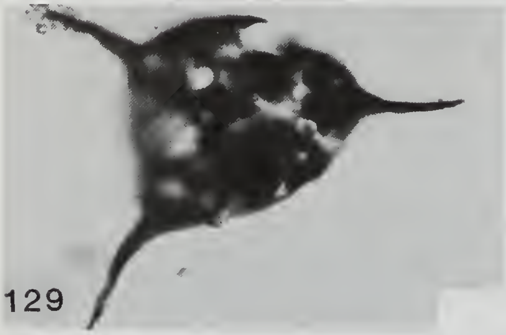
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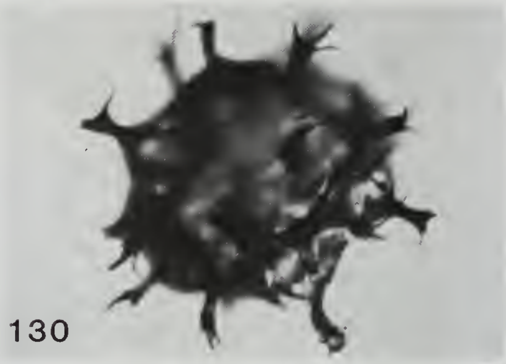
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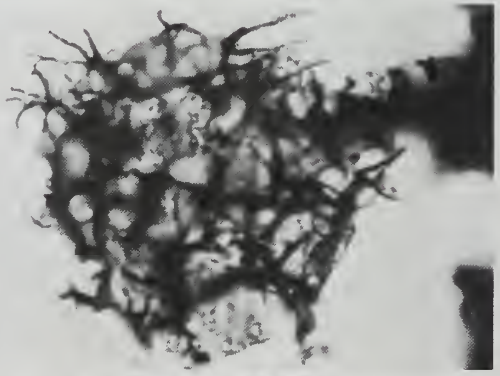
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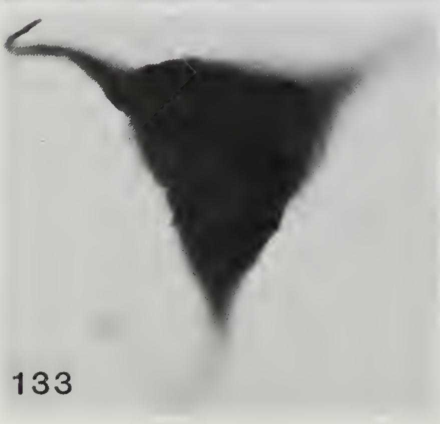
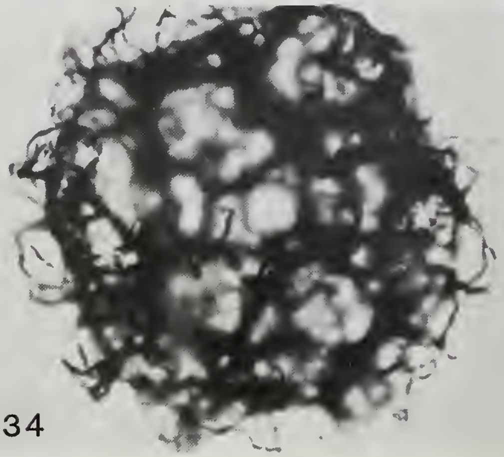

133


134

Genus *VOGTLANDIA* Burmann, 1970

TYPE SPECIES. *Vogtlandia ramificata* Burmann 1970.

?*Vogtlandia flosmaris* (Deunff 1977) Dean & Martin 1978
Fig. 128

?1977 *Evittia flosmaris* Deunff: 143; pl. 1, fig. 18; pl. 2, figs 7, 9, 11, 14.
?1978 *Vogtlandia coalita* Dean & Martin: 9–10; pl. 2, figs 3, 7.
?1978 *Vogtlandia flosmaris* (Deunff) Dean & Martin: 19.
?1982 *Vogtlandia flosmaris* (Deunff) Dean & Martin: Martin; pl. 1, fig. 3.

MATERIAL. One specimen.

OCCURRENCE. Allt Cystanog Member: MPA 20074.

DESCRIPTION. The vesicle is subpolygonal in outline but the vesicle sides are masked to some extent by the wide process bases. The processes, of which there are 12, have stout stems and divide distally to the fourth order, terminating in long, slender filaments.

DIMENSIONS. Vesicle diameter: 24 μm × 24 μm.
Process length (overall): 14 μm.
Process length from proximal contact to first bifurcation: 8 μm.
Process length from first bifurcation to distal termination: 6 μm.

REMARKS. The specimen has relatively long distal filaments like those on the specimens illustrated by Deunff (1977) and Martin (1982), but there is no evidence they are intertwined (cf. Dean & Martin 1978: 10; pl. 2, figs 3, 7). This difference might be explained by the poor preservation of the specimen from the Allt Cystanog Member.

Genus *VULCANISPHAERA* Deunff, 1961

TYPE SPECIES. *Vulcanisphaera africana* Deunff 1961.

Vulcanisphaera britannica Rasul 1976
Fig. 130

1976 *Vulanisphaera britannica* Rasul: 482–484; pl. 1, figs 2, 7–9, 13–16; text-fig. 1: 4, 5.

MATERIAL. One specimen.

OCCURRENCE. Pontyfenni Formation: MPA 20099.

DESCRIPTION. The vesicle is subpolygonal and bears at least twenty processes, which have stout stems dividing distally into three or four branches. All the branches arise from a common point and are acuminate and possibly acicular.

DIMENSIONS. Vesicle diameter 32 × 28 μm; process length *c.* 12 μm.

Fig. 127 *Timofeevia lancarae* (Cramer & Diez 1972) Vanguestaine 1978; MPK 4958, sample MPA 20099, Pontyfenni Formation; slide 1, N34/4, × 1200.

Figs 129, 131, 133 '*Veryhachium trispinosum*' group; × 1200. Fig. 129, MPK 4960, sample MPA 20103, Cwm yr Abbey Member; slide 2, D74/4. Figs 131, 133, sample MPA 20091, Pontyfenni Formation. Fig. 131, MPK 4962; slide 1, U29/2. Fig. 133, MPK 4964; slide 1, O46/0.

Fig. 128 ?*Vogtlandia flosmaris* (Deunff 1977) Dean & Martin 1978; MPK 4959, sample MPA 20074, Allt Cystanog Member; slide 2, K51/4, × 1200.

Fig. 130 *Vulcanisphaera britannica* Rasul 1976; MPK 4961, sample MPA 20099, Pontyfenni Formation; slide 1, G26/2, × 1200.

Figs 132, 134 *Vulcanisphaera turbata*? Martin *in* Martin & Dean 1981; × 1200. Fig. 132, MPK 4963, sample MPA 20099, Pontyfenni Formation; slide 1, L37/3. Fig. 134, MPK 4965, sample MPA 20103, Cwm yr Abbey Member; slide 1, L38/2.

REMARKS. The specimen is most like *Vulcanisphaera britannica, forma* 2 of Rasul (1976), recorded from the Shineton Shales (of Tremadoc age), Shropshire. It indicates probable reworking of Tremadoc forms into the lower part of the Pontyfenni Formation.

***Vulcanisphaera turbata*? Martin 1981**
Figs 132, 134

?1981 *Vulcanisphaera turbata* Martin *in* Martin & Dean: 23–24; pl. 1, figs 2–4; text-fig. 6.

MATERIAL. Two specimens.

OCCURRENCE. Cwm yr Abbey Member: MPA 20103. Pontyfenni Formation: MPA 20099.

DESCRIPTION. The vesicle is subspherical. The processes are rarely single, more usually grouped into clusters of two, three or four. Filamentous threads arise laterally from some of the processes. A number of polygonal fields are delimited by dark folds or protuberances on the surface of the vesicle.

DIMENSIONS. Vesicle diameters 40 × 36 μm and 48 × 45 μm; process length 8 × 10 μm.

REMARKS. The specimens resemble *V. turbata*, and also show some similarity to *Vulcanisphaera cirrita* Rasul, 1976, and *V. africana* Deunff, 1961, as understood by Martin (*in* Martin & Dean, 1981). The determination is tentative on account of poor preservation. *V. turbata* was described from late Middle Cambrian and Upper Cambrian rocks of Random Island, eastern Newfoundland, and its presence may indicate the possible reworking of Cambrian forms into the Arenig Series of south-west Wales.

Systematic descriptions: Chitinozoa

The descriptive terminology used in this section is that of Laufeld (1974). The general remarks on p. 319–20 apply here also.

Genus ***BELONECHITINA*** Jansonius, 1964

TYPE SPECIES. *Conochitina micracantha robusta* Eisenack 1959.

Belonechitina spp.
Figs 135–137, 139

Eight specimens from the Pontyfenni Formation (MPA 20091) are assigned to this genus. There are two distinct forms, distinguished by size, but it is possible that they represent a single species.

DESCRIPTIONS. Four specimens have cylindro-conical vesicles which are poorly divided into a chamber and a neck by weakly-developed flexures and shoulders. The chamber is subconical, the basal edge rounded and the base flat to slightly convex. The neck is cylindrical and slightly narrower than the chamber. The vesicle bears an ornament of short hairs and grana which are most prominent on the basal edge. Dimensions of the four specimens are as follows: vesicle length 76–84 μm, mean 81 μm; chamber width 61–72 μm, mean 66 μm; neck width 34–53 μm, mean 44 μm. (See Figs 137, 139).

The other four specimens also have cylindro-conical vesicles, but the neck is not differentiated from the chamber, or is only poorly differentiated by a weakly-developed flexure. The basal edge is rounded and the base is flat or concave. The neck of all four specimens is broken orally. An ornament of fine hairs is present on the vesicle. Dimensions of these specimens are: vesicle length 118–152 μm, mean 133 μm; chamber width 57–74 μm, mean 65 μm; neck width 29–48 μm, mean 34 μm. (See Figs 135, 136).

REMARKS. *Belonechitina henryi* Paris 1981 has a longer vesicle than either form from the Pontyfenni Formation. *B. micracantha typica* (Eisenack 1965) has similar dimensions, is variable in shape and has an ornament well developed on the basal edge but not on the flanks. All the specimens from the Pontyfenni Formation resemble *B. micracantha typica*, but the ornament may be more widely distributed over the vesicle surface than in that species.


135


136


137a


138a


139b


139a


140


137b


138b

Figs 135–137, 139 *Belonechitina* spp.; Pontyfenni Formation; × 480 (Fig. 139B × 1200). Fig. 135, MPK 4966, sample MPA 20092; slide 2, L21/0. Fig. 136, MPK 4967, sample MPA 20091; slide 1, K22/4. Fig. 137A, B, high and low focus, MPK 4968, sample MPA 20091; slide 2, H25/3. Fig. 139A, B (B detail of surface ornament × 1200), MPK 4970, sample MPA 20092; slide 2, J22/1.

Fig. 138A, B *Lagenochitina cylindrica*? Eisenack 1931, high and low focus; MPK 4969, sample MPA 20091, Pontyfenni Formation; slide 1, U25/3, × 480.

Fig. 140 *Conochitina* cf. *chydaea* Jenkins 1967; MPK 4971, sample MPA 20092, Pontyfenni Formation; slide 1, P19/0, × 1200.

Genus *CONOCHITINA* Eisenack, 1931

TYPE SPECIES. *Conochitina claviformis* Eisenack 1931.

Conochitina cf. ***chydaea*** Jenkins 1967
Fig. 140

cf. 1967 *Conochitina chydaea* Jenkins: 453–454; pl. 70, figs 4–8.

MATERIAL. Six specimens.

OCCURRENCE. Pontyfenni Formation: MPA 20091.

DESCRIPTION. The vesicle is cylindro-conical, the base flat or slightly convex and the basal edge rounded. Flexures and shoulders are not developed. The neck is poorly developed and may flare aborally of the aperture.

DIMENSIONS. Vesicle length: range 93–148 μm; mean 111 μm.
Width (chamber): range 44–57 μm; mean 53 μm.
Width (neck): range 30–38 μm; mean 35 μm.
Width (aperture): range 23–42 μm: mean 33 μm.

REMARKS. *Conochitina chydaea* is variable in morphology. The specimens recorded from the Pontyfenni Formation bear some resemblance to the type material (Jenkins 1967) from the Llanvirn of Shropshire, but are smaller.

Genus ***LAGENOCHITINA*** Eisenack, 1931

TYPE SPECIES. *Lagenochitina baltica* Eisenack 1931.

***Lagenochitina cylindrica*?** Eisenack 1931

Fig. 138A, B

?1931 *Lagenochitina cylindrica* Eisenack: 81; pl. 2, figs 18, 19.
?1967 *Lagenochitina cylindrica* Eisenack; Jenkins: 463; pl. 74, figs 1–3.

MATERIAL. One specimen.

OCCURRENCE. Pontyfenni Formation: MPA 20091.

DESCRIPTION. The vesicle has a conspicuous flexure and shoulder that differentiate the chamber from the neck. The chamber is subcylindrical with a flat base and a rounded basal edge. The neck is cylindrical.

DIMENSIONS. Vesicle length 112 μm; length of chamber 65 μm; length of neck 48 μm; width of chamber 48 μm; width of neck 36 μm.

REMARKS. The specimen is small for *Lagenochitina cylindrica* but resembles those illustrated by Jenkins (1967) from the Llanvirn of Shropshire.

Lagenochitina sp. A

Figs 141–143

MATERIAL. Thirty specimens.

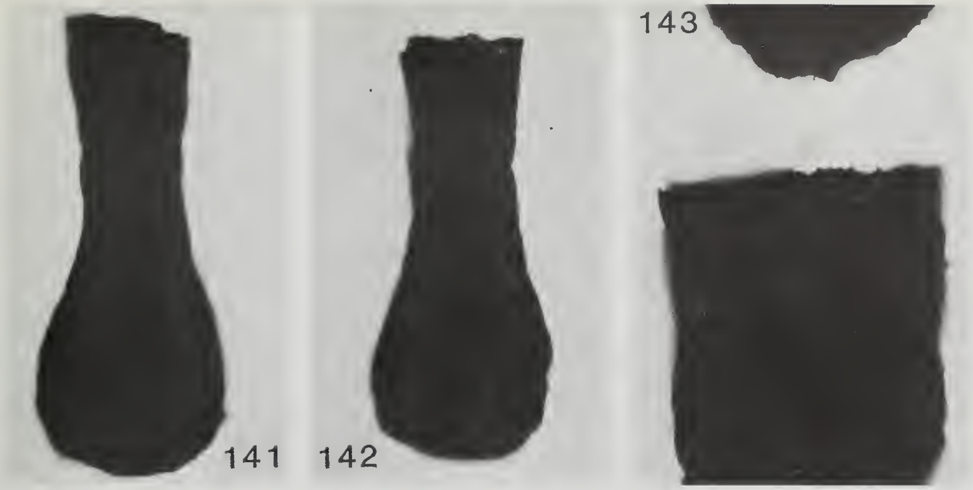
OCCURRENCE. Pontyfenni Formation: MPA 20091–3.

DESCRIPTION. The chamber is subcylindrical to subconical and rarely sphaeroidal. The flexure is usually more conspicuous than the shoulder, the latter being broadly rounded. The basal edge may or may not be present; when present it is convex and rounded to broadly rounded. The base is flat or convex. The neck is long and cylindrical, widening slightly near the aperture. The length of the neck is usually a little over half the total length of the vesicle. The aperture is fringed by short spines but the vesicle is otherwise smooth.

DIMENSIONS. Vesicle length: range 110–162 μm; mean 141 μm.
Length of neck: range 53–99 μm; mean 76 μm.
Length of chamber: range 49–84 μm; mean 66 μm.
Width of neck: range 29–42 μm; mean 36 μm.
Width of chamber: range 44–68 μm; mean 59 μm.
Width of aperture: range 29–42 μm; mean 38 μm.

REMARKS. *Lagenochitina* sp. A is the most commonly occurring chitinozoan in the Pontyfenni Formation near Maesyrwyn. It is unlike other species of *Lagenochitina*, being distinguished by its relatively long neck, fringed aperture and the shape of its chamber.

Lagenochitina obeligis Paris 1981 is larger, has a relatively shorter neck, an ovoidal chamber and a more convex base, and its aperture is not fringed. *L. esthonica* Eisenack 1955 has a very characteristic shape that distinguishes it from the present *Lagenochitina* sp. A. *L. shelvensis*



Figs 141–143 *Lagenochitina* sp. A; Pontyfenni Formation; × 480 (Fig. 143 × 1200). Fig. 141, MPK 4976, sample MPA 20091; slide 2, T31/2. Fig. 142, MPK 4975, sample MPA 20092; slide 1, P40/3. Fig. 143, detail of aperture × 1200, MPK 4974, sample MPA 20091; slide 2, G32/3.

Jenkins 1967 and *Lagenochitina* sp. of Achab (1982) are both larger than the present form, and both have relatively shorter necks. Achab's *Lagenochitina* sp. also has a more or less quadrangular chamber.

Acknowledgements

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Sample localities

1. *Ogof Hên Formation*: Allt Cystanog Member.
    - MPA 20074. 140 m at 112° from Star Cottage (SN 4305 1979). Loc. 4b of Owens & Fortey (1982).
2. *Ogof Hên Formation*: Bolahaul Member.
    - MPA 20075–6. 10 m at 227° from Star Cottage (SN 4291 1981). Loc. 8 Fortey & Owens (1978).
    - MPA 20079. Roman Road, Pensarn. 105 m at 140° from chapel at Pensarn (SN 4141 1911). Loc. 6 of Fortey & Owens (1978).
    - MPA 20080. Roman Road, Pensarn. 80 m at 149° from chapel at Pensarn (SN 4137 1914). Loc. 6 of Fortey & Owens (1978).
3. *Carmarthen Formation*: Cwmffrŵd Member.
    - MPA 20077–8. Nantycaws dingle. 410 m at 233° from Ty-cerig (SN 4510 1844). Loc. 7 of Owens & Fortey (1982).
    - MPA 20086. Nant y Glasdwr. 50 m at 130° from Nant-y-Glasdwr-fâch (SN 4239 1756). Loc. 3E of Fortey & Owens (1978).
    - MPA 20087. Nant y Glasdwr. 95 m at 131° from Nant-y-Glasdwr-fâch (SN 4242 1753). Loc. 3D of Fortey & Owens (1978).
4. *Carmarthen Formation*: Cwm yr Abbey Member.
    - MPA 20081. Nant y Glasdwr. 40 m at 169° from Gwynion Dale (SN 4272 1748). Loc. 3A of Fortey & Owens (1978).
    - MPA 20082. Nant y Glasdwr. 55 m at 218° from Gwynion Dale (SN 4267 1748). Loc. 3A of Fortey & Owens (1978).
    - MPA 20083. Nant y Glasdwr. 75 m at 228° from Gwynion Dale (SN 4265 1747). Loc. 3A of Fortey & Owens (1978).

MPA 20084. Nant y Glasdwr. 100 m at 235° from Gwynion Dale (SN 4263 1746). Loc. 3A of Fortey & Owens (1978).

MPA 20085. Nant y Glasdwr. 120 m at 238° from Gwynion Dale (SN 4261 1746). Loc. 3A of Fortey & Owens (1978).

MPA 20088. Nant y Glasdwr. 160 m at 252° from Gwynion Dale (SN 4256 1747). Near loc. 3B of Fortey & Owens (1978).

MPA 20089. Nant y Glasdwr. 165 m at 251° from Gwynion Dale (SN 4255 1747). Near loc. 3B of Fortey & Owens (1978).

MPA 20090. Nant y Glasdwr. 185 m at 257° from Gwynion Dale (SN 4253 1748). Near loc. 3B of Fortey & Owens (1978).

MPA 20103. Cwm yr Abbey. 400 m at 322° from Abbey Farm (SN 5002 1978). Loc. 16 of Fortey & Owens (1978).

5. *Afon Ffinnant Formation.*

MPA 20104–5. Cwm yr Abbey. 400 m at 322° from Abbey Farm (SN 5001 1979). Loc. 16 of Fortey & Owens (1978, 1987).

6. *Colomendy Formation*: Whitland Abbey Member.

MPA 20094. 340 m at 290° from Whitland Abbey (SN 2060 1822). Near loc. 27 of Fortey & Owens (1987).

MPA 20095. 210 m at 287° from Whitland Abbey (SN 2072 1818). Near loc. 27 of Fortey & Owens (1987).

MPA 20096. 210 m at 285° from Whitland Abbey (SN 2072 1818). Near loc. 27 of Fortey & Owens (1987).

MPA 20097. 210 m at 284° from Whitland Abbey (SN 2072 1817). Near loc. 27 of Fortey & Owens (1987).

MPA 20098. 200 m at 278° from Whitland Abbey (SN 2072 1815). Near loc. 27 of Fortey & Owens (1987).

7. *Pontyfenni Formation.*

MPA 20091. 560 m at 260° from Maesyrwyn (SN 2379 1694). Loc. 23 of Fortey & Owens (1987).

MPA 20092. 540 m at 262° from Maesyrwyn (SN 2381 1696). Loc. 23 of Fortey & Owens (1987).

MPA 20093. 520 m at 264° from Maesyrwyn (SN 2383 1699). Loc. 23 of Fortey & Owens (1987).

MPA 20099–100. 400 m at 353° from Penlan (SN 1984 1948). Loc. 38 of Fortey & Owens (1987).

MPA 20101–2. 400 m at 356° from Penlan (SN 1986 1949). Loc. 38 of Fortey & Owens (1987).

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Miocene geology and palaeontology of Ad Dabtiyah, Saudi Arabia

Compiled by **P. J. Whybrow**
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Fig. 1 Qarn Abu Wayil. The locality where in 1933 H. St J. Philby first found Miocene fossils. Photographed in 1979 from Qatar; the Saudi Arabian–Qatar border, left to right, passes the foot of the hill.

Summary

P. J. Whybrow

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The importance of the eastern Saudi Arabian Miocene mammal-bearing localities lies in their intermediate palaeogeographical position between the eastern African Miocene sites and those of Turkey and Pakistan, and their proximity to the shores of the contracting Tethys epicontinental sea.

The eastern Arabian deposits consist of three units. These are, from oldest to youngest, the continental Hadrukh Formation, which unconformably overlies Eocene rocks, the marine Dam Formation and the continental Hofuf Formation. The Hadrukh can always be distinguished from the Hofuf when the intervening marine Dam is present, but where continental equivalents of the Dam occur, such as at Ad Dabtiyah, they are difficult to separate from the underlying Hadrukh.

In the Mesopotamian region of the Middle East the ancient marine connection between the Mediterranean and the Indian Ocean—the Tethys—had been lost at the time of deposition of the Dam Formation. The break in the marine sequence, indicated in part by the continental Hadrukh and its equivalent chronostratigraphic units in the region, suggests the presence of a land connection between Saudi Arabia and southwestern Asia by *at the latest* mid-Burdigalian times, at about 18 Ma (Adams, Gentry & Whybrow 1983; Whybrow 1984). Keller & Barron (1983) report worldwide low sea level between 20 and 18 Ma, while Barry, Johnson, Raza & Jacobs (1985) believe an Africa to southern Asia land connection must have existed before 18 Ma and possibly even before 20 Ma as suggested by Whybrow *et al.* (1982).

The Ad Dabtiyah fauna, described here, represents part of a fauna of cosmopolitan distribution in Africa, Europe and Asia during a time equivalent to the mid-Orleanian of Europe, 17–19 Ma. The Asian mastodon *Gomphotherium cooperi*, previously known only from the basal Miocene deposits at Dera Bugti, Pakistan, is present. Of the two rhinoceros species found, both are early and primitive members of their genera; one is not unlike the European *Dicerorhinus sansaniensis*. Even so, the poor ruminant and suid fauna, together with the mastodon and rhinoceroses, does not on balance suggest any discrete palaeobiogeographical affinities for the Ad Dabtiyah fauna. Part of its African element is a new genus of hominoid which is interpreted as the sister group of the great ape and man clade and is more closely related to the African members of that clade than to their Eurasian representatives.

The palaeoenvironment at Ad Dabtiyah appears to have been a tropical ponded area of fresh water with centropomid and cyprinid fishes. Logs, probably of palm, are found encrusted with cyanophyte algal material of fresh-water origin, and large stromatolitic bioherms occur. The ruminants and rhinoceroses suggest a woodland habitat near to the Ad Dabtiyah depositional area.

From the marine Dam Formation near its type locality at Jabal Lidam, the first cetacean fossil to be reported from Saudi Arabia is described (p. 447).

Acknowledgements

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Appendix. Table of eastern Saudi Arabian Miocene vertebrates

Hofuf Formation—vertebrate fauna from Al Jadidah

From Sen & Thomas 1979; Thomas *et al.* 1978; Thomas 1983.

- **Rodentia**
  - Sciuridae: *Atlantoxerus* sp.
  - Ctenodactylidae: *Metasayimys intermedius* Sen & Thomas 1979
- **Carnivora**
  - Hyaenidae: *Percrocuta* sp.
- **Proboscidea**
  - Gomphotheriidae: *Gomphotherium angustidens*
- **Perissodactyla**
  - Rhinocerotidae: *Dicerorhinus* cf. *primaevus*
- **Artiodactyla**
  - Suidae: cf. *Lopholistriodon*
  - Giraffidae: *Palaeotragus* sp.
  - Bovidae:
    - *Pachytragus ligabuei* Thomas 1983
    - *Caprotragoides* aff. *potwaricus*
    - *Protragocerus* sp.
    - cf. *Homoiodorcas*?
- Indeterminate Pisces, Chelonia and Crocodilia.

Dam Formation (continental equivalents)—vertebrate fauna from Ad Dabtiyah

- **Hominoidea**
    - *Heliopithecus leakeyi* Andrews & Martin 1987 (herein)
- **Proboscidea**
  - Gomphotheriidae: *Gomphotherium cooperi*
- **Perissodactyla**
  - Rhinocerotidae:
    - *Dicerorhinus* sp. aff. *sansaniensis*
    - *Brachypotherium* sp.
- **Artiodactyla**
  - Suidae:
    - *Listriodon* cf. *lockharti* or *L.* cf. *akatikubas*
    - ? *Kenyasus* sp.
  - Tragulidae:
    - *Dorcatherium* sp.
    - *Dorcatherium*, larger sp.
  - Giraffoidea: *Canthumeryx* sp.
  - Bovidae:
    - *Eotragus* sp.
    - Bovid species 2.
    - Bovid species 3.
- **Chelonia**
- **Crocodilia:** cf. *Crocodylus pigotti*
- **Osteichthyes:** Cyprinidae
- **Acanthoptergii:** ? Centropomidae

Vertebrates from the As Sarar (Al Sarrar) locality

Provisional list from Thomas *et al.* 1982.

- **Insectivora:** Erinaceidae
- ? **Primates** gen. et sp. indet.
- **Lagomorpha:** Ochotonidae
- **Rodentia**
  - Cricetidae
  - Ctenodactylidae: *Metasayimys* cf. *intermedius*
  - Gerbillidae
  - Pedetidae:
    - *Megapedetes* cf. *pentadactylus*
    - cf. *Protalactaga*
  - Thryonomyidae: *Paraphiomys* sp.
- **Carnivora**
  - Viverridae: *Viverra* sp.
  - Mustelidae:
    - cf. *Martes*
    - *Mionictis* sp.
  - Felidae: *Pseudaelurus turnauensis*
  - Amphicyonidae: *Amphicyon* sp.
- **Proboscidea**
  - Deinotheriidae: cf. *Deinotherium*
  - Gomphotheriidae: *Gomphotherium* sp.
  - ? Amebelodontinae
- **Sirenia** indet.
- **Hyracoidea**
  - Saghatheriinae: *Pachyhyrax* aff. *championi*
- **Perissodactyla**
  - Rhinocerotidae:
    - *Aceratherium* sp.
    - *Dicerorhinus* sp.
- **Artiodactyla**
  - Suidae:
    - *Listriodon* sp.
    - gen. et sp. indet.; giant species.
  - Tragulidae: *Dorcatherium* cf. *libiensis*
  - Bovidae gen. et sp. indet.
- **Aves**
  - Threskiornithidae
  - Ciconiidae:
    - *Mycteria cinereus*
    - ? *Mycteria* sp.
  - Scolopacidae: Charadriinae indet.
  - spp. unidentified.
- **Crocodilia**
  - Crocodylidae: *Crocodylus* cf. *pigotti*

Chelonia
  Pelomedusidae:
    cf. *Schweboemys*
    aff. *Stereogenys*
  Trionychidae: aff. *Cycloderma*
  Carettochelyidae
  Testudinidae: *Geochelone* sp.
Serpentes
  Scolecophidia
  Boidea:
    Python sp.
    Eryx/Gongylophis spp.
  Colubridae
  Elapidae: *Naja/Palaeonaja* spp.
  Viperidae
Squamata
  Sauria: Lacertidae
  Amphisbaenia: Amphisbaenidae
Amphibia
  Bufonoidea
  Ranoidea
Pisces
  Mormyridae: *Hyperopisus* sp.
  Cyprinidae:
    Barbus sp.
    Labeo sp.
  Clariidae:
    Heterobranchus sp.
    Clarias sp.
  Centropomidae: *Lates* sp.
  Sphyraenidae: *Sphyraena* sp.
  Sparidae indet.
Selachii
  Hemigaleidae: *Hemipristis serra*
  Carcharhinidae:
    Carcharhinus aff. *priscus*
    Carcharhinus aff. *plumbeus*
    Galeocerdo cf. *aduncus*
    Scoliodon sp.
    Negaprion eurybathrodon
  Sphyraenidae: *Sphyraena* sp.
  Dasyatidae: *Dasyatis* sp.
  Myliobatidae:
    Myliobatis sp.
    Aetobatus arcuatus
  Rhinopteridae: *Rhinoptera*

Hadrukh Formation—vertebrates from Jabal Midra ash-Shamali

From Whybrow *et al.* 1982.

Rodentia
  Zapodidae: *Arabosminthus quadratus* Daams 1982
  Cricetidae: *Shamalina tuberculata* Daams 1982
Artiodactyla
  Bovidae: cf. *Oioceros* sp.

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Miocene stratigraphy, geology and flora (Algae) of eastern Saudi Arabia and the Ad Dabtiyah vertebrate locality

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Synopsis

Studies of the Miocene deposits in eastern Saudi Arabia are briefly reviewed. The stratigraphical succession is explained and the geological details of the vertebrate-bearing, non-marine deposits at Ad Dabtiyah presented. The stratigraphical position of the fossiliferous beds is believed to lie near the boundary of the continental sequence of the Hadrukh Formation and continental equivalents of the Dam Formation, the beds themselves locally close to, and the lateral equivalent of, the basal deposits of the Burdigalian marine carbonates of the Dam Formation. The fresh-water depositional environment at Ad Dabtiyah contains many bones of terrestrial vertebrates, found in close association with several large stromatolitic bioherms. These, and similar encrustations also of a fresh-water origin, are associated with *in situ* logs, probably of palm trees. Overall, both the stratigraphical position of the Ad Dabtiyah deposits and their contained fauna suggest an age of about 17–19 Ma; middle Orleanian (European land-mammal age equivalent); early Burdigalian (marine chronology).

Introduction

Until the 1930s, almost nothing was known of the geology of the central part of the Arabian Peninsula. Observations on its general geology had been carried out by Philby (1933) during his explorations of Saudi Arabia, and his fossil collections were presented to the British Museum (Natural History) by King Abdul Aziz ibn-Saud. Cox (1933) studied the Tertiary fossils Philby had found at a hill called Qarn Abu Wayil (Fig. 2) and identified the oyster *Ostrea latimarginata*, and natural casts of *Mytilus*, *Anomia*, *Cardium*, *Clementia*, *Anadara* and other molluscs previously known from the Lower Fars rocks of Iran. South of Qarn Abu Wayil at Jaub Anbak (Fig. 2), Philby had noted the marine beds were overlain by a considerable thickness of red sandstones which Cox suggested might also be of Miocene age, but equally might be equivalent to the Pliocene Bakhtiyari deposits of Iran (Cox, *in* Philby 1933: 386–387). Cox's work therefore provided the first evidence of the presence of Miocene rocks in Arabia.

Mapping and surface collecting by geologists of the Arabian American Oil Company, ARAMCO, started in the mid-1930s and revealed in detail the extent of Miocene deposits in eastern Saudi Arabia. Three formations were formally designated (Steineke *et al.* 1958), together with the lithological details at their type localities. Later, the first published evidence that vertebrate fossils occurred in the region was given by Powers *et al.* (1966: D97) who recorded 'vertebrate fragments' in their lists of the Miocene biota.

In 1974 a collection of Miocene crocodile, turtle, antelope, rhinoceros and proboscidean remains was presented to the British Museum (Natural History), representing the first known

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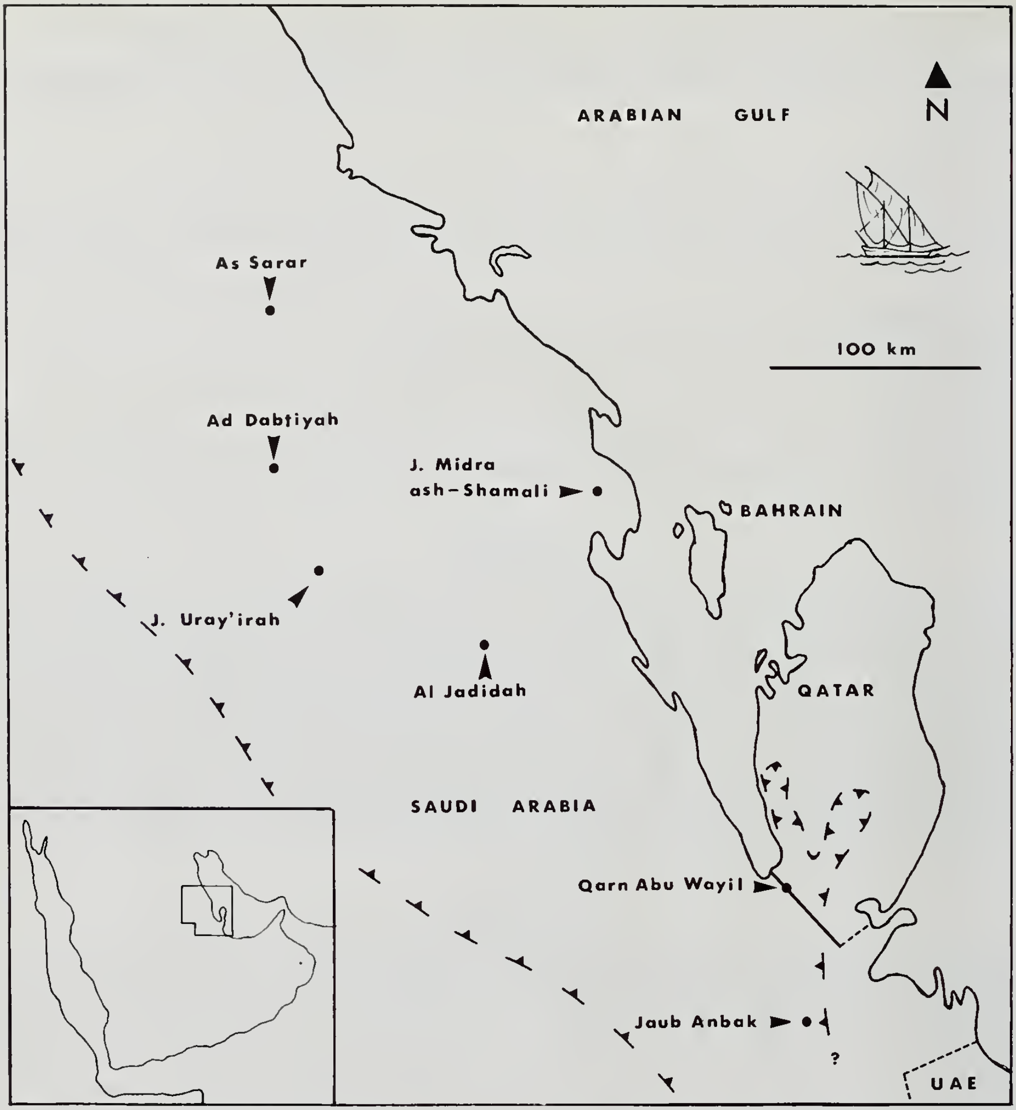

Fig. 2 Eastern Saudi Arabia, the State of Qatar and part of the United Arab Emirates showing localities referred to in the text. The most western extent of the Miocene deposits in Saudi Arabia and their location in south-western Qatar is indicated.

vertebrate palaeofauna from Arabia (BM(NH) 1975: 18). In the same year staff of the Palaeontology Department added more material by collecting from Miocene continental deposits at Ad Dabtiyah (Fig. 2). They also collected vertebrate-bearing rocks near a hill called Jabal Midra ash-Shamali, *c.* 6 km north-west of Dhahran (Fig. 2) where Tleel (1973) had discovered 'artiodactyl' remains. Chemical breakdown of these rocks yielded rodent, lagomorph and bovid teeth and preliminary reports on the faunas from both localities were published (Hamilton *et al.* 1978; Andrews *et al.* 1978). Further work on the Ash-Shamali material showed a new genus of fruits of aquatic plants, *Midravalva arabica* (Collinson 1982), to be present, together with new rodents, *Arabosminthus quadratus* and *Shamalina tuberculata* (Daams, *in* Whybrow *et al.* 1982: 111–116).

In 1978, H. Thomas of the Museum National d'Histoire Naturelle, Paris, and colleagues excavated vertebrate fossils, *Percrocuta, Gomphotherium angustidens, Dicerorhinus, Lopholistriodon, Pachytragus, Protragocerus, Caprotragoides* and a new rodent, *Metasayimys intermedius*, from red-coloured sandstones at Al Jadidah (Fig. 2); see Thomas *et al.* (1978), Sen & Thomas (1979), Thomas (1983). Later, they collected from the As Sarar region (Fig. 2) in collaboration with the Saudi Arabian Department of Antiquities. Abundant vertebrate remains were found including two gomphothere species, a deinothere, several carnivores and cricetid, ctenodactylid, dipodid, gerbellid, pedetid and phiomorph rodents (Thomas *et al.* 1982).

These discoveries of terrestrial vertebrates in eastern Arabia have now bridged the palaeogeographical gap between the better-known Miocene faunas of Africa and those of south-western Asia. In addition, interpretations of the eastern Arabian palaeoenvironments have been made (Whybrow & McClure 1981; Thomas *et al.* 1982; Whybrow *et al.* 1982) and, because of the proximity of the fossil localities to the contracting Tethys epicontinental seaway, there have been suggestions concerning the location of a Neogene land connection between Arabia and south-western Asia (Adams *et al.* 1983; Rogl & Steininger 1983; Whybrow 1984; Thomas 1985).

The collected papers in this issue of the *Bulletin*, with the exceptions of the descriptions of a delphinoid ear bone and a gomphothere tooth from other localities, are the results of studies on the Ad Dabtiyah fauna and flora collected and donated in 1974.

Stratigraphy and the age of the deposits

Towards the end of the middle Eocene, widespread emergence of the eastern Arabian shelf coincided with continued uplift and a slight north-easterly tilting of the Arabian plate, events that began in the late Cretaceous and continue today as a consequence of the movement of the Arabian plate against the more stable south-western Asian plate. Red Sea rifting was also a contemporaneous consequence of this plate activity (Schmidt *et al.* 1983; Sellwood & Netherwood 1984). Since that time mainly continental deposition, with the exception of a marine transgression from the Indian Ocean, has prevailed in eastern Arabia. Rocks of Oligocene age have not been recognized in the region; Miocene deposits unconformably overlie rocks of Ypresian or Lutetian age.

Where the rocks formed by the marine transgression (represented by the Dam Formation) occur, the continental Neogene has been divided into units. From the oldest, these are the Hadrukh Formation (*c.* 20–120 m thick), succeeded by the Dam Formation itself (*c.* 30–100 m thick), and the Hofuf Formation (*c.* 30–100 m thick).

Towards the western interior, where the marine marker beds of the Dam intercalate with the continental deposits, become thin and eventually disappear, the eastern divisions of Hadrukh, Dam and Hofuf no longer apply. The undifferentiated deposits are treated as a single un-named unit—Tertiary continental sandstone, marl and limestone, marked 'Tsm' in Figs 3 and 5 (Steineke *et al.* 1958). In such deposits a gomphothere $M^2 + M^3$ (M.42946) was found in the 1930s; see Gentry, p. 401 in this issue.

The age of the Hadrukh is important and is currently controversial (see Whybrow 1984) as it contains a new cricetid rodent, *Shamalina tuberculata*, whose descendant relatives appear to be present in the Miocene Lower Siwaliks of Pakistan (Daams, *in* Whybrow *et al.* 1982; E. H. Lindsay, personal communication 1985). The Hadrukh is undoubtedly coeval with the Ghar Formation of Kuwait and southern Iraq and, in the neighbouring part of Iran, 215 m (700 ft) of sandstone (subsurface section from a drill hole) is said to be the eastern wedge-end of the Ghar Formation and called the Ahwaz Sandstone (James & Wynd 1965: 2229). Adams *et al.* (1983: 278) indicated that at least part of the Ahwaz Sandstone is of Late Oligocene (Chattian) age, but Murris (1980: 614) suggested an Early Miocene, Aquitanian, age for these deposits, which he called the Ahwaz delta formed from eroded Saudi Arabian pre-Neogene rocks. Thin beds near to the top of the Hadrukh contain poorly-preserved marine molluscs and the oyster *O. latimarginata* which indicates a Burdigalian (marine chronostratigraphy) age. These beds crop out in a small area near the modern coastline; their lithology has not been described and

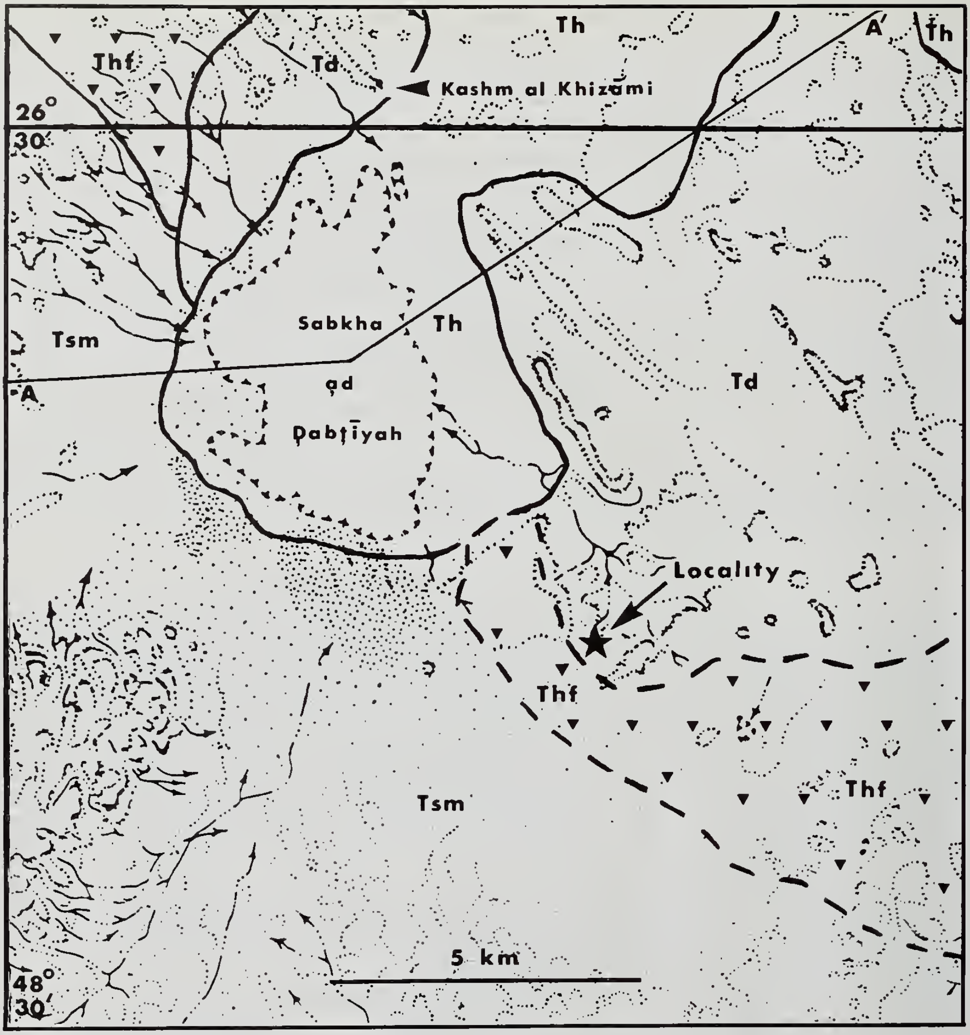

Fig. 3 Geology and topography around Sabkha Ad Dabtiyah and the position of the vertebrate-bearing locality. Tertiary units are: Th = Hadrukh Formation, Td = Dam Formation, Thf = Hofuf Formation, Tsm = undifferentiated continental equivalents of the Dam and Hofuf Formations. Broken line indicates that the contact is uncertain. A–A′ refers to the schematic cross-section in Fig. 5. Adapted from Steineke *et al.* (1958).

they are the only evidence of marine Hadrukh in Saudi Arabia (Powers *et al.* 1966: D93). They may be in part coeval with the basal Miocene of Qatar; see below.

The continental Hadrukh must be older than the overlying marine carbonates of the Dam Formation, and its thickness in Kuwait of 244 m, together with regional stratigraphy, suggests that a 21–18 Ma age for its deposits in eastern Arabia is a plausible estimate.

Adams *et al.* (1983: 278) pointed out that there should be a distinct ‘discontinuity between the Hadrukh and the overlying Dam Formation’. The top of the Hadrukh as defined by Steineke *et al.* (1958: 1313) is ‘at the base of the *Echinocyamus*-bearing limestone and marl of the basal Dam’. This echinoid *Echinocyamus* was described by Kier (1972) as *Fibularia damensis*. The limestone in which it occurs is known as the ‘Button bed’; it is an echinoid coquina, which has been used as a Miocene marker horizon throughout eastern Saudi Arabia and Qatar. It also marks the change from mainly clastic continental deposition to a shallow-water marine carbonate environment. A local discontinuity has been observed in the basal Miocene sequence of Qatar. Here marine carbonates and the Button bed overlie thinly bedded ferruginous claystones showing desiccation and rainspot structures and an intraformational conglomerate in erosional contact with underlying medium-bedded sandstones (Whybrow & Bassiouni 1986).

The marine biota of the Dam Formation is of an Indo-West Pacific origin and dated as Burdigalian, about 16–19 Ma, a time when there was no marine connection with the Mediterranean (Kier 1972; Adams *et al.* 1983).

Basal continental extraformational conglomerates and sandstones of the Hofuf Formation unconformably overlie the Dam Formation marine carbonates. The contact is well represented in Qatar where the Dam terminates in a regressive evaporitic phase. The vertebrate-bearing Hofuf locality of Al Jadidah lies stratigraphically about 30 m above the contact of Hofuf conglomerates with the underlying Dam Formation. Some 70 m of red-coloured sandstones overlie the vertebrate horizon (Thomas 1978; Fig. 2). From his study of the bovids found at Al Jadidah, Thomas (1983) concluded that their age is close to that of the Fort Ternan, Kenya, vertebrate locality dated at 14 Ma (Shipman *et al.* 1981).

The Ad Dabtiyah locality

Sabkha ad-Dabtiyah, a large salt flat (*sabkha*), from which the vertebrate-bearing site takes its name, is the dominant topographic feature of the area. It occupies the central part of a local drainage depression, itself probably a reflection of an underlying minor post-Miocene structure, and is surrounded by low hills and long mesa-topped escarpments of Neogene rocks. The whole region, generally bare of both vegetation and Recent sediments, is heavily dissected by small wadis (Fig. 3).

The vertebrate-bearing sediments (26° 27′ 02″ N, 48° 35′ 24″ E) were first discovered during geological mapping surveys in the late 1930s (Fig. 4). The locality is about 4 km from the

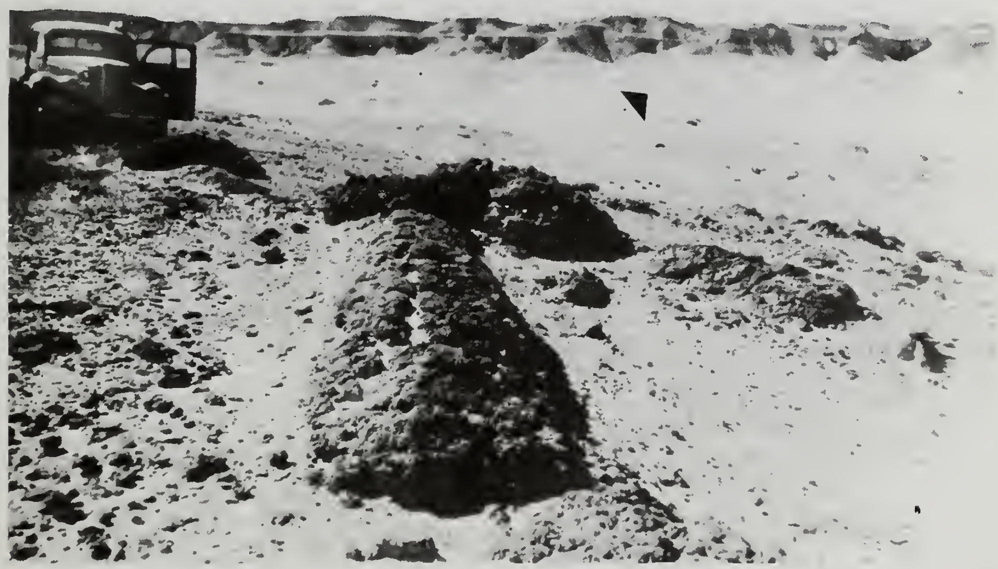

Fig. 4 Photograph of part of the Ad Dabtiyah locality taken by geologists of the Arabian American Oil Company in the early 1930s; note the Ford field vehicle. In the foreground are *in situ* 'logs' encrusted with stromatolite. View is south-west; compare drainage channel (arrow) with Fig. 6.

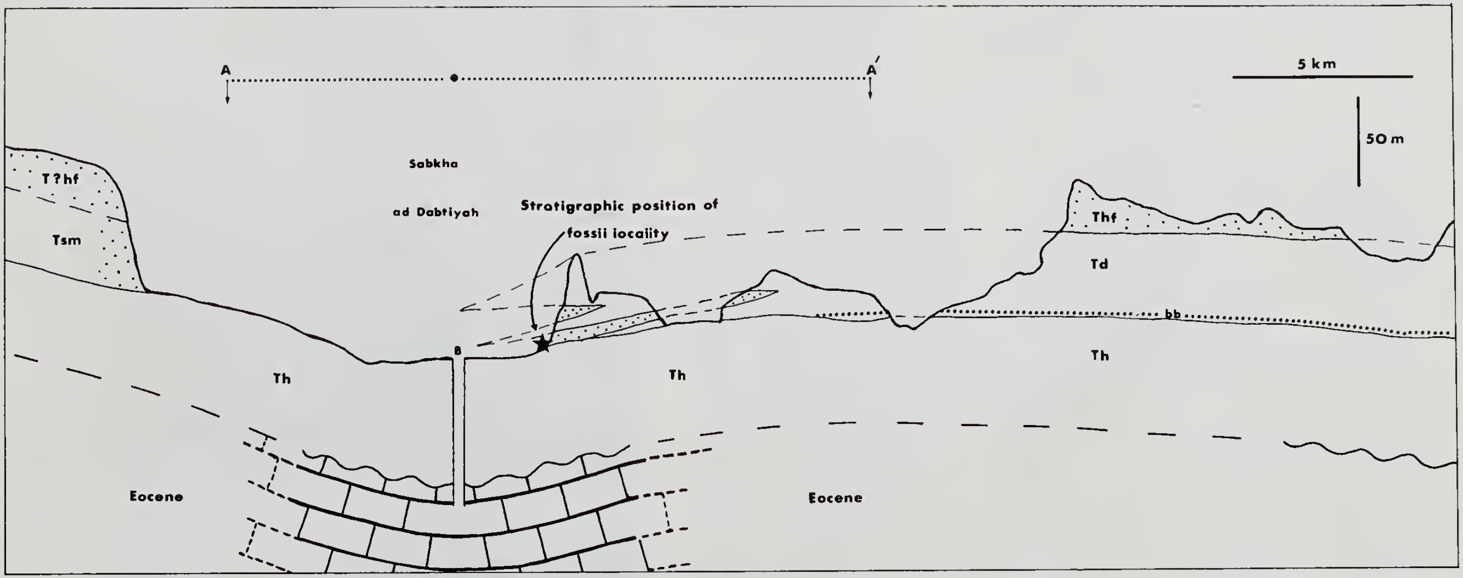

Fig. 5 Schematic cross section around the Ad Dabtiyah locality. The unconformity between Neogene and Eocene rocks is indicated; B = a bored water well that provided subsurface information, bb = 'Button bed'. See Fig. 3 for other abbreviations.

south-eastern edge of the sabkha, in hummocky terrain. The low-lying area with centripetal drainage into Sabkha ad-Dabtiyah is floored by continental sediments mapped as Hadrukh Formation. Along a north-westerly line and to the east, low hills mapped as Dam Formation flank the sabkha, while stratigraphically higher and to the north-west and south-east gravels and sandstones of the Hofuf Formation occur. To the south-west, beyond the limits of marine Dam outcrops, the Neogene formations cannot be divided, see p. 373.

Fig. 6 Similar view to Fig. 4 (photo taken 1979) showing the *in situ* 'logs'. The drainage channel, shown in Fig. 4, indicates little erosion in over 40 years. Tape = 1 metre.

Fig. 7 Large stromatolitic bioherms found to the north-east of the vertebrate locality. S measured 223 cm in width.

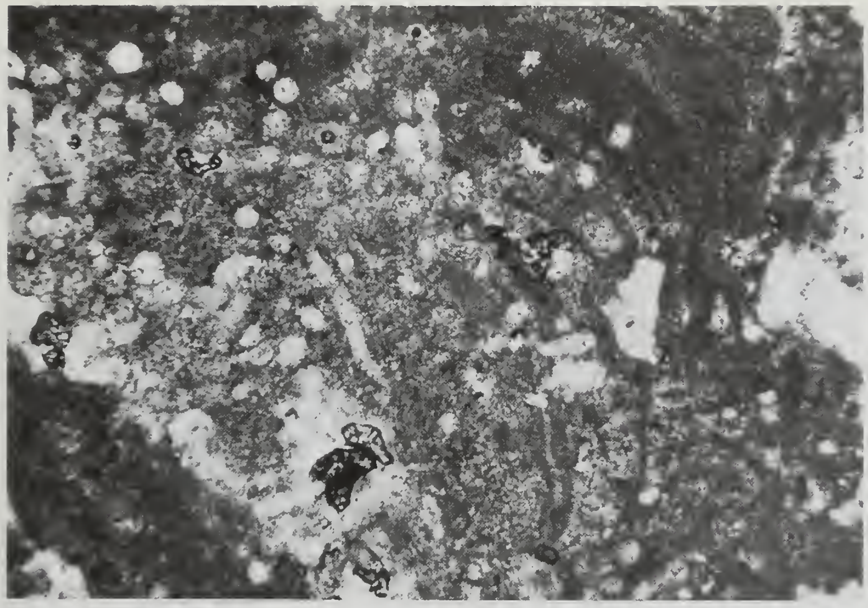

Fig. 8 Photomicrograph of a thin section of calcareous crust (V.60434c) found covering the skull of a rhinoceros. Banded algal growth of radial cyanophyte filaments are at top right. × 45.

The vertebrate site lies at or near the contact of the Hadrukh Formation with other continental sediments coeval with and laterally equivalent to the basal parts of the marine Dam sequence. The basal Dam marker horizon—the 'Button bed' with *Fibularia damensis*—is absent at the locality, but is found about 10 km to its east. The south-western limit of the Dam sea in

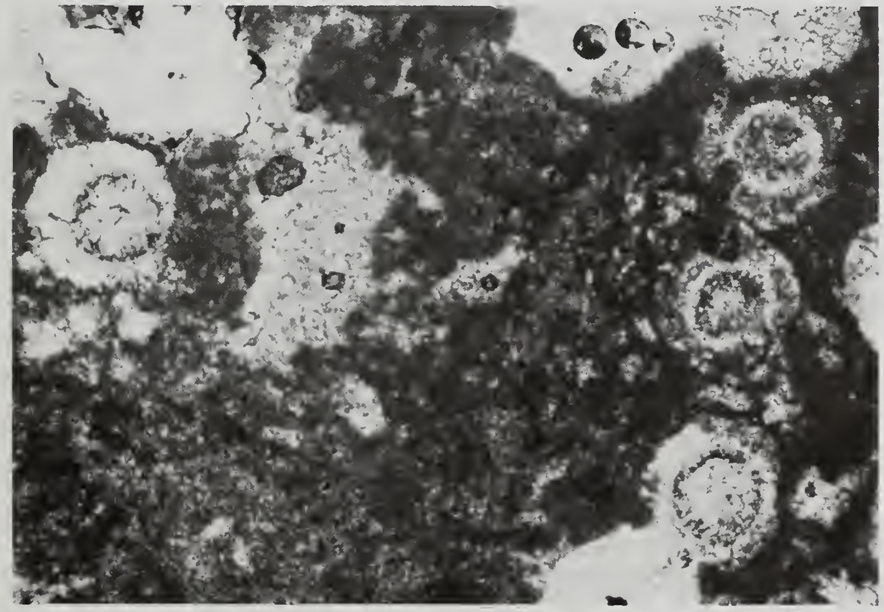

Fig. 9 Algal crust showing conspicuous charophyte oogonia, left and right. Same sample as Fig. 8. × 45.

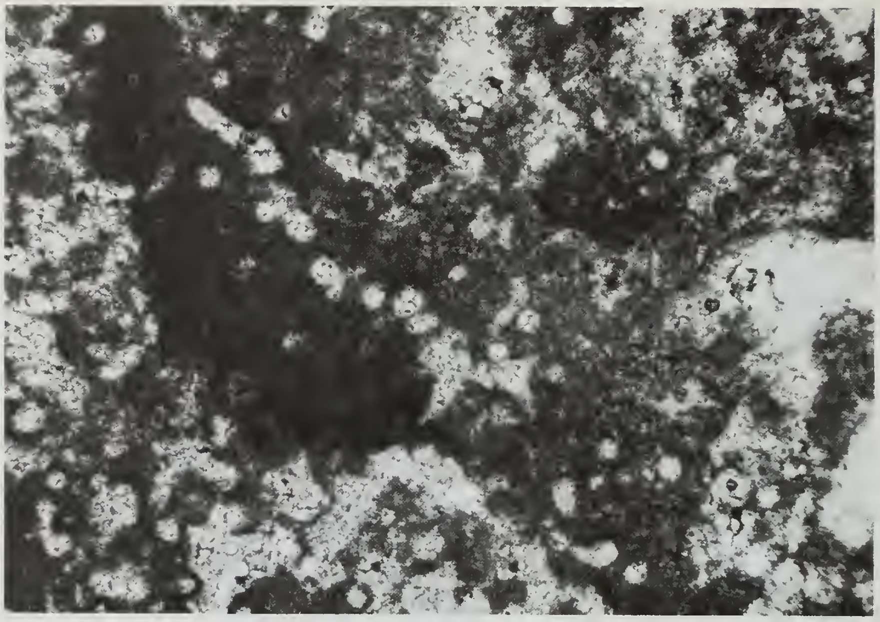

Fig. 10 Algal crust with probable traces of chironomid larval tubes, centre. Same sample as Fig. 8. × 45.

the area appears to have been near Kashm Khizami (Fig. 3), where marine fossils are associated with beach boulder conglomerates. A schematic cross section of the area indicating the relationship of the stratigraphy to the vertebrate site is shown in Fig. 5.

The main excavation was carried out in hard, unbedded White N9 (United States Geological Survey Rock-Color Chart 1980) sandstones. These were well sorted with fine-grained (about 280 μm), angular to subrounded, micrite supported quartz clasts. Occasionally, rounded micritic pebbles were present. Voids in the sandstones were sometimes filled with sparry calcite or, rarely, a form of manganese oxide known as wad. The excavation (about 22 m × 17 m, 50–80 cm in depth) produced scores of isolated bones, mainly lower jaws, teeth, limb bones, pectoral and pelvic elements, mostly of rhinoceros. None was preferentially orientated. Vertebrae and ribs were rare and, although none of the bones showed sign of depositional transport, rhinoceros mandibles had been broken and their anterior parts were missing. Except for the dryopithecine maxilla (see Andrews & Martin, this issue, p. 383), no other cranial bones were excavated.

About 5 m stratigraphically higher than the main excavation, and 110 m to its west, the sediments exposed on a ridge trending north-east showed a change in lithology. They consisted of an unsupported conglomerate formed of pebbles and cobbles of micritic limestone. In these sediments a proboscidean scapula and incomplete but uncrushed fish skulls were found (see Greenwood, this issue, p. 451). On top of this ridge were five *in situ* fallen logs encrusted with stromatolite (Fig. 6). Three measured 3·0 m, 5·3 m and 7·2 m in length and all, including the encrustation, were about 1·5 m in diameter. At one end of each of these logs stromatolitic crusts, 2 m in diameter, suggested the position of the bole of the fallen tree. The microstructure of a large amount of silicified wood found in this area resembled palm wood. At the same level and 11 m east of the logs, a bioherm had been fractured to reveal a fragmented rhinoceros skull encrusted with a 3-cm layer of algal material. Surface collecting in the area of the conglomerate produced proboscidean, giraffoid and tragulid remains. The conglomerate facies continued to the east and on the northern flank of a parallel ridge, many large stromatolitic bioherms were present (Fig. 7).

The bioherms and the crusts are largely of cyanophyte (myxophyte) algal origin. In thin section the rock shows marked banding with differential growth, and in places a ragged radial structure survives from the original microscopic thread-algae (Fig. 8). The rock shows intrinsic evidence of freshwater origin with embedded charophyte oogonia and debris, and what are probably chironomid larval tubes. All are poorly preserved and filled with sparry calcite (Figs 9, 10).

The depositional environment

Immediately prior to or at about the time of the deposition of basal transgressive marine sediments of the Dam Formation coming from the east, the environment at Ad Dabtiyah appears to have been a fluvial regime, transporting sandy carbonate muds, with laterally discontinuous conglomerates suggestive of channel sediments. Remains of terrestrial mammals, freshwater fish, turtle and crocodile (cf. *Crocodylus pigotti*, see Buffetaut, 1984) occur in these sediments. Subsequently, clastic deposition ceased and ponded fresh water was present; this was perhaps as a lake high in dissolved carbonates and deep enough to allow continuous growth of large stromatolitic bioherms and thick stromatolite crusts on hard substrates.

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The phyletic position of the Ad Dabtiyah hominoid

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Synopsis

The hominoid maxilla and four isolated teeth from Ad Dabtiyah, Saudi Arabia, are assigned here to a new genus and species *Heliopithecus leakeyi*. It shares numerous primitive characters with *Proconsul* (for example, molar cingula and premolar cusp heteromorphy), and a few advanced characters with *Kenyapithecus* (for example premolar enlargement and molar enamel thickening). The latter characters are also characteristic of the great ape and human clade, and for this reason it is grouped with that clade, but it is a more primitive member than *Kenyapithecus* because it retains more primitive characters. Molar enamel is intermediate in thickness and all pattern 3, the first hominoid so far described to have this combination, and this places it intermediate between gibbons and *Proconsul* which have thin pattern 3 enamel, and *Kenyapithecus* and the ancestral great ape and human morphotype which have thick pattern 3 enamel.

Introduction

We describe here a new genus and species of hominoid primate from continental equivalents of the basal deposits of the marine Dam Formation near Ad Dabtiyah, Saudi Arabia: see Whybrow *et al.* (this issue, p. 371). The hominoid specimens from these early middle Miocene deposits were first described by Andrews *et al.* (1978), and the associated fauna and geology were described by Hamilton *et al.* (1978). The hominoids were not named, but were considered to be intermediate in morphology between the early Miocene species of *Proconsul* from east Africa and later Miocene species of *Ramapithecus* and *Sivapithecus* from Eurasia. Comparison was made with the type specimen of what was originally called *Sivapithecus africanus* (Le Gros Clark & Leakey 1950) and subsequently *Kenyapithecus africanus* (Leakey 1967), but the taxonomic position and provenance of this species was too uncertain itself for this comparison to be particularly helpful.

Much progress has been made recently which has improved our ability to determine the phylogenetic status of the hominoid from Ad Dabtiyah. Both the hominoid clade and its constituent clades have now been better defined (Harrison 1982, Andrews 1985, Martin 1986). In particular, work on the structure and thickness of molar enamel has clarified its significance in hominoid evolution (Martin 1983, 1985), and comparisons with Spanish and Hungarian material, all assigned to *Dryopithecus* (Martin & Andrews 1982), have expanded our knowledge of this middle Miocene genus. Some new material is also available for *Kenyapithecus* (Pickford 1982, Ishida *et al.* 1984). The Ad Dabtiyah material is considered to resemble both *Dryopithecus* and *Kenyapithecus* in derived characters and to be linked with them in the great ape and human clade. *Proconsul*, by contrast, cannot be shown to share any derived characters with this clade although it does appear to have some hominoid synapomorphies (Andrews 1985, Fleagle 1986). It is now clear that the Ad Dabtiyah hominoid shares only primitive characters with *Proconsul* and is not therefore uniquely related to it; it would also appear that the characters it shares with *Kenyapithecus* and *Dryopithecus* are synapomorphies of the great ape and human clade and are also not indicative of special relationship. On the contrary, both *Kenyapithecus* and *Dryopithecus* share derived characters with the great apes and humans not present in the

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Ad Dabtiyah specimens. For these reasons, we have decided to name a new genus and species for this material while recognizing its taxonomic relationship with *Kenyapithecus* and the great apes and man.

Systematics

Superfamily **HOMINIODEA** Simpson 1931

Genus ***HELIOPITHECUS*** gen. nov.

DIAGNOSIS. A genus of hominoid with the enlarged premolars characteristic of the great ape and human clade; the P^3 is elongated with a massive buccal cusp and with great buccal flare, and the P^4 is also elongated but without the buccal flare; the premolars are large relative to M^1, both in length and breadth, and are comparable to *Kenyapithecus* in this respect; they differ from this genus in the greater cusp heteromorphy of the premolars and the greater cingulum development on the upper molars; the tooth enamel is all pattern 3 and is intermediate in thickness, that is thicker than in *Proconsul* but thinner than in *Kenyapithecus*; the teeth wear with the dentine separation pattern.

NAME. Greek, *Helios*, the sun, and *pithekos*, an ape.

TYPE SPECIES. *Heliopithecus leakeyi* sp. nov.

Heliopithecus leakeyi sp. nov.

HOLOTYPE. M.35145, a slightly crushed maxilla from the left side with the crowns of P^3 to M^2 and the lingual alveolar margins of I^2 and C. The specimen is housed in the Department of Palaeontology, British Museum (Natural History).

TYPE LOCALITY. Ad Dabtiyah, Saudi Arabia: 4 km south-east of the salt flat named Ad Dabtiyah, 26° 27′ 02″ N, 48° 35′ 24″ E.

PARATYPE. M.35146, isolated upper third molar.

REFERRED MATERIAL. Three isolated teeth, M.35147–9.

DIAGNOSIS. As for genus.

NAME. In honour of Louis Leakey, who did so much to add to our knowledge of hominoid evolution.

DESCRIPTION. The descriptions of this fossil hominoid can be added to in three ways from the previous descriptions (Andrews *et al.* 1978): variability within the sample; the significance of premolar enlargement; and changes in enamel thickness. Measurements, see Table 1.

Table 1 Measurements of the teeth of *Heliopithecus leakeyi*. md = mesiodistal length, bl = buccolingual breadth; all measurements in millimetres.

Specimen	md	bl	bl/md	Crown module	Crown height	
					buccal	lingual
P^3 M.35145	7·7	11·6	150·1	9·7	8·4	4·0
P^4 M.35145	7·0	11·4	162·8	9·2	5·8	5·4
M.35149	5·3	9·7	183·0	7·5	5·7	4·2
M^1 M.35145	8·8	10·5	119·3	9·7	—	—
M^2 M.35145	9·5	11·9	125·3	10·7	—	—
M^3 M.35146	10·4	12·9	124·0	11·7	—	—
dP^4 M.35147	6·9	8·3	120·3	7·6	—	—
dC M.35148	5·9	4·9	83·1	—	5·0	—

Fig. 11 Occlusal view of the type specimen of *Heliopithecus leakeyi* (M.35145). Below right are three of the isolated teeth, from left to right, M.35147, right dP^4; M.35148, right dC; and M.35149, right P^4.

Sample variability

It was originally suggested (Andrews *et al.* 1978) that the isolated P^4 (M.35149) might belong to a separate species from the maxilla M.35145. This is no longer considered likely on the basis of metrical dimensions in comparison with other closely related taxa. For instance, in the genus *Kenyapithecus* we would now combine *K. wickeri* from Fort Ternan and *K. africanus* from Maboko (Andrews & Walker 1976, Pickford 1982) into a single species (Greenfield 1979), and recognize this species as being distinct from the Asian genera *Sivapithecus* and *Ramapithecus* which themselves have now been grouped together (Greenfield 1980, Andrews & Cronin 1982). The metrical and morphological differences in the premolars of the *wickeri* and *africanus* specimens are very similar to those seen in the two specimens from Ad Dabtiyah: for instance the buccolingual variation of the P^4 is 10·5 to 12·0 mm in the African specimens and 9·7 to 11·4 mm in the Ad Dabtiyah specimens (Fig. 12). Similarly, the ranges in P^4 buccolingual dimensions for *Proconsul africanus* (from Rusinga only) is 8·5 to 9·9 mm and for *Proconsul nyanzae* is 9·6 to 11·7 mm (Andrews 1978), both similar to the range seen in the Ad Dabtiyah specimens; greater if the Rusinga *africanus* is combined in a single species with the Rusinga *nyanzae*. In comparison with these there is no good reason for not including all the Ad Dabtiyah specimens in the one species *Heliopithecus leakeyi.*

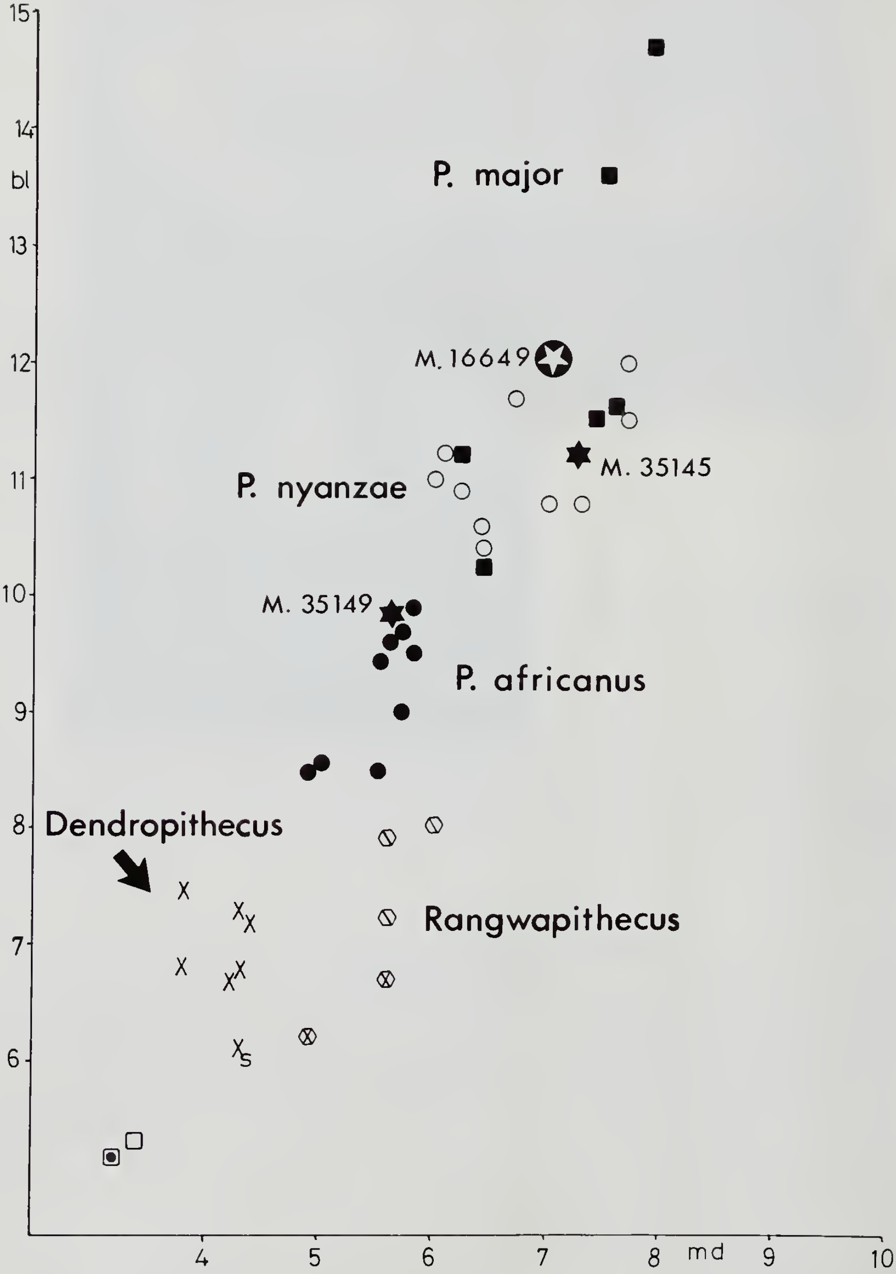

Fig. 12 Size variation of the upper fourth premolar. The two specimens from Ad Dabtiyah (M.35145 & M.35149) are identified by closed stars and the type specimen of *Kenyapithecus africanus* (M.16649) by an open star. The sample ranges of three species of *Proconsul* and two species of *Rangwapithecus* are shown for comparison.

Premolar enlargement

The main characteristic of *Heliopithecus leakeyi* is the great enlargement of the premolars. The P^3 is larger than the P^4 and both are nearly as large as the first molar in cross-sectional area (Andrews *et al.* 1978). Fig. 13 shows this to be an important feature: the extant great apes have a relatively larger P^3 than do most Miocene hominoids, and *Heliopithecus* and *Kenyapithecus* are both within the great ape range and outside the range of other Miocene hominoids. For the P^4, on the other hand, they differ from both living and fossil apes. They both have unusually large P^4s, and in this they resemble the palate from Moroto, Uganda, which has previously been incorrectly referred to *Proconsul major* (Pilbeam 1969, Andrews 1978), but which would seem on this evidence to belong either to *Kenyapithecus* or *Heliopithecus.* There is evidence here, therefore, both for the relationship of these two genera based on premolar morphology, and for their relationship with the extant great apes; and it may be that the Moroto palate also belongs with this group. (See Note added in proof, p. 391.)

The premolars and molars of *Heliopithecus* generally have low rounded cusps, the exception being the buccal cusp of P^3, which is more than twice the height of the lingual cusp. In this latter feature it differs from *Kenyapithecus* and *Dryopithecus* but resembles the Moroto palate, and it would seem likely to be a primitive retention which has been lost in *Kenyapithecus* and

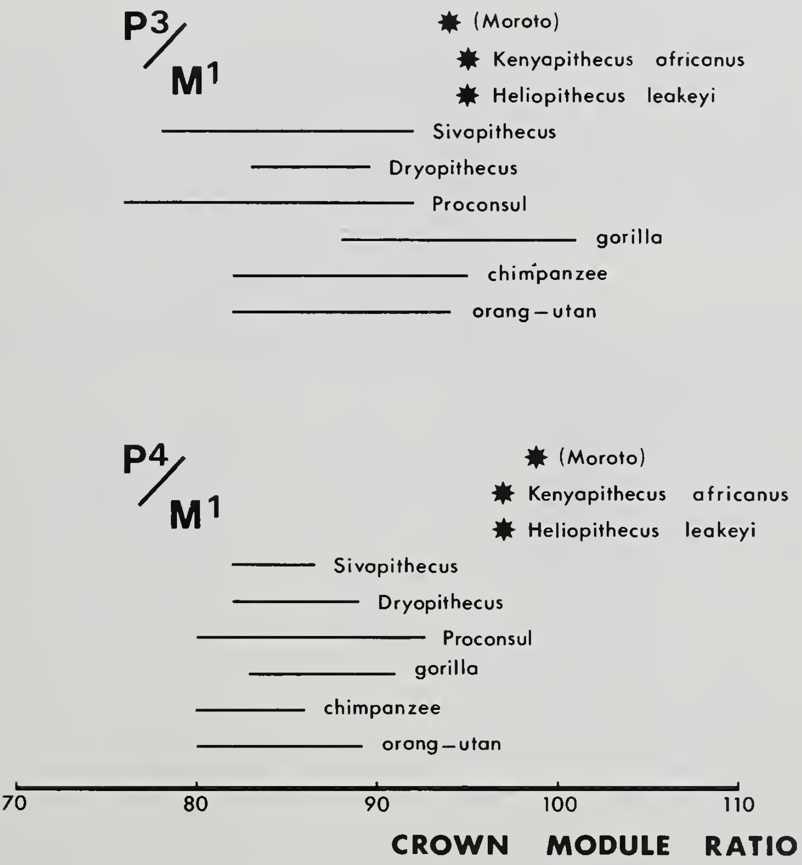

Fig. 13 Size ranges of the third and fourth premolars. The horizontal axis shows the premolar/molar size ratios calculated for the crown modules (length + breadth/2). The total ranges for a number of living and fossil taxa are shown (*Proconsul* = 3 species; *Sivapithecus* = 2 species) for comparison with *Heliopithecus leakeyi.*

Dryopithecus. Other characters of the molars show this same combination, particularly the presence of upper molar and premolar cingula, which have been lost in later Miocene fossil hominoids and in the extant great apes. The type specimen of *Kenyapithecus africanus* has only a slight lingual and mesial cingulum on its P^4 and M^1, but material described more recently by Pickford (1982) from Majiwa includes some upper teeth with at least as great a cingulum development as on the Ad Dabtiyah specimens.

Our reason for interpreting premolar cusp heteromorphy and presence of cingula as primitive in this instance is the widespread occurrence of these characters in earlier Miocene and Oligocene hominoids and catarrhines. Neither character is present throughout the living catarrhines, and on this basis their absence would appear more likely to be primitive for this group. In this case, however, we feel that the fossil evidence can add to the evidence of living forms and suggest the alternative interpretation. Cusp heteromorphy and cingula are ubiquitous among early catarrhines like *Propliopithecus* (including *Aegyptopithecus*), *Dendropithecus*, *Micropithecus* and *Limnopithecus*; they are also present on early Miocene hominoids like *Proconsul* and *Rangwapithecus*, and they are now seen to be present in *Heliopithecus* and *Kenyapithecus* of the early middle Miocene. It is not until later in the middle Miocene that hominoids lacking these characters first appear, such as *Dryopithecus* and *Sivapithecus*, and we consider these hominoids to be derived in this respect.

These morphological changes can be put into phylogenetic perspective as follows: the primitive hominoid condition is considered to include premolars that were small relative to molar size, were mesiodistally compressed and had heteromorphic cusps; upper molars and the fourth premolar had low rounded cusps and well-developed lingual and mesial cingula. *Kenyapithecus* and *Dryopithecus* differ from this condition in the enlargement of the premolars, loss of premolar cusp heteromorphy, and the partial reduction of the cingulum, which is not developed on most specimens. *Heliopithecus* is intermediate in these characters, retaining a greater degree of cusp heteromorphy and cingulum development than seen in *Kenyapithecus* and *Dryopithecus* but linked with them through premolar enlargement.

Enamel structure and thickness

It has been possible to examine the enamel of one of the specimens from Ad Dabtiyah. The isolated M^3 (M.35146) is naturally fractured, and the fractured surface has been exploited to study enamel thickness and enamel microstructure. The naturally fractured face passing through the paracone revealed a nearly ideal plane of section which minimized obliquity (Martin 1983, 1985). The slightly ragged fracture was flattened by diamond polishing to facilitate enamel thickness measurements and to produce a relief-free surface for back scattered (high energy) electron imaging. The plane in which enamel thickness was measured is shown in Fig. 14. Although this does not correspond exactly with the buccolingual plane of section through the mesial cusps recommended by Martin (1983), it is clear that it approximates to a section passing through the maximum diameter of the dentine horns and should produce results little affected by obliquity of section and therefore comparable with those from sectioned teeth.

The enamel thickness was measured for a number of linear dimensions which have been used previously (Martin 1983). Linear enamel thickness over the tip of the paracone of the M^3 is 1·0 mm, and lateral enamel thickness on the buccal cusp is 0·92 mm (average 0·96 mm). The breadth of the tooth across the cervix is 8·1 mm, approximately the size of a chimpanzee M^3, and comparable mean dimensions for chimpanzee enamel thickness are 0·5 mm at the tip of the paracone and 0·7 mm laterally. The enamel of *Heliopithecus leakeyi* is thus considerably thicker in absolute terms than that of the chimpanzee.

An attempt was made to scale enamel thickness by comparing enamel and dentine areas (Martin 1983, 1985). The area of enamel visible in section (as shown in Fig. 14) was measured, and this was then divided by the length of the enamel dentine junction in the same section; this approximates to the dimension c/e of Martin (1983, 1985) for the whole tooth. This dimension, which is called the Average Enamel Thickness, was then scaled for body size using the area of

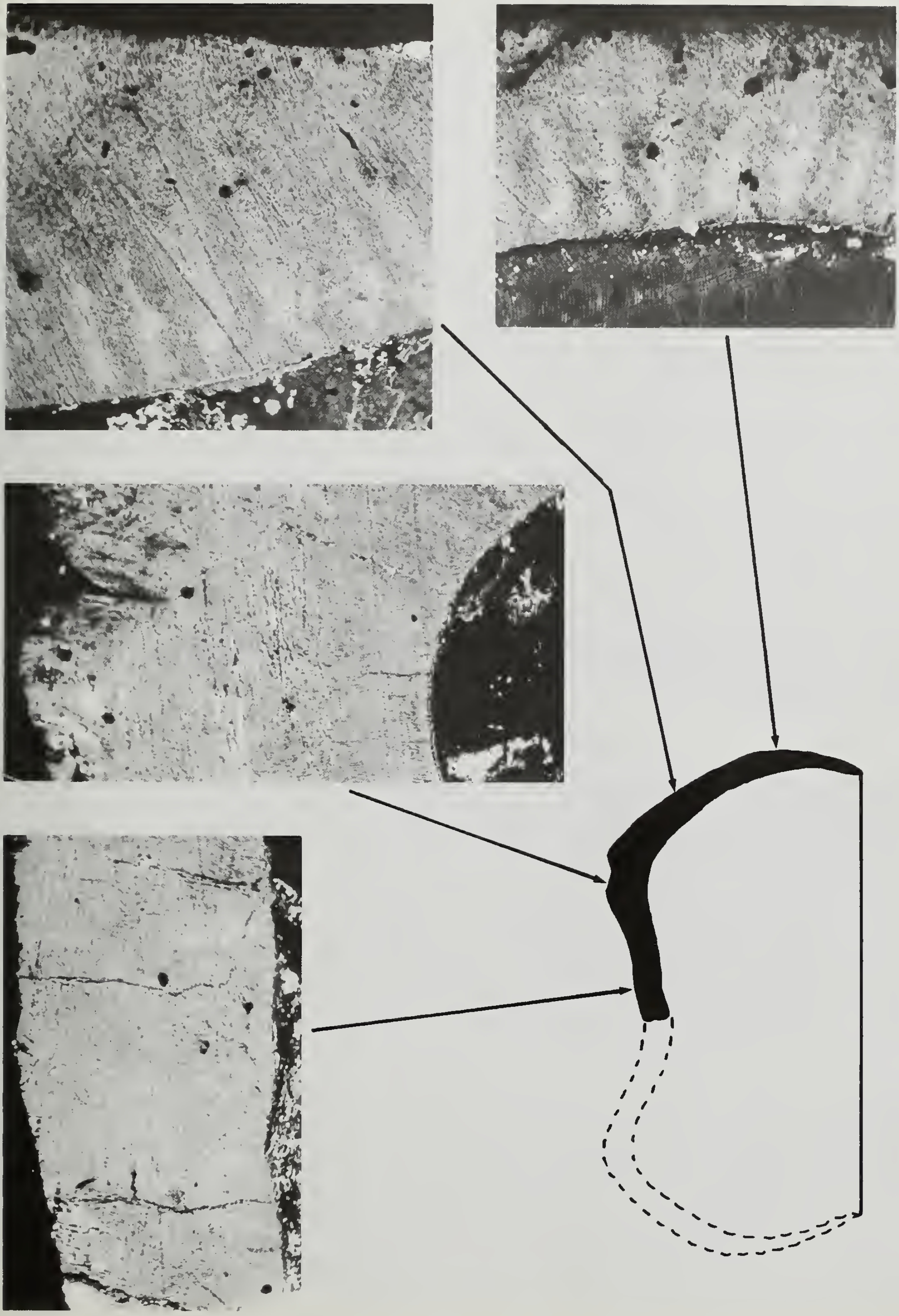

Fig. 14 Sections across the mesial face of the crown of the isolated M^3 (M.35146). The buccal half of the crown was broken when discovered and has been polished and etched to expose the prism structure and the enamel–dentine junction.

dentine in the same section (Martin 1983) as the estimator of body size. This gives the scaled dimension called the Relative Enamel Thickness, which in the case of the Ad Dabtiyah M^3 has a value of 17·35. This compares with values of 8·90–11·30 for thin enamel (for instance in the chimpanzee and gorilla); 11·31–14·64 for intermediate/thin enamel; 14·65–17·49 for intermediate/thick enamel (as seen in the orang-utan); and 17·50–26·20 for thick enamel, which is seen in *Homo* and *Sivapithecus*. The enamel of *Heliopithecus* falls at the top end of the range of the intermediate/thick category, and although obliquity of section may have slightly increased the apparent enamel thickness, it is quite clear that *Heliopithecus leakeyi* has significantly thicker enamel than in chimpanzees, gorillas or gibbons, once size has been taken into account. Although the errors inherent in this estimation are recognized, we are confident that they have been reduced to a minimum and that *H. leakeyi* has enamel which is of intermediate thickness (as defined by Martin, 1985).

This result is significant in the light of the ancestral conditions for hominoid enamel determined by Martin (1985). The ancestral hominoid is thought to have had thin enamel, with thickened enamel as a derived character of the great ape and human clade. The presence of thickened enamel in *Heliopithecus* therefore represents a shared derived character with the great ape and human clade. Of the living members of this clade, only the orang-utan has enamel of intermediate thickness, and this might appear to be a point of resemblance to *H. leakeyi* in simple thickness terms. However, the enamel in the orang-utan is intermediate in thickness as a result of secondary reduction from thick enamel, while the enamel microstructure of *H. leakeyi* shows no such reduction, with the enamel being formed at a fast, pattern 3, rate throughout the enamel thickness. In *Pongo* the outer 20% of the enamel is formed at a reduced rate, as measured from prism cross-striation repeat intervals, but this is not the case in *H. leakeyi*. The enamel in *H. leakeyi* is of intermediate thickness in relation to the time available to develop enamel, and is not due to secondary reduction. As such it could represent an early stage in the evolution of thick enamel in the common ancestor of the great ape and human clade. It is interesting to note that this is the first evidence for intermediate-thickness enamel, all of which is fast-formed pattern 3 enamel, that has been seen in any hominoid species, these conditions having previously been predicted solely on the basis of end conditions of change (Martin 1983, 1985).

Phylogenetic interpretation

The new pieces of evidence presented here, from examination of the enamel and the reinterpretation of premolar and molar morphology, are consistent in their placement of *Heliopithecus leakeyi* in hominoid phylogeny. Premolar enlargement with retention of what are interpreted as ancestral characters, such as retention of molar cingula and premolar cusp heteromorphy, place *Heliopithecus* as an intermediate between the hominoid ancestral pattern and the great ape and human ancestral pattern which is shared also by *Kenyapithecus* and *Dryopithecus*. In other words, it is more closely related to the great apes and man than are the gibbons but less closely than are *Dryopithecus* and *Kenyapithecus*. The evidence from the enamel shows the same thing: the ancestral hominoid pattern is thin pattern 3 enamel such as is present in gibbons, while the ancestral great ape and man pattern is thick pattern 3 enamel which is retained unchanged in modern and fossil man; the intermediate thickness of enamel (all pattern 3) in *Heliopithecus* shows that it lacks the full development of this character, and our interpretation is that it is the sister group to the great ape and man clade, with some of its characters developed but not others.

These relationships are shown in Fig. 15. This shows *Proconsul* as the sister group to all other hominoids, living and fossil, and branching off before the divergence of the gibbons. After the gibbon divergence, first *Heliopithecus* and then *Kenyapithecus* diverged, so that both are successively sister groups to the living great apes and humans. The position of *Dryopithecus* with respect to *Kenyapithecus* is not certain. The basal split of the great ape and human clade is shown as that separating the orang-utan from the African apes and man (Andrews & Cronin 1982, Ward & Pilbeam 1983, Martin 1983), with the orang-utan joined with *Sivapithecus*. The remaining divergence is that between the African apes and man.

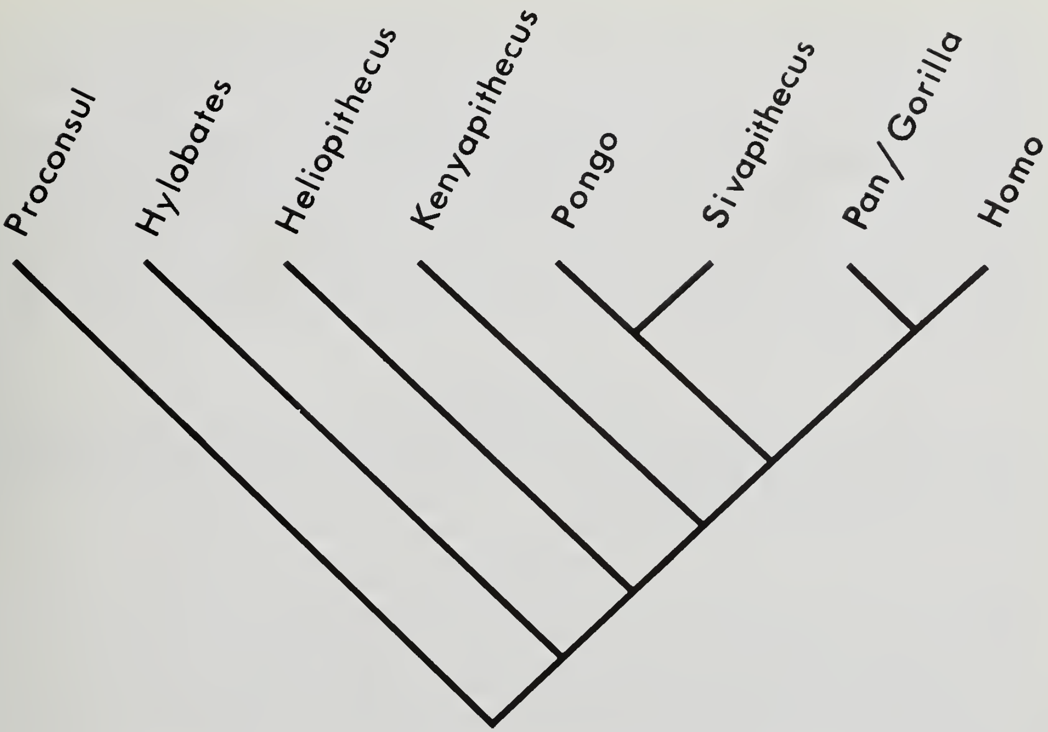

Fig. 15 Cladogram showing the proposed relationships of *Heliopithecus leakeyi.*

Note added in proof

Since this paper was submitted for publication in September 1984 new specimens have been found and named from East Africa (Leakey & Leakey 1986). We have not yet had the opportunity of making direct comparisons of *Heliopithecus leakeyi* with this new material, but the published descriptions and examination of casts indicates that there is a strong similarity between them.

The new material is from the site of Kalodirr west of Lake Turkana. It has been named *Afropithecus turkanensis* by R. E. and M. G. Leakey (1986) and the type specimen consists of a relatively complete skull with a number of unusual and rather baboon-like characters of the facial skeleton. In addition there are less complete specimens from the same site and from Buluk, east of Lake Turkana, which had been described in an earlier paper (Leakey & Walker 1985). The much less complete specimen from Ad Dabtiyah described here is not so well preserved as the East African material, but the parts that are preserved in common show a high degree of similarity.

Many characters of the *Afropithecus* specimens which are shared with other early Miocene and earlier fossil anthropoids would appear to represent primitive retentions for the Hominoidea. This applies to the wide interorbital distance, the massive glabellar region, the narrow and lightly built supraorbital tori not linking across the glabella, the oval-shaped nose, the nasal floor morphology, the single infra-orbital foramen, the relatively large lateral incisors compared with medial incisors, the heteromorphic premolars, and molars retaining distinct lingual cingula. These last two characters are seen to be present also in *Heliopithecus*, and the two genera also share the distinctive premolar enlargement described here. For example, the P^3/M^1 crown module ratio for *Afropithecus* is just over 100%, which is at the limits of the gorilla range, and the P^4/M^1 ratio is 96%. In both cases the greatest similarities are with the Miocene genera *Heliopithecus* and *Kenyapithecus* together with the Moroto palate, which we have subsequently suggested represents a second species of *Heliopithecus* (Andrews, Martin & Whybrow 1987).

In terms of size, the *Afropithecus* specimens appear to group with the Moroto palate from Uganda and are considerably larger than *Heliopithecus* from Saudi Arabia. Because of this, there is little doubt about the species differentiation between the Saudi Arabian and African material, but it is unclear whether the generic distinction is justified. Without changing the main text of the present paper, we would like to place on record our doubts about the generic distinction. Additional material from Saudi Arabia providing data on the face of *Heliopithecus*, or information on the enamel structure and thickness of the teeth of *Afropithecus*, would either confirm or remove these doubts.

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Mastodons from the Miocene of Saudi Arabia

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Synopsis

Mastodon dental remains from Ad Dabtiyah, Saudi Arabia, are assigned to *Gomphotherium cooperi*, a species hitherto known only from the basal Miocene of Dera Bugti, Pakistan. The Ad Dabtiyah population would best fit a late Lower Miocene or earliest Middle Miocene date—equivalent to the middle Orleanian of Europe and coming between Rusinga and Maboko in east Africa. A right $M^2 + M^3$ from 60 km south of Ad Dabtiyah is tentatively included in *G. cooperi*.

Introduction

All but one (M.42946) of the Proboscidea described in this paper come from Ad Dabtiyah, Saudi Arabia, and were collected by P. J. Whybrow, H. A. McClure and the late W. R. Hamilton in 1974. The locality is situated at 26° 27′ 02″ N, 48° 35′ 24″ E (Hamilton *et al.* 1978; see also Whybrow *et al.*, this issue, p. 375) where the fossils occur in continental deposits thought to be laterally equivalent to the nearby extreme limits of the marine Miocene Dam Formation.

Register numbers of specimens refer to the collection of the British Museum (Natural History), London. Measurements (Table 2) are given in millimetres.

In mastodons the pretrite is the lingual half of an upper molar loph and the labial half of a lower molar lophid. The posttrite is the remaining half of each loph or lophid. Pretrites become worn in advance of the corresponding posttrites.

Systematics

Order **PROBOSCIDEA** Illiger, 1811

Family **GOMPHOTHERIIDAE** Hay, 1922

Genus ***GOMPHOTHERIUM*** Burmeister, 1837

Gomphotherium cooperi (Osborn, 1932)
Figs 16–22

1932 *Trilophodon cooperi* Osborn: 3; figs 1–2.

MATERIAL. Measurements are given in Table 2.

M.42940 Conjoined left M_3 and back of M_2. The rear lophid of M_3 has begun to wear. Figs 16, 22.

M.42941 Left lower tusk. Fig. 17.

M.42942 Much of right mandible with M_3. M_2, present in life, is now missing. All lophids of M_3 are in wear. Only the back of the rostrum is present. Fig. 18.

M.42943 Right M^3. The front loph has begun wear. Figs 19, 22.

M.42944 Back of left M_3. Lophids not yet in wear.

M.42945 Left M_3. Wear has barely started on the second lophid; incomplete posteriorly. Figs 20, 22.

M.42946 Conjoined right M^3 and M^2. M^2 is heavily worn and the front two lophs of M^3 are worn. Rear of M^3 is damaged and incomplete. Figs 21–22. The locality for this specimen is about 10 km west of Jabal Uray'irah, an area about 60 km south of Ad Dabtiyah, where undifferentiated deposits are thought to include equivalents of the Dam and Hofuf Formations (Steineke *et al.* 1958). The specimen was collected 40–50 years ago by oil company geologists. It is questionably included in *G. cooperi*.

M.42947 Lateral part of proximal left ulna from Ad Dabtiyah. It can be assumed to be conspecific with the teeth M.42940–5.

M.42948 Partial right scapula from Ad Dabtiyah. Again conspecificity with the teeth can be assumed.

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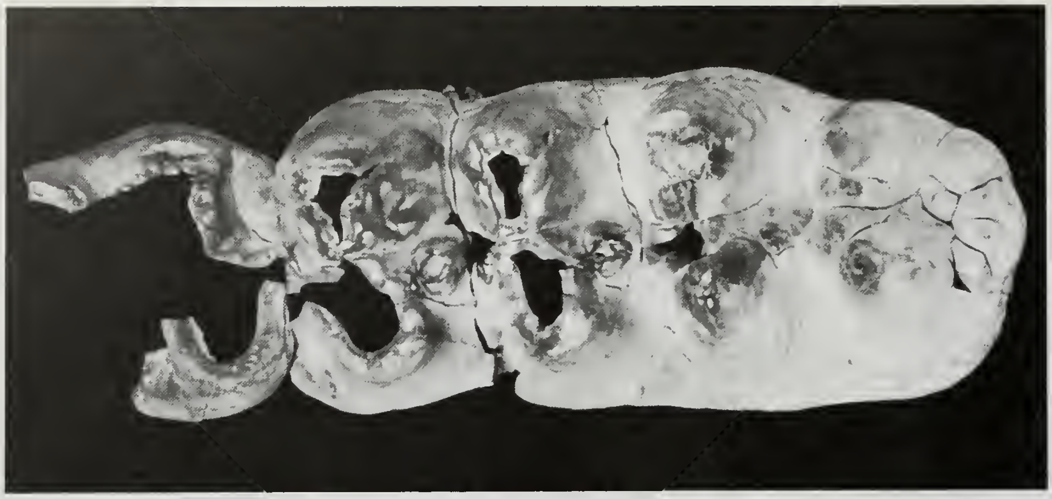

Fig. 16 *Gomphotherium cooperi.* Occlusal view of left M_3 and back of M_2, M.42940, from Ad Dabtiyah. Anterior side to the left. × 0·75.

DESCRIPTION. The teeth all come from one or more species of bunodont, trilophodont mastodon. Except for M.42942 they are preserved only as crowns which has made identification as uppers or lowers less secure in some cases.

The M_3s have four lophids plus a posterior cingulum; the M^3 M.42943 has three lophs and that of M.42946 has four. The third and fourth lophs and lophids show signs of chevroning (forwardly-directed indenting in their centres). The cones and conules of the lophs and lophids are moderate- to high-crowned. In M.42940 and M.42943 they give the appearance of growing out of a basal shelf and the lower parts of their sides are not closely pressed to one another. Small cingular tubercles may be visible between cones. Besides the main (outside) cone in each half loph or lophid there is one additional conelet budded off towards the longitudinal median line of the tooth. M.42943 shows an irregularly surfaced swelling on the rear of the posttrite of the anterior loph, which could be taken as a rudimentary posterior conelet.

The lower tusk M.42941 is peg-like, has a slight twist, a concave upper surface and convex lower surface in cross section, and longitudinal grooves and striations on its lower surface. The latter feature is reminiscent of hippopotamus canines. No enamel band is visible along its outer surfaces. The length, as preserved, is 345 mm and its mid-length diameters 45·3 × 28 mm.

The two postcranial bones, M.42947-8, will not be considered further.

Table 2 Measurements in mm of molars of *Gomphotherium cooperi* (Osborn) from Saudi Arabia.

Specimen		Maximum length	Width across 1st loph(-id)	Maximum width
M_3	M.42940	136	*c.* 60·0	64·2
M_3	M.42942	147	64·3	70·6
M_3	M.42945	*c.* 157	*c.* 69·0	*c.* 76·1
M^3	M.42943	148	*c.* 63·0	66·8
M^3	M.42946	*c.* 147	76·1	*c.* 78·0
M^2	M.42946	*c.* 108	—	67·0

Fig. 17 *Gomphotherium cooperi.* Above: dorsal view of left lower tusk, M.42941, from Ad Dabtiyah. Below: lateral view of same tusk. Inset: transverse section across middle of tusk, medial side to the left, dorsal to the top. × 0·5.

Background to comparisons

Work by Tobien and Tassy since 1970 has greatly improved our grasp of mastodon evolution. Even if not found to be correct in all details their various proposals do at least add up to a comprehensible framework (see Tassy 1983*a*, *b* and references; Tobien 1973). It seems that the following groups of Neogene (effectively post-Egyptian Fayum) Old World mastodons can be recognized.

1. Zygodont or ridge-toothed mastodons of Family Mammutidae, *Eozygodon* Tassy & Pickford (1983) in Africa and *Zygolophodon* Vacek in Eurasia, the latter surviving until the later Pliocene. The remaining mastodons mentioned below are all bunodont.
2. *Gomphotherium*, an early trilophodont mastodon of Family Gomphotheriidae. The European type species, *G. angustidens* (Cuvier), has been known since Cuvier's time and *G. cooperi* and *G. browni* (Osborn) come from the basal Miocene Nari Formation (its upper part) at Dera Bugti, and from the Middle Miocene Chinji Formation, respectively, of Pakistan. Raza & Meyer (1984: 45) place Bugti in the Chitarwata Formation.
3. Shovel-tusked trilophodont mastodons belonging to *Platybelodon* Borissiak, *Protanancus* Arambourg and *Archaeobelodon* Tassy 1983*b*, best known from Asia and Africa. This group is put in the subfamily Amebelodontinae of the Gomphotheriidae, named after the North American type genus.
4. The persistently trilophodont *Choerolophodon* Schlesinger, which develops a crowded and irregular pattern of cones and conules on its molars. This genus also is accorded subfamily rank within the Gomphotheriidae.
5. The tetralophodont mastodons *Tetralophodon* Falconer & Cautley, mainly from the *Hipparion* faunas of Europe, and *Paratetralophodon* Tassy 1983*a* from the Dhok Pathan Formation of the Siwaliks. They are put into subfamily Gomphotheriinae.
6. More advanced relatives of *Tetralophodon*, comprising *Stegolophodon* Schlesinger and *Stegotetrabelodon* Petrocchi which could in their turn be close to *Stegodon* Falconer, *Primelephas* Maglio and later elephants. The differences in molar teeth of these four genera, present though they are, are outweighed by the similarities. Their family affiliation has long been variably interpreted.

The Arabian mastodon remains are clearly trilophodont and bunodont and the central questions are whether they belong to *Gomphotherium* or the Amebelodontinae and how far these groups can be separated anyway.

Until recently *Gomphotherium angustidens* was thought to have lived in Europe from the middle of the Orleanian (late Lower Miocene) as at Artenay, France, until the Vallesian (early Upper Miocene). The name of *G. angustidens* has been used as a blanket and convenient designation for any trilophodont, bunodont mastodon and Osborn (1936: 340; fig. 299) selected as lectotype an M_2 from Simorre, a middle or late Astaracian locality. However Tobien (1973: 255) drew attention to finds of shovel-like mastodon tusks in western Europe and Tassy (1983*b*: 462) founded the genus *Archaeobelodon* for them. Tassy has also emphasized that at Sansan, France (early Astaracian) and in Africa and southern Asia the most abundant early mastodons appear to be amebelodontines.

Gomphotherium is held to have strong upper tusks of oval or triangular cross section, twisting outwards and downwards, and with a broad enamel band along the lateral to ventral surface. The lower tusks are short with a rounded oval cross section (Tobien 1973: fig. 3 nos 1–3) and concave dorsal surface. They are set in a long rostrum and Tobien refers to them as peg-tusks. Amebelodont lower tusks are more flattened and can reach enormous dimensions, as in the Asiatic *Platybelodon* (see Osborn 1936: figs 426, 437). Internally they may acquire a medulla of close-packed dentine tubercles instead of laminated dentine (Tassy 1983*a*: pl. 1, fig. 2; Gaziry 1976: pl. 3, fig. 2). Much taxonomic weight has been put on these tubercles, which are presumably a mechanical response to either pronounced flattening or increased size (as in Schlesinger 1917: pl. 34, fig. 2) of lower tusks. However they are not yet present in early amebelodonts (Tassy 1983*a*: 126–127) so cannot help to define the subfamily. Upper tusks of amebelodonts

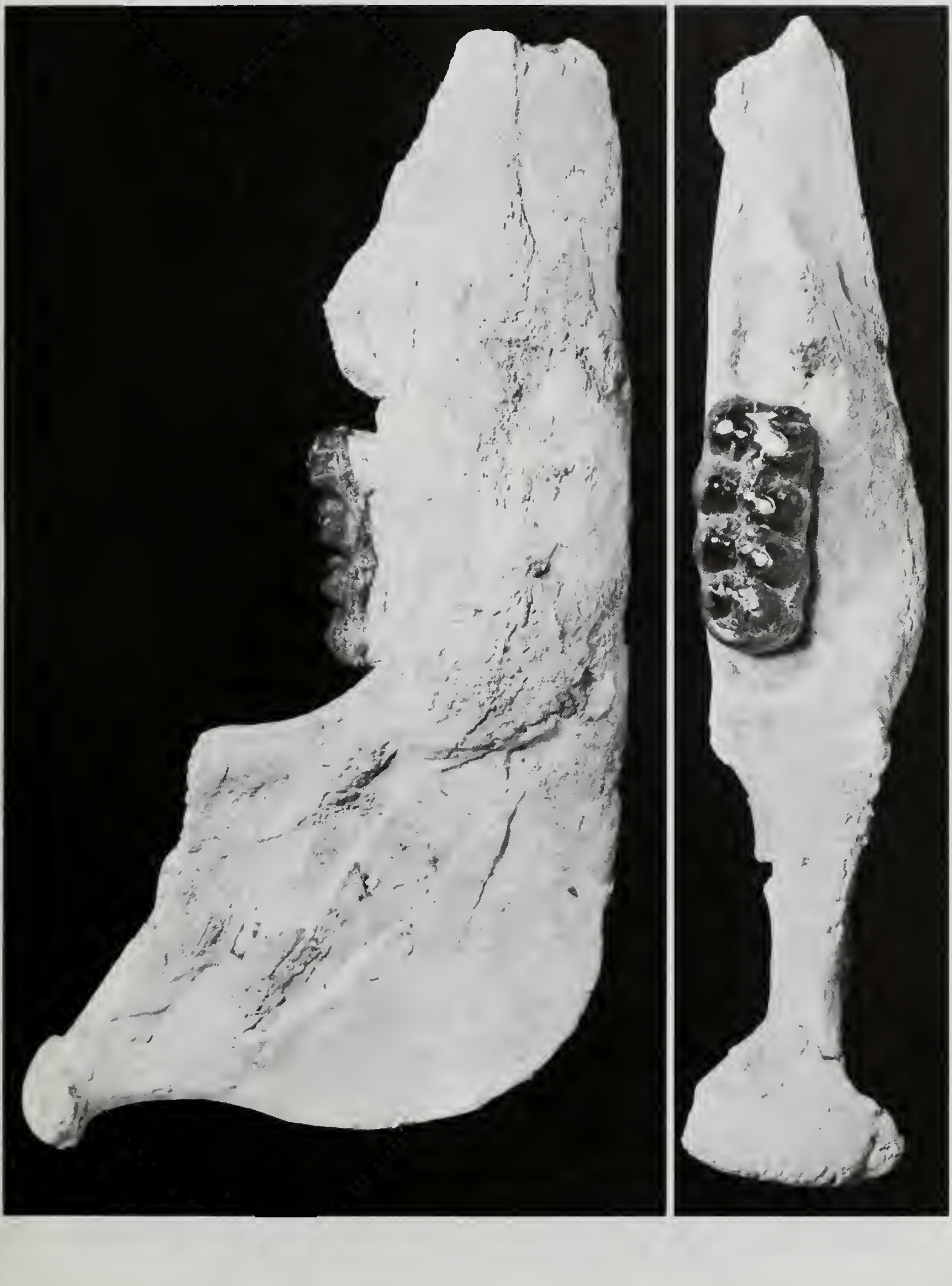

Fig. 18 *Gomphotherium cooperi*. Lateral and dorsal views of right mandible with M_3, M.42942, from Ad Dabtiyah. × 0·25.

Fig. 19 *Gomphotherium cooperi.* Occlusal view of right M^3, M.42943, from Ad Dabtiyah. Anterior side of the right. × 0·75.

are alleged to be small; this is obviously true in relation to their own lower tusks, but less so in relation to *Gomphotherium* upper tusks (Osborn 1936; compare figs 416 A2 and 436). Another feature of amebelodonts is the narrowness of their molars and Tobien (1973: fig. 9) demonstrates this as between Asiatic *Platybelodon* and European and North American *Gomphotherium.* Also considered helpful is the development of posterior conules on the posttrites which may give rise to a more fully trefoil pattern as on the pretrites.

Tassy (1979: 267; 1983*b*: 466) referred *Protanancus macinnesi* Arambourg of the lower Middle Miocene of Maboko, Kenya, to the Amebelodontinae. Its molars are certainly narrower than in European *Gomphotherium* and sometimes there is an indication of posterior conules on the posttrites (MacInnes 1942: pl. 4, fig. 2). Moreover somewhat widened lower tusks are known from Maboko. Tassy (1979: 267) took the mastodon of the Lower Miocene of

Fig. 20 *Gomphotherium cooperi.* Occlusal view of left M_3, M.42945, from Ad Dabtiyah. Anterior side to the left. × 0·75.

Fig. 21 *Gomphotherium cooperi*. Occlusal view of right M^2 and M^3, M.42946, from 60 km south of Ad Dabtiyah. Anterior side to the right. × 0·75.

Rusinga, Kenya, as also an amebelodontine; the flattened lower tusk from Loperot (Maglio 1969) may be another earlier record than Maboko, although Pickford (1981: 90) has some doubts. Tassy (1983*a*: 116) put into *Protanancus* the common mastodon of the Chinji Formation, *P. chinjiensis* (Pilgrim), which is somewhat advanced on *P. macinnesi* in, for example, the more obvious posterior conules of the posttrites (Tassy 1983*a*: fig. 10).

The narrow molars and high cones of *Protanancus* and *Platybelodon* are definitely different from *Gomphotherium*, either *G. angustidens* of Europe or the more rarely preserved *G. browni* (Osborn 1936: fig. 416) which is contemporaneous and sympatric with *Protanancus chinjiensis*. As regards posterior conules of the posttrites, these can sometimes be seen in *Gomphotherium*, as on the front lophid of M_3 of the *G. browni* holotype.

The relationships of *Gomphotherium cooperi* are problematical and it could be a junior synonym of *G. inopinatus* (Borissiak & Beliaeva) of Kazakhstan (see Osborn 1936: fig. 224). The holotype of *G. cooperi* is a mandible, M.12181 (Osborn 1936: fig. 222). Its M_3, and others from Bugti, have length/width proportions closer to the Maboko and Rusinga amebelodontines than to European *G. angustidens*. However, three Bugti M^3s, M.12185, M.12190 and the smaller M.12180 are as wide as in *Gomphotherium*. Tassy (1983*a*: 259) surprisingly assigned a Bugti M_3 to *Choerolophodon*. The tooth (cast M.11050) is longer than *Choerolophodon* M_3s from Maboko and his idea may be that some shortening of M_3 occurred in the earliest *Choerolophodon*.

In western Europe the distinction between the amebelodontine *Archaeobelodon* and *Gomphotherium* can be a matter of some difficulty, especially where isolated cheek teeth are involved (Tassy 1983*b*: 463). It is also noticeable that the amebelodont incisors recorded by Tobien (1973: fig. 15, nos 4–8) come from Sansan and La Grive, France, localities considerably post-dating the arrival of Proboscidea in Europe. If the amebelodontine did evolve from earlier peg-tusked gomphotheres (Tobien 1973: fig. 3, nos 1–3), this would be out of line with Tassy's (1979: 265) view of the plesiomorphy of flattened incisors, but Tassy himself (1983*b*: 465) affirms that *Archaeobelodon* was present in Europe well before the time level of Sansan. The less extreme widening of the tusks of *Archaeobelodon* than in the Asian *Platybelodon* suggests the possibility of regional or continental variation in this character. The documentation of the all-important *Gomphotherium* remains from En Péjouan (Tassy 1983*b*: 463) is needed to establish that *G. angustidens* is indeed a species additional to and continentally sympatric with the western European amebelodontine.

The rest of this paper is mainly concerned with molar teeth, and those coming from Europe and used in comparisons will be referred to in the traditional manner as *Gomphotherium* or *G. angustidens*.

Comparisons

Against this background comparisons can be made between the Ad Dabtiyah mastodons and other relevant material.

M.42940. The M_3 is the only tooth worth considering in detail. It differs from M_3s of Sansan by being smaller, less robust, lower-crowned, and the lophids being more separated at their bases. This last character gives the appearance of the lophids having grown from a basal shelf and is reminiscent of *Zygolophodon*.

It is similar to the Rusinga M_3 M.15300 (MacInnes 1942: pl. 6, fig. 8) but lacks the irregular cingular tubercles evident in M.15300. It also seems to have less sign of swellings (? incipient conelets) around the lophids. It is not so narrow (Fig. 23, smallest reading for X) and is widest across the third instead of the second lophid. It is also very like the Bugti M_3s but shorter than M.12183, with less chevroning of the third lophid than in M.11050, and perhaps with smaller posterior conules of the pretrite trefoils, i.e. smaller conules between the lophids.

It has one less lophid than M_3s of Maboko *Protanancus macinnesi* and less or no chevroning of the fourth lophid. It has a better developed fourth lophid and less chevroning than Maboko *Choerolophodon* M.15542 (MacInnes 1942: pl. 6, fig. 7).

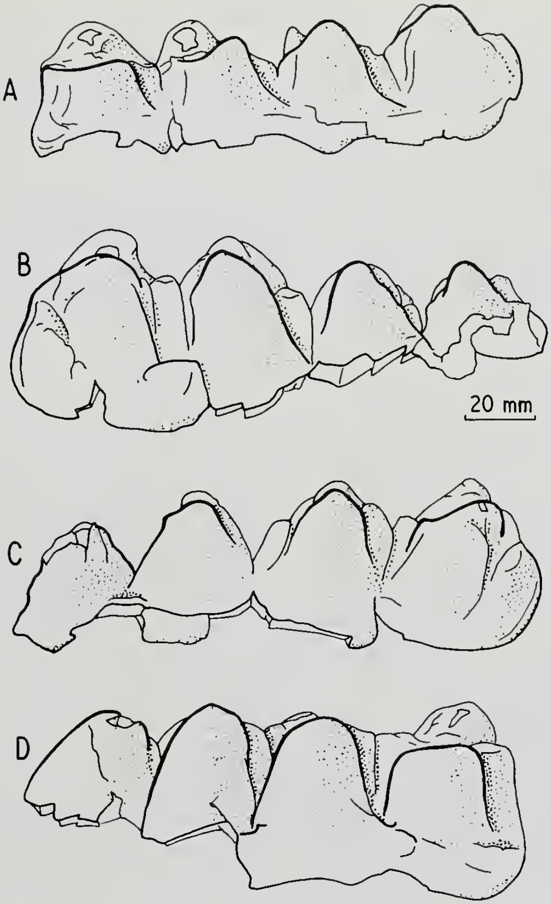

Fig. 22 *Gomphotherium cooperi.* Labial views of molars. A–C, from Ad Dabtiyah. A, left M_3, M.42940. B, left M_3, M.42945. C, right M^3, M.42943. D, right M^3 from 60 km south of Ad Dabtiyah, M.42946.

It looks very like the Artenay M_3 of Ginsburg & Antunes (1966: pl. 3, fig. 2) but is possibly lower-crowned. At first sight it also looks narrower but this is not borne out by Ginsburg & Antunes' measurements of length × breadth (179 × 82 mm) nor by my own measurements from their picture.

M.42941. The dorsal concavity of the tusk is very evident but the width is not sufficient for it to fit an amebelodontine (Tobien 1973: fig. 15).

M.42942. The M_3 in the mandible is better preserved and slightly more worn than the very similar M.42940. Its lophids look less as if they are growing out of a shelf. It is more evenly wide along its length instead of having the third lophid noticeably the widest. The posterior lobes of the pretrite trefoils, consituting the conules which lie centrally between the lophids, are small as in M.42940 and no larger than in Rusinga M.15300. These conules appear to be smaller than in M_3s from Bugti. The third lophid is less chevroned than in Bugti M.11050.

Its length/breadth proportion looks similar to the Artenay M_3 of *G. angustidens* (see Ginsburg & Antunes 1966: pl. 3, fig. 2), but the latter looks as if it has less marked anterior conules of the pretrite trefoils and a more obvious shelf from which grow the lophids.

M.42943. This M^3 differs from Sansan examples, e.g. 32534, by being smaller, narrower, lower-crowned, with three instead of four lophs and with less of an anteromedial cingulum. It also has only one, not two, conelets budded off towards the median line on each posttrite loph.

It is higher-crowned than the Rusinga M^3 M.15318 (MacInnes 1942: pl. 5, fig. 3) and has less of a cingular shelf and no obvious tubercles decorating the shelf labially and lingually.

It is narrower than the Bugti M^3s M.12185 and M.12190, and shows stronger development of the posterior lobes of the pretrite trefoils on lophs 2 and 3.

It differs from the Maboko *Protanancus* by having three instead of four lophs somewhat more widely spaced, being lower-crowned and showing less exaggerated anterior lobes on the pretrite trefoils of lophs 2 and 3.

M.42944. Little can be noted about this back of a left M_3.

M.42945. This M_3 looks more advanced than M.42940 in that it is larger and higher-crowned.

It differs from Sansan M_3s by being slightly lower-crowned and less robust and having more trace of a basal shelf between the front and second lophid row.

Its fourth lophid is less developed than in most of the M_3s illustrated by Bergounioux *et al.* (1953) from the Lisbon 'middle Helvetian Vb' faunas, thought to be of late Orleanian age. It is also lower-crowned than some of these M_3s. It would fit better with the small number of M_3s illustrated from the earlier 'upper Burdigalian IVb' faunas of middle Orleanian age (Bergounioux *et al.* 1953: figs 125, 143, 147, 148, 266). The IVb fauna, later called the R2 fauna, is stratigraphically positioned between the start of N7 and somewhere within N8 of the Blow marine planktonic foraminiferan scale (Van Couvering & Berggren 1977: 299). All the non-zygodont Portuguese mastodons were accepted as *G. angustidens* by Tobien (1973: 207).

It is higher-crowned and wider than Rusinga M.15300.

It is difficult to judge whether, when complete behind the fourth lophid, it would have been as long as the Maboko *Protanancus*, i.e. longer than in Rusinga M.15300. The third lophid may be less chevroned than in Maboko or Chinji *Protanancus*.

The front two lophs of M.42945 are very similar to the same part of the M_3 of *Gomphotherium browni* (AMNH 19417, BM(NH) cast M.15035). Possibly the posterior lobe of the posttrite of the first lophid is less marked than in *G. browni*. The tooth is longer and more robust than in *G. cooperi* M.12181, but has about the same crown height.

M.42946. The M^3 is as long as M.42943 and wider as well. There appear to have been four lophs and the second posttrite had a posterior conule. There were probably two conelets budded off medianwards on each posttrite loph, although preservation and wear impose some uncertainty about this.

At the back of the M^2 the talon has been incorporated into the third pretrite wear facet. The size of the talon in earlier wear would have been about as in the M^2 on the Bugti palates M.12178–9, the normal *Gomphotherium* size.

Its relatively great width is like the Artenay M^3 of Ginsburg & Antunes (1966: pl. 4, figs 2, 3), but its fourth loph is more advanced. It is very like the Sansan M^3 32534, except for the absence of a medianmost lobe on the first pretrite trefoil of the latter which may be fortuitous.

Compared with Maboko *Protanancus macinnesi*, the M^3 on M.42946 is wider but otherwise very similar. Possibly the wings of the pretrite trefoils are better developed in *P. macinnesi*.

It is similar to the M^3 of *G. browni* (cast M.15035; Osborn 1936: fig. 416) but the chevron effect on the third loph may be more pronounced and the lobes of the pretrite trefoils have less of an appearance of being gathered into the line of the lophs. A median longitudinal groove, incipient on M.15035, is not apparent on M.42946.

Compared with the Bugti M^3s M.12185 and M.12190 it is more advanced in its fourth lobe and higher cones. Again the posterior lobe of the pretrite trefoil on the first loph of M.42946 is better developed than in the Bugti teeth. The Bugti teeth could be foreshadowing the condition of *G. browni*.

Coming from a different locality and with a definitely advanced morphology, M.42946 may be a different species from the other Arabian mastodon teeth but for the present it need not be separated from them.

Conclusions

There is evidently a range of variation among the Arabian mastodon teeth. M.42940 is small like Rusinga and Bugti M_3s but less narrow than in the single Rusinga example. M.42945 is larger and higher-crowned. All three Ad Dabtiyah M_3s are wider than in the Maboko *Protanancus* and could most probably belong to a *Gomphotherium*, an attribution compatible with the peg-like lower tusk, M.42941.

The M^3 M.42943, however, is narrower than in the Sansan, Artenay or Bugti gomphotheres, and hence appears more akin to an amebelodont.

On balance it seems best not to split these teeth into different species but to take them all as one species of *Gomphotherium. G. browni* is poorly known and it differs in that its molars appear too large and advanced and the lower incisors have a more rounded cross section

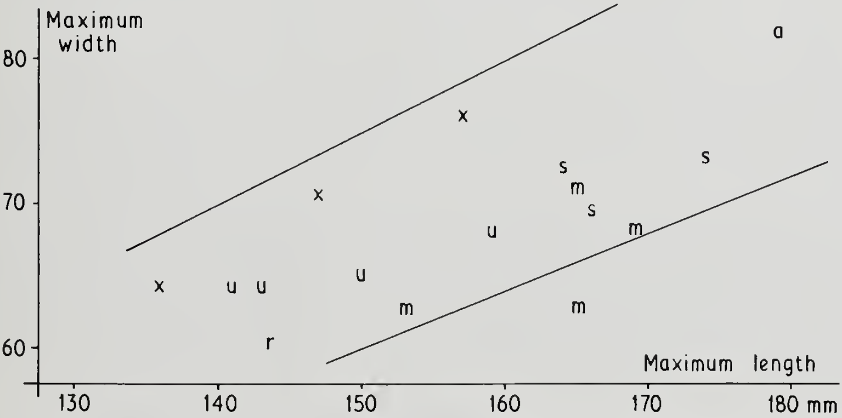

Fig. 23 Width/length proportion for some mastodon M_3s. X = Ad Dabtiyah *Gomphotherium cooperi*; a = Artenay *G. angustidens*; m = Maboko *Protanancus macinnesi*; r = Rusinga amebelodontine; s = Sansan *G. angustidens*; u = Dera Bugti *G. cooperi.* Upper diagonal line is that along which width is 50% of length; the lower line is 40%.

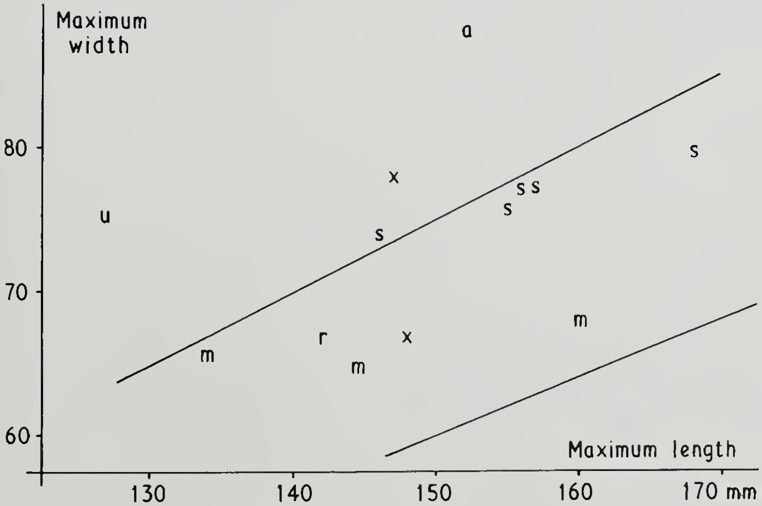

Fig. 24 Width/length proportion for some mastodon M^3s. Symbols and diagonal lines as in Fig. 23.

(Tassy 1983*a*: fig. 25A). *G. angustidens*, at least as represented in Sansan and later localities, is also more advanced. Probably the best designation for the Arabian species is *G. cooperi*. Bugti specimens included in this species show a wide range of variation between narrow M_3s and wide M^3s, but the unerupted M_3 of the holotype mandible M.12181 could not be improved upon as a match for a species embracing M.42940 and M.42945.

Size alone is not a good guide for correlation since European *G. angustidens* has a considerably greater size range than shown on Figs 23–24 for the small BM(NH) sample from Sansan. It would not be reliable to take the small size of the Arabian teeth on these graphs as indicating a pre-Astaracian time of occurrence. Nor is the appearance that the lophs or lophids are growing up from a basal shelf or plate a satisfactory character to use for correlations. Such a shelf is seen in M.42940 and some other early mastodon teeth, but it may also be found in later mastodons, e.g. M.7228, a cast M_3 of '*Mastodon pyrenaicus*' Lartet identified by Tassy (1977: 1391) as an Astaracian occurrence of *Tetralophodon longirostris* (Kaup). Hence the similar structure of M.42940 cannot be regarded as a primitive character indicating an early time level.

We are left with the number and height of lophids and lophs, and these suggest that the Ad Dabtiyah specimens lived at a period before the Maboko level in Africa or Sansan in Europe. They are probably not as old as Rusinga in east Africa, and in the European sequence they would best fit a middle Orleanian time level. They are probably younger than the Dera Bugti *G. cooperi*.

M.42946, from 60 km south of Ad Dabtiyah, looks like a *Gomphotherium* as advanced as that at Sansan and could come from a higher stratigraphical level than at Ad Dabtiyah. It does not appear to be evolving towards *G. browni*.

The Arabian mastodon teeth have not improved understanding of the relations between *Gomphotherium* and amebelodontines, although the dorsal concavity of the tusk M.42941 supports the idea that they were closely linked.

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Rhinoceroses from the Miocene of Saudi Arabia

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Synopsis

Dental and postcranial remains of the rhinoceroses from the Miocene of Ad Dabtiyah, Saudi Arabia, are compared with Oligocene and Miocene Old World representatives of *Ronzotherium*, *Diceratherium*, *Brachypotherium*, *Aceratherium*, *Dicerorhinus*, *Paradiceros*, *Rhinoceros* and *Hispanotherium*. From this it is concluded that two species are present, *Dicerorhinus* aff. *sansaniensis* and *Brachypotherium* sp. Both are primitive, and by implication early, members of their genera. Attention is drawn to the absence of *Aceratherium* and its occurrence in Africa is questioned.

The rhinoceroses suggest a woodland habitat at Ad Dabtiyah and a geological age early in the Middle Miocene, not later than the Orleanian in European terms.

Introduction

The fossils described below were collected in 1974 from continental deposits, thought to be the lateral equivalent of the Dam Formation, at Ad Dabtiyah, Saudi Arabia. This locality is situated at 26° 27′ 02″ N, 48° 35′ 24″ E (Hamilton *et al.* 1978; see also Whybrow *et al.*, this issue, p. 375).

Register numbers of individual specimens refer to the collection of the British Museum (Natural History), London. Nomenclature for rhinoceros teeth is shown in Fig. 26, p. 410.

Systematics

Order **PERISSODACTYLA** Owen, 1848

Family **RHINOCEROTIDAE** Owen, 1845

Genus ***DICERORHINUS*** Gloger, 1841

Dicerorhinus sp. aff. ***sansaniensis*** (Lartet, 1851)

Figs. 25, 27–32, 33A, 34–37, 38A, 39A, B, 40, 42–43, 44A, B

MATERIAL. Measurements in mm.

M.36890 Anterior part of conjoined nasal bones. Fig. 25.

M.36891–2 Left M^1 and M^2, early middle wear, possibly from one individual, occlusal lengths 41·8 and 51·6. Figs 27B, C.

M.36893 Left P^4, middle wear, occlusal length 37·7. Fig. 27A.

M.36894 Right upper molar, probably M^2, early middle wear, occlusal length 49·3.

M.36895 Right M^2, middle wear, occlusal length 40·4. Figs 28B, 33A.

M.36896 Left M^2, middle wear, occlusal length 40·5.

M.36897 Right M^3, early wear, occlusal length 41·1. Fig. 28A.

M.36898 Right P^4, middle wear, occlusal length 32·4. Fig. 29B.

M.36899 Left P^3, middle wear, occlusal length 30·6. Fig. 29A.

M.36900 Left P^2, anterolabial parts missing, late middle wear.

M.36901 Right P^2, middle wear, occlusal length 27·3. Fig. 29C.

M.35012 Left deciduous P^1, late wear, occlusal length 24·1.

M.36902 Left mandible with labial side of P_1, P_2–P_4, much of M_1, much of the labial side of M_2. Early middle wear. The front premolar is identified as P_1 and not P_2 because M_1, itself identified by being more worn than P_4, is the fifth tooth from the front of the cheek tooth sequence. Occlusal lengths: P_1 19·4, P_2 25·4, P_3 31·7, P_4 36·8, P_1–P_4 113·4, M_1 *c.* 43·0. Fig. 30.

M.36903 Left mandible with P_3 to M_3, early middle wear. Occlusal lengths: P_3 30·3, P_4 31·2, M_1 37·2, M_2 42·6, M_3 41·2, M_1–M_3 124·0. Fig. 31.

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Fig. 25 Dorsal (above) and lateral (below) views of *Dicerorhinus* nasal, M.36890 from Ad Dabtiyah. Anterior side to the left. × 0·5.

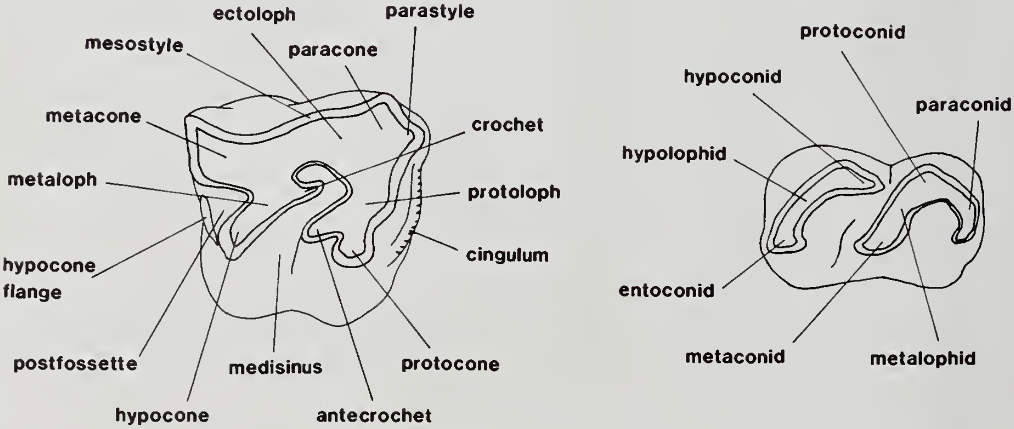

Fig. 26 Nomenclature in rhinoceros upper molar (left) and lower molar (right). Anterior side to right and labial side to top.

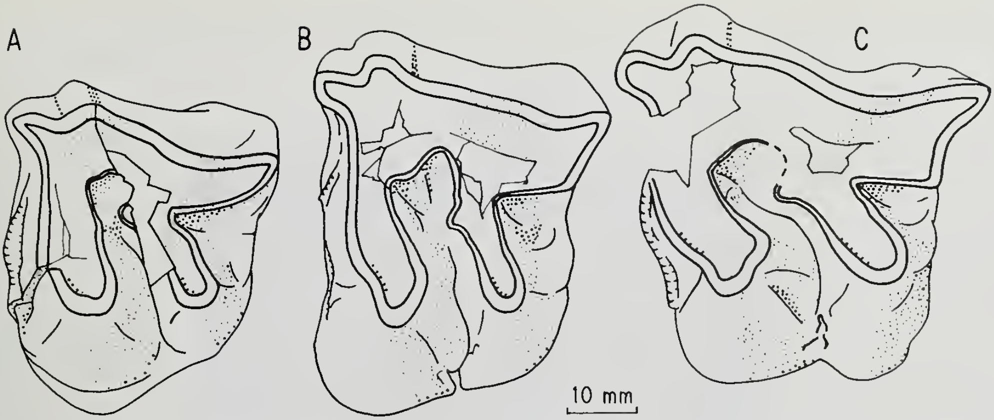

Fig. 27 Occlusal views of teeth of *Dicerorhinus* from Ad Dabtiyah. Anterior sides to left. A, left P^4, M.36893. B, left M^1, M.36891. C, left M^2, M.36892.

M.36904 Back of right mandible with M_2–M_3 and part of M_1, early middle wear. Occlusal lengths: M_2 45·0, M_3 42·7. Possibly the same individual as the last specimen.

M.36309 Right P_4, middle wear, occlusal length 32·8. Possibly belongs to mandible M.36904.

M.36905 Most of the crown of a right P_3, early middle wear, occlusal length 29·5.

M.36906 Most of the crown of a right P_2, middle wear, occlusal length 25·5. Fig. 32.

M.36907 Right I_2, little worn. Fig. 34 (top).

M.36908a, b Paired I_2s, about half worn by comparison with last specimen. Fig. 34 (bottom).

M.35076 Two pieces of mandibular symphysis with alveoli for I_1 and I_2. Fig. 35.

M.35075 Ventral part of right scapula, doubtfully rhinocerotid.

M.36909 Right humerus, complete and undistorted. Length from top of lateral tuberosity to base of medial condyle 460; length from top of articular head to base of medial condyle 410; least transverse width of shaft 64. Fig. 36.

M.36910 Left humerus, less complete and crushed anteroposteriorly in proximal part.

M.36912 Right ulna, complete. Overall length 440. Fig. 37.

M.36913 Right metacarpal IV complete but partially shattered. Overall length 155; transverse width in middle of shaft 32. Fig. 39A.

M.36914 Proximal left metacarpal III.

M.36915–6 Two right scaphoids. Fig. 38A.

M.36917–8 Parts of left and right unciforms.

M.36919 Right magnum.

M.36782 Partial right magnum.

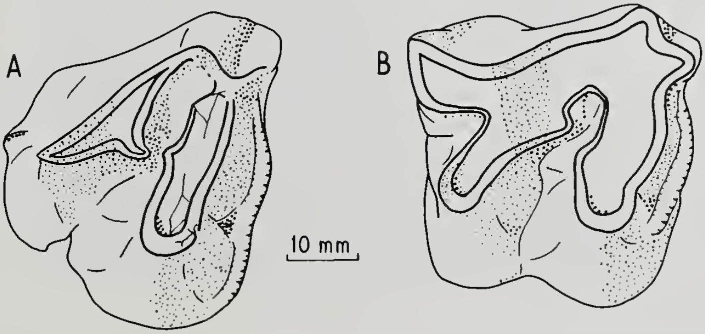

Fig. 28 Occlusal views of teeth of *Dicerorhinus* from Ad Dabtiyah. Anterior sides to right. A, right M^3, M.36897. B, right M^2, M.36895.

M.36783 Left femur, complete. Length from top of great trochanter to base of lateral trochlear ridge 520. Fig. 40.
M.36784 Left tibia, complete. Length from centre of medial facet proximally to posterior tip of medial facet distally 371; transverse width in middle of shaft 60. Fig. 42.
M.36785 Left astragalus, damaged mediodistally. Fig. 43.
M.36786–7 Trochleae of one left and one right astragali, both slightly smaller than preceding specimen.
M.36788 Left calcaneum.
M.36789 Medial side of left cuboid.
M.36299 Left metatarsal III, proximal end damaged anteromedially. Overall length 169; transverse width in middle of shaft 41·4. Fig. 39B.
M.35077 First phalanx of median digit. Fig. 44A.
M.36911 Second phalanx of median digit. Fig. 44B.
Many other more fragmentary bones have been left unregistered.

Description. The nasal fragment, M.36890, has a small protuberance for a horn base, but its dorsal surface is not very rugose. The tip of the anterior end is missing but it is clear that the portion of bone in front of the horn base is neither long nor at all downturned.

The cheek teeth are brachyodont and the premolar row relatively long. The upper molars show a hypocone flange spreading up from the cingulum and meeting a corresponding but smaller flange from the ectoloph to close the postfossette, no lingual cingula, a prominent paracone rib, no mesostyle, the merest trace of constriction of the protocone and no antechrochet, a small or very small crochet on M^1 and M^2 and a moderate-sized one on the M^3, and a straight ectometaloph on M^3. However, the M^3 ectometaloph would become more curved in late wear. The upper premolars have only an occasional trace of the lingual cingulum, no fusion between hypocone and protocone, hypocone somewhat narrowly connected with more labial cusps to make a metaloph, and only a poor metacone rib on the labial wall. The lower molars have fewer distinctive characters; they show no anterolabial or posterolabial cingula, and the vertical indentation centrally on the labial wall is weak. The lower premolars show poor anterolingual cingula, a moderate depth of the ventral indentation centrally on the labial wall, an anterolabial concavity on the wall of P_2, and a large P_1 or persistent dP_1. The central vertical indentation on the labial wall of P_2 is quite narrow behind the sharp-angled protoconid, and the effect is accentuated by the labial flange developed from the protoconid. This may be an individual or a species character.

It is possible to split the adult upper teeth into two groups: M.36891–4 on the one hand and M.36895–901 on the other. The second group consists of smaller-sized teeth which are also small in comparison with the rhinocerotid mandibular and postcranial remains at Ad Dabtiyah. The premolars and molars are less wide than in M.36891–3, although M.36894 may be in an intermediate state. The upper premolars of this second group have a hypocone less completely bound in with the metaloph, and in fact in the P^3 it is altogether isolated—probably an individual variation. The metacone rib is also probably slightly larger giving a less flat or concave appearance.

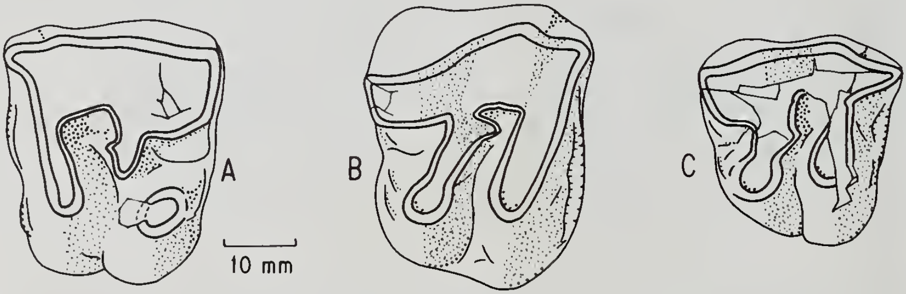

Fig. 29 Occlusal views of teeth of *Dicerorhinus* from Ad Dabtiyah. A, left P^3, M.36899, anterior side to left. B, right P^4, M.36898, anterior side to right. C, right P^2, M.36901, anterior side to right.

Fig. 30 Lateral view of left mandible, M.36902, of *Dicerorhinus* from Ad Dabtiyah. × 0·33.

Fig. 31 Occlusal view of P_3–M_3 in left mandible of *Dicerorhinus* M.36903. Anterior side to the left. × 0·5.

The pair of I_2s in later wear have retained more of their roots than the unworn one and these roots are more or less straight. The unworn incisor may have a more curved course of its crown and root but this is very uncertain.

Each lower jaw has preserved nearly all of its vertical ramus. The angle of the jaws projects or bulges a little posteriorly. The lower edges of the horizontal rami are very slightly convex in outline, but only M.36902 is visible as far forwards as diastema level. The back of the symphysis in M.36902 is about level with the back of P_1.

The postcranial bones are further considered on p. 423, following the comparisons of cranial and dental remains.

GROUPS USED IN COMPARISONS. In order to identify and understand these remains, comparisons were made with fossils and illustrations of the following Eurasian and African rhinoceroses:

1. *Ronzotherium* Aymard, mainly from the illustrations of Brunet (1979), Heissig (1969) and Roman (1912). This was the earliest rhinoceros in Europe at localities like Ronzon and survived until the end of the Oligocene.
2. *Diceratherium pleuroceros* (Duvernoy), a small rhinoceros from the Upper Oligocene and basal Miocene of Europe. It has two horns side by side at the front of its nasals. Upper cheek teeth in middle wear are illustrated in Piveteau (1958: 440, fig. 77), lowers in Roman (1912: pl. 6, figs 4–6).
3. The hornless rhinoceros *Aceratherium* Kaup, mainly as illustrated in Guérin (1980), Bonis (1973) and Heissig (1969). It is first known in Europe in the middle of the Oligocene. The small Agenian '*Dicerorhinus tagicus*' (Roman), possibly conspecific with *Protaceratherium minutum* (Cuvier) as used by Abel (1910: pl. 2, fig. 8), has crochets on its upper molars, at least in earlier wear, and no fifth metacarpal (Roman 1924). It could be an offshoot of Oligocene *Aceratherium.* It also occurs in the basal Miocene of Dera Bugti, Pakistan (Cooper 1934: 602) and near the Oligocene/Miocene boundary in Russia (Borissiak 1938*a*). Larger and smaller sized *Aceratherium* continued into the Upper Miocene (Vallesian).
4. The large, short-legged and usually hornless *Brachypotherium* is known from the Agenian onwards and replaced *Ronzotherium.* It may have originated from a form near *Diceratherium* Marsh, judged by traces of paired horns in some early examples, or one close to *Aceratherium,* judged by the difficulties with generic classification of the early species *lemanense* Pomel (Bonis 1973: 124). It is illustrated in Depéret & Douxami (1902), Hooijer (1966), Viret (1929) and Roman (1912).
5. Miocene species of the horned rhinoceros *Dicerorhinus,* as in Guérin (1980) and Hooijer (1966). [*Dicerorhinus* has been validated in preference to *Didermocerus* by the International

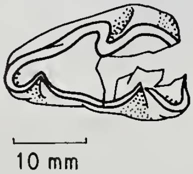

Fig. 32 Occlusal view of left P_2, M.36906, of *Dicerorhinus* from Ad Dabtiyah. Anterior side to left.

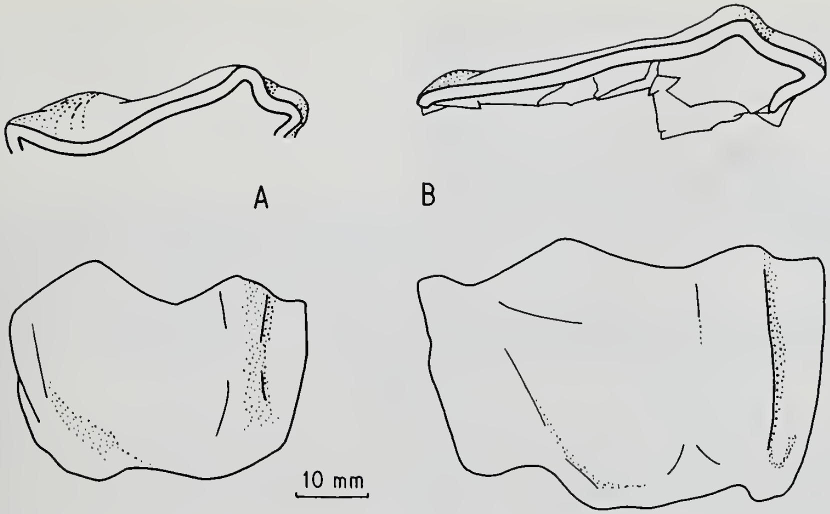

Fig. 33 Occlusal and labial views of labial sides of rhinoceros upper molars from Ad Dabtiyah. Anterior sides to right. A, *Dicerorhinus*, a right tooth, M.36895 (occlusal and reversed labial views). B, *Brachypotherium*, a left tooth, M.36300 (labial and reversed occlusal views).

Commission of Zoological Nomenclature (1977).] *Dicerorhinus sansaniensis* (Lartet) and the smaller *D. steinheimensis* Jäger are best known from the Middle Miocene of Europe, *D. leakeyi* Hooijer from the Lower Miocene of east Africa, *D. primaevus* Arambourg from the Upper Miocene of north Africa and *D. schleiermacheri* (Kaup) from the Upper Miocene (Vallesian and Turolian) of Europe. *Diceros pachygnathus* (Wagner) from the Turolian of Pikermi, Greece, lacks lower incisors but is otherwise very similar to *Dicerorhinus schleiermacheri. Dicerorhinus sansaniensis* is known back to the Orleanian or late Lower Miocene in Europe (Heizmann *et al.* 1980: 7; Guérin 1980: 201). Finally it may be mentioned that '*Aceratherium*' *abeli* Cooper (1934: 596) from Dera Bugti appears to be a *Dicerorhinus*, as already noted by Heissig (1972: 27).

6. The African horned rhinoceros *Paradiceros mukirii* Hooijer (1968) from the Middle Miocene of Fort Ternan, Kenya (Shipman *et al.* 1981), related to *Diceros*.

7. A rather incompletely known group of Miocene horned rhinoceroses held to be related to the Pliocene and Pleistocene *Elasmotherium* Fischer of Asia and centred on *Hispanotherium* Crusafont & Villalta, within which Ginsburg & Antunes (1979) would also include the Asiatic *Beliajevina* Heissig and *Caementodon* Heissig. *Hispanotherium* appeared for only a limited duration in Spain and Portugal (Antunes 1979: 20) and is known at what is probably a later horizon in Turkey (Heissig 1976). The African *Chilotheridium pattersoni* Hooijer (1971) and possibly the *Chilotherium* Ringström of the Chinese *Hipparion* faunas (Ringström 1924), as well as the much earlier *Chilotherium blanfordi* (Lydekker), the commonest true rhinoceros at Dera Bugti, could also belong here. All these rhinoceroses were hypsodont and had upper molars with constricted protocones and strong antecrochets; the (? primitive) protocone/hypocone fusion on upper premolars persisted until the start of the late Miocene. There are, however, some differences among them. In particular the Turkish *Hispanotherium* has a reduced mandibular symphysis and no enlarged lower incisors (Heissig 1976: 33, fig. 2), whereas the Bugti *Chilotherium* shares a very wide symphysis (Cooper 1915: figs 4, 5) with the *Chilotherium* of the Chinese *Hipparion* faunas. The Chinese *Chilotherium* has no horns, the state of *C. blanfordi* is unknown, *Chilotheridium* possessed a nasal horn and pneumatized frontals (Hooijer 1971: pls 2, 4) and *Beliajevina* Borissiak had what must have been a horn base towards the back of the nasals (Borissiak 1938*b*: 8). In addition to the foregoing references, see also Heissig (1972, 1974), Antunes (1972) and Antunes *et al.* (1972).

Fig. 34 Incisors of *Dicerorhinus* in medial view to show differences in root curvature. Right I_2, M.36907 (above), left I_2, M.36908b (below). × 0·5.

8. *Rhinoceros browni*, first described by Colbert (1934) under the generic name *Gaindatherium* and figured by him and by Heissig (1972). It is known from the Chinji Formation and other pre-*Hipparion* localities of the Siwaliks Group in Pakistan, where it predates other rhinoceroses like *Aceratherium* and *Brachypotherium* (Guérin *in* Pilbeam *et al.* 1979: 36; Barry *et al.* 1982: 113–4).

The taxonomy and history of Oligocene and earlier Miocene rhinoceroses is confused. Many generic names have been used besides those so far mentioned while multitudes of species-level names have been founded and used in differing combinations with the generic names.

Comparative material in the British Museum (Natural History) comprised mainly fossils and casts from the Upper Miocene of Eppelsheim, Germany and the Lower and Middle Miocene of some French localities, the Lower Miocene of Jebel Zelten, Libya, the Lower Miocene of some Kenyan localities and the basal Miocene of Dera Bugti, Pakistan.

COMPARISONS. In *Ronzotherium* upper molars it is mainly the massive lingual and posterolabial cingula, the stronger indication of a mesostyle, the posteriorly open postfossette and the curved ectometaloph of M^3 which differ from the Arabian teeth. Strong cingula also occur on *Ronzotherium* lower molars and premolars.

The upper premolars differ by having strong cingula as in the molars, a stronger metacone rib and fusion between the protocone and hypocone. Radinsky (1967: 5) and Heissig (1969: 15) agree that primitively rhinocerotid P^3s and P^4s would have had a protocone linked or almost linked by a protoloph to the ectoloph. The hypocone was definitely linked with the protocone-protoloph but only more weakly via the metaloph to the ectoloph. This is the condition found in *Ronzotherium*, whereas in other rhinoceroses the hypocone is part of a metaloph and linked only weakly or in later wear, if at all, to the protocone. They thus look much more like molars.

Fig. 35 Anterior view of mandibular symphysis of *Dicerorhinus*, M.35076. Notice alveoli for I_1s as well as I_2s. Natural size.

The change has been carried less far in *Aceratherium* in which a narrow protocone–hypocone link may be present (e.g. *A.* cf. *platyodon* Mermier, of Roman & Viret 1934: pl. 8, fig. 1). In *Hispanotherium* (Heissig 1976: pl. 1, figs 14, 15) this same link has survived undiminished from its ancestral *Ronzotherium*-like condition (or has been strengthened anew, helped perhaps by antecrochet growth from the protoloph, from an *Aceratherium*-like condition). Against this background the Arabian P^3 is interesting in that the hypocone is separated both from the

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Fig. 36 Anterior view of right humerus of *Dicerorhinus*, M.36909. × 0·33.
Fig. 37 Medial view of right ulna of *Dicerorhinus*, M.36912. × 0·33.

protocone and from a metaloph growing towards it from the ectoloph. It has, however, already developed a posterolabial flange (perhaps a raising of the old posterior cingulum) which is closing off the postfossette posteriorly.

The P_1 or persistent dP_1 on M.36902 is almost as large as in a *Ronzotherium filholi* from Bournouncle I, France (Heissig 1969: fig. 15C; table 14), although in other *Ronzotherium* the P_1 may be only a single-rooted peg or altogether absent.

The upper premolars of *Diceratherium pleuroceros* do not have the primitive *Ronzotherium*-like fusion of protocone and hypocone but the teeth are otherwise little advanced. They differ from the Arabian species by being smaller, the M^3 having a curved ectometaloph (only available from the aged specimen 28845, a cast of the holotype skull), and anterolabial and anterolingual cingula being present on the lower molars. '*Dicerorhinus*' *tagicus* has stronger cingula on the premolars and molars, stronger crochets and mesostyles, some sign of antecrochets on the upper molars and only a peg-like P_1. The only figured specimen also lacks a nasal horn.

Aceratherium differs very distinctly by its tendency to have a reduced paracone rib and by the antecrochets and constricted protocones on the upper molars, by the curved ectometaloph and localized posterolabial cingulum on M^3, and by an internal cingulum and narrow protocone–hypocone fusion on the upper premolars. The lower molars have a stronger labial indentation between the metalophid and hypolophid, and small but definite anterolabial and anterolingual cingula. P_1 is smaller.

Brachypotherium has rather primitive teeth but has nonetheless developed some specializations of its own. The large size, wide and evenly flat or slightly concave ectoloph surface behind the rather insignificant paracone rib, persistence of internal cingula on its upper cheek teeth and of external cingula on its upper and lower molars are all different from the Arabian form. Orleanian *Brachypotherium* already had a smaller P_1 (Mayet 1908: pl. 2, fig. 2). The P^3 of '*Rhinoceros* (*Diceratherium*) *asphaltense*' Depéret & Douxami (1902: pl. 2, fig. 1), which Bonis (1973: 123), following Schlosser (1904: 443), includes in *B. lemanense*, is one of the few in which the hypocone is not linked by a metaloph to the ectoloph. Other cases are found in some *Ronzotherium* P^4s, e.g. that shown by Heissig (1969: fig. 13).

The distinctive *Hispanotherium* has hypsodont upper molars, often with abundant cement; the paracone rib is probably weaker than in the Arabian specimens, the protocone strongly constricted and an antechrochet is present. On the upper premolars the protocone and hypocone are fused and the metacone rib is strong. The lower molars have more of a labial

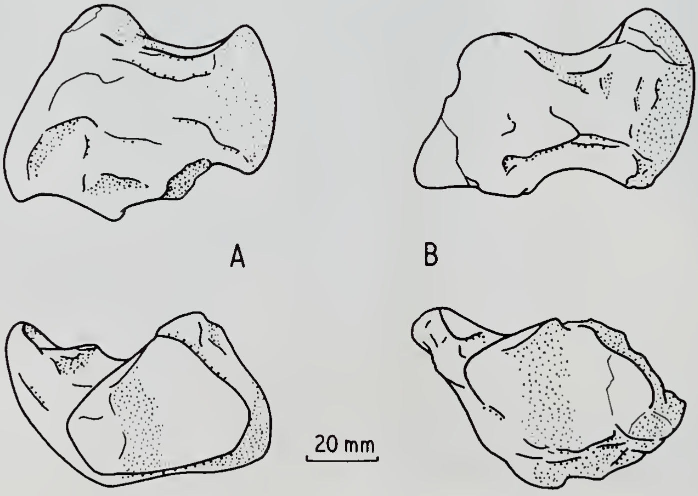

Fig. 38 Right scaphoids of rhinoceros from Ad Dabtiyah in medial view (above) and dorsal view (below). Anterior sides to left. A, *Dicerorhinus*, M.36916. B, *Brachypotherium*, M.36302.

indentation between metalophid and hypolophid. As regards reduction of the anterior premolars, even P_2 has diminished in size (Heissig 1976: 33, fig. 2).

Paradiceros mukirii was described as an early relative of the living African black rhinoceros, *Diceros bicornis*, apparently about twice as old as the well-known Turolian *Diceros pachygnathus*. *Paradiceros* differs most notably from the Arabian species by the absence of lower incisors. Other differences are its shorter premolar row without a P_1, stronger anterolingual cingula on the lower premolars, and probably the larger crochets of the upper molars.

It is not clear why *Rhinoceros browni* need be generically separated from *Dicerorhinus* as used here (cf. Groves 1983: 310). Alleged differences are that it has no sign of a horn base on the frontals, the top of the nasals are less bent downwards and the anterior border of the orbit lies above the middle of M^1. The first two characters resemble later *Rhinoceros* but could as easily fit a female *Dicerorhinus*. As to the third, the front of the orbit lies above P^4 in adult modern *R. unicornis*, above M^1, perhaps even its back half, in *D. sumatrensis*, and above the M^1/M^2 boundary in Miocene *Dicerorhinus*. Here again the state of *R. browni* could fit *Dicerorhinus* as easily as *Rhinoceros*. The union of the posttympanic and postglenoid processes beneath the external auditory meatus, mentioned by Colbert (1934), is like *Rhinoceros* and Miocene *Dicerorhinus* but unlike *D. sumatrensis*. Modern *R. unicornis* and *sondaicus* have a longer P^3 and P^2 than *D. sumatrensis* (Guérin 1980: table 5) but there is no foreshadowing of this in *R. browni*.

Rhinoceros browni differs from the Arabian species in having a smaller crochet and curved ectometaloph on M^3, a shorter premolar row, a more prominent metacone rib on the upper premolars and probably a stronger mesostyle rib on the upper molars. Crochet size on M^1 and M^2 of *R. browni* must be variable according to the illustrations of Colbert (1934: fig. 4) and Heissig (1972: pl. 1, figs 7, 8). P_1 was reckoned by Colbert (1934: 9) to be absent in *R. browni* and although Heissig (1972, pl. 2, fig. 3) figured one, it was nevertheless smaller than in the Arabian rhinoceros. The anterolabial wall of P_3 is very slightly concave in the Arabian species—more so than in many later rhinoceroses but like *R. browni* in Heissig (1972: pl. 2, fig. 3).

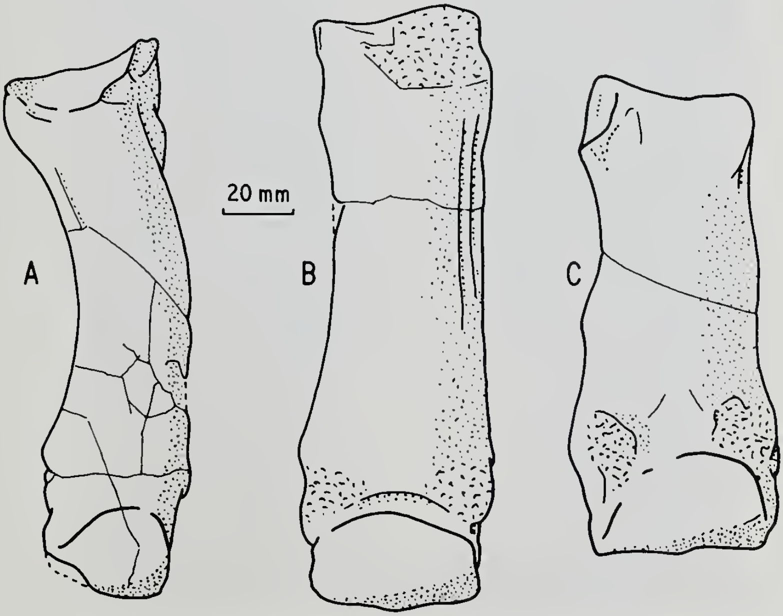

Fig. 39 Metapodials of rhinoceros from Ad Dabtiyah in anterior view. A, *Dicerorhinus*, right metacarpal IV, M.36913. B, *Dicerorhinus*, left metatarsal III, M.36299. C, *Brachypotherium*, left metatarsal III, M.36308.

Fig. 40 Anterior view of left femur of *Dicerorhinus*, M.36783. × 0·33.

Dicerorhinus shows fewer differences in its teeth from the Arabian species than genera already mentioned and some species-level comparisons are needed.

Dicerorhinus primaevus Arambourg (1959: 56) comes from the Upper Miocene of Bou Hanifia (= Oued el Hammam), Algeria. It has larger teeth than the Arabian species and larger crochets on M^1 and M^2. Unfortunately premolars are known only from the milk dentition.

Dicerorhinus abeli differs from the Arabian species by having larger crochets on its upper molars, a smaller P_1, a lingual cingulum at the medisinus entrance on the upper premolars, a stronger metacone rib on the upper premolars, antero- or posterolabial cingula on the lower molars and a shallow anterolabial concavity on the wall of P_2.

D. leakeyi appears to show fewer differences: a less straight ectometaloph in M^3 (Hooijer 1966: pl. 7, fig. 5), a more prominent metacone rib on the upper premolars, more fusion between hypocone and protocone in later wear on the upper premolars and deeper labial grooves on the lower premolars. P_1 is present in one of the two specimens but is not quite as large as in M.36902.

D. sansaniensis, known to me only from illustrations, differs by the probably stronger fusion between hypocone and protocone of the upper premolars in later wear. It also has better lingual cingula on both its upper molars and premolars and larger labial grooves on its lower molars. One mandible (Guérin 1980: pl. 9C) has a P_1 almost as large as in the Arabian specimen, but the holotype (Guérin 1980: pl. 6) has a smaller P_1.

D. steinheimensis is a smaller species. According to Guérin (1980: table 47), the smaller Arabian upper teeth (M.36895–901) would match *D. steinheimensis* in size and the larger ones (M.36891–4) *D. sansaniensis.* I shall not, however, split the Arabian material at species level.

D. schleiermacheri is a later form. Its upper molars contrast with the Arabian form in their weaker paracone rib but stronger mesostyle rib. The closure of the postfossette by flanges from hypocone and ectoloph is also more apparent. Its upper premolars show fusion between the protocone and hypocone in middle and late wear and a stronger metacone rib. The lower molars have more of a central indentation on their labial walls and the P_1 is smaller or absent.

The lower incisors from Arabia, M.36907–8, are smaller than the large ones assigned to *Aceratherium* in the Eppelsheim collection but larger than BM(NH) 21490 in the same collection assigned to *D. schleiermacheri.* The more or less straight roots of the more worn pair make them more akin to *Dicerorhinus* according to Hooijer (1966: pl. 4, figs 2–5). Guérin (1980: 218), following Heissig (1972), points out that incisors of *Dicerorhinus* differ from those of *Aceratherium* in possessing a neck. The worn pair from Saudi Arabia do not have such a neck whereas the unworn one does. It may also be noted that the mandible M.35076 shows alveoli for two small I_1s, thereby agreeing with *D. leakeyi* (Hooijer 1966: 123) and *D. schleiermacheri* (M.2781).

The posterior projection of the angle of the lower jaws differs from *Aceratherium*, in which the back of the vertical ramus descends in more of a straight line. The Arabian mandibles resemble two casts of *Dicerorhinus schleiermacheri* from Eppelsheim, *Dicerorhinus sansaniensis* (Guérin 1980: pls 5, 6), *D. leakeyi* (Hooijer 1966: pl. 2, fig. 4) and *Brachypotherium* (Mayet 1908: pl. 2, figs 1, 2; Roman 1912: pl. 8, figs 1, 3). The lower edge of the horizontal ramus in M.36902 does not curve upwards anteriorly so much as in *Diceratherium pleuroceros* (Roman 1912: pl. 6, fig. 4) or as in *Aceratherium* or *Dicerorhinus schleiermacheri.* Like *D. sansaniensis* and *D. leakeyi*, in *Brachypotherium* it looks curved but less so than in *Aceratherium.* Heissig (1972: 21) gives a forwardly-directed mandibular symphysis as a character of the subfamily Rhinocerotinae.

The nasal fragment M.36890, with its small horn base, is unlike *Aceratherium* and most *Brachypotherium* which are hornless. It is also unlike the twin-horned *Diceratherium* or some early *Brachypotherium* with vestiges (?) of paired horns (Osborn 1900: 253, figs 12B, D; Dietrich 1931: 210, figs 10, 11). The smallness and absence of surface rugosity could suggest that the bone is from a female, juvenile, primitive or geologically old animal. The absence of downturning anteriorly is unlike *Dicerorhinus sansaniensis* or *D. leakeyi* but like *D. schleiermacheri* and *Rhinoceros browni.* Whether or not there was a frontal horn in the Arabian species is not known.

Fig. 41 Anterolateral view of left femur of ?*Brachypotherium*, M.36305. × 0·4.

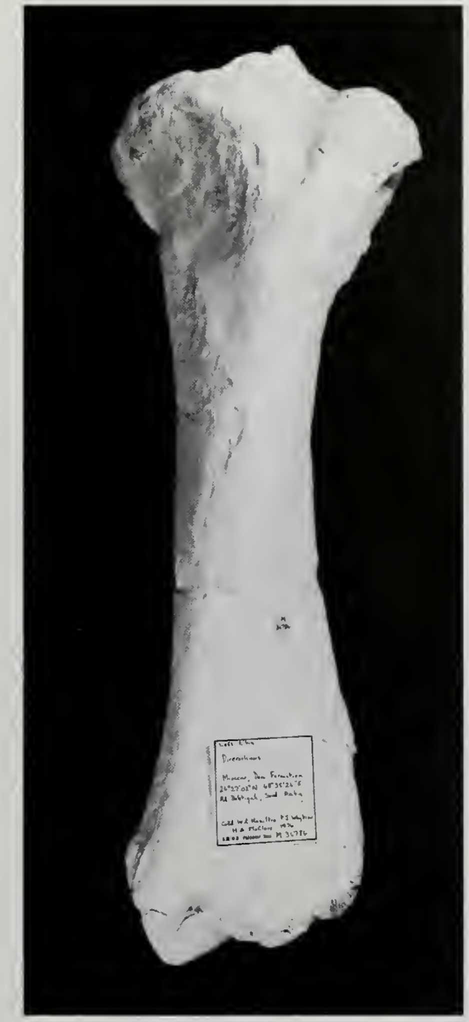

Fig. 42 Anterior view of left tibia of *Dicerorhinus*, M.36784. × 0·33.

POSTCRANIAL BONES. The ventral part of a damaged right scapula, M.35075, could belong to a rhinoceros but the glenoid facet is very narrow transversely. It is probably too small to fit a mastodon.

The well-preserved right humerus, M.36909, is about the size of those of *Dicerorhinus leakeyi*, *schleiermacheri* and *orientalis* (Schlosser) listed in Hooijer (1966: 160, table 28). It is about as wide at the proximal as at the distal end. The olecranon fossa is deep at the distal end. Compared with the humeri of Pikermi rhinoceroses, the shaft looks longer between the base of the deltoid crest and the supinator ridge distally. The humerus of *Ronzotherium filholi* (Osborn), as figured by Brunet (1979: pl. 20b, c), is a slighter bone and that part of the distal end lateral to the condyles is narrower. It agrees well with M.2783, the cast of a specimen from Eppelsheim labelled as *D. schleiermacheri*.

The right ulna, M.36912, is again complete; even the top of the olecranon is present in its entirety. The process at the top of the olecranon projects strongly medially and the mid-shaft diameter from front to back is considerably less than in Pikermi examples of *Diceros pachygnathus*.

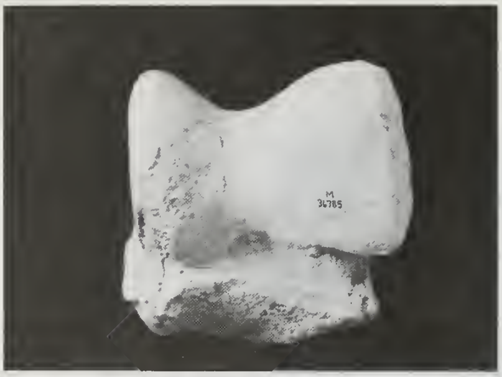

Fig. 43 Anterior view of left astragalus of *Dicerorhinus*, M.36785. × 0·5.

The right metacarpal IV, M.36913, is as curved and less thickset than M.18814 from Rusinga (perhaps belonging to *D. leakeyi*; Hooijer 1966: pl. 12, figs 2, 3); the latter is itself less thickset than Pikermi examples probably belonging to *Diceros pachygnathus*. M.36913 has no facet for articulation with a metacarpal V.

The two right scaphoids, M.36915–6, are less thickset than examples from Pikermi probably belonging to *Diceros pachygnathus*. There is only poor development of a downwards projection posteroventrally and this may be a resemblance to *Dicerorhinus* rather than to *Aceratherium* (see Bonis 1973: fig. 36).

The complete left femur, M.36783, is about the size of Pikermi examples but more gracile especially at the distal end. The third trochanter is smaller and higher on the shaft and in lateral view the top of the great trochanter slopes downwards anteriorly. These are additional differences from the Pikermi bones and the downward slope of the great trochanter may be linked with the third trochanter appearing to be higher on the shaft. The Arabian femur is not quite so long as a cast of an Eppelsheim femur (M.1283, labelled *D. schleiermacheri*), on which the great trochanter has a similar slope and the third trochanter is about the same size as the Arabian one.

The left tibia, M.36784, is the size of the *Dicerorhinus leakeyi* and *D. orientalis* listed in Hooijer (1966: 171, table 40) but a bit longer than the *D. schleiermacheri*. It is about the size of a rhinoceros tibia 27458 from Sansan, but less gracile as shown by the wider distal part of the shaft and distal articular surface. Compared with Pikermi rhinoceros tibiae it is slightly more gracile, the tibial tuberosity at the proximal end is less massive in proximal view and in anterior view there is less of a deep groove at the proximal end.

The left astragalus, M.36785, matches M.2786 from Eppelsheim which is labelled as *D. schleiermacheri* and is unlike 1290 and M.2785 labelled as *Aceratherium incisivum* from the same locality. The agreement with M.2786 lies in the prominent overhang of the lateral parts of the proximal trochleae and in the top edge of the front of the cuboid facet being widely separated from the base of the more proximal trochlear facets on the anterior surface, but it must be stated that Pikermi examples of astragali of *D. schleiermacheri* or *Diceros pachygnathus* do not match the Eppelsheim bone in these respects. M.36785 is taller than the Pikermi astragali and its proximal lateral trochlea is less bulbous. M.36785 is larger than most of the east African *Dicerorhinus* and *Aceratherium* listed by Hooijer (1966: table 42) but is not as large as the only one listed as definitely *Dicerorhinus*—that which belongs to the associated skeleton no. 2.

The left calcaneum, M.36788, has its tuber less thick, front to back, than in Pikermi examples.

The left metatarsal III, M.36299, is more slender than Pikermi ones.

The first and second phalanges of the median digit, M.35077 and M.36911, by comparison with Hooijer (1966: pl. 10, figs 4–7) are seen to match *Dicerorhinus* rather than *Brachypotherium*. There is also another, more damaged, median second phalanx and a number of phalanges of the side toes.

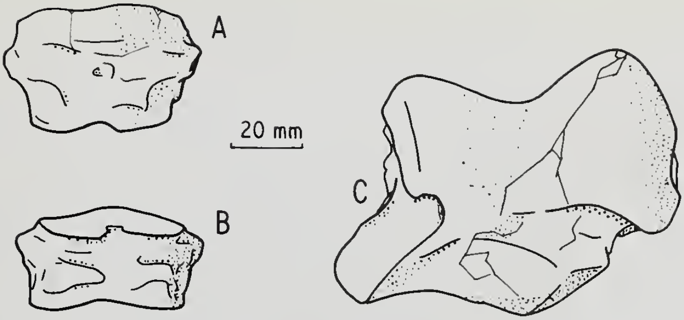

Fig. 44 Rhinoceros bones from Ad Dabtiyah. A, *Dicerorhinus*, median 1st phalanx in anterior view, M.35077. B, *Dicerorhinus*, median 2nd phalanx in anterior view, M.36911. C, *Brachypotherium*, left astragalus in anterior view, M.36306.

Discussion. Early *Dicerorhinus* species and *Rhinoceros browni* emerge as close to the Arabian material. The *Dicerorhinus* species with which comparisons have been made come from continentally-separated localities and the one which differs least could be *D. sansaniensis*. It has to be noted, however, that the characters of the latter were available to me only from plates in Guérin (1980) and Filhol (1891). Many characters in this assessment would also probably turn out to be variable in large samples in spite of their long-standing use in rhinoceros taxonomy. Furthermore, on dental morphology alone the Arabian species could only be distinguished from *Diceratherium pleuroceros* by its greater size.

The Arabian species can be named as *Dicerorhinus* sp. aff. *sansaniensis*, but this may reflect no more than the attainment of a similar evolutionary level of tooth morphology. In particular it need not imply zoogeographical relationship with Europe. A skull from Ad Dabtiyah would be needed to make a reliable identification. As far as geological age is concerned, Sansan itself is of Astaracian age but *D. sansaniensis* is known back to the Orleanian as noted previously. In Africa *D. leakeyi* is best known from the time range 20–16·5 Ma, which probably corresponds to the Orleanian in Europe, and Hooijer (1978: 374) regards Alengerr, Kenya (12–14 Ma?) as the latest reasonable record. The preorbital part of its skull is longer than in *D. sansaniensis* (Hooijer 1966: pl. 1; Guérin 1980: pls 5, 6) which would fit with the suggestion of an earlier age than Sansan. The Dera Bugti *D. abeli* could well date from the basal Miocene (Eames 1950, Khan 1968), i.e. have an age equivalent to the Agenian in Europe. Some of the other Dera Bugti mammals support this assessment, for example the mandibular piece (M.12339) of '*Amphicyon*' *shahbazi* (Pilgrim), which looks like *Pseudocyonopsis* Kuss, a genus extinct in Europe after the Agenian (Springhorn 1977: 37). All this suggests that the rather primitive *Dicerorhinus* of Ad Dabtiyah could be of an age equivalent to the Orleanian land mammal age in Europe. The rather large size of the dP^1 (M.35012) could also support an early date for Ad Dabtiyah. It appears to be about 10% longer relative to M^2 than in *D. primaevus* or Astaracian *D. sansaniensis* (Guérin 1980: 233), and thereby in closer agreement with *D. leakeyi* and *D. abeli.*

Numerical approaches. As an alternative to the above comparisons a matrix was drawn up of 25 cranial and dental character differences in 18 taxa of Oligocene and Miocene rhinoceroses. The characters used were:

SKULL:

1. Paired horn bases present or absent at front of nasals.
2. Horn bases present or absent posteriorly on nasals.
3. Lower incisors directed forwards or upwards.
4. Lower edge of mandible convex or straight.
5. Premolar row short or long compared with molar row.
6. Cheek teeth higher- or lower-crowned.

UPPER MOLARS:

7. Paracone rib prominent or weak.
8. Trace of mesostyle absent or present.

9. Protocone partially constricted or not.
10. Hypocone partially constricted or not.
11. Antecrochet present or absent.
12. Crochet present or absent.
13. Hypocone flange closing postfossette or not.
14. M^3 ectometaloph straight or curved.
15. Lingual cingula absent or present.

UPPER PREMOLARS:
16. Lingual cingula absent or present.
17. P^3 and P^4 with hypocone and protocone unfused or fused.
18. Metacone rib absent or present on labial wall.
19. Crenulations present or absent on front of metaloph.

LOWER MOLARS:
20. Antero- or posterolabial cingula absent or present.
21. Central labial indentation deep or shallow.

LOWER PREMOLARS:
22. Anterolingual cingula absent or present.
23. Concavity on anterolabial wall of P_2 absent or present.
24. Central labial indentation shallow or deep.
25. P_1 absent or present.

In the above list the first mentioned alternative was considered advanced.

The state of all characters was ascertainable in the Arabian material, but not invariably in the other taxa. Every character state existed in more than one taxon so there were no unique occurrences. Two dendrograms were constructed from this matrix. The first was a phenetic dendrogram (Gentry 1974: 184, based on a method of Corbet & Hanks), for which one counts the differences of the taxa from one another, standardizes the totals as percentages of the number of characters compared, and associates on the dendrogram those forms which are least different. The second dendrogram associates forms sharing the largest numbers of supposedly advanced similarities. Neither dendrogram allows for parallel evolution or displays the contribution of individual characters but each has a percentage scale of difference or similarity.

There were difficulties in constructing these dendrograms. Once a character difference had been spotted between two taxa it was often hard to assign other taxa to one or other state and adoption of intermediate categories was not always satisfactory. Secondly, consistency of assessment was hard when using photographic illustrations, despite the excellent reproduction in many older publications. And finally, on the second dendrogram some character polarities were in doubt. As noted earlier, several early *Brachypotherium* specimens have traces of bipartite horn bases and this could imply descent of hornless rhinoceroses from ancestors with *Diceratherium*-like horns. Again, if Radinsky (1966: 636) is right that procumbency of I_2s is part of the initial family-level specialization of rhinocerotids, then the more upright I_2s of *Aceratherium* should be counted as secondary despite their unspecialized appearance. Alternatively *Aceratherium* could be removed from the Rhinocerotidae. The following comments can be made on the two dendrograms (Fig. 45).

1. The Arabian rhinoceros forms part of a grouping of *Dicerorhinus* species and *Rhinoceros browni* on both dendrograms and within that grouping it associates with early or primitive *Dicerorhinus* rather than with *D. schleiermacheri.*

2. The phenetic dendrogram presents comprehensible major groupings of the rhinoceroses despite the limitations on its construction. One sees on it the three clusters of (A) the mid-Tertiary hornless rhinoceroses plus the primitive *Ronzotherium* and *Diceratherium*; (B) horned rhinoceroses centred upon *Dicerorhinus*; (C) the *Hispanotherium* group. The last two groups are also recognizable on the second dendrogram but here advanced *Brachypotherium* and *Aceratherium* attach themselves to *Hispanotherium* presumably because of parallel advances. The closeness of many of the horizontal linking lines on the chart suggests that repeats of the same exercise would be unlikely to produce the same result.

3. The association of *Chilotherium*, *Chilotheridium* and *Hispanotherium* on both dendrograms supports the view of their similarities taken above. If they should be a natural group, the early Miocene irruption of *Hispanotherium* into Iberia may have come from an African origin close

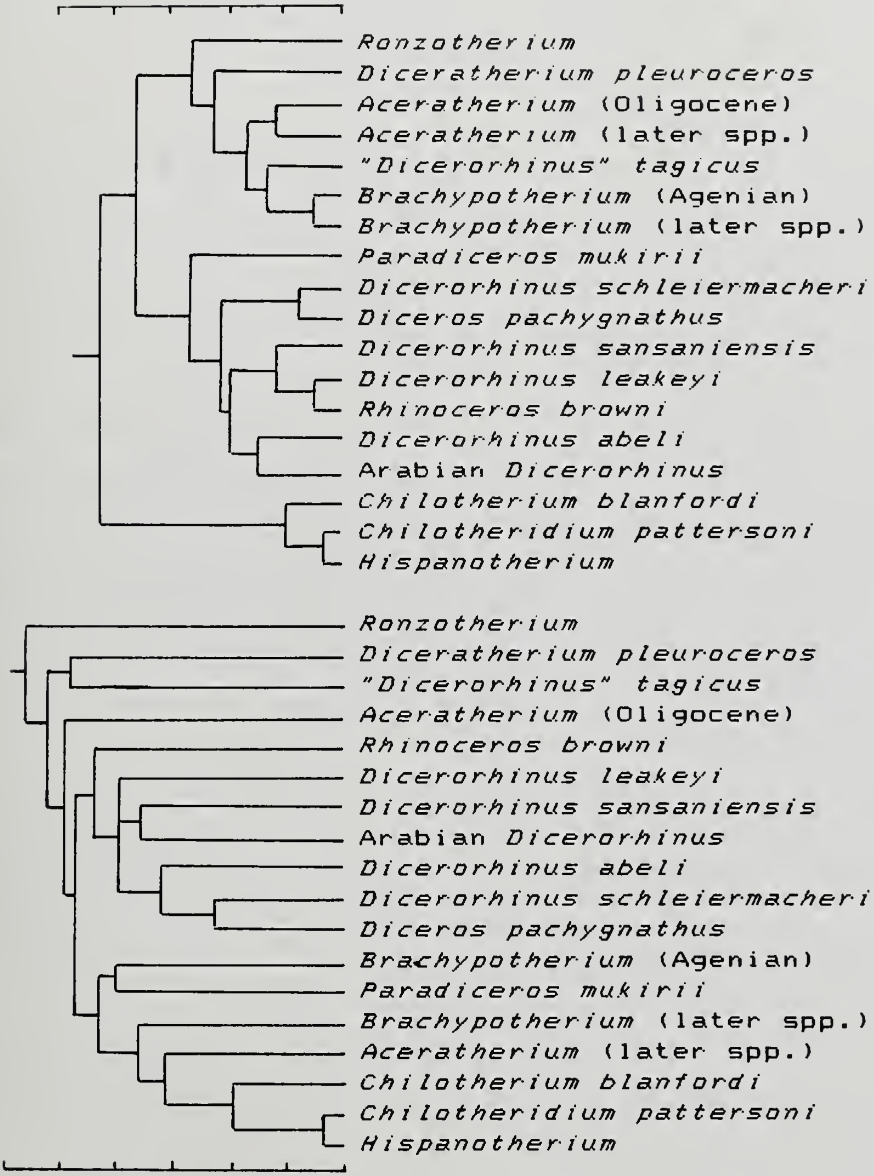

Fig. 45 Above, phenetic dendrogram of relationships among some Oligocene and Miocene rhinoceroses. The scale runs from 10% nearest the names to 60% nearest to the base of the tree. Below, advanced characters dendrogram for the same rhinoceroses. The scale runs from 0% nearest the base of the tree to 60% nearest the names.

to *Chilotheridium* instead of from east to west dispersal along the northern side of Tethys (cf. Antunes 1979).

Genus *BRACHYPOTHERIUM* Roger, 1904

Brachypotherium sp.

Figs 33B, 38B, 39C, 41?, 44C

MATERIAL. Measurements in mm.

M.36300 Tooth fragments including a reassembled labial wall of a left upper molar in middle wear. Occlusal length 56·5. Fig. 33B.
M.36301 Right radius preserved over its complete length but without anterior parts. Overall length 308.
M.36302 Right scaphoid. Fig. 38B.
M.36303 Right metacarpal III, much damaged. Overall length *c*. 148.
M.36305 Left femur without posteroproximal part and with damage medially on patellar groove. Overall length 432. Fig. 41.
M.36306 Left astragalus, much damaged. Dimensions (after Guérin 1980: fig. 22): height 76, anteroposterior dimension (DAP int) 51, breadth (DT) 95. Fig. 44C.
M.36307 Right cuboid.
M.36308 Left metatarsal III, proximal posterior part damaged. Overall length 133; transverse width in middle of shaft 48·5. Fig. 39C.

DESCRIPTION. The large size of the labial wall of an upper molar (M.36300), its flatness and the small size of the paracone rib in comparison with the large flat area leave no doubt of the generic identity being with *Brachypotherium*.

The right radius M.36301 is a little shorter than rhinocerotid radii from Pikermi belonging to either *Diceros* or *Dicerorhinus*, but its shaft width is about the same. Its proportions match closely a radius from Rusinga, M.18908, identified by Hooijer (1966: 148; pl. 9, fig. 1) as *Brachypotherium heinzelini* Hooijer. It is too short to match the complete ulna M.36912.

The scaphoid M.36302 is less high in side view than the other two from Ad Dabtiyah.

Judged from the anterior facet at its distal end, the metacarpal III, M.36303, looks less wide than a corresponding metacarpal III, M.18813, from Rusinga identified by Hooijer (1966: pl. 10, fig. 2) as *Brachypotherium*.

The femur, M.36305, is appreciably smaller than the *Dicerorhinus* femur. Its third trochanter is smaller, it lacks a vertical ridge running down from its great trochanter anterolaterally, and the lateral and medial condyles are less widely separated in ventral view. The presence of any third trochanter at all shows that it must belong to a perissodactyl. If not of a rhinoceros it could perhaps be a chalicothere. Although not very like the femur of the middle Miocene *Chalicotherium grande* (Blainville) figured by Zapfe (1979: 184, fig. 107), it is like the North American *Moropus* Marsh of earlier geological age (Coombs 1978: fig. 13B). However, a right femur of a *Brachypotherium* (Mayet 1908: pl. 2, fig. 3) also looks as if it lacks the vertical ridge, so the present bone is tentatively placed in that genus.

The measurements of the astragalus M.36306 show that it is low and wide, as befits a *Brachypotherium* astragalus. In anterior view the lateral part of the proximal trochleae has quite an overhang. The process low on the medial side also projects well transversely. The top edge of the front of the cuboid facet is widely separated from the base of the more proximal trochlear facets on the anterior surface. The ventral facet for the navicular has a very concave profile in anterior view.

The right cuboid, M.36307, is less deep than that in the associated skeleton of *Dicerorhinus leakeyi* figured by Hooijer (1966: pl. 13, fig. 4) but not quite as shallow as the *Brachypotherium* figured by Guérin (1980: fig. 48G).

The left metatarsal III, M.36308, is shorter and has a wider shaft than the left metatarsal III referred to *Dicerorhinus*. It is longer than the upper Miocene examples of *Brachypotherium* measured by Guérin (1980: 342), but Hooijer (1966: table 17) quoted *Brachypotherium* measurements which match it.

Table 3 *Brachypotherium* species from Europe and Turkey: proportions of astragali (height × 100/breadth) and third metatarsals (breadth × 100/length).

Bone	Proportion	Likely age	Source
Astragalus	89%	Agenian	Measured from Bonis (1973: fig. 32).
	77%	Late Orleanian	Ginsburg & Bulot (1984: 358).
	74%	Late Orleanian	BM(NH) M.7760 from Thenay, France.
	76%	Middle Ataracian	Steinheim (Hooijer 1966: 148, quoting Roger).
	72%	Middle Astaracian	BM(NH) 33529 from Villefranche d'Astarac.
	72%	Late 'Astaracian'	Heissig (1976: 88).
	64%	Late Astaracian	Guérin (1980: 311).
Metatarsal III	31%	Agenian	Mean of three readings from Repelin (1917: 35, 36); Viret (1929: 267).
	37%	Orleanian	*B. stehlini* (Hooijer 1966: 147).
	37%	Middle Astaracian	*B. brachypus* (Lartet) (Hooijer 1966: 147, quoting Roger).
	37%	Late Astaracian	Heissig (1976: 89).
	41%	Late Astaracian	Guérin (1980: 342).

Discussion. A distinctive feature of *Brachypotherium* is the progressive shortening and widening of its limb bones. If this evolved in a straightforward manner during the course of the Miocene it ought to be possible to see how far along the line the Arabian species fits in. Unfortunately there is a shortage of specimens with recorded measurements, but some data for European and Turkish astragali and metatarsals is assembled in Table 3.

The Arabian species has these astragalus and metatarsal ratios at 80% and 36% respectively, which show that it is fairly primitive for a *Brachypotherium* and is likely to date from the Lower or lowest Middle Miocene. One would not expect it to postdate the early Astaracian. However, it should be noted that a Rusinga astragalus measured by Hooijer (1966: 148) has a ratio of 70% yet would probably date in European terms from the earlier Orleanian.

Palaeoecology of Arabian rhinoceroses

Guérin (1980: 380) and many others have commented on the 'hippopotamid' aspect of *Brachypotherium* as manifested by its large skull, barrel-like body and short, stubby limbs. The usual and reasonable conclusion from this is that it was an animal of aquatic habitats. A wooded environment is also often mentioned, which would be a point of difference from *Hippopotamus amphibius*. However, Webb (1983: 289) quotes taphonomic evidence that the north American *Teleoceras* Hatcher, very like *Brachypotherium*, 'lived in the water but grazed on adjacent dense grasslands' exactly as does the modern hippopotamus (Kingdon 1979: 250)—an amazing parallelism for two mammals in different orders and with different digestive strategies.

Miocene *Dicerorhinus* stands close to the ancestry of the extant horned rhinoceroses and what is known of their ecology can be used as a guide to that of the fossil form. The somewhat specialized African rhinoceroses live in lightly wooded areas, preferably with thickets (*Diceros bicornis*) or in more open environments with grasses (*Ceratotherium simum*); both species need access to water (Kingdon 1979: 80–119). *Rhinoceros unicornis* was in historic times an inhabitant of the grassed and wooded Indian alluvial plains and it feeds mainly on grasses (Laurie 1982: table 2). *Dicerorhinus sumatrensis* inhabits densely wooded areas but prefers their margins and disturbed areas. It can ascend and descend steep slopes with agility and, a century or two ago, may have been found in hillier country than the sympatric *R. sondaicus* (Groves & Kurt 1972; van Strien 1975: 37).

One can therefore conclude that the Arabian *Dicerorhinus* is likely to have fed by browsing in wooded habitats with easily available water.

Zoogeography of Arabian rhinoceroses

If the Arabian *Brachypotherium* really is of Lower Miocene age, as implied by the proportions of its astragalus and metatarsal, it could be conspecific with *B. snowi* (Fourtau 1918) from Moghara, Egypt. The occurrence of *Brachypotherium* at this period as far east as Ad Dabtiyah would be interesting inasmuch as Guérin (*in* Pilbeam *et al.* 1979: 36) does not find it in the Siwaliks sequence until after *Hipparion* is present. However, Heissig (1972: 103) claimed to have identified *Brachypotherium* as far back as in the Kamlial Formation.

A comment may also be made here on the question of the occurrence of *Aceratherium* in Africa. The holotype skull of *Turkanatherium acutirostratus* Deraniyagala 1951 from the Middle Miocene of Moruorot, Kenya, was subsequently referred to *Aceratherium* by Arambourg (1959: 74). This fossil was the first described from Africa adequate to sustain an identification as either *Aceratherium* or something else. Its upper cheek teeth are large and wide by comparison with European *Aceratherium.* They do show moderate or strong antecrochets, but in this, as in the two preceding characters, they agree well with the later Miocene *Brachypotherium lewisi* Hooijer & Patterson from Lothagam (Hooijer & Patterson 1972: 2). It is possible that Deraniyagala's skull is the same species or lineage as the short metapodials, phalanges and other elements found in east Africa and referred to *Brachypotherium*, e.g. those of Hooijer (1966: pl. 10, figs 1–3, 6–8). The skull material of *Aceratherium campbelli* Hamilton (1973: table 3; pls 1, 3) from Zelten, Libya, may also have been incorrectly placed at generic level. Its teeth were large and appear to have been wide; it looks very like the Moruorot skull. The high occiput and concave profile of the cranial roof in both skulls is unlike European *Aceratherium* (Mermier 1896: pl. 2, fig. 2; Guérin 1980: pl. 3) but can be matched from within *Brachypotherium* (Mayet 1980: pl. 2, fig. 1). African *Brachypotherium*, as in Europe identified by its short limb extremities, may have been an entirely separate development and have evolved *Aceratherium*-like antecrochets on its upper molars. This idea needs further investigation. If it were correct, the absence of *Aceratherium* at Ad Dabtiyah could be held to align the fauna with Africa rather than with Europe. Unfortunately the concurrent absence of *Chilotheridium* could be held to indicate the reverse. Hence the rhinoceroses reported in this paper remain zoogeographically inconclusive.

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Ruminants from the Miocene of Saudi Arabia

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Synopsis

Six ruminant species have been identified from the Miocene of Ad Dabtiyah, Saudi Arabia. These comprise two tragulids belonging to *Dorcatherium*, the giraffoid *Canthumeryx*, and *Eotragus* and two other bovid species. The tragulid teeth, known only from the smaller of the two species, are well worn. This fauna seems to date from the early Middle Miocene, which would be the later Orleanian or earliest Astaracian of the European scale.

Introduction

The ruminant fossils to be described in this paper come from Miocene continental deposits thought to be laterally equivalent to the Dam Formation, at Ad Dabtiyah, Saudi Arabia. This locality is situated at 26° 27′ 02″ N, 48° 35′ 24″ E. Further details are given in Hamilton *et al.* (1978) and Whybrow *et al.* (this issue, p. 375).

Register numbers of individual specimens refer to the collection of the British Museum (Natural History), London.

Systematics

Order **ARTIODACTYLA** Owen, 1848

Infraorder **TRAGULINA** Flower, 1883

Family **TRAGULIDAE** Milne Edwards, 1864

Genus ***DORCATHERIUM*** Kaup, 1833

Dorcatherium sp.
Figs 46, 48D

Some tragulid remains from Ad Dabtiyah are about the size of *Dorcatherium pigotti* Whitworth (1958: 9) of the east African early Miocene and *Dorcatherium* sp. of Colbert (1935: 311) of the Siwaliks Group, Pakistan. They are smaller than *D. libiensis* Hamilton (1973: 80; pl. 1, fig. 1) from Gebel Zelten, Libya. The first is part of a fragmentary right mandible with P_2 and P_3, M.34278 (Fig. 46C), in which P_3 and the back of P_2 are well worn. The occlusal lengths of P_2 and P_3 are 6·5 and 8·5 mm respectively.

Two pieces of right mandibles (Fig. 46D, E) also show M_2 (M.34279a) and M_3s (both M.34279a and b) in late wear. What can be discerned of the occlusal pattern on the M_3s does not look like a pecoran. The central cavities have wide posterior openings to the outside and the labial lobes are insufficiently narrow and pointed. They lack basal pillars and are thus unlike *D. libiensis*. The occlusal lengths of the M_3s are 12·8 and 13·2 mm.

Three right upper molars and two right upper molars, M.30131 (Fig. 46A) and M.30132 respectively, belong to a tragulid of similar size to the above pieces. They are very well worn. They have a cingulum around the lingual lobes, especially the anterior one, as is usual in tragulids. The posterolabial rounding of the anterior lingual lobe (protocone) also looks tragulid rather than pecoran. The rib between parastyle and mesostyle is less deflected anteriorly than in the Siwaliks *Dorcatherium* of Colbert (1935: figs 138, 141, 143), which perhaps indicates that the Arabian fossils are geologically older. The occlusal lengths of M^1 and M^3 in M.30131 are 8·3 and 9·7 mm; the two upper molars in M.30132 measure 8·7 mm (front one) and 9·1 mm (rear one).

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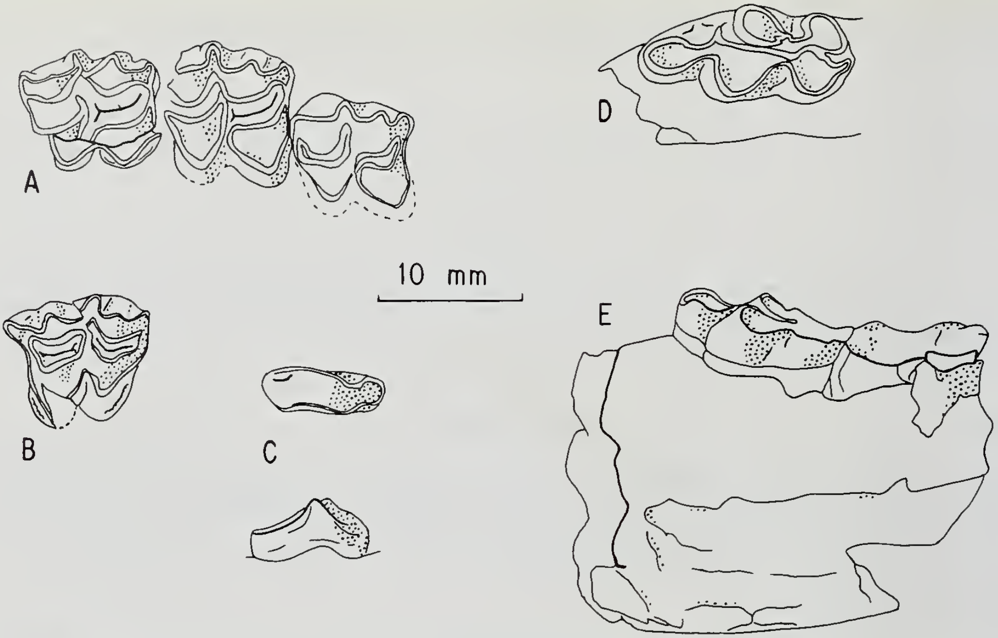

Fig. 46 Teeth of *Dorcatherium* from Ad Dabtiyah. Anterior side to right (except B). A, occlusal view of right M$^{1-3}$, M.30131. B, occlusal view of left dP^4, M.30133. C, occlusal and lateral views of right P$_3$, M.34278. D, occlusal view of right M$_3$ in mandible, M.34279b. E, lateral view of another right mandible with M$_{2-3}$, M.34279a.

M.30133 is a left dP^4 in late middle wear with an occlusal length of 9·3 mm (Fig. 46B). It has a notably large parastyle and a cingulum on its lingual lobes. The strong parastyle and the convergent front and back walls of the tooth suggest it is a dP^4 and not a molar.

Thomas *et al.* (1982: 127) have reported a similar-sized *Dorcatherium* from Al-Sarrar.

A right and a left astragalus (M.35265; M.35266, Fig. 48D), a left naviculocuboid plus ectocuneiform (M.35267) and a proximal left metatarsal (M.35268) have tragulid morphology and are about the size of *D. pigotti.*

Dorcatherium, larger sp.
Fig. 48A–C

A further left astragalus, M.35269 (Fig. 48C), is larger than those assigned to the above *Dorcatherium* sp. and matches the size of *D. chappuisi* Arambourg of the east African early Miocene (see Whitworth 1958: 4). Much of a left tibia including the distal end, M.35079 (Fig. 48A, B), could also belong here. It is larger than the tibia of the living *Hyemoschus aquaticus* and the distal articular facet is longer anteroposteriorly and less wide transversely. These proportions are nearer to those of Suidae and therefore presumably nearer to the ancestral state. The total length of the tibia would have been in the region of 150 mm.

Infraorder **PECORA** Linnaeus, 1758

Superfamily **GIRAFFOIDEA** Simpson, 1931

Genus ***CANTHUMERYX*** Hamilton, 1973

Canthumeryx sp.
Fig. 48E

A much damaged but practically complete giraffoid left metatarsal, M.34277, is about 320–330 mm long and about 36 mm wide across its distal condyles. It is close in size to the metatarsal of *Canthumeryx sirtensis* Hamilton from Moruorot, Kenya (Arambourg 1947: pl. 22, fig. 5; Hamilton 1978: 178) but about 25%–30% longer and thereby presumably more advanced. It is too gracile to belong to a *Palaeomeryx* such as that known from Sansan, France.

A left unciform, M.35078 (Fig. 48E), is also of an appropriate size to belong to *Canthumeryx*. Compared with modern Bovidae it shows more resemblance to Tragelaphini than to Alcelaphini, in that the back of the facet for the cuneiform is less deeply excavated towards the ventral edge of the bone, and also in that there are separate dorsal and ventral facets on the posterior part of the medial side. It differs from examples of extant giraffids, cervids and bovids in having a prominent downturned flange posteriorly.

Thomas *et al.* (1982: 124) recorded a probable *Canthumeryx* from the Al-Sarrar locality. They illustrated an upper molar (1982: pl. 116, fig. 5) on which the rather bulky condition of styles and anterior rib are presumably owing to late wear. They draw attention to the difficulty in identifying giraffoids from isolated upper teeth. Among their other remains was a metacarpal with a length and distal condylar width of 360 mm and 38 mm respectively. According to Pickford (1981: 96) *Canthumeryx* belongs to 'Set II' faunas in east Africa, dating from 18·5–16.5 Ma and possibly to 'Set III' ones at 16·5–14·5 Ma. It is zoogeographically interesting that the mandible with M_{2-3} of *Progiraffa exigua* from Dera Bugti (Pilgrim 1911: pl. 1, fig. 1) looks as if it could be congeneric with *Canthumeryx* (as Hamilton had independently recognized—Patterson 1981: 462). This slightly later faunal element contrasts with the antique aspect of most of the Bugti mammals and perhaps came from a higher level; Pilgrim (1912: 2) and Pascoe (1964: 1656) refer to bones in the deposit being scattered through most of its thousand-foot (305 m) thickness. *Canthumeryx* precedes and may be ancestral to *Giraffokeryx* Pilgrim, and also to pre-*Hipparion* representatives of *Palaeotragus* Gaudry which Hamilton (1978: 200) believed to be not congeneric with the type species *P. roueni*. *Canthumeryx* is unknown from Europe.

Superfamily **BOVOIDEA** Simpson, 1931

Family **BOVIDAE** Gray, 1821

Genus ***EOTRAGUS*** Pilgrim, 1939

Eotragus sp.

Figs 47A, 48F

This is represented by M.30134, a left P_3, P_4 and M_1 in early wear and with occlusal lengths 9·3, 11·1 and 12·0 mm respectively (Fig. 47A). The central parts of the M_1 are missing. The size and proportions of the teeth would be similar to *Protragocerus* Depéret, e.g. *P. labidotus* Gentry (1970: 247) of Fort Ternan, except that they are lower-crowned and the basal pillar on the molar is smaller, both of which make them like *Eotragus* as illustrated in Thenius (1952). A trace of an anterior cingulum on the molar is like both *Eotragus* and *P. gluten* (Pilgrim) of the Siwaliks. The premolars match *Eotragus* and *Protragocerus* in that the anterolabial wall is not turned to lie in a transverse plane, in the diagonal alignment of the metaconid, and in the weak differentiation of a paraconid. The molar is about the size of a bovid lower molar from Maboko, Kenya (Whitworth 1958: Fig. 10a–c), but the labial lobes may be more narrowly pointed. The teeth are a little larger and higher-crowned than in the bovid-like pecoran *Walangania africanus* (Whitworth 1958) from the east African early Miocene (Hamilton 1973: 146), and the molar has a smaller basal pillar, no diagonal fold on the rear wall of the protoconid (*Palaeomeryx* fold), a weaker metastylid and a weaker anterior rib on its lingual wall. A probable bovid from Arrisdrift, Namibia (Hendey 1978: fig. 12) is smaller and has quite a strong paraconid on its P_4.

Eotragus is the most likely identity for M.30134. This genus is known in Europe from the Orleanian and Astaracian (MN 4–7 of Mein 1975, 1979). It also appears to be represented at Gebel Zelten, Libya by horn cores M.26688 and M.26689 (Hamilton 1973: 127; pl. 13, fig. 1), and comes in at Maboko in the east African succession of Miocene faunas with a cranial roof

M.15544 (Gentry 1970: 303; Thomas 1979: 296). It may be present at the later Fort Ternan locality (Gentry 1970: 261; pl. 15, figs 6, 7). Pickford (1981: 96) has Maboko as one of his 'Set III' faunas with a probable age back to 16·5 Ma.

A partial right horn core of a bovid, M.34270, has only the anterior part of its base preserved, along with the supraorbital pit and part of the frontal. Its insertion angle is inclined backwards at about the same angle as in *Eotragus*. The supraorbital pit is narrow. Not enough is left of the horn core above the pedicel for definite identification as *Eotragus*.

The greater part of a left astragalus, M.34271 (Fig. 48F), rather larger than in *Walangania*, could also belong to the same species as M.30134.

Bovidae, Genera indet.

Bovid species 2

Fig. 47B

The back part of an unworn right M_3, M.34272, looks like a bovid and comes from a larger species than M.30134. It is like M.42005, the back of an M_3 identified as cf. *Oioceros* sp. and coming from Jabal Midra ash-Shamali in the Hadrukh Formation (Whybrow *et al.* 1982: 110). It is smaller than M.42005 but about as hypsodont. Further, the entostylid part of the middle lobe on the lingual side of the tooth is at a markedly lower level than the entoconid constituting the rest of this lobe, a character unlike other bovids but probably present in M.42005.

Bovid species 3

Figs 47C–F, 48G–K

The back of a right M_3, M.34273 (Fig. 47C), is in early middle wear and may belong to a species smaller than M.30134 and about the size of the bovid from the Dam Formation at Al-Sarrar (Thomas *et al.* 1982: 126; pl. 116, figs 6, 7). It is about as high-crowned as *Eotragus*.

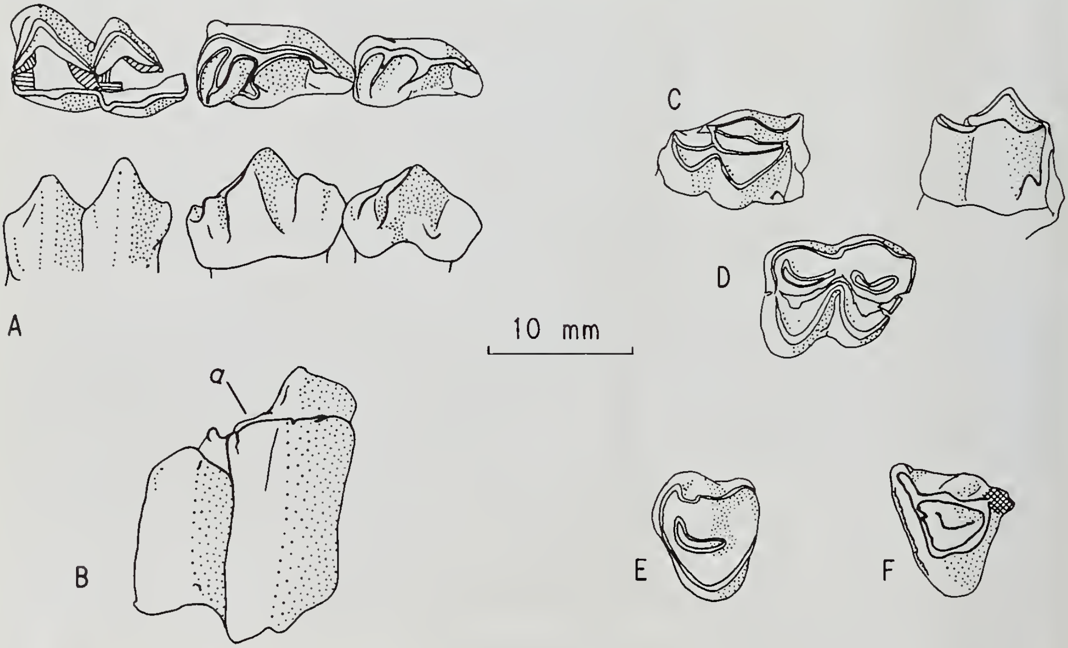

Fig. 47 Bovid teeth from Ad Dabtiyah. Anterior side to right (except E). A, *Eotragus* sp., occlusal and medial views of left P_3–M_1, M.30134. B, bovid sp. 2, lateral-occlusal view of back part of right M_3, M.34272; *a* indicates low entostylid behind entoconid. C–F, bovid sp. 3. C, occlusal and lateral views of back part of right M_3, M.34273. D, occlusal view of right lower molar, M.34274. E, occlusal view of left P^4, M.34275. F, occlusal view of right P^4, M.34276.

The hypoconulid, or the main part of the rear lobe, has a flat lingual wall. A flange, present at its posterior end, does not loop round anteriorly to meet the entostylid or entoconulid and thus enclose a central cavity. This makes the specimen unlike *Walangania* but more like most *Eotragus* and the Arrisdrift, Namibia (Hendy 1978) species. But its condition is not like the early *Eotragus* which at Artenay, France (Ginsburg & Heintz 1968; pl. 1, figs 4a, b) has a completely enclosed central cavity. The entostylid of M.34273 is less large than in the Arrisdrift specimen. The central cavity on the second lobe does not open to the exterior posteriorly.

Thomas *et al.* (1982: 126) suggested that the Al-Sarrar bovid was congeneric if not conspecific with the Arrisdrift species. However, it can be seen from their figure (1982: pl. 116, fig. 6) that P_{3-4} are about as long as in the Arrisdrift specimen whereas M_{1-3} is considerably longer. From my own measurements the premolar row length would have been around 75% of that of the molar row length in the Arrisdrift specimen whereas on the two illustrated Al-Sarrar specimens the same ratio is around 61%. It is thus unlikely that they could be conspecific.

A right lower molar in middle wear with an occlusal length of 9·5 mm, M.34274 (Fig. 47D), could also belong to the same species. It is smaller than the M_1 of M.30134 and is close in size to the molars of *Gazella* from Gebel Zelten (Hamilton 1973: 128; pl. 13, figs 2, 3). It has transversely long labial lobes, a tiny basal pillar, and may be higher-crowned than M.30134.

A left P^4 in middle wear, M.34275 (Fig. 47E), has an occlusal length of 7·1 mm and a right P^4 in early wear, M.34276 (Fig. 47F), has an occlusal length of *c.* 7·8 mm. They are low-crowned but smaller than *Eotragus*. The second can be seen to differ from *Eotragus* by its stronger metastyle and stronger rib in front of it, and by a narrower lingual part of the tooth. The last feature is presumably primitive.

A proximal right tibia, M.35080 (Fig. 48G, H), smaller than *Protragocerus labidotus* (Gentry

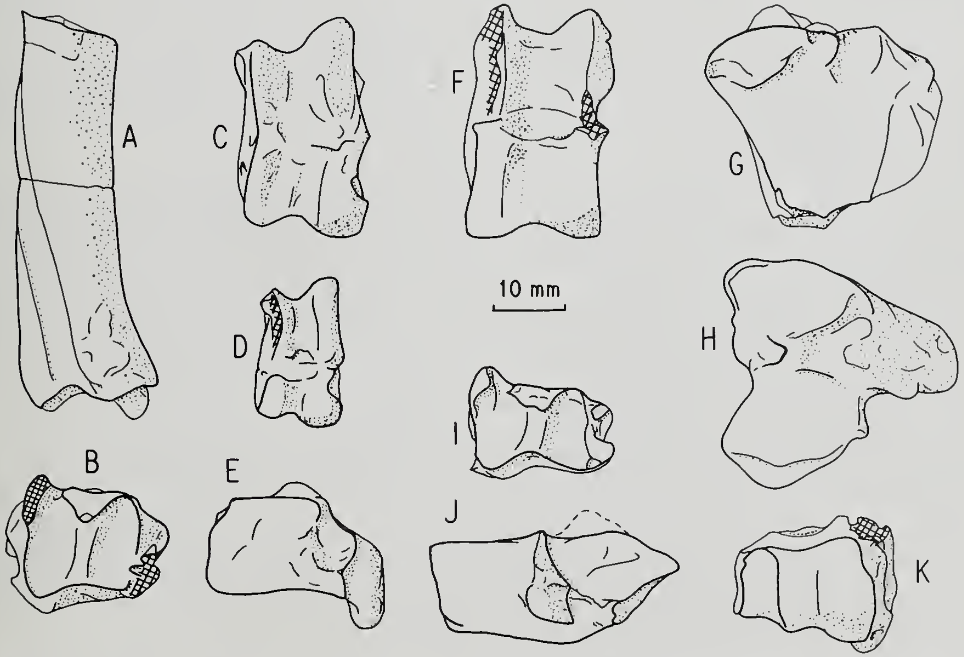

Fig. 48 Ruminant postcranial bones from Ad Dabtiyah; cross-hatching indicates areas of broken bone. A–C, *Dorcatherium*, larger sp. A, medial view of distal left tibia, M.35079. B, articular surface of same, anterior side towards top. C, anterior view of left astragalus, M.35269. D, *Dorcatherium* sp., anterior view of left astragalus, M.35266. E, *Canthumeryx* sp., lateral view of left unciform, M.35078. F, ?*Eotragus* sp., anterior view of left astragalus, M.34271. G–K, bovid species 3. G, lateral view of proximal right tibia, M.35080. H, articular surface of same, anterior side towards right. I, articular surface of distal left tibia, M.35070, anterior side towards top. J, medial view of partial left calcaneum, M.35071. K, anterior view of distal right humerus, M.35074.

1970: pl. 11, fig. 2) or *Walangania*, may also be of this species. It shows boselaphine or possibly primitive characters like *P. labidotus* in that there is only a shallow hollowing between the two flanges in the centre of the top articular surface, there is little differentiation of a tubercle and medial hollow in the area in front of the flanges, and the lateral edge of the lateral facet is not upwardly turned. A distal left tibia, M.35070 (Fig. 48I), has an anterior as well as a posterior facet for the fibula.

Three partial calcanea, M.35071–3 (Fig. 48J), look pecoran but come from animals smaller than *Walangania*. A distal right humerus, M.35074 (Fig. 48K), could also be of the same species.

Either or both of two first phalanges, M.35081–2, also belong to a species smaller than *Walangania africanus*. The central groove on the proximal articular surface passes completely to the front edge of the bone. In this they look fully pecoran, i.e. more advanced over the tragulid condition than in some BM(NH) examples of early Miocene '*Dremotherium*' from Allier, France. Of course it is conceivable that in early pecorans the front and back legs might be different for such a character as this. The Ad Dabtiyah phalanges have at best only indistinct facets at the back of the proximal articular surfaces for the sesamoid bones.

Discussion of ruminant fauna

The tragulid teeth from Ad Dabtiyah are well worn but appear to belong to *Dorcatherium*, first known from the early Miocene (*c.* 19–20 Ma) of east Africa and probably contemporaneously in Europe. It may also be noted that *Dorcatherium* occurs in the basal Miocene of the upper part of the Nari Formation at Dera Bugti, Pakistan; a cast M.11080 of M_2–M_3 of '*Gelocus ?gajensis*' Pilgrim (1912: pl. 25, fig. 5) is very close or identical to the east African *D. chappuisi*.

A larger species of *Dorcatherium* is represented by postcranial bones.

Canthumeryx has been recorded, but no remains definitely identifiable as Cervidae.

The main bovid species from Ad Dabtiyah resembles an *Eotragus*; the second and larger species is like the primitive cf. *Oiceros* sp. of the Hadrukh Formation (Whybrow *et al.* 1982: 109); a third probable bovid is smaller than the *Eotragus* and is possibly the same species as that described by Thomas *et al.* (1982: 126) from Al-Sarrar.

Ruminants like these suggest that the fauna dates from before the period of Fort Ternan and is about equivalent to Maboko in the east African Miocene. It would thus be from the early Middle Miocene and would be expected to correspond to later Orleanian or early Astaracian in European terms. This is a more precise temporal placing than was possible with the rhinoceroses (Gentry, this issue, pp. 425, 429) and is later than suggested by the mastodon (Gentry, this issue, p. 406). Thomas *et al.* (1978: 71) and Thomas (1983) record *Protragocerus*, *Gazella* and *Caprotragoides potwaricus* (Pilgrim) from the Hofuf Formation overlying the Dam Formation. Such an assemblage would match Fort Ternan and kindred sites and gives support for the earlier age suggested for the underlying fauna herein described.

Palaeoecologically it may be noted that *Dorcatherium* is an important constituent of the Kenyan early Miocene communities held by Evans *et al.* (1981: 116) to have inhabited forests. Modern tragulids too are inhabitants of forests. With *Canthumeryx* the difficulty would be to choose between okapi (forest) and giraffe (savanna) as analogues for habitat choice. The appearance of any bovids at all in a Miocene fauna can be held to herald less closed habitats, but only one of the species shows possible beginnings of hypsodonty which could, but need not, be correlated with grazing. Maboko is the African locality with the most similar list of ruminant taxa and here the deduced habitat was woodland (Evans *et al.* 1981: 112).

The ruminants, as well as the mastodon and rhinoceroses described elsewhere in this issue, largely fail to indicate zoogeographical relationships for the Ad Dabtiyah fauna. *Canthumeryx*, being unknown in Europe, would have suggested an African affinity but for the Manchar Formation, Pakistan (Raza *et al.* 1984: 591) and Bugti occurrences of the probably congeneric *Progiraffa exigua*. Detailed study of original material of *Gomphotherium*, *Dicerorhinus*, *Dorcatherium* and perhaps *Eotragus* in various museum collections might, or might not, allow one to discriminate morphologically between allied species living on different continents during the Miocene, but hitherto there has been little consideration of this question.

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Miocene Suidae from Ad Dabtiyah, eastern Saudi Arabia

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Synopsis

Two of four suid teeth from Ad Dabtiyah, Saudi Arabia, are ascribed to *Listriodon*; the others are fragmentary. A Middle Miocene (Mein Zone 4a or 4b) age is suggested. The wider significance of the assemblage is discussed.

Introduction

Four suid teeth from Ad Dabtiyah, Saudi Arabia, have been examined and assigned to two taxa, one of which is a reliable marker for the Middle Miocene period in Europe, India and Africa. The best preserved specimens, an M^3 and an M_3, belong to a bunodont, thick-enamelled listriodont similar to *Listriodon lockharti* (Pomel) from early Middle Miocene strata of Europe, and to *Listriodon akatikubas* Wilkinson from sites of similar age in Kenya. The remaining two specimens are fragmentary, one of them being an incompletely formed tooth germ. Both, however, are bunodont and recall the genera *Conohyus* Pilgrim and *Kenyasus* Pickford, but the material is too incomplete for the purposes of specific identification. A specimen from another collection from Saudi Arabia suggests affinities with *Kenyasus*, a relatively common genus in the Kisingiri sites of Rusinga, Karungu and Uyoma, dated about $17{\cdot}8 \pm 0{\cdot}2$ Ma (Drake *et al.*, in prep.).

Viewed as an assemblage, the four teeth would not be out of place in early Middle Miocene strata of East Africa and Europe, perhaps 16–17 Ma old. The listriodont teeth in particular appear to represent a period of evolution prior to *Listriodon splendens* von Meyer of Europe and *L. pentapotamiae* (Falconer) of late Middle Miocene strata of Pakistan. Correlation of the Ad Dabtiyah site with Mein Zone 4a or 4b, and Maboko (Kenya), is indicated. This leads us to postulate that the Ad Dabtiyah site preserves faunal elements which lived just after the closure of the Tethys at the beginning of the Langhian Stage, an event which not only provided 'dryshod' access for Eurasian faunas to Africa and *vice versa*, but also resulted in major global climatic changes recorded in western Kenya, the Tethys, and as far afield as Japan. Zoogeographic boundaries shifted latitude during this event, which resulted in the widespread establishment of African faunal elements in southern Eurasia and a marked influx of Eurasian faunal elements into Africa. *Listriodon* was one of these widespread genera, which makes it a useful biostratigraphic marker for this and immediately subsequent periods.

Systematics

Subfamily **LISTRIODONTINAE** Simpson, 1945

Genus ***LISTRIODON*** Von Meyer, 1846

Type species. *Listriodon splendens* von Meyer, 1846

Listriodon cf. ***lockharti*** (Pomel, 1848)

Figs 49–50

Material. Right M_3 M.42949; right M^3 M.42950.

Description. M.42949 is a right M_3 lacking the anterior buccal cusp. The cusp morphology and simple talonid of this tooth indicate that it belongs to the genus *Listriodon*, although its

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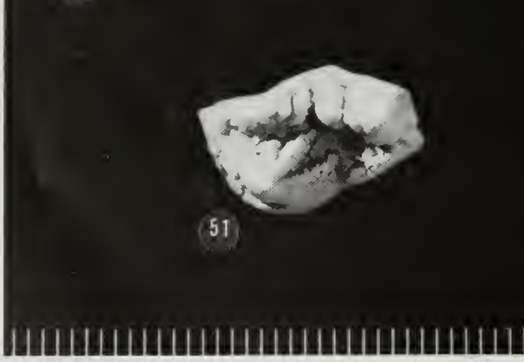
enamel is somewhat thicker and the cusps more bunodont than in *L. splendens* and *L. pentapotamiae*. The median accessory cusp is large but closely joined to the cross lophs which are well formed, but low. The 'furchen' or grooves are well marked considering the wear stage of the tooth and its listriodont affinities. The talonid is simple and strongly joined to the posterior loph *via* the posterior accessory cusp. There are cingular remnants in the ends of the buccal valleys. The overall morphology of this tooth resembles that seen in bunodont listriodonts from Europe and Africa.

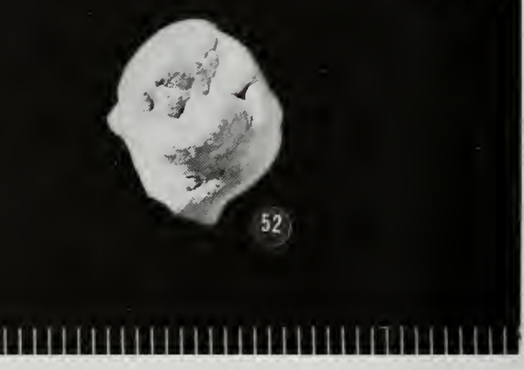
The length and estimated breadth of M.42949 at the base of the crown are 32·8 and 19·5 mm respectively.

M.42950 is a right M^3 lacking only the roots and small fragments of enamel at the cervix level. Its enamel is thicker than is usually found in *L. splendens* and the tooth is more bunodont and lower-crowned, while the lophs are less well formed than in *L. pentapotamiae*. The 'furchen' are not clear, because they have apparently been eradicated by wear which has advanced to the stage where dentine is exposed on the two lingual cusps. The talon is simple and the lingual flare is marked.

The length and breadth of M.42950 are 25·9 and 22·0 mm respectively.

DISCUSSION. These two teeth probably belong to the same taxon, a bunodont listriodont close to *Listriodon lockharti* (Pomel, 1848) or *L. akatikubas* Wilkinson 1976. Teeth like these have





Figs 49–50 M.42949 and M.42950, respectively lower and upper third molars of a bunodont *Listriodon*. Ad Dabtiyah, Saudi Arabia.

Fig. 51 M.42951, fragment of lower molar of a bunodont suid, possibly *Kenyasus*. Ad Dabtiyah, Saudi Arabia.

Fig. 52 M.42952, fragment of unerupted and incompletely formed lower molar of a bunodont suid. Ad Dabtiyah, Saudi Arabia.

never been reliably recorded from Lower Miocene sites in Kenya, despite the reports of Wilkinson (1976). Indeed, the subfamily Listriodontinae is unknown in Kenyan Lower Miocene deposits. The genus *Bunolistriodon* is a synonym of *Listriodon* (see Leinders 1975). In any case the material identified as *Bunolistriodon* by Arambourg (1963) and Wilkinson (1976) belongs to the subfamily Kubanochoerinae Gabunia, 1960 (Pickford 1985). The Ad Dabtiyah listriodont teeth do not resemble the species ?*L. akatidogus* Wilkinson, which is probably not a listriodont suid, but possibly a tayassuid (Pickford 1985). The only African species which resembles the Ad Dabtiyah sample is *Listriodon akatikubas*, which is known from Maboko, Nyakach, Kirimun and Fort Ternan, all Middle Miocene sites in Kenya.

From the European viewpoint, the Ad Dabtiyah listriodont teeth resemble those of *L. lockharti* known from a number of lower middle Miocene sites in southern Europe such as La Romieu (France), and from Pasalar (Turkey). The teeth are considerably more lophodont than the most lophodont Orleanian suids of southern Europe, such as *Palaeochoerus giganteus* described by Golpe-Posse (1972). The Saudi Arabian teeth are considerably more bunolophodont than teeth assigned to *L. splendens*, which is characteristic of late Vindobonian localities of Europe. As far as is known, the genus *Listriodon* has at most only minimal overlap in time with *Hipparion*, its stratigraphical range being nearly totally limited to the Middle Miocene.

From the Asian viewpoint the Saudi listriodonts compare with some of the teeth identified as *Listriodon guptai* from the Sind in Pakistan (Pilgrim 1926), although much of this material is more likely to represent *L. pentapotamiae*, a very lophodont form from Chinji levels in the Potwar Plateau. *Listriodon affinis* from Bugti is inadequately known, and the holotype may well represent a kubanochoere, (Pickford, in prep.). In any case it does not match the Saudi specimens. It therefore seems that in Asia *Listriodon* is confined to Middle Miocene deposits as it is in Africa and Europe.

Taking everything into consideration, I consider it likely that the Ad Dabtiyah listriodonts indicate an age close to Mein Zone MN 4a or 4b or perhaps a little later (Mein 1977, 1979, 1985). This would correspond to middle Orleanian deposits.

Subfamily ? **KUBANOCHOERINAE** Gabunia, 1958

Genus indet.

Figs 51–52

MATERIAL. M.42951, less than half the crown of a left lower molar; M.42952, distal half of an incompletely formed left lower molar.

DESCRIPTION. M.42951 is less than half of the crown of a left lower molar. The enamel is relatively thick, the cusps appear to be rounded and the 'furchen' are relatively shallow. There is a beaded cingular remnant in the buccal end of the median valley and the median accessory cusplet is small. These features suggest that we might be dealing with the genus *Kenyasus* Pickford (1985) or *Conohyus* Pilgrim. It is unlikely that the tooth belongs to *Hyotherium* von Meyer, although in view of the fragmentary nature of the specimen there must be room for doubt. The somewhat open labial notch is wider than is usually the case in *Conohyus*, which possibly tilts the balance in favour of this specimen representing a kubanochoerine such as *Kenyasus*.

M.42592 is the distal half of an incompletely formed lower molar. Considering that it was not fully formed at the time of death of the individual, it is difficult to make a valuable statement about this tooth. It may perhaps represent the same taxon as the previously described fragment.

DISCUSSION. I have seen a small kubanochoerine tooth in another collection from Saudi Arabia, which seems to be close in morphology to the Lower Miocene *Kenyasus rusingensis*. It is likely that this tooth and M.42591–2 described above belong to a single taxon. If these suppositions are correct, then it would follow that we are examining a suid which is usually Lower Miocene in age, although it extends up to lower Middle Miocene sites in Kenya such as Nachola.

In view of the fragmentary nature of these two specimens, I weigh the listriodont teeth as far more valuable from the point of view of biostratigraphy. Nevertheless, the presence of *Kenyasus* at Ad Dabtiyah, if it is eventually sustained, would not invalidate an age estimate of lower Middle Miocene, but would suggest that it was very early in that period. Kubanochoeres seem to have evolved in Africa, spreading into Eurasia during the Middle Miocene, where they have been recorded from Turkey, Georgia, China and India (Pickford 1985). It is possible that Ad Dabtiyah records the first of these emigrant kubanochoeres.

Palaeozoogeography

Ad Dabtiyah has yielded only a small sample of suids, but they are exceptionally interesting from the point of view of zoogeography. Suids often seem to be in the vanguard of emigrations. Along with gomphotheres, they seem to comprise a sort of 'chef de file', appearing in new regions in advance of many other taxa. They are therefore generally good indicators for changes in environment or for the opening up of migration pathways.

At Ad Dabtiyah, it is possible that a crossing of the ways has been sampled, with the genus *Listriodon* making its way into Africa and the genus *Kenyasus* emigrating to southern Eurasia. I would be happier, however, if we had more definitive samples of the bunodont suid from the site before fully accepting this.

Although we need not postulate the existence of 'dryshod' access across the Tethys to account for the migration of suids and proboscideans, it would appear that the Tethys had indeed closed by the time the Ad Dabtiyah sediments accumulated (Adams *et al.* 1983, Whybrow 1984, Thomas 1985). Closure of the Tethys would surely have had marked effects on regional and perhaps global climates as a result of changes in circulation of the Atlantic and Indian Oceans. It was at about the time of the postulated closure that widespread 'heating' events occurred in the western Tethys (Anon. 1984), Japan (the Kurosedani event, Karyu *et al.* 1984) and western Kenya (Pickford & Senut, in prep.). In west Kenya the regional climate, as inferred from fossil terrestrial gastropods, was humid and hot during the Lower Miocene (at Koru, Songhor and Rusinga) but changed dramatically by the time the Maboko sediments accumulated. At Maboko, the gastropods suggest that the region was a semi-desert with gallery forests fringing the rivers. Somewhat later, at Fort Ternan, cooler, wetter conditions were re-established.

The Kurosedani event in Japan is characterized by the establishment of tropical to sub-tropical mangroves and associated mollusc assemblages in many parts of Japan, at least 1000 km north of their closest living occurrences. Sea temperatures in Japan rose by 10°C (summer temperatures) or 20°C (winter temperatures). This event has been dated between 15–16 Ma (Karyu *et al.* 1984).

It is tempting to ascribe these 'heating' events at the beginning of Langhian times, observed in three widely separated areas, to a single cause, occurring as they do at about the same time (as far as current datings indicate). If this is so, then a single major geological event such as closure of the Tethys might represent the fundamental root cause of such a global effect.

Confirmatory evidence is afforded by the faunas, which underwent marked changes in many parts of the Old World at about the same time. The faunas of western Kenya underwent a major turnover between Rusinga (Lower Miocene) and Maboko (Middle Miocene) (Pickford 1981). West European faunas underwent comparable changes, which have been utilized in defining the boundary between Lower and Middle Miocene faunas in that part of the world (Mein 1979). Although the Asian evidence is not so well dated, it seems that similar changes in fauna may have occurred at the beginning of the Middle Miocene.

For these widespread and apparently synchronous faunal changes to have occurred, it seems likely that tropical and sub-tropical zoogeographic conditions extended appreciably further north during the Middle Miocene than they did before. Even the suid evidence on its own supports this contention because at present, and at times during the past, suids have shown marked latitudinal stratification, with well-defined Palaearctic elements clearly distinguishable from their more southerly tropical counterparts (Pickford 1985, and in prep.). At Ad Dabtiyah and penecontemporary sites we have what I consider reasonable evidence that the Ethiopian zoogeographic realm had spread northwards at the expense of the Palaearctic realm, and that it incorporated Saudi Arabia and much of southern Eurasia. In this respect the evidence of the suids from Ad Dabtiyah is most intriguing: clearly, however, better samples are required. In particular, the reports of giant kubanochoeres at Al-Sarrar (Thomas *et al.* 1982) may provide further support for the hypothesis that zoogeographic boundaries shifted northwards during the Middle Miocene.

In conclusion, on the basis of the suids from Ad Dabtiyah, I see no reason to consider the locality as being Lower Miocene in age, unless one either is prepared to re-arrange the upper boundary of the Lower Miocene period to include Mein Zone 4a, or wishes to postulate that the genus *Listriodon* appeared substantially earlier at Ad Dabtiyah than it did in Europe, Africa or Asia.

Acknowledgements

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A delphinoid ear bone from the Dam Formation (Miocene) of Saudi Arabia

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Synopsis

A right periotic of a dolphin-like cetacean was found in near-shore marine rocks of Burdigalian age in eastern Saudi Arabia. Its resemblance to ear bones of primitive Delphinidae suggests that a primitive delphinid, or an advanced kentriodontid, lived in the Tethys epicontinental sea in Burdigalian times.

Introduction

A single delphinoid ear bone was collected by P. J. Whybrow in 1979 from the type locality of the Dam Formation at Jabal Lidam, 26° 21′ 42″ N, 49° 27′ 42″ E, eastern Saudi Arabia. It is the first cetacean fossil to be reported from Saudi Arabia. Fragmented ribs of sirenians were also found at the locality.

Systematic palaeontology

Order **CETACEA** Brisson, 1762

Suborder **ODONTOCETI** Flower, 1867

Superfamily **DELPHINOIDEA** Flower, 1864

Delphinoidea, gen. et sp. indet.

Fig. 53

MATERIAL. A right periotic, M.42836.

DESCRIPTION. Among the holdings of the United States National Museum of Natural History (USNM 258859), a periotic of the living species *Sousa chinensis* Osbeck 1765 from the Gulf of Siam, is most similar to the fossil. The pars cochlearis is similarly prominent (transverse measurement from apex of pars cochlearis to posterior border of anterior process = 20·2 mm in M.42836 and 21·2 mm in USNM 258859), although in the fossil, its dorsal side is slightly more bulbous than in *S. chinensis*. In both the fossil and *S. chinensis*, the foramen singulare and the internal aperture of the Fallopian aqueduct are included in the depression of the internal auditory meatus (Fig. 53a); this depression is slit-like, is widest in the area of the internal auditory meatus, and is orientated at an angle of about 45° to the transverse axis of the pars cochlearis. It is separated from the triangular hollow surrounding the opening of the endolymphatic duct by a keel on its lateral margin (see Kasuya 1973: 34, fig. 65).

In both the fossil and *S. chinensis*, the anterior process is only slightly elongated, is turned only slightly in a medial direction, and has a rectangular end (Fig. 53b); the posterior process, seen laterally (Fig. 53c), is in the same plane as the anterior process; its articular surface in both specimens bears fine grooves where it was attached to the tympanic (Fig. 53b). The fossil periotic is 28·75 mm long; its pars cochlearis is 16·2 mm long at the base. The ratio between these measurements reflects the shortness of the anterior and posterior processes. In both specimens, the superior process is divided into lateral and dorsal planes by a longitudinal keel.

Barnes (1978) raised the Kentriodontinae of Slijper 1936, a subfamily of the Delphinidae, to family rank as the Kentriodontidae, a family of middle and late Miocene delphinoid cetaceans which are more primitive than the Delphinidae. The Arabian specimen differs from the periotics of species of Kentriodontidae in having derived characters typical of Delphinidae. It differs from *Kentriodon*, *Liolithax kernensis* Kellogg 1931, and *Delphinodon dividum* True 1912 in

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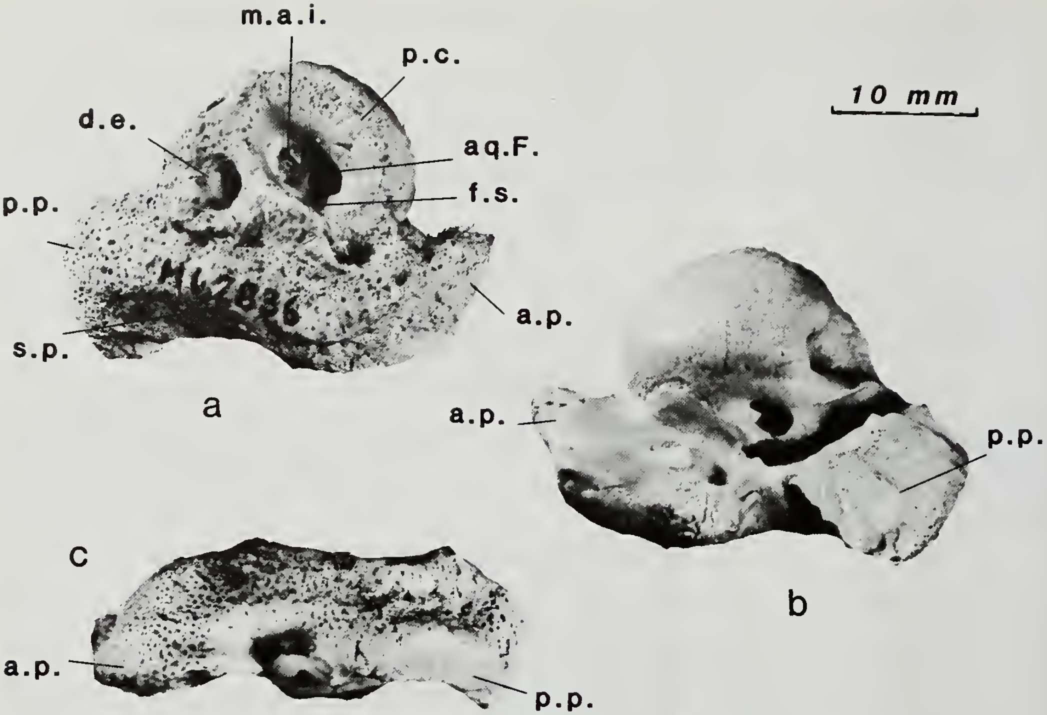

Fig. 53 Delphinoidea, genus and species indeterminate. Right periotic, BM(NH) M.42836. a, cerebral (dorsal) view; b, ventral view; c, lateral view. × 2. Key: a.p., anterior process; aq.F., opening of Fallopian aqueduct; d.e., opening of endolymphatic duct; f.s., foramen singulare; m.a.i., internal auditory meatus; p.c., pars cochlearis; p.p., posterior process; s.p., superior process. From Dam Formation, Jabal Lidam, Saudi Arabia. Burdigalian.

having the anterior and posterior processes in the same horizontal plane, and in having a flat superior process, grooved articular surface of the posterior process, and relatively short anterior process. From *Liolithax pappus* (Kellogg 1955) it differs in having a relatively short anterior process and relatively larger pars cochlearis. It differs from *Kentriodon*, *Lophocetus calvertensis* (Harlan 1842), and *Delphinodon dividum* in having a slit-like depression for the internal auditory meatus, which also contains the foramen singulare and the internal aperture of the Fallopian aqueduct. The Arabian specimen was also compared with a periotic from Lee Creek, North Carolina (USNM 183001), probably from the Pungo River Formation (early and middle Miocene), that was identified by L. G. Barnes (oral communication, September 17, 1975) as identical to the periotics accompanying a skull of *Pithanodelphis* from the late Miocene of California. In the shape of its anterior and posterior processes, this *Pithanodelphis* specimen closely resembles the Arabian specimen and the periotics of Delphinidae; however, its pars cochlearis is smaller than that of the Arabian periotic.

The Arabian specimen also closely resembles a periotic (USNM 317874) of an undescribed ondontocete from the Pungo River Formation of North Carolina. The major difference between the two specimens is that the periotic from North Carolina has a smaller pars cochlearis.

Although they are smaller, two unidentified periotics (UCMP 88582 and UCMP 88583) from the San Diego Formation (Pliocene) of California resemble the Arabian specimen in the slit-like internal auditory meatus, in the shape of the pars cochlearis and anterior process, and in the articular surface of the posterior process being in the same plane as the anterior process (see Barnes 1973: fig. 2g–j).

Discussion

The single cetacean periotic from the Dam Formation possesses characters typical of primitive Delphinidae, and possibly of advanced Kentriodontidae. Its morphology is closest to that of the living genus *Sousa*, the humpbacked dolphin, now living in coastal waters and the mouths of rivers from the South China Sea west through the Straits of Malacca, the Bay of Bengal, and the Arabian and Red Seas to the Suez Canal, and in waters off South Africa and west Africa (Hershkovitz 1966: 18–25). However, definite generic assignment can be made only in the basis of the skull. The only conclusion that can be reached from study of a single ear bone is that a possible close relative of *Sousa* is present in the Dam Formation. *Sousa* itself has never been reported as a fossil.

Remington Kellogg, in a letter to D. W. Rice (December 4, 1962: Smithsonian Institution Archives, Record Unit 88, Box 6), pointed out the resemblance between the periotics of the Miocene genus *Kentriodon* and the living New World freshwater porpoise *Sotalia*. He wrote:

> The fresh water porpoises of the genus *Sotalia* all possess periotic bones with similar characteristics. If you will refer to the following article . . . [Kellogg 1927] . . . you will find illustrations . . . [pl. 3, figs 2–4] . . . of this fossil porpoise which resemble those of *Sotalia* rather closely. The configuration of the cerebral surface and the shape of the internal acoustic meatus is similar in both. *Kentriodon* which was present in the Miocene period in the Chesapeake embayment may have been an antecedent of the fresh water porpoise *Sotalia*. . . .
>
> Dr Fraser and I have not come as yet to any final conclusion as to the family allocation of *Sotalia*. Relatively few specimens have been received by museums. On the basis of present information it would appear that *Sotalia* may possibly be somewhat closely related to *Steno* and *Sousa*, but in my opinion this allocation should be deferred until more adequate information is available.

The family Kentriodontidae, as defined by Barnes (1978), reflects a middle to late Miocene delphinoid radiation of animals that were more primitive than, but in part contemporaneous with, members of the more advanced family Delphinidae. True (1912) favourably compared *Delphinodon dividum* True 1912 with *Pithanodelphis* Abel 1905 of the Miocene, and with living *Steno* and *Sotalia*. Barnes (1978) placed *Delphinodon* and *Pithanodelphis* with *Kentriodon* in the Kentriodontidae; I include *Sousa* with *Steno* and *Sotalia* as structurally primitive living Delphinidae.

The periotic from the Dam Formation is delphinoid in that the articular surface for the bulla on the posterior process is in the same horizontal plane as the ventral side of the anterior process and, concomitant with this, the superior process is low and flat. The Arabian periotic has a longer, straighter anterior process than do those of advanced Delphinidae, whose anterior process is directed medially and is partly appressed against the anterior side of the pars cochlearis. This combination of characters is probably a morphological stage between the relatively primitive periotics of the Kentriodontidae and the derived condition in the Delphinidae.

If the Arabian periotic is accepted as representing a species in the Delphinidae, this record extends the range of the Delphinidae farther back in time than has previously been reported. Barnes (1976: 330, tab. 4; fig. 2) reported a late Miocene species of Delphinidae *sensu stricto*, known from a complete skull from California. This specimen is at least ten million years old, but even this is at least five million years younger than the specimen from the Dam Formation. On the slim evidence that we have, familial assignment of the Arabian periotic to the Delphinidae or to the Kentriodontidae must await collection of more material.

Tethyan Distribution of Miocene Delphinoidea

In Burdigalian time the area that is now eastern Saudi Arabia was separated from the ancestral Mediterranean by an evaporite realm that formed a land bridge between Asia and Africa (Steininger *et al.* 1985). Earlier in the Miocene the land area was occupied by a strait allowing access by its marine fauna to the western Tethys. The marine mammal fauna represented by the specimen from the Dam Formation could, therefore, have been related to forms from farther west in the Tethys Sea. Unfortunately, only one penecontemporary delphinoid, '*Delphinus*' *vanzelleri* Fourtau 1918, is known from the Mediterranean Tethys. This species, represented only by a partial jaw from the Lower Miocene Moghara Formation of Egypt, is probably generically unidentifiable (Barnes & Mitchell 1978) and cannot be compared to the Saudi Arabian specimen.

Five genera of Delphinoidea are known from the late Miocene (Sarmatian) of the Caucasus. Three of these, *Leptodelphis* Kirpichnikov 1954, *Sarmatodelphis* Kirpichnikov 1954, and *Microphocaena* Kudrin & Tatarinov 1965, have been placed in the Kentriodontidae by Barnes (1978). The other two, *Anacharsis* Bogachev 1956 and *Imerodelphis* Mchedlidze 1959, are tentatively assigned to the Delphinidae. These genera have not been identified elsewhere, and it is possible that they were endemic to Paratethys.

The resemblance, pointed out above, of the Saudi Arabian specimen to isolated periotics from North Carolina and California may indicate distribution of related Delphinoidea throughout the Tethys in Miocene time.

Conclusions

A primitive delphinoid, similar to and perhaps related to *Sousa*, was present in the ancestral Arabian Gulf in Burdigalian time. Confirmation of the taxonomic position of this cetacean must await collection of more material from the Dam Formation. Despite this taxonomic uncertainty, the morphology of the periotic makes it clear that we have here another bit of evidence of the radiation of the earliest modernized dolphins. Similar bones (unfortunately usually unaccompanied by skulls) from the middle Miocene to lower Pliocene of North Carolina may indicate a Tethyan distribution of related primitive delphinoids. A continuous range of these forms from the Tethys to the west coast of North America would have been possible because of the existence of the Panama seaway (see Whitmore & Stewart 1965).

Acknowledgements

I thank Peter J. Whybrow of the British Museum (Natural History) for making the specimen available for study. Cary T. Madden, then of the U.S. Geological Survey, encouraged discussion of the Miocene vertebrate faunas of Saudi Arabia among the specialists working in different parts of the Kingdom. I am grateful to Lawrence F. Barnes and Samuel A. McLeod for reviewing the manuscript. The photographs were taken by Robert H. McKinney of the U.S. Geological Survey.

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Early Miocene fish from eastern Saudi Arabia

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Synopsis

Fish remains collected from early Miocene (Burdigalian marine chronology, middle Orleanian European land-mammal age equivalent, *c.* 17–19 Ma) continental deposits at Ad Dabtiyah, Saudi Arabia, can be referred to the family Cyprinidae and, possibly, to the Centropomidae. Teeth resembling those found in certain members of the family Labridae are also present.

Introduction

The fish remains were recovered from a continental white, pebbly, calcareous grit thought to be laterally equivalent to the basal deposits of the nearby marine Dam Formation (see Whybrow, McClure & Elliott, this issue, p. 371). In a preliminary report on the vertebrate fauna from the Saudi Arabian Miocene (Hamilton *et al.* 1978: table 1), the fish described here were erroneously stated to have been collected from the Jabal Midra ash-Shamali locality.

Register numbers refer to the collections of the Department of Palaeontology, British Museum (Natural History), London.

Systematic description

Subclass **OSTEICHTHYES** Huxley, 1880

Superorder **OSTARIOPHYSI** Sagemehl, 1885

Family **CYPRINIDAE** Bonaparte, 1837
Fig. 54

The Cyprinidae is a family of essentially freshwater species, a very few of which have a limited tolerance of brackish water.

The family is represented by a single, well-preserved pharyngeal tooth, P.61555. Judged from the nature of its basal attachment area and from the unworn occlusal surface, it was probably an unattached replacement tooth.

The ornate cusp pattern on the occlusal surface is most unusual (Fig. 54) and cannot be matched with that from any extant species represented in the Zoological collections of the British Museum (Natural History), nor with any species which has been described in the literature. Thus it is impossible to suggest an infrafamilial taxon to which the fossil might be allied.

Gayet (*in* Thomas *et al.* 1982: 116) identified cyprinid pharyngeal teeth from Lower Miocene deposits of the Al-Sarrar region (Eastern Province, Saudi Arabia) as derived from fishes referable to the genera *Barbus* and *Labeo*, with certain of those from the former taxon closely resembling median row teeth of *Barbus bynni*, an extant Nilotic species. The presence of *Barbus* and *Labeo* in Miocene deposits of Saudi Arabia supports, according to Gayet, Menon's (1964) suggestion that these fishes '. . . entered Africa (from Asia) as late as Plio-Pleistocene times'. The presence of a presumed *Barbus* from the Upper Miocene of Tunisia (Greenwood 1972), however, would appear to weaken that argument. None of the cyprinid fossil evidence available so far would seem to indicate, as Gayet suggested, either the routes or the dispersal pattern of the family, if indeed there was dispersal on this scale. Those questions are more likely to be elucidated by evidence ultimately obtained from a detailed phylogenetic analysis of living taxa. For the moment it would seem preferable only to use the fossil record as indicative of cyprinids occurring in both Africa and Saudi Arabia during the Miocene.

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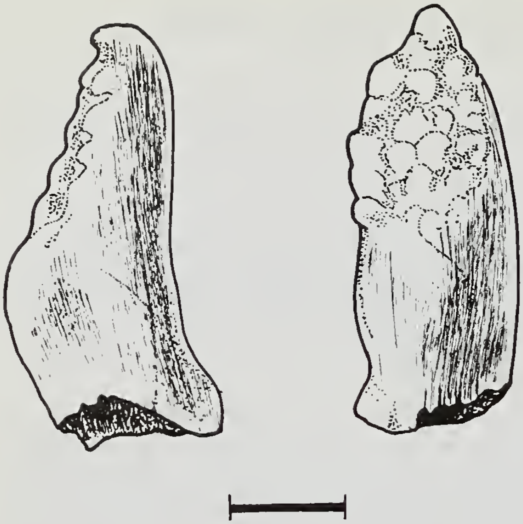

Fig. 54 Lower pharyngeal tooth from a cyprinid fish in lateral (left) and anterior (right) views. Bar = 1 mm. Early Miocene, Ad Dabtiyah, Saudi Arabia.

Superorder **ACANTHOPTERYGII** Gouan, 1770

Group **PERCOMORPHA** Bleeker, 1859

Family **?CENTROPOMIDAE** Poey, 1865

An extensively damaged and incomplete neurocranium, P.61556, is referred tentatively to the Centropomidae, on the basis of its overall proportions taken in combination with the shape and proportions of individual skull bones.

The skull is elongate and slender and is noticeably narrow across the otico-occipital region. The supraoccipital is long-based and protracted anteriorly, thereby entirely and widely separating the elongate parietals, and also, but more narrowly, the frontals over the greater part of their medial faces. The exoccipital is an elongate and expansive bone with the foramen for the occipitospinal nerve situated immediately above the buttress extending upwards from the exoccipital facet.

In all these features the morphology of the fossil skull resembles that in extant *Lates* species (the African and Indo-Pacific, predominantly freshwater, representatives of the family) more closely than it does the neurocranial form in any *Centropomus* species (the American, and predominantly marine–brackish water representatives) or in *Psammoperca waigiensis* Cuvier & Valenciennes, a coastal marine centropomid of the Indo-Pacific area; see Greenwood (1976) for details and figures. It differs, however, in the great forward extension of the blade-like anterior supraoccipital prolongation. In no extant centropomid species does the supraoccipital separate more than the posterior third to quarter of the frontals. Likewise, in none of the serranid or percichthyids (the other presumed basal percoids) I have examined does the supraoccipital extend forward beyond that level.

The bones present and recognizable in the fossil are: the left and right frontals in part (those portions medial to the frontoparietal crests), the supraoccipital (missing its crest and the ventral portion of its posterior median extension), the parietals in part (the bone medial to the crest), the greater part of the right epioccipital, virtually the entire right exoccipital, the posterior region of the right prootic (but lacking its ventral margin), part of the dermethmoid, and the proximal part of the right lateral ethmoid.

Based on comparisons with skulls from *Lates calcarifer* (Bloch) and *Lates niloticus* (L.), it is estimated that the fossil skull, when entire, measured *c.* 10 cm from the anterior tip of the vomer to the ventral rim of the basioccipital condyle. It would thus be derived from a fish of about 30–35 cm standard length.

Part of a right dentary, P.61557 (that region of the bone immediately anterior to its separation into an ascending coronoid and a horizontal lower limb), is also thought to be derived from a centropomid fish. In its gross morphology, and in having small tooth scars densely packed into a broad alveolar surface, this dentary closely resembles that found in extant *Lates* species. It is probably from a fish of about the same size as that from which the skull was derived.

When compared with the dentary in specimens of extant *Lates* species of comparable size, the fossil is more robust and the alveolar surface is, relatively, somewhat wider.

The distal end of a proximal dorsal fin radial (pterygiophore), P.61558, compares closely with the third pterygiophore in the anterior dorsal fin of *Lates*. It is difficult to estimate the size of the individual from which the fossil came, but certainly it would not have been of more than 35–40 cm standard length.

A fragment from the proximal end of a spinous fin ray, P.61559, could also be derived from a centropomid fish within the size range 30–35 cm standard length.

Many extant species of the Centropomidae are known to be euryhaline; a few species are apparently confined to marine habitats, and some of the African species are apparently confined to fresh waters, with a number physiographically restricted to lakes.

Remains of a *Lates* species are recorded by Gayet (*in* Thomas *et al.* 1982: 116) from the Lower Miocene of the Al-Sarrar region, Eastern Province, Saudi Arabia.

Material of indeterminate origin

Two small teeth, P.61560, with molariform crowns, cannot be referred with certainty to any taxon. In their gross morphology they resemble a type of pharyngeal tooth frequently found in members of the Labridae, a family whose living members are exclusively marine.

Superficially these teeth do bear some resemblance to those from the parasphenoidal and basihyal tooth plates in members of the mormyrid genus *Hyperopisus*. However, on closer examination of the gross morphology, overall proportions and details of wear pattern, they are quite unlike those found in extant *Hyperopisus* specimens.

One tooth is squat, its maximum height (2 mm) is equal to the greatest diameter of its subcircular crown. The occlusal surface is slightly convex, with a well-defined wear facet occupying about one-third of its area; the entire surface slopes gently into the plane of its greatest diameter.

The other tooth is more elongate, its height measured from the crown to the lowest point of the neck preserved is 4·5 mm, and the maximum and minimum crown diameters are 2·0 mm and 1·5 mm respectively. Almost the entire occlusal surface is worn, the wear plane sloping to one side across the narrow diameter of the crown.

The third specimen of indeterminable origin, P.61561, is a small fragment of bone which resembles the head region of a percoid pleural rib.

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