

## NOTES.

### ON THE SYSTEMATIC POSITION OF ISOËTES, L.—

The systematic position of this genus has been the subject of much speculation on the part of botanists. By some it has been placed among the Phanerogams<sup>1</sup>, by others among the Mosses<sup>2</sup>, and by the majority among the Vascular Cryptogams, the last being undoubtedly its true position. There has also been considerable difference of opinion as to its place among the Vascular Cryptogams. The earlier botanists all associate *Isoëtes* with *Pilularia* and *Marsilea*. Thus Linnaeus<sup>3</sup> associates these genera as a group of the Filices having '*fructificationes radicales*,' and Gleditsch<sup>4</sup> assigns to *Isoëtes* a similar position. The affinity of *Isoëtes* with *Pilularia*, *Marsilea*, *Salvinia*, and *Azolla*, is affirmed more definitely by Willdenow<sup>5</sup>, who associates them in the group Hydropterides; and by Batsch<sup>6</sup>, who unites these genera in the group Rhizocarpeae, as does also Bischoff<sup>7</sup>. Bartling<sup>8</sup> takes the same view, classifying the Rhizocarpeae into the three orders, Salviniaceae, Marsiliaceae, and Isoëteae.

On the other hand, De Candolle<sup>9</sup> removes *Isoëtes* from the Rhizocarpeae, the group being now termed Rhizospermae, and incorporates it with the Lycopodiaceae, on the following grounds: 'Ce genre semble se rapprocher, par son port, des rhizospermes, mais il touche réellement aux lycopodes; 1<sup>o</sup> par ses fructifications axillaires, et non

<sup>1</sup> Reichenbach (Conspectus, 1828) places *Isoëtes* together with Potamogetoneae and Aroideae in a group which he terms Limnobiae. Adanson (Fam. des Plantes, 1763) makes it a genus of Aroideae.

<sup>2</sup> Dillenius (Hist. Musc. 1741) places *Isoëtes*, together with *Pilularia* and *Subularia* in the Musci, under the name *Calamaria*. B. Jussieu (Ht. Trien. 1759) also places it among the Mosses.

<sup>3</sup> Linnaeus, Systema Vegetabilium, 1751.

<sup>4</sup> Gleditsch, Syst. Plant. 1764.

<sup>5</sup> Willdenow, Bem. Farrenkräuter, 1802; Species Plantarum, t. v, 1810.

<sup>6</sup> Batsch, Tab. affinitatum Regni Vegetabilis, 1802.

<sup>7</sup> Bischoff, Die Kryptogamischen Gewächse, 1828.

<sup>8</sup> Bartling, Ordines Naturales Plantarum, 1830.

<sup>9</sup> Lamarck et A. P. de Candolle, Flore Française, t. ii, 1815 (Lycopodiaceae, fam. Monocotyledonum cryptogamarum).

pas proprement radicales; 2<sup>o</sup> par l'existence des deux genres de coques qu'on trouve dans plusieurs lycopodes, savoir, les coques à poussière et les coques qui portent des globules chagrinés et munis de trois côtes rayonnantes à leur base.' In this he is followed by Brongniart<sup>1</sup>. Endlicher<sup>2</sup>, recognising the affinity between *Isoëtes* and the Lycopodiaceae, does not, however, unite them, but founds the class Selagines which includes the two orders Lycopodiaceae and Isoëteae. The attitude of Lindley on this point is curious. In his Natural System of Botany (Ed. 2, 1836) he follows De Candolle in including Isoëtes in the Lycopodiaceae, founding at the same time the cohort Lycopodales, consisting of the orders Lycopodiaceae, Marsiliaceae, and Salviniaceae; whereas in his later works (Vegetable Kingdom, Ed. 2, 1846, Ed. 3, 1853), he removes *Isoëtes* from the Lycopodiaceae and places it, with *Marsilia*, *Pilularia*, *Salvinia*, and *Azolla*, in an order Marsiliaceae. Payer<sup>3</sup> retains *Isoëtes* in the Lycopodiaceae, uniting it with *Psilotum* and *Tmesipteris* in the group Psiloteae. Berkeley<sup>4</sup> says with regard to it, 'on the whole, therefore, notwithstanding the difference in tissue, it should seem that it is a true Lycopod.'

The next important step in the classification of the Vascular Cryptogams was made by Sachs. Recognising the importance of distinguishing the homosporous (or isosporous) from the heterosporous forms, and at the same time overestimating it, in the three earlier editions of his Lehrbuch, he divides the Vascular Cryptogams into two groups, the isosporous, containing Filices, Equisetaceae, Ophioglosseae, and the heterosporous, containing the Rhizocarpaceae and the Lycopodiaceae, pointing out at the same time that, among the Lycopodiaceae, heterospory only occurs in the Selaginelleae and Isoëteae. The fourth edition of the Lehrbuch<sup>5</sup> (1874) shows a marked advance. The classification here adopted brings to light the appreciation of the fact that heterospory has arisen within the limits of the several groups, each group (ex. Equisetaceae) therefore including both heterosporous and homosporous forms; the Rhizocarpaceae are recognised as the heterosporous forms of the Fern-alliance,

<sup>1</sup> Ad. Brongniart, in Dict. Classique d'Hist. Nat. t. ix, 1826.

<sup>2</sup> Endlicher, Genera Plantarum, 1836-40.

<sup>3</sup> Payer, Botanique Cryptogamique, 1850.

<sup>4</sup> Berkeley, Introduction to Cryptogamic Botany, 1857.

<sup>5</sup> English edition, Oxford, 1882.

and the Selaginelleae and Isoëteae, united into the group Ligulatae, as the heterosporous forms of the Lycopodium-alliance. It is as follows:—

Class I, Equisetaceae.

„ II, Filicinae.

Order 1. Stipulatae (incl. Ophioglosseae, Marattiaceae, Osmundaceae?, Schizaceae?).

„ 2. Filices.

„ 3. Rhizocarpace.

„ III, Dichotomae.

Order 1. Lycopodiaceae (Lycopodiaceae, Psiloteae, Phylloglosseae).

„ 2. Ligulatae (Selaginelleae, Isoëteae).

In the edition of the systematic portion of the Lehrbuch by Goebel<sup>1</sup>, the classification is in the main adhered to, though with some modifications. Thus, the class Equisetaceae is reconstituted as Equisetinae, certain heterosporous fossil forms probably belonging to this group being included. The orders of the Filicinae are arranged in two groups in accordance with the results of Goebel's researches on the development of the sporangia: the majority of the Ferns being grouped with the Rhizocarpace (now termed Hydropterideae) as Leptosporangiate Filicinae, the remainder (Ophioglosseae, Marattiaceae) constituting the Eusporangiate Filicinae. Sachs' class Dichotomae is re-named Lycopodinae<sup>2</sup>, as Sachs' name is misleading. There are three orders of Lycopodinae: Lycopodiaceae (*Lycopodium*, *Phylloglossum*), Psilotaceae (*Psilotum*, *Tmesipteris*), Ligulatae (Selaginelleae, Isoëteae). The proposal is made to distinguish homosporous and heterosporous forms in the order Lycopodiaceae, the heterosporous forms being represented by the fossil genus *Lepidodendron*, but the value of this is questionable. *Selaginella*

<sup>1</sup> Goebel, Grundzüge der Systematik, 1882; Outlines of Classification and Special Morphology, Oxford, 1887.

<sup>2</sup> It should be borne in mind that the term Lycopodinae had been previously used in a different sense by Link (Enumeratio, 1822) as the equivalent of Lycopodiaceae of De Candolle. The order Lycopodineae was founded by Swartz (Syn. Fil. 1806) to include the genera *Lycopodium*, *Tmesipteris*, and *Psilotum*, and this term has since been used in many different senses by various writers.

appears to be the real heterosporous form corresponding to *Lycopodium*, and probably the fossil heterosporous Lycopodinous forms belong really to the Selaginelleae.

Although this position of *Isoëtes* has met with general acceptance, yet it is a question whether it really corresponds to its true affinities. Goebel himself says<sup>1</sup>, 'The groups which have been brought together under the name of Ligulatae have scarcely anything in common but the presence of a ligule, and it would be better perhaps to make separate divisions of them.' But if there is little in common between the Isoëteae and the Selaginelleae, there must be still less in common between *Isoëtes* and the Lycopodiaceae. The question at issue is, therefore, not merely whether the Selaginelleae and the Isoëteae should be separated, but whether *Isoëtes* really belongs to the Lycopodinae at all. This raises the further question; if *Isoëtes* be removed from the Lycopodinae, with what group of Vascular Cryptogams shall it be associated? It is the object of the present note to endeavour to answer these questions.

Taking first the question of the affinity of *Isoëtes* with the Lycopodinae, it becomes at once apparent that there are many important differences between them. The general characteristic of the sporophyte of the Lycopodinae is that the stem is slender and much branched, the leaves being small and numerous; in *Isoëtes*, on the contrary, the stem is short, thick, and unbranched, and the leaves are relatively large. It is true that in habit *Phylloglossum* more nearly resembles *Isoëtes* than it does the other Lycopodinae; but even here<sup>2</sup> there is a branching of the stem, at least in the sporangiferous forms, in connexion with the formation of the tubers. Again, the sporangia of the typical Lycopodinae are borne on sporophylls which are confined to special branches; and in the majority the sporophylls differ from the foliage-leaves and are aggregated together into cones on special shoots: in *Isoëtes* all the foliage-leaves are sporangiferous. Further, so far as the embryogeny of the sporophyte is known in the Lycopodinae, that is, in the case of *Lycopodium* and *Selaginella*, there is a suspensor but no primary root; whereas in *Isoëtes* there is a primary root but no suspensor. As regards the gametophyte, the mode of germination of the microspores is much the same in *Isoëtes*

<sup>1</sup> Outlines, p. 196.

<sup>2</sup> Bower, On the development and morphology of *Phylloglossum Drummondii*, Phil. Trans. II, 1885.

and in *Selaginella*, but there is the well-known difference in the germination of the macrospores.

These differences between *Isoëtes* and the recognised members of the Lycopodinae are surely sufficiently striking to raise a doubt as to the propriety of continuing to include them all in one group, and thus the question is raised as to what other position can, with any probability, be assigned to *Isoëtes*.

In its general habit, and in the absence of sporangiferous cones and specially differentiated sporophylls, *Isoëtes* resembles the Filices, as also in the more general features of its embryogeny. This relationship is emphasised in a remarkable manner if, as Sadebeck suggests<sup>1</sup>, the velum of *Isoëtes* be truly homologous with the indusium present in many Filices and in the Salviniaceae. It must be admitted, however, that both the male and female gametophytes of *Isoëtes* resemble rather those of *Selaginella* than those of the Hydropterideae.

The general tendency of these remarks would seem to be towards a reunion of *Isoëtes* with the Rhizocarpae; but in view of Goebel's researches on the development of its sporangium this cannot be done. *Isoëtes* is distinctly eusporangiate, whereas the Rhizocarpae are as distinctly leptosporangiate. If *Isoëtes* is to be included in the Filicinae, it must be connected with the eusporangiate forms of that group. This is, in fact, the answer to the question as to the systematic position of *Isoëtes*, if removed from the Lycopodinae: it is a heterosporous form, the only one hitherto recognised as such, of the Eusporangiate Filicinae. It certainly resembles the Ophioglosseae and the Marattiaceae in its general habit; in *Isoëtes* as also in these forms the stem is remarkable for its extremely small longitudinal growth, for the consequent absence of internodes and of branching, for the entire concealment of its surface by the insertions of the leaves, and for the formation of roots in acropetal succession close behind its apex. There is a more special point of resemblance, though it may amount to no more than an analogy, between the imperfectly multilocular sporangia of *Isoëtes* and the compound sporangium of most of the Marattiaceae.

Doubtless, many objections will be raised to this view of the

<sup>1</sup> Sadebeck, Die Gefässkryptogamen, in Schenk's Handbuch der Botanik, I, p. 326 k, 1879.

systematic position of *Isoëtes*, some of which I will now endeavour to meet by anticipation.

In the first place, it may be objected that, in the growth in thickness of its stem, *Isoëtes* differs from the Filicinae and indicates a relationship with the extinct Lycopodinae. In reply to this it may be pointed out that secondary growth in thickness of the stem is by no means a peculiarly Lycopodinous character; and further, that some indication of such secondary thickening is to be found in the rhizome of existing Ophioglosseae.

Secondly, the absence of a single apical cell in the growing-point of either stem or root may be urged as an objection to the incorporation of *Isoëtes* with the Filicinae. This is not, however, an objection of any weight; for among the Lycopodinae, on the one hand, the presence of a single apical cell is common in *Selaginella*, and among the Filicinae, on the other, the presence of a single apical cell is not universal, there being in the roots of the Marattiaceae a group of apical cells.

It may be added here that Russow<sup>1</sup> has already drawn attention to certain histological resemblances between *Isoëtes* and the Ophioglosseae.

Further, the resemblance between the male and female gametophytes of *Isoëtes* and *Selaginella* may be urged as a ground for keeping these genera together, and therefore also for retaining *Isoëtes* among the Lycopodinae. It has been already pointed out that the two genera do differ in this respect, and it may be further suggested that the reduction of the gametophytes of *Isoëtes*, as compared with those of the Hydropterideae, is just what might be expected in higher and lower groups of the same series. In fact, the comparison of the gametophytes of *Isoëtes* and *Selaginella* rather supports the view that they are forms, not belonging to one group, but occupying corresponding positions in two different series: that is to say, that *Isoëtes* occupies in the Filicinae the same relative position as *Selaginella* in the Lycopodinae.

The presence of a ligule in both *Isoëtes* and *Selaginella* might also be brought forward as a reason for classing them together; but, when contrasted with the wide difference in the class-characters, the importance of this common feature is but small. Moreover, it

<sup>1</sup> Russow, Vergleichende Untersuchungen, Mém. de l'Acad. imp. de St. Pétersbourg, sér. 7, t. xix, 1872, p. 192.

is easy to imagine that a ligule may have been developed in the Filicinae as it has been in the Lycopodinae, to say nothing of other groups of plants.

On summing up the evidence, it appears to be proved that there is quite as much resemblance between *Isoëtes* and the Eusporangiate Filices, as there is between *Selaginella* and the Lycopodiaceae; and further, that there is a closer resemblance between *Isoëtes* and the Eusporangiate Filices than there is between *Isoëtes* and the recognised Lycopodinae. At the same time, it must be admitted that there is some affinity between *Isoëtes* and the Lycopodinae. But it has long been recognised that the Eusporangiate Filices are those Filices which have most affinity with the Lycopodinae; and, in uniting *Isoëtes* with the former group, this affinity merely becomes more marked.

In conclusion, I would point out that the proposed change in the systematic position of *Isoëtes* throws an altogether new light on the evolution of the Phanerogams from the Pteridophyta, but I reserve the discussion of this question for a future occasion.

S. H. VINES.

**PRELIMINARY NOTE ON THE DEVELOPMENT OF THE ROOT OF EQUISETUM.**—I undertook, as the result of some discussion with, and at the suggestion of, my friends Dr. Vines and Mr. Gardiner, to determine the somewhat doubtful point of the development of the double endodermis of the root of Equisetum. As I have not, at present, time to prepare a full account of my investigations I propose to give in this note the main results obtained.

The apical cell of the root gives rise to two kinds of tissue which can at once be distinguished from one another by the sequence of divisions. Of these, one forms an outer layer or cylinder constituting the *exomeristem* of Russow; the other is enclosed by it forming a central cord of tissue constituting the *endomeristem* of the same author.

The exomeristem is distinguished from first to last by its cells being arranged in radial rows, most distinctly so in the zone of cells immediately surrounding the endomeristem. The endomeristem may be said to be chiefly distinguishable by the fact that its cells are not arranged in radial rows, and are also smaller than the cells of the exomeristem. No one can possibly fail to see at the first glance where the line passes separating the two meristems. This is especially



Vines, Sydney Howard. 1888. "On the systematic position of Isoetes, L." *Annals of botany* 2, 117–123. <https://doi.org/10.1093/aob/os-2.1.117>.

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