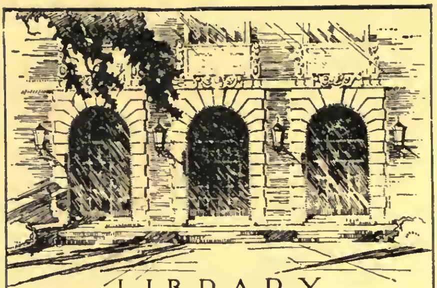

EVOLUTION AND CLASSIFICATION OF THE OSTEOSTRACI

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FIELDIANA: GEOLOGY
VOLUME 11, NUMBER 3
Published by
CHICAGO NATURAL HISTORY MUSEUM
JANUARY 19, 1951

PRINTED IN THE UNITED STATES OF AMERICA
BY CHICAGO NATURAL HISTORY MUSEUM PRESS

INTRODUCTION

The past twenty-five years have seen a tremendous increase in our knowledge of the Osteostraci. In two monumental works on the cephalaspids of Spitsbergen and Great Britain, Stensiö (1927, 1932) has made a notable contribution to our understanding of the detailed anatomy of the group. The ateleaspids (hemicyclaspids), particularly those from Norway, have been exhaustively treated by Heintz (1939). Robertson has produced a number of papers dealing with the fauna from the Island of Oesel in the Baltic. New forms from Spitsbergen, Great Britain, Poland, Norway and North America have been described by other authors. In spite of all this work, however, there is still a lack of agreement concerning the general evolutionary trends within the order, and a poor understanding of the relationships of the various genera.

The present paper is the result of a study of the Late Silurian Osteostraci from Oesel, collected by William Patten and preserved in the Dartmouth College Museum. This fauna is of particular interest not only because it includes the earliest known members of the order, but also because of the considerable variety of forms by which it is represented. The Oesel genera are of the utmost importance in the study of the evolution and classification of the Osteostraci, with which this paper is primarily concerned.

TAXONOMIC REVISIONS

There is no attempt in this paper to present a complete taxonomic revision of the Osteostraci. In the course of this study, however, the need for certain changes has become apparent, and they are discussed at this time in order to avoid confusion and misunderstandings in later sections of this work.

Robertson (1939a) established the genus *Witaaspis* with *Cephalaspis schrenkii* Pander[1] as genotype. In 1940, he described a second species of the genus, *W. patteni*. Both are from the Wita Quarry on the Island of Oesel, and both are of similar dimensions. *W. patteni* was distinguished in part by the ornamentation of its

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[1] Not *C. schrenckii* as used by Robertson, nor *C. schrencki* as used by Stensiö, 927.

cephalic shield, but such differences as appear are due to the manner of preservation; they depend on whether the matrix has broken away fully from the surface of the shell, or has removed with it part or all of the exoskeleton. The apparent large size of the dorsal field and the low median crista of *W. schrenkii* are again due to faulty preservation. In the absence of any other characteristics to distinguish it, *Witaaspis patteni* Robertson must be referred to *W. schrenkii* (Pander).

In another study of the Oesel Osteostraci, Robertson (1938a, p. 288) established a new cephalaspid genus, *Saaremaaspis*, for the species *Tremataspis mickwitzi* Rohon. In a later paper (1938b, p. 489) he described *Rotsiküllaspis obrutchevi*, a new genus and species, and referred it to the Dartmuthiidae. According to Robertson, there are only two known specimens of *S. mickwitzi*, the holotype in the Academy of Sciences in Moscow (No. 256:536) and one specimen in the Dartmouth College Museum (No. 38–71–9526). It appears that Robertson's differentiation of *Rotsiküllaspis* from *Saaremaaspis* was the result of a misinterpretation of the inadequate material of the latter genus. The two species agree quite closely in size. Robertson was in error in giving the length of *S. mickwitzi* as 18 mm. and the maximum width as 19 mm. A comparison of the measurements is given below:

	Total length mm.	Maximum width mm.
S. mickwitzi (type from Robertson, 1938b, pl. 60, fig. 8)	27	28
S. mickwitzi (measured from D.C.M. 38-71-9526)	29 (estimated)	26
R. obrutchevi (type, D.C.M. No. 38-71-9404)	29	24

The most striking differences that are apparent from Robertson's restorations (1938b, text figs. 1, 2) are the lengths of the shields of the two, and the presence of short, broad cornua and deep pectoral sinuses in *Saaremaaspis*. His restoration of *Saaremaaspis* is based largely on the photograph of the type (1938b, pl. 60, fig. 8) in which the posterior boundary appears to be a break rather than an actual edge of the shield. Cornua in Osteostraci are developed at the posterior corners of the cephalic shield, not far back in the trunk region as Robertson has shown them. Thus there is good reason to believe that *Saaremaaspis* lacked cornua, that the type was incomplete, and that the total length of the shield was greater than 27 mm. None of the other differences of shape and proportion that Robertson mentions is particularly significant when it is considered that all of the known specimens are crushed or distorted to some extent. Another character used by Robertson to distinguish these genera is the length of the lateral fields. The boundaries of these fields are indistinct in the type of *Saaremaaspis mickwitzi*, but, according to my interpretations, the fields are similar in extent to those of *Rotsiküllaspis obrutchevi;* this is certainly true of D.C.M. No. 38–71–9526, referred by Robertson to *Saaremaaspis*. Robertson mentions differences in the ornamentation of the exoskeleton, but does not state what they are; none is apparent.

No valid grounds for the separation of these two species are left, so it becomes necessary to refer *Rotsiküllaspis obrutchevi* to *Saaremaaspis mickwitzi* as a synonym. The relationships of this species to other Osteostraci are discussed below.

For reasons to be presented in the discussion of the classification of the Osteostraci that follows, the following taxonomic changes are proposed:

Cephalaspis oeselensis Robertson is referred to *Procephalaspis,* gen. nov.

Cephalaspis staxrudi Stensiö is referred to the genus *Securiaspis* Stensiö.

Cephalaspis woodwardi Stensiö is referred to *Stensiopelta,* gen. nov.

In order to avoid confusion in the discussion of the evolution of the Osteostraci, a classification is presented below. This differs from earlier classifications in many respects, but a discussion of it will be deferred until the evolution has been considered.

Order Osteostraci	
Family Tremataspidae	
Subfamily Tremataspinae	*Trematapis*
Subfamily Dartmuthiinae	*Dartmuthia* *Saaremaaspis*
Subfamily Oeselaspinae	*Oeselaspis*
Subfamily Didymaspinae	*Didymaspis*
Family Sclerodontidae	*Sclerodus*
Family Ateleaspidae	*Hemicyclaspis* *Hemiteleaspis* *Micraspis* *Aceraspis* *Ateleaspis* *Witaaspis*
Family Cephalaspidae	
Subfamily Cephalaspinae	*Thyestes* *Procephalaspis* *Cephalaspis*

Subfamily Benneviaspinae	*Securiaspis* *Benneviaspis* *Hoelaspis* *?Boreaspis* *Stensiopelta*
Family Kiaeraspidae	*Kiaeraspis*

THE EVOLUTION OF THE OSTEOSTRACI

The Osteostraci are a relatively compact group, first appearing in the Late Silurian, flourishing in the Early Devonian, but represented by only a few survivors in the Middle and Late Devonian. Throughout this time they were quite conservative in many respects, although there are obvious differences in certain characteristics. The evolutionary significance of these differences has been variously interpreted. Stensiö (1927, 1932) came to the following conclusions:

(1) The trunk carapace was lengthened by the incorporation of trunk scales.

(2) The pectoral fins, pectoral sinuses, and cornua have been reduced in such forms as *Kiaeraspis* and *Didymaspis,* and lost in *Tremataspis.*

(3) Both the exoskeleton and endoskeleton have shown a degeneration of ossification.

(4) The paired lateral fields of *Tremataspis* are the result of a subdivision of primitive single fields.

(5) The originally metameric nerves supplying the lateral fields have been modified and reduced in number by fusion.

These views have been supported recently by Wängsjö (1946). On the other hand, Westoll (1945) has come to diametrically opposed conclusions. In his opinion, the Osteostraci with long carapaces and small or absent pectoral sinuses and cornua are primitive, this view being based largely on their supposed dominance in the earliest deposits. The solution to the problem is not obvious, however, when we consider the variety of forms described from the Late Silurian of Oesel. Among them are genera with long carapaces and those with short, genera with well-developed pectoral sinuses and those without, genera with subdivided lateral fields and those with only one pair, and, finally, genera with strong endo- and exo-skeletons as well as those with poorly developed skeletons.

In order to clarify the situation, an attempt has been made in the present paper to study the controversial characters as objectively as possible, in order to determine whether any evolutionary trends are demonstrable. Where possible, the characters are expressed as

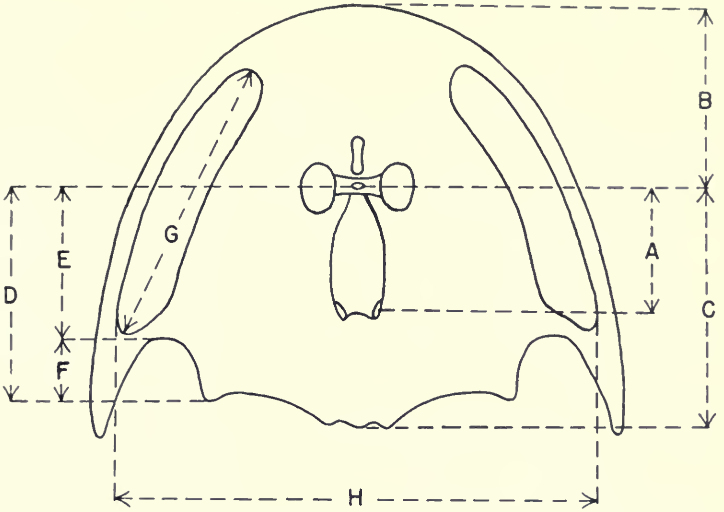

FIG. 20. Dorsal shield of *Procephalaspis*, illustrating the measurements used in this paper. A. Distance from pineal opening to line connecting centers of external openings of endolymphatic ducts. B. Prepineal length (excluding rostral process, if present). C. Postpineal length, median. D. Postpineal length, measured to level of postero-lateral corners of cephalic or trunk shield. E. Distance from pineal opening to line connecting the anterior ends of the pectoral sinuses. F. Depth of pectoral sinus. G. Length of lateral field. H. Maximum distance between external borders of lateral fields.

measurements, or more often as ratios of measurements. Since most actual specimens are crushed, distorted, or incomplete, the data have been derived mainly from restorations, some original but many from the published figures of Stensiö (1927, 1932), Wängsjö (1937) and Zych (1937). The species are grouped by age in three categories, Ludlow, Downtonian and Early Devonian, and the numerical expression of the characters is represented graphically.

It has been found necessary at the outset to eliminate a considerable number of the described Osteostraci from this evolutionary study. Many are too poorly preserved to furnish the required measurements. This, unfortunately, is true of all the Middle and Late Devonian species. Others have been found in strata whose geological age is uncertain, or whose age is determined in large part by the supposed evolutionary stage of their contained Osteostraci. This applies at present to the forms from Norway and Scotland. Thus, this study is limited to the species found in the West Midlands of England, Spitsbergen, and Oesel, and the one species described as yet from Poland. The measurements used are indicated in figure 20.

The approximate stratigraphic occurrence of the genera is indicated in figure 31, page 194.

THE SIZE OF THE LATERAL FIELDS

Tremataspis and *Oeselaspis* are unusual among the Osteostraci in having two pairs of lateral fields; all the other described genera have but a single pair. This characteristic has been used in classification as a primary basis for distinguishing these genera as separate families (Stensiö, 1927; Robertson, 1938a), suborders (Heintz, 1939), or even orders (Berg, 1940). Two pairs of lateral fields might be considered as a primitive character since they occur in the earliest fauna, or they might be regarded as the result of subdivision of originally single lateral fields. The latter view was apparently taken by Stensiö (1927, p. 308; 1932, p. 180). Wängsjö (1946, p. 360) mentions an undescribed form from Spitsbergen which "shows a still more advanced subdivision of the lateral electric fields into separate portions than we find in *Tremataspis* and *Oeselaspis*. . . ."

It is proposed here to determine whether there is any evidence supporting a trend towards an increase or decrease in the size (that is, the length) of the lateral fields in the Osteostraci. The length is denoted by G (fig. 20); in *Tremataspis* and *Oeselaspis* the sum of the lengths of the two fields is used. Since we are concerned in this case not with the absolute length, but with the relative length, a suitable base measurement has been sought with which G can be compared in the form of a ratio. The distance from the pineal opening to the level of the apertures of the endolymphatic ducts (A, fig. 20) is the only measurement of this sort that has been discovered. Determined, as it is, by brain structures, it is presumably stable, but unfortunately is not available in a large number of species.

The ratio, G/A, is plotted against an arbitrary time scale in figure 21. This demonstrates the relatively small size of the lateral fields in all of the Ludlow species (G/A less than 2.5). On the other hand, the Early Devonian forms have relatively large lateral fields (G/A greater than 2.5). The Downtonian fauna, though inadequately represented, is of an intermediate nature. Clearly the geological evidence favors the view that small lateral fields were primitive and that there was a trend towards an increase in size through the Downtonian and Early Devonian. On purely theoretical grounds this might be expected. The lateral (and dorsal) fields are peculiar to the Osteostraci, and thus must have developed within the group as a specialization, perhaps as electric organs for defense. Such specialized structures would first appear in the course of evolu-

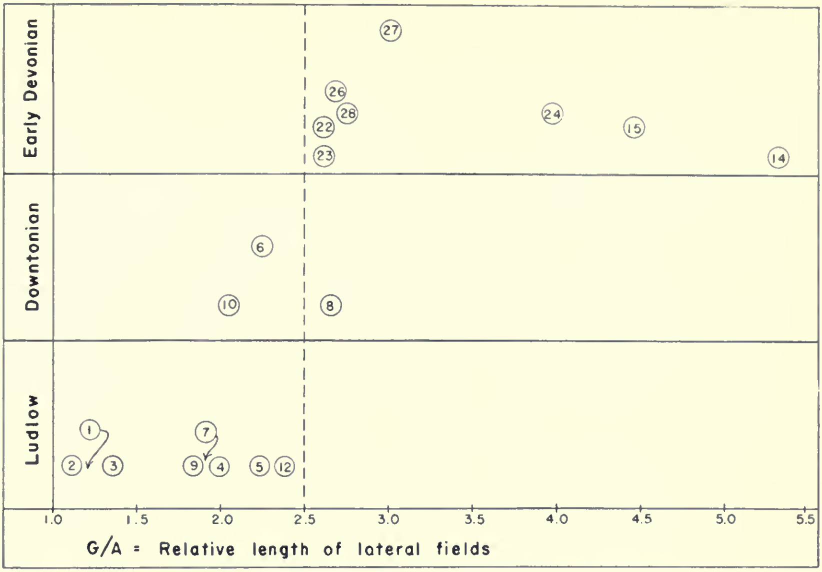

FIG. 21. Relative length of lateral fields (G/A) plotted against an arbitrary time scale. The encircled figures refer to different species plotted here and in figures 24–26 as follows: 1, *Tremataspis mammillata;* 2, *T. schmidti;* 3, *Oeselaspis pustulata;* 4, *Dartmuthia gemmifera;* 5, *Saaremaaspis mickwitzi;* 6, *Didymaspis grindrodi;* 7, *Witaaspis schrenkii;* 8, *Hemicyclaspis murchisoni;* 9, *Thyestes verrucosus;* 10, *T. egertoni;* 11, *T. salteri;* 12, *Procephalaspis oeselensis;* 13, *Cephalaspis kozlowskii;* 14, *C. lankesteri;* 15, *C. salweyi;* 16, *C. heintzi;* 17, *C. whitbachensis;* 18, *C. hoeli;* 19, *C. arcticus;* 20, *C. whitei;* 21, *C. langi;* 22, *Securiaspis kitchini;* 23, *Benneviaspis lankesteri;* 24, *B. holtedahli;* 25, *B. anglica;* 26, *Hoelaspis angulata;* 27, *Boreaspis rostrata;* 28, *Kiaeraspis auchenaspidoides.*

tion as rudiments, and these are most closely approximated among known forms by the two pairs of lateral fields of *Tremataspis* and *Oeselaspis*. The single lateral fields of other Osteostraci are presumably the result of enlargement and fusion of such rudiments. The maximum development is shown by *Cephalaspis;* the observed range of G/A in this genus, including several species not plotted because of uncertainty regarding their age, is 3.8 to 5.3. The determination of the status of the species with subdivided fields from Spitsbergen mentioned by Wängsjö (1946, p. 360) must await its description, but secondary subdivision may be involved.

No separate study of the dorsal field is presented, since it shows the same tendencies as the lateral fields. It is always single, but is smallest in the Late Silurian *Tremataspis* and *Oeselaspis* and largest n the Early Devonian *Cephalaspis.*

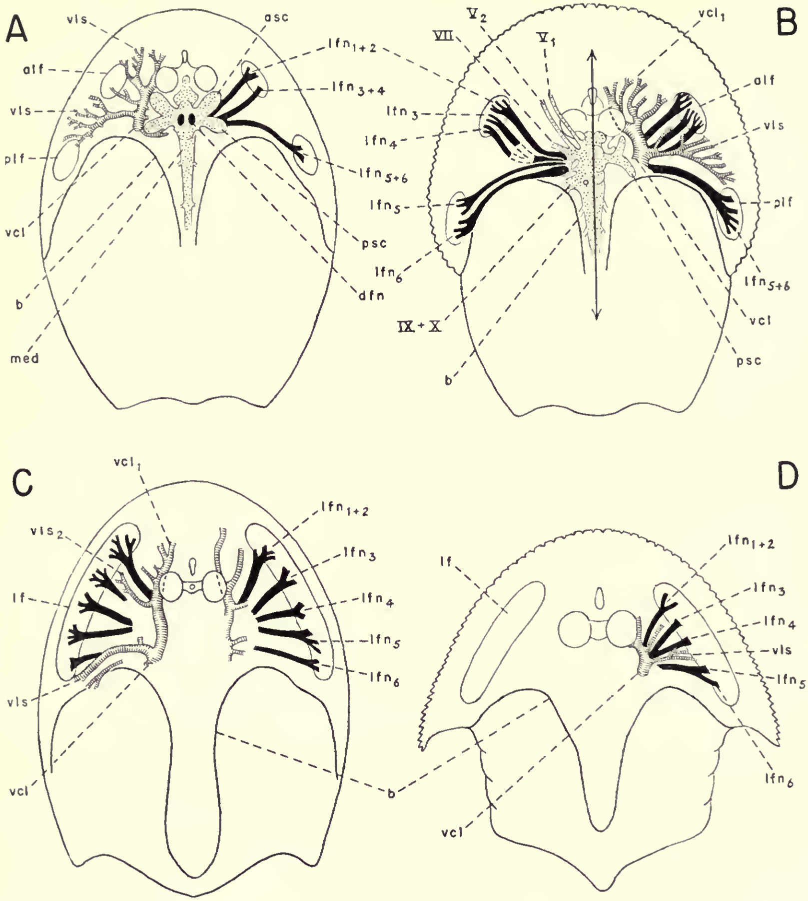

FIG. 22. Cranial nerves and blood vessels of Ludlow Osteostraci. A, *Tremataspis mammillata*, dorsal (×1.5); B, *Oeselaspis pustulata*, dorsal on right, ventral on left (×2.0); C, *Dartmuthia gemmifera*, dorsal (×1.1); D, *Thyestes verrucosus*, dorsal (×2.2). *alf*, anterior lateral field; *asc*, anterior semicircular canal; *b*, boundary of endoskeletal component; *dfn*, dorsal field nerve; *lf*, lateral field; *lfn*1–6, nerves of lateral fields; *med*, medulla oblongata; *plf*, posterior lateral field; *psc*, posterior semicircular canal; *vcl*, vena capitis lateralis; *vcl*1, preorbital part of vena capitis lateralis; *vls*1–6, dorso-lateral superficial veins; *V*1, N. profundus; *V*2, N. trigeminus; *VII*, N. facialis; *IX*+*X*, root of N. glossopharyngeus and N. vagus.

THE NERVES OF THE LATERAL FIELDS

The arrangement of the nerves supplying the lateral fields and their relationship to other cranial nerves have been used by Stensiö (1932, p. 75) and accepted by Westoll (1945, p. 351) as primary bases for distinguishing the families and subfamilies of Osteostraci. Thus the Cephalaspinae were defined in large part by the fact that the first two nerves of the lateral fields divide close to the orbit, and N. trigeminus mandibularis lies between them. On the other hand, the Kiaeraspinae were distinguished by having the first two nerves of the lateral fields united most or all of the way, and lying behind N. trigeminus mandibularis. Stensiö (1927, p. 241) considered that the nerves of the lateral fields were primarily metameric in disposition, as was suggested to him by their alternation with the

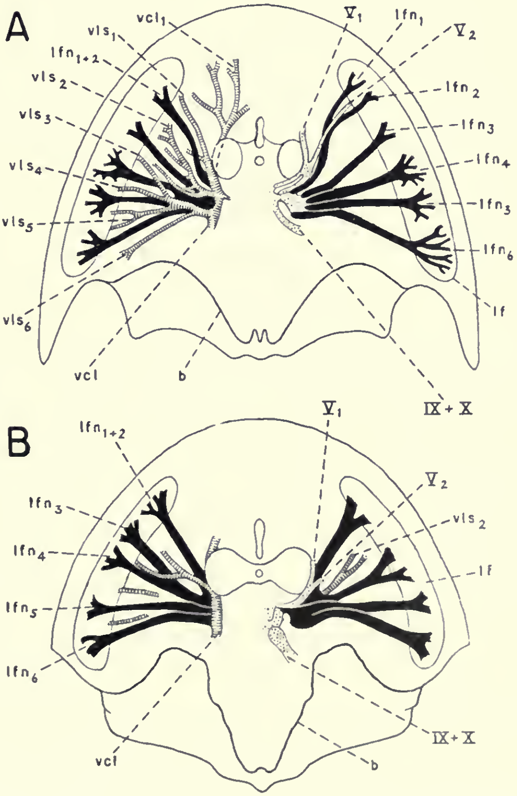

FIG. 23. Cranial nerves and blood vessels of Ludlow Osteostraci, dorsal view on left, ventral on right. A, *Procephalaspis oeselensis* (×2); B, *Witaaspis schrenkii* (×3). For abbreviations, see figure 22.

branchial nerves in *Cephalaspis;* other arrangements, such as that found in *Tremataspis,* he considered as secondary, due to fusion of nerves.

Caution in the use of nerves of the lateral fields in classification is demanded by the fact that their disposition may vary within a species, or even on the two sides of one individual. Thus Heintz (1939, fig. 27) demonstrated considerable differences within individuals of *Micraspis gracilis.* The same variation is shown in *Securiaspis kitchini* (Stensiö, 1932, p. 39, footnote). Among the species from Oesel, variations have been noted in different individuals of *Oeselaspis pustulata, Witaaspis schrenkii,* and *Procephalaspis oeselensis.* Figures 22 and 23 show the disposition of the cranial nerves of the Oesel Osteostraci as far as has been determined by dissections. It should be noted that *Tremataspis* has only three lateral field nerves, as recognized by Wängsjö (1946, p. 360), not "at least four" as stated by Stensiö (1927, p. 305), and Robertson (1938a, pp. 201–202).

As an approach to the problem of the evolution of the nerves of the lateral fields, the number of nerves has been counted in each species where they are known, and the number plotted against an arbitrary time scale, just as in the analysis of the lateral fields. A nerve that divides half way between the brain and the lateral field is counted as one and a half. By this system, *Cephalaspis* has 5.4 to 5.7 nerves. Where the number varies, the median value is taken.

The evidence from the temporal distribution of the Osteostraci, as represented graphically in figure 24, supports the view that there was a trend towards an increase in the number of nerves supplying the lateral fields. Only one of the Ludlow species has more than five nerves (that is, shows any subdivision of the first two nerves), while this is true of all the Early Devonian representatives, with the exception, perhaps, of certain individuals of *Kiaeraspis.* The Downtonian fauna again appears to be intermediate. Stensiö's theory that the number of nerves was reduced by fusion is plainly contrary to the geological evidence.

There is certainly a high degree of correlation between the size of the fields and the number of nerves supplying them. Thus *Tremataspis,* which was shown above to have the smallest lateral fields, has only three pairs of nerves; the evidence indicates that this is the most primitive state among the known Osteostraci. On the other hand, *Cephalaspis,* with the largest fields, has 5.4 to 5.7 nerves, exhibiting as advanced a subdivision as is known in the group. Genera intermediate in this respect—including the Benneviaspine

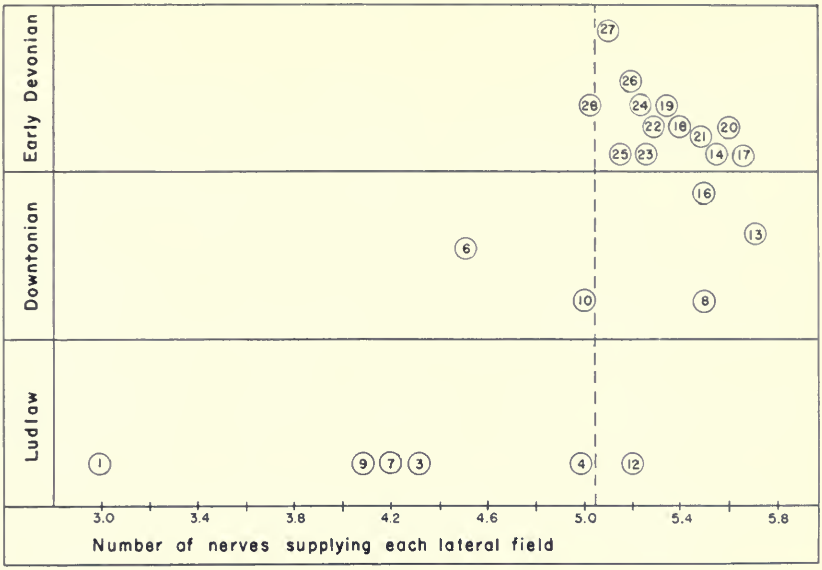

FIG. 24. Number of nerves supplying each lateral field plotted against an arbitrary time scale. For a key to the species represented by the encircled numbers, see figure 21.

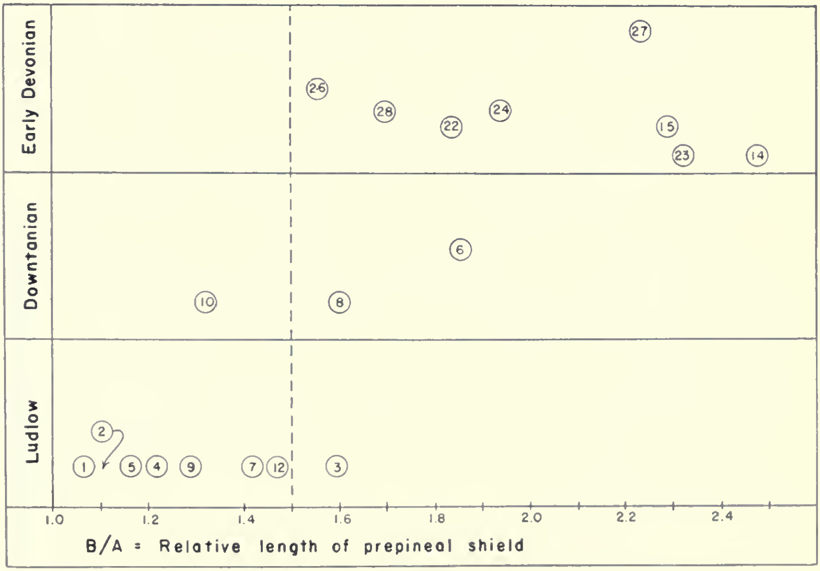

FIG. 25. Relative length of the prepineal shield (B/A) plotted against an rbitrary time scale. For a key to the species represented by the encircled numbers, ee figure 21.

forms, also *Kiaeraspis, Thyestes, Didymaspis* and *Sclerodus*—were grouped together by Stensiö in the Kiaeraspinae. As is shown below, this is an artificial assemblage, since it includes otherwise divergent forms that have arrived at a similar stage in the enlargement of the lateral fields and in the subdivision of their nerves.

If the condition found in *Tremataspis* is primitive, the basic metamerism of the nerves, which Stensiö believed was exemplified by *Cephalaspis,* is questionable. To be sure, it is probable that the nerves of the lateral fields were derived from branches of metameric cranial nerves. They are closely associated with the roots of the facial and glossopharyngeal nerves, and may also be related to the trigeminal and vagus. Their only claim to metamerism is in probable derivation from some of these nerves. As the lateral fields enlarged in the evolution of the Osteostraci, the primitive three nerves of *Tremataspis* subdivided and spread out, culminating in the *Cephalaspis* condition, where they came to alternate more or less with other cranial nerves. But this is a secondary condition, not a primary metameric arrangement.

THE PREPINEAL SHIELD

As is illustrated in figure 25, there is clear evidence that the prepineal shield was lengthened in the course of evolution of the Osteostraci. This is measured by the ratio of the prepineal length, B, to the base measurement, A (see fig. 20). B/A is less than 1.5 in all but one of the Lower Ludlow Osteostraci, and greater than 1.5 in all of the Early Devonian species; the Downtonian forms are intermediate. As is the case with the other characters discussed above, *Tremataspis* is to be considered most primitive in having the shortest prepineal shield, while *Cephalaspis* is most advanced in possessing the longest. *Oeselaspis* and *Didymaspis,* which in other respects are very primitive, show a precocious lengthening of the prepineal shield.

The meaning of the enlargement of the anterior part of the shield is not at once obvious. It would, of course, give added space for the expansion of the lateral fields, but it is improbable that there is any relation, since the available space is never completely occupied. It is probably related to the enlargement of the oralo-branchial chamber. As Romer (1946, p. 43) has stressed, the Osteostraci were "food strainers" in which the oralo-branchial chamber has more to do with food intake than with respiration. The living "food strainers," the whalebone whales and the whale shark, have a much enlarged mouth and pharynx that allow a greater intake of water with its contained food particles. Thus it is logical to assume that the enlargement of the prepineal shield was connected with a perfection of this type of food-getting mechanism in the Osteostraci.

EXTENT OF THE TRUNK CARAPACE

Of paramount importance in the study of osteostracan evolution is the problem of whether the portion of the carapace covering the trunk was reduced, as thought by Westoll (1945, pp. 349–350), or lengthened by the incorporation of trunk scales, as Stensiö believed (1927, p. 30). For analysis, it has not been possible to measure the length of the trunk carapace directly, since there is no way by which the carapace can be separated into its cephalic and thoracic portions externally. Used as a substitute measurement is the postpineal length (C, fig. 20), which includes a portion of the cephalic shield, but whose magnitude is dependent to a large degree on the amount of thoracic shield included. The relative length of the postpineal shield is given by the ratio, C/A.

Plotting this character against the time scale (fig. 26) does not give as clear a picture of an evolutionary trend as is the case with the characters discussed above. Analysis of the graph, however, does bring out the following points: (1) With one exception, the Early Devonian species have short postpineal shields, with C/A less than 3.2 (the exception is *Kiaeraspis*, in which the trunk shield is very long, with C/A estimated to be 4.5); (2) the earliest Osteostraci from Oesel show a wide range, but *Tremataspis*, which is surely primitive in other characters, has the longest shield (C/A greater than 4.1). Thus the evidence favors the theory that there was a trend towards the reduction of the trunk shield. This view is supported by Westoll's point (1945, p. 349) that the short-shielded forms were much more efficient swimmers. In the absence of any convincing evidence supporting Stensiö's contrary theory, it will be assumed that a long trunk shield is a primitive character in the Osteostraci, and that this has been reduced in most later genera by subdivision into body scales.

In this connection an interesting point is to be observed in *Thyestes verrucosus*. In the restoration made by Patten (1912, fig. 235, A), transverse grooves indicate the presence of two thoracic segments included in the shield posterior to the pectoral sinus. This may be the most common condition in this species, but certain specimens have a longer thoracic shield, including three, or even four segments. Thus, within the species, C/A may range between 2.7 and 3.3. The same variability may occur in *Thyestes egertoni*. A specimen figured by Stensiö (1932, pl. LII, fig. 3) clearly shows three segments and may contain a fourth in its thoracic shield. In another specimen (ibid., pl. XL, fig. 2) the segments are not clear, but there is not room for more than two or three. Stensiö interprets these as transverse rows of scales that have fused to form the thoracic shield. In view of the evidence that the shield was reduced, the apparent segmentation should be considered as a preliminary stage of the subdivision into scales of the solid thoracic shield.

DEVELOPMENT OF EXOSKELETON AND ENDOSKELETON

As a result of his study of the Spitsbergen forms, Stensiö (1927, pp. 31, 34) concluded that the Osteostraci represent a degenerating series with regard to the degree of ossification of both the exoskeleton and endoskeleton. A trend toward reduction of ossification has recently been demonstrated in other groups of fishes, but apparently it is not clearly shown by the Osteostraci. In the first place, Stensiö's conclusions were based originally on a comparison of species from the Red Bay and Wood Bay Series, whose ages are Late Downtonian and Early Devonian, respectively. In other words, they are all relatively late forms in the evolutionary history of the group. Secondly, the Wood Bay Series includes forms with well-developed exoskeletons and endoskeletons, *Cephalaspis lata*, *C. isachseni*, and probably *Boreaspis* and *Cephalaspis brevicornis*. Third and finally, a good proportion of the earliest species from the Ludlow of Oesel have a much reduced skeleton.

Considering first the exoskeleton, the species may be classified in four categories. (The information is derived from Stensiö [1927, 1932] and from study of the Oesel Osteostraci.)

Group 1. Exoskeleton unreduced; superficial layer complete; sensory canals opening to surface by pores.

Group 2. Superficial layer slightly reduced; sensory canals continuously open to surface, resulting in external division of shield into polygonal areas.

Group 3. Superficial layer considerably reduced or absent, except perhaps on tubercles; middle layer may be slightly reduced between tubercles.

Group 4. Superficial layer absent, except perhaps on tubercles; middle layer greatly reduced or absent, so that the sensory canals are exterior to the exoskeleton.

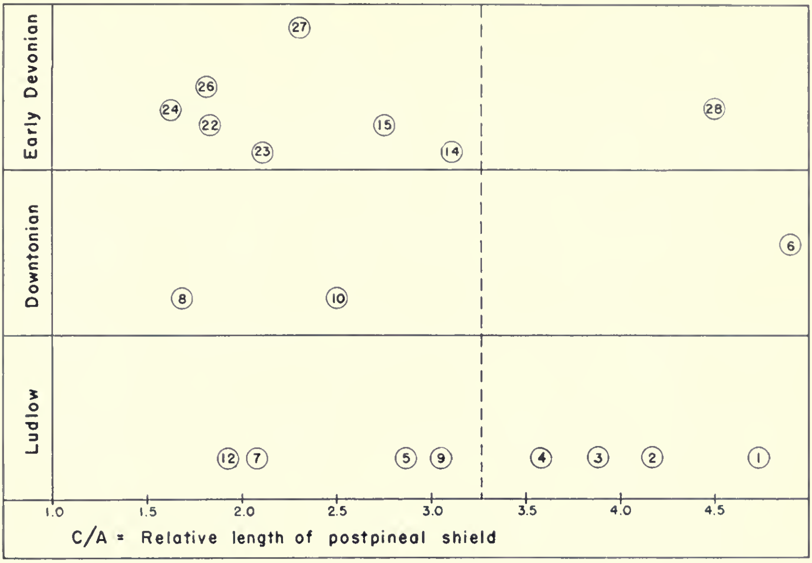

FIG. 26. Relative length of the postpineal shield (C/A) plotted against an arbitrary time scale. For a key to the species represented by the encircled numbers, see figure 21.

The species whose stratigraphic position and exoskeletal development are known, are grouped in the above categories and by age as follows:

	Group 1	*Group 2*	*Group 3*	*Group 4*
Wood Bay Series	2	5	0	1
Dittonian and Upper Red Bay Series	15	2	4	0
Downtonian and Lower Red Bay Series	5	0	2	4
Ludlow	4	1	5	1

This grouping gives little support to Stensiö's theory; in fact, it would be possible to make a case for strengthening of the exoskeleton. For example, in the family Cephalaspidae the majority of the Early Devonian species have a well-developed exoskeleton with unreduced superficial layer, yet *Thyestes* and *Procephalaspis*, which are the earliest and in other respects the most primitive members of the family, have a greatly reduced exoskeleton. The same apparently applies to the Ateleaspidae. The exoskeleton is most strongly developed in *Hemicyclaspis murchisoni*, and perhaps in *Hemiteleaspis heintzi*, both relatively late members of the family. The earliest ateleaspid, *Witaaspis*, and the contemporary and probably related genus, *Saaremaaspis*, have much reduced exoskeletons. Genera that are presumed to occupy an intermediate stratigraphic position—

Ateleaspis, Micraspis, and *Aceraspis*—appear to be intermediate in exoskeletal development, judging from Heintz's descriptions (1939); in all of them the network of the sensory canals is open to the surface by grooves, at least on part of the shield, forming polygonal areas or "tesserae." But this is not conclusive, since *Hemicyclaspis lightbodii,* contemporaneous with *H. murchisoni,* has the exoskeleton reduced, retaining the superficial layer only on tubercles.

On the other hand, *Tremataspis* might be used to support the view that a well-developed exoskeleton is primitive within the Osteostraci. This genus, which has been shown in other characters to occupy a central and basal position as regards osteostracan evolution, has a continuous superficial layer pierced by pores of the sensory canal network (Denison, 1947). These sensory canals have a relatively simple structure when compared to the apparently secondarily subdivided canal systems described by Stensiö in many Downtonian and Early Devonian species. The vascular canals of the middle layer form an irregular network, differing from the more highly organized "radiating canals" of *Cephalaspis.* All in all, the exoskeletal structure is simple and probably primitive.

Whether a highly ossified or a reduced exoskeleton be considered primitive, it becomes obvious that there is no clear and general trend within the Osteostraci towards reduced or increased ossification. The variable development of the exoskeleton within two species, *Cephalaspis pagei* and *C. powriei brevicornis* (Stensiö, 1932, pp. 99, 111), suggests that it may have been subject to genetic fluctuations throughout much of the evolutionary history of the order. Study of the histology of various exoskeletons does not support Westoll's suggestion (1945, p. 351) that the loss of the superficial layer may be due to resorption or wear from burrowing in the sand or to post-mortem abrasion.

It is not possible at present to make a satisfactory analysis of the degree of endoskeletal ossification. Since we are not dealing with surface structure, the determination of its presence and development depends upon the availability of enough specimens so that suitable preparations can be made. Usually this is not possible in species known from only a very few specimens. Stensiö's experience with the Spitsbergen Osteostraci (1927) led him to believe that there was a trend towards reduction of ossification. It is worth noting, however, that one of the latest members of the order, *Boreaspis,* from the Wood Bay series, has the most completely ossified endoskeleton of any of the Osteostraci; in fact, it is the only known form in which the actual body of the endoskeleton, rather than just its surfaces, is ossified. At the other extreme, the Oesel fauna includes three species in which the perichondrial ossification is thin: *Saaremaaspis mickwitzi, Witaaspis schrenkii,* and *Thyestes verrucosus.* The other Oesel Osteostraci have a strongly ossified endoskeleton; this includes *Tremataspis, Dartmuthia, Oeselaspis,* and *Procephalaspis.*

In the present state of our knowledge, it seems hardly possible to demonstrate any well-defined evolutionary trend with regard to the ossification of either the exoskeleton or the endoskeleton.

CORNUA AND PECTORAL FINS

In the consideration of the evolution of the Osteostraci, one of the most interesting and at the same time most difficult questions is whether or not the ancestral members of the group possessed paired fins. Stensiö (1927, p. 302) believed that they did. According to his theory, they have been reduced in such forms as *Didymaspis* and lost in *Tremataspis.* This belief is hard to reconcile with the relative stratigraphic occurrence of genera with and without pectoral fins, and requires the postulation of a hypothetical ancestral form that on the one hand could give rise to groups retaining the fins, and on the other hand to those losing them. It is reasonably certain that all the Early Devonian genera possessed pectoral fins. They are known to be present in *Cephalaspis,* and are clearly implied by the proven presence of canals for nerves and blood vessels in *Kiaeraspis* and *Hoelaspis.* Although they have not been demonstrated in *Benneviaspis, Boreaspis,* and *Securiaspis,* the possession of pectoral sinuses, and the close relationship of these genera to *Cephalaspis* and *Hoelaspis,* makes it safe to infer their presence. Turning to the earliest osteostracan fauna, it is important to note that paired fins were absent in the majority of genera and species. *Witaaspis, Thyestes,* and *Procephalaspis* may well have possessed them, although their presence has not been demonstrated as yet. But the strongest argument against Stensiö's theory is their undoubted absence in *Trematаspis, Dartmuthia,* and *Saaremaaspis,* and almost certain absence in *Oeselaspis,* for these are the genera that have been shown to be most primitive in other respects.

Stensiö argues that *Trematаspis* possessed an endoskeletal shoulder girdle component, but this has not been demonstrated. There are, to be sure, in the postero-lateral cephalic region endoskeletal structures that are concerned with the enclosure of nerves of the lateral fields, marginal blood vessels, etc., and the postbranchial wall is closely associated with them. It is more probable that these structures later came to support the pectoral fins in such forms as *Cephalaspis,* than that they are primarily shoulder girdle elements.

The evidence points to the independent acquisition of paired fins *within* the order Osteostraci. From a general evolutionary point of view this is an important point, since it means that they were acquired more than once by the vertebrates. (As a matter of fact, it is probable that paired fins were evolved independently at least three or four times among the vertebrates—within the Anaspida, within the Osteostraci, within the Placodermi, and perhaps independently by the ancestors of modern fish groups.) To make the evolutionary origin of fins more complicated, it appears that within the Osteostraci, fins were evolved concurrently yet independently in two different lines; the manner in which they evolved was in general similar, but differed in details, and the overall phylogenetic picture, to be discussed later, indicates that the phyla separated prior to the acquisition of paired fins.

Admitting for the Osteostraci the primitive nature of *Tremataspis* and the advanced position of *Cephalaspis,* the stages in the evolution of pectoral fins are moderately well documented. The first step is the development of a lateral fold that may properly be considered, in part at least, as a "fin fold." No such fold is present in *Tremataspis mammillata.* A transverse section through the exoskeleton of the body in the thoracic region suggests that this part of the body completely filled the carapace. Laterally the exoskeleton is unthickened and unconstricted, and there is no indication of any structure that might be morphologically ancestral to a fin (fig. 27, A). In other species of *Tremataspis* a thickening of the lateral curve of the carapace may be seen in transverse sections; it is pronounced in both *T. schmidti* (fig. 27, C) and *T. milleri* (fig. 27, B), where it may be discerned on superficial inspection of the shield. This thickening is interpreted as the first indication of the development of a lateral fin fold, and is correlated with a lateral constriction of the thoracic and abdominal parts of the body. The posterior part of the shield of *Didymaspis* shows a similar development of the lateral rim, judging by the section figured by Stensiö (1932, fig. 61, C). *Oeselaspis* exhibits an interesting stage in this evolution. In the posterior cephalic and anterior thoracic regions there is pronounced lateral thickening of the exoskeleton, especially of its basal layer, and it is probable that there was dorso-ventral compression to form a real rim (fig. 27, E). More posteriorly, in the narrower part of the exoskeletal shield (that is, in the region of the so-called "pectoral

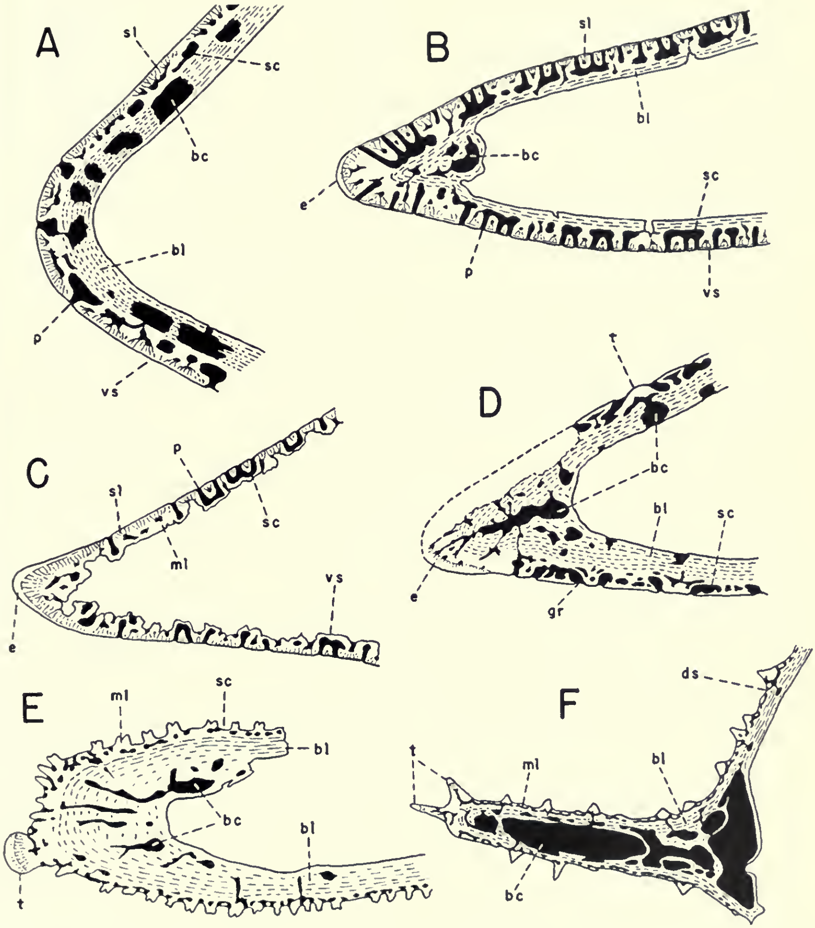

FIG. 27. Transverse sections of the lateral margin of the shield in various Ludlow Osteostraci. A, *Tremataspis mammillata* (×20); B, *T. milleri* (×25); C, *T. schmidti*, juvenile (×25); D, *Dartmuthia gemmifera* (×25); E, *Oeselaspis pustulata* (×25); F, *Thyestes verrucosus* (×15). *bc*, basal vascular cavity; *bl*, basal layer; *ds*, dorsal shield; *e*, enamel; *gr*, groove by which sensory canal opens to surface; *lfo*, lateral fold; *lr*, lateral rim of lateral fold; *m*, margin of oralo-branchial fenestra; *ml*, middle layer; *p*, pore by which sensory canal opens to surface; *pf*, pectoral fin; *sc*, sensory canal; *sl*, superficial layer; *t*, tubercle; *vs*, ventral shield.

sinus"), this rim is not developed, and it is presumed to have been lost. In *Dartmuthia* the lateral fold is very strong and distinct (fig. 27, D). In both *Oeselaspis* and *Dartmuthia* it may be considered to consist of two elements. First is the more lateral part, or lateral rim proper, which consists of the three exoskeletal layers separated only by channels for nutrient vessels and nerves. Second is the more medial part, which is distinguished from the rest of the body only by the fact that it is somewhat compressed dorso-ventrally, yet is still appreciably open to the mesodermal and endodermal tissues of the body. It is suggested that the lateral rim was morphologically ancestral to the cornua of the Cephalaspidae and to the thickened lateral edge of the ateleaspid fin, while the more medial part was to give rise to the fin proper in both groups. For the most part the genera illustrating the stages described above form a morphological but not a phylogenetic series.

For reasons to be entered into below, it is thought that *Saaremaaspis* is close to the ancestry of the Ateleaspidae. Unfortunately, this genus is rare and incompletely known, but, since it is not far removed from *Dartmuthia,* it is probable that the two genera were similar in the development of the lateral fold. In any case it is likely that such a stage was passed through by the ancestors of those Osteostraci that evolved paired pectoral fins. The evolution of the paired fins within the Ateleaspidae has been discussed by Heintz (1939, p. 101). Since the morphological stages in the evolution of their fins do not correlate with the presumed evolution of other characters, it is probable that the known genera do not represent a phylogenetic series; nevertheless they do illustrate more clearly than any other group of Osteostraci some of the details of fin evolution. The processes involved are:

(1) Further emphasis of the lateral fold, particularly of its more medial part, which is to give rise to the fleshy fin. As the lateral fold is compressed, the thoracic part of the body is laterally constricted more and more. An advanced stage is well illustrated by Heintz's sections of *Aceraspis* (fig. 28, C, D).

(2) Reduction and sometimes complete loss of the posterior part of the lateral fold. An early stage in this change is shown by *Oeselaspis* (which is not related to the Ateleaspidae), and more advanced reduction is shown by *Ateleaspis, Aceraspis,* and *Micraspis.* It is probable that the posterior reduction has a functional importance, since a pectoral fin of the length of the post-cephalic fold of *Dartmuthia* or *Saaremaaspis* would be an awkward appendage. It is

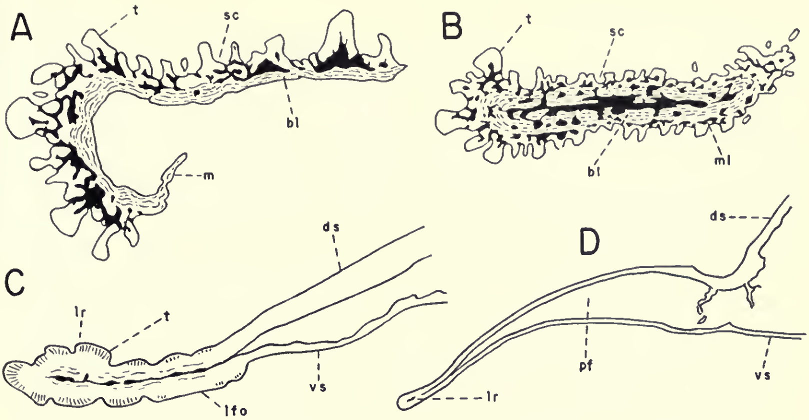

FIG. 28. Transverse sections of the lateral margin of the shield in some early Osteostraci. A, *Procephalaspis oeselensis* (×30); B, Cornua of same (×20); C and D, *Aceraspis robusta* (from Heintz, 1939). For explanation of abbreviations, see figure 27.

correlated in this family, but not in all Osteostraci, with the assumption of mobility in the abdominal and posterior thoracic regions.

(3) Subdivision of the exoskeletal shield of the lateral fold into scales to give mobility to the incipient fins. This process is correlated with the segmental breakup of the carapace of the body proper into scales, which gives mobility to the whole post-cephalic body.

(4) Separation of the "pectoral flaps" from the thorax so that they become freely movable fins. Heintz has shown that *Ateleaspis, Aceraspis, Micraspis,* and *Hemicyclaspis,* in that order, exemplify stages in this separation (Heintz, 1939, pp. 101–102).

Nothing is known of the stages of fin evolution within the Cephalaspidae. Heintz (1939, p. 101) considered that the cephalaspid cornua was derived by fusion and separation of the thickened lateral rim of the ateleaspid fin, leaving a free and separate fin in the resulting pectoral sinus. This is unlikely since, as will be shown below, the different phyletic lines represented by the two families may have been distinct prior to the evolution of fins. The manner of fin evolution within the Cephalaspinae was probably similar to that described for the Ateleaspidae, with one exception: the lateral rim, retaining a solid, undivided exoskeleton attached to the cephalic shield, became the cornua (fig. 28, B), while the more medial part of the lateral fold, attaining mobility and freedom from the thorax and cornua, became the fin.

In the Cephalaspinae, the development of pectoral fins probably went hand in hand with the reduction and subdivision of the thoracic and abdominal shield. This is not so in *Kiaeraspis*. This genus retains a long trunk shield. In section (Stensiö, 1927, fig. 79, D) this shield has broadly rounded lateral contours showing no trace of a lateral fold. However, the thoracic and abdominal regions have been constricted laterally, indicating that a lateral fold was developed and then lost by the ancestors of *Kiaeraspis*. The anterior part of it was modified as a pectoral fin, whose presence is indicated by canals and foramina for the subclavian and brachial arteries. *Kiaeraspis* lacks prominently projecting cornua, and it is not known whether the lateral rim was lost, or whether it was retained as a thickened margin on the fins.

It is unlikely that *Oeselaspis* possessed paired fins. Only the posterior part of the lateral fold has been lost, and the position, contour and serrate edge of the posterior boundary of the remaining lateral fold all argue against the possession of pectoral fins.

Didymaspis, judging from Stensiö's description (1932, p. 172, fig. 61, C), possessed a small lateral fold. This is present along the lateral edge of the shield except in the posterior part of the cephalic region, where there is a constriction forming the so-called "pectoral sinus." But the weak development of the lateral fold and the small size of the sinus indicate that fins, if present, must have been small and ineffectual organs.

Sclerodus, which occupies an isolated position among the Osteostraci, probably did not possess any paired fins. But the lateral fold is exceedingly strongly developed, even in the head region, where it is fenestrated. The exoskeleton of the trunk proper has been reduced (or more probably subdivided into scales), but the lateral fold retains its solid exoskeletal sheath in this region, remaining as greatly elongate "cornua." It is probable that the "cornua" include the whole lateral fold, not just its lateral rim, so for this reason they are not exactly comparable with the cornua of cephalaspids.

CLASSIFICATION AND PHYLOGENY

It was not until the appearance of Stensiö's important descriptions of the Spitsbergen and British Osteostraci that the group was well enough understood to allow any satisfactory analysis of the interrelationships of the various genera. Thus the first important classification appeared in those works (1927, 1932). Since that time, Heintz (1939) has described certain Ateleaspidae (Hemicyclaspinae) in detail, and discussed their classification in relationship to the rest of the order. Robertson (1945) has studied the Oesel representatives and has suggested changes and additions based on his knowledge of those forms. Westoll (1945), in describing a Scottish ateleaspid, has considered the relationships of the various genera of the order. All of these later classifications have been founded largely on that of Stensiö, who used as primary characters the following:

(1) The length of the trunk shield.

(2) The presence or absence of pectoral sinuses and fins.

(3) The subdivision and development of the lateral fields.

(4) The subdivision of the lateral field nerves, and their relationship to other cranial nerves.

It has been shown above that all of these characters are involved in general evolutionary trends that pervade the order. A classification based almost entirely on such characters is apt to be a purely horizontal one in the sense that it may well include forms belonging to quite unrelated phyletic lines that have happened to arrive at the same stage of evolutionary development in these respects. Such is certainly the case with most of Stensiö's (1932) groups. To take a specific example, a subgroup of the family Kiaeraspidae, including *Thyestes*, *Didymaspis*, and *Sclerodus*, was characterized by the relatively weak development of the lateral and dorsal fields, the coalescence of the first two nerves of the lateral fields, and the position of the trigeminus and facial nerves in front of the nerves of the lateral fields. It is contended here that these three genera are almost as distantly related as any Osteostraci can be, that the three characters used to unite them are closely correlated, and that they agree only in exemplifying a rather primitive stage in the evolution of these traits.

An alternative classification was presented in outline form above (p. 159). It is based primarily on such characters as the manner of development of the pectoral fins, pectoral sinuses and cornua, and on the proportions of the shield, as well as on other traits that sometimes appear to characterize phyletic lines. It also considers those features that show progressive evolution throughout the Osteostraci, but with due regard for the fact that their rates and modes of evolution may be characteristic of certain phyla. Such characters include:

(1) The relative length of the lateral (and dorsal) fields.

(2) The number and arrangement of nerves to the lateral fields.

(3) The amount of reduction of the thoracic shield.

(4) The lengthening of the prepineal part of the shield.

(5) The development of pectoral sinuses and fins.

The grouping is largely phylogenetic or vertical. Since, however, the Osteostraci converge as they are traced backwards into the Late Silurian, it has been found impractical to hold entirely to a phylogenetic subdivision of the more primitive forms; they are therefore grouped together in one horizontal or primitive family: the Tremataspidae. The proposed classification is defined and discussed below.

Order **OSTEOSTRACI** Lankester 1868

Family TREMATASPIDAE[1] Woodward 1891

Originally named for *Tremataspis* Schmidt alone, this family is here extended to include a number of primitive genera from the Ludlow, as well as one from the Downtonian. It includes the basal stock from which other Osteostraci were derived, yet within the family may be recognized the beginnings of phyletic divergence in a number of directions, some of which trend towards later families. The classification of such an assemblage is a matter of convenience, and depends on the bias of the individual investigator. Here it is considered more practical to group them together in one family, emphasizing the convergence towards a central ancestral type, and at the same time to subdivide them into subfamilies, recognizing their incipient phyletic divergence. The Tremataspidae, as used in this way, may be characterized by the following primitive traits:

(1) Long, relatively unreduced trunk shield (C/A greater than 2.8).

(2) Relatively short lateral fields (G/A less than 2.2).

(3) Nerves of the lateral fields few (3 to 5 in number).

(4) Pectoral fins and sinuses absent, or at the most in an incipient stage of development.

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[1] Fowler (1947, p. 4) referred *Tremataspis* to *Stigmolepis*, and the family Tremataspidae to Stigmolepidae. He was not aware, apparently, that a recent student of this group considered *Tremataspis* and *Stigmolepis* doubtfully cogeneric (Robertson, 1947). And he could not have known that the difficult taxonomic problem involving the genotype of *Tremataspis* had been referred to the International Commission on Zoological Nomenclature. It was agreed at the 1948 meeting of this body in Paris to designate *T. schmidti* Rohon 1892 as the type species of *Tremataspis* Schmidt 1866, making Fowler's use of *Stigmolepis* and Stigmolepidae entirely unnecessary.

Subfamily TREMATASPINAE new rank

(=TREMATASPIDAE Woodward, 1891)

Represented only by *Tremataspis* Schmidt (fig. 29, A; Lower Ludlow, Oesel), this subfamily includes forms considered to be the most primitive known Osteostraci, which from a morphological point of view could well be ancestral to all the other genera. It is characterized by its primitive features, as follows:

(1) Trunk shield long, covering both the thoracic and abdominal regions (C/A=4.2–4.8).

(2) Two pairs of small lateral fields (G/A=1.2).[1]

(3) Only three lateral field nerves, two supplying the anterior field and one the posterior field.

(4) No pectoral sinuses, pectoral fins, or cornua, and the lateral fold absent or only moderately developed.

(5) Prepineal part of shield very short (B/A=1.1).

(6) Exoskeleton well developed with unreduced superficial layer, simple sensory canal network, and unspecialized vascular canal system.

Other characteristics, some or all of which may be primitive, include a well-ossified endoskeleton, strong sclerotic ossifications, large oralo-branchial plates, absence of a definite dorsal fin, and relatively few and large caudal scutes.

Subfamily DARTMUTHIINAE new rank

(=DARTMUTHIIDAE Robertson 1935)

Dartmuthia Patten and *Saaremaaspis* Robertson (including *Rotsiküllaspis* Robertson) form a group that is very primitive in most respects. These two genera show tendencies suggesting that they may be close to the basal stock from which both the Cephalaspidae and Ateleaspidae arose. The subfamily is characterized as follows:

(1) Trunk shield only slightly reduced (C/A=2.9–3.6).

(2) Lateral fields single, but still relatively short (G/A=2.0–2.2).

(3) Nerves of lateral fields five in number (in *Dartmuthia*); the first two nerves united all the way to the lateral fields. (*Saaremaaspis* is not well known in this respect.)

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[1] G is the sum of the lengths of the two fields.

(4) No pectoral sinuses, pectoral fins, or cornua, but the lateral fold strongly developed.

(5) Prepineal part of the shield relatively unexpanded (B/A=1.2).

(6) Superficial layer of exoskeleton may be reduced or absent.

In most of these respects the Dartmuthiinae are still very primitive. However, they do show an advance over the Tremataspinae in the following: the slight reduction of the trunk shield; the moderate elongation of the single pair of lateral fields; the greater subdivision of the nerves of the lateral fields; the strengthening of the lateral fold; and exoskeletal modifications.

Saaremaaspis (Lower Ludlow, Oesel; fig. 29, C) exhibits tendencies suggesting that it may have been close to the ancestry of the Ateleaspidae. Many of these are so slight that they are hardly definable, but it does possess a moderately narrow shield (H/A=3.1), the lateral fields are quite long for the Ludlow (G/A=2.2), and the nerves of the lateral fields may be subdivided more than in *Dartmuthia*. In all of these respects it approaches the early Ateleaspidae.

Dartmuthia (Lower Ludlow, Oesel; fig. 29, D) is considered to be closer to the base of the cephalaspid stem. Its head shield is slightly broader (H/A=3.2), its lateral fields are shorter (G/A=2.0) and comparable in relative length to those of *Thyestes*, and large tubercles are developed in longitudinal rows in the exoskeleton, a feature of certain Cephalaspidae.

Subfamily OESELASPINAE new rank

(=OESELASPIDAE Robertson 1935)

Only *Oeselaspis* Robertson (Lower Ludlow, Oesel; fig. 29, B) is included in this subfamily. In the following respects it is very primitive:

(1) The trunk shield is long (C/A=3.9).

(2) There are two pairs of small lateral fields (G/A=1.3).[1]

(3) The nerves of the lateral fields are relatively few (4.0–4.6 in number).

On the other hand, *Oeselaspis* is definitely advanced beyond *Tremataspis* in the following characters:

(4) A lateral fold is strongly developed anteriorly, and presumably has been lost posteriorly in the trunk region; this is probably to be considered as an intermediate stage in the evolution of pectoral fins.

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[1] G is the sum of the lengths of the two fields.

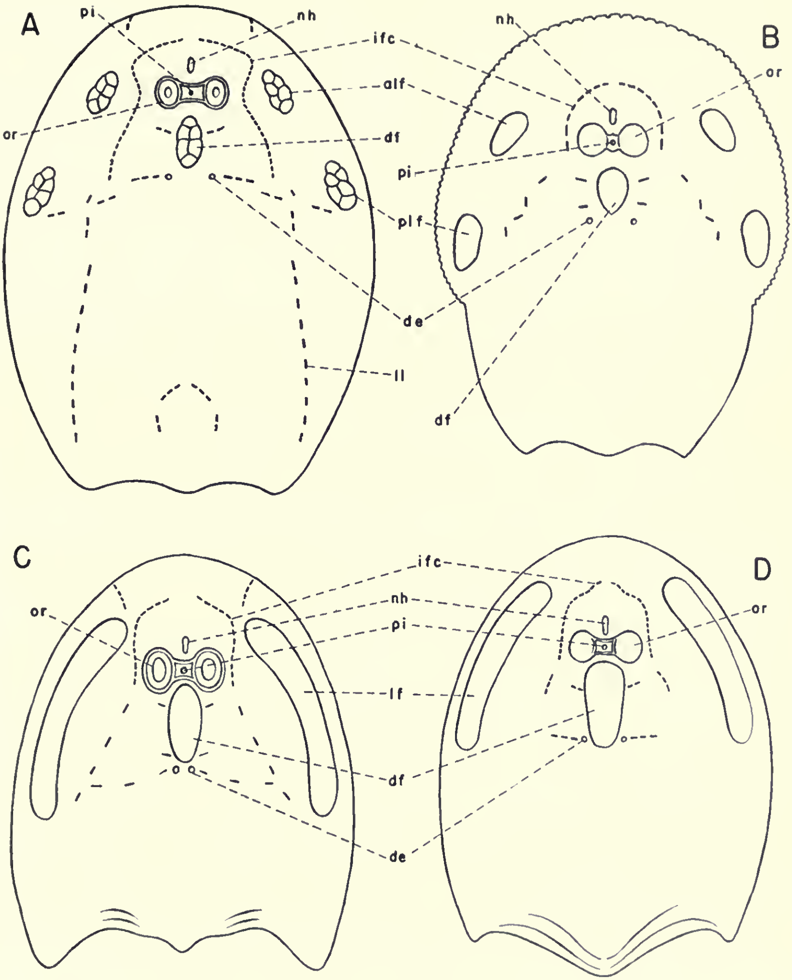

FIG. 29. New restorations of dorsal shields of Ludlow Tremataspidae. A, *Trematapsis mammillata* (×2); B, *Oeselaspis pustulata* (×2); C, *Saaremaaspis mickwitzi* (×1.9); D, *Dartmuthia gemmifera* (×1.2). *alf*, anterior lateral field; *co*, cornua; *de*, external opening of endolymphatic duct; *df*, dorsal field; *ifc*, infraorbital lateral line canal; *ll*, main lateral line canal; *lf*, lateral field; *nh*, nasohypophysial opening; *or*, orbit; *ps*, pectoral sinus; *pi*, pineal opening; *plf*, posterior lateral field.

(5) The prepineal shield is expanded (B/A=1.6).

(6) The superficial layer of the exoskeleton is lost except on the large tubercles, and the middle layer is reduced.

(7) The cephalic shield is moderately broad (H/A=3.9).

It is possible that *Oeselaspis* was descended from a *Tremataspis*-like form. Any relationship to any of the other genera of Osteostraci is unlikely. An affinity with *Didymaspis* has been suggested, but the very long trunk shield and the unique manner in which the lateral fold is reduced in the latter makes this highly improbable. Because of the wide gap between *Oeselaspis* and other Osteostraci, it is safer at this time to consider that it diverged from the primitive stock in early times and left no known descendants in later periods.

Subfamily DIDYMASPINAE new rank
(=DIDYMASPIDAE Berg 1940)

This is another monotypic subfamily, including only the genus *Didymaspis* Lankester (Downtonian, England). It retains the following primitive characters:

(1) Very long trunk shield (C/A=5.0).

(2) Moderately short lateral fields (G/A=2.2).

(3) Relatively few nerves of lateral fields (4.5 in number).

It is definitely specialized as compared to *Trematapsis* in:

(1) The presence of small "pectoral sinuses" that may or may not have contained rudimentary pectoral fins.

(2) Long prepineal shield (B/A=1.8).

(3) Loss of the superficial layer and reduction of the middle layer of the exoskeleton.

(4) Moderately broad cephalic shield (H/A=4.5).

As far as its ancestry is concerned, *Didymaspis* might have been derived from *Trematapsis,* but that is not certain, since the trunk shield is even longer than in the latter genus. *Oeselaspis* has been considered as a possible relative, but, as was stated above, the manner in which the lateral fold is reduced is entirely different in the two genera. Among other long-shielded forms, *Dartmuthia* and *Saaremaaspis* are excluded from an ancestral position by being more advanced in several respects.

It is probable that *Didymaspis* represents a sterile side branch of the primitive tremataspid stock, not ancestral to any of the known later genera. There is, however, a remote possibility that *Boreaspis* was descended from *Didymaspis.* This is suggested by the inturning of the posterior ends of the lateral fields and by the anterior position of the pectoral sinuses, and is supported by a similarity in general proportions. As will be shown in the discussion of the Benneviaspinae, *Boreaspis* differs in certain respects from other members of that subfamily and might possibly represent a parallel development from a non-cephalaspid stock. But because of the many resemblances of *Boreaspis* to other Benneviaspinae, and because of the large structural and temporal gap between *Boreaspis* and *Didymaspis,* the former is retained provisionally in the Benneviaspinae, and the relationship of the two genera is considered as insufficiently supported by the available evidence.

Family SCLERODONTIDAE Fowler 1947
(=SCLERODIDAE Berg 1940)

This is an aberrant family of Osteostraci, including only the genus *Sclerodus* Agassiz (Downtonian, England).

This genus is characterized particularly by the very long, so-called "cornua," which have been shown above to consist of the entire lateral fold encased in exoskeleton. Between the "cornua" the trunk shield has been reduced, and presumably subdivided into scales. Pectoral fins were surely not developed. The wide lateral fold is continued onto the head where it is fenestrated. The peculiar nature of the exoskeleton has been emphasized by Stensiö and Wängsjö. It is considerably reduced superficially but not necessarily much specialized in other respects and is probably derivable from the primitive *Tremataspis* type.

In spite of its peculiar specializations, *Sclerodus* retains some very primitive features, as follows:

(1) The lateral fields are very short.

(2) The nerves of the lateral fields are few; the first two nerves are not subdivided, and it is possible that the posterior two may be united for part of their course.

(3) The prepineal part of the shield is moderately short.

Stensiö (1932, p. 176) and with less certainty Westoll (1945, p. 352) considered that *Sclerodus* was related to *Thyestes* and *Didymaspis.* The only similarity between these genera is that they have all progressed to about the same degree in the lengthening of the lateral and dorsal fields, and in the subdivision of the nerves of the lateral fields. *Sclerodus* is more probably an early and divergent branch from the central *Tremataspis* stock, highly specialized in the development of the lateral fold and in the reduction of the trunk shield, yet retaining some very primitive characteristics.

Family ATELEASPIDAE Traquair 1899
(=HEMICYCLASPINAE Heintz 1939)

A clearly defined and natural group recently discussed by Heintz (1939) and Westoll (1945). It includes the following genera: *Witaaspis* Robertson (Lower Ludlow, Oesel); *Ateleaspis* Traquair (Ludlow or Downtonian, Scotland); *Aceraspis* Kiaer (Ludlow or Downtonian, Norway); *Micraspis* Kiaer (Ludlow or Downtonian, Norway); *Hemiteleaspis* Westoll (?Downtonian, Scotland); *Hemicyclaspis* Lankester (Downtonian, England; ?Downtonian, Norway).

The Ateleaspidae are distinguished by the following characters:

(1) The cephalic shield is relatively narrow (H/A=2.8–3.7). Narrowness of the shield is a trait that clearly distinguishes the Ateleaspidae from the Cephalaspidae.

(2) Pectoral fins are developed, but there are no cornua or distinct pectoral sinuses; the cornua of the Cephalaspidae find their homologues in the thickened marginal rim of the ateleaspid pectoral fin.

(3) The thoracic shield is greatly shortened (C/A=1.4–2.0). Ateleaspids are more progressive even than later cephalaspids in this respect.

(4) The lateral fields are only moderately long (G/A=2.0–3.0). They may extend far anteriorly, but because of the absence of cornua and the shortness of the shield, they cannot extend far posteriorly.

(5) The number and disposition of the nerves of the lateral fields vary because of evolution within the group; the first two nerves are always subdivided to some extent, except in *Witaaspis*.

(6) The prepineal shield is not much expanded (B/A=1.3–1.6); this is less than in most Cephalaspidae.

(7) The posterior contour of the cephalic shield is emarginate medially (except in *Witaaspis*) instead of having a posteriorly projecting spine as in the Cephalaspidae.

(8) There are usually strong sclerotic ossifications.

Witaaspis was referred by Robertson (1939a, p. 652) to the Cephalaspidae, but as restored here (fig. 30, B) it agrees closely

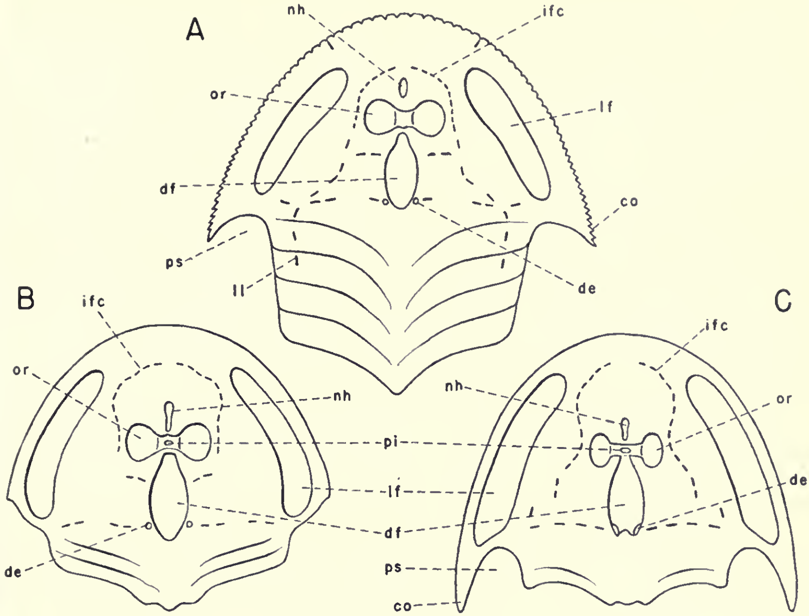

FIG. 30. New restorations of dorsal shields of Ludlow Cephalaspidae and Ateleaspidae. A, *Thyestes verrucosus* (×2.3); B, *Witaaspis schrenkii* (×2.3); C, *Procephalaspis oeselensis* (×1.5). For abbreviations, see figure 29.

with the Ateleaspidae. Pectoral fins have not been preserved, but the configuration of the postero-lateral corner of the cephalic shield agrees with that of other members of this family. As would be expected, since this is the earliest known genus assignable to the family, it is more primitive in some respects than the Scottish and Norwegian genera. The lateral fields are relatively short (G/A=2.0), the first two nerves of the lateral fields are completely united, the third and fourth nerves are partly fused, and the thoracic shield is longer (C/A=2.0).

The evolution of the Ateleaspidae has been discussed at some length by Heintz (1939), who demonstrates a convincing series of stages in the development of the pectoral fins in various genera. Unfortunately, the evolution of other characters does not coincide with that exhibited by the fins. The obvious conclusion is that the Ateleaspidae do not represent a monophyletic group, but, instead, several branches in which various characteristics were differently developed. At the present time any study of the evolution of this family is impractical, since the relative stratigraphic position of most of the known forms is highly controversial. It is quite certain that *Witaaspis* is the oldest known form. It is beyond doubt that *Hemicyclaspis kiaeri* is younger than *Aceraspis* and *Micraspis*. But correlation of deposits containing these genera with the geologic sections in which *Ateleaspis*, *Hemiteleaspis*, and *Hemicyclaspis murchisoni* occur is not yet possible.

Family CEPHALASPIDAE[1] Huxley 1861

(=CEPHALASPIDES Agassiz 1843)

This family forms a well-defined and apparently natural group when restricted to the two subfamilies, Cephalaspinae and Benneviaspinae. Among the Osteostraci it is clearly the most successful family, judging by the number of genera, species, and individuals that have been discovered; moreover, it is the only family known to have survived the Early Devonian, for a few species referred to *Cephalaspis* have been recorded from the Middle and Late Devonian. It is characterized primarily by:

(1) The presence of cornua and distinct pectoral sinuses.

(2) Pectoral fins developed, but lacking the thickened lateral rim of the ateleaspid fin, this being represented by the cornua.

(3) Shield broader than in the Ateleaspidae (H/A=3.7–7.3).

(4) Postero-median spine on the dorsal shield (with one or two exceptions).

The Cephalaspidae may be considered as progressive in the following tendencies:

(1) Elongation of the prepineal shield.

(2) Reduction of the thoracic shield.

(3) Elongation of the lateral and dorsal fields.

Subfamily CEPHALASPINAE Stensiö 1932

The following genera are included: *Thyestes* Eichwald (Lower Ludlow, Oesel; Downtonian, England); *Procephalaspis*, gen. nov. (Lower Ludlow, Oesel); *Cephalaspis* Agassiz (Dittonian, England; Lower and Middle Old Red Sandstone, Scotland; Red Bay Series

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[1] Fowler (1947, p. 4) has felt called upon to emend many of the names of ostracoderms. Thus the name Pteraspidae is altered to Pteraspididae, apparently with some orthographical justification. Why he did not feel that this correction should apply to Cephalaspidae, Atelaspidae (sic), and Kiaeraspidae is not explained when he does apply it to the subfamily name Cephalaspidinae. In view of the inconsistency with which the emender uses this correction, and the awkwardness which would result from its use, it has not been followed in the present work.

and Wood Bay Series, Spitsbergen; Czortkower Stage, Podolia; Upper Siegen and Lower Koblenz Beds, Germany; Early Devonian, New Brunswick and Wyoming; Middle and Late Devonian, Quebec).

Cephalaspis, which does not appear until the late Downtonian, is typical of the subfamily, while *Procephalaspis* and *Thyestes* are early and primitive representatives. The subfamily may be defined as follows:

(1) Thoracic shield typically less shortened than in the Benneviaspinae (C/A=2.4–3.4; 1.9 in *Procephalaspis*).

(2) Pectoral sinuses shallower than in the Benneviaspinae (F/D=0.1–0.5); the shallowness is due largely to their more posterior position (E/A=1.2–1.9).

(3) Shield generally narrower than in the Benneviaspinae (*Cephalaspis hoegi*, *C. lata*, *C. brevicornis* and *C. laticornis* have very broad shields, but they are incompletely known and of uncertain systematic position).

(4) Lateral fields with simple posterior termination.

The later Cephalaspinae are more progressive than the contemporaneous Benneviaspinae in the following respects:

(1) The lateral fields are greatly elongate (in *Cephalaspis* G/A=3.8–5.3).

(2) The nerves of the lateral fields are highly subdivided (5.4–5.7 in number).

(3) The prepineal shield is much expanded (B/A=2.2–2.5).

"*Cephalaspis*" *oeselensis* Robertson (1939b), from the Ludlow, resembles later species of *Cephalaspis* in general form and characteristics, but differs in a number of traits which are to be considered as primitive. These include the short dorsal and lateral fields (G/A=2.4), undivided or only slightly divided anterior nerves of the lateral fields (number of nerves=5.0–5.2), and relatively short prepineal shield (B/A=1.5). Other features, which may debar it from actual ancestry of *Cephalaspis*, are the specialized exoskeletal structure, the greatly reduced thoracic shield (C/A=1.9), and the more anterior position of the pectoral sinus (E/A=1.2; in other cephalaspids, E/A=1.3–1.9). It is necessary to distinguish this form as a distinct genus for which the name **Procephalaspis** is proposed (fig. 30, C).

Thyestes (fig. 30, A) is the most primitive of the Cephalaspidae and may represent the stock from which both the later Cephalaspinae and Benneviaspinae arose. The thoracic shield has been reduced somewhat, but it is still longer than in most of the later members of the family, and contains a variable number of segments (C/A=2.5–3.4). The lateral fields are short (G/A=1.9–2.0) and the nerves of the lateral fields are relatively undivided. The prepineal part of the shield is short (B/A=1.3). It is also probably primitive in having undivided lateral body scales, and in lacking any indication of a dorsal fin, even a median series of dorsal ridge scales. The greatly reduced exoskeleton, specialized in its large tubercles, may indicate that the known species of *Thyestes* are not ancestral to most later cephalaspids.

Subfamily BENNEVIASPINAE, subfam. nov.

With the exception of *Stensiopelta*, all of the genera referred to this subfamily, as well as *Kiaeraspis*, *Thyestes*, *Didymaspis*, and *Sclerodus*, were included by Stensiö (1932, p. 151) in his subfamily Kiaeraspinae. In this paper, *Kiaeraspis* has been referred to a family of its own, the Kiaeraspidae, while *Thyestes*, *Didymaspis*, and *Sclerodus* have been referred to the Cephalaspinae, Tremataspidae and Sclerodontidae, respectively. The following genera are included in the Benneviaspinae: *Securiaspis* Stensiö (Dittonian, England; Upper Red Bay Series, Spitsbergen); *Benneviaspis* Stensiö (Dittonian, England; Middle and Upper Red Bay Series, Spitsbergen); *Hoelaspis* Stensiö (Upper Red Bay Series, Spitsbergen); *Boreaspis* Stensiö (Lower Wood Bay Series, Spitsbergen); *Stensiopelta*, gen. nov. (?Dittonian, England).

They are definitely Cephalaspidae in possessing cornua and presumably the cephalaspid type of fin. Their close relationship to the Cephalaspinae is shown by intermediate forms, namely, *Securiaspis* and *Stensiopelta*, and it is probable that they were derived from the Cephalaspinae at a relatively late date. The Benneviaspinae are characterized by the following features, which distinguish them from the Cephalaspinae:

(1) Thoracic shield greatly reduced, more so than in the Cephalaspinae (C/A=1.7–2.3; 2.8 in *Stensiopelta*).

(2) Pectoral sinus deeper than in the Cephalaspinae (F/D=0.6–0.8); this is due in large part to the greater anterior invagination of the sinus (E/A=0.4–0.8).

(3) Shield generally broad, with a decided tendency towards a lateral flare in the postero-lateral region.

(4) The lateral fields usually show a two-pointed posterior termination, one point extending onto the cornua, and one postero-mesially. Exceptions to this are *Stensiopelta* and *Securiaspis*, al-

though the latter may show an incipient development of this character.

The Benneviaspinae were less progressive than contemporary Cephalaspinae in the following respects:

(1) The lateral fields only moderately lengthened (G/A=2.6–4.0).

(2) Nerves of the lateral fields less subdivided than in the Cephalaspinae (5.1–5.3 in number).

(3) The prepineal part of the shield, excluding the rostrum, generally less expanded (B/A=1.5–2.3).

Securiaspis is clearly intermediate morphologically between the Benneviaspinae and *Cephalaspis,* which it resembles in the general shape and proportions of the shield, and in the absence of any clearly indicated branching of the lateral fields posteriorly. It differs from *Cephalaspis,* however, and is shown to be related to the Benneviaspinae, by the greatly reduced thoracic shield (C/A=1.8), relatively unexpanded prepineal shield (B/A=1.8), only moderately lengthened lateral fields (G/A=2.6), and deep pectoral sinus (F/D=0.6) extending far anteriorly (E/A=0.6). On the basis of these characters, *"Cephalaspis" staxrudi* Stensiö (1927, p. 272, text fig. 68) certainly belongs to *Securiaspis.*

"Cephalaspis" woodwardi Stensiö (1932, p. 140, text fig. 50) differs markedly from other members of that genus. Its lateral fields extend posteriorly far onto the cornua without any indication of a medially directed lobe, as is typical in *Cephalaspis,* and it agrees with the latter in the moderately long thoracic shield (C/A=2.8). But in other characters it clearly resembles the Benneviaspinae: The prepineal shield is relatively short (B/A=1.8) and the lateral fields are not greatly lengthened (G/A=3.4). Very characteristic of the Benneviaspinae are the deep pectoral sinuses (F/D=0.6) extending far anteriorly (E/A=0.6), and the broad shield with a pronounced postero-lateral flare. These features indicate that *"Cephalaspis" woodwardi* should be separated from other species of *Cephalaspis;* it is here referred to **Stensiopelta,** gen. nov. and is referred to the Benneviaspinae. It is considered to be a relatively unspecialized member of the subfamily which has paralleled the Cephalaspinae in some respects.

Benneviaspis and *Hoelaspis* are highly specialized and divergent members of the subfamily, characterized particularly by the greatly broadened shield.

Boreaspis differs in certain respects from other Benneviaspinae. In spite of its late age, the thoracic shield is less reduced than in other members of the subfamily (C/A=2.3) and the shield is relatively narrow. The highly ossified endoskeleton is a distinctive feature that may be a specialization. The remote possibility has been suggested above that *Boreaspis* was descended from *Didymaspis*, but this is not demonstrable at present.

It is unlikely that the ancestry of the Benneviaspinae is to be sought within the genus *Cephalaspis* in spite of the annectent forms, *Securiaspis* and *Stensiopelta*. The few known Downtonian species of *Cephalaspis* were already more advanced in the lengthening of the lateral fields, subdivision of their nerves, and in the expansion of the prepineal part of the shield. On the other hand, there is nothing (excepting perhaps exoskeletal structure) to debar *Thyestes* from the ancestral position, and it is possible that this genus gave rise to both *Cephalaspis* and the Benneviaspinae.

Family KIAERASPIDAE Heintz 1939

As used here, this group is restricted to the genus *Kiaeraspis*, and is raised to family rank. Kiaeraspinae was originally used by Stensiö (1932) to include not only those genera here referred to the Benneviaspinae, but also *Thyestes*, *Didymaspis*, and *Sclerodus*. The classification of *Kiaeraspis* with these forms was based largely on a similarity in the degree of enlargement of the lateral and dorsal fields and on the position of the first two nerves of the lateral fields, as well as on their lack of subdivision. In an earlier part of this study it has been shown that these are characters subject to general evolutionary trends within the Osteostraci, so by themselves they are of little value in demonstrating relationships. In other respects *Kiaeraspis* occupies a rather isolated position.

Among the Osteostraci, only the Cephalaspidae can be considered as possible relatives, but the resemblances to any known members of that family are not particularly close. The form of the trunk segments and the posterior outline of the trunk shield, as well as the shape of the pectoral sinus and the postero-lateral corner of the cephalic shield, are not far from the condition of *Thyestes verrucosus*. On the other hand, *Kiaeraspis* differs widely from all Cephalaspidae in the following important respects:

(1) The trunk shield is long and apparently unreduced in length. This is to be considered as a primitive character that has been retained into the Devonian by this genus alone. All of the Cephal-

aspidae, even the earliest representatives from Oesel, have greatly shortened shields.

(2) No distinct cornua are developed. It is perfectly possible that they were present in the ancestors of *Kiaeraspis* and have been reduced, but it is also possible that they were never developed and that the lateral rim of the lateral fold was incorporated in the pectoral fin as in the Ateleaspidae. Only the discovery of the fins themselves can solve this problem.

(3) The peculiar inturning of the posterior ends of the lateral fields is unusual, and can be compared only with the situation in *Didymaspis* and the Benneviaspinae. In the former it is certainly related to the anterior position of the "pectoral sinuses," which have, in a sense, forced the posterior part of these fields to turn inward. In the Benneviaspinae, it is correlated with the angulation and restriction of the size of the cornua, which permitted further posterior expansion of the lateral fields only in a medial direction. In *Kiaeraspis,* however, the pectoral sinuses are posterior to the lateral fields, and the space on the postero-lateral corners of the cephalic shield is unoccupied; so the inturning of the fields is apparently related to other factors.

These differences make any close relationship to the Cephalaspidae improbable. But the few resemblances, slight though they are, suggest that *Kiaeraspis* may have been derived from the same stock as that family. Phyletic separation must have taken place earlier than the *Thyestes* evolutionary stage, where reduction of the trunk shield was already well under way. Since the manner in which the pectoral fins evolved in the Cephalaspidae is unknown, two possibilities must be considered: (*a*) The common ancestor had begun to develop pectoral fins from its lateral fold, but retained a long trunk shield, in which case both *Thyestes* and *Kiaeraspis* could be derived from this hypothetical form. (*b*) Pectoral fins evolved concurrently with the reduction of the trunk shield in the Cephalaspidae, in which case the common ancestor of *Thyestes* and *Kiaeraspis* must be sought in some such form as *Dartmuthia,* and *Kiaeraspis* must have developed its fins independently.

The Kiaeraspidae, as the name is here used, may be briefly defined by the following characters:

(1) Trunk shield unreduced in length.

(2) Pectoral fins present, but cornua absent or perhaps reduced.

(3) Lateral fields of moderate length, curving inwards posteriorly.

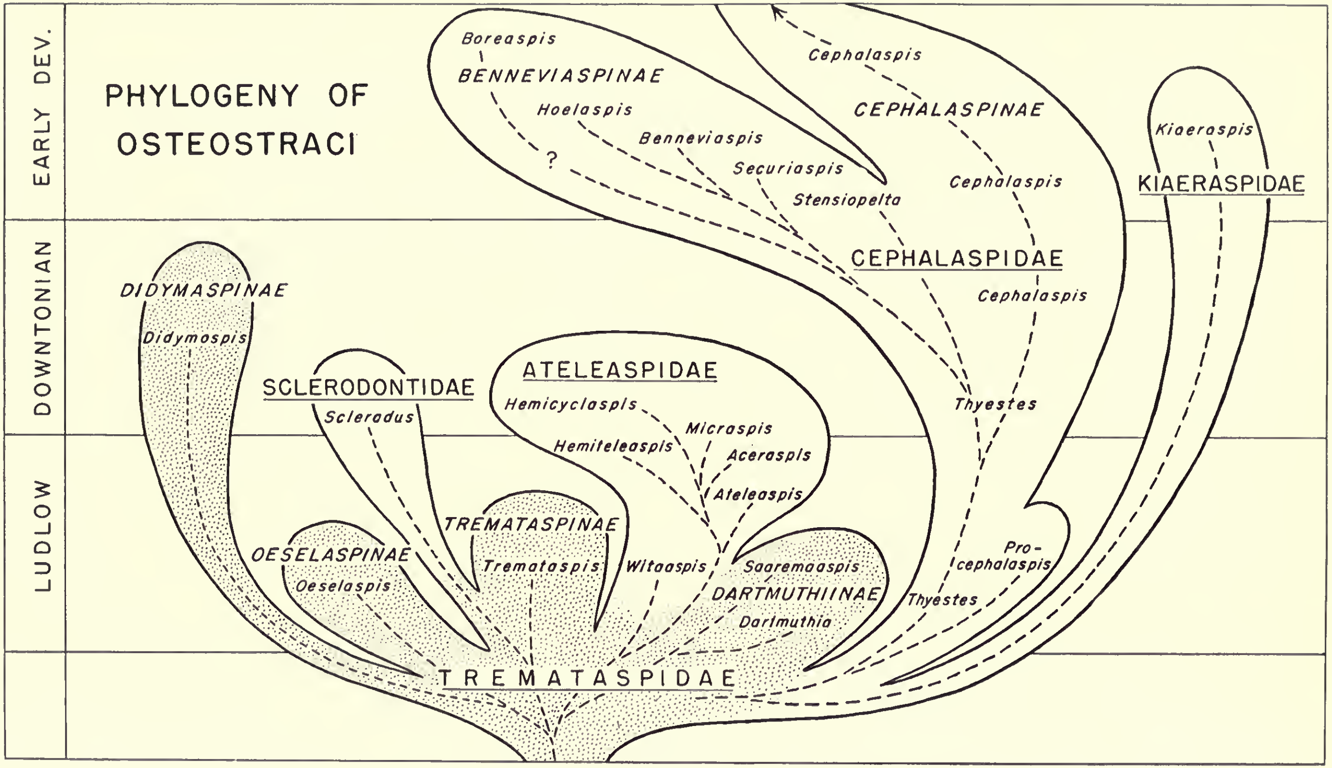

FIG. 31. Tentative phylogeny of the Osteostraci; the family Tremataspidae is indicated by stippling.

(4) First two nerves of lateral fields undivided, or perhaps very slightly separated.

(5) Prepineal shield of moderate length.

SUMMARY

The conclusions reached in this paper concerning the evolution and relationships of the Osteostraci are most concisely summarized by the accompanying phylogenetic chart (fig. 31). This suggests—especially during the early history of the group—many contemporaneous phyletic lines, each with its own particular specializations, yet all sharing the general evolutionary trends of the order. The first part of this work has been concerned with the demonstration of these general trends in a few of the more obvious characteristics of the Osteostraci, and, through this approach, the determination of what characters may be considered as primitive within the order. In the second part of this paper an attempt has been made to distinguish different phyletic lines and to base a classification upon them; the phyla have been distinguished not only by qualitative characteristics, but also by different rates of evolution in certain features.

The phylogeny represented in figure 31 is admittedly tentative. The Osteostraci from Oesel indicate that a wide evolutionary radiation had already taken place by Lower Ludlow times. Many of these early genera are clearly not ancestral to known later Osteostraci, while the suggested phyletic connections of some of the other genera to subsequent groups is unfortunately based upon less complete evidence than could be desired. It is hoped that future research and discoveries will help to clarify the many uncertainties that still remain in the evolution, classification and phylogeny of the Osteostraci.

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THE EXOSKELETON OF EARLY OSTEOSTRACI

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FIELDIANA: GEOLOGY
VOLUME 11, NUMBER 4
Published by
CHICAGO NATURAL HISTORY MUSEUM
JANUARY 19, 1951

PRINTED IN THE UNITED STATES OF AMERICA
BY CHICAGO NATURAL HISTORY MUSEUM PRESS

INTRODUCTION

This paper is primarily a discussion of the structure of some of the earliest known vertebrates, the Osteostraci from the Lower Ludlow of the Island of Oesel in the Baltic. Recent descriptions of most of these forms have disregarded the microscopic structure of the exoskeleton. That of *Tremataspis* is well known from the researches of several authors, and the *Dartmuthia* exoskeleton is the subject of a recent paper; but as far as the other Oesel Osteostraci are concerned, only brief, inadequate, and often incorrect notes have appeared.

The exoskeletal structure is often a diagnostic character of at least the higher categories, and for this reason alone it is desirable that descriptions be available. Added significance has been given to the structure of the exoskeleton by the recent suggestion that the heavy armor of the earliest vertebrates is to be considered a primitive trait, and that subdivision, reduction, and even loss of armor came later. With this in mind, I have made some comparisons of the Ludlow Osteostraci with later genera, and have given general consideration to the problem of the evolution of the exoskeleton within the order.

Genus **Tremataspis**

Since the exoskeleton of *Tremataspis* has been described in detail in earlier publications (Stensiö, 1927; Gross, 1935; Denison, 1947), I have given here only a brief account of its structure. This has been included so that there will be a basis for comparison in the discussion of other genera, and also to define the terminology here used.

The surface of the exoskeleton of *Tremataspis mammillata* (fig. 32, A) is smooth except for occasional small dorsal tubercles, and he pores and grooves of the sensory canal system and of the related ateral lines. Externally there is a thin layer of enamel, underlain y a much thicker layer of dentine-like tissue, the two forming the uperficial layer. The dentine is pervaded by tubules that arise rom a network of small vascular canals at the very top of the middle ayer. This network, called the subepidermal vascular plexus by

Stensiö, is divided in this species into polygons that are delimited by the sensory canals deeper in the middle layer; within the polygons the arrangement of the vascular canals is irregular. The subepidermal vascular plexus is connected by vertical canals (external branches of the ascending vascular canals) with a deeper vascular network near the bottom of the middle layer. The canals of this network have been called radiating canals in *Cephalaspis* by Stensiö, but since in *Tremataspis* they have no regular arrangement, the name is not appropriate; Wängsjö (1946) calls them horizontal submucous vascular canals. In *Tremataspis* this network of vascular canals lacks a well-defined polygonal arrangement and has numerous connections below the sensory canals. The thick and strongly laminated basal layer contains large cavities (basal cavities of Wängsjö, 1946) thought to have housed vascular sinuses and connected by narrow passages (ascending vascular canals) with the submucous vascular network of the middle layer. Small canals also pass internally from the basal cavities, either emerging from the inner surface of the exoskeleton, or passing into a subaponeurotic vascular plexus in the endoskeleton, where this is present. Finally, and definitely characteristic of the Osteostraci, is the very regular polygonal network of canals in the middle layer, called "mucous canals" by Stensiö (1927), but more recently shown to be sensory canals (Denison, 1947). In *T. mammillata*, these form relatively large and simple polygons, opening to the exterior by pores, or by open grooves where this system is specialized to form lateral line canals.

Other species of *Tremataspis* show some modifications of this simple structure. In both *T. schmidti* and *T. milleri* (Denison, 1947, text figs. 4–5) there is clear evidence of subdivision of the polygons of the sensory canals by the development of smaller and more superficial connecting canals across the primary polygons. These secondary connecting canals are homologous with the intra-areal canals of cephalaspids, while the larger primary canals are equivalent to the circumareal canals (of Gross, 1935; equals interareal canals of Stensiö, 1927). There are differences in the vascular networks of the middle layer, but the canals lack any regular arrangement; in fact, even their polygonal subdivision is not apparent in *T. schmidti*.

Genus **Dartmuthia**

The exoskeleton of *Dartmuthia* was the subject of a recent paper by Wängsjö (1946). In spite of the fact that he had very limited

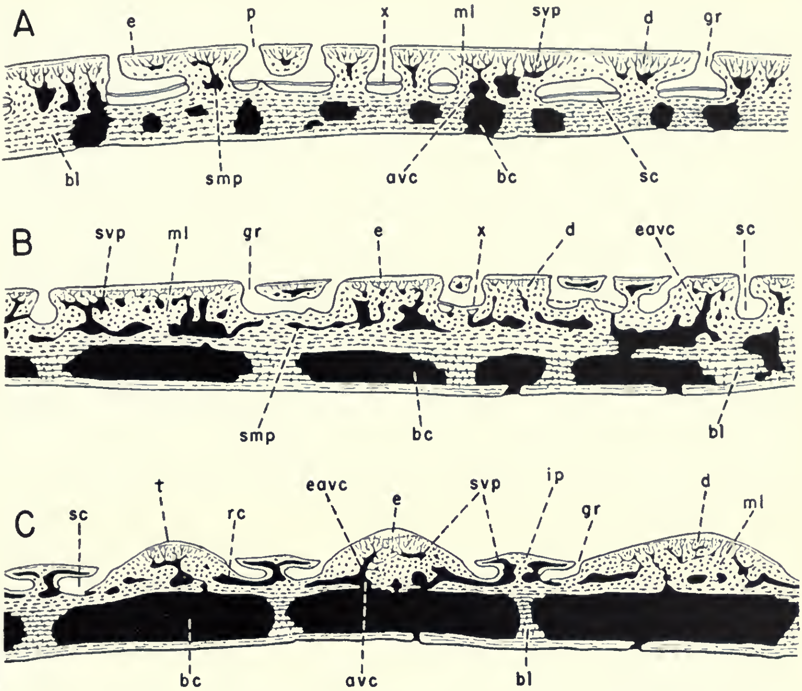

FIG. 32. Transverse sections of exoskeletons of Oesel Osteostraci. A, *Trem-ataspis mammillata* (×35); B, *Dartmuthia gemmifera*, ventral shield (×45); C, *D. gemmifera*, dorsal shield (×40). *avc*, ascending vascular canal; *bc*, basal vascular cavity; *bl*, basal layer; *d*, dentine; *dvc*, descending vascular canal; *e*, enamel; *eavc*, external branch of ascending vascular canal; *gr*, groove by which sensory canal opens to surface; *ip*, intertubercular process; *ml*, middle layer; *p*, pore by which sensory canal opens to surface; *rc*, radiating canal; *sc*, sensory canal; *smp*, submucous or lower vascular plexus of middle layer; *src*, sinus in radiating canal system; *svp*, subepidermal vascular plexus; *t*, tubercle; *x*, horizontal septum dividing sensory canal.

material at his disposal, his description is for the most part correct, although it is incomplete since it does not include the ventral shield. However, his conclusion (1946, p. 359) that "*Dartmuthia*, as far as its exoskeleton is concerned, on the whole agrees more closely with the Cephalaspids proper than with other Osteostraci" is not supported by the facts that he himself marshalls; it is hardly defensible when the ventral shield is considered, since the latter is very similar to the *Tremataspis* exoskeleton.

Excepting the marginal region, the ventral shield of *Dartmuthia* (Figs. 32, B; 33, A) is smooth, without any of the elevated tubercles that characterize the dorsal surface. It is subdivided into polygonal areas by the network of sensory canals which open to the surface by grooves (fig. 33, A, *gr*), instead of opening by pores as in *Tremataspis.* The grooves are extremely sinuous superficially, as if they had been formed by the union of numerous adjacent pores (fig. 34, B). The superficial layer is well developed, and consists of a shiny enamel film on the surface, underlain by a layer of dentine-like substance; it is similar to that of *Tremataspis,* although thinner. In the middle layer, the system of sensory canals is, for the most part, comparable to that of *Tremataspis.* Its polygons are relatively large, and there is no indication of any secondary canals except near the marginal area. Along the ventral surface of the marginal area, there are elongated areas with scalloped edges, capped with enamel, which correspond to the tubercles of the dorsal shield, except that they are flatter (fig. 33, B, *st*); these are separated by areas in which the polygons are small and lack enamel. The small size of the polygons here suggests that the canals separating them are comparable to intra-areal canals, while the canals separating the polygons of the rest of the ventral shield are similar to those of *Tremataspis mammillata* and to the circumareal canals of cephalaspids. It is possible to recognize in some of the sections the thin horizontal septum, first discovered in *Tremataspis* (Denison, 1947, p. 341), which divides the sensory canals into an outer part in direct communication with the exterior, and an inner part that presumably housed the sensory endings, and into which the vascular canals open (fig. 32, B, *x*). The vascular canals of the middle layer are much as in *Tremataspis.* The subepidermal vascular plexus is divided into polygonal areas by the grooves of the sensory canals, but the submucous plexus extends freely below the sensory canals and shows no indication of any regular arrangement as radiating canals. The ascending vascular canals from the basal layer are concentrated near the center of the polygons, but their external branches are numerous throughout the whole polygonal area. The basal layer resembles that of *Tremataspis;* the basal cavities are larger in the sections studied, but this may not be characteristic of fully adult exoskeletons.

The dorsal shield (figs. 32, C; 34, A) is much modified, its most obvious specialization being the presence of tubercles, some of which are large and arranged in rows. The tops of the tubercles show thin enamel and thick dentine layers, representing the superficial layer of the exoskeleton. Just below are canals of the subepidermal vascular plexus, connected by external branches of the ascending

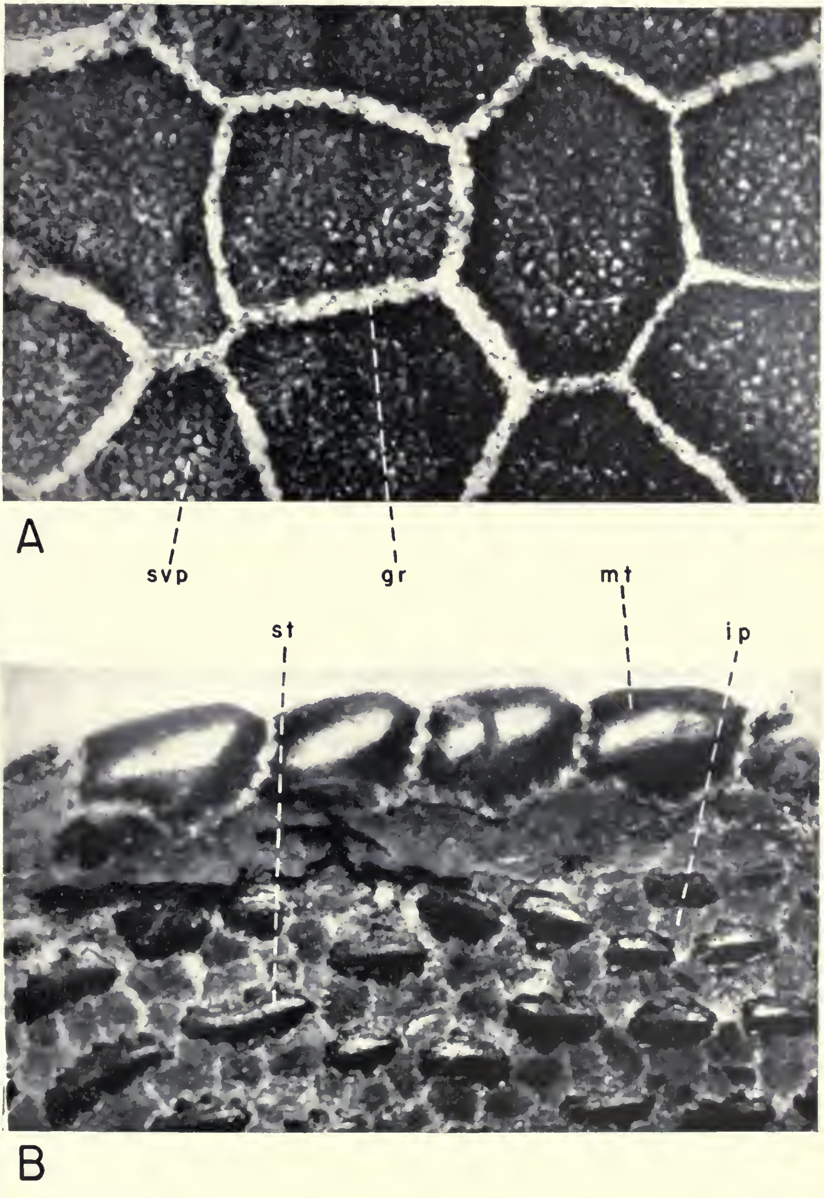

FIG. 33. *Dartmuthia gemmifera.* A, Surface of ventral shield seen as a semitransparency under liquid (×35); B, Ventral surface of lateral marginal area (×30). *gr,* groove by which sensory canal opens to surface; *ip,* intertubercular process; *mt,* marginal tubercles; *st,* small tubercle-like areas; *svp,* subepidermal vascular plexus.

vascular canals with the submucous vascular plexus at the base of the tubercles. The arrangement of the latter plexus is modified from the primitive condition found in the ventral shield and in *Tremataspis,* and approaches the cephalaspid pattern. In the center of the tubercles an irregular plexus is formed by canals uniting the ascending vascular canals from the basal cavities; but radially disposed branches extend from this central plexus in all directions, passing under the sensory canals to unite with radiating canals from other tubercle areas (fig. 34, A, *smp*). Although it is obvious there must have been a blood supply both to and from the exoskeleton, it does not seem possible to distinguish, as in cephalaspids, any clearly differentiated canals representing the beginnings of the venous system; the canal labeled "descending vascular canal" by Wängsjö (1946, pl. VI, fig. 3) is not strictly comparable to the canals so named in *Cephalaspis.*

Between the tubercles, and nearly enclosing the sensory canals that surround the tubercles, arise processes with vertical columns basally, and horizontal laminae superficially (fig. 32, C, *ip*). The latter were named "intertubercular plates" by Wängsjö, although they are not separate from the rest of the exoskeleton. The vascular supply of the intertubercular processes is derived from branches of the underlying radiating canals; there are ascending canals in the vertical columns, from which branches spread out irregularly in the more superficial horizontal lamellae. The latter are certainly part of the subepidermal vascular plexus, which is significant, since it shows that the processes consist largely of the middle exoskeletal layer. Wängsjö (1946, p. 355) considered that the "intertubercular plates" belonged to the superficial layer, but this is disproved by the presence in them of the subepidermal plexus. It is probable that a very thin layer coating the intertubercular processes represents the superficial layer here, but I have not been able to identify any structures that would characterize this coating as dentine; it is certainly not enamel. In any case, it is clear that the superficial layer has been largely lost between the tubercules.

The sensory canals ("mucous canals") have been described in some detail by Wängsjö, who gave different names to canals surrounding the tubercles and to those lying between tubercles. It should be noted that the canals are in the central or lower part of the middle layer, and that they are always open to the surface by grooves (fig. 32, C, *gr*), in contradiction to statements by Wängsjö. The lateral line canals are interstitial canals (as distinguished from

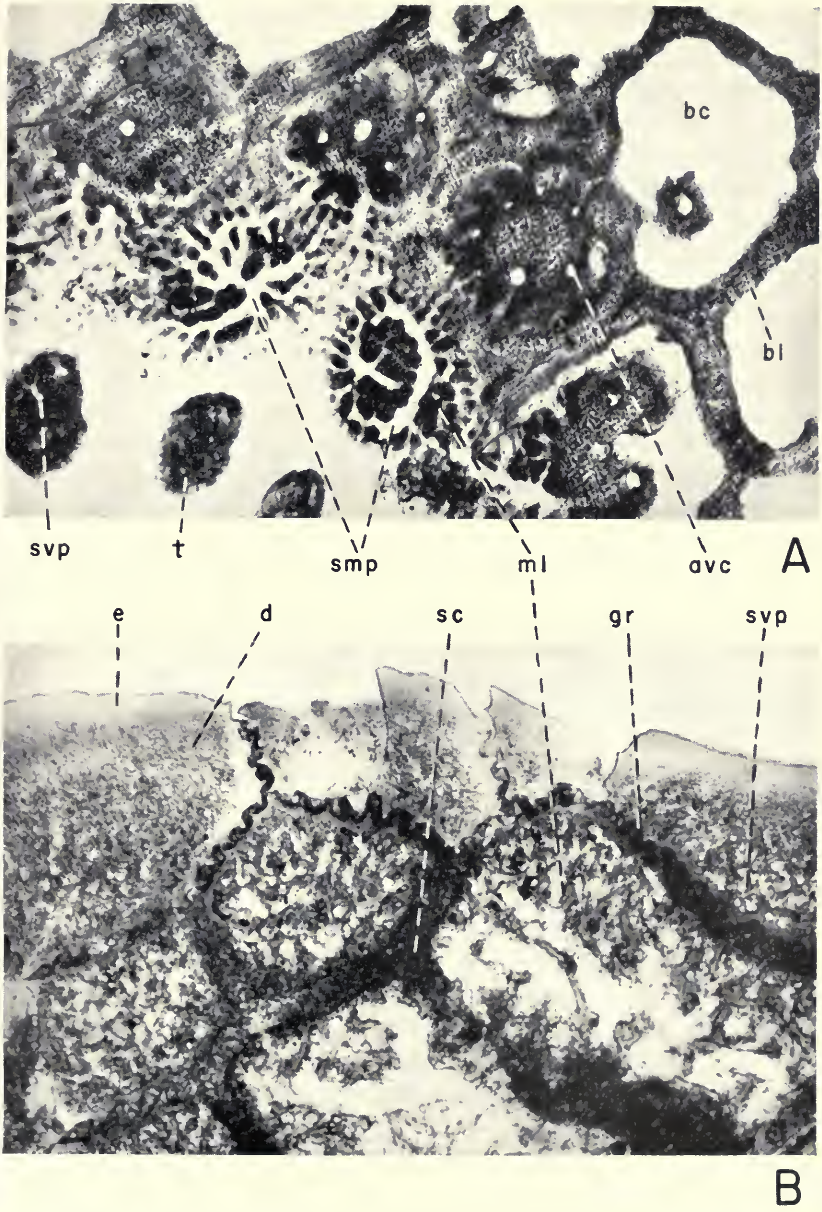

FIG. 34. *Dartmuthia gemmifera* (×30). A, Obliquely tangential section of dorsal shield; B, Obliquely tangential section of ventral shield. *avc*, ascending vascular canals; *bc*, basal vascular cavity; *bl*, basal layer; *d*, dentine; *e*, enamel; *gr*, groove by which sensory canal opens to surface; *ml*, middle layer; *sc*, sensory canal; *smp*, submucous or lower vascular plexus of middle layer; *svp*, subepidermal vascular plexus and external branches of ascending vascular canals; *t*, tubercle.

canals called circumtubercular and cross commissural by Wängsjö) that are specialized only in their linear arrangement. Thus in essentials, the relationship of the lateral line system to the sensory canal network is the same as in *Tremataspis*, where it has been described more fully in an earlier work (Denison, 1947, pp. 350–353).

The basal layer does not differ from that of the ventral shield or from the basal layer of the *Tremataspis* exoskeleton. The relatively large basal cavities in the figured sections (figs. 32, C; 34, A, *bc*), as in the case of the ventral shield, probably indicate that the exoskeleton was not completely grown in these individuals, since in other sections, not figured, the basal cavities are much smaller. That there were horizontal connections between the basal cavities as indicated by Wängsjö (1946, p. 351) is doubtful; in the section he figures to demonstrate this (1946, pl. VI, fig. 2), these connections are clearly due to breaks and displacement, not to natural perforations. Such breaks are invariably present in this relatively weak part of the exoskeleton in the sections examined, but in no case was there any clear evidence of a natural communication.

The structure of the ventral shield of *Dartmuthia* strongly supports the view that this genus is closely related to *Tremataspis*. The dorsal shield, although considerably specialized superficially, is still unspecialized basally. It could have been derived from the simple *Tremataspis* type by the emphasis of tubercles, by their arrangement in rows, by the reduction of the superficial layer between the tubercles, and by the partial acquisition of a radial pattern in the submucous vascular plexus.

There is good evidence that the growth of the exoskeleton was similar to that described in *Tremataspis* (Denison, 1947). One individual that has been sectioned lacks the basal layer and has the middle layer only partly developed, incompletely enclosing the vascular canals. As I mentioned above, the large cavities in the basal layer in the figured specimens would probably have filled in partly, upon maturity.

Genus **Oeselaspis**

The structure of the exoskeleton of *Oeselaspis* has not been described before, except for brief notes derived from observation of the surface by Robertson (1935). The dorsal and ventral shields are similar and exhibit a characteristic and somewhat specialized condition (fig. 35, A).

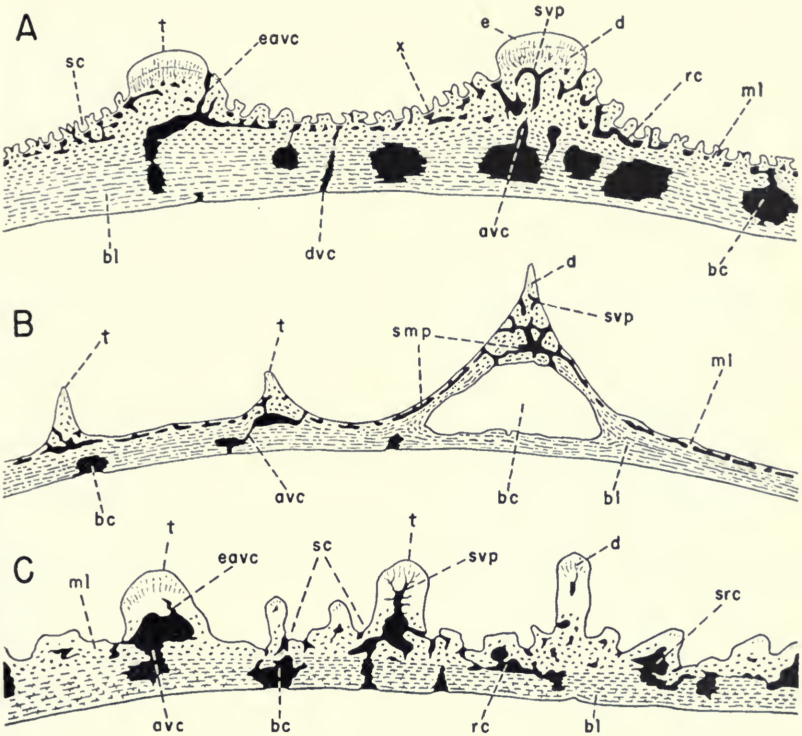

FIG. 35. Transverse sections of dorsal exoskeletons of Oesel Osteostraci. A, *Oeselaspis pustulata* (×40); B, *Thyestes verrucosus* (×35); C, *Procephalaspis oeselensis* (×40). For abbreviations, see figure 32.

Large, widely scattered tubercles with broadly rounded tops are the outstanding superficial feature. The outer part of the tubercles is covered with a rather thick layer of enamel, penetrated by numerous fine tubules perpendicular to the surface. Below is a layer of dentine exhibiting tubules continuous with those of the enamel layer. Sometimes these tubules look like ordinary cell lacunae of the middle layer, except that they are elongated perpendicular to the surface. This, and the fact that the superficial and middle layers are not clearly differentiated, suggest that this tissue is intermediate n character between true dentine and bone. Only in the tubercles s the superficial layer preserved.

Vascular canals at the top of the middle layer in the tubercles are shown to belong to the subepidermal vascular plexus by the fact that the dentinal tubules arise from them. Lateral branches descending more or less parallel with the surface of the tubercles connect them with a network of canals just below the grooves of the sensory canals, while external branches of the ascending vascular canals unite the subepidermal vascular plexus with the vascular plexus near the base of the middle layer. The latter, which is equivalent to the submucous vascular plexus in *Tremataspis,* is specialized in *Oeselaspis* by the development of an irregular radiating pattern centered under the tubercles.

In the intertubercular spaces, the superficial layer and the uppermost part of the middle layer are absent. The surface consists of open grooves that house the sensory canals (fig. 35, A, *sc*) and that are separated by projections of the middle layer, giving the "minutely spiculate" effect described by Robertson (1935, p. 457). The middle layer is thinner here. Near its base are the radiating canals, from which vascular canals extend toward the surface; many of them pass the short distance to the base of the sensory canal grooves, where they expand and are separated from the grooves only by a thin bony partition (fig. 35, A, *x*). It is probable that this partition is homologous with the thin, horizontal septum dividing the sensory canals of *Tremataspis* and *Dartmuthia,* and that the "vascular" expansion below the partition is to be identified with the lower part of the sensory canals of those genera. There is good indication in certain sections of *Oeselaspis* that this thin septum is pierced by a few minute pores, perhaps for sensory endings. A few of the vascular branches from the radiating canals appear to extend into, or along the edge of, the bony projections between the sensory canals; they probably lead to a part of the subepidermal vascular plexus external to the exoskeleton.

The sensory canals form a fine-meshed network over the entire shield, except on the top of the tubercles (fig. 37, C, *sc*), and are housed in open grooves, since in these regions the superficial layer and the top of the middle layer are absent. No large polygonal sensory canal areas are recognizable, and the small size of the polygons suggests that most of the canals are intra-areal or secondary, rather than circumareal. The lateral lines are clearly a part of this sensory canal system (fig. 37, C, *ifc*).

The basal layer is thick and strongly cross-laminated. It possesses numerous basal cavities, widely distributed both below and between the tubercles. Ascending vascular canals feed the vascular networks of the middle layer and extend superficially, while basal canals lead to the internal surface of the exoskeleton. The only indication of a large polygonal pattern in the shield is given by the partitions between the basal cavities. Large polygons, corresponding to the tubercle areas, are subdivided by the partitions between the basal cavities within those areas. In certain cases the partitions appear as ridges on the inner surface of the skeleton because the intervening weaker parts of the basal layer have been crushed. Narrow vertical canals in the basal layer of the intertubercular region are occasionally seen in sections. They extend from the radiating canals to the internal surface of the exoskeleton, and may represent venous canals, comparable to the descending vascular canals of *Cephalaspis* (fig. 35, A, *dvc*).

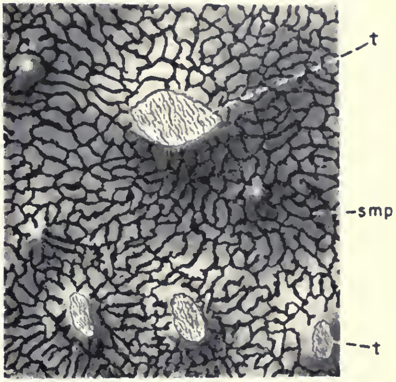

FIG. 36. Superficial view of the exoskeleton of *Thyestes verrucosus* (×40), showing the tubercles (*t*), and the submucous or radiating vascular canals (*smp*), which are drawn as transparencies.

Genus Thyestes

A few notes on the minute structure of the shield of *Thyestes egertoni* and *T. salteri* have been given by Stensiö (1932). In those species, as also in *T. verrucosus* to be described here, the exoskeleton is specialized and greatly reduced.

The tubercles are the most striking feature of the dorsal shield of *Thyestes verrucosus* (fig. 35, B; 36, *t*). Some of them are arranged in longitudinal rows and are very large and wide-based, tapering to a rather sharp tip. Between the rows of large tubercles, and sometimes on their lower slopes, are numerous smaller tubercles, often rregularly arranged but similar in shape. Along the margin of the shield are two or three rows of moderate-sized tubercles, with straight crests and very much flattened dorso-ventrally, so that they appear very slender and sharp in transverse sections. The only enamel that has been observed in this species is on the tips of these marginal tubercles. The other tubercles are capped with dentine of the usual type found in Osteostraci. Elsewhere on the shield the superficial layer is completely lacking.

The middle layer is also greatly reduced. In the tubercles it is represented by a thickness of non-laminated bone, pervaded by a complicated network of vascular canals representing the subepidermal vascular plexus, ascending canals, and submucous plexus or radiating canals. The latter may be expanded into a sinus from which the lower network of vascular canals extends in all directions toward the periphery of the tubercle as an irregular network, with only a slight suggestion of a radiating pattern (fig. 36, *smp*). Between the tubercles, the middle layer may be completely missing on the lateral part of the shield. More medially it is just thick enough to enclose a stratum of vascular canals that open frequently to the surface. These represent the submucous vascular plexus, a continuation of that of the tubercles. The polygonal areas are marked only by the pattern of these canals, each polygon containing a central tubercle. The subepidermal vascular plexus (except in tubercles) and the network of sensory canals is completely outside the exoskeleton. Lateral lines may be recognized superficially on the shield; they are marked only by the linear arrangement of the tubercles on either side, and by the faintly indicated edges of the polygons that underlie the lateral lines.

The basal layer is well developed and very strongly laminated, making up the bulk of the exoskeleton. It contains relatively few small basal cavities, communicating with the interior of the shell and with the submucous vascular plexus by means of ascending vascular canals. Under the large tubercles, the basal cavities are tremendously enlarged (fig. 35, B, *bc*), so that the upper part of the basal layer bends sharply upward and extends high into the tubercle.

Sections of the exoskeleton of *Thyestes egertoni* and *T. salteri* have not been figured, but judging from Stensiö's descriptions (1932, pp. 167, 169) the structure is similar to that of *T. verrucosus*. The greatly reduced exoskeleton, apparently characteristic of the genus, is presumably a specialization and is surprising in so early a form, which in other respects could very well have been ancestral to later Cephalaspidae.

Genus **Procephalaspis**

Procephalaspis oeselensis was originally described as a species of *Cephalaspis* (Robertson, 1939), but it differs from any described member of the latter genus in its exoskeletal structure as well as in other characters. Superficial reduction, affecting the superficial layer and to some extent the middle layer, is considerable, though less than in *Thyestes*. The most striking specialization is the peculiar development of tubercles (fig. 35, C, *t*). Over the dorsal shield these tubercles are generally tall, and often slender and columnar, with a rounded top; on the lateral rim they are smaller, close set, elongated, and usually expanded distally. No evidence of any enamel has been found in any sections. The cap of the tubercles is nearly structureless in most of the sections examined, only occasionally showing tubules. But, since this tissue is superficial to the most external vascular canals, it is certainly part of the superficial layer and is considered to be a modified osteo-dentine.

Judging by the extent of the vascular canals, the middle layer extends well up into the tubercles, although bone cell lacunae have not been found as far superficially as the canals. The system of vascular canals is simple, but not unmodified from the *Tremataspis* type. Ascending vascular canals from the basal layer are centered below the tubercles and lead into large sinuses in the middle layer at the base of the tubercles (fig. 35, C, *src*). From these sinuses the submucous vascular plexus extends horizontally below and to the bases of the grooves of the sensory canals; it has a typically cephalaspid radiating pattern. External branches of the ascending vascular canals continue in a superficial direction from the sinuses into the subepidermal vascular plexus in the tubercles.

Between the tubercles the sensory canals are represented by relatively large grooves, left open superficially by the absence of the outer part of the middle layer. Separating the sensory canals are processes of the middle layer, among which the tubercles may be included (fig. 37, A, *pml*). Superficial inspection indicates that both circumareal and intra-areal canals are present, the former represented by the larger polygonal grooves surrounding the tubercle areas, the latter by the complex network within the polygons and around the tubercles (fig. 37, A, *cac, iac*). In the limited number of thin sections available, it has not been possible to distinguish these two types of sensory canals. The canals of the lateral line are circumareal canals differing only in that they are arranged in a linear fashion (fig. 37, A, *ifc*).

The basal layer shows no obvious modifications. It is clearly laminated, contains moderate-sized basal cavities below the tubercles, and occasionally exhibits between the tubercles narrower canals that may represent descending vascular canals.

Genus **Saaremaaspis**

Since few specimens belonging to *Saaremaaspis* are known, no thin sections have been made, and the following rather incomplete description has been derived from a study of the inner and outer surfaces and broken edges of the dorsal and ventral shields.

The exoskeleton is very thin. Along the lateral margin there are small, flattened tubercles that appear to be coated with enamel, but only on these tubercles has the superficial layer been recognized. Over the rest of the shield the middle layer forms the surface and seems to be reduced to some extent. The fine, "granular ornamentation" that covers the whole surface and that Robertson identified as tubercles of the superficial layer (1938, p. 493) are not comparable to the tubercles of other Osteostraci but are small projections of the middle layer, similar to those of *Oeselaspis* (fig. 37, D, *pml*). Between these projections are open canals forming a polygonal network of very fine mesh. Their identification as canals of the sensory canal network is confirmed by the fact that they communicate freely with the canals of the lateral line, which have the appearance of linear, larger, and somewhat deeper members of the same canal system (fig. 37, D, *ifc*); circumareal and intra-areal canals cannot be differentiated. Below the sensory canals in the middle layer, the submucous vascular plexus is occasionally discernible, and probably lacks any regular arrangement. The basal layer is sometimes present, and is typically cross-laminated; it has numerous small basal cavities, each with a pore beneath it on the smooth inner surface of the exoskeleton.

As has been noted elsewhere (Denison, 1951), there are no recognizable differences in the structure of the exoskeleton of *Rotsiküllaspis*, which, for this and other reasons, has been referred to *Saaremaaspis*.

Genus **Witaaspis**

Witaaspis is another genus so rare that thin sections of the exoskeleton have not been made. A few slides, made by Patten from his Oesel collections, and labeled "*Thyestes reticulata*," almost certainly belong to *Witaaspis*, but are unsatisfactory and show little that cannot be observed by study of the surface of the exoskeleton.

The exoskeleton is very poorly developed except marginally and around the median dorsal structures, where it may be considerably thicker. As in *Saaremaaspis*, the superficial layer is present only

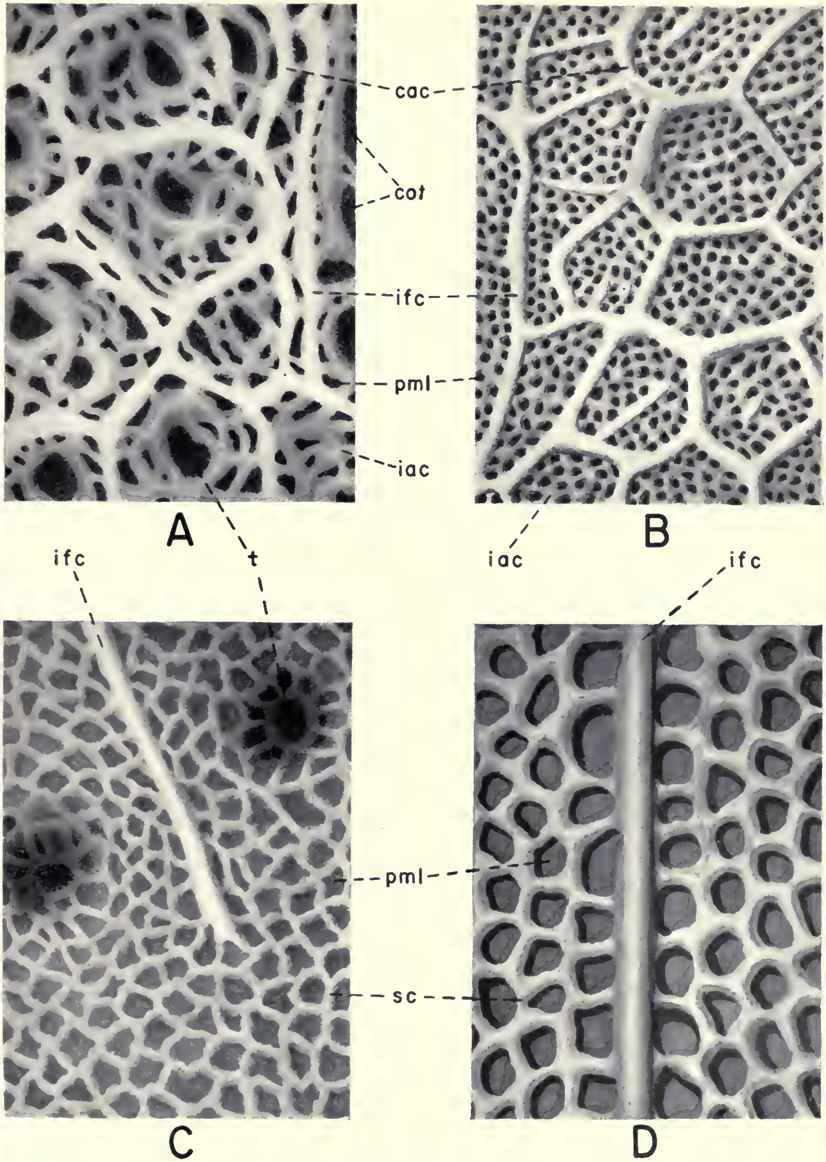

FIG. 37. Preparations of the exoskeleton in which some of the shell material has been removed from below so as to show the relationships of the sensory canal network to the lateral lines; all are viewed from the inside. A, *Procephalaspis oeselensis* (×25); B, *Witaaspis schrenkii* (×30); C, *Oeselaspis pustulata* (×60); D, *Saaremaaspis mickwitzi* (×75). *cac*, circumareal sensory canals; *cot*, circumorbital tubercles; *iac*, intra-areal sensory canals; *ifc*, infraorbital lateral line canal; *pml*, processes of middle layer between intra-areal sensory canals; *sc*, sensory canals (probably intra-areal); *t*, tubercle.

on the tips of the small tubercles of the lateral margin. The surface of the rest of the shield is formed by the middle layer and is marked by grooves forming polygons of moderate size, which undoubtedly housed the circumareal sensory canals (fig. 37, B, *cac*). The polygons are subdivided by shallower and narrower grooves for the intra-areal sensory canals, which form a fine network (fig. 37, B, *iac*). Lateral line canals may be seen to be part of the sensory canal system, closely resembling the circumareal canals in size and depth (fig. 37, B, *ifc*). Between the sensory grooves are processes of the middle layer, often pointed in section, and pierced by canals of the vascular system.

The basal layer is very poorly developed and cannot be observed in many specimens. In one of Patten's sections of "*Thyestes reticulata,*" possibly a juvenile individual, only a thin layer representing the most superficial part of the basal layer or basal part of the middle layer is present. Another section shows a very thin basal lamina, connected infrequently with the more superficial exoskeleton by vertical columns of laminated bone. Whether the basal layer was really reduced in this genus, or whether the specimens examined are juvenile individuals with incomplete development of the basal layer, it is not possible to say with certainty.

Genus **Sclerodus**

The peculiar nature of the exoskeleton of the Downtonian genus *Sclerodus* has been emphasized by Stensiö (1932, pp. 176, 179) and Wängsjö (1946, pp. 356–357), who considered it to be distinct from that of all other Osteostraci. Unfortunately it has not been figured, except for a section of one of the "cornua" (Stensiö, 1932, pl. LVI, fig. 1), which cannot be considered as typical. The superficial layer is reported to be reduced or entirely absent, and the middle layer to be well developed. The latter contains a complicated system of vascular canals, but no trace of the sensory canals has been recognized. Stensiö argues that the irregular arrangement of the submucous vascular plexus ("radiating canals") indicates that the sensory canal system had been lost, since the polygonal arrangement of the latter system determines the arrangement of the vascular canal areas. It is more likely, however, that the superficial part of the middle layer was lost, that the sensory canal system was exterior to the exoskeleton, and that the irregular arrangement of the vascular network was a primitive feature, comparable to that in *Tremataspis* and in the ventral shield of *Dartmuthia*.

EVOLUTIONARY MODIFICATIONS OF THE EXOSKELETON

In a recent general analysis of the exoskeleton of the Osteostraci (Denison, 1951), it was concluded that there was no clearly demonstrated trend towards the reduction of ossification in the evolution of this order. In the same paper *Tremataspis* was shown to be primitive among the Osteostraci in so many respects that the assumption was made that its well-developed exoskeleton with unreduced superficial layer was also primitive. Although it is not always true that evolution proceeds in the direction of increasing complexity, this is usually the case, so the relatively simple structure of the *Tremataspis* exoskeleton is an added argument in favor of its primitive condition. The surface shows only an insignificant development of tubercles, and these are merely swellings of the superficial layer. The system of sensory canals, at least in *T. mammillata,* consists of a simple network of large polygons, uncomplicated by secondary subdivisions. The vascular networks of the middle layer are irregular, lacking any orderly pattern or well-defined subdivision into areas. The basal layer does not reflect the polygonal arrangement of the middle layer to any degree, and lacks any recognizable distinct canal systems for the return of venous blood.

Turning to other Osteostraci, the following modifications, all presumably specializations, appear in various genera and species:

(1) Development of tubercles, involving a protuberance of the middle as well as the superficial layer. Since tubercles are superficial structures, they often retain an enamel crown, as in the dorsal shield of *Dartmuthia,* and also in *Oeselaspis, Aceraspis, Hemicyclaspis lightbodii,* and many species of *Cephalaspis.* In other genera, *Procephalaspis* and *Thyestes,* the enamel is lost and the tubercles are capped with dentine. In *Witaaspis, Saaremaaspis,* and perhaps *Sclerodus,* tubercles are present only on the margins of the shield; the projections that cover the rest of the shield consist only of the middle layer and are not to be considered as tubercles in the strict sense.

(2) Superficial reduction of the exoskeleton. Except in *Tremataspis,* the superficial layer is always reduced between the tubercles and may be completely lost. Reduction and loss of the superficial layer is also common in non-tuberculated forms. The outer part of the middle layer may also fail to ossify, leaving the sensory canals widely open. In a few species only the base of the middle layer is ossified, so that the entire system of sensory canals is outside the exoskeleton; this is the case in *Thyestes, Didymaspis,* and probably

in *Sclerodus* and some species of *Cephalaspis*. In the most extreme cases of reduction the middle layer is completely absent, as in *Cephalaspis borealis, C. oblongus,* and parts of the shield of *Thyestes* and *Didymaspis*. There is no well-established case where the basal layer is also reduced; this may be so in *Witaaspis,* but the fact that this layer ossifies last in ontogeny suggests the possibility that those exoskeletons lacking a well-developed basal layer may be those of juvenile individuals.

(3) Subdivision of the sensory canal network. The sensory canals of *Tremataspis mammillata* and of the ventral shield of *Dartmuthia* form a polygonal network of relatively large mesh; these are the primitive circumareal canals. Subdivision of the polygons by the growth of smaller, and usually more superficial, intra-areal canals has taken place in other forms. The beginnings of this subdivision may be seen in *Tremataspis milleri* and *T. schmidti* (Denison, 1947, fig. 4), and both circumareal and intra-areal canals can be distinguished in most of the other genera whose exoskeletal structure is sufficiently well known. The network of sensory canals may become very complex in Downtonian and Early Devonian forms, especially in some species of *Cephalaspis,* such as *C. campbelltonensis* and *C. powriei,* where the circumareal canals themselves are multiple (Stensiö, 1932, fig. 5).

(4) Organization of the vascular system of the middle layer. In *Tremataspis* and in the ventral shield of *Dartmuthia* both the subepidermal vascular plexus and the submucous plexus are irregular. In most other Oesel genera, and in the majority of later Osteostraci, the polygonal pattern defined by the circumareal sensory canals conditions a subdivision of the vascular network into polygonal areas. Typically, the blood vessels are supplied from within at the center of a polygon, or under the center of a tubercle, and blood is transported to the periphery of the polygon or tubercle area by canals with a clearly radiating pattern at the base of the middle layer. While originally the radiating canals occupied a single level, they may subdivide so as to occupy a considerable thickness of bone in *Cephalaspis*.

(5) Modifications of the basal layer. The basal layer is remarkably conservative in its structure throughout the Osteostraci. The basal cavities are consistently placed below the centers of the polygons, the partitions between them reflecting to varying degrees the polygonal pattern of more superficial layers. In some species of *Cephalaspis,* such as *C. salweyi* and *C. powriei,* the polygonal

pattern of the basal layer is emphasized by the development of descending vascular canals and ring sinuses beneath the periphery of the polygons. An unusual modification of the basal layer is found in *Thyestes verrucosus*, where the basal cavities are tremendously expanded under the larger tubercles.

This review of exoskeletal modifications supports the view that there was a trend towards increasing complexity of structure in the history of the Osteostraci. The various specializations do not as yet appear to fit into any phyletic pattern. The exoskeletal structure may be characteristic of a genus, but families (excepting monogeneric ones) cannot now be recognized on this basis. Superficial reduction is common, but the absence of any well-defined trends in this respect, and the presence of considerable variability not only between species but also within species (*Cephalaspis pagei* and *C. powriei*) make it unsafe to assume that the loss of the superficial part of the exoskeleton must necessarily debar a species from the ancestry of forms in which the exoskeleton is well developed. Thus the possibility cannot be excluded that such genera as *Saaremaaspis* and *Witaaspis*, which have greatly reduced but relatively simple exoskeletons, may still be ancestral to later Ateleaspidae in which the superficial layer is usually present. On the other hand, the enormous tubercles of *Thyestes*, underlain by greatly enlarged basal cavities, are unique, a specialization that would seem to exclude the known species of this genus from the ancestry of most later Cephalaspidae. Our present knowledge of the exoskeleton of most Downtonian and Devonian Osteostraci is insufficient to permit the distinguishing of phyletic groups on the basis of their exoskeletal structure alone, although eventually this feature may help to indicate their relationships to Ludlow genera.

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