remarkable plant will bear the name of my colleague, A. G. More, Esq., who first called attention to it, and who has contributed in so many instances to the furtherance of British botany.

DESCRIPTION OF TAB. 199. — *Isoetes Morei*, D. Moore, from specimens collected at Lough Bray, Ireland. 1. A complete plant. 2. Vertical section of the corm. 3. Transverse section of the same. 4. Lower portion of a leaf, showing macrosporangium, veil and lingula. 5. Transverse section of microsporangium. 6. Transverse section of leaf. 7. Macrospores.

[N.B.—In section No. 4 the lingula is shewn *too narrow* at base, with margins more entire than they usually are.]

THE "PRO-EMBRYO" OF *CHARA*: AN ESSAY IN MORPHOLOGY.

By SYDNEY H. VINES, B.A., B.Sc., F.L.S., Fellow and Lecturer of Christ's College, Cambridge.

IT is to the researches of Pringsheim* that we are indebted for our knowledge of the fact that the fertilised oosphere of *Chara* does not immediately give rise, as had been stated by previous observers, to the sexual plant, but that a comparatively inconspicuous "pro-embryo" (Vorkeim) is developed from it, which presents no differentiation of stem and leaf, from one of the cells of which the axis of the sexual differentiated plant is formed as a lateral outgrowth. The details of the development of the "pro-embryo" have been recently described by De Bary.† From his description and figures it appears that the first stage in its development consists in the disappearance of the granules of starch and fatty matter from the protoplasm occupying the apex (free end) of the cell, and in the formation of a wall at right angles to its long axis as to divide it into two unequal cells—a small apical cell filled with hyaline protoplasm, and a much larger basal cell, the protoplasm of which is full of granules. The basal cell appears to act merely as a depository for nutrient materials to be used in the growth of the "pro-embryo," which is formed from the small apical cell in the following manner:—It is divided into two equal parts by the formation of a wall perpendicular to the first, lying therefore in the plane of the long axis of the oospore.‡ Each of the two cells thus formed grows out into a multicellular filament, the one being the "pro-embryo," the other the "primary root."

It is not necessary to follow the succession of cell-divisions which lead to the formation of these structures, nor is it essential to reproduce here Pringsheim's account of the development of the axis of the sexual plant from one of the cells of the "pro-embryo." What has been said above will be found sufficient to render intelligible the following discussion, which has for its object the elucidation of the morphological significance of the "pro-embryo."

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* 'Jahrb. für wiss. Bot.' Bd. iii. 1864, p. 294.

† 'Bot. Zeitg.' 1875, p. 377 (trans. in Journ. Bot., 1875, p. 298); also 'Nordstedt, and Wahlstedt, Flora,' 1875.

‡ Oospore = fertilised oosphere (central cell, gynosphere, ovum).

The interpretation given by Pringsheim* of the facts discovered by him is to this effect:—He considers that the structure which springs from the oospore of *Chara*, and to which he gives the name of " pro-embryo " (Vorkeim), is the exact morphological equivalent of the protonema which is developed from the spore of a Moss, and he infers from the existence in these plants of leafless structures intervening between the spore and the leafy plant, that the *Characeæ* and the *Muscineæ* are closely allied. This close relationship is, he believes, placed beyond doubt by the fact that Mosses alone of all plants possess organs which are analogous to the " pro-embryonic branches " (Zweigvorkeime) of *Chara*. The researches of Schimper † shew that " rhizoid prothallia " occur on the stem and leaves of many Mosses.

In proceeding to inquire into the adequacy of this interpretation, it may be at once admitted that the *Characeæ* resemble the *Muscineæ* in many points. Pringsheim does not fail to note in his above-mentioned work the similarity in structure and development existing between the nucule of *Chara* and the archegonium of a Moss. It is usual at the present time ‡ to place the *Characeæ* in the class *Carposporeæ*, and to speak of the nucule as a carpogonium. The soundness of such a classification becomes questionable when it is remembered that both in structure and development, as well as in the changes which it undergoes in consequence of fertilisation, the nucule of *Chara* differs absolutely from a typical carpogonium. The central cell (oosphere) of the nucule is surrounded from the first by a multicellular investment, and consequently that formation of a cystocarp around the oosphere after its fertilisation, which is so characteristic of the *Carposporeæ*, does not take place in the *Characeæ*. It is probably more correct to speak of the nucule of the *Characeæ* as being an archegonium.

In a recent paper upon the alternation of generations among the Thallophytes,§ Pringsheim groups the *Characeæ* with the *Fucaceæ* and the *Conjugatæ*, as being plants which do not present that dimorphism of the organs of fructification which is essential to the occurrence of alternation of generations. In making this statement he becomes unconsciously illogical. If, as he insists in his first paper, the " pro-embryo " of *Chara* be homologous with the protonema of a Moss, and if, as he asserts in his second paper, there be no stage in the life-history of *Chara* which corresponds to to the asexual generation (sporophore ‖) of the Moss, it must be admitted that the product of a fertilised oosphere is morphologically equivalent to the product of a germinating spore; that, for instance, the sporogonium of a Moss is equivalent to its pro-

* *Loc. cit.* p. 318, quoting from 'Monatsber. d. Berl. Akad.', 1862.

† 'Recherches anat. et morphol. sur les Mousses.' Strasbourg, 1848, pp. 13, 15, 19.

‡ 'Sachs, Lehrbuch,' 4te Auflage, 1874.

§ 'Jahrb. für wiss. Bot.', Bd. xi. 1877, p. 32.

‖ Thiselton Dyer has suggested the word " oophore " as a general expression for the sexual and " sporophore " for the asexual generation of plants. These terms are used in this sense throughout this paper.

tonema—a result which is obviously incorrect. An attempt might be made to escape from this dilemma by surrendering the supposed homology of the "pro-embryo" with a protonema, maintaining, however, the assertion that no alternation of generations presents itself in the life-history of *Chara*; but this would only lead to further difficulties. Such a view would at once isolate *Chara* from all other living organisms as being an individual the fertilised "ovum" of which produces an embryo quite unlike its parent, from which the sexual individual is subsequently formed by a process of budding. The life-history of *Chara* can be satisfactorily accounted for only on the assumption that an alternation of generations occurs in it.

It is admitted by those who agree in placing the *Characeæ* among the *Carposporeæ* that an alternation of generations does exist in the life-history of *Chara*, and the following is a brief account of the supposed mode of its occurrences. To make it quite clear a comparison may be instituted between *Chara* and a typically carposporous plant such as *Coleochæte*. As the result of fertilisation, the oosphere of *Coleochæte* undergoes successive divisions, which give rise to a number of similar cells. This mass of cells, invested by the walls of the mother-cell, is the sporophore of *Coleochæte*, for, at a later period, these cells become isolated; each of them is in fact a spore (carpospore), and from each of them a zoospore is emitted, from which the oophore is developed. In *Chara* the fertilised oosphere does not give rise even to so simple a spore-producing apparatus as that of *Coleochæte*. It remains unicellular; it is, in fact, converted directly into a single carpospore, and this is all that represents the sporophore in the life-history of *Chara*. It is only when this spore is about to germinate that it becomes multicellular by the formation of cell-walls within it in the manner described by De Bary. This comparison may be conveniently expressed in the following tabular form:—

	Oophore.			*Sporophore.*
Coleochæte ...	———	———	Plant.	Oospore.
Chara	Proembryo.	———	Plant.	Carpospore.
Moss	Protonema.	———	Plant.	Sporogonium.

This view certainly harmonises with Pringsheim's theory of the homology of the "pro-embryo" with a protonema, but it presents obvious difficulties. It is not easy to realise that the so-called carpospore of *Chara* is the morphological equivalent of the whole oospore of *Coleochæte*, and therefore also of so complex a structure as the sporogonium of a Moss, and these difficulties are very much increased by Pringsheim's recent paper above referred to. In it he satisfactorily demonstrates that the spore of a Moss or of a Fern, for instance, is not the final stage of the sporophore, but that it is the first stage of the oophore. This being the case, the table given above is incomplete, all mention of the spore (except in the case of *Chara*) being omitted. In its complete form it is as follows:—

	Oophore.			*Sporophore.*
Coleochæte ...	Carpospore.	———	Plant.	Oospore.
Chara	Carpospore.	Proembryo.	Plant.	Carpospore.
Moss	Spore.	Protonema.	Plant.	Sporogonium.

This statement of the case makes it evident at a glance that the hypothesis of the direct conversion of the oosphere of *Chara* by fertilisation into a single carpospore results in a paradox. It compels us to regard the carpospore of *Chara* as being not only the sporophore but also the first stage of the oophore of the plant; or, in other words, to consider the carpospore of *Chara* as being the morphological equivalent of the oospore of *Coleochæte* and of the sporogonium of a Moss, and, at the same time, of a single spore of either of these plants, a view which is quite untenable. Moreover, such a direct conversion of an oosphere into a single spore is quite unparalleled among plants which exhibit an alternation of generations. In all such plants the result of the development of the fertilised oosphere is the production of *numerous* spores. Further, the mode of "germination" of this "carpospore" of *Chara* is quite different from that of the spores of other plants. When a spore germinates it usually protrudes a germinal filament (Keimschlauch) from any portion of its surface, but in *Chara* the protrusion of the filament is confined to a definite spot, and its formation is preceded by certain well-defined and apparently constant cell-divisions. It appears, therefore, that this view of the alternation of generations in *Chara* is unsatisfactory, for it is based upon an unwarrantable assumption, and it fails to explain all the phenomena of the life-history of the plant.

An attempt may now be made to give an interpretation of these phenomena which shall have a more secure foundation, and which shall interpret them in a more satisfactory manner. The first cell-divisions which take place in the fertilised oosphere of *Chara* are not unlike those which take place in that of *Coleochæte*, but the final result is different in the two cases; in *Coleochæte* the cells formed fall apart, but in *Chara* they remain connected and certain of them give rise to the "pro-embryo" and to the "primary root." The processes of growth exhibited by the "germinating carpospore" of *Chara* correspond much more nearly to those which accompany the development of an embryo from a fertilised oosphere than to those which occur in a germinating spore. It is interesting to compare, from this point of view, the embryology of *Chara* with that of the *Hepaticæ*. In *Chara*, the first division of the oosphere takes place, as we have seen, in a plane at right angles to the long axis of the archegonium, and this is the case also among the higher *Hepaticæ* (Jungermannieæ); but this difference exists, that in *Chara* two unequal cells are formed, whereas the two cells of the *Hepaticæ* are equal in size. The more superficial of the two cells in the *Hepaticæ*—the one, that is, which immediately underlines the neck of the archegonium—undergoes numerous divisions, by means

of which the tissue of the future sporogonium is formed, and the more deeply-placed cell gives rise to the tissue of the seta and foot (embryophore). In *Riccia*, however, the whole oosphere is devoted to the formation of the sporogonium. In *Chara*, the more superficial of the two cells gives rise to the "pro-embryo" by repeated divisions, whereas it appears that the deeply-placed larger cell undergoes no change. Since their mode of origin is the same, it is reasonable to suggest that the "pro-embryo" of *Chara* is the homologue of the sporogonium of the *Hepaticæ*, and that the basal cell of the former is the homologue of the seta and foot of the latter,—that the "pro-embryo" and the basal cell together are equivalent to the sporogonium with its seta and foot. It must not be forgotten, however, that in *Chara* the "primary root" is derived from the apical cell as well as the "pro-embryo." From the researches of Nordstedt and Wahlstedt * it appears that this development of a "primary-root" is not absolutely constant, and that when it does not take place the whole of the apical cell gives origin to the "pro-embryo." This fact affords some ground for regarding this root not as a "primary" root, in the strict sense of the term, but rather as an adventitious root. As I have endeavoured to establish elsewhere,† a "primary root" is an organ developed from that segment of the oosphere which is diagonally opposite to that one in which the apex of the stem is formed. Of this the Ferns and *Equisetaceæ* and also the *Phanerogams* offer good examples. When, as in *Chara*, the first root is formed from that half of the oosphere which gives rise also to the stem, it must be regarded as being adventitious. Of this *Selaginella* and the *Coniferæ* afford examples. It may be objected that the inequality of the two cells in *Chara* destroys the homology which is here suggested, but this objection has not much weight. It is not denied that the sporogonium of *Riccia* is homologous with the sporogonium, seta, and foot of one of the other *Hepaticæ*, because in *Riccia* the sporogonium is formed from the whole instead of from half of the oosphere, and therefore the homology of the "pro-embryo" of *Chara* with the sporogonium of one of the *Hepaticæ* cannot be denied on the ground that it is formed from a small part of an oosphere the greater part of which is devoted to the formation of a foot.

On this view the "pro-embryo," or rather the true "embryo" of *Chara* must be regarded as the sporophore of the plant. The following table will illustrate this view in all its consequences:—

	Oophore.			*Sporophore.*
Coleochæte ...	Carpospore.	———	Plant.	Oospore.
Chara	———	———	Plant.	Embryo.
Moss...	Spore.	Protonema.	Plant.	Sporogonium.

* *Loc. cit.*

† On the Homologies of the Suspensor, 'Quart. Journ. Micr. Sci.', January, 1878.

A very obvious objection is at once suggested by this table, viz., that if it be correct the sporophore of *Chara* is represented by an organ which has never been known to produce spores. It must not be forgotten, however, that the transition from the sporophore to the oophore in plants which present a well-marked alternation of generations is not necessarily effected by means of spores. The recent researches of Pringsheim * and of Stahl † have shewn that the seta and the sporogonium (*i. e.* the sporophore) of a Moss may, under certain conditions, give rise to a protonema upon which the moss-plant (oophore) is subsequently developed as a lateral outgrowth. From the observations of Müller ‡ we know that the protonema of a Moss is merely the simplest possible form of its leaf-bearing stem. These facts warrant the assertion that a direct transition from the sporophore to the oophore can be effected in Mosses without the intervention of spores. It is not so paradoxical, therefore, as it appears to be at first sight, to apply the term "sporophore" to an organ which does not actually produce spores. It may be inferred that the condition which is accidental in Mosses is permanent in *Chara*, in which plant the sporophore remains rudimentary, producing no spores, but giving rise to the oophore by lateral budding from one of its cells.

The vegetative reproduction by means of the "pro-embryonic branches"—or, as should now be said, "embryonic branches"—which has been described in detail by Pringsheim, and which is of common occurence in *Chara*, affords some indirect but valuable support to the views here advanced. These embryonic branches spring from the nodes of the stem, and closely resemble the embryo in their structure. Like the embryo, an embryonic branch gives origin to a sexual plant by a process of budding from one of its cells which lies behind its apical cell. Expressing these facts in general terms this process may be described as the development of numerous sporophores (embryonic branches) by budding from the oophore (*Chara*-plant), as an instance, that is, of a transition from an oophore to a sporophore without the intervention of sexual reproductive organs (Apogamy, *De Bary*). Other instances of this occur among Ferns. It has been found § that the prothallus (oophore) of certain Ferns (*Aspidium filix-mas cristatum*, *Aspidium falcatum*, *Pteris cretica*) gives rise to the fern-plant (sporophore) by a process of budding without the development of any sexual reproductive organs, and that this is the only means by which these Ferns are reproduced.

It appears from the foregoing facts and deductions (1) that a well-marked alternation of generations occurs in the life-history of *Chara*, and (2) that the *Chara*-plant with its reproductive organs is

* 'Jahrb. für wiss. Bot.' Bd. xi. 1877, p. 1.

† 'Bot. Zeitg.' 1876.

‡ 'Die Sporenvorkeime etc., der Laubmoose.' 'Arb. d. bot. Inst. in Würzburgh,' Bd. I., Heft. iv., 1874.

§ Farlow, on asexual growth from the prothallus of *Pteris cretica*. 'Quart. Journ. Mic. Sci.', vol. xiv., 1874.
De Bary; Ueber apogame Farne, &c. 'Bot. Zeitg.', 1878.

the oophore, the sporophore being represented by the embryo, *i.e.*, the product of the development of the central-cell of the archegonium. In order to indicate the fact that no spores are ever produced, so far as is at present known, by the sporophore of *Chara*, we may speak of this plant as being "aposporous," using a word which is symmetrical with the term "apogamous," applied by De Bary to those Ferns in whose life-history no process of sexual reproduction occurs.

If this interpretation of the facts in the life-history of *Chara* be in any measure a correct one, it will necessarily have an important bearing upon the question of the systematic position of the *Characeæ*. This question has been recently discussed in these pages by Bennett* and by Caruel.† The former, accepting the prevailing account of the life-history of *Chara*, and perceiving the many features which the *Characeæ* and the *Muscineæ* possess in common, suggests that the *Characeæ* may be Mosses, rendered abnormal by their aquatic habit, in which the formation of the non-sexual generation (sporophore) is altogether suppressed. There is nothing in the views advanced in this paper to contradict the existence of a relationship between the *Characeæ* and the *Muscineæ;* on the contrary, there is much to establish it. It is true that the "pro-embryo" of *Chara* cannot any longer be regarded as the homologue of the protonema of a Moss, but, on the other hand, it is here contended that the embryo is the homologue of the sporogonium of a Moss; so that although these views destroy one link in the chain of analogies and homologies which connects the *Characeæ* and the *Muscineæ*, they replace it by a stronger one. I quite agree with Bennett's conclusion, on account of the facts detailed in the earlier part of this paper, that it is incorrect to place the *Characeæ* among the *Carposporeæ*, for they have stronger affinities with the Mosses.

Still it must not be overlooked that the *Characeæ* do possess certain features in common with some of the *Carposporeæ*. such as a very simple histological composition and their peculiar corticatation. And further, although, as Bennett states and as I have already pointed out, the "nucule" of *Chara* is essentially different from a carpogonium,—is, in fact, an archegonium,—yet it presents a peculiarity in which it resembles the carpogonium of certain *Carposporeæ*, and in which it differs from the archegonium of a Moss. This peculiarity consists in the existence of one or more cells (Wendungszellen, *A. Braun*) at the base of the central-cell, which have been divided from it. These cells are usually regarded as being the representatives of those forming the trichopore of the *Florideæ*, that is, as the rudiments of an organ which exists fully developed in allied plants, the antherozoids of which are not endowed with the power of movement, but which is unnecessary in the *Characeæ*, because in them the antherozoids are actively motile.

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* 'Journ. of Botany.' New Series. Vol. vii., July, 1878, p. 202.

† *Idem.* New Series, Vol. vii., September, 1878, p. 258. Also 'La Morfologia Vegetale.' Pisa. 1878.

I cannot proceed, therefore, as Bennett does, to unite the *Characeæ* with the *Muscineæ*.* I regard them as forming an independent group intermediate between the *Carposporeæ* and the *Muscineæ*. This is really to say that they link the Thallophytes to the Cormophytes, and this I believe to be actually the case. In the structure of their vegetative and reproductive organs they resemble the cormoid Thallophytes on the one hand and the thalloid Cormophytes on the other.

Caruel proposes to place the *Characeæ* (his Schistogams) between the Vascular Cryptogams (his Prothallogams) and the Phanerogams. He rejects, as I do, the supposed homology of the "pro-embryo" of *Chara* with the protonema of a Moss, and partly on this ground and partly on the ground that in Mosses the "neutral form" (sporophore ?) is definite in its evolution, whereas in *Chara* it is indefinite, he separates widely the *Characeæ* from the *Muscineæ* in spite of many obvious resemblances. Of these reasons the former is quite insufficient, as a consideration of the foregoing paragraphs of this paper will shew. As to the latter, the observations of Pringsheim and of Stahl, to which reference has been made above, shew that the "neutral form" of a Moss is not necessarily definite in its evolution. I am unable to ascertain exactly from his paper or from his book what Prof. Caruel considers to be the "neutral form" of *Chara*, but if it is either the oospore or the "pro-embryo," these surely are definite in their evolution. He goes on to separate the *Characeæ* from the Prothallogams on account of the absence from the former of "anything like the sexual prothallus so peculiar to the Prothallogams," and also on account of "the complex organisation of the antherocyst (globule) compared to the simpler antheridium, and of the oogemma (nucule) compared to the archegonium, and of the different origin of both, which in *Characeæ* proceed directly from the neutral form and not from spores produced by it." Are we then to cease to regard the sexual *Chara*-plant as corresponding to the prothallus of a Fern, and are we to consider the sexual organs which it bears as a separate sexual generation? Surely this is a view which has no foundation in true morphology. Can there be any reason for regarding the archegonia and antheridia of *Chara* as constituting a generation distinct from the plant which bears them, whilst no such distinction is made in the case of the prothallus of a Fern? The feature of the *Characeæ* to which importance is attached as indicating a relationship with the Phanerogams is the "marked resemblance of structure, coupled with the same origin, between the oogemma of the one and the gemmule (misnamed ovule) of the other," and further, "the similarity of origin in the male forms of both the groups, equally proceeding from bodies which are modifications of leaves." Even if we admit, as Caruel does, that Celakovsky † has satisfactorily proved that the central-

* This has been done also by Trevisan. (Conspectus ordinum Prothallophytorum, in 'Bull. Soc. Bot. Belg.', 1877.) He unites the *Bryophyta* and *Phycophyta* (*Characeæ*) into one group which he calls *Anthogamæ*.

† 'Flora,' 1878, p. 49.

cell of the archegonium of *Chara* (oogonium, Celakovsky) and the ovule of a Phanerogam are both phyllomes, and that the investment of the former is comparable to that of the latter (ovary), still this fact does not necessarily establish the existence of a close relationship between these plants. Do we not find among Mosses archegonia which are morphologically phyllomes, and are not these organs usually invested by leaves forming either a perichætium or a perigynium? It is scarcely necessary to go so far as to the Phanerogams to find female organs which resemble those of the *Characeæ* in their morphological nature when they occur close at hand in the *Muscineæ*. The same remarks may be applied also to the male organs. It cannot be doubted that the antheridium of *Chara* much more closely resembles that of a Moss (which may be also a phyllome) than the stamen of a flowering plant. Caruel himself admits that great differences exist between the structure of the male organ of *Chara* and that of a stamen. This, together with the differences in the embryology of the two groups, suffices to keep them distinct.

The permissibility of such a comparison of the reproductive organs of *Chara* and those of a Phanerogam is very questionable. It is admitted on all hands that these organs in *Chara* belong to the oophore, whereas the ovules and stamens of a Phanerogam belong to the sporophore. It is difficult to imagine from what morphological stand-point it is that Caruel proceeds to institute it.

The ground upon which it is sought to establish the existence of a close relationship between the *Characeæ* and the *Phanerogamæ* cannot be considered to be satisfactory, and if the interpretation of the facts of the life-history of *Chara* which is given in this paper be the correct one, they lose even the appearance of plausibility.

NOTES ON NEW ZEALAND FERNS.

By H. C. Field, Esq.

[The following notes, made from long observation of the Ferns of New Zealand in their native localities, were sent by Mr. Field in a letter merely intended for my own private instruction; but they contain so much that is interesting and valuable that I have asked and obtained his permission to publish them.—J. G. Baker.]

I think *Gleichenia circinnata* and *G. dicarpa* are merely forms of the same plant. Here the lobes of both fold tightly back, so as to cover the sori, the only apparent difference being that, while those of the former are reflexed symmetrically, so as to cover all up closely, those of the latter fold back lopsidedly, so as to leave a sort of deep cup-shaped cavity on the upper side of each lobe, or perhaps I should rather say on the side of it farthest removed from the stipes of the frond. I hardly fancy this distinction sufficient to justify their being separately classed; and moreover, they