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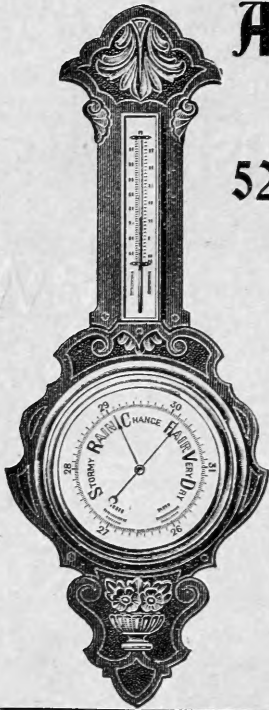
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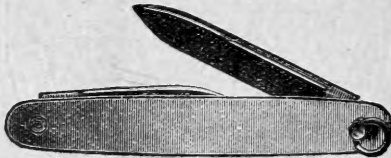
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The Scottish Botanical Review

No. 4]

1912

[OCTOBER

Morphological Notes. By K. von Goebel,
Sc.D. (Camb.), LL.D. (St And.),

Director of the Botanic Garden, Munich.

(With One Plate.)

I. THE INFLORESCENCES OF THE AMBROSIACEÆ.

THE large family of the Compositæ, as is well known, is one of those groups whose individual representatives, in spite of all their variation, still show such a close agreement in the structure of the flowers and the inflorescences that one can offhand recognise them as members of one family. Only a few groups deviate to any great extent, and of these one of the most interesting is the Ambrosiaceæ.

Ecologically they are interesting in the manner in which pollination on the one hand and the distribution of the fruit on the other hand are accomplished among them.

The Compositæ as a rule exhibit insect-pollination, but the Ambrosiaceæ have reverted to wind-pollination.

Hardly any greater contrast can be presented than between the resplendent flower-head of a *Helianthus* or a *Dahlia*, with its remarkable arrangements for dehiscence and for transference of the pollen, and the insignificant male and female floral attire of a *Xanthium* or an *Ambrosia*. There is a clear indication here that, quite apart from the lack of a corolla conspicuous in its coloration, the structure of the floral organs is in strict correlation with their functions. In the

flowers no nectar is formed, there is no "concrecence" (in reality it is only agglutination or sticking together) of the anthers, and the pollen is formed in great quantity, as is the case with other anemophilous flowers. The condition of the exine indicates, however, that originally pollination took place by insects as in other Compositæ.

It is well known that the pollen in entomophilous plants is provided with a spiny or sticky exine, whereas in anemophilous plants the exine of the pollen-grains is smooth and not sticky. The Ambrosiaceæ, so far as I have been able to examine them, still show in the exine the remains of spinose thickenings such as are found in numerous other Compositæ, but these are so reduced that the pollen is no longer adapted for adhering.

The male flowers still show on the rudiment of the stigma a hairiness which recalls the "stigmatic brush" of other Compositæ. In the female flowers, in which the stamens have dwindled without leaving a trace, there is no longer any indication of this stigmatic brush. Thus the Ambrosiaceæ, in contrast to other Compositæ, are retrogressive in structure. On the other hand, it is evident that they have developed new characters not attained by other Compositæ. This is seen more especially in the character of the noteworthy envelopes with which the fruit is enclosed. The fruiting heads of *Xanthium* are well enough known to the wool-grower as the detested "burrs" (Kletten), which by means of their bent hooks attach themselves to the woolly coats of animals, and are so dispersed. We shall see that as regards these fruiting heads the other Ambrosiaceæ have also undergone retrogression in contrast with *Xanthium*.

It is not surprising that such noteworthy plants have repeatedly formed subjects for investigation. So far as the developmental history is concerned, and apart from Payer's¹ contributions, which in the present instance need only be indirectly considered, there are available only the investigations of Rostowzew,² and these I propose in the following to supplement on some points.

¹ Payer, "Traité d'Organogénie comparée de la fleur" (Paris, 1857, p. 638).

² T. Rostowzew, "Die Entwicklung der Blüten und des Blütenstandes bei einigen Arten der Gruppe Ambrosiæ" ("Bibliotheca botanica," 20).

Thus one topic will be the male inflorescence, while another will be the "fruit" of *Ambrosia*.

A. The Male Inflorescences.

As is known, the Ambrosiaceæ are monoecious to this extent, that the male inflorescences occupy the apex of shoots at the base of which are placed the female ones.

The individual flower-heads ("capitula") of *Ambrosia tripartita* are arranged in large numbers indefinitely (botryose) on an elongated axis, which in turn is terminated by a flower-head.

The lateral capitula have this noteworthy characteristic, that the flowers are not placed as usual on the upper (adaxial) side, but on the under side—that is, the side turned away from the primary axis of the whole inflorescence (abaxial). It is natural, at first sight, to ascribe this occurrence to a *torsion* of the flower-stalk. This is indeed the opinion of Rostowzew, who says that the flower-head undergoes a torsion, in that the peduncle grows more rapidly on its upper side than on its lower.

This interpretation in itself does not agree with the developmental history. If one examines the early stages, it is seen that the position of the capitula is "reversed" at a *very early stage*.

The capitula are differentiated from the embryonal tissue as hemispherical primordia. The cells of the primordia on the adaxial (upper) side pass first into the phase of elongation-growth, with the exception of the terminal part (*a*, fig. 1), which develops as the first leaf. On the other hand, the lower side remains embryonal. This is utilised for the development of the growing-point of the capitulum (*b*, fig. 1), except the basal part (nearest the primary axis), which later gives rise to the intercalary meristem in the elongating peduncle of the capitulum.

How shall we interpret this peculiar development? Two different views are obviously possible.

It may be that the first leaf (*a*, fig. 1) arising from the growing-point of the capitulum is the first leaf of the involucre of the capitulum, the individual leaves of which,

united together, form an apparently entire envelope. This is the concept of Rostowzew, which, however, has thus far to be supplemented, that the "torsion of the capitulum"—if one assumes such a thing—is not a subsequent event, but it existed from the first; in other words, it is "congenital." Rostowzew does not mention that if this interpretation be assumed, then the lateral capitula of the *Ambrosia* would present one of the rare cases in which the "bracts" (Deckblätter) of lateral shoots have aborted completely. This occurrence is known in the flowers of the cruciferae, etc., in which one can correlate the abortion of the bracts with excessive crowding originally undergone by the flower-primordia before the elongation of the axis of the inflorescence. In the case of *Ambrosia*, this would be all the more striking because the female inflorescences possess well-developed bracts, although they are quite as closely crowded together as the male ones. In no instance have I observed in the male capitula even a trace of a subtending bract.

The second possibility is that the first leaf (indicated by *a* in fig. 1) is the bract (Deckblatt) of the capitulum. The manner in which (*a*) develops from the primordium that gives rise to (*a*) and (*b*) is similar to what occurs frequently in flowers and inflorescences. In this instance the bract, so to speak, is late in being formed. It does not develop in advance of its axillary shoot, but from a primordium common to both. The thing that surprises one is that the axillary shoot should arise on the under side of the bract, and not, as usual, on the upper side. But, after all, this is no more wonderful than the "congenital torsion" already referred to, nor is it quite without precedent amongst other Dicotyledons. The remarkable flowers of *Erythrochiton hypophyllanthus* are situated on the under side of the leaf; also the axillary branches on the creeping shoots of some of the terrestrial Utriculariæ arise on the side of the leaf furthest away from the growing-point.¹

In other respects it may be assumed that the position of the male capitula of *Ambrosia* means the same thing as the torsion (entirely brought about by their weight) of the male inflorescences of *Corylus*, *Alnus*, *Juglans*, or the torsion of

¹ K. Goebel, *Utricularia* ("Annal. du jardin botan. de Buitenzorg," vii. 1889).

the anther of grasses : by this means the shaking out of the pollen is facilitated in all these anemophilous plants.

Returning now to the morphological question, one might, in arriving at a decision, also take the anatomical facts into account. If (a) (fig. 1) represents the bract of the capitulum, then one might expect that the normal orientation would be shown in the constitution of the vascular bundle, phloem on the lower side, xylem on the upper. Of course, I do not regard the anatomical conditions as decisive, since, in my opinion, these are determined by the morphological, not the reverse. In the present instance this would mean that, in the event of a relatively limited development and retardation in time on the part of the bract in comparison with the axillary shoot, it appears quite natural that the former (the bract) should be provided with its vascular system from the latter (the shoot). This being so, one expects the xylem to be uppermost, with the phloem underneath.

The conditions actually existing are briefly as follows: The thin, much-flattened peduncle of the capitulum contains two vascular bundles (rarely three); the phloem-groups of these are set towards the narrow margins, and the xylems are turned towards one another and somewhat obliquely downwards (fig. 3). This anatomical structure is interesting because unusual in a shoot-axis.

A certain biassed school of anatomists assumes that shoots are distinguished from leaves by their anatomical structure, particularly in the arrangement of the vascular bundles. The shoot of the capitulum of *Ambrosia* does not differ in structure from many leaf-stalks, except that in the latter the xylem of the vascular bundle is directed upwards.

There is little doubt that this anatomical structure is the result of reduction; that is, the peduncle of the primitive type possessed more than two vascular bundles. Linked with these bundles are those which ramify throughout the involucreal leaves and the flower, but I have not followed these in detail. It may be mentioned, however, that the vascular bundles of the involucreal leaves are normally orientated in that their xylem lies towards the growing-point of the capitulum. The orientation is that described above, and for the reasons given it does not seem to me possible to arrive at any definite con-

clusion as to the morphological interpretation of this leaf (*a*) from the anatomical structure.

It might be advanced in opposition to the view that the leaf (*a*) is a bract, that later on it does not always stand opposite the peduncle; this might, however, result from displacement. In the younger stages I saw it in the median position occupying the whole breadth of the inflorescence-primordium (fig. 4). As regards the further development of the male capitula, two facts may be pointed out. Firstly, that the external side (that on which the letter (*a*) is placed) appeared to be much further advanced than the inner side; this is seen at once in fig. 4. Secondly, that the arrangement of the flowers is not "dichasial" sympodial (as one of the recent authors wrongly states), but corresponds essentially with the other Compositæ. One sees quite clearly the broad growing-point of the capitulum (V., fig. 4), from which the individual flowers arise; some of the outer ones have bracts even now. The characteristic arrangement of the flowers is determined by the fact that the capitulum as a whole is dorsiventral in structure, with a more advanced development on the outer side.

B. The Female Inflorescences.

As indicated by Rostowzew, these are dichasially arranged (fig. 5). Each consists of a single flower enclosed by an "envelope" (fig. 8). To understand their constitution it will be necessary to first compare the inflorescences of other *Ambrosiæ*. Here one finds the following series:—

1. Mixed inflorescences with female marginal florets.
2. Inflorescences with sexes distinct, in so far that in the female only the marginal florets flower, and only the minority of these, while in the male inflorescence the formation of female flowers is entirely suppressed.
3. There is also a diversity in the arrangement of the female and male inflorescences. Whereas the arrangement was originally indefinite (botryose), this is retained only in the case of the male inflorescences, the female ones showing dichasial arrangement.¹

¹ With regard to diversity of male and female, compare Goebel, "Ueber sexuellen Dimorphismus bei Pflanzen" ("Biolog. Centralblatt," p. 657, 1910).

In *Xanthium* the male inflorescences are orientated normally; the structure of a young male inflorescence in longitudinal section is shown in fig. 6, I. The female capitulum consists of two flowers enclosed in the many-spined envelope. This envelope originates from the fusion of two bracts (*Sa*, *Sb*, fig. 6, III.) in whose axils the female flowers are placed. With reference to the development, the reader is referred to my recent account.¹ This is noteworthy in this respect, that the two floral bracts entirely monopolise the growing-point of the capitulum (except what is required for the flowers arising in their axils), as is shown in the view from above (fig. 6, IV.), and that the flowers are deeply sunk in the axis of the capitulum.

Comparing this inflorescence with that of *Ambrosia*, it will be found to have undergone still further reduction. Firstly, we see that the spines or barbed hooks outside the envelope are here reduced to a few small processes (figs. 7 and 8, *st*); secondly, each envelope contains only one flower. The processes referred to can no longer be of use in the dispersal of the fruits by animals.² How dispersal is effected can only be ascertained in the native land of the plant. The fruits are relatively light, and float in water for a short time at least, and they may even be rolled to a distance by wind.

It is evident that the envelope of the fruit of *Ambrosia* corresponds to that of *Xanthium*. But is it, like the former, a double one, or is it single? That there is some suggestion of a double envelope is evident by the fact that the apex of the envelope (originally laid down as a closed ring; see fig. 7, right-hand figure) is distinctly two-lobed in the later stages of growth. This indicates that two leaf-primordia take part in the formation of the envelope. Only one of these, however, has an axillary flower-primordium. Obviously a characteristic retrogression has taken place here: the flower monopolises the whole area within the envelope; hence it arises not as a lateral outgrowth on the growing-point of a capitulum, but is terminal. There are, of course, many examples of an organ genetically lateral in origin becoming ultimately terminal. We may cite the spikelets of many

¹ Goebel, *l.c.* ("Biolog. Centralblatt," xxx., 1910, p. 722).

² They might, of course, become lodged between the claws or in the hoof.

grasses, also the carpels which in many flowers monopolise all the residual part of the growing-point of the flower, and the terminal stamen of *Naias*, *Callitriche*, etc. *Ambrosia* is, however, a specially well-marked example of this procedure. The development of the female flower need not be described further, except to point out that there is only a mere trace of the corolla, while the stamens and calyx have disappeared without leaving a trace.

Thus we see that *Ambrosia* has carried still further in its female inflorescence that reduction already indicated in *Xanthium*. Even in *Xanthium* the male organs of the capitulum are completely suppressed and the number of female flowers is reduced to two. As new structures there are present the hook-like spines on the outside of the concrescent floral-bracts, which, taking the place of the pappus originally present, facilitate dispersal of the fruit. In *Ambrosia* these spines dwindle to a few rudiments and the number of flowers diminishes to a single one.

In the male inflorescences, however, the number of capitula is probably increased considerably in comparison with the type-form with hermaphrodite flowers. With this may also be correlated, that these male capitula have departed from the prevailing scheme of development, and as seen in their "reversal" have progressed along new lines. Thus with no great effort, and with a basis of facts admissible in any new speculation, we are able to trace, in what seems to me a satisfactory manner, the historical evolution of the structure of the inflorescences of *Ambrosia*. At the same time, the case dealt with here illustrates once again the phenomenon to which the author has frequently made reference: namely, that our phylogenetic series, so far as we can depict them with any degree of probability, all represent a reduction-series.

The following may be advanced in support of this:—

1. In a descending series we have a definite starting-point (that is, some one of the more completely equipped forms as distinct from the more reduced ones) with which we can compare the less completely equipped members of the series.
2. In many instances the organs in question may still be recognised as rudiments.

3. The descending series arise latest ; hence they are more completely preserved and easier to recognise than the ascending with a history extending much further back, and whose members are as a rule very incompletely preserved.

Descending series of this kind are known to every botanist, since they appear again and again in almost every family. Other facts also indicate that organisms become modified mainly through retrogression and simplification : thus "mutations," for example, are essentially of this nature, since in them there is a loss of some definite characteristic.¹

Has then the "nisus formatoris" of the ancient philosophers itself become antiquated? Not at all ; botany at least has remained youthful. To be convinced of this, one need only glance at what is only possible where youthful aspirations exist, namely, the construction of genealogical trees from below upwards. "Alas, alike in their tenure of life, they are mostly ruins, not of the trees, however, but of the ephemeral day-flies !"

MUNICH, April 1912.

EXPLANATION OF THE FIGURES.

Fig. 1. Longitudinal section through an inflorescence of *Ambrosia tripartita*. V, growing point of the male inflorescence ; the individual capitula (with the exception of the terminal one) are placed laterally on the primary axis. *a*, the first leaf of a male capitulum of which *b* is the growing-point. *Bl*, female flower with its envelope, H.

Fig. 2. *Ambrosia tripartita*. Longitudinal section through an older male capitulum. V, the growing-point.

Fig. 3. Transverse section through the peduncle of a male capitulum of *Ambrosia tripartita*. The xylem in each of the two large conductive bundles is shaded.

Fig. 4. Capitulum of *Ambrosia tripartita* seen from above. Around the growing-point, V, there are seen fifteen embryonal flowers in various stages of development ; the involucre surrounds the whole.

Fig. 5. *Ambrosia tripartita*. Transverse section through a young female inflorescence-group. In the axil of a bract (Deckblatt), D, is a one-flowered female inflorescence, I, with its envelope, H ; this has two

¹ E. Baur, "Einführung in die experimentelle Vererbungslehre" (Berlin, 1911), says : "The large majority of mutations which have been closely investigated depend simply on the loss of some single Mendelian unit character. I have not found, up till now, any absolutely certain case in which one or more unit characters have arisen *de novo*."

prophylls (Vorblätter), V, in the axils of which other inflorescences are present.

Fig. 6, I.-III. *Xanthium spinosum*.

- I. Longitudinal section through a young male inflorescence. B, male flower with its bract, S.
- II. Longitudinal section through a female inflorescence. Sa, Sb, the bracts (Deckblätter) of two flowers, Sa₁, Sb₁, which on the side towards the incurved margins of the bracts are proceeding to develop the floral organs.
- III. Older inflorescence in which each female flower has now the stigma developed, st.
- IV. *Xanthium strumarium*. A young female inflorescence seen from above.

Fig. 7. *Ambrosia tripartita*. On the left a female inflorescence, seen from the outside. st, primordia of the spines which remain rudimentary. H, the envelope (clearly two-partite). Bl, flower-primordium seen through the envelope (which is regarded as transparent). On the right a young inflorescence seen from the outside.

Fig. 8. *Ambrosia tripartita*.

- I. Fruit with its envelope, bisected longitudinally. H, envelope; st, spines; P, pericarp; S, seed-coat (very thin); E, embryo.
- II. Fruit with envelope seen from outside.

Notes on some Mosses from the Three Lothians. By James M^cAndrew,

Assoc. of the Botanical Society of Edinburgh.

PERHAPS the following notes may prove interesting to local and Scottish bryologists. They consist principally of new records of British mosses gathered in the Lothians since the "Census Catalogue of British Mosses" was published in 1907. I am indebted to Mr. William Evans, Edinburgh, for about one-half of them; the others were gathered by myself and from time to time reported to Mr. R. H. Meldrum, and will no doubt in due course appear in the next edition of the "Census Catalogue."

HADDINGTON, v.c. 82. *Sphagnum cymbifolium* Ehrh.; *S. rigidum* Schp.; *Andreaea petrophila* Ehrh.; *And. Rothii* W. and M. (Traprain Law, East Linton); *Polytrichum*

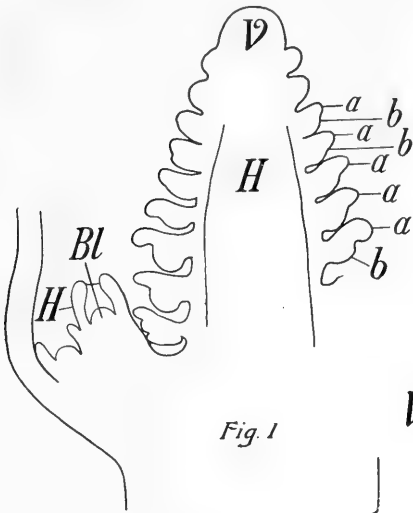


Fig. 1

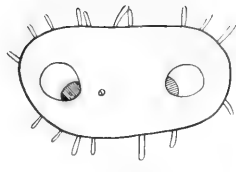


Fig. 3

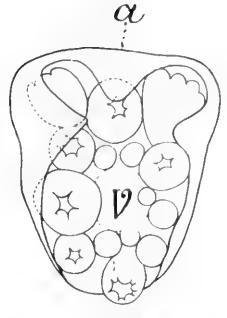


Fig. 4

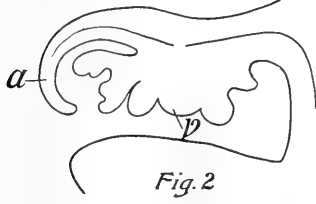


Fig. 2

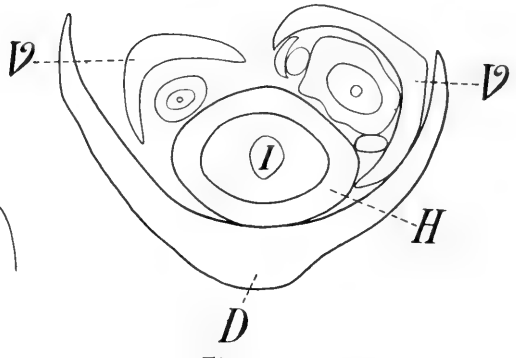


Fig. 5

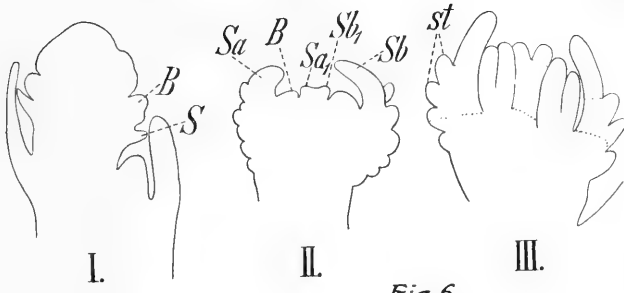


Fig. 6

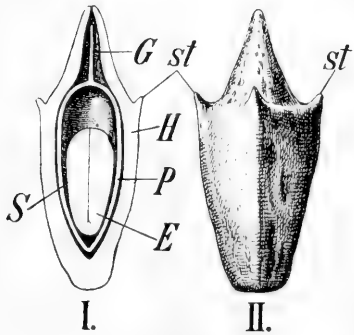
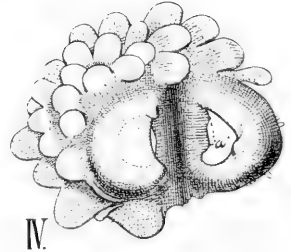


Fig. 8



Fig. 7

urnigerum L. ; *P. alpinum* L. (Traprain Law) ; *P. formosum* Hedw. ; *Pleuridium subulatum* Rabenh. ; *Rhabdoweisia fugax* B. and S. (Traprain Law) ; *Dicranella squarrosa* Schp. ; *Blindia acuta* B. and S. (Traprain Law) ; *Grimmia apocarpa* Hedw., var. *rivularis* W. and M. (East Linton) ; *G. patens* B. and S. (Traprain Law) ; *G. decipiens* Lindb. (Traprain Law—cum fructu) ; *G. montana* B. and S. (Traprain Law) ; *G. Stirtoni* Schp. (Garleton Hills, by W. Evans) ; *Rhacomitrium protensum* Braun (Traprain Law, by W. Evans) ; *R. canescens* Brid., var. *ericoides* B. and S. ; *Hedwigia imberbis* Spruce (Traprain Law) ; *Pottia bryoides* Mitt. (Gosford Bay, by Mr. John Hunter) ; *Barbula fallax* Hedw., var. *brevifolia* Schultz (west of Dunbar) ; *Weisia microstoma* C. M. (Gosford Bay) ; *Cinclidotus fontinaloides* P. Beauv. (river Tyne) ; *Zygodon Mougeotii* B. and S. (Traprain Law) ; *Orthotrichum stramineum* Hornsch. ; *Bartramia pomiformis* Hedw., var. *crispa* B. and S. (Traprain Law) ; *Leptobryum pyriforme* Wils. (W. Evans) ; *Plagiobryum Zierii* Lindb. (Traprain Law) ; *Webera proliger*a Bryhn (W. Evans) ; *Bryum alpinum* Huds., and var. *viride* Husn. (Traprain Law) ; *B. argenteum* L., var. *lanatum* B. and S. (Gullane Links) ; *Mniuni stellare* Reich. (Gullane Links) ; *Pterygophyllum lucens* Brid., and *Heterocladium heteropterum* B. and S. (Traprain Law) ; *Brachythecium salebrosum* B. and S. (Gullane Bay) ; *B. plumosum* B. and S. (East Linton) ; *Plagiothecium pulchellum* B. and S. (Traprain Law) ; *Amblystegium serpens* B. and S., var. *salinum* Carr. (Gullane Links) ; *Hypnum elodes* Spruce ; *H. aduncum* Hedw., var. *paternum* Sanio (all Gullane Links) ; *H. Sendtneri* Schp. (Gullane Links). Regarding this moss Mr. J. A. Wheldon, F.L.S., Liverpool, writes me: "Your plant is typical *H. Sendtneri* Schp. It is new to Haddingtonshire, and as a matter of fact it is the first specimen I have seen from Scotland, although recorded from v.c.'s 86 and 87. I have for years been trying to get a specimen of the inland plant, but without success so far." It grows in a shallow lagoon on Gullane Links, and covers the whole bottom with a mass of several acres exclusively of this moss. *H. fluitans* L. ; *H. cupressiforme* L., var. *filiforme* Brid. ; *H. Patientiæ* Lindb.

Traprain Law, East Linton, has several very interesting mosses such as *Hedwigia imberbis* Spruce; *Grimmia montana* B. and S.; *Grimmia decipiens* Lindb., all three in great abundance, the latter in fruit; *Andreaea Rothii* W. and M.; *Bryum alpinum* Huds. Gullane Links also, like Tents Muir, Sands of Barrie, Dunbarnie Links, etc., have also several rare mosses already recorded as *Ditrichum flexicaule* Hpe., var. *densum* B. and S.; *Swartzia montana* Lindb., and *S. inclinata* Ehrh.; *Barbula Hornschuchiana* Schultz; *Trichostomum flavo-virens* Bruch; *Encalypta rhabdocarpa* Schwæg.; *Amblyodon dealbatus* P. Beauv.; *Meesia trichoides* Spruce; *Catascopium nigratum* Brid.; *Bryum calophyllum* R. Br.; *Amblystegium filicinum* De Not., var. *Whiteheadii* Wheldon; *Hypnum chrysophyllum* Brid.; *H. giganteum* Schp., *Thuidium recognitum* Lindb., etc.

EDINBURGH, v.c. 83. This vice-county has been better searched for mosses than the two adjoining counties, and hence the new records for it are fewer. *Sphagnum cuspidatum* Ehrh. var. *submersum* Schp.; *S. molle* Sull.; *Polytrichum strictum* Banks (all from Bavelaw Moss); *Oligotrichum hercynicum* Lam., recently got in Corstorphine Hill wood, is now extinct; *Fissidens crassipes* Wils. (Colinton Dell); *Barbula Hornschuchiana* Schultz (waste ground north of Donaldson's Hospital); *Physcomitrella patens* B. and S. (Torduff reservoir, by Mr. W. E. Evans. I got this moss in plenty on the dried-up bottom of a lagoon west of S. Queensferry last year); *Bryum argenteum* L., var. *lanatum* B. and S.; *Brachythecium glareosum* B. and S. (Flotterstone Bridge); *Hypnum polygamum* Schp.; *H. aduncum* Hedw., var. *polycarpon* Bland.; *H. fluitans* L., var. *Jeanbernati* Ren., and var. *atlanticum* Ren.; *H. exannulatum* Gümbl., var. *pinnatum* Boul., f. *stenophylloides* Ren., and var. *pinnatum* Boul., f. *gracilescens* Ren.; *H. intermedium* Lindb., var. *tenellum* Roth (= *H. pellucidum* Wils.) (all in Bavelaw Moss); *H. cupressiforme* L., var. *tectorum* Brid.; *H. imponens* Hedw. (Bavelaw Moss). I got this also last year near West Linton in Peeblesshire, v.c. 78.

LINLITHGOW, v.c. 84. *Sphagnum rigidum* Schp., and var. *compactum* Schp.; *S. cymbifolium* Ehrh.; *S. tenellum*

Ehrh.; *S. fimbriatum* Wils.; *S. Girgensohnii* Russ. (all in Drumshoreland Moss); *Pleuridium subulatum* Rabenh.; *P. alternifolium* Rabenh. (N.B. railway embankment); *Cynodontium Bruntoni* B. and S. (Cocklerue); *Fissidens recurvus* Starke; *Barbula lurida* Lindb.; *Barbula Hornschuchiana* Schultz; *Physcomitrella patens* B. and S. (all west of S. Queensferry); *Bartramia ithyphylla* Brid., *Leptobryum pyriforme* Wils. (Kirkliston distillery); *Webera annotina* Schwæg. (Drumshoreland); *Bryum alpinum* Huds. (Cocklerue); *Thuidium recognitum* Lindb. (west of S. Queensferry); *Hypnum riparium* L. (Linlithgow Loch); *H. stellatum* Schreb., var. *protensum* Rohl; *H. exannulatum* Gümb.; *H. cordifolium* Hedw. (Drumshoreland curling pond); *H. loreum* B. and S. (W. Evans).

In the "Census Catalogue of British Mosses" for 1907 there are several mosses which require rediscovery, for their records are old. For instance, the rare *Grimmias* on Arthur's Seat have evidently disappeared. *Grimmia leucophæa* Grev., is the last one of the group I have seen on Arthur's Seat, and I suspect that now it too is extinct. The following among others require refinding:—*Sphagnum Austini* Sull. (v.c. 83); *Bryum Warneum* Bland. (v.c. 82); *Cryphæa heteromalla* Mohr (v.c. 82); *Hypnum eugyrium* Schp. (v.c. 83); *Grimmia orbicularis* Bruch (v.c. 83); *G. anodon* B. and S. (v.c. 83); *G. conferta* Funck (v.c. 83); *G. commutata* Hübn. (v.c. 83); *G. ovata* Schwæg. (v.c.'s 82 and 83); *Antitrichia curtispindula* Brid. (v.c. 83), and several others. *Trichostomum mutabile* Bruch.; *T. inclinatum* Dixon; *T. nitidum* Schp., have yet to be gathered in v.c. 82.

Saxifraga Hirculus, L., in Caithness, and its Distribution in the British Isles. By Arthur Bennett, A.L.S.

MR. G LILLIE has kindly sent me good flowering specimens of the above species which he found growing "in a floating bog about ten yards across each way. It was very shaky,

but there was not much danger of one sinking in it as there was considerable growth of grasses, plants, and mosses." It occurred between Lybster and Loch Rhuard, altitude 430 feet, 58° 22' N. lat., about 1½ miles from the loch. The loch itself afforded *Lobelia Dortmanna* and *Subularia aquatica*, rare plants in the county. As the water from the loch and the stream running into it is discharged into the Loop river, thence to the Little river, and finally into the Thurso river, the plant belongs to the north-west watershed, not to the east.

S. Hirculus is not on record north of West Perth and Kincardine, 57° N. lat.; the extension of range north to Caithness is interesting, though it is a high arctic and northern species.

As a rare species it may be well to summarise its distribution in our Isles.

91. Kincardine. Wet moor on the farm of Jacksburns, Glenbervie. 21.6.1839.—Mr. James Rae. This is the station erroneously given in "Topl. Botany" as "Aberdeen, J. Rae."

87. Perth, W. Madie Moss, above Tillicoultry, c. 2000 feet. Northern side of the Ochils, Clackmannanshire.—Mr. W. Thompson.

83. Edinburgh. On a wet moor between Fala and Stow.—G. J. Blackie. Three miles beyond Blackshiels, Pentland Hills, Midlothian. 11.8.98.—F. C. Crawford sp.

81. Berwick. Moor south of Langton Lees farmhouse, plentiful.—Dr. Johnston, c. 1831; sp. Cardiff Museum!.

78. Peebles. Pentland Hills, source of the Medwin, about 1000 feet. 11.9.1836.—Dr. A. Hunter. J. H. Balfour sp., 19.9.1838.

77. Lanark. Boorland Moss, Walston, Sept. 1850.—G. F. Blackie. No altitude given, but the parish ranges from 660 to 1000 feet alt.

69. Westmoreland. Neathheath Syke, alt. 1800 feet, Sept. 1840.—John Bell. Backhouse in Herbarium, York!.

66. Durham. Wet moor, Inishope, Weardale, 2.8.1885.—J. P. Soutter sp.

65. York, N.W. Sedbergh.—J. Handley, "Yorkshire Naturalist" (1903), p. 408. Cotherstone Fell, 1847.—D. Oliver sp. The actual station is swamps at the junction of

the river Balder with the Black Beck. Discovered here by J. Backhouse, 1810; sp. in York Herbarium.

58. Cheshire. Knutsford Moor, where it was associated with *Andromeda*, *Melampyrum pratense*, *Carex linosa*, *curta*, and *stellulata*;¹ also with *Sium angustifolium*, *Cicuta*, *Potamogeton polygonifolius*, *Carex ampullacea*, *Lastrea spinulosa*, *L. thelypteris*, and *Osmunda regalis*.

The date of its first record here (and for Britain) is 1724, Dill. in Ray, "Syn.," 3rd. ed., p. 355; but the plant had been gathered some time between then and 1696, as in an old volume of coloured impressions of Cheshire plants² the locality is given, and the names are those of the 2nd ed. of the "Synopsis." Specimen sent from here by Mr. Okell of Chester, and figured in "Eng. Botany," t. 1009,³ Aug. 1801. Extinct in 1842. The species did not become extinct here altogether through natural causes, as the following extract will show:—

"Still exists on Knutsford Moor, but is almost destroyed by the rapacity of some individuals who have dug it up for sale in the most remorseless manner."—Dr. J. B. Wood, in "Phytologist," i. (1842), p. 282.

In Ireland in the middle and north-east (*i.e.* in six of Mr. Praeger's divisions), but characterised as very rare.

In Europe it is a species of Arctic Norway to 69° 29' N. lat., Swedish, Finnish, and Russian Lapland, Iceland, along the Siberian coast to Behring's Straits.⁴ The American Arctic coast to Labrador, south to Saskatchewan. E. and W. Greenland, as var. *alpina*, Engler Mon. Warming, "Om Groenlands Vegetation," 1886-7, does not give any height for this, though citing many species up to 4000 feet. It will bear intense cold, as on the island of Kolegew, where "the thermometer never rose above 9° R. in July and August 1841";⁵ there it is common. It also occurs on Spitzbergen and Bear Island.

I am not sure whether the first Scottish record was the

¹ Lord de Tabley, "Fl. Cheshire" (1899), p. 142.

² Perry, "Phyt.," i. (1843), p. 700.

³ This plate is not quoted in the 3rd ed., iv. (1865), t. 550.

⁴ Kjellman, "Vega Expedition" (1882), 263, 302.

⁵ Erman, "Arch. Wiss. Kimde v. Russlandes" (1852), x. 313-16; quoted by Fielden and Geldart, "Trans. Nor. and Norf. N. Soc." (1896), p. 169.

Berwick one in Watson's "Outlines," 1832, or the Blackshields one in the "Edin. Phil. Journal," as I have not access to the latter. It is not given in Dr. Johnston's "Flora of Berwick," ii., 1831.

Along with the Saxifrage there was a form of *Cerastium vulgatum*, L. (*triviale*, Link.), which looked very different from the ordinary form of the species, no doubt induced by the place of growth. Still thinking it might be one of the Swiss forms so found, I sent specimens to Dr. Schinz of Geneva; he referred them to Dr. Keller of Berne. Dr. Keller reports: "They are only a form of *C. cæspitosum*, Gilib.¹ (= *vulgatum*, Wahn.), but the plant ought to be observed. Like all species of *Cerastium*, *cæspitosum* shows a great variation in all parts according to the medium in which it lives." Dr. Keller writes: "*C. vulgatum*, L. (= *glomeratum*, Thuill, *viscosum*, Fr.)," which opens the door to a war of words. One accepts the decision; at the same time, the plant is easily distinguished by the eye. Another addition to the county was growing with it—*Ranunculus scoticus*, Marshall.

A New Japanese Grateloupia. By E. M. Holmes, F.L.S., F.B.S.E.²

(With One Plate.)

AMONGST some marine algæ collected in Japan by Mr. S. Okubo, and brought to me for identification, I noticed one which I was unable to match either at the Kew Herbarium or at South Kensington. Although bearing some resemblance to *Grateloupia filicina*, it differs so much in habit and colour that I have decided to describe it as a new species.

Grateloupia subpectinata, n. sp.—Fronde compressa, plana, ad 15 cm. longa, et 3 mm. lata, pinnatim ramosa, ramis a basi angustiore. longe subuliformibus, inferioribus longioribus, infra medium latere inferiori ramellis brevibus subpectinatis, latere superiori dentibus paucis præditis, ramis supremis simplicibus, brevibus. Color pulchre roseus.

¹ Gilibert, "Fl. Lithuanica," v. (1782), p. 159.

² Read before the Botanical Society of Edinburgh.



Grateloupia subpectinata, nov. sp.

Hab.: Japan, S. Okubo, 1912.

The nearest approach to this species, in the mode of branching, is *Grateloupia Pennatula*, Kuetzing, a native of Cuba ("Tab. Phyc.," vol. xvii., tab. 27, a, b), which has similar ramelli, but both the ramuli and ramelli are lanceolate-linear rather than subuliform, and are much shorter in proportion. The rose colour, so far as I know, is never found in forms of *Grateloupia filicina*, although I have seen many forms referred to this species. The structure, is however, typical of *Grateloupia*, and not of loose texture as in the section *Gloiozenia*, to which a rose-coloured species, *G. acuminata*, from Japan, previously described by me, belongs.

Kenfig Burrows: An Ecological Study. Communicated by M. Y. Orr.¹

KENFIG Burrows forms the southern extremity of a fringe of blown sand which borders the south-west coast of Glamorgan as far as Swansea, a distance of fifteen miles. The breaks in its continuity are brought about by the rivers Avon and Neath. At Kenfig the sand dunes extend inland for over two miles at the broadest part, and occupy an area of approximately 1500 acres. The general drift of the sand is in an easterly direction.

Apart altogether from the biological problems involved, the area is of great historical interest, for a waste of sand now covers what was at one time a prosperous town. A few scattered ruins on the northern dunes are all that remain to mark the site of the castle and buried city of Kenfig. The invasion of the sand since Roman times appears to have been gradual, but, according to tradition, sand storms of considerable magnitude occurred in the fourteenth century. In 1538 ruin had overtaken the town and castle, and both were abandoned to the advancing sand.

Kenfig is now represented by a little hamlet, situated about half a mile from the castle ruins, on a ridge overlooking the sheet of water known as Kenfig Pool. This water occupies the central portion of the landward margin of the dunes. From its eastern shore the ground slopes gradually upwards to the ridge, the height of which, and of the adjacent fixed dunes, varies from ninety to one hundred feet above sea-level. The pool forms the apex of a triangular wedge of fertile land which has not been invaded by the sand to any great extent. No doubt, the pool, owing to its position, forms a natural barrier to the further incursions of the sand. The

¹ Read before the Botanical Society of Edinburgh.

area of this sheet of water is 68 acres, and its greatest depth is 11 feet. The water is fresh and fed by springs on the landward side. It has existed in its present form since 1876, but is of less extent and slightly different outline to the pool of 1814. It was originally a marsh, and its eastern margin is still, in part, characterised by a marsh vegetation. At that time it was drained by a stream which flowed in a northerly direction and emptied itself into Kenfig river. To-day there is no visible outlet, but it is possible that its waters filter through the sand and ultimately enter the river in that way.

Geology, Climate, and Rainfall.

The blown sand rests on the Keuper marls of the Trias formation. Rocks which project here and there through the sand nearly all consist of conglomerate, which is more or less calcareous in composition. The wedge of land which has the pool as its apex is boulder clay resting on Triassic conglomerate, while the southern boundary of the "white" dunes is of like glacial origin. A broad stretch of alluvium marks the northern limit, and an irregular alluvial tract extends from the margin of the pool to within a short distance of the shore. The climate is mild and humid. Owing to the prevalence of warm south-westerly winds the mean January temperature is about 41° F., and it is probable that the resultant mild winters have a modifying effect upon the vegetation. The corresponding July temperature is 62° F. The average annual rainfall, estimated over a number of years, is a little over 33 inches. The wettest months of the year are July to January inclusive. A complete analysis of the soil and sand taken from different stations on the dunes is now being carried out, and a detailed account of soil conditions will be embodied in a future publication. Cattle and horses are pastured on the dunes, and the soil is thus enriched with manure. Molluscan shells are abundant in many of the hollows.

The plant formation which covers this area is a natural one, and presents many interesting biological features. A comprehensive ecological study of its vegetation, on modern lines, is now being undertaken, and it is hoped to extend this investigation so as to include the entire belt of sand dunes from Porthcawl to Swansea. So far, detailed observations have been chiefly confined to the Kenfig district. This communication is, therefore, not intended to be exhaustive, and is merely a brief account of the more salient features of the vegetation.

THE PLANT ASSOCIATIONS.

The three most prominent and well-marked associations in this formation are the following: 1. The association of *Ammophila arenaria*; 2. the association of *Salix repens*; 3. the association of *Pteris aquilina*.

1. The association of *Ammophila arenaria*.—This association is

characteristic of the "shifting" dunes, with the Marram grass as the dominant species. This species occupies the first seaward line of sand hills, the *Agropyretum juncei* (sea couch-grass association) of the Somerset and Lancashire dunes being practically absent in this area. It is worthy of notice that *Elymus arenarius*, which in Norfolk gives rise to low dunes, is entirely absent from this coast. The higher inland dunes, many of them over fifty feet in height, bear on their crests the characteristic tufts of Marram grass. It descends on the leeward slopes and colonises the sandy hollows, and in many of the latter, its rhizomic habit of growth is particularly obvious. As a "sand-binder" it is pre-eminent, and it is interesting to note that in the Charters of Kenfig of 1330 special provision was made for its protection and preservation. *Ammophila* also occurs in abundance on some of the "fixed" dunes.

2. The *Salix repens* association.—*Salix repens* occurs on the "shifting" dunes as a "sand-binder," producing a well-marked association. In the sandy dune valleys it forms a carpet of low-growing scrub, but in the more exposed stations it collects around it the blown sand and gives rise to "hummocks" and small dunes. In the damp hollows it forms a fringe round the marshy ground and the dependent species vary accordingly. *Salix* represents the second stage in succession on the dunes, as *Ammophila* represents the first. In the more open stations of this association Marram grass is the subdominant species. *Salix repens* occurs on the Lancashire dunes, but Moss describes it as a comparatively rare plant on the Somerset sand hills.

3. The *Pteris aquilina* association.—The bracken covers acres of the "fixed" dunes in this area, and its outliers blend with the willow of the preceding association. Its rhizomic habit of growth makes it likewise a successful sand-binder, and it forms the last stage in succession. According to Massart, *Pteris* is entirely absent from, or very rare, on the Belgian dunes. It has here undoubtedly adapted itself to life on the dunes and grows luxuriantly. The fronds are regularly harvested for cattle-bedding. Although it is such an abundant type on the "grey" dunes near Kenfig pool, it is sparsely represented on the adjoining boulder clay. This may be due, in part, to the fact that the latter is under cultivation, or perhaps its absence may be accounted for by the more or less calcareous nature of the clay; the bracken being regarded by some authorities as a calcifuge.

In these three chief associations the subordinate species vary according to the character of the association. The Marram grass association is essentially an open one, and on the seaward side of the first range of "mobile" dunes it is an almost pure association. As a result of this open character, competition among the associated species is reduced to a minimum. The *Salix repens* association is of a less open nature. The habit of growth of the *Salix* affords protection from blowing sand, and excessive insolation, to the types which it shelters. At the same time, a certain amount of humus is

present, especially in damper stations. On the embryonic dunes formed by this species few associated plants occur, principally on account of the more exposed situation. These hummocks are subjected to frequent denudation by the wind, and their bases commonly present a weathered appearance. In the fixed dune association where *Pteris* is the dominant plant, the amount of shade cast by its fronds is relatively greater, and the dependent species are mostly grasses, *Agrostis* sp., etc. These three dominant species are rhizomic in habit, and are specially adapted to hold their own under apparently unsuitable edaphic conditions.

Extent and Distribution of these Associations.

The Marram grass association extends inland as far as Kenfig Pool, where its outlying stations dovetail with those of the *Salix* association. This latter covers a broad area on the alluvium on the seaward side of the pool, and extends laterally on its flanks. It gradually loses its identity in the bracken association of the fixed dunes. Distributed throughout these chief associations are minor associations which are of local occurrence. *Rubus caesius*, the dew-berry, for instance, forms a community of this description. This species occurs in certain situations on the dunes, and represents, with *Pteris* and *Salix*, the last stages in succession. Sometimes associated with it is a hybrid form of *Rubus* which gives rise to hummocks. In addition to these principal associations many sub-associations and plant societies exist. These will be described at a later stage.

The term "plant association" implies a plant community, and it therefore follows that the dominant types, mentioned above, have associated with them species which may be regarded as subdominant, abundant, or occasional, according to the frequency of their occurrence. Some species are apparently always associated with a particular dominant, but on the dunes there are many cosmopolitan types which are not limited in their distribution to any one association. A list of subordinate species occurring in any one plant community does not therefore imply that they are characteristic of that association alone, or that they do not occur as frequently in any other association. The majority of associated species colonise the sheltered "flats" and dune valleys which wind in all directions among the high dunes. The configuration of these valleys is varied, and some are characterised by a flora quite distinct in composition from that of a neighbouring depression. Some are marsh-like in character, while others are undulating plains of blown sand, with embryonic dunes in various stages of formation. The species which occupy the dry hollows are psammophilous, although some, like *Cnicus arvensis*, which frequently occurs, are as characteristic of other formations. On the fixed dunes sward-forming plants and others are associated with *Pteris* and *Anemophila*, while many species of moss form patches

of bright green colour everywhere, and are particularly obvious during the early spring.

The following detailed description of the associations is not intended to be exhaustive. Many problems arising out of the distribution of the dependent species in this formation have yet to be solved, and the listing of associated types is but a step on the way to their complete elucidation. No sharp line can be drawn between two associations, and it is often difficult to determine whether a certain species belongs to one association or to another.

In the Kenfig sand-dune area the *Salix repens* association is of a transitional type. In its more open stations on the mobile dunes the majority of its subordinate species are those of the Marram grass association. Towards its inner limit, fixation of the sand is complete, and the included species are those of the fixed dunes.

Before enumerating the species which are found in the chief associations, it is necessary to call attention to the plants which occupy the foreshore, above high-water mark. These plants are usually included in the sand-dune formation, although, as a rule, they are more of a halophilous nature. This association of strand plants is not well developed on this part of the coast; only a few species occurring here and there. The following are the commoner species: *Cakile maritima*, Scop.; *Arenaria peploides*, Linn.; *Salsola Kali*, Linn.

Marram Grass Association.

In the "flats" and sheltered hollows among the "shifting" dunes the following species occur:—

DOMINANT SPECIES.

Ammophila arenaria, Link.

ABUNDANT SPECIES.

| | |
|--|--------------------------------------|
| <i>Erodium cicutarium</i> , L'Hérit. | <i>Euphorbia Paralias</i> , Linn. |
| <i>Anaphalis margaritacea</i> , B. & H. fil. | <i>Euphorbia portlandica</i> , Linn. |
| <i>Senecio Jacobæa</i> , Linn. | <i>Iris fetidissima</i> , Linn. |
| <i>Cnicus arvensis</i> , Hoffm. | <i>Carex arenaria</i> , Linn. |

FREQUENT OR OCCASIONAL SPECIES.

| | |
|--|---------------------------------------|
| <i>Erigeron acre</i> , Linn. | <i>Cynoglossum officinale</i> , Linn. |
| <i>Taraxacum erythrospermum</i> , Andrz. | <i>Verbascum Thapsus</i> , Linn. |
| | <i>Verbena officinalis</i> , Linn. |

The variety *glandulosum*, Bosch., of *Erodium cicutarium* has been recorded from this district. *Anaphalis margaritacea* is well established on the dunes, and apparently succeeds best where competition is reduced to a minimum. *Cnicus arvensis* colonises the sandy hollows

towards the inner limit of the mobile dunes. It is also abundant on the fixed dunes, as in Norfolk. *Euphorbia portlandica* is absent from the Somerset sand hills.

Salix repens Association.

As already mentioned, this association includes within its limits plants of the mobile dunes, as well as those of the fixed dunes. The following species occur:—

DOMINANT SPECIES.

Salix repens, Linn.

SUBDOMINANT SPECIES.

Rubus cæsius, Linn.

Ammophila arenaria, Linn.

FREQUENT SPECIES.

Viola ericetorum, Schrad.

Leontodon (nudicaule), B. & S.

Viola Curtisii, Forster.

Euphorbia Paralias, Linn.

Erodium circuitarium, L'Hérit.

Iris fetidissima, Linn.

Rosa spinosissima, Linn.

Carex arenaria, Linn.

Erigeron acre, Linn.

Phleum arenarium, Linn.

Cnicus arvensis, Hoffm.

Viola Curtisii was recorded from the sand dunes near Aberavon, over sixty years ago. It is not found in Somerset. The damp sandy hollows which occur within the limits of the *Salix* association possess a characteristic vegetation. These depressions lie at a low level, and during the winter months are frequently submerged. A layer of humus is formed in places, and in conjunction with an increased water content produce a plant society of a definite type. The *Salix* forms a fringe round the margin of these hollows, which are colonised by the following species:—

Samolus Valerandi, Linn.

Littorella uniflora, Aschers.

Erigeron canadense, Linn.

Helleborine longifolia, R. & B.

Hydrocotyle vulgaris, Linn.

Orchis incarnata, Linn.

Anagallis tenella, Murr.

Juncus effusus, Linn.

Blackstonia perfoliata, Huds.

Equisetum palustre, Linn.

Mentha aquatica, var. *hirsuta*
(Huds.).

The occurrence of these species in the different hollows depends upon the relative amount of moisture present. Practically pure societies of one particular species are not uncommon.

Kenfig Pool is situated within the limits of the *Salix* association, and its general features have already been described. On its sandy margin the vegetation met with is mainly that of the damp hollows. A sheltered bay on its landward side is rich in species, and the

vegetation here and there is of the marsh type. On the opposite shore, which is exposed to frequent sand-blasts from the adjoining dunes, very few plants occur. Space does not permit of a detailed description of the flora and its distribution, but the following list of commoner species will suffice to indicate its character and composition :—

| | |
|---|---------------------------------------|
| <i>Ranunculus peltatus</i> , Schrank. | <i>Polygonum amphibium</i> , Linn. |
| <i>Castalia alba</i> , Wood. | <i>Rumex Hydrolapathum</i> , Huds. |
| <i>Hydrocotyle vulgaris</i> , Linn. | <i>Iris fœtidissima</i> , Linn. |
| <i>Menyanthes trifoliata</i> , Linn. | <i>Alisma ranunculoides</i> , Linn. |
| <i>Scutellaria galericulata</i> , Linn. | <i>Eleocharis palustris</i> , R. & S. |
| <i>Scutellaria minor</i> , Huds. | <i>Carex leporina</i> , Linn. |
| <i>Littorella uniflora</i> , Aschers. | <i>Carex Goodenowii</i> , Gay. |

Limosella aquatica, var. *tenuifolia*, Lej., was recorded as occurring in great quantities on the sandy shores of the pool in 1898, but it has not been observed in this locality since 1908. Trees are practically absent from the mobile dunes. On the northern limit of the fixed dunes sand plantations occur, while the alder grows freely on the banks of Kenfig river, and follows its course for a considerable distance on the alluvium. Stunted, wind-pruned specimens of *Sambucus nigra* are met with here and there on the "shifting" dunes, usually in somewhat exposed situations. *Hippophæ rhamnoides*, which forms a dense scrub on the Norfolk dunes, and is also reported by Moss as frequent on the Somerset sand hills, does not occur.

Vegetation of the Fixed Dunes.

The transition from the associations of the "mobile" dunes to those of the "fixed" dunes is gradual. Fixation by *Salix*, *Rubus*, and sward-forming plants, like *Festuca rubra*, begins in the more sheltered hollows, near the inner limit of the shifting dunes. In the more exposed stations the Marram grass still holds its own, and on the dune grassland, where *Pteris* is absent, it remains a dominant type. Where dune grassland gives place to cultivated land, bush vegetation and trees form a final barrier to the invasion of the sand.

Pteris aquilina Association.

In the more open stations of this association the following species occur, in addition to many of those already mentioned :—

| | |
|---|---|
| <i>Erophila verna</i> , E. Meyer. | <i>Saxifraga tridactylites</i> , Linn. |
| <i>Cerastium semidecandrum</i> , Linn. | <i>Carduus nutans</i> , Linn. |
| <i>Cerastium tetrandrum</i> , Curt. | <i>Sedum acre</i> , Linn. |
| <i>Stellaria apetala</i> , Ucria. | <i>Lycopsis arvensis</i> , Linn. |
| <i>Sagina nodosa</i> , Frenzl. | <i>Myosotis collina</i> , Hoffm. |
| <i>Vicia angustifolia</i> , Linn. | <i>Koeleria gracilis</i> , Pers. |
| | <i>Festuca rubra</i> , Linn. and its different maritime forms. |

On those fixed dunes, from which *Pteris* is absent, *Ammophila* is almost a dominant type, and the association is a closed one. Many of the included plants are those of cultivated land. In addition to some of the species already mentioned as occurring in the bracken association, the following are abundantly represented :—

| | |
|------------------------------------|--------------------------------------|
| <i>Geranium molle</i> , Linn. | <i>Leontodon nudicaule</i> , B. & S. |
| <i>Galium saxatile</i> , Linn. | <i>Rumex Acetosella</i> , Linn. |
| <i>Bellis perennis</i> , Linn. | <i>Urtica dioica</i> , Linn. |
| <i>Cnicus lanceolatus</i> , Willd. | <i>Luzula campestris</i> , D. C. |
| <i>Cnicus arvensis</i> , Hoffm. | |

On the innermost margin of these fixed dunes *Ulex europæus* is occasionally met with. Mosses and lichens are common here, and in the transitional associations. They play an important part in preparing the ground for the growth of flowering plants. Here and there on these fixed dunes limited areas have been enclosed and are now under cultivation. It is impossible at this preliminary stage in the study of the vegetation of this formation to form any opinions on its composition and distribution which will be of lasting value. The particular area which forms the subject of this communication is too restricted in extent, in any case, for generalised deductions. The mere listing of species included in the different associations is but the initial stage in any ecological study. Were these lists complete, much would yet remain to be done. Critical forms must be made the subjects of careful investigation. A thorough investigation of the dependent species and their habit of life must be undertaken, to determine the relationship existing between them and the dominant type, in the association in which they occur.

The powers of adaptation and adjustment to environment of the individual plants, and many other kindred problems, still await solution.

The Past History of Monocotyledons, with Remarks on their Origin. By A. R. Horwood.

(With Two Plates.)

(Continued from p. 180.)

4. THEORIES AS TO THE ORIGIN OF MONOCOTYLEDONS.

There have been many theories as to the origin of monocotyledons. They may be regarded as (i.) systematic, (ii.) morphological and embryological in character.

According to the former evidence monocotyledons are generally

regarded as the more primitive and dicotyledons as derived from them.

As an exponent of this view we may select the classification of Engler with some modifications, and follow the generalisations of Dr. Rendle,¹ whose conclusions must largely be based upon the vast and unequalled collections of dried specimens in the National Herbarium, supplemented by a knowledge of the living forms represented in the Royal Botanic Gardens at Kew.

Dr. A. B. Rendle² adopts Engler's view that Pandanales are the most primitive. The flower of *Typha* recalls the gymnospermic strobiloid flowers. They are held to represent developments from a common ancestor along different lines.

Helobieæ are next in order, and *Najas* is the most primitive, with micro- and mega-sporangia, axial in origin. Glumifloræ have flowers typically naked, and "correlated with this is the suggestion that the group represents a primitive and not a reduced type of monocotyledons, which have developed on their own lines." It is said to "suggest a derivation from an earlier, more strictly aquatic group," and "that it was the first group to become established upon the drier land surface."

In regard to Spadicifloræ, similarity of seed-structure serves to unite palms and aroids here. Dr. Rendle thinks they may represent a further development of Pandanales.

Lemnaceæ are a reduced type of Aroideæ, whose huge herb type is an adaptation to a hot, moist climate, and an outcome of this is the epiphytic form, whose origin may be traced in *Philodendron*. Assuming Glumifloræ to be primitive, the higher types follow on from them.

Farinosæ (including Restiaceæ, Eriocaulaceæ, Commelinaceæ, Pontederiaceæ, Bromeliaceæ) are limited in range and highly specialised. The Restiaceæ suggest a glumiflorous type, adapted to dry conditions which Glumifloræ in many points appear to confirm. The Eriocaulaceæ and other families are also highly specialised.

The Liliifloræ include Juncaceæ, which appear to be derived from Glumifloræ. Liliaceæ are closely related to them. Iridaceæ, however, appear to exhibit reduction. In these and in the Liliaceæ and Amaryllidaceæ there is a marked development of corms and bulbs, and the plants are adapted to land areas not occupied by a mesophyte vegetation.

In aloes and yuccas we find an increase in stem by secondary growth to meet xerophytic conditions on a larger scale; the leaves also are larger and more numerous. In *Smilax* both leaf and flower structure are adapted to a climbing habit.

The Scitamineæ are derived from some of the Liliifloræ. *Musa* is the most primitive, and all are adapted in their herbaceous characters to a moist climate.

¹ "The Classification of Flowering Plants," 1904, p. 378 *et seq.*

² *Ibid.*

Amongst Microspermæ the Burmanniaceæ exhibit an affinity with Liliifloræ.

Thus far we have reviewed the results attained by the study of the systematist. Let us see what morphology and embryology, with some ecological facts, have to tell us.

The opinion expressed by Schimper and Schenk in their text-book of Palæobotany¹ largely coincides with the decision arrived at by some of those who have based their researches upon the facts of morphology or embryology. They consider that dicotyledons are the older race. They remark upon the late appearance of monocotyledons and their rare occurrence as fossils. They consider the stem-structure proves that monocotyledons are the higher group. It is pointed out that the dicotylous type of stem-structure is found in fossil vascular Cryptogams and Gymnosperms. The simple floral structure is thought to point to a group in process of evolution.

Dr. W. C. Worsdell² holds the view that dicotyledons are derived from monocotyledons, that the cotyledon is always terminal, and that the stem-structure is not due to reduction but is primitive. He regards the fruiting stem and petiole as alone able to unfold the true ontogeny of the individual whereby the stages in the race-history may be made out. Dr. Worsdell's latest view is that monocotyledons and dicotyledons are variants of one form and that there is only *one* cotyledon. He has found a similar stem-structure of scattered bundles in about thirty orders of dicotyledons, and considers the dicotylar vascular system derived from the monocotylous. Many other characters also are correlated with it.

In Jungermanniæ (*cf.* Pl. II. fig. 3, part i. p. 180) the seta is derived from the two epibasal quadrants, and it is considered that the cotyledon is homologous with it, and terminal. It arises before other organs, bearing out the sporogonial or phyton theory of the plant, but not the lateral appendage view. If their development is similar, then the single cotyledon has dichotomised to form two; and the plumule is then lateral to both cotyledons, and between the two. And the bifid cotyledon is primarily terminal. "The actual ontogenetically terminal position of the plumules is a secondary adaptation," and in some plants, *e.g.* in palms, "it becomes enclosed in the basal sheathing petiole of a single tubular cotyledon, which is terminal to the hypocotyl."

In the moss the seta is terminal. If we regard the cotyledon as homologous and the monocotylous embryo an index of the history of the leafy angiosperm, we have a succession of shoots arising, the second like the first, and so on, till a terminal apex or growing point is formed upon the axis thus produced by sympodial arrangement. This monopodial axis with apparent lateral appendages is purely illusory, and "we need to entirely amend our artificial conception

¹ 1891, p. 348.

² *Vide* "A Study of the Vascular System in certain Orders of the Ranales," "Ann. Bot.," Oct. 1908, p. 651 *et seqq.*

of the leaf as a purely lateral appendage to an axis. We are misled all along the line into believing these secondary modifications to be the original types" (Pl. III. fig. 1).

From the embryonic segmentation and the dominant cotyledons the usual view as to the appendicular nature of the leaf is wrong. The plant is built up of a number of individuals (phytons) by "anaphytosis," or sympodial arrangement. On this view monocotyledons are the older. Angiospermous plants may be placed in one of two categories according to their habit, viz. :—

Grandifoliate plants (monocotylous), stem subsidiary, with bundle-system like that of the leaf, reduced internodes, leaves dominant, closely succeeding, with wide sheathing base; e.g. palms, water-lilies.

Parvifoliate (dicotylous), stem dominant, bundle-system differing from that of the leaf, elongated internodes, small leaves, unsheathed bases; e.g. elm, wall-flower.

The grandifoliate is the more primitive, and is due to the precocious assertion of the axis, displacing the terminal cotyledon, which is constantly repeated and gives rise to the short internodes.

Dr. Worsdell points out in regard to the fusion or abortion of one cotyledon to account for the deviation of the monocotylous from the dicotylar type, that in no instance has a monocotylous plant been found to develop a bifid cotyledon or two cotyledons. On the other hand, the converse is found where amongst dicotyledons one is found.

This is held to be a *reversion*. Bifurcation of cotyledons is common, and the polycotyledonary form seems to be the direction evolution is taking.

Thus we come to the novel view recently promulgated by Dr. Worsdell as follows: "Hence I hold that the presence of two cotyledons in dicotyledons is merely an illusive appearance. There is only one cotyledon, as in monocotyledons; this has become so deeply bifurcated in the great majority of cases as to give the appearance of two distinct leaves."

The sympodial arrangement of the stem and leaves is a recapitulation of that of the seedling monocotyledon, and as such lends support to their relatively primitive character.

In regard to the ancestry of Angiosperms generally, Dr. Worsdell remarks :—

"I feel more and more inclined to hold the view that Angiosperms have developed directly from an ancestor belonging to the Bryophyte level, and that they have not come from either Gymnosperms, Pteridosperms, or Ferns. On the other hand, it is quite possible that they have descended from a fern-like ancestor."

The tendency of Dr. Worsdell's view is thus largely in the direction of the point reached by Celakovsky and Bower.

Ontogeny does not always visibly repeat phylogeny. In seedling structure some stages are omitted, and there is no room for scattered bundles. The adult, however, should include all previous stages.

Leaves retain their primitive character longer than stems which carry all the organs.

The stem is parvifoliolate in Umbelliferæ, the leaves grandifoliolate. If the monocotylous type be derived from dicotylar forms, the stem would not remain the same and leaves become grandifoliolate; but if dicotylous forms are derived from monocotylous, the stem might become parvifoliolate and the leaves remain grandifoliolate and stem become parvifoliolate. Scattered bundles are found in the stem of Umbelliferæ, and it is not truly parvifoliolate.

In Ranunculaceæ the flower is primitive and the habit grandifoliolate. They have evidently not been derived from a woody parvifoliolate type; nor are Nymphæaceæ—said to retain their grandifoliolate habit owing to adaptation to an aquatic habit, for that induces reduction and concentrated bundles, to form a compact mass in the centre of the stem. Indeed, they retain their habit although aquatic. Berberidaceæ, Calycanthaceæ, Magnoliaceæ possess primitive flowers, sheathing leaf-bases, and retain something of the grandifoliolate habit. The bundles are amphivasal where scattered—a character common to both groups of Angiosperms.

Miss Ethel Sargent holds the view that both monocotyledons and dicotyledons are monophyletic. The absence of a cambium is said to be due to reduction. The stem-structure of Liliaceæ is regarded as primitive, e.g. in *Anemarrhena*, with its bisymmetrical structure: the last stage in the fusion of the cotyledons. Other groups of Liliifloræ exhibit the same type. Comparison with pseudomonocotyledons and with *Eranthis* and *Podophyllum*, the latter arrested on its way to become a monocotyledon, confirms this. The correlation of this feature with the geophilous habit suggests that it is the cause of the fusion of the two cotyledons to form one, which is regarded as a necessary economy by reduction of material expended in assimilating tissue, owing to the short growing season of such plants as Alpine, bulbous, and tuberous plants. In such plants the leaves are crowded, giving rise to concentric or scattered bundles. Linear leaves assist in elongation. Short-lived roots characterise lowland plants habituated to a short growing season. Albuminous seeds are found in dicotyledonous geophytes. Thus Miss Sargent holds the view that the monocotylous forms are reduced owing to a geophytic habit.

Darwin, in his "Movements of Plants,"¹ says: "We may infer that there is some close connection between the reduced size of one or both cotyledons and the formation, by the enlargement of the hypocotyl or of the radicle, of a so-called bulb."

Pseudomonocotyledons are geophytes as well as many monocotyledons, and thus the common habit is taken to be the cause of the single cotyledon.

As to the possession of a cambium, Queva has found this in second-year tubers of *Gloriosa superba*, from which he regards dicotyledons

¹ 1880, p. 97.

as the older group. Professor Jeffrey finds cambial activity in monocotyledonous seedlings in their third period when they become ascending axes, and considers they are derived from dicotyledons by adaptation to an amphibious habit.

The single cotyledon is terminal, but, if derived from dicotyledons, is thought to be only apparently terminal, really lateral. In *Delphinium nudicaule* (see Pl. III. figs. 2 and 3) at eight weeks the cotyledon is terminal, but at fourteen weeks the plumule is. In *Alisma* (Pl. III. fig. 4, A), *Tamus communis* (*ibid.*, 4, D), and the pseudomonocotyledon *Corydalis cava* (*ibid.*, 4, B, C) the cotyledon is formed before the plumule and is terminal; but when the plumule is developed the cotyledon is forced to one side. This is explained as due to the early formation of the plumule, or to the partial union of one margin only, as in *Ranunculus ficaria*.

The other characters, parallel venation of leaf, short duration of primary root, albuminous seeds, trimerous symmetry—except the last—are regarded as adaptations to mode of life.

Miss Sargent reviews the theory of Professor Henslow. This is based largely on the great number of aquatic monocotyledonous orders. He considers monocotyledons are derived from dicotyledons by suppression of one cotyledon, due to their aquatic habit. But aquatics and geophytes have characters in common. Vascular structure is reduced by an aquatic habit. Parallel venation is found only in aquatic monocotyledons. Tufted roots are found in aquatic monocotyledons and dicotyledons. Aquatic dicotyledons do not tend to become monocotylous nor produce albuminous seeds. The floral structure is not uniform, and may be derived from an ancestor between Ranales and Liliifloræ. Probably aquatic monocotyledons were not primitive but driven by severe competition on land to the water, where conditions are more uniform. Aquatic conditions tend to modify vegetative organs, but not the flower. This is because it is a physiological phase.

Geophytes can adapt themselves either to an aquatic or a climbing habit. Arboreal monocotyledons are not aquatic, but possess anomalous thickening rings as in *Aloe*, *Dracæna*, etc. Palms, again, recall the characters of geophilous plants, being semi-bulbous.

Of phylogenetic schemes, which embrace the other characters, e.g. parallel venation, trimerous floral structure, ephemeral primary root, albuminous seeds, etc., there is Professor Lyon's theory of the origin of dicotyledons from monocotyledons by fission of one to form two cotyledons, of use to the cotyledon in forcing itself from the seed. Agardh first proposed the alternative theory, but only applied it to a few monocotyledons.

Professor G. Henslow extended this theory, deriving monocotyledons from dicotyledons by suppression of the one cotyledon due to the aquatic habit. This is based to a great extent on the large proportion (33 per cent.) of aquatic orders. Miss Sargent regards monocotyledons as a decadent race driven to an aquatic habit to

escape competition. The arrest of the cotyledon is found to be confined to one aquatic dicotyledon. The others are geophilous. The sheathing leaf-base is common to both groups, and is correlated with suppression of internodes. The absence of a cambium and substitution of concentric rings of growth may be due to the number of broad-based leaves inserted on a short axis in the case of underground aquatics, e.g. *Nymphæa*.

In *Peperomia* Mr. A. W. Hill found one cotyledon, but there were probably originally two, and one is hypogeal, acting as a sucker; the other looks like and performs the function of a true leaf. He extends this theory to monocotyledons generally. It is geophilous, with stem-structure like *Alisma*.

Then we have Miss Sargent's own theory in which fusion of cotyledons is correlated with a geophilous habit. Suppose the primitive Angiosperm were geophilous. The green parts of the seedling would be reduced in early seasons and fusion would result.

Podophyllum affords an example of a plant with united cotyledons and scattered stem bundles which is a geophyte.

The suggestion is thrown out that the glacial period may have produced conditions most favourable to geophytes and afforded scope for monocotyledonous development.

In attempting to reconstruct the character of a race of primitive Angiosperms¹ Miss Sargent discusses the question of monocotyledons in a new light. The development from Pteridosperms, first as a pro-anthostrobilus, then as a eu-anthostrobilus, up to the primitive *Magnolia* and *Liriodendron*, as recently sketched out by Messrs. Arber and Parkin,² is accepted, and she reconsiders the evidence for regarding Angiosperms as monophyletic, and the reconstruction of the pro-Angiosperm. As to the first, the community of descent of monocotyledons and dicotyledons is proved by the many characters they share in common. And it is pointed out that the angiospermic flower is unique. The homologue of the flower, carpel, or endosperm is by no means settled.

The germination of the embryo-sac and formation of endosperm, where the first nuclear division, origin of endosperm from three nuclei, and the uniform nature of the two processes is so characteristic, supports the monophyletic origin. Double fertilisation is by no means uncommon. The history of the development of the endosperm is not known. Commenting on Miss Berridge's suggestion as to the resemblance between the endosperm of *Ephedra* and that of Angiosperms, Miss Sargent says: "No tissue then in *Gnetum*, nor, so far as we know, in *Welwitschia*, can be considered as the direct representative of the angiospermic endosperm";³ and she

¹ "The Reconstruction of a Race of Primitive Angiosperms," *Ann. Bot.*, 1908, vol. xxii, p. 121 *et seq.*

² "On the Origin of Angiosperms," *Jour. Linn. Soc.*, 1907, vol. xxxviii, p. 29. See further, Dr. D. H. Scott, "The Evolution of Plants," 1911, Williams & Norgate.

³ See, however, Professor Pearson's recent researches on *Welwitschia*.

thinks "the germination of the embryo-sac and the history of the endosperm isolate monocotyledons and dicotyledons from all other plants." The flower also is distinct from other "flowers," and characteristic.

In the reconstruction of the primitive Angiosperm Miss Sargent relies on the evidence adduced by Arber and Parkin as to the form and character of the primitive flower, with angiospermic foliage, flowers, seeds, and ovules enclosed in an ovary, three nuclei in the pollen-tube, etc. The flower was elaborate in structure, with sepals, stamens, carpels, spirally arranged in acropetal succession, as in *Magnolia*.

The early types were of the form of a bisexual strobilus as in *Magnolia*, with ♂ sporophylls below, ♀ above, protected by a series of sterile bracts forming a basal perianth. Such a type is found in the Jurassic *Bennettites*. The immediate ancestor had an anthostrobiloid flower, with perianth leaves, stamens, carpels, arranged acropetally. The strobilus was the primitive form, and *Bennettites* stands midway between it and *Magnolia*.

Monocotyledons and dicotyledons differ in stem-anatomy and number of cotyledons. How did the primitive Angiosperm differ from or resemble either? As to stem-anatomy, monocotyledons do not possess a cambium, or rarely. *Gloriosa*, however, exhibits collateral traces and a cambium in second-year tubers. Gymnosperms exhibit cambial activity, and so did many fossil vascular cryptogams. Dicotylar seedlings early exhibit a cambium. Some monocotyledons, as *Yucca*, etc., do. Thus evidence points to the primitive Angiosperm possessing a cambium. As to the number of cotyledons, monocotyledons possess one, dicotyledons two. No monocotyledon possesses two, but several dicotyledons possess one. Many groups of Gymnosperms are dicotylar, and the most primitive Araucariæ are polycotyledonous. In what respect did the primitive Angiosperm differ from or resemble either recent group? Analogy, as above, favours the primitive nature of the dicotylar type. What do we learn from embryology within the embryo-sac? The whole of the evidence in this connection centres around the position of the cotyledon. The terminal position of the monocotyledonous form with the derivation therefrom by fission of the two is not favoured by Miss Sargent. Can a terminal cotyledon be a true leaf? Opinions differ as to this. If extensions of the axis, they are terminal and not true leaves. The difficulty is thought to be avoided by considering the cotyledon as only apparently terminal, and so lateral.

In *Alisma* (Pl. IV. figs. 1-6) the cotyledon is terminal at first, then lateral as the plumule displaces it. In *Pistia* and *Sparganium* early leaves are terminal. Are they cauline? Or are they due to suppression of the axis? They are primitive forms and aquatic. The stem exists in the mature *Pistia*, but not in the embryo. The reduction in stem is due to the aquatic habit, and causes terminal leaves. Can it cause the cotyledon to be terminal? The form of

the embryo and development of embryo-sac are affected by (1) space rotations, (2) mode of food-supply, (3) shape of embryo, and depend on future form of seedling and mode of freeing itself from the seed-tissue. The embryo-sac is long and narrow, and bent upon itself, evidently due to nature of surroundings. The suspensor conveys food. The cotyledons are absorptive, and endosperm prepares and draws upon the store. Is the function of the cotyledons to absorb food and pass it on? The embryo exhibits adaptation to present, past, and future environments. Wide embryo-sacs have a lateral cotyledon, and narrow embryo-sacs, as in *Alisma*, an apparently terminal cotyledon.

If the single cotyledon was lateral, was that of the primitive Angiosperm lateral? It is possible to imagine a lateral member split into two, and that one member has revolved through 180° . If it was dicotylar, the monocotylous form might be derived by suppression of one or fusion of two members. The cotyledon was single in pseudomonocotyledons, and derived from two presumably. The development is like that of *Tamus*. Sterckx found in *Ranunculus ficaria* a bilobed venation in the cotyledon which suggested fusion of two cotyledons. Analogy with Gymnosperms favours this, but development of the embryo-sac yields no evidence, its shape being due to environment.

As regards embryology after germination, certain types of monocotylous plants have primitive vascular tissue. In dicotyledons the tetrarch type is found as well as the diarch type.

In *Nigella* it is diarch, but there is transition to a tetrarch root. In *Althea*, which is tetrarch, there is an approach to diarch structure, like *Liriodendron*. The oldest Gymnosperms exhibit tetrarch structure and also diarch structure. In Pteridosperms probably the structure was tetrarch. Thus presumably the primitive forms were either tetrarch or diarch. In monocotyledons the structure is more variable, but there is a series of extreme types and also intermediates.

The common origin indicates presumably a primitive type. Such are Liliaceæ, e.g. *Anemarrhena*, which is tetrarch; and they are connected with others, e.g. Iridaceæ, Aroideæ, whilst it is in fact a radicle of Liliifloræ, and hence may be of monocotyledons in general, recapitulating ontogenetically the history of the group. There is a strong resemblance between the structure of *Anemarrhena* and the dicotylar *Althea*, which is near the primitive gymnospermous type, and probably primitive. Hence probably the primitive Angiosperm type had a tetrarch stem-structure. Would this necessarily be correlated with two cotyledons? Dicotylar forms with cotyledons each symmetrical about the median plane are symmetrical about two vertical planes. There is no symmetry about one plane, where reduction occurs. In monocotylous stems receiving traces from a single lateral there is only symmetry about the median plane. The primitive *Anemarrhena*, *Galtonia*, etc., are exceptions. That the tetrarch skeleton symmetrical about two planes is found in these suggests

that dicotylar forms gave rise to monocotylous by fusion of the two cotyledons. In Ranales, e.g. *Eranthis*, the root is diarch, and tetrarch structure is found in the hypocotyl. In *Podophyllum peltatum* the same occurs. *Anemarrhena* and *Althea* are recalled in these. In both the cotyledons are united for some distance. Reduction of the tetrarch type has progressed further than in *Althea*, of which *Anemarrhena* is a reduced form, and with it *Podophyllum* and *Eranthis* agree, showing that the union of cotyledons in a tetrarch dicotyledon may result in a monocotylous type with structure of *Anemarrhena*.

Professor G. Henslow, in a paper¹ read before the Linnean Society, brought forward the theory of the origin of endogens from exogens by adaptation to an aquatic habitat due to suppression of one cotyledon. This theory, which is an extension of Agardh's, is based upon the large proportion of monocotylous aquatic orders in the group, viz. 33 per cent. There are, however, some characters which are found in both monocotyledons and dicotyledons, and those which are thought to be confined to aquatic plants alone are also found in geophytes and other groups. Aquatic conditions have certainly helped to reduce the stem-structure and to modify foliage, but are not responsible for the reduction in cotyledons, nor so far as is known, the character of the flowers.

Messrs. E. A. N. Arber and J. Parkin,² in a paper on the "Origin of Angiosperms," trace the ancestry of the group. They disagree with Engler's view that the present-day primitive Angiosperms have unisexual flowers, e.g. Piperales, Pandanales, etc. But the perianth is to be regarded as arising *de novo*, and to be an organ *sui generis*.

The plants cited have a sharply defined complicated structure. This theory has proved barren. The strobiloid theory is held to solve the question, the primitive form being amphisporangiate with micro- and megasporophylls and a well-defined perianth. The parts of the flower were numerous, arranged spirally, the female sporophylls above the male. Such a type is found in some Magnoliaceæ, Ranunculaceæ, Alismaceæ. The apetalous unisexual flowers are regarded as derived from these. The flower is an anthostrobilus of which a gymnospermic and an angiospermic form can be distinguished. But they are modelled on the same plan, the female and male sporophylls occupying the same relative position, and the perianth is differentiated. These authors consider that some important change in the mode of pollination caused the advent of Angiosperms.

Dealing with the ontogeny of Angiosperms in the paper already cited, Bessey defines the difference in the development of the embryo in monocotyledons and dicotyledons as follows:—

"The only histological difference which is measurably constant is

¹ "A Theoretical Origin of Endogens from Exogens by self-adaptation to an Aquatic Habit," Journ. Linn. Soc., vol. xxix., 1892, p. 485. But see a more recent paper, *ibid.*

² *Ibid.*, "Jour. Linn. Soc.," 1907, p. 29.

that the longitudinal division of the embryo takes place *before*¹ the formation of transverse walls in dicotyledons, and *afterwards*¹ in the monocotyledons. To this rule, however, there are numerous exceptions."

Commenting on the further progress of this division, he says, "It is at least an interesting coincidence that in the young embryo the undivided foliar cells give rise to the single cotyledon, and the epibasal cell to the pair of cotyledons."

The following remarks are so *à propos* that they are quoted at length:—

"Are there any indications which may help us to answer the question of the origin of these two groups? Have dicotyledons been derived from monocotyledons, monocotyledons from dicotyledons, or both from a common ancestor? It must be admitted that on theoretical grounds it is no more difficult to pass from two cotyledons to one, than from one to two. Indeed, there have been not a few botanists who have suggested the derivation of the monocotyledons from the dicotyledons. When, however, one compares the two embryos there is a slight preponderance in favour of the view that the structure is a little higher in dicotyledons than in monocotyledons. The row of undivided cells in the embryo of the monocotyledon after the third or fourth segmentation is certainly a lower structure than the compact mass of cells constituting the 'octant stage' of the dicotyledonous embryo. The cotyledons themselves afford a slight suggestion as to the relationship of the two groups. It is a well-established principle in embryology that embryonic stages of higher organisms resemble the adult stages of the organisms which are lower in the same genetic line. Applying this principle to the cotyledons, we observe that while they bear some similarity to the leaves of both monocotyledons and dicotyledons, the similarity is a little more marked in the case of the monocotyledons. Compare the mostly sessile, often clasping, usually elongated leaves of monocotyledons with the cotyledons of either class, and contrast these with the mostly petiolated, generally not clasping, and usually broad-bladed leaves of the dicotyledons."

Bessey also refers to the fact which Sir J. Lubbock (now Lord Avebury) points out, that the earlier leaves of a plant are generally quite different from the later ones. Young plants are the most alike, and they begin to get more unlike as they mature. So that it is often only possible with seedlings to distinguish the subclass, later the family, and then the genus, whilst until the flower is produced the specific characters are hidden.

The deductions he makes from ontogeny are:—

1. All Angiosperms are essentially alike.
2. The two subclasses (monocotyledons and dicotyledons) appear to be modifications of a common type which diverged from one another at an early period.

¹ Present writer's italics.

3. There is no indication that either subclass was derived from the other.
4. There are some structural indications that the monocotyledons must rank lower than the dicotyledons.
5. The vegetative rank of most cotyledons is so nearly the same as to have left no vestiges on the young plant, which is itself vegetative.
6. The groups into which dicotyledons and monocotyledons are divided are "flower subdivisions" of a greatly multiplied rather common vegetative structure. Therefore, we may not expect to find upon the embryo or immature plant any vestigial record of their origin.

In discussing the results derived from morphology, Bessey, in speaking of tissue systems, draws attention to the short life of monocotyledons and the long life (often amounting to hundreds of years) of dicotyledons. But the ephemeral type of the former occurs amongst the latter, which indicates, he suggests, the close relationships of the two subclasses.

He points out that the young stems of monocotyledons and dicotyledons differ less than old stems, and remarks that "the important difference between these two types of stem is that the skeletal tissues continue to form a single solid column in the dicotyledons while they do not in the monocotyledons," and the further fusion of bundles in the former, due to cambial activity, marks them out as a higher group.

From the normal type of stem seen in lilies, naiads, and orchids, there are two departures in the stem with elongated internodes of grasses and sedges, and the shorter internodes of palms and screw-pines. As to their leaves he says:—

"The leaves of monocotyledons are usually entire, elongated, parallel-veined blades, placed alternately or scattered upon the stem, to which they are attached directly (in sessile leaves) or indirectly (in petioled leaves) by a common broad base which is rarely supplied with stipules."

When contrasting these with dicotyledonous leaves which are dentate or lobed, usually broad, net-veined, opposite and alternate, attached by a narrow base, commonly supplied with stipules, these differences are said to be "due to differences in development." The parallel veins of monocotyledonous leaves are due to localisation of growth at the base of the blade or indefinite bands on each side of its axis. The broad basal attachment of the monocotyledonous leaf may be due to the looser disposition of the fibro-vascular bundles in the stems, or perhaps may be owing to the fact that they are not so far advanced as the leaves of dicotyledons, there being an articulation at the base of the latter only. In the monocotyledons the common leaf type is especially modified in the Gramineæ.

The flower is held to consist of a strobilus of "flower-leaves" consisting of sterile leaves and spore-bearing leaves, the former being derived according to Bower, from the latter. The perianth as a

ring of sterile leaves may be united by symphysis, or may be apetalous. The last condition is no indication of affinity, but is simply a case of reduction.

The pollen leaves (microsporophylls, stamens) lie between the sterile and ovule leaves, and are largely adapted to the seed-producing or pollen-distributing capacity.

The ovules (macrosporophylls, carpels) occupy the highest portion of the strobilus, being usually separate, and the carpels are often separate as in *Alisma*, etc., forming apocarpia, or united as in lilies, to form a syncarpium, with some portions still free as in the latter, or with styles united all their length as in Commelinaceæ.

When some other organs are attached to the syncarpia as in the epigynous irids and orchids, "there has been such a fusion of the originally separate parts of the strobilus as to result in a single compact structure."

"The primitive syncarpia of the monocotyledons appears to have contained three carpels as in lilies." In the fusion some parts are suppressed. In some dicotyledons, *e.g.* Caryophyllales, etc., "there is a tendency to a reduction in the number of parts with increased fusion of the strobilar leaves."

"The same law is illustrated in the genetic line, which includes the lilies (Coronarieæ), pipeworts (Eriocaulaceæ), sedges (Cyperaceæ), the lower grasses (Bambuseæ), and higher grasses (Agrostidæ and Paniceæ); or possibly still better in the line from lilies to amaryllids (Amaryllidaceæ), irises (Iridaceæ), burmannias (Burmanniaceæ), and orchids (Orchidaceæ)."

There are then two modifications of the strobilus by (*a*) *symphysis*, fusion of parts; (*b*) *aphanisis*, a suppression of parts.

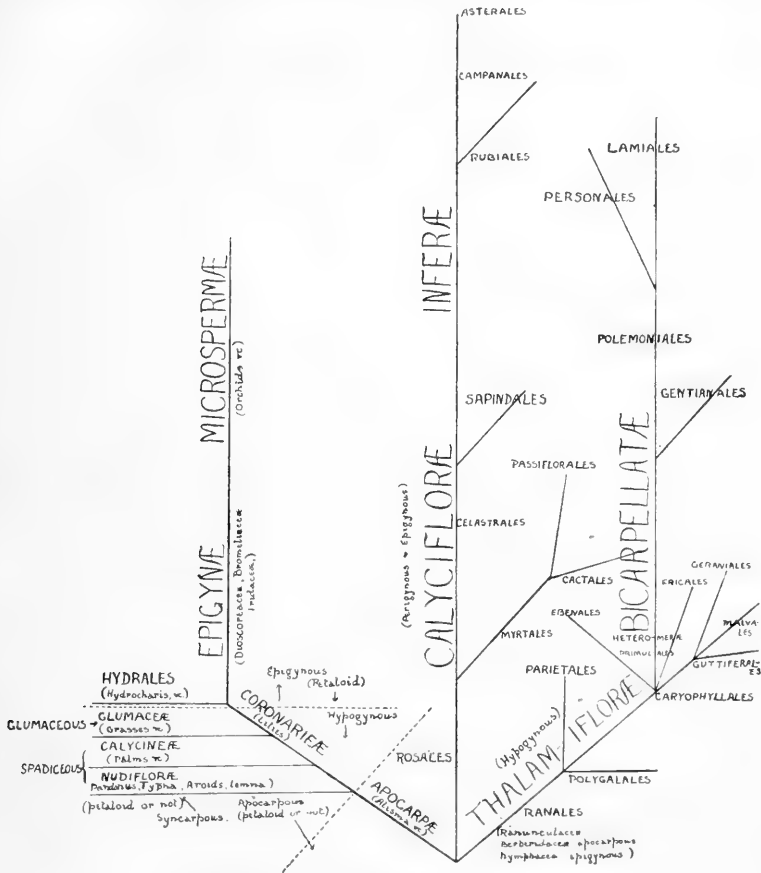
They may affect some or all organs of the strobilus separately or jointly.

The conclusions arrived at from morphology are:—

1. The identity of the cells and tissues of the two subclasses of Angiosperms indicates their close relationship.
2. The fibro-vascular tissue-system of the dicotyledons indicates that the subclass is higher than the monocotyledons.
3. The roots of dicotyledons indicate that this subclass is higher than monocotyledons, and suggest the possibility of the origin of the former from the latter.
4. The structure of the dicotyledonous stem indicates the highest rank of this subclass.
5. Among monocotyledons the external morphology of the stem indicates the derivation from lily-like plants of the palms and screw-pines by an excessive shortening of the internodes, and of sedges and grasses by a corresponding elongation.
6. The general morphology of the leaves of monocotyledons and dicotyledons, as has already been indicated many times, emphasises the close relationship of the two subclasses, and repeats the suggestion that the former includes plants which must take rank below the dicotyledons.

In dealing with the hypothetical phylogeny of Angiosperms, Bessey refers to the monocotyledons as follows:—

“The modifications which gave us the main lines of monocotyledons were first the fusion of the carpels with one another and the production of a syncarpium, and, second, the progressive fusion of



The Phylogeny of Angiosperms. (After Bessey.)

the syncarpium with the other strobilar leaves. These resulted in the phylum, which begins with Apocarpæ and passes to Coronariæ, Epigynæ, and Microspermæ. In some Apocarpæ and many plants of the type of the Coronariæ the perianth has been more or less reduced (by aphanisis), in some cases amounting to complete suppression, as in palms (Calycineæ), aroids (Nudifloræ), and sedges and grasses (Glumaceæ).”

As to their *taxonomy*, he writes:—

“The Angiosperms are separable into two diverging subclasses—the monocotyledons (Monocotyledoneæ), and the dicotyledons (Dicotyledoneæ), the first ranking structurally lower than the second. The monocotyledons are well divided by Bentham and Hooker into seven series, and these we may accept unchanged, with the single exception that the water-worts (Hydrocharitaceæ) should probably be removed from the Microspermæ to constitute an additional co-ordinate group. These eight groups, which appear to be deserving of no more than ordinal rank, should then be arranged so as to have the following sequence, namely, Apocarpæ, Coronariæ, Nudifloræ, Calycinaæ, Glumaceæ, Hydrales, Epigynæ, Microspermæ. Here it must be understood that the Nudifloræ, Calycinaæ, and Glumaceæ are separate orders radiating from the present order Coronariæ, and that the Hydrales constitute a diverging order from the base of the Epigynæ.”

Some researches made by Professor H. H. W. Pearson¹ in regard to *Welwitschia* are of interest in this connection. In studying the endosperm he found all the cells are multinucleate. Later, each cell possesses only one nucleus by fusion of nuclei in young cells. The original nucleus by division has become a thousand. The embryo-sac elongates, and there is a redistribution of nuclei. Two poles are formed: one at the micropylar, the other at the opposite end. In the former the nuclei are not crowded, in the latter they are. Then a division into compartments or segmentation takes place, with 2 to 6 nuclei at the micropylar end, 12 or more elsewhere. When there are more than 6 nuclei they are divided up into cells with single nuclei; but those at the micropylar end are not so affected, as each wall grows up into the prothallial tube. The nuclei and cytoplasm pass into this, and the nuclei become functional gametes. This unusual characteristic has led Professor Pearson to regard the endosperm as representing a new stage, which he calls the trophophyte, which serves to mark its intercalation into the life-history—a terminology now familiar to us from Professor Bower's theory of the antithetic generation or intercalation of the sporophyte into the life-history of the moss plant. This trophophyte is neither the sporophyte nor gametophyte, but is regarded as phylogenetically related to the endosperm of Angiosperms by a series of reductions and specialised stages. The fact that in Angiosperms a similar procedure takes place is corroborative of this view. In a more recent paper² Professor Pearson finds that the ovule in *Welwitschia* is cauline, and it is considered that the female cone and male flower are derived by reduction and specialisation from an amphisporangiate strobilus of a type similar to *Bennettites*. After division 1024 nuclei are contained in the embryo-sac, and it is repeatedly divided. The endosperm of the primitive Angiosperm

¹ “Rep. Brit. Assoc. Dublin,” 1908.

² “Further observations on *Welwitschia*,” “Proc. Royal Soc.,” Nov. 1908.

is thought to have been homologous with that of *Welwitschia*. *Gnetum* and *Welwitschia* are derived from the Angiospermic stock, but before the carpel became the pollen-receiver.

In the Penæaceæ, a group of dicotyledons, Miss E. L. Stevens¹ finds that there is no polarity in the early stages of development of the endosperm, as in most Angiosperms. The embryo-sac contains not 8 but 16 nuclei which form four egg-apparatus. By the fusion of 4 nuclei a definitive nucleus results. By this reductional process the same features met with in *Welwitschia* are recalled. A very similar process is recognised in *Gnetum* by Lotsy in the germination of the megaspore or embryo-sac, and the development of the endosperm.

5. CONCLUSIONS.

Summing up the evidence afforded by the different views held by the writers cited, and by personal observation and experience, it seems to us that systematic researches have failed to appreciate the results of palæontology and of morphology, and in considering *Pandanus*, etc., as the oldest group sufficient attention has not been given to the comparative results of floral structure or of morphology.

As to the theories based upon either embryology or morphology, Dr. Worsdell's view seems to us to be based upon the most stable evidence.

The view that there is only one cotyledon in both groups, indeed, is perfectly reasonable; and if the cotyledon and the seta of Bryophytes are conceded to be homologous, then their respective order in time is also practically settled, for the single cell in the latter gives rise to two, and so on until, just as in *Capsella*, Pl. II. fig. 3 (part i.), p. 180, we arrive, in due course, at the bifid cotyledon. The fact of the subdivision from an original single cell presupposes the primitive character of the latter, and the derived nature of the double row of cells.

As to the position of the cotyledon, if the above view is accepted the originally terminal character of the cotyledon also follows. The lateral position subsequently, if we adopt the sympodial arrangement, does not affect the question. The lateral appendage view does more harm, it seems to us, in obscuring the sequence of the ontogeny (and so the phylogeny), and the morphological significance of organs than any other theory promulgated.

The reversionary nature of the monocotyledonous type in Ranales is in itself more or less favourable to the earlier age of monocotyledons and the derivation of dicotyledons from them.

Miss Sargent's views are in direct contrast to those of Dr. Worsdell's. This is readily understood when it is seen that she has based her evidence mainly upon the earlier embryological features of the species studied, too early in the ontogeny for a proper recapitulation to be observed. Dr. Worsdell, however, takes the most mature

¹ "Proc. Roy. Soc. S. Africa," 1908.

structures in his investigations, and there he obtains the full history. One is specially grateful to both of these able investigators for thus, in their several fields, enabling us, by their combined researches, to study both early and late stages. However much we may differ in theory from either one or the other, the data upon which they have been based lose none of their value whatsoever. In some respects the plants Miss Sargent studied were anomalous forms, e.g. Pseudo-monocotyledons, and primitive Liliaceæ, and the evidence is thus inconclusive. The lateral appendage view only leads back again to an unnecessary transposition, in time, of the mono- and di-cotylar types.

The interpretation of certain features, e.g. the absence of a cambium, as due to reduction, instead of being held as a primitive character, is a necessary consequence.

There may really be some truth in Professor Lyon's view that the fission of the cotyledons has to do with the freeing of the cotyledon from the testa.

Professor G. Henslow's theory that one cotyledon has been suppressed in monocotyledons is based upon the preponderance of aquatic orders in monocotyledons—and thought to be due to their adaptation to an aquatic habitat, a physiological cause, which is not universally applicable.

In so far as it touches the origin of monocotyledons Messrs. Arber and Parkin's paper is favourable to the view that a primitive Angiosperm gave rise very early to both mono- and di-cotylar types, the divergence being close to the origin of the primitive ancestor.

Bessey's views seem to us to be so reasonable that, taken in conjunction with Dr. Worsdell's, they lie nearest the truth.

It is a remarkable fact that the earliest forms of both monocotyledons and dicotyledons exhibit a sort of parallelism of development. The first monocotyledons are apocarpous, just as are Ranunculaceæ, amongst the latter (except Nymphæaceæ, which are epigynous).

Then there is a higher series which becomes hypogynous, from which the Calycifloræ early diverge and are perigynous or epigynous.

So in monocotyledons the apocarpous forms (rarely petaloid) become syncarpous, and then spadiceous or glumaceous, or hypogynous, and finally epigynous.

The researches of Professor Pearson and Miss E. L. Stevens as to the embryology of *Welwitschia* and Penæaceæ favour the derivation of Angiosperms from Gymnospermic or Bennettitean stock, but, as yet, throw no light upon the Angiospermic origin nearer the present time, and the differentiation into mono- and di-cotyledons.

Speaking generally, it seems to us that the monocotyledons and dicotyledons have diverged from a common primitive Angiospermous stock. The earlier types of the former appear to belong to Alismaceæ, leading on to Liliaceæ; and the earlier forms of the latter the Ranales, represented by *Magnolia* and *Liriodendron*, from which *Ranunculus* and its allies are later derivatives. This would allow of the retention of some primitive characters in both groups which are apparently explained only by supposing dicotyledons derived from

monocotyledons or *vice versa*, or from a stock capable of transmitting either.

Primitively we may consider that there was an adaptation from aquatic to terrestrial conditions, which then gave rise to the geophilous habit, whilst other forms in the harder struggle on land retained or sought refuge again in an aquatic habit.

The derivation of Angiosperms from the same synthetic type as Gymnosperms seems clear. The near approach of the unique Bennettiteæ with two cotyledons and copious endosperm would alone suggest this. The derivation of the latter from Pteridosperms is again more or less clear. The fact that two cotyledons is so characteristic a feature of Gymnosperms is again confirmatory of the early differentiation of a dicotylous type. The polycotyledonary¹ forms are also the more ancient, so that there is some evidence from analogy for reduction. In Gymnosperms a suspensor is not always present. Many of the Gymnosperms exhibit other characters, though these may be homoplastic—*e.g.* parallel-venation and strap-shaped nature of leaves, *e.g.* in *Cordaites*.

It should be noted in regard to stem anatomy being a distinctive character, that the arborescent Lycopods sometimes, though not invariably, exhibit cambial activity, whilst herbaceous forms do not.

As to cotyledons the number is extremely variable amongst Gymnosperms within the same group. So that although dicotyledons and monocotyledons are remarkably uniform in this respect, yet the character is apparently due to physical selection and is homoplastic, like the stem anatomy.

Probably Dr. Worsdell's suggestion that the two are phases of one group is nearer the mark. Amongst fossil Cephalopods the group Nautiloidea is more or less constant in the central or dorsal position in the siphuncle, whereas in Ammonoidea the siphuncle is ventral. In Clymenioids, an Ammonite group, however, it is dorsal.

Triassic Ammonoids, again, exhibit a curious type of sutural development. In Nautiloidea Triassic Pleuronautilids exhibit what may be called an homologous arrangement.

Thus monocotyledons and dicotyledons may be compared with Nautiloidea and Ammonoidea, and although the first two are plants, and the last two animals, they exhibit a sort of parallel mode of development, in respect of the degree and not the kind of difference. The phenomenon is what Hyatt has described as morphic equivalents.

Summing up the evidence in regard to the relative antiquity of the monocotyledons and dicotyledons, and the bearing this has upon the origin of the latter, we find ourselves reduced to the following conclusions:—

1. There is evidence from palæontology that monocotyledons came into existence almost contemporaneously with dicotyledons, not, as once held, long prior to the latter.

¹ There may be 3 to 18 cotyledons as in *Pinus*, 3 to 8 in *Abies*, 3 to 11 in *Picea*, 6 to 11 in *Cedrus*.

2. All but a few of the families and orders (6) have been recognised in a fossil state, and most of these in the Tertiary.

3. The group appears to have diverged from the primitive Angiospermic stock, evolved from a line of ancestors connecting Pteridosperms, Bennettitales, and eventually such dicotyledons as *Magnolia*, *Liriodendron*, *Nymphaea*, and the monocotylous Alismaceæ and Liliaceæ.

4. There is every appearance of reduction in the floral symmetry, but the characters of the cotyledons, stem, and leaves are apparently as primitive as those of the primitive dicotyledons—further than which latter they have not progressed. The uniform aquatic habit would account for a great deal of this in stem and leaves, and even cause some reduction. In other words, monocotyledons are retrogressive and dicotyledons progressive types.

5. The prevalence of aquatic, geophytic, and climbing genera lends support to the view that they are a weaker or degraded race of Angiosperms which have sought refuge in aquatic habits, thus avoiding the severer struggle for existence upon land.

6. The view is held that the difference in cotyledons is due partly to the shape of the embryo-sac and supply of endosperm, partly to the mode of life of the plants after germination.

7. The stem structure is due to physiological causes, since the tree type is more or less absent, and where present traces of a cambium often occur.

8. The absence of any recapitulation during the ontogeny of monocotyledons of a supposed previous dicotylar stage is regarded as conclusive evidence that the former are not derived from the latter.

9. It is held that the primitive Angiosperms resembled an Alismaceous or Liliaceous type, on the one hand, and a Ranalian type on the other, and that the monocotyledons and dicotyledons are divergent series from a common ancestor, recalling the common characteristics of the two as the one or the other were called into being by either physical or natural selection. In the one case, dicotyledons, there has been progression and differentiation; in the other, monocotyledons, retrogression and even some reduction from a common ancestor of the primitive Angiospermic type.

PLATE III.

- Fig. 1. (A) A shoot of *Polyalthia*, to illustrate sympodial arrangement. Every stem segment is terminated by a leaf. (B) Monocotyledonous embryo, to show similar arrangement. (After Worsdeil, "A Study of the Vascular System in certain Orders of Ranales," Oct. 1908. "Ann. Bot.," p. 653.)
- Fig. 2. *Delphinium nudicaule*, seedling after eight weeks, to show position of leaf and cotyledon.
- Fig. 3. *Delphinium nudicaule*, seedling after fourteen weeks.
- Fig. 4. A = *Alisma plantago*; B, C = *Corydalis cava*; D = *Tamus communis*. Mono- and di-cotyledons for comparison to show position of cotyledon.
- (Figs. 2, 3, and 4 after Sargent, "The Evolution of Monocotyledons.")

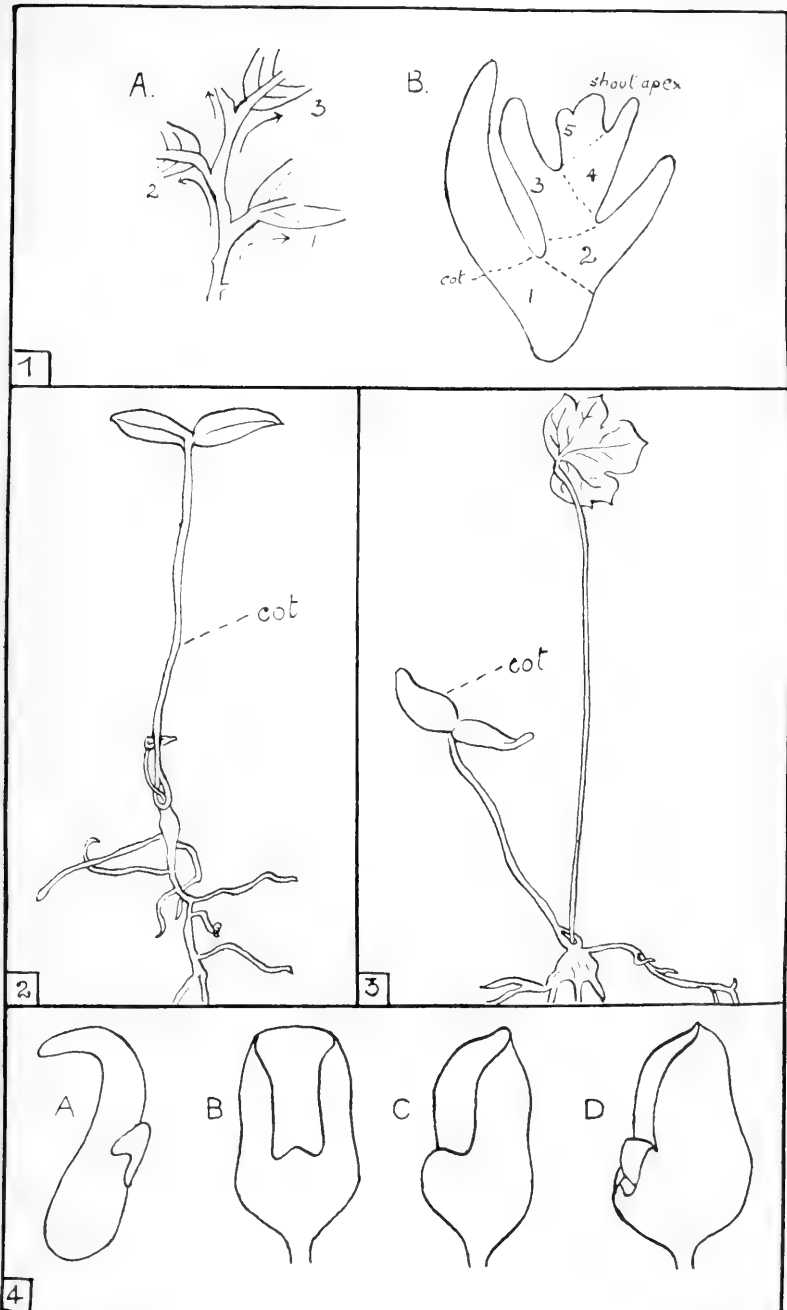




PLATE IV.

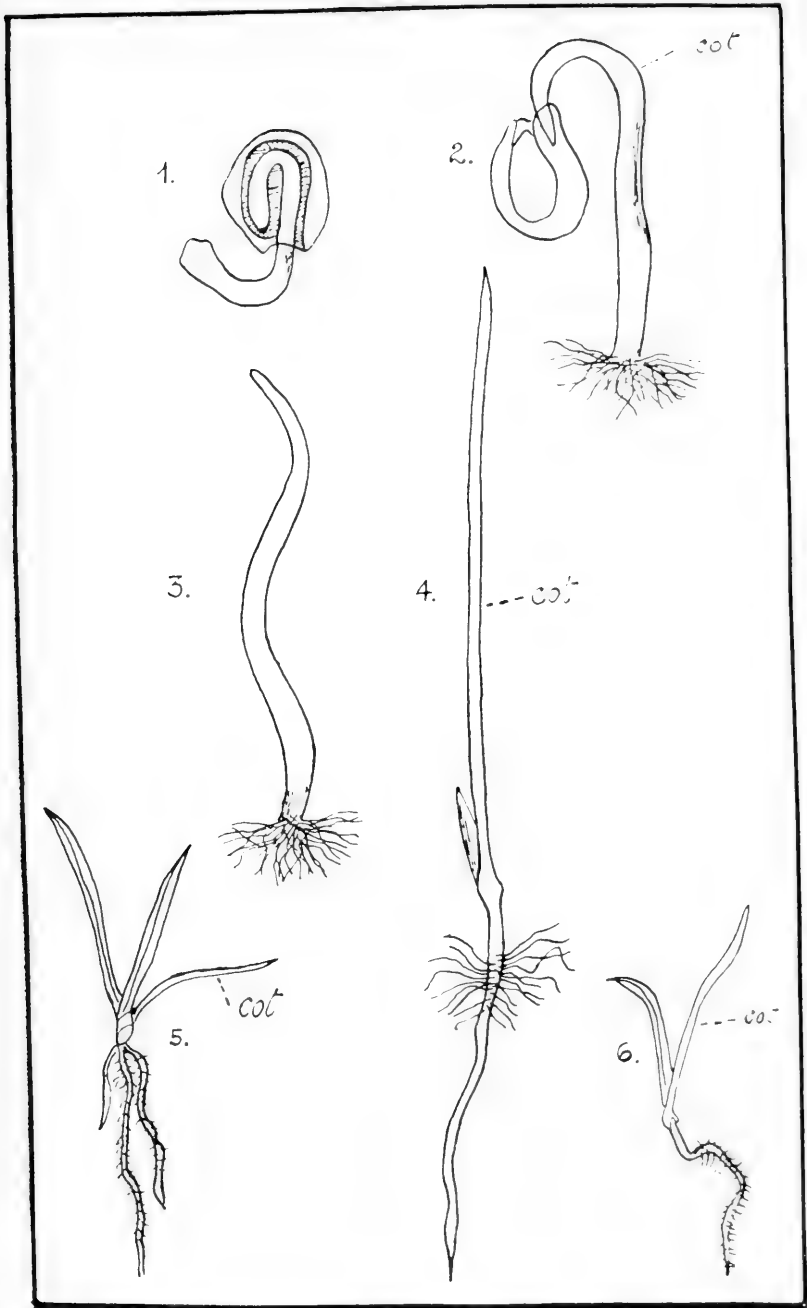
Figs. 1, 2 and 3. Stages in the germination of the seedlings of *Alisma plantago* :
eight times natural size.

Fig. 4. The same $\times 4$.

Fig. 5. ,, natural size.

Fig. 6. ,, ,,

(Figs. 1-6 after Lord Avebury, "Seedlings." *Cot.* = cotyledon.)





Short Notes.

Saxifraga aizoides, L.—Among plants from Orkney sent by Mr. M. Spence are two specimens of the above Saxifrage, and answering to the description of the *f. aurantia* of Hartmann, "Vet. Ak. Handl.," 1818. The leaves are orange, shading to yellow at the apex. The lower stem leaves are suffused with red, and the fruit is orange-red (only half-ripe). The leaves are quite entire, very thick, with here and there a long patent hair. This form occurs in Norway, with the ordinary form in Sweden, and rarely in Russian and Finnish Lapland. Is not the figure in "English Botany," t. 59, quite a rare form? I have not seen such stem leaves on any specimen as there represented, and the description says "rarely denticulate." A. BENNETT.

Utricularia vulgaris L., in Caithness.—Good specimens of the above (though not in flower) have been sent me by Miss I. Lillie and Mr. G. Lillie from Loch Watten on the east coast of Caithness. There are several of the winter buds; these are strongly setose, with translucent, spinose-like hairs, and the young leaves are spinose-setose. The young bladders are semi-transparent, the older ones also, but with the addition of a yellowish nucleus. This definitely records the species for the county. A. BENNETT.

Cnicus oleraceus Lin. = *Cirsium oleraceum* Scop.—This plant has occurred this season on a marshy meadow by the side of the Tay, left bank, about a mile below Perth. It forms a small patch comprising about sixty or seventy flowering shoots and was certainly not there, at least in the flowering stage, till this season. How it came I am unable to conjecture, as it is certainly not a plant likely to be cultivated, and the meadow, though cut, consists of natural herbage only, and is never sown. Mr. Arthur Bennett informs me that it occurred in Lincolnshire from 1832 to 1840 on the Fen banks, and I believe it has been found in Scotland amongst other casuals. The plant was named for me at the Herbarium of the Royal Botanic Garden, Edinburgh. It has yellow flowers. Near to the same place a little patch of *Sanguisorba canadensis* Lin. has kept its place amongst some alder bushes for more than half a century. Till this year I have never seen any signs of its spreading. But this summer at least three other patches, at about a hundred yards further down and clear of the bushes, have made their appearance and have flowered freely. One patch in the middle of the meadow forms a circle of a good many yards in diameter and comprises a considerable number of plants. Possibly the very hot summer of last year may have more thoroughly ripened the seeds and thus enabled the plant to extend its area.

Juncus tenuis Lin.—In growing through Glen Ogle in July this sedge

occurred in great plenty by the roadside about half-way between Lix and the summit of the pass. For about a quarter of a mile it formed a close band along the left side of the road. For about another half mile I traced it in patches and isolated plants. It seemed as if carts loaded with American fodder had been passing along the road dropping seeds at first thickly and then more thinly. Certainly the plant is not native in any of the Perthshire stations in which it has been found.

W. BARCLAY.

Notes from Current Literature.

"Quel est le vrai caractère biologique du *Raphanus Raphanistrum*, L., et du *Sinapis arvensis*, L.," by A. Verhulst ("Contributions from the U.S. Nat. Herbarium," vol. xvi. part iii.).

"The North American Species of *Nymphæa*," by G. S. Miller, jun., and P. C. Standley ("Contributions from the U.S. Nat. Herbarium," vol. xvi. part iii.).

"Studies in Tropical American Ferns," by W. R. Maxon ("Contributions from the U.S. Nat. Herbarium," vol. xvi. part iii.). Particularly valuable in containing a monographic account of the species of *Hemitelia*, subgenus *Cnemidaria*, fully illustrated.

"*Spiræa Ulmaria*, L., and its Bearing on the Problem of Xeromorphy in Marsh Plants," by R. H. Yapp ("Annals of Botany," July 1912).

"*Polygala vulgaris*, L., var. *grandiflora*, Bab.," by Arthur Bennett ("Journal of Botany," July 1912).

"A New Variety of *Parnassia palustris*," by W. G. Travis and J. A. Wheldon ("Journal of Botany," August 1912).

"Le genre *Balsamocitrus* et un nouveau genre voisin, *Æglopsis*," by W. T. Swingle ("Bull. Soc. Bot. de France," vol. xi.).

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"A Beehive Fungus, *Pericystis alvii*, Gen. et Sp. Nov.," by A. S. Betts ("Annals of Botany," July 1912).

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"Nouvelles maladies de plantes cultivées," by Arsène Puttemans ("Contributions from the U.S. Nat. Herbarium," vol. xvi. part iii.).

"Écologie d'une petite panne dans les dunes des environs des Dunkerque (Phanerogames et Cryptogames)," by M. Bouly de Lesdain ("Bull. Soc. Bot. de France," vol. xiii.).

"Nouvelle contribution à la Géographie Botanique du Jurassique Belge: Dispersion du *Circium acaule*, Allioni," by A. Verhulst ("Bull. Soc. Royale de Bot. de Belgique," 1911).

"Vegetationsskizze der Umgebung von Czernowitz," by Dr. K. Rudolph ("Annals of Botany," July 1912).

"Leaf Movements in the Family Oxalidaceæ," by E. B. Ulrich ("Contributions from the Botan. Laboratory of the University of Pennsylvania").

"Ein neuer Typus der Spaltöffnungen bei den Saxifragaceen," by B. Hryniewiecki ("Bull. International de l'Académie des Science, Krakaw," March 1912).

"Azotobacter Studien: I. Morphologie und Cytologie," by A. Prazmowski ("Contributions from the U.S. Nat. Herbarium," vol. xvi. part iii.).

Reviews, Book Notices, etc.

CLARE ISLAND SURVEY. PARTS XI. and XII.: MUSCI AND HEPATICÆ.
CANON H. W. LETT, M.A. 1912. Price 6d.

THE investigation of the cryptogamic flora of the Clare Island survey district is one which cannot fail to stimulate survey work elsewhere. If so remote a region, though botanically important, can receive such systematic attention at the hands of busy specialists, it is to be hoped that other areas may in due course be similarly dealt with, including the many unexplored parts of Scotland, Wales, and England.

Canon Lett in his interesting paper describes the district from a bryological point of view, noting the absence of glens, the exposed surfaces, the peaty districts much denuded by peat-cutting, which in Ireland has helped to restrict the distribution of turfophilous plants on a wide scale, though here it supports few mosses or hepatics. They abound, however, in well-sheltered nooks and corners which absorb the abundant rain. Croaghmore affords shelter to leeward

on the N.E. slopes for a rich flora, while on several low hills running N.W. by S.E., with intervening valleys owing to peat-cutting, they are rare. Saxicolous species are also rare. Though the district is now intersected by walls, they have not as yet been covered by mosses, and rupicolous species grow best near Knocknaveen (729 feet). Salt is not responsible for their scarcity, for many appear to be halophytes here. The loughs yielded no good results, sphagna being mainly restricted to Creggan Lough. Arboreal species are absent, except in plantations, and cutting down of forests has been a factor in extinction here, leaving only sphagna as relics. Some arenicolous species occur on the shore. Canon Lett indicates the most favourable spots for bryological observation as at Croaghaun Mountain and Knockacurram. No work had been done in Clare Island previous to this survey, though Achill Island had been investigated.

Interest attaches to the statistics of the flora given, the total being 221, of which seven hepatics are new to Ireland and two are second records. Notes are given as to the distribution of the flora, and the absence of some is emphasised. The flora of Clare Island is said to owe its origin to dispersal of spores by the wind. Following the list of mosses and also that of hepatics come notes on the rarer species, in which the respective areas of occurrence are indicated by I. and M., indicating Clare Island and the mainland. A useful bibliography is appended.

Part XIII.: FUNGI. By CARLETON REA, B.C.L., M.A., and Sir H. C. HAWLEY, Bart., 1912. Price 1s.

THE account of the fungi is divided into two sections, Clare Island being described by the second author, the mainland by the first. In so far as the mycology is concerned this region was previously quite unexplored, *two species only* being recorded by Adams in 1910, and of 1400 Irish species 100 only were known in Connaught. The species and varieties discovered number 802, including 295 species and 12 varieties new to Ireland, 11 new to Britain; whilst Hawley describes a new genus, *Candelospora*, genotype *C. ilicicola* sp. nov. (figured), and Rea a new species, *Hygrophorus squamulosus* (unfigured). The flora of the island differs from that of the mainland, especially in the number of Autobasidiomycetes. The island is bare and wind-swept, the mainland sheltered, fertile, and wooded. It is remarkable that *Hypoxylon coccineum*, so common on beeches in S. England and elsewhere, is unknown. Hawley's work consisted of some three weeks' collecting, resulting in a list of 283 species, with but few coprophilous species and the minute Fungi Imperfecti. The chief woodland is in the N.E. There are two districts: (1) exposed pastures, and (2) cultivated tracts. Several interesting maritime specimens were collected, on *Plantago maritima*, etc. The absence of woodland determines the relative poverty of Autobasidiomycetes here, though there is an excess of twenty found in

the Faeroes, with the flora of which comparison is made, and where too it is to be remarked that there were few pratal species. In this list 101 are new to Ireland, eight are new to Britain, one new to science. Mr. A. D. Cotton found all the maritime fungi. Notes follow the list, in which no localities are given, though most were found near Westport. Hawley here separates *Hypoxyylon pileatum* and *H. terrigenum*. He found the spores of *Microglossum atropurpureum* Karst. variable, and suggests *Epicymatia Balani* Wint. is better placed under *Mycosphærella*. A South American species, *Phomatospora argentina* Spegg., first found here, is said to differ but little from the European *P. ovalis* (Pass.) Sacc. The genus *Candelospora* is regarded as allied to *Microsporium* in the penicillate branching well shown in the figure, differing in the single terminal conidia. It is found on dead holly leaves.

Rea was unfortunate in his choice of weather, meeting on the mainland with snow and drought. The best wood he found was Brackloon, where there are oak, beech, pine, sycamore, holly and alder, and much leaf mould. The species of *Cortinarius* were especially numerous and in good condition. He records 667 species and varieties, 232 new to Ireland, five new to Britain. In this list localities are given, which is a distinct advantage. *Corynella glabrovirens* is regarded as allied more closely to Calloriaceæ than Bulgariaceæ. *Urceolella incarnatina* (Quel.) Bond., new to Britain, is not considered to be related to any other British genus. *Anthostoma saprophilum* E. and E. is new to Europe. The new species *Hygrophorus squamulosus* resembles *Tricholoma repens* in the tomentose margin of the piles, and differs from *H. olivaceoalbus* Fr. in the floccose squamules, characters sufficiently distinct to warrant a new name. Both accounts of the Clare Island fungi are worthy of careful study.

THE GENUS FUMARIA IN BRITAIN. By H. W. PUGSLEY, B.A.
Supplement to the "Journal of Botany," January to July
1912. Pp. 1-76, with one Plate.

MR. PUGSLEY here distributes the British plants of this genus into eight species, two sub-species, and fourteen varieties with sub-varieties and one hybrid.

The number of pages here used to describe and treat on these will at once show how full the work is; the only fear one has is, will it be the fate of all British genera? If so, one can but pity the student when wading through the series. Even the artificial key on pages 72 and 73 makes one wonder if any person will ever try to name a specimen by it. Certainly, if all this has to be learnt, the oft-repeated remark as to botany, "all hard names," will be exemplified.

Still, the trend of all botany is to specialise, and it is hard to find fault with good honest work simply because it is long in telling.

Mr. Pugsley has evidently studied the genus very closely and with

much care, and if means could be adopted to shorten the matter for a flora, it would represent good and painstaking work.

In addition to the former new species (*occidentalis* and *purpurea*),¹ we have now a third described (*F. paradoxa*), two sub-species, one hybrid ($\times F.$ *Painteri*), and several varieties, etc.

Under *F. paradoxa* Mr. Pugsley certainly seems to have scored, as four Continental botanists referred this to quite another section of the genus, and I think in a case like this we may be forgiven for being a little proud of our countryman.

Lastly, the index of 121 names shows how much is included in the work.

PLANT LIFE AND EVOLUTION. Professor D. H. CAMPBELL.
 "American Nature Series," Holt & Co., New York, 1911.
 Price \$1.60 net.

MUCH has recently been written upon the subject of evolution following upon the celebration, both here and in America, of the jubilee of the publication of Darwin's "Origin of Species." In these discussions plants have not played so prominent a part as animals, hence we may welcome this book all the more, coming as it does from one of the American school, reared up in the traditions of Agassiz, Hyatt, Ribot, Cope, Marsh, Beecher, Osborn, and many other valiant supporters of Neolamarckism. In Europe we can point to Hering, Herbert Spencer, Pfeffer, Semper, F. Darwin, and Semon as able exponents of similar views. Moreover, Professor Campbell has done pioneer work on the development and structure of mosses and ferns, apart from other important studies. He may be said, in fact, to occupy that place in the New World which in the Old World we accord to Professor Bower, as doyen of cryptogamic morphology. Both have reached much the same conclusions (*vide* the "Origin of a Land Flora," "Plant Life on Land"), if by somewhat different methods, which is perhaps the best criterion of accuracy.

The book, which may be thoroughly recommended to English students, is admittedly written from a Neolamarckian standpoint, but whilst the author discusses in a masterly way all the theories of evolution, he accepts none as explaining the ultimate cause of evolution. Though primarily written for American students, it is safe to say it is of international interest, since the treatment of the subjects, discussed by one who is a specialist in his own particular field, displays so wide and intimate a knowledge of current work and thought in other fields, with so well balanced and critical an estimate of the value and relative bearing or otherwise of each upon the matter in hand, that the book may be placed on the shelf as an important study in origins, especially applicable to the plant world. Whilst it provides all the material for a text-book of morphology or

¹"Jour. of Botany," 1902, p. 129; 1904, p. 217.

physiology, general ecology and etiology, it is written from a genetic standpoint, so that the *meaning* of structures or phenomena discussed is at once apparent. Moreover, not only are the latest discoveries in botanical work, recent or fossil botany, referred to, but many of the more important zoological facts are contrasted with them. It will illustrate the scope of the work best perhaps to refer to a few of these. In connection with the origin of life, Winogradsky's researches on nitrogen bacteria are mentioned. In discussing the lower plants, Bower's theory of sterilisation finds a place, and the antithetic alternation of generations of pteridophytes and bryophytes is affirmed.

In relation to heredity, F. Darwin's views on memory are accepted, and, we think, with good reason. Bower's theory of sterilisation is however, not accepted, an entirely separate origin for the sporophyte in club-mosses and ferns being assumed. Researches amongst the carboniferous and mesozoic floras as to the origin of seed plants by Scott, Seward, and Wieland are given due prominence. By the way, Seward's view that conifers such as *Araucaria* are related to the Palæozoic lycopods is favoured. The cumulative effects of stimuli are illustrated by Jennings' work on Infusoria. In determining the value of current theories of the origin of species, the mutation theory of De Vries and Mendel's laws of heredity are fully discussed, but Lotsy's views as to the cause of mutations are preferred, the germ-plasm theory, in so far as plants are concerned (since they are more plastic and respond to external stimuli more readily), not being considered to apply. The nature of the Palæozoic climate is explained on Manson's view that a mantle of cloud excluded sunlight. Great stress is laid upon Kleb's experiments as to the effect of stimuli in determining sex and regulating other factors of the environment. All the important results of plant breeders bearing on the questions discussed are surveyed, and Bailey and Burbank are cited here. Winckler's work on graft hybrids also receives adequate notice.

The book is divided into ten chapters, including an introduction, the factors in evolution; the lower plants; the origin of land plants (which are derived from green algæ); seed plants, leading on from heterospory in pteridophytes from the zygote or resting stage in algæ required by dry conditions; the Angiosperms, where the division into monocotyledons and dicotyledons is regarded as artificial, and their characters considered as adaptive, developed in parallel series; environment and adaptation, the terrestrial phase being the cause of seed plants, and their possession of fruit is regarded as the cause of their dominance. The chapter on plant distribution is especially interesting and will appeal particularly to American students. The human factor in plant evolution is dealt with from an original outlook, and the great importance of extinction is adequately recognised.

The origin of species is lucidly expounded, and it is justly remarked that plants differ from animals in this respect, for while the germ-plasm may play a part in the case of the latter, in the case of plants, "to assume that there is a special germ-plasm, which is passed

on from the tiny gametophyte to the non-sexual and long-lived sporophyte, and finally segregated in the spores, and again passed along to the next generation of gametophytes, is, to say the least, improbable." Here indeed lies the secret of the whole matter.

We miss any reference to sphagnales in the discussion of the origin of the lower plants. The term prothallus is neglected, and pollen spore is used for pollen grain. Owing to subdivision of the matter there is an unavoidable amount of repetition. Generally speaking, there is an absence of Americanisms, but we notice mold, meter, center, color, gray for grey, skepticism, fiber, canyon, favorite, meager, behavior, armor. The diæresis is used in re-established pre-eminently, zoospore. Sperms is substituted for spermatozoa. A few typographical errors occur: ax (p. 290), especialy (p. 229), futher (p. 335), unequaled (p. 147). The terms horsetail and clubmoss in reference to Palæozoic types are used literally; "forbears" is used for "ancestors" in reference to plants.

Each section leads up to the next admirably. The use of common types to illustrate facts, *e.g.* cross pollination in the nasturtium and scarlet geranium, is an excellent feature. The personal element is not entirely lacking. Visits to South Africa, where sunbirds were studied, and Krakatau, in 1906, are related.

We believe that this book if, as it is hoped, it is read widely in this country, will do much to stimulate inquiry upon new and right lines, and can thoroughly recommend its adoption as a standard text-book on plant life and problems of evolution.

BRITISH PLANT GALLS. By E. W. SWANTON. Methuen & Co., London. 8vo, cloth, pp. 251, sixteen coloured and sixteen photographs, with numerous blocks in the text. 7s. 6d. net.

THIS book should supply a long-felt want. Up to the present time we have had only one good work dealing with British galls, and that was mainly a translation by C. R. Straton of Dr. H. Adler's German work "Über den Generationswechsel der Eichengallen," and was limited to the galls occurring on the oak. E. T. Connold subsequently published some fine photographs of our British galls, but the accompanying text was of little assistance. The present work condenses into a readily accessible form a mass of information on this subject which for the most part is hidden away in various systematic works and scattered papers published by numerous scientific societies. Mr Swanton in his opening pages deals in a lucid manner with the origin of our British plant galls, and devotes a separate chapter to those that are caused by the Hymenoptera, Coleoptera, Lepidoptera, Diptera, Homoptera, Acari, Nematoda, Fungi, and Mycetozoa. In the detailed catalogue of British plant galls which succeeds the opening chapters the galls are arranged in botanical sequence on their hosts in accordance with the classification adopted by Engler in "Die Naturalischen Pflanzenfamilien," and

the specific name accepted by "The London Catalogue of British Plants," 10th edition. Eight hundred and eighty British plant galls are enumerated in this catalogue, but we fail to see that this number is justified, as we presume that it includes the same gall when present in the stem, leaf, or flower as a distinct gall, and it certainly includes the same fungus when growing on different hosts, whilst the hard woody excrescences so common on our ash trees caused by the fungus *Daldinia concentrica* are omitted from the work. The book is well got up, and the numerous coloured illustrations and photographs should make it a useful guide to the identification of our more common plant galls.

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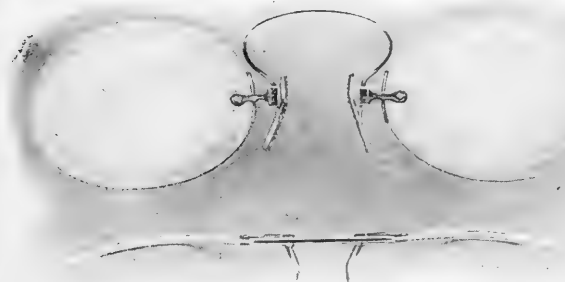
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