THE
NEW PHYTOLOGIST

A BRITISH BOTANICAL JOURNAL,

EDITED BY A. G. TANSLEY, M.A., F.R.S.

UNIVERSITY LECTURER IN BOTANY, CAMBRIDGE,

IN CONSULTATION WITH THE STAFF OF THE CAMBRIDGE BOTANY SCHOOL.

VOLUME XVIII.

PP. VII. AND 298.
WITH SIX PLATES AND NUMEROUS FIGURES IN THE TEXT.

WILLIAM WESLEY & SON,

28 Essex Street, Strand, W.C.2.

LONDON, 1919.

INDEX OF SUBJECTS.

INDEX OF AUTHORS.

THE
NEW PHYTOLOGIST

VOL. XVIII, NOS. 1 & 2. JAN. & FEB., 1919.
[PUBLISHED MARCH 9TH, 1919.]

THE ORIGIN AND DEVELOPMENT OF THE COMPOSITÆ.

BY JAMES SMALL, M SC. (LOND.), PH.C.

CHAPTER X.

GEOGRAPHICAL DISTRIBUTION OF THE COMPOSITÆ.

ALTHOUGH morphological characters must always be the primary data in the determination of the apparent affinities and evolutionary history of species, geographical distribution furnishes an obvious but somewhat neglected test of the truth of any deductions from structure. For instance, the Calenduleæ are practically confined to Africa and are unknown in America with the exception of one monotypic genus, *Eriachaenium*, which occurs in the Magellan region. Although this genus may be placed quite properly in the Calenduleæ from a taxonomic point of view, it is clear that its evolutionary history differs from that of the other genera in the tribe.

Up to the present point the affinities and evolutionary history of the tribes and sub-tribes have been traced only from morphological and physiological data. This chapter, which is an extension of a paper by the author (67) on the same subject, includes, in addition to the main outlines of the history of the subject, an account of the distribution of *Senecio* in some detail and of other genera, together with a discussion of these data in the light of recent developments in geographical botany and of the phyletic suggestions contained in the previous chapters.

A. HISTORY.

The most important contribution to the subject of this chapter is Bentham's elaborate exposition (I, 7), which covers the whole field from the older, purely taxonomic point of view.

General problems are dealt with by De Candolle (IX, 11). Darwin (II, 16), and Wallace (IX, 41). Don (I, 25) gives an analysis of the distribution of the Cichorieæ known at that date

(1825), while Lindley (I, 56) and Schultz Bipontinus (I, 77) treat of of the subject in a somewhat perfunctory manner. The last developed his preliminary remarks in a later contribution (61). Nees (I, 67) gives a table of the distribution throughout the world of the then (1833) known genera of the Heterochrominæ. As illustrations of the new outlook on the problems of geographical distribution the papers by Andrews (3-4) and Capitaine (13) on the Leguminosæ, by Himmelbauer (39) on the Berberidaceæ and by Gates (28-29) on certain Liliaceæ may be quoted. These accounts correlate all, or at least most, of what is known about the plants with their distribution, and sound views on the evolution of the groups are more likely to result from this method than from the older method of purely morphological comparisons.

Land bridges in various parts of the world are brought in to solve many problems (cp. 74 and 82) and the Antarctic connection between Fuegia and New Zealand has been much written about (58, 66, etc.), but Hutton (42) points out that such a bridge probably did not exist after the origin of the Angiosperms, except in the form of an archipelago. In the Compositæ, as was indicated in Chapter IX, we must explain the distribution with the land surface of the world as it is to-day.

Concentration at High Levels. The extreme abundance of the Compositæ at high levels is noted in almost all alpine investigations ; it is mentioned by Cassini (I, 18, Tome I, p. 324.), Spruce (69, p. 288), Whymper (73, pp. 199 and 352) and Guppy (IX, 21, Vol. II, p. 238) who quotes Hemsley (37), Hooker and Ball (40) and Schimper (IX, 32) as authorities. Hemsley (37) quotes figures for concentrations along the mountains from the Caucasus to Japan and suggests the pappus mechanism as the cause. Ball (5a) gives 25-30% as the proportion of Composites in the higher Andean flora.

The local dominance of Composites over other plants is well known from common experience with daisies, dandelions and thistles. Interesting cases of complete dominance are given by Darwin (21, p. 113), who mentions beds of the cardoon thistle (*Cynara cardunculus*) "many (probably several hundred) square miles" in extent where "nothing else can now live", and also by Geddes (30), who found the Great Ragweed (*Ambrosia trifida*) covering a ravine with a dense growth of plants 12 to 18ft. high.

Action of Environment. The direct effect of environment on the individual is rapidly becoming one of the most fertile fields in the domain of experimental evolution. Although the origin of new

Linnean species has not yet been effected, changes in the individual in response to definite factors of the environment have been obtained which certainly give greater differences than those between a very large number of taxonomic species.

Some instances have already been mentioned of the effect of injury, food supply etc., on the floral characters: see Molliard (IV, 55-56a) and his explanation of the dioecism of *Pulicaria* (II, 26), also Daniel (IV, 23-24) and the reduction of doubling, Chapter IV, C, under Causal Morphology,

The value of this type of work is recognised by Massart (53), who considers that the effects of the environment are hereditary in some cases at least and, as a consequence, recognises the possibility of a polyphyletic origin for genera or even species. Warming (71, Chap. 100) and the Reports of the Carnegie Institution of Washington furnish abundant references to such experimental evolution. The last chapter of Warming's *Oecology of Plants* is of great interest in this connection (see below Chapter XI). An important point is developed by Harshberger (35) under the term "generic coefficient," which expresses the percentage relation between the number of genera and that of species in any region: *i.e.* $\frac{\text{number of genera}}{\text{number of species}} \times 100 = $generic coefficient. Simple topography, as on the plains, gives a high generic coefficient, while the highly diversified topography of regions such as the Rockies and Andes gives a low generic coefficient.

The subject cannot be dealt with in detail here, but it may be useful to bring together some references. Taylor (70) mentions habitat endemics. Cockayne (17) uses the term *epharmonic variation* in the sense of "a change in its form or physiological behaviour *beneficial* to an organism evoked by the operation of some environmental stimulus. Such a change may be called epharmonic adaptation, as distinguished from such adaptations as cannot be traced to any direct action of the environment" Poweraker (26), who gives some experiments on anthocyan changes in *Raoulia* in response to environment, suggests natural selection as the cause of the origin of cushion-plants but he agrees, in conversation with the writer, that the most probable explanation of his chief problem, "What causes this espalier shape?", lies in the direct action of the heat radiation from the sun-baked shingle on the permeability of the protoplasm of the cells of the under surface of the lateral branches (cp. 68a). This seems to be a clear case of epharmonic variation. The observations by Poweraker (loc. cit.), Hauri (36), and Schröter and Hauri (60) furnish other examples of similar epharmonic variation in cushion-plants of widely different taxonomic affinities (cp. Schimper IX, 32, pp. 704-716).

It is a significant fact that the first detailed studies of the peculiar insular floras both of New Zealand (15-17) and of the Sandwich Islands (51) have resulted in the emphasis of epharmonic variation. Bews (6-7) dealing with the many peculiar Composites of Natal seems to take the same view although he uses epharmony in Vesque's sense, not in Cockayne's (see below Chapter XI). He writes (7) of the study of epharmony as giving a deeper insight into the causal relationship of environment to plant form.

One of the most extraordinary cases is the change observed in *Cnicus arvensis* by Compton (18) who records that after a flood in the fens all herbaceous plants were killed except *Cochlearia armoracia*, the rootstocks of which sprouted after drainage, and a few specimens of *Cnicus arvensis*, which seemed normal but were attached to the soil by two to three feet of slender, leafless stem, exactly like the woodless stem of a true aquatic. Considering that the thistles probably owe their origin to the heat and dryness of the centre of origin (see below) this epharmonic adaptation in a few weeks to an aquatic habitat is very striking (cp. Warming on *Polygonum amphibium*, 71, p. 371).

Other cases are (*a*) woodiness in the stem of a marsh plant as the effect of water at 30-40° C (27), (*b*) various modifications similar to those of arctic plants as the effect of continuous or discontinuous electric illumination (8), (*c*) desiccation and excessive insolation as the cause of spines (48), (*d*) the alpine habit in *Senecio Jacobaea* etc. induced by the alternation of low temperatures and darkness with high temperatures and strong insolation (9).

There are also other experimental or observational papers by Oger (56), Harris (33), Dauphiné (22), Constantin (19), Shreve (63-64), Bailey and Sinnott (5) and Jeffrey (43, Chap. XXX).

Age and Area. The Age and Area Law which has been demonstrated by Willis (75-82) is the most important contribution to geographical botany since the *Origin of Species*. As the original accounts and various reviews (20,23-24,49,65,67) are easily accessible it will be sufficient to note that the formal expression of the law is that "the geographical distribution of a species (*i.e.* the area which it includes within its outer localities) within a fairly uniform country not broken by serious barriers depends, so long as conditions remain constant, upon the age of that species within the country."

The truth and value of this contribution to the subject is obvious when it is noted that the composition of and many other points concerning the flora of a country can be predicted with a reasonable degree of accuracy. It has been applied very successfully to the evolution of the Podostemaceæ by Willis (IV, 93) and has been confirmed for the Gramineæ of Australia by Breakwell (10). Taylor (70) dealing with only 22 endemic species, finds it true in as detailed a fashion as can be expected when dealing with single species, but he transgresses the Willisian dictum that comparisons must be made in groups of 20 or more species. Under these circumstances the exceptions he finds are quite in accordance with expectations. Taylor effects a compromise between the views of Sinnott (65) and Willis. He finds that of 22 endemic species 16 are young and 5 relicts, the remaining case being doubtful. Of the 16 young species 14 are considered to be due to generic or specific instability and 2 to the direct action of the environment (cp. Chap. XI, B).

The theory of "the differentiation of primitive, world-ranging, generalised types in response to the differentiation of their conditions" (Guppy, IX, 22, p. 313) is quite in accordance with the facts of Age and Area, and the idea of the differentiation, especially of insular endemic species, *in situ* is in close agreement with what is known of epharmonic variations. This also solves one of the problems of Age and Area, *i.e.* the occurrence on islands of endemic species of wide spread genera, which are there the only representatives of these genera. If the individuals were confined on arrival to a particular area they would naturally all show the same epharmonic variation, with the result that the original species as represented on the island would be entirely transformed into the new species.

Guppy, however, seems to use primitive in a peculiar sense (op. cit., p. 315) since he classes the Compositæ as primitive! He also appeals very much to geological changes, but no authentic fossil Composites are known below the Oligocene, and the differentiation of climate since has not been sufficient to account for all the differentiation in the family.

Other accounts of phenomena bearing on Age and Area and Differentiation are given by Kroeber (46), Andrews (4), A. Jordan (44, pp. 18-19), D. S. Jordan (45), Lloyd (47) and Samuelsson (59) The most important contribution for present purposes is that by Bentham, who was never an enthusiastic Natural Selectionist. He says (I, 7, p. 481) "The result of the best-founded opinions on this subject which to my knowledge have been propounded is that a race of plants, be it tribe or genus or species, in its period of full vigour, is widely dispersed, accommodates itself to a great variety of climatological, physical or other external influences, is numerous and varied in subordinate races, as well as individuals, these subordinate races, especially those immediately subordinate, not being separated by wide structural gaps, and not having acquired any marked local characters, but for the most part passing, as it were, into each other, their respective distinctive characters not having yet acquired any marked degree of correlation. On the other hand, a race in a state of decay is represented by subordinate races very distinct in structural characters, of restricted areas, and requiring for their preservation special climatological or other physical conditions, and consequently comparatively few in number . . . . Old decaying and apparently expiring races may, however, in some of their branches, owing perhaps a slight change in constitution, habit or external circumstances, start into new life . . . . These young progressive races will be very prolific, ready colonisers; and their subordinate races will be generally numerous and so blended together as to defy all positive determinations of their limits, and be variously estimated as subgenera, sections, species, subspecies or varieties." Again writing of the sections of *Vernonia* (I, 7, p. 393) he says "the section *Lepidaploa*, which, rather from its wide geographical range and connections than from its happening to include the species first taken as the type, may be conjectured to be nearest to the original form."

These views, it will be seen, form what is probably the best pre-Willisian account of the relation of Area to Age. But, whereas these are suppositions fairly obvious but unproved, the hypothesis is raised to the status of a fundamental law by the statistical proof furnished by Willis for age within a given country, and its proved extension to absolute age and total area seems to be only a question of time and application.

B. GEOGRAPHICAL DISTRIBUTION OF *Senecio*.

The Senecioneæ are indicated in previous chapters as the primitive tribe; the distribution of the chief genus, *Senecio*, is therefore of fundamental importance. If the numerous species of *Senecio* were confined to one locality or even to one continent, it would be difficult to uphold the view that they had been the source, for example, of the Arctotideæ in South Africa, the Vernonieæ in

South America, and the Cichorieæ in the Mediterranean region. The present investigation, however, shows that the distribution of this genus is quite in accordance with previous suggestions.

Method.

In dealing with the Compositæ the world may be divided into a few large regions, which do not always correspond to the regions delimited in the study of other families.

America is divided thus:—

U. S. A. region:—including Canada and Alaska.
Mexican region:—including Central America and California.
West Indian region:—including all the West Indian Islands in the widest sense,
Andine region:—including west tropical South America.
Brazilian region:—including east tropical South America.
Chilian region:—including extra-tropical South America.

The rest of the world is divided thus:—

Eur-Asiatic region:—including north and central Europe, Siberia and the eastern parts of subtropical Asia.
Mediterranean region:—including south Europe, north Africa and the western parts of subtropical Asia.
Tropical Asiatic region:—including India south of the Himalayas, the East Indies and the Malay Archipelago.
Tropical African region.
South African region:—including extra-tropical South Africa.
Australian region:—including the Australasian islands.[1]

These regions serve for a preliminary analysis of distribution and will be frequently referred to later, but in the case of *Senecio* a detailed investigation was made. An alphabetical list of the 2300 species of *Senecio* in the *Index Kewensis* and its Supplements to 1910 was made, including amongst other data the habitat as there recorded. A number of floras and papers (84-135)and the Herbaria at Kew and Edinburgh were then examined for further details. During this investigation about 50 new species were added to the list, so that it is more or less complete. The results of this study are naturally too bulky to be included in the present condensed

---

[1] A somewhat similar division for mammals is made by Sclater (62) and it is interesting to note that his Cape sub-region connects directly in East Africa with the Saharan sub-region; and that his Western or Arid sub-region includes most of Mexico and the western U.S.A (see below on Paths of Migration).

account of the family, so that only a general outline of the more striking features will be given.

A map (Plate I, Fig. 29) is given in which the areas of the more important species are delimited by a thick red line, those of less important species with more than a local habitat by a thin red line and those of species which are limited to one state or country by red dots. Accuracy in detail has not been aimed at on account of the small size of the map and because it is unnecessary for the elucidation of the chief points, namely the centre of origin, the paths of migration and the centres of concentration.

The Centre of Origin.

In a number of other widespread genera the centre of origin is clearly indicated by the coincidence of the point of overlapping of the areas of widespread species with the centre of concentration (see Pl. II, 31, Pl. III, 34, Pl.V, 37,38), but in *Senecio* there is no such indication. Evidence will be given in Chapter XI for the origin of *Senecio* in or about the Bolivian region. The north of South America is the probable centre of origin for most large Angiospermous families (cp. 4). One point which confirms this hypothesis for *Senecio* is the very large concentration of species along the Andes and on the campos, savannahs and the margins of the Brazilian forests, but as there are other equally intense concentrations in South Africa and Mexico this does not form conclusive evidence.

Taking this point as granted in the meantime we can consider the South American species. The species with only a local distribution number in Chili 318, in Peru 66, in Bolivia 56, in Ecuador 36, in Colombia 45, in Brazil 56, in Argentina 36, and in Patagonia 46. These numbers are, however, of little importance for comparison among themselves as they depend perhaps more on our present knowledge of each country than on the actual number of species present. The large number in Chili, for instance, is due to the activity of two botanists Remy (130-131) and Philippi (126-127). It is clear, however, that the Andean is a particularly favourable region for specific differentiation in the genus. On the other hand, not a single species of *Senecio* is recorded from Honduras, our knowledge of the flora of that Central American state having been limited until recent years to a list of some seventy species mentioned by Morris (54). More recent collections have added somewhat to our knowledge of this flora (cp. 41 & 83).

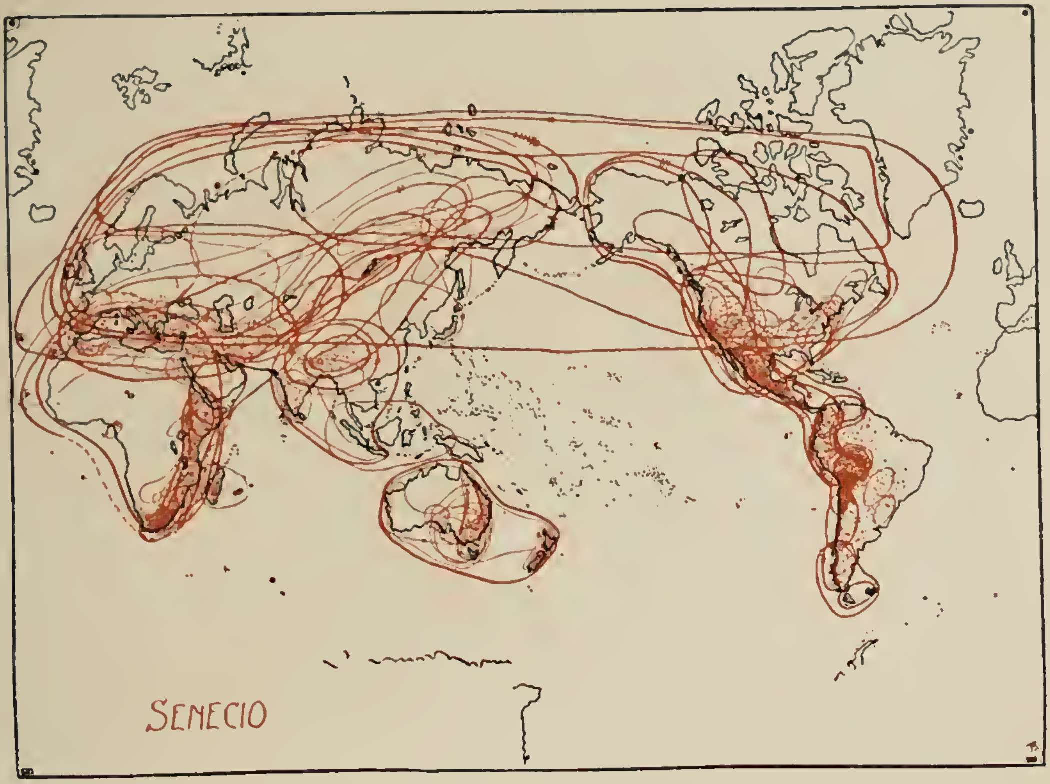

SENECIO

FIG. 29.

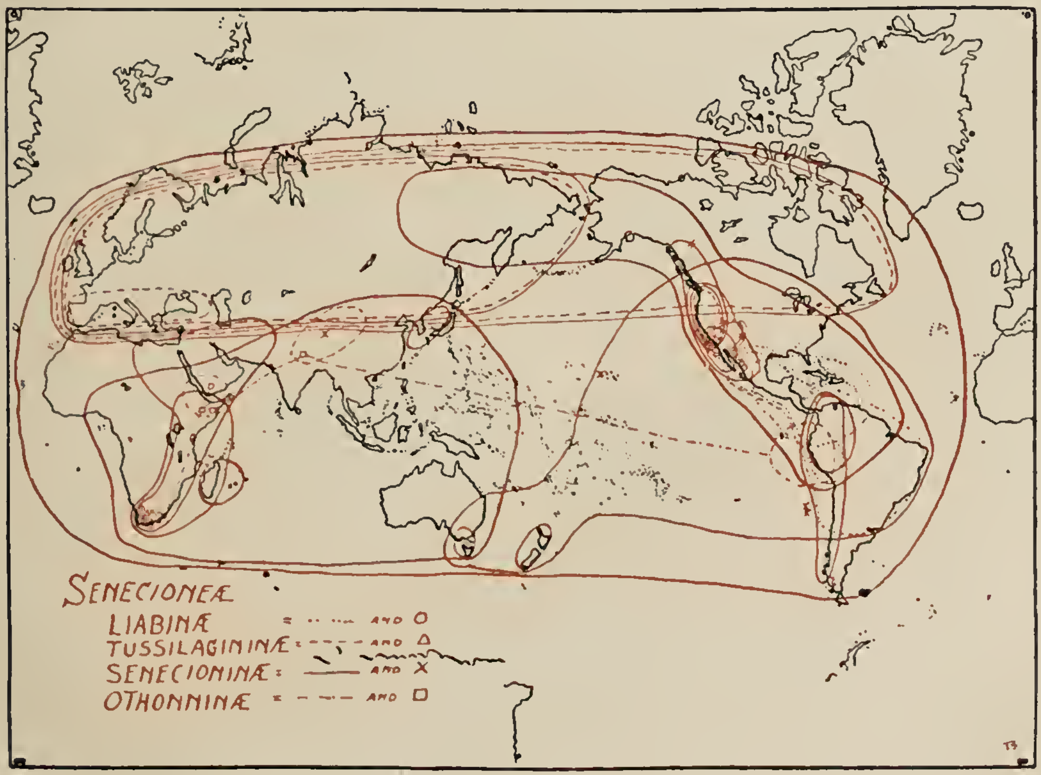

SENECIONEÆ
LIABINÆ and O
TUSSILAGININÆ and △
SENECIONINÆ and X
OTHONNINÆ and □

FIG. 30.

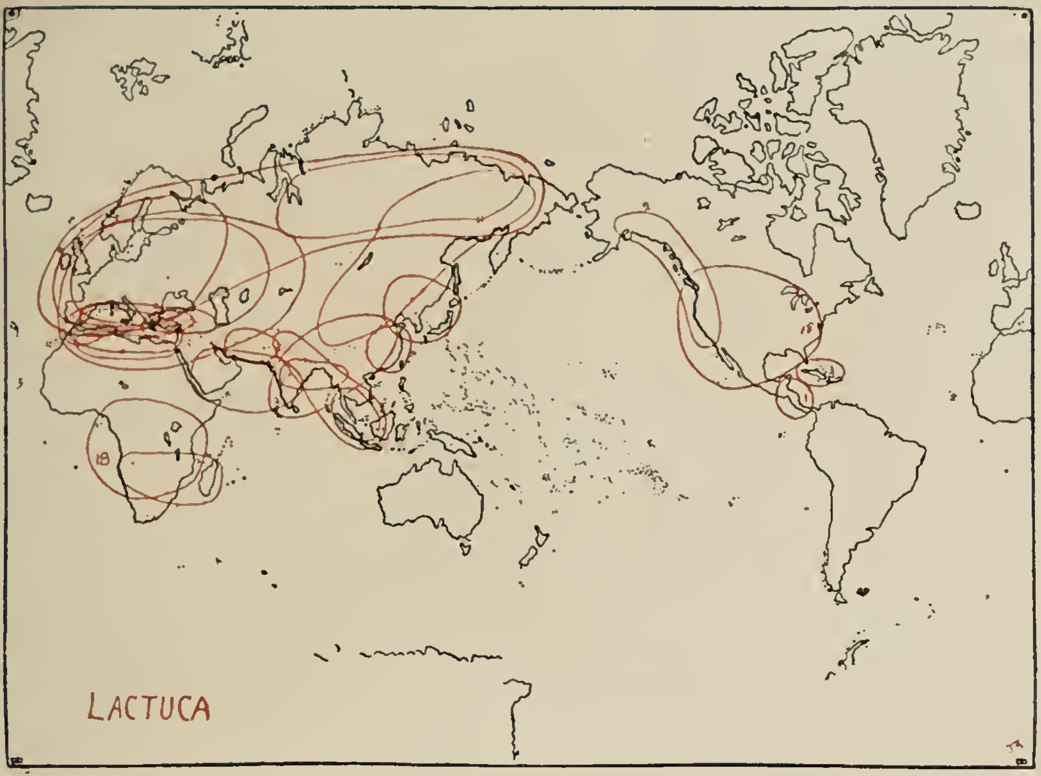

LACTUCA
18
15

FIG. 31.

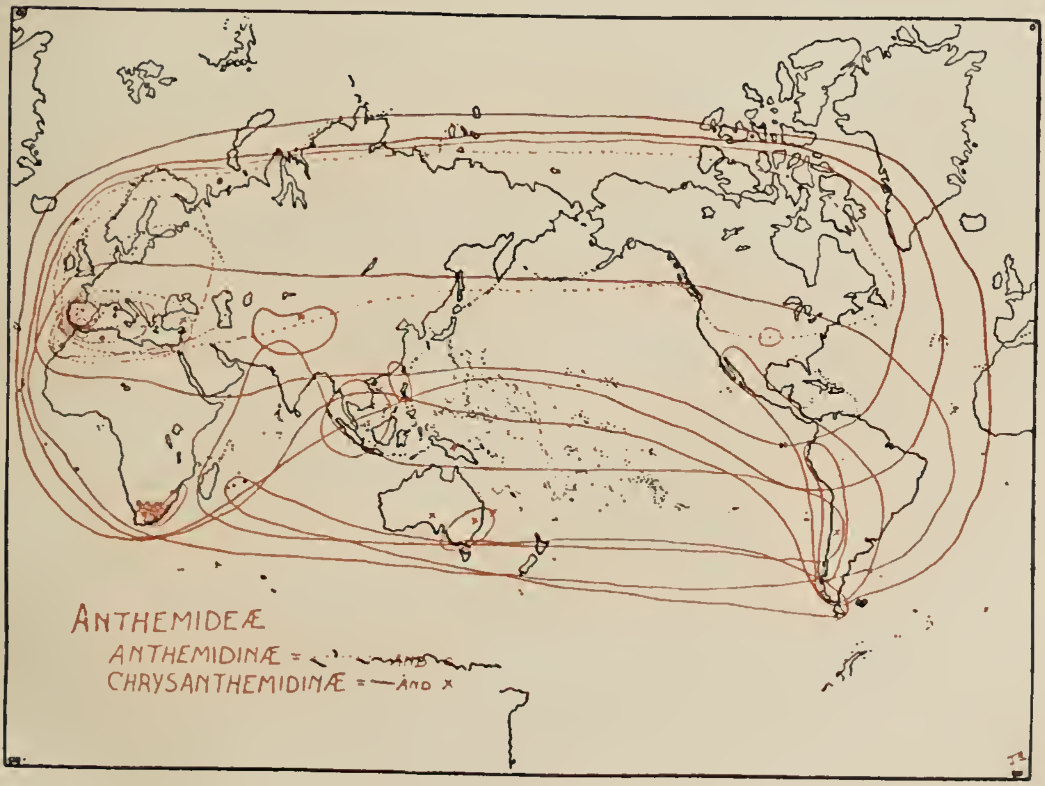

ANTHEMIDEÆ
ANTHEMIDINÆ = ··· AND
CHRYSANTHEMIDINÆ = — AND ×

FIG. 32.

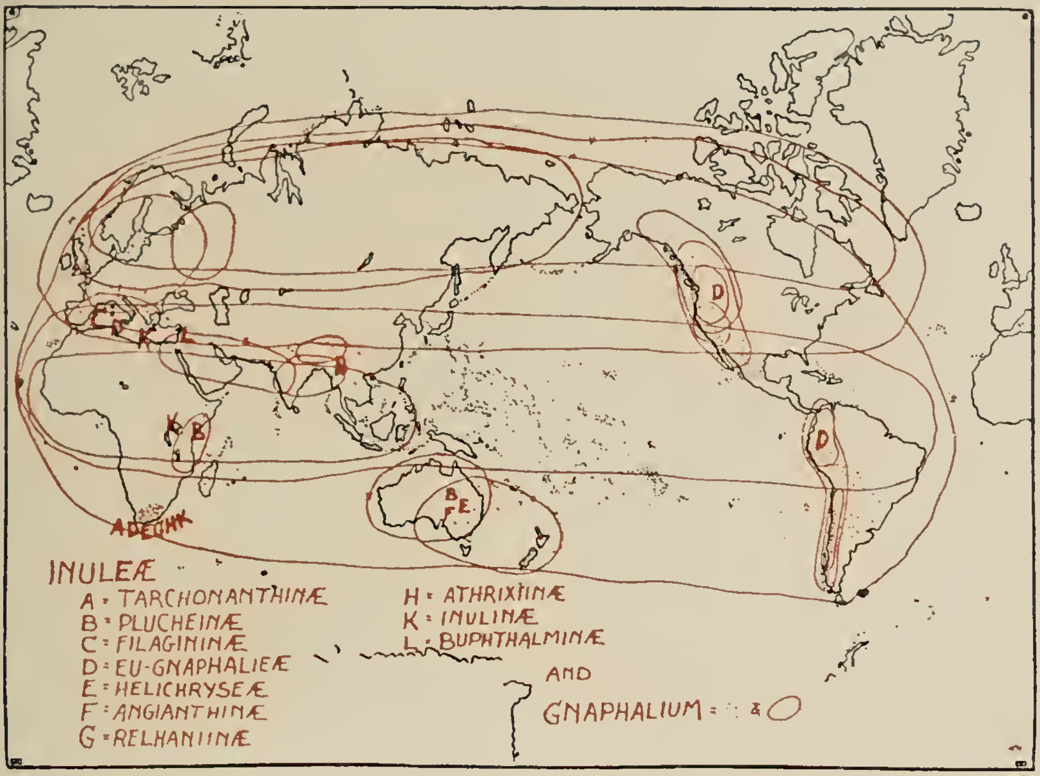

D
D
B
B
E
F
C
K
L
K
B
ADEGHK
INULEÆ
A = TARCHONANTHINÆ
B = PLUCHEINÆ
C = FILAGININÆ
D = EU-GNAPHALIEÆ
E = HELICHRYSEÆ
F = ANGIANTHINÆ
G = RELHANIINÆ
H = ATHRIXIINÆ
K = INULINÆ
L = BUPHTHALMINÆ
AND
GNAPHALIUM = ⁚ & ○

FIG. 33.

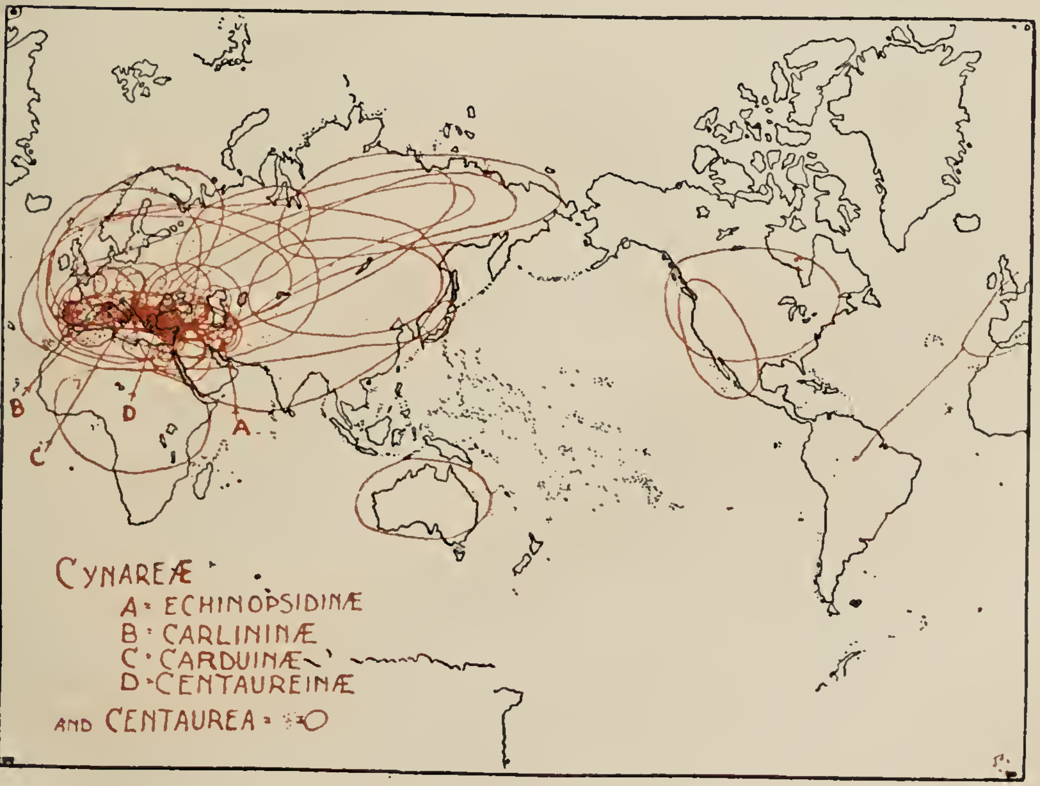

B
C
D
A
CYNAREÆ
A = ECHINOPSIDINÆ
B = CARLININÆ
C = CARDUINÆ
D = CENTAUREINÆ
AND CENTAUREA = ⁚ & ○

FIG. 34.

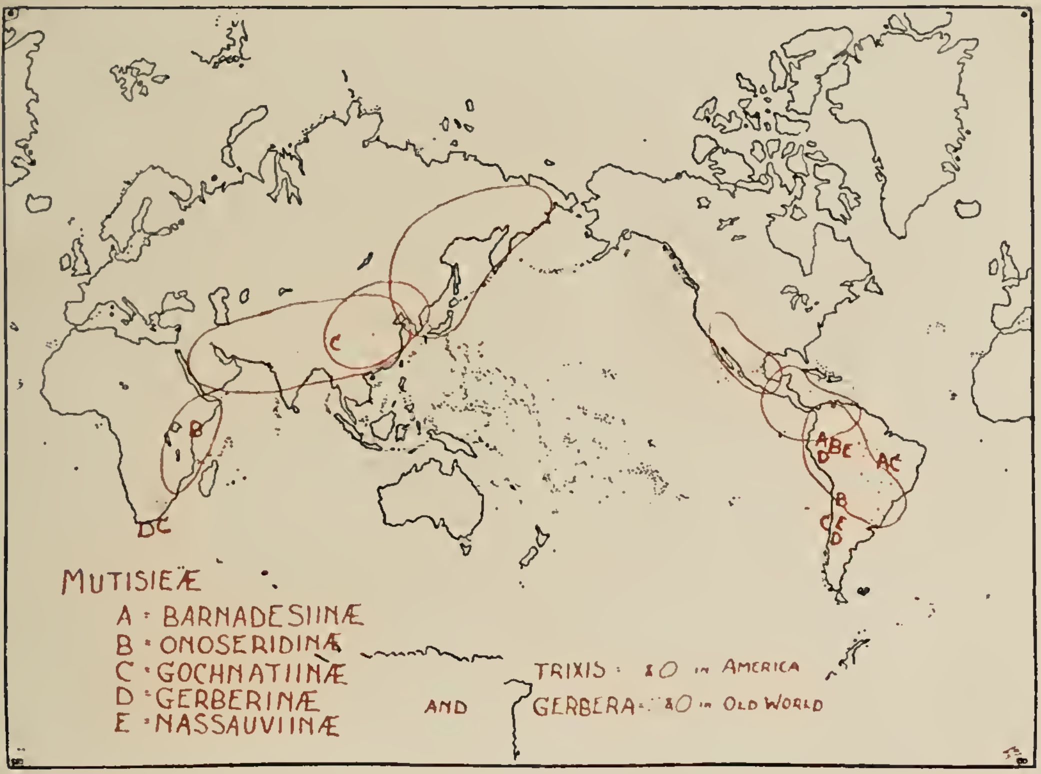

C
B
DC
ABE
D
AC
B
CE
D
MUTISIEÆ
A = BARNADESIINÆ
B = ONOSERIDINÆ
C = GOCHNATIINÆ
D = GERBERINÆ
E = NASSAUVIINÆ
TRIXIS : & O in AMERICA
AND
GERBERA = ∴ & O in OLD WORLD

FIG. 35.

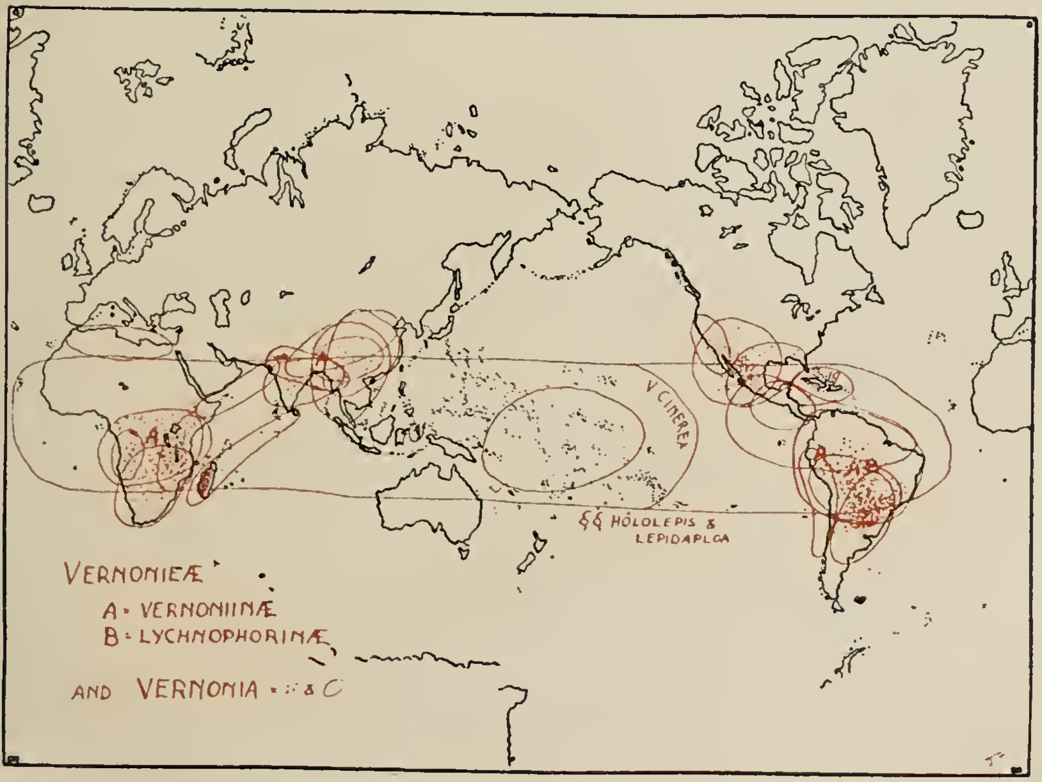

A
A
AB
V. CINEREA
§§ HOLOLEPIS & LEPIDAPLOA
VERNONIEÆ
A = VERNONIINÆ
B = LYCHNOPHORINÆ
AND VERNONIA = ∴ & C

FIG. 36.

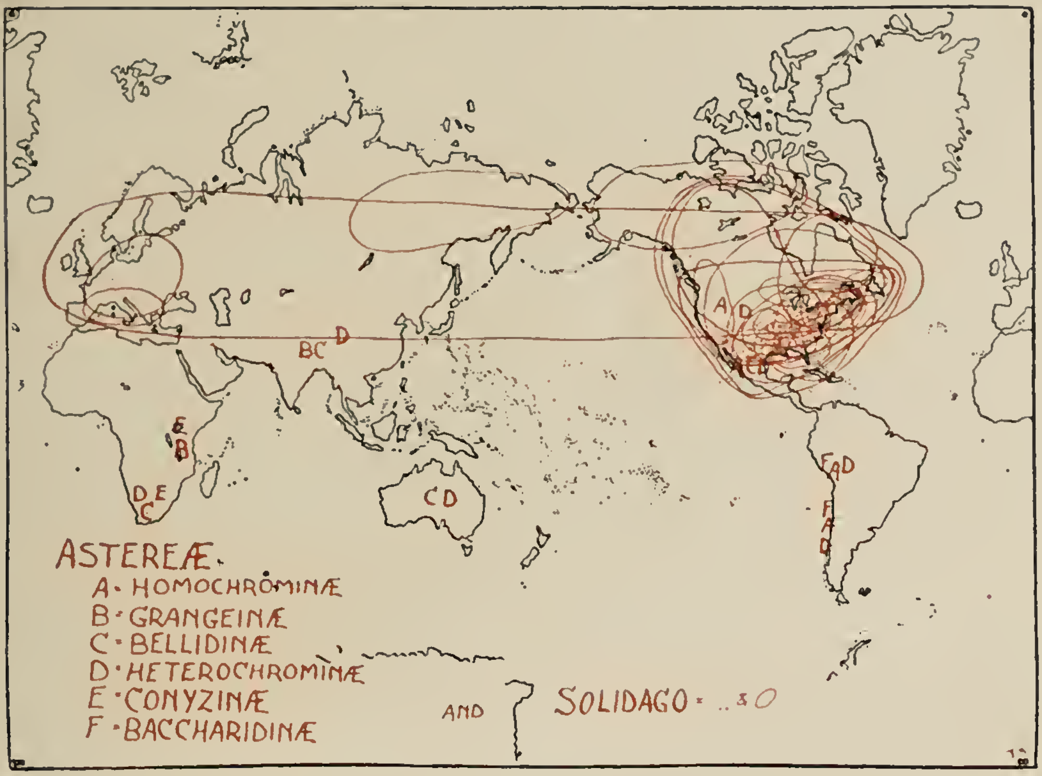

ASTEREÆ.
A. HOMOCHROMINÆ
B. GRANGEINÆ
C. BELLIDINÆ
D. HETEROCHROMINÆ
E. CONYZINÆ
F. BACCHARIDINÆ
AND SOLIDAGO .. & O
BC
D
CD
E
B
D E
C
A D
F A D
F
A
D

FIG. 37.

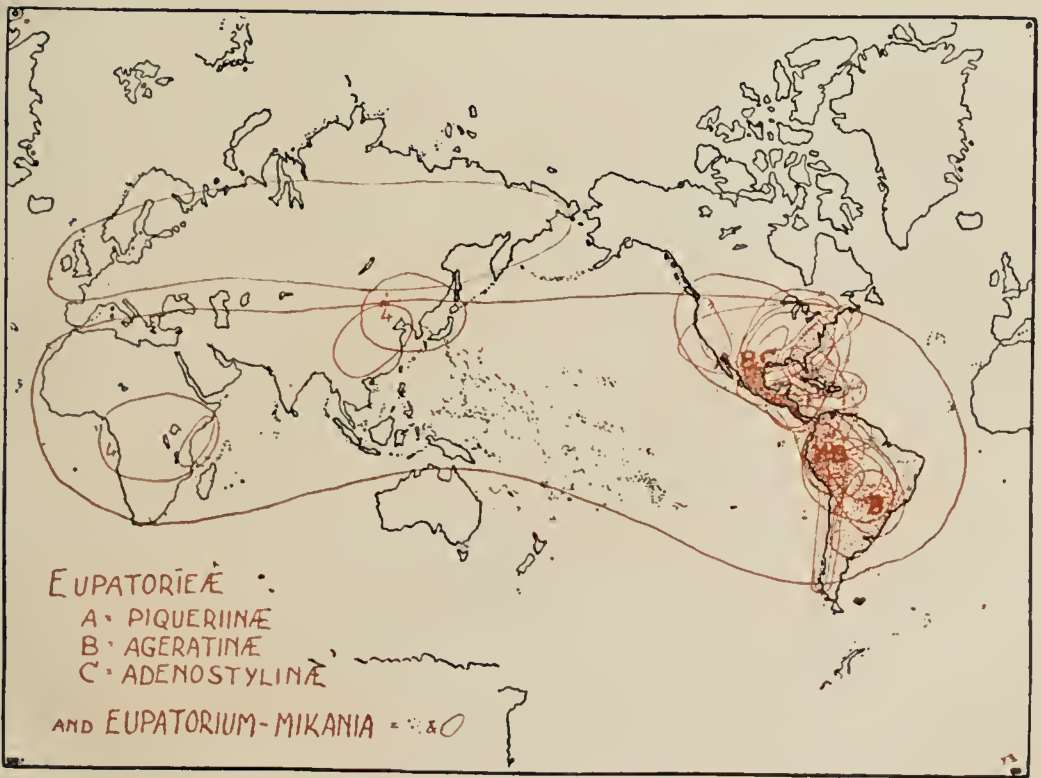

EUPATORIEÆ.
A. PIQUERIINÆ
B. AGERATINÆ
C. ADENOSTYLINÆ
AND EUPATORIUM-MIKANIA .. & O
4
4
B C
A B
B

FIG. 38.

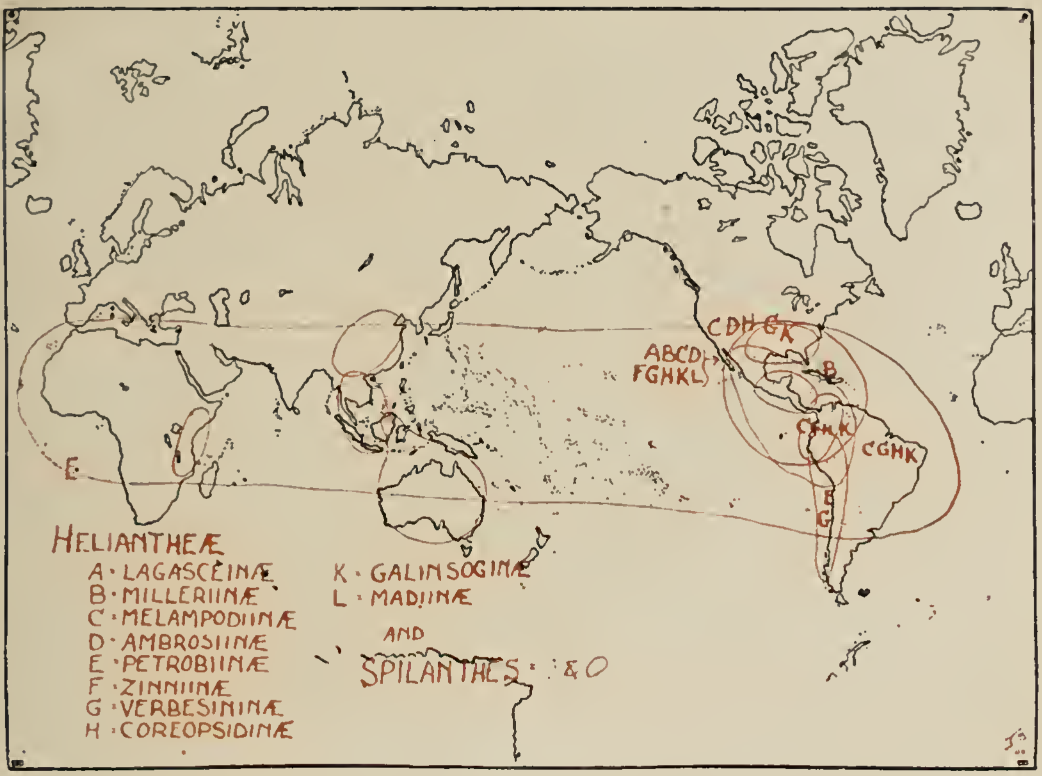

CDHGK
ABCD
FGHKL
B
CFHK
CGHK
E
E
G
HELIANTHEÆ
A · LAGASCEINÆ
B · MILLERIINÆ
C · MELAMPODIINÆ
D · AMBROSIINÆ
E · PETROBIINÆ
F · ZINNIINÆ
G · VERBESININÆ
H · COREOPSIDINÆ
K · GALINSOGINÆ
L · MADIINÆ
AND
SPILANTHES · &O

FIG. 39.

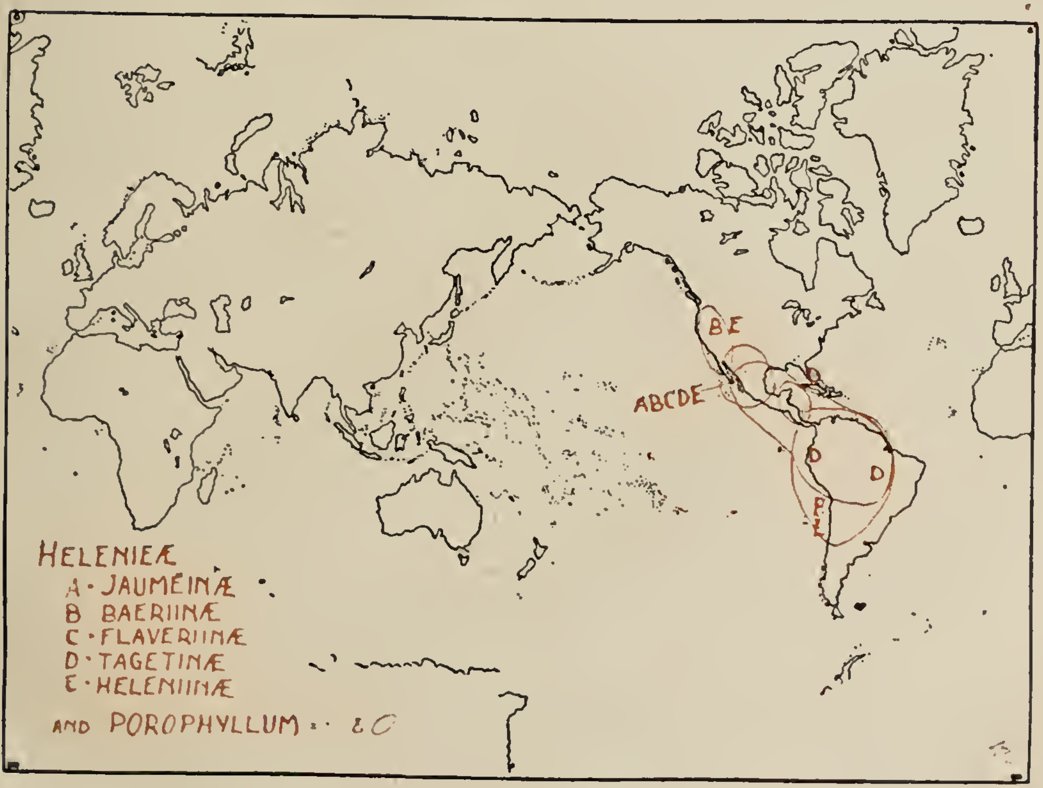

BE
ABCDE
D
D
E
L
HELENIEÆ
A · JAUMEINÆ
B BAERIINÆ
C · FLAVERIINÆ
D · TAGETINÆ
E · HELENIINÆ
AND POROPHYLLUM · · &O

FIG. 40.

The Paths of Migration.

If the centre of origin is taken as the Bolivian region (see Pl. I, Fig. 29) the study of the widespread species indicates clearly that the path of migration has been southward along the Andes to Fuegia and northwards along the same range towards Central America and the Cordilleran system from Panama to Alaska. Throughout the rest of the world the path of migration is commonly along the mountain ranges, usually above 3,000 ft., frequently above 6,000 ft.

South America. Extending in the southern direction into Chili we get *S. Bridgesii*, Hook. A connection is traced between Chili and the Argentine and between Chili and Patagonia. There are two species, *S. Smithii*, D.C. and *S. candidans*, D.C. which are of interest. The former extends from southern Chili into the Magellan and Fuegian regions and to the Falkland Islands. The latter occurs in Fuegia and the Falklands. The Falkland Islands are about 300 miles from the nearest land, but, instead of raising a very hypothetical land-bridge to explain the distribution, we can point with some certainty to the westerly trade winds and remind the reader of the fact demonstrated in the previous chapter that the minimum wind for dispersal to any distance of an average fruit of *Senecio vulgaris* is 1.5 m.p.h. In the region in question we have a wind of the necessary velocity in the proper direction and sometimes though not always the air has the necessary low relative humidity.

Extending northwards we have *S. medullosus*, S.B. from Bolivia to Colombia, *S. superbus*, S.B. from Peru to Colombia, and *S. rhizocephalus*, Turcz. from Ecuador to Colombia, while other species with smaller ranges connect other parts of the Andine path.

South America to North America. The connection between the two halves of the American continent is made by two species, *S. decompositus*, Hieron. and *S. formosus*, H.B.K. The latter occurs in Bolivia, Colombia and Mexico, the former in Venezuela, Colombia and Mexico. Greenman (100) also mentions *S. ledifolius*, D.C. as connecting North and South America.

Central America to North America—The bridging species between these two regions are *S. lanicaulis*, Greenm. and *S. Aschenbornianus*, Schau., the latter occurriug at levels over 6000 ft. on the Central American mountains.

North America. The widespread species in this region usually belong to the Cordilleran flora, and there is a considerable affiinity between Texas, Arizona, California and Mexico, so much so that these states are included in the "Mexican" region by Bentham, (I, 7). The most important species are *S. lugens*, Rich., *S. canus*, Hook. and *S. triangularis*, Hook., which occur all along the Cordilleran system from California to the Arctic region, each species showing a number of forms and occurring sometimes as high as 12,000 ft. or, especially in the Arctic region, coming down to sea level. These three species also extend eastward to a varying degree, as far as Saskatchewan, Manitoba and Iowa. *S. Fremontii*, T. & G. does not extend north of British Columbia, but occurs further south in Mexico, while *S. eremophilus*, Rich., which extends to the Mackenzie River, is confined in its southern area to the eastern spur of the Cordilleras.

The northern region is covered by *S. Hookeri*, T. & G., which extends from the Arctic regions southwards only to the high northern Rockies. The eastern path along the Appalachian system is indicated by *S. lobatus*, Pers., which extends from Mexico to Florida, Carolina and Illinois, and even more clearly by *S. suaveolens*, Ell., which occurs along the mountains from Maine to Florida.

The gap between the Appalachian species in the east and those of the Cordilleras in the west is bridged by *S. aureus*, L., which with many variations in form extends from the west coast to the east coast and from Newfoundland, the North-west Territories and Alaska in the north to Mexico and Florida in the south. Other species with smaller areas link up the parts of both eastern and western paths.

North America to Asia and Europe—The Behring Strait presents no impassable barrier to fruits which can be blown long distances by winds of less than 4 m.p.h. and the result is a strong connection between arctic America and Siberia. *S. Pseudo-Arnica*, Less., extending in America from Maine and Newfoundland to Alaska, occurs also in northern Asia. Three other species make use of this "Alaska-Siberian bridge": the most wide spread of these is *S. palustris*, Hook., which occurs all over the northern temperate and Arctic regions including Greenland. The other two are *S. resedifolius*, Less., and *S. frigidus*, Less.: the last like *S. Pseudo-Arnica* occurs near the coast and in habit it is similar to that species. The Alaska-Siberian bridge is mentioned by many writers (see 55, 118, etc.).

Asia. The first path to be noted in Asia lies along the Altai and Thian Shan Mountains from Siberia to Turkestan (cp. 25a). This is shown by *S. Ledebouri*, S.B., and *S. altaicus*, S.B., and is extended along the mountains of Afghanistan and Persia to the Persian Gulf by *S. dubius*, Ledeb. The second path lies along the east of Mongolia and Tibet by way of the Yablonoi, Khin-gan and Sin-ling Mountains from Siberia to the eastern Himalayas. This path is taken by *S. Ligularia*, Hook. The eastern Himalayan region is connected with the southern Chinese provinces by at least seven species of *Senecio*, and *S. scandens* extends beyond that region to Ceylon, the Neilgherries and Burma. A further extension from the eastern Himalayas is shown by *S. araneosus*, D.C., which occurs from China through Sikkim to Ceylon and Java. India and Java are also connected by *S. tenuifolius*, Burm. Other species with smaller areas again link up the parts of both the eastern and western paths through Asia.

Asia to Europe. The extension of the west Tibetan path into Europe is shown in detail by *S. sibiricus*, L., which occurs from Dahuria and the Yablonois via the Altai Mts. and Turkestan, the extension being along the Caucasus and Carpathians to the Alps. Part of this path together with a much wider extension of area into the plains of the Eur-Asiatic region is covered by *S. sarracenicus*, L., *S. paludosus*, L., *S. sylvaticus*, L., *S. erucifolius*, L., *S. præaltus*, Bertol., and *S. brachychætus*, D.C. The Siberia-Caucasus-Carpathians part of the path is covered by *S. capitatus*, Steud., and other shorter parts by other species.

Asia and Europe to Africa. The further extension of the west Tibetan path into Africa is shown in detail by *S. coronopifolius*, Desf. This species occurs all over Europe and northern Asia, and through Turkestan, Afghanistan, Baluchistan, Persia, Syria, Palestine to Egypt, the Sudan and Abyssinia. *S. erraticus*, Bertol., and *S. Jacobæa*, L., extend this area to north-west Africa, including Algeria and the region north of the Atlas Mts.; the former species extends even to the Azores.

An interesting species is *S. Decaisnei*, D.C., which, although it extends north-east into Asia only as far as Afghanistan, occurs also in India, and from northern Arabia across Africa to Morocco and the Canary Islands, and south through Nubia, probably as far as South Africa. This connection between north and south Africa is confirmed by *S. maritimus*, L., which occurs commonly in the Mediterranean region and in South Africa. In addition to the above-mentioned species *S. Schimperi*, S.B., links up Arabia and Abyssinia, while *S. arabicus*, L., connects Arabia, Egypt and

Nubia. There are also a number of species, such as *S. nebrodensis*, L., *S. vernalis*, Wald., and *S. squalidus*, L., which are widespread within the Mediterranean region, thus linking up Asia, Europe and Africa.

Europe to Africa. A connection is made between Europe and Africa at the western end of the Mediterranean by a number of species with areas varying from that of *S. crassifolius*, Willd., which extends from France and Spain to Italy, Sardinia, Algeria, Morocco and the Canary Islands, to that of *S. Auricula*, Bong., which occurs only in Spain and Algeria.

Africa. The path of migration in Africa is clearly along the mountains of the east coast. The first step is shown by *S. tuberosus*, S.B., which extends from Abyssinia into Galla. The path is extended to Mozambique by *S. subscandens*, Hochst., and to Natal and the Transvaal by *S. picridifolius*, D.C. The southern part is covered by *S. paucifolius*, D.C., which extends from the Zambesi into the east and south of Cape Colony, and the northern part is covered by *S. longiflorus*, S.B., which extends from Abyssinia to the Kalahari Desert. Other species again form smaller links in the chain.

Two interesting species in the west are *S. Mannii*, Hook., and *S. clarencianus*, Hook, which both occur in the Cameroons and Fernando Po. This is a case similar to that of Fuegia and the Falkland Islands species, but the distance between the two localities is only about 70 miles. A more striking case is *S. Leucadendron*, Benth., which occurs on St. Helena and on Prince's Island,[1] the distance in this case being nearly 1,500 miles. In this region the south-east trade winds may well be the distributing agent of the pappose fruits, and in view of the evidence given in Chapter IX, a journey of 1,500 miles over the sea is not improbable for a fruit of the *Senecio* type.

Centres of Concentration.

As the basal genus of the family it is to be expected that *Senecio* will have a considerable share in the predominance of the Compositæ in the higher regions of the mountains throughout the world. There are many species with very limited areas, but as shown above there are also the usual proportion of widespread species. It will be obvious from the distribution of the red dots on the map (Fig. 29) that these local species are most abundant along

---

[1] This extension to Prince's Island is supported only by one specimen in Herb. R.B.G., Edinburgh, concerning the collection of which there is no detail known.

the ridge which extends around the Pacific and Indian Oceans from Fuegia to South Africa.

In South America 70% of the species of *Senecio* occur in the Andes; the percentage is somewhat lower in North America, but some idea can be gained of the development of *Senecio* in the Cordilleran system from the descriptions by Harshberger (34). *Senecio* and *Gutierrezia* (op. cit., p. 224) are the dominant genera of the mesas in the autumn. *Senecio* again forms a considerable part of the rich vegetation of the hanging meadows on the hillsides (op. cit., p. 260) and is mentioned among the important genera of most Cordilleran regions. Weberbauer (72, p. 111 and p. 113) also gives *Senecio* first place among the genera with many Andine species. Greenman (100), who gives a general account of the 22 sections of North aad Central American species of *Senecio*, also notes that the greatest development of the genus in both North and South America occurs on the mountains. The abundance of Composites in these and similar regions frequently impresses non-botanical writers, *e.g.*, Petrocokino (57) mentions "fields golden with a kind of yellow marguerite" in the Andes of Bolivia.

A noteworthy point is that Honduras is a complete blank and Harshberger (op. cit., p. 663) mentions no *Senecio* in the Guatemalan region, which includes Honduras, nor is there any endemic species recorded from Nicaragua or San Salvador (cp. Hemsley, 107).

In the arctic and subarctic regions there is naturally no abundance of local species. The next region of concentration is in China, especially the south-eastern region, which is closely connected with the eastern part of the Himalayan concentration. The western part of the Himalayan concentration connects with a smaller development of local species along the Hindu Kush and Elburz Mts. This in its turn leads on to a stronger development along the Caucasus and through Asia Minor to the Balkans, Carpathians, Alps and Pyrenees.

Still following the path of migration along the mountains there is some slight development of local species in Arabia, connecting with a larger development in Abyssinia. The region of concentration extends in some degree along the mountains of east tropical Africa, culminating in the 54 endemic species of *Senecio* in Madagascar and the 280 local species which have been recorded for South Africa.

Rather isolated developments of local species occur in Australia and New Zealand, which are connected by *S. lautus*, Forst., and *S. odoratus*, Horn.

The six Javan species and the five Phillippine species indicate the two probable paths for the Australian supply of *Senecio*, the one from India *via* Burma and the Malay Peninsula and the other from China, *via* the Phillippines and East Indies (cp. Gibbs, 31, on New Guinea as the source of Australian types).

Ecology.

It will be clear from the above considerations that the regions of concentration for local species lie along the paths of migration as shown by widespread species, and that both are more or less co-extensive with the 3,000 ft. level throughout the world. The reason is to be sought in the aut-ecology of the genus, but as this forms the subject of a more extensive account now being prepared it will be sufficient to indicate briefly some of the more salient points,

The genus *Senecio* includes herbaceous annuals, biennials and perennials, which may be anything from aquatic to xerophytic in structure, also semi-shrubby and shrubby forms, which are erect or climbing, and trees of various growth forms.

The weedy type is the commonest and occurs in all the mesophytic habitats, but there are a number of distinct types which are characteristic of the regions where they occur. In common with many other Compositæ these weedy species of *Senecio* show a general tendency to develop a single, rather large capitulum, instead of the common branched inflorescence, as the altitude of the habitat increases. This type, sometimes called the *Arnica* type, occurs along the very high regions of the Andes and Cordilleras, and also lower down in the Arctic region. *S. Pseudo-Arnica* and *S. frigidus* have this uni-capitulate habit, while *S. resedifolius* is similar but smaller and more like *Bellis perennis*. Along the west Thibetan path this *Arnica* type is replaced by species which with the same general structure are of ranker growth with medium-sized capitula arranged in corymbs. Along the east Thibetan path the *Arnica* type is replaced by larger species with racemes of large capitula. Further south these two types are replaced by less rank but similar growth forms.

The shrubby species of South America are scandent in Brazil but usually erect in the Andes, and show several peculiar types.

Bolivia has a number of very dwarfed shrubs, only an inch or two high, the majority, however, are erect and from six inches to two feet high, as in the other Andine regions. An interesting spiny species *S. spinosus*, D.C., occurs in the Lake Titicaca region, where the dryness and excessive insolation (cp. Sect. A above) may be judged from the fact that the lake is gradually drying up by evaporation although supplied by seven rivers which are of considerable volume during the rainy season (52).

The shrubby forms of India and China are scandent in open forest or at the edges of denser forests as in Brazil; the erect shrubs are more or less confined to the Deccan and the mountains above the tree level, as in South America.

In Africa shrubby erect and scandent forms occur along the mountains from Abyssinia to Cape Colony, and a number of trees occur at high altitudes; of these none is more striking than *S. adnivalis*, which forms an open forest on Mt. Ruwenzori (14) similar to that formed by *Espeletia grandiflora* on the Paramos of Colombia (cp. I, 42, Fig. 109 and Goebel 32, Teil II, Pl. X and p. 17). In South Africa the peculiar shrubby form is more coniferous or "abietoid," and is to be compared with ericoid species of the same latitudes in the Andes.

The shrubby species of New Zealand are also of a distinct and peculiar type, but most of the Australian arborescent species are more allied to the South African forms. Each region in fact has its characteristic type of shrubby *Senecio*.

From the account given in Chapter IX it will be clear that the fruit dispersal of *Senecio* is easy on grassy plains and on mountain sides, both above the tree level and in the unwooded regions which are common below a certain altitude (cp. 34, p. 243 and I, 7, p. 484). The tundra zone of the northern latitudes also holds no obstacle to the dispersal of pappose fruits and the wide areas of the Arctic species is the result.

In migrating from its place of origin along the mountain ranges of the world *Senecio* has obviously followed the line of least resistance and avoided all forests and low-lying regions where fruit-dispersal by wind becomes distinctly problematical. The diversity of conditions along such a path (cp. 35) as well as constitutional instability is probably responsible to a great extent for the concentrations of local species which occur at all favourable points.

Conclusions.

Taking Bolivia as the still hypothetical centre of origin for

Senecio it is clear from the detailed study of the genus, of which the above is a very meagre and fragmentary account, that its history can be epitomised somewhat as follows. The genus, arising in the Andes, spread comparatively rapidly (cp. Willis, 82, p. 342.) along the unwooded regions of the mountain ranges of the world; while the floral structure which characterises the genus remained practically the same, the extreme diversity of conditions combined with a marked constitutional instability in the vegetative structure producing in each region several distinct variations in habit and a large number of local species. Because of this free reaction of the vegetative part of the *Senecio* plant to its environment there is no species which completely covers the range of the genus. *S. vulgaris* is cosmopolitan but has been largely introduced from Europe. Instead of a species we have the weedy *type*, which is cosmopolitan, and also various species with wide areas of distribution, a few of which taken together cover the chief regions occupied by the genus.

Finally it is abundantly clear that the geographical distribution of *Senecio* is quite in accordance with the view that a number of tribes have arisen from this genus in widely separated regions of the world.

C. GEOGRAPHICAL DISTRIBUTION OF THE TRIBES.

Although not up-to-date, Bentham's statistical summary (I, 7) of the geographical distribution of all the genera of the Compositæ remains sufficiently accurate for a general view of the distribution of the tribes and sub-tribes. The centres of origin and paths of migration, however, cannot be deduced from his table with any certainty. An analysis was therefore made of the distribution of some fifty widespread genera, including 8,600 species, by similar but not such detailed methods as were used for *Senecio*. Maps were made and the centres of origin and paths of migration were traced. In these maps a line around a country with a number included is used where the distribution within the country is not given in detail, and many dots are used where the map is too small for the useful employment of lines which indicate wider areas. Genera from all the tribes except the Calenduleæ and Arctotideæ were examined. Bentham's table was used in some cases to elucidate the centres of concentration of the sub-tribes and the results will now be discussed.

Senecioneæ. As the basal tribe the Senecioneæ have been studied specially and the distribution of all the genera in each sub-tribe is given (Fig. 30). The close similarity between this map and the previous one (Fig. 29) will be obvious at a glance. The local genera occur in the more important regions of concentration for *Senecio*. The widespread genera follow the mountain ranges of the world and the more or less treeless arctic zone, just as the widespread species of *Senecio* do. The exceptions are (*a*) *Gynura*, which connects tropical Asia with Australasia, thus supplying a link which is missing in *Senecio*, (*b*) *Erechtites*, which connects America with Australia, and (*c*) *Werneria*, which shows a curious discontinuous distribution from the Andes to the Himalayas and Abyssinia.

The centre of origin for the Liabinæ is Colombia or Mexico. Hoffmann's African genera (I, 42) require reconsideration. The Tussilagininæ are seen to be the further development of the *Arnica* and *Ligularia* types of the northern regions, originating probably in Siberia and spreading all over the arctic and sub-arctic zone. The Senecioninæ, the basal sub-tribe, is characterised by a number of widespread genera, the local genera occurring in the regions of concentration shown by *Senecio*. The Othonninæ are clearly of South African origin extending north along the mountain ranges to Abyssinia; the genus *Werneria* requires special consideration.

Cichorieæ. All the sub-tribes here, with the exception of the insular Dendroseridinæ, have their centres of concentration and region of overlapping of the areas of widespread species in the Mediterrannean region. The centre of origin is thus clearly defined, but the paths of migration are not so clearly marked as in the Senecioneæ. *Lactuca* may be taken as the type of distribution shown by the widespread genera (Fig. 31).

Details of the distribution are not necessary to show that from the Mediterranean the genus has spread to America and Africa by the same route as that by which *Senecio* arrived. *Hieracium*, *Hypochæris* and other genera have spread further along the mountain ranges of the world, extending into the Chilian Andes; while *Sonchus* has spread still further, extending to Australasia.

Calenduleæ. Most of the genera of this tribe are confined to Sonth Africa, but *Calendula* and *Dipterocome* are Mediterranean, while *Eriachænium* is Chilian. The systematic position of the last genus requires reconsideration. *Tripteris* extends into Tropical Africa. There is very little doubt of the South African origin of the tribe.

Arctotideæ. Except for the small genera *Gundelia* in the Mediterranean region and *Cymbonotus* in Australia, the Arctotideæ are South African with a very slight extension into tropical Africa. It is interesting to note that this northern extension occurs chiefly in *Ursinia*, and to a lesser degree in *Arctotis* and *Berkheya*.

Anthemideæ. The distribution of this tribe is peculiar. There is a distinct centre of concentration for both sub-tribes in the Mediterranean region, but the Chrysanthemidinæ shows a subsidiary concentration in South Africa, with more genera but fewer species than in the Mediterranean concentration. This is a case where the diversity of conditions gives a low generic co-efficient apart from the differentiation at the centre of origin.

The map (Pl. II, Fig. 32) illustrates the point; there are quite a number of small genera endemic in South Africa, but the areas of most of the widespread genera of both sub-tribes overlap in the Mediterranean region. The primary importance of this geographical centre is clearly shown when maps are made of the species in the larger genera. These practically all show a marked Mediterranean centre for local species and for overlapping of the areas of the widespread species, notably so in *Achillea*, *Chrysanthemum* and *Artemisia*. The paths of migration are the same in these and most other genera of the Anthemideæ as in *Senecio*.

Inuleæ. A number of genera in this tribe have been examined by the map method, but on account of the limitations of space, only *Gnaphalium* is given in the map (Fig. 33), while the centres of concentration for the sub-tribes are indicated. It has been suggested (Fig. 7) that the Gnaphaliinæ are the primitive sub-tribe, and the Helichryseæ the primitive section. When examined geographically there is little doubt that *Gnaphalium* is the primitive genus, so that the relative positions of the two sections of the Gnaphaliinæ should be reversed. This will be discussed later.

A map of all the genera of the Inuleæ shows that a marked proportion of the widespread genera belong to the Eu-gnaphalieæ. The map of the species of *Gnaphalium* shows centres of concentration and paths of migration corresponding closely to those of *Senecio*. It is of interest also that several species of *Gnaphalium* are more widely distributed than any one species of *Senecio*. This is probably due to a more stable constitution, corresponding to the more advanced evolutionary position of the genus. These matters are discussed below (Sect. D). The Helichryseæ are clearly South African in origin, as are several sub-tribes (see Fig. 33).

The only other wide spread sub-tribes are, (*a*) the Plucheinæ, which, with their chief centre in tropical Africa, have subsidiary centres in tropical Asia and Australia, and also extend into all the American regions, (*b*) the Filagininæ, which, although rather diffuse and extending to Mexico, have a distinct centre in the Mediterranean region.

The Inulinæ, although fairly widespread in the Old World, are markedly Mediterranean in origin, as is shown by maps of the species of the widespread genera, especially *Inula* and *Pulicaria.* Another point of interest is the centre of the Buphthalminæ at the eastern end of the Mediterranean region.

Cynareæ. The centre of origin, as indicated by the coincidence of the region of concentration of local species with the region of the overlapping of the areas of the widespread species, is nowhere more clearly indicated than in *Centaurea* (Fig. 34). The centre for all the sub-tribes is at the eastern end of the Mediterranean region, and the same type of map is shown by all the wide spread genera of the Cynareæ. The paths of migration are the more arid regions along the mountain ranges, but this is shown better by *Cnicus* and *Echinops* than by *Centaurea.* Only the last genus extends to Chili but *Cnicus* extends to Mexico and *Saussurea* to the U.S.A.

Mutisieae. There is in this tribe no genus common to the Old World and America with the exception of the South American genus *Trichocline,* which has one species in Australia. An analysis of all the genera in each sub-tribe shows that the chief centre for each is in South America (Fig. 35). The Nassauviinæ and the Barnadesiinæ are confined to America, but the other three sub-tribes have some genera in Africa. The two geographical groups of genera are illustrated by two of their most wide spread members, *Trixis* and *Gerbera. Trixis angustifolia* extends north to California and Arizona, while *Gerbera Anandria* extends to north Siberia. The paths of migration are the same as in *Senecio,* but a gap exists between Siberia and California. The Nassauviinæ show a marked concentration of both species and genera in Chili; although the local species of *Trixis* are chiefly Mexican, there are a number of local species in Brazil, and the commonest species, *T. divaricata,* is South American.

Vernonieæ. The type of distribution here is quite a simple one. The centre of concentration is in Brazil, and there is an inter-tropical connection. This applies equally to *Vernonia* (Fig. 36) with 948 species and the bridging sections *Hololepis* and *Lepidaploa*, and to *Elephantopus* with 24 species and the bridging species *E. scaber*. In both genera there is also an extension north into the U.S.A. region. A path of migration across the islands of the Pacific is indicated by the above-mentioned sections of *Vernonia*, by *E. scaber* and by *V. cinerea* (11).[1] The stretch of ocean between Peru and the Marquesas is not an impassable barrier, given a pappose fruit and the south-east trade winds (cp. Chapter IX). The occurrence of *V. Zeylanica* in Ceylon and Madagascar is probably explicable in the same way by a pappose fruit and the monsoons, although this case requires further examination. An Atlantic path of migration is indicated by *Sparganophorus Vaillantii*, which connects east tropical America with east tropical Africa.

Except for *E. scaber* and one other species in Senegambia the Lychnophorinæ are confined to America, but there are a number of African genera in the Vernoniinæ.

Astereæ. The distribution of the primitive genus, *Solidago*, is typical (Fig. 37). A concentration in the U.S.A. region is clear, and the path of migration is that of *Senecio*. This point, however, is much clearer and more distinct in the maps of *Aster*, *Erigeron* and *Conyza*, which are too complex for inclusion in the present account. The centres of the sub-tribes are indicated by letters. The Homochrominæ extend south into the Mexican region to a marked degree. The Bellidinæ are rather diffuse, occurring in all the regions of the world, as do also the Heterochrominæ with a chief centre in the U.S.A. and other concentrations in Mexico, South Africa, Australia and the Eur-Asiatic regions. The Conyzinæ are markedly African and the Grangeinæ occur chiefly in tropical Africa and Asia. The Baccharidinæ are another diffuse group but are chiefly Andine.

Eupatorieæ. For the present purpose *Mikania* and *Eupatorium* have been united into the basal group which has been referred to previously. The distribution of this group (Fig. 38) shows the characteristics of the Eupatorieæ very well. There is a concentra-

---

[1] A migration to the Sandwich Islands from the Australian and Malayan regions as well as from America is proved by Campbell (12), and was previously suggested by Hooker (IV, 39), who gave only general evidence. Hutton's idea of a continental bridge across the Pacific in Tertiary times (42) is modified by Macloskie (118) into an "archipelagian" bridge from New Guinea and New Zealand to Chili, very similar to but perhaps more developed than the existing Pacific archipelago.

tion in the Mexican region, but the Andine and Brazilian regions show others almost equally well developed. There is a tropical connection by *Mikania scandens* and also by *Ageratum conyzoides.* In addition there is some indication both in its present and its Pliocene distribution of the use of the Alaska-Siberian bridge by *Eupatorium.*

The Piqueriinæ are best developed in Mexico and the Andes, the Adenostylinæ in Mexico and the U.S.A. regions. The main sub-tribe, Ageratinæ, have the distribution of the *Eupatorium-Mikania* plexus, extending more or less into all the regions of the world.

Heliantheæ. The Verbesininæ have been suggested as the primitive sub-tribe (Fig. 7), and *Spilanthes*, with type 4 stamens, type IV style, setiferous aristæ in the pappus and a sub-biseriate involucre seems a probable primitive genus. The distribution of this genus is, therefore, given (Fig. 39) together with the centres of the sub-tribes.

The detailed distribution of this tribe is somewhat complex, as there are several more of less cosmopolitan genera, but the *Spilanthes* type of distribution is common among these widespread genera ; *Ambrosia*, *Xanthium*, *Siegesbeckia* and *Eclipta* are examples, the last two belonging to the same sub-tribe as *Spilanthes.* A northern connection *via* the Alaska-Siberian bridge in addition to the usual tropical one is indicated in *Bidens.*

All the sub-tribes, except the peculiar Petrobiinæ, have a Mexican concentration. The Verbesininæ and Coreopsidinæ extend into all the regions of the world. The Lagasceinæ, Madiinæ and Zinniinæ have only a slight extension from Mexico, and the other sub-tribes are practically confined to America, extending more or less strongly into the Andine and Brazilian regions.

Helenieæ. All the sub-tribes of the Helenieæ are practically confined to America, and *Porophyllum* (Fig. 40) is taken as one of the widespread genera, although it is probably not the most primitive. *Jaumea*, *Flaveria* and *Cadiscus* are the only genera which extend to the Old World, but there is only one species of each outside America. The distribution of the Tagetinæ is very closely similar to that of the Galinsoginæ, both sub-tribes developing in the same regions and almost to the same degree. There is a distinct extension to the Chilian region in the Baeriinæ and the Heleniinæ, but only one or two species of the Jaumeinæ and Flaveriinæ extend to that region.

Ecology of the Tribes.

The causal relationship of a number of ecological conditions to the arborescent habit, the spiny habit, the cushion and espalier habit, and other plant forms in the Compositæ, can be taken as proved to a degree of comparative certainty.

Scapigerous Perennials. In the grasslands herbaceous perennials are the chief type and, as in *Senecio*, this type tends to become dwarfed, scapigerous, and finally uni-capitulate in the alpine and arctic regions. The origin of the *Cremanthodium* from the *Ligularia* type of *Senecio* (see Chapter II, E) seems to be almost entirely due to the arid alpine conditions of the screes which form the typical habitat of that genus.

Scramblers. The climbing or scrambling habit is clearly due to the direct action of the environment (see Henslow, 38, p. 44) and Cockayne gives some very good evidence for this explanation (15, p. 21). The presence of open forest or scrub is necessary for the development of the typical Composite scramblers. These are most abundant on the western margins of the Brazilian forests and in the tropical African scrub.

Erect Shrubs. The erect shrubby forms of the Andes are probably the effect of an aridity of environment which does not obtain in the Cordilleras, with the result that the shrubby Composites are not so common in the northern region. Quite a number of genera with many arborescent species in the Andes are represented in the Cordilleras by perennial herbs. The erect shrubs reappear at high altitudes in tropical Africa and more abundantly in South Africa (cp. 6-7), Australia and New Zealand, where the ecological conditions are somewhat similar to those of the Andes. The shrubs peculiar to so many oceanic islands are probably also the result of the direct action of aridity, wet and cold, or hot and dry conditions (cp. 50-51).

Trees. The large shrubs and trees are obviously the extreme development of the shrubby condition. These trees usually occur as more or less isolated specimens high up on the mountain sides where there are open associations and consequently very little competition, and where all the ecological conditions tend to slow growth and lignification. The trees of the oceanic islands have long been objects of interest, usually regarded as relics of an ancient flora, but in the light of the new views on the origin and dispersal of species they are to be considered as more or less recent species which have become arborescent under the influence of external conditions. In addition most of these species have lost the means of wide dispersal possessed by their ancestors, and the localised distribution may be due to any or all of the following facts : (*a*) the species is recent, (*b*) the fruit is epappose, (*c*) the plant does not bear fruit until several years old, (*d*) the supply of fruits from the few specimens which represent the species is not sufficient to cover all the casualties sustained in travelling across the wide stretches of ocean, and in the attempt to establish the species in a region usually quite different ecologically and already well stocked with other plants.

These various forms, scapigerous perennials and arborescent species, occur in almost every tribe and their detailed evolution in each group is very interesting.

Spiny Forms. It is clearly easier for the appropriate ecological conditions to produce spines from leaf structures which are already reduced. The result of this is seen in the spinescent involucral bracts characteristic of the Cynareæ and common in the Buphthalminæ (Inuleæ), Gorteriinæ and Gundeliinæ (Arctotideæ). Spiny leaves occur also in the above-mentioned groups and in *Scolymus* (Cichorieæ). All these spiny forms occur either in the Karroo (Gorteriinæ) or in the semi-desert area at the eastern end of the Mediterranean region.

Aquatics. Although many Composites, but not a large proportion, are marsh plants there are very few aquatics (15, p. 17 and I,43), and, as these belong to various tribes, any phyletic value they possess is strictly limited. It will be sufficient to indicate the possibilities of the basal genus as shown by *Senecio hydrophilus*, Nutt, which grows in wet ground or even in brackish water, and the possibilities of the most advanced tribe as shown by the extraordinary production of an aquatic stem by a species which owes its spiny condition to the excessive insolation and dryness of the original habitat of its ancestors (see Sect. A and 18).

D. THE PHYLOGENETIC SIGNIFICANCE OF GEOGRAPHICAL DISTRIBUTION.

Absolute age is not considered at all by Willis in his exposition of the law of Age and Area. He limits his conclusions to age within the given country. Although proved only for age within the country the law receives its logical expansion to absolute age from Sinnott (65, p. 214), who says "there is doubtless much truth in Willis's main contention that, other things being equal, the longer a species lives, the wider the range it will cover." In this way we return to the views expressed by Bentham (Sect. A).

Physiological Differentiation and Restriction of Area. Considering the list given by Willis (78, p. 206) of causes which may modify the application of the law of Age and Area, and considering also Bentham's remarks quoted in Section A, we can trace an underlying principle which may be expressed as above. In a paper read before Section K of the British Association in 1916 (67) the writer applied the law of Age and Area to absolute age and total area and indicated the relation of physiological differentiation to restriction of area somewhat as follows: "We find in the Compositæ that the morphologically higher or more differentiated groups are well developed in the same regions as their morphologically lower or less differentiated ancestors. As these groups of ancestors and descendants occupy the same areas and show their maximum concentrations in these areas it is evident that the survival of the fittest in so far as it applies to morphological development has not exercised any very rigorous action, otherwise the ancestral groups would have been eliminated by their more highly developed offspring."

"On the other hand we know nothing very definite about the physiological differentiation of these groups and from analogy it would seem probable that within the limits of any particular family a morphologically primitive plant would be physiologically primitive and that a morphologically advanced plant would be physiologically highly differentiated also. The result of this would be that, although the higher forms would be more successful in those areas peculiarly well suited to their physiological constitution, this advantage would be more or less counterbalanced by the greater range, or greater choice of habitat, which would be enjoyed by the lower forms on account of their lack of special physiological differentiation. This compensation of the advantages of adaptation to one habitat by the power of living in many different habitats seems the most probable explanation of the continued existence in such profusion of *Senecio*, the primitive genus of the family."

"Of course, morphologically reduced forms must be carefully distinguished from the primitive forms, as these reduced forms would probably have a relatively highly differentiated physiological constitution." It should be further noted that a genus with an unstable constitution, (*i.e.*, abnormally susceptible to environmental conditions and liable to spontaneous mutations) will probably not show a species covering the range of the genus, while a more stable genus may have this characteristic (cp. 75, p. 336).

Guppy in the following year independently expressed the same principle thus:— "That differentiation and decrease of range go together is a principle that seems to prevail through the whole plant world" (IX, 22,p.314).

Age and Area. The most striking example of the action of the law of Age and Area is the world-wide distribution and numerous centres of concentration of the basal genus *Senecio.* No genus in the family has a distribution at all approaching that of *Senecio,* except *Gnaphalium,* the basal genus of the Inuleæ-Cynareæ branch, which is of comparatively ancient origin. Along this line we can follow the genus *Gnaphalium* in its period of full vigour and the gradually higher physiological differentiation and restriction in area which culminates in the Buphthalminæ; then from this "apparently expiring race" we have the vigorous "young progressive race" starting into new life in the Cynareæ with all the characteristics given by Bentham (see above Sect. A). The significance of these small groups, such as the Buphthalminæ and Liabinæ, which give much larger and more widely spread groups will be made clearer in the following chapter, Sect. C.

The wide distribution of some genera of the Heterochrominæ, and Verbesininæ also illustrate the principle of Age and Area. Other examples are *Liabum,* the *Eupatorium-Mikania* plexus, *Vernonia, Trixis* and *Ursinia*; in fact the primitive genus in almost every sub-tribe and the primitive sub-tribe in almost every tribe, in addition to the primitive genus of the whole family show the greatest area occupied by the oldest member of the group. There are exceptions such as the Buphthalminæ and Nassauviinæ, but these are peculiar groups, and their rejuvenescence to give larger, wider spread, more prolific races is in accordance with the general life history of a race as given by Bentham.

One point, however, requires consideration. Bentham regards these "decaying races" as ancient, but the facts of the individual cases show that they are more probably derivative races, arising comparatively recently from the widespread vigorous races. In Bergson's phraseology they are the last, small reverberations of the explosions which scarcely interrupt, and certainly do not stop, the progressive unrolling of the main theme. As a rule one genus in each restricted sub-tribe is closely allied to the immediate ancestor of the sub-tribe and, retaining the relatively primitive condition, physiological and otherwise, is capable of expansion, while the other more distant derivatives remain restricted more or less to their original sphere. Whether these restricted forms are really dying out or not is uncertain; the only relevant evidence is that given by Willis for the absence of any considerable dying out in the Angiosperms (77).

If the facts of distribution of the sub-tribes as given in the maps and Section C are compared with the phyletic scheme (Fig. 7) it will be seen that only in a very few details does the scheme fail to answer the test of geographical distribution.

Senecioneæ. The Senecioninæ have all the characteristics of a primitive race, either from the " Age and Area " point of view or from Guppy's " Differentiation " point of view. The Liabinæ (Fig. 30) in the Andine region, the Tussilagininæ in the Asiatic region, and the Othonninæ in South Africa all arise at points where specific differentiation in *Senecio* is well developed.

Cichorieæ. The Mediterranean centre for the majority of this tribe and the comparatively restricted area of most genera and species is in accordance with its suggested recent origin from the Mediterranean Senecioninæ.

Calenduleæ. The South African centre for this tribe and its marked restriction in area, in addition to its close similarity to the Senecioneæ in morphology and physiology, suggest an origin from the South African Senecioninæ at a date even more recent than that of the origin of the Cichorieæ.

Arctotideæ. The South African centre and the distribution of this tribe suggest an origin very similar in source, time, and place to that of the Calenduleæ. The wider areas of *Ursinia*, *Arctotis* and *Berkheya* confirm the positions of the Arctotidinæ and Gorteriinæ, while the restriction in area of *Gundelia* and *Platycarpha* confirms the position of the Gundeliinæ.

Anthemideæ. The Mediterranean centre and wide distribution of a number of genera in this tribe suggests an origin from the Senecioneæ of that region at a time previous to the origin of the Cichorieæ. The wider distribution and larger development in South Africa of the Chrysanthemidinæ (Fig. 32) confirm the suggestion made in Chapter IV, F, of the primitive position of at least the main genera of that sub-tribe.

Inuleæ. The Gnaphaliinæ are confirmed as the primitive sub-tribe, but the Eu-gnaphalieæ are shown to be the primitive section of the sub-tribe. In various morphological characters the Helichryseæ as a whole have appeared to be more primitive, but at this stage it is permissible to compare the main genera rather than the groups as a whole, because the smaller genera are seen to be little more than local variations of the larger genera. *Gnaphalium*, with a wide distribution (Fig. 33), with type IV style, type 10 stamens, simple setose pappus and foveolate or naked receptacle, is obviously more primitive than *Helichrysum*, which does not extend to America and which has type IV style, type 13 or 14 stamens, simple setose pappus, and a naked, foveolate or alveolate receptacle. Five of the Old World genera of the Eu-gnaphalieæ extend to America and only one genus of the Helichryseæ. The Helichryseæ in America are limited to two genera, while there are about a dozen Eu-gnaphalieæ.

The separation of the Angianthinæ (Australian) from the Relhaniinæ and Athrixiinæ (South African) which was suggested in Chapter VI, C, is confirmed. The arrangement of the other sub tribes is in accordance with the facts of distribution, especially the suggested origin of the Buphthalminæ from the Inulinæ; both are Mediterranean with extension to South Africa and the latter sub-tribe has the wider area.

Cynareæ. The derivation of the Centaureinæ from the Buphthalminæ is confirmed by the co-incidence of the centres of those two sub-tribes. The relatively primitive position of the Centaureinæ and Carduinæ is confirmed by the extension of these two groups into America, while the other two are limited to the Old World.

Mutisieæ. The derivation of the Nassauviinæ from the Senecioninæ is confirmed by the co-incidence of centres of concentration in these two groups. The primitive position of *Trixis* in the Nassauviinæ is confirmed by its comparatively wide area; the position of *Mutisia* and *Onoseris* as the basal genera of the Onoseridinæ (cp. Chaps. IV, F, and V, C-D) is confirmed by the wide South American distribution of these two genera. The distribution of the genera of the Onoseridinæ and Gochnatiinæ is also in accordance with their origin from *Mutisia*; *Chuquiragua* in South America and the *Ainsliæa-Dicoma* plexus in the Old World are indicated as the primitive genera of the Gochnatiinæ. The distribution of the Gerberinæ is in accordance with the origin of that subtribe from *Onoseris*; *Chaptalia* with a wide distribution connecting with *Gerbera* in the Old World forms the primitive plexus of the subtribe. The Barnadesiinæ are probably a group which has arisen independently of the rest of the Mutisieæ in the same place from the same source, but probably at a later date.

As the Mutisieæ develop chiefly in tropical and sub-tropical America and Africa, it is probably a result of their physiological differentiation that present conditions make the Alaska-Siberian bridge impassable for this group. The probable use of the bridge before the last period of glaciation in the north is indicated by the distribution of *Gerbera* and *Trixis* (Fig. 35) and by the close affinity of the wider spread genera of both hemispheres in each of the sub-tribes which reach the Old World.

Vernonieæ. The derivation of the Vernoniinæ from the Liabinæ is confirmed by the very close proximity, if not the actual co-incidence, of the centres of origin of these two sub-tribes (Figs. 30 & 36). The derivative position and relative youth of the Lychnophorinæ are confirmed by the smaller development of this sub-tribe in those regions where it occurs, and by the absence of any considerable development to compare with the tropical African concentration of the Vernoniinæ.

Astereæ. Various suggestions have been made for alterations in the positions of the sub-tribes in the Astereæ (see Chapter IV, D and Chapter V, D). The evidence of the distribution is also somewhat uncertain. The origin of the Homochrominæ from the Senecioninæ is confirmed by the co-incidence of the centre of origin of the former with a large concentration of the latter in Mexico and the U.S.A. The predominance in genera and species of the Homochrominæ over the Heterochrominæ in the region of origin supports the relative age of the former, while the wide distribution of the latter suggests that it is the group which has given most of the other sub-tribes.

The greatest development of the Baccharidinæ coincides with a considerable development of both the basal sub-tribes (Fig. 37), so that the evidence of structure decides the balance in favour of the Heterochrominæ as the source of that sub-tribe. The African development of the Conyzinæ and Grangeinæ confirms the origin of these sub-tribes from the Heterochrominæ as suggested (Chapter IV, D). The Mexican concentration and wide area of the Bellidinæ confirm the origin of this sub-tribe from the Homochrominæ, as suggested (Chap. V, D).

Eupatorieæ. The co-incidence of the chief centre of the Ageratinæ with one of the most important centres of the Heterochrominæ confirms the origin of the former sub-tribe as suggested in Chapter IV, F). The wider area of the Ageratinæ compared with that of the Adenostylinæ or Piqueriinæ and the co-incidence of all three centres in the Mexican region confirms the derivative position of those two sub-tribes. The exceptional distribution of *Adenostemma viscosum* (Piqueriinæ) is clearly the result of its very effective means of dispersal (IV, 98.)

Heliantheæ. The wide areas of a number of genera in the Verbesininæ (Fig. 39) and the slightly less wide distribution of the Coreopsidinæ confirm the basal positions of those two groups. The Mexican centres and distribution of the Madiinæ, Zinniinæ and Lagasceinæ, and the Mexican-West Indian development of the Milleriinæ confirm the positions of these sub-tribes. The Chilian centre of the Petrobiinæ co-incides with a considerable development of the Verbesininæ. The position of *Petrobium* on St. Helena can only be accounted for by a polyphyletic origin of this sub-tribe: the probability of polyphylesis will be considered in the next chapter. The wide distribution in America of the Galinsoginæ and their diffuse development from the U.S.A. to the Andes confirms the direct origin of this group at a comparatively early date from the Verbesininæ.

Helenieæ. Except for their almost complete absence from the U.S.A. the Tagetinæ show a remarkable similarity in their distribution to that of the Galinsoginæ, so that the origin of the former from the latter sub-tribe is more or less confirmed, but the facts of distribution would also support an origin of the Tagetinæ from the Senecioninæ as suggested in Chapter V, D. The Mexican centres and areas occupied by the other sub-tribes are in accordance with their relationships, as suggested in Fig. 7 and modified in Chapter IV, D. The extension of *Jaumea* and other details of the distribution of the Jaumeinæ confirms the suggestion (Chapter IV, D) that this sub-tribe arose not later than the Baeriinæ. The independent origin of the Heleniinæ suggested in Fig. 7 and confirmed in Chapter III, E, is in accordance with its distribution, which is more like that of the Baeriinæ than that of the Tagetinæ.

Conclusions. It is clear, therefore, that (except for the derivation of the Conyzinæ from the Homochrominæ and the reversal of the positions of the sections of the Gnaphaliinæ) the views on the origin and development of the tribes of the Compositæ which have been given in Fig. 7 (Chapter II) and modified slightly in subsequent chapters receive complete confirmation in considerable detail from the study of the geographical distribution of the family.

The value of the graphic method of using maps for each genus or tribe, instead of the statistical method used by Bentham, is clearly proved.

The elucidation of the principle of physiological differentiation and restriction of area enables us to understand many peculiarities of distribution.

The usefulness and fundamental truth of the Law of Age and Area in its wider application to absolute age and total area are demonstrated with a considerable degree of certainty by the striking way in which the action of the law can be traced as agreeing with the phyletic conclusions based on the floral morphology and physiology of the family.

BIBLIOGRAPHY X.

1. Abrams, L. R. and Smiley, F. J. Taxonomy and Distribution of *Eriodictyon*. Botan. Gazette. Vol. LX, 1914.
2. Abruzzi, Duca degli. See Chiovenda.
3. Andrews, E. C. The development and distribution of the Leguminosæ. Jour. Proc. Roy. Soc., N.S. Wales, Vol. XLVIII, p. 333, 1914.
4. ,, ,, The development of the Myrtaceæ. Proc. Linn. Soc., N.S. Wales, Vol. XXXVIII, p. 529, 1913.
5. Bailey, I. W. and Sinnott, E. W. The climatic distribution of certain types of angiosperm leaves. Amer. Jour. Bot., Vol. III, p. 24, 1916.

5a. Ball, J. Notes of a Naturalist in South America, pp. 102 and 157, London 1887.

6. Bews, J. W. The growth forms of Natal plants. Trans. Roy. Soc., S, Afr., Vol. V, p. 605, 1916.
7. ,, ,, The plant ecology of the Drakensberg range. Ann. Natal Mus., Vol. III, p. 511, 1917.
8. Bonnier, G. Influence de la lumière électrique continue et discontinue sur la structure des arbres. Comptes Rendus, Tome 115, p. 447 and p. 475, Paris, 1892.
9. ,, ,, Expériences sur la production des caractères alpins des plantes par l'alternance des températures extrêmes. Ibid. Tome 127, p. 307, 1898.
10. Breakwell, E. The Gramineæ and the Age and Area Hypothesis. Proc. Linn. Soc. N.S. Wales, Vol. XLII, Pt. 2, p. 303, 1917.
11. Burkill. I. H. The Flora of Vavau. Jour. Linn. Soc., Bot. Vol. XXXV, p. 20, 1902.
12. Campbell, D. H. The origin of the Hawaiian flora. Mem. Torr. Bot. Club, Vol. XVII, p. 90, 1918.
13. Capitaine, L. Répartition géographique des Legumineuses. Bull. de Géographie Botan., Nos. 319-321, 1916.
14. Chiovenda, E. Asteraceæ—in Il Ruwenzori by Duca degli Abruzzi, Milan, 1909. (Italian)—see also French Edition, Paris. 1909.
15. Cockayne, L. Observations concerning Evolution derived from Ecological Studies in New Zealand. Trans. N.Z. Inst., Vol. XLIV, p. 1, 1912.

16. Cockayne, L. On the Peopling by Plants of the Subalpine River-bed of the Rakaia. Trans. Bot. Soc. Edin., Vol. XXIV, Pt.3, p. 104, 1911.

17. ,, ,, and Foweraker, C. E. The Principal Plant Associations in the immediate vicinity of Canterbury College Mountain Biological Station. Trans. N.Z. Instit., Vol. 48, p. 166, 1916.

18. Compton, R. H. The Botanical Results of a Fenland Flood. Journal of Ecology, Vol. IV, p. 15, 1916.

19. Constantin, M. Etude comparée des tiges aériennes et souterraines des Dicotyledons. Ann. des Sci. nat. Bot. ser. 6, t. XVI, 1883.

20. Coulter, M.C. Endemism. Rev. Bot. Gaz., Vol. LXV, p. 116, 1918.

21. Darwin, C. The Voyage of the Beagle. London, 1845.

22. Dauphiné, A. Sur la lignification des organes souterraines chez quelques plantes des hautes régions. Compt. Rend., Paris, Tome 138, p. 592, 1904.

23. De Vries, H. Die endemischen Pflanzen von Ceylon und die mutierenden Oenotheren. Biol. Centralbl. Bd. XXXVI, p. 1, 1916.

24. ,, ,, The Relative Age of Endemic Species. Science, Vol. XLVII, p. 629, 1918.

25. Dunn, R. The Youngest World. P. 204, London, 1914.

25a. Etherton, P. T. Across the Roof of the World. London, 1911.

26. Foweraker, C. E. The Mat-plants, Cushion-plants and allied forms of the Cass River-bed. Trans. N.Z. Instit., Vol. XLIX, p. 1, 1917.

27. Gates, F. C. A Woody Stem in *Merremia gemella* induced by High Warm Water. Amer. Jour. Bot., Vol. II, p. 86, 1915.

28. Gates, R. R. A Systematic Analytical Study of certain North American Convallariaceæ considered in regard to their origin through Discontinuous Variation. Ann. Bot., Vol. XXXII, p. 253, 1918.

29. ,, ,, A Systematic Study of the North American Melanthaceæ from the Genetic Standpoint. Jour. Linn. Soc., Bot. Vol. XLIV, p. 131, 1918.

30. Geddes, W. N. Some great Ragweeds (*Ambrosia trifida*, L.). Bot. Gaz., Vol. I, p. 14, 1875 6.

31. Gibbs, L. S. A Contribution to the Plant Geography and Flora of the Arfak Mountains in Dutch N.W. New Guinea. London, 1916. (abst. Rep. Brit. Assoc., Newcastle, p. 509, 1916 and rev. Jour. of Ecol., Vol. VI, p. 159, 1918).

32. Goebel, K. Pflanzenbiologische Schilderungen. Marburg, 1889-91.

33. Harris, J. A. Sap Concentration and Plant Communities. Amer. Jour. Bot., Vol. IV, p. 268, 1917. Science, N. S. Vol. 46, p. 25, 1917, and rev. Bot. Gaz., Vol. LXV, p. 285, 1918.

34. Harshberger, J. W. Phytogeographic Survey of North America. In Die Vegetation der Erde, Bd. XIII, New York, 1911.

35. ,, ,, The Diversity of Ecological Conditions and its Influence on the Richness of Floras. Proc. Acad. Nat. Sci., Philadelph., p. 419, 1915.

36. Hauri, H. Anatomische Untersuchungen an Polsterpflanzen nebst morphologischen und ökologischen Notizen. Beihefte Bot. Centralbl., Bd. 33, p. 275, 1916.

37. Hemsley, W. B. The Flora of Tibet or High Asia. Jour. Linn. Soc., Bot., Vol. XXXV, p. 124, 1902.

38. Henslow, G. The Heredity of Acquired Characters in Plants. London, 1908.

39. Himmelbauer, W. Die Berberidaceen und ihre Stellung im System. Denkschriften Ksl. Akad. Wiss. Wien. Math.-nat. Kl. LXXXIX, p. 733. (abst. Bot. Centralbl, 131, p. 10, 1916),

40. Hooker, J. D. and Ball, J. Journal of a Tour in Morocco and the Great Atlas. London, 1878.

41. Hooper, E. D. M. Report upon the Forests of Honduras. London, 1887. Rev. in Garden and Forest, Vol. 1, p. 167, 1888.

42. Hutton, F. W. Ancient Antarctica. Nature, Vol. LXXII, p. 244, London, 1905.

43. Jeffrey, E. C. The Anatomy of Woody Plants. Chicago, 1917.

44. Jordan, A. Remarques sur le fait de l'existence en société a l'état sauvage des espèces végétales affines. Lyons, 1873. (Read to the Congrès de l'Assoc. française pour l'Avanc. des sciences, 1873.

45. Jordan, D. S. The Origin of Species through Isolation. Science, Vol. XXII, p. 545, 1905.

46. Kroeber, A. L. Floral relations among the Galapagos Islands. Univ. Calif. Publ., Bot. VI, p. 199.

47. Lloyd, F. E. Isolation and the Origin of Species. Science, Vol. XXII, p. 710, 1905.

48. Lothelier, A. De l'influence de l'humidité de l'air sur le développement des épines de l'*Ulex europaeus*. Rev. gen de Bot., Tome 24, p. 296, 1912.

49. Lotsy, J. P. Die endemischen Pflanzen von Ceylon und die Mutations-hypothese. Biol. Centralbl. Bd. XXXVI, p. 207, 1916.

50. MacCaughey, V. A Survey of the Hawaiian Land Flora. Bot. Gaz., Vol. LXIV, p. 89, 1917.

51. ,, ,, Vegetation of Hawaiian Lava Flows. Ibid., Vol, LXIV. p. 386, 1917.

52. Markham. C. R. Peru, p. 29, London, 1880.

53. Massart, J. Le rôle de l'expérimentation en géographie botanique. Rec. Inst. Bot., Leo Errara, Vol. IX, p. 68, 1912.

54. Morris, D. The Colony of British Honduras. London, 1883.

55. Nakai, T. Notulæ ad plantas Japoniæ et Koreæ. XIV, etc., Bot. Mag. Tokyo, Vol. 31, p. 97, 1917, etc, rev. Bot. Gaz. Vol. LXIV, p. 341, 1917.

56. Oger, A. Étude expérimentale de l'action de l'humidité du sol sur la structure de la tige et des feuilles. Compt. Rend., Paris, Tome, 115, p. 525, 1892.

57. Petrocokino, A. Along the Andes. p. 9, London, 1903.

58. Rodway, L. Botanic evidence in favour of land connection between Fuegia and Tasmania during the present floristic epoch. Proc. Roy Soc. Tasmania, p. 32 1914., abst. Bot. Centralbl. 132, p. 359, 1916.

59. Samuelsson, G. Ueber die Verbreitung einiger endemischer Pflanzen. Arkiv. f. Botanik, Stockholm, Bd. 9, No. 12, 1910.

60. Schröter C, and Hauri, H. Versuch einer Uebersicht der siphonogamen Polsterpflanzen. Engl. Bot. Jahrb., Bd. 50, p. 618, 1914.

61. Schultz Bipontinus, C. H. Beiträge zur Geschichte und geograph. Verbreit. der Cassiniaceen. Durkheim, 1866.

62. Sclater, W. L. and P.L. The Geography of Mammals. London, 1899.

63. Shreve, F. The physical control of vegetation in rain forest and desert mountains. Plant World, Vol. 20, p. 135, 1917., rev. Bot. Gaz., Vol. LXV, p. 198, 1918.

64. ,, ,, The weight of physical factors in the study of plant distribution. Plant World, Vol. 19. p. 53, 1916.

65. Sinnott, E. W. The "Age and Area" Hypothesis and the Problem of Endemism. Ann. Bot., Vol. XXXI, p. 209, 1917.

66. Skottsberg, C. Notes on the relations between the floras of Sub-antarctic America and New Zealand. Plant World, Vol. 18, p. 129, 1915.

67. Small, J. Geographical Distribution of the Compositæ. Rep. Brit. Assoc., Newcastle, p. 509, 1916.

68. ,, ,, The Age and Area Law. Science Progress, Vol. XII, p. 439, 1918.

68a. ,, ,, Changes of Electrical Conductivity under Geotropic Stimulation. Proc. Roy. Soc., B, Vol. 90, p. 349, 1918.

69. Spruce, R. Notes of a Botanist on the Amazon and Andes. Vol. II, pp. 212 and 288, London, 1908.

70. Taylor, M. Endemism in the flora of the vicinity of New York. Torreya, Vol. 16, p. 18, 1916.

71. Warming E. Oecology of Plants. Oxford, 1909.

72. Weberbauer, A. Die Pflanzenwelt der peruanischen Anden, in Die Vegetation der Erde. Vol. XII, Leipzig, 1911.

73. Whymper, E. Travels amongst the Great Andes of the Equator. London, 1891-2.

74. Willis, J. C. The Geographical Distribution of the Dilleniaceæ. Ann. Roy. Bot. Gdns., Perad , Vol. IV, Pt. II, p. 69, 1907.

75. ,, ,, The Endemic Flora of Ceylon with reference to geographical distribution and evolution in general. Phil. Trans. Roy. Soc., B, Vol. 206, p. 307, 1915.

76. ,, ,, The Distribution of Species in New Zealand. Ann. Bot., Vol. XXX, p. 437, London, 1916.

77. ,, ,, The Evolution of Species in Ceylon with reference to the Dying out of Species. Ibid., Vol. XXX, p. 1, 1916.

78. ,, ,, The Relative Age of Endemic Species etc. Ibid., Vol. XXXI, p. 189, 1917.

79. ,, ,, Further Evidence for Age and Area. Ibid., Vol. XXXI, p. 335, 1917.

80. ,, ,, The Distribution of the Plants of the outlying islands of New Zealand. Ibid., Vol. XXXI, p. 327, 1917.

81. ,, ,, The Age and Area Hypothesis. Science, Vol. XLVII, p. 626, 1918.

82. ,, ,, The Sources and Distribution of the New Zealand Flora. Ann. Bot., Vol. XXXII, p. 339, London, 1918.

83. Wilson, P. Report on Exploration in Honduras. Jour. N.Y. Bot. Gdns., Vol. IV, p. 99, 1903.

FLORAS.

84. Arvet-Touvet, C. Hieraciorum praesertim Galliæ et Hispaniæ Catologus Systematicus. Paris, 1913.

85. Bailey, F. M. The Queensland Flora. Pt. III, Brisbane, 1910.

86. Baker, J. G. Compositæ in Flora Brasiliensis (Martius and Eichler) Vol. VI, Pts. 2-3, Leipzig, 1873.

87. Balfour I. B. Botany of Socotra. Trans. Roy. Soc. Edin., Vol. XXXI, p. 128, 1888.

88. Ball, J. Spicilegium Floræ Maroccanæ. Jour. Linn. Soc., Vol. XVI, p. 494, 1878.

89. Bentham. G. and Mueller, F. Flora Australiensis. Vol. III, London, 1866.

90. Boissier, E Flora Orientalis. Vol. 3. p. 152, Geneva, 1875.

91. Britton, N. L. and Brown, A. An Illustrated Flora of the Northern United States, etc. New York, 1898.

92. Brown, R. Florula Discoana. Contrib. to the phyto-geography of Greenland. Trans. Bot. Soc. Edin., Vol. IX, 1867-68.

93. Cheeseman, T. F. Manual of the New Zealand Flora. Wellington, 1906.

94. Forbes, F. B. and Hemsley, W. B. Flora Sinensis. Jour. Linn. Soc. Vol. XXIII, p. 400, 1886-88.

95. Franchet, M. A. Les genres *Ligularia*, *Senecillis*, *Cremanthodium*, et leurs espèces. Bull. Soc. Bot., France, Tome XXXIX, p. 279, 1892.

96. „ ,, Mutisiaceæ japonicæ. Mém. Boissier, No. 14, Gèneve, 1900.

97. Grant, J. A. The Botany of the Speke and Grant Expedition. Trans. Linn. Soc., Vol. XXIX, p. 1, 1873.

98. Gray, A., and Torrey, J. Flora of North America. New York, 1838-40.

99. Gray, A. Synoptical Flora of North America. New York, 1884.

100. Greenman, J. M. Monograph of the North and Central American Species of the Genus *Senecio*. Pt. I., Engl. Bot. Jahrb. Bd. 32, p. 1, 1902.

101. ,, „ ibid. Pt. II., Ann. Miss. Bot. Gdn., Vol. 3, p. 85. 1916, and Vol. 5, p. 37, 1918.

102. „ ,, New Species of Cuban Senecioneæ. Field Mus. of Nat. Hist., Bot. Ser. Vol. II, No. 8, p. 327, 1912.

103. ,, ., Descriptions of North American Senecioneæ. ibid. Vol. I, p. 263, and Vol. II, p. 573, 1914-15.

104. Grisebach, A. H. R. Flora of the British West Indian Islands. p. 352, London, 1859-64.

105. Harvey, W. H., and Sonder, O. W. Flora Capensis. Vol. III, Dublin, 1864-65.

106. Hayata, B. Compositæ Formosanæ. Jour. Coll. Sci., Imp. Univ., Tokyo, Vol. XVIII, Art 8, 1904.

107. Hemsley, W. B. Biologia Centrali-Americana. (Godman and Salvin). Botany, Vol. II, London, 1881-2.

108. ,, ,, See IX, 23.

109. Hieronymus, G. Compositæ in Plantæ Ecuadorenses, II by S. J. Aloysius Sodiro. Engl. Bot. Jahrb., Bd. XXIX, p. 1, 1900.

110. ,, ,, Plantæ Lehmanniæ Colombia et Ecuador collectæ. Compositæ II. Ibid. Bd. XXVIII, p. 558, 1901,

111. Hooker, J. D., and Thomson, T. Introductory Essay to the Flora Indica. London, 1885.

112. Hooker, J. D. Flora of British India. Vol. 3, p. 219. London, 1882.

113. ,, ,, Origin and Distribution of Arctic Plants. Trans. Linn. Soc., Vol. XXIII, p. 251, 1860.

114. ,, ,, New Zealand Flora. London, 1867.

115. Humboldt, A., and Bonpland, A. Plantes équinoctiales. Paris, 1808-9.

116. ,, „ and Kunth, K. S. Nova Genera et Species Plantarum. Tome IV, Paris 1820.

117. Jepson, W. L. A Flora of Western Middle California. California, 1901.

118. Macloskie, C. Reports of the Princeton Expedition to Patagonia. Vol. VIII, 2., Botany p. 764, 1896-9.

119. Macoun, J. N., and Malte, M. O. The Flora of Canada. Canad. Geog., Survey, Mus. Bull. No. 26, Biolog. Ser., No. 6. 1917.

120. Maiden, J. H., and Betche, E. A Census of New South Wales Plants. Sydney, 1916,

121. Moore, C. Flora of New South Wales. Sydney, 1893.
122. Mueller, F. Key to the System of Victorian Plants. 1885.
123. Nyman, C. F. Conspectus Floræ Europaeæ. Örebro, 1878-82., Vol. II, p. 348, and Suppl. II, 1889-90.
124. Oliver, D. Flora of Tropical Africa. Vol. III, London, 1887.
125. Pearson, H. H. W., and Hutchinson, J. see VI, 11.
126. Philippi, R. A. Plantarum novarum Chilensium. Linnæa, Vols. XXVIII, XXIX, XXX, and XXXIII, 1859-64.
127. ,, ,, Plantas nuevas Chilenas. (Ann. Mus. nac. Chile and Anal. Univ. Chile, 1891-6). Santiago de Chile, 1893-6.
128. Porsild, M. P. On the genus *Antennaria* in Greenland. Medd. om Greenland., Vol. LI, p. 265, 1915.
129. Reiche, C. Flora de Chile. Tome III, p. 255, IV-V, p. 49., Santiago de Chile, 1902-10.
130. Remy, E. J. Compuestas, in Historia de Chile by P. R. Gay, Botany, Tome III, p. 257 and IV, Paris, 1847-9.
131. ,, ,, Monografia de las Compuestas de Chile. Paris, 1849.
132. Rendle, A. B., Baker, E. G., and Moore, S. Le M. An account of the Plants collected on Mt. Ruwenzori. Jour. Linn. Soc., Bot., Vol. XXXVIII, p. 228, 1908.
133. Rydberg, P. A. North American Flora. Vol. 34, Pt. 143, 1917.
134. Small, J. K. Flora of South-Eastern United States. New York, 1913.
135. Weddell, H. A. Chloris Andina. Tome 1, Paris, 1855.

THE INFLUENCE OF TEMPERATURE ON THE SOAKING OF SEEDS.

By Franklin Kidd and Cyril West.

(*Imperial College of Science and Technology.*)

IN a previous communication (Kidd and West, 1) we have dealt with the effect upon germination and upon subsequent development of soaking seeds of red dwarf beans (*Phaseolus vulgaris*, var.) in excess of water previous to sowing. Soaking these seeds for periods up to 24-48 hours at ordinary room temperatures increased the rate and vigour of germination; but the effect under the conditions of the experiment upon the subsequent development of the plants produced was injurious, even in the case of short periods of soaking.

In this communication a further fact was noted for which no explanation is at present forthcoming, namely, an unexpected effect of the temperature which obtains during the process of soaking the seed. We did not find as might have been expected that the injurious effect upon germination and upon the yield per plant was less when the temperature during soaking was low. What did appear, on the other hand, was a markedly greater injury at 10°C than at 20°C. This effect showed itself by a reduction in the number of germinations at 10°C and a still more marked reduction in the number of plants surviving at the end of three weeks.[1] This effect was very clear, even for such short periods of immersion as six hours (Table I).

TABLE I.

Period of soaking under 4 cms. of distilled water.		0 hrs.	6 hrs.	24 hrs.	48 hrs.	72 hrs.
Percentage of plants that survived after 3 weeks.	Soaked at 10°C	96%	40%	36%	32%	60%
	,, ,, 20°C	96%	66%	48%	60%	64%
		gms.	gms.	gms.	gms.	gms.
Dry Weight of 100 plants.	Soaked at 10°C	23·27	21·34	20·05	13·92	17·80
	,, ,, 20°C	23·27	21·47	21·04	17·93	16·28

The seeds were sown in good garden soil in a cool greenhouse immediately after the soaking treatment.

Further experiments have since been carried out with peas (Sutton's "Maincrop"), and the results obtained were essentially the same as those recorded above for dwarf beans. The results of a typical experiment are given in the following table and figure.

TABLE II.

The seeds were soaked under 4 cms. of distilled water and were sown (together with the untreated controls) in good garden soil in a cool greenhouse immediately after the soaking treatment. 25 seeds were used in each experiment.

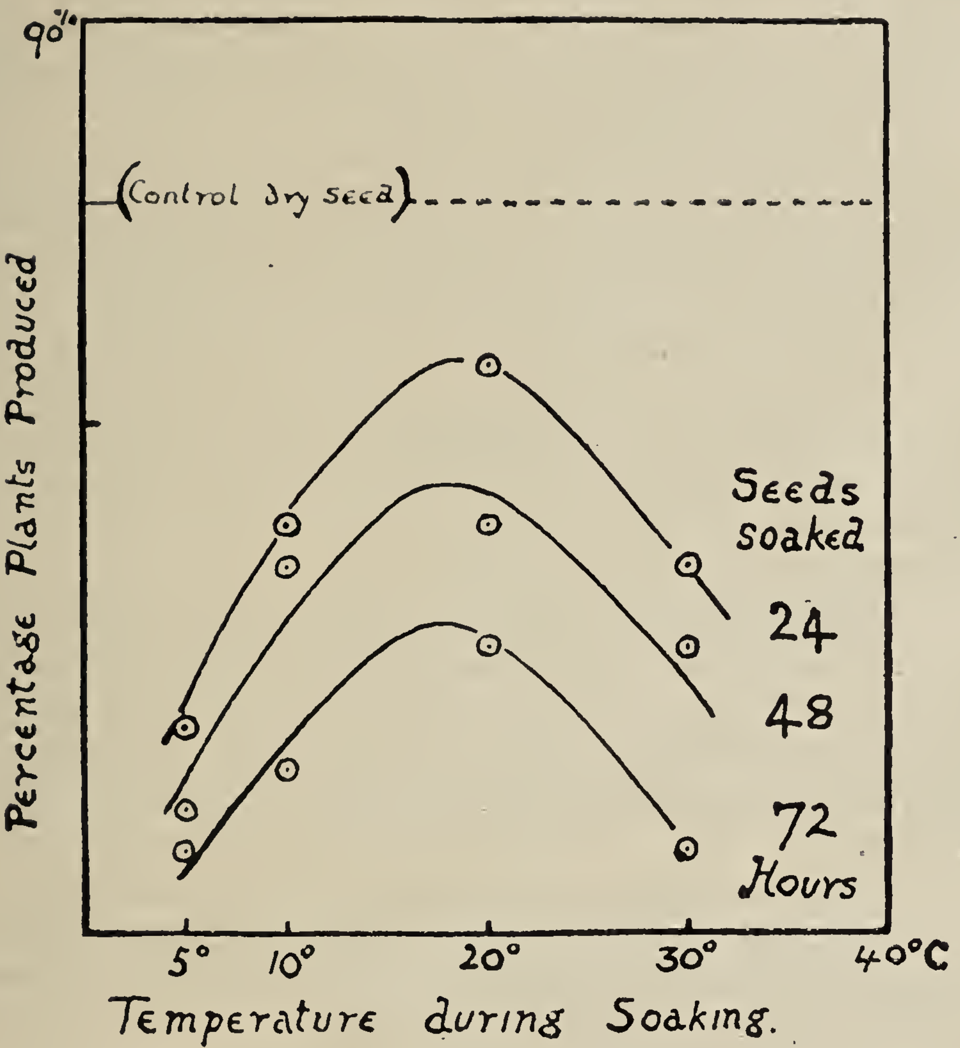
Period of Soaking		0 hrs.	24 hours.				48 hours.				72 hours.			
Temp. of the water used			5°C	10°C	20°C	30°C	5°C	10°C	20°C	30°C	5°C	10°C	20°C	30°C
Number of Germinations after:—	7 days	17	5	9	13	11	2	8	9	6	1	4	5	1
	14 ,,	18	5	9	13	9*	2	9	10	7	1	4	7	1
	21 ,,	18	5	10	13	9	3	9	10	7	2	4	7	2
	28 ,,	18	5	10	14	9	3	9	10	7	2	4	7	2
	35 ,,	18	5	10	14	9	3	9	10	7	2	4	7	2

* Two died.

---

[1] This curious temperature effect appears to be observed only under conditions of actual immersion in water, for it has frequently been found in exhaustive experiments dealing with the question of seed storage that whereas at ordinary temperatures (20°C circa) seeds very quickly lose their vitality if their water-content is high, cold storage at about 5°C is efficient in maintaining the vitality of such seeds (cf. Heinrich, 2).

Fig. I.



It appears from the above table that at all temperatures soaking the seed in excess of water very markedly decreases the number of plants produced and that this injurious effect increases progressively as the time of soaking is lengthened; and again we have the remarkable fact that the injurious effect becomes more pronounced as the temperature falls below 20°C. The total number of plants produced five weeks after sowing was 10, 23 and 31 out of 75 in the case of seeds soaked at 5°C, 10°C and 20°C respectively, while the control (75 seeds, not previously soaked) produced 54 plants. Above 20°C the injurious effect of soaking increases with temperature.

This effect of the temperature during the soaking treatment upon the number of plants produced is reflected in the subsequent development of the plants that survive.

The cause of the deleterious action of soaking seeds in water under certain conditions has not yet been cleared up by experimental work. There appear to be three plausible hypotheses in the field, viz. (1) that the injurious effect is due to disorganised metabolism resulting from deficiency in oxygen supply and accumulation of carbon dioxide (cf, Jodin, 3; and Mazé, 4), (2) that it is due to the leaching out of essential soluble food-reserves, (3) that it is due to a combination of (1) and (2).

In the case of seeds soaked under the same conditions except as regards temperature, although no direct data are available, it would appear that at the lower temperatures there would be more available oxygen for the following reasons: (1) the greater solubility of oxygen at lower temperatures, and (2) the relatively greater decrease in the rate of respiration as compared with the rate of diffusion of oxygen at lower temperatures. Hence the question of oxygen supply must be eliminated in seeking to explain the differences in the effect of soaking seeds at higher and lower temperatures.

We may assume that at lower temperatures the amount of carbon dioxide in the water of soaking (other conditions being the same) will not be greater than at higher temperatures; there is evidence, however, that at low temperatures carbon dioxide is more active in producing inhibition and injury than at higher temperatures (Kidd, 5).

In connection with the above experiments we obtained data as to the exosmosis or leaching out of soluble food-reserves which occurred at various temperatures, and the following tables (Tables III and IV) give the results obtained.

TABLE III.

Effect of various temperatures on the exosmosis of soluble substances that occurs when Dwarf Runner Beans *(Phaseolus vulgaris, var.)* are soaked in excess of distilled water.

Period of soaking: 3 days. Seeds soaked under 4 cms. of water. 25 seeds used in each experiment.

Temp. of the water used	10°C.	20°C	25°C	30°C
Total weight of solid matter leached out of 25 bean seeds during experiment	0·572 gms.	0·528 gms.	0·563 gms.	1·270 gms.

TABLE IV.

Effect of various temperatures on the exosmosis of soluble substances that occurs when Peas (Suttons "Maincrop") are soaked in excess of distilled water.

Period of soaking: 3 days. Seeds soaked under 4 cms. of water. 50 seeds used in each experiment.

Temp. of the water used	5°C	10°C	20°C	30°C
Total weight of solid matter leached out of 50 pea seeds during experiment	0·278 gms.	0·253 gms.	0·220 gms.	0·659 gms.

At the lowest temperatures the figures for exosmosis are in both cases slightly higher than at the medium temperatures, but the differences are probably too small to be significant. At higher temperatures, however, the rate of exosmosis is greatly increased.

We cannot at present offer any satisfactory explanation to account for the greater exosmosis at the lower temperatures and for the markedly more injurious effects observed in the later development of the plants produced from seeds soaked in excess of water at lower temperatures as compared with medium temperatures.

SUMMARY.

The soaking of pea seeds (*Pisum sativum*) and of bean seeds (*Phaseolus vulgaris*) in excess of water is injurious at all temperatures, that is, the number|and vigour of the plants produced are diminished. This injurious effect is more marked with low temperatures of soaking (5°-10°C) than with medium temperatures (15-20°C). At higher temperatures the amount of injury resulting again increases, so that the curve of the number of plants produced from seeds soaked at different temperatures rises and falls about an optimum in the region of 15°-20°C.

LITERATURE CITED.

1. Kidd, F. and West, C. Physiological Pre-determination : The Influence of the Physiological Condition of the Seed upon the Course of Subsequent Growth and upon the Yield. I. The Effects of Soaking Seeds in Water. Ann. Applied Biology, 5, 1918, p. 1.
2. Heinrich, M. Der Einfluss der Luftfeuchtigkeit, der Wärme und des Sauerstoffs der Luft auf lagerndes Saatgut. Landw. Versuchsstat., 81, 1913, pp. 289-376.
3. Jodin, V. Recherches sur la Germination. Ann. Agronom. 23, 1897, p. 433.
4. Mazé, P. Recherches sur le Rôle de l'Oxygène dans la Germination. Ann. de l'Inst. Pasteur, 14, No. 5, 1900, p. 350.
5. Kidd, F. The Controlling Influence of Carbon Dioxide in the Maturation, Dormancy and Germination of Seeds. Part II. Proc. Roy. Soc. (Lond.), B, 87, 1914, p. 609.

ON THE RELATION OF PLASMOLYSIS TO THE SHRINKAGE OF PLANT TISSUE IN SALT SOLUTIONS.

By Walter Stiles and Ingvar Jörgensen.

[With Two Figures in the Text]

IN the March-April number of this journal,[1] D. Thoday fired the maroon, as it were, for a warning of the bomb he intended to drop on us in the May-June number. Now that the attack has been delivered,[2] we think it was brought about by a complete misrepresentation of our views in regard to a very elementary and generally understood matter, in which our opinions do not differ from those of anyone else who has interested himself in the subject of the osmotic relations and permeability properties of the plant cell.

The essence of the business is that Thoday represents us as supposing that the sap of a cell which neither gains nor loses in weight when placed in a solution of a salt is of the same osmotic concentration as the solution. This is manifestly absurd. On page 420 of the paper,[3] which, according to Thoday, moved him to call attention to the existence of turgor pressure in plants, will be found a passage in which we give the explanation usually advanced to explain how plant tissue can remain in equilibrium, as regards water exchange, with a solution of lower osmotic concentration than the cell sap. Thoday merely gives the same explanation.

It should have been clear to anyone who had read the part of our paper dealing with the swelling of tissue in distilled water, and the maintenance of an equilibrium condition between distilled water and the cell sap in regard to water exchange, that we did not consider a cell which neither gained nor lost in weight when placed in a solution as necessarily isotonic with the cell sap. In regard to the one case in which we spoke of a solution as isotonic with the cell sap of tissue which altered only slightly in weight after immersion in the solution, it should thus have been obvious that we regarded the hydrostatic pressure of the solution in the cells as small in comparison with the osmotic pressure of the sap. It would have been a legitimate ground for criticism if Thoday could have produced evidence that the hydrostatic pressure of the water in the cells of potato normally possessed a value approaching that of the osmotic

[1] New Phyt., 17, p. 60, 1918.

[2] New Phyt., 17, p. 108, 1918.

[3] Ann. of Bot., 31, pp. 415-434, 1917.

pressure of the cell sap, but no attempt even was made in Thoday's note to bring forward such evidence.

The question of the relation of loss in water by the cell to plasmolysis is one on which we had projected experiments, but circumstances have necessitated their abandonment for the present. In view of Thoday's recent note we have therefore thought it worth while to publish a few preliminary results we have obtained in regard to this question in order to show the sort of assumption we made in supposing that with the potato tissue which underwent only slight change in weight when immersed in a salt solution, the latter could be regarded as approximately isotonic with the cell sap.

In the experiments described below the gain or loss in weight of tissue immersed in solutions of sodium chloride of different concentrations was measured in the manner described in an earlier paper,[1] while observations were made at the same time as regards the plasmolysis of the cells of the same tissue in various concentrations of the same salt.

Thoday[2] implies that the solution which just brings about plasmolysis is to be regarded as isotonic with the cell sap. This neglects the observation of Pfeffer[3] that "at the commencement of plasmolysis the osmotic pressure of the external fluid is slightly higher than that of the turgid cell." Generally that solution is regarded as isotonic which just fails to produce plasmolysis. Theoretically these two concentrations should be the same within the limits imposed by the gradation of solutions used for the plasmolysis test. If Pfeffer's statement cited above is to be accepted, it would therefore appear that values for the osmotic concentration of the cell sap obtained by plasmolysis are more or less approximate.

The matter is complicated in the case of a tissue, since, as is well-known, all the cells of a tissue do not require the same concentration of salt solution to bring about plasmolysis. Thus the value obtained for the concentration of a solution isotonic with the cell sap of a tissue is necessarily an approximation.

While potato tissue is not a favourable material for plasmolytic observations, red beetroot on the other hand, is much more favourable for this purpose on account of the colour of the cell sap. In the experiments recorded below red beetroot, and not potato, was used.

[1] Ann. of Bot., 31, pp. 415-431, 1917.

[2] New Phyt., 17, pp. 110, 111, 1918.

[3] Physiology of plants, English Edit., Vol. I, p. 145, Oxford 1900.

In these experiments three series of observations were made on the swelling of the tissue in solutions of sodium chloride of different strengths. In each series all the tissue used was obtained from the same root and at the same time sections were cut from this root and placed in various strengths of solution for plasmolytic observations.

As regards the experiments on swelling and shrinkage, about 10

TABLE I

Swelling of Root of Red Beet in Sodium Chloride solution. Series 1 (Beet No. 1).

Distilled Water.		0·125 N.		0·25 N	
Time in hrs.	Percentage gain in weight.	Time in hrs.	Percentage gain in weight.	Time in hrs.	Percentage gain in weight.
0·60	10·8	0·61	9·8	0·69	9·9
3·82	17·9	3·94	14·0	4·11	13·1
5·72	18·9	5·78	14·4	5·87	12·6
22·84	20·9	22·78	14·6	22·81	12·8
30·42	22·3	30 33	15·2	30·28	13·1
47·02	23·3	46·95	15·1	46·85	13·0
70·85	25·0	70·70	15·3	70·6	13·0
95·00	24·2	95·0	15·2	94·5	13·0
143·0	25·4	143·0	14·5	142·5	12·1
167·0	24·5	167·0	14·2	166·5	12·3
191·0	24·3	191·0	12·0	190·5	12·5
235·0	23·7	235·0	11·7	234·5	12·3
259·0	22·9	259·0	9·5	258·5	12·7
283·0	21·5	283·0	6·3	282·5	12·8
331·0	19·6	331·0	4.9	330·5	6·1

TABLE II.

Swelling and Shrinkage of Root of Red Beet in Sodium Chloride solution. Series 2 (Beet No 2).

0·25 N		0·33 N		0·40 N		0·45 N	
Time in hours	Percentage gain in weight	Time in hours	Percentage gain in weight	Time in hours	Percentage gain in weight	Time in hours	Percentage gain in weight
0·52	6·1	0·57	3·9	0·62	—0·6	0·69	—4·9
2 27	10·4	2·28	7·9	2·32	—0·1	2·21	—6·2
5·42	11·1	5·41	8·1	5 47	—0·2	5·53	—6·4
				22·52	+1·9	22·52	—5·2
				46 8	+3·5	46·82	—5·2
				95·0	+1·6	95·0	—5·1
				118·8	—0·9	118·82	—6·1
				134·8	—4·3	134·82	—7·2
						159·7	—9·1
						182·8	—10·4

grams of discs were used prepared as described in an earlier paper[1], and the precautions there described for reducing the sampling error were taken. The percentage changes in weight observed in each of the three series are shown in Tables I to III.

TABLE III.

Swelling and Shrinkage of Red Beet in Sodium Chloride solution. Series 3 (Beet No. 3).

0·33 N		0·40 N		0·45 N	
Time in hrs.	Percentage gain in weight	Time in hrs.	Percentage gain in weight	Time in hrs,	Percentage gain in weight
0·62	3·2	0·63	—0·2	0·67	—4·1
3·20	7·0	3·20	—0·4	3·25	—4·2

In the first series all the solutions employed were below the equilibrium concentration. In both the second and third the solution of sodium chloride in which neither gain nor loss in weight took place was approximately 0.4 N, and on the assumption that the hydrostatic pressure is small in comparison with the osmotic pressure we should say that a solution of 0.4 N is approximately isotonic with the cell sap. The changes in weight during the first five hours are shown graphically in Fig I.

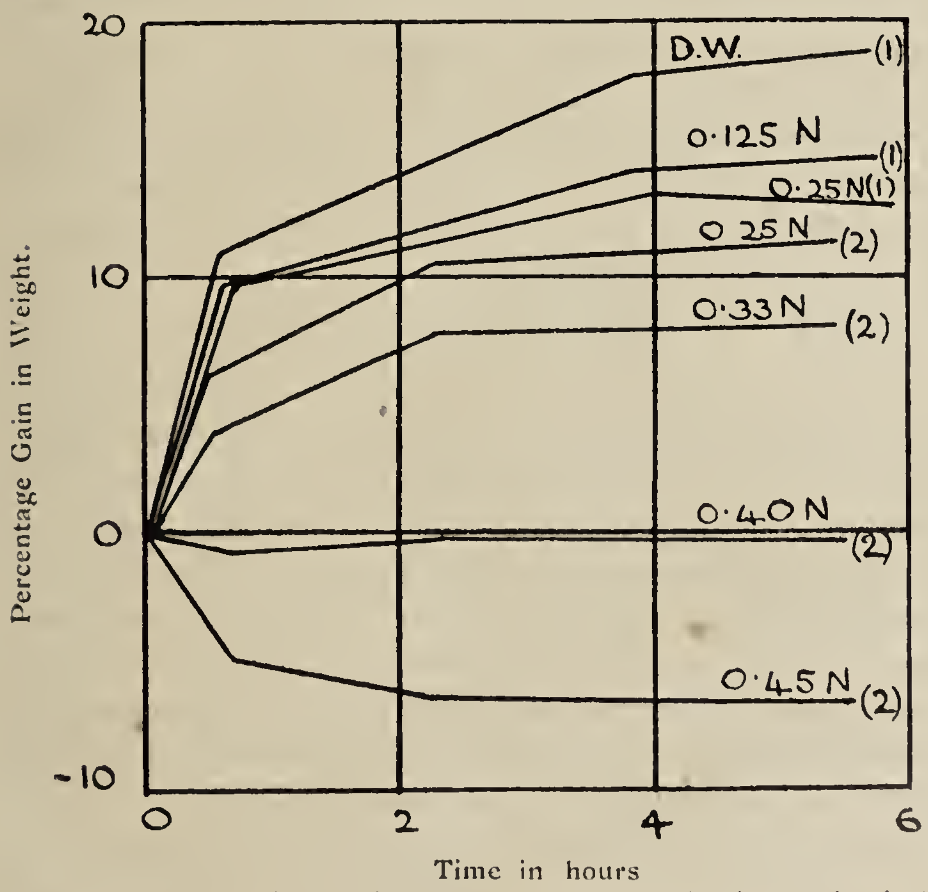


FIG. 1. Change in weight of red beet-root during immersion in distilled water and sodium chloride solutions of different concentrations.

---

[1] Ann. of Bot., 31, pp. 416-419, 1917.

In Tables IV to VI we give the results of the plasmolytic experiments on sections cut from the same three roots. We have already touched on the difficulty arising from differences between different cells of the same tissue as regards the concentration of the salt solution required to produce plasmolysis, so that when we speak of a plasmolysing concentration for the tissue as whole we are necessarily involved in an approximation. However, in the cases of all three series we should say that the concentration which just failed to produce plasmolysis in the majority of the cells was 0.4 N, and we should therefore conclude that a solution of 0.4 N sodium chloride is approximately isotonic with the cell sap.

TABLE IV.

Plasmolysis of Beet Root Cells in solutions of Sodium Chloride.
(Beet No. 1).

Concentration of Salt.	Condition of cells after 30 minutes.
0·33 N	No plasmolysis.
0·44 N	Plasmolysis slight but noticeable.
0·50 N	Good plasmolysis.
0·67 N	Strong ,,
0·80 N	,, ,,
1·00 N	Very strong plasmolysis.

TABLE V.

Plasmolysis of Beet Root Cells in solutions of Sodium Chloride.
(Beet No. 2).

Concentration of Salt.	Condition of cells after 60 minutes.
0·25 N	No plasmolysis.
0·33 N	,, ,,
0·40 N	Plasmolysis just starting in a few cells.
0·45 N	Slight plasmolysis in practically all cells.

TABLE VI.

Plasmolysis of Beet Root Cells in solutions of Sodium Chloride.
(Beet No. 3).

Concentration of Salt.	Condition of cells after 60 minutes.
0·25 N	No plasmolysis.
0·33 N	,, ,,
0·40 N	Incipient plasmolysis in a few cells.
0·45 N	Slight plasmolysis in most cells.

Thus the change in weight method and the plasmolytic method gave the same value for the concentration of sodium chloride approximately isotonic, on the osmotic hypothesis, with the cell sap in the case of the three beet roots examined.

In order to avoid misunderstanding we would emphasize that the values found for the concentration of sodium chloride isotonic with the cell sap of a tissue, whether the change in weight method or the plasmolytic method is used, is of necessity only a crude approximation. Nothing more than this was claimed in our earlier paper, where on the basis of the change in weight method we spoke of a solution of sodium chloride of concentration 0·125 N as approximately isotonic with the cell sap of potato. Of course the degree of approximation depends on the gradation of the solutions used in the swelling and the shrinkage experiments, as well as on the hydrostatic pressure of the solution in the cell, a quantity itself depending on a variety of conditions. It is perfectly clear that the change in weight method could not be used for the accurate determination of isotonic coefficients; on the other hand the plasmolytic method for the measurement of isotonic coefficients is not free from pitfalls and difficulty, and requires considerable caution in its use, so that it will only give accurate results under special circumstances.[1]

However, if we assume that the water relations in potato are similar to those of beetroot, an assumption which appears to us in no way unreasonable, the facts recorded in this paper indicate that our statement to the effect that a solution of sodium chloride of concentration 0·125 N is approximately isotonic with the cell sap of potato, was correct. We may also point out that the two sentences in which we spoke of an isotonic solution were very incidental remarks and had nothing to do either with the facts or the general theme of that paper. Nevertheless, we think the observations recorded above indicate that, as passing remarks, they were justified.

There are a few other matters connected with the contents of this paper which we think deserve mention.

In the first place we would call attention to the length of time that beet-root tissue remains in apparent equilibrium with salt solution as regards exchange of water. In Fig. 2 are shown graphically the results obtained from experiments in which beet discs remained immersed in solutions of sodium chloride for a period extending over 200 hours in the cases of distilled water, 0·125 N sodium chloride and 0·25 N sodium chloride, and for a shorter period in the case of 0·40 N and 0·45 N (see Tables I and II). No

---

[1] See especially H. Fitting, Jahrb. f. wiss. Bot., 57, 553-612, 1917.

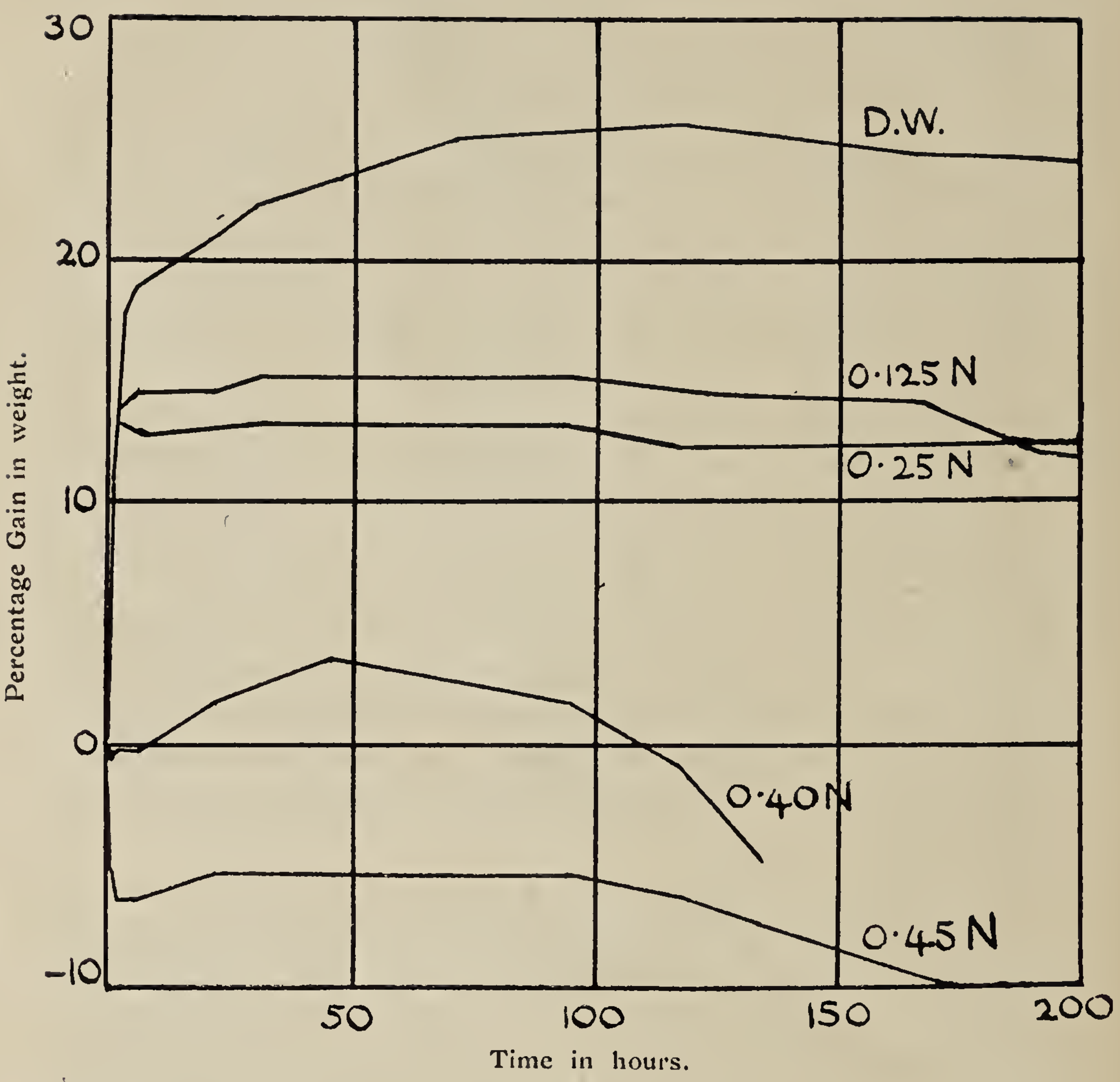


FIG. 2. Change in weight of red beet-root during immersion in distilled water and sodium chloride solutions of different concentrations.

special precautions were taken to keep the liquids sterile, although the solutions were renewed daily. How far therefore the shrinkage which ultimately supervenes, and which is one of the features of death of the tissue, is due directly to the action of the salt on the tissue or to the secondary action of micro-organisms cannot be said. It can at any rate be concluded that the tissue remained in approximate equilibrium with distilled water up to the 200th hour of immersion, with 0·125 N and 0·40 N and 0·45 N up to the 100th hour of immersion, and with 0·25 N up to about the 300th hour of immersion (see Table I). These times are all minimum values. The longer resistance to injury in the case of 0·25 N sodium chloride may be simply accidental in this instance; if not it might be explained on the ground that in the concentrations higher than this the injurious action of the salt comes into evidence sooner, while diluter solutions do not inhibit the injurious action of micro-organisms. It is clear in any case that beet-root remains uninjured by comparatively strong solutions (0·25 N) of sodium chloride for a surprisingly long time.

A second point we wish to emphasize is that the conditions in a tissue in regard to tissue tensions and water relations must be exceeding complex. To enter into a discussion of these questions is outside the scope of this note, but we may refer for example to the discussion of this question by Pfeffer,[1] in which the complexity of the matter is made very clear. While we may agree with Thoday that, "in all applications of physical and chemical principles to the analysis of complex physiological phenomena a clear understanding of their action in simple cases is an essential preliminary to the consideration of observed complications or discrepancies,"[2] it seems to us Thoday makes this an excuse for attempting to explain phenomena which are actually complex on the hypothesis that they are simple. Thus Thoday attempts to explain the water relations of the cells of a tissue in terms of osmotic pressure and the tension of the cell wall. How little further this takes us is obvious when we realise that the two quantities are not independent of one another, and that the tension of the cell wall must depend on a number of factors including the modulus of elasticity of the cell wall, the permeability of the cell wall to water, the osmotic pressure of the ceil sap, etc. We do not know how far the permeability of the cell wall influences the modulus of elasticity and what factors influence the permeability. We know little enough about the elasticity of the cell wall. In considering the water relations between different cells of the same tissue Thoday assumes that the colloidal properties of the cell contents can be neglected. This reduces the applicability of Thoday's remarks to those tissues in which the protoplasm forms a negligible part of the volume of the cell, and also assumes in this case that the colloidal properties of the cell sap are negligible. It seems to us that while the osmotic theory of the cell may be used as a working hypothesis to explain observed facts while our knowledge is in its present incomplete state, it is going too far to accept the osmotic theory as a fact and to derive from it "important corollaries" not founded on fact but on the unproved theory, especially since we know the conditions are certainly more complex than the theory assumes. As we pointed out in our earlier paper,[3] mathematical treatment of the subject is possible and in the future will no doubt be helpful, but

---

[1] Physiology of Plants, English Edit., Oxford. Vol. I, pp. 134 147, 1900, Vol. II, pp. 50-67, 1903.

[2] New Phyt., 17, p. 109. 1918.

[3] Ann. of Bot., 31, p. 431, 1917.

until we have more facts would be premature. Once again we would emphasize that what are wanted at present for the solution of permeability and related problems are facts. There are already too many theories and explanations based on the insufficient data available.

Finally we can scarcely pass over the statement made by Thoday in a footnote to his paper,[1] to the effect that we confuse elasticity with extensibility. This statement is, we think, unwarranted and misleading. In our paper there was no shadow of doubt whatever as to our meaning, and not the least confusion. "Elasticity" says Professor Love "is the property of recovery of an original size and shape. A body of which the size, or shape, or both size and shape, have been altered by the application of forces may, and generally does, tend to return to its previous size and shape when the forces cease to act. Bodies which exhibit this tendency are said to be elastic."[2]

There appears to us to be nothing in our use of the term elasticity which is contradictory to the spirit of the meaning of the term as defined above. The first sentence in which we used the term was as follows: "If the cell wall were absolutely elastic the intake of water should continue indefinitely." Thoday appears to have misread this expression "absolutely elastic" as "perfectly elastic" a term with a definite physical meaning. What we meant to indicate by the expression "absolutely elastic" was the condition of a cell wall which was indefinitely extensible and tended to return to its original shape. Thoday appears to assume that by "absolutely elastic" we meant simply "absolutely extensible." It would be as reasonable to assume that by "white" we meant "black" and then criticise us for not meaning "white." One might regard a piece of wax as indefinitely extensible, but no one would ever regard it as absolutely elastic.

In our other sentence in which we used the term we said: "If the cell wall were perfectly inelastic and quite incapable of stretching" etc. The meaning of this is perfectly clear and there is no scope for confusion. Of course, for a body to be perfectly inelastic it is not necessary that it should be incapable of change of shape. A piece of plasticene would be practically perfectly inelastic since it exhibits no tendency to return to its original shape after deformation. But for a body to be elastic, as it is commonly understood, that is, to return more or less to its original shape on deformation, we generally assume that deformation is possible.

---

[1] New Phyt., 17, p. 109, 1918.

[2] Encyclopædia Britannica. 11th Edit., Vol. 9, p. 141, Cambridge, 1910.

Hence we think our remarks involving the use of the word "elastic" were perfectly clear, and we regard Thoday's statement that we "have confused elasticity with extensibility" as incorrect and unwarranted.

SUMMARY.

1. The swelling and shrinkage of beet root in distilled water and aqueous solutions of sodium chloride of various concentration was measured by the change of weight method previously described by us. In solution of sodium chloride of concentration 0.40 N the tissue examined underwent almost no change in weight.

2. Sections of the same roots were mounted in aqueous solutions of sodium chloride and examined microscopically. The solution which was just not strong enough to produce the first signs of plasmolysis was one of concentration 0.40 N. For reasons given in the paper this value must of necesssity be an approximation.

3. It can be thus said with truth that in the case of the particular tissues examined the solution of sodium chloride which produced neither loss or gain in weight of beet root was approximately isotonic with the cell sap on the basis of the osmotic hypothesis. If it be assumed that potato has similar properties to beet root in regard to water relation, then it may also be said in regard to potato that a solution which produces neither gain or loss in weight is approximately isotonic with the cell sap of the tissue.

4. But it is obvious that this is only a crude approximation, and no more than this is now or has been claimed for it. In the case of cells with a high degree of turgor the cell will remain in equilibrium as regards water exchange with a solution of lower concentration than the cell sap, or even with distilled water, as we have explained in a recent paper. (Ann. of Bot., XXXI, 415-434, 1917).

5. In view of our having deliberately explained how on the osmotic theory of the cell, a tissue can remain in equilibrium with distilled water, Thoday's statement that we "have not succeeded in freeing our minds from the misconception that a solution in which a turgescent tissue shows no gain or loss of water is isotonic with the cell-sap," is as surprising as it is misleading.

6. Thoday's statement that we "have confused elasticity with extensibility" is also incorrect.

UNIVERSITY COLLEGE,
LONDON,

August, 1918.

THE RECONSTRUCTION OF ELEMENTARY BOTANICAL TEACHING.

ACADEMIC BOTANY AND THE FARM AND GARDEN.

In justification of the note of alarm sounded in the article initiating this discussion, the most disturbing aspect is that I can find no instance of a botanist whose services (as a botanist) were considered "essential" during the crisis we have just passed through; notwithstanding the fact that the objects of his study are essential to man's existence. The following incident is suggestive. In the early days of the war, a young man, descended from a long line of farmers and gardeners, and himself a very capable son of the soil, being unable to "join up," entered one of our large Universities in the hope of increasing his usefulness. After he had been some months in the laboratories I enquired about his progress. His reply was this: "When I go to the University I feel I am in another world, and one which has no connection with either the garden or the farm." That there should be a real and practical connection seems obvious, but we appear to have missed it.

T. W. WOODHEAD.

December, 1918.

ON SOME ASPECTS OF THE PLEA FOR RECONSTRUCTION.

The signatories to the memorandum on the Reconstruction of Elementary Botanical Teaching may, I think, congratulate themselves on the amount of support they have received. The plea that it was inadvisable that comparative morphology should be the central or dominating part in an elementary cause has clearly found a sympathetic response in the minds of many. It is to be regretted, however, that a number of other botanists with a wide experience of elementary teaching have taken no part in the discussion. This aloofness bears out the complaint, made by the Editor of The New Phytologist shortly after the journal was started, that it seems almost impossible to persuade English botanists generally to take part in a discussion.

It has been suggested that the memorandum was of the nature of an encyclical and the words "oppression," "dragooning," "bolshevism" have been used in criticism of it. It is true that the article was vigorously worded, but that was necessary if it were to succeed in its object. Surely it is clear that the memorandum was simply a plea for reconstruction on certain lines with a request for the support of those in agreement with the views put forward. Even if a committee were appointed to further those views, as suggested by one writer, its recommendations could not possibly be mandatory. To those who know Professor Bower and "Witness" the idea of a body of other botanists attempting to coerce or oppress them is distinctly humorous. It is of course, an axiom, which all botanists would accept, that no course can be satisfactory in which the teacher does not "express himself": no two elementary courses would be exactly alike; they would vary according to the special knowledge and predilection of the teacher. What the memorandum urges is that every teacher should examine his elementary course and consider whether it could be modified in the directions indicated. The signatories contend that in the light of our present knowledge of plants, and of the manifold points of contact of botany with other sciences and with human activities generally, the elementary course should no longer be centric to evolution or have phylogeny as its *leitmotif.* The main problem to be presented to the student seems to them to be that of living, not that of origin. Such a view necessitates the reduction of comparative morphology to a subordinate position, a view to which all the signatories will certainly hold firmly. Anatomy, *i.e.*, a description of the facts of structure, is bound to preponderate in any elementary course, as pointed out by the Editor, but such facts of structure should be mainly used to develop a picture of plants as living and struggling organisms rather than a picture of the phylogeny of plants.

Several writers have referred to the important question of the psychology of the student and the relative claims of morphology and physiology upon his interest. Everyone will agree with Professor Bower that the rapid development of the British school of morphologists was largely due—apart from the natural stimulus to workers from co-operation in the growth of the most rapidly developing branch of the subject—to the enthusiastic interest of its votaries. I do not think that physiologists are in any way wanting in admiration and respect for the achievements of the British school of morphology, achievements in which Professor Bower has played so striking a part. They would be the first to admit that they could do no better than attempt to emulate the enthusiasm of the followers of that school. With the advance of time, however, other aspects of Botany have opened out; and most botanists would admit that comparative morphology cannot now claim to be, as formerly, in the main current of botanical progress. The signatories to the memorandam, therefore, can hardly be accused of presumption or of a tendency towards bolshevism in claiming that the time has come to reconsider the balance of various parts of the subject most suitable for elementary teaching. In asking that comparative morphology, though "good in itself," should yet occupy a subordinate position in an elementary course I find it difficult to understand how the signatories have laid themselves open to the accusation of Professor Bower, that they are exhibiting "the spirit that has ruined Russia, and endangered the future of civilisation."

A proper subordination of parts is the test of a satisfactory work of art and of a sound elementary course in botany; a subordination of personal freedom in the interest of the community —and freedom is "good in itself"—is surely a test of civilisation. In fact the simile might be inverted, and the domination of comparative morphology to the detriment of other branches of the subject might be compared to the autocratic rule of the bolsheviks which has been so serious for other classes of Russian society.

Dr. McLean has contended that, apart from the special enthusiasm of the teacher, the morphological aspects of plants make a more general appeal to students than the physiological, though this is denied by others. Mr. Small has developed an ingenious analogy between the receptive student and a synthesising organism, and claims that in physiological teaching a much smaller proportion of the energy radiated by the teacher "must impinge upon the organism" (student). If the "photosynthate" to be obtained is simply a "true and accurate knowledge of plants" the analogy may be accepted. It is a truism however that an object of teaching even more important than the acquirement of knowledge is the development in the student of a capacity to think for himself. For the purpose of encouraging a critical habit of mind a discussion of the work of others, which Mr. Small appears to deplore in physiological teaching, may be of far more value to the student than the assimilation of large quantities of "solid fact." The accumulation in the mind of the student of a vast amount of structural detail which is really inessential and indeed useless to anyone but the comparative morphologist may be more satisfying, at all events at its first impression, than the collection of quantitative and qualitative data which result from a physiological study, because of the greater concreteness of the mental images produced. But it is often found that students who have been attracted at first to comparative morphology later transfer their attention to the physiological side when they realise its state of active development. And the greater appeal at first of the complete picture formed in the mind by a thorough study of structure is certainly no argument against the treatment from a physiological standpoint of the material (which is necessarily mainly structural) of an elementary course in which the object should be to give a picture of the plant as a living organism. A desire to know "how things work" is exhibited by most active youthful minds unless they have been stunted in this direction by a too severely literary training. It is to this mental characteristic that a more physiological treatment of the elementary course would appeal, especially as it can be shown—until at least we reach the "higher synthesis" of morphology and physiology—that both the main line of progress of the subject and contact with practical life lie in this direction.

The question of treatment is not, of course, quite simple. Some of the difficulties, such as that of physiological work with large classes, are only concerned with special conditions, and do not affect the question as to the direction in which an ideal elementary class lies. The difficulty of large classes can be surmounted to a certain extent by the demonstration of physiological experiments, but there is no doubt that large classes, except under the very best conditions, of ample space, an adequate staff of demonstrators, etc., are inimical to the most satisfactory teaching. Then again there is the difficulty that most of the fundamental processes of plants cannot yet be fully explained in terms of chemistry and physics, and that for the proper consideration of some processes a knowledge of the more recondite aspects of physical chemistry is necessary. There is however a very considerable body of physiological knowledge, not requiring for its due appreciation a special knowledge of other sciences, which might be incorporated in elementary work. There can be no doubt that a teacher concentrating his attention on the presentation of aspects of the subject other than comparative morphology can produce a more vital and stimulating elementary course than is at present customary.

It is perhaps unfortunate that the clue to some of the details of the structure and relations of the reproductive organs of the higher plants can only be gained by a study of alternation of generations with its many complexities. The result has been that "alternation" has tended to dominate the elementary course, though it is a phenomenon of very special nature, a detailed knowledge of which is not essential to a general elementary training in botany. The undue importance which is attached in an elementary course to alternation of generations was once brought home to me very sharply. I chanced to be asked to take the chair at a meeting of a Natural History Society at which a local medical man was to give an address. The members of the audience had had no special training in biology but were brought together by a general interest in natural history. When the address began I discovered to my dismay that the lecturer's idea of a subject suitable to such an audience was that of alternation of generations. So he proceeded to plod steadily through mosses, ferns, gymnosperms, and angiosperms, stating the homology of the reproductive organs of the various groups. It was obvious that to the lecturer alternation of generations was the kernel of the elementary botanical teaching which he had received as a preliminary to his medical studies. Clearly in his case a great opportunity for sound biological training had been missed by the teacher responsible for the course. Matters are possibly better now, but in my opinion the detailed complexities of alternation of generations must upset the proper balance of an elementary course for medical students, especially as this course is for most of them their first introduction to the study of living things. I have found by experience the advantage of practically eliminating alternation of generations from an elementary course for medical students. The question of the proper content of a course for such students is however a large one, and requires, as Mr. T. G. Hill suggests, separate discussion.

As to the immediate practical possibilities nothing of course can be done without the sympathy and goodwill of those in charge of elementary courses. No one desires, or has the power, to coerce those botanists who may think that changes in the direction indicated are retrograde. Some points however have been brought out in the discussion which are of interest in connexion with practical measures. It has seemed to the writer for some time that most elementary courses (including those which he has given) are too static in character. Professor Thoday has put this point very clearly in the demand that students should have the "opportunity of handling the evidence of growth and change." This I would tentatively suggest might be combined with Mr. Hiley's proposal of an intensive study of a small number of types, which could be grown in, or brought into, the laboratory in all stages, and studied from the morphological, physiological and ecological aspects. Such types as sunflower, wheat, an arborescent type, and a type chosen especially with an eye to the study of its ecological relations might be suggested. Such types would enable one to bring out agricultural and some of the other economic aspects of the subject.

There is a further point to which reference may be made. The problem of the content of the primary academic course in botany is not the same in all Universities. There are in the main two types of elementary academic courses. On the one hand we have the condition, as at Cambridge, where the degree course and the primary course are one and the same. On the other hand we have the condition, as at London, where the degree course is in two parts, the primary or "Intermediate Science" course and the more advanced "Pass B.Sc." courses. The "Intermediate Science" course is only a short one, but it is attended not only by degree students but also by students, such as those of physics and chemistry, who are not proceeding to a degree in botany. For the last class of students this course is often the only biological training which they will receive; it is therefore of especial importance that the course should be so designed as to bring before them the most vital aspects of the subject. In connexion with this "Intermediate Science" course the question is raised as to whether it should not be mainly confined to a study of seed-plants. The idea that in a restricted course of this kind it is necessary to give the student a bird's-eye view of the vegetable kingdom by studying in detail types of algæ, fungi, liverworts, mosses, ferns, etc., should, I suggest, be given up. Such a survey, if too great insistence is not laid upon comparative morphology with its concomitant elaboration of structural detail, is of course eminently desirable and would be given later as a part of the degree course. But in a short one year course of the "Intermediate" type such a survey of the vegetable kingdom can hardly be obtained except at the expense of a proper working picture of the plant as a living, struggling organism.

There are many other aspects of the matter which might be discussed, but I should like to support the suggestion of Mr. T. G. Hill that a number of botanists who are in sympathy with the idea of reconstruction on the lines indicated in the memorandum should meet and consider what changes are possible. They might suggest a syllabus for an elementary course, but it is unlikely that any teacher would accept such a syllabus *en bloc*; it would however be of value as a basis to be modified to suit the special predilections of the teacher or the special needs of his students. Lastly, I would add that in my opinion the appearance of a satisfactory elementary text-book treating the subject on the lines laid down in the memorandum would do more than anything else to rouse interest in the subject and make converts among botanists generally.

V. H. BLACKMAN.

December, 1918.

"NO DEPARTMENT THE DOOR OF WHICH SHOULD NOT BE OPENED."

It will I think be conceded that the discussion which the original memorandum has provoked has fully justified its publication. That memorandum was inspired by a certain fear lest the morphological bias which has been predominant in Britain for many years past should have outstayed its usefulness. The very enthusiasm with which morphology (including anatomy) has been pursued in this country has perhaps blinded us not so much to the fact that there are other points of view as to the possibility that the time has come when the elementary course could with profit be presented in some other form than is often the case. It seems to me that the place for the development of morphology should be at a later stage than in the elementary course, where by over-elaboration on the structural side we run a risk of losing sight of the living plant within. However, it is not my object here to rewrite the original memorandum, with which I am in substantial agreement.

In view of the discussion that has taken place there is no further need to emphasise here the importance of making the life functions of the plant the *pointes d'appui* around which the course as a whole should be built up, but a word or two may be permitted as to its scope.

I am satisfied that an ideal elementary course should give quite clear indications of all the various vistas which the subject presents and this equally in the interests of students who are going to pursue botany and of those who are not. There is no department of botany the door of which should not be opened sufficiently wide for an impression to be gained of the treasure within. I include here not only the applications of botany, such as brewing, milling of wheat, manufacture of paper, vegetable textiles, etc., but also definite departments of the subject such as ecology, plant pathology, genetics, and even fossil botany. It is perfectly clear that whilst these by-ways and applications, many of them, can only claim passing reference in an elementary course, such references are likely to make a more lasting impression when attached to those parts of the main subject matter to which they strategically belong. Genetics probably might be developed with advantage to some little extent; no branch has more important applications, nor does it ever fail to appeal to the student.

As regards ecology, I am in cordial agreement with the Editorial Note appended to Dr. Harold Jeffreys' letter. The student should at least make acquaintance with a selection of the different ways in which plants subjugate their environments and comport themselves under a variety of conditions; particularly useful being water plants, maritime plants and woodlands. In this connection it is eminently desirable that students should have an opportunity of viewing plants in the field for several days continuously (*e.g.*, a long week-end). Indeed, having regard to the exhilarating and enjoyable attendant circumstances of such visits and the lasting impressions gained, it is throwing away one of the most valuable assets of botany not to develop the excursion.

A good deal has been said in the course of this discussion on the practical applications of botany and the desirability of giving prominence to these in elementary teaching. Half-a-century or more ago the applied side of the subject was kept before students much more fully than has been latterly the case, and there I think our forebears were right and we wrong. Applied botany has a human interest going far outside academic circles, and its proper use places a valuable instrument in the hands of the teacher; moreover it is decidedly attractive to students, who naturally respect a subject which gives them the scientific foundation for this or that operation in agriculture or industry. Among the many reasons why the applications of botany should not be neglected in the class room I reckon the most important to be that it may encourage a student eventually to choose a vocation in one of these fields. Too often what are really botanists' jobs are filled by chemists who know very often little or nothing about botany at all. We need to develop the applied side and ourselves indicate the scientific foundations of practice, thus gradually building up a connection with industry in addition to that with the medical and teaching professions. I would go so far as to say that a botanist might do worse than take a practical and sympathetic interest in some branch of applied work. It will bring him into touch with extra-academic circles—growers, planters, foresters, technologists, hobbyists, etc.—with mutual advantage. We botanists need not only to do our work to the best of our ability, but also continually to broaden our circle if botany is to come by its own.

F. W. OLIVER.

January, 1919.

WHAT IS BOTANY?

To the Editor of THE NEW PHYTOLOGIST.

Botany, as the Science of Plants, claims dominion over some ninety-nine per cent of the living matter on the surface of the earth and over most of the fossil remains under the surface. In extent and diversity of interest no other single science can equal it.

As plants alone provide food and energy for the other small fraction of living matter they still form the one essential background to every human activity. At all times plant existence has loomed large in the minds of both practical and scientific men. Throughout the ages students have sat at the feet of those who knew, and the sages have taught with authority and enthusiasm what they would, probably all they could, with little reflection or current criticism as to what they should be teaching.

Now, in this critical hour of a self-conscious age, it has come to be widely questioned what botany really consists of and what we ought to teach in centres of learning and education. With this problem in mind and realising the continued growth of our subject in depth and in extent, it has seemed to me worth while to run lightly through the phases of botany that have successively come to birth and dominance in the past; and to pursue the same idea on beyond the present. No great pains have been taken to define phases critically; the phases have just been indicated, and any guidance that emerges comes from this general presentation of our science.

The problems, phases and sections of botany are not really inherent in vegetation though they are often projected on to it: they are phases of outlook of the human mind with its changing vistas and varying needs. Let us then take man's outlook on plants from the beginning, indicating some nine successive phases of scientific or sub-scientific enquiry.

I. *The Phase of Economic Plant Exploitation.* From the prehistoric beginnings of our race there must have been times of earnest research and experimentation, involving indeed life and death. What countless negative results must have gone to the discovery of the edible in all climates and what delicate experimentation has led to the conclusion that capers should be eaten in bud, and medlars, alone of all fruit, rotten. A still more surprising achievement is the early discovery of nearly all condiments and spices; and the uses and abuses of such drugs as opium, quinine or the "hellish oorali." Who started experimental physiology by using animal ordure for vegetable nurture or discovered the value of leguminous crops for improvement of the soil and its subsequent returns?

II. *The Phase of the Herbals.* In early historic times the science of botany centres round the *Hortus Sanitatis* and the medicinal uses of plants. Here some of the names of teachers and text-books survive, but the methods are more like those of the lower journalism than of science. Slowly however, by selection, an accepted *Materia Medica* clarified itself from the jumble of alleged virtues of plants.

III. *The Phase of Taxonomy.* Gradually some scientific spirit of knowledge for its own sake pervaded man's contemplation of botany, and existing types were grouped and sifted and regrouped by men whose life-long devotion to "plants" gave them great unformulated insight into affinities. Systematic botany was then the chief science of botany, with its subsidiary descriptive work on the forms of flowers, fruits and the vegetative parts of plants. Indefatigable collectors ransacked the globe for new species as an end in itself.

IV. *The Phase of Comparative Anatomy and Morphology.* Isolated anatomical investigations of the insides of plants of course began early and morphology grew up with classification but it was the vitalising theory of evolution which gave a scientific significance to the *comparative* aspect of these studies. Plants were not the chaos of a special creation but an orderly if complex phylogenetic sequence, to be analysed and, in spite of the imperfection of the whole record, to be reconstructed by attention to the minute birth-marks of insignificant structure. The harvest of the main phyla is now mostly reaped and further study seems likely to proceed on the principle of diminishing returns. There have been some stirring pieces of detective work, as the piecing together of the evolution of the seed from fossilised types; or the discovery that pollen-tube-fertilisation still bears the class-marks of alternation of generations.

V. *The Phase of Plant Physiology.* Stephen Hales, in the early eighteenth century, was the first to apply to living things a general scientific "chymio-statical" outlook, and so laid the foundations of several chapters of plant physiology. The rest waited for the discovery of protoplasm, the physical basis of life, and the realisation that what was known of animal functions could, in essentials, be transferred to plants. Combining with all this the special botanical studies of photosynthesis and tropisms, Sachs put together, in a masterly way, the outlines of a coherent physiology of plants in the middle of the nineteenth century. Since then physiology has received definite recognition as an indispensable but rather detached section of the subject. The first English text-book of physiology appeared in 1886: in general text-books, physiology was the smallest of the three traditional main divisions.

VI. *The Phase of Genetics.* The twentieth century has seen the rise of several new phases of man's outlook on plants. The general study of variation and heredity received such an access of vigour from the Mendelian rediscoveries that it rapidly developed a body of genetic principles which no biological science can ignore, and is making the phenomena of evolution assume quite a new aspect. Apart from the gain in understanding of plants, the power that genetics has conferred on the botanist has brought honour to the whole science. Millions of years of Nature's evolution have not achieved for us so desirable a wheat as the special creation of "Little Joss."

VII. *The Phase of Ecology.* In a quiet gradual way a new section of botany has segregated itself in our midst from devotion to Nature Study and Vegetation as it actually exists upon the surface of the earth. Ecology widens the botanical horizon enormously by insisting upon our adding what may be called the sociological outlook to the various other ways in which plants have been regarded. That a new section should thus materialise in these later days based merely upon phenomena of vegetation which have been before the eyes of botanists from the beginning, illustrates the huge content of the science and the human, subjective nature of the sections into which it is divided. All this certainly adds to the difficulty of devising for students a general but comprehensive introduction to botany as a whole.

VIII. *The Biology of the Individual.* Further I think one may indicate a group of phenomena, associated with the existence and development of every plant as a living individual, which is perhaps now cohering and in process of segregation to form a definite section of our science. These are essentially matters of life, but hardly included in physiology in the narrow sense of physiology of functions and organs: the outlook is upon the plant as an individual life-history, and its associated problems are brought most vividly before those who carry on the culture of plants *in horto* or *in agro.* Enumeration of a few will suffice to indicate the scope of this section ; ripeness and viability of seeds ; dormancy of seeds in soil ; retardation and forcing of vegetative activity ; the laws of growth-rate and of dry-weight increase ; intensive cultivation, vegetative growth versus reproductive activity; crop yield and predetermination of it.[1]

In the future other phases must arise and acquire a measure of autonomy: we all await a constructive philosophy of plant-form—a crystallography of the organised plant—which will interpret such strange things as the sickle-shaped cells of some green Algæ and the mimicry forms of Caulerpa as well as the problems of polarity and regeneration.

The specialised study of one group of plants is not to be counted as an independent phase from our present point of view.

---

[1] It is true that many of these matters are already regarded as part of the subject of Ecology in its widest sense. Ecology is so comprehensive that it can be presented as including the whole of physiology and practically all the phenomena of living vegetation, but the history of the growth of the phases of Botany shows that Physiology as a human outlook has an independent existence and so also the matters collected in this section have their independent origin and inspiration in growth and culture of plants, and not in the ecological outlook.

The phases that we have here gone through have all been focussed upon the normal healthy plant as subject-matter but, as phases of human outlook, they should, if soundly drawn up, repeat themselves and be equally valid even if one set out to exemplify the whole of botanical science on one group only of plants, as for instance, Algæ or Fungi.

IX. *The Last Phase.* To cast a glance much further ahead, what may we imagine botanical outlook and teaching to be when every biological phenomenon has been considered to the full both in its historical and functional aspects?

When our knowledge becomes quantitative and completed botany may in great part look like a special branch of applied mathematics. An attempt might then be made to set out the life of the plant in terms of chemical dynamics for the single functioning unit, in statistical form for aggregates of units, and as correlation-coefficients for the influence of the environment. Meanwhile there would be an infinite number of biological constants to be determined for different plants.

Though most of us feel relieved to think that this phase is still infinitely remote and that the atmosphere of mystery and ignorance is left to fascinate us, it must be recognised that there is already enough mathematical treatment of biological phenomena to call for a sound understanding of certain sides of mathematics as part of the equipment of students who hope to go far with work on the living plant.

The only compensation that this last phase could bring would be that the power of man had increased as greatly as his knowledge, and that vegetation had become as plastic in his hands as the inorganic is now.

* * * * *

What light do we gain by thus setting out the science of botany as a series of shifting phases of development, each of which has its infancy, its period of growth and dominance when vigorous additions to knowledge are being made, and then tends to yield diminishing returns to further research, leaving finally a definite corpus of truths of structure, function or relationship as a permanent addition to the Pantheon of Botanical Science.

The steady drift of phases makes it clear that no one of the federated sections can expect to take precedence of the other sections on grounds of an absolute nature, which will be valid through all time. At any epoch there will be some older sections that can claim the classical beauty of clearly worked out ideas, while newer sections boast the romantic beauty of the primitive.

Another obvious point is that what is known and taught as Botany in successive ages shifts. In earlier days advance was slow and to be a generation behind the times was no great matter. Now new sections come fast into the field, start their own journals and societies, and materialise at a rate which makes it a considerable effort for those nurtured in the earlier phases to follow. The collective thought of botanists in council should therefore be given to laying the foundations of a general course of practicable length which will serve as an introduction to all modern phases of the subject. Some material must from time to time be dropped as we move forward and the teaching term does not expand. The better established and more clearly worked out a section has become, the easier it should be to get the essentials formulated so that repeated exemplification in detail can be spared. This process has been at work already and many things taught 20 years ago have faded out. *Materia medica* has gone[1]; taxonomy has been greatly reduced in bulk and now the down-turning thumbs of recent contributors seem to point to comparative morphology as the next section to submit to the stigma of being called a classic.

With regard to the new accessions to our federation, we must hold it vitally important that students should, in any general introduction to botany, be brought definitely to realise the existence of these new sections and their respective points of view. A difficulty arises in that the new, developing sections are by no means homologous. While the central attraction and justification of genetics is a definite discovery—the Mendelian achievement—the claim of ecology is much more a way of looking at plants, the focussing of scattered existing knowledge and the accumulation of fresh knowledge from new and fruitful points of view. Imparting to students a conception of ecology is thus a very different task from that involved in dealing with genetics. The best way of doing these things must be sought out.

With the new national patronage of science, which chiefly means expectation of commercial or political benefit to the state, one aspect of any section of botany that may not be overlooked is the possibility it presents of translating knowledge into power.

If this presentation of botany and its diversity in unity is a

---

[1] The use of coloured plates for poisonous plants alone, in the earlier editions of the Bonn text-book, may to the phylogenist appear to be the last trace of this phase.

sound one, it cannot be a tenable position to claim that the scope of the general teaching at any school of botany is a personal matter of minor importance. Such a position fails when examined either from the point of view of the reputation of the school or the equipment of its students.

The living plant yields place to nothing in its scientific interest for investigation at the present and in the immediate future ; partly because of the wealth of problems presented and partly because the scope of experimentation is almost unlimited, not even checked yet by sentimentality. Whole ranges of experimental work exhibit the plant as amazingly labile, while other types of experiment bring out equally impressive stability. To correlate all this into a well-balanced whole is an attractive and imposing objective.

Finally it may be urged, without any real paradox, that it is just for students who do not propose to become botanists and whose sole experience of our science will be one general course of botany, that it is most important that the course should give a survey of the whole sweep of aspects here indicated, so that these students may not pass through our schools without being compelled to feel respect for the scope of the subject and the problems that lie before us, as well as satisfaction in acquiring the body of knowledge already organised: for while in truth their acquired knowledge will certainly fade their respect may often remain to our permanent gain.

F. F. BLACKMAN.

January, 1919.

THE
NEW PHYTOLOGIST

VOL. XVIII, NOS. 3 & 4. MARCH & APRIL, 1919.
[PUBLISHED MAY 14TH, 1919.]

THE ORIGIN AND DEVELOPMENT OF THE COMPOSITÆ.

BY JAMES SMALL, M.SC. (LOND.), PH.C.

CHAPTER XI.

THE ORIGIN OF THE COMPOSITÆ.

IN the previous chapters phylesis has been studied by the methods of comparative morphology, and a comparison of the details of the movements of the styles and stamens has been added. The conclusions arrived at have been tested by the geographical distribution of the groups (Chap. X). The phyletic data which have been elucidated would seem to support the origin of species by mutation and by the direct action of environment. Evidence is also given of the action of the Age and Area Law and, to a certain extent, the Differentiation Theory of Guppy is supported. It appears that Natural Selection has acted only on broad lines, such as the large development of Compositæ in the best situations for the dispersal of the fruits, and the selection of the mountain ranges as the path of migration.

In view of the multiplicity of evolutionary theories at the present time it is necessary to examine these and to endeavour to state precisely the evolutionary theory which appears to be most in accordance with the results of the present study before proceeding to any detailed enquiry on the actual origin of the family. The problem of this origin has four main facets—(1) From what group of plants did the family arise? (2) By what method? (3) In what region? (4) At what geological time? The first three points are discussed in the present chapter, the second being taken before the others in order to make the discussion of the first problem more circumscribed and precise. A brief summary of previous views on the origin of the family is given in the first section.

A. HISTORY.

Linné (I, 59, p, 415) classed *Dipsacus* and *Jasione* with the Compositæ in his "Communes" and later (I, 59, p, 441) he placed

Lobelia and *Jasione* in the Syngenesia. These suggested affinities cover the range of almost all subsequent views on the origin of the Compositæ. Allen (IV, 1) covers even a wider range when he writes of the "closely allied Dipsaceæ, Valerianeæ, Lobeliaceæ and Campanulaceæ."

The Dipsaceous origin is upheld by Bessey (I, 10) and by Bentham (I, 8), see Chap. I, B. The latter, although he classed the Compositæ with the Dipsaceæ in the Asterales and was "unable to see any grounds for supposing, with Delpino, that the Lobelieæ are the parents of the Compositæ" (6, p. 8), gave the other view in his phylogenetic scheme (Chap. I. Fig. 2), where he follows Cassini (Chap. I, Fig. 1) in suggesting an affinity between the Cichorieæ and the Campanulaceæ through the Lobelioideæ.

The origin of the Compositæ from Lobelioideæ has been upheld by all other writers on the subject, beginning with Batsch (see Chap. I, B). Delpino (Chap. I, Tab. III), Höck (I, 41), Wernham (Chap. I, B), Hallier (21-22 and I, 38) and Engler (I, 30) are others who have expressed this view.

The present writer has suggested other points of affinity between the Compositæ and the Lobelioideæ (IV, 74, p. 198 and III, 49, p. 267), but the most detailed comparison yet made is by Kirchner (33). This author follows the development of the various genera of the Campanulaceæ into the Compositæ and a summary of the points which he finds to be common to the two groups may be useful. These are (1) protandry, (2) pollen presented on outside of style, (3) autogamy by curving of style, (4) capitula as in *Jasione* and *Phyteuma*, (5) syngenesy which is suggested in *Jasione* and accomplished in *Symphandra*, (6) nectar stored in the narrow, lower part of the corolla tube as in *Trachelium* and Compositæ, (7) nectary at the base of the style as in *Adenophora* and Compositæ.

No other family except those mentioned above has been seriously considered as the source of the Compositæ, and although some may show involucrate heads, syngenesy etc., these characters occur combined with numerous others which are quite different from those of the Compositæ, while the remarkable number of characters which are common to the Lobelioideæ and the Compositæ leaves very little doubt of the true affinity of the two groups.

B. THEORIES OF EVOLUTION.

Although the literature of evolution is extensive very few writers give a general account of modern theories, and none except

Bergson has yet attempted to expound a synthetic theory. This exposition by Bergson of evolution (7) is only partly scientific; it is rather metaphysical and transcendental as beseems the work of a philosopher. It is, however, of the greatest importance to the student of evolution who desires to appreciate the true meaning of the development and progress of life.

Perhaps this brings the expression "life force" to the mind of the reader; if so it is necessary to point out that the original phrase "un élan de la vie" is translated by "vital impetus" or "impulse of life" and not by "life force." These phrases give a better idea of what Bergson means than the popular "life force" does (cp. 47).

According to Bergson (op. cit., p. 103) evolution "proceeds rather like a shell, which suddenly bursts into fragments, and these fragments, being themselves shells, burst in their turn into fragments destined to burst again, and so on for a time incommensurably long. We perceive only what is nearest to us, namely, the scattered movements of the pulverized explosions."

Other general accounts of less importance are given by Bernard (8) and the writer (47), and various aspects are treated by different authors in *Darwin and Modern Science* (45).

Natural Selection.

The theory of the origin of species by the elimination of all except the fittest of a series of infinitesimal variations (II, 16) has been widely accepted since 1858, but few recent experimentalists support this view, although not many deny it altogether.

One of the few supporters is Stout (50-51) but there is much in his work on *Cichorium* that requires revision. For example, he makes a strong point of the fact that the mode of the flower number *per head* in *Cichorium* does not fall in the Fibonacci series. The vast majority of the data refer to the ray florets (which are not present in *Cichorium*) and, as Church (IV, 18, p. 116) has shown, the Fibonacci series in the number of rays depends on the number of long spirals in the inflorescence and the sub-division of these spirals according to the 2 : 1 : 2 : 1 : 2 arrangement (see Chap. VIII). The number of spirals in the disc is definite and usually in the Fibonacci series but the number of flowers in each spiral is very indefinite (cp. IV, 18, p. 133). There is, therefore, no apparent reason why the total flower number *per head* should be in the Fibonacci series or discontinuous at all, although the discon tinuity in the number of ray florets and the occurrence of Fibonacci numbers among them is abundantly proved.

Willis (58-60, X, 74 and IV, 93) is one of the few who have in recent years written for the specific purpose of controverting natural selection but many have expressed doubts as to the causative action of such a negative principle as elimination. Walton (54) writing of the direct connection between the rotation of the earth and the rotation of aquatic micro-organisms says "Any attempt to account for it on the basis of natural selection can scarcely gain credence." The denial of the theory is also not uncommon among amateur naturalists who have spent many years in close observation of wild life. Thus Fountain (16), as a result of his observations on the celerity with which animals detect their prey in spite of so-called protective colouring, regards the whole theory of protective colouration as the result of insufficient observation in the field followed by inaccurate fireside reasoning, and pours scorn on the the natural selectionists in general (cp. op. cit., p. 95).

The elimination of the unfit by natural selection is a biological axiom which is not controverted by anyone, but its effect as an originating cause of species is not so evident.

Hybridisation

The most extreme views on the theory of the origin of species by hybridisation are expressed by Lotsy (35-36). This theory receives substantial support from the well-known and completely proved phenomena of Mendelism and from the work of Jeffrey and his collaborators (29, etc.). In spite of the extremeness of his views Lotsy has given definitions of "Linneon" and "Jordanon" (36) which should prove very useful if applied in future experimental work, since he distinguishes carefully between taxonomic species and genetically pure species.

It seems very clear from the Mendelian work that distinct forms or even species may arise by Mendelian segregation and recombination. The segregates of *Senecio vulgaris* obtained by Trow (IV, 84) would almost certainly have been described as separate species if they had been examined and described in the usual way by the usual taxonomists. Cockayne (X, 15) gives specific cases of confusion between hybrids and true species.

The cytological work of Morgan and others (38-39) has furnished a reasonable foundation in structure for the origin of very varied types by Mendelian segregation. The origin of new characters which is necessary for progress is not, however, explained by Mendelism (cp. 11). This difficulty is avoided by some Mendelians who claim that little or no progress but only loss of characters and diversification have taken place (cp. Bateson, 35, p. 89).

An interesting point is the variability of Mendelian factors or genes. That they are invariable is accepted more or less as an axiom by many Mendelians and the point was made precise by Johannsen (31) in the theory of pure lines or genotypes. Cockerell (IV, 19), who finds that a few genes or potentialities can give many varieties, concludes that new genes, though rare, do occur in the annual sunflowers. The variability of genes is upheld by Castle (12), and also by Stout (50) and Harris (23-24) : the last two authors criticise Johannsen's work and the genotype theory very adversely, and this criticism is supported by the details of Jennings' work on *Paramœcium* (30 and Gates 35).

Mutations.

That mutations or discontinuous variations occur in the Compositæ is clear from the evidence which has already been mentioned (see Chap. IV, A). The truth of the phenomena described by De Vries (IV, 87-88) has never been denied, but Mendelians claim that all the phenomena can be explained by hybridisation and subsequent segregation, with occasional loss of genes (cp. 35).

White (56) claims priority for his observations (1898-99) of mutations in *Lycopersicum*. Cockayne (X, 15) makes a similar claim for Armstrong (1881). Davenport (14) mentions mutations which are sterile with the parent species (the accepted proof of specific differentiation). Willis throughout his work on Age and Area supports the views of De Vries, especially in his earlier papers (58-60, X, 74 and IV, 93) and in his special studies of the hill-top floras (IX, 43-45). The facts in the latter papers are supported by those given by Gibbs (X, 31).

Two interesting points are mass mutation and tetraploid mutation. The former is described by Bartlett (3-4) as the production of a large proportion (sometimes 100% of progeny) of mutants from certain parents. These mutants are themselves very unstable but do not throw off the type form of the species. This phenomenon is inexplicable by Mendelian segregation, but the loss of a factor giving a 100% mutant progeny is quite in accordance with Mendelian ideas. Mass mutation is also another possible reason for the occurrence on islands of endemic species of genera which are otherwise unrepresented in the same region (cp. Differentiation, Chap. X, A).

Tetraploid mutation giving pairs of species, one species usually larger in every way than the other, is described by Gates (IV, 32) who also gives a general account of the part played by mutation in evolution (18) and applies the conception very successfully and in considerable detail to special systematic groups (X, 28-29), thereby proving that the theory of mutation is distinctly useful in the study of the details of classification. The mutation in this case is frequently, if not always, to be interpreted as a result of hybridisation (see Chap. XII, B).

The occurrence of mutations in the Compositæ is either suggested or proved by many observations (see X, 59; VI, 15; IV, 8a, 40, 45, 66, 68, 82 and 84). Besides *Oenothera*, the Compositæ and the cases given by De Vries (IV, 87-88), there is *Capsella Hoeggeri* (49), *C. Vigueri* (9), *Juglans* (1), *Matthiola* (17), *Solanum* (26), *Gossypium*, (32), *Pleodorina* (20) and *Drosophila* (38). Few cases (cp. Lotsy, 35) of progressive mutations from a pure, homozygous stock have yet been thoroughly proved. Retrogressive mutation by the loss or suppression of a factor explains most, but not all, the cases which are inexplicable by segregation.

Orthogenesis.

According to Bergson, orthogenesis or "the continuity of direction of successive mutations" is due to the direction of the "élan originel de la vie," but somewhat less metaphysical ground is adopted by Wernham (I, 88, p. 136), who says that "Critical tendencies are no less important than critical characters," and also that "In the progeny . . . . the characters are constant and completely evolved; and the line which unites ancestor and descendants represents the transition between tendencies and their realisation." To the student of Bergson the "tendency" is clearly the direction of the "becoming" and the fixity of the characters in the progeny is a lapse on the part of the author into the artificial, cinematographic point of view which is the normal attitude of the scientist.

The importance of orthogenesis in evolution is emphasised by Himmelbauer (X, 39) and Benedict (5). The facts given by the latter are very striking and his phrase "orthogenetic saltation" summarises very aptly in scientific phraseology Bergson's view of evolution as a combination of "*déroulement*" and "*déclanchement*," the unrolling being orthogenesis and the explosion resulting from the "*déclanchement*" being saltation or mutation (cp. 7, pp. 78 and 91).

Coulter (13) defines orthogenesis as "progressive evolution in a given direction, in contrast with the more or less successful variations in several directions involved in the theories of natural selection and mutation." He considers orthogenesis to be a response to evolution of climate (cp. X, 43, Chap. XXX), *i.e.* to "a persistent change in the conditions of living." This, as he points out, makes orthogenesis a physical rather than a vitalistic phenomenon and such a view explains most, if not all, orthogenetic development.

Throughout the Compositæ Coulter's explanation is satisfactory. Such cases as the tendency to dorsiventrality in the Tristichaceæ and Podostemaceæ, however, seem to require correlation in addition to epharmosis for their complete explanation. It is noteworthy also, that most lines of orthogenesis can be explained by *loss* of factors. All the cases of reduction or aggregation of parts, which form the chief examples of orthogenesis, are clearly retrogressive mutations, *e.g.* the keynote of the evolution of green plants is generally recognised to be the progressive sterilisation of potentially reproductive cells.

Epharmosis

In its original sense, as used by Vesque (53) epharmosis is distinguished from adaptation; adaptation is described as the effect of epharmosis after the effect has been transmitted by heredity and fixed by selection (op. cit., p. 44), but it is proposed to use the term epharmosis here as meaning the act of developing epharmony in Cockayne's sense of the word (see above, Action of Environment, Chap. X, A). This limits epharmony to adaptations which are the direct result of an environmental stimulus and excludes such changes as may be due to mutations or other spontaneous variations, and which may happen to be advantageous, while at the same time it removes the distinction between fixed and unfixed variations. There is as yet no direct evidence either for or against the fixation of epharmonic characters, but there are a large number of facts, which can be used to prove the probability of such fixation in plants.

The powerful effect of environment in producing advantageous modifications of structure or physiological behaviour is implicit in much of the theorising on the origin of land plants. It is very significant also that Sargant, Hill, and Henslow, with three different theories, all attribute the origin of monocotyledony to an action of environment, which in all three cases is more or less direct (see

Bancroft, 2, and Sinnott, 46, p. 566). Jordan apparently had some idea of epharmosis when he wrote (X, 44, p. 17) " Si l'on entend que la sélection naturelle ou sélection inconsciente de la nature, comme disent Darwinistes, s'opére indépendamment des causes extérieures il suffira de faire remarquer que cette sélection n'existe pas."

It is noteworthy that ecologists and most botanists who have made a careful study of plants in the field are among the chief supporters of the causative action of epharmosis in the origin of species. Spruce (X, 69, Vol. II, p. 357) says " Of the riparial plants, nearly every species has its congener on terra firma, to which it stands so near that, although the two must of right bear different names, the differences of structure are precisely such as might have been brought about by long exposure even to the existing state of things, without supposing them to date from widely different conditions in the remote past." Warming (X, 71, Chap. 100) gives a summary of various aspects of epharmosis, a term which he uses for self-regulation or direct adaptation, implying in his expression " they directly adapt themselves " a metaphysical view of evolution closely akin to that of Bergson. The definition given above in accordance with Cockayne's view does not imply any teleological action.

Warming gives many references, one of the most important being Goebel (19). Some of the points he mentions may be applied to the Compositæ—(1) illumination altering leaf-position, *e.g.* the compass-plants, *Lactuca Scariola* and *Silphium laciniatum* ; (2) aerial and subterranean conditions as affecting external structure, *e.g.* various Compositæ (X, 19) ; (3) epharmonic xeromorphy, *e.g.* various Compositæ (see 41 and X, 6, 16, 36, 48, 51, 56, 60 and 63) ; (4) hydrophytes : the changing of *Polygonum amphibium* in a few weeks from the land-form to the aquatic form is paralleled by the even more striking case of *Cnicus arvensis* (X, 18, and Chap. X, A), (5) changes in food-supply inducing distinctions in floral structure, *e.g. Dimorphotheca pluvialis* (Chap. IV, C) ; (6) internal structure as affected by external conditions, *e.g. Raoulia, Senecio,* etc. (X, 26 etc.) ; (7) plasticity of biological characters, *e.g.* action of climate on irritability (see Chap. III, especially *Torenia* and notes 14, 15, 18, 31 and 33) ; (8) specially marked plasticity and genera in a condition of active evolution, *e.g. Hieracium* (II, 55).

Warming (loc. cit.) mentions that epharmosis is more or less confined to the vegetative organs and to the metabolism of the plant. " The flowering shoot in its development follows laws that, in some ways, differ entirely from those concerning vegetative organs." The effect of food and light on the corolla in the Compositæ has already been noted (cp. *Helianthus*, V, 21 and Chap. IV), and that external conditions may have a marked effect even on the inflorescence in the Compositæ is shown by the production of a solitary capitulum, instead of a compound inflorescence in *Rudbeckia* under adverse conditions (IV, 44), by the seasonal variation in the number of ray and disc florets described by Nakano (VIII, 19) and others, and also by the floral changes produced by injury (IV, 23), grafting (IV, 24) and parasites (IV, 55-56a). That the modifications caused by the environment in such details are of taxonomic importance is shown by the fact that hairs may be diagnostic characters, *e.g.* in *Senecio* (25); many of the other characters are also used in diagnostic keys to the species.

The permanence in heredity of epharmonic variations is accepted by Warming as proved, but more detailed evidence on this point is given by Henslow (27 and X, 38). Cockayne (X, 15, p. 13) cites quite a number of workers who have given reasons for their adherence to this neo-Lamarckian doctrine. Even Weismann was "driven to the conclusion that the ultimate origin of hereditary individual differences lies in the direct action of external influences upon the organism" (55, p. 279 and cp. Macbride, 35). Whether such inheritance of acquired characters is true or not for the species or genotypes (Jordanons, etc.) as defined by the Mendelians, it seems certain that many *taxonomic* species (which are based on morphological structure and which have not been examined genetically) are the result of the direct action of the environment

The remarkable plasticity of the Compositæ is apparent throughout most of the work on epharmosis. For example, the Compositæ give more than one-seventh of the species in New Zealand (X, 93, p. 278), but this does not altogether account for the fact that Cockayne draws examples from the family for every one of his sections on response to ecological factors (X, 15, pp. 15 sqq.); soil—*Cotula Haastii, C. Featherstonii, Senecio antipodus*; light—*Olearia insignis*; wind—*Olearia ilicifolia*; water—*Cotula, coronopifolia*; altitude—*Celmisia argentea*: as well as for the after-effect of stimuli—*Olearia Lyalli, O. Colensoi*; for convergent epharmony—*Celmisia, Haastia, Psychrophyton*, and for persistent juvenile forms—*Helichrysum*,

The most recent example has been worked out by Wall (53a), who has shown that two New Zealand species of *Senecio*, *S. saxifragoides* and *S. lagopus*, are microspecies of the same aggregate. They are distinguished only by the sparseness or abundance of the bristle-like, glandular hairs on the leaves. "Those differences in degree, being certainly hereditary, constitute true unit characters." It is further suggested that the difference is "of climatic origin" and that "the drier climate of the Port Hills has directly determined the development of *S. saxifragoides*."

Other papers of interest in connection witb epharmosis are by Harshberger (X, 35), Raunkiaer (43), Poole (42), Bonnier (X, 8-9), Cockayne and Foweraker (X, 17), Dauphiné (X, 22), Foweraker (X, 26), Gates (X, 27), Harris (X, 33), Oger (X, 56), Schröter and Hauri (X, 60), Shreve (X, 63-64), Sinnott and Bailey (46 and X, 5), Massart (X, 53), and Eames (15). For further literature the reader is referred to Goebel (19), Warming (X, 71), Henslow (X, 38), Cockayne (X, 15-17), Schimper (IX 32) and De Vries (IV, 87, pp. 438 seq.).

Isolation and Differentiation.

A. Jordan's theory of the origin of species by isolation was revived by D. S. Jordan (X, 45) and is expressed thus. "Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighbouring district separated from the first by a barrier of some sort." This is shown to be true for *Eriodictyon* by Abrams and Smiley (X, 1) and the idea is applied by some taxonomists, when they raise geographical forms to specific rank (cp. 37). It is not, however, recognised as a general truth in the plant kingdom, for as Lloyd (X, 47) points out, the more general phenomenon is the occurrence of the most closely related species in the same region. Cockayne (X, 15) gives a number of specific instances of the occurrence of closely related species side by side in the same region and quotes Leavitt (34), who considers this phenomenon to be evidence in support of the action of mutation rather than that of natural selection or epharmosis. "Mutation breaks the species, and momentarily at least must give a polytypic aspect to the group within a specific area" (*loc. cit.* p. 211).

The theory of "the diffentiation of primitive world-ranging types in response to the differentiation of their conditions" (Guppy, IX, 22, p. 313) has already been mentioned (Chap. X, A) and is closely akin to the action of isolation and epharmosis. Of these theories which attempt to explain more or less the same phenomena, epharmosis is supported by the most conclusive evidence. Even Andrews (X, 3-4), who is quoted by Guppy in support of his theory writes (X, 4, p. 536) of "an organic response to severer conditions of climate and to a greater poverty and porosity of soil."

Fountain's opinion is interesting as that of an amateur, who knew little of botany and less of the literature of epharmosis. He writes (16, p. 227) "In fact, the peccary, as all, or nearly all, other animals bears out my theory that species (that is variations from *original types*) are the outcome of locality, and not of 'natural' or any other kind of 'selection.'"

Conclusions.

The action of orthogenetic saltation is discussed by Davenport (IV, 25), whose chief point is that internal laws give a breaking up of the complex germ plasm. He gives the origin of radium as an analogy but does not develop the analogy in the detail which it deserves.

Considering the "evolution" of the Uranium-Actinium Series (Fig. 41),[1] it will be noticed that, whereas some of the elements (to be regarded as species) have a long life, others are very unstable and exist only for a short time. Orthogenesis finds its analogue in the straight series from Uranium I to Radium C (Fig. 41) and from Thorium to Thorium C (Fig. 42), each step in the series being dependent on the preceding steps. Divergence of types finds its analogue in the splitting of Radium C (Fig. 41) and of Thorium C (Fig. 42) to give two distinct series each. The irreversibility of evolution (cf. 41a) is the same as that of the disintegration series.

Both infinitesimal variation and mutation have analogues, the former in those cases where the imponderable particle is thrown off, giving a new form and the latter in those cases where a perceptible explosion takes place and the helium particle is thrown off. It will be noticed that it is always by *loss* of something that a "mutant" arises. It is perhaps stretching the analogy too far to extend it to cytology, the first case corresponding to the loss of one gene from a chromosome and the second to the observed loss

---

[1] I am indebted to Dr. J. F. Spencer for the details given in Figs. 41-42 The times given are half life-periods, or the time taken for 50% of any given quantity of an element to change into the next of the series. The numbers within the circles are the atomic weights. The β particle is imponderable and the α particle (helium) has an atomic weight of 4. The dotted lines indicate probable but unconfirmed lines of development.

of a complete chromosome from the nucleus (cp. Gates on *Oenothera* mut. *lata* and mut. *gigas*, 18), but the suggestion may be useful.

The rapidity with which some of the elements break up to form the next of the series is analogous to the unstable mutants which De Vries suggests may intervene between successive stable forms, and which are said to be specially noticeable when mass mutation takes place (3). The analogous changes in the plant might take place either during nuclear division or in successive generations; the former case might well lead to the very marked mutations which are supposed by Willis (IV, 93) to occur, since the different stages in the disintegration of the parent would not be identified with corresponding external stages.

Polyphyly of genera or even of species, which is becoming

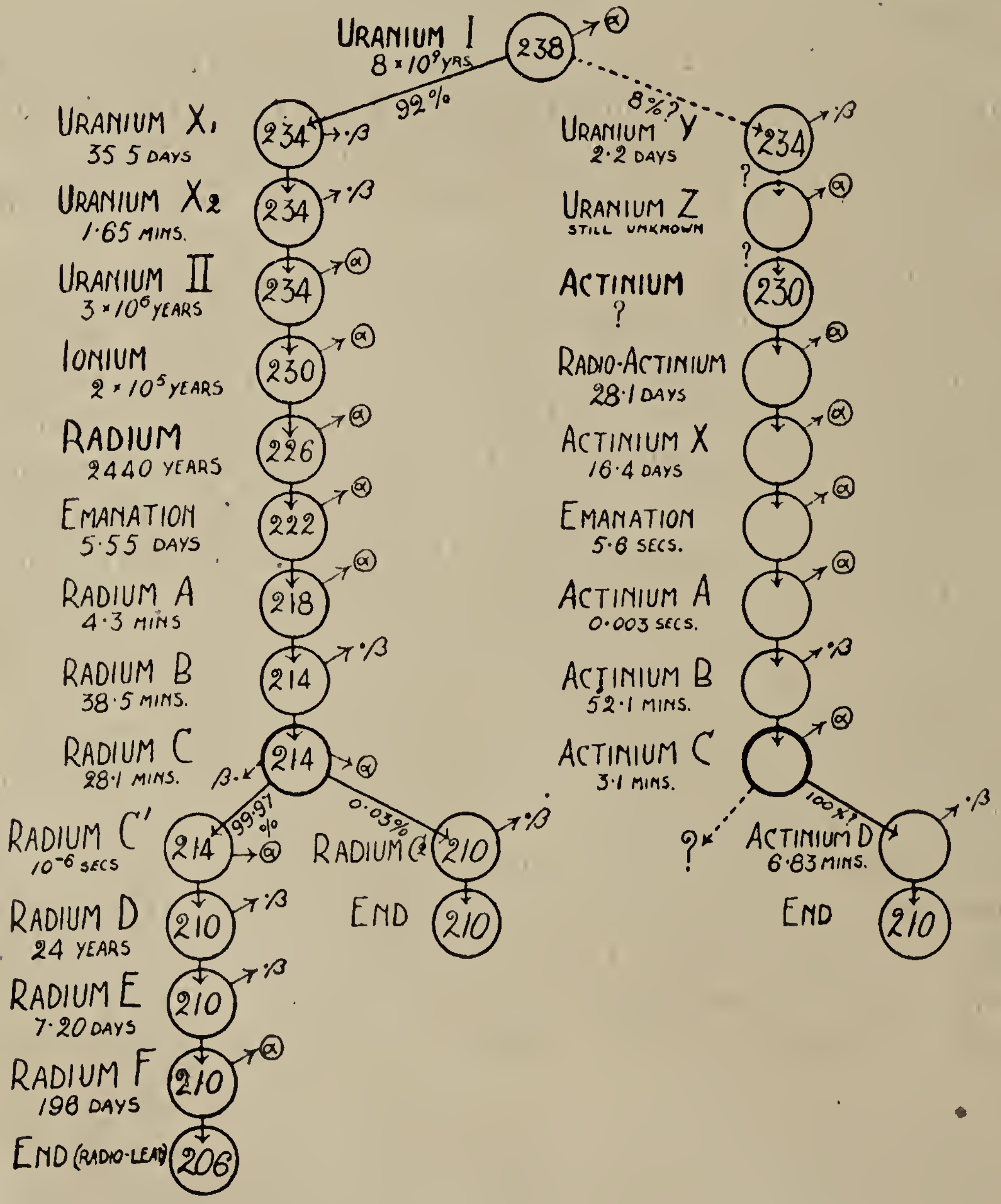


FIG. 41. Uranium-Actinium Disintegration Series.

generally recognised as not uncommon (cp. 10 and 40), and convergence, epharmonic or otherwise, which is also becoming recognised as an important point in evolution (cp. 10, 57 and X, 15 and X, 69, Vol. II, p. 115) have analogues here also. Convergence may be noted in Radium F and the end-products of the Radium C² and Actinium D lines, and also in the similarity of the end-products of all the disintegration series in both Figs. 41 and 42. Parallel evolution and polyphyly may be noted in the identity of the end-products of the last two lines in Fig. 41 and and of the Thorium C¹ and Thorium D lines (Fig. 42). Allotropic modifications, such as occur in sulphur, are unknown in the radio-active elements so that there is no analogy here for tetraploid mutations, although these find their analogue amongst the other elements.

The radio-active analogy holds good, therefore, for most of the details of orthogenetic saltation; it fails, however, to be complete for evolution because external circumstances have apparently no effect on the course of the disintegration and the form of the constituent members of the uranium and actinium series. This is more or less true for orthogenetic saltation alone but epharmosis finds no analogue in radioactivity. Such an analogue does, however, occur in crystallisation and other chemical phenomena which simulate the processes of life.

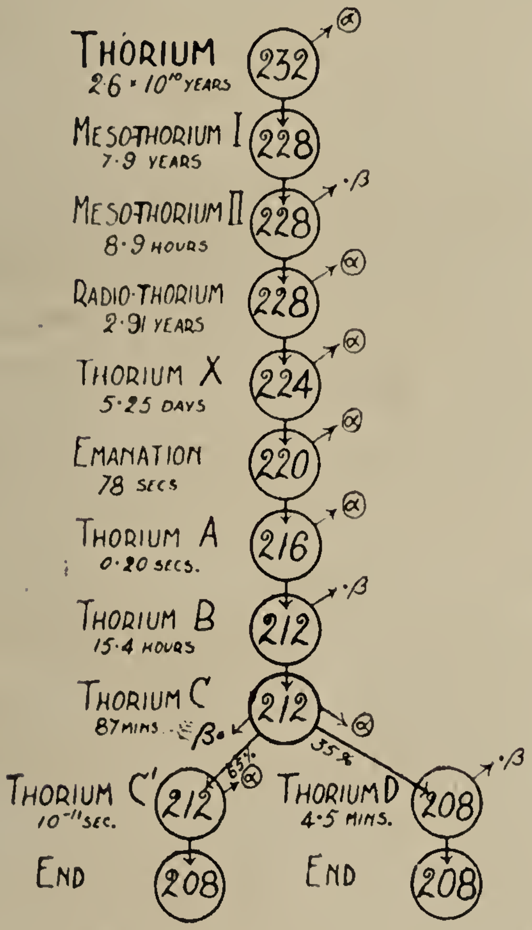


FIG. 42, Thorium Disintegration Series.

"The truth is that adaptation explains the sinuosities of the movement of evolution, but not its general directions, still less the movement itself." (Bergson, op. cit. , p. 107). Elsewhere this philosopher compares life and evolution to a river—"The movement of the stream is distinct from the river bed, although it must adopt its winding course," (op. cit., p. 284). Dendy (35) uses the analogy of a piece of music with its main theme and the variations but applies it in rather a different way. He agrees with Bergson, however, in regarding evolution as a dual process. That the analogy of a stream cannot be followed without reserve is clear from the passage quoted at the beginning of Section B and from another which emphasises the part played by contingency in in evolution; "Two things only are necessary: (1) a gradual accumulation of energy; (2) an elastic canalization of this energy in variable and indeterminable directions, at the end of which are free acts."

If we place a number of water-falls and anastomosing back-waters at intervals along the metaphorical stream, we get some approach to the "explosions" and "free acts". Bergson's view of evolution can then be translated into scientific phraseology thus —the smooth flowing stretches of the "stream" correspond to orthogenetic development; the water-falls, explosions or free acts are saltations which give rise to the branches or back-waters of the stream; the river bed with its sinuosities is the environment, which by epharmosis and elimination of the unfit keeps the stream within definite limits. In this way we get a synthetic, eclectic theory of evolution which includes all the diverse points of view and assigns to them their proper place in the complete scheme.

In evolution by *orthogenetic saltation*[1], with *epharmosis* and *elimination of the unfit* exercising a directing and delimiting function on the actual forms assumed by organised life[2], we have the best of Darwinism, neo-Lamarckism, neo-vitalism, Mendelism and the mutation theory.

Something of this kind, but without the precision rendered possible by recent work is foreshadowed by Bentham (cp. quotation,

---

[1] Orthogenetic saltation may decide the inner constitution of a species, but the expression of that constitution is modified by epharmosis. Probably the inner constitution, as well as its expression in the form and structure of the plant, is altered by the cumulative effect of continued epharmonic adaptation The saltation may be either Mendelian or De Vriesian or both, Mendelian segregation having most evidence to support it as an originating cause of a large number of *taxonomic* species or even genera (cp. Rendle, 35). Progressive mutations seem to be as rare as the proved origin of new genes, but their rarity in quite in accordance with their place in the general scheme of evolution, as will be readily evident to anyone who tries to solve the Biochronic Equation of any highly organised species (see IV, 88, p. 674). It is remarkable how few characters which are not epharmonic are present in such a species and absent in others of lower systematic position.

[2] It is certain at least that epharmosis and, to a lesser degree, natural selection, decide the habit and many of the details of the structure of a species, even if the genetic constitution remains the same throughout a series of variations, a supposition which is, to say the least, unsupported by the necessary detailed evidence,

Chap. X, A), and by De Candolle (LX, 11, p. 1119), where after discussing the origin of species from one individual or from many individuals he writes "J'insiste sur ces doubles explications."

C. THE LOBELIOIDEÆ.

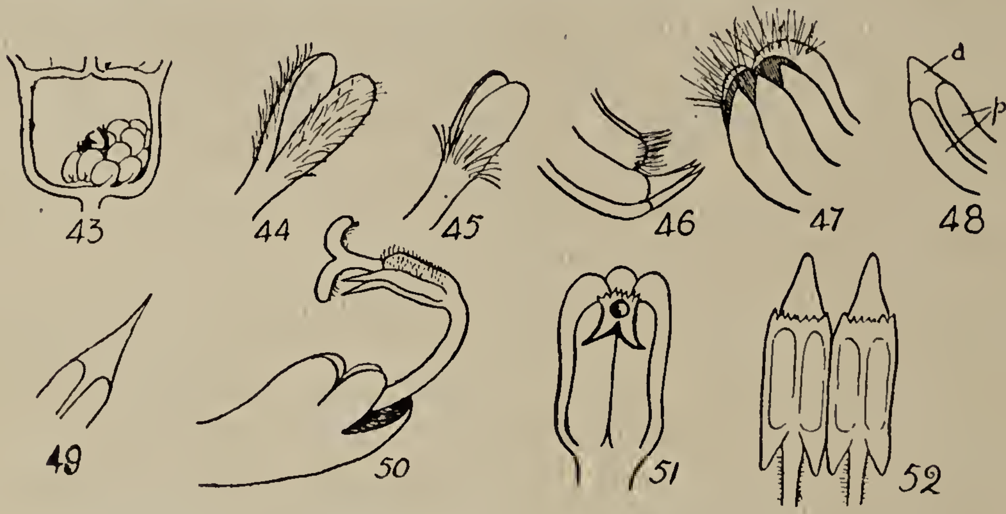
If the theory of evolution by orthogenetic saltation and epharmosis is sound, we should find the chief characters of the Compositæ foreshadowed in the ancestral group.

The general characteristics of the Lobelioideæ as given by Schönland (44) are the following:—Flowers usually distinctly zygomorphic, in a few cases unisexual; almost without exception pentamerous; calyx regular or bilabiate; corolla usually tubular, often slit down one side, rarely with the petals quite free; stamens usually more or less fused with each other and sometimes with the corolla also; anthers always syngenesious, usually with hairs or bristles at the apex; three anthers usually larger than the other two; style with a ring of hairs; ovary usually bilocular; fruit a berry or capsule, usually loculicidal at the apex, more seldom dehiscing laterally; herbs, shrubs or trees.

Gynœcium—To begin with the gynœcium, the ovary is inferior or semi-inferior and bi-carpellary and the ovules are anatropous, all as in the Compositæ except the occasional semi-inferior ovary. Although the ovary is usually bilocular with axile placentation, the partition is incomplete in *Rhizocephalum* and absent altogether in *Apetahia* which has numerous ovules on parietal placentæ. A further stage is reached in *Lysipomia* where one loculus aborts and the ovules are few, grouped together on a more or less basal placenta (Fig. 43). If this is compared with the occasional occurrence of more than one ovule in the Compositæ (cp. Don, Chap. II, A, and 182), especially with the case of a bilocular, biovulate ovary in *Senecio vulgaris* (1,82), it will be clear that in this character there is a tendency in the Lobelioideæ towards the condition in the Compositæ.

The style in the Lobelioideæ has sweeping-hairs on the outside; these may be in a ring, as in *Siphocampylus asper* (Fig. 45) or scattered as in *Lysipomia muscoides* (Fig. 44). This should be compared with the types in the Compositæ (Chap. II, Fig. 5). The two style branches are usually shorter than in the Compositæ, but they act as pollen-presenters in exactly the same way, even to the coiling back on themselves to give self-pollination.

Andrœcium—The syngenesy of the anthers is a well-known feature of the Lobelioideæ but the appendages are of scarcely less importance in view of the great significance of these structures in the Compositæ. Apical appendages are present in most genera. In *Siphocampylus* some of the anthers have rigid, horny or membranous elongations of the connective, and the others have a tuft of hairs at the apex. There may be three teeth as in *S psilophyllus*, *S. asper* (Fig. 46) and *S. lantanifolius* (Figs. 47-48), or only two as in *S. aggregatns* (Fig. 50). The lateral anthers in *S. lantanifolius* have the appendages very slightly developed but it is quite clear in the median anther (Fig. 48). The appendages may be obtuse or acute (cp. Figs. 48, 49 and 52). There are two teeth in *Lobelia corymbosa* (Fig. 51), *Pratia macrodon* (Fig. 52) and *Rhizocephalum*, and three in *Laurentia repens*.



FIGS. 43-52. Floral details of the Lobelioideæ.

FIG. 43. *Lysipomia muscoides*, ovary; 44, ditto, style; 45, *Siphocampylus asper*, style; 46, ditto, apical part of anther tube; 47, *S, lantanifolius*, apical part of anther tube; 48, ditto, median anther to show (a) appendage, and (p) pollen sacs; 49, *Laurentia repens*, apical appendage of anther, 50, *Siphocampylus aggregatus*, style and stamens to show apical appendages , 51, *Lobelia corymbosa*, anther tube to show apical appendages ; 52, *Pratia macrodon*, two of the five appendaged stamens.

All five anthers may have hairy appendages and be more or less equal, as in *Monopsis* and *Brighamia*; or the two smaller anthers only may be hairy, as in *Clermontia*, *Delissea*, *Sclerotheca* and *Hovellia*; or the condition may vary in the genus; all or only the two smaller anthers have hairy appendages in *Cyanea* and *Lysipomia*, or the appendages of these two anthers may be teeth or hairs, the other three being naked as in *Pratia* and *Isotoma*; while in *Centropogon* one section has the two smaller anthers with teeth, another has them with hairs and the third has all five anthers with no appendages at all. *Lobelia* shows a variation similar to that in *Centropogon*. In *Hypsela* there may be one tooth or a few bristles at the apex of the two smaller anthers.

Another point to be noticed is the incipient basal appendages in *Pratia macrodon* (Fig. 52), which are specially interesting as they occur where the filaments are free, a rather unusual condition in the Lobelioideæ, where the filaments are usually fused to form a tube.

The frequent occurrence of apical appendages and the rare occurrence of basal appendages to the anthers in the Lobelioideæ compare well with the prevalence in the Compositæ of the former and the gradual development of the latter from a type in which they are absent. That the biological significance of the apical appendages is the same as in the Compositæ is obvious when the more or less horizontal position of the anther tube is noted together with the position of the appendages (cp. Figs. 46, 47, 50 and 51). In the cases such as *Lysipomia muscoides*, where all the anthers are equally appendaged, the anther tube is usually, if not always, erect.

Irritability of the style or stamens has not yet been observed with certainty (cp. III, 49, p. 267), but in *Lobelia thapsoides* and *L. cardinalis* a very slight touch on the filaments or anther tube, is sufficient to produce the presentation of a small quantity of pollen. It has not yet been ascertained whether this is due to a contraction of the filaments, which are united into a tube, or to the delicate adjustment of the style with its sweeping hairs inside the anther tube. Observations on this point in the natural habitats of the species would be of interest (cp. *Torenia*, Chap. III, B).

Corolla. Although typically bilabiate or irregular, the corolla is not infrequently almost or quite radially symmetric, as in some species of *Centropogon*, *Siphocampylus* (Figs 53-55), *Dialypetalum*, *Laurentia*, *Hypsela*, *Lysipomia*, *Rhizocephalum*, *Isotoma*, *Brighamia*, and *Downingia*. Indeed, there is a general tendency for the corolla to become more or less radially symmetric whenever the flowers become crowded or reduced in size (cp. Fig. 54 and *Dialypetalum*).

The colours of the corolla are usually of the higher types, blue red or purple, but orange and yellow occur in some species of *Siphocampylus*, *Centropogon*, *Heterotoma* and *Downingia*.

Calyx. The progressive reduction of the free lobes of the calyx from more or less foliose structures to mere undulations at the top of the receptacle is illustrated in the genus *Siphocampylus* (Figs. 53-55). The other genera show even more foliaceous sepals as a rule, but reduction is comparatively common ; the extreme condition, as in Fig. 55, is reached in several genera.

Inflorescence. Solitary axillary flowers occur in a number of genera; simple and corymbose racemes are common. The tendency of the corymb to form a racemose umbel develops in various species of *Siphocampylus*, including *lantanifolius* (Fig. 53), *microstoma*, *corymbiferus*, *gracilis*, *aggregatus*, and *reticulatus*, and also in *Jasione* and *Phyteuma* of the Campanuloideæ (cp. also *Campanula glomerata*). A dense, short corymb which is a close approach to a capitulum occurs in *Lobelia corymbosa*. The inflorescence of *Centropogon densiflorus* varies from a short raceme almost to a racemose umbel, and the more umbellate it is the more flowers are ebracteolate. This occurs in a number of other species of the genus.

FIGS. 53-55. Inflorescence etc. of *Siphocampylus*.
FIG. 53, *S. lantanifolius*, complete inflorescence; 54, *S. asper*, portion of raceme; 55, *S. eximus*, portion of raceme (after Planchon).

Bracts. The general tendency throughout the tribe is the same as in *Centropogon*: the closer the inflorescence approaches an umbel the fewer and more reduced are the inner bracts. This reduction of the bracts in *Siphocampylus* is more or less correlated with the reduction of the calyx (cp. Figs. 53-55). Even in the simple racemes there is a tendency for the upper bracts to disappear, as in *S. angustifolius* and *S. flagelliformis*.

Involucre. In the cases where the inner or upper bracts are reduced or even completely absent, the outer or lower bracts usually remain more or less foliaceous (cp. Fig. 53), although they may be reduced to a certain extent. *Siphocampylus reticulatus*, for instance, shows in some specimens an inflorescence which might almost be described as an involucrate umbel. *S. corymbiferus* also shows a very close approach to a capitulum, but the inner bracts and the calyx are only moderately reduced (see also *Lysipomia acaulis*, X, 72, p. 198). In the Campanuloideæ the involucre is diffuse in *Phyteuma*, uniseriate in *P. comosum*, biseriate in *Hedraeanthus tenuifolius* and multiseriate in *Jasione*.

Habit. A very good account of this subject is given by Bentham (6). The more widespread types are herbaceous, perennials or annuals, as in the Compositæ, and, as in that family and many others, the insular species are more or less woody. As in the Compositæ also, the scrambling climbers are most abundant in open scrub and around the edges of the tropical forests, especially in South America. Erect woody forms occur at high altitudes, especially in the Andes, where the ericoid, abietoid and lycopodioid forms are very interesting. Similar forms occur in the Compositæ, (see Chap. X and Weberbauer, X, 72, Fig. 26, C and F, Goebel, X, 32, Pl., VIII, Figs. 2a-2b and Schimper, IX, 32, Fig. 409). The perennial herbs develop large, coarse plants with a racemose inflorescence in some regions and the erect Lobeliæ of Africa may be compared with the Ligulariæ of Asia. It remains to note that the leaves are usually alternate.

Latex. The occurrence of laticiferous vessels in the Lobelioideæ is also of interest. Our knowledge of these structures in the Lobelioideæ is by no means complete, and the absence of latex in the species of *Rhizocephalum* and a few other genera which have been examined is significant. Latex is present in some species of *Siphocampylus*, *Centropogon* and many other genera; *Lysipomia* does not seem to have been examined (see Chap. XII, C).

Summarising the points in which the Lobelioideæ show characters and tendencies, or lines of orthogenesis, leading towards the Compositæ we have—

1. Inferior or semi-inferior ovary with anatropous ovules.
2. Reduction of the quinquelocular ovary of the lower Campanuloideæ to a bilocular ovary and finally to a few ovules on more or less basal placenta.
3. Bifid style with collecting hairs; scattered or in a ring, and recurving of style branches to give ultimately self-pollination.
4. Pollen-presentation mechanism, protandrous and the same in principle, with the nectary at the base of the style and a suggestion of irritability of the stamens.

5. Syngenesious anthers, stamens sometimes epipetalous.

6. Prevalence and varying development of apical appendages to anthers.

7. Slight development of basal appendages to the anthers.

8. Actinomorphy of corolla in lower Campanulaceæ, zygomorphy with a return to actinomorphy, especially under conditions of reduced food supply (cp. Causal Morphology, Chap. IV,C) in the Lobelioideæ.

9. Variation in colour of corolla from yellowish-green to yellow, white, orange, purple, etc.

10. Reduction of calyx limb under crowded conditions of the flowers, progressing to complete absent of free lobes.

11. Progressive aggregation of the flowers with consequent reduction in corolla and calyx, together with the progressive disappearance of the inner or upper bracts of the racemose umbel.

12. Development of an involucre, diffuse in the Lobelioideæ but completely organised in certain special Campanuloideæ.

13. Alternate arrangement of leaves.

14. Laticiferous vessels present or not (see Chap. XII, C).

15. General habit and range of variation in habit.

16. Haustorial antipodal cells and prominent integumentary epithelium of embyro sac (see Chap. XII, B).

D. THE ORIGIN OF *Senecio.*

The above summary of the lines of orthogenesis in the Lobelioideae is in complete accord with the basal position of *Senecio.* The floral characters would apply to the whole family more or less, but the complete disappearance of the free calyx limb affords additional evidence in support of the secondary nature of the pappus (cp. Chap. V and Chap. XII, D). The occurrence of the racemose umbel as a form of condensed inflorescence is in accordance with the view expressed on the origin of the capitulum (Chap. VI, B.) The complete disappearance of the inner bracts is in accordance with the primitively naked condition of the receptacle and the atavistic nature of the receptacular paleæ (Chap. VII). The diffuse, slightly developed condition of the involucre in the umbellate Lobelioideae is in accordance with the view expressed on the primitively uniseriate pericline with a slightly developed calyculus (Chap. VI). The alternate phyllotaxis of the leaves is in accordance with the view expressed on the primitive phyllotaxis in the Compositæ (Chap. VIII).

The range of habit is the same as in the Compositæ as a whole but *Siphocampylus* shows a number of herbs with the common *Senecio* habit, while a number of the arborescent species of that genus are very similar in general appearance to some arborescent species of *Senecio*. We may also mention *Isotoma senecioides* (see 44, p. 66) with the habit of a weedy *Senecio*.

The final test, that of geographical distribution, may now be applied. In the Lobelioideæ there are six genera endemic in the Sandwich Islands, one in the Company Islands, and one in Madagascar. Of the other local genera one is Mexican, one extends from Abyssinia to South Africa, another from South Africa to Australia and three, *Lysipomia*, *Hypsela* and *Rhizocephalum*, are Andine. *Isotoma* has six species in Australia and one each in the West Indies and the Company Islands; *Laurentia* extends from North America to the Mediterranean and South Africa, and *Lobelia* is widespread, occurring in the Old World and in South America.

The genera which show the best development of anther appendages, aggregation of the flowers, etc. are the three Andine genera and the remaining widespread genera. These are *Pratia*, which extends from South America to Australia and tropical Asia, *Downingia*, which extends from Oregon and California to Chili. *Centropogon* and *Siphocampylus*, both of which extend from tropical South America to Central America and the West Indies. These last two genera have about 100 species each and show many of the above-mentioned tendencies. It should now be clear why the north of South America was taken in Chap. X as the centre of origin for *Senecio*,

I will now try to help the student to visualise the origin of the first *Senecio* as a living, moving process—in fact attempt the kind of presentation which has already been advocated in this journal. This attempt being necessarily descriptive cannot be other than cinematographical, but with a little mental effort and a little study of Bergson (7, pp. 314—330) the student may be able to perceive the "becoming" from *Siphocampylus* to *Senecio*. It will be sufficient to say that the following is an attempt to present the origin of one definite kind of living organism from another definite kind of living organism as a normal, natural result of the actual *living* of the parent organism in a particular region.

Let us suppose a certain species of *Siphocampylus* grows as an arborescent scrambler on the edge of the forest about the sources of the Amazons. It has already developed a racemose umbel as an inflorescence, the outer bracts remain more or less foliaceous, while the inner bracts and the calyx limb are much reduced. The corolla is yellow in colour and zygomorphic. The stamens have the usual syngenesious anthers unequally appendaged. The ovary is bilocular with numerous ovules on axile placentæ.

As the years pass the species spreads (cp. Age and Area, Chap. X, A) until it reaches the zone, about 5000 ft. up on the slopes of the Andes, where the forest gives way to open scrub and grassland. Under the influence of the unfavourable conditions, (dryness, high winds, alternation of extreme temperatures,) the individual plants which become established in this region are stunted in growth and instead of scrambling over bushes become dwarf, trailing shrubs.

In this form the species extends to higher altitudes where true alpines grow among the dwarfed, shrubby forms of species which are characteristic of the lower zone (cp. X, 69, Vol. II, p. 264). Under the more arid conditions the individuals which become established there are still more dwarfed. Coincident with the dwarfing of the individual, the reduction of the food supply causes the flowers to be smaller, the pedicels to be shorter (cp. *Lysipomia acaulis*, X, 72, p. 198), and the inner bracts and free calyx segments to disappear completely. This reduction enables the pressure of orthogenesis (as represented possibly by the climatic conditions) to crowd the flowers still closer (cp. I, 81, p. 30 and Chap. IV, B) and the corolla as a consequence becomes actinomorphic. The stamens as a result of correlation cease to be unequally developed, the anther tube becomes erect, the tooth-like appendages become equally developed on all the anthers (cp. *Lysipomia muscoides*). As a result of the reduced food-supply only a few ovules are developed near the base of the ovary and the septum aborts (cp. *Rhizocephalum* and *Lysipomia*).

Continued existence under these unfavourable conditions of excessive insolation, alternating with intense cold and combined with growth on the arid, wind-swept mountain slopes, would produce crowding of all parts of the plant to give a rosette or ericoid form (cp. alpine *Senecio Jacobea*, Chap. X, A, also IX, 32, pp. 704—716 and X, 72, numerous figures). These epharmonic variations would include the complete disappearance of the pedicels, the formation of a properly protective, uniseriate pericline, an indefinite calyculus, and a head of small flowers (cp. the close aggregation of the capitula and formation of secondary involucres in alpine Composites), and also the development of only one ovule in each indehiscent ovary for the further protection of the seed. The development of the hairs on the fruit into the pappus mechanism may be a fortunate accident or an epharmonic variation; there is no clear evidence on this point at present. Thus we arrive at a plant with all the essential characters of a *Senecio.*

It must be noted that we started with a *Siphocampylus* with characters and tendencies which are known to be present in the genus, and we have appealed only to those orthogenetic lines or critical tendencies and to the direct influence of the external conditions to effect the change from a species of the Lobelioideæ to a species of the primitive genus of the Compositæ. The orthogenetic saltation in almost every detail involves the loss or suppression of a character and presumably of a factor, This is in accordance with Bateson's view of mutation (35). The progressive development of appendages to the stamens, may also be due to loss, if the view given in Chap. II of the origin of the appendages by the sterilisation of potentially sporogenous tissue is correct. The steps in the change from one genus to the other are natural and occur in related forms in the same region. Indeed, there is a distinct possibility that even at the present time a close examination of the variation of the species of the Lobelioideæ and *Senecio* in the critical region from the edge of the Matto Grosso to the *puna* of the Sierra would show the actual occurrence of forms such as have been suggested. These forms have already been observed in closely related genera in that particular region.

In any case, from the strictly scientific point of view a close affinity can be traced between the Lobelioideæ of the Andes and *Senecio.* So close is the affinity that we may be permitted to suggest a doubt as to the truth, in the case of the Compositæ, of the dictum of De Vries which is quoted by Horne (28) that "the great lines of evolution of whole families and even of genera...... obviously lie outside the limits of experimental observation."

The first three questions given in Section A of this chapter have been answered. The fourth—"at what geological time did the Compositæ arise?"—is considered in Section A of the following chapter.

BIBLIOGRAPHY XI.

1. Babcock, E. B. Walnut mutant investigations. Proc. national Acad. Sci., Vol. I, p. 535, 1915.
2. Bancroft, N. A Review of Literature concerning the Evolution of Monocotyledons. NEW PHYTOLOGIST, Vol, XIII, (Rep. No. 9), 1914.
3. Bartlett, H. H. Mass Mutation in *Oenothera praticola.* Bot. Gaz., Vol. LX, p. 425, 1915.
4. „ „ Mutation en masse. Amer. Nat., Vol. XXXIX, p. 129, 1915.

5. Benedict, R. C. The origin of new varieties of *Nephrolepis* by orthogenetic saltation. I. Progressive variations. Bull. Torr. Bot. Club, Vol. 43, p. 207, 1916.

6. Bentham, G. Notes on the Gamopetalous Orders belonging to the Campanulaceous and Oleaceous Groups. Jour. Linn. Soc., Vol. XV, p. 1, 1877.

7. Bergson, H. Creative Evolution. Eng. trans., London, 1914.

8. Bernard, N. L'Évolution des Plantes. Paris, 1916.

9. Blaringhem, L. and Viguier, P. Une nouvelle espéce de Bourse-à-Pasteur. *Capsella Viguieri* Blar. née par mutation. Comptes Rend., Vol. CL, p. 988, 1910.

10. Bower, F. O. Studies in the phylogeny of the Filicales, VI. Annals of Botany, Vol. XXXI, p. 1, 1917.

11. ,, ,, On the Natural Classification of Plants, as exemplified in, the Filicales. Jour. Linn. Soc., Bot., Vol. XLIV, p. 107, 1918.

12. Castle, W. E. Piebald rats and multiple factors. Amer. Nat., Vol. LI, p. 102, 1917 (and other papers, see bibliography by Stout and Boas, 50).

13. Coulter, J. M. A suggested explanation of "orthogenesis" in plants. Science, N. S. Vol. XLII. p. 859, 1915.

14. Davenport, C. B. Principal Advances of the Year. Department of Experimental Evolution. Carneg. Inst. of Washington, Year Book No. 16, p. 111, 1917.

15. Eames, A. J. On the Origin of the Herbaceous Type in the Angiosperms. Annals of Botany, Vol. XXV, p. 215, 1911.

16. Fountain, P. The River Amazon. London, 1914.

17. Frost, A. B. Mutation in *Matthiola annua*, a "Mendelizing" species. Amer. Jour. Bot., Vol, III, p. 377, 1916.

18. Gates, R. R. The Mutation Factor in Evolution. London, 1915.

19. Goebel, K. Einleitung in die experimentelle Morphologie der Pflanzen. Leipzig, 1908.

20. Grove, W. B. Note on *Pleodorina illinoiensis*. NEW PHYTOLOGIST, Vol. XVI, p. 180, 1917.

21. Hallier, H. Provisional Scheme for the Natural (Phylogenetic) System of Flowering Plants. NEW PHYTOLOGIST, Vol. IV, p. 151, 1905.

22. ,, ,, L'Origine et le Systéme Phylétique des Angiospermes. Archives néerlandaises. Ser. III, B. Tome I, 1912.

23. Harris, J. A. The biometric proof of the pure line theory. Amer. Nat., Vol. XLV, p. 346, 1911.

24. ,, ,, The distribution of Pure Line Means. Ibid, Vol. XLV, p. 686, 1911.

25. Hayek, A. von. Die Trichome einiger heimischer *Senecio*-Arten. Oesterr. bot. Zeitschr., Bd. LXV, p. 292, 1915.

26. Hayes, H. K. Tobacco Mutations. Journ. of Heredity. Vol. VI, p. 73 1915.

27. Henslow, G. The Origin of Plant Structures. London, 1895.

28. Horne, A. S. A contribution to the Study of the Evolution of the Flower. Trans. Linn. Soc., B. Ser. 2, Vol. VIII, p. 239, 1915.

29. Jeffrey, E. C. Hybridism and the rate of evolution in Angiosperms. Amer. Nat.. Vol. L, p. 129, 1916.

30. Jennings, H. S. Pure lines in the study of genetics in lower organisms. Amer. Nat., Vol. XLV, p. 79, 1911.

31. Johannsen, W. The genotype conception of heredity. Ibid., Vol. XLV, p. 129, 1911.

32. Kearney, T. H. Mutation in Egyptian Cotton. Jour. of Agric. Research, Vol. II, p. 287, 1914.

33. Kirchner, O. Die Blüteneinrichtungen der Campanulaceen. Jahreshefte des Vereins für vaterl. Naturkunde in Württ. 1897, p. 193.

34. Leavitt, G. G. The Geographic Distribution of closely related species Amer. Nat., Vol. XLI, p.207, 1907.

35. Lotsy, J. P. On the Origin of species (and discussion). Proc. Linn. Soc., 1914. p. 73.

36. ,, ,, Evolution by means of hybridisation. The Hague, 1916.

37. Nelson, A. and Macbride, J. F. Western Plant Studies. Bot. Gaz., Vol. LXII, p. 143, 1916.

38. Morgan, T. H. The Mechanism of Mendelian Heredity. London, 1915.

39. ,, ,, A Critique of the Theory of Evolution. London, 1916.

40. Oswald, F. The Sudden Origin of New Types. Science Progress, No. 19, p. 396, 1911.

41. Parish, S. B. Notes on some Southern California Plants. Bot. Gaz., Vol. LXV, p. 334, 1918.

41a. Petronievics, B. Sur la Loi de l'Evolution Irréversible. Science Progress, Vol. XIII, p. 406, 1919.

42. Poole, H. S. *Senecio Jacobæa* and *Callimorpha Jacobæa.* Proc. Nova Scotia Instit. Sci., Vol. XIII, p. 279, 1915.

43. Raunkiaer, C. Om Livsformen hos *Tussilago Farfara.* Bot. Tidsk. Copenhagen, Bd. 28, p. 203, 1908.

44. Schönland, S. Campanulaceæ in Engler and Prantl's *Pflanzenfamilien.* Teil IV, Abt. 5, p. 63.

45. Seward, A. C. Darwin and Modern Science. Cambridge, 1909.

46. Sinnott, E. W. and Bailey, I. W. Investig. on the Phylogeny of the Angiosp. 4. The Origin and Dispersal of Herbaceous Angiosperms. Annals of Botany, Vol. XXVIII, p. 547, 1914.

47. Small, J. Modern Theories of Evolution. Pharm. Journ., Vol. XCVII, p. 612, 1916, and Vol. XCVIII, p. 3, 1917.

48. Solms-Laubach, H. Cruciferien-studien. I, *Capsella Hoeggeri.* Bot. Zeit. Bd. LVIII, p. 167, 1909.

49. Stout, A. B. and Boas, H. M. Statistical studies of flower number per head in *Cichorium Intybus.* Mem. Torr. Bot. Club, Vol. XVII, p. 334, 1918.

50. Stout, A. B. The establishment of varieties in *Coleus* by the selection of somatic variations. Publ. Carneg. Inst. Washington, 1915, p. 1.

51. Vesque, J. L'espéce végétale considérée au point de vue de l'anatomie comparée. Ann. des Sci. Nat., Bot., ser. 6, tome XIII, p. 5, 1882.

52. Wall, A. On the Distribution of *Senecio saxifragoides*, Hook. f., and its Relation to *Senecio lagopus*, Raoul. Trans. N. Z. Instit., Vol. L, p. 198, 1917.

53. Walton, L. B. The Axial Rotation of Aquatic Micro-organisms and its Significance. The Ohio Journal of Science, Vol. XVIII, No. 1, 1917.

54. Weismann, A. Essays upon Heredity and Kindred Biological Problems. Eng. trans. 1st edit., p. 279, Oxford, 1889.

55. White, C. A. The Saltatory Origin of Species. Bull. Torr. Bot. Club, Vol. XXIX, p. 511, 1902.

56. Willey, A. Convergence in Evolution. London, 1911.

57. Willis, J. C. Some Evidence against the Theory of the Origin of Species by Natural Selection. Ann. R.B.G., Peradeniya. Vol. IV, p. 1, 1907.

58. ,, ,, Further Evidence against the Origin of Species by Infinitesimal Variations. Ibid., Vol. IV, p. 17, 1907.

59. ,, ,, On the Lack of Adaptation in the Tristichaceæ and Podostemaceæ. Proc. Roy. Soc. Vol. LXXXVII, B p. 532, 1914.

A CONTRIBUTION TO THE LIFE-HISTORY AND CYTOLOGY OF *SYNCHYTRIUM ENDOBIOTICUM* (SCHILB.) PERCIVAL, THE CAUSE OF POTATO WART DISEASE.

By K. M. Curtis, M.A., M.Sc.

Preliminary Notice.

AN investigation of the life-history and cytology of *Synchytrium endobioticum*, the cause of Wart Disease in potato, has been carried on by the writer for several years. As it may be some time before the full results of the research can be published it seemed advisable to make a statement of the main results attained, which accordingly are embodied in the outline of the life-history given below.

The stage of the organism which is most commonly observed is that of the resting sporangia, one of which, in cases of heavy infection, may occupy each cell of the three or four outermost layers of tissue of the tumour. The sporangia continue their development after the decay of the host plant and eventually give rise to numerous uniciliate zoospores. After a period of motility the zoospore enters an epidermal cell of any actively dividing region of eye, stem or leaf, passes to the lower end of the cell, and there rapidly enlarges. As the result of infection a two-fold effect is produced on the neighbouring cells. The ring of epidermal cells actually in contact with the infected cell grows out to form a rosette-like structure consisting of elongated, curved cells which arch over the parasitised cell at their base. The other cells in the neighbourhood divide repeatedly and a somewhat cup-shaped tumour is produced, at the bottom of which lies the infected cell with its rosette. Fresh infection frequently takes place at this stage, and the tumour eventually becomes a more or less spherical mass of tissue with the surface thrown into innumerable ridges. Passage of the organism from one host cell to another was never observed.

By the time the parasite has grown to a size sufficient to fill the lower half of the cell it has developed a firm envelope. The uninucleate contents, surrounded by a thin membrane, now push up through a small area of the free surface of the envelope and pass into the upper half of the host cell. The nucleus divides repeatedly and the extruded mass segments into five to seven portions; each segment is the initial of a zoosporangium and the whole is a young sorus. Nuclear divisions continue and finally the so-called zoospores are formed; when these are nearly mature the sporangia absorb water and swell, the soral envelope and host cell walls are ruptured, and the sporangia are set free on the irregular surface of the tumour.

The motile cells, hitherto described as zoospores, are now liberated. They are smaller than the zoospores of the resting sporangium but similar in shape. These motile cells are facultative gametes for when the contents of different sporangia are discharg-together, which frequently occurs, fusion takes place and a zygote is formed. The gametes however may infect the host without fusion. The result of infection by the zygote, which becomes uninucleate before entry, is a resting sporangium ; the result of infection when fusion is omitted is a sorus.

A tumour may bear several series of sori before the production of resting sporangia becomes general. As, however, the development of the sorus may be completed and its gametes liberated in less than three weeks while the growth of the resting sporangium extends over months, and, as in addition, the tumours when bearing only sori are small and liable to be overlooked, it is not surprising that the occurrence of sori as a regular stage in the cycle of development of the fungus has not hitherto been recognised.

IMPERIAL COLLEGE OF SCIENCE AND TECHNOLOGY,
SOUTH KENSINGTON, LONDON.

ON THE RETENTION OF VITALITY BY ALGÆ FROM OLD STORED SOILS.

By B. Muriel Bristol, M. Sc.

[With Two Figures in the Text].

I. Method of Culture and General Observations.

DURING the course of a series of experiments on Soil-Algæ which have been under investigation for the last three years, a number of cultures were made, in October 1915, of some old stored soils from the Rothamsted Experimental Station, Harpenden, and as a result of these cultures some very interesting facts have been observed in regard to the length of time during which algæ are able to retain their vitality under adverse conditions.

The samples of soil used were collected from the various experimental plots at Rothamsted, and after being partially air dried were passed through a sieve having ¼-inch meshes. They were then placed in large bottles and sealed with leaden capsules, so that neither foreign infection from outside nor evaporation of the contained water could take place. The first soils examined had been taken from Broadbalk in 1893, 1881, 1869, 1868, 1865, 1856 and 1846 respectively, from Agdell in 1867, from Barnfield in 1870, from Hoosfield in 1868 and from Geescroft in 1865. They remained in the original bottles until 1912 when representative samples were taken by Dr. T. Goodey, to whom I am greatly indebted for the material, and placed in small sterilised bottles closed with a plug of cotton-wool. The water-content of the soils at this time varied rather considerably, some containing only about 3-5%, while others contained as much as 10% of water; but in no case was there sufficient water present for active vegetative growth to have been taking place. From 1912 onwards a gradual desiccation of the soils took place through the cotton-wool stoppers until, in October 1915, they contained only about 3% of water. The samples from Broadbalk 1865 and 1856 and from Geescroft 1865 differed from the others in that they had been moistened in November 1913 to bring the water-content up to 18%; they had then undergone gradual desiccation as the others had done.

In April, 1916, cultures were made of additional samples of the Barnfield 1870 soil obtained from the original bottles at Rothamsted which had remained sealed since 1912; and I take this opportunity of thanking Dr. E. J. Russell for so kindly providing me with this valuable material.

The cultures were set up in small glass boxes or in small conical flasks closed with a plug of cotton-wool, great care being taken to ensure that perfectly sterile conditious were obtained. The sterile culture solution was introduced into the vessel to a depth of about half an inch, and 3 or 4 grams of the soil were then added by means of a sterilised spathula, 3 cultures of each soil being made.

The closed vessels were placed under glass bell-jars in a north window and allowed to remain untouched until signs of growth appeared in the cultures.

The culture-medium used was an aqueous mineral-salt solution having the following composition :—

Potassium dihydrogen phosphate (KH_2PO_4)	1·0 gm.
Sodium nitrate ($NaNO_3$)	1·0 gm.
Magnesium sulphate ($MgSO_4$)	·3 gm.
Calcium chloride ($CaCl_2$)	·1 gm.
Sodium chloride ($NaCl$)	·1 gm.
Ferric chloride ($FeCl_3$)	·01 gm.
Distilled water.	1000 cc.

Very slow evaporation took place from the surface of the liquid, and this was remedied by very occasional watering with sterilised culture solution of about a quarter to one-half of the original strength.

The first growth observed in the cultures was the appearance of a white scum over the surface of the liquid; this was found to consist of bacteria. Later, the scum began to assume a green tinge of colour and was found to contain numbers of small unicellular green algæ.

The growth of moss protonema from some of these soils has already been recorded[1] but at the time of writing the algæ had not developed sufficiently for their identity to be determined; the first trace of moss protonema was observed in the Barnfield soil on Dec. 30th, 1915, whereas algæ were not detected in the cultures until about four months later. Green algæ grew first and were found in all of the cultures early in May, 1916; they produced chiefly a green stratum on the surface of the liquid and on the sides of the vessel, but the whole liquid assumed a light green colour owing to the

---

[1] Bristol, B. M. "On the Remarkable Retention of Vitality of Moss Protonema." New Phytologist, Vol. XV, No.7, July 1916.

presence of free-floating unicells. In December, 1916, blue-green algæ appeared from the Broadbalk and Hoosfield soils, forming strata below the surface of the liquid, usually attached to the soil, but later extending up the glass sides of the vessel. The colours of these strata varied very much not only with the species but also with their state of development; young strata were usually a light blue-green, but at later stages they became olive-green or even brownish-black. When once they had begun to develop, the blue-green algæ grew much more rapidly than the green algæ until eventually they very strongly predominated in the cultures.

A considerable time elapsed before the identity of the various forms could be established, since it was necessary in most cases to follow the complete life-history of the alga before it was possible to arrive at a definite conclusion; little or no imformation could be obtained from the developmental stages which at first predominated. In the final identification of the species considerable difficulty has been experienced, in that many of the forms found in the cultures do not agree exactly with any of the species previously described, though bearing a very strong resemblance to one particular type. In these cases it has been necessary to take into consideration not only the somewhat abnormal conditions under which the algæ have been growing in the cultures, but also the extended period of drought which they had experienced before being introduced with the soil into the culture. Where the differences might be ascribed to one of these two causes, the form under consideration has been referred to the particular species which it most nearly resembles, a special note being made of the distinctions between the two forms.

II. RESULTS OF CULTURAL EXPERIMENTS.

Name of Plot.	*Date of Collection.*	*Algæ Found.*
Broadbalk	1893	*Chlorococcum humicola* (Næg.) Rabenh. *Nostoc muscorum* Kütz. *Anabæna oscillarioides* Bory var. *terrestris* (n. var.) forma *major.* *Plectonema Battersii* Gomont. *Hapalosiphon flexuosus* Borzi forma (?)
Broadbalk	1881	*Chlorococcum humicola* (Næg.) Rabenh. *Nostoc muscorum* Kütz.

Name of Plot.	*Date of Collection.*	*Algæ Found.*
Broadbalk	1881	*Nostoc* Sp.? Juvenile form.
		Anabæna laxa (Rabh.) A. Br. (?)
		Plectonema Battersii Gomont.
		Hapalosiphon flexuosus Borzi forma. (?)
Broadbalk	1869	*Chlorococcum humicola* (Næg) Rabenh.
		Nostoc muscorum Kütz.
		Anabæna laxa (Rabh.) A. Br. (?)
		A. oscillarioides Bory var. *terrestris* f. *major*
		Plectonema Battersii Gomont.
		Hapalosiphon flexuosus Borzi forma. (?)
Broadbalk	1868	*Chlorococcum humicola* (Næg.) Rabenh.
		Stichococcus bacillaris Næg.
		Nostoc muscorum Kütz.
		Anabæna oscillarioides Bory forma.
		Cylindrospermum licheniforme (Bory) Kütz.
		Plectonema Battersii Gomont.
		Hapalosiphon flexuosus Borzi forma. (?)
		Phormidium tenue (Menegh) Gomont.
Broadbalk	1865	*Chlorococcum humicola* (Næg.) Rabenh.
		Nostoc Sp ? juvenile form.
		Anabæna oscillarioides Bory var *terrestris* forma *minor.*
Broadbalk	1856	*Chlorococcum humicola* (Næg.) Rabenh.
		Nostoc muscorum Kütz.
		Nostoc Passerinianum Bornet et Thuret.
		Nostoc Sp? juvenile form.
		Anabæna oscillarioides Bory var. *terrestris.* forma *major.* n. var.
		Cylindrospermum licheniforme (Bory) Kütz.
Broadbalk	1846	*Nostoc muscorum* Kütz.
		Nodularia Harveyana (Thwaites) Thuret.
Agdell*	1867	*Trochiscia aspera* (Reinsch) Hansg.
		Chlorococcum humicola (Næg.) Rabenh.
		Stichococcus bacillaris Næg.
		Nitzschia Palea (Kütz.) W. Sm.
Barnfield*	1870	*Trochiscia aspera* (Reinsch) Hansg.
(3·3% water-content)		*Chlorococcum humicola* (Næg.) Rabenh.
Barnfield*	1870	*Trochiscia aspera* (Reinsch) Hansg.
(10% water-content)		

* These soils also contained moss protonema.

Name of Plot.	*Date of Collection.*	*Algæ Found.*
Barnfield* (10% water-content)	1870	*Chlorococcum humicola* (Næg.) Rabenh. *Stichococcus bacillaris* Næg.
Barnfield* Plot 1a.	1870	As from last sample above.
Hoosfield*	1868	*Trochiscia aspera* (Reinsch) Hansg. *Chlorococcum humicola* (Næg.) Rabenh. *Nostoc muscorum* Kütz.
Geescroft	1865	*Chlorococcum humicola* (Næg.) Rabenh.

It was hoped that a comparison of the algæ found in the various Broadbalk soils would indicate in what order the different species were eliminated by successively increased periods of drought. The results, however, are not sufficiently regular to admit of this to any great extent, though in a few cases some deductions may be made; for this purpose the following comparative table (p. 97) is useful.

It is very conspicuous that the Broadbalk 1865 sample contains far fewer species than the sample collected from the same field nine years earlier; this difference cannot be due to the relative periods of drought, hence some other factor or factors must have been at work in eliminating certain of the species, since it is scarcely likely, in view of the much more uniform results obtained from the other samples, that the discrepancy has arisen from the absence of the algæ from the soil at the time of its collection. It is possible that such a factor is the degree of dryness of the soil during the period of storage. Unfortunately no exact information on this subject is available, but the theory is supported by the fact that the sample containing the greatest amount of water in 1912 was that collected in 1868, and this sample is the one from which the largest number of species have been obtained. The sample collected in 1846 differs from the others in that in about 1880 the bottle was opened and the soil spread out in a warm room to finish drying, so that when it was bottled again it contained only 3% of water. The presence of only two species of algæ in this soil may therefore be due not only to the great age of the soil but also to the extremely low water-content of the soil.

In the case of *Chlorococcum humicola*, the presence of this alga in all the cultures except those of the 1846 Broadbalk sample seems to indicate that its power of retaining its vitality in these old soils is more or less independent of their water-content, hence it is

---

* These soils also contained moss protonema.

probable that the chief factor causing its elimination from the 1846 sample is the great length of the period of desiccation, and that between sixty and seventy years is about the limit of its endurance.

No. of Culture.	2	3	4	7	5	6	8	9	10	59	60	11	12
Name of Field.	Broadbalk	Broadbalk	Broadbalk	Broadbalk	Broadbalk	Broadbalk	Broadbalk	Agdell	Barnfield	Barnfield	Barnfield, plot 1a	Hoosfield	Geescroft
Water-Content.				12% (?)			3%		10 p.c. in 1912 3·3 p.c., 1915	10%	10%		
Date of Collection.	1893	1881	1869	1868	1865	1856	1846	1867	1870	1870	1870	1868	1865
Date of Removal from Original Bottle.	1912	1912	1912	1912	1912	1912	1912	1912	1912	1915	1915	1912	1912
Date of Moistening of Soil.					5.xi.13	,,							
Date of Inoculation of Culture.	9.x.15	,,	,,	13.x.15	11.x.15	,,	13.x.15	,,	,,	15.iv.16	,,	13.x.15	,,
Nostoc muscorum Kütz.	1	1	1	1		1	1					1	
Nostoc Passerinianum Bornet et Thuret.				1				1		1	1		
Nostoc sp ? Juvenile form.	1	1	1	1	1	1		1	1	1	1	1	1
Anabæna laxa (Rabh.) A Br. ?								1	1	1	1	1	
Anabæna oscillarioides Bory forma.								1					
A. oscillarioides Bory var. *terrestris* forma *minor.*				1									
A. oscillarioides Bory var. *terrestris* forma *major.*	1	1	1	1									
Nodularia Harveyana (Thwaites) Thuret.	1	1	1	1									
Cylindrospermum licheniforme (Bory) Kütz.				1		1							
Plectonema Battersii Gomont.							1						
Hapalosiphon flexuosus Borzi forma (?)	1		1			1							
Phormidium tenue (Menegh.) Gomont.					1								
Nitzschia Palæ (Kütz.) W. Sm.				1									
Trochiscia aspera (Reinsch) Hansg.		1	1										
Chlorococcum humicola (Næg.) Rabenh.		1			1	1							
Stichococcus bacillaris Næg.						1							

The two algæ with the greatest power of resistance are *Nostoc muscorum* and *Nodularia Harveyana* whose spores germinated after a period of desiccation extending over seventy years, during the last half of which the soil contained only 3% of water.

That the degree of dryness of the soil during the period of desiccation affects *Stichococcus bacillaris* is clear from a comparison of the Barnfield samples. The alga was present in the cultures of all the samples obtained from the original bottles in 1916, the water-content of these being about 10%, but it was absent from the cultures of the samples which had been taken in 1912 and which in 1915 contained only 3·3% of water. The fact of its occurrence in only one of the Broadbalk samples, that containing the greatest percentage of water, may perhaps be explained in the same way.

The absence of *Plectonema Battersii* and of *Hapalosiphon flexuosus* forma (?) from all the earlier Broadbalk soils, irrespective of their water-content, probably indicates that 48 years is very near the limit of the period during which they are able to retain their vitality.

III. DESCRIPTIVE NOTES ON THE SPECIES FOUND.

A. BACILLARIEÆ.

Nitzschia Palea (Ktz.) W. Sm.

This is the only diatom found in the cultures of these old stored soils, and was obtained from the Agdell sample; it had thus retained its vitality for a period of nearly fifty years. The specimens examined agree in all particulars with the description given by Van Heurck,[1] except in habitat which is said to be aquatic Petersen,[2] however, has also found it growing on the surface of the ground in Denmark, so that the species is evidently not entirely aquatic in habit, as has generally been thought.

B. CHLOROPHYCEÆ.

Trochiscia aspera (Reinsch) Hansg.

The alga described under this name is not exactly typical in character but can probably be regarded only as a cultural form of the species. Though the alga agrees in essential points of structure and life-history with the typical form, the cell-wall exhibits considerable variation in its markings. Some individuals

---

[1] Van Heurck, H. Traité des Diatomées, p. 401, Anvers, 1899.

Petersen, J. B. Studier over Danske Aërofile Alger, p. 295, D. Kgl. Danske Vidensk. Selsk. Skrifter, 7 Række, Nat. og Mathematisk Afd. XII, 7. 1915.

bear on their surface the denticulations that are characteristic of the species, but in the majority these are suppressed to a greater or less degree, and every gradation can be observed between the typical form and a form with almost smooth walls. Many of the cells enter into a palmella state; a number of the cells also tend to assume a much larger size than is typical, but these differences are probably due only to the conditions under which the alga is growing, and there is no reason for considering that it is a different species.

The alga has been obtained from the following soils: Agdell 1867, Barnfield 1870, Hoosfield 1868; its resting-cells have thus germinated after nearly fifty years.

Chlorococcum humicola (Næg.) Rabenh.

This alga, as observed in soil-cultures, exhibits a far more complicated life-history than has previously been thought to be the case; it forms the subject of a separate paper that is in course of publication by the Linnean Society, and further details are therefore unnecessary here. It has been obtained from all of the plots examined, and is able to retain its vitality for at least sixty years.

Stichococcus bacillaris Næg.

The form of this alga obtained from the cultures differs in no way from the typical form. It was observed in the Barnfield, Agdell and Broadbalk soils, hence the maximum time after which it has developed is forty-eight years.

C. MYXOPHYCEÆ.

Nostoc muscorum Kütz.

Forms of this alga have appeared from all the Broadbalk samples, with the exception of that collected in 1865, and also from the Hoosfield sample. It has retained its vitality for nearly seventy years even under conditions of extreme drought. The forms obtained from the different samples, though agreeing in mode of growth and in general characters show considerable variation in details. In certain of the cultures, notably in those of the 1893, 1881, and 1868 Broadbalk samples, the form observed agrees almost entirely with the description and dimensions given by Lemmermann, the chief difference being that the spores are on the whole rather smaller, rarely exceeding 7–8μ in length. Lemmermann[1] describes the cells as shortly barrel-shaped or cylindrical, and in many filaments of the cultures this is the case; there can be observed, however, a tendency of the cells of other filaments to become rounded off from one another and to assume a somewhat more spherical form. It is likely that small differences such as these are the result of the treatment to which the algæ have been subjected, and are not to be regarded as of specific importance.

A different form of *N. muscorum* was found in the 1881, 1869, 1856 and 1846 Broadbalk samples and in the Hoosfield sample, and this differs much more considerably from the typical form. The vegetative cells are usually almost spherical, 3–3·5μ in diameter, though in some filaments the typical barrel-shaped cells can be observed, and in this case are 3–4μ in length. The heterocysts are infrequent, and are generally very much smaller than in the typical form, rarely exceeding 4–5μ in diameter, though occasional hetercysts have been found measuring 5·5–6μ in diameter. The spores are oval, 4–5μ broad, by 7–8·5μ long, and grow in long irregular chains of a very characteristic form, as is shown in Text-Fig. 1. The walls of the spores are smooth and shiny, and become at first yellowish and later a darker brownish colour.

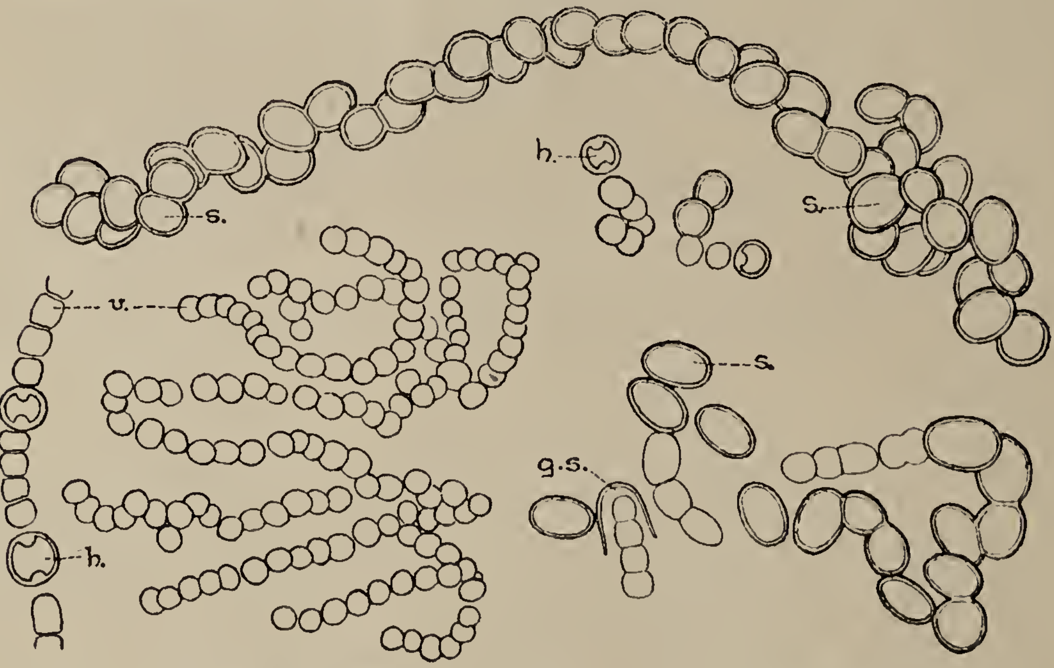


FIG. I. *Nostoc muscorum* Kütz. forma. *v.* vegetative cells, *h*, heterocysts, *s.* spores, *g.s.* germinating spore.

In those cultures in which both of these forms of *N. muscorum* occur, viz., in those of the 1881 Broadbalk soil, other forms

---

[1] Lemmermann, E. Kryptogamenflora der Mark Brandenburg III, Algen I, p. 168, Leipzig, 1910.

intermediate between the two can be observed, showing beyond any possibility of doubt that the two are only forms of the same species, and not even different varieties.

Nostoc Passerinianum Bornet et Thuret.

The *Nostoc* that has been been identified as this species appeared only in the 1856 Broadbalk sample, so that it had germinated after a period of about sixty years. Unfortunately, probably owing to cultural conditions, no heterocysts were produced so that full particulars could not be obtained. The size of the vegetative-cells and of the spores agrees very well with Lemmermann's description, while the almost parallel arrangement of the filaments makes it very probable that this identification is the correct one. It is very conspicuous that the long parallel strands of filaments often undergo a slight spiral twist, and the long rows of spores with their yellowish-brown walls often assume the appearance of the strands of a rope that has been frayed out in places.

Nostoc Sp.? Juvenile form.

In the cultures of the three Broadbalk samples, 1881, 1865 and 1856, a blue-green alga has been observed that is certainly a *Nostoc*, but the characters have never become sufficiently distinct for any identification of the species to be made. The cells constitute filaments that are twisted together in close irregular spirals to form irregularly lobed or cylindrical colonies invested with a close gelatinous covering which gradually assumes a yellowish colour. As the colonies become larger the spiral arrangement of the filaments becomes less distinct until finally the colony appears to consist of an irregular mass of closely packed cells. In the young colonies the cells are usually barrel-shaped, being 4–6μ in diameter and rather shorter than broad, but in the older colonies they become more globose and are sometimes even angular by compression. Heterocysts are exceedingly rare in these colonies, but when found they are spherical and about 5μ in diameter. Very occasionally the cells become converted into spores with yellowish-brown shiny walls; they are only slightly bigger than the vegetative cells.

It is probable that these colonies are only juvenile forms of some well-known species, which owing to cultural conditions have retained their juvenile characters for a considerably longer period than would be the case under quite normal conditions; and the production of spores directly from the juvenile cells is possibly the outcome of the same conditions.

Anabæna laxa (Rabenh.) A. Br. (?)

In the cultures of the two Broadbalk samples collected in 1881 and 1869 an alga appeared which agrees in its characters much more nearly with *A. laxa* than with any other described form. The filaments are straight or slightly curved, usually single, and invested with a colourless sheath that is most distinct in the region of the spores. The vegetative cells are barrel-shaped, mostly 4–5μ broad, and about the same length or a little longer. Heterocysts have not been found, but as no mention of them is made either by Lemmermann[1] or by Tilden[2] this appears to be a very general character of the species. The spores are cylindrical or somewhat oval in shape and vary in length from 14–20μ; they differ, however, from those previously described in being mostly from 7–9μ broad instead of only 6μ. They are produced either singly or in series, as many as six being frequently seen in a series.

Anabæna oscillarioides Bory forma.

In all of the Broadbalk soils, with the exception of the 1881 sample, forms of this species have been found, but their deviation from the original description is so marked and so constant that it has been decided to include all of the forms except that from the 1868 sample in a new variety of the species. The form from the 1868 sample resembles the typical form in all respects except the size of the heterocysts which are only 4·5–5μ in diameter, but a diminution in the size and frequency of the heterocysts appears to be a character common to many soil forms grown in cultures, and is therefore not to be regarded as of specific importance. The vegetative cells are barrel-shaped, 4·5–5μ broad and about the same length; the spores are cylindrical 8–9μ broad and 17–21μ long. When ripe they have a smooth yellowish-brown wall.

Var. *terrestris* nov. var.

In mode of growth and general characters this variety agrees with var. *tenuis* Lemm. rather than with the typical form. It possesses, however, distinctive characters which are constant not only in the cultures of these old soils but also of a number of recent soils that have been dried and set up in cultures within six weeks of the date of collection. The filaments grow singly, or a

---

[1] *Loc. cit.*, p. 181.

[2] Tilden, J. Minnesota Algæ I, p. 192, 1910.

variable number may lie more or less parallel within a structureless gelatinous sheath which later becomes diffluent and very difficult to see. Probably owing to unequal growth, the parallel strands of

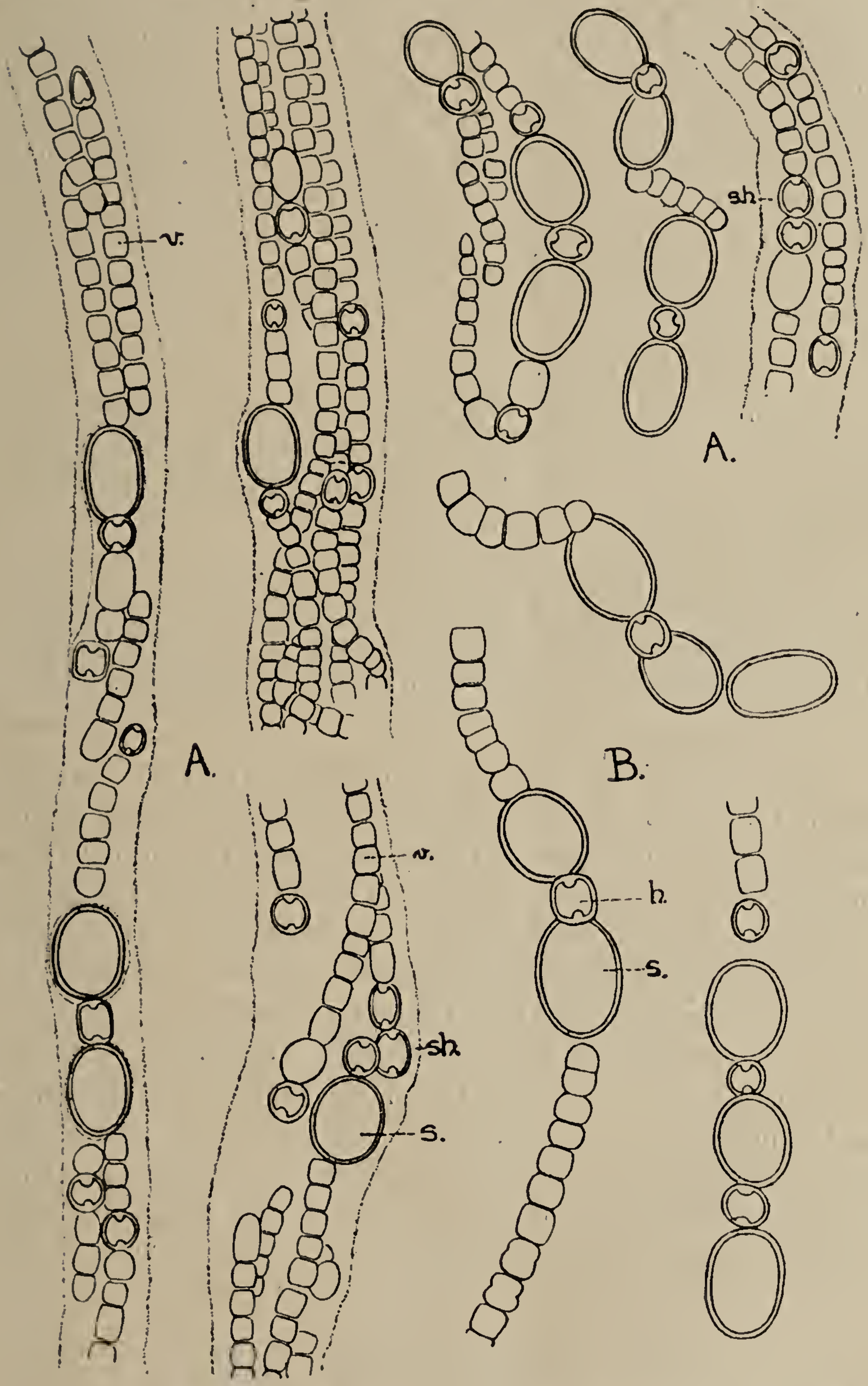


FIG. 2. – *Anabæna oscillarioides* Bory var. *terrestris* nov. var. *A* forma *minor*, *B* forma *major*. *h*. heterocyst, *s.h*. seriate heterocysts, *s*. spore, *v*. vegetative cell.

filaments often assume a strong spiral twist within the mucous sheath, points of reversal of the spiral being very conspicuous.

The vegetative cells are barrel-shaped, about as long as they are broad, and the end cells are conical. The heterocysts are spherical or occasionally oval and of a yellowish colour; they may form short series of two or three together. The spores lie either singly or in pairs, generally on both sides of the heterocysts, but they differ from the typical form in being almost invariably oval and very much broader in proportion to their length. When ripe the walls of the spores become yellowish-brown in colour.

Two forms of this variety have been observed, differing from one another only in size:

(a) forma *minor*.

From the old stored soils this form has been observed in the cultures of only one sample, Broadbalk 1865, but it has also been obtained from five recently dried soils, and is therefore probably to be regarded as the more usual form.

The vegetative cells are generally 2·5–3·5μ broad though they may occasionally be as much as 4μ; the heterocysts are about 4–5μ in diameter and the spores are 9–10μ broad by 13–17μ long. In this old soil it has retained its vitality for fifty years.

(b) forma *major*.

This occurred in the cultures of the 1893, 1869 and 1856 samples of the Broadbalk soil, but has not been observed in any of the recently dried soils. The vegetative-cells are usually 4–5μ in diameter, occasionally a little less; the heterocysts are 5–7μ in diameter, and the spores 11–12·5μ broad by 15–19μ long.

It germinated after a resting-period of fifty-nine years.

Nodularia Harveyana (Thwaites) Thuret.
[=*Nodularia turicensis* (Cramer) Hansg.]

This species was obtained from the 1846 Broadbalk sample and is interesting for two reasons. In the first place it shows, more than any other alga except *Nostoc muscorum*, an extraordinary power of retaining its vitality, having germinated after nearly seventy years extreme drought.[1] The absence of this species from the later Broadbalk soils must therefore probably

---

[1] The first record of longevity in algæ was made in connection with this species; and it was this observation which led Professor G. S. West to suggest the present investigation.—*Vide* West, Algæ, *Cambridge Botanical Handbooks*, Vol. I, p. 28, 1916.

be due to the absence of the alga from the original soil-samples rather than to the influence of drought on the spores themselves. Secondly, the alga as observed in these cultures shows a suppression of one of the most characteristic features of the genus, viz., the regular and frequent occurrence of the heterocysts. In young filaments only are heterocysts to be found, and in these cases they agree in shape and size with the typical form. The vegetative cells are 3·5–5μ broad and little more than half as long the spores are sub-spherical, about 7μ in diameter.

Cylindrospermum licheniforme (Bory) Kütz.

This species occurred in the 1868 and 1856 samples of the Broadbalk soil, and the spores have consequently retained their vitality for a period of nearly sixty years. The spores are oval with flattened ends, and the walls assume a deep red-brown colour when ripe; they are 13–15μ broad and 21–29μ long. The heterocysts are oval or sub-spherical, 6–7·5μ broad by 8–9μ long.

Plectonema Battersii Gomont.

Up to the present time this species has been described only from sea-water, hence its appearance in the cultures of the 1868, 1869, 1881 and 1893 samples of the Broadbalk soil is extremely surprising. The form that appeared in the cultures agrees in every particular, except that of habitat, with that of Tilden's description of the species, and it is quite distinct from any other, hence it is probable that this species has a far wider distribution than has hitherto been believed. The cells of the filaments are usually about 3μ broad and 2μ long, with a firm thin colourless sheath.

In view of its previously described aquatic habit, the power that this terrestrial form has exhibited of retaining its vitality in a dry condition for nearly fifty years is very remarkable.

Hapalosiphon flexuosus Borzi forma. (?)

In the cultures of the 1868, 1869, 1881 and 1893 samples of Broadbalk soil a species of *Hapalosiphon* appeared which seems to stand nearest to *H. flexuosus* Borzi, though it does not exactly agree with it. The difference of habitat is very marked, though this is not unique since an even greater difference was observed in the species *Plectonema Battersii* Gomont; and it its ability to withstand dessiccation for forty-eight years is therefore extremely interesting.

The alga is richly branched, and the branches may be either single or more rarely in pairs on any side of the filament, though they are much more frequent on one side than on the other. The sheath is very definite and, though colourless at first, gradually assumes a deep reddish-brown colour; the breadth of the main filaments varies from 11–13μ and that of the branches from 7–13μ Towards the ends of the branches the sheaths are seen to be constricted at more or less regular intervals, and exhibit also a few indistinct longitudinal striations; they are much thicker than those of the main filaments and rather less definite in outline. The trichomes do not always completely fill the cavity of the sheath, especially in some of the older filaments; the cells are usually elliptical-depressed in the main filaments, and are 9-11μ broad by 3·5–6μ long. The cells of the branches are usually somewhat less depressed, and may occasionally become much distended and bead-like, or more rarely very narrow and elongated; they are usually 5-6·5μ broad and 3-7μ long. Heterocysts have not been found; but in certain of the filaments the cells were seen to have become somewhat enlarged and to have acquired thick cell-walls in addition to the sheath, and it is probable that this represents some stage in the formation of spores.

In Borzi's species the filaments are 6-8μ broad, and no mention is made of the colour of the sheaths, while the species has been described up to the present only from standing or from running water. The alga found in the cultures thus differs in three quite noticeable particulars from Borzi's species, but with the information obtainable it is not possible to do more than suggest that it may be a terrestrial form of the same species.

Phormidium tenue (Menegh.) Gomont.

This species has been found only in the 1868 sample of the Broadbalk soil, though it frequently occurs in cultures of recently dried soils. It is probable therefore, since the 1868 sample possessed the highest water-content of all the stored samples, that this species is more affected by the degree of dryness of the soil than are the other species. The form found in the cultures exactly resembles the typical form.

SUMMARY.

From cultural experiments with old stored soils it is found that certain algæ belonging to the groups *Myxophyceæ*, *Bacillarieæ* and *Chlorophyceæ* possess extraordinary powers of retaining their vitality

during very long periods of rest, and that the length of time after which they can resume growth appears to be affected, in some cases at least, by the degree of dryness of the soil during the resting period.

The greatest power of resistance against desiccation was shown by the two algæ *Nostoc muscorum* Kütz. and *Nodularia Harveyana* (Thwaites) Thuret, which resumed growth after extreme desiccation for seventy years: *Nostoc Passerinianum* Bornet et Thuret, *Anabæna oscillarioides* Bory var. *terrestris* n. var., *Cylindrospermum licheniforme* (Bory) Kütz. and *Chlorococcum humicola* (Næg.) Rabenh. resumed growth after fifty-nine years' rest; *Trochiscia aspera* (Reinsch) Hansg. *Stichococcus bacillaris* Næg. and *Nitzschia Palea* (Kütz.) W. Sm. after forty-eight years' rest; *Plectonema Battersii* Gomont, *Hapalosiphon flexuosus* Borzi forma (?) and *Phormidium tenue* (Menegh.) Gomont after forty-seven years' rest and *Anabæna laxa* A. Br. (?) after forty-six years' rest.

The algæ described from these cultures differ in some respects from typical forms, but are probably only cultural forms of the given species.

In conclusion I desire to express my thanks to Professor G. S. West, not only for suggesting that I should undertake this work, but also for his valuable help and advice throughout the course of the investigation.

Botanical Laboratory,
University of Birmingham.

THE RECONSTRUCTION OF ELEMENTARY BOTANICAL TEACHING.

POSTSCRIPT.

By the Editor.

THE discussion which is now brought to a close has well served its purpose of thoroughly ventilating the questions raised in this journal in December, 1917; and it is superfluous, as it would be wearisome, to add any further arguments to those which have already been employed. There are however two points which seem to call for remark, both concerned with misunderstandings of the original memorandum.

The first has formed the foundation of more than one criticism, and though these criticisms have already been countered, it is desirable that no trace of misunderstanding should be left in the minds of readers. The words " morphology " and " morphological " were used, not with reference to the study of external and internal structure as such, but as indicating the study of these with a view to elucidating phylogeny, whether of organs or of organisms. This is so clearly apparent in the original memorandum as to make it a little curious that anyone should have been misled. The close study of structure is an essential element in the work of the student of biology and affords an unsurpassed training in accuracy of observation. That is common ground, and it is doubtful if any teacher of biology would wish materially to lessen the amount of time devoted to the study of structure. What was urged is a change in the *main centre of interest* of elementary teaching—a change from interest in lines of descent to interest in the plant in all its manifold aspects as a living organism. As Professor V. H. Blackman aptly expresses the idea: " The main problem to be presented to the student seems to them [the signatories of the original memorandum] to be that of living, not that of origin." The study of structure is most certainly essential: the question is the point of view from which it should be undertaken, and, as a corollary, which structures should have most attention paid to them.

Secondly it has come to the editor's knowledge that a certain remark in the memorandum: " Side by side with this [the teaching of facts of structure and their interpretation from the phylogenetic standpoint] there generally goes a discussion of function which is often limited by a crude Darwinian teleology," has aroused some resentment; though this has not found overt expression in any contribution to the discussion. It is certainly strange that such a remark should be thought to imply any slight upon Darwin's work. It is clearly the misuse of the theory of natural selection by teachers which is aimed at. And that misuse, unhappily still prevalent, is not a new discovery on the part of the signatories of the memorandum, but has long been evident to all who are interested in the current teaching of biology. The criticism was put tersely and vigorously by Professor Farmer, for instance, in his Presidential Address to Section K of the British Association at Leicester in 1907. "Many people still find consolation and satisfaction in an anthropomorphic and somewhat slipshod application of a kind of doctrine of free-will to matters that really call for rigorous examination into the causes which, under given conditions must inevitably and of necessity bring about their definite result." "It is *not* enough to explain the appearance of a structure on the ground of its utility; properly speaking, such attempts, so far from providing any explanation, actually tend to bar the way of inquiry just where scientific investigation ought to commence."

It is obvious that this barrier to enquiry is falsely justified in the minds of those who erect it by the doctrine of natural selection, which professes to give a causal explanation of the origin of useful structures and reactions on the ground of their usefulness. In very many cases no attempt is made to analyse for students the absolutely fundamental matter of the relation of the doctrine of natural selection to physico-chemical causation of structure and process, with the result that too many students are allowed to slip into the habit of looking at living things in the anthropomorphic and slipshod way of which Professor Farmer complained. Of the widespread prevalence of this vicious habit of mind answers to examination questions give abundant evidence. That is what was meant by "a crude Darwinian teleology," and it is certainly not Darwin's fault that his teaching has been so much abused. It seems hardly necessary to say that one of the objects of all teachers of biology should be to free their students' minds from the anthropomorphic bias which is present in every untutored human mind; but unhappily the evidence is conclusive that this is not successfully done. It is indeed an irony that Darwin, who freed the world from the narrow teleology of the doctrine of the special creation of useful structures for useful ends, should be used as cover for a new teleology almost as narrow, and much less logical. It is true that the best and most vigorous-minded students avoid or emancipate themselves from this slipshod habit, but in dealing with general questions, such as the method and content of elementary teaching, it is the mass of students that has to be considered.

Similarly in regard to the general nature of the elementary courses that are at present given. Some of these are no doubt framed on thoroughly enlightened lines, and there has certainly been a development in the direction of paying more attention to the more vital and fundamental parts of the subject. No one has contended that the subject is dead or even moribund, and development of the kind must take place in any living department of knowledge. What prompted the original memorandum was the conviction that elementary teaching in general requires to be brought more consciously and rapidly into accord with the newer developments, if serious dangers are to be avoided and the subject is to discharge its duty to the community.

The suggestion that the syllabus of an elementary course, on the lines indicated in the memorandum, should be drawn up and published has been made from several quarters. In accordance with this suggestion a meeting of botanists known to be in sympathy with the ideas of the memorandum was held in London in January, and a small committee was appointed to compile such a syllabus. The demand that concrete form should be given to the ideas expressed could not be refused, but the task of the committee is not easy if the right combination of definiteness and elasticity is to be attained and the impression that the authors desire to dictate to their fellow botanists to be avoided. Already deprecation of a "cast-iron" or "stereotyped" course has been expressed. Is it necessary to say that nothing of the kind is intended or desired? But an effort will be made to give detailed form and structure to the ideas expressed, and thus to help towards the realisation of the widespread desire for elementary courses which shall more nearly meet the needs of the present time than those framed on the older models. Substantial help in the way of results of experience with elementary classes has already been obtained, and further co-operation from all who are willing to give the benefit of their knowledge and experience is invited.

PAPAVER RHÆAS, P. DUBIUM AND THE HYBRID BETWEEN THEM.

By C. E. Salmon, F.L.S.

[With Seven Figures in the Text]

During June, July and August, 1918, I had many exceptional opportunities for observing Poppies in some cornfields at Chilworth, Surrey, and happened to alight upon an example that seemed at first sight a variety of *P. dubium* (*Lamottei*) with spreading hairs upon the peduncles. Upon a more detailed examination of the plant, however, I was not satisfied with this conclusion and believing that I had a hybrid between *P. dubium* and *P. Rhæas* before me, it became necessary to note closely the finer differences between these two species and their relation to my particular plant.

Colour of Flower. Our handbooks scarcely lead one to expect such a striking difference in colour between the flowers of *Rhæas* and *dubium.*

Babington (*Man.* ed. 9, 18, 1904) says of the former, "deep scarlet, often nearly black at the base"; of *dubium*, "pale red." Hooker (*Stud. Fl.*, ed. 3, 17, 1884) mentions that *Rhæas* has scarlet flowers, but omits any note of colour under *dubium.* Syme (*Eng. Bot.* I, 89, 1863) notes, however, that in the flowers of *P. dubium* (*Lamottei*) "the scarlet colour . . . is much paler than that of *P. Rhæas.*" Bentham and Hooker (*Handb. Brit. Fl.*, ed. 6, 18, 1892) give no indication as to the distinctive colour of *dubium*, merely stating that *Rhæas* has flowers "of a rich scarlet, with a dark eye" —which, by the bye, is by no means always the case. Mr. Druce (*Fl. Berks*, 33, 1897) mentions that the petals of *dubium* in their unopened stage are very much paler in colour than those of *Rhæas* in a similar condition. Dr. F. N. Williams (*Prod. Fl. Brit.* II, 603, 1912) describes the petals of *Rhæas* as "cinnabarina" and those of *dubium* as "miniata"; Dr. B. D. Jackson (*Journ. Bot.*, 1899, 101) considers the former term to indicate a scarlet, "the fullest in hue," and the same authority (*Gloss. Bot. Terms*, 235, 1916) translates the latter as "the colour of red lead; more orange and duller than vermilion."

As far as my observations go, I should describe the flowers of *P. dubium* (*Lamottei*) as pale red with an orange flesh tint, the paler forms reminding one of the delicately tinted state of *P.*

alpinum grown in gardens. *P. Rhœas* is normally of a vivid scarlet, often with rich black spots or markings internally at the base of the petals, sometimes very pronounced, whilst plants may frequently be found bearing paler red flowers almost similar to those of *dubium*[1]; rarely, the petals are of a "crushed strawberry" tint or of a purplish hue, recalling *Rœmeria hybrida.* In short, the colour is distinctly variable.

On the other hand, the flowers of *P. dubium* seem to be much more constant in colour and I could not find blossoms either with black spots at the base or of the vivid scarlet of *Rhœas.*

To sum up, the general effect of a flower of typical *Rhœas* is a bright scarlet blossom with a dark centre, whilst that of *dubium* is a more pallid flower with a paler centre.

It may here be noted that all our "red" poppies are thus really distinct in tint, the flowers of *P. Argemone* being small, pale-red with a black base to the petals, whilst those of *P. hybridum* are distinctly purplish, as already noted by Mr. H. S. Thompson (*Journ. Bot.*, 1913, 172), who may, I think, rest assured that our British form does not differ in tint from the Continental plant.

Buds. In *P. Rhœas* these are coarsely and roughly tuberculately-hairy, irregular in shape, obvoid, blunt at the apex, broadest *above* the middle (rarely at the middle) (Fig. 3); in *dubium* the buds are less roughly-tubercular with whiter and more silky hairs, they are more symmetrical and graceful in shape, ovoid, tapering to a more acute apex and are broadest *below* the middle (Fig. 2).

Hairs on peduncles. These, in typical *Rhœas*, appear to be ± numerous, irregularly horizontally-patent and yellowish in colour (red in the form *Pryorii*); in *dubium* they are copious and appressed, more regular in character, white and more abundant than in *Rhœas.*

Summit of peduncles. The dilated summit, in *P. Rhœas*, is *broader* than the base of the capsule and its pronounced carpophore; in *dubium*, the enlarged summit is slightly *narrower* than the base of capsule, which has a shorter carpophore.

Anthers and Pollen. The anthers of *P. Rhœas* are distinctly dark, greenish-or-violet tinted, often nearly black; the pollen, greenish-yellow. In *dubium* the anthers are not so dark in tint, of a slaty-green colour and their pollen is a clear yellow.

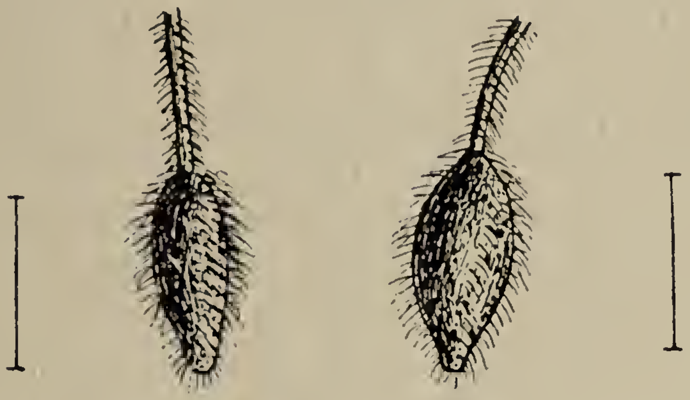
Stigma disc. Whilst the plant is in flower the rays of the disc in *P. Rhœas* are dark in colour, often purplish (rarely yellow), whilst those of *dubium* during a corresponding period are *invariably* yellow and I could not

---

[1] These *may* be of hybrid origin.

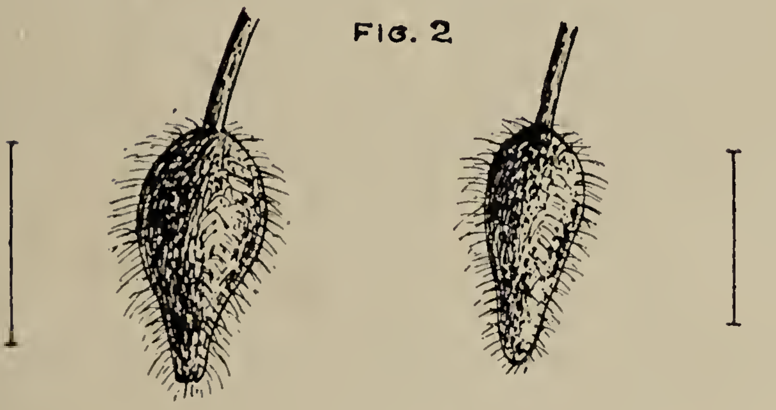
find a single example of dark tint. After the petals have fallen, however, the rays of the latter darken in colour and became almost similar in tint to those of *P. Rhœas.*

FIG. 1



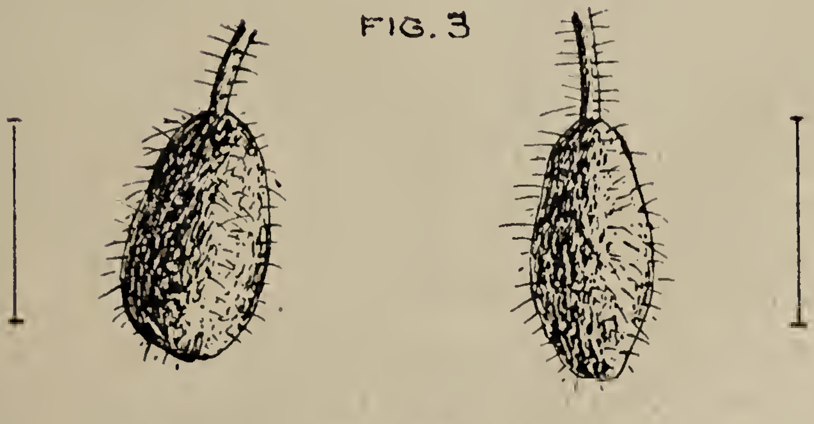
P. DUBIUM × RHÆAS

FIG. 2



P. DUBIUM

FIG. 3



P. RHÆAS

Figs. 1-3, Flower buds of *P. Rhœas*, *P. dubium* and hybrid.
(lines indicate natural size).

The number of the rays of the disc of *P. Rhœas* is more than in *dubium:* of 45 capsules from different plants of the former, seven had 9 rays, eight had 10, fifteen had 11, seven had 12, five had 13, two had 14, and one had 15. In *P. dubium*, similarly examined, one had 5, nine had 6, eleven had 7, twenty had 8 and four had 9.

Thus, as far as these observations go, one may summarize—*P. Rhœas*, rays of disc 9-13 (15), *dubium* (5) 6-8 (9).

Shape of ripe capsule. In *P. Rhœas* sub-rotund (Fig. 6) and all stages between that and the elongated obovoid form shown in Fig. 7. In *dubium*, clavate (Fig. 5), tapering from just below the summit.

Seeds. I am unable to find any appreciable difference between the ripe seeds of *P. Rhœas* and *dubium* as regards size, colour, or sculpture.

Upon examining closely, in the light of the above observations, specimens of the presumed hybrid (of which I found some half-dozen scattered examples) the following notes were made, and it will be seen that their characteristics belonged some to one parent, some to the other, whilst a few were perfectly intermediate in a most suggestive and instructive manner.

Colour of Flower. This was of the pale *dubium* character.

Buds. These seemed practically intermediate between *P. Rhœas* and *dubium* as regards shape and hairiness. They were broadest about the middle, slightly tapered to the apex and were rather smaller than those of *dubium*; the surface was not so coarsely tuberculately-hairy as in *Rhœas* and the hairs were whiter (see Fig. 1).

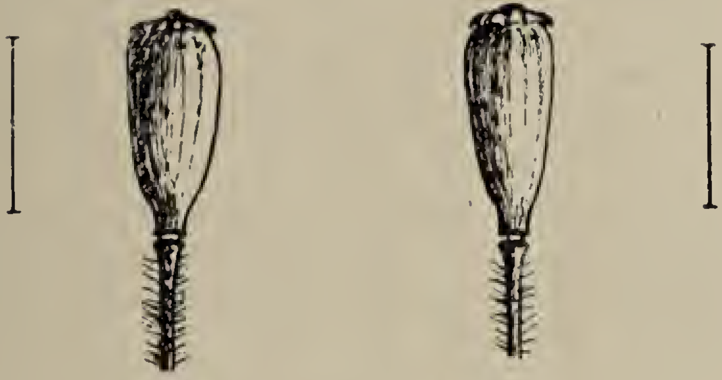
Hairs on peduncles. These again were of an intermediate type; whilst being abundant and white as in *dubium*, the *Rhœas* influence was evident in their not being closely appressed but standing away from the peduncles in an ascending-patent direction. This conspicuous feature enabled one to pick out the isolated examples of the hybrid along the cornfield margins at some distance, the light catching the abundant spreading white hairs in a remarkable way.

Summit of peduncles. Again intermediate, the dilated summit being more or less *equal* in width to the base of the capsule. The carpophore is of the shorter *dubium* type.

Anthers and pollen. Both showing the characters of *P. dubium.*

Stigma disc. This combined the distinctive features of both parents, the colouring of the rays being dark as in *P. Rhœas* but their number—(5) 6-8 (9)—being entirely *dubium* in character.

FIG. 4



P. DUBIUM X RHÆAS

FIG. 5

P. DUBIUM

FIG. 6

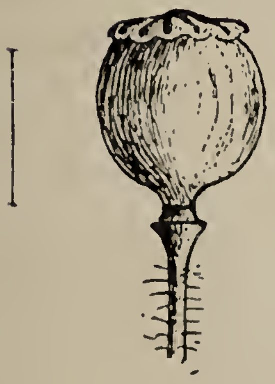
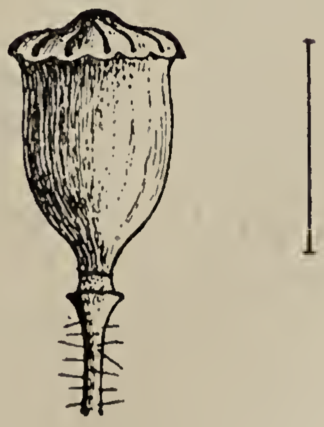


FIG. 7



P. RHÆAS

FIGS. 4-7, Capsules of *P. Rhæas*, *P. dubium* and hybrid.
(lines indicate natural size)

Shape of ripe capsule. Whilst these were decidedly of *dubium* shape they were always smaller, slightly more parallel sided and with a faint though distinct "neck" near the base (Fig. 4) recalling *Rhœas*.

Seeds. In all the plants discovered capsules were produced or in process of being formed but in all the mature ones examined, although there was plenty of seed of a dust-like character not a single fertile one was to be found.

It is perhaps normal in the genus *Papaver* for hybrids to prove usually sterile and this may account for the comparative rarity of the one now described considering the overlapping areas and often extreme abundance of both parents.

In *Gard. Chron.*, Aug. 17, 1918, p. 67, it is stated in a note by Mr. S. Arnott that a hybrid between *Papaver orientale* and *P. rupifragum* has not been observed to produce any perfect seeds although it forms seed capsules.

In Hooker's *Student's Flora* (ed. 3, 17, 1884) we find "A form entirely intermediate between *P. dubium* and *P. Rhœas* has been found in Surrey by Mr. G. Nicholson." By the kindness of Professor Trail of Aberdeen University where Nicholson's Herbarium is preserved, I have been able to examine a series of the "intermediates" to which Hooker refers.

The examples are all from "Cornfield, Ham, Surrey" and were collected in July, 1881. There are undoubted specimens of typical *P. dubium* and *P. Rhœas* and a number of sheets of the latter possessing capsules rather more elongated than usual, very like my f. 7; I do not think these are of hybrid origin. *One* sheet, however, contained a specimen that I should consider *Rhœas* × *dubium*, although the material is not so complete as one would wish.

The Rev. E. F. Linton (*Journ. Bot.*, 1907, 270) has referred to Mr. Nicholson's plant and mentioned that he saw *P. Rhœas* in Norfolk "with similar intermediate capsules" but "did not arrive at any conclusion."

In 1911 Mr. C. E. Britton distributed a Poppy gathered at Banstead, Surrey (*B.E.C. Report*, 1911, 67) and the majority of those to whom it was referred considered it *P. Rhœas* × *dubium*. I have lately, in the light of my Chilworth notes, re-examined my example of this poppy (supplemented by other specimens kindly lent me by Mr. Britton), and, whilst still of the opinion that the plant (Ref. No. 197) was of hybrid origin, I find it shows more evidence of *Rhœas* in buds, peduncles and hairs than my Chilworth examples. On the other hand, Mr. Britton's Ref. No. 184 (l.c.) seems to me a not infrequent form of *P. Rhœas* with rather more elongated capsules than usual, but scarcely so extreme as that I have figured (f. 7).

In 1912, Mr. Britton again gathered and distributed some Poppies from Banstead (op. cit. 1912, 227) and he has kindly lent me examples of these. A plant bearing the Ref. No. 795 is, I believe, the hybrid under discussion showing more of the *Rhœas* parentage but, unlike his No. 197 and my Chilworth plants which were barren, this example had set apparently fertile seed. The Chilworth poppy that Mr. Britton gathered in 1895 (l.c. 228) I find upon examination to be very different to the hybrid plants from that locality described in this note, and seems in all essentials to be *P. Rhœas* with the rather elongated capsule noted above.

Miss M. Cobbe has quite recently sent me a Poppy which she gathered at Pyrford, Surrey, in August last; it agrees exactly with my Chilworth hybrid as regards peduncle, hairs, stigma-disc and capsule and is, moreover, apparently quite sterile.

Specimens of the Chilworth hybrid are being deposited in Herb. Mus. Brit. and at Kew and Cambridge so that future workers on the genus who may read these notes may know exactly the form of the hybrid to which I refer. As the Chilworth details I have noted are simply the outcome of a few observations made *in one locality*, they are given in the hopes that others may report similar plants from their district or record in some detail the points in which their conclusions differ from those to which I have attempted to arrive.

Since writing the notes above, I have come across the Rev. E. A. Woodruffe-Peacock's interesting article upon Poppy hybrids in Journ. Bot., 1913, 48. His examination of the comparative number of stigmatic rays in *P. Rhœas* and *dubium* brings out a result which coincides with my observations at Chilworth, but his hybrid, which he calls *strigosum* and which presumably possesses strigose hairs on the peduncles, is obviously not the same form of the cross as I have described and figured.

TRACHELOMONAS INCONSTANS, A NEW FLAGELLATE

By Nellie Carter, M.Sc.

IN May, 1918, a collection was made from a small rain-water pool near Longmoor Pool at Sutton Park, Warwickshire, which proved on examination to contain, in addition to other Flagellates, a species of *Trachelomonas* which is not like any other previously recorded and is presumably a new species. The distinctive feature seems to be the presence of a prominent nodule or spiny excrescence at the posterior end of the organism.

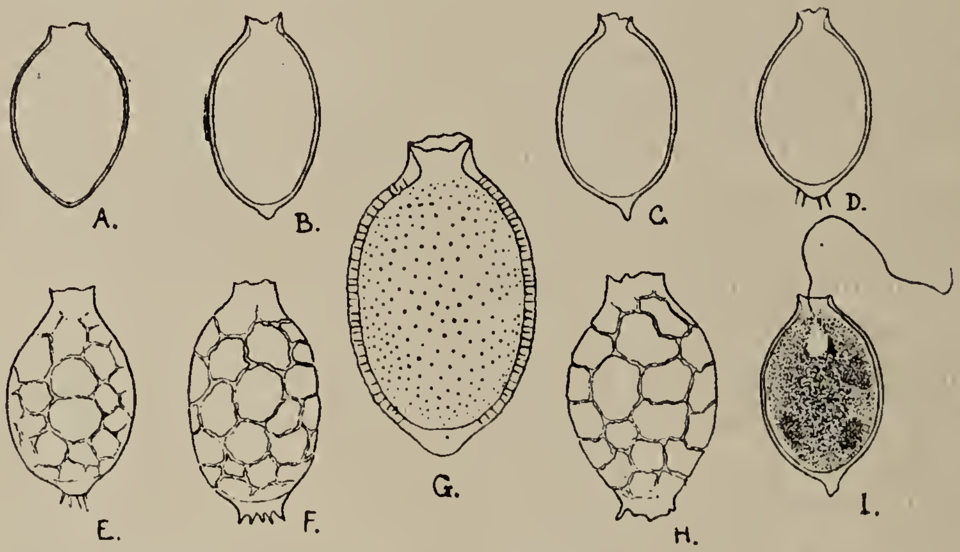


Fig. 1. A, B, C, D, E, F and H, cases of various individuals × 510; G, showing the structure of the case × 810; I, living individual × 519.

The living cell is provided with a case, the shape of which is variable within certain limits. In the majority of specimens it is egg-shaped, the widest part usually being posterior (Fig. 1, D and E), but occasionally anterior (Fig. 1, A and H), although in certain individuals it may be more or less oval in shape (Fig. 1, F and G). The basal nodule is also capable of considerable variation, its size probably depending on the age of the individual. In delicate and probably newly-formed cases, the nodule may be entirely wanting (Fig. 1, A). As a rule it forms a rather button-like thickening or conical outgrowth (Fig. 1, B, D, E and G) and frequently there are several delicate spicules projecting from it (Fig. 1, D and E). Very often it is in the form of a spike (Fig. 1, C and I), or it may be two or more fid (Fig. 1, F and I) whilst in older individuals the nodule often becomes very large and irregular in form (Fig. 1, H). At the anterior end, the case is prolonged to form a distinct neck with a collar-like thickening at its base (Fig. 1, G).

The whole case is strongly impregnated with iron, particularly in the older specimens, and this often gives the empty cases a slightly yellowish colour. The iron penetrates into the basal nodule, and even the tiny spicules attached to it, if these are present, show traces of iron.

In the living condition the external surface of the case is apparently densely covered with very short spines, but examination with higher magnification, or after the use of various stains shows that this is not so. The appearance is due to the presence of minute pores within the thickness of the wall (Fig. 1, G). These pores are brought out particularly well after staining with hæmatoxylin, and also by the Prussian Blue test for iron. The general mass of the case, by virtue of its iron content, stains very deeply with either of these reagents, whilst the pores remain unstained and are clearly visible. In specimens having fairly thick cases these pores are particularly noticeable, and give the appearance of small spicules projecting from the surface[1].

In very old specimens the cases tend to break up into irregular angular plates (Fig. 1, E, F and H), losing their shape and collapsing slightly, although the plates still remain in contact with one another for some considerable time.

The living cell is densely green in colour, and is provided with a bright red stigma whilst a long flagellum protrudes from the neck of the case. There are several contractile vacuoles (Fig. 1, I).

Trachelomonas inconstans sp. n. Integumentum oviforme vel ellipticum, plerumque inferne aut interdum superne amplius, tuberculo basali fibuliformi vel conico, senio latiore ac irregulari præditum, ad collum magis incrassatum, provectiore ætate ferro valde coloratum, atque grosse punctatum ita ut prima specie spinulis curtis horrescens videatur, postremo in plagulas polygonales dirumpendum.

Long. 35-47μ, Lat. 20-28μ.

Cellula viva saturate viridis, stigmate vivide rubro ac flagello instructa.

Hab. in stagnis palustribus, Longmoor Pool, Sutton Park, Warwickshire.

In conclusion, I wish to express my thanks to Professor G. S. West for much help during the investigation.

THE BOTANICAL LABORATORY,
UNIVERSITY OF BIRMINGHAM.

---

[1] The typical form of *T. hispida* (Perty) Stein actually has its case covered with short spines. In a certain variety, however, var. *coronata* Lemm. which occurred in the same collection with the species under consideration, these spines are wanting, and the case shows a similar punctate structure.

ETHEL SARGANT.[1]

October 28, 1863 – January 16, 1918.

[WITH TWO FIGURES IN THE TEXT.]

ETHEL Sargant was the daughter of Henry Sargant, barrister-at-law, and his wife, Catherine Emma Beale. She was educated at the North London Collegiate School under Frances Mary Buss, at a time when schools of this type represented an adventurous experiment. From 1881 to 1885 she studied natural science at Girton College, Cambridge, but nearly all her subsequent work was carried out at home, where domestic ties involved continuous demands upon her time and vitality, and often interrupted her own private pursuits for long periods together. The conditions of her life made any professional undertaking—in the sense of a teaching post—impossible for her, but she was far from regretting this disability, since she was convinced that lecturing and demonstrating would, in her case, have paralysed the faculty for original work. She was in her element, however, in initiating research students into the methods of discovery, and to those who from time to time worked under her direction in her little laboratory, she gave a unique training. We are here concerned with her rather as a botanist than in her human relations, so we must be content with a bare allusion to a single aspect of her wise and helpful attitude towards younger workers—an aspect which found expression in her advice to a student who was hesitating on the threshold of research, discouraged by the renunciations to which those who embrace that life must be prepared to commit themselves. If after a year of tackling some biological problem "you find yourself," she wrote. "restless, dissatisfied, half-starved, don't attempt to follow up that line—'Look in your heart and write' as Sidney said 300 years ago . . . . . The question is not whether any work you may take up will not atrophy some faculties to some degree, It is almost bound to do so. But if you have sufficient taste for the work to delight in it, appetite will come as you eat, and you will develop not only the faculties you use but your whole being through their exercise.

---

[1] Since Ethel Sargant's death, the following notices of her life and work have appeared:—by Dr. D. H. Scott, *Annals of Botany*, Vol. 32, 1918, pp. i-v; see also letter by Dr. Scott in *Times Literary Supplement*, Thursday, Jan. 31, 1918, reprinted in Journal of Bot. Vol. 56, 1918, pp. 115-6; by Dr. E. N. Thomas, *Proc. Linn. Soc.* 130th Session, Oct. 1918, pp. 41-42; by the present writer in *The Cambridge Magazine*, Vol. 7, Jan. 26, 1918 p. 361, reprinted in *The Common Cause*, Vol. 9, 1918, p. 567; see also *Nature*, Vol. 101, 1918, pp. 428-9. Reference may also be made to a forthcoming article by the present writer, "Ethel Sargant, 1863-1918, A study of the mind of a morphologist," in *Studies in the History of Science*, edited by Dr. C. Singer, Vol. III.

Besides there is much choice in biological work, and a great field for the philosophical naturalist, and I have always felt a sense of beauty a most essential faculty for the biologist."

Ethel Sargant's own botanical research was concerned with two widely separated branches—Cytology and Anatomical Morphology. Her studies on the Cell, though admirable of their kind, scarcely revealed her powers so fully as the morphological work, in which she entirely "found herself," and to which the greater part of her writings relate. Her first research in Cytology was directed to the question of whether centrosomes exist in the higher plants—a problem which excited keen interest in the early nineties of the last century. This gave rise to no published results, but paved the way for a general study of oögenesis and spermatogenesis in *Lilium Martagon*, from which she drew the conclusion that there was no evidence, in the heterotype and homotype divisions, of the "transverse fission" postulated by Haecker. At this time there was considerable doubt as to the nature of the "synapsis" stage—certain cytologists holding it to be an artefact, due to the action of the reagents employed. By examining, under the immersion lens, thin sections of fresh anthers of the Turk's Cap Lily, mounted in the plant's own sap, Ethel Sargant succeeded in demonstrating the existence of the synaptic phase in living cells, thus settling this critical question once and for all.

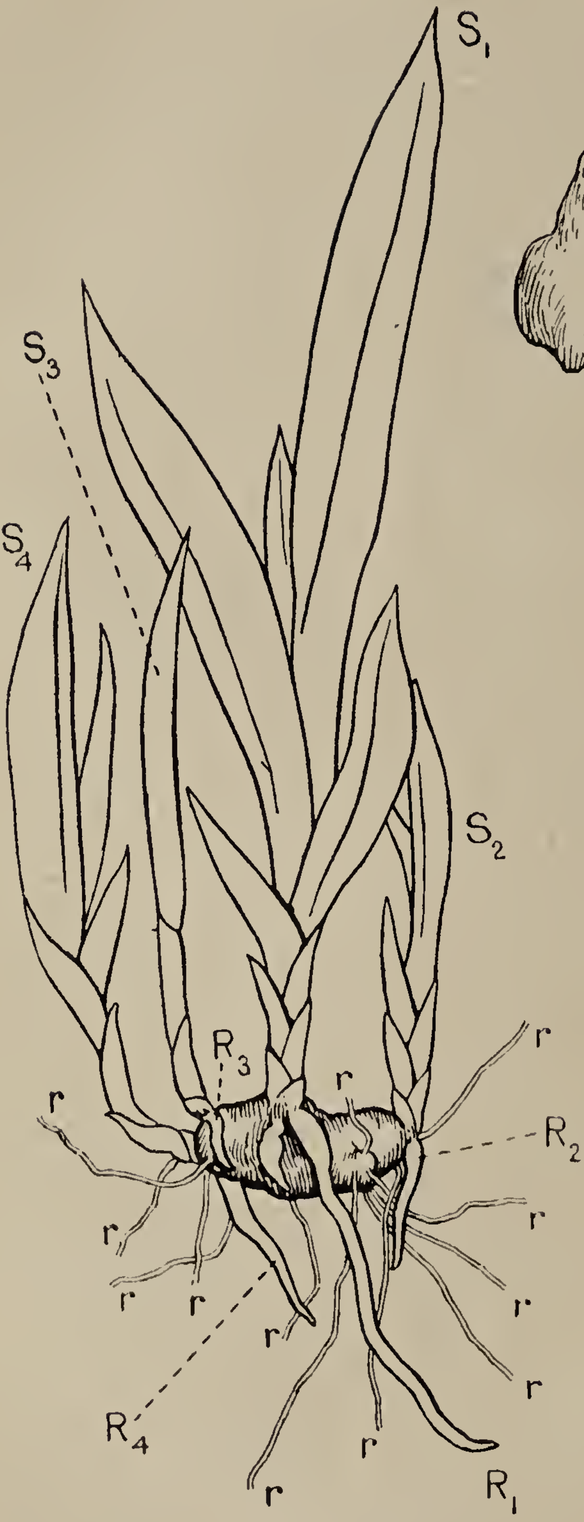
In 1897—the year in which the second of her papers on *Lilium Martagon* appeared—Ethel Sargant visited various Continental laboratories in company with Professor Margaret Benson. At Bonn she had a memorable meeting with Strasburger, with whom she had previously corresponded. In a letter soon after her return she wrote, "He is a very highly wrought man, nervous, unbalanced but he impresses one as a genius. I shouldn't think his influence altogether good on his pupils—he dominates the whole place and they learn to think that the cell can only be studied in the Bonn laboratory. 'But, Sir, he is a very great man,' as Johnson said of Goldsmith. We conversed in French . . . . and I had to beat my French out very thin to make it cover the ground. But by hook or by crook the thing was done, and it is something to look back on all one's life."

In 1899 the work of Nawaschin and Guignard on "double fertilisation" became known to English botanists. The accounts of these discoveries led Ethel Sargant to look again at a few hand sections of fertilised ovules of *Lilium Martagon*, which had been cut some years before, but scarcely glanced at; the re-examination showed that these slides perfectly displayed both the fertilisation of the egg and the "triple fusion" of the second male nucleus with the two polar nuclei. These preparations were shown at a meeting of the Royal Society, and elsewhere, and served to convince botanists in this country of the accuracy of the observations made by Nawaschin and Guignard. In a letter dating from this juncture, Ethel Sargant wrote—somewhat ruefully—"I missed a splendid chance four years ago, and all this fuss comes to writing myself down an Ass in large gold letters." But though she did not achieve priority of discovery, her work came to fruition in a later paper on the Results of Fertilisation in Angiosperms, In this discussion she propounded the ingenious theory that the triple fusion in the embryo-sac corresponds to a second fertilisation, "spoilt" by the intrusion of the lower polar nucleus. The endosperm is thus, as it were, a monstrous embryo, degraded to the position of a short-lived food tissue by the presence of the redundant nuclear elements introduced by the lower polar nucleus. This theory is now nearly twenty years old, and it is greatly to be wished that some botanist, familiar with the recent developments in our knowledge of the embryo-sac, should give us a critical review of the evidence relating to the problem, as it stands at the present day.

After her work on *Lilium Martagon*, Ethel Sargant did not again return to Cytology, partly because her eyes were not strong enough for continuous work with high powers. But she closely watched the progress of the subject and marked, with some distress, the tendency—which became particularly rife in the first decade of this century—to obscure cytological issues by presenting the facts coloured beyond recognition by some preconceived theory; as she wrote in 1905, "I am feeling moved to write a Cytology as a protest against the confusion of observation with induction."

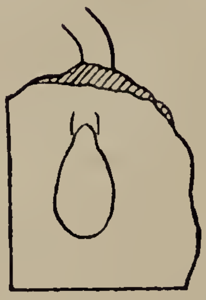
While Ethel Sargant was pursuing her cytological work, she was at the same time developing a line of thought which was destined to find its ultimate expression in that study of seedlings with which her name is chiefly associated. Immediately after she went down from Girton, she began to read Hegelmaier's work on Vegetable Embryology, and the notes which she made at the time show how deeply she was impressed with the subject. These notes form, as it were, the germ out of which her Presidential Address (Brit. Ass., Sect. K, 1913) was to develop nearly thirty years later. In 1889 and 1890 she made her first attempts at research, examining and recording the arrangement of the vascular bundles in a number of flowers. This work, which she never published, reveals the birth of that *flair* for detecting morphological clues in the skeletal system of the plant, which led, in its maturity, to her theory of the origin of Monocotyledons. From 1892-3 she worked under the direction of Dr. D. H. Scott at the Jodrell Laboratory, Kew—an experience to which she always referred as having been of untold value as a training in research in general and in the methods of anatomy in particular. It was at Kew that both her cytology and the main line of her morphological work came into active existence. Her natural capacity for balanced thought developed to an exceptional pitch in the congenial atmosphere of the Jodrell Laboratory. This capacity—none too common, it must be confessed, among anatomists, since it has an unfortunate tendency to atrophy under the influence of the microscope—prevented her ever consenting to the divorce of structure from function, and in 1897 and 1898 she made a thorough study of the literature dealing with the transpiration stream, and also carried out a number of elaborate experiments on the ascent of sap in trees. She did not publish the results of this work, but it gave a sound quality of concreteness to her anatomical conceptions. It was perhaps this quality, combined with her constant reference to the historical standard in morphology, that led her so profoundly to distrust certain developments of the stelar theory, which in her view had become so academic as to have lost all touch with reality.

Some work on the seedlings of the Wild Arum, begun in 1895 in association with Mrs. D. H. Scott, was one of the outcomes of the Jodrell Laboratory period. This collaboration was a fortunate episode, for Ethel Sargant's later work was permanently influenced by her colleague's rare capacity for natural history observation. This paper served as the starting point for a study of the life history of Monocotyledons, more especially their methods of lowering themselves into the soil—a subject to which Ethel Sargant returned again and again throughout her life. In 1911 she stayed at La Mortola, near Mentone, in order to examine the Monocotyledons in the Hanbury garden, and here she met with some examples of contractile roots, an especially notable case being that of one of the Iridaceæ, *Antholyza aethiopica*, L. (Fig. 1), which she always intended to work out fully. In her incomplete notes on the subject she left the following statement :—"Clearly *Antholyza aethiopica* produces two kinds of root: one slender, of which there are many



I

II A



II B

FIGS. 1 and 2. Unpublished drawings by Ethel Sargant made at La Mortola in the Autumn of 1911. [illegible]

I, *Antholyza æthiopica*, L. Habit drawing of plant, one-third nat. size, showing S_1—S_4, leafy shoots; r, r, r, some of the numerous slender spreading roots; R_1—R_4, stout roots, probably contractile.

II, *Crinum Powelli*, A, seedling (slightly reduced), B, apex of cotyledon in endosperm (nat. size).

to each leafy shoot. These spread about at various angles to the vertical. The other kind—of which I have only seen one (in one instance two) to one leafy shoot—is much stouter and descends vertically into the soil. It appears almost like a prolongation of the ascending shoot to which it is directly attached by a very broad basis." These stout roots—which were found to be polyarch and which were compared with certain *Crocus* roots which are externally similar—are probably contractile, but it would be necessary to collect material later in the season in order to determine this point with certainty.

Many years ago Ethel Sargant had an idea—which she was never able to carry out—for field work of a type which might even to-day be well worth pursuing. "I have long had plans," she wrote, "for systematic work as to the conditions of life of native plants in their wild state—what determines the extinction or survival of a species in a particular locality and particularly the mode of reproduction which actually operates. How far are perennials reproduced by seed for example? The *Arum* business first attracted my attention to this question, and little work has been done on it systematically. Perhaps we might find England almost an unexplored country from this point of view!"

In addition to having formed the basis for Ethel Sargant's study of the bionomics of Monocotyledons, the *Arum maculatum* paper was of importance in another connexion, since it initiated the comparative work on seedlings, begun at Dr. Scott's suggestion, which was, later on, to present such remarkable developments. Ethel Sargant had, as we have already mentioned, been impressed at a very early stage by the historical importance of the vascular system of flowers, and had begun to work at this subject in 1889. Twenty-eight years later, only three months before her death, in a letter to the present writer, she reaffirmed in fulness of experience her considered opinion regarding the value of the vascular system as giving indications of ancestral history. In her own words, "For a long time—much longer really than dating from my seedling work—I have looked on the number and arrangement of vascular bundles within a member—axial or lateral—as a useful guide to descent. Being interpreted, that conviction of course means that such characters are slow to alter and therefore often betray ancestry. But if I try to recollect the evidence on which that belief is founded, I can't be sure of much exclusive of experience in seedlings. And of course . . . the exceptions even there are so numerous and so puzzling that any given genus or larger group might quite likely tell against me. Only in that department have I the right to say (as I do say) that in spite of many obscurities and some positive difficulties, my observations convince me that the characters of the vascular symmetry within the Monocotyledonous seedling are more valuable guides to descent than its external characters. And on any theory of Evolution we must suppose that to mean that the race alters its seedling skeleton less readily than the external characters of the seedling."

An examination of the vascular structure of Monocotyledonous seedlings, especially those of the Liliaceae, occupied Ethel Sargant for many years. This research was exceedingly exacting, and it could never have been accomplished but for the assistance of Dr. E. N. Thomas, who took a large part in the work. For a long time no general hypothesis came into being to illumine the facts observed, but in the spring of 1902 the light broke, and a possible interpretation of the knowledge so laboriously acquired, rapidly revealed itself. In a letter dated April 26th, Ethel Sargant wrote, "My seedlings have suddenly turned up trumps. Did I ever tell you that for some years I have been convinced that the single 'cotyledon' of Monocotyledons is not homologous with one, but with both the cotyledons of a Dicotyledon? This conviction has been growing up in my mind ever since I cut and appreciated *Anemarrhena*. It is down in black and white in a little Abstract of results dated Aug., 1900. Now quite lately I have found the *Anemarrhena* structure in *Galtonia* and *Albuca*, both belonging to the Scilleae—that is, some distance systematically from the Asphodeleae where *Anemarrhena* belongs. Of course this confirms the theory that this is really a primitive structure, and so I resolved to drop the Liliaceae for a time and beat about among likely Dicotyledons. Well on March 25th, when I was just beginning to collect material from Nymphæaceæ and Ranunculaceæ, Williams and Norgate sent me a paper by a Belgian [Sterckx], on the anatomy of seedling Ranunculaceæ. I had ordered it on the chance of its containing useful information. And behold I found pictures of seedlings with their cotyledons united almost to the top, and showing (so far as I could make out) a vascular structure extraordinarily like that of *Anemarrhena*! In the past five weeks I have collected, and pickled, and cut, and a preliminary account of my theory has been sent off to-day to the New Phytologist."

In another letter, ten days later, she gave expression to the central idea which was soon to develop into her theory of the geophilous origin of Monocotyledons, "I am inclined to think," she wrote, "that the habit of a stem shortened to a mere root-stock or tuber or bulb is what originally differentiated the Monocotyledons and I suspect that the specialization of the cotyledon(s) as a sucking organ chiefly, is bound up with this, but all this is rather inchoate as yet."

It would lead us too far to attempt to trace the history of the reception of Ethel Sargant's theory of the origin of Monocotyledons, which was fully developed in the papers numbered 11, 13 and 15, in the accompanying list of her memoirs. But it may be worth mentioning that so acute a thinker as the late Professor Léo Errera of Brussels, gave the hypothesis his immediate adhesion. On receiving the NEW PHYTOLOGIST paper of 1902 he wrote, "It appears to me to throw really the first ray of light on the obscure phylogeny of Angiosperms." The temptation to discuss and analyse the theory must be resisted for lack of space; it is, indeed, scarcely necessary to deal with it in detail, since it is fully and lucidly explained in the papers cited, and the criticism to which it has been subjected is also well-known to botanists.

The fact that Ethel Sargant was President of the Botanical Section at the Meeting of the British Association in 1913, had a definite value in her scientific life, since it gave her the necessary incentive for writing a critical summary of the rise and progress of botanical embryology, including in this term the study of seedlings —a laborious task which, without this stimulus, she might never have attempted. Her discussion will remain as conspicuous a landmark for the subject as Hanstein's work of 1870, from which she dated her review. It was entirely characteristic of her that she brought the Address to a close with certain lines from Milton. Her sympathies in poetry, leaned essentially to the grand style and the large manner; she was at home in regions swept by an air "not dim from human hearth-fires." Her spacious nature gave forth chords answering to Milton's music— even, indeed, to the height of his great argument.

A. A.

MEMOIRS BY ETHEL SARGANT.

1. [Conjointly with D. H. Scott]. On the Pitchers of *Dischidia rafflesiana* (Wall.). Ann. Bot., Vol. VII, 1893, pp. 243-269, 2 pls.
2. Some Details of the First Nuclear Division in the Pollen-Mother-Cells of *Lilium Martagon* L. Journ. Roy. Micr. Soc., 1895, pp. 283-7, 9 text-figs.
3. Direct Nuclear Division in the Embryo-sac of *Lilium Martagon*. Ann. Bot., Vol. X, 1896, pp. 107-8.
4. The Formation of the Sexual Nuclei in *Lilium Martagon:* I. Oögenesis. Ann. Bot., Vol. X, 1896, pp. 445-77, 2 pl.
5. The Formation of the Sexual Nuclei in *Lilium Martagon;* II. Spermatogenesis. Ann. Bot., Vol. XI, 1897, pp. 187-224, 2 pls.
6. [Conjointly with Rina Scott]. On the Development of *Arum maculatum* from the Seed. Ann. Bot., Vol. XII, 1898, pp. 399-414, 1 pl.
7. On the Presence of two Vermiform Nuclei in the Fertilised Embryo-sac of *Lilium Martagon*. Proc. Roy. Soc., Vol. LXV, 1900 for 1899, pp. 163-5, 1 text-fig.
8. A New Type of Transition from Stem to Root in the Vascular System of Seedlings. Ann. Bot., Vol. XIV, 1900, pp. 633-8, 1 pl.
9. Recent Work on the Results of Fertilization in Angiosperms. Ann. Bot., Vol. XIV, 1900, pp. 689-712,
10. The Origin of the Seed-Leaf in Monocotyledons. New. Phyt., Vol. I, 1902, pp. 107-13, 1 pl.
11. A Theory of the Origin of Monocotyledons founded on the Structure of their Seedlings. Ann. Bot., Vol. XVII, 1903, pp. 1-92, 7 pls., 10 text-figs.
12. [Conjointly with Agnes Robertson (Arber)]. The Anatomy of the Scutellum in Zea Maïs. Ann. Bot., Vol. XIX, 1905, pp. 115-123, 1 pl.
13. The Evolution of Monocotyledons. Bot. Gazette, Vol. XXXVII, 1904, pp. 325-45, 6 text-figs.
14. The Early History of Angiosperms. Bot. Gazette, Vol. XXXIX, 1905, pp. 420-3.
15. The Reconstruction of a Race of Primitive Angiosperms. Ann. Bot., Vol. XXII, 1908, pp. 121-86, 21 text-figs.
16. The Development of Botanical Embryology since 1870. Presidential Address to Section K (Botany). Brit. Ass. Rep., Birmingham, 1913, pp. 692-705, 1 text-fig.
17. [Conjointly with Agnes Arber]. The Comparative Morphology of the Embryo and Seedling in the Gramineæ. Ann. Bot., Vol. XXIX, 1915, pp. 161-222, 2 pls. and 35 text-figs.

THE
NEW PHYTOLOGIST

VOL. XVIII, NOS. 5 & 6. MAY & JUNE, 1919.
[PUBLISHED JULY 15TH, 1919.]

THE ORIGIN AND DEVELOPMENT OF THE COMPOSITÆ.*

By JAMES SMALL, PH.C., F.L.S.

CHAPTER XII.

MISCELLANEOUS TOPICS.

THE preceding chapters have each dealt as far as possible with only one aspect of the origin and development of the Compositæ. There remain to be considered some subsidiary aspects, such as the palæobotany, cytology, laticiferous and secretory systems, seedling structure, etc. These are dealt with in the present chapter.

A. FOSSIL COMPOSITÆ.

An extensive but not quite exhaustive search through the literature of tertiary fossil plants has yielded the records for Compositæ given in Tables XII and XIII. The localities and geological dates are given in Table XII. The numbers in the second column of Table XIII refer to the bibliographical references given at the end of this chapter; with one or two exceptions the reference to the original description is given and comes first. The numbers in the third column of Table XIII refer to the numbered localities given in Table XII, which was drawn up to avoid a cumbersome repetition in Table XIII of geographical localities.

The value of the palæobotanical evidence for our present purpose depends largely upon the soundness of the identifications. This point will, therefore, be reviewed before we proceed to draw any conclusions from the fossil record.

The first part of Table XIII is occupied mainly by the records of the Reids. In all these cases the fossils were fruits which, after being preserved by special methods, were examined for the details of structure, such as shape, ribs, sculpture, etc. It may appear strange that determination of such fossils can be made with specific accuracy, especially in large genera such as

---

* Part of a Thesis approved for the Degree of Doctor of Science in the University of London.

Eupatorium and *Senecio*. The method apparently folowed by these authors of comparing the fossil fruits in the first instance with the fruits of species now existing in the same localities avoids the difficulties and uncertainties which would undoubtedly arise if the comparison were wider. It is seldom impossible but sometimes very difficult to assign recent well-preserved fruits to a particular species. The deposits dealt with are, however, comparatively recent, and the limited comparison is, therefore, probably quite justified and the determinations can be accepted as accurate.

Opinions differ on the exact age of the peperino from which the leaves of *Tussilago Farfara* are described by Antonelli (cp. 15). As that tufa is, however, certainly post-glacial and the fruits are recorded from both neolithic and Cromerian beds the determination of these very distinctive leaves can be taken as corroborated by Reid's evidence. Antonelli's record of *Bellis perennis* from the same locality, although not corroborated in the same way, may be accepted.

The second part of Table XIII is occupied by a series of unclassified genera and species which require more critical consideration. The genus *Baccharites* of Saporta rests on a resemblance of these fossil leaves to those of *Baccharis*. For present purposes they may be classed with the *Silphium*-like leaves described by Massalongo as *Silphidium*. Bentham's comment (see Table XIII) on the identification of these leaves is echoed by more than one palæobotanist. The fossil leaves of *Hieracites Salyorum*, Sap. and *Parthenites priscus*, Sap. appear to the writer to be very probable determinations resting on much the same ground as Reid's identifications. The leaves of *Hyoserites Lingua* Ettingsh, associated as they are with beaked achenes, seem to be the most authentic Compositæ leaves of the older strata.

The other fossils are chiefly fruits; *Bidentites antiquus* as figured by Heer (2, Pl. 101, Fig. 20) and Zittel (38, Fig. 404), is a fruit with a bidentate apex, but there its similarity to the fruits of *Bidens* ends. The teeth or awns arise close together on the contracted apex of the fruit and diverge at an angle rarely met with in *Bidens*, where the awns are erect, almost parallel and arise on opposite sides of a more or less truncate apex. The identification would certainly not survive the application of the criteria adopted by the Reids.

Carpolithus hyoseritiformis, Berry, is placed by its author among the genera "incertæ sedis" (3, p.353), at the same time he says " it is almost certainly an achene of some Wilcox species of Compositæ." As figured and described by Berry this fruit has the characteristic ridges and is crowned by about ten bristles which have lateral projections like those of *Coreopsis.* This solitary American representative would seem, therefore, to belong to the Heliantheæ, if it is a Composite at all.

The large genus *Cypselites*, Heer, includes some undoubted Compositæ. Saporta's determinations may be accepted as being accurate in most cases, but those by Heer require critical revision. Saporta left the position of the gypsum beds to be decided by later workers. Zeiller (37) gives the period as lower Oligocene, while Ward (36) gives it as Eocene. *C. bisulcatus*, because of the paucity of the ridges, and *C. ellipticus*, because of the numerous ridges, although possibly Cynareæ, come under suspicion, which is increased by the curious projections from the beak in both cases. *C. Lessingii* also has very numerous ridges and a very peculiar group of rigid hairs. *C. rostratus* might also be excluded from the present discussion because of the absence of the characteristic ridges and the peculiar irregularity in length of the hairs. Some of these exclusions may seem severe but only thoroughly authentic Compositæ can be admitted for the purpose of elucidating the past history of the family. The genera *Hieracites* and *Hyoserites* contain several interesting species, all of which may be accepted as well defined Compositæ.

One of the most striking features of the well authenticated fossil Compositæ is the predominance of the simple setose type of pappus. Although the American tertiary has as yet yielded practically no Compositæ, and the European forms, even from the Lower Oligocene, cannot be accepted as the earliest types, the evidence, as far as it goes, supports the view that the setose type of pappus is the primitive form (cp. Chap. V). The plumose setæ of *Cypselites Regelii* and *C. Ungeri*, the outer setæ with flattened, dilated bases (paleaceo-setose) of *Hyoserites Schultzii*, of *C. gypsorum* and those of *C. costatus* which are connate at the base, are all comparatively primitive types according to the view expressed in Chapter V.

In connection with the writer's opinion that the small, almost flat receptacle is the primitive type (see Fig. 19 and Chap. VI, B), it is noteworthy that the earliest known receptacula (*Hieracites stellatus* and *H. nudatus*) are small and almost flat. Concerning the latter species, which is interpreted as a receptacle with only the scar of the involucre showing and no bracts, but a densely packed mass of florets or achenes, Saporta (32b, p. 57) says " L'empreinte est difficile à interpréter." The figure (Pl. 20, Fig. 5a) which he gives, however, is quite clearly a typical Cichoriaceous capitulum just before anthesis. The calyculus in that group is frequently soft, herbaceous and easily removed without disturbing the rest of the capitulum. The narrow, elongated structures on the outside of the fossil are too flat and undulate to be achenes: on the other hand they cannot be florets because they are attached directly to the receptacle without the least vestige of an ovary. The writer suggests, therefore, that this fossil is a capitulum with only the outer bracts or calyculus missing, and that it shows a sub-biseriate involucre similar to that which is the chief part of the fossil *Hieracites stellatus*, but with the equal involucral bracts which are common in the Cichorieæ.

We have then two fossil examples of involucre, *H. stellatus* and *H. nudatus*, which are both sub-biseriate. The latter is of a Cichoriaceous type but the former, although compared by Saporta with that of *Inula pulicaria*, is very closely similar to the involucre of *Senecio glaucus* figured above (Chap. VII, Fig. 21). Leaving the exact affinity as impossible to determine in the meantime, one point is clearly proved, namely, that the only involucres known in the fossil condition are sub-biseriate, and one of them shows the scar of a distinct calyculus. This is in accordance with the view expressed in Chap. VI, B, on the primitiveness of the involucre with an uniseriate pericline and a slightly developed calyculus.

Considering now the evidence which has a bearing on the dates of appearance in Europe of the various tribes, we find the Cichorieæ indicated by a number of beaked achenes, by the capitulum of *Hieracites nudatus*, and by leaves similar to those of recent species of the tribe. These occur in the lower Oligocene, so that, if the views expressed in Chap. X on the successive origin of the tribes from the Senecioneæ are correct, most if not all of the tribes had been differentiated at the beginning of the Oligocene period. The absence of any fossils from the Aix deposits which could be ascribed to the Calenduleæ or Arctotideæ, although only negative evidence, is interesting on account of the suggestion in Chap. X, D, of the origin of these tribes at a later date than that of the Cichorieæ. The decided development of the Cichorieæ in Oligocene and Miocene times is in accordance with the occurrence of a number of the same tribe in the Pliocene and later floras. An interesting point in connection with the suggested age of the genus *Lactuca* (Chap. X, C, and Fig. 31) is the similarity of *Cypselites spoliatus* to the fruits of that genus. The Asiatic affinity of two species of *Crepis* from the Middle Pliocene is in accordance with the suggested migration of the present Asiatic Cichorieæ from the Mediterranean region. The absence of any fossil species of

Hieracium, except *H. Pilosella*, is in accordance with the suggested recent origin by mutation of the thousands of micro-species described in that genus.

Although no palæobotanist has yet suggested an affinity between any of the earlier fossil Compositæ and Senecioneæ, it is significant that an unidentified species of *Senecio* is described by the Reids from the lowest beds (Middle Pliocene) examined by them. Quite a number of the fruits figured by Heer and Saporta might well be ascribed to *Senecio* and its allies.

The presence of the Cynareæ in the Mediterranean region in Miocene times and the absence of any clear evidence of their development in the Oligocene is in accordance with the date of origin as deduced from the structure and geographical distribution of the tribe. They are more restricted in area and more specialised in structure than the Cichorieæ, so that the action of the Law of Age and Area, as shown by the present distribution, receives some corroboration in this case from the fossil evidence. It will be noticed that both *Centaurea* and *Carduus* occur in the Upper Pliocene, so that the development of the Cynareæ at that date is in accordance with the greater age of the two sub-tribes represented.

The leaves of *Parthenites priscus* are so much like the characteristic leaves of species of *Chrysanthemum* that they may be used as corroborative evidence for the statement in Chap. X, D, that the main genera of the Chrysanthemidinæ are older than those of the Anthemidinæ, while the suggestion that the tribe arose before the Cichorieæ is not invalidated by the simultaneous occurrence of representatives of both tribes in the Lower Oligocene. The coroniform pappus of *Hyoserites Schultzii* from the Upper Miocene may be another indication of the presence of the Anthemideæ in these early times, while the occurrence of living species of the tribe in the early glacial deposits is further evidence of an antecedent development of the group.

The Inuleæ are represented only by an unidentified species of *Helichrysum* from the Middle Pliocene. Such meagre evidence is of little phyletic value; that the fruit belongs to the Gnaphaliinæ is in accordance with the views previously expressed on the primitiveness of that sub-tribe, while the absence of other representatives of the group, especially of *Gnaphalium*, is easily accounted for by the small size of the fruits and the alpine habitat of most species.

The Astereæ are represented only by the leaves of one living species and the fruits of another. As they are both Pleistocene they give no interesting data. The well confirmed derivation of the Eupatorieæ from the Astereæ, however, lends a doub interest to the records of *Eupatorium*. *E. cannabinum*, which occurs all over the Eur-Asiatic region at the present time, seems to have been common in England in Pleistocene times, another small piece of evidence supporting the Law of Age and Area. The obscure variety of *E. japonicum* is interesting, but, as the identity is not fully verified, no special conclusion can be drawn, since it is quite possible that the fossil fruit represents an old derivative of *E. cannabinum*, rather than the former extension of the living, local variety of *E. japonicum*. The Middle Pliocene development of *Eupatorium*, when considered in relation to the ancestry of the tribe, can, however, be taken as evidence in favour of the relatively early origin of the Astereæ.

The Heliantheæ are represented by *Bidens* from the Upper Pliocene to the Roman Period. The wide extension of this genus at such a date, combined with the Lower Eocene Helianthoid *Carpolithus hyoseritiformis*, indicates an early origin of the Heliantheæ as suggested in Chap. X, D. The available evidence concerning the development of the Compositæ in America is, however, so meagre that it does not furnish any information about the relative age in America of the various tribes. This field for research is still very open and investigations on the early Tertiary Compositæ of America would prove very interesting.

From the above brief account of fossil Compositæ it will be seen that so far as our present knowledge extends the details are quite in accordance with the phyletic suggestions given in previous chapters; they add little it is true, but slight confirmation is all that can be expected from such an incomplete record.

According to Chamberlin and Salisbury (6) the Angiosperms arose in late Jurassic or early Comanchean times in the eastern part of North America. This theory is regarded by Stopes (34) as possibly true but unproven (35). The evidence of the present geographical distribution of most of the Sympetalæ and of the higher Archichlamydeæ is in favour of a more southern place of origin—the northern part of South America. Fossil evidence is scanty, but other data point quite clearly to the region of the Amazons and northern Andes as the geographical source of the Angiosperms in general and of the Compositæ in particular.

Late Cretaceous or early Eocene times are indicated as the time of origin of the Compositæ. This is in agreement with the suggested early Tertiary origin deduced by Guppy (IX, 21, p. 245) from the absence of endemic genera of Compositæ from the Fiji Islands and their presence in the Hawaiian Islands. That phenomenon, however, can be explained equally well by the hypothesis of an immigration of Compositæ into the Fiji Islands from the east at a date much later than the migration from America of the ancestors of the Hawaiian endemics. The peculiar, insular endemic genera occur on the islands (Galapagos, Juan Fernandez and Hawaiian) which are much nearer America than Fiji. The last mentioned probably received its present Compositæ after New Zealand had been stocked from New Guinea via Australia (see Chap. X).

It has been shown above that the migration of most of the Compositæ, and of *Senecio* in particular, took place along the mountain ranges. The dispersal of the Compositæ must, therefore, have taken place after the formation of the ridges which constitute the main path of migration. According to the geological evidence

TABLE XII.

List of Localities for the Records in Table XIII.

Pleistocene	Roman Period	1.	Silchester, Hampshire
	Neolithic	2.	Redhall, near Edinburgh
		3.	Hailes, ,, ,,
		4.	Fillyside ,, ,,
		5.	Gayfield ,, ,,
		6.	Close y Garey, Isle of Man
		7.	Elie, Fife
		8.	Tilbury Docks, Essex
	Paleolithic	9.	Reuver, (alluvial beds) see 31
	Post-Glacial	10.	Albano, Rome
	Late Glacial	11.	Angel Road, Lea Valley
		12.	Hedge Lane, ,,
		13.	Ponder's End ,,
		14.	Temple Lane, ,,
		15.	Hoxne (bed C), Suffolk
		16.	Hailes (lower bed), near Edinburgh
		17.	Corstorphine, near Edinburgh
		18.	Garvel Park, Clyde Beds
		19.	Roxburgh Street, Greenock
	Interglacial	20.	Allenton, near Derby
		21.	West Wittering, Sussex
		22.	Southelmham, Suffolk
		23.	Hoxne (bed D), Suffolk
		24.	Shacklewell, London
		25.	Hitchin, Hertfordshire
	Early Glacial (Arctic Plant Bed)	26.	Beeston, Norfolk
Upper Pliocene	Cromerian Beds	27.	Pakefield, Suffolk
		28.	Mundesley, Norfolk
	Teglian Beds	29.	Tegelen, Limburg.
Middle Pliocene	Reuverian Beds	30.	Swalmen, Dutch-Prussian Border
		31.	Reuver, ,, ,, ,,
Upper Miocene	—	32.	Oeningen, near Constance
		33.	Rochesauve, Ardéche
		34.	Priesen, Bohemia
		35.	Savine (Stellen), Alps
Middle Oligocene	—	36.	Chiavon, Vicentin, Italian–Tirol frontier
		37.	Salcedo ,, ,, ,,
Lower Oligocene	—	38.	Aix en Provence
		39.	Gergovie, Puy-de-Dôme
Lower Eocene	Wilcox Beds	40.	Puryear, Henry County, Tenn.

TABLE XIII.

List of fossil fruits, leaves, etc., which have been classed as Compositæ

Species Classified.	References.	Dates and Localities.	Remarks.
SENECIONEÆ			
TUSSILAGININÆ			
Tussilago farfara, L.	Reid, 22, 23	Neolithic, 2	Only one fruit
	Antonelli, 1	Post Glacial, 10	Leaves in volcanic tufa [or peperino
	Zittel, 38		
	Reid, 27	Upper Pliocene, 27	Fruits
SENECIONINÆ			
Senecio aquaticus, Huds.	Reid, 23	Interglacial, 21	
,, *sylvaticus*, L.	Reid, 22, 23	Neolithic, 2	
Senecio sp.	Reid, 29	Middle Pliocene, 30	Near *S. sylvaticus*
CICHORIEÆ	Bentham, 2	Upper Miocene	Heer's species of [Cypselites
LAPSANINÆ			
Lapsana communis, L.	Reid, 22, 23	Neolithic, 2, 3	
	,, 17, 22, 23	Interglacial, 21	
	,, 16, 22, 23	Upper Pliocene, 27	
CREPIDINÆ			
Picris hieracioides, L.	Reid, 16, 22, 23, 27, 29	Upper Pliocene, 27	
Crepis cf. *blattaroides*, Vill.	Reid, 29	Middle Pliocene, 30	Very near *C. blattaroides* but also resembles certain spp. of China
Crepis fuscipappus, Benth.	Reid, 29	Middle Pliocene, 30	A mountain species of India & Chinese forests
Crepis succisæfolius Tausch.	Reid 27, 29	Upper Pliocene, 27	Not uncommon
Crepis virens, L.	Reid 22, 23	Neolithic, 2	
	,, 30	Late Glacial, 11	
Crepis, sp.	,, 29	Middle Pliocene, 31	
Crepis ?	,, 25	Paleolithic, 9	In alluvium
HIERACIINÆ			
Hieracium Pilosella, L.	,, 23	Interglacial, 21	No trace of any other species of *Hieracium* has been found fossil in [Britain
HYPOCHŒRIDINÆ			
Leontodon autumnalis, L.	Reid 22, 23	Neolithic, 2	
	,, 30	Late Glacial, 12, 13	
	,, 22, 23	Interglacial, 20	
	,, 27, 29	Upper Pliocene, 27	Rare
Leontodon hispidus, L.	,, 24a	Roman Period, 1	
Taraxacum officinale, Web.	,, 22, 23	Neolithic. 2, 4	4 is a raised beach
	,, 19, 22, 23	Late Glacial, 15	
	,, 22, 23	,, ,, 16, 17, 18	
	,, 22, 23	,, ,, 19	In glacial clay
	,, 22, 23	Interglacial, 20, 21, 22	
Taraxacum sp.	,, 30	Late Glacial, 11, 12, 13, 14	
LACTUCINÆ			
Sonchus arvensis, L.	,, 18, 22, 23	Neolithic, 2, 5	
	,, 22, 23	,,	Lacustrine deposits of Scottish lowlands
Sonchus oleraceus, L.	,, 24a	Roman Period, 1	
,, *palustris*, L.	,, 24a	,, ,, 1	
ANTHEMIDEÆ			
CHRYSANTHEMIDINÆ			
Chrysanthemum Leucanthemum, L.	Reid 23, 24a	Roman Period, 1	
Chrysanthemum segetum, L.	,, 18. 22, 23	Neolithic, 2, 3	
Matricaria inodora, L.	,, 18, 22, 23	Neolithic, 2, 3	

TABLE XIII (continued)

Species Classified.	References.	Dates and Localities.	Remarks.
Tanacetum vulgare, L.	Reid, 22, 23	Early Glacial, 26	Base of Arctic Fresh-[water beds
INULEÆ			
GNAPHALIINÆ			
Helichrysum, sp.	Reid, 29	Middle Pliocene,30	Similar to several species
CYNAREÆ	Bentham, 2	Upper Miocene, 32	Two or three of Heer's species of *Cypselites*
CARDUINÆ			
Arctium Lappa, L.	Reid, 24a	Roman Period, 1	
,, sp.	,, 27	Upper Pliocene, 27	Two different forms
Carduus crispus, L.	,, 22, 23	Neolithic, 6	Bed B
,, *nutans*, L.	,, 24a	Roman Period, 1	
	,, 30	Late Glacial, 13	
	,, 27, 29	Upper Pliocene, 27	Not uncommon
	Zittel, 38		
,, cf. *nutans*, L.	Reid, 27, 29	Upper Pliocene, 27	Differs in sculpture and absence of longitudinal ridges.
	,, 26	Upper Pliocene, 29	
,, sp.	,, 29	Middle Pliocene, 31	Near *C. nutans*
,, sp.	,, 25	Paleolithic, 9	In alluvium
Cnicus lanceolatus, Willd.	,, 24a	Roman Period, 1	
	,, 24b	,, ,,	In two places, in a well and in a pot
	,, 22, 23	Neolithic, 2	Fruits rather small
	,, 22, 23	,, 7	
	,, 17, 22, 23	Interglacial, 21	
	,, 16, 27	Upper Pliocene, 27	Recorded in 16 with a ? as rare, fruit small
Cnicus (Carduus) sp.	,, 29	Middle Pliocene, 31	Near *C. lanceolatus*
,, *palustris*, Willd.	,, 23	Neolithic, 3	
	,, 22, 23	,, 2	
	, 30	Late Glacial, 11	
	,, 22, 23	Interglacial, 22	Fruits small
	,, 27	Upper Pliocene, 27	
	,, 28	,, ,, 29	
Cirsium heterophyllum, Hill.	,, 27, 29	,, ,, 27	
CENTAUREINÆ			
Centaurea Calcitrapa, L.?	,, 27, 29	,, ,, 27	One of two forms found
,, *Cyanus*, L.	,, 18, 22, 23	Neolithic, 2	
,, sp.	,, 27	Upper Pliocene, 27	The other of two forms found
ASTEREÆ			
BELLIDINÆ			
Bellis perennis, L.	Antonelli, 1 Zittel, 38	Post Glacial, 10	Leaves in volcanis tufa [or peperino
HETEROCHROMINÆ			
Aster Tripolium, L.	Reid, 23	Interglacial, 21	
EUPATORIEÆ			
AGERATINÆ			
Eupatorium cannabinum, L	, 22, 23	Neolithic, 8	In peat below sea-level
	,, 22, 23	,, 2	
	,, 19, 22, 23	Late Glacial, 15	Bed C in "blackearth," below Paleolithic deposits
	,, 17, 23	Interglacial, 21	
	,, 21, 23	,, 24	In peaty clay below 8 or 10 ft. of gravel
	,, 20, 23	,, 25	Ancient alluvium, below Paleolithic brickearth

TABLE XIII (continued)

Species.	References.	Dates and Localities.	Remarks.
Eupatorium cannabinum, L	Reid, 19, 22, 23	Interglacial, 23	Bed D, in lignite, below bed C
	,, 23	,, 20	
Eupatorium japonicum, Thunb. var.	,, 29	Middle Pliocene, 30, 31	Very near to, if not identical with a variety collected in the mountains of Japan
Eupatorium, sp.	,, 27, 29	Upper Pliocene, 27	
HELIANTHEÆ			
COREOPSIDINÆ			
Bidens cernua, L.	,, 22, 23	Neolithic, 2	
,, *tripartita*, L.	,, 24a	Roman Period, 1	
	,, 19, 22, 23	Late Glacial, 15	Bed C, a starved fruit
	,, 19, 22, 23	Interglacial, 23	Bed D, associated with a variety with four equal awns
	,, 16, 23 27, 29	Upper Pliocene, 28	
	,, 16, 23, 27	,, ,, 27	
	Zittel, 38		
	Reid, 23, 28	,, ,, 29	
Bidens tripartita, L. var.	,, 19	Interglacial, 23	Bed D, four equal awns
UNCLASSIFIED			
Genus ?	Reid, 29	Middle Pliocene, 31	Fruit poorly preserved and apparently germinated
Genus ?	,, 29	,, ,, 30	Fruit of some large Composite, but apex not preserved and base obscure
Baccharites, Sap. =*Lomatites*, Sap. (part.)	Saporta, 32b Zeiller, 37 Zittel, 38	Lower Oligocene, 38	Leaves like those of *Baccharis* and other Conyzinæ, first referred to Proteaceæ
B. acerosus, Sap.	Saporta, 31b, 31k, 32b Ward, 36 Zittel, 38	,, ,, 38	
B. aquensis, Sap.	Saporta, 31b, f, k, 32b Ward, 36 Zittel, 38	,, ,, 38	
	Boulay, 5	,, ,, 39	
B. obtusatus, Sap.	Saporta, 31k, 32b Ward, 36 Zittel, 38	,, ,, 38	
B. salicinus, Sap.	as above	,, ,, 38	
B. sinuatus, Sap.	Saporta, 31b, k, 32b Ward, 36 Zittel, 38	,, ,, 38	
Bidentites, Heer.	Heer, 11	Upper Miocene, 32	
	Bentham, 2	,, ,,	Heer's specimens, "probably the achene of an aquatic species"
	Zeiller, 37	Upper Pliocene	Reid's achenes of *Bidens*
B. antiquus, Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	

TABLE XIII (continued)

Species.	References.	Dates and Localities.	Remarks.
Carpolithus hyoseritiformis Berry	Berry, 3	Lower Eocene, 40	Fruit 8 mm. long, with about 10 simple awns or bristles; among "Incertæ Sedis."
Cypselites, Heer.	Heer, 11 Saporta, 31, 32 Zeiller, 37	Upper Miocene, 32 Lower Oligocene, 38	Fruits of Compositæ
C. angustatus, Herr.	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 8 mm. long, pappus 16 mm., sparse and setose, resembling *Crepis* fruits. Ettingshausen says this is like fruit of *Echitonium*.
C. aquensis, Sap.	Saporta, 32b	Lower Oligocene, 38	Achene 6·5 mm. long, pappus of scabrid setæ, longer than achene, very rare.
C. bisulcatus, Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 6mm. long, pappus stipitate, duplex, of slightly waved setæ, 13 mm. long
C. brachypus, Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 8mm. long, pappus stipitate, beak short, setose, 19 mm. long.
C. cincinnatus, Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 8mm. long, pappus 20 mm. long, of numerous wavy setæ, connate at the base.
C. costatus, Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 9mm. long, pappus 18mm. long, of setæ connate at the base. Greatly resembles *Arctium lanuginosum* of central Europe (Heer, 9)
C. deletus, Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	Pappus twice length of the achene. Probably Cynareæ (Heer, 9)
C. dubius (Al. Br.) Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	=*Achænites dubius*, Al. Br., achene 7mm. long, pappus slightly longer.
C. ellipticus, Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 7mm. long, pappus shortly stipitate, of very long slightly curved setæ. Compared with *Sonchus* by Heer, 9.
C. elongatus, Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 17 mm. long, shortly beaked.
C. Fischeri, Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 6mm. long, pappus 18 mm. long, of slightly wavy setæ. Perhaps a species of *Arctium*, Heer, 9
C. fractus, Sap.	Saporta, 32b	Lower Oligocene, 38	Pappus of very fine setæ, shorter than the achene, very rare.
C. grandis, Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 11 mm. & pappus 21mm, long, shortly stipitate, setose.
C. gypsorum, Sap.	Saporta, 31 b, k Schimper, 33 Ward, 36 Zittel, 38	Lower Oligocene, 38	Achene small & ribbed, pappus duplex, inner setæ numerous, outer 5-7 with dilated bases.

TABLE XIII (continued)

Species.	References	Dates and Localities	Remarks.
C. latinus, Massal.	Meschinelli, 14	Middle Oligocene, 37	Name only, quoted from Massalongo, Syll. pl. foss. p. 126
C. Lessingii, Heer	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 7 mm. long, pappus stipitate, of thick, rigid setæ
C. Miegi, Fliche	Fliche, 8a	(Tertiary)	In chalk or hard marl at Riedisheim, Mulhouse. Like *C. Ungeri*
C. Nægelii, Heer	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Pappus twice as long as achene, obliquely inserted (cp. I, 7), of wavy setæ. Probably Cynareæ. Heer 9
C. Philiberti, Sap.	Saporta, 31k	Lower Oligocene, 38	Achene 5 mm. long, pappus setose
C. Regelii, Heer	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 15 mm. long, pappus 15 mm. long, of plumose setæ, obliquely inserted (cp. I, 7)
C. rostratus, Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 8mm. long, pappus stipitate, setose
C. Schultzii, Heer	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 7 mm. long, pappus 18 mm. long, of numerous curved setæ
C. spoliatus, Sap.	Saporta, 32b	Lower Oligocene, 38	Achene 6 mm. long, no trace of pappus but a very obtuse beak, very rare. Rather like *Lactuca* with pappus off, Saporta, 32b
C. stenocarpus, Sap.	Saporta, 31k	Lower Oligocene, 38	Whole fruit 1·5 cm. long, pappus sessile, of compact setæ, very rare
C. striatus, Heer	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 8 mm. long, pappus 21 mm. long, stipitate, setose
C. tenuirostratus, Sap.	Saporta, 32b	Lower Oligocene, 38	Achene 5 mm. long, with truncate beak and no pappus, very rare
C. tenuis, Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 4·5 mm. long, pappus shorter, of wavy setæ
C. trisulcatus, Sap.	Saporta, 32b	Lower Oligocene, 38	Achene 7 mm. long, pappus sessile, only vestiges left, very rare
C. truncatus, Heer	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Pappus twice as long as fruit. Probably Cynareæ, Heer, 11
C. Ungeri, Heer	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 16mm. long, pappus markedly stipitate, of elongated plumose setæ, compared to *Podospermum laciniatum*, Heer, 2
Cypselites, sp.	Boulay, 4	Upper Miocene, 33	Not identified with any spec. described by Heer
Hieracites, Sap.	Saporta, 32b Zeiller, 37	Lower Oligocene, 38	Defined by Saporta (32b) as the receptacle and involucre of fossil Compositæ.

TABLE XIII (continued)

Species.	References	Dates and Localities	Remarks
H. stellatus, Sap.	Saporta, 32b Zittel, 38	Lower Oligocene, 38	Avignon, in calcareous marl, very rare. Sub-biseriate involucre and small receptacle, compared to *Inula Pulicaria* and referred tentatively to that genus by Saporta
H. nudatus, Sap.	Saporta, 32b Zittel, 38	Lower Oligocene, 38	Receptacle after flowering, with involucral bracts missing & achenes or florets densely packed, Saporta, cp. text
H. Salyorum, Sap.	Saporta, 31b Schimper, 33 Zittel, 38	Lower Oligocene, 38	Leaves in marly schist above gypsum beds; compared by Saporta with *Taraxacum obovatum*.
Hyoserites, Ettings.	Ettingshausen, 7 Schimper, 33	Upper Miocene	In plastic clay, achenes like those of the "Hyoseridées"
H. Lingua, Ettings.	Ettingshausen, 8	Upper Miocene, 35	Achenes lanceolate acuminate very shortly beaked, pappus absent, leaves also present
H. Schultzii, Ettings.	,, 7 Schimper, 33 Zittel, 38	Upper Miocene, 34	Achenes, pappus short, coroniform and paleaceous
Lychnophorites, Martius	Bentham, 2		Since referred to a Monocotyledon of the *Vellozia* type
Parthenites priscus, Sap.	Saporta, 31b Schimper, 33 Ward, 36 Zittel, 38	Lower Oligocene, 38	Leaves compared by Saporta to *Chrysanthemum Parthenium* and *C. Hysterophorus*
Silphidium, Mass.	Massalongo, 13 Bentham, 2 Meschinelli, 14 Schimper, 33 Zeiller, 37 Zittel, 38	Middle Oligocene, 36	Leaves, like *Silphium laciniatum* (Massalongo); "it is probable that the four species are really only one" (Schimper); "a wild guess without a particle of evidence in support of it" (Bentham)
S. gracile, Mass.	Massalongo, 13 Meschinelli, 14 Schimper. 33	Middle Oligocene, 36	
S. heteromallum, Mass.	Massalongo, 13 Meschinelli, 14 Schimper, 33	Middle Oligocene, 36	
S. Proserpinæ, Mass.	Massalongo, 13 Meschinelli, 14 Schimper, 33	Middle Oligocene, 36	Also a variety, *subdenticulatum*
S. Visianicum, Mass.	Massalongo, 13 Meschinelli, 14 Schimper, 33	Middle Oligocene, 36	Compared to *Silphium gummiferum* of N. America by Massalongo; also a variety, α *denticulatum*

the Andes had begun to appear in late Cretaceous times, the height being increased by the Miocene uplift all around the Pacific.

In the previous chapter it was shown that the origin of the Compositæ was most probably due to the ecological conditions at high altitudes in the Andes. The palæobotanical evidence shows that the origin of the family took place at approximately the same date as the first upheaval of the Andes. This synchronising of events in climatic evolution with events in plant evolution is in accordance with Coulter's explanation of orthogenesis (see XI, 13, and Chap. XI, B). The rapidity of dispersal, which is characteristic of the family, would readily account for the appearance of representatives in the Mediterranean region within a geologically short interval of the origin of the earliest forms. The time available for this dispersal and the differentiation of the types is nearly the whole of the Eocene Period and opinions concerning even the approximate length of that period vary very considerably.

It is more than probable that the Compositæ were among the first arrivals in the new mountainous habitats (cp. Krakatau and Taal, Chap. X), and this would account, in part at least, for their predominance in those regions at the present time. The Compositæ, indeed, seem to have been formed with the mountains by the mountains for the mountains.

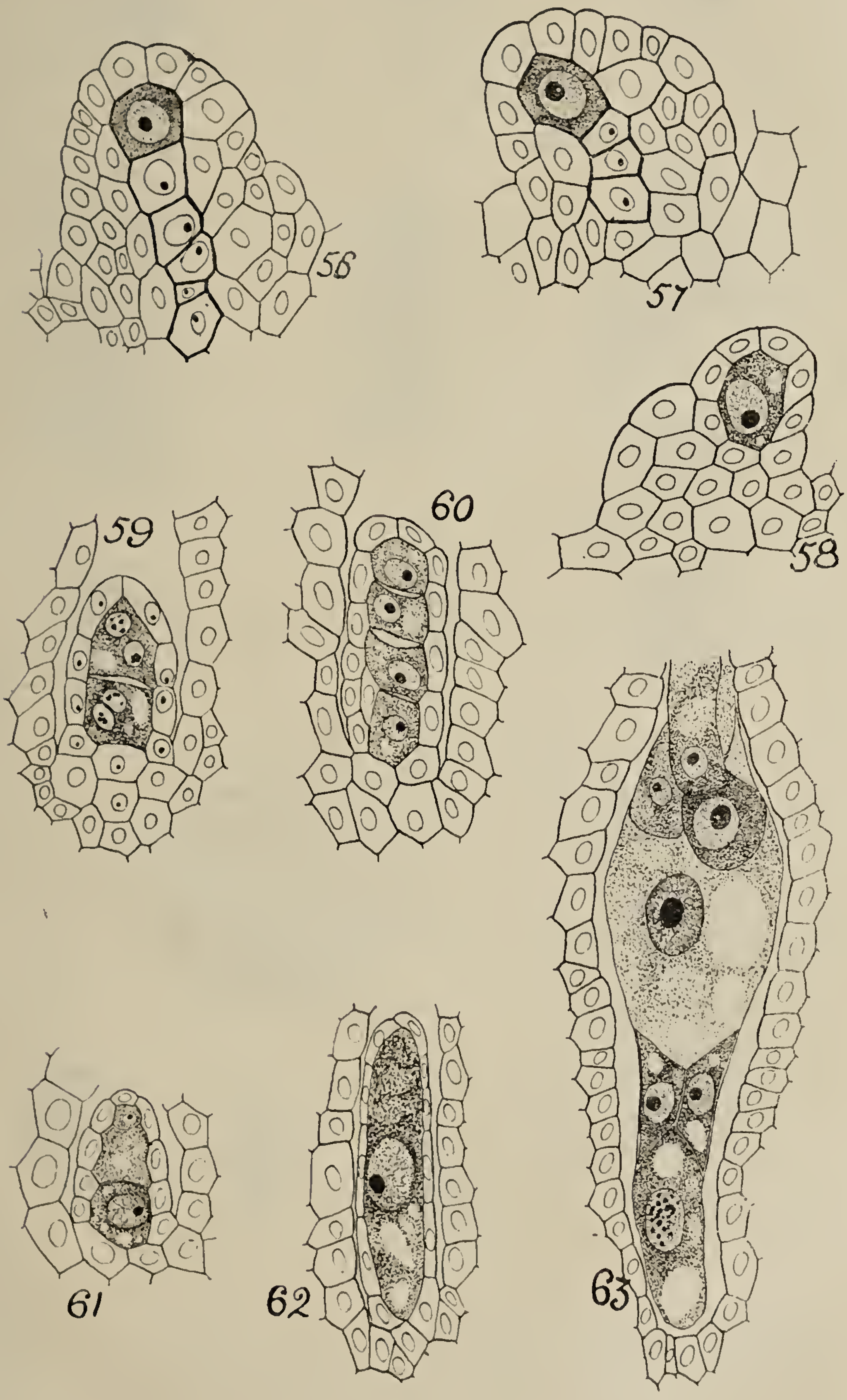
B. CYTOLOGY OF THE COMPOSITÆ.

This part of the subject has been worked out in considerable detail but only in a comparatively small number of genera. The chief papers will be found mentioned in Section B of Bibliography XII. Parthenogenesis, apogamy and double fertilisation have claimed attention but such data have little phyletic value, except as an explanation of the large numbers of microspecies in some of the genera. Spermatogenesis and oogenesis have been described in a number of forms and the figures given of *Senecio vulgaris* may be regarded as typical.

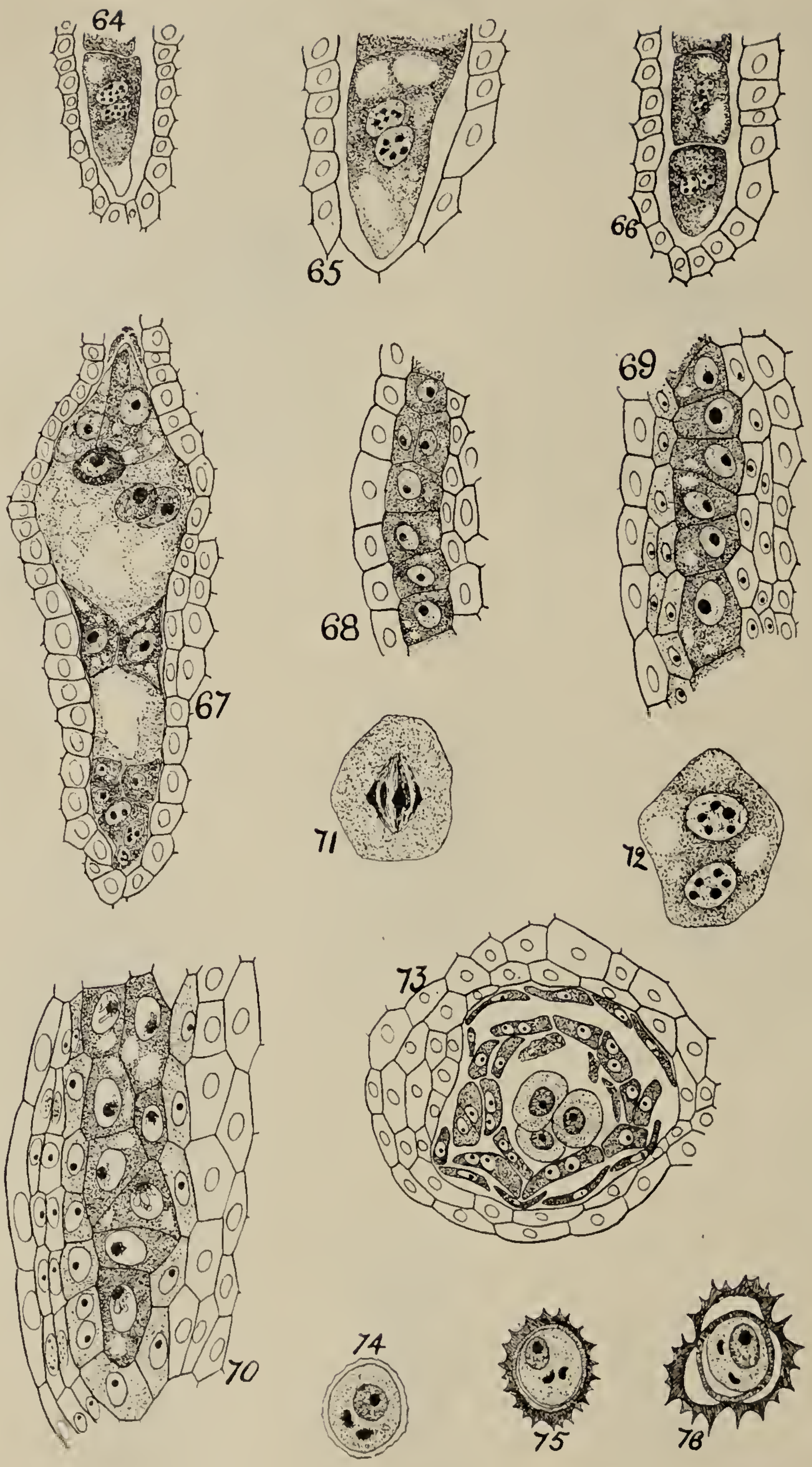
Spermatogenesis :—Considering spermatogenesis first, the archesporium is sub-epidermal, usually only one row of cells (Fig. 68), which cuts off a single layer outside (Fig 69). This layer divides into three (Figs. 69-70); the innermost of the layers forms the tapetum, the cells of which are frequently bi-nucleate (Figs. 70-73). The middle layer finally degenerates and functions as a subsidiary tapetum (Fig. 73). The single row of archesporial cells rarely undergo more than one division before the pollen mother cells are formed (Fig. 70), so that only one tetrad of microspores is usual in tranverse sections of the sac (Fig. 73). The separation of the spore mother cells from each other takes place between synapsis (Fig. 70) and the metaphase of the reduction division (Fig. 71). The differentiation of the exine has already been mentioned (Chap. IV, B) as being sometimes intermediate in *Senecio* between the Tubulifloræ and the

Liguliforæ (see Figs. 22-24). There is a large vegetative nucleus and two small, more or less vermiform male nuclei.

Oogenesis. Considering oogenesis next, the first controversial point is the cauline or lateral origin of the ovule. Most writers are



Figs. 56-63. Oogenesis in *Senecio vulgaris.*



Senecio vulgaris.
FIGS. 64-67. Antipodal development. FIGS. 68-76. Spermatogenesis.

agreed that the single ovule belongs to one or other of the carpels, but Campbell (44) considers it to be primitively cauline. The cauline vascular bundle ends in a flattened or cup-shaped disc (cp.

11, 63), and the primitively lateral position of the ovule is confirmed by the anomalous cases figured by the writer (99) in which all the four lateral ancestral placentæ of the two carpels are indicated.

The single archesporial cell is differentiated at an early stage as the end cell of a row in the middle of the young ovule (Figs. 56-57). The integument shows an unilateral development almost from its first appearance (Figs. 56-58). While reduction division is taking place, the integument develops very rapidly, so that the following stages occur within a single-layered nucellus enclosed by the integument with its peculiar epithelium. A row of four megaspores is formed, with the middle or first formed wall very thick (Figs. 59-60). This wall disappears and the two middle megaspores degenerate (Fig. 61); the apical megaspore also degenerates and the basal one develops into the embryo sac (Fig. 62). Palm (84) considers that in *Solidago* and *Aster* the sac is formed from the micropylar megaspore and that the three lower megaspores develop into the haustorium. He is, however, adversely criticised by Chamberlain (49); and most other workers on the embryo sac of the Compositæ agree in describing the sequence of events as above.

This question has recently become rather controversial. Holmgren (64) describes six methods of embryo sac development in the Compositæ.

A. with a row of four *cells* as megaspores,
    (1). Sac from the chalazal megaspore, normal and eight-nucleate, as in most cases (69, 77, 91, 93, etc.);
    (2). Sac from one of the other three megaspores and not always eight-nucleate, as in *Senecio vulgaris* (Winge, 113), *Solidago serotina* and *Aster novæ-angliæ* (Palm, 84), all three species with persistent megaspores in the antipodal region.

B. With only one wall formed after the heterotypic nuclear division,
    (3). Sac from the two micropylar megaspores, as in *Tanacetum vulgare* (Palm, 85);

C. With no wall formed during meiosis;
    (4). Sac from the micropylar megaspore nucleus and eight-nucleate, as in *Anthemis tinctoria* (Holmgren, 64);
    (5). Sac from the two micropylar megaspore nuclei and eight-nucleate with persistent chalazal megaspores as in *Tanacetum vulgare* (Palm, 85);

(6). Sac from all four megaspore nuclei and sixteen-nucleate, as in *Pyrethrum parthenifolium* var. *aureum* (Palm, 85).

Winge's interpretation of his figures is rather unsatisfactory and has been shown to be wrong by Carano (47). In his English summary he states that three megaspores degenerate but in the text he figures and describes three large bi-nucleate megaspores and three very minute, degenerate antipodals in the region of the egg-apparatus. He considers that the micropylar megaspore develops into the embryo sac, but his Fig. 3 shows the chalazal megaspore slightly larger than the others, and his Fig. 4 shows three small megaspores and a large one, the row being isolated so that the micropylar or chalazal position of the large megaspore cannot be determined.

Winge's figures, apart from the very problematical degenerate antipodals, are similar to those given here and are best interpreted in a similar way, as Carano (46-47) and others maintain.

Palm's interpretation of the phenomena in *Aster* and *Solidago* has already been more or less discredited by Chamberlain (49). There remain the anomalies of types 3-6; these all occur in the Anthemideæ and it is possible that further investigations will confirm the presence in this tribe of anomalous embryo-sac development, as in *Plumbagella* (51), *Lilium*, etc.

The disappearance of the upper megaspores is very clear in *Senecio* and *Silphium*. Even in the interesting case of an aposporic embryo sac described by Rosenberg (90) in *Hieracium*, the tetrad was formed and the chalazal megaspore was the last to disappear before the nucellus was pushed on one side by the growth of the abnormal sac. The origin of the chalazal haustorium from the antipodals can be taken as without any properly authenticated exception.

In the mature embryo sac there is the normal arrangement of synergids, oosphere, endosperm or fusion nucleus, and three antipodals (Fig. 63). The nucellus disappears completely, leaving the embryo sac surrounded by the epithelial layer of the integuments, or a few remnants may be left to form the so-called nucellar cap (Fig. 67).

Antipodal Cells. In *Senecio vulgaris* the basal or chalazal antipodal elongates (Fig. 63) and divides (Figs. 64-67), the basal portion showing as many as four extra antipodal cells in one longitudinal section, each cell having one or more nuclei (Fig. 67). This is the structure of which it is said that "the antipodals of many of the Compositæ are organised into an aggressive haustorium

TABLE XIV

List of Antipodal Cells in Compositæ.

Species	Nos.	References	Remarks.
SENECIONEÆ			
TUSSILAGININÆ			
Tussilago sp.	4 usually	Guignard, 60 Coulter and Chamberlain, 50	
Petasites sp.	3	ditto	Active and haustorial
SENECIONINÆ			
Doronicum sp.	3	ditto	,, ,,
Cineraria maritima	10-12	Goldflus, 58	Uniseriate, polygonal or rounded, and continued into pseudochalaza
Senecio aureus	3-6	Mottier, 78 C. and C., 50	haustorial
S. Doria	8-9	Goldflus, 58	Uniseriate, upper large lower pass gradually into chalazal cells
S. vulgaris	3	Strasburger, 101 Warming, 112	Normal arrangement, one chalazal & the other two side by side above
		Guignard, 61	Uniseriate
	3-4	Strasburger, 100	Normal or 4, uniseriate, the chalazal antipodal having divided
	3-6	Small (Figs. 63-67)	Chalazal antipodal dividing & multinucleate
Cacalia hastata (*Senecio*)	3	Goldflus, 58	Chalazal antipodal elongates to give tube
CICHORIEÆ			
HYOSERIDINÆ			
Catananche lutea	3	Goldflus, 58	Normal or uniseriate
Cichorium Intybus	3	Hegelmaier, 62	
HIERACIINÆ			
Hieracium amplexicaule	3	Hegelmaier, 62	
HYPOCHOERIDINÆ			
Hypochæris maculata	3	Hegelmaier, 62	
Taraxacum officinale	3	Schwere, 98	
	4-5	Hegelmaier, 62 C. and C., 50	Haustorial
Taraxacum sp.	3	C. and C., 50	Haustorial
LACTUCINÆ			
Sonchus oleraceus	3	Lavialle, I, 52	Uniseriate
SCORZONERINÆ			
Tragopogon floccosus	7-9	Hegelmaier, 62	Haustorial
Scorzonera alpina	3-4	Goldflus, 58	Haustorial, normal arrangement or with chalazal antipodal divided
S. hispanica	4-7	Goldflus, 58	Haustorial
CALENDULEÆ			
Calendula arvensis	3	Carano, 46	One synergid develops into large micropylar haustorium
C. lusitanica	3	Billings, 42 C. and C., 50	ditto
ANTHEMIDEÆ			
CHRYSANTHEMIDINÆ			
Pyrethrum balsaminatum (*Chrysanthemum*)	3	Ward, 111	Normal
Leucanthemum lacustre (*Chrysanthemum*)	3-7	Goldflus, 58	In two rows, chalazal antipodal enlarges and shows abnormal nuclei as in *Senecio vulgaris*

TABLE XIV (continued)

Species.	Nos.	References.	Remarks
Chrysanthemum Leucanthemum	3	Goldflus, 58	Chalazal antipodal much enlarged and elongated
INULEÆ			
GNAPHALIINÆ			
Antennaria alpina	at least 19	Juel, 70 C. and C. 50	Quite a tissue by continued division
INULINÆ			
Inula Helenium	6	Goldflus, 58	In two rows or scattered
BUPHTHALMINAE			
Telekia speciosa (*Buphthalmum*)	3	Goldflus, 58	All large, elongated chalazal gives a long tube
CYNAREAE			
CENTAUREINAE			
Serratula coronata	3	Goldflus, 58	Uniseriate
Centaurea cirrhata	3	Lavialle, I, 52	Uniseriate
C. crocodylium	3	Goldflus, 58	Normal
C. dealbata	4	Goldflus, 58	Uniseriate, haustorial
C. macrocephala	4	Goldflus, 58	Uniseriate, haustorial
ASTEREAE			
HOMOCHROMINAE			
Solidago serotina	3	Palm, 84	Haustorial, interpreted by Palm as the three chalazal megaspores
BELLIDINAE			
Bellis perennis	6-7	Carano, 45	One cell with 3 nuclei, another very large containing a pseudo-oosphere (cp. Chamberlain 48)
HETEROCHROMINAE			
Aster Novæ-Angliæ	3-13	Chamberlain, 48 C. and C., 50	Up to 20 nuclei in 1 cell pseudo-oosphere present
	3-13	Goldflus, 58	No trace of pseudo-oosphere
Galatella rigida (*Aster*)	20-25	Goldflus, 58	Forming a parenchyma
CONYZINAE			
Conyza sp.	8 10	Guignard, 60 C. and C., 50	Haustorial
HELIANTHEAE			
MELAMPODIINAE			
Silphium spp.	2-7	Merrell, 77	One case of 7 cells, 8 nuclei in one of them "with indications of amitotic divisions"
	3-8	C. and C., 50	
ZINNIINAE			
Zinnia tenuiflora	3-4	Hegelmaier, 62	Uniseriate or with upper cell divided
VERBESININAE			
Dracopis amplexicaulis (*Rudbeckia*)	3-4	Goldflus, 58	Uniseriate
Echinacea intermedia (*Rudbeckia*)		Goldflus, 58	A small number, polygonal
Rudbeckia speciosa	2-3	Nawaschin, 80	Two antipodals figured, one enlarged and very like an oosphere
Helianthus annuus	3	Hegelmaier, 62	Chalazal antipodal enlarged
	2	Hofmeister, 63	Both cells large and elongated
		Nawashin, 80	ditto
		Carano, 46	ditto, upper cell multinucleate
H. Maximiliani	3	Goldflus, 53	Uniseriate, upper antipodal enlarged & as long as the rest of the sac

TABLE XIV (continued)

Species	Nos.	References	Remarks
H. tuberosus	2-3	Goldflus, 58	Uniseriate
Helianthus sp.	3	Täckholm, 103	Chalazal antipodal degenerates but upper cell is very large and long
CORROPSIDINAE			
Dahlia gracilis	2-3	Goldflus, 58	Uniseriate or normal, binucleate or multinucleate
Bidens leucantha	3	Hegelmaier, 62	One small and two large
Cosmos bipinnatus	2	Täckholm, 103	Both large, 19 nuclei figured in one cell
Cosmidium Burridgeanum (*Cosmos*)	2	Täckholm, 103	Both large, one very long with 16-25 nuclei
HELENIEAE			
HELENIINAE			
Gaillardia bicolor	3	Goldflus, 58	Uniseriate, lower short, middle long and narrow, upper short

which can only be regarded as a very specialised organ" (50 p. 108).

In connection with the origin of the Compositæ from the Lobelioideæ it is interesting to note that an antipodal haustorium is recorded in *Campanula americana* (40), *C. rotundifolia* (39) and *Lobelia inflata* (97), and that most of the Campanulaceæ develop either micropylar or chalazal haustoria or both (50). Another point of similarity is that in both families the epithelium of the integument is conspicuous, always in the Compositæ, sometimes in the Campanulaceæ.

The general phylogenetic value of the endosperm and haustorium is considerable, as shown by Jacobsen-Stiasny (68). In the Compositæ the antipodal haustorium, presumably derived from the similar structure in the ancestral Lobelioideæ, has been described in a number of genera and the results, which are summarised in Table XIV, will now be discussed.

According to our present knowledge there are two methods by which the antipodals develop into a special haustorial apparatus, one by elongation and free nuclear division or amitosis or both, and the other by elongation accompanied by cell division giving a tissue. Both these methods occur to a certain extent in *Senecio vulgaris*.

The tube haustorium is more developed in other Senecioneæ (*Cacalia hastata*) and so is the tissue haustorium (*Senecio Doria* and *Cineraria maritima*). The Tussilagininæ have the haustorium only slightly developed.

In the Cichorieæ the haustorium is only slightly developed throughout, especially in the Lactucinæ; the exception is the advanced, rather special group, Scorzonerinæ.

In the Calenduleæ the antipodals are more or less normal but a special micropylar haustorium is developed.

The development of the haustorium in the Chrysanthemidinæ closely approximates to that in *Senecio*.

Although the data in the Inuleæ are very meagre, what there is tends to support the diphyletic development of that tribe, the Inulinæ being near the Senecioninæ and leading to the Centaureinæ through the Buphthalminæ.

In the Centaureinæ the slight development of the haustorium is rather surprising considering the advanced position of the tribe, but is, nevertheless, quite in keeping with the slight development of the haustorium in the ancestral Buphthalminæ.

The haustorium in the Astereæ is slightly developed in the primitive Homochrominæ, more developed in the more advanced Bellidinæ and Conyzinæ, and most developed in the advanced Heterochrominæ. An investigation of the antipodals of the Eupatorieæ should prove interesting in view of the derivation of that tribe from the Heterochrominæ.

The coenocytic tube type of haustorium is best developed in the Heliantheæ. The structure of the organ in the primitive Verbesininæ is sometimes quite simple and in most, if not all cases, it is less developed than it is in the Coreopsidinæ, especially *Cosmos*. The haustorium in the Zinniinæ is simple, in the Melampodiinæ it is more developed (cp. Fig. 79).

The development, as far as it is known, in the Helenieæ agrees with the origin of that tribe from the Senecioneæ directly and not indirectly via the Heliantheæ.

In spite of the very restricted number of species in which the antipodal development is known, it is clear from the above that the data are drawn from sufficiently representative genera to furnish some interesting confirmation of previous phyletic suggestions.

Chromosomes. Meek's theory (76) of a constant diameter for the chromosome with a gradual elongation of each chromosome during evolution, and conjugation of the chromatin units in fours when the length-limit has been reached to give chromosomes with twice the original diameter, has been criticised by Farmer and Digby (54), who agree, however, that although the chromosome width cannot be strictly correlated with the evolutionary sequence, many of the lower animals and plants have smaller and narrower chromosomes, as compared with those of higher forms. The chromosome width varies so much in plants that it is certainly not very useful in dealing with phylesis within a family.

Apart however from these considerations, the variation in the chromosome number in the Compositæ shows some interesting points. These numbers are recorded in various lists by Gates (57), Winge (114), and Ishikawa (66-67), and all the known numbers are given in Table XV. Tischler (109) and Winkler (115) have given general accounts of the phenomena, but they are not yet available. Winge (114) considers the Compositæ specially, distinguishing as cardinal numbers 9 for the Anthemideæ and 8 for the Heliantheæ; his classification of the genera seems, however, to be mainly on the chromosome number rather than on any generally accepted system, *e.g.*, he puts *Bellis* in the Anthemideæ and *Calendula* in the Heliantheæ. Rosenberg (94) mentions the Compositæ series of numbers and shows how they may arise by unequal heterotypic divisions, with or without the formation of subsidiary nuclei with a small number of chromosomes.

The known chromosome numbers of the Compositæ are given in Table XV, with calculated numbers in brackets. Where no gametic number is given the species is apogamous and where a (v) is appended to the name of an author he has given verbal information to the authority quoted below.

Considering the numbers as given in Table XV, the first case is *Senecio vulgaris* for which Ishikawa (67) records 19. The present investigation shows 5 at reduction division, the metaphase (Fig. 71) is very clear and in the telophase (Figs. 59, 72) the number again appears as 5, with some indication of an idiochromosome which shows also in some of the divisions of the chalazal antipodal cell (Figs. 65-66). The anomalous nuclear divisions in the basal antipodal show other numbers also, about 20 (Fig. 63) or 10 (Fig. 64). As *S. vulgaris* is an aggregate species it is probable that Ishikawa examined some other member of the aggregate, in which apogamy or hybridisation may have led to complications. The figures 56-76 were drawn in 1914, when the writer was unaware of the only two examples of 5 then known as a chromosome number in the Compositæ, but quite a number of other examples with 5 have since been described.

It will be seen from Table XV that the 9, 18, 27, 36, 45 series holds good for all the Anthemideæ except *Achillea Millefolium*, in which the number is not known with certainty, and *Centipeda orbicularis*, which has 10. The series 8, 16, 32 likewise holds good for the Heliantheæ with certain exceptions.

If we seek any phyletic data in the chromosome numbers, the 5, 10, 15, 20, 30, 60 series is indicated as the primitive one in accordance with the phylesis of the family as shown by other data. This is the series of the Senecioneæ, with the cardinal number

TABLE XV.

Chromosome Numbers in the Compositæ.

Species.	Numbers Gametic	 Somatic	References
SENECIONEAE			
SENECIONINAE			
Senecio vulgaris	19		Ishikawa, 67
	5		Small, figs. 59, 65, 66, 71, 72
S. sagittatus	5		Ishikawa, 67
S. nikœnsis	10		,,
Ligularia tussilaginea	30		Miyaji
(*Senecio*)			Ishikawa, 67
L. tussilaginea var. *crispata*	30, 31		Miyaji
			Ishikawa, 67
L. japonica	±60		Miyaji (v)
			Ishikawa, 67
CICHORIEAE			
LAPSANINAE			
Lapsana humilis	8		Ishikawa, 67
L. apogonoides	22		,,
CREPIDINAE			
Picris hieracioides	5		,,
Crepis virens	3	6	Rosenberg, 92
			Beer, 41
			Digby, 52
			Gates, 57
			Ishikawa, 66, 67
C. tectorum	4	8	Juel, 70
			Beer, 41
			Gates, 57
			Ishikawa, 67
C taraxacifolia	4	8	Digby, 52
			Ishikawa, 67
C. lanceolata var. *platyphyllum*	5	10	Tahara and Ishikawa, 108
C. japonica	8	16	Tahara, 104
			Gates, 57
HIERACIINAE			Ishikawa, 66, 67
Hieracium venosum	7	14	Rosenberg, 91
			Gates, 57
			Ishikawa, 67
H. auricula	9	18	Rosenberg, 91, 94
			Gates, 57
			Ishikawa, 66, 67
H. umbellatum	9	18	Juel, 70
			Gates, 57
			Ishikawa, 66, 67
,, (apogamous race)		27	Rosenberg, 94
H. excellens	17	34	Rosenberg, 91
			Gates, 57
			Ishikawa, 66, 67
	18+18+6	42	Rosenberg, 94
H. Pilosella	18	36	,, ,,
H. aurantiacum	c. 18	c. 36	,, ,,
H. flagellare	21	c. 42	,, 91
			Gates, 57
			Ishikawa, 66, 67
H. boreale	27		Rosenberg, 94
H. lævigatum	27		,, ,,
H. lacerum	27		,, ,,
H. pseudoillyricum	27		,, ,,
HYPOCHOERIDINAE			
Taraxacum confertum	8	16	Rosenberg, 93
			Gates, 57
			Ishikawa, 66, 67

TABLE XV (continued)

Species	Numbers		References
	Gametic	Somatic	
T. platycarpum	8	16	Osawa, 82
			Ishikawa, 67
T. officinale	12-13	24-26	Juel, 70
	12-13	26-30	Gates, 57
	12-13	20-30	Ishikawa, 66, 67
T. albidum		36-40	Osawa, 82
			Ishikawa, 67
LACTUCINAE			
Lactuca denticulata	5		Ishikawa, 67
L. Keiskeana	5		Miyaji
			Ishikawa, 67
L. lanceolata	5		,,
,, var. *platyphylla*	5		Tahara and Ishikawa, 108
			Ishikawa, 67
L. tamagawensis	8, often 7		,, ,,
L. stolonifera	8		,, ,,
L. villosa	9		,, ,,
L. laciniata	9		,, ,,
L. Thunbergia	12,often 11		,, ,,
L. debilis	24		,, ,,
Sonchus oleraceus	16		,, ,,
SCORZONERINAE			
Tragopogon pratensis	6		Beer, 41
	7		Ishikawa, 67
CALENDULEAE			
Calendula officinalis	14	28	Lundegardh, 74
			Ishikawa, 66, 67
			Winge, 114
Calendula sp.	16	32	Rosenberg, 88
			Ishikawa, 66, 67
			Winge, 114
ANTHEMIDEAE			
ANTHEMIDINAE			
Achillea Millefolium	24 ?	48 ?	Lundegardh, 74
			Ishikawa, 66, 67
			Winge, 114
Anthemis tinctoria	9	18	Lundegardh, 74
			Holmgren, 64
			Ishikawa, 66, 67
			Winge, 114
CHRYSANTHEMIDINAE			
Chrysanthemum carinatum	9		Tahara, 106
			Ishikawa, 74
			Winge, 114
C. coronarium	9		ditto
C. japonicum	9		ditto
C. lavandulæfolium	9		ditto
C. lineare	9		Tahara (v)
			Ishikawa, 67
C. Marchalli	9		Tahara, 106
			Winge, 114
C. myconis	9		Tahara (v)
			Ishikawa, 67
C. Nipponicum	9		Tahara, 106
			Ishikawa, 67
			Winge, 114
C. roseum	9		Tahara, 106
			Ishikawa, 67
C. segetum	9		Tahara (v)
			Ishikawa, 67
C. indicum	18		Tahara (v)
			Ishikawa, 67

TABLE XV (continued)

Species	Numbers		References
	Gametic	Somatic	
C. Leucanthemum	18		Tahara, 106
			Ishikawa, 67
			Winge, 114
C. hakusanense	27		Tahara (v)
			Ishikawa, 67
. *morifolium* var. *genuinum* f. *japonicum*	27		Tahara, 106
			Ishikawa, 67
			Winge, 114
C. Decaisneanum	36		ditto
C. arcticum	45		ditto
C. marginatum	45		Tahara (v)
			Ishikawa, 67
Matricaria ambigua	9		Tahara (v)
			Ishikawa, 67
M. Chamomilla	9		Lundegardh, 74
			Beer, 41
			Ishikawa, 67
			Winge, 114
Centipeda orbicularis	10		Ishikawa, 67
Tanacetum vulgare	9		Rosenberg, 89
			Ishikawa, 66, 67
			Winge, 114
INULEAE			
GNAPHALIINAE			
Antennaria dioica	12-14	24 ?	Juel, 69
		20	Coulter and Chamberlain, 50
		24-28	Gates, 57
		24	Ishikawa, 67
A. alpina	12-14	45 ?-50	Juel, 69
		40-50	Coulter and Chamberlain, 50
		45-50	Gates, 57
		45-50	Ishikawa, 66, 67
CYNAREAE			
CARDUINAE			
Saussurea affinis	18		Ishikawa, 67
ASTEREAE			
BELLIDINAE			
Bellis perennis	9		Ishikawa, 67
			Winge, 114
HETEROCHROMINAE			
Erigeron philadelphicus	8	16	Land, 72
			Ishikawa, 66, 67
E. strigosus	8	16	ditto
E. dubius var. *glabrata*	9		Tahara (v)
			Ishikawa, 67
E. annuus	13	26	Tahara, 107
			Ishikawa, 67
E. linifolius	26		Tahara, 107
			Ishikawa, 67
EUPATORIEAE			
AGERATINAE			
Ageratum conyzoides	10		Ishikawa, 67
Eupatorium glandulosum		49-52	Holmgren, 65
HELIANTHEAE			
MELAMPODIINAE			
Silphium integrifolium	8		Merrell, 77
			Coulter and Chamberlain, 50
			Ishikawa, 66, 67
			Winge, 114
S. laciniatum	(8)	16	Land, 72
			also 60, 66, 67, 114

TABLE XV (continued)

Species	Numbers		References
	Gametic	Somatic	
S. terebinthinaceum	8		Merrell, 77
		16	Land, 72
			Ishikawa, 66, 67
			Winge, 114
AMBROSIINAE			
Xanthium Strumarium	18		Ishikawa, 67
ZINNIINAE			
Zinnia elegans	12		Ishikawa, 67
VERBESININAE			
Wedelia prostrata	15		Ishikawa, 67
Helianthus annuus	9		Tahara, 105
			Ishikawa, 67
	16 ?		Bönicke, 43
			Winge, 114
COREOPSIDINAE			
Dahlia coronata	16	32	Ishikawa, 66, 67
			Gates, 57
			Winge, 114
D. variabilis	32	64	ditto
Dahlia, garden varieties such as *D. Juarezii* and *D. gracilis* believed to be derived from *D. variabilis* and *D. coccineum*	32	64	Ishikawa, 66, 67

occurring in *Senecio*. As *Lactuca* has been suggested to be the primitive genus of the Cichorieæ, derived from the Senecioneæ, it is interesting to note that the most frequently occurring number in this genus is 5. In the same genus, *Lactuca*, both 8 and 9 occur also (cp. *Erigeron*), so it is clear that the number may vary in one genus between the various cardinal numbers, 5, 8, 9. This being so, the derivation of the various numbers from the primitive series may quite easily follow the derivation already suggested of the various tribes from the Senecioneæ.

The various types of hybridisation, especially the forms of philozygoty and pathozygoty distinguished by Winge (114, pp. 196-201), account for the variation in number *within* each of the three main series. The origin of the 8 and 9 series from the 5 series may be accounted for by the passing of n—1 chromosomes to one pole and of n+1 to the other, as observed by Winge (*loc. cit.*) in *Callitriche verna*. More unequal division of the chromosomes has been observed by Rosenberg (94) in *Hieracium*; the variations which he describes as semi-heterotypic include the migration of 3 gemini to one pole and 21 unpaired chromosomes to the other, and similar, very unequally balanced numbers.

C. LATEX IN THE COMPOSITÆ.

The phyletic value of the facts concerning the distribution of latex throughout the family and in the individual plants is considerable, but must always be subordinate to that of floral details. Col, who has investigated the latex of the Compositæ more closely than any other author, clearly recognised this. He writes (120d, p. 155) " On juge en général de l'importance d'un caractère anatomique á sa constance dans une famille ou une tribe établie sur d'autres caractères ; cela n'est un moyen certain qu'autant que ces dernieres, tirés le plus souvent des organes reproducteurs, ont valeur réelle."

The interpretation of these anatomical facts depends to a large extent on the theory which is adopted of the physiological function of latex and laticiferous tubes and vessels. Many theories have been given, such as the excretion theory of Treviranus, 1827, (see 124), who compared the laticiferous vessels with gum-resin canals That latex is an excretion has been held by De Candolle (Physiologie végétal, 1832) and Richards (Eléments de botanique, 7th edit.). That latex is a secretion with a protective function has been held by Schimper (140), Groom (130), Tschirch (150), Kny (135), Czapek (120) and Sharples (142). The analogy of latex to the blood suggested by Schultz (1841) was developed by Trécul (146), who considered the laticiferous vessels to be " le systéme veineux " and the xylem vessels to be " le systéme artériel."

Many others have considered that latex has a nutritive function and is translocated, such as Treub (148), Biffen (117) who got positive experimental results for the translocation of sugar and proteid, Schwendener (141), Faivre (123, 125-6), Jussieu, Decaisne, Naudin, Hanstein (132), Schullerus, Haberlandt (131) and the writer (143). This theory is opposed by Schimper, Groom (130), Kniep (134), Leblois (136) and to a certain extent by Mangham (137).

Spence (145) considers that caoutchouc is a food reserve, rich in chemical energy, which is rendered available by oxydases, and he compares it with the glycogen in the liver which is broken down by glycolytic enzymes. The proteids are rendered available by proteolytic enzymes (127-8). That the laticiferous system has a dual function, nutritive and excretory, has been held by Sachs (Physiol. of Plants) and Faivre (124). Finally, a water-storage function has been suggested by Parkin (138).

The latex-containing elements in the Compositæ are cells, sacs or vessels. Comparisons in this family and in others, especially in the Nymphæaceæ, show that a series of transitions occur even in the same genus, from isolated, isodiametric cells containing latex through elongated, isolated, latex cells to sacs consisting of two or three elongated cells placed end to end, as in *Nuphar* and *Nelumbium*, or longer sacs consisting of numerous cells in long rows, as in *Brasenia* and *Cabomba* (144, Vol. I, pp. 48-9).

Numerous cases of transitions from such sacs to vessels are known; the vessels, indeed, frequently show the sac stage before the walls break down to produce the typical anastomosing system. Transitions between vessels and tubes are recorded for *Hevea* and *Manihot* (Euphorbiaceæ) and for *Tupa salicifolia* (Lobeliaceæ), cp. Trécul, 146, Tome VII, p. 178. Transitions from the common oleo-resin canals of the Compositæ to laticiferous vessels are recorded by Trécul (op. cit., p. 181) in *Gundelia Tournefortii* of which he remarks " Ces vaisseaux donnent donc un degré de transition de plus entre le canaux oléo-résineux des autres Composées et les laticifères les plus parfaits." See also 137a for somewhat similar canals in the primary and secondary phloem of *Rhus*.

Cells containing oleo-resins are so common in higher plants as excretory organs that the widespread occurrence of cells which also contain reserve proteid and carbohydrate does not call for any particular explanation.

The elongation of these cells and their organisation into sacs and vessels, with the extreme and peculiar case of the development of tubes instead of vessels, is best regarded as part of the epharmonic variation which produces climbing plants.

Before developing this suggestion it will be advisable to consider the function of laticiferous tissue in general. The oleo-resin cells are in the first place mere receptacles for excretory products; the same may be said of these cells as Record says of resin tracheids (139), *i.e.* they " represent one form of reservoir for excretions." The addition of reserve food material—proteid (129), etc., caoutchouc (145), carbohydrate, etc.—need not change or eliminate the excretory function. The second class of material is rendered available for immediate use by specific enzymes, which would separate the secretions from the excretions by solution and diffusion. The simple, isolated latex cell has, therefore, two functions; it is a receptacle for excretions and for food reserves.

The organisation of the cells into sacs produces no change in this duality of function. The food reserves still require to be dissolved before they can pass from one cell to another, from one part of the plant to another. The breaking down of the dividing walls when the sacs become vessels renders possible the translocation of the solid materials from one part of the vessel to another part of the same vessel no matter how distant it may be. That such translocation of solids does take place is considered proved for *Lactuca* by the preliminary experiments described by the writer (143). That translocation of sugars in solution takes place is proved for *Euphorbia* by Biffen's quantitative analysis of the sugar-content of the latex in undarkened and darkened leaves (117). That both sugars and proteids are manufactured in the leaf and pass at once into the laticiferous vessels or tubes is rendered very probable by the above experiments, by the fact recorded by Biffen (*loc.cit.*) and others that the blind-endings of the laticiferous system are generally connected with the palisade cells of the chlorenchyma, and by the fact that in the Compositæ "it often happens that the laticiferous ducts are actual sieve tubes or are at least continuous with elements of that nature" (133, p. 433).

Laticiferous tubes can be considered as a special development of the vessels. The first stage is seen in *Tupa salicifolia*, where some of the cells comprising the vessel are branched.

The conclusion from the known facts is then that the tubes or vessels forming the laticiferous system exercise two functions; they are reservoirs for excretory products and at the same time are canals along which food materials can be easily and rapidly translocated to considerable distances either in solution or in the solid condition, and in which these same substances can also be stored until required.

If an explanation is sought for the development of this particular method of translocation in some groups of plants and not in others, the general prevalence of the climbing habit in those groups which show laticiferous tissue becomes significant. The four families in which laticiferous tubes occur, Euphorbiaceæ, Moraceæ, Apocynaceæ and Asclepiadaceæ, are well known to contain quite a number of climbing species. The same is true of many of the groups in which laticiferous vessels occur, *e.g.*, Araceæ, Convolvulaceæ, Lobelioideæ and Clusioideæ (cp. Trécul, 146). Other families which show laticiferous sacs or vessels, such as the Nympheaceæ and Musaceæ, are herbs which develop long stems, petioles or peduncles by rapid growth. It is of interest to note also that in the Gymnosperms one of the few genera with many climbing species, *Gnetum*, has latex tubes in some species, *e.g.*, *G. africanum* (122) and *G. Gnemon* (119).

Oleo-resin or mucilage canals occur in a still larger number of families. The use of such canals by climbing plants or giant herbs for the translocation of food materials easily and quickly along stems where the cross section of the phloem is small compared with the size of the plant and the length of stem is just what might be expected. The writer, therefore, suggests that the development of the oleo-resin canals into a laticiferous system is part of the response to environment (epharmonic variation) which produces a climbing plant from an erect one. Such an advantageous character would not readily be lost if the climber again developed the habit of an erect shrub or herb, especially if the phloem had become reduced in the interval. This would explain the relatively few cases, such as the Papaveraceæ and the non-climbers in the above mentioned groups, in which latex occurs in comparatively low-growing herbs or shrubs.

The present is not a suitable opportunity to develop this theory fully and we will proceed to apply it to the particular problem of the development of latex in the Compositæ. Laticiferous vessels and the climbing habit are concomitant characters in the *Siphocampylus-Centropogon* ancestors of *Senecio.* In that genus and in all the Senecioneæ which have been examined there is a system of oleo-resin ducts throughout the root, rhizome and aerial stem (see Fig. 77). The explanation of the absence of food materials from the canals in this case is to be found in the facts given in Chap. XI, C-D. It was shown there that the dominant feature of the evolution of *Senecio* from the *Siphocampylus* group must have been the dwarfing of the plant in an Andine habitat and the aggregation of all the aerial parts. This is the very opposite of the phenomena which, on the above theory of latex, lead to the development of a laticiferous system. In these circumstances it is not surprising that the duality of function ceases and the laticiferous vessels degenerate into oleo-resin ducts with only an excretory function. For this reason an examination of *Lysipomia* from the latex point of view would be very interesting. *Rhizocephalum* (another Andine genus) and *Apetahia*, the other two genera which show considerable reduction in the gynoecium (cp. Chap. XI, C) have already been examined for latex with negative results (144 and 156). It is probable, therefore, that the change to oleo-resin canals had taken place during the dwarfing of the Andine plants before the origin of *Senecio.*

We thus arrive at a definite point of view with regard to the primitive condition of the secretory apparatus in the Compositæ: *i.e.*, *Senecio*, being derived by a dwarfing process from the Lobelioideæ in which a laticiferous system extends to root, rhizome and aerial stem, has that system modified by the loss of its nutritive function into a series of oleo-resin canals, which also extends to rhizome and aerial stem.

Although many authors have contributed to our knowledge of the secretory apparatus of the Compositæ (see Faivre, 125-6, Kny 135, Triebel 149, Van Tieghem 151-3, Vuillemin 154-5, Leblois 136, Trécul 146-7 and Bibliography in Solereder 144) Col has given the most complete account (120) with numerous bibliographical refer-

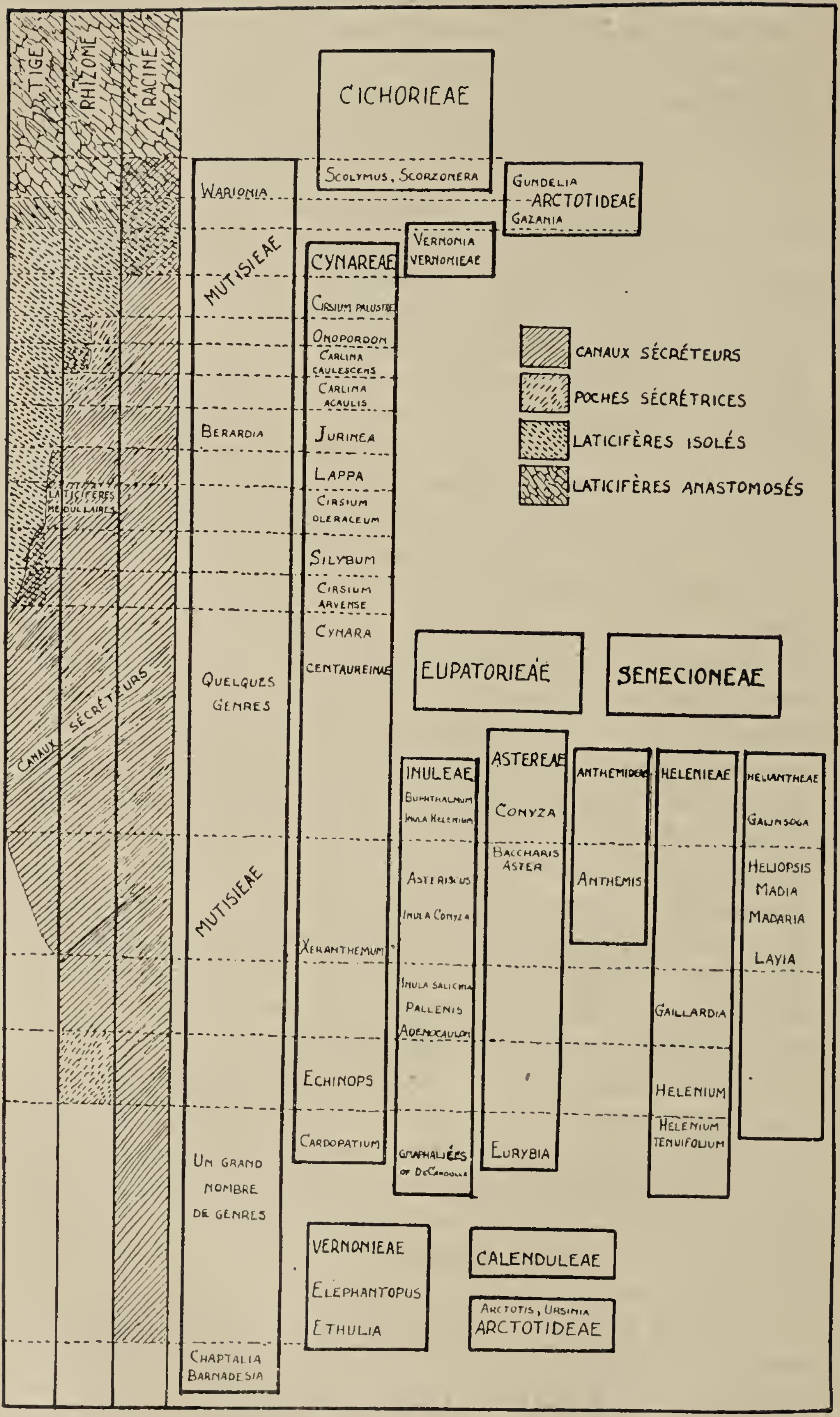


FIG. 77. Distribution of Secretory Tissue in the Compositæ: modified from Col. For explanation, see text.

ences and he summarises the facts conveniently in a series of figures (120d). Fig. 77 is a copy of his Tab. II with some modification in the nomenclature and some additional genera added from his Tab. III. The three columns on the left indicate by the hatching, etc. the character of the secretory apparatus present in root, rhizome and aerial stem of the genera and groups on the right.

In his final contribution Col considers the phyletic value of the facts and gives two hypotheses for the development of the secretory canals in the Compositæ. According to the first the canals are in the process of disappearing completely or of being replaced by laticiferous elements. On this view he points out that the Senecioneæ and Astereæ are the primitive groups and the other tribes are grouped around them. According to the second the canals are in the process of appearing and in this case no primitive groups are indicated.

Although he says he prefers the latter hypothesis, he also states very definitely that he has given the tables and the two hypotheses "pour mettre . . . . les taxinomistes futurs de tenir compte des données de l'appareil sécréteur interne de l'axe des Composées. Les affinités entre les groupes de cette famille sont si grandes, qu'il faudrait renoncer à une classification basée sur l'ensemble des caractères, avant de connaître d'une façon précise la valeur de ces caractères, et les causes de leurs variations." The problem is, therefore, quite an open one as far as Col is concerned, but in view of the preceding investigation of phylesis in the Compositæ and the origin of the family from a group in which a secretory apparatus is fully developed, there can be no doubt that the first hypothesis is the correct one.

The facts are given in Fig. 77, and there is little that it is necessary to add, except that in the Senecioneæ and Astereæ the canals of the aerial stem are situated opposite the vascular bundles, are usually only feebly developed in or immediately within the endodermis, and are very similar to the simple canals of the rhizome. In all those cases, also, where canals of any kind are absent from a part of the aerial stem (as in *Asteriscus*, *Inula*, *Madia*) the canals which are present in the rest of the stem are situated at the sides of the vascular bundles. *Echinops* and *Helenium* have only sacs but they also are laterally placed. Further, the species in which the secretory tissue is present in the rhizome and entirely absent from the aerial stem belong to those tribes in which canals or sacs are lateral when present.

Considering Fig. 77, the Senecioneæ are again indicated as the primitive group. The Astereæ-Eupatorieæ line is quite clear, with the advanced position of at least some of the Heterochrominæ (*Aster* and *Eurybia*) and of the *Baccharis* group confirmed. The

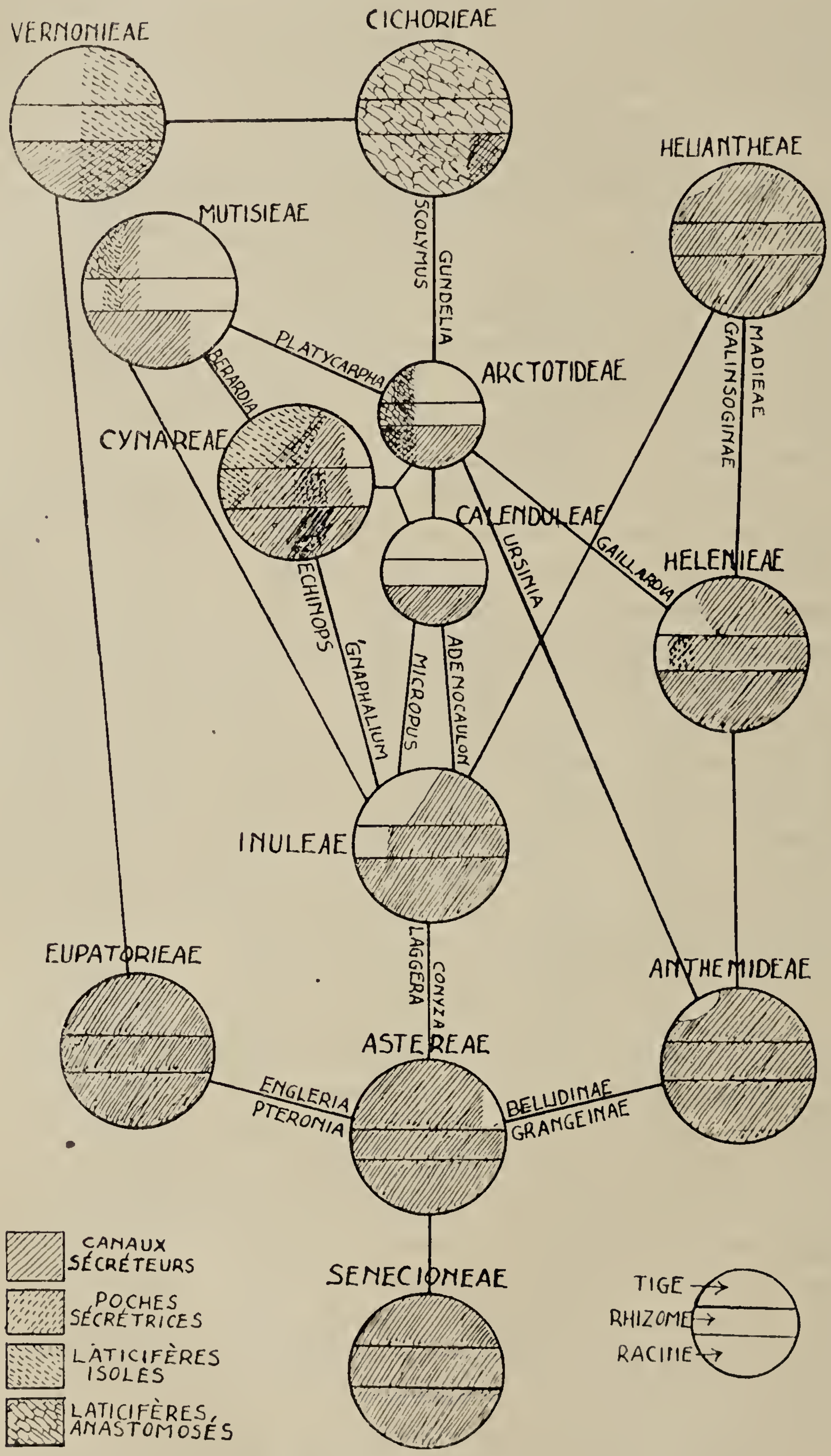


FIG. 78. Affinities among the Compositæ as shown by the distribution of secretory tissue; modified from Col.

position of the Anthemideæ, Heliantheæ and Helenieæ is in accordance with Fig. 7, except that a close affinity has again to be noted between the Senecioneæ and Helenieæ (cp. Chaps. V, D and X, D). The somewhat abrupt disappearance of the canals from the stem in the Calenduleæ and Arctotideæ (*Ursinia* and *Arctotis*) is not surprising when the variation in a single tribe (as in the Cynareæ, Mutisieæ, etc.) is observed.

In the Vernonieæ two distinct types occur; the appearance of laticiferous sacs in *Vernonia* may be correlated with the climbing habit of many of the species and a thorough examination of the climbing species of *Senecio* would be of interest in this connection. The derivative position of the Lychnophorinæ is confirmed by the total absence of secretory canals from the stem.

The distribution of the canals in the Inuleæ raises again the question of the monophyletic origin of that tribe. The "Gnaphaliées of De Candolle" includes the first seven sub-tribes of the Inuleæ of Bentham. The facts indicate a diphyletic origin, as suggested in Chaps. IV, F and VI, C. The variation in *Inula* would account for the distribution of the secretory apparatus in the Athrixiinæ and Relhaniinæ.

One of the most interesting points is that the secretory apparatus is equally developed in the Senecioneæ, *Inula Helenium*, *Buphthalmum* and the Centaureinæ. The only difference is that in the first and last groups the canals are opposite the vascular bundles, while in the other two they are placed laterally or between the bundles. The origin of the Cynareæ from the Buphthalminæ thus receives comfirmation. In *Cynara* and *Saussurea* (Carduinæ) the development of the canals is the same as in the Centaureinæ, so that the position of the Echinopsidinæ as derived from the Carduinæ (Figs. 7 and 77) is confirmed. The Carduinæ show a gradual development of laticiferous sacs possibly connected with the ecological conditions which have played so conspicuous a part in the development of the Cynareæ (cp. Col's conclusion from his experiments that the environment determines the appearance of the secretory organs in some Compositæ but not in others (120d, p. 164). The change in the case of the Cynareæ would be rendered easy by the ancestral laticiferous characters, which, although suppressed, do not appear to have been completely lost. The Carlininæ show a wide range from *Carlina acanthifolia* with anastomosing laticiferous vessels to *C. caulescens*, *Xeranthemum* and *Cardopatium*. This is in accordance with the derivation of this sub-tribe from the Carduinæ (Fig. 7), the *Carlina* group corresponding to the *Cirsium* line and the *Xeranthemum* group corresponding to the Echinopsidinæ.

The somewhat anomalous genera, *Warionia* and *Berardia*, were removed from the Carduinæ of Bentham and placed in the Mutisieæ by Hoffmann, for reasons which are not given but may be found in Bentham's note on the latter genus (I, 8, p. 474). Although he was not quite certain about the position of these two genera, Bentham's opinion as expressed in his classification is to be preferred to Hoffmann's, who seems to have followed on more than one occasion the former's suggestions of alternative affinities with no further evidence or reason. The Mutisieæ can, therefore, be regarded as a more or less homogeneous group as far as the secretory canals are concerned. The tribe shows a clear gradation from genera similar to the Senecioneæ to the extreme cases of *Chaptalia* and *Barnadesia*.

Considering the fact that reversion to the ancestral condition is shown in the Cynareæ, the appearance of laticiferous vessels or sacs in *Gundelia* and *Gazania* (Arctotideæ) may be taken as confirming the derivative position of the Gundeliinæ and Gorteriinæ (cp. Fig. 7).

The Cichorieæ have the laticiferous system well developed; the only genera which show oleo-resin canals in the root are *Scolymus* and *Scorzonera*. In Chap. VII, C, it was suggested that the receptacular paleæ are atavistic; the Cichorieæ also show reversion to their Lobelioid ancestors in the posterior split of the corolla. This atavism is easily understood if the tribe is closely related to the Senecioneæ. There is then only one step between the Lobelioideæ and the Cichorieæ, so that reversion should be comparatively easy. This close affinity, combined probably with the environment at the time of the origin of tribe, explains the reversion of the Cichorieæ in the secretory apparatus as well as in the corolla and receptacle.

Col gives a figure (120d, Tab. IV) representing "sur un plan la terminaison de l'arbre généalogique de la famille de Composées," in which he indicates affinities as shown by radiate capitula, presence of receptacular paleæ and tailed anthers, in addition to the characters of the secretory apparatus. As his treatment of the first three characters is somewhat superficial and inaccurate, it has been omitted from Fig. 78, which is a reproduction of Col's Tab. IV, modified to occupy less space but with the affinities as indicated by that author.

Although this (Fig. 78) is considered to represent the ends of the phyletic lines, the capitula of the corymb so to speak, several of the affinities which have been considered in previous chapters can be traced.

As shown above, however, much more evidence can be adduced in favour of the phylesis as expressed in Fig. 7, Chap. II, and modified in subsequent chapters. The facts concerning the secretory apparatus are not only in agreement with the general lines of evolution but confirm a number of detailed affinities in a very interesting fashion. As this conclusion is arrived at by the use of the theory of latex outlined above it serves as a confirmation of the usefulness of such a theory, if not also of its actual truth.

In spite of the extensive work by Col and others on latex in the Compositæ, much remains to be done as our knowledge is still incomplete. This fact is well illustrated by the recent description (116) of latex sacs in a species of *Parthenium* (Melampodiinæ), one of the advanced Heliantheæ, in which latex is present in sufficient quantity to be of possible commercial value as a source of Guayule rubber. Another source of rubber is *Hymenoxys floribunda* (Heleniinæ) but the quality is said to be inferior (see 119a).

D. Some Isolated Data.

There remain to be considered some isolated data referring to morphological and physiological characters which are of minor importance or which do not extend to a representative number of genera and tribes.

Seedling Structure.

The work of Dufour (I, 26) and Lebard (I, 53), which was mentioned in Chapter I, is now of more interest. Lebard derived the Cichorieæ from the "Tubuliflores" through the genera with long, narrow cotyledons, the Leptocotylées of Dufour. The examination of an extensive and representative collection of seedlings grown for the purpose shows that the broad cotyledon is the predominant type throughout the Tubulifloræ; it may be long or short but only in a minority of genera do we find the long cotyledon also linear and in still fewer is the short cotyledon at all narrow. Lubbock (167) considered that "One of the simplest types of embryo is that seen in the species of *Senecio*," where the cotyledons are short and oblong-obvate.

Lee's work (I, 54) on the seedling anatomy of the Compositæ led him to the conclusion that such data are of no use in questions of affinity. There is a marked divergence of opinion on the primitive type of root, diarch or tetrarch (cp. Thomas, 170). Only one type of transition with variations occurred in the fifty species of Compositæ examined; these were all diarch or tetrarch and showed variations between these extremes in nearly related species or in different examples of the same species. This is only to be expected after Compton's proofs (160) that in the Leguminosæ the type of vascular anatomy in the seedling is correlated with the size of the latter. Hill and de Fraine (164), using examples from the Compositæ and other families, found that the area of the cross-section of the vascular bundles in the seedlings is correlated with the surface area of the cotyledons. Lee (*loc. cit.*) found that in the Compositæ there are also variations which cannot be correlated with any external factors or characters.

The cause of much of the variation in the anatomy of the seedling is thrown a step further back by Lubbock (*op. cit.*, p. 102), who says "The prevailing type of the cotyledons in the seedling stage is spathulate, a shape due to that of the seed, which in turn strictly conforms to the interior of the fruit." The shape of the fruit clearly depends on the conditions under which it matures, for example, the fruits in the centre of the capitulum of most thistles are quite straight, but those around the outside are curved and have the pappus inserted obliquely. The narrow fruits of *Scorzonera* and *Tragopogon* mature on a flat receptacle, while enclosed by a long, rigid involucre. The result is the long, narrow cotyledon characteristic of these genera. In other genera where the fruits have more room to expand radially instead of longitudinally the short, broad type of cotyledon results.

In the seedling, as in the embryo, *Senecio* shows the primitive type, and Lebard's scheme (Table IV, Chap. I) must be reversed. This brings the genus *Lactuca* into the primitive group of the Cichorieæ and the scheme, with some modification, is then in accordance with the views on the evolution of the Cichorieæ given in Chap. X. With the *Senecio* or *Lactuca* type as primitive the variation in the other tribes, although in most cases considerable, is in accordance with the general lines of phylesis as deduced from other data.

Pericarp.

Various authors (61, p. 283; 169, 172, etc.) have investigated the detailed structure of the ovule, but Lavialle's extensive work on the pericarp is the only one which yields interesting phyletic data. His conclusions are given in Fig. 3, Chap. I, and are of interest as far as the Cynareæ are concerned. The Centaureinæ and Carduinæ appear as a large basal group from which the Carlininæ are given off, with *Atractylis* as an intermediate genus and *Xeranthemum* connecting with the Mutisieæ. The Echinopsidinæ are given as derived from the Carlininæ (cp. Figs. 7 and 79).

Anatomy.

The general anatomical characters of the Compositæ are of little use in classification of groups above the rank of genera (cp. Vuillemin and Hildebrandt, Chap. I, B, also Michael, 168), but a critical analysis of the facts might well lead to the elucidation of evolutionary principles, if the main lines as laid down in Chapter XIII and Fig. 79 were taken for guidance.

An interesting point is mentioned by Whitaker (173), namely, the occurrence of internal phloem in the leaf traces as they pass through the cortex; this is figured for *Solidago* and mentioned as a general feature "of the genus and probably of the family." Various types of phloem development have been observed in these leaf traces; it may be all round the xylem, as it is sometimes in *Olearia Haastii*, or almost completely encircling the xylem, as in some species of *Senecio*, or of the bicollateral type, as in other species of *Senecio*. These facts are of interest on account of the bicollateral bundles of the Cucurbitaceæ, one of the lowest families of the Campanulatæ. For other anatomical anomalies, such as "inverted" bundles, medullary bundles, etc., the reader is referred to Solereder (144) and the papers there mentioned.

Phytochemistry.

Systematic phytochemistry is a subject which must be largely developed in the future if there is to be any rational exploitation of plants. Hallier (163) deals with it in a general exposition of what is known and Greshoff (162) makes a strong plea for this eminently utilitarian study. Comparative phytochemistry is sometimes of distinct value in cases of doubtful affinity (cp. 163 and X, 39), and if the subject were properly developed it would at least remove the stigma from science which results from the fact that up to the present our knowledge of the medicinal properties of plants rests, in practically every case, on the experience of savages or barbarians. Only in a very few cases has civilised man discovered a new medicinal plant, either in his own or in any other country.

The literature of the subject, so far as the Compositæ are concerned, is so scattered through chemical and pharmaceutical publications that only one or two interesting points can be noticed here. The subject awaits a proper systematic investigation both practically and bibliographically.

The medicinal properties of the Compositæ are discussed in a general way by Lindley (I. 56, pp. 199-201). Greshoff (*loc. cit.*) records the occurrence of cyanogenetic glucosides in a number of genera, notably in the Cynareæ and Anthemideæ, also of saponin in a smaller number of genera. Two alkaloids, senecionine and senecine, are recorded for *Senecio vulgaris* (161). The intimate relationship of *Senecio* and *Ligularia* is emphasised by the occurrence of senecioic acid in *Ligularia tussilaginea* (157), while the less close relationship of *Arnica* and *Tussilago* is confirmed by the occurrence in the latter of faradiol, a bivalent dextrophytosterol closely related to arnidiol, a constituent of *Arnica* (165-166).

Many of the constituents of the latex, oleo-resins and gum-resins have a commercial value, but the most interesting case is *Stevia Rebaudiana*, the dried, powdered leaf of which is 40-50 times sweeter than any other natural product and can be used in the crude condition as a non-toxic substitute for saccharin. The sweet constituent is a glucoside, estevin or eupatorin, and the sweetening power of the pure substance is 150-180 times that of cane-sugar (see 171 for review of facts and literature)·

Much more is known of the chemical constituents of the Compositæ but much more still remains to be added before the facts can be used in a rational manner, either in the investigation of phylesis or in the utilisation of the plant products for economic purposes.

Pappus.

Since Chapter V was written some adverse criticism has been made of the views there expressed on the trichome nature of the pappus. Further evidence has arrived also, which supports the trichome theory in a very interesting way. As no decided opinion on the fundamental nature of the pappus was expressed in the previous account, the issue will now be made clear. The present writer holds that the pappus is a trichome structure or an emergence and not a divided calyx, for the following reasons:—

(1). The structure of the mature pappus, even in the paleaceous forms, is that of a series of hairs which have become fused throughout all or part of their length, either side by side to give a scale or in a mass to give a seta or awn.

(2). The development of the members of the pappus is either that of a typical trichome or that of an emergence, such as the surface spine of the thistle-leaf, which is comparable with some of those anomalous cases in which vascular bundles have been found in the pappus.

(3). The primitiveness of the scabrid seta is in conformity with the evolution of the family as deduced from other data.

(4). The predominant type of pappus in the fossil forms is the setose type. No fossil foliose pappus is known.

(5). The similarity of the setæ to the achenial hairs is very marked. In the primitive genus the latter are already biseriate and have a bicellular pulvinus (Fig. 11, Chap. V) which causes the hairs to diverge in moist conditions; the former are pauciseriate and have a pulvinus which causes the setæ to diverge in dry conditions. This difference in the action of the pulvinus may be due to the position of the setæ on the top of the pericarp and in any case is probably epharmonic.

(6). Blake has pointed out (159, p. 6) the general concomitance of the presence of pappus and the presence of achenial hairs or the absence of pappus and the absence of achenial hairs. This "pair of linked characters (pappus and pubescence of the achene)." is used by Blake (*op. cit.*, p. 48) to separate two varieties of *Viguiera flava*, which are "sometimes growing together and not separable by any other character.' An extensive examination shows that the linkage of these two characters is very common throughout the Compositæ in tribes, genera, species, varieties and forms. There are a few exceptions but the great predominance of the linkage is sufficient to render it almost, if not quite, certain that the two characters are inherited together. As they apparently behave as one character, there seems to be no real reason why they should be regarded as two distinct units in the genetic constitution of the plants. One systematist aptly summarised the point, when he said that "one could not properly describe a pappose achene as glabrous."

Since there is no conceivable reason why the character of a free calyx-limb should be linked with the character of pubescence of the achene, this new point is regarded as decisive.

The teratological specimens of Treub (V, 66) and Worsdell, (IV, 96) are properly explained by Buchenau's observations (see Chap. V, A) of a pappus inserted upon five green leaflets, which were developed in inverse proportion to the pappus. As the true sepal aborts the hairs upon it become larger until they are the only structures left. In this sense only can the pappus be regarded as a reduced calyx. This would also account for the occasional grouping of the setæ in five more or less obscure bundles and the subsequent fusion of these bundles of setæ to give five awns or paleæ.

Pubescence of the sepals is very frequently linked with pubescence of neighbouring parts such as the pericarp, the outer layers of which may be formed in the Compositæ from the fused calyx tube. Another point in favour of this view is that where hairs occur on the corolla they may be organised into a pappus as in *Leontopodium* (cp. Worsdell, IV, 95, p. 77 and Chap. V, A).

Since all the facts adduced in support of the phyllome theory can be easily and adequately explained by assuming that the pappus is in part, at least, a development of the hairs which were inserted on the now aborted free calyx segments, the evidence in favour of the trichome or emergence nature of the organ admits of no other conclusion regarding the origin and essential homologies of the pappus.

BIBLIOGRAPHY XII.

SECTION A. FOSSIL COMPOSITÆ.

1. Antonelli, M. Contributo alla flora foss. del suolo di Roma. Rome, 1889.
2. Bentham, G. See Bib. I, 7.
3. Berry, E. W. The lower Eocene floras of south-eastern North America. U.S. Geol. Survey. Professional paper, 91, Washington, 1916.
4. Boulay, M. l'abbé. Notice sur la flore tertaire des environs de Privas (Ardéche). Bull. Soc. Bot. France, Tome XXXIV, p. 265, 1887.
5. ,, ,, Flore fossile de Gergovie (Puy-de-Dôme). Ann. Soc. sci., Bruxelles, Vol. XXIII, 1899.
6. Chamberlin, T. C. and Salisbury, R. D. Geology, Vol. III, pp. 130-133, New York, 1906.
7. Ettingshausen, C. von. Die fossile Flora des Tertiär-Beckens von Bilin. Pt. 2, p. 18, 1868.
8. ,, ,, Die fossile Flora von Sagor in Krain. Denkschr. der math.-nat. Classe der K. Akad. d. wiss. Wien. Bd. XXXVII, Th. II, p. 2, Vienna, 1877.

8a. Fliche, M. Note sur les flores tertaires des environs de Mulhouse. Bull. de la Soc. Industrielle de Mulhouse, 1886, p. 357.

9. Heer, O. Die Urwelt der Schweiz. Zurich, 1883.
10. ,, ,, The Primaeval World of Switzerland (Eng. trans. of above). London, 1876.
11. ,, ,, Flora tertiaria Helvetiæ. Winterthur, 1855-59.
12. Massalongo, D. A. Plant. foss. nov. in format. tert. regni veneti super inventæ, p. 15. Verona, 1853.
13. ,, ,, Monogr. del genere *Silphidium*. Mem. Soc. Ital. delle Scienze. Ser. 2, Tome I, p. 18, Modena, 1858.
14. Meschinelli, A., et Squinabol, X. Flora tertiaria italica, p. 510. Padone, 1893.
15. Murchison, R. I. On the Earlier Volcanic Rocks of the Papal States and the adjacent parts of Italy. Q. J. Geol. Soc., Vol. VI, p. 300, 1850.
16. Reid, C. Pliocene Deposits of Britain. General Memoirs of Geol. Surv. of U.K., p. 231, 1890.
17. ,, Pleistocene Deposits of the Sussex Coast. Q. J. Geol. Soc., Vol. XLVIII, p. 344, 1892.
18. ,, On Scottish Interglacial Deposits. Geolog. Mag., Decade IV, Vol. II, No. 371, p. 217, 1895.
19. ,, and others. The relation of Palæolithic Man to the Glacial Epoch, Rep. Brit. Assoc., Liverpool, p. 400, 1896.
20. ,, Palæolithic Deposits of Hitchin. Proc. Roy. Soc., Vol. LXI, p. 40, 1897.
21. ,, Pleistocene Plants from Casewick, Schacklewell and Grays. Q. J. Geol. Soc., Vol. LIII, p. 463, 1897.

22. Reid, C. Further Contributions to the Geological History of the British Flora. Annals of Botany, Vol. XII, p. 243, 1898.

23. ,, The Origin of the British Flora. London, 1899.

24. ,, Notes on the Plant-Remains of Roman Silchester. (*a*) Archæologia, Vol. LVII, London, 1901. (*b*) Ibid, Vol. LVIII, 1902.

25. Reid, C. and E. M. Les éléments botaniques de la détermination de l'âge des argiles a briques de Tegelen, etc. Bull. Soc. Belge de Géol., et de Paléont., et d'Hydrol., Tome XXI, p. 583, Brussels, 1907.

26. ,, ,, The Fossil Flora of Tegelen-sur-Meuse. Verhand. Kon Akad. v. Wetensch., Amsterd. Tweede Setie, Deel, XIII, No. 6, 1907.

27. ,, ,, On the Pre-Glacial Flora of Britain. Jour. Linn. Soc. Bot., Vol. XXXVIII, p. 206, 1908.

28. ,, ,, A further Investigation of the Pliocene Flora of Tegelen. Versh. Kon. Akad. Wetensch., Amsterd., 1910, p. 192.

29. ,, ,, The Pliocene Floras of the Dutch-Prussian Border. Mededeel. van de Rijksopsporing van Delfstoffen, no. 6, The Hague, 1916.

30. Reid, C. The Plants of the Late Glacial Deposits of the Lea Valley. Q. J. Geol. Soc., Vol. LXXI, Pt. 2, p. 155, 1916.

31. Saporta, G. de. Études sur la végétation du Sud-Est de la France à l'époque tertiare. Paris, 4 Vols., 1862-74. Also in Ann. Sci. nat., Bot., (*a*) Ser. 4, T. XVI, p. 309; (*b*) ibid. T. XVII, p. 191; (*c*) ibid. T. XIX, p. 5; (*d*) Ser. 5, T. III, p. 5; (*e*) ibid. T. IV, p. 5, (*f*) ibid. T. VIII, p. 5; (*g*) ibid. T. IX, p. 5; (*h*) ibid. T. XV, p. 277; (*i*) ibid. T. XVII, p. 5; (*k*) ibid. T. XVIII, p. 23.

32. ,, ,, Derniéres adjonctions à laflore fossile d'Aix en Provence, (*a*) ibid. Ser. 7, T. VII, p. 1, 1888; (*b*) ibid. Ser. 7, T. X, p. 1, 1889.

33. Schimper, W. P. Traité de Paléontologie Végétal. Tome II, p. 865, Paris, 1870 74.

34. Stopes, M. C. Petrifactions of the Earliest European Angiosperms. Phil. Trans. Roy. Soc., B. Vol. 233, pp. 75-100, 1912.

35. ,, ,, Catalogue of the Mesozoic Plants in the British Museum. The Cretaceous Flora, Pt. II, p. 259, 1915.

36. Ward, Lester F. Synopsis of the Flora of the Laramie Group. U.S. Geol. Surv. 6th Ann. Rep. 1884-85.

37. Zeiller, R. Eléments de Paléobotanique. Paris, 1900.

38. Zittel, K. A. v. Handbuch der Paläontologie. Palæophytologie. Abth. II, p. 795, Munich and Leipzig, 1876-90.

Section B. Cytology of Compositæ.

39. Balicka-Iwanowska, G. P. Contribution à l'étude du sac embryonnaire chez certaines Gamopetales. Flora, Bd. 86, p. 47, 1869.

40. Barnes, C. R. The Process of Fertilisation in *Campanula americana*. Bot. Gazette, Vol. X, p. 349, 1885.

41. Beer, R. On the Structure and Division of Nuclei in the Compositæ. Ann. Bot., Vol. XXVI, p. 705, 1912.

42. Billings, F. H. Beiträge sur Kenntniss der Samenentwicklung. Flora, Bd. 88, p. 325, 1901.

43. Bönicke, L. v. Zur Kenntniss der Prophasen der heterotypischen Teilung einiger Pollenmutterzellen. Ber. d. deutsch. Bot. Gesell., Bd. 29, p. 59, 1911.

44. Campbell, D. H. Notes on the Structure of the Embryo Sac in *Sparganium* and *Lysichton*. Bot. Gaz., Vol. XXVII, p. 153, 1899.

45. Carano, E. Su particolari anomalie del sacco embrionale di *Bellis perennis*. Annali di Botanica, Vol. XI, p. 435, Rome 1913.

46. „ „ Ricerche sull embriogenesi delle Asteraceæ. Ibid., Vol. XIII, p. 251, 1915.

47. ,, ,, Sull' embriologia di *Senecio vulgaris*, L. Rendiconti d. R. Accad. d. Lincei, Vol. XXIV, p. 1244, 1915.

48. Chamberlain, C. J. The Embryo Sac of *Aster Novæ-Angliæ*. Bot. Gaz., Vol. XX, p. 215, 1895.

49. ,, ,, The Embryo Sac of *Aster* and *Solidago*. Bot. Gaz., Vol. LXV, p. 571, 1918.

50. Coulter, M. C. and Chamberlain, C. J. Morphology of Angiosperms. London, 1903.

51. Dahlgren, K. V. O. Der Embryosack von *Plumbagella*. Arkiv für Botanik Bd. 14, p. 1, 1915.

52. Digby, L. A Critical Study of the Cytology of *Crepis virens*. Archiv für Zellforschung, Bd. 12, p. 97, 1914.

53. Eichler, A. Ueber die doppelte Befr. bei *Tragopogon*. Sitzber. Wiener Akad., Bd. 115, 1906.

54. Farmer, J. B. and Digby, L. On the Dimensions of Chromosomes in Relation to Phylogeny. Phil. Trans., B. Vol. CCV, p. 1, 1914.

55. Fleischer, E. Beiträge zur Embryologie der Monocotylen und Dicotylen (*Helianthus annuus*) Flora. Bd. 67, p. 369, 1874.

56. Gates, R. R. See IV, 32.

57. ,, ,, See XI, 18.

58. Goldflus, M. Sur la structure et les fonctions de l'assise épithéliale et des Antipodes chez les Composées. Journ. de Botanique, Tome XII, p. 374, 1898 and T. XIII, pp. 9, 49, 87, 1899.

59. Guignard, L. Sur l'origine du sac embryonnaire et le rôle des antipodes. Bull. Soc. Bot. de France, Tome XXVIII, p. 197, 1881,

60. ,, ,, Recherches sur le sac embryonnaire des Phanerogames Angiospermes. Ann. Sci. nat., Bot., Ser. 6, T. XIII, p. 136, 1882.

61. ,, ,, Recherches sur le développement de la graine (*Senecio vulgaris*, p. 283). Journ. de Botanique, T. VII, pp. 1, etc., 1893.

62. Hegelmaier, F. Ueber den Keimsack einiger Compositen und dessen Umhüllung. Bot. Zeitung, Bd. 47, pp, 805, 821, 837, 1889.

63. Hofmeister, W. Die Entstehung des Embryo der Phanerogamen. Leipzig, 1849.

64. Holmgren, J. Die Entwicklung des Embryosackes bei *Anthemis tinctoria*. Svensk. Bot. Tids., Bd. 9, p. 171, 1915.

65 ,, ,, Apogamie in der Gattung *Eupatorium*. Ibid, Bd. 10, p. 263, 1916.

66. Ishikawa, M. Cytologische Studien von Dahlien. Bot. Mag., Tokyo, Bd. XXV, No. 288, 1911.

67. ,, ,, A List of the Number of Chromosomes. Ibid, Bd. XXX, p. 404, 1916.

68. Jacobsen-Stiasny, E. Versuch einer phylogenetischen Verwertung der Endosperm-und Haustorialbildung bei den Angiospermen. Sitzungsber. Kaiserl. Akad. Wiss., Wien. Bd. 123, p. 1, 1914.

69. Juel, H. O. Vergleichende Untersuchung über typische und parthenogenetische Fortpflanzung b. d, Gattung *Antennaria*. Kungl. Svenska Vetenskaps-Akad. Handl. XXXIII, No. 5, p. 1, Stockholm, 1900.

70. ,, Die Tetradenteilungen bei *Taraxacum* und anderen Cichorieen Ibid, XXXIX, No. 4, p. 1, 1905,

71. Juel, H. O. Untersuch. über die Auflösung der Tapetenzellen in den Pollensäcken der Angiospermen (*Doronicum grandiflorum*). Jahrbüch. f. Wissensch. Bot., Bd. LVI, p. 337, 1915.

72. Land W. J. G. Double fertilisation in the Compositæ. Bot. Gaz., Vol. XXX, p. 252, 1900.

73. Leavitt, G. G., and Spalding, L. J. Parthenogenesis in *Antennaria*. Rhodora, Vol. VII, 1905.

74. Lundegardh, H. Ueber Reduktionsteilung in den Pollenmutterzellen einiger dicotylen Pflanzen. Svensk Bot. Tids., Bd. III, p. 78, Stockholm, 1909.

75. Martin, G. W. Development of the flower and embryo-sac in *Aster* and *Solidago*. Bot. Gaz., Vol. XVII, pp. 353, 406, 1892.

76. Meek, C. F. U. A Metrical Analysis of Chromosome Complexes. Phil. Trans. Roy. Soc., B. Vol. CCIII, p. 1, 1913.

77. Merrell, W. D. A Contribution to the Life History of *Silphium*. Bot. Gaz., Vol. XXIX, p. 99, 1900.

78. Mottier, D. M. On the embryo-sac and embryo of *Senecio aureus*. Bot. Gaz., Vol. XVIII, p. 245, 1893.

79. Murbeck, S. Parthogenese bei den Gattungen *Taraxacum* und *Hieracium*. Botaniska Notiser (Lund), 1904, p. 285.

80. Nawaschin, S. Ueber die Befruchtungsvorgänge bei einigen Dicotyledonen. Ber. de deut. bot. Gesell., Bd. XVIII, p. 224, 1900.

81. Opperman, M. A contribution to the life-history of *Aster*. Bot. Gaz., Vol. XXXVII, p. 353, 1904.

82. Osawa, J. Studies on the Cytology of some species of *Taraxacum*. Arch. f. Zellforsch., Bd. X, 1913.

83. Ostenfeld, C. H. Experiments on the Origin of Species in the Genus *Hieracium*. New Phytologist, Vol. XI, p. 347, 1912. (And other papers on the same genus).

84. Palm, B. Zur Embryologie der Gattungen *Aster* und *Solidago*. Acta Horti Bergiani, Bd. V, p. 1, 1914.

85. ,, Ueber die Embryosackentw. einiger Kompositen. Svensk. Bot. Tids. Bd. VIII, 1914.

86. Portheim, L. R. v. Beiträge zur Entwick. der Achæne und des Embryos der Compositen. I. *Senecio vulgaris*, L. Sitz.-ber. deutsch. naturwiss.-med., N.F. 21, 1901.

87. Raunkiaer, C. Kundannelse uden Befruchtning hos Maelkbötte (*Taraxacum*). Bot. Tidssk., Köbenhavn, Bd. XXV, Heft 2, 1903.

88. Rosenberg, O. Ueber die Individualität den Chromosomen in Pflanzenreich. Flora, Bd. XCIII, p. 251, 1904.

89. ,, Zur Kenntniss der Reduktionsteilung in Pflanzen. Botan. Notis. (Lund), p. 1, 1905.

90. ,, Ueber die Embryobildung in der Gattung *Hieracium*. Ber. d. Deut. bot. Gesell., Bd. XXIV, p. 157, 1906.

91. ,, Cytological studies in the Apogamy in *Hieracium*. Bot. Tidssk., Copenhagen, Bd. XXVIII, Hf. 1-2, 1907.

92. ,, Zur Kenntniss von den Tetradenteilung der Compositen, Svensk Bot. Tids., Bd. III, p. 64, 1909.

93. ,, Ueber die Chromosomenzahlen bei *Taraxacum* und *Rosa*. Ibid, Bd. III, Hf. 2, 1909.

94. ,, Die Reduktionsteilung und ihre degeneration in *Hieracium*. Ibid, Bd. XI, p. 145, 1917.

95. Schiller, J. Zur Embryogenie der Gattung *Gnaphalium* (double fertilis.) Oest. bot. Zeitschr., Jahrg. 55, p. 312, 1905.

96. Schkorbatow, H. Parthenogenetische und apogame Entwicklung bei den Blütenpflanzen (*Taraxacum officinale*). Travaux Soc. nat. Univ. imp. Kharkow, Tome XLV, p. 15, 1911.

97. Schlotterbeck, J. O. Beiträge zur Entwicklungsgeschichte pharmakognostischwichtiger Samen. Bern, 1896.

98. Schwere, S. Zur Entwickelungsgesch. der Frucht von *Taraxacum officinale* Flora, Bd. 82, p. 32, 1896.

99. Small, J. Anomalies in the Ovary of *Senecio vulgaris*, L. Annals of Botany, Vol. XXX, p. 191, 1916.

100. Strasburger, E. Angiospermen und Gymnospermen (*Senecio vulgaris*), 1879.

101. ,, ,, Zellbildung und Zelltheilung (*Senecio vulgaris*), 1880,

102. ,, ,, Ueber den Bau und das Wachstum der Zellhäute (*Senecio vulgaris*). Jena, 1882.

103. Täckholm, G. Zur Antipodenentwicklung der Kompositen Gattungen *Cosmidium* und *Cosmos*. Svensk Bot. Tids., Bd. X, p. 423, 1916.

104. Tahara, M. On the Number of Chromosomes of *Crepis japonica*. Bot. Mag. Tokyo, Vol. XXIV, p. 1, 1910.

105. ,, Cytological Investigations on the Root-tips of *Helianthus annuus*. Ibid, Vol. XXIX, p. I, 1915.

106. ,, Cytological Studies on *Chrysanthemum*. Ibid, Vol. XXIX, pp. 5, 45, 92, 1915.

107. ,, Parthogenesis in *Erigeron annuus*. Ibid, Vol. XXIX, p. 245, 1915.

108. Tahara, M., and Ishikawa, M. The Number of Chromosomes of *Crepis lanceolata*, var. *platyphylla*. Ibid, Vol. XXV, p. 119, 1911.

109. Tischler, C. Chromosomenzahl, Form und Individualität im Pflanzenreiche. Prog. Rei Bot., Bd V, p. 164, 1915.

110. Vesque, J. Nouvelles recherches sur le développement du sac embryonnaire des Phanérogames Angiospermes (*Senecio vulgaris*). Ann. d. Sci. nat. Bot., Ser. 6, T. VI, p. 237 and p. 285, also ibid, Ser. 6, T. VIII, p. 261, and Comptes Rendus, T. LXXXVIII, p. 1359, 1879.

111. Ward, H. Marshall. A Contribution to our Knowledge of the Embryo Sac in Angiosperms. Jour. Linn. Soc., Vol. XVII, p. 534, 1879.

112. Warming, E. De l'Ovule. Ann. d. Sci. nat. Bot., Ser. 6, T. V, p. 178, 1877.

113. Winge, O. Oogenesis hos *Senecio*. Botan. Tidssk., Copenhagen, Bd. 33, p. 245, 1914.

114. ,, The Chromosomes. Their numbers and general importance. Comptes rendus des travaux du Laboratoire de Carlsberg. Vol. XIII, Livr. 2, 1917.

115. Winkler, H. Ueber die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. Zeitschr. f. Bot., Bd. VIII, 1916.

SECTION C. LATEX IN THE COMPOSITAE.

116. Bartlett, H. H. *Parthenium Lloydii*, a new Mexican Guayule. Torreya, Vol. XVI, p. 45, 1916.

117. Biffen, R. H. The Functions of Latex. Ann. Bot., Vol. XI, p. 334, 1897.

118. ,, ,, The Coagulation of Latex. Ibid. Vol. XII, p. 165, 1898.

119. Bower, F. O. The Germination and Embryology of *Gnetum Gnemon*. Q. J. Microscop. Sci., Vol. XXII, 188:.

119a. Cockerell, T. D. A., and others. On *Picradenia floribunda* (*Hymenoxys*) as a source of rubber. Kew Bulletin, 1906, pp. 218-219 and ibid, Additional Series, VII, Rubber, 1906.

120. Col, M. Recherches sur l'appareil sécréteur internes des Composées. Jour. de Botanique, (*a*) Tome XIII, p. 2, 3, 4, 1899; (*b*) Tome XV, p. 166, 1901, (*c*) Tome XVIII, p. 110, 1904; (*d*) Tome XVIII, p. 153, 1904.

121. Czapek, F. Biochemie der Pflanzen. Vol. II, pp. 698-701, 1905.

122 Duthie, A. V. Anatomy of *Gnetum africanum*. Ann. Bot., Vol. XXVI, p. 593, 1912.

123. Faivre, E. Recherches sur la circulation et sur la rôle du latex dans *Ficus elastica*. Ann. d. Sci. nat., Bot., Ser. 5, T. VI, p, 23, 1866.

124. ,, Etudes physiologiques sur le latex du Mûrier blanc. Ibid Ser. 5, T. X, p. 97, 1869.

125. ,, Le latex pendant l'évolution germinative du *Tragopogon porrifolius*, effectuée dans les conditions diverses de milieu extérieur. Comtes Rendus, T. 88, p. 369. Paris, 1879.

126. ,, Recherches sur la formation du latex et des laticiféres pendant l'évolution germinative chez l'embryon du *Tragopogon porrifolius*. Ibid, T. 88, p. 269, 1879.

127. Gerber, C. Le latex du Figuier, suc pancreatique végétal à diastase protéolytic prédominante. Ibid, T. 155 p. 56. Paris, 1912.

128. ,, Caséase et trypsine des latex du *Ficus Carica* et du *Broussonetia papyriforme*. Bull. Soc. bot., France, T, LX, LXXXVIII.

129. Green, J. R. Proteid Substances in Latex. Proc. Roy. Soc., Vol. IXL, p. 28, 1886.

130. Groom, P. On the Function of Laticiferous Tubes. Ann. Bot., Vol. III, p. 157, 1889.

131. Haberlandt, G. Physiological Plant Anatomy. Eng. Trans, 1914.

132. Hanstein, J. Die Milchsaftgefässe und die verwandten Organe der Rinde. Berlin, 1864.

133. Jeffrey, E. C. The Anatomy of Woody Plants. Chicago, 1917.

134. Kniep, H. Ueber die Bedeutung des Milchsafts der Pflanzen. Flora, Bd. 92, p. 129, 1905.

135. Kny, L. Ueber die Milchsafthaare der Cichoriaceen. Sitzungber. d. Ges. naturf. Frenade. Berlin, 1893.

136. Leblois, A. Canaux sécréteurs et poches sécrétrices. Ann. d. Sci. Nat., Bot. Ser. 7, T. VI, 1887.

137. Mangham, S. Translocation of Carbohydrates Science Progress, Nos. 18-19, pp. 279 and 476, 1910-11.

137a. McNair, J. B. Secretory Canals of *Rhus diversiloba*. Bot. Gaz., Vol. 65, p. 268, 1915.

138. Parkin, J. Observations on Latex and its Functions. Ann. Bot., Vol. XIV, p. 193, 1900.

139. Record, S. J. Significance of Resinous Tracheids. Bot. Gaz., Vol. LXVI, p. 61, 1918.

140. Schimper, A. F, W. Ueber Bildung und Wanderung der Kohlenhydrate in den Laubblättern. Bot. Zeitung, Bd. 43, col. 739, 1885.

141. Schwendener, H. Einige Beobachtungen an Milchsaftgefässen. Sitzb. d. k. Akad. Wissensch., Bd. XX. Berlin, 1885.

142. Sharples, A. The Laticiferous System of *Hevea brasiliensis* and its Protective Function. Ann. Bot., Vol. XXXII, p. 247. 1918.

143. Small, J. The Translocation of Latex and the Multiple Razor. NEW PHYTOLOGIST, Vol. XV, p. 194, 1916.

144. Solereder, H. Systematic Anatomy of the Dicotyledons. Eng. Trans., 1908.

145. Spence, D. On the presence of oxydases in India-rubber, with a theory in regard to their function in the latex. Biochem. Journ., Vol. III, p. 165, 1908.

146. Trécul, A. Recherches sur les vaisseaux laticiféres. Adansonia. T. VII-VIII. Paris, 1866-67.

147. ,, *Vernonia præalta*, canaux sécréteurs. Journ. de l'Instit, 1862.

148. Treub, M. Notice sur l'amidon dans les laticifères des Euphorbes. Ann. Jard. d. Buitenzorg, Vol. III, p. 37, 1883.

149. Triebel, R. Ueber Oelbehalter in Wurzeln von Compositen. Nov. Act. Acad. Cæsar, Leop. Carol. 1887.

150. Tschirch, A. Die Harze und die Harzbehälter. 2nd edit., Vol. II, 1906.

151. Van Tieghem, P. Sur les canaux oléifères des Composées. Bul. Soc. bot. de France, T. XVIII, 1871.

152. „ „ Sur les situation d'appareil sécréteur dans les Composées. Ibid, T. XXX, p. 310, 1883.

153. „ „ Memoires sur l'appareil sécréteur. Ann. d. Sci. Nat., Bot., Ser. 5, T. XVI, 1872, and ibid, Ser. 7, T. 1,1885.

154. Vuillemin, P. Tige des Composées. Paris, 1884.

155. „ „ Remarques sur la situation de l'appareil sécréteur des Composées. Bull. Soc. Bot. d. France, T. XXXI, p. 108, 1884.

156. Ydrac, F. L. Appareil lacticifére des Lobeliacées. Jour. de bot., T. XIX, p. 12, 1905.

SECTION D. PHYTOCHEMISTRY, SEEDLINGS, ETC.

157. Asahina, Y. Senecioic Acid from the rhizomes of *Ligularia tussilaginea* (*Senecio Kæmpferi*). Arch. Pharm., Bd. 251, p. 355, ex Yearbook of Pharmacy, p. 147, 1914.

158. Beauverd, G. Contribution à l'étude des Composées. Suite IV. Recherches sur la tribu des Gnaphaliëes. Bull. Soc. bot., Genéve, Vol. II, p. 207, 1910.

159. Blake, S. F. A revision of the genus *Viguiera*. Contrib. from the Gray Herbarium of Harvard Univ., N. S. XLV, 1918.

160. Compton, R. H. An Investigation of the Seedling Structure in the Leguminosæ. Jour. Linn. Soc. Bot., Vol. XLI, No. 279, 1912.

161. Grandval, A., et Lajoux, H. Etude de la sénécionine et de la sénécine. Comptes Rendus, T. 120, p. 1120, 1895.

162. Greshoff, M. Phytochemical Investigations at Kew. Kew Bulletin, 1909, No. 10, p. 397. See also Ber. d. D. pharm. Gesell., Bd. III, p. 191, 1893.

163. Hallier, H. Ueber die Anwendung vergleichenden Phytochemie in der systematischen Botanik. Compte Rendu de XIme Congrés International de Pharmacie, T. XI, p. 969. La Haye, 1913.

164. Hill, T. G., and de Fraine, E. A Consideration of the Facts relating to the Structure of Seedlings. Ann. Bot., Vol. XXVIII, p. 257, 1913.

165. Klobb, J. L'arnisterine, phytosterine de l'*Arnica montana*, L. Comptes Rendus, T. 138, p. 768, 1904.

166 „ Recherches sur la composition chimique des fleurs de Tussilage (*Tussilago Farfara*, L.) Ann. Chim. et Physique, Ser. 8, T. XXII. p. 5, 1911.

167. Lubbock, J. Seedlings. London, 1892.

168. Michael, H. Vergleichende Untersuchungen über den Bau des Holzes der Compositen, Caprifoliaceen und Rubiaceen. Leipzig, 1886.

169. Monnier, G. Le. Recherches sur la nervation de la graine. Ann. d. Sci. Nat., Bot., Ser. 15, T. XVI, 1872.

170. Thomas, E. N. Seedling Anatomy of Ranales, etc. Ann. Bot., Vol. XXVIII, p. 695, 1914.

171. Turrill, W. B. *Stevia Rebaudiana*. Kew Bulletin, 1918, Nos. 8 and 9. p. 343.

172. Van Tieghem, P. Note sur les divers modes de nervation de l'ovule, etc. Ann. d. Sci. Nat., Bot., Ser. 5, T. XVI, 1872.

173. Whitaker, E. S. Anatomy of Certain Goldenrods. Bot. Gaz., Vol. LXV, p. 250.

ON THE CYTOLOGY OF TWO SPECIES OF *CHARACIOPSIS.*

[WITH THREE FIGURES IN THE TEXT.]

BY NELLIE CARTER, M.Sc.

IN November, 1918, a collection of epiphytes was made from a small stagnant rain-water pool in Pool Hollies Wood at Sutton Park, Warwickshire. The fallen leaves lying in the water were covered with a pale blue-green incrustation, which proved on examination to consist almost entirely of two species of *Characiopsis* Borzi, together with developmental stages of spores of *Microthamnion* and filamentous bacteria. One of the species of *Characiopsis* was identified as *Ch. Nægelii* (A.Br.) Lemm., but the other has never previously been recorded, and is therefore described here as a new species under the name of *Ch. saccata.*

Since the material was available in considerable quantity a study of the cytology of the two species has been made, and several interesting facts have been revealed. Thus the great difference in the internal structure observed in these two species belonging to the same genus is rather surprising, and not what one would have expected. This difference is obvious, even in the living condition, and although in the case of very young individuals the size and shape of the cell is often similar in both species, there is no possibility of confusing them.

The larger species, *Ch. Nægelii,* varied in size from 16-50μ long and 6-28μ broad, and the individuals were usually oval, elliptical, or sometimes subspherical in shape, and except in the case of very young individuals the apex of the cell was always broadly rounded (Fig. 1, A-G).

The smaller species reached in fairly large specimens a length of 82μ and a breadth of 15-16μ, but in this case there was very much more variation in the shape of the individuals (Fig. 2). Usually they were somewhat lanceolate, the apex being distinctly acuminate (Fig. 2, E, I, L, M and P). It not unfrequently happened, however, that distorted forms occurred, in which the cells were rather irregular in outline, being very often more or less triangular (Fig. 2, A-D, F, G, H and J). These abnormal forms were very common amongst the smaller individuals, although occasionally some of the larger specimens also showed similar distortions.

In both species there is a very distinct, though short basal stalk, with a disc-like holdfast by means of which the organism is attached to the substratum. In the case of the triangular forms, the individual is usually, though not invariably, attached at one corner.

Eichler and Gutwinski ('94) figured some time ago a new alga under the name of *Sycidion polonicum*, which shows some superficial resemblances to these abnormal forms of *Characiopsis saccata*, but there are one or two differences between the alga described by the above authors and the one under consideration, which make it rather unlikely that the two are identical. In the first place the one figured by Eichler and Gutwinski is somewhat larger than the triangular forms observed here, and again their description of the cell-wall would scarcely apply. In *Sycidion polonicum* there is a thick cell-wall which increases in thickness at the upper angles of the cell, whilst in *Characiopsis saccata* the cell-wall is always very thin and delicate, in the triangular forms as well as in the more elongated cells, and there is never any visible increase in thickness at the angles.

Another epiphyte of very peculiar form was figured by Braun ('55) under the name of *Characium horizontale*, which is rather suggestive of some of the irregularly shaped specimens of *Characiopsis saccata*, cf. Fig. 2, D. Since only one of these peculiar individuals was observed by Braun, and it occurred amongst other allied species, including *Characium longipes* [=*Characiopsis longipes* (Rab.) Borzi], *Characium clavatum*, *Ch. ornithocephalum* and *Ch, obtusum*, it would seem highly probable that this particular individual was simply an abnormal specimen of one of these other species, and does not represent a distinct species at all. Braun himself seems to have considered this possibility and to have come to the conclusion that the form of this individual was too peculiar for it to have been merely an abnormal specimen of *Ch. ornithocephalum*, but in view of the wide variability of form which has been observed in the collection from Sutton Park, it seems quite probable that the individual called *Ch. horizontale* by Braun really was simply an abnormal specimen of one or other of the species amongst which it was living.[1]

These two examples, *Sycidion polonicum* Eichl. and Gutw. and *Characium horizontale* A. Br. are merely mentioned as showing some similarities to the unusual forms often observed amongst individuals of *Characiopsis saccata*, but as has already been shown, it is most unlikely that either of these is identical

---

[1] This idea is supported by Dr. E. Lemmermann in Algologische Beiträge. XII, Die Gattung *Characiopsis* Borzi, Abh. Nat, Ver. Brem. Bd. XXIII, H. 1, 1914. Lemmermann only includes *Characium horizontale* A. Br. in *Characiopsis* as a doubtful species.

with the alga in question. In all other characters than shape, the elongated and irregularly shaped cells are identical with each other, even in the cytological details of the cell-structure, and there is not the slightest doubt that these individuals of peculiar form are to be considered merely as abnormally developed specimens.

Characiopsis saccata sp. n. Cellulæ adultæ plerumque elongatæ cylindricæ vel subfusiformes, apice acuminato, stipite brevi discoque basali præditæ, juniores sæpissime forma irregulari quinetiam triangulari, chromatophoris copiosis vel prima juventute singula, parietalibus, foliorum ad instar tenuissimis; cytoplasmate grosse granuloso, nuculeis 1-32.

Long. 15-82μ.
Lat. 4-16μ.

Hab. in foliis *Quercus* emortuis, Pool Hollies Wood, Sutton Park. November, 1918.

CYTOLOGY.

In 1895 Borzi established the genus *Characiopsis* to include a number of epiphytic algæ previously described as species of *Characium.* The distinguishing features of *Characiopsis* are the presence of usually two or more parietal chloroplasts, the absence of pyrenoids and starch, and the storage of oil. *Characiopsis* thus belongs to the Heterokontæ, whereas *Characium* belongs to the Protococcales. Later Lemmermann ('14) removed a number of other species from *Characium* on these grounds, and placed them in *Characiopsis.* Nevertheless it is true that the two genera greatly resemble each other, and there is undoubtedly some confusion with regard to them. Thus it was hoped that the examination of these two species of *Characiopsis*, *Ch. Nægelii* and *Ch. saccata*, and the comparison of them with an undoubted species of *Characium* would help to clear up the misunderstanding which at present exists concerning these two genera.

METHODS. The algæ were fixed in a hot solution of corrosive sublimate consisting of—

Corrosive sublimate ...	3 gms.
Glacial acetic acid ...	3 ccs.
50% Alcohol	100 ccs.

The material was first washed in 50% alcohol, and finally in alcohol to which a little iodine had been added. It was taken down to water and stained in Heidenhain's iron hæmatoxylin, and finally mounted in Venetian turpentine. In the case of the sections the epiphytes were fixed *in situ* on the leaf on which they were living, the leaf being finally embedded and sectioned.

In all cases the transference of the material from one liquid to another was made as gradual as possible, and the strength of the solution was rarely increased by more than 10% at a time.

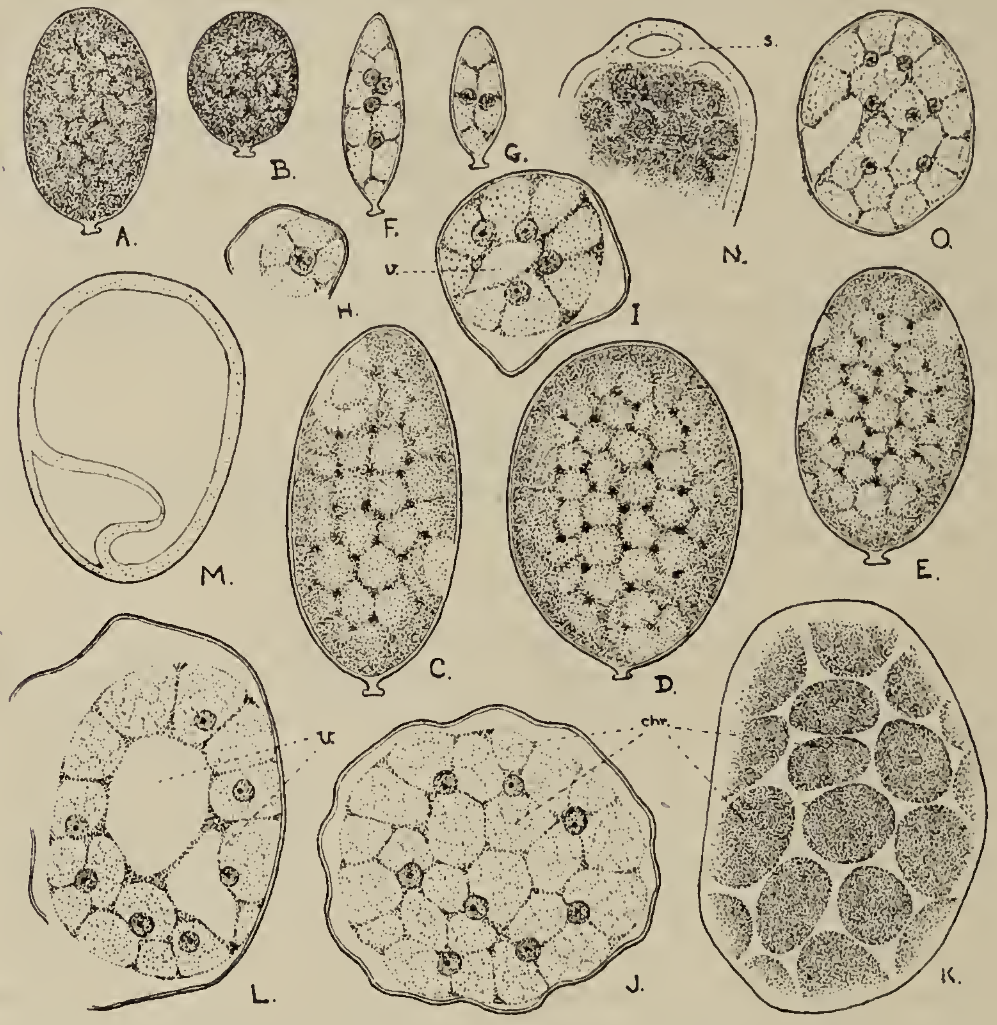


Fig. 1. *Characiopsis Nægelii* (A. Br.) Lemm. A and B, living individuals ×510; C, D and E, stained specimens showing cavities in the protoplast caused by internal projections of the cell-wall ×910; F and G, very young individuals ×910; H, I and J, transverse sections ×1720; K, surface longitudinal section, showing chromatophores ×1720; L, longitudinal section, showing vacuolate protoplast ×1720; M, section treated with chlor-zinc-iodine, showing the internal invagination of the cell-wall ×910; N, section through an internal projection treated with chlor-zinc-iodine, and showing the space (s) between the layers of the cell-wall ×910; O, longitudinal section showing the protoplast and internal projection of the cell-wall ×910. chr, chromatophores; v, vacuoles.

Characiopsis Nægelii.

The cell-wall of this species is of some thickness and is peculiar in the frequent production of internal processes penetrating the cell-cavity. These processes are not present in all specimens, but they are frequently found in the larger individuals. They vary in size from small button-like thickenings (Fig. 1, E and N) to fairly long tubular processes projecting half-way or even more through the cell (Fig. 1, M and O). Sometimes more of these projections than one are present in a single cell, cf. Fig. 1, C and E. On treating with chlor-zinc-iodine the wall increases somewhat in thickness and gives the cellulose colour reaction. The projections do not seem to be solid, however, since a colourless gap is often seen in the middle of the thickening (Fig. 1, N). It looks as if the wall were laminate, and at certain points the lamellæ separated, the inner layers being invaginated to form a kind of vesicle or hollow tubular process penetrating the cytoplasm (Fig. 1, M and O). The arrangement of the cell-contents is disturbed by these projections, and sometimes even in living specimens it is possible to distinguish the cavities in the dense cell-contents caused by them. These are far more obvious in stained specimens (Fig. 1, C, D, E and O).

Bristol ('17) and Moore ('17) have described internal projections of cellulose in the cells of two species of *Chlorochytrium* but these are not exactly similar to those observed in *Characiopsis Nægelii*. In *Chlorochytrium grande*, according to Bristol, the internal projections were solid, lamellose and irregular in form, and were characteristic of cells about to be transformed into zoogonidangia. In the case of *Characiopsis Nægelii* no evidence has been obtained in support of the suggestion that the particular cells showing the internal projections are zoogonidangia, since no reproductive stages have yet been observed in the culture. Here the projections also differ from those of *Chlorochytrium* in their apparent hollow structure, and in that they are never so irregular in form as in the latter genus.

In the living condition *Characiopsis Nægelii* is very densely green, and there is apparently a large number of small green disc-like chromatophores which line the whole cell-wall. Very little else can be distinguished.

After staining, the appearance of the cell is rather different. The disc-like chromatophores are no longer visible, and the whole cell appears to be full of very lightly stained protoplasm in which a coarse network, rather more deeply stained, can be distinguished. On focussing into the interior of the cell, numbers of small dark rounded bodies come into view (Fig. 1, C, D and E).

The structure of the cell-contents is better understood from the examination of sections, cf. Fig. 1, J and O. There is a large number of rounded globular bodies, which may be angular by compression, and do not stain very deeply. These are the chromatophores. Between these, and filling up the space between them, is the colourless cytoplasm, which, being so compressed between the chromatophores is very dense in texture, and consequently stains rather deeply: Scattered throughout the films of cytoplasm are the nuclei, which are found chiefly at the angles between the chromatophores, where there is naturally more room for them. They rarely occur in the extreme peripheral lining layer of protoplasm, and are usually confined within the outermost layer of chromatophores.

It usually happens that the chromatophores stain more lightly in Heidenhain's iron hæmatoxylin than the colourless cytoplasm. The opposite, however, is seen in Fig. 1, K, which shows a surface section in which the chromatophores have stained more deeply than the protoplasm. The chromatophores are differentiated very well by the use of chlor-zinc-iodine (Fig. 1 N) or fuchsin, in both of which they usually become more deeply coloured than the intervening protoplasm.

The chromatophores were usually so numerous that the whole of the cell-cavity was completely filled, and only very occasionally were vacuoles present as seen in Fig. 1, L and I.

The nuclei in *Ch. Nægelii* are often very numerous, but vary very much in number according to the size of the individual (Fig. 1, C-G). In some of the larger cells the number of nuclei present must often be more than sixty, but they are very difficult to count in entire specimens because of the thickness of the cell,

FIG. 2. *Characiopsis saccata* sp. n. A-G, various living individuals, E being the most usual form, × 610; H-L, stained specimens showing the varying numbers of nuclei × 610; M and N, stained specimens showing chromatophores and nuclei × 1720; O, transverse section × 1720; P, showing probable formation of zoogonidia × 1720.

and the dense cell contents. They are quite small, and usually show a distinct nucleolus (Fig. 1, H, I, J, L and O).

Characiopsis saccata.

Ch. saccata is quite different from *Ch. Nægelii* in its internal structure. The cell-wall is of cellulose; it is thin and delicate, and no attempt at the formation of the internal projections was observed.

In the living condition it is usually very difficult to locate the chromatophores. The granular cell-contents appear faintly green, and on focussing on to the edge of the individuals it may be possible to distinguish a deeper green lining layer, with occasional paler interruptions (Fig. 2, A-G). After staining, the chromatophores are often still obscure, but can be seen in some individuals as very thin delicate plates closely adhering to the cell-wall (Fig. 2, M). Unlike the globular chromatophores of *Ch. Nægelii*, which are so large and numerous as usually to fill the whole cell, in this species they occupy only a very insignificant part of the interior of the cell, and in transverse section are only to be distinguished as very thin plates bounding the protoplast (Fig. 2, O). In some very small individuals there is only one chromatophore which does not entirely cover the cell-wall (Fig. 2, N).

The remaining protoplasm is very homogenous, and appears to be coarsely granular. Neither vacuoles nor a definite network were ever noticed. The conspicuous granules are presumably only denser parts of the general mass of protoplasm, since they only assume a pale yellowish colour when treated with iodine, and do not give the characteristic reaction of any definite substance.

The nuclei in this species are again very numerous, although they never reach such large numbers as in *Ch. Nægelii.* In general the number of nuclei present is dependent on the size of the individual, and eight or sixteen are the usual numbers, although in one individual thirty-two were counted (Fig. 2, L). In many of the smallest specimens only one nucleus was present (Fig. 2, N), and the nuclei apparently divide by simultaneous bipartitions, since the commonest numbers of nuclei present are those of the progression 1, 2, 4, 8, 16, etc. (Fig. 2, H, I and K-M). In one case six nuclei were present, evidently owing to the more rapid division of two of the four nuclei which were previously present (Fig. 2, J). The nuclei very often take up a somewhat peripheral position, usually occupying the spaces between the chromatophores (Fig. 2, I and M). They are much larger than those of *Ch. Nægelii*, and appear very conspicuous in stained specimens. There is very rarely a definite karyosome, the chromatin being usually scattered (Fig. 2, M, N and O).

Both *Ch. Nægelii* and *Ch. saccata* are quite destitute of pyrenoids and starch, but contain quantities of oil.

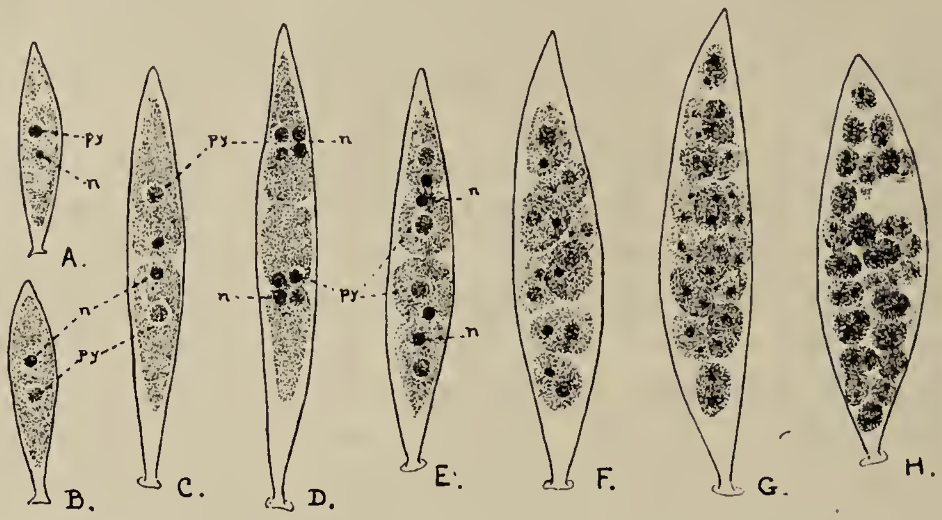


FIG. 3. *Characium angustum* A. Br. A and B, rather small individuals; C-H, successive stages in the formation of zoogonidia. All × 610 : py, pyrenoid ; n, nucleus.

Characium angustum.

This alga, occurring in large numbers on some stained filaments of *Cladophora* sp., was thoroughly examined for comparison with the two species of *Characiopsis* described above.

There was considerable variation in the size of the individuals, and most of the larger specimens showed cleavage of the protoplasm preparatory to the formation of zoogonidia (Fig. 3, A-H). The cell-contents in individuals whose protoplast had not yet divided contained a single pyrenoid and a single nucleus (Fig. 3, A and B). The rest of the protoplast was perfectly homogeneous except for the very rare occurrence of vacuoles (Fig. 3, A). No chromatophores could be distinguished in the stained specimens, and it is therefore highly probable that the chlorophyll is diffuse, and not confined to a definite chromatophore. The chlorophyll has also been shown to be diffuse in *Characium Sieboldii* by Smith ('16), as well as in other members of the Protococcales.

Apparently in *Ch. angustum* a multinucleate condition never occurs, the division of the nucleus being followed immediately by the cleavage of the protoplast (Fig. 3, C-H). The division of the nucleus is accompanied by the simultaneous division of the pyrenoid, and the cleavage of the protoplast soon follows it (Fig. 3, D). After the division the newly formed pyrenoids separate rapidly, and move to opposite ends of the constricting protoplast, whilst the daughter nuclei remain near the division plane for some time (Fig. 3, E). By repeated divisions of this kind, eight, sixteen and thirty-two small protoplasts are produced, each containing a tiny nucleus and pyrenoid (Fig. 3, F, G and H). The small protoplasts round themselves off, and presumably become zoogonidia. In Fig. 3, H, the zoogonidia seem to have been swarming within the zoogonidangium at the time of fixation.

Before accepting the characters of this species as typical of *Characium* it must first be compared with the only other species of the genus whose cytology has been investigated. It will be seen that the two species by no means agree in all respects.

Smith ('16) found that in *Ch. Sieboldii* there was no definite chromatophore, the chlorophyll being diffuse. In this *Ch. angustum* and *Ch. Sieboldii* agree, but in their cytological characters they have, beyond this, very little in common. For in the adult condition the latter species is multinucleate, containing usually thirty-two or sixty-four nuclei, and one or more pyrenoids, whereas *Ch. angustum* contains only one nucleus, and one pyrenoid previous to the beginning of cleavage. In the formation of zoogonidia the protoplast of *Ch. Sieboldii* undergoes progressive cleavage, forming first a number of multinucleate portions, and then by further division smaller uninucleate protoplasts. The original pyrenoids disappear during the process of cleavage, but a new one reappears in each uninucleate protoplast before it rounds itself off and becomes a zoogonidium. This method contrasts strongly with the regular successive cleavage of the protoplast in *Ch. angustum*, where each cleavage is always preceded by the simultaneous division of both nucleus and pyrenoid. Thus in cytological characters *Ch. angustum* and *Ch. Sieboldii* only agree in the absence of a definite chromatophore and in the possession of pyrenoids and starch.

On comparing now the structure of *Characiopsis Nægelii* and *Ch. saccata* with these two species of *Characium*, it will be seen that the distinctions between the two genera are still very slight. Both species of *Characiopsis* are in the adult condition multinucleate, but this is also the case in *Characium Sieboldii*. In *Characiopsis saccata* the youngest individuals, those which have presumably just been formed from the coming to rest of the zoogonidia, contain only one nucleus, which divides by successive bipartitions as the individual increases in size, until in the adult condition there are sixteen or thirty-two. In *Ch. Nægelii* the same thing probably occurs since specimens containing two and four nuclei were often observed (Fig. 1, F and G), but owing to the much greater thickness of the cell in this species, and the more complicated nature of the cell-contents, the later stages in the increase in number of the nuclei are much more dfficult to follow.

Characium angustum differs widely from these two species of *Characiopsis* with regard to nuclei, but on the other hand *Characium Sieboldii* is almost exactly similar, the young individuals containing only one nucleus, which divides by successive bipartitions as in *Characiopsis saccata* until in adult specimens there are thirty-two to sixty-four.

Thus as far as the nucleus is concerned there are no essential differences between *Characiopsis* and *Characium*, since the uninucleate condition of the cell is not constant in the latter genus.

In the chromatophores there are apparently great differences between the species of *Characiopsis* and *Characium* under consideration, since in *Ch. angustum* and *Ch. Sieboldii* there are no definite chromatophores, whilst in both *Characiopsis Nægleii* and *Ch. saccata* the chromatophores, whilst not being in the least similar to each other, are nevertheless well-defined from the colourless cytoplasm. On the other hand, however, it has still to be proved that chromatophores are universally present in *Characiopsis* and altogether absent in other species of *Characium*, so that this difference of chromatophores is only a possible distinction between the two genera.

Thus after the consideration of these four species the only constant differences which can be distinguished between the two genera remain, as before, in the presence of pyrenoids and the occurrence of starch in *Characium* and their entire absence from *Characiopsis*, the latter genus storing its food reserve in the form of oil.

In conclusion, I wish to express my thanks to Professor G. S. West for much help and advice during the course of the investigation.

BIBLIOGRAPHY.

Borzi, A. ('95). Studi Algologici. Fasc. 11, Palermo, 1895.

Braun, A. ('55). Algarum unicellularium genera nova et minus cognita, etc. Lipsiæ, 1855.

Bristol, B. M. ('17). On the Life-history and Cytology of *Chlorochytrium grande*, sp. nov. Annals of Botany, Vol. XXXI, 1917.

Eichler, B., and Gutwinski, R. ('94). De nonnullis speciebus algarum novarum. Rozpraw Wydzialu matematyczno-przyrodniczego. T. XXVIII, 1894.

Lemmermann, E. ('14). Algologische Beiträge. XII, Die Gattung *Characiopsis* Borzi. Abh. Nat. Ver. Brem. Bd. XXXIII, 1914.

Moore, G. T. ('17). Algological Notes. 1. *Chlorochytrium glœophilum* Bohlin. Annals of the Missouri Botan. Gardens, 4, 1917.

Smith, G. M. ('16). Cytological studies of the Protococcales. 1. Zoospore formation in *Characium Sieboldii* A. Br. Annals of Botany, Vol. XXX, 1916.

THE BOTANICAL LABORATORY,
UNIVERSITY OF BIRMINGHAM.

AN ACCOUNT OF SOME FIELD OBSERVATIONS ON THE DEVELOPMENT OF POTATO BLIGHT.

By F. T. Brooks, M.A.

[With Two Figures in the Text]

Introduction.

EVER since the fungus *Phytophthora infestans* first became the subject of scientific investigation, there has been a good deal of obscurity as to the way in which it is carried over from year to year. The conidia are short-lived and therefore do not serve to tide the fungus over the winter.

In spite of prolonged search, de Bary[1] failed to find resting oospores in diseased potato plants, the fungus in this respect being unlike many other species of *Phytophthora.* He was of the opinion, therefore, that potato blight was carried over from year to year by means of mycelium hibernating in partly diseased tubers, and he obtained definite evidence that mycelium of this kind sometimes passed from the tubers into young shoots, on which the fungus developed its spores above ground, thus forming starting points for an epidemic.

In 1875, Worthington Smith[2] reported the discovery of resting oospores of the blight fungus in tissues of diseased potato plants, but the evidence was not conclusive and, in the absence of confirmation by other observers, there has always been doubt whether these bodies really belonged to *Phytophthora infestans.*

With the discovery in America by Jones[3] and Clinton[4] that *Phytophthora infestans* developed oospores in pure culture, attention was again directed to the possibility of infection arising from such resting bodies during the early summer, and Pethybridge[5] followed up this line of enquiry in Ireland, Although he confirmed the development of oospores in culture, he failed to find them in diseased plants. In connection with this work, Pethybridge put to the test the view that the fungus is carried over the winter by mycelium in partly diseased tubers, and, obtained some experimental evidence that, when planted in pots chiefly under greenhouse conditions, a very small percentage of blighted tubers functioned in this way, the great majority either giving rise to perfectly healthy

---

[1] de Bary, A. Researches into the nature of the potato-fungus—*Phytophthora infestans.* Journ. Roy. Agric. Soc. England, 1876, pp. 239-269.

[2] Smith, W. G. The resting spores of the potato disease. Gardeners Chronicle, 1875, p. 35.

[3] Jones, L.R. Resting spores of the potato fungus. Science, 1909, p, 813.

[4] Clinton, G. P. Oospores of potato blight. Conn. Agric. Exp. Stat. Rept. 1909-10, p. 753.

[5] Pethybridge, G. H. Investigations on potato diseases. 5th., 6th., 7th., Reports, 1914-6. Journ. Irish Bd. Agric.

tubers or decaying completely in the soil. Under field conditions however, none of the blighted tubers planted experimentally by him were seen to throw up shoots invaded by mycelium of *Phytophthora infestans* derived from the seed sets. In the light of these investigations, the blight problem has also been discussed by Horne.[1]

Melhus[2] in America obtained a considerable amount of evidence in favour of the view that primary infection arises from mycelium which hibernates in the seed tubers. Thus a number of partly diseased tubers planted experimentally in the open threw up one or more shoots which were infected by *Phytophthora* and served as starting points for an epidemic.

In connection with the perennation of potato blight by means of mycelium in diseased tubers, mention may be made of the possibility of shoots becoming infected while the tubers are stored in clamps or after being discarded from these and left lying near them. Such shoots may give rise to spores in the late spring or early summer under favourable weather conditions, and these may serve to infect growing crops close at hand, although there is no published evidence of the occurrence of an outbreak arising in this way.

Portions of blighted tubers left in the soil from the previous crops or introduced with the manure (*e.g.*, from pigs) may also, perhaps give rise to conidia of *Phytophthora* when lying near the surface of the soil, but such diseased tissues usually become invaded by secondary organisms which cause complete disintegration.

There are of course other ways in which the blight fungus might hibernate. Its mycelium may perhaps live saprophytically in the soil but this is unlikely for *Phytophthora infestans* is by no means an easy fungus to grow artificially and in competition with other organisms would probably soon collapse. The intervention of an alternate host has sometimes been invoked but there is no evidence that such exists, and other plants *e.g.*, tomatoes, which occasionally become infected by *Phytophthora infestans* in this country, are only attacked after an epidemic has begun in potatoes. Massee[3] considered that the mycelium hibernating in the tubers passed thence into the growing shoots, remaining dormant in the stems and leaves until weather conditions suitable for the sporulation of the fungus intervened, but no evidence in support of the dormancy of the mycelium in the aerial parts of the plants was given. Recently, Eriksson has advanced his mycoplasm theory

---

[1] Horne, A. S. Potato diseases. Ann. App. Biol., 1914.

[2] Melhus, I. E. Hibernation of *Phytophthora infestans* in the Irish potato. Journ. Agric. Res., 1915, V, p. 71.

[3] Massee, G. Diseases of Cultivated Plants and Trees, 1910, p. 123.

in explanation of the rapid onset of epidemics of potato blight, but without any evidence more critical than has hitherto been brought forward in his other papers on mycoplasm; it is obvious that the possibility of explaining the propagation of potato blight from year to year by the agency of mycoplasm will stand or fall by the mycoplasm theory in general, which, it may be said, is still entirely unproven.

Nearly all the work on the means of over-wintering of potato blight referred to above, has been done on a small scale under experimental conditions, and few careful observations have been made in the field as to the way in which the fungus first develops in potato fields planted under ordinary conditions. On account of the uncertainty still existing as to the means by which the earliest appearance of blight in epidemic form in the growing crop is brought about, Dr. A. S. Horne and the writer decided to carry out observations in certain parts of the country with a view to throwing further light on this matter, if possible. It was clear that the districts chosen for these observations should be areas in which the fungus develops in epidemic form, as it were endemically, *i.e.*, without infection by spores brought by air currents from other quarters. Consideration of the progress of the epidemic of potato blight in 1917 shewed that the Penzance district and the Isle of Wight fulfilled this requirement, for in that year *Phytophthora* developed in both these areas before it appeared in the adjacent parts· Although the observations around Penzance were the first to be taken, those made in the Isle of Wight will first be described, as operations there were conducted in greater detail and with better facilities. In the original program, it was arranged that the writer should make observations in the Penzance district, and that Dr. Horne should do the same in the Isle of Wight, but after making some preliminary visits to the island, the latter was unfortunatly prevented by illness from continuing the work, the direction of which then devolved upon Professor F. W. Oliver and the writer.

Observations in the Isle of Wight.

Through the financial asistance of the Food Production Department, and the kind interest of Mr. Lawrence Weaver, C.B.E. (Food Production Department) and of Professor F. W. Oliver, F.R.S., certain members of the staff and students of University College, London, including Misses E. Goodyear, E. A. Fraser, M. L. Hett, M. Munro, E. J. Whitehead, B. Russell Wells, M. A, Sutton, H. S. Pearson, H. A. Bond, A. Gotlieb, together with Mr. H. Stansfield of the Imperial College, and Miss Osborn and Miss Barker of Bedford College, spent several weeks in the island during

June, July, and August, examining potato fields in detail, under the general direction of Professor Oliver and the writer, the latter being then Plant Pathologist to the Food Production Department of the Board of Agriculture. As the exigencies of the war prevented the continued presence of the same observers throughout this period, continuity was maintained by relays of workers.

The plan of operations was as follows:

The observers were divided into three groups stationed in different parts of the island. At each centre two series of observations were carried out;

(*a*) By rapid examination of a considerable number of potato fields scattered in the neighbourhood.

(*b*) By intensive inspection of each individual plant in small plots.

If any of the plots under rapid survey became suspiciously affected, it was the intention to place them under detailed observation. Plots of early and second early varieties were usually chosen for this work as it is well known that these are usually affected by blight before the later varieties.

The mode of procedure in the detailed inspection was as follows:—each plant was minutely examined, as far as possible from day to day, and any discolouration in the haulm that came under suspicion of being an early stage in the development of blight was noted, and the plant marked for further observation. Sometimes the affected part was removed and incubated under conditions suitable for the development of *Phytophthora* and then examined microscopically in a room near the plots, temporarily used as a laboratory. Dark patches on the stem and lower leaves were the symptoms especially looked for.

Unfortunately two of the centres had to be closed before *Phytophthora* appeared and it is not worth while to describe the negative evidence alone obtained at these centres. At the third centre the potato fields under rapid observation gave only negative results but *Phytophthora* appeared in two of the plots under detailed examination and a summary account of these results will now be given. Many of the following notes are based upon observations made by Mr. H. Stansfield by whom also the plans of the plots were drawn.

PLOT 1.

This plot, situated at Haven Street, contained about 130 plants of the second-early variety, White Beauty of Hebron, grown from own-saved seed. In 1917 the crop was onions and two years previously the ground was a fowl run. All these plants were of vigorous growth. The position of the plants particularly noted is shewn on the accompanying plan (Fig. 1).

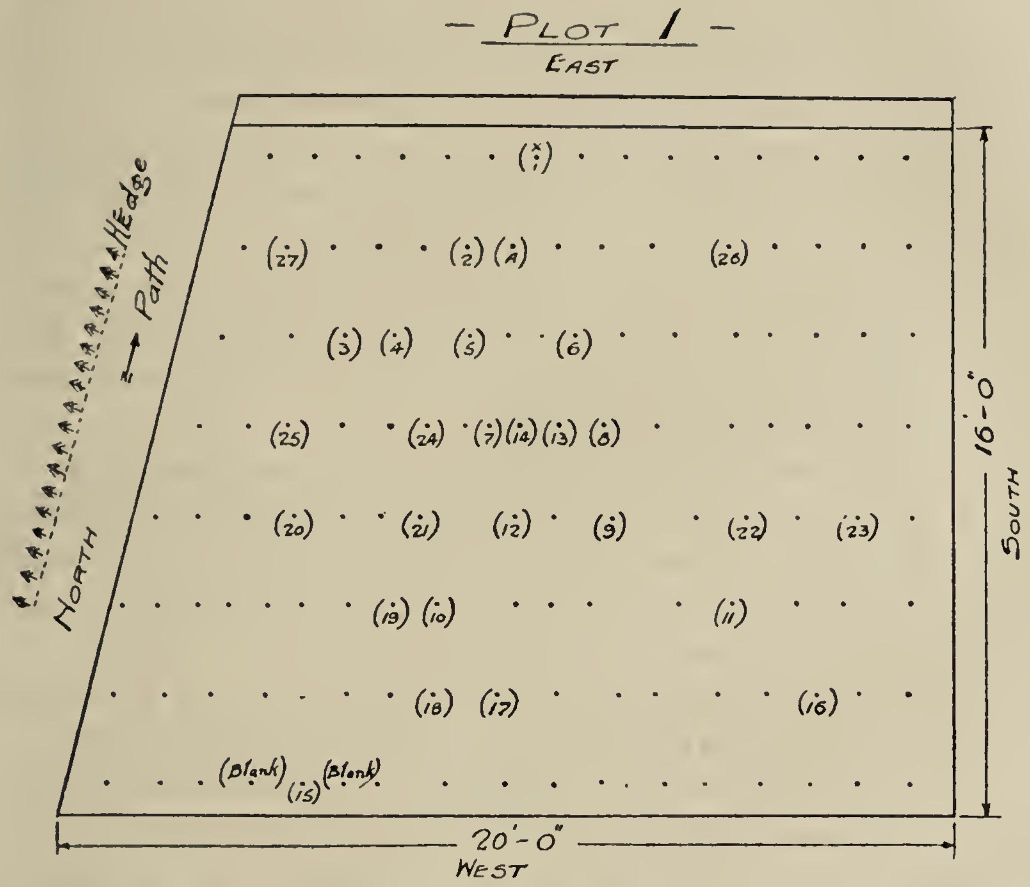


Fig. 1. Plan of Plot 1.

The record of the observations on Plot 1 is as follows:—

June 25. A plant, subsequently called plant A, shewed three separate brownish-black zones on one of the two main stems arising from the parent tubers. These discoloured areas extended about two inches upwards from one and a half inches above soil level and were suspected of being affected by *Phytophthora.* Careful search in the vicinity, however, failed to reveal any shoot bearing spores which might have been the source of infection.

A portion of one of these discoloured areas was removed for microscopic examination, but by the time (July 1) it reached the writer in London, bacterial decomposition was so advanced as to prevent the certain diagnosis of *Phytophthora* although spores similar to those of blight were found on the surface. It was therefore probably affected by blight.

On the same day two of the lower petioles were seen to be partly withered.

On this date no similar discolouration was seen in any other plant in this plot.

As regards the previous weather conditions, rain fell on June 21st and 24th.

June 30. One of the lower petioles of plant A part of which shewed a brownish discolouration, was placed in a collecting tube and despatched to London where it developed spores of *Phytophthora infestans* freely by July 3rd on the discoloured parts, thus shewing that this petiole had been affected by the blight fungus.

July 4. There was no change in plant A. Other plants were as before.

July 6. The brownish-black zones on one of the main stems of plant A had spread considerably.

July 7. Another stem of plant A arising as a lateral from the main stem already mentioned, shewed discolouration all round at about the same distance above soil level and extending upwards about two inches. This black zone was not in continuity with the discoloured areas noted on June 25th.

The plant A was now dug up and a second smaller main stem arising from the old tuber was found healthy throughout. On the main stem which shewed discoloured areas above ground no blackening was found below soil level, but three tubers were diseased. One of these, the largest, showed a large discoloured area which might have been infected *via* the stolon, another of intermediate size was attacked in more than one place and was certainly not infected *via* the stolon, and the third was a small tuber found at a lower level than the others shewing more than one diseased area, one of which was not connected with the stolon. The diseased parts of the two larger tubers were incubated and both developed *Phytophthora* in abundance by July 12th.

Search was made on July 7th as before for any diseased shoot arising from the parent tuber of this plant or from a plant close by which might have been the source of infection of these blighted tubers, but without success. Spores may possibly have developed at some previous date on the discoloured areas already observed on plant A, but *Phytophthora* was not seen on them in the field.

The old tuber of plant A was completely rotten by this date.

Subsequent examination of the discoloured areas on the stems shewed that the fungus was confined to the cortex.

There is no doubt that plant A was affected by *Phytophthora*, but the manner in which it became infected is obscure. The possibilities are discussed later. It appears certain that the fungus developed *within the plot* and was not brought there from outside.

July 6-8. Seven other plants (Nos. 1-7) in this plot were found to be affected in the same way as A, *i.e.*, discoloured zones appeared on the stems or petioles a little distance above soil level. Some of the portions under suspicion were removed but only the discoloured petioles developed *Phytophthora*. The fungus was not observed to fructify on these black zones in the field prior to the leaf infection noticed on July 22nd, although in the absence of continuous observation one cannot be certain that it did not. Even during an epidemic it is exceptional for the fungus to fructify on the stems in the field, and the fact that the lower petioles are often splashed with soil may have prevented the observation of fructifications on them even if present. Rain fell on July 10th, 11th, 12th, 14th, 15th, and 17th.

July 9. A plant (No. 8) shewing several small blackened areas on the branches, was dug up. The tubers were sound but there were several small discoloured zones on the stem below soil level.

July 10. A plant (No. 9) shewed blackening of the stem just above soil level. This plant was dug up on July 12th and all underground parts except the stem immediately below soil level, which was discoloured, were healthy.

July 14-17. Plants 10-27 shewed discolouration on the basal parts of the stems and lower petioles, similar to those previously described.

July 22. On this date plants (1), (2), (4), (5) and (13) were each affected by a few typical blight spots on the leaves, chiefly the lower ones. Microscopic examination confirmed the presence of *Phytophthora*. This was the first occasion on which the fungus was found producing spores in the field. The source of this leaf infection was not discovered. The blight spots rapidly increased in numbers on the leaves of these plants, and the number of discoloured areas on the stems and petioles of these plants developed considerably after the appearances of the fungus in epidemic form, although the fructifications were not seen on these particular parts in the open.

July 23. Plants (6), (11), (14), (15), (19) shewed blight spots on the leaves.

July 24. Plants (23), (24), (26) ditto.
July 25. Plants (7), (10), (20), (21), (22) ditto.
July 28. Plant (12) ditto.
Aug. 1. Plant (25) ditto.

At this date plants (3), (8), (9), (16), (17), (18) and (27) which had been under suspicion of being affected by *Phytophthora* on account of having discoloured areas towards the base of the plant were still free from undoubted blight spots on the leaves. Likewise all other plants in the plot except those mentioned were still unaffected by blight.

Between July 24th and 28th several small garden plots near Plot 1 in Haven Street shewed blight spots on the leaves.

The weather conditions between June 24th and Aug. 2nd were as follows ;—Rain fell on July 10, 11, 12, 14, 15, 17, 22, 23, 24, 26, 27, and Aug. 2, the other days being dry and warm. It will be noted that no rain fell between June 24th and July 10th and this dry spell probably delayed the appearance of the disease in epidemic form.

There are several possible explanations of the way in which plant A became infected :—

1. The seed tuber may have thrown up a diseased shoot which escaped observation, from which spores were (*a*) splashed upwards by rain to infect the base of the stem and lower leaves, and (*b*) washed down into the soil to infect the tubers. As stated, however, there was no trace of such a diseased shoot.

2. A diseased shoot which escaped observation may have grown up from some other tuber near by, but it is more difficult in this case to understand why other plants did not shew discoloration at the same time as plant A and why the tubers of the latter should be infected.

3. The plant may have become infected by spores existing *in situ*. It might be supposed, for example, that resting spores in the soil at this spot germinated, giving rise to conidia or zoospores which may have been splashed upwards to the lower parts of the plant and also washed down to the tubers. If so, it is uncertain how such spores got into the soil as the previous crop was onions, although in view of the widespread opinion amongst practical men that potato disease is often propagated by way of the manure, it is perhaps of some significance that two years previously the site was a fowl run.

4. A blighted tuber or portion of such near the surface of the soil may have given rise directly to conidia, but in view of the previous crop, this is unlikely.

From July 22nd onwards, certain other plants in this plot already under suspicion of being affected by *Phytophthora*, became attacked by typical blight spots, chiefly, but not exclusively, on the laminæ of the lower leaves and it appears likely that these were derived from spores which arose on certain of the discoloured areas noted before this date, but which escaped observation. It is of interest that, in this plot, of the plants which did not shew discoloured areas before July 22nd, none exhibited typical blight spots, ont he leaves up to the end of the period.

From an examination of the plan of the plot it is evident that there was no regularity in the sequence of the plants shewing first, suspicious symtoms, and then definite blight spots, except that the plants first affected were grouped rather towards that part of the plot which contained plant A. After the end of July the production of spores on the plot was so great that there would be no lack of material to infect the remaining plants under favourable conditions

It is thus uncertain how the plants in Plot 1 were infected. The phenomena observed are capable of explanation either by infection *via* the soil or *via* the seed tubers.

PLOT 2.

This Plot, which was about a mile from Plot 1, contained about 60 plants of each of two varieties—Great Scot and Dunbar—and 120 of Arran Chief, all Scotch seed and planted in April. The land was under strawberries during 1917 and before being planted with potatoes was dressed with farmyard manure. On a part of the area planted with the variety Dunbar many blighted tubers of the 1917 crop had been thrown from a shed near by, in which the tubers had been sorted the previous autumn. A search in the top layer of soil revealed many decayed tubers and other tubers partly shrivelled but apparently sound, giving rise to weak shoots. Several of the latter were incubated but *Phytophthora* did not develop.

A plan of this Plot is appended :

During the period of detailed observations, none of the Great Scot plants and only two plants of Arran Chief came under suspicion of being affected by *Phytophthora*, but it was subsequently concluded that these were not so attacked.

The following record was taken of the Dunbar potatoes:—

July 9. A plant B in the area (cross shaded in the plan) containing last year's blighted tubers shewed one stem blackened all round from soil level upwards for about two inches. Two other stems of the same plant were healthy. All the neighbouring plants were sound.

July 10. No change.

July 17. No change. Another plant E in the same area shewed blackening of one of the lower petioles.

July 21 (morning). No change observed.

July 22 (evening). The plant B noted on July 9 as having a discoloured stem now shewed many petioles blackened and numerous typical blight spots on the leaves, especially the lower ones. This plant was dug up but all the tubers were sound and there was no discolouration of the stem below soil level.

All the other plants in this area containing last year's blighted tubers, shewed one or more leaves—especially the lower ones, attacked by *Phytophthora* on this date, but no plants outside this area, whether Dunbar or other variety, were affected. The owner picked off all the diseased leaves the same evening.

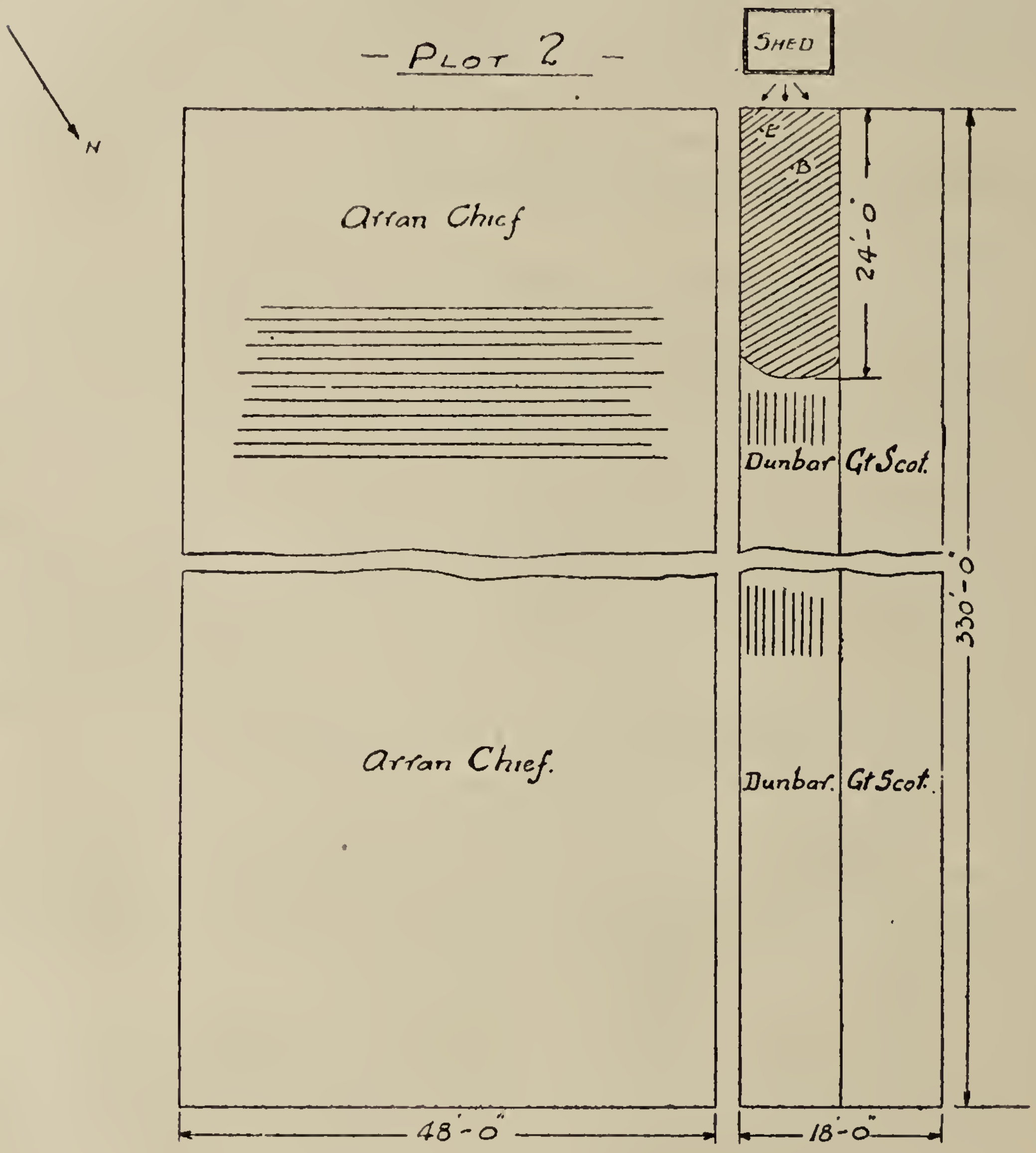


FIG. 2. Plan of Plot 2.

July 24. The same area shewed a slight increase in the number of affected leaves but these were picked off every morning. No plants were affected outside this area.

July 29. There was about twice as much leaf infection as that visible a week ago but it was still confined to the same area.

July 30. There was some increase in the amount of infection.

July 31. Some of the leaves of Great Scot plants adjoining the affected area shewed blight spots.

Aug. 2. The disease was now present on the leaves at the far end of the Dunbar bed about 100 yards away from the area first affected.

At this date the disease was not found in any other potato areas in the immediate vicinity of Plot 2.

As in Plot 1, this outbreak of the disease in epidemic form was was very circumscribed in area and was preceded by the appearance of discolouration on a stem of one of the plants in the infected area. It is noteworthy that when the fungus was first found fructifying in the field it was on this plant that it was most abundant.

Although careful search was made, no shoots from last year's blighted tubers bearing *Phytophthora* were found but strong suspicion was aroused that these blighted tubers had something to do with the outbreak, though in what way could not be ascertained.

These blighted tubers may have sent up diseased shoots bearing spores, which escaped detection, or they may have been the means of introducing resting spores into the plot. It is significant that for some time the only plants affected in the plot were those within the limits occupied by blighted tubers of the previous year. The occurrence of typical blight spots on the leaves at the same date as these were observed in Plot 1 is probably to be correlated with the incidence of similar weather conditions.

No report of the appearance of *Phytophthora* in epidemic form in other parts of the Isle of Wight was received until July 28th when it appeared at Whippingham, a few miles from Haven Street. At Whitwell, 10 miles away, I was informed that the disease was seen during the last week of July on the leaves of a single prostrate plant (Sharp's Express, an early variety) growing under very moist conditions, but blight did not become widespread there until the middle of August.

No records of the appearance of blight in the adjoining mainland counties of Dorset and Hampshire were received by the Food Production Department until the first week of August, hence it is probable that the blight fungus developed "endemically" in the Isle of Wight as regards Plots I and 2.

Observations in the Penzance District.

These were carried out by the writer alone and, on account of circumstances were of a more rapid nature than the observations made in the Isle of Wight. Nevertheless they are of interest. As is well known, early varieties of potatoes are grown on an extensive scale in this part of Cornwall. The soil is particularly suitable for potato growing, being a light sandy loam of good quality, and usually enriched with heavy dressings of farmyard manure and sea-weed. Potatoes are frequently grown on the same land year after year and as soon as the tubers are lifted in May and June, broccoli are planted. These early potatoes are grown very closely together, the rows being only about 10 inches apart and the seed sets 8 inches from one another. The plants are not earthed up as is the custom in most parts of the country. Successive visits were paid to the neighbourhood and the following is a record of the observations which are given as recorded on the spot.

May 27. At this date the lifting of early varieties had already commenced. Blight was found in a field of the variety Sharp's Express near Newlyn. The seed sets, which were obtained from Lincolnshire, had been sprouted and cut prior to planting during the third week of March. Before May 27th the weather had been dry with the exception of an occasional sea fog. In this field there were two areas on the sheltered side of a high hedge, each about a yard across, in which every plant was more or less attacked by blight in sporing condition, but in neither area could the disease be traced downwards to parts of the stems below soil level. In these two spots all parts of the plants above ground were attacked, including the flower buds, the stems often appearing to be invaded by way of the axils of the lower leaves. The fungus was fructifying on the laminæ of the leaves, but suspected discoloured portions of petioles and stems also developed *Phytophthora* spores after incubation. In addition to these two areas, there were a few scattered spots of blight on the upper leaves in other parts of this and other fields close at hand. These had presumably arisen by secondary infection, probably from spores found in the two areas referred to. As regards this particular place there could be no doubt that blight first developed in these two well defined spots in the field.

May 31. The same field was visited again. Blight had spread very little since the last visit, the weather having been dry. Another centre of infection was found, however, every plant within a circular zone two yards across being attacked, especially in the lower leaves and the parts of the stem just above soil level. As before, the disease could not be traced downwards to parts of the stems below soil level.

Two other centres of infection were found in two other fields in the same locality showing the same appearances as already described. In one of these the site was relatively dry, being situated on a slope with a southerly aspect.

Many other fields of early potatoes in this vicinity were found to be free from blight.

A centre of infection—about 3 yards across, was found in a large plot of Sharp's Express in a low-lying situation in Penzance, shewing the same symptons as noted previously. At the margin of the infected area there were a few spots of blight on the upper leaves, but beyond these all plants were healthy.

At Madron a group of Royal Jersey potatoes—about 3 yards across, was affected by blight in the midst of a large plot of this variety. The symptoms were the same as before, but in this case opportunity was afforded of lifting some of the plants, with the result that a few tubers were found already affected by blight, *Phytophthora* subsequently developing on slices of these diseased tubers kept in Petri dishes. In these tubers the disease had not entered *via* the stolons. They may have been infected by spores which had fallen from the aerial parts, or by the fungus present in some form *in situ* in the soil. One of the upper leaflets of a plant about fifty yards away from the centre of infection was blighted, but otherwise the remaining plants were healthy. At this date neighbouring fields of early varieties were quite unaffected by blight.

June 2. One patch of blight, about three yards across, was found in a field of Sharp's Express at Gulval, the disease being chiefly present on the lower parts of the stems and the lower leaves, with typical blight spots on the latter. The disease could not be traced downwards to parts of the stems below soil level.

A group of the second early variety—British Queen—about three yards in diameter was affected in the middle of about four rods of this variety at Penzance. The symptoms and distribution of the disease were the same as before. On the circumference of the affected group, blight spots were found only on the upper leaves but in the centre of the disease area, the lower parts of the stem, the petioles,and midribs of the lower leaves were chiefly affected. Here again the disease could not be traced from above soil level to the parts of the stems below the soil. Some of the diseased plants were lifted and blighted tubers were found, but these were only exceptionally affected at the heel end, thus showing that in most cases at any rate the disease did not enter *via* the stolons. *Phytophthora* subsequently developed on these tubers after incubation.

June 23. The area last mentioned was again visited but there had been only a slight extension of blight since June 2, the weather having been dry in the meantime, but on a neighbouring plot there were a few blight spots on the upper leaves and also on a main crop variety growing partly under trees about fifty yards away. By this date nearly all early varieties had been dug in this district.

Numbers of other potato areas were examined in the vicinity of Penzance at this time with negative results, and it is noteworthy that up to June 23rd not a trace of blight was found on varieties of potatoes other than earlies and second-earlies. The weather remained dry until about the middle of July and there was no appreciable development of blight on main crop potatoes in the western parts of Cornwall until the end of that month. Of course had wet intervened when the early varieties were first affected the disease would have spread with its usual rapidity.

Conclusions.

The observations taken in the Penzance district agree in kind with those made in the Isle of Wight and shew with the latter that the earliest outbreaks of blight developing *in situ* are of strictly limited extent and that from them the fungus develops centrifugally under favourable conditions until the spores are so widely distributed in the air that infection of susceptible plants becomes universal. The observation that blight affects the tubers at a very early stage in the development of the disease is noteworthy, as is also the evidence presented that these do not generally become infected from the main stem *via* the stolons. The facts observed are capable of interpretation either by infection from the soil through the agency of some form of resting body or by infection from blighted shoots growing upwards from diseased sets. The latter were not found in spite of careful search, although it is known that they have occasionally functioned under experimental conditions. The fact that the first plants to be affected are in limited groups may at first thought appear to invalidate the possibility of infection from the soil, but it does not follow that resting bodies, if formed, would be regularly distributed in the soil and it is likely that only a few would function and be successful in causing blight to develop on the plants. One is reluctant to give up the idea of some form of resting body in the life-history of this fungus in nature, for it would be suprising if this fungus, which can produce oospores in artificial culture, were unable to form these in nature under certain, at present unknown, conditions.

These observations shew that it will be a matter of difficulty, and perhaps also of considerable luck, to obtain critical evidence as to the mode in which the blight fungus is carried over from year to year in crops of potatoes grown under ordinary conditions. In shewing that the first attacks are strictly limited where extraneous infection is not operative, the solution of the problem is advanced slightly, and by continued attack along these and other lines the obscurity which still exists in regard to the life-history of *Phytophthora infestans* in the field should be removed.

In conclusion, the grateful thanks of the observers and the writer are due to all those in the Isle of Wight and in the Penzance district who provided facilities for carrying out these observations, especially to Mr. C. Martin, Instructor in Horticulture for the Isle of Wight, and also to Professor Oliver, F.R.S. for his great interest and help throughout the work in the Isle of Wight.

THE
NEW PHYTOLOGIST

VOL. XVIII, No. 7. JULY, 1919.
[PUBLISHED SEPTEMBER 10TH, 1919.]

THE ORIGIN AND DEVELOPMENT OF THE COMPOSITÆ.*

BY JAMES SMALL, D.SC., F.L.S.

CHAPTER XIII.

GENERAL CONCLUSIONS.

THE results of the present investigation of the Compositæ are chiefly of two kinds; the phylesis of the family and of its chief groups has been elucidated, and various theories have been given to account for the origin and development of the structures and physiological and cytological phenomena which occur in the family. The historical evolution of the tribes is discussed briefly in the first chapter, together with previous phylogenetic suggestions. As these suggestions were in most cases based upon only one or a few characters it is unnecessary to discuss them in detail. It will be sufficient to point out that the affinities of the tribes suggested in the present account have almost all been recognised by previous synantherologists.

The results of general importance are summarised below.

Styles and Stamens. The evolution and biological significance of the appendages of the styles and stamens have been elucidated and the general economy-tendency has been shown to extend to the polliniferous tissue. The two general principles, "the progressive sterilisation of potentially sporogenous tissue" and the elaboration of the sterilised tissue, are exemplified in the evolution of the anther appendages.

Irritability of the Stamens. Our knowledge of thigmotropism of the stamens has been extended to all the tribes, except the Eupatorieæ and Vernonieæ, and to most of the sub-tribes of the family. Subsidiary results of the investigation of irritability are the new record of thigmotropism in the style of *Gazania splendens*, the differentiation of five types of movement of the stamens, and the theory of the differential changes in the permeability of the cells of the filaments as the cause of the movement.

---

* Part of a Thesis approved for the Degree of Doctor of Science in the University of London.

Corolla. The ray florets are shown to be essentially bilabiate in development and structure, and the occurrence of inner rows of ray florets is shown to be related to the food-supply of the capitulum. Other results of the investigation of the corolla are the elucidation of the evolution of colour in the family from yellow, through orange and white, to red, purple, violet and blue, and the recognition of the filiform corolla as a reduced type.

Pappus. The setose pappus is proved to be primitive by its mature structure (Chap. V), by the presence of a pulvinus, by its development in the individual and in the family, by its common occurrence in the earlier known fossil Compositæ, and by the correlation between pubescence of the achene and presence of pappus (Chap. XII, D). Subsidiary results of the investigation of the pappus are a re-affirmation with new evidence of its trichome nature, and the elucidation of the evolution of the various types from the scabrid setæ by fusion and reduction, two tendencies which are recognised as general in the other parts of the flower and inflorescence of the family.

Origin of the Capitulum. The development of the capitulum is shown to be due to the abortion of the pedicels in a racemose umbel rather than the non-elongation of the main axis of a spike. All the essential characters of the capitulum are explained by this theory.

Involucre. Two parts are differentiated in the involucre, the pericline and the calyculus. The primitive involucre is shown to be one with an uniseriate pericline and a slightly developed calyculus. This is confirmed by the structure of the earliest known fossil involucres.

Receptacle. The receptacular alveoles and setæ are shown to be new outgrowths, and the detailed structure and distribution in the family of these and other receptacular appendages are explained. The paleæ of the receptacle are regarded as atavistic to a pre-Composite ancestor when they subtend the florets, and as a development of the fimbrillate type of appendage where, as in the Cynareæ, they do not subtend the florets.

Phyllotaxis. The pericline and calyculus are shown to be distinct structures; the pericline is the row of members transitional between the curve-system of the cauline leaves or calyculus and the curve-system of the disc florets. These transitional members subtend the ray florets in radiate capitula. The pericline is, therefore, primitively uniseriate. Other results of the investigation of the phyllotaxis are the proof of the primitiveness in the family of alternate phyllotaxis in the cauline leaves, and the elucidation by Church's work of the rules governing the number of rays and the general symmetry of the capitulum.

Fruit Dispersal. Winds of comparatively small velocities are proved to be sufficient to disperse pappose fruits to any distance under proper conditions of atmospheric humidity. A method and a formula are given for calculating from the rate of fall in quiet air the minimum wind necessary for the dispersal of pappose fruits. A new type of anemometer of considerable accuracy is described. New experimental methods for determining the rate of fall in quiet air and the minimum wind necessary for dispersal are given. The hydrodynamics of the wind-dispersal of pappose fruits are elucidated.

A preliminary explanation is given of the general phenomenon of the elongation of the stalk of the fruit or spore-sac which in most cases immediately precedes fruit- or spore-dispersal. This explanation is also applicable to the elongations of the axis which take place in the female cone of *Pinus*.

Geographical Distribution. The previous phyletic conclusions and the validity of the Law of Age and Area are confirmed by the geographical distribution of the species, genera and tribes of the family. The principle of physiological differentiation and restriction of area is elucidated. Other points illustrated are the irreversibility of evolution, the development of peculiar types in each well-defined climatic region, the correlation between ecological conditions and the vegetative forms assumed in the various tribes, and the existence of definite centres of origin and paths of migration for the various tribes.

The explanation (Chap. X, A) of the espalier and cushion forms of plants by permeability changes which are directly due to the environment is of particular interest, since this view of epharmosis is capable of extensive development both experimentally and theoretically (cp. Chap. III, D, and Bib. III, 49-50, and X, 68a).

Origin of the Compositæ. It is shown to be highly probable that *Senecio* originated from the Lobelioideæ by orthogenetic saltation and epharmosis in late Cretaceous or early Tertiary times in a particular region of South America. An eclectic theory of evolution is suggested and a close analogy is traced between orthogenetic saltation and the disintegration process of the radioactive elements.

Fossil Compositæ. A list is given of most, if not all, known fossil Compositæ. The occurrence of the various types of fossil Compositæ fruits is shown to be in accordance with the phyletic suggestions in previous chapters.

Cytology. Considering relationships within the family, the chromosome number is shown to be of some phyletic value. The development and type of haustorial antipodals also agree with previous phyletic suggestions.

Latex. A general theory is given of the evolution and functions of laticiferous tissues; the functions are excretory and nutritive; the evolution is suggested to be the result of epharmonic adaptation to a climbing or rapidly-elongating habit, which requires the easy and rapid translocation of food materials obtained by the development of a laticiferous system.

These are the general results, as distinguished from the phyletic results, which will now be discussed for each tribe.

PHYLETIC CONCLUSIONS.

Senecioneæ. The main thesis of the preceding chapters is that *Senecio* was the first genus of the Compositæ to come into existence and that it has directly or indirectly given rise to all the other genera of the family. That *Senecio* is the basal genus of the Compositæ is a theory which is supported by all the details of its vegetative and floral morphology, physiology and cytology, *i.e.*, the chromosome number, the antipodal haustorium, the anomalous septa and lateral placentæ in the ovary, the simple structure of the seed and seedling, the simple appendages of the styles and stamens, the simplicity of the pollen-presentation mechanism as a whole, the simple type of irritability of that mechanism, the numerous species and varieties with discoid capitula, the variation in form, development, colour and vascular anatomy of the corolla, the setose-scabrid pappus, the pulvinate achenial hairs, the small, flat, simple receptacle, the uniseriate pericline, the slightly developed calyculus, the alternate phyllotaxis of the cauline leaves, the development and contents of the secretory system, and the extreme plasticity of vegetative organisation or low physiological differentiation as shown by the marked response to a variety of ecological conditions. This theory is also confirmed by the geographical distribution of the genus and its close approach in the details of floral structure to the ancestral genera in the Lobelioideæ. The 2500 species of *Senecio*, constituting 10% of the Compositæ, form a very substantial "trunk" for the family tree (Fig. 79).

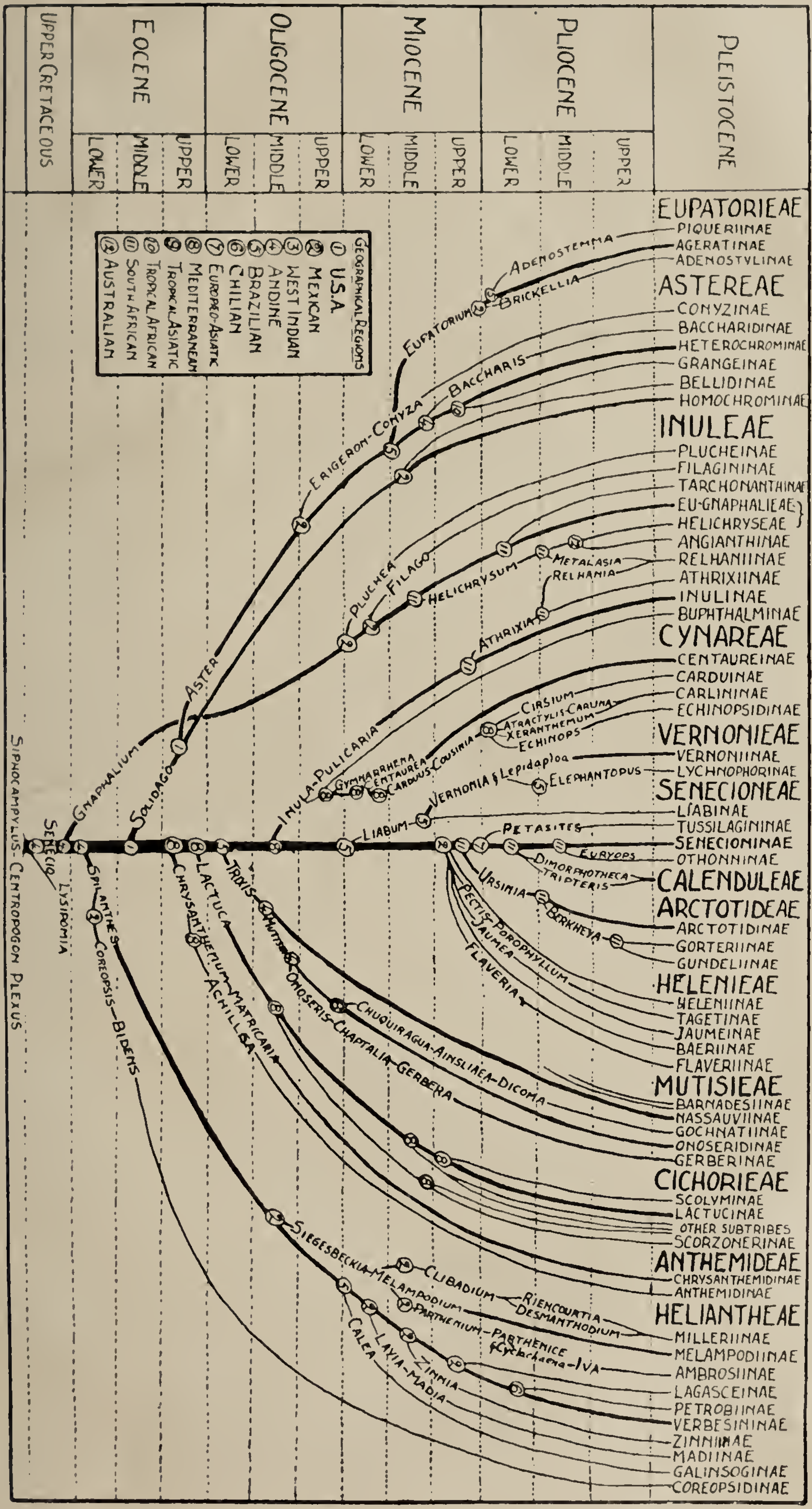


FIG. 79. The Evolution of the Compositæ in Time and Space.

The origin of *Senecio* from the *Siphocampylus-Centropogon* group of the Lobelioideæ somewhere between the forests of the Amazons and the heights of the Andes has been proved as clearly as is possible without actual ocular demonstration of the process. The evolutionary processes involved in this origin are shown to be orthogenetic saltation and epharmosis, and the date of the event is indicated by the geological evidence to be the late Cretaceous Period and approximately the same as the date of the first upheaval of the Andes.

The Senecioninæ consist of a group of genera closely related to *Senecio*. The detailed evolution of the genera in this sub-tribe is interesting, but is reserved, together with the detailed generic evolution of the other tribes, for future contributions. The facts of floral morphology and geographical distribution which are available should be supplemented by other data before any attempt is made to deal with the details of phylesis in the smaller subdivisions of the family. It will be sufficient for the present to suggest possible basal or transitional genera where these are clearly indicated.

Liabum is the primitive genus of the Liabinæ; this is shown by the floral morphology and geographical distribution. This genus may be regarded as the *Gynura* of America, the type VIIIa style of *Gynura* being very similar to the type III style of *Liabum;* other characters also show a parallelism. It is interesting to note that these two genera flourish in the same latitudes, the one in America and the other in the Old World. The transition from the discoid species of *Liabum* to *Vernonia* is more a matter of the corolla colour and the phyllotaxis of the cauline leaves than anything more serious.

In Chapter II, E, the very close proximity of one genus of the Tussilagininæ, *Cremanthodium*, to *Senecio* is discussed. This sub-tribe is probably not monophyletic in the sense that a single primitive genus in the group has given rise directly or indirectly to the other genera; it is probably monophyletic in the sense that all the primitive genera have arisen directly from *Senecio*. Thus *Cremanthodium* is a comparatively recent genus which has arisen directly from the *Ligularia* section of *Senecio*. It is very probable, although less certain, that *Petasites* also arose in the same Asiatic region, but at an earlier date, from *Senecio* and *Ligularia*, and that it has given rise to the other genera of the Tussilagininæ. *Alciope* in South Africa is probably a third offshoot from *Senecio*. The derivation of this sub-tribe from the *Ligularia* type of *Senecio* is confirmed by the floral morphology, by the general habit and by the slight or slow irritability of the stamens or its complete absence in that type of *Senecio.*

Apart from *Werneria*, which is possibly a polyphyletic genus, the Othonninæ are clearly of recent South African origin, with *Euryops* as a probable primitive genus. *Euryops* is distinguished from *Senecio* only by its fused periclinal bracts and the wavy setæ of the pappus. The Othonninæ are also connected with *Senecio* through *Othonna* and *Othonnopsis*, but the differences are greater along that line, and although *Othonna* has more species than *Euryops* the area occupied by the latter genus is greater.

Cichorieæ. The derivation of the Cichorieæ from the Senecioneæ involves very few changes of any magnitude. The pollen-presentation mechanism is of a simple type; the peculiar folding of the exine is approached in *Senecio vulgaris*; the homogamous, non-radiate capitulum is similar to the discoid species of *Senecio*; the predominance of yellow as a corolla colour and the simpler types of pappus which occur are other characters which show the affinity; still others are the simple, small, almost flat receptacle, the uniseriate pericline with or without a slightly developed calyculus, and the alternate phyllotaxis of the cauline leaves. The occasional occurrence of receptacular paleæ is to be considered a reversion to a pre-Composite ancestor. The posterior split of the corolla and the development of laticiferous vessels are the two chief changes and these also are clearly of the nature of reversions to the Lobelioid ancestors of the Senecioneæ.

The sub-tribes are rather artificial, but we can distinguish the *Lactuca-Sonchus* group as primitive and the *Scorzonera* group as advanced. *Lactuca* is indicated as the primitive genus by all the characters of the florets and inflorescence, the seeds and seedlings, the chromosome numbers, and the geographical distribution.

The time and place of origin of the tribe are both clearly shown; the centre of origin is shown to be the Mediterranean region by the present geographical distribution; the occurrence of the *Lactuca* type and other Cichoriaceous material in the Lower Oligocene of Aix-en-Provence is in accordance with this conclusion and at the same time gives the date of origin as that period or a little earlier.

Calenduleæ. The Calenduleæ are closely allied to the Senecioneæ in the structure of the styles and stamens, in the irritability of the stamens, in the colour and anatomy of the corolla, in the simple receptacle and involucre and in the phyllotaxis of the cauline leaves. The chief differences are the usual absence of pappus and the usual heteromorphy of the achenes. It is not surprising, therefore, that Bentham wrote (I, 7, p. 463) that the Calenduleæ "might almost have been enumerated amongst the sub-tribes of the Senecionideæ." *Dimorphotheca*, with type IV style, type 4 or type 10 stamens, disc florets sometimes fertile, no pappus, plain receptacle, simple involucre and alternate phyllotaxis, is indicated as the primitive genus, but *Tripteris* is almost equally primitive; it has the disc florets always sterile and occasionally opposite phyllotaxis, but the pappus is coroniform and the involucre is very simple ; it also has a wider geographical area. It is practically certain that the tribe is polyphyletic on account of the Chilian genus *Eriachænium*, and it is quite probable that the remainder of the group is at least diphyletic, if it is not only a mere collection of African Senecioneæ with heteromorphous achenes.

The place of origin is clearly South Africa and in the complete absence of fossil evidence the date may be taken as quite recent, probably Pliocene.

Arctotideæ. This tribe is separated from the Senecioneæ by a number of characters, such as the type of style, pappus, receptacle and involucre. The primitive genus, *Ursinia*, with the widest geographical area, is more closely related to the Senecioneæ than any of the other genera. *Ursinia* has the *Senecio* type of style and stamens, shows no irritability of the style and has yellow as the predominant corolla colour. The paleæ of the pappus and receptacle are comparatively advanced features, but are secondary to the inner floral characters. *Berkheya* by its floral structure and geographical distribution is indicated as the primitive genus of the Gorteriinæ, which sub-tribe has the Gundeliinæ as a small, possibly diphyletic, off-shoot.

The place of origin of the tribe is clearly South Africa and the date is probably a little earlier than that of the origin of the Calenduleæ : considering the extension of the tribe into Australia it is probably lower Pliocene.

Anthemideæ. In the pollen-presentation mechanism the Anthemideæ are very similar to the Senecioneæ, except for the type V style of the sterile florets. The corolla colour is higher and the chief differences are the almost complete absence of any pappus except the reduced, paleaceous coroniform type, and the scarious margins of the involucral bracts. The epaleaceous receptacle and geographical distribution indicate the Chrysanthemidinæ as the primitive sub-tribe, while these characters and those of the florets indicate *Chrysanthemum* as the primitive genus with *Matricaria* as more or less comtemporaneous in origin. If *C. segetum* is carefully compared with a radiate *Senecio* with the calyculus well developed only the two chief tribal characters and general habit are found to distinguish the two types, and *C. segetum* has a fairly extensive geographical area.

Achillea is indicated by its floral characters and geographical distribution as the basal genus of the Anthemidinæ, the chief difference being the paleaceous receptacle, which here, as in the Cichorieæ, is considered to be an atavistic character. That it occurs in both cases in genera which are advanced in other characters is confirmation of the reversionary nature of this type of receptacular appendage.

The place of origin of the tribe is shown by the present geographical distribution to be the Mediterranean region. The date of origin is indicated by the same facts to be earlier than that of the Cichorieæ. The presence of the *Chrysanthemum*-like leaves of *Parthenites priscus* in the Mediterranean region in the lower Oligocene, and the occurrence of the Anthemidean type of pappus and achene (*Hyoserites Schultzii*) in the Upper Miocene in another locality of the same region confirm, as far as is possible with our present knowledge, both time and place of origin. The *Cypselites trisulcatus* of the lower Oligocene has certain resemblances to the achenes of the Anthemideæ and it is possible that further investigation may show that those epappose achenes have in most cases been passed over on account of the absence of the pappus.

Inuleæ. Throughout the analysis of the various characters of this tribe there has been some difficulty on account of the synthetic nature of the group. The diphyletic origin suggested by the filiform or bilabiate outer florets is confirmed by the structure of the involucre, the haustorial development of the antipodals, the secretory apparatus and the geographical distribution.

If Tables VI and VII are examined in the light of these suggestions various points can be seen. In Table VI the Tarchonanthinæ can be neglected as a small, special group. The other four sub-tribes with a filiform corolla (Plucheinæ, Filagininæ, Gnaphaliinæ and Angianthinæ) show a large proportion of type IV styles; type XIII styles are also well represented in the "filiform" sub-tribes. In the last three sub-tribes (Athrixiinæ, Inulinæ and Buphthalminæ) type XII is the dominant form of style. The Relhaniinæ show an exceptional proportion of type IV styles for a radiate sub-tribe.

Turning now to Table VII it will be noted that with one exception all the genera showing the simpler types of stamens occur in the "filiform" group, the first five sub-tribes. The predominance of type 10 stamens in the Gnaphaliinæ and Inulinæ mark these sub-tribes as the primitive groups of the two divisions of the Inuleæ. The four chief types of stamens in the tribe are 10, 12, 13, 14. All four types occur in the two basal sub-tribes and among the other sub-tribes only in the Relhaniinæ. A more detailed examination of the floral characters of the Relhaniinæ shows that sub-tribe to be a mixture of genera, some with radiate capitula and others with few-flowered, homogamous capitula. A diphyletic origin of this sub-tribe is clearly indicated, one line coming from the Helichryseæ with *Metalasia* as the primitive genus, the other coming from the Athrixiinæ with *Relhania* as the primitive genus.

In the Inuleæ, therefore, we have two main phyletic lines. The first line begins in the Eu-gnaphalieæ with a South American origin from the Senecioneæ at an early date and passes to the Filagininæ with a Mediterranean centre of origin, the Plucheinæ with a tropical African centre, the Helichryseæ, Tarchonanthinæ and part of the Relhaniinæ with their centres in South Africa, and finally to the Australian Angianthinæ. The second line begins with the Inuleæ, originating from the Senecioneæ at a later date than the Eu-gnaphalieæ in the Mediterranean region, and passes in the same region to the Buphthalminæ and in South Africa to the Athrixiinæ and the rest of the Relhaniinæ. This development harmonises with all the known characters of the groups, including the geographical distribution, and exemplifies the parallel evolution, polyphyly and convergence which are discussed in Chap. XI, B.

In Fig. 7 the Helichryseæ are shewn as preceding the Eu-gnaphalieæ, but the geographical distribution indicates and the other data on more critical analysis confirm the view that the latter group is the primitive one for the "filiform" sub-tribes of the Inuleæ. Beauverd (XII, 158) places *Helichrysum* before *Gnaphalium* when he gives the chief genera of the sub-tribe "dans l'ordre évolutif présumé." He, however, used the fertility or sterility of the flowers as his chief guide and the work of Uexküll-Gyllenband (II, 69) shows that this cannot be taken as of primary importance in phylesis; it is also proved by the fact that the other characters which are analysed by Beauverd do not follow the same sequence as the homogamy or heterogamy of the capitulum.

The data available for the determination of the times of origin of the two main lines are confined to the probable origin of the Senecioneæ in the Upper Cretaceous, the known development of the Cynareæ in the Upper Miocene and the present geographical distribution of all the groups concerned. From these data, however, the date of the first development of the Eu-gnaphalieæ can be placed soon after the origin of *Senecio*, probably early Eocene; and the date of the origin of the Inulinæ must have been later than that but some time before the Upper Miocene. Taking all the facts into consideration the date indicated is the middle Oligocene. Such a date would account for the absence of the Cynareæ from the lower Oligocene and would also give a sufficient interval for the development of the *Arctium* type of the Cynareæ in the Upper Miocene (see below under Cynareæ). At the same time it would account for the similarity in the present distribution of the Inulinæ and Cichorieæ, as well as for the greater area occupied by the latter, which is the older group.

Cynareæ. Two possible sources, the Plucheinæ and Buphthalminæ, have been suggested for the Cynareæ and a diphyletic origin of the tribe has been indicated as a possibility. As diphylesis is supported only by the evidence from the pappus it will be neglected until a more detailed examination has been made of the evolution in the tribe. The rest of the characters, including the geographical distribution and the secretory apparatus. support a monophyletic origin of the tribe from the Inuleæ *via* the Buphthalminæ, *Gymnarrhena*, *Centaurea* and the Centaureinæ. So close is the affinity that a microscopic investigation is necessary to distinguish some plants of *Gymnarrhena micrantha* (Inuleæ, Buphthalminæ) from *Centaurea furfuracea* (Cynareæ, Centaureinæ) and these two species grow in the same region.

The development of the Carduinæ from the Centaureinæ with the *Carduus-Cousinia* group as the basal plexus is clear, as is also the development of the Carlininæ and Echinopsidinæ from the Carduinæ. The evolution of these two sub-tribes along different lines from the same source is well shown in the secretory apparatus, the *Carduus* plexus gives the *Cirsium* line in the Carduiinæ and the parallel *Carlina* line in the Carlininæ; the same plexus gives the Echinopsidinæ line and the parallel *Xeranthemum* line in the

Carlininæ. A slight degree of diphylesis is thus indicated for the Carlininæ and this is supported by other details, which suggest the *Atractylis-Carlina* plexus and *Xeranthemum* as the two basal groups (cp. Lavialle above, Chap. XII, D).

Considering the date of the origin of the Cynareæ, the facts are that this tribe is not represented with any certainty previous to the upper Miocene and that the *Arctium* type (Carduinæ) had then developed. If the above views on the phylesis of the tribe are correct this involves the previous existence of the *Carduus* type, which is also represented at the same horizon, and of the *Centaurea* type, which is not as yet reported fossil below the upper Pliocene. The time interval necessary for this development takes the origin of the Cynareæ back to the lower Miocene or Upper Oligocene. As the shrinking of the Central Sea reached its maximum about this time, the semi-desert condition of the eastern Mediterranean region would appear to have developed then. The connection between the origin of the Cynareæ and the ecological conditions in the place of origin has been discussed previously, and the synchronising of events in climatic evolution with events in plant evolution appears to be exemplified in the origin of the Cynareæ as well as in the origin of *Senecio*.

Mutisieæ. The basal group of the Mutisieæ is undoubtedly the Nassauviinæ and the basal genus is shown to be *Trixis* by the characters of the styles, stamens, pappus and other achenial hairs, receptacle and involucre. This is confirmed by the geographical distribution of the genus and sub-tribe and by the Senecionoid habit of many species of *Trixis*. The colour of the corolla in *Trixis* is also primitive and the distinguishing feature is the homogamous capitulum of bilabiate florets. Since the ray floret of *Senecio* and other radiate genera has been shown to be essentially bilabiate, and since it has also been shown, though with less certainty, that the number of rows of bilabiate florets, *i.e.*, the the amount of "doubling," depends on the food supply of the capitulum, the change from *Senecio* to *Trixis*, from the Senecioneæ to the Mutisieæ, is evidently one which is largely dependent on ecological conditions.

In Chap. V, D, it was suggested that *Mutisia* gave rise to the rest of the Onoseridinæ and to the Gochnatiinæ, while *Onoseris*, as the other member of the basal plexus of the Onoseridinæ, gave the Gerberinæ. The evolution of these groups is further discussed in Chap. X. *Chuquiragua* is suggested as the basal genus of the

American Gochnatiinæ and the *Ainsliæa-Dicoma* group as the source of the Old World Gochnatiinæ. As *Ainsliæa* is more closely allied to *Mutisia* than *Dicoma*, that genus may be substituted for the double group.

Gerbera and *Chaptalia*, which are separated only by the abortion of the posterior lip of the ray florets in the latter and its presence in the former genus and by their geographical localities, form a very good basal plexus for the Gerberinæ. The differences between these two genera and *Onoseris* are of no more than specific rank in other genera, except for the type XII style of *Gerbera* and *Chaptalia* and the type IX style of *Onoseris*. A glance at Fig. 5 will show that the type IX style could be regarded as a type XIIa style in which the stigmatic papillæ had spread over the whole of the inner surface and in which the style branches had closed up. The former style would be the more primitive, but the difference is so slight that the evolution of the Gerberinæ from *Onoseris* is quite probable. These suggestions involve a slight change in Fig. 7 which would bring off the Gochnatiinæ from the Onoseridinæ instead of from the Gerberinæ.

The two genera of the Barnadesiinæ, *Barnadesia* and *Schlechtendahlia* with type 3 or type 4 stamens and type IX styles have probably arisen separately from distinct sources, and this sub-tribe is another example of polyphyly and convergent evolution. Until a detailed examination of their affinities has been made they can be regarded as a separate development, as shown in Fig. 7.

The separation of the Mutisieæ into two geographical groups furnishes some clue to the early history of the tribe. That the separation is geologically recent is proved by the affinity of *Gerbera* and *Chaptalia*. That the separation was due to the last Glacial Epoch is rendered probable by the recency of the event and by the fact that the Mutisieæ are tropical and subtropical plants. Such species, although they probably crossed the Alaska-Siberian bridge during the pre-glacial and interglacial warm periods, were unable to survive in the more northern latitudes during the period of glaciation and only a few primitive, *i.e.*, physiologically undifferentiated, species, such as *Gerbera Anandria*, are even now becoming acclimatised to sub-arctic conditions.

The origin of *Trixis* is thus thrown back some considerable time to allow for the differentiation and dispersal of the higher types, such as *Gerbera*. Since the area occupied by the tribe is considerably larger than that of the Cynareæ and since the differentiation of types within the tribe is greater than in the Cynareæ, a date antecedent to the origin of the latter tribe is indicated; taking into account the similarity in the areas occupied by the Inulinæ and by the Old World Mutisieæ, and the greater area of the whole of the Mutisieæ, the lower Oligocene is a probable date for the origin of the Nassauviinæ, with an extension into the Old World about middle Oligocene times.

Vernonieæ. The evolution of this tribe from the Senecioninæ *via* the Liabinæ is abundantly proved by most of the details of the florets and capitulum. The affinity between the Liabinæ and the Vernonieæ may be judged from the fact that *Gongrothamnus*, a genus of the Liabinæ according to Bentham, is Sect. IV of the genus *Vernonia* according to Hoffmann. The primitive genus, *Liabum*, of the Liabinæ is closely connected on the one hand with the Senecioninæ and on the other hand with *Vernonia*, the primitive genus of the Vernonieæ. The derivative position of the Lychnophorinæ is confirmed by most of the floral details and by the geographical distribution of the sub-tribes. The primitive genus is probably *Elephantopus*; the only character which raises any doubts of the primitive position of this genus is the form of the corolla, which sometimes has a posterior split.

The generic differentiation in the tribe is comparatively slight. Bentham (I, 7) remarks that the Vernonieæ "consists principally of one large genus with a number of smaller ones closely connected with it forming altogether one sub-tribual or generic group of a higher order." The distribution is entirely tropical or sub-tropical and the use of the Alaska-Siberian bridge by the tribe is not in any way indicated. These facts and the close affinity with the Senecioninæ point to a comparatively recent origin for the group, but the wide tropical distribution indicates an origin precedent to that of the Calenduleæ or Arctotideæ. Taking all the data into consideration the date of the origin of the Vernonieæ seems to be about the middle Miocene; the place of origin is clearly the Brazilian region.

Astereæ. Various changes have been suggested in the evolution of the Astereæ as given in Fig. 7. The most important of these is the reversal of the Homochrominæ and Heterochrominæ, which has been completely vindicated by the analysis of other details than the styles and stamens, and also by a more critical examination of these structures.

The Homochrominæ is the basal sub-tribe and *Solidago* the primitive genus. An examination of any of the ordinary keys to the British flora, such as that in *Hayward's Botanist's Pocket Book* will show how closely allied are the three genera, *Senecio*, *Solidago* and *Inula*. The case of the Inulinæ is discussed above. The imbrication of the involucral bracts and the rigidity of the pappus hairs are apparently the best characters which can be found to distinguish *Solidago* from *Senecio*, and these apply only to the British species. The rigidity or silkiness of the pappus varies, especially in *Senecio*, while that same genus has exotic species in which the calyculus is so well developed that the involucre must be described as imbricate. The type VIII styles of *Solidago* are the real tribal distinguishing feature, but even this distinction is not absolute, since various species of *Senecio* show the type VIII and type VII styles.

The place of origin of the Homochrominæ is clearly somewhere about the borders of the Mexican and U.S. regions. This sub-tribe has in all probabililty given the Bellidinæ, while the Grangeinæ and Conyzinæ have probably come from the Heterochrominæ (see Chap. X, D), the Conyzinæ *via Erigeron*, which passes on the one hand into *Aster* and on the other into *Conyza*.

The transition from the Homochrominæ to the Heterochrominæ can be located in the region of origin of the former sub-tribe. The chief genera of the latter sub-tribe are *Aster*, *Erigeron*, *Olearia*, *Felicia* and *Celmisia*; of these *Olearia* and *Celmisia* are restricted to the Australian region, while *Felicia* is almost confined to South Africa. The other two genera are more or less cosmopolitan and are so very closely allied that the transitional species are comparatively numerous and the genera in these cases are distinguished only by the so-called indefinable characters of the taxonomist. On the other hand *Solidago* is "only distinguished technically from *Aster* and its immediate allies by the homochromous florets, the ray-florets, when present, being yellow, like the disk—a character in general of so little value that it cannot, in *Senecio* for instance, be admitted as of more than specific importance" (Bentham, 1, 7).

The Baccharidinæ, which include only the large genus *Baccharis* and two very small genera, show affinities with the Heterochrominæ and especially with the Conyzinæ in styles and stamens (see Fig. 7), corolla-form, pappus, involucre, receptacle and phyllotaxis. The chief distinctions are the dioecious capitula and the habit. The Baccharidinæ can, therefore, be regarded as a special American development of the African Conyzinæ type either from *Conyza* or more probably by parallel evolution from the *Erigeron* type of the Heterochrominæ.

The data available for the determination of the date of origin of the Astereæ include the occurrence of *Eupatorium* in the middle Pliocene of Europe. The origin of the Eupatorieæ from the Heterochrominæ may be considered proved, so that the origin of the Homochrominæ is thrown back a considerable time to allow for the wide dispersal and differentiation of the various types. The fossil record of authentic Astereæ is very meagre and does not extend beyond the Glacial Epoch. Several of the achenes from the lower Oligocene and upper Miocene are of the Asterean type. Taking into account the wide dispersal of not a few genera of the tribe and the wide dispersal also of the derivative Eupatorieæ, as well as the considerable differentiation of types in the Astereæ and Eupatorieæ, the date of origin for the Homochrominæ can scarcely be later than the middle Eocene, and might well be earlier still.

Eupatorieæ. The hypothesis of the origin of the Eupatorieæ from the Heterochrominæ has been more or less confirmed by all the characters of the group. The basal sub-tribe is the Ageratinæ and the basal group of this sub-tribe is the *Eupatorium-Mikania* plexus. The affinity of *Eupatorium* with the Heterochrominæ in styles, stamens, corolla colour, pappus, involucre, receptacle, and to a lesser degree the phyllotaxis, is distinct. The difference in the styles is the difference between type II and type VIIIa, and the chief distinction is in the complete absence of ray florets. Turning again to the above-mentioned key to the British flora we find that the discoid *Aster Linosyris* is distinguished from *Eupatorium* by the colour of the corolla and the shape of the leaves, characters which are in most cases of only specific rank.

The reduction in the complexity of the floral structures extends to the stamens in the Piqueriinæ (see Chap. II, E). The basal genus of this sub-tribe is *Adenostemma*, with its one wide spread species *A. viscosum*. The basal genus of the Adenostylinæ is probably the American genus *Brickellia*; *Adenostyles*, however, shows an approach to the *Cacalia* type of *Senecio* in habit and involucre (cp. Bentham, I, 7, p. 401). As *Adenostyles* is chiefly developed in the Eur-Asiatic region this case requires further investigation; the genus may be a development of the *Ligularia* section of *Senecio*, which approaches the Eupatorieæ, particularly in the characters of the style.

The place of origin for all three sub-tribes of the Eupatorieæ is clearly the Mexican region.

In discussing the age of the Eupatorieæ Bentham (*loc. cit.*) showed more than his usual remarkable perspicacity. He considered that the Eupatorieæ "may be regarded as one large and natural essentially American group or genus in an extended sense of the term;" that they "must, therefore, either not be so ancient as some other groups of the Compositæ, or some other reason must have interfered with their early dispersion." Discussing the truncate anther-tips of the Piqueriinæ he says, "This remarkable deviation from the almost absolute uniformity of Compositæ is probably, therefore, of West American origin, and not ancient enough to have spread into other continents now severed from America."

The fossil evidence of the early history of the Eupatorieæ is interesting. The species of *Eupatorium* which now occupies the greatest area is identified in the fossil condition in Interglacial times, and other species are described from the upper and middle Pliocene. Considering these points and those indicated by Bentham, the date of origin of *Eupatorium* must be not later than the lower Pliocene. Taking into account the comparative development of the Eupatorieæ and the Arctotideæ (which is assigned above to the lower Pliocene) and the fact that *Eupatorium* had apparently arrived in Europe as early as the middle Pliocene, the most probable date of origin for the genus and tribe seems to be the middle Miocene.

The Eupatorieæ and Vernonieæ would on this hypothesis have arisen more or less at the same time. This would account for the similarity in sub-tribal and generic differentiation in these two tribes, as well as for the similarity in their geographical distribution (cp. Figs. 36-37).

Heliantheæ. Throughout the preceding chapters no reason has appeared for making any change in the phylesis suggested for the Heliantheæ in Fig. 7. A more detailed analysis of the genera, however, suggests certain modifications. The Verbesininæ is clearly the primitive sub-tribe and *Spilanthes* is the most probable primitive genus for the sub-tribe (see Chap. X, C). In connection with the setiform aristæ of this genus it is interesting to note that Blake (159), discussing the few-membered, paleaceous pappus of *Hymenostephium*, says that it "is certainly not to be looked upon as primitive." Although he does not say which type is to be looked upon as primitive, the derivative position of the paleaceous type agrees with the views expressed above and in Chap. V on the primitiveness of the setose type.

The Coreopsidinæ are very closely allied to the Verbesininæ and the primitive genus is probably *Coreopsis*, although the oligotypic genera *Guizotia* and *Microlecane* are even more closely allied to the parent group. As the centre of origin for all the sub-tribes of the Heliantheæ, except the Petrobiinæ, is clearly the Mexican region, and as the two above-mentioned genera are African, the affinity is evidently another case of convergent evolution. The intimate connection between *Bidens* and *Coreopsis* indicates that these genera have been contemporaneous almost from the origin of the sub-tribe.

The Galinsoginæ are closely connected with *Spilanthes* through *Calea*, the chief genus of the sub-tribe. which has type IV style, type 4 or type 5 stamens, and differs chiefly in the numerous scales of the pappus, which are, however, sometimes as few as four, and narrow, rigid, acuminate, approaching the setiform tvpe of *Spilanthes*.

The Lagasceinæ and Petrobiinæ are two small, somewhat anomalous groups, which in the absence of a detailed investigation can be taken as coming from the Verbesininæ as in Fig. 7.

The Madiinæ, with the *Layia-Madia* group indicated as the primitive plexus, are more closely allied to the Galinsoginæ than is suggested in Fig. 7.

The Zinniinæ, especially *Zinnia*, is so closely connected with the lower Verbesininæ that it is impossible to give a precise source for the sub-tribe without more detailed investigation.

The Ambrosiinæ are more closely connected with the Melampodiinæ than with the Verbesininæ as suggested in Fig. 7. The affinity between *Iva* (Ambrosiinæ) and *Parthenice* (Melampodiinæ) is so close that there can be no doubt of the systematic position of the Ambrosiinæ in the Heliantheæ and also very little doubt, if any, of the origin of the sub-tribe from the Melampodiinæ via *Parthenium*, *Parthenice*, *Cyclachæna* (= Sect. I of *Iva* Hoffmann) and *Iva*.

The affinities of the Verbesininæ, Melampodiinæ and Milleriinæ are quite clear. Bentham (I, 7, p. 434) points out that the Melampodiinæ are " intermediate between Millerieæ and the great mass of the Helianthoideæ (Verbesineæ), differing from the former in the completely paleaceous receptacle, from the latter in the constant sterility and undivided styles of the disk-florets."

The transition from the Melampodiinæ to the Milleriinæ is effected according to the same author by the Milleriinean genera *Riencourtia, Desmanthodium* and *Clibadium.* As the last genus has since been shown by Blake (VII, 2) to belong to the Melampodiinæ the affinity is apparently closer than is suggested by the arrangement in Fig. 7, *i.e.* the Milleriinæ have been derived directly from the Melampodiinæ, not from the Coreopsidinæ on the same phyletic line.

Melampodium by its floral characters and distribution is indicated as the primitive genus of the Melampodiinæ. A comparative examination of the genera of the Coreopsidinæ and Verbesininæ shows that the differences between *Melampodium* and these genera are slight. Only the first seven genera of the Verbesininæ agree with *Melampodium* in having the outer achenes enclosed by the periclinal bracts. Of these seven only *Siegesbeckia* and *Enhydra* have some of the disc florets sterile, thus approaching the completely sterile condition of the disc florets in *Melampodium.* The involucre in *Enhydra* is rather special, consisting of two outer and two inner bracts, but that of *Siegesbeckia* is biseriate as in *Melampodium* ; the former genus has often five outer or calycine members and the latter has four or five. Other affinities between these two genera can be traced. The type XIII style of *Melampodium* can be regarded as a closed type VII style and this type occurs in *Siegesbeckia,* where the branches are already short. In both genera the stamens are type 3, the ray-florets are uniseriate, the pappus and other achenial hairs are absent, the receptacular paleæ sometimes encircle the disc florets, the corolla colour is yellow, the cauline leaves are opposite and sometimes dentate. *Siegesbeckia* plants are annuals and so are some species of *Melampodium.* Both genera occur in the Mexican and Andine regions and extend to the Old World. The areas of the two genera are very similar but that of the older one, *Siegesbeckia,* is larger, since *Melampodium* extends in the Old World only into the tropical Asiatic region, while the weedy *S. orientalis* extends into all the Old World regions. The Melampodiinæ are, therefore, derived, not from the Coreopsidinæ as suggested in Fig. 7, but from the Verbesininæ via *Siegesbeckia* and *Melampodium.*

The date of the origin of the Heliantheæ is shown to be early by the common occurrence in Europe of the American genus *Bidens* in the upper Pliocene That it is probably much earlier than this epoch is indicated by the Coreopsidean achene of *Carpolithus* *hyoseritiformis* from the lower Eocene of America. The wide distribution of some of the higher types and the more extensive generic differentiation in the Heliantheæ than in the Astereæ renders it probable that the lower Eocene is the latest date which can be regarded as probable for the origin of the tribe. Taking all the data into account the origin of the Heliantheæ can be placed very soon after the origin of the family, and it is possible that the more primitive genera of the tribe originated in South America. *Spilanthes* shows a considerable Andine development as well as a centre of overlapping in South America. (See Fig. 39 and also the suggestion by Blake (159) that the South American section *Eu-aureæ* of *Viguiera* is the primitive one). Although the Heliantheæ probably arose in South America they undoubtedly attained their greatest development in the Mexican and U.S. regions, and the origin of most of the sub-tribes is probably to be located in these last two regions.

Helenieæ. Throughout this investigation affinities have been indicated for the Helenieæ with two tribes, the Heliantheæ (Galinsoginæ) and the Senecioneæ. With the possibilities of polyphyly and convergent evolution which have been discussed, the close connection of the Helenieæ with the Senecioneæ, which was recognised by Bentham, and the affinities which are also shown with the Anthemideæ and the Heliantheæ, the probability is considerable that this tribe is an artificial one, distinguished only technically from the Senecioneæ by the paleaceous pappus. If this view is correct the tribe requires reclassification on a more natural basis and it would serve no useful purpose to discuss the affinities of the sub-tribes at the present stage.

That the origin of most or all of the genera is comparatively recent is indicated by the restricted distribution and the comparatively slight generic differentiation within the tribe. The date of the origin of the oldest genera, such as *Pectis* and *Porophyllum* (Tagetinæ) *Flaveria* (Flaveriinæ) and *Jaumea* (Jaumeinæ) can scarcely be earlier than the upper Miocene.

Chapter XIV.

THE STORY OF THE COMPOSITÆ IN TIME AND SPACE.

THE conclusions arrived at in the preceding section are summarised in Fig. 79. The geographical centre of origin of each tribe is indicated by a number corresponding to the table of regions on the left. The primitive genera are indicated in those cases where they are obvious without any detailed discussion of all the genera in the group. In some cases the centre of origin as given in Fig. 79 does not coincide with the main centre of concentration as given in Chap. X; this is because the probable primitive genus has its centre of origin in a region different from that of the chief development of the genera of the group. The change is made at this stage so that Fig. 79 may form the basis of future discussions and for that reason it should be as nearly a true representation of the history of the family as it is possible to attain without a detailed consideration of each one of the 23,000 species. The time of the origin of each sub-tribe, as deduced from the palæobotanical evidence and from the present development, generic and specific differentiation and area of the various groups, is also indicated.

An attempt will now be made, using Fig. 79 as a basis, to give that "coherent account of the evolution of the family" which, as mentioned in the Introduction, can be attained by the use of "the modern theories of heredity, evolution and geographical distribution." The writer's problem is to convey to the mind of the reader something of the activity and individuality which have been shown in the development of this immense family. A similar attempt was made in Chap. XI to picture the evolution of *Senecio*, but the cross-references given there interrupt the flow of the narrative and, in the present case, the reader is referred to all that precedes this last chapter for the proofs, the evidence for suggestions and the discussion of the various problems raised.

In the days immediately preceding the Cretaceous uplift on the west coast of South America, the Angiosperms had developed a multitude of forms which represented most of the larger families now existing. The forests of the Amazons to this day retain the very mixed character of this nursery of the Angiosperms: no one group was or is dominant, while the vegetative characters varied comparatively slightly owing to the similarity of conditions throughout a wide expanse of country. The inherent instability of this comparatively new plexus was the cause of the many mutations in the reproductive parts which differentiated the larger families. The arborescent habit of the ancestors of the Angiosperms was continued in the new group, so that there were only trees, shrubs and woody plants growing on trees, lianes and other climbers, in that particular region. Certain of the groups had already sent out colonisers which, especially the arborescent forms, had begun to make some headway, chiefly in the flat lands which formed the bulk of the earth's surface at that time. This period, in fact, was the Mesozoic Pre-differentiation Era of Guppy.

When the Cretaceous uplift raised the Andes well above the tree-limit a new habitat was produced, inaccessible to the trees and climbers as such, but offering a clear, unoccupied region to such of the climbers as were sufficiently plastic to develop into low-growing shrubs.

Among these plastic plants were the members of the *Siphocampylus-Centropogon* group, which proceeded to colonise first the lower and then the higher slopes of the new mountain range. Under such altogether strange conditions many epharmonic variations took place and the Differentiation Era or Age of Compositæ (cp. Guppy) was initiated. The first form of Compositæ was a low-growing, woody, dwarf plant with the inflorescence and flowers of *Senecio*, as explained in Chap. XI.

The new form of fruit, with a dispersal mechanism eminently suited to the wide, windy, more or less barren, mountain regions, combined with the simplicity of the physiological constitution of the plant which was its inheritance from the Pre-differentiation Era, led to a very large development and wide dispersal of the *Senecio* form throughout the Andine region during the evening of the Cretaceous day. A similar form, which, however, may be of much more recent origin from the same plexus, is seen in *Lysipomia*, where the calyx persists in a clumsy, leafy form, so that this genus possesses no particular means of distribution and is still confined to the region of its origin.

Eocene Period.

Among the many forms developed by *Senecio* one of the earliest distinct types, *Gnaphalium*, with more complete aggregation of parts, was produced by the conditions near the snow-line. Another of the early types was the result of the re-invasion of the lower, more temperate regions by the now very definitely organised and aggressive *Senecio*. The annual and rhizomatous, perennial, herbaceous forms of *Senecio* probably developed in connection with local, slightly sheltered conditions in the mountains and also with the short "summer" season. Such forms rendered possible the invasion of the open tracts in the lower regions and the *Spilanthes* type was the result.

The lower Eocene was now well advanced and *Senecio* had proceeded north to the Rockies, where the greater rainfall and less intense insolation rendered both the stunted, shrubby habit and the large-leaved xerophytic habit unnecessary. The usual *Senecio* of these regions was, therefore, of a herbaceous perennial type. The earliest progeny of the genus naturally accompanied the parent, *Gnaphalium* travelling along the higher mountain levels and *Spilanthes* along the foot-hills and alpine meadows.

The mountain habitat formed by the slowly rising Rockies was comparatively restricted and the successful invaders from the Andes extended their zone of occupation to the wooded regions of the plains. There the setose pappus would be of little use as a means of wind-despersal. Accordingly, the tendency to fusion of the setæ had more or less free play and the ten-awned type of fruit represented by *Carpolithus hyoseritiformis* was developed, the rest of the plant remaining very similar to the parent *Spilanthes.* Animal denizens of the forest would be much more efficient seed-dispersers than the gales which scarcely penetrated below the forest roof. The development of the free ends of the setæ into hooks, erect as in *Coreopsis* or recurved as in *Bidens*, was, therefore, a very successful experiment; so successful indeed that the latter of these experimental forms spread in time all over the surface of the earth.

Senecio travelled far and wide along the paths mapped out by the isolated hills and mountains, which by the end of the Eocene had appeared in most of the now mountainous regions of the world. The development of the different types would naturally be greatest nearest the Andine centre, where the numbers of individuals would also be greatest. The less arid conditions of the Rockies favoured a large development of the herbaceous forms. The lapse of time had given the tendency to elaboration of the style branches an opportunity to develop the elongated appendages characteristic of the Astereæ; the evolution of the fimbrillæ and alveoles of the receptacle and the aggregation of the cauline leaves to form a multiseriate calyculus had also been carried forward several stages. The most noteworthy result of these changes was the development of *Solidago* during the middle Eocene in the central region of North America. By that time the four main types of Compositæ had been initiated, *i.e.*, the Senecioneæ, Inuleæ, Heliantheæ, and Astereæ

New conditions were required for further marked differentiation and these were attained when *Senecio* reached the Mediterranean region, by way of Alaska, Siberia and the Asiatic mountain ranges. The shrinkage of the Great Central Sea, which at one time stretched from the Gulf of Mexico to the Deccan, and the initial development of the Alps in upper Eocene times prepared a new land for *Senecio* to conquer. The low hills with abundance of marshland, and the sub-tropical climate combined to produce marshy woods and low-lying meadows in which the setose pappus was again of little use. Other experiments in fruit dispersal were, therefore, made here. Animal dispersal, especially by birds, was obtained by the reduction of the pappus to a ring or auricle, and the edible fruit was thus exposed to view. An occasional improvment was effected by the development of a mucilaginous pericarp, which would be very efficient in such a marshy environment. These changes, combined with a few slight and probably mutational changes in the styles and sexual arrangements within the capitulum, sufficed to produce the Anthemideæ as represented by *Chrysanthemum* and *Matricaria*.

Another method of getting rid of the superfluous pappus was tried with success; the pulvini of the setæ, which normally act only in dry air, having no opportunity of exercising their usual function, degenerated into regions of abscission, and the pappus became caducous. A preliminary attempt at raising the pappus was probably due to the fruit continuing growth under the predominantly moist climatic conditions. The initiation of both these experiments is seen in *Lactuca*, but the two methods became distinct in the progeny of that genus. The very rapid growth of these Cichoriaceous herbs was probably responsible for the re-development of latex which had been suppressed from the time when *Siphocampylus* first started to climb the Andes. The profound disturbance of the organism under a climate so different from that of the Andine home of *Senecio* was probably responsible for the mutation which produced the ligulate florets and also for the fact that the bulk of the Senecioneal colony in the Mediterranean region were transformed partly into Anthemideæ and partly into Cichorieæ. The origin of two more large groups is thus traced to the evolution of climate, particularly in the Mediterranean region during late Eocene times, combined with the arrival of the aggressively migrating *Senecio*.

About this time also the *Solidago* type underwent anthocyan changes in the corolla, possibly as the result of the decrease in the insolation of the North American as compared with that of the Andine region, or possibly as the result of a mutation similar to that which produced the red sunflower. The result of these and other slighter changes was the origin of *Aster* from the *Solidago* type.

Oligocene Period.

While these events were occurring in the Mediterranean and North American regions, the ancestral home of *Senecio* was becoming rather crowded by its numerous progeny. The accompanying spread of the genus led, during the lower Oligocene, to another invasion of the *caatingas* among the Andine foothills near the sources of the Amazons. These regions were wooded but the altitude and soil conditions combined to produce well lighted, sunny woods with comparatively small trees, rather than the dense, umbrageous type of forest characteristic of the lower parts of the Amazons valley. Such conditions favoured the development of the herbaceous perennial type of *Senecio*, and as the tendency to economy in polliniferous tissue became effective tails were developed to the anthers. This economy was counter-balanced by an extravagance in the development of a bifid upper lip in the ray florets. These two changes, the former an example of orthogenesis, the latter an example of a mutation which can scarcely be called orthogenetic, together with some very slight changes which did not involve any change in general habit, resulted in the production of *Trixis*.

This habitat, it will be remembered, is that of the scandent Lobelioid ancestors of the Compositæ. It is not surprising, therefore, to find that these invaders from the mountains, both *Senecio* and *Trixis*, developed scandent forms. In the former the flower remained typical of the genus at least until the end of the Oligocene. In the latter, which was a comparatively new form not at that time quite stabilised, floral changes accompanied the change in habit. The barbellæ of the pappus setæ elongated to give a plumose type and the anther tails became somewhat longer; at the same time the supply of extra material for the inner lip of the corolla was cut down by the innate economy of the family. These changes, all of which are expressions of general orthogenetic tendencies in the family, together with slight anthocyan changes in the corolla, combined to originate the genus *Mutisia* during the middle Oligocene.

By the end of the lower Oligocene all but the more restricted groups of the Compositæ had been initiated, so that the considerable variety in the *Cypselites* of that period, even in the Mediterranean region, is what might be expected.

During the middle Oligocene a considerable amount of differentation took place, chiefly along the lines already laid down. Thus *Inula* was developed in the Mediterranean region by a series of orthogenetic changes all of which had already been initiated in *Senecio*. These changes included the spreading of the stigmatic papillæ all over the inner surfaces of the style branches, the elongation of the anther tails, the greater aggregation of the cauline leaves into the calyculus, and the increased development of bilabiate florets. This last change was probably due to the moist climate, where food material was abundant both for the greater vegetative growth shown by *Inula* and for the extra floral material required to produce numerous rows of bilabiate corollas. In the Mediterranean also, the same moist environment led to a development of the beaked achene with which *Lactuca* had been experimenting at an earlier date and the *Scorzonera* group was originated.

Events were meanwhile progressing in the Mexican region, where considerable geological changes were occurring. Similar conditions to those of the Mediterranean prevailed for a time and *Erigeron* was developed from *Aster* by an increased outlay in bilabiate corollas and a decrease in the number of protective involucral leaves, but, as the western end of the Great Central Sea continued drying up, the climate, at least locally, became much drier and a proportion of the Erigerons began to find conditions less favourable. The bilabiate florets were therefore reduced to filiform female florets and at the same time the protective action of more aggregated cauline leaves was required. *Erigeron* in these local dry regions thus became *Conyza*.

Before this time the moist conditions of the wooded parts of the Mexican region had induced *Spilanthes* to reduce the protective calyculus to a few leaves, and in the absence of opportunities for wind-dispersal the pappus and other achenial hairs ceased to be developed. Other changes had led to the production of a number of genera now classed as Verbesininæ, but these particular developments produced *Siegesbeckia*. Continued existence under such favourable conditions gave the innate economy an opportunity to act by sterilising a number of the disc florets, thus reducing the number of fruits produced by each capitulum. This economy, initiated by *Siegesbeckia*, was carried further until all the disc florets were sterile; then the style branches remained permanently closed, since the style survived only as a pollen presenter, and *Melampodium* came into being about the time of the middle Oligocene.

Meanwhile, further south, among the headwaters of the Amazons, *Mutisia* was being developed from *Trixis* by floral changes accompanying a recovery of the ancestral scandent habit as described above. The *Mutisia* type repeated the travels of its grandparent *Senecio* and re-ascended the Andes, undergoing the changes necessary for existence on the more arid and windy mountain slopes. Food material for the capitulum being scarcer, the ray florets became reduced or sometimes ceased to be developed; the pappus regained its wind-dispersal function and was developed to a greater extent. In addition the scapigerous form was taken in the more barren regions where it was necessary. During this interesting journey *Mutisia*, in fact, became *Onoseris*.

Having regained an efficient wind-dispersal mechanism, the *Onoseris* type spread quickly. By a few slight changes, including the abortion of the inner lip of the corolla in the outer row of florets, which was quite natural under the unfavourable conditions of the Andine habitat, *Chaptalia* was evolved. The pappus being retained in an efficient condition, the mountain path north along the Rockies, across the Alaska-Siberian bridge and south along the mountains of Asia, was open for *Chaptalia*. This migration took place in the upper Oligocene and on reaching the plains of China the genus suffered the natural changes on regaining a mesophytic habitat. Increased food supply led to a redevelopment of the aborted inner lip of the outer corollas and a reduction in the number of protective calyculine leaves; *Chaptalia* in this way became *Gerbera* on crossing the Alaska-Siberian bridge.

The end of the Oligocene saw the initiation of a number of subsidiary lines of evolution, the most important of which was again connected with important geological events. The Mediterranean end of the Central Sea was undergoing considerable shrinkage, and this led to the development of spines in the *Inula* group. At the same time mutational changes developed the fimbrillæ of the receptacle into deeply lacerate alveoles, which surrounded the young fruits and to a certain extent prevented the pappus from exercising its normal function. The pappus setæ, therefore, fused in various ways and the Buphthalminæ originated.

The shrinkage of the Central Sea continuing into the lower Miocene, a strongly insolated, semi-desert region was produced at the eastern end of the Mediterranean, of which the dwarfed, reduced, spinescent *Gymnarrhena* was a natural inhabitant. The progressive elaboration of the style branches included the formation of the ring of hairs characteristic of the Cynareæ and the orthogenetic economy in polliniferous tissue led to the further elaboration of the anther tails. By an elongation of the achene and a reduction in the length of the receptacular setæ the pappus was again freed and *Centaurea* was produced. Being economical and easily dispersed by wind this type multiplied and spread to occupy the new habitat.

About the same time (end of the Oligocene and beginning of the Miocene) another of the periodical invasions of the Amazonian headwaters took place. Two mountain tribes took part in this invasion and the new environment of moist woods and *caatingas* had the same effect in both cases. The pappus was again rendered of little use and as a consequence became more or less atrophied by fusion. This change was most pronounced in the *Spilanthes* coterie and the *Calea* (Galinsoginæ) type was the result. The numerous progeny of the Andine Senecios were not so susceptible, and the fusion of pappus hairs was more or less confined to the outer rows; the style branches in this case, however, underwent considerable elongation and *Liabum* was the result. This genus afterwards re-ascended the Andes, undergoing the usual changes, becoming dwarfed and unicapitulate.

A neighbouring region, the Chilian part of the Andes, was invaded more or less simultaneously by *Mutisia* and its fellow genera from the foot-hills. This regaining of a region where the conditions rendered the food-supply of the capitulum rather problematical led to the complete suppression of the large corollas of the ray florets. At the same time the plumose pappus was once again in a position to exercise its natural efficiency and reduction in the number of fruits was possible. This was affected by the sterilisation of some or all of the florets of the capitulum and *Chuquiragua* came into existence.

Just as its cousin, or rather niece, *Chaptalia* raced along the mountain ranges on regaining an efficient pappus in a suitable environment, so did *Chuquiragua*. Like *Chaptalia* also, this new genus was transformed on crossing the Alaska-Siberian bridge by an increase in the corolla material, which was rendered possible by the mesophytic conditions of the upland plains of China. *Ainsliæa* is the name now giving to the transformed *Chuquiragua*. This

Ainsliæa type reached South Africa at a much later date (lower Pliocene) by means of a greater development of the pappus which made migration easier. During the journey it underwent a few other slight changes and became *Dicoma*.

To the north, in the Mexican region, the end of the Oligocene saw a descent from the mountains by the progeny of *Gnaphalium*. Such a migration to the moist wooded plains rendered the closely aggregated capitula of that genus unnecessary. Larger and less densely involucrate heads were developed, with some rounding off of the tips of the style branches, and a weedy habit was acquired. The result was *Pluchea*, another wanderer, which spread and developed largely on the other side of the Pacific.

Miocene Period.

Beyond a larger development of the Cynareæ, with the initiation of the *Carduus* type, in response to the continued evolution of the semi-desert area of the eastern Mediterranean region, the lower Miocene was comparatively uneventful. The only other events were confined to the Mexican region.

Gnaphalium again descended from the mountains, this time into the Californian valleys and, undergoing changes similar to those which originated *Pluchea* in a similar environment, it became *Filago*. This type, which like *Pluchea* spread to Asia, finally became well-developed in the Mediterranean and other regions lying on the path of migration.

In the Mexican region also, about the same time, the descendants of *Spilanthes* having reverted to their distant Lobelioid ancestors in producing receptacular bracts, again came into line with the rest of the Compositæ by omitting these accessory structures. Continued existence in the favourable mesophytic environment of the Mexican woods rendered the numerous involucral leaves of those forms unnecessary and the result of these two changes was the initiation of the *Layia-Madia* group,

The middle Miocene, a geologically active period, was more eventful for the Compositæ. The orthogenetic elongation of the appendages of the style branches continued in the *Aster* plexus and the production in the open Brazilian woods of forms which, with the abundant food supply, produced dense masses of capitula had an interesting result. The crowding of the heads gave little room for ray florets and the food supply of the dense inflorescence being limited by the conductivity of the peduncle, each capitulum would get a distinctly limited supply. These factors led to the suppression of the ray florets and the discoid *Eupatorium* was produced. A very similar development occurred in the *Liabum* group of the same region and *Vernonia*, which is very similar to *Eupatorium* in general form, was evolved. Both these genera spread across the Pacific archipelago during the succeeding periods.

The tendency to economise in fruit production was more or less general in these favourable regions at the foot of the Andes and it became very marked in some of the Brazilian Asters. Some of the capitula became completely sterile. Thus *Baccharis* originated, and by travelling up and along the Andes reached such a diversity of habitats that it gave rise to a very varied group of species.

In the Mexican region a considerable differentiation occurred, which was probably connected with the geological activity during the middle Miocene in and around what is now the Caribbean Sea. By changes in the colour of the ray florets in the Golden-rod tribe, similar to those which produced the Asters, combined with the always recurring suppression of the pappus, the Bellidinæ originated.

The tendency to reduction in the number of fruits produced by each capitulum, which had become well developed in the *Melampodium* plexus, was carried still further: the capitulum was reduced to a few flowers; at the same time the large anterior lip of the ray florets became reduced and *Clibadium* (Milleriinæ) was developed. The same two tendencies were carried to extremes along another line in the same plexus. *Parthenium*, losing the aristæ of the pappus and reducing the corolla of the female ray florets, became *Parthenice*. A still further reduction of the rays resulted in the genus *Iva*, in which the tendency to unisexuality of the flowers became so strong that unisexual capitula were developed in some of the other Ambrosiinæ. These series, the Milleriinæ and Ambrosiinæ, represent the working out to the last possible stage of orthogenetic lines commenced under the influence of the success of the capitulum as a seed-producing arrangement, together with the reduction in available food material resulting from the gradual drying up of the originally mesophytic environment as the shrinking of the Central Sea continued. In the mesophytic wooded localities which were left the *Spilanthes* group continued to thrive, and in some rather unsuccessful forms the awned pappus of the ray florets was lost by the mutation, common throughout the family, which resulted in the suppression of the achenial hairs and pappus.

Conditions being favourable these forms continued to exist, and, requiring something to replace the lost pappus, developed a substitute by rendering the corolla of the ray florets persistent. When the disc florets were fertile the awns were present or, if the loss mutation extended to all the flowers in the capitulum, tuberculations of the pericarp in the achenes of the disc were sometimes developed for dispersal purposes to replace the lost stuctures. These cases and the original development of the achenial hairs into a pappus are examples of the general rule that lost structures are not re-developed but are replaced by something similar developed from parts which are still present.

The other end of the Central Sea in the Mediterranean region was also active geologically during the middle Miocene. The continued evolution of the semi-desert region, with dryness and strong insolation as predominant characteristics, produced the spiny group (Scolyminæ) of the Cichorieæ. The changes in climate resulting from the alternating sinkings and uprisings of considerable stretches of the land surface were doubtless responsible for a considerable proportion of the diversity of forms produced in the Cichorieæ at this time.

One of the most interesting events of the middle Miocene was the origin of *Helichrysum* from the *Gnaphalium* line in South Africa. *Senecio* and *Gnaphalium* had by that time become established in this region, and finding the climate in these similar latitude srather like that of their Andine home, as far as aridity, insolation, etc. were concerned, these two genera multiplied abundantly. *Gnaphalium*, more accustomed to living near the snow-line, yielded earlier than *Senecio* to the difference in altitude, and *Helichrysum* was produced. This genus was so suited to the conditions on account of its epharmonic origin that its numbers soon exceeded in a very marked degree those of its parent.

Probably on account of its lower physiological differentiation *Senecio* was slower in yielding, but in the succeeding period, the upper Miocene, it gave *Ursinia* by the changes which usually resulted from the attainment of a more favourable environment, where food material was abundant and wind-dispersal rather uncertain. The ray florets became neuter and the reduction in the number of fruits per capitulum was carried further by the sterilisation of the inner disc florets. At the same time fusion of the pappus setæ was accompanied by a development of the fimbrillæ of the receptacle to form flat setæ.

As time went on this new genus spread to the arid, semi-desert regions which were increasing in South Africa in the evening of the Miocene day; the dryness and strong insolation had the same result as they had at an earlier date in the Mediterranean region. The type became spinescent (*Berkheya*); reduction and aggregation continuing, as they did again later to produce *Echinops* among the thistles, the dense glomerules of the spinescent *Gundelia* and *Platycarpha* originated.

In addition to the origin of *Ursinia* the upper Miocene in South Africa saw the origin of the *Athrixia* line. The *Inula* group was by this time well represented in South Africa and a reduction in the corolla of the ray florets occurred, similar to that which had previously taken place in the similarly arid part of the Mediterranean region. This with other very slight changes gave the Athrixiinæ. On account of the continued drying up of the region, which produced a distinctly xerophytic habitat, the flat or slightly recurved leaves of *Athrixia* became much reduced and practically ericoid. The semi-shrubby habit changed at the same time into the typical xeromorphic shrubby habit. These conditions also led to a reduced or depauperate condition in the capitulum: very few flowers were developed in each head and this led to the usual aggregation. By these epharmonic adaptations *Relhania* and its congeners were originated.

Helichrysum by this time was well developed in South Africa and the xerophytic conditions had almost the same effects on this genus as they had on *Athrixia*. So much so that epharmosis, in this case as in many others, led to convergent evolution, and the present systematic group Relhaniinæ includes both *Relhania* and *Metalasia*, which latter was the product of the second series of epharmonic variations.

A neighbouring event of this time was the origin of the Grangeinæ in tropical Africa. The Asters and Erigerons had followed *Senecio* along the lower levels of the mountains and on attaining the very favourable conditions yielded by the tropical African scrub underwent the usual reductions. The pappus first became reduced or caducous and then disappeared completely. At the same time the tendency to reduction of the rays, which was so well developed in the *Aster* plexus resulted in reduced ray florets.

Meanwhile the Senecioneæ in Mexico were again being affected by the mesophytic conditions which had previously led to the fusion of the pappus setæ in the origin of the Galinsoginæ, Madiinæ and Liabinæ near the beginning of the Miocene. In this case the

Helenieæ were originated. In all four cases a tendency to lateral fusion of the pappus hairs was present, and similar climatic and other ecological conditions are indicated by other data.

About the same time the tendency to reduction in the number of fruits, which is seen in the *Melampodium* line, became effective in the ancestral plexus of that genus and the one-flowered capitulum of *Lagascea* was developed in the Mexican region. In the northern sub-arctic regions of Asia the cold and other adverse conditions, including the short vegetative season, induced some of the Senecioninæ to assume the geophilous habit of *Petasites.*

Pliocene Period.

Events in the lower Pliocene occurred chiefly in the Old World and notably in South Africa. The above-mentioned origin of the *Metalasia*, *Relhania* and *Berkheya* groups and of the Tarchonanthinæ took place then. In addition those Senecioninæ in South Africa which were fortunate enough to have occupied the moist valleys found a reduction in fruit-number possible and the disc florets became sterile. As usual such conditions resulted in the reduction or complete suppression of the pappus, which was replaced in this case by bent apical beaks, tuberculations, and other structures suitable for animal dispersal. In this way the Calenduleæ were developed.

Differentiation in the Mediterranean region was active chiefly in the Cynareæ as far as sub-tribes were concerned; the two groups of the Carlininæ and the Echinopsidinæ with aggregated, few-flowered capitula are probably the result of the working out to the furthest limits of efficiency of the two tendencies, aggregation and reduction. A large development of the Carduinæ is also suggested.

Reduction and aggregation were nearing the limits of efficiency in other tribes also and similar "end-products" can be traced in other geographical regions. Within the limits of efficiency but showing reduction came the Adenostylinæ via *Brickellia*, but in the same *Eupatorium* plexus the limits were passed in the Piqueriinæ which, originating in *Adenostemma*, remained as a consequence of their inefficiency a small, restricted group. These were Brazilian events and in the same region a parallel development occurred in the Vernonieæ, where the few-flowered, aggregated capitula of the Lychnophorinæ were developed in *Elephantopus*. Another very similar development occurred in the origin of the reduced, dioecious and geographically restricted Petrobiinæ in the Chilian region.

By the time the middle Pliocene was reached most of the sub-tribes of the Compositæ had been differentiated and events occurred only in rather outlying regions. In Australia the *Helichrysum* line developed the same "end product" as the above groups in the reduced, few-flowered, aggregated capitula of the Angianthinæ. In South Africa the main stock of the family, the Senecioninæ, retaining its vitality to the last, gave off the Othonninæ by the fusion of the periclinal bracts. The only later sub-tribe to arise was the small group Gundeliinæ, another few-flowered, aggregated "end-product," which as mentioned above was produced in the same region from the *Berkheya* line in the upper Pliocene.

The upper Pliocene and the succeeding geological period were characterised by generic, specific and varietal differentiation rather than by the origin of larger groups. This is probably due to the short period of time which has elapsed since the middle Pliocene and, perhaps even in a greater degree, to the more settled climatic conditions of the earth as a whole.

It will be seen that a few fundamental tendencies or orthogenetic lines, largely if not entirely due to epharmonic variation, can be traced throughout the various tribes in their wanderings over the surface of the earth during the Tertiary evolution of climate. Little else is required to account for the main variations in form and physiology of the Compositæ and that little can be supplied by mutational phenomena such as we are accustomed to at the present time.

This is the story of the Compositæ in time and space and it is hoped that what has been lost in scientific accuracy has been regained to some extent in the coherence of the narrative. In any case the strictly scientific synantherologist is referred for facts to the preceding chapters and he can neglect and forget this attempt to bring a real, living picture of the origin and development of the Compositæ before the mind of the ordinary student.

THE ANDROECIUM IN *PLAGIOCHASMA APPENDICULATUM* L. ET L. AND *P. ARTICULATUM* KASHYAP.

By S. R. Kashyap, M.Sc. (Punjab), B.A. (Cantab).

Professor of Botany, Government College, Lahore.

[With Two Figures in the Text.]

THE genus *Plagiochasma* was worked out, both as regards its structure and development, by Leitgeb who gave a detailed account of it in his classical treatise, " Untersuchungen über die Lebermoose," Vol. VI, 1881. *Plagiochasma appendiculatum* was one of the five species which he examined. He gave a fairly full account of the structure of the thallus and the female receptacle in the genus but only a single paragraph is devoted to the male receptacle, and although he gives many figures of the female receptacle at various stages of development, the male receptacle is not figured even once. More recently, Evans, in the Bulletin of the Torreya Botanical Club (Vol. XLII, 1915), has given a comprehensive account of the genus with very full descriptions of the American species. He refers to Leitgeb's and the present writer's work, and says : " The androecia vary in outline from circular to more or less crescentic or cordate, with the convex side turned towards the base of the thallus. These crescentic androecia, as Leitgeb notes, should not be confused with the dichotomous androecia occasionally found in *Lunularia*, where two growing points are involved. They represent, according to his ideas, a persistence of the two-lobed condition at the apex of the ordinary thallus, where the single growing point lies in the indentation between the lobes. Kashyap, however, says that in both *P. appendiculatum* and *P. articulatum* the androecium has usually two growing points, and implies that the horse-shoe shape is therefore due to a forking. Unfortunately, he adduces no conclusive evidence to support his position." According to the present writer's experience it is so easy to satisfy oneself regarding the two growing points in the androecium in spirit material that the failure of two such accurate observers as Leitgeb and Evans to notice them can only be due to unsatisfactory herbarium material. As the importance of this point lies even far beyond the genus *Plagiochasma* itself, it was decided to clear it up by examining a large number of spirit specimens collected by the writer in various parts of the western Himalayas, chiefly Mussoorie.

As is well known both the male and female receptacles are surrounded by scales which are smaller than those present on the ventral surface of the thallus. The cells of these scales in both the species examined contain small round grains in addition to the nucleus which stains blue with iodine indicating the presence of starch. They may be starch grains, but the writer is inclined to think that they probably represent reduced chloroplasts. As the material was preserved in alcohol no chlorophyll, if it ever was present, could be seen. The grains are certainly much smaller than ordinary chloroplasts. Chloroplasts in ventral scales have been described in several genera, *Aitchisoniella*, *Stephensoniella*, and *Cyathodium*, by the writer (NEW PHYTOLOGIST, Vol. XIII, 1914), and *Monoselenium*, by Goebel (Flora, Bd. 101, 1910). Both the ventral and the receptacular scales of *Gollaniella* contain chloroplasts as was described by the writer in an earlier paper (NEW PHYTOLOGIST, Vol. XIV, 1915). The grains in the two species of *Plagiochasma* examined usually occur in the basal half of the scale, though sometimes the whole scale is full of them except one or two cells at the apex. From the margins of the basal portion of the young scales numerous club-shaped mucilage hairs are given off resembling those found on the ventral scales. The terminal cell of the scale is also often hyaline resembling a mucilage hair (Fig. 1)

FIG. 1. *Plagiochasma appendiculatum.* Scales from the male receptacle. × 75.

The scales of the receptacles often show a distinction into a body and an appendage, but this distinction is never so marked as in the ventral scales.

The usual form of the androecium is cordate or deeply bilobed. The tip of each lobe is covered with closely applied young scales while in the posterior portion the scales are older and more or less spreading. By teasing out antheridia under a dissecting microscope it can very easily be seen that the chambers at the tips of the lobes in both the species contain the youngest antheridia while those behind have older ones, and the chambers near the base are usually empty even in comparatively young androecia, the antheridia having discharged their contents. In older androecia all the chambers are naturally empty. It is clear, therefore, that in these cases two growing points are involved. The same sequence of development is also seen in longitudinal sections of the lobes. The antheridia near the apex may not even have formed the sperm mother-cells while those behind may have well developed sperms, and still further back they may be quite empty.

Each antheridium is an ovoid structure with a slender stalk and a conspicuous beak. The sperms are long, narrow, coiled bodies.

Unfortunately no androecia were found in very early stages of development so that it was not possible to study the early stages of development of the antheridium. Similarly the apical cell, if it was ever present, could not be made out.

Only the bilobed condition of the androecium is met with in *Plagiochasma articulatum*. In *P. appendiculatum* the androecium shows a great variety of form.

In some plants of *P. appendiculatum* it was found that the two lobes of the androecium showed a second forking. In some robust plants growing in a shady and moist place it was seen that the androecium went on growing as a simple cushion-like structure in the mid-dorsal line for some time, forming a linear-oblong structure which divided later into two, and each of the lobes thus formed again forked (Fig. 2, e). These ultimate lobes showèd an acropetal succession in the development of the antheridia. This condition is particularly interesting as showing undoubtedly the dichotomy of the androecium. In still other cases it was found that the androecium was more or less irregulary lobed (Fig. 2). Some of these lobes were of a small size and were probably due merely to irregularities of growth, but others showed distinct signs of growing points, from the arrangement of the scales and the sequence of the antheridia. Most of these specimens were quite old and the antheridia had discharged their contents, but enough was seen to conclude that some of the lobes undoubtedly possessed growing points.

Three different considerations, therefore, show that the androecium of *P. appendiculatum* and *P. articulatum* is really homologous with that of the higher Marchantiales in being a branch-system. The dorsal position, like the dorsal position of the female receptacle, is quite secondary as has already been shown by the writer (New Phytologist, Vol. XIII, 9). In *P. articulatum* the androecium is quite terminal at first. The three considerations are:— (1). The arrangment of the scales at the tip of the lobes which is very similar to that at the tip of the vegetative lobe. (2). The repeated branching of the receptacle, two or three times in some specimens. (3). The invariably acropetal succession of the antheridia in all lobes exactly as in *Marchantia*, the highest genus of the Marchantiales.

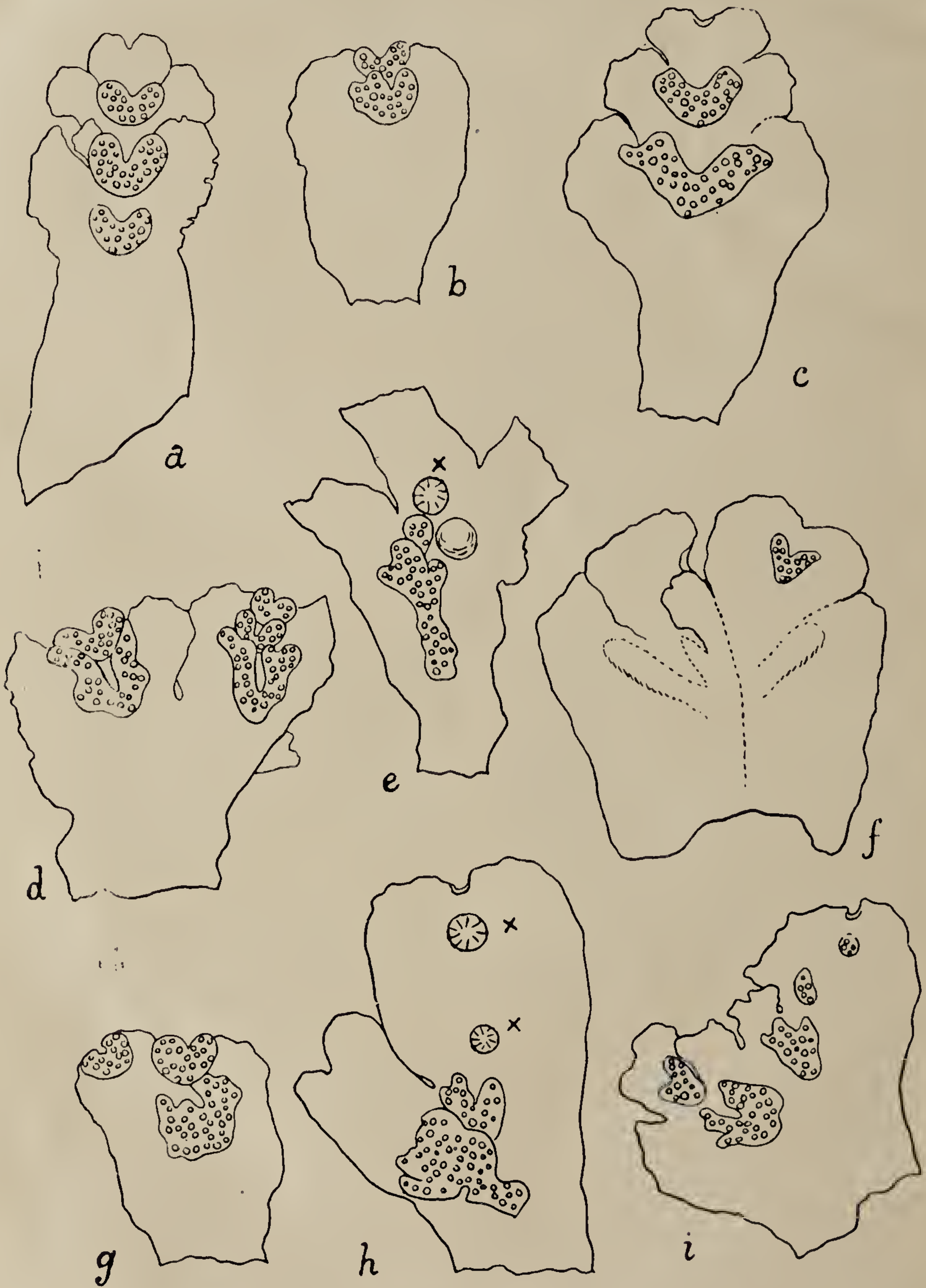


FIG. 2. *Plagiochasma appendiculatum*. Various forms of the male receptacle. x female receptacle, × 3.

THE
NEW PHYTOLOGIST

VOL. XVIII, NO. 8. OCTOBER, 1919.
[PUBLISHED DECEMBER 4TH, 1919.]

THE IONIC PHASE OF THE SEA.

BY A. H. CHURCH.

TO the subaerial botanist brought up on an extended course of laboratory cultures involving a "food-solution" with the extreme dilution of about 3½ grams per litre, sea-water with 3½% of salts, or just ten times the amount, appears as a strongly plasmolytic solution, the utility of which as a nutritive medium seems almost ludicrous in view of an osmotic value of over 20 atmospheres, great content of common salt, and microscopic proportions of compounds of Nitrogen and Phosphorus. Such an attitude is reflected in the discussion of the problems of halophytes, and one is asked to admire the biological equipment of such plants as *Salicornia* and *Suæda fruticosa* in this country, or the more arboreal Mangroves (*Rhizophora* and *Avicennia*) established in forest-association in the seas of more tropical latitudes; though further out one is brought into contact with *Zostera*, an Angiosperm living permanently submerged in the sea on our own coasts; while *Posidonia*, a possibly allied form, extends commonly to 30 fathoms in the clear water of of the Mediterranean, and Schimper does not scruple to record it at 50. The continued existence of such plant-forms which derive their sustenance from a substratum soaked in sea-water, leads on to the recognition of the fact that in the case of the benthic (algal) vegetation of the sea, as "hormon" or anchored somata without absorptive roots, the sea does represent the actual food-solution of the entire series of marine algæ, as in fact it is the sole food-solution of all earlier phyla of simple plankton-forms. At last it begins to be realized that the sea may not only be on occasion a food-solution to higher organism, but that it is the essential and only food-solution of all primitive forms of plant-life; and not only the sole source of food-salts, but at once the actual and original medium permeating the entire body of marine organisms; that is to say, the medium from which they draw all supplies of food-materials, and even the medium in which all the cytoplasmic organisms of the sea have been evolved in the first instance. The conclusion is not only warranted, but generally accepted, that living plasma, as the primitive source of what is termed biological life of land-organism, is evolved directly from sea-water itself, as a medium which is not known to have been markedly different in composition from what it is to-day, at any preceding epoch of the world's history, so long as an aqueous envelope has existed on the crust of the earth.

Sea water still covers more than three-quarters of the surface of the world, in quantity sufficient to submerge the levelled crust to a depth of over two miles (2000 fathoms). The actual quantity of the medium has been estimated at 1.3×10^{18} tons; though on a model of the globe a metre in diameter such an ocean might be indicated by sponging the surface to give a wet film of ¼ mm. It constitutes a watery solution containing very approximately 3.5% of dissolved salts by weight; 3.5%, or a salinity of 35 per thousand may be taken as accurate for the English Channel. The salt-content may be regarded as comprised essentially of 8 elementary ions:—4 electro-positive (kations), Na', K', Mg'', Ca'', and 4 electro-negative (anions) Br', Cl', SO_4'', CO_3'', with the possibility of at least 16 salts, as also with traces of such elements as Nitrogen, Phosphorus, Iodine, Iron, Manganese, Gold, Silver, etc., or 32 in all (Krümmel). The general run of these elements follows the sequence of the Periodic Law from A.W. 12—40, in which Al and F are conspicuously deficient, while Fe appears accessory, as if of meteoric origin. Such a solution of 3.5% salt-content presents a freezing-point of —1.910°C, and an osmotic value of 23.12 atmospheres (Krümmel). From similar physical data it would appear that the solutes are ionized to the extent of 90% (Krümmel), and the excess salt-molecules are mainly NaCl; *i.e*, all minor constituents (N, P, Si, compounds) must be regarded as fully ionized. The water itself is also ionized to an extent of approximately one part in ten million; the ionization coefficient being taken as $C_{H^{\cdot}} \times C_{OH'} = 10^{-14}$ The solution is very fairly neutral, *i.e*, balanced at $10^{-7}(H^{\cdot}) \times 10^{-7}$ (OH'); but many seas are distinctly alkaline, the latter effect being the expression of a predominance of OH' ions, as noted for Pacific water off the Californian coast, as opposed to water of the North Atlantic (Loeb). Alkalinity has been found to increase normally from Northern Seas towards the warmer Mediterranean; possibly largely as the effect of plankton-photosynthesis in withdrawing CO_2 from the solution. The $H^{\cdot}$ ion concentration is given as 7.95 to 8.35×10^{-7} for the Mediterranean (Palitzsch), while the high estimate of 22.4×10^{-7} is recorded by Gaarder (1917) for Norwegian Fjords. Loeb and others have shown that such alkalinity is favourable for animal life: for practical demonstration "acid" water gives yellow to red coloration with Methyl Orange; "alkaline" water red with Phenolphthalein (Palitzsch, p. 243).

The general facts of the ionic relations of sea-water are accepted from the work of physical chemists; and with their methods of arriving at such conclusions the botanist has little to do; he has to fit his ideas to suit these new conceptions, and try to see to what they tend in the study of the plant-life of the sea. The standpoint that protoplasm is "non-molecular," in the sense that "life" implies a continuous sequence of physical and chemical reactions, in which all molecules are so far "dead" end-products —and that it may be regarded as comparable, for example, with a flame "burning" at 300°A—is now extended by the view that quite a large proportion of sea-water (the primary source of "life") is also non-molecular, consisting of free "ions," which may be visualized as in a perpetual state of combination and dissociation, in an "*ionic phase*." The fact that sea-water contains very uniformly 3.5% of salts, of which again 90% is fully ionized, implies that sea-water is also *non-molecular* to the extent of over 3% by weight; and this commonplace medium, hitherto commonly regarded as a molecular fluid, appears as an organization of inconceivable complexity.

It would appear that biological "life" may be similarly regarded as the expression, at any rate partially, of an ionic phase; and that living protoplasm continues the relations of the ions of sea-water: what is termed "life" biologically being a state of organization evolved in a highly ionized medium (including atmospheric derivatives), and working in terms of nothing else except solar energy. All purely molecular theories are so far to be scrapped. It is news to many botanists, brought up on the molecular conventions of a past generation, that water does not consist wholly of H_2O molecules; but that one ten-millionth exists in the form of $H^{\cdot}$ and OH' ions; and this one ten-millionth seems a small amount, as if almost negligible. But it must be remembered that such data are spatial (cubic), and not linear dimensions as generally employed by biologists. A simple sum in arithmetic shows that OH' and $H^{\cdot}$ ions in the sea run to over 400 tons in a cubic mile (a small unit in dealing with the North Atlantic averaging three miles deep); or, on an estimate of one in ten million, the $H^{\cdot}$,OH', ionic-value of the world-ocean is 1.3×10^{11} tons (over a hundred thousand millions). Again, owing to the inevitably indirect method of approaching these problems on the part of subaerial scientists, the ionic hypothesis is proposed in terms of "dissociation," involving possibly some relation between the ions of a dissolved substance and the inert molecules of the water. But, however much this conception may apply to the effect of placing a salt in water, in terms of the solute, it can scarcely hold in the case of the solvent, in this case the primary water-supply of the world itself. To the biologist, whose conceptions are necessarily based on some sort of evolutionary scheme, it would appear that, just as the special chemical attributes of the elements comprising the crust of the earth, by the accident of the earth's position in the solar system, in their aggregated condition unite to give the chemical possibilities of sea-water,—so at the aqueous condensation special physical attributes of the dielectric constitution of this remarkably ionizing medium become apparent, as marking the introduction of a new asset in the possible progression of the world, the results of which would have been so far wholly unforeseen. The fact emerges that sea-water, although the commonest thing on the world, as a mass of material of fairly uniform constitution, is physically an organization of extreme complexity; as the original fluid of a world-condensation at about 100°C, in which at a lower temperature biological "life" has become established; and of a nature quite distinct from that of any other "anhydrous" medium. It is with these peculiar properties of the medium termed sea-water that the first and most fundamental factors of life are involved.

It thus follows that in dealing with "life" in terms of ions, as a phase presumably non-molecular, though even this view may not include the whole truth, all older molecular conceptions require readjustment. Cytoplasm, in so far as it is living, probably consists essentially of active ions; all molecules being end-phases, so far "dead," and passive, or in reserve. Colloidal cytoplasm in the first place adsorbs ions, not molecules; there are practically no molecules of nutritive significance in the sea; the excess molecular salts are largely useless NaCl. There is no definite evidence that an autotrophic plant deals with any molecule in the sea. Present exceptions include large quantities of molecular debris of dead organism, as "organic" carbon, "organic" nitrogen, "organic" phosphorus. The question of the utilization of free oxygen in katabolic processes is equally secondary: it is not possible to say what may be the exact condition of oxygen "in solution" in the water; photosynthetic organisms may be said to manufacture their own, in which case it may be described as "nascent"; while its essential utility may be doubted in the presence of available solar radiation. There is no such thing conceivable as a molecular anabolyte; vast energy is not required to dissociate H_2O molecules to build up the living substance ; they are provided in " dissociated " form, and all other anabolic requisites similarly. Theories of photosynthesis involving molecular conceptions also require to be scrapped. There is little " CO_2 " in the sea; the ions of H_2CO_3 are H', HCO_3', and CO_3''. Experimental observations on the action for example, of radium or ultra-violet light on CO_2, on land, or in air, and the synthesis of formaldehyde, have as little to do with the primary problems of photosynthesis as Bastian's observations on " spontanous generation " in boiled solutions of beef-tea had to do with the direct synthesis of protoplasm. There is only one thing to be considered,—The ultimate structure and organization of sea-water, with regard to its ionic content : all molecules are but a reserve on which to draw, as existing ions may be segregated in the higher expression of organization we call *living* entities.

From the known composition of aqueous protoplasm (about 90% water), it would follow that the ions of ordinary sea-water would suffice at any given moment, without renewal, to supply 500 tons of living ionic matter per cubic mile; without allowing for vast quantities of inevitable molecular debris. While there is no present reason to suppose that cytoplasm in sea-water presents a higher coefficient of ionization than the medium itself (3%), it is interesting to note that the net amount of primary autotrophic organism in the sea is appreciably within the scope of such an estimate; and one part in ten million may be even suggested as a possible average " plankton-rate " for autotrophic organism in British Seas. For example, the amount of cytoplasm in a flagellated algal zoid, approximately 5μ diam., and 100cμ in volume, at a plankton-rate of a million per litre, may be visualized as one part in ten million of the medium. Allen (1919) from cultural observations (Plymouth Sound) suggests the possibility of a million autotrophic organisms per litre; these being mostly Diatoms, and their cytoplasmic value still obscure. Lohmann (1908) for the nutritive waters of Kiel Bay (August), gives maximum " autotrophic " plankton as equivalent to a total volume of 105.4 c.mm per 100 litres, or little more than 10 times this amount (and his figures include holozoic Peridiniaceæ and Flagellates) : no other estimate approaches this.

A further very special biological interest is associated with the connection between the ions of carbonic acid and those of the water as expressed in the conception of Sörensen and Palitzsch

(1909) that it is the carbonic acid which acts as a "buffer" in regulating the Hydroxyl-ion concentration of the sea; and this suggestion is of the greater value as bearing possibly on the primary relation of the carbon-compounds in the evolution of autotrophic pelagic life, in which the carbon atom under the influence of solar radiation apparently comes into a still more intimate association with the ions of water to initiate the CHOH chains $(\text{H-}\overset{|}{\underset{|}{\text{C}}}\text{-OH})$, in terms of which it has been usual to visualize the chemistry of the carbohydrate series.

Thus the complex relations of the ions of carbonic acid in sea-water may be first approached by considering that:—

(1) A portion of the CO_2 of the sea will be absorbed from the atmosphere, just as will any other gas, in amount depending on the temperature, pressure and salinity; one litre dissolving approximately .3 cc. physically (3 in 10,000), giving a concentration equal to that of the air at 15°C[1].

(2) The rest of the CO_2 of the sea, 150 times as much (or more) may be regarded as combining chemically with the water as H_2CO_3 and the latter dissociating to $H^\cdot$ and HCO_3', the dissociation-constant being $H^\cdot, HCO_3' = 3 \times 10^{-7} (H_2CO_3)$[2].

(3) The HCO_3' ion further dissociates to $H^\cdot$, CO_3''; but the dissociation-constant for this reaction is many times less than that of the preceding (5,000 times less, Palitzsch)[3].

Only a small part of the H_2CO_3 is thus completely dissociated, not 1% (Ruppin), and the greater part of the CO_2 of the sea occurs as HCO_3' ions in equilibrium with calcium ions or other kations, or as undissociated carbonates and bi-carbonates. There in no reason to suppose that any great amount of carbonate exists in molecular form among the 10% residual non-ionized part of the total salts; and theoretical discussions of the constants of one substance taken separately in pure water do not go very far in explaining the complex relation of such a mixture of ions as that presented in sea-water.

Whether the plant in photosynthesis utilizes dissolved CO_2 HCO_3' or $CO^{3''}$ is still disputed; quite possibly the last as the most completely ionized form, to which the HCO_3' ion constitutes the main reserve.

The complications that are involved in such phenomena of ionization may be briefly considered as follows:—Assuming a condition of equilibrium to be in existence, if CO_2, physically absorbed by the solution, be removed from the water, as in the hypothetical case of the action of a photosynthetic submerged plant,

---

[1] Palitzsch, *loc. cit.*, p. 242.

[2] Thiel and Stroheeker (1914) give 5×10^{-4}; Gaarder, *loc. cit.* p. 33.

[3] Ruppin (1910) assumes a dissociation-constant for $H^\cdot$, CO_3'' as 1.295×10^{-11}: Palitzseh (1912) takes 6×10^{-11} (Auerbaeh and Pick, 1911).

some of the combined H_2CO_3 (present in large quantity) must automatically decompose into H_2O and CO_2 until the equilibrium is restored. To get this, if the H_2CO_3 is all ionized, some $H^{\cdot}$ and HCO_3' ions must recombine; while if the CO_3'' ions be removed by the plant, more HCO_3' must dissociate, and so on. In either case, in the long run, the plant may be said to utilize HCO'_3 of the acid carbonates, although there may be no acid carbonate molecules in the sea, but only the corresponding ions.

The preceding action may be made good in the course of time by the absorption *physically* of more CO_2 from the atmosphere by ordinary diffusion-rate, but this requires time; hence the ionic processes are in a state of constant flux, since one ionic operation upsets the equilibrium of all the other ions.

As examples of ionic reactions involved by the "dissociation" effects of H_2CO_3 and water, the following may be considered (Gaarder);—

(1) $CO_2+H_2O \rightleftarrows H_2CO_3$
(2) $H_2CO_3 \rightleftarrows H^{\cdot}, HCO_3'$.
(3) $HCO_3' \rightleftarrows H^{\cdot}, CO_3''$.
(4) $H^{\cdot}, OH' \rightleftarrows H_2O$.

as also, involving the relations of monocarbonate or bicarbonate;—

(5) $CO_3''+H_2CO_3 \rightleftarrows 2\,HCO_3'$
(6) $CO^{3''}+2\,HOH \rightleftarrows H_2CO_3+2OH'$
(7) $HCO'_3+HOH \rightleftarrows H_2CO_3+OH'$
(8) $CO_3''+HOH \rightleftarrows HCO_3'+OH'$

and representing 8 reversible reactions for which distinct constants will obtain; while any interference with one reaction sets all the others in motion, as all require to be readjusted. From a botanical standpoint the arrangements are further complicated, as plant-life removes CO_2 in sunlight, but gives it back in hours of darkness.

Since it is not possible to follow mathematically the mutual relations of the ions of more than two substances, it thus follows that the sea presents an organization of inconceivable physical complexity, constituting phases of molecular association and dissociation; so that if one cares to extend the conception of "life" to such non-molecular processes, the *aqueous phase of the sea may be conceived as one vast mass of "life," the primordial material of which protoplasmic units are but individualized particles or segregated centres of actions, still more complex, but of the same category.* Further if the ionic relations of such apparently simple chemical substances as CO_2 and H_2O may be so complex, one gets a faint idea of the infinite possibility of elaboration in the relations of all the ions of living cytoplasm and their molecular reserves.

To the biologists of a preceding generation, brought up on animal physiology as presented in the human body, the distinction of " living " as opposed to " non-living " organization was based on the conception of *Katabolism*, as involving a " combustion-process," or internal liberation of energy for vital operations; and so far the flame is the legitimate image of biological life. The work of Pasteur on *Saccharomyees*, of Sachs on photosynthesis, and later of Winogradski on Nitro-bacteria, showed that other *external* sources of energy are available to organism; and, since the idea of breaking down demands a preceding effort of building up, the primary definition of life was extended to anabolism; the synthetic processes of organism being clearly more essential than the destructive operations associated with the performance of animal work.

From a botanical standpoint, autotrophic organism working in terms of an external source of solar energy must be regarded as the primary case; and the recognition of the initiation of " Life " thus extends still further back in the problem of more and more elementary syntheses of protoplasm; as for example to proteid-complexes of more elementary nature, as considered in the synthesis of polypeptides, and even to the non-nitrogenous synthesis of presumably carbohydrate material. So that while animal physiologists may discuss the more fundamental efforts of "life," as expressed in the elaborations of proteid from sugar and ammonia, the antecedent synthesis of sugar involves the apparent adoption of formaldehyde as " non-nitrogenous protoplasm " (Cross and Bevan, 1912). But it is evident that all such syntheses are the necessary preliminary stages of a continued sequence of anabolic processes; and it is not possible to say that " life " began at any one stage more than at any other. Further complications only continue the same story, and "reversible enzyme-actions" are possibly but of the same class of phenomena as reversible ionic reactions involving interchange of OH' and $H^{\cdot}$ ions. Taking the actual starting point as the introduction of an *external* source of energy, beyond that provided by the inorganic material of a world-condensation, this may be traced in the action of solar radiation, a factor of the solar-system, again older than the earth itself. The point at which it is applied, so far as is known, is to be sought in the chemical reactions antecedent to the production of a monosaccharide sugar, initiated by the dissociation of the ions of CO_2 in sea-water, and the building of open chains of CHOH groups. In so far as this non-material action only increases the complexity of material organization on lines previously existing, the still more fundamental physical factors may be recognisably brought within the same sequence of phenomena; and beyond the introduction of solar energy, itself a component factor of the solar system, it is not possible to draw any sharp line between "living" and "non-living" reactions in the sea. To this extent the ionic organization of the sea may be said to constitute the link between the "life" of aqueous protoplasmic organism, included within the province of the biologist, and the more generalized life of the stellar universe: the wider view of life being thus brought within the provisional definition as *organization pressing to the mathematical limit of possibility*, as determined by the progressive cooling of the solar system, of which the earth and its ocean form but a special case. The expression "organization" being again a term masking some unknown factor, yet suggesting that the biological segregation of spheroidal plasmatic entities in ionic sea-water may be in some way a parallelism of the causation of the more immense phenomena associated with the segregation of spheroidal suns in a period of material organization indefinitely more remote. On the other hand if there be still an inherent distaste for extending the connotation of the term "life" in the biological sense to such a medium, it may be at any rate accepted that these fundamental physical properties of ionized sea-water constitute also the most fundamental asset of organic matter, requiring only the addition of the phenomena of "chemical growth" to bring it even more clearly within the comprehension of this jealously guarded term. But that plasmatic life arose in the sea with its complex ionic phase, and that such life out of the available elements of sea-water, has followed the carbon-atom, so far fairly expresses the facts of the case; both the *locus* and the *material* for the evolution of plasmatic life being clearly defined.

GENERAL LITERATURE.

Anglestein (1911), Cohn's Beiträge, p. 87.

Allen (1919), Journal Marine Biolog. Assoc.

Church (1919), Plankton Phase and Plankton Rate, Journal of Bot., Supp. III.

,, ,, The Building of an Autotrophic Flagellate: Bot. Mem. 1, Oxford.

Gaarder (1917), Bergen Aarbok, p. 32. Die Hydroxylzahl des Meerwassers.

Krümmel (1907), Ozeanographie, Vol. I, p. 242.

Lohmann (1908), Wiss. Meeres. Kiel, X, p. 351.

Murray and Hjort (1912), Depths of the Ocean, p. 175.

Palitzsch (1912), Danish Oceanograph. Exped., "Thor," p. 240, p. 251, Measurement of the Hydrogen Ion Concentration.

Ruppin (1910), Wiss. Meeres. Kiel, Alkalinity of Sea Water, p. 290.

LABORATORY EXPERIMENTS ON THE SPROUTING OF POTATOES IN VARIOUS GAS MIXTURES.

(Nitrogen, Oxygen and Carbon Dioxide).

By Franklin Kidd, D.Sc.

Food Investigation Board, Department of Scientific and Industrial Research.

METHOD. Potatoes were enclosed in glass desiccators of about 3,000 cc. capacity and the artificial gas mixtures were made up by the method previously described.[1] This method involves partial or complete evacuation of the vessel containing the tubers before passing in from cylinders of compressed gas the different gases in the proportions required. Five potatoes were the most that could be used in any experiment. With such a small number the probable error due to individual variation is large. To decrease this the following precautions were taken. In any comparative series the potatoes were carefully selected so that in all experiments they should be of the same weight, size and number, and of the same sprouting capacity as estimated by previous tests.

The sprouting capacity was judged by (1) the number of sprouts, (2) their vigour (*i.e.* size). Every time an observation was made all the sprouts which had appeared were broken off. The results are given in number of sprouts, total weight of sprouts, and weight per 100 sprouts. From a series of controls the average error of a single reading from 5 potatoes was calculated to be under 15 per cent. Even with five potatoes it was found necessary to renew the gas-mixtures every two days. The variation in concentration of O_2 and CO_2 during the experiments was not more than from 2 to 3 per cent.

The experiments were conducted in a dark room the daily temperature variation of which was from 1-2 degrees. The season was from June to December, 1918. The average monthly temperature of the dark room was as follows:—

June	...	17°C.	Oct.	...	13°C
July	...	19°C.	Nov.	...	13°C.
Aug.	...	20°C.	Dec.	...	13-14°C.
Sept.	...	15°C.			

Material. The "Factor" potatoes used were taken on the 24th April from the clamp where they had already sprouted somewhat. From 24th April to 31st May they were kept in a dark, cool and dry place in the laboratory. Sprouts had again developed in this interval, and these were removed before using the potatoes for the following experiments. The "King Edward's," which were not used until late in the season, had several times produced sprouts which had been removed.

---

[1] Kidd, F., Proc. Roy. Soc. (Lond.), B. 87, 1914, 411.

Results. Three series of experiments were carried out. (1) The influence of oxygen and of carbon dioxide upon sprout formation were simultaneously tested, the following twelve mixtures being used :—5%, 10%, and 20% oxygen combined respectively with 0% CO_2 10% CO_2, 20% CO_2, and 40% CO_2, (Table 1 and 2). The influence of oxygen alone was tested in the following concentrations:—5%, 10%, 20%, 50% and 80% (Tables 3, 4 and 5).

Carbon dioxide at a concentration in the atmosphere of 20% or higher inhibited sprouting. Carbon dioxide in a 10% concentration greatly reduced the number of sprouts formed and also reduced to a less degree the size of the sprouts that appeared, that is, their rate of growth. The retarding and inhibiting action of carbon dioxide was not markedly influenced by the amount of oxygen present as far as tested, *i.e.*, between 5% and 20% oxygen.

Injury and death occurred after 6–7 weeks in 40% carbon dioxide. This injury was accelerated by oxygen concentrations above a certain minimum in proportion to the amount of oxygen present. It occurred more quickly where 20% oxygen was present, in conjunction with CO_2, than where 10% was present, and more quickly in this case again than where only 5% was present.

In the case of 10% and 25% carbon dioxide no injurious effect was shown during the two months the potatoes were in the presence of the artificial gas mixtures, but subsequently the sprouting did not return to its normal value, and rotting set in earlier than with the controls. This premature rotting was most pronounced in the potatoes which had been in 20% oxygen, and least in those from 5% oxygen. It appears, therefore, that oxygen becomes harmful to the potato in concentrations above 5—10%, and that this harmful action is increased in proportion to the amount of oxygen present.

The results of the experiments in which the effect of different oxygen concentrations (in the absence of CO_2) was tested supports this conclusion (Tables 3 and 4). In concentrations above 20% oxygen clearly depressed sprouting. The number of sprouts produced was fewer and the size smaller. The effect became more marked in higher concentrations of oxygen. A concentration of 50% oxygen caused injury in 4 to 5 weeks. Cell death occurred in localised areas, and moulds became established. A concentration of 80% killed the potatoes in the same period. A decrease in oxygen concentration below 20% did not lessen sprouting. On the contrary the optimal concentration for sprouting appeared to be 10% or even 5% oxygen.

After the middle of June the natural sprouting capacity of the potatoes fell off regularly from week to week (Table 6).

The Influence of Carbon Dioxide and of Oxygen on the Sprouting of Potatoes (Factor).

	Date.	Growth interval in days.	Fresh weight of sprouts in grams.			
			0% CO_2	10% CO_2	20% CO_2	40% CO_2
20% Oxygen.	14/6/18.	14.	1·2.*	0·6.	0	0
	28/6/18.	14.	1·5.	0·5.	0	0
			[7·1] (21).	[5.0] (10).		
	12/7/18.	14.	1·1.	0·4.		
			[3·3] (19).	[2·1] (19).	0	0
	1/8/18.	20.	1·6.	0·1.	0	Discarded All bad.
	All removed to air (1/8/18).					
	22/8/18.	21.	0·9.	0·2.	0	
	16/1/18.	147.	3·3. All sound.	0 Half number dead.	All dead.	
10% Oxygen.	14/6/18.	13.	2·0.*	0	0	0
	28/6/18.	14.	5·2.			
			[12.7] (41)	0·3.		
				[6·0] (5).	0	0
	12/7/18.	14.	1·5.	0·2.		
			[3·6] (41).	[4·0] (5).	0	Discarded Half number bad
	1/8/18.	20.	1·7.	1·6.	0	
	All removed to air (1/8/18).					
	22/8/18.	21.	0·9.	0·8.	0	
	16/1/19.	147.	1·3. All sound.	0·1. All sound.	0 Half number dead.	
5% Oxygen.	14/6/18.	13.	0·5.	0	0	0
	28/6/18.	14.	1·6.	1·7.	0	0
			[4.1] (39).	[5·6] (30.)		
	12/7/18.	14.	1·4.	1·1.	0	Discarded All sound.
			[3.2] (43).	[2·9] (38).		
	1/8/18.	20.	1·6.	0·45.	0	
	Removed to air (1/8/18.)					
	22/8/18.	21.	0·9.	0·5.	0	
	16/1/19.	147.	2·2. All sound.	0·3. All sound.	0·5 All sound.	

The figures in square brackets are weights (grams) per 100 sprouts.

The figures in round brackets are numbers of sprouts.

* In the first two weeks the potatoes in 10% Oxygen had produced a greater weight of sprouts than those in 20% Oxygen. To check this difference, as due to the experimental conditions and not to individual variation, the two lots were transposed. In the succeeding periods the potatoes in 10% Oxygen continued to produce more sprouts than those in 20% Oxygen.

The Influence of Carbon Dioxide on the Sprouting of Potatoes (Factor). Summary from Table 1.

		Carbon Dioxide.		
		0%	10%	20%
Fresh weight (grams) of sprouts. (Time 9 weeks).	Oxygen 20%	5·4.	1·6.	0
	,, 10%	10·4.	2·1.	0
	,, 5%	5·1.	2·8.	0·1.
	Total.	20·9.	6.5.	0·1.
Fresh weight (grams) per 100 sprouts. (Time 4 weeks.)	Oxygen 20%	10·4.	7·1.	0·5.
	,, 10%	16·3.	10·0.	0
	,, 5%	7·3.	8·5.	1·0.
	Total	34·0.	25·6.	1·5.
Total number of sprouts (Time 4 weeks).	Oxygen 20%	55	29	2
	,, 10%	82	10	0
	,, 5%	82	68	11
	Total.	219	107	13

The Influence of Oxygen on the Sprouting of Potatoes (King Edward). First Experiment.

Date.	Growth interval in days.	Fresh weight of sprouts in grams.				
		5% Ox.	10% Ox.	20% Ox.	50% Ox.	80% Ox.
26/7/18.	14.	0·5. [2·5.]	**0·8.** **[5·3.]**	0·7. [3·5.]	0·6. [2·4.]	0
9/8/18.	14.	**3·3.** **[7·2.]**	1·1. [4·4.]	1·0. [4·0.]	0·4. [1·6.] injured.	0 [0·4.]
Total.	28.	**5·2.** **[4·9.]**	2·6. [4·9.]	2·1. [3·6.]	2·3. [2·0.]	[0·4.]
Removed to air 9/8/18 22/8/18.		1·4.	0·7.	0·4.	1·3. Injured.	All dead.

The figures in square brackets are weights (grams) per 100 sprouts.

The Influence of Oxygen on the Sprouting of Potatoes (King Edward). Second Experiment.

Date.	Growth interval in days.	Fresh weight of sprouts in grams.				
		5% Ox.	10% Ox.	20% Ox.	50% Ox.	80% Ox.
22/8/18.	13.	0·4. [1·8.]	1·6. [3·2.]	1·8. [4·0.]	0·9. [2·9.]	0
11/9/18.	19.	4·0. [18·2.]	2·2. [5·4.]	3·3. [6·9.]	0·8. [5·0.] Injured.	Dead.
Total.	32.	4·4. [10·0.]	3·8. [4·3.]	5·1. [5·4.]	1·7. [4·0.]	

The figures in square brackets are weights (grams) per 100 sprouts.

The Influence of Oxygen on the Sprouting of Potatoes (Factor) Extract from Table 2.

Fresh weight of sprouts in grams in nine weeks.		
5% Ox.	10% Ox.	20% Ox.
5·4.	10·4.	5·1.
2·8.	2·1.	1·6.

The fall off in natural sprouting capacity of Potatoes from June to January.

Weeks.		Sprouts per week per 5 potatoes (Factor)
June	0 to 2.	2·2 grams.
	2 ,, 4.	5·4 ,,
July	4 ,, 6.	2·9 ,,
	6 ,, 9.	2·2 ,,
Aug.	9 ,, 12.	1·4 ,,
Sept. —Jan.	12 ,, 33.	0·34 ,,

CONCLUSIONS.

1. Oxygen is harmful to the potato tuber in concentrations above 5-10%. Oxygen 80% kills in 4 to 5 weeks. Oxygen 5-10% is the optimal concentration for sprouting.

2. The harmful action of Oxygen is increased in the presence of Carbon Dioxide.

3. Carbon Dioxide inhibits sprouting in a concentration of 20%. This concentration is at the same time to some extent harmful.

4. Higher concentrations of Carbon Dioxide cause marked injury and death.

28th April, 1919. THE BOTANY SCHOOL, CAMBRIDGE.

OBSERVATIONS ON THE PERIANTH IN *RANUNCULUS AURICOMUS* AND *ANEMONE CORONARIA*.

BY W. B. TURRILL, B.Sc.

[WITH THREE FIGURES IN THE TEXT.]

THE origin of the perianth in the Angiosperms has already been discussed from different points of view by Worsdell (1) and Rendle (2) in an early volume of this journal and it is unnecessary to recall in detail the theories which are there debated. The two extreme views are that the perianth has been derived entirely and directly from either the bracts or the stamens. Compromising suggestions are that the calyx has been derived from bracts and the corolla from stamens, and that the perianth in some group or groups of plants has arisen by metamorphosis of bracts and in other groups by metamorphosis of stamens. Genera and species of Ranunculaceæ have frequently been mentioned in the controversy, especially by those who have accepted the staminoid origin of the perianth, and it seems worth while to record some observations made this spring on flowers of *Ranunculus auricomus* and also to describe an anomalous specimen of *Anemone coronaria* recently received at Kew.

Ranunculus auricomus is a species of buttercup common throughout a large part of Europe and known from most parts of the British Isles except the extreme north of Scotland. A large patch grows in the shade under a walnut-tree north of the Aroid House in Kew Gardens, and last May the opportunity was taken of making a careful examination of some hundreds of flowers. The results may be most conveniently summarized as follows:—

1. The majority of the flowers had no petals (" honey leaves " of Prantl) or staminodes. In such flowers five sepals were constantly present.

2. The normally developed sepals were greenish-yellow with a deeper tinge of green towards the apex, or green with a yellow margin of greater or less width, they had no trace of a nectary and were always hairy on the back and glabrous on the inner (upper) surface.

3. The fully developed petals were bright deep yellow in colour, quite glabrous on both surfaces, and each was provided on the inside a short distance above the base with a small, oval-orbicular, shallow pit which served as a nectary.

4. The stamens had a relatively broad connective and 2-lobed anthers, each lobe having two pollen-sacs and dehiscing longitudinally.

5. A few flowers were found which were functionally female. These were usually situated low down on the plants and were therefore more or less covered by foliage and by taller plants. Their stamens were very much reduced in size and produced little or no pollen. Similar unisexual states of both *Ranunculus bulbosus* and *R. acris* have been found on the lawns at Kew.

6. A series of interesting transition stages between stamens and petals were found and a selection are here figured. It will be noted that the filament is usually very short or entirely suppressed. Fig. 1*a*, is a normal stamen with two of the four pollen-sacs showing. Fig. 1, *b* represents a staminode from a flower with five ordinary green sepals and no petals. The staminode was short, narrow, and showed clear indications of two anther-lobes each with two pollen-sacs which dehisced by a common longitudinal slit setting free a small amount of pollen.

Fig. 1, *c* is very similar to the last but the pollen-sacs are not so well developed and only a little incomplete pollen was found at the base. Fig. 1, *d* is a staminode from a flower with five sepals and one fully developed petal. One anther-lobe was complete and had two pollen-sacs which produced a small amount of pollen, the other was formed below but was replaced above by a small pocket.

Fig. 1, *e* represents a staminode from a flower with five sepals and one normal petal. In side view it strongly recalls the honey-leaves of species of *Helleborus* and *Eranthis*. No pollen was produced and both anther-lobes ended above in pockets.

Fig. 1, *f* is a staminode taken from a flower which also possessed five sepals and one normal and one nearly normal petal. A double pocket was present in the lower half and near the base there was an indicatation of a nectary.

Figs. 1, *g* and *h* are staminodes from a flower which also had five sepals and one normal petal. Some incomplete pollen grains were found near the margins.

Fig. 1, *i* is a staminode from a flower which also had four sepals and one normal petal. No pollen grains were found.

Fig. 1, *j* represents a staminode which may be termed a petal, for a nectary is present near the base and no pollen was produced though the remnant of one of the anther-lobes was present.

Fig. 1, *k* from a flower with five sepals, is a petal with a well-formed nectary but with thickened ridges parallel to the margins in the lower half.

Fig. 1, *l* represents a fully developed petal.

7. It was frequently noticed that when only four sepals were present the place of the fifth was taken by a more or less normally formed petal. It was always the sepal innermost in the whorl which was thus replaced.

8. In one flower with four normal sepals and no normal petals or staminodes a perianth-leaf, half sepaloid, half petaloid, was found occupying the position of a fifth sepal and internal to the others, Fig. 2, *m*. The lower part was green, externally hairy, and sepaloid, the upper yellow, glabrous, and petaloid. There was no trace of a nectory.

9. In one flower, which unfortunately had partly fallen to pieces when gathered, one of the sepals was replaced by a leaf intermediate between a sepal and an involucral bract. It was greenish-yellow and hairy on the back only, like the sepals, but was regularly lobed (Fig. 2, *n*).

Specimens of *Anemone coronaria* with a fully developed sepal in the position of a segment of the involucre have several times been reported in cultivated plants, but no previous record has been found of the occurrence of this abnormality in wild specimens. *Anemone coronaria* is a native of South Europe and the Orient. In Palestine it is one of the commonest and most beautiful of the native flowers, and is probably the "lilies of the field" of the

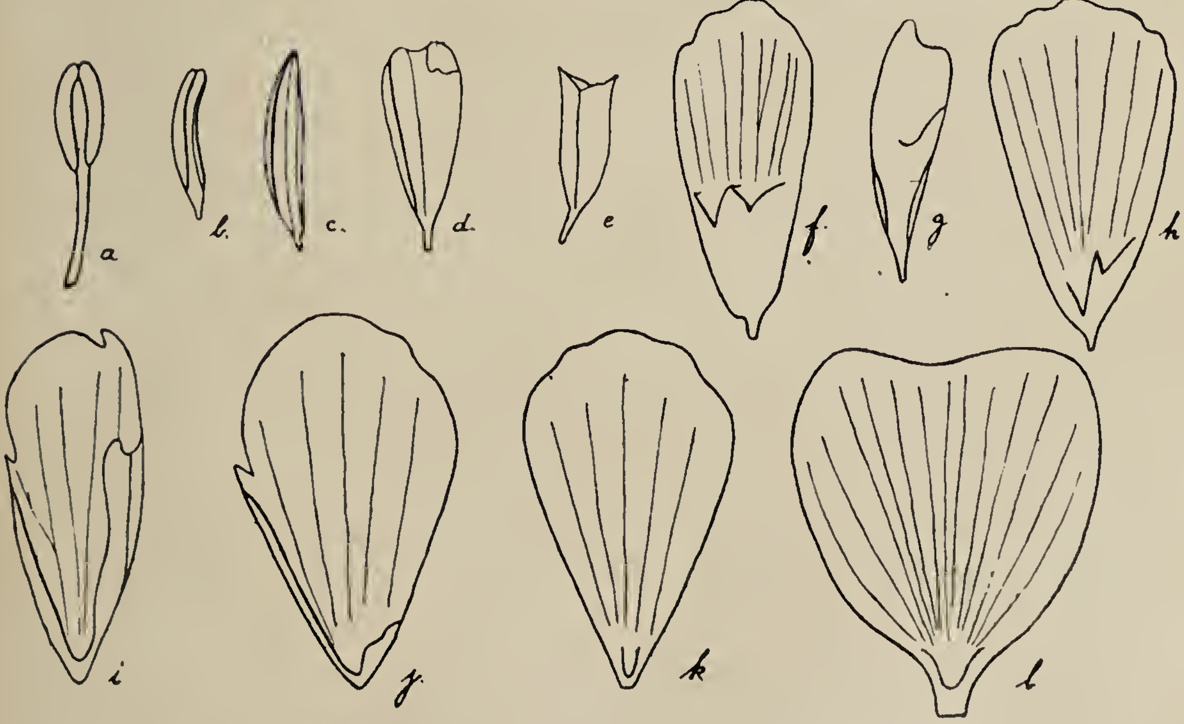


FIG. 1. *Ranunculus auricomus.* Transition forms between stamens and "petal," *a*, normal stamen, *l*, normal "petal."

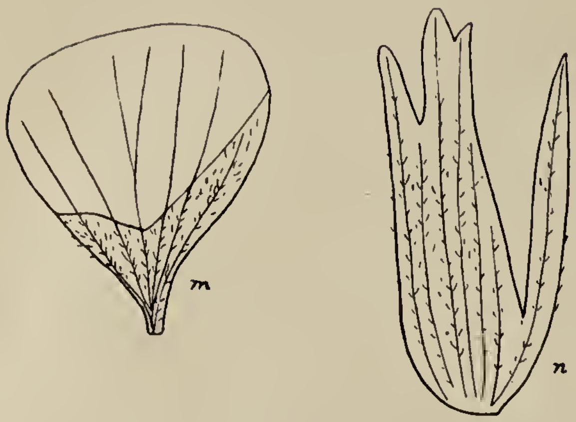


FIG. 2. *Ranunculus auricomus.* *m*, Transition forms between "petal" and "sepal," *n*, bract-like sepal.

Fig. 3. *Anemone coronaria.* Displacement of "sepal" into the involucral whorl.

Bible. The majority of the flowers have from six to nine deep scarlet petaloid sepals and no petals. From 1 to 6 cm. below the flower an involucre is situated and usually consists of three separate bracts which are deeply and irregularly lobed. Amongst a consignment of well dried specimens of this species collected in Central Palestine by Capt. G. H. Ogilvie was found one which shows a sepal, normal in size, colour, venation and indumentum, but arising in the involucral whorl 2 cm. below the remaining nine sepals of the flower, Fig. 3. One of two explanations is possible, that a sepal has become misplaced, its primordium having been left behind when the pedicel above the bracts lengthened, or that an involucral bract has become abnormally metamorphosed into a sepal. The former seems the more probable because three normal bracts are present in the involucral whorl in addition to the sepal.

REFERENCES.

1. Worsdell. "The origin of the perianth of flowers." New Phytologist 2, pp. 42, 116, 1903.
2. Rendle. "The origin of the perianth in seed-plants." l.c., p. 66.
3. Davis. Knuth's "Handbook of flower pollination." 2, pp. 28-29.

THE "OSMOTIC HYPOTHESIS:" A REJOINDER.

In a recent number of this journal[1] exception has been taken to certain criticisms in a paper on "Turgescence and the Absorption of Water"[2] in which I drew attention to the need for a stricter use of terms in dealing with the water relations of cells and tissues and suggested the conception of water-absorbing power, which depends on the water-deficit of a cell or system and not solely on the osmotic strength of the cell-sap.

Stiles and Jörgensen admit the assumption involved in their use of the term isotonic, *viz.* that the turgor pressure was negligible in the potato tissue used in their experiments. When, however, they claim that the implicit assumption should have been obvious, I must demur. On the contrary, it is surely a contradiction in terms to call a tissue turgescent in which the turgor pressure is practically nil.

The word turgescent is, it is true, used loosely. The borderline between turgidity and flaccidity is not sharply defined. Appearance and rigidity change gradually as turgor is lost; and even when there is no turgor pressure deformation will bring the elasticity of the wall into play, so that the loss of rigidity is not complete. At the same time the term turgescent does imply the existence of turgor pressure, and the unqualified use of the term isotonic was calculated to mislead.

Moreover, the assumption that turgor pressure is negligible must be justified by experiment for each kind of tissue used. Stiles and Jörgensen's new experiments with beet-root indicate that the roots they used were in a condition bordering on flaccidity; but it does not follow that their potato tissue was in a comparable condition, nor that beet-root would always be in that condition.

I must confess that the point of some of their counter-criticism escapes me.

The implication "that the solution which just brings about plasmolysis is to be regarded as isotonic with the cell-sap" does *not* involve neglect of the observation of Pfeffer that "at the commencement of plasmolysis the osmotic pressure of the external fluid is slightly higher than that of the turgid cell." It is clear from the context that Pfeffer is referring to the original turgid condition of a cell and had in mind the contraction of the vacuole

---

[1] Vol. XVIII, 1919, p. 40.

[2] Ibid., Vol. XVII, 1918, p. 108.

and consequent increase of concentration that takes place. This is not inconsistent with the statement that when equilibrium is reached, involving plasmolysis, whether incipient or pronounced, the solution bathing the protoplast and the sap within the protoplast are isotonic (that is, of course, ignoring inward pressure due to viscosity and surface tension). But, as Pfeffer points out in the passage referred to, when cells with extensible walls are turgid the osmotic pressure of the sap can be determined by de Vries' method only if the contraction in volume can be measured with sufficient accuracy and a correction applied for it.

It should hardly be necessary to emphasise that in giving a definite value for the osmotic pressure of the sap of a cell it is necessary to define exactly the condition of the cell. In the treatment of the conditions of equilibrium in my paper it is made perfectly clear that reference is to the actual condition of the cell-sap at the moment, not to any previous or "normal" condition.

As for "attempting to explain phenomena which are actually complex on the hypothesis that they are simple," I have merely, like Stiles and Jörgensen themselves, taken the osmotic hypothesis of Pfeffer and de Vries as a working hypothesis which as a first approximation, fits the facts. I do not think they would wish their own views to be judged on the principle that to adopt a simple working hypothesis is to declare the facts to be as simple as the hypothesis.

We are admittedly ignorant of many things that it would be desirable to know, in this field as in others. Stiles and Jörgensen seem to suggest that because we "know little enough about the elasticity of the cell-wall" we are hardly justified in using the fact that it *is* elastic. The difference between us seems to be that whereas I frankly find the old working model still useful, they are looking beyond it to the complexities. I do not ignore the complexities; but surely, if "the osmotic theory of the cell may be used as a working hypothesis to explain observed facts while our knowledge is in its present incomplete state" one should attempt to the best of one's ability to understand the theory *and* its corollaries.

And in what sense is the theory still hypothetical? Do Stiles and Jörgensen doubt that the cell-wall is elastic and in varying degree extensible, or that the protoplasm is hardly permeable to the solutes of the cell-sap? The osmotic hypothesis, so-called, is merely a working model framed on the basis of of these facts. It applies in its simple form to vacuolated cells, but as most plant-cells are vacuolated the range of its applicability is not inconsiderable. Nothing that has been said has yet convinced me that the model will have to be discarded, though it will certainly need to be modified and complicated as our knowledge increases.

I take this opportunity of pointing out that in my paper on "Some Observations on the Behaviour of Turgescent Tissue, etc."[3] the blocks for Figs. 5 and 6 have been unfortunately interchanged.

D. THODAY.

Botanical Department,
University of Cape Town.
August, 1919.

---

[3] N.P., Vol. XVII, 1918, pp. 64-5.

REVIEWS.

"Botany of the Living Plant," by F. O. Bower, Sc.D., F.R.S , Regius Professor of Botany in the University of Glasgow. Pp. X. and 580, with 447 figures in the text. Macmillan & Co., 1919. Price 18s.

THIS is the first general presentation of the elements of botanical science by a leading British botanist that has appeared for a very long time. It is framed, according to the author's preface, on the lines of the annual course of elementary lectures on botany given in the University of Glasgow for more than thirty years. This course has been constantly remodelled and developed, and is now recast in the form of a series of self-contained essays with additional facts and some fresh subject matter. The material is throughout, says the author, such as will be reckoned elementary, but "elementary and fundamental," he adds, "should be held as equivalent terms when applied to those facts and principles upon which a Science is built." We may therefore fairly consider that this book contains, in the author's judgment, the fundamental facts and principles of modern botany, which should, first of all, be presented to the attention of the student.

The plan of the book as regards about half of its contents is somewhat unusual, and as the author remarks, will probably be criticised. After a short introduction and a substantial Division I (280 pages) which deals with the life history, anatomy and physiology of the seed plant along familiar lines, the author takes the other chief groups of the plant kingdom in *descending order*, finishing up with the bacteria. The book closes with two chapters, on "Sex and Heredity" and on "Alternation of Generations, and the Land Habit," and with two appendices on "Types of Floral Construction in Angiosperms" and on "Vegetable Food-Stuffs." The justification of the progress in description from the complex to the simple which the author hopes will be found "in the accessory and in the employment of materials later in the book" is not very obvious to the reader. The advantage of first describing and analysing the structure and functions of the complex seed plant, which is the type most familiar to the layman, and from the study of which many different kinds of everyday facts can be readily explained, has been very generally recognised; but once this has been done it is difficult for most lecturers and writers to resist the appeal of gradual progress from the simpler to the more complex and from aquatic to subaerial life. Nor are the positive advantages of the descending order quite clear. We presume the author finds them in the facility of immediate comparison of each group with a preceding one, beginning with a comparison of Gymnosperms and Angiosperms.

The space devoted to the different groups is not always in accord with their intrinsic importance in the scheme of plant life. Fourteen pages are devoted to Gymnosperms, thirty-seven to Pteridophytes, eighteen to Bryophytes, twenty-five to Algæ and as many as fifty-nine to Fungi. We should have liked to see more space given to Algæ, which are from so many points of view fundamental to an understanding of the higher plants. As Mr. Church has recently pointed out,[1] algæ have always been rather scandalously neglected by the land botanist: yet among them we learn facts of cell structure and reaction, of tissue arrangement and reproductive mechanism, without a knowledge of which we cannot hope to understand the original equipment which the landward migrants had at their disposal to meet the special problems of subaerial life. The Bacteria only get three pages of Professor Bower's book, a space which is quite inadequate to do the slenderest justice to their enormous interest and importance in the world. It is most desirable that the medical student, especially, should have his attention directed to this group by a biologist, who is or should be able to give the beginner some vivid and comprehensive idea of the stupendous and varied parts bacteria play in the world, on their own account and in relation to other organisms, so that the student should not wait until he is compelled to view them, at a much later stage of his course, almost entirely as causative agents in disease.

The two concluding general chapters deal with their respective subject in the light of modern knowledge, and they are decidedly harder reading than the body of the book. No attempt is made to deal with the process of evolution itself, except incidentally in the discussion of mutations. Though so little is actually known of the process of evolution it would seem desirable to have made a direct attempt to give the elementary student some idea of what is thought and held as to this process, and of the evidence on which current theories are based.

---

[1] *Thalassiophyta and the Subaerial Transmigration*, Oxford Botanical Memoirs, 1919.

But the thing we chiefly miss in the book, regarded as representing the content of a somewhat extended course for the student of the elements of botany, and especially having regard to the author's statement of the equivalence of "elementary" and "fundamental," is the absence of any serious attempt to grapple with the constitution and biochemistry of the plant cell, topics which must form the basis of any real understanding of "the Living Plant." We may still be very far from being able to "explain" the whole mechanism of a living cell in terms of chemistry and physics, but after all we do know *something* of what the protoplast is and of the way in which the protoplast works, and we can directly relate some of its activities to its physical and chemical nature and properties. It is no more difficult to frame an account of this subject which is intelligible and interesting to the student than to deal similarly with heredity and alternation of generations; and it is impossible to deny that the former is even more fundamental than the two latter. Until these things are faced it is impossible to carry the basic scientific concept of Causation into the necessary foundation of the study of the plant as a living organism. We must confess to a great deal of ignorance, but the student never minds that if we make an honest effort to explain to him what we do know, and what we only think, and why. To avoid this task seems to be to abrogate the first and most vital function of the teacher of science. And it is the too common avoidance of it among even the most distinguished teachers of botany, such as the author of this book, and the consequences of that avoidance, which lead one to the conviction that the teaching of elementary botany is in need of radical reform.

The book is written with that ease, fluency and lucidity of style of which its author is a master. It deals with the familiar story of the seed plant and with the stories of the other groups in an attractive and most readable way, and, it is unnecessary to say, with an assured mastery of discrimination between the essential and the unessential among the morphological and "biological" features which the different groups display.

We have noticed two slips, to which the author would no doubt like to have his attention drawn. The description of the corm of *Crocus* (p. 165) is misleading if not inaccurate, and the statement on p. 372 that the brown colour of Phæophyceæ depends on a pigment "phycophæin" is now obsolete.

The illustrations are exceedingly good, many of them drawn by the practised and skilful hand of the author, and many others—among the most admirable—by Dr. J. M. Thompson: the selection from figures already published is judicious; and all are excellently reproduced.

THE LIVING CYCADS.

" The Living Cycads." By C. J. CHAMBERLAIN. (The University of Chicago Science series).

IN this particularly attractive little book Professor Chamberlain introduces the layman to one of the most interesting classes in the plant kingdom and provides the botanist with an appetiser for the more serious repast which, we hope, will be ready at an early date. No author is better qualified than the Chicago Professor to deal with recent Cycads: his account of the nine genera makes his less fortunate readers envious of his good fortune in having been priviliged to make the intimate acquaintance of plants known to most botanists only in cultivation or as dried specimens. In the summer of 1914 I experienced the thrill caused by the first sight of a Cycad growing in the Australian bush and I am therefore able to appreciate the pleasure enjoyed by one who is on speaking terms with the whole family in both the West and East hemispheres. Within a small compass, though his account is not too condensed to be intelligible to the general reader, Professor Chamberlain describes the habits, habitats, and distribution of the Cycads, their life-history, and general morphology. In the third part of the book the difficult problem of the evolution of the group is handled with skill and on orthodox lines. Both the Cycads and the Bennettitales are regarded as offshoots of an ancient filicinean stock; it is recognised that the female part of the cone of the Mesozoic Bennettitales cannot be regarded as the source of the female cone of a recent Cycad. We are still far from having solved the question of the degree of relationship between the Cycadofilices and the Ferns. It may be, as Dr. Scott suggested at the recent meeting of the British Association, that we must substantially modify opinions which have been prevalent during the last two decades. Our knowledge of the past history of the true Cycads as distinct from the Bennettitales is exceedingly meagre: the two classes of the Cycadophyta are in some respects strikingly alike, while in others they are far apart, and the pre-Mesozoic history of the group is by no means clear.

The volume is admirably illustrated and, while one may be unconvinced by the evolutionary views, there can be no difference of opinion as to the success with which the author has presented the story of one of the most fascinating groups of seed-plants. It is pertinent to ask why the volumes in the University of Chicago Science series bear no date on the title-page or elsewhere.

A. C. SEWARD.

THE

NEW PHYTOLOGIST

Vol. XVIII, Nos. 9 & 10. Nov. & Dec., 1919.
[Published March 20th, 1920.]

FESTUCA RUBRA NEAR CARDIFF:

A TAXONOMIC, MORPHOLOGICAL AND ANATOMICAL STUDY OF THREE SUB-VARIETIES OF *FESTUCA RUBRA* L. SUBSP. *EU-RUBRA* HACK., VAR. *GENUINA* HACK., GROWING NEAR CARDIFF, S. WALES.

By W. O. Howarth, M.Sc.

[With Fourteen Figures in the Text.]

I.—Introduction.

THE present paper is the result of a morphological and systematic study of three forms of *Festuca rubra* L., which had been observed by Professor (now Principal) Trow of the University College of South Wales (Cardiff), and grown in his garden side by side, maintaining their distinctness for several years.

The interest of these forms was enhanced by their local economic importance (sward consisting of these grasses being in great request for bowling-greens, &c., and saleable at 6d. per square yard, or £121 per acre, as a standing crop to be removed at the cost of the purchaser): by the difficulty of assigning the three forms to their proper positions in the current scheme of taxonomy; and by the interesting ecological relations of the habitats affected by them.

II.—Systematic.

It will be convenient to begin with a description of the forms included in Hackel's Section *Ovinæ* of the genus *Festuca* which correspond with the plants variously known to English authors as *Festuca ovina*, *duriuscula* and *rubra*.

1. *Section* Ovinæ, *Hackel*.

Radical sheaths not thickened at the base. Ligules very short, truncate, often biauriculate. Laminæ either all complicate or those of the culm more or less flat; vernation conduplicate. Spikelets elliptical or oblong-elliptical. Fertile glumes narrow, margins scarious, in fruit the margins very involute. Ovary obovate-oblong, glabrous, rarely sparingly hispidulous, style exactly terminal. Caryopsis oblong, pale, with deep ventral furrow, glume closely adherent, and mark of hilum extending nearly the whole length.

This section Hackel divides into two sub-sections.

1. *Intravaginales*, characterised by their branches growing apogeotropically that is, they grow up inside the sheath which subtends them and emerge from the top of the sheath where the latter passes into the lamina. Each bears a dorsal prophyll followed by normal leaves (*i.e.*, having sheath and lamina). This includes nine species among which is *F. ovina*.

2. *Extravaginales* and *Mixtæ*. Branches either all, or only the lower ones, diageotropic, growing out through the base of the subtending sheath, and up external to it. Dorsal prophyll very small and with a gradual transition through various scale-leaves to normal foliage leaves. In the typical Extravaginales all the branches are extravaginal; the Mixtæ connect these with the Intravaginales. The three forms under investigation come in this intermediate group. Here Hackel places only two species, *F. rubra* L. sens. ampliss. and *F. Porcii* n.sp.

2. *Festuca rubra* L. sens. ampl.

Sheaths of the radical leaves all entire; ligules glabrous.

Further details which Hackel considers of importance in his description are: sheaths of the radical leaves on withering break up into irregular fibres, laminæ persist after death, ligules the same throughout, scarious margins not producing auricles, those of cauline leaves not equally biauriculate or nearly uniauriculate.

Following Hackel's key to the sub-species and varieties one is led to subsp. *eu-rubra* and var. *genuina*.

3. Subsp. *eu-rubra*.

About as many intravaginal as extravaginal branches. Laminæ obtuse; those of radical leaves obtusangled, 5 to 7 nerves, single sclerenchymatous strands corresponding to these on the lower surface, those of cauline leaves with motor cells clearly arranged.

Var. 1 (6) *genuina*. Loosely cæspitose, basal extravaginal branches creeping. Laminæ difformed: radical complicate, and angulate, obtuse-hexagonal in trans. sect., sclerenchymatous bundles separately arranged, motor-cells absent; cauline flat.

Seven sub-varieties of *genuina* are described :—

a vulgaris. Tall, radical leaves soft, setaceous (0·6—0·7 mm. diam.) dark-green; panicle loose (6—15 cm. long). Spikelets small (7—8 mm. long), lanceolate or oblong, green or slightly grey-violaceous; fertile glumes 4—4·5—5 mm. long, mucronate or shortly aristate, glabrous.

β. grandiflora. As the preceding, but spikelets large, 10 mm. and more long; fertile glumes 6—7 mm. long, with long awns.

γ. glaucescens. As *α*, but leaves glaucous-green, with spikelets often pruinous.

δ. juncea. Creeping at length. Laminæ of radical leaves juncaceous (0·8—1·2 mm. diam.), rigid, glaucescent, strengthened with stout sclerenchymatous strands; panicle somewhat loose, large, spikelets large (9—10 mm. long) glabrous, reddish hue.

ε. barbata. As *α* or *β* but spikelets shortly pubescent.

ζ. arenaria. Creeping at great length. Leaves rigid, sub-juncaceous, culm leaves generally subcomplicate. Panicle large; spikelets large, elliptic-lanceolate, 9—10 mm. long and more, densely hispid or villous.

η. dasyphylla. Celakovsky Prodr. d. Fl. Boehm. IV, 723 (1881).

4. *Position in Hackel's scheme of the three forms under investigation.*

The first form I have investigated, which is dark-green in colour, and which occurred as a weed in Professor Trow's garden, agrees with *β. grandiflora* and compares well with herbarium specimens of this in the British Museum. The second form is yellow-green and was found near Chepstow. While possessing the large spikelets of *grandiflora* it agrees fairly closely in other respects with *γ. glaucescens.* Herbarium specimens so named at South Kensington are rathermore glaucous and have smooth rachides. The third form is glaucous-green and came from the Barry pebble-ridge. It undoubtedly falls under var. *genuina*, but does not correspond with any of the sub-varieties described. One specimen only at the South Kensington Museum appears to agree with it (No. 1570, *Festuca* 504^3 Sp. 6 *rubra*). This was collected by Augustin Ley, June 25th, 1879, from "banks just above tidal mud under Wynd Cliff, Mon., Alluvial." The position and locality further suggest an agreement, but the specimen, if this is the case, is not a typical one, since it has a creeping habit. This might, however, be a fault easily committed by a collector unacquainted with the special habit of the plant. It is described as follows: "*Festuca repens*=*F. rubra* sp. pl.=*F. cambrica* Huds." "A variety of *duriuscula*" (Rev. Hugh Davies). "Doubtless under this as a super sp. . . . Another form of *F. rubra*" (A. Bennett).

The spikelets agree with those of *β. grandiflora*, but it differs in form of panicle, fineness of leaves and stoloniferous habit, as well as in other details which will be described later. It has therefore, been ranked as a new sub-variety of *genuina* under the name *tenuifolia*.

For the present, at any rate, it is just as well to keep to Hackel's analysis of the group as the basis for comparison of our British forms; otherwise there is much confusion. Boswell Syme's description (2, p. 145) of *Festuca rubra* subsp. *duriuscula*, "Linn.," Sm., includes the three forms A, B and C and Hackel's α, β and δ. He is inclined to think that *F. duriuscula*, Fries, also really represents the shortly stoloniferous plant which he supposes to be *F. duriuscula*, Linn.; but Fries, (4, p. 6), Koch (8, p. 705), and Babington (1, p. 440) place the forms of this *F. duriuscula* with longer stolons under *F. rubra*. Watson (13, p. 220) also regards *F. duriuscula* as "not strictly cæspitose; more shortly stoloniferous than *F. rubra*, with usually plane stem leaves; distinguished from *F. ovina* by larger panicles and more awned pales." In his records of distribution he confesses to great confusion between *F. duriuscula* and *F. ovina*, and between *F. rubra* and *F. duriuscula*. In his "Flora of Hampshire" Townsend (11, p. 423) regards *F. rubra* L., Bab., Gren. and God. as equivalent to *F. duriuscula* Sm.,?Syme; whilst J. W. White (14, p. 664) in his "Flora of Bristol" describes under "*F. rubra* L., *F. duriuscula* auct. angl., hard Fescue grass, the slightly creeping sub-cæspitose form which has commonly borne the name of *F. duriuscula* in this country." Druce's description (3, p, 245) of *F. duriuscula* applies to *β. grandiflora* of Hackel and does not include the forms *tenuifolia* and *glaucescens*. Whilst one might perhaps accept all three forms as *duriuscula*, this name does not go far enough, and it becomes necessary to distinguish between them. The differences are emphasised in the following diagnoses:—

5. *Description of the three forms.*

A. *Festuca rubra* subsp., *eu-rubra*, var. *genuina*, subvar. *β. grandiflora* Hackel, Monogr. Fest. Europ., 1882, p. 139. *F. rubra diversifolia β.* Gaud.! (Fl. helv. I, 288) and *F. rubra megastachys* Gaud.! (l.c. 287).

Stock perennial, loosely cæspitose. Extravaginal branches more numerous than, or equal to intravaginal ones; the former creep at length, diam. 0·8—1·0 mm., bear 5—6 (occasionally 9) scale-leaves, root at the nodes, older ones branch (Fig. 1).

Radical leaves 4—5 per shoot; sheath entire throughout, green at first, becoming more or less reddish-purple on drying, pubescent marcescent; ligule slightly bilobed; lamina almost appressed to shoot and in straight line with sheath, dark-green, lower surface with polished cuticle, complicate, length 33 mm., broadest diam. when closed 1·0 mm., fairly rigid (compared with B), 5 longitudinal ridges, 7 vascular bundles, 7 strands of sclerenchyma below abaxial surface (including margins) and a small strand along each ridge of adaxial surface.

Cauline leaves 3; sheath split throughout with overlapping edges, slightly pubescent or glabrous, generally slightly longer than the internode, base swollen, dark-coloured; ligule with broad, rounded sheath-lobe, abrupt transition from sheath to lamina; lamina as long as, or slightly longer than its sheath, highest with 9 longitudinal ridges, 9 vascular bundles and 11 strands of sclerenchyma abaxially, flat.

Haulm slightly curved at the base, then erect, terminated by panicle; length from base (including panicle) 76 cm., diam. varies between 1·8 and 1·0 mm. from base to apex; upper two-thirds naked, almost cylindrical, but 12—15 slight longitudinal ridges, more obvious on drying.

Panicle sub-secund, erect, length 18 cm., loose, open during anthesis, lower rhachillæ widely separated, internodes almost or quite smooth. Lower rhachillæ paired, unequal, with long stalks.

Spikelets large, 13 mm. long, green or slightly violaceous, 2 basal sterile glumes, 5—7 flowering glumes, axis jointed. Sterile glumes unequal, mucronate; lower smaller, 1-nerved, somewhat keeled; higher, larger, 3-nerved. Fertile glumes 5-nerved, all aristate, awns 3 mm. long; broadly lanceolate, 6—8 mm. long without the awn. Palea superior, 2-keeled, 2-nerved, pilose apex, Lodicules 2, massive, lower part becomes globular, upper unequally forked with blunt apices. Stamens 3. Ovary broadly ovoid or nearly globular, furrow glabrous, slight posterior; 2 nearly sessile terminal stigmas. The caryopsis has not been found to develop.

B. Subvar. *tenuifolia* (new subvar.).

Stock perennial, more densely cæspitose. Extravaginal branches about equal to intravaginal ones, the former generally short, gently curving upwards from their base, bearing 1—4 (6) scale-leaves, rarely rooting at the nodes and more rarely branched,

Radical leaves 4—5 per shoot; sheath-surface slightly rough hispidulous, due to minute downwardly directed reflexed hairs, otherwise as in *grandiflora* ; ligule slightly bilobed ; lamina making a small angle with the shoot axis, dark glaucous green having the appearance of a "bloom," complicate, length 25 cm., broadest diam. when closed 0·8 mm., therefore more slender than in *grandiflora*, rather lax, 5 longitudinal ridges, 5—7 vascular bundles, 5—7 small strands of sclerenchyma below abaxial surface, absent from adaxial surface.

Cauline leaves 2—3; sheath split, quite smooth, only two-thirds length of internode, base swollen, green ; ligule with lower (sheath) lobe raised into a definite auricle ; lamina, usually shorter than its sheath, highest with 5—7 vascular bundles and 7—9 strands of sclerenchyma abaxially, flat or canaliculate.

Haulm, shorter and more slender than in *grandiflora* ; length (including panicle) 52 cm. ; diam. varies between 1·0 and 0·8 mm., upper half naked, almost cylindrical, but 10 slight longitudinal ridges, more apparent when dry.

Panicle subsecund, erect, total length 9 cm., much smaller than in *grandiflora*, somewhat dense, open during anthesis ; lower rhachillæ paired, unequal, short-stalked, not widely separated, internodes flanked with upwardly directed hairs, slightly prickly to the touch.

Spikelets large, 12 mm. long, green or slightly violaceous, 2 basal sterile glumes and 5—7 (occasionally 8) flowering glumes ; axis jointed. Sterile glumes as in *grandiflora*. Fertile glumes, lower mucronate, upper becoming aristate, awns 2·5 mm. long, narrowly lanceolate, 5—7 mm. long excluding awn. Palea superior, apex somewhat hispid. Lodicules 2, not so swollen below, unequally forked above, with acute apices. Stamens 3. Ovary ovoid. Caryopsis enclosed with persistent and closely adherent paleæ with portion of axis attached ; 3 mm. long, 1 mm. broad, pericarp brown, with pronounced posterior furrow. Comes true from seed.

In accordance with the Vienna rules a diagnosis is given in Latin :

Subvar. *tenuifolia* (subv. nov.).

Elatior ; folia innovationum mollia, setacea (0·8 mm. diam.), obscure glauco-viridia ; vaginæ hispidulæ. Panicula densiuscula (9 c.m. lg.). Spiculæ magnæ (12 mm. lg.) ; glumæ fertiles 5—7 mm. lg., brevitus-longius aristatæ.

C. *Subvar. glaucescens.*

Stock perennial, fairly densely cæspitose. Extravaginal branches equal to intravaginal ones ; the former may creep to a distance, diam. 0·8—1·0 mm., bearing 8 scale-leaves, rooting at nodes and sometimes branching.

Radical leaves 5 per shoot; sheath perfectly glabrous; ligule slightly bilobed; lamina makes a slight angle with shoot axis, light yellow-green (glaucescent) complicate, fairly rigid, length 23 cm., greatest diam. when closed 0·8 mm.

Cauline leaves 2 (occasionally 3); sheath split, quite glabrous, only about half length of internode, base swollen green; ligule as in *grandiflora*, lamina very poorly developed and of short duration.

Haulm erect from near base, terminated by panicle; length including panicle, 46 cm., slender, upper half naked cylindrical, few striations visible when dry.

Fig. 1. Subvar. *grandiflora*. Base of shoot, nat. size.

Panicle sub-secund, erect, length 6 cm., fewer spikelets than B, densiusculous, open during anthesis, lower rhachillæ not widely separated, internodes as in *tenuifolia*.

Spikelets fairly large, 12 mm. long, distinctly violaceous and hispidulous, having a "bloom"; 2 basal sterile glumes; 4—6 (occasionally 7) flowering glumes, axis jointed. Sterile glumes as A. Fertile glumes all aristate, lanceolate, length 9 mm., excluding awn, awns 3 mm. Palea superior as in B, but more hispidulous. Lodicules, stamens, ovary and caryopsis, as in *tenuifolia*.

6. *Habitats of the forms.*

Sub-variety *grandiflora*: confined to soils more or less calcareous formed from the softer mesozoic rocks, fertile and, on the whole, moderately humid. Its general habitat is therefore a more or less mesophytic one. In the coastal area of Glamorgan it is only found along the cliffs well beyond the reach of the sea, and usually well protected by higher strata of vegetation such as scrub or open canopy wood, or by the lie of the land, from the force of the prevailing winds. Inland it is found along roadsides, growing amongst the loose stones of less frequented roads, or on hedge-banks, especially upon the dust-heaps and sweepings, or even in the crevices of old limestone walls.

Sub-variety *tenuifolia*, confined to the sea-coast, is either the dominant, or a co-dominant plant in the following habitats:—

(i.) the salt-marsh, where it descends into the *Glycerietum* and is dominant above it, associated with typical halophytes.

(ii.) the pebble ridge, associated with xerophytes, e.g., *Poa bulbosa*, var. *vivipara*.

(iii.) the hard exposed rocks in scanty soil, calcareous and well-drained, associated with halophytes or more extreme xerophytes.

(iv.) the calcareous tufa of the cliff-face.

Fig. 2. Subvar. *grandiflora*. Transition from foliage leaf to prophyll. Nat. size.

In all these situations it occasionally comes under the influence of salt water, either by complete inundation or from spray.

Sub-variety *glaucescens*, so far as known, grows in the higher zones of the salt-marsh and of the littoral, generally out of reach of the salt water. Not in Glamorgan; the nearest point at which it has been found to Cardiff is the mouth of the Usk (Mon.) and stretching along the coast well into Gloucestershire.

III.—COMPARATIVE MORPHOLOGY.

1. *The Branch-system.*

The subvariety *grandiflora* is loosely sub-cæspitose. Its lower branches are typically extravaginal, creeping for varying distances and then erect, bearing the characteristic prophyll and series of scale-leaves, 5—6 (occasionally 9) in number (Fig. 2). Under normal conditions the branches reach a total length of about 8 cm. and their diameter varies from ·8 to 1 mm. If grown in the garden they are much longer, branch from the axils of the scale-leaves, and root at the nodes.

The subvariety *tenuifolia* is sub-cæspitose, that is its extravaginal branches are much shorter; and they are more slender (·7 mm. diam.). Even those first produced curve gently upwards from their base, rarely branch, and only occasionally root at the nodes. Only two or three such branches are produced, the rest are typically intravaginal (Fig. 3).

Fig. 3. Subvar. *tenuifolia.* Base of shoot. Nat. size.

The typical extravaginal branches are rarely found in the earlier stages of development of seedlings. In the majority of seedlings the first branch is intravaginal (Fig. 4 a) ; but in some the branch grows through the base of the subtending sheath, and then almost erect, having a more or less elongated prophyll followed by a scale-leaf, and then a normal leaf (Fig. 4 b). Occasionally the first branch has a shorter prophyll followed by two scale-leaves, then normal leaves (Fig. 4 c) and is therefore more typically extravaginal. The second and succeeding branches of these seedlings are all intravaginal. From these observations it would appear that the intravaginal branch is the more primitive type, and that development has proceeded towards extravaginal branches accompanied by a change in the direction of growth, a reduction in the size of the prophyll, and a reduction in the succeeding leaves to scales by partial or complete loss of laminæ.

The third subvariety, *glaucescens*, in respect of the cæspitose habit approximates more to *tenuifolia*. Transference to garden soil affects both these forms by encouraging them to produce longer stolons, but even under these conditions they remain quite distinct from *grandiflora*.

Fig. 4. Subvar. *tenuifolia*. Seedlings showing transition from true intravaginal to true extravaginal branch.

2. *The Vegetative Shoot.*

All branches develop a shoot which remains purely vegetative during the first season's growth. The extent of development depends upon whether it is laid down early or late in the season. The usual number of leaves on a shoot is four or five. They are produced according to a regular alternation but become twisted out of position by a torsion of the axis. From the axils of these "radical" leaves branches arise; extravaginal from the older ones, intravaginal from the younger. Each shoot thus becomes the centre of a rapidly increasing branch system. The intravaginal branches form a compact turf; the extravaginal ones spread out in all directions. All become new centres of growth, thus tending to a raising of the general level of the turf. When, as frequently happens, the turf becomes covered with loose soil, débris or alluvium, not only do the new growths extend upwards but the short internodes of the vegetative axes elongate, often quite considerably, and take on the appearance of stolons. The same may also occur with the intravaginal branches. The result is, in the case of a shortly creeping form like *tenuifolia*, a false appearance of creeping at length; hence the necessity of selecting typical specimens for determination (see p. 265).

The sheath of the radical leaf is entire at first but later splits from above and below, ultimately separating into irregular fibrous strands which persist for some time after withering. The sheath surface serves to distinguish the three subvarieties; that of *grandiflora* is pubescent, especially in the upper exposed portion of the older sheaths; that of *tenuifolia* is hispidulous, having minute, retrorse, sharply-pointed hairs; that of *glaucescens* is perfectly glabrous. The sheaths of all develop a reddish-purple colour before withering.

The ligule is a slight ridge or cushion across the base of the lamina, and ends laterally on each side in a slight lobe at the edge of the sheath. The edges of the lamina also thicken somewhat as they pass into the sheath forming a second (upper) lobe which is often rather more pronounced in *tenuifolia* than in the other two forms. But the differences between the three subvarieties in this respect are too minute to be of real value for determination.

The lamina of subvar. *grandiflora* is rather more rigid than are those of the other two forms. It stands erect at first and in a straight line with the sheath. Fully developed it attains a length of 25—33 cm., and the broadest diameter of the elliptical transverse section is 1·0 mm. It is complicate with acute apex, polished and dark-green below, the "mat" upper surface raised into five longitudinally-running ridges. That of subvar. *tenuifolia* attains a total length of 20—25 cm., and is slender (·8 mm. diam.) and flexible. The lower surface is dark glaucous green, having the appearance of a "bloom"; the upper surface is just as in *grandiflora*. The leaves form densely matted masses when their growth is not interfered with. Subvar. *glaucescens* has laminæ also with a "bloom," like those of *tenuifolia* except that their colour is a lighter more yellowish green. These colour differences are a ready means of distinguishing the three forms.

3. *The Haulm.*

The stronger vegetative shoots continue their development in the second season to produce a haulm terminated by the inflorescence.

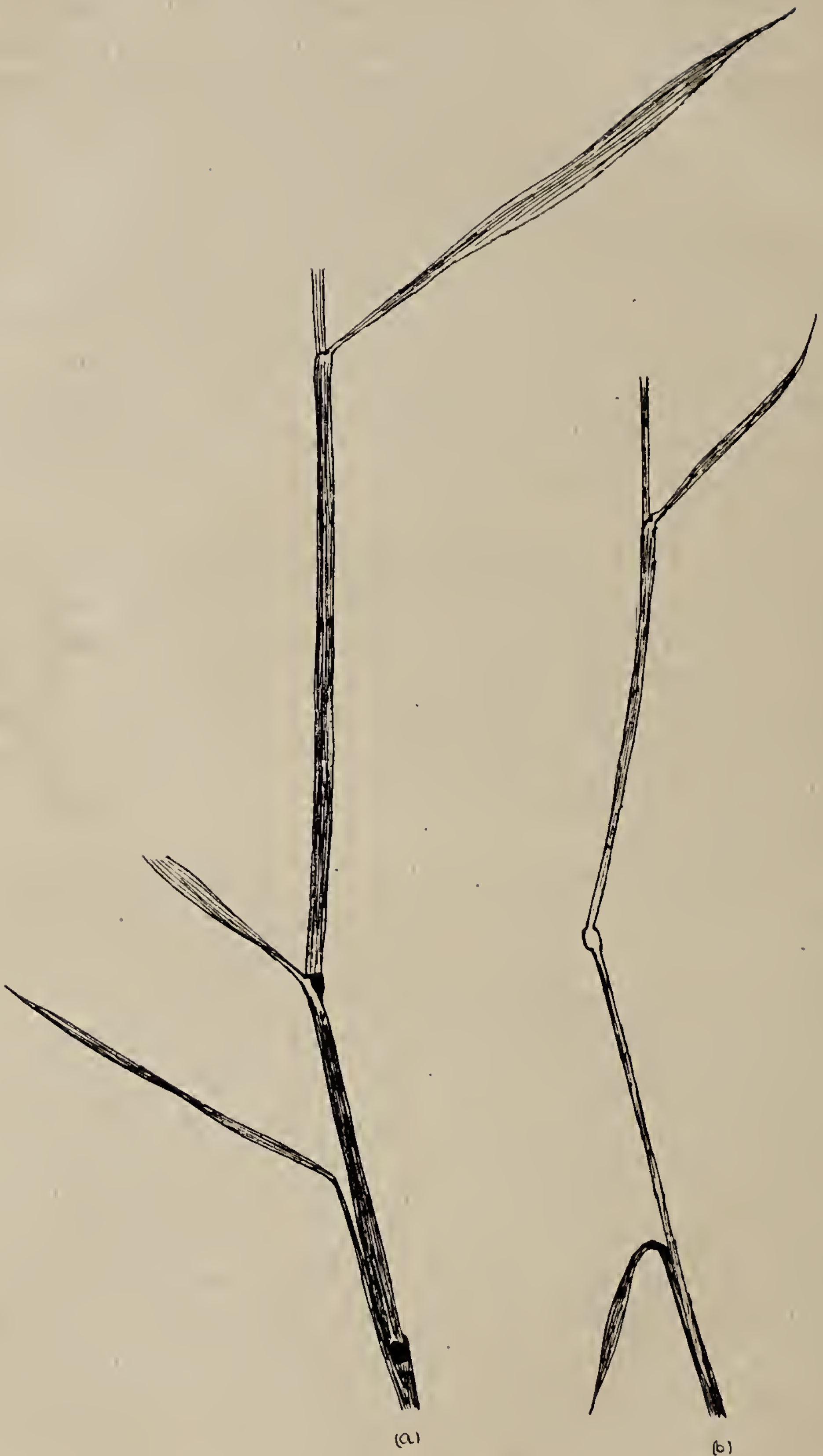


Fig. 5. Haulms of (a) *grandiflora* and (b) *tenuifolia*.

The latter makes its appearance about the end of May and has attained its maximum height about the middle of June. That of *grandiflora* is the largest of the three. Two well developed samples of (1) *grandiflora* and (2) *tenuifolia*, collected on June 14th, 1914 and compared showed:—

	grandiflora.	*tenuifolia.*
Height - - - -	76 cm. - - - - - -	52 cm.
Diameter -	1·8 mm.—1·0 mm. -	1·0 mm.—0·8 mm.
	Upper ⅔rds. naked	Upper ½ naked.

The number of cauline leaves is generally three for *grandiflora*, two to three for *tenuifolia*, and only two for *glaucescens*. The cauline leaf sheaths of *grandiflora* are as long as or slightly longer than the internode; they may be slightly pubescent above, or perfectly glabrous (Fig. 5 a). In *tenuifolia* the sheaths are usually, shorter than the internodes (Fig. 5 b), and quite smooth. In all, the sheath is split from top to base and the edges overlapping considerably. The lateral lobes of the ligule are broad and rounded in *grandiflora*, but raised into a definite pointed auricle in *tenuifolia*. The lamina is flat, somewhat involute when dry. The highest lamina on the haulm of *grandiflora* has nine longitudinal ridges along its upper surface; that of *tenuifolia* has only five to seven and is shorter; that of *glaucescens* is very poorly developed.

4. *The Panicle.*

The panicle of subvar. *grandiflora* is well developed and loose, attaining a total length of about 18 cm. (Fig. 6 a), That of subvar. *tenuifolia* is only about half this size (6—9 cm. long) and is of quite different shape, especially at anthesis (Fig. 6 b). That of subvar. *glaucescens* is smaller and less well developed in every respect.

In subvar. *grandiflora* the lower rhachillæ are widely separated and long-stalked. The following numbers were obtained from specimens of *grandiflora* and *tenuifolia*:—

Lengths of internodes (from below).

grandiflora, 5·5 cm., 3·0, 2·0, and the rest 1·0.
tenuifolia, 1·8 cm., 1·3, 1·0, 0·8, and the rest 0.6.

Number of spikelets on branches of panicle (from below)

grandiflora, 8 and 5, 6 and 3, the rest 2 each to terminal 1.
tenuifolia, 4 and 2, 2 and 1, ,, ,, 1 ,, ,, ,, 1.

The flanks of the internodes of axis and rhachillæ in subvar. *tenuifolia* are lined with small, upwardly directed barbs which makes the axis somewhat prickly to the touch; in subvar. *grandiflora* they are practically smooth.

Each axis of the panicle is terminated by a spikelet. The spikelet is shortly stalked and bears two basal sterile glumes, of which the lower shorter one is narrow, somewhat keeled, one-nerved, and the higher larger one broader and three-nerved. Both are mucronate. Above these in regular alternation are borne from five to seven or eight fertile glumes, the last one terminating the spikelet axis. Each is five-nerved; in *grandiflora*, aristate, the awns up to 3 mm. long; in *tenuifolia* the lower ones are mucronate, the upper aristate with awns up to 2·5 mm. long. The upper edges of the glumes of *grandiflora* are more broadly scarious, and more abruptly narrowing into the awn than in *tenuifolia*. In both the awns and margins the glumes are covered with minute upwardly directed prickles. The spikelets are green at first, but may become slightly tinged with violet in *tenuifolia*, more so in *glaucescens* where they are covered with minute hairs and a "bloom."

Fig. 6. Panicles of (a) *grandiflora* and (b) *tenuifolia*. × ½.

Fig. 7. Lodicules of (a) *grandiflora* and (b) *tenuifolia*. × 18.

The apex of the superior palea is rather pilose in *grandiflora*, more hispid in *tenuifolia* and *glaucescens*. The lodicule forks above unequally; in *grandiflora* one prong is thicker than the other and each has a blunt apex (Fig. 7 a), in *tenuifolia* and *glaucescens* the arms are more nearly equal and have acute apices (Fig. 7 b). The lower portion is much more swollen in *grandiflora* than in either of the other two forms. The result is that the flowers of *grandiflora* open widely, whilst those of the other two open just sufficiently to allow the projection of stamens, between the two points of the paleæ, and later the stigmas, between the two overlapping edges of the paleæ. At this stage the larvæ of *Thrips* attack the flowers of *grandiflora* and the young ovules shrivel.[1] On the other hand the flowers of *tenuifolia*, even though growing side by side, are immune. Possibly *Thrips* has easy access to the ovules of *grandiflora* through the well separated glumes, whilst the closed glumes of *tenuifolia* make access difficult or impossible. Massee (10) has "frequently seen the ear (of barley) well out of the leaf sheath, and many or all of the grains presenting a shrivelled appearance . . . due to the work of *Thrips ceralium* Halid."

The anthers dehisce about the second week in June. The almost sessile feathery stigmas are receptive about a week later. In subvar. *tenuifolia* the ovary after fertilisation elongates considerably and when full grown is about three mm. long. It has a deep median posterior furrow. It is ready for dispersal about the end of August.

IV.—COMPARATIVE ANATOMY AND HISTOLOGY.

1. *The Rhizome* (*Stolon*).

Extravaginal branches of *grandiflora* and *tenuifolia* were sectioned across their basal internodes (Fig. 8). In *grandiflora* the epidermis is slightly cuticularised, but in *tenuifolia* the walls are thickened, with a well developed cuticle. The cells of the hypodermis in the latter are also somewhat thick-walled. In *grandiflora* there are only three to four layers of cortex, and when mature the cells below the hypoderm break down in places, forming large cavities; in *tenuifolia* there are about six layers of cortical cells which persist. The mechanical tissue is in the form of a tube which is more centrally placed in *tenuifolia* than in *grandiflora*. The radial and inner walls of the external fibres are much more thickened than the outer walls; those placed between and within the vascular bundles are uniformly thickened (Fig. 8 c). In *grandiflora* there are about twenty-five vascular bundles; in *tenuifolia* only about ten. They vary in size individually, but on the whole those of *grandiflora* are larger. They are of the usual grass type (Fig. 8 a and 8 b).

---

[1] Whether *grandiflora* would set good seed if protected from *Thrips* remains to be determined.

Sections taken across the younger internodes of *grandiflora* show the cortex to be entire and composed of large parenchymatous cells loosely placed. Stomata occur occasionally in the epidermis of both forms.

In older rhizomes the scale-leaves wither and split into shreds. In *grandiflora* the tissues outside the fibrous zone practically disappear, but in *tenuifolia* they tend to persist, though shrivelled.

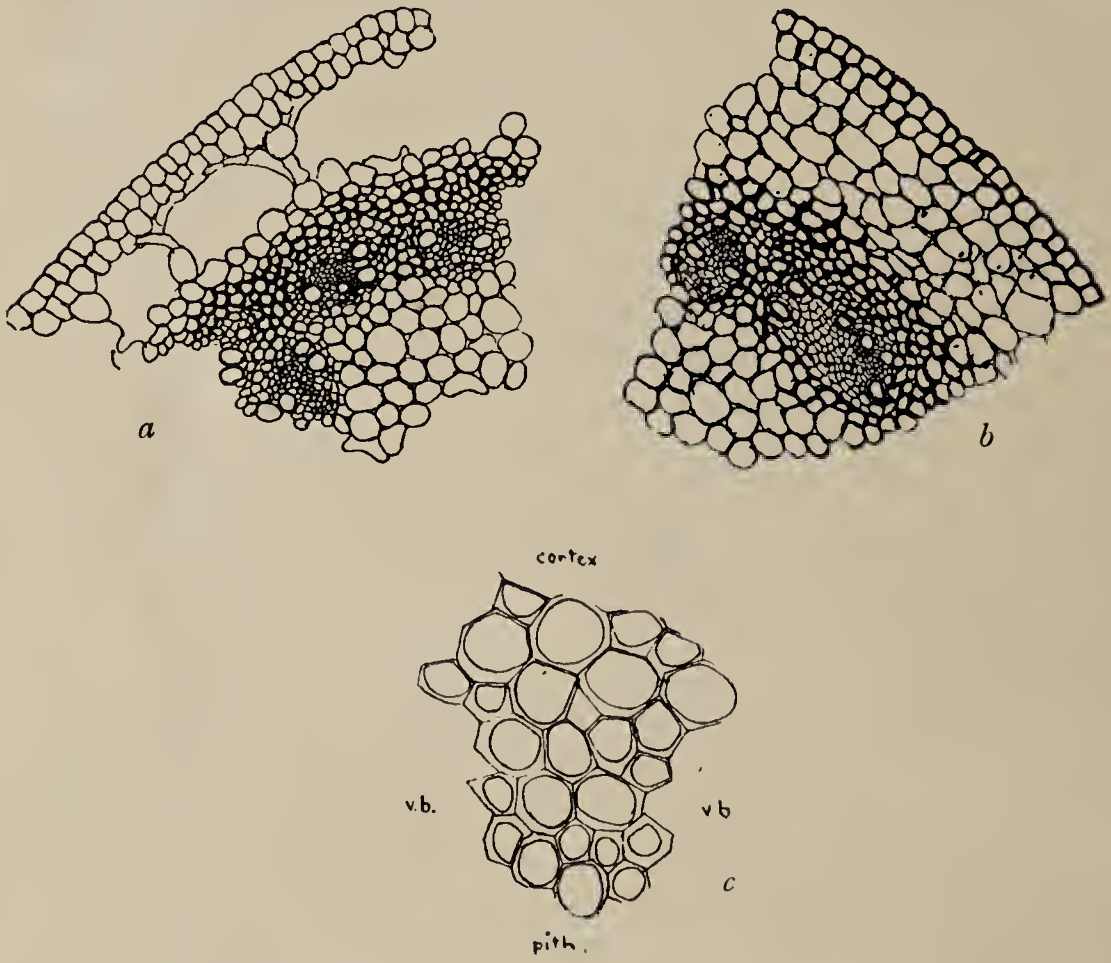


Fig. 8. *a*, Transverse section of internode of *grandiflora*. *b*, Ditto of *tenuifolia*. ×75. *c*, Fibres of pericycle in trans. sect. ×360.

2. *The Shoot.*

As the rhizome axis continues into that of the shoot, and successive leaf-sheaths are given off, there is a gradual diminution in its diameter. The vascular bundles from the sheaths pass into the axis. The midrib maintains its identity through two internodes, but the lateral bundles form lateral plates on which the steles of the nodal roots are inserted. The rest of the ground tissue is parenchymatous; the cells are rich in protoplasmic contents and starch. The tissues maintain their extensibility, the internodes remaining capable of elongation.

3. *The Adventitious Root.*

In *grandiflora* two or three adventitious roots arise simultaneously with the axillary branch and below it; in *tenuifolia* there is usually only one root, which is almost exactly below the midrib of the subtending leaf. This may be supplemented by others, according to the nature of the soil. As the young root grows out through the cortex the cells of the latter form a sheath of two to three layers which grows out with it, acting like the coleorhiza to the radicle The first roots are all tetrarch, their finer branches diarch.

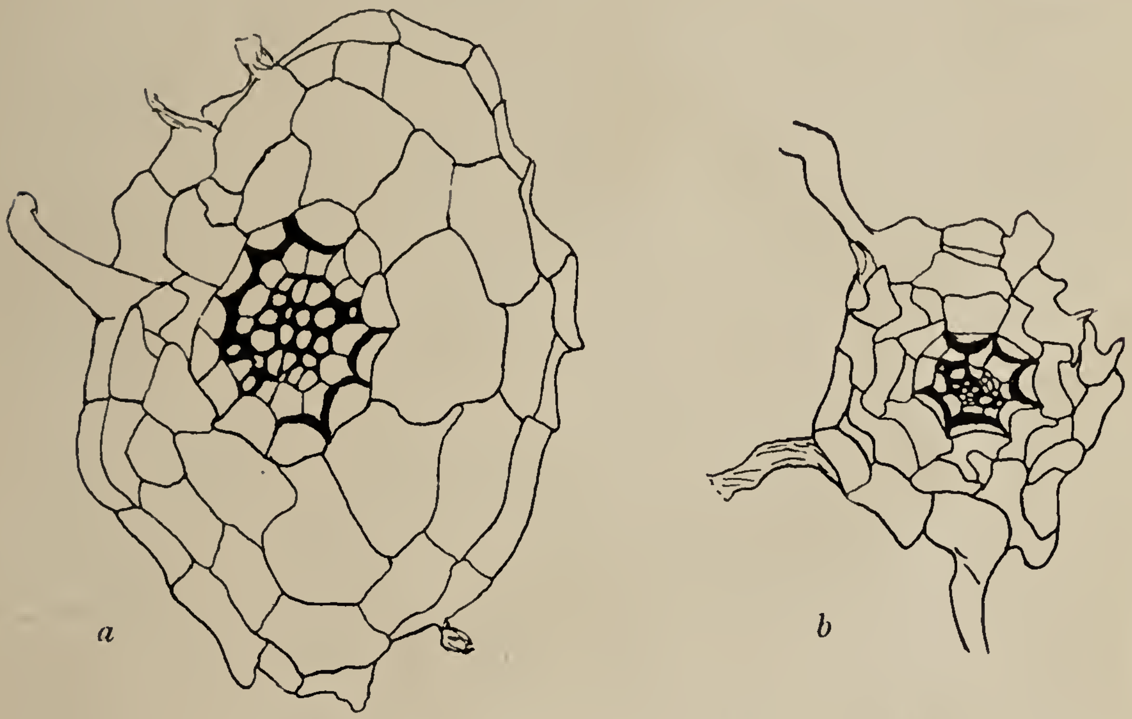


Fig. 9. Transverse section of fine root of (a) *grandiflora*, (b) *tenuifolia*. × 330.

Transverse sections show the root of both subvarieties to have much the same general structure. The piliferous layer of *grandiflora* (Fig. 9 a) has few root hairs, a cortex of two layers of parenchyma, an endodermis with "horseshoe" thickening broken by two sets of passage cells, a pericycle of one layer of regular cells alternating with those of the endodermis, and a diarch xylem plate. In *tenuifolia* (Fig. 9 b) the root is similar, but has less than half the diameter; the root hairs are quite as stout and relatively more numerous. In later formed roots of both forms, when the root-hairs have ceased to function, the piliferous layer collapses, the exodermis becomes suberised and the endodermis uniformly thickened; the xylem is tetrarch to polyarch. The whole of the cortex may later wither, but it persists around the endodermis and in *tenuifolia* the cell-walls of the pericycle become thickened so that it forms a second protective layer within the endodermis.

4. *The "Radical" Leaf.*

The outer epidermis of both sheath and lamina is composed of elongated cells, from twelve to fifteen times as long as broad, alternating with short cells. The short cells of the outer epidermis of the sheath may grow out as hairs (Fig. 10), or may develop into stomata, which are found especially in the cell rows close to the vascular bundles. The short cell divides longitudinally but unequally, and the larger of the two again divides longitudinally. Thus a central cell is cut off from two lateral ones. The latter become the subsidiary cells, and the central cell now divides longitudinally into two cells, each of which becomes a guard cell. The structure and mechanism of the guard cells has been fully described by Haberlandt (6, p. 451). The main differences between the sheath of the two forms are that in *grandiflora* there are about nine vascular bundles and a loose mesophyll; in *tenuifolia* only five to seven bundles, a compact mesophyll, and more thickened epi- and hypo-dermis. The outer sheaths decay and split, the vascular bundles being preserved intact by the protective endodermis and thus the lamina is enabled to continue its function for some time, after the sheath has split.

Fig. 10. Subvar. *tenuifolia*. Surface of sheath. × 120.

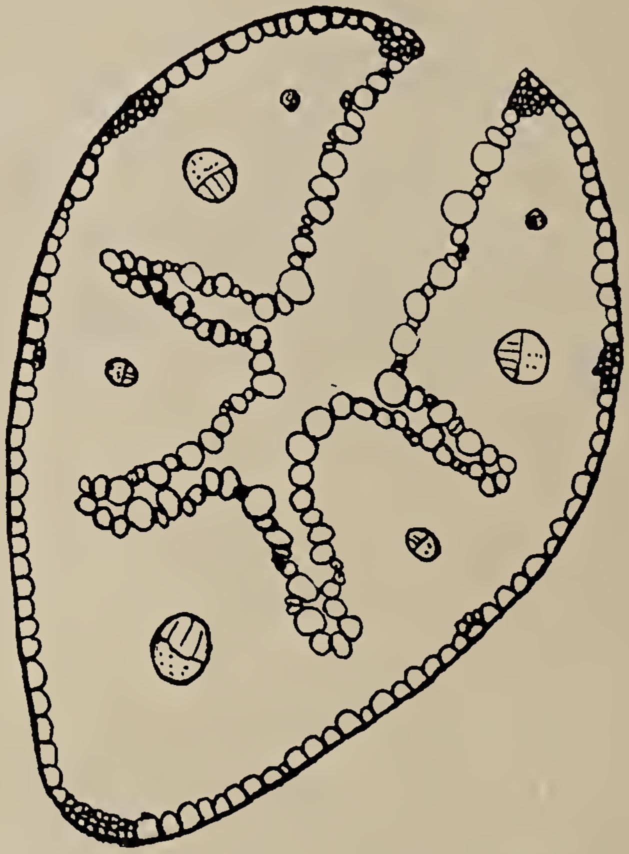


Fig. 11. Subvar. *tenuifolia*. Trans. sect. of lamina. × 120.

At the top of the sheath there is a slight overfolding of the tissue; then the upper fold becomes free from the lower and the edges pass round into the ligule and lamina.

The sheath is cylindrical for the greatest part of its length, but just previous to splitting a slight fold appears in it on the side opposite that from which the lamina passes off. The upper limb of this fold becomes free from the lower by the disappearance of the connecting plate of tissue and the sheath is now split, the free edges passing into the ligule and lamina.

The ligule is merely a slight ridge or cushion of thin walled parenchyma. The cells of the outer surface grow out as short papillæ or trichomes.

The lamina is complicate (Fig. 11). Along the upper surface are five longitudinal ridges, clothed with minute hairs, which give a dull green appearance to the surface. The shape of transverse sections varies slightly in passing from ligule to tip. From Hackel's description it would appear that he used herbarium material in which the softer tissues had shrunk, the resulting shape depending upon the position and amount of resistant tissues. The vascular bundles, five to seven in number, pursue a straight course from base to apex. At intervals branches pass out into the mesophyll. Each branch consists of a row of short, stout, spirally-thickened tracheides, connected at one end with the reticulate narrower elements of the main bundle, and ending either in contact with mesophyll cells or with an intercellular space. Each branch strand is surrounded by cells containing large nuclei and granular protoplasm. These branch strands are more numerous in *grandiflora.* The sub-epidermal strands of sclerenchyma are larger in *grandiflora* than in *tenuifolia*: hence the somewhat greater rigidity of the lamina of the former.

The lower (outer) epidermis in surface view consists of alternating long and short cells. The former are from six to fourteen times as long as broad and their long anticlinal walls are corrugated. The surface walls are furnished with the so-called marginal pits, which occupy the troughs of the undulations of the anticlinal walls on one side only, and extend obliquely upwards and outwards from the cell-cavity towards the surface (Fig. 12). The short cells in the neighbourhood of the ligule project beyond the general surface as hairs. The outer walls are strongly thickened, and the thickening extends to about midway along the anticlinal walls.

The upper (inner) epidermis also consists of long and short cells. The former are thin-walled, narrow at either end, but swelling out in the middle where their diameter is greatest. They are arranged in longitudinal rows and the cells of each row alternate with those of adjacent rows. As a result the short cells are sunk in depressions or troughs between the broad, protruding portions of the long cells. The long cells are more or less circular in transverse section and in the middle portion of their length from $\frac{1}{3}$ to $\frac{1}{2}$ of their surface is free and exposed. The short cells may produce short hairs or stomata. The latter are thus to some extent protected even when the leaf is open. The ratio of the number of stomata on equal areas of surface of *grandiflora* and *tenuifolia* is 12 : 11. The epidermal cells situated along the bottoms of the longitudinal furrows are not clearly differentiated from the rest of the epidermis either in size or in the thickness of their walls. They cannot therefore be said to form specialised structures, though the lamina, in folding, hinges on these cells.

Fig. 12. Subvar. *tenuifolia.* Lower epidermis of lamina showing marginal pits. *a*, Surface view, ×300. *b*, Trans. sect. ×860.

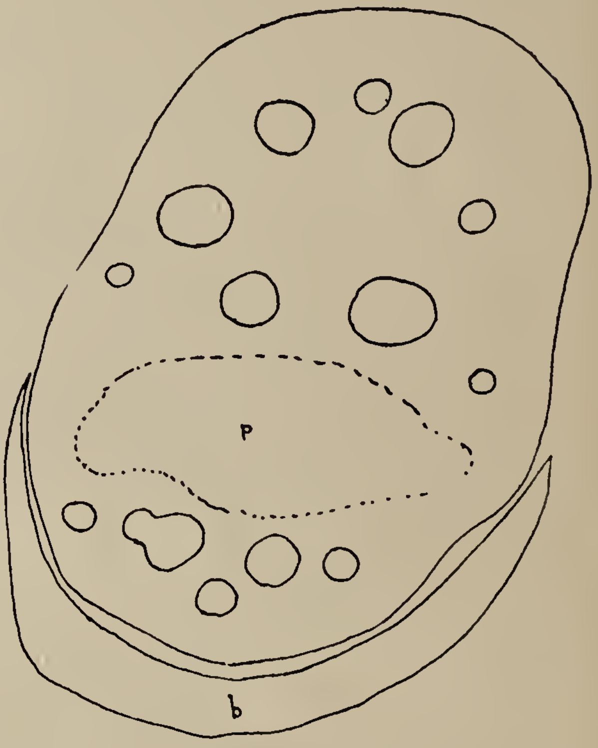


Fig. 13. Subvar. *tenuifolia.* Trans. sect. of node of panicle. *b*, bract. *p*, parenchyma. ×85.

Seen in transverse section the cells of the mesophyll radiate outwards from the vascular bundles, but in longitudinal section the palisade cells can be distinguished as being regular and compact, each cell directed slightly obliquely upwards from the bundle towards the outer epidermis of the lamina.

5. *The Cauline Leaf.*

The lamina of the cauline leaf has a comparatively short life, but is nevertheless a specialised structure as regards drought resistance. When open it is more or less flat and stands out practically at right-angles to the axis. A transverse section of the highest lamina on the axis of *grandiflora* showed nine longitudinal ridges along the upper surface, and in the furrows there are specialised " motor " cells, larger than the rest, which are scarcely raised above the general level of the surface. The hairs on the surface are more numerous and longer than those of the radical leaves. Groups of sclerenchyma occur below both upper and lower surfaces, in some cases in contact with the vascular bundles. Stomata are numerous on the upper epidermis. In *tenuifolia* the cauline lamina has only five to seven ridges, and is poorer in sclerenchyma.

6. *Rhachillæ.*

The lowest rhachilla is subtended by a small bract, whose base encircles the axis, but whose upper part is free and crescent-shaped in section (Fig. 13). It is composed of parenchymatous cells whose somewhat thickened walls are pierced by numerous pits. These cells are continued into the cortex of the axis at the node. At the higher nodes there is no obvious bract, but the cortical cells are developed in the same way.

The morphology of the paired rhachillæ is evident from a study of serial transverse and of longitudinal sections through the node. The bract is a simple structure ; it is present as a slight ridge of tissue around the stem just below the insertion of the paired rhachillæ, highest on the side from which these are given off, lowest on the opposite side. It does not suggest any fusion, so that there is every reason to believe that it subtends a single primary branch, which is the larger of the pair of rhachillæ. From this is given off almost immediately a weaker secondary branch, the smaller member of the pair. There is no trace of a bracteole.

This view is supported by tracing the various vascular bundles from the axis below the node into the rhachillæ. The vascular

Fig. 14. Subvar. *tenuifolia*, dwarfed seedling. × $\frac{3}{4}$.

system of the axis divides into two distinct groups of bundles ; the larger group remains in the axis whilst the smaller group belongs to the primary branch. This latter, slightly higher up, resolves itself into six distinct bundles which appear as two groups of three, one group of which consists of larger bundles and passes up the primary branch axis, the other group of smaller bundles belonging to the secondary branch. Thus the vascular system of the secondary branch joins up with that of the primary forming a single group which takes its place in the main axis.

V.—TEMPORARY MODIFICATIONS

The effect of certain types of habitat is seen in modifications of external form and internal structure which are of a temporary nature, and there is a reversion to normal when the plant is transferred to normal conditions.

Specimens of *tenuifolia* collected from scanty soil on exposed rocks have proved difficult to identify until transferred to the garden and their subsequent growth observed. They show a peculiar stunted growth, a kind of nanism, induced by the extreme xerophytic conditions under which they grow (Fig. 14). The leaves are shorter and more fleshy ; the laminæ stand out from the axis and gently curve upwards. The base of the shoot is stouter and the plant more densely cæspitose. The panicle is reduced to a few small spikelets. These modifications are the result of a very exposed situation, extreme dryness of habitat, and probably also halophytic influence. Similar modifications, though not quite so marked, are seen in the plants which grow on the scantier soil of the pebble-ridges, where great extremes of moisture and temperature on and near the surface must be encountered.

VI. SUMMARY.

The three forms studied, which have been referred to the subvarieties *grandiflora*, *tenuifolia* and *glaucescens* respectively, are quite stable, distinct in both vegetative and floral characters, and in choice of habitat.

The first form corresponds with *Festuca rubra*, var. 1 *genuina*, subvar *β. grandiflora* (Hack). Its general habitat is a more or less mesophytic one and its morphological and anatomical characters are practically those of a mesophyte, though with certain xerophytic tendencies. It possesses fairly long, creeping rhizomes and is loosely sub-cæspitose; well fitted for producing a rich carpet of vegetation. It has a well developed root-system and its dark green leaves are perfectly glabrous. Its panicle is loose and well-developed, and the spikelets are large.

The second form also belongs to the variety *genuina* (Hack) and is entitled to rank as a new subvariety; it is given the subvarietal name *tenuifolia.* It is capable of growing under the most extreme xerophytic conditions and is generally associated with halophytic conditions. Its morphological and anatomical structure support the view that it is certainly a xerophyte, and under the influence of salt water it shows certain halophytic tendencies. It is fairly densely cæspitose; its rhizomes are short and more or less curved and ascending from the base. The leaves are slender and dark glaucous green, having a "bloom." The panicle is more compact than in *grandiflora*; the internodes rough; the spikelets fewer, but the individual glumes large and as numerous as in *grandiflora,* with shorter awns. This new form is of special interest because it appears to be peculiar to certain habitats.

The third form also comes under Hackel's variety *genuina* and probably corresponds to subvar. *glaucescens* Hack. Its main points of difference are the yellowish-green colour of its leaves, the perfectly glabrous sheaths, and the size of the panicle, with fewer spikelets, and fewer glumes with longer awns than in the other two subvarieties. It is distinctly violaceous and hispidulous with a "bloom."

I am indebted to Professor Trow for drawing my attention to these grasses and placing his garden material at my disposal: to Mr. G. Claridge Druce for kindly examing specimens and confirming my determinations; and to Mr. R. S. Adamson for helpful criticism of the manuscript.

BIBLIOGRAPHY.

1. Babington. Manual of British Botany, Ed. VIII, p. 440.
2. Boswell-Syme. Sowerby's English Botany XI, Gramina, 1872.
3. Druce, G. C. Hayward's Botanists' Pocket Book, 1914.
4. Fries, E. Novitiæ Floræ Suecicæ, Mant. III, p. 6.
5. Grenier and Godron. Flore de France III, 1856 pp. 572, 574.
6. Haberlandt, G. Physiological Plant Anatomy, Eng. Trans. by Drummond, 1914.
7. Hackel, E. Monographia Festucarum europæarum, 1882.
8. Koch. Synopsis Floræ Germanicæ et Helveticæ, Ed. iii, pp. 705-6.
9. Lewton-Brain, L. On the Anatomy of the Leaves of British Grasses, Trans. Linn. Soc., London, 2nd Ser. Botany, Vol. VI, Pt. 7., Feb., 1904.
10. Massee, G. Diseases of Cultivated Plants and Trees, 1910.
11. Townsend. Flora of Hampshire, 1883.
12. Trow, A. H. Flora of Glamorgan, Vol. I, 1911 p. 181.
13. Watson. Cybele Britannica III, 1882.
14. White, J. W. Flora of Bristol, 1912.

A PHÆNOLOGICAL STUDY.

By Francis Darwin.

IN the Spring of 1917 I was struck by the fact that *Ranunculus Ficaria* did not flower until April 1st, whereas the average date according to Blomefield[1] is February 28th: the earliest recorded date being January 21st, and the latest March 28th.[2] It seemed worth while to follow up the observation and the following pages give a record of the flowering dates of the commoner plants near Brookthorpe, Gloucestershire, for the years 1917, 1918 and 1919.

I have only recorded one of the elements which make up the environment and which may influence the date of flowering:—namely the temperatures. These are taken from the *Weekly Weather Report of the Meteorological Office:* and I have taken the temperatures at Clifton as probably giving those for the neighbourhood of Gloucester with fair accuracy. I have not only given the actual temperatures, but what is more important:—the weekly " deviations from the normal."

Table 1. Clifton, 1917.

Week ending.	Mean Temp. °F.	Deviation from Normal.	Week ending.	Mean Temp. °F.	Deviation from Normal.
1 Jan. 6	46·4	+6·9	27 July 7	59 3	– 2·6
2 ,, 13	37·9	—1·4	28 ,, 14	65·4	—1·8
3 ,, 20	33·7	- 5·6	29 ,, 21	63·3	+0·7
4 ., 27	30·3	—9·0	30* ,, 28	63·8	+3·5
5 Feb. 3	29·3	—10·3	31 Aug. 4	60·0	- 2·5
6 ,, 10	26·5	—13·5	32 ,, 11	62·8	+0·6
7 ,, 17	34·2	– 5·9	33 ,, 18	62·2	+0·4
8 ,, 24	41·5	+1·3	34 ,, 25	61·3	+0·2
9 Mar. 3	41·8	+0·9	35 Sept. 1	57·1	--2·8
10 ,, 10	35·4	—5·9	36 ,, 8	60·6	+1·5
11 ,, 17	43·0	+0·4	37 ,, 15	59·3	+1·1
12 ,, 24	39·2	—3·5	38 ,, 22	58·9	+2·2
13 ,, 31	39·4	—5·0	39 ,, 29	57·3	+2·4
14 Apr 7	37·8	--8·1	40 Oct. 6	54·0	+1·1
15 ,, 14	39·7	—6·8	41 ,, 13	47·8	—3·4
16 ,, 21	46·0	—1·8	42 ,, 20	45·9	—4·0
17 ,, 28	50 9	+1·4	43 ,, 27	46·6	—1·1
18 May 5	56·7	+6·2	44 Nov. 3	46·1	—1.0
19 ,, 12	54·6	+2·4	45 ,, 10	47·1	+1·2
20 ,, 19	54·2	+0·4	46 ,, 17	43·4	0·0
21 ,, 26	60·5	+5·4	47 ,, 24	50·7	+5·4
22 June 2	58·9	+1·7	48 Dec. 1	47·7	+4·7
23 ,, 9	60·7	+2·5	49 ,, 8	39·2	--2·8
24 ,, 16	65·2	+7·2	50 ,, 15	40·0	– 1·8
25 ,, 23	61·7	+2·1	51 ,, 22	32·1	—8·7
26 ,, 30	56·5	—4·9	52 ,, 29	35·9	—4·4

* Hereford.

---

[1] *A Naturalist's Calendar* by Leonard Blomefield (formerly Jenyns), edited by Francis Darwin, Cambridge University Press, 1903.

[2] My results for 1917 were published in the *Proceedings of the Cotteswold Nat. Field Club*, Vol. XX, Pt. i, 1918.

TABLE 2. CLIFTON, 1918.

Week ending.	Mean Temp. °F.	Deviation from Normal.	Week ending.	Mean Temp. °F.	Deviation from Normal.
1 Jan. 5	34·1	–5·6	27 July 6	63·8	+1·9
2 ,, 12	36·5	–2·5	28* ,, 13	58·1	–1·9
3 ,, 19	39·6	—0·1	29* ,, 20	60·3	—0·4
4 ,, 26	50·1	+9·8	30 ,, 27	60·2	—2·0
5 Feb. 2	44·6	+3·9	31 Aug. 3	64·1	+1·6
6 ,, 9	48·5	+8·1	32 ,, 10	62·7	+0·5
7 ,, 16	46·7	+6·2	33 ,, 17	62·9	+1·1
8 ,, 23	40·9	+0·7	34 ,, 24	64·0	+2·9
9 Mar. 2	40·9	0·0	35 ,, 31	58·3	–1·6
10 ,, 9	39·0	—2·3	36 Sept. 7	58·9	—0·2
11 ,, 16	45·1	+2·5	37 ,, 14	55·5	—2·7
12 ,, 23	47·0	+4·3	38 ,, 21	58·1	+1·4
13 ,, 30	46·3	+1·9	39 ,, 28	53·2	–1·7
14 Apr. 6	46·1	+0·2	40 Oct. 5	48·9	—4·0
15 ,, 13	46·8	+0·3	41 ,, 12	52·0	+0·8
16 ,, 20	40·1	—7·7	42 ,, 19	46·5	–3·4
17 ,, 27	49·6	+0·1	43 ,, 26	47·7	—0·2
18 May 4	49·9	—0·6	44 Nov. 2	52·0	+4·5
19 ,, 11	54·2	+2·0	45 ,, 9	45·5	—1·0
20 ,, 18	57·3	+3·5	46 ,, 16	43·3	—0·8
21 ,, 25	62·4	+7·3	47 ,, 23	38·7	—4·4
22 June 1	60·9	+3·7	48 ,, 30	46·6	+3·6
23 ,, 8	61·0	+2·8	49 Dec. 7	51·7	+9·7
24 ,, 15	56·5	—1·5	50 ,, 14	49·8	+8·0
25 ,, 22	55·3	—4·3	51 ,, 21	44·5	+3·7
26 ,, 29	57·0	–4·4	52 ,, 28	42·0	+1·7

* Hereford.

TABLE 3. CLIFTON, 1919.

Week ending.	Mean Temp. °F.	Deviation from Normal.	Week ending.	Mean Temp. °F.	Deviation from Normal.
1 Jan. 4	39·1	+2·8	21 May 24	57·7	+2·6
2 ,, 11	40·4	+1·4	22 ,, 31	60·0	+2·8
3 ,, 18	43·0	+3·8	23 June 7	60·6	+2·4
4 ,, 25	37·3	—3·0	24 ,, 14	61·0	+3·0
5 Feb. 1	33·6	—7·1	25 ,, 21	58·2	—1·4
6 ,, 8	32·8	—7·6	26 ,, 28	55·9	—5·5
7 ,, 15	31·8	—8·7	27 July 5	54·2	—7·7
8 ,, 22	40·7	+0·5	28 ,, 12	59·9	—2·3
9 Mar. 1	38·7	—2·2	29 ,, 19	60·3	—2·3
10 ,, 8	42·5	+1·2	30 ,, 26	59·6	—2·6
11 ,, 15	42·6	0·0	31 Aug. 2	60·9	—1·6
12 ,, 22	38·2	—4·5	32 ,, 9	63·6	+1·4
13 ,, 29	36·2	—8·2	33 ,, 16	68·0	+6·2
14 Apr. 5	39·6	—6·3	34 ,, 23	63·3	+2·2
15 ,, 12	47·6	+1·1	35 ,, 30	57·9	—2·0
16 ,, 19	47·8	0·0	36 Sept. 6	59·6	+0·5
17 ,, 26	46·5	—3·0	37 ,, 13	63·3	+5·1
18 May 3	45·4	—5·1	38 ,, 20	55·5	—1·2
19 ,, 10	53·3	+1·1	39 ,, 27	52·0	—2·9
20 ,, 17	58·6	+4·8	40 Oct. 4	48·5	–4·4

1917. Of the 16 weeks up to April 21st, 1917 (No. 26 in 1919 curve), only three showed a temperature above the normal, and all the 1917 plants were markedly later than the corresponding species for 1919, and still more markedly later than 1918. It will be noted that the Spring temperatures for 1919 are below normal, and on the whole only slightly above those of 1917; so that the lateness of the Spring flowers in 1917 in comparison with 1919 seems hardly explicable by temperature difference.

Between the flowering dates of 1917 and 1918 the difference is much more striking. This is clearly shown on the curves. That for 1917 (×) running through April and May, while the 1918 (+) record shows the same species flowering in January, February and March, and one in April. Here the differences between the flowering dates agree with the differences between the 1917 and 1918 temperatures. The 1919 curve (·) shows a few flowerings in January, none in February, a few in March, and a considerable number of April readings. In fact a general inspection of the 1919 curve from January to the end of April shows clearly that it is intermediate between the curve of 1918, in which the flowerings are (on the whole) early, and that of 1917. But it must be repeated that the difference in temperature between the Spring of 1919 and that of 1917 is not nearly as obvious as is the difference in flowering dates.

The May readings of 1917 are obviously late, and not till No. 42 (*Acer Pseudoplatanus*) do we find a case in which the flowering date (May 9) is the same as that for 1919. And not till No. 51 (*Ajuga reptans*) is the 1917 date earlier than in 1919. This is only a temporary difference, and the 1917 readings are equal to, or more commonly later, than 1919 dates up to No. 73 (*Vicia sativa*), May 23. Taking the later 1919 readings in May, from No. 75 to No. 95, we find the 1917 readings still markedly later than in 1919. One plant, No. 76 (*Asperula odorata*), flowers earlier in 1917, and two or three are synchronous with 1919. But the general result is:—the 1919 plants flowering near the end of May, and 1917 scattered through June; and this in spite of the temperature of 1917 being above the normal from the end of April to nearly the end of June. In the same way the 1917 dates for the plants flowering early in June, 1919, are on the whole later.[1]

From No. 130 to 149 the cases in which the 1917 flowerings are earlier than, or equal to, those of 1919 become more frequent, *e.g.*, 135, 139, 140, 141, 142, 143, which are all equal to the 1919

---

[1] Except for Nos. 101, 109, 120, 125, 129, 130.

readings, while Nos. 147, 148, 149, of 1917 are earlier than the 1919 readings. And for the 23 weeks ending June 9th, 1917, and also for the 24th and 25th weeks, the 1917 temperatures are markedly higher than the corresponding weeks in 1919.

The general result for 1917 from No. 150 to the end of the curve is that the flowerings are somewhat later than in 1919, but afterwards become equal to or earlier than the readings for the last named year. And this in spite of the cold weather in 1917 from June 30th to July 14th.

1918. With regard to 1918 the general impression is that for Nos. 1 to 5, inclusive, the 1919 flowerings are earlier than those of 1918. And the 1918 temperature deviations for the first three weeks of the year are—5·6,[1]—2·5,—0·1; the same period for 1919 showing + deviations. But from No. 6 onwards the 1918 flowerings are clearly earlier than those of 1919. And the 1919 temperatures from the week ending January 25, to that ending February 15, are markedly below normal, the corresponding temperatures for 1918 being strikingly above the average. The higher temperature for 1918 (except for a fortnight of normal temperatures, or slightly below normal, in March) continued until the middle of April, the corresponding temperatures for 1919 being markedly lower. The flowering dates for May, 1918, are only slightly earlier than in 1919, while the corresponding temperatures are roughly identical.

The 1918 flowerings in the middle of June are later than those of the same plants in 1919, when the 1918 temperatures are below, and those of 1919 above, normal. The 1918 plants flowering towards the end of June are on the whole later than those of 1919, but this does not seem explicable as a result of temperature.

In the middle and end of July occurs a period when the 1918 plants flowered earlier than those of 1919. The temperatures were at this period often below the normal in 1918 and in 1919, though more strikingly so in 1919.

1919. It is unnecessary to enter into detail on the 1919 flowerings, which are intermediate between those of 1917 and 1918. But since, in the graphic representation of the dates of flowering, the continuous line of the 1919 flowerings serves as a standard of comparisons with the scattered readings of 1917 and 1918, I have thought it best to give some details which are not given for the

---

[1] That is as above explained 5·6 below normal.

other years. I have compared the flowering dates of 100 plants in 1919 (some at the beginning of the year and others in the summer) with Blomefield's dates for these species. In the early part of the year, out of 45 dates, 15 are earlier and 30 are later than Blomefield's dates. Of the 55 readings from June onwards 33 are earlier, and 22 later than Blomefield's. Thus out of 100 readings 48 of my flowerings are earlier than his, and 52 are later. In other words my results for 1919 are broadly speaking the same as Blomefield's.

Alphabetical List of Plants whose first flowering is recorded in the following charts. The numbers refer to the order in which the species appear in the charts (pp. 296-298). The date of flowering in each of the three years, 1917, 1918, 1919 is also given.

No.	Species.	Date of first flowering.		
		1917.	1918.	1919.
75	Acer campestre		May 5	May 24
42	,, Pseudo-Platanus	May 6	,, 9	,, 9
164	Achillea millefolium	July 7	July 8	June 26
19	Adoxa moschatellina		Mar. 16	April 8
117	Ægopodium podagraria...		June 6	June 7
192	Æthusa cynapium	July 17	July 2	July 12
166	Agrimonia Eupatoria	June 27	,, 3	June 27
	Agropyrum caninum		,, 10	
177	,, repens			July 4
215	Agrostis alba		July 7	,, 24
51	Ajuga reptans	May 7	April 28	May 14
	Alchemilla vulgaris	,, 21		
220	Alisma Plantago			July 27
37	Alliaria officinalis	May 14	April 8	May 6
53	Allium ursinum	,, 16	May 10	,, 14
	Alnus glutinosa ♀		Feb. 18	
63	Alopecurus pratensis		May 9	May 17
185	Anagallis arvensis		July 2	July 8
22	Anemone nemorosa		Mar. 26	April 10
225	Angelica sylvestris			July 31
212	Anthemis arvensis		July 2	,, 23
54	Anthoxanthum odoratum		May 9	May 15
74	Anthriscus cerefolium			,, 23
172	Anthyllis vulneraria	July 11	June 6	June 30
201	Apium nodiflorum	,, 18	July 7	July 14
208	Arctium Lappa	,, 19		,, 20
124	Arrhenatherum avenaceum			June 8
33	Arum maculatum	May 10		April 28
173	Asperula cynanchica			June 30
76	,, odorata	May 15	May 17	May 24
106	Avena pratensis		,, 29	June 2

No.	Species.	Date of first flowering.		
		1917.	1918	1919.
87	Barbarea vulgaris			May 27
191	Bartsia Odontites	July 17	July 12	July 11
5	Bellis perennis	April 4	Jan. 20	Jan. 8
228	Brachypodium pinnatum		June 24	Aug. 9
115	Briza media	June 11	,, 6	June 6
81	Bromus arvensis			May 26
209	,, asper		July 16	July 22
	,, erectus		June 24	
213	,, giganteus		July 12	July 24
	Bromus racemosus[1]		May 21	
92	Bryonia dioica ♂	June 9	,, 30	May 28
70	Bunium (Conopodium) flexuosum		,, 15	May 20
202	Butomus umbellatus			July 14
183	Calamintha Clinopodium	July 6	July 9	,, 7
21	Caltha palustris	April 22		April 9
	Campanula glomerata	Aug. 21	June 19	
189	,, rotundifolia	July 6	July 9	July 10
200	,, trachelium	,, 17	,, 11	,, 13
82	Cardamine amara			May 26
10	,, hirsuta			Mar. 18
17	,, pratensis	May 2	Mar. 17	April 7
	Carduus acanthoides		July 11	
180	,, acaulis	July 7	,, 8	July 4
169	,, arvensis	June 27	June 30	June 27
203	,, lanceolatus		July 16	July 15
126	,, palustris	June 14	May 31	June 9
49	Carex pendula ♂	May 22	,, 4	May 12
40	,, ,, ♀			May 9
227	Carlina vulgaris			Aug. 4
205	Caucalis Anthriscus		July 5	July 17
135	Centaurea nigra	June 17	June 6	June 19
142	,, Scabiosa	,, 21	June 29	,, 21
61	Cerastium vulgatum		May 18	May 16
38	Chœrophyllum sylvestre (Anthriscus sylvestris)	May 18	April 16	,, 6
97	Chœrophyllum temulum		May 29	June 1
217	Chenopodium ficifolium			July 26
89	Chrysanthemum Leucanthemum	May 30	May 22	May 28
12	Chrysosplenium oppositifolium		Mar. 17	April 4
146	Circœa lutetiana	June 26	June 17	June 22
193	Clematis vitalba	July 10	July 10	July 12
149	Convolvulus arvensis	June 18	,, 2	June 22
178	,, sepium	,, 27	,, 11	July 4
129	Cornus sanguinea	,, 6	June 2	June 10
8	Corylus Avellana		Jan. 23	Mar. 15
67	Cratœgus Oxyacantha	May 18	May 1	May 18
	Cynosurus cristatus		June 13	
96	Dactylis glomerata	June 10	,, 3	June 1
206	Daucus Carota	July 11	July 12	July 18
160[2]	Digraphis arundinacea		,, 6	June 24
181	Epilobium hirsutum		,, 6	July 6
107	,, montanum	June 12	May 28	June 3
190	,, parviflorum		June 30	July 10
	Erigeron acris	Aug. 11		
88	Euonymus europœus	June 6	May 17	May 28
210	Eupatorium cannabinum	Aug. 19	July 13	July 23
223	Euphrasia officinalis	,, 3		,, 28
128	Festuca ovina			June 10
16	Fragaria vesca	April 21	Mar. 16	April 6
26	Fraxinus excelsior ♀		April 14	,, 21
	Galeopsis Tetrahit		July 11	
90	Galium aparine	June 4	May 23	May 28
139	,, mollugo	,, 13		June 20

[1] A form of *B. arvensis.* [2] see also 134.

No.	Species.	Date of first flowering.		
		1917.	1918.	1919.
144	Galium verum	,, 21	June 29	,, 21
125	Genista tinctoria	,, 14	,, 11	,, 9
231	Gentiana Amarella	Aug. 20		Aug. 28
150	Geranium dissectum			June 22
161	,, pratense			,, 25
56	,, robertianum	May 12	May 10	May 15
71	Geum urbanum	,, 28	,, 14	,, 21
224	Habenaria viridis...	Aug. 11		July 28
100	Helianthemum vulgare	June 12	June 4	June 2
69	Heracelum Sphondylium		May 11	May 20
105	Hieracium Pilosella		June 10	June 2
133	Holcuslaurtus			June 19
152	Hordeum pratense		July 2	,, 22
155	Hypericum hirsutum	June 27	June 20	,, 23
	,, perforatum		July 9	
182	,, quadrangulum		,, 14	July 6
95	Hypochæris radicata		May 27	May 29
219	Inula Conyza	Aug. 3		July 27
211	,, Dysenterica...	July 29		,, 23
	Iris Pseudacorus		May 30	
154	Lactuca muralis			June 23
24	Lamium album	May 10	Feb. 16	April 15[1]
44	,, Galeobdolon	,, 11	April 10	May 10
34	,, maculatum			,, 2
3	,, purpureum	April 17	Jan. 22	Jan. 1 (Dec. 19)
140	Lapsana communis	June 18	June 16	June 20
130	Lathyrus pratensis	,, 8	,, 17	,, 12
	Leontodon hispidus	May 31		
114	Ligustrum vulgare			June 6
64	Linaria Cymbalaria	June 12	May 16	May 18
113	Linum catharticum	,, 8	,, 25	June 6
	Listera ovata	,, 12		
	Lolium italicum		June 13	
119	,, perenne		,, 10	June 7[2]
145	Lonicera Periclymenum			June 21
65	Lotus corniculatus		May 22	May 18
36	Luzula campestris ♂		Mar. 25	May 4
	,, ,, ♀			April 15
43	Lychnis diurna		April 28	May 9
78	,, Flos-cuculi	May 31	May 18	,, 25
123	,, vespertina		,, 29	June 8
176	Lysimachia nummularia	July 5	July 7	July 2
141	Malva moschata	June 21	June 29	June 21
170	,, sylvestris			,, 27
147	Matricaria Chamomilla	June 12	July 10	,, 22
195	Medicago sativa			July 12
77	Melica uniflora			May 24
229	Mentha aquatica	Aug. 8		Aug. 12
218	,, arvensis			July 26
6A	Mercurialis perennis		Feb. 4	Mar. 14
85	Milium effusum			May 27
	Myosotis arvensis	May 12		
	Nasturtium officinale		May 31	
23	Nepeta Glechoma	May 2	Mar. 21	April 12
132	Œnanthe crocata	June 18		June 13
102	Onobrychis sativa	July 3	June 6	,, 2
214	Ononis arvensis	,, 1	July 5	July 24
179	,, spinosa			,, 4
	Ophrys apifera	July 11	July 16	
	Orchis latifolia	June 25	May 24	
98	,, maculata	,, 11	,, 24	June 2

[1] Date of main flowering: a few plants flowered in Dec. 1918. See No. 2.

[2] See also No. 131, full flower June 13, 1919.

No.	Species.	Date of first flowering.		
		1917.	1918.	1919.
98	Orchis mascula	May 16	,, 4	
57	,, morio	,, 23		May 15
153	,, pyramidalis	June 21	June 13	June 22
199	Origanum vulgare	July 17	July 16	July 13
31	Oxalis Acetosella		Mar. 16	April 22
143	Papaver Rhœas	June 21	July 2	June 21
186	Parietaria officinalis	July 12	,, 6	July 14
52	Paris quadrifolia		April 27	May 3
196	Pastinaca sativa	July 7		July 18
39	Pedicularis sylvatica	May 6	May 24	May 7
171	Phleum pratense			June 29
41	Plantago lanceolata	May 12	April 14	May 9
35	,, ,, ♀			May 3
138	,, major	July 13	July 5	June 20
104	,, media	June 6	May 22	,, 2
110	Poa (Glyceria) fluitans		,, 30	,, 5
	,, trivialis		June 8	
79	Polygala vulgaris	June 12	May 21	May 25
216	Polygonum aviculare			July 24
	,, Bistorta	June 8		
108	Potentilla anserina		May 27	June 4
127	,, reptans	June 18	June 13	,, 10
86	,, Tormentilea	,, 25	May 10	May 27
72	Poterium Sanguisorba ♂	June 8	May 17	,, 22
	,, ,, ♂		,, 10	
20	Primula acaulis		Mar. 24	April 9
136	Prunella vulgaris			June 19
32	Prunus communis	May 3	,, 23	April 23
68	Pyrus aucuparia			May 19
	Quercus Robur		April 30	
60	Ranunculus acris	May 16	May 13	May 16
50	,, aquatilis			,, 12
158	,, arvensis	June 3		Jnne 24
45	,, auricomus (f. depauperatus)	May 10	April 12	May 10
48	,, bulbosus	,, 13	,, 28	,, 11
6	,, Ficaria	April 1	Feb. 10	Mar. 13
55	,, repens		May 10	May 15
	,, sceleratus		June 20	
165	Reseda luteola	July 27		June 26
109	Rhinanthus Crista-Galli	May 31	May 20	,, 5
	Rosa sp.	June 11	,, 21	
184	,, arvensis			July 7
111	,, canina			June 6
91	Rubus cœsius	May 28	May 21	May 28
188	,, fruticosus	June 22	June 24	July 10
118	,, ,, [1]			June 7
80	Rumex acetosa ♂	May 29	May 21	
80	,, ,, ♀		May 27	May 25
167	,, crispus *var.* elongatus			June 27
84	,, obtusifolius	June 10		May 26
18	,, cinerea *var.* aquatica ♂	April 19		April 7
25	,, ,, ,, ,, ♀			April 17
94	Sambucus nigra	?June 10	May 21	May 29
93	Sanicula europœa		,, 16	,, 28
162	Scabiosa arvensis	July 1		June 25
197	,, Columbaria	,, 7	July 16	July 13
230	,, succisa			Aug. 17
27	Scilla nutans	May 11	April 15	April 22
99	Scrophularia aquatica			June 2
	,, nodosa	June 7	May 29	
	Sedum album	July 11	July 1	
137	,, acre			June 19
156	Senecio erucœfolius			June 23
204	,, Jacobœa	July 11	July 14	,, 15

[1] A form with small leaves, white flowers and glandular flower stalks.

No.	Species.	Date of first flowering. 1917.	 1918.	 1919.
204	Sherardia arvensis		May 10	
163	Silene inflata			June 26
222	Sison Amomum			July 28
112	Solanum Dulcamara	June 6	May 27	June 6
159	Sonchus oleraceus	,, 21		,, 24
148	Spiræa Ulmaria	,, 17	June 5	,, 22
207	Stachys Betonica	July 11	July 13	July 18
157	,, germanica			June 24
116	,, sylvatica	May 30	June 2	,, 6
29	Stellaria Holostea	,, 11	April 14	April 22
11	,, media			Mar. 23
103	Tamus communis	June 6	May 28	June 2
7	Taraxacum Dens-leonis	April 25	Jan. 22	Mar. 15
15	Taxus baccata ♂		Mar. 8	April 5
174	Thymus Serpyleum	June 12	June 24	June 30
187	Tilia europœa	July 2	,, 30	July 9
121	Tragopogon pratense			June 8
66	Trifolium agrarium		May 17	May 18
221	,, fragiferum			July 27
62	,, pratense	May 12	May 14	May 16
122	,, repens	June 13	June 8	June 8
13	Tussilago Farfara		Mar. 13	April 5
9	Ulmus montana			Mar. 16
101	Urtica dioica ♂	June 5	May 25	June 2
175	,, ,, ♀	June —	May —	June 30
198	Verbascum nigrum	July 7		July 13
226	,, Thapsus			Aug. 1
	Verbena officinalis	July 25		
4	Veronica agrestis		Mar. 26	Jan. 1 (Dec. 26)
83	,, Beccabunga	May 29	May 17	May 26
28	,, Buxbaumii			April 22
46	,, Chamœdrys	May 12	April 29	May 10
	,, montana		May 13	
58	,, serpyllifolia		,, 9	May 15
168	Vicia cracca		July 7	June 27
73	,, sativa	June 3		May 23
59	,, sepium	May 12	April 30	,, 15
30	Viola canina			April 22
1	,, odorata		Mar. 13	Jan. 1
14	,, ,, (white)			(about Dec. 5) April 5
47	,, tricolor			May 10

The chronological charts on the following pages show the species whose first flowerings were noted in 1919, arranged in the order of their appearance in that year. The time of appearance in each month being indicated by a dot. The times of first flowering of the same species in 1917 and 1918 are indicated by × and + respectively.

× First flowering 1917 + First flowering 1918 • First flowering 1919

1919			No.	Jan.	Feb.	Mar.	Apl.	May	June
Jan.	1	*Viola odorata abt Dec. 5 (1918)*	1	•		+			
	1	*Lamium album Dec. 19 (1918)*	2	•	+			×	
	1	*Lamium purpureum Dec. 19 (1918)*	3	• +			×		
	1	*Veronica agrestis Dec. 26 (1918)*	4	•		+			
	8	*Bellis perennis*	5	• +			×		
Mar.	13	*Ranunculus Ficaria*	6		+	•	×		
	14	*Mercurialis perennis*	6*a*		+	•			
	15	*Taraxacum Dens-leonis*	7	+		•	×		
	15	*Corylus Avellana*	8	+		•			
	16	*Ulmus montana*	9			•			
	18	*Cardamine hirsuta*	10			•			
	23	*Stellaria media*	11			•			
Apl.	4	*Chrysosplenium oppositifolium*	12			+	•		
	5	*Tussilago Farfara*	13			+	•		
	5	*Viola odorata* (*white*)	14				•		
	5	*Taxus baccata* ♂	15			+	•		
	6	*Fragaria vesca*	16			+	• ×		
	7	*Cardamine pratensis*	17			+	•	×	
	7	*Salix cinerea* var. *aquatica* ♂	18				• ×		
	8	*Adoxa Moschatellina*	19			+	•		
	9	*Primula veris*	20			+	•		
	9	*Caltha palustris*	21				• ×		
	10	*Anemone nemorosa*	22			+	•		
	12	*Nepeta Glechoma*	23			+	•	×	
	15	*Lamium album* *	24		+		•	×	
	17	*Salix cinerea* var. *aquatica* ♀	25				•		
	21	*Fraxinus excelsior* ♂	26				+ •		
	22	*Scilla nutans*	27				+ •	×	
	22	*Veronica Buxbaumii*	28				•		
	22	*Stellaria Holostea*	29				+ •	×	
	22	*Viola canina*	30				•		
	22	*Oxalis acetosella*	31			+	•		
	23	*Prunus communis*	32			+	•	×	
	28	*Arum maculatum*	33				•	×	
May	2	*Lamium maculatum*	34					•	
	3	*Plantago lanceolata* ♀	35					•	
	4	*Luzula campestris* ♂ †	36			+		•	
	6	*Alliaria officinalis*	37				+	• ×	
	6	*Chærophyllum sylvestre*	38				+	• ×	
	7	*Pedicularis sylvatica*	39					ו +	
	9	*Carex pendula* ♀	40					•	
	9	*Plantago lanceolata* ♂	41				+	• ×	
	9	*Acer Pseudoplatanus*	42					+ו	
	9	*Lychnis diolca*	43				+	•	
	10	*Lamium Galeobdolon*	44				+	• ×	
	10	*Ranunculus auricomus* ‡	45				+	ו	
	10	*Veronica chamædrys*	46				+	• ×	
	10	*Viola tricolor*	47					•	
	11	*Ranunculus bulbosus*	48				+	ו	
	12	*Carex pendula* ♂	49					+ • ×	
	12	*Ranunculus aquatilis*	50					•	
	14	*Ajuga reptans*	51				+	× •	
	14	*Paris quadrifolia*	52				+	•	
	14	*Allium ursinum*	53					+ • ×	
	15	*Anthoxanthum odoratum*	54					+ •	
	15	*Ranunculus repens*	55					+ •	
	15	*Geranium Robertianum*	56					+ ו	
	15	*Orchis morio*	57					• ×	
	15	*Veronica serpyllifolia*	58					+ •	
	15	*Vicia sepium*	59				+	ו	
	16	*Ranunculus acris*	60					+ ו	
	16	*Cerastium vulgatum*	61					+•	
	16	*Trifolium pratense*	62					+× •	
	17	*Alopecurus pratensis*	63					+ •	
	18	*Linaria cymbalaria*	64					+•	×
	18	*Lotus corniculatus*	65					• +	
	18	*Trifolium agrarium*	66					+•	
	18	*Cratægus oxyacantha*	67					+ ו	
	19	*Pyrus aucuparia*	68					•	
	20	*Heracleum sphondylium*	69					+ •	
	20	*Bunium flexuosum*	70					+ •	
	21	*Geum urbanum*	71					+ • ×	
	22	*Poterium sanguisorba* ♂	72					+ •	×
	23	*Vicia sativa*	73					•	×
	23	*Anthriscus Cerefolium*	74					•	

---

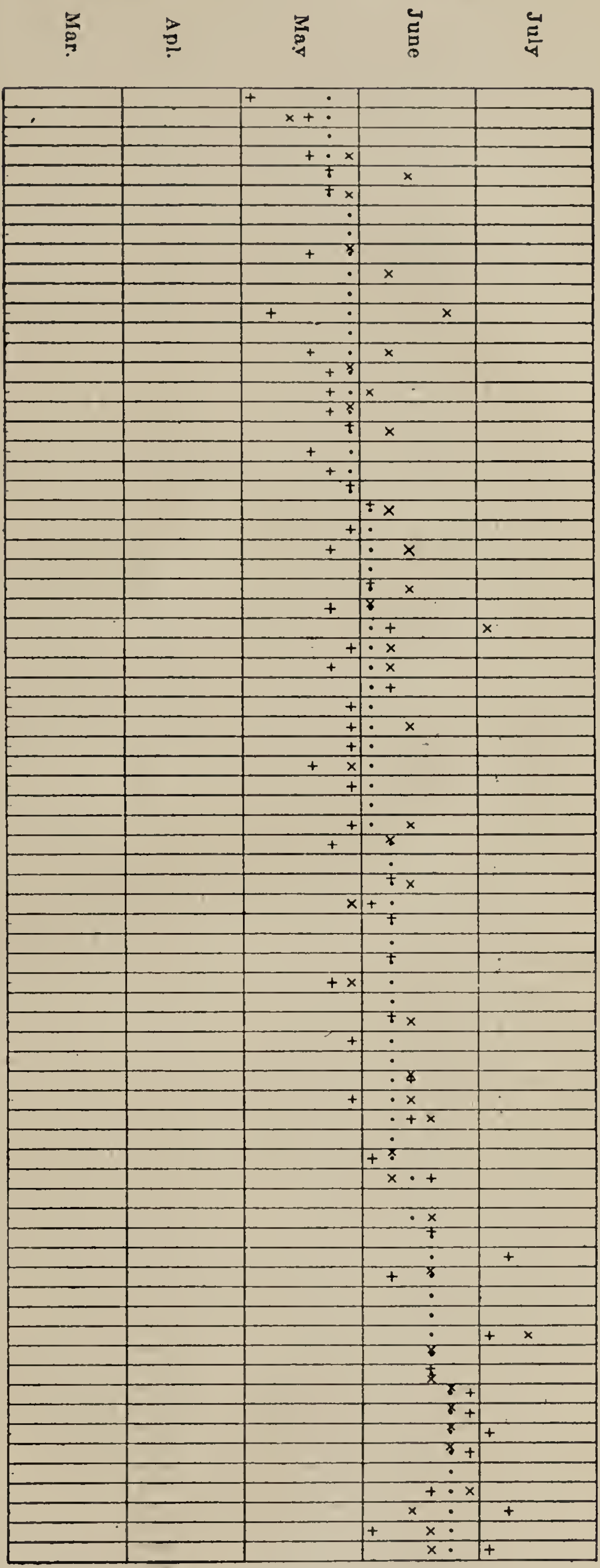
* The date of general flowering, though a few were seen in Dec. 1918.

† *Luzula campestris* ♀ Apl. 15.

‡ The "depauperate" form.

× First flowering 1917 + First flowering 1918 • First flowering 1919

1919			No.
May	24	*Acer campestre*	75
	24	*Asperula odorata*	76
	24	*Melica uniflora*	77
	25	*Lychnis Flos-cuculi*	78
	25	*Polygala vulgaris*	79
	25	*Rumex Acetosa* ♂ and ♀	80
	26	*Bromus arvensis*	81
	26	*Cardamine amara*	82
	26	*Veronica Beccabunga*	83
	26	*Rumex obtusifolius*	84
	27	*Milium effusum*	85
	27	*Potentilla Tormentilla*	86
	27	*Barbarea vulgaris*	87
	28	*Evonymus europæus*	88
	28	*Chrysanthemum Leucanthemum*	89
	28	*Galium aparine*	90
	28	*Rubus cæsius*	91
	28	*Bryonia dioica* ♂	92
	28	*Sanicula europæa*	93
	29	*Sambucus nigra* *	94
	29	*Hypochæris radicata*	95
June	1	*Dactylis glomerata*	96
	1	*Chærophyllum temulum*	97
	2	*Orchis maculata*	98
	2	*Scrophularia aquatica*	99
	2	*Helianthemum vulgare*	100
	2	*Urtica dioica* ♂	101
	2	*Onobrychis sativa*	102
	2	*Tamus communis*	103
	2	*Plantago media*	104
	2	*Hieracium Pilosella*	105
	2	*Avena pratensis*	106
	3	*Epilobium montanum*	107
	4	*Potentilla anserina*	108
	5	*Rhinanthus Crista-galli*	109
	5	*Poa (Glyceria) fluitans*	110
	6	*Rosa canina*	111
	6	*Solanum Dulcamara*	112
	6	*Linum catharticum*	113
	6	*Ligustrum vulgare*	114
	6	*Briza media*	115
	6	*Stachys sylvatica*	116
	7	*Ægopodium podagraria*	117
	7	*Rubus fruticosus* †	118
	7	*Lolium perenne*	119
	8	*Rubus cæsius*	120
	8	*Tragopogon pratense*	121
	8	*Trifolium repens*	122
	8	*Lychnis vespertina*	123
	8	*Arrenatherum avenaceum*	124
	9	*Genista tinctoria*	125
	9	*Carduus palustris*	126
	10	*Potentilla reptans*	127
	10	*Festuca ovina*	128
	10	*Cornus sanguinea*	129
	12	*Lathyrus pratensis*	130
	13	*Lolium perenne* (in full flower) ‡	131
	13	*Œnanthe crocata*	132
	19	*Holcus lanatus*	133
	19	*Digraphis arundinacea* §	134
	19	*Centaurea nigra*	135
	19	*Prunella vulgaris*	136
	19	*Sedum acre*	137
	20	*Plantago major*	138
	20	*Galium mollugo*	139
	20	*Lapsana communis*	140
	21	*Malva moschata*	141
	21	*Centaurea scabiosa*	142
	21	*Papaver Rhœas*	143
	21	*Galium verum*	144
	21	*Lonicera Periclymenum*	145
	22	*Circæa lutetiana*	146
	22	*Matricaria Camomilla*	147
	22	*Spiræa ulmaria*	148
	22	*Convolvulus arvensis*	149



---

* May 29 *Sambucus*. Some deformed flowers mingled with normal ones. Normal flower noted June 6.

† A white-flowered small-leaved form with glandular flower-stalks.

‡ *Lolium perenne* 119 is given in the curve, not 131.

§ Variegated garden form: the wild form is 160.

× First flowering 1917 + First flowering 1918 • First flowering 1919

1919		No.	May	June	July	Aug.
June 22	*Geranium dissectum*	150		•		
22	*Scrophularia aquatica*	151		•		
22	*Hordeum pratense*	152		•	+	
22	*Orchis pyramidalis*	153		+ ו		
23	*Lactuca muralis*	154		•		
23	*Hypericum hirsutum*	155		+ • ×		
23	*Senecio erucæfolius*	156		•		
24	*Stachys germanica*	157		•		
24	*Ranunculus arvensis*	158		× •		
24	*Sonchus oleraceus*	159		ו		
24	*Digraphis arundinacea*	160		•	+	
25	*Geranium pratense*	161		•		
25	*Scabiosa arvensis*	162		•	×	
26	*Silene inflata*	163		•		
26	*Achillea millefolium*	164		•	+ ×	
26	*Reseda luteola*	165		•	×	
27	*Agrimonia Eupatoria*	166		ו	+	
27	*Rumex crispus* var. *elongatus*	167		•		
27	*Vicia cracca*	168		•	+	
27	*Carduus arvensis*	169		+×		
27	*Malva sylvestris*	170		•		
29	*Phleum pratense*	171		•		
30	*Anthyllis vulneraria*	172		+ •	×	
30	*Asperula cynanchica*	173		•		
30	*Thymus Serpyllum*	174		× + •		
30	*Urtica dioica* ♀	175		•		
July 2	*Lysimachia nummularia*	176			ו +	
4	*Agropyrum repens*	177			•	
4	*Convolvulus sepium*	178		×	• +	
4	*Ononis spinosa*	179			•	
4	*Carduus acaulis*	180			• ×+	
6	*Epilobium hirsutum*	181			+•	
6	*Hypericum quadrangulum*	182			• +	
7	*Calamintha clinopodium*	183			+×	
7	*Rosa arvensis*	184			•	
8	*Anagallis arvensis*	185			+ •	
8	*Parietaria officinalis*	186			+• ×	
9	*Tilia europæa*	187		+	× •	
10	*Rubus fruticosus*	188		×+	•	
10	*Campanula rotundifolia*	189			+×	
10	*Epilobium parviflorum*	190		+	•	
11	*Bartsia Odontites*	191			+• ×	
12	*Æthusa cynapium*	192			+ • ×	
12	*Clematis vitalba*	193			×+ •	
12	*Hypericum hirsutum*	194		×+	•	
12	*Medicago sativa*	195			•	
13	*Pastinaca sativa*	196			× •	
13	*Scabiosa Columbaria*	197			× • +	
13	*Verbascum nigrum*	198			× •	
13	*Origanum vulgare*	199			• ×+	
13	*Campanula Trachelium*	200			+• ×	
14	*Apium nodiflorum*	201			+ • ×	
14	*Butomus umbellatus*	202			•	
15	*Carduus lanceolatus*	203			• +	
15	*Senecio Jacobæa*	204			+×	
17	*Caucalis Anthriscus*	205			+ •	
18	*Daucus Carota*	206			×+ •	
18	*Stachys Betonica*	207			×+ •	
20	*Arctium Lappa*	208			ו	
22	*Bromus asper*	209			+ •	
23	*Eupatorium cannabinum*	210			+ •	×
23	*Inula dysenterica*	211			• ×	
23	*Anthemis arvensis*	212			+ •	
24	*Bromus giganteus*	213			+ •	
24	*Ononis arvensis*	214			×+ •	
24	*Agrostis alba*	215			+ •	
24	*Polygonum aviculare*	216			•	
26	*Chenopodium ficifolium*	217			•	
26	*Mentha arvensis*	218			•	
27	*Inula Conyza*	219			•	×
27	*Alisma plantago*	220			•	
27	*Trifolium fragiferum*	221			•	
28	*Sison amomum*	222			•	
28	*Euphrasia officinalis*	223			•	×
28	*Habenaria viridis*	224			•	×
31	*Angelica sylvestris*	225			•	
Aug. 1	*Verbascum Thapsus*	226				•
4	*Carlina vulgaris*	227				•
9	*Brachypodium pinnatum*	228		+		•
12	*Mentha aquatica*	229				× •
17	*Scabiosa succisa*	230				•
28	*Gentiana amarella*	231				× •