On the Fossil Genus *Sporocarpon*.

BY

R. C. McLEAN.

With Plates VIII-X.

SOME years ago the present writer gave a short description (1) of a group of fossil structures, occurring in the coal-balls of this and other countries, of which the true nature has long been problematical.¹ Minute and complex as these bodies are, they have often been misunderstood, and they have in consequence undergone many vicissitudes of classification since they were first described by Williamson (2). Although they are preserved in a typically vegetable manner, and constantly associated with abundant plant remains, it was thought proper, when the previous description above referred to was published, to establish the several genera as a group of extinct Protozoa. At the same time it was maintained that they should be included in the class Rhizopoda and that their affinities amongst living organisms were most nearly with the Radiolaria.

Notwithstanding this allegation of their animal nature they are historically the property of botanists, since only botanists have written or interested themselves about them, and they are, moreover, constantly passing under the notice of fossil botanists, so that perhaps one may be permitted to introduce an account of them into a strictly botanical journal, as being, so to speak, in our own province.

The question of affinities was fully discussed in the previous article, and it is needless to cover the same ground again, except to point out that no other explanation has offered anything like so satisfactory an exegesis of their structure, and that fresh observations have only tended to confirm the opinion previously advocated, while rendering any of the rival hypotheses practically untenable.

As fossil Rhizopoda (= Sarcodina) these organisms are remarkably isolated, for the only other orders in the class which have been found fossil are, of course, the Radiolaria themselves, and (to a much smaller extent) the Foraminifera; while as an *extinct* group of Protozoa they are unique.

¹ The present descriptions are intended to be *supplementary* to those details which were originally given.

Neither in the fossil Radiolaria nor in the Foraminifera is there any notable change of character between their earliest known forms and those of the present day. In the former case this covers nearly the whole period of the geological record, so that we may conclude that the Protozoa as a class are not only conservative of morphological character, but so fundamentally adaptable that the probability of any large group suffering complete extinction is correspondingly reduced. It is suggested that in these fossils we are dealing with a highly specialized offshoot from a stock normally oceanic in habitat, which had become adapted to life in the vast swampy lagoons of the Coal Measures period, in water, that is to say, probably brackish, and certainly highly charged with organic matter. Under these conditions they underwent a change of nature, the originally mineralized skeleton becoming a chitinized structure, with a consequent degradation of rigidity, while the quiet waters appear to have favoured a higher elaboration of the extra-thecal cytoplasm than is to be found in related pelagic forms. Life in a less highly oxygenated medium would indeed render it obligatory.

If these suggestions as to their origin from known forms of Protozoa be accepted as probable, it makes it easy to understand how liable they were to be extinguished when secular changes of level finally abolished the topographical conditions which had favoured them, and upon which they depended, as a parasite does upon its host, in a balance of adaptation.

The former account, which has been already referred to, included the four genera which were provisionally united into the family Traquairidae; namely *Traquairia*, *Sporocarpon*, *Oidospora*, and *Zygosporites*, while a fifth genus, *Calcisphaera*, morphologically similar, but found in limestones and preserved in calcite, was briefly dealt with, as being probably confamiliar with the other forms.

The first of these genera, *Traquairia*, has already been the subject of a memoir by Mrs. D. H. Scott (3), who is collecting further information with a view to more comprehensive treatment on a future occasion. In regard to *Zygosporites* nothing can, so far, be usefully added to what has already been written about it, while *Calcisphaera* calls for a much wider range of investigation, not only in the Carboniferous Limestones, but also in rocks of similar character from other Palaeozoic formations,¹ before a satisfactory presentation of its nature can be made. From the casual notes of its occurrence made by various geologists it appears to be widely distributed both in space and time, and it may have played a large part as a rock-former in the older calcareous strata. While not clearly differentiated in many cases from fossil Radiolaria, or what are accepted as such by geologists, yet its calcareous preservation and some details of its organization appear to give it a claim to separate consideration as an organism

¹ Possibly in Mesozoic formations also, e. g. the grey shales of the Keuper marl.

allied in both directions to Traquairidae and Radiolaria, and probably affording links of connexion between the two. It may be regarded as a parallel development to the Traquairidae, but with a mineralized skeleton. There remain then only the genera *Sporocarpon* and *Oidospora*, which it is here proposed to treat as one, giving a more detailed account of the species, with more complete illustration than was possible in the preliminary treatment, and sketching the probable lines of affinity between them and living Rhizopoda.

SPOROCARPON. Williamson.

1878. Williamson, On the Organization of the Fossil Plants of the Coal Measures. Part IX. 'Phil. Trans.', pp. 169–346.

The delimitation of the genus cannot be regarded as satisfactory, even for a fossil, inasmuch as it is scarcely possible to frame a definition which will reduce the divergent structures to a common denominator. Strictly speaking, almost all the six or more 'species' should be segregated as distinct generic types, and were it not for the fact that each genus so constituted would be practically monotypic this should be done now. Should it become possible in the future to distinguish more than one type within the limits of what is now called one species, as has been done in *Traquairia*, then the larger species thus subdivided will inevitably have to receive new generic titles. For the present, however, there is much to be said in favour of retaining the old name *Sporocarpon* to cover all the forms, since all are obviously closely connected, and, in the absence of fuller knowledge, too fine a subdivision would unquestionably be valueless. It should be clearly laid down at the start that *Sporocarpon* is no true genus, but a plexus of somewhat heterogeneous ingredients, imperfectly separable from one another and only referable in one or two particulars to a common type. The error of nomenclature is even greater in this case than in fossil plants in general, since so much depends, in lower organisms, on cytological details of the plasma, here no longer available as criteria.

The genus *Oidospora*, founded by Williamson at the same time as *Sporocarpon*, differs from the latter only in its smaller size. Indeed, it is not improbably merely a juvenile stage of *S. compactum*, though this cannot be regarded as established. It is monotypic, and it does not seem possible to frame any definition of the larger genus which will exclude the smaller, save only on the point of size, which is, on the other hand, so variable within the genus *Sporocarpon*, as at present constituted, as to make it unwise to lay stress upon it as a generic distinction. Considering this close approximation I propose to suppress its generic isolation and to treat it here as a species of the *Sporocarpon* group under the name of *S. Oidospora*.

To define the limits of *Sporocarpon* brings us against considerable difficulties. In my first account of the Traquairidae I gave a short

definition intended to cover all the known genera, but to lay down a stricter definition of one alone is less easy, if it is to be carried into any particularity. Nor is it a matter of much importance, if we bear in mind the reservations made above regarding the status of the genus.

Confining ourselves, then, to the widest generalities, the following is the taxonomic basis of the forms selected for description here. The description is, of course, subsidiary to that previously given for the group.

Sporocarpon.

Spherical or spheroidal organisms of minute but very variable size (0.03–0.35 mm.); without attachments, and surrounded by a stereomatic envelope composed of vesicles which may be radially or tangentially developed. These vesicles contained protoplasm and possessed the power of extension and development during the life of the organism. Reproduction as in the group as a whole.

Without proposing to split the genus up into new genera it is a matter of convenience to subdivide it into sections, the better to exhibit the interrelationships of the species.

These are as follows :

Sporocarpon § *Eu-sporocarpon* (i)

S. compactum.

S. tubulatum.

S. Oidospora.

§§ *Fredaia* (ii)

S. elegans.

§§§ *Diadematis* (iii)

S. cellulosum.

§§§§ *Sirion* (iv)

S. asteroides.

§§§§§ *Perichoderma* (v)

S. pachyderma.

In the classification originally proposed, only one subgenus, *Perichoderma*, was recognized, including the three latter species as given above, but they are obviously so divergent that nothing much was thus to be gained in clarity over the integral genus *Sporocarpon*. Consequently it has seemed better now to subdivide them further, while retaining the old generic title for all.

We will proceed to their description in order :

§ *Eu-sporocarpon*.

(i) *S. compactum*. Williamson, 'Phil. Trans.', pp. 169–349, 1878.

I look upon this as the central and typical species, as it is the most generalized type, and the others can be satisfactorily regarded as declensions or modifications from this as a primitive form.

The external envelope is formed, in the young state, of cylindrical cells, closely contiguous in the tangential direction and arranged with their long axes radially. There is only one layer, and the outer extremities of all are more or less abruptly acuminate. Although they are almost truly circular in cross-section there are no interspaces between the cells, for the spaces between the lines of actual contact are filled in by extra thickening of the walls, and the cells are slightly broader at the distal ends. In most specimens, and in those the best preserved, the outer pointed extremities of these cells or vesicles bear small dark papillae which may be seen to have finely tufted points, if a high magnification be used. By comparison with *Traquairia*, in which all the radial spines bear fibroid processes, which are clearly hollow, and serve to connect the interior lumen of the spine with the outside, it seems legitimate to conclude that these minute papillae are of similar nature.

The centripetal ends—the bases—of the cells abut upon the wall of the sphere, which is smooth and often fairly thick. The average length of the cells of the envelope is only about one quarter the diameter of the spherical interior space. The question of proximal openings into the interior cavity has not been at all easy to decide in this species. In some of the others, and in *Traquairia*, there can be no doubt that such do exist, a fact which strengthens greatly the unicellular view of the organism. Extremely thin, perfectly radial sections are scarcely possible, and it is generally in a somewhat thick tangential section, giving a hemispherical view, that the structure of the sphere wall is best seen. Those that have been available to me have shown no sign of any large openings, but in several specimens the sphere wall and the radial walls of each cell for a short distance up from the base can be seen to be covered with a very fine punctate marking, like the 'dots' on diatom frustules and just about as minute. Quite possibly this may have been a porose sieve-area which permitted junction of the protoplasm between the cells, and with the interior cavity.

That the cells of the envelope did contain living matter it is impossible to doubt, for they show a marked power of radial elongation. In older specimens many of the cells will be found lengthened into spines, three or four times as long as the original cells. These spines are rather obtuse, never acuminate as in the embryonic condition, so that it is evident that in growing the pointed apical portion of the cell must have shared in the extension of surface, and not have been merely pushed outwards from within by the intercalary elongation of the thinner radial walls. The whole mature spine, above the level of the surrounding cells, tapers gradually, and is covered with the minute nipples spoken of before, whose porose nature can sometimes be clearly seen. Some at least of these must have been added during the secondary growth of the cell. No instance of all the cells of an individual becoming elongated has come to my notice. Usually

only three or four are present in any given section, often grouped closely together, which is a clear distinguishing character between this species and *S. elegans*, where all the peripheral cells develop, though not all at the same time.

This elongation demonstrates clearly that protoplasm lived in the cells of the envelope; and, secondly, that the walls, even the thickened external walls, were not merely skeletal as in the Radiolaria, but were formed of organic material capable of extension. It is probable that the secondary growth of the cells was conditioned by the demand for an increased number of pores of communication in the adult reproductive organism, since it is through these atria that absorption would be chiefly carried on.

The whole organism bears a certain resemblance to *Volvox*, though with obvious differences. The formation of reproductive cells in the interior cavity, unless the protoplasm migrated there centripetally, hardly seems compatible with colonial nature. Most species show clearly that the various spaces of the organism were in open communication, and the localization of reproduction in the large interior cavity suggests strongly that this was a living part of the organism, not merely a mucilaginous medulla. No segmentation of the contents has been noticed except at sporulation, so that all the evidence points to their being truly unicellular, or at least coenocytic organisms. The method of reproduction in all the species is essentially similar, so that one description will serve for all.

Within the outer wall of the sphere comes a delicate 'capsule wall' normally in close contact with the sphere wall, but often shrunk away from it. This may bear fine markings, and is sometimes apparently formed of two separable thicknesses. The capsule contains a closely packed mass of thin-walled vesicles (the so-called *sporoids* of my first account), frequently embedded in frothy *periplasm*. Commonly these sporoids are empty, but one frequently finds specimens in which each one, more or less, holds a small dark-walled *spore* with a sculptured coat. These last may be fungal, but their mode of occurrence leans me to the view that they are the real reproductive cells; the sporoids being of the nature of mother-cells. There is no evidence to show how they were dispersed.¹ Diminutive or otherwise juvenile individuals have no sporoids in their capsules, spore formation only taking place at maturity.

Very little can be said about the subsequent history of these spores. Truly embryonic stages in the development of the spheres have not been recognized with certainty, and I am inclined to think that they were not, until approaching maturity, of a suitable consistency for fossilization. It is possible that *S. Oidospora* may be a young stage of

¹ Since the above was written I have received a very interesting drawing from Mrs. Scott (Fig. 9), in which a specimen of *S. asteroides* is shown (Scott Collection, 1788) apparently extruding the contents of its capsule through a dehiscence of the envelope, not by means of any definitely organized aperture.

S. compactum, and questionable juveniles of *S. tubulatum* and *S. pachyderma* have been found, but there is nothing to add on this point to what was said at the beginning of my first account, i. e. that the spores are apparently asexual autospores, developing directly into mature individuals by increase of size. Minute vesicles are apparently responsible for the markings on their surface, and these are thought to develop into the envelope 'cells' of the mature organism.

Average dimensions:

Total diameter, 320 μ .

Diam. of cells: Base, 16.5 μ .

Internal sphere, 220 μ .

Near top, 22 μ .

Length of cells, 50–60 μ .

Diam. of sporoids, 25–45 μ .

(ii) *S. tubulatum*. Williamson, 'Phil. Trans.', pp. 169–349, 1878.

This species is anomalous in being oval, though the difference in length of the two axes is not very considerable. All the same it affords a parallel to *Zygosporites oblongus*, although not so markedly elongated, and thus helps to illustrate the homogeneity of the group. Taking an average of the few specimens available, the greater diameter is about one-eighth more than the lesser.

The structure of the envelope in *S. tubulatum* is superficially similar to that in the preceding species, so that it is not surprising that it was originally named as a variety of *S. compactum*.¹ In the young condition there are contiguous tubular vesicles all over the exterior surface, their long axes disposed radially, as in the first species, though here the vesicles are nearly five times as long as broad. They are slightly broader distally, and their outer ends, instead of being sharply pointed, are smoothly rounded off, without any papillae or openings of any kind.

At the base of each such cell is a well-marked pore communicating with the interior of the sphere. Indeed in this species this form of opening is better shown than in any other. There can be no doubt that free interplay of living material existed between the interior cavity and the peripheral cells during life.

It is remarkable that both in this and the former species the cells of the envelope are very constant in size and regular in their adjustment each to the other. Just as in *S. compactum*, the vesicles of the envelope matured into long spines; but here we have definite evidence that they all elongated as in *S. elegans*, although probably in succession, not simultaneously.

Maturation of the spines was accompanied by swelling out into a globose bulb, at about the summit level of the young vesicles, in such a way as to thrust aside the neighbouring ones and clear a space round the proximal portion of the new spine. The apical half tapered regularly to a sharp, solid point, without any sign of perforations on its wall, the whole mature spine being more than twice as long as its parent vesicle

¹ Williamson, in his slide catalogue, not published.

and equal to more than half the diameter of the whole organism. A slight constriction develops just above the basal pore. In the oldest stages all the apical moiety of the spines may get knocked off, leaving only the disorganized basal portions. This can hardly have taken place during life, for the protoplasm would have been thus exposed through the broken ends. The breaking off of the spines in this way, found similarly in *S. elegans*, is evidence of fragility, which we might well predict from the general delicacy of the walls throughout development, but which is in striking contrast to the great flexibility that is evident in the spines of *Traquairia*.

A somewhat rare species. I have not seen more than half a dozen specimens, and none of these contained any reproductive cells or capsule. In size it is somewhat smaller than *S. compactum*, even in its greater diameter, though the spines are much longer, both relatively and absolutely.

The following are the principal elements:

Diameter over all :	Length of vesicles, (<i>circa</i>) 67 μ .
Greatest, 286 μ .	Breadth, 16 μ .
Least, 276 μ .	Length of mature spine, 155 μ .
Diameter of interior :	Breadth at swelling, (<i>circa</i>) 25 μ .
Greatest, 149 μ .	Proximal pore, 2.5-4 μ .
Least, 133 μ .	

(iii) *S. Oidospora*: mihi. *Oidospora anomala*. Williamson, 'Phil. Trans.', pp. 169-357, 1878.

This species is anomalously small, but otherwise seems to fall suitably into line with the two preceding organisms, in the present class. It consists of a spherical central portion, enclosed within an envelope of somewhat rounded vesicles, as closely set as their shape permits, and flattened at their bases, where they are attached to the wall of the sphere. No perforations have been observed, either to the exterior or to the interior, and the walls are all perfectly thin and smooth. The vesicles of the envelope are about equal to the diameter of the sphere in length. Although somewhat like *S. compactum* no intermediates between the two are known. The present species is probably therefore a substantive one.

Only two preparations have come under my notice, so that it is probably the most infrequent of the known forms. One of these is in the Williamson Collection at the British Museum (section numbered in catalogue 1552), containing large numbers, from among which Fig. 102 in Williamson's ninth memoir was taken. The other slide, containing only a pair, is in the University College London, Collection. Like most of the others, this species appears to have been gregarious, judging from the large numbers on one slide, but there is no definite sign of union into colonies. On slide W. 1552 there are a few individuals with markedly enlarged and elongated vesicles, suggesting, though not conclusively, elongation into spinous processes. No interior capsule or spores have been found.

*Dimensions:*Total diameter, 55 μ .Length of cells, 14 μ .Diameter of sphere, 28 μ .Breadth of cells, 10 μ .§§ *Fredaia*.*S. elegans*. Williamson, 'Phil. Trans.', pp. 169–348, 1878.

This was taken in my last paper as the type species of the genus, but I now refer *S. compactum* to that position, as the least specialized type. The present organism has an envelope formed of tapered spines, with a median and a proximal swelling, between which—that is, in the lower half—the shaft is constricted to a slender stalk. The median and basal swellings are contiguous all over the sphere, so that there is formed a 'colonnade' of the slender portions of the shafts and the continuous space which lies between them. As in *S. tubulatum* the spines must have been somewhat brittle, for only a few survive at full length even in the best-preserved specimens. They were broken off all about the same level, just above the median swelling, and it is easy to see, by the broken stumps which form the greater part of the envelope in most specimens, that originally each cell of the envelope formed a spine. Where the 'cells' of the colonnade touch one another their walls are thickened, so that where the spines break off, just above this level, there is a thickened honeycomb-like framework left behind at the outer surface of the colonnade layer. (See Pl. VIII, Figs. 1 and 3.) Occasionally spines may be observed flexed, but not often. The walls of the spines are perfectly smooth and free from perforations, but the tips are often bifid or trifid, with widely divergent segments, a character which has its counterpart in *Traquairia*. The lumen connects with the interior of the sphere by a single pore.

Williamson believed the spaces of the 'colonnade' to be filled by thin-walled cells, relying upon the appearances shown in tangential sections. I myself, finding that the walls of these 'cells', cut in tangential sections of the envelope, were double throughout, came to the conclusion that they were really the remains of a system of tangential tubuli, homologous with those of *Traquairia*, connecting up the proximal ends of the 'colonnade' units. The spaces of the 'colonnade' are not, I believe, occupied at all, but the appearance of traversing walls or tubuli may possibly be due only to the overlapping of the margins of the basal swellings, which can easily be observed in transverse section, and which may lead to this appearance of tangential connexions when seen from above.

The species is a fairly common one, and is often singularly plentiful when met with. Good specimens well deserve the specific name. Curiously enough, no specimens have been found which throw any light on the development of *S. elegans*, although we have good evidence of the history in both *S. compactum* and *S. tubulatum*. There is little doubt that the

young stage must have been very like the young stage of the former species, and may have been confounded with it.

The interior capsule and sporoids have been found very well preserved, with abundant periplasm. In the spines of this species, as well as others, I have sometimes seen very small spheres, not unlike the spores. They can hardly be true spores in such a position, and I believe they may be commensal protophytes, analogous to the testiculate flagellata sometimes found in modern Radiolaria.

Dimensions:

Total diameter, 480 μ .	Width at swelling, 25–35 μ .
Diam. of sphere, 360 μ .	Width at base, 25–35 μ .
Length of spines (base to tip), 180–240 μ .	Width of constricted part, 8–9 μ .
	Height of colonnade, 50–65 μ .

§§§ *Diadematis*.

S. cellulorum. Williamson, 'Phil. Trans.', pp. 169–347, 1878.

In this subgenus the true structure of the envelope is in some doubt. So far as can be judged there appear to have been divaricate spines in groups round the periphery, each group having something of a tiara-like appearance in side view. I have never seen any specimen in which these spines were fully developed, and it is open to question whether any elongation took place further than what has been observed. In this condition they form stout, comparatively short tubes, with dark and rather thick walls, blunt and open distally. Each group consists of longer tubes in the middle, the remainder declining in length outwards, in both directions, giving the impression of a kind of sorus with basipetal development.

That development did actually run in this order seems evidenced by the way in which the neighbouring elements of the envelope are deflected from the truly radial position, pushed away as it were by the elongation of the elements of the sorus. Between these widely separated groups of spinous processes the envelope is composed of similar, but quite short tubes, evenly distributed. In tangential section all appear to be hexagonal and close fitting, but in radial view the appearance is that of alternating cells and vacant spaces.

Running tangentially between all these tubular processes are several series of fine dark lines. These may be either very fine tubules themselves, or thickening bands upon the radial cell-walls, or, more probably, pairs of them may be the edges of comparatively stout tubes in longitudinal section, or they may be the walls of true cell elements, filling in the interspaces between the radial tubes. As I said before, the specimens available have not been sufficient to elucidate the point, though I incline to the second view. If they are really cells, there would be afforded a welcome link with the structure of the following species, which otherwise is extremely isolated.

Proximal pores communicating with the interior have been seen at the base of the radial tubuli. Central capsule and reproductive cells normal.

No certain developmental phases have been observed, but a spherical body with an envelope of a single layer of small square cells with dark walls, once found, suggests a possible juvenile form.

Dimensions:

Total diameter, 400–420 μ .

Diam. of sphere, 350 μ .

Length of best-developed processes, 65–70 μ .

Width of such processes, 20–23 μ .

Length of short processes, 15–20 μ .

§§§§ *Sirion*.

S. asteroides. Williamson, Phil. 'Trans.', pp. 171–510, 1880.

A strikingly peculiar species, in which the envelope consists of a firm parenchymatous tissue, or what appears to be such, though it may actually be paraplectenchyma, the difference being obscure even in isolated sections of living plants, and almost indecipherable in a fossil. The great regularity in size and arrangement of the cells does, however, look very like true parenchyma. The envelope is produced into large lobes, nearly as long as the organism is wide, five or six of which may appear in any section. Hence the specific name.

The walls of most of the cells are quite thin, except at the outer surface and in particular at the tips of the rays, where there is marked induration and darkening. Faint markings are sometimes discernible on the walls, but no cell-contents have been seen. The inner layers of the envelope are sometimes markedly meristematic in appearance, and this, in conjunction with the thickened walls and absence of divisions in the outer layers, points clearly to centrifugal growth of the envelope. The outer surface is very seldom well preserved; in fact, the only perfect outer surface I have seen, and that one irregular, was in a young specimen with very small lobes, which suggests that the outer surface was subjected to erosion during later life and was worn away and renewed internally like so much periderm.

The average depth of the envelope is 5–6 cells, but a lobe when mature may be more than a dozen layers in depth, while in the bays between lobes there may be only one layer. No perforations of any sort are visible, and it is rather difficult, with this in mind, to envisage any but a holophytic method of nutrition.

The capsule wall is peculiar, for it can be clearly seen under high magnifications (500 diam. *et supra*) to be patterned with very minute and closely set dots. In transverse section these dots show up as raised papillae on the outer surface of the capsule wall, while especially favourable examples

show a complementary jutting of the inner surface of the sphere wall. The sporoids and periplasm are exactly as in other species.

Williamson described and named as species of *Sporocarpon* (*S. anomalum* and *S. ornatum*)¹ two objects with just such a parenchymatous investment as this, which have since been shown to be the transverse sections of small Pteridospermic seeds.² Indeed they show many features which might have aroused suspicion of their nature. One might easily dismiss the present species as an impostor and thus be rid of a peculiar difficulty, were it not for the very clear evidence of the capsule and its spore contents, which are perfectly in accord with the same structures throughout the group.

Similarly, *S. asteroides* agrees with other species in secondary points; in the matter of size, for example (though this is rather variable, within limits), and in its gregarious habit, so that I cannot but regard it as an established member of the genus, albeit not easy to bring into line with the remainder.

The diameter of the sphere is rather more variable than is usual, although all species exhibit some plasticity in this respect, strengthening the view that the interior cavity is an integral living part of the organism. Growth is straightforward, the original form being without projecting lobes, which develop secondarily, but early, upon a narrow, spherical envelope of cells.

Dimensions:

Width of sphere, 180–330 μ .

Length of lobes, 120–140 μ .

Width of lobes at base, 90–120 μ .

Average thickness of envelope between lobes, 25 μ .

Size of individual cells, 8–16 μ .

§§§§§ *Perichoderma*.

S. pachyderma. Williamson, 'Phil. Trans.', pp. 171–510, 1880.

An interesting and frequent species. The envelope is composed of large interlacing tubules, anastomosing closely with one another in all directions. Neither beginning nor end is traceable for any given tubule: all are fused into a closed system round the stout wall of the sphere. At the external surface certain tubes form extruding apertures which there is reason to believe may have formed the bases of radial processes, usually lost or crushed, but as they stand they merely provide communication between the lumen of the tubular network and the outside. Usually all the ramifications are approximately of equal diameter, but there is a second type distinguishable where certain larger and darker walled tubes form

¹ Phil. Trans., 1880 and 1883.

² Oliver, Ann. Bot., xxiii. 74, 1909. The statement that *S. anomalum* is a mere slip for *S. ornatum* is not correct, for the original specimen, W. 1326, is so labelled by Williamson. Nor are the two altogether identical, though the differences may be due to their respective states of preservation.

a wide meshwork, as viewed in tangential section, the interspaces being filled in with slighter tubules. The larger tubes in this type bear the external orifices at the nodes of their mesh. These two forms are not, however, sufficiently distinguished by this peculiarity alone to warrant their specific segregation from one another. All the tubes are quite thin walled, and there is no appearance of contents, or of finer lateral openings, or appendages such as might be suggested by the analogy of the investment of tangential tubules in *Traquairia*. Openings to the interior exist, and the capsular contents of sporoids and small spores are quite normal, except that the capsule wall may show a very delicate reticulation (slide 1503, Williamson), an appearance also noted in *Traquairia Carruthersii* (W. Coll. 1066, 1074, 1077). The capsule sometimes shows a double wall, but this is met with occasionally in all species and may be the universal condition. On the other hand, the external surface is peculiarly interesting. It often appears to be covered with a dark membrane, double in places, through which the exoscopic apertures thrust themselves, while many specimens have small thin-walled vesicles like bubbles, borne attached organically to the outside of the tubular envelope.

Putting these aside for the moment, let it be noted that the species is not only highly gregarious, but actually colonial, several individuals being massed together in one confluent envelopment of tubes. This marks a distinct departure from the usual *Traquairidean* type and bespeaks an approach to the *Pharetrone* sponges. Many cases of confluent individuals show one or more of the attached individuals collapsed, and when this is the case the collapsed one always has a very exiguous envelope of tubes, with a dark and well-marked sphere wall. Now I would suggest that these are the younger members of the colony, as yet unstrengthened by the full development of their envelope, and that they are formed on the outside of older members by the growth of the round vesicles previously spoken of, building up a sort of *Globigerina*. Thus the colony would be regarded as formed by superficial budding, each new sphere forming from an enlargement of one of the peripheral tubes in the older organism; which is in a manner a parallel phenomenon to the secondary enlargement of the cells in § *Eu-sporocarpon*.

One very peculiar specimen (U.C.L. Collection), mentioned in my last paper, shows three confluent individuals, in one of which there is an internal ring of wide oblong cells arranged radially, with very dark contents. These are very puzzling and suggest further uncomprehended possibilities in regard to the group as a whole (Pl. X, Fig. 19).

The lumen of each cell is confluent outwardly with a tube of the envelope, so that they are part and parcel of the investment system and not special reproductive cells of any sort.

Taking into consideration the colonial habit, I would hazard the view

that this is the mother-cell of a colony, and that the ring of radial elements is the precursor in development (from the spore) of the tangentially arranged tube network, and therefore only found in the mother-cell, while absent from the proliferous outer daughter-spheres of the colony. Such a scheme affords a useful hypothesis, and serves to exhibit a possible connexion of this anomalous form with the typical envelope of radial vesicles in § *Eusporocarpon*. It will be desirable to advert to these possible affinities later on.

A very probable spore, with irregular wall, has been found in close proximity to a large nest of individuals (see Pl. IX, Fig. 14).

Dimensions:

Total diameter, 330–390 μ .

Diam. of sphere, 240–270 μ .

Average thickness of integument, 60–90 μ .

Average width of tubules, 8–16 μ .

INTERRELATIONSHIPS.

It would be fallacious to try to unite these few species into anything like a phyletic sequence, but it would not be undesirable to emphasize here the points in which they seem to connect with one another.

Taking *S. compactum* as the standard, we can see that separation of the vesicles from one another and grouping of the scattered spines into 'sori' would produce a type resembling *S. cellulosum*. Again, complete development of the vesicles into spines, as shown in the closely allied *S. tubulatum*, leads us to the *S. elegans* type, where the constriction of the basal moiety of each spine—indicated in one peculiar example of *S. compactum* itself (T. 8, in my own possession) and normal in *S. tubulatum*—has been carried to the extreme. As before stated, *S. asteroides* stands somewhat apart. Its nearest relative would appear to be *Traquairia stellata*, R. Scott, where the spinose arms are divided into cellular compartments, but I think the two are really parallel developments, and not genetically connected. *S. asteroides* might be reached by a proliferation of the juvenile vesicles of *S. compactum* into a pseudo-parenchyma, in place of their normal individual development into spines.

S. pachyderma, in the light of the specimen with an inner radial investment of cells, is best regarded as a derivation from the *S. compactum* form, in which a colonial habit has been established and a general envelope formed by the prolongation and anastomosis of the distal portions of the radial envelope cells into a complex outer stereome of tubules, beyond which their free apices may have projected. Obviously this yields points of contact with the envelope of *Traquairia*, where ramification of the spines is general. But the envelope is formed by the anastomosis of proximal rather than distal ramifications. Postulating a type of *S. compactum* in

which every vesicle was developed into a spine (one of Williamson's specimens approaches this condition), we would possess a feasible working hypothesis of a prototype from which not only the remaining species of *Sporocarpon* may be derived, but which might give indications (chiefly through *S. cellulsum*) of the origin of the more specialized genus *Traquairia*.

RELATIONSHIPS TO OTHER PROTOZOA.

The comparison of the genus as a whole with living Protozoa is not easy, for there is no resemblance in an aggregate of particulars such as to point indubitably to one group with which detailed morphological homologies might be shown. There are indications of affinity to both Foraminifera¹ and to Radiolaria, but especially the latter. Not that these present real homologies with the Traquairidae. At most it can be said there are suggestive analogies. Chiefly interesting, perhaps, is the central capsule, in the Radiolaria the seat of the nucleus and of sporulation. A fundamental divergence is the absence in these fossils of any system of perforations of the capsule wall, unless the fine punctations occasionally observed are to be so interpreted, in which case their affinities would obviously be with the primitive group of Peripylaria, possessing an evenly porose capsule. Association with the Peripylaria raises naturally the question as to whether we are not dealing in a *Sporocarpon* sphere with a colony of individuals, after the fashion of *Collozoum inerme*, each sporoid being then regarded as the homologue of a complete central capsule. I have already indicated that the balance of evidence is against this opinion, but it cannot altogether be discounted. The spores, again, present difficulties, for the spores of *Sporocarpon* are furnished with a palpable wall, enclosing protoplasmic relics, while those of modern Radiolaria are quite unsubstantial and indeed self-motile. Here a comparison with Foraminifera may help us out, for among them the reproductive amoebulae surround themselves with a minute one-chambered cell as the starting-point of a new individual. How the spores were exerted from the interior chamber of the organism there is no evidence to show, unless they may be imagined to escape by the dissolution of the envelope.² This envelope appears to be held together chiefly by its attachment to the sphere wall, but the sphere wall may not have been so substantial as it appears, for it may be looked upon as the correlative of the dark fatty assimilative layer of protoplasm closely surrounding the capsule in the Radiolaria, and thus perhaps much more readily disintegrated than a solid non-plastic membrane would be.

¹ The relationship to Foraminifera has not been considered here so fully as that to Radiolaria, but it may be pointed out that the genus *Polytrema* has several features suggesting affinity with the present group.

² But *vide supra*, p. 76, and Fig. 9.

The Radiolaria form both isospores and heterospores, the latter being sexual gametes, and some species even show a complete dimorphism according to the type of spore formed. Among the Traquairidae isospores are predominant, but specimens frequently show spores of different size which may be true heterospores, or may be mere irrelevancies due to fungal intrusion during decay. In some cases it is very difficult to accept this latter explanation (*vide Traquairia* in W. 1063).

One further point of interest presents itself. There is only one class of Radiolaria in which no 'zooxanthellae' (endobiotic Chrysomonad flagellates) are present, namely, the Phaeodaria. Among the Phaeodaria we find close analogies in form and composition with the skeleton of the Traquairidae, but each individual invariably contains a large dark excretory aggregation. This is quite absent in our fossils, unless the dark mass in the capsule of *S. elegans*, Pl. VIII, Fig. 3, be so interpreted, so that one can scarcely associate the two groups very closely, but at the same time the absence of this aggregation of excretory granules raises the interesting possibility that endophytic algae may have played a part in the life-history of these fossil organisms as in the true Radiolaria. The development of elaborate systems of external apertures leaves little doubt that their main method of nutrition was, as in the Radiolaria, holozoic, but variation in this respect is probably evidenced by the structure of *S. asteroides*. The skeletal affinities were treated pretty fully in my first paper. I still maintain that a chitinous substance seems the most likely material. Evidently it was something pretty hard, since the preservation is meticulously accurate in the smallest details, and it was in most cases flexible.¹ Among the Phaeodarian Radiolaria the skeleton often suggests the Traquairian form, and it consists of an organic silicate, which is at least nearer in nature to the fossils than is the strontium sulphate skeleton of the Acantharia. At the same time the internal arrangements in the present group are much more nearly those of the Peripylaria. Therefore I would suggest that the nearest living analogues of the Traquairidae are to be found in the group Orosphaeridae, removed from Phaeodaria to Peripylaria by Häcker (4), which shows a union of the characters of the two groups parallel to that observed in the Traquairidae.²

Since, as Cavers (5) has pointed out, the Radiolaria may be derived from ancestors like the Gymnodiniaceae, it is not improbable that the Tra-

¹ The Foraminifera possess a chitinous test between the protoplasm and the calcareous test. This may develop excessively, not as a consequence of starvation or wandering into brackish water, as formerly suggested, but as a variation in any species under any conditions (Heron-Allen, Rep. Brit. Ass., Bournemouth, 1919). Wholly chitinous forms may appear as monstrosities.

² The Coccolithophoridae (see Murray and Blackman, Nature, lxx. 510, 1897) must also be considered as possible descendants, on the evidence of their armour characters, though their cytology is not fully known. Indeed, I would be nothing loath to postulate a common plexus of origin for the Coccolithophoridae, Traquairidae, Radiolaria, Diatomaceae (as represented by the early liassic genus *Pyxidicula*), Prorocentraceae, and Peredineae.

quairidae may have sprung from some similar group of Peredinian affinities, with spores possessing a hard cell-wall, in place of the lower, flagellate type represented by the spores of Radiolaria. It has been maintained all along that their homoeomorphy with the latter group is rather the result of parallel descent than of homology.

Sporocarpon pachyderma has particular affinities of its own with the Keratosa group among the sponges, and represents an advance in their direction, which brings it into relation to a parallel living group of Protozoa, the little-known Xenophyophoridae (6), which also, though widely asunder, have developments tending similarly to a sponge-like facies.

I have previously suggested that the present group represents a line springing from common ancestors with the Radiolaria, probably not very far back from the present level of that class, the modifications being traceable to life in shallow, highly organic waters with a low saline content. Such habitats have not often been extensive in geological history, but as the Carboniferous Coal Measures are the only period of the sort sufficiently closely investigated, it is impossible to deny the existence of similar organisms at other epochs similarly constituted. Not improbably Mesozoic and Cainozoic coal deposits may yield allied or identical forms when they have been more fully examined. At present, however, so far as we can tell, they are exclusively Palaeozoic and limited to the Coal Measures, though on those horizons they attained a wide distribution. The mineralized skeleton of the pelagic Radiolaria is by no means an insuperable difficulty in the way of associating the groups, since such skeletons are also found in several isolated groups, for example among the Diatomaceae and the Silicoflagellata, without the occurrence of anything but an organic test in their nearest relatives. Fossil Radiolaria are found extensively in Lower Palaeozoic rocks, even the lowest, notably in the Lower Culm of Devon and Somerset (7) and in the European Culm in general, almost at the base of the Carboniferous succession (8). Use has been made, by geologists, of their presence in these rocks to argue very deep water conditions at the opening of this geological period, and a gradual shoaling until the Carboniferous Limestone is reached, with subsequent elevation and the commencement of the Upper Carboniferous rocks.

There can be little doubt of the affinity of the organisms figured by Hinde and Fox (7) both with Radiolaria and with Traquairidae, though clearly their skeletons have undergone resolution and replacement, so much so indeed that the generic and specific assignments awarded them are more than dubious. The interesting point at the moment is the presence of a class of organisms resembling modern Radiolaria, widely and plentifully distributed in the seas preceding the formation of the Coal Measures. From this organismal reservoir it is, as I conceive, that the Traquairidae were drawn, during the subsequent shallowing of the waters.

The genus *Calcisphaera*, too, may have originated in this period, although it makes its appearance earlier, in the Carboniferous Limestone. Hill and Jukes-Browne (9) have shown how unstable chemically is the Radiolarian skeleton during fossilization, and *Calcisphaera* may likewise have suffered chemical replacement of either a siliceous, strontium sulphate, or organic test by calcite. Apart from its chemical nature there is little to separate it from true Radiolaria, and it affords several morphological links between them and the Traquairidae. Taking into account its earlier appearance and its intermediate distribution, in the moderately deep water limestone deposits, it may well be a connecting group.

SUMMARY.

1. The present article is an attempt to give in full detail the facts, in so far as they have been determined, of the structure of the genus *Sporocarpon*, Williamson, one of the group of Traquairidae, previously established (1).

2. The genus is shown to cover a multiplicity of divergent types, represented only by single species, which it is impossible to regard as generically related in the present-day sense. The old generic name is retained for convenience, but five subgenera are proposed.

3. A revised monographic description of the seven species is given. The organism called by Williamson *Oidospora anomala* is added to the present genus under the name of *Sporocarpon Oidospora*.

4. Taking *S. compactum* as the simplest and least specialized type, it is shown that it is possible to derive the structure of the other species from it by divergent changes, while *Traquairia* may also be derived from a *Sporocarpon* type, probably in the neighbourhood of *S. cellulolum*. This emphasizes the homogeneity of the group.

5. The relationships of structure between *Sporocarpon* and recent Protozoa are examined in detail and the conclusion pointed that the nearest living analogues of Traquairidae are the Peripylarian Radiolaria. At the same time the material of the skeleton and the appearance of the spores suggest that, like the Radiolaria, they may ultimately have sprung from flagellate ancestors of a Peridinium type.

6. Evidence is adduced for the widespread existence of Radiolarian organisms at the base of the Carboniferous period in abyssal waters; while in the shallower water limestone deposits of the Lower Carboniferous, the intermediate organisms called *Calcisphaera* are enormously prevalent. The bearing of this upon the phyletic origin of *Sporocarpon*, afterwards typically developed in the non-saline waters of the Coal Measures, is pointed out and suggested as a probable trace of their evolution.

7. These organisms are specially characteristic of sections taken from coal-seam nodules (coal-balls) of the Lower Coal Measures, and in particular

the Burntisland and Halifax Hard beds. It was in the latter that they were noticed for the first time by Messrs. Spencer and Binns.

The sections which I have chiefly consulted are those in the Williamson Collection at the British Museum; the University College, London, Collection; Prof. Seward's Collection at Cambridge, and some in the possession of Dr. D. H. Scott and myself. I wish to express my indebtedness to Prof. F. W. Oliver and Dr. D. H. Scott for the kind loan of their preparations, and to Mrs. Scott for a similar kindness with regard to photographs and drawings.

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EXPLANATION OF PLATES VIII-X.

Illustrating Prof. McLean's paper on *Sporocarpon*.

PLATE VIII.

Fig. 1. *Sporocarpon elegans*. Tangential section, showing the numerous spines arising from the honeycomb-like framework which forms the outer limit of the 'colonnade' layer. Towards the centre the attenuated waists of the colonnade units may be seen in cross-section, and between them their delicate tangential connexions. Tams phot. Lent by Mrs. Scott. This specimen is figured in Williamson, Part X, and the slide is in his collection. $\times 100$.

Fig. 2. *S. elegans*. Median section, showing a shrunken capsule and several spines, the extremities of certain of which (at A) may be seen to branch. Tams phot. Lent by Mrs. Scott. $\times 100$.

Fig. 3. *S. elegans*. Median section, showing the structure of the colonnade of spine base units with exceptional clarity. Capsule and sporoids well preserved. Where the spine bases are in contact

at the region of the intercalary swelling, it will be seen that their walls are somewhat thickened, forming the framework referred to under Fig. 1. Tams phot. Lent by Mrs. Scott. $\times 100$.

Fig. 4. *S. elegans*. A truly tangential section through the colonnade with the units cut at different levels; upper swellings on the periphery of the section, lower (foot) swellings in the centre and 'waists' intermediately. The photograph shows the tangential connexions running between the units, with here and there a double contour, as if they were tubular. (Williamson Collection.) $\times 450$.

Fig. 5. *S. compactum*. Restoration of a single unit (cell) of the envelope, at the beginning of its elongation into the mature spine form. The tuberculae shown near the apex are really minute openings with pores at the tip of each of their very fine ramifications. $\times 2,000$ approx.

Fig. 6. *S. compactum*. Part of the envelope, showing two cells at A in process of elongation. (Author's Collection.) $\times 450$.

Fig. 7. *S. asteroides*. Median section of a specimen with unusually long lobes. Interior capsule faintly shown. (U. C., London, Collection.) $\times 20$.

Fig. 8. *S. asteroides*. Young specimen in median section, showing part of the outer surface of a young lobe at A, with convex outer 'cell-walls'. (U. C., London, Collection.) $\times 80$.

Fig. 9. *S. asteroides*. Two specimens, one containing a capsule with sporoids, the other apparently dehiscing and extruding a mass of spores (?) united by filaments. A unique specimen. Drawing by Mrs. Scott from a specimen in the Scott Collection. $\times 100$.

Fig. 10. *S. tubulatum*. A young specimen in median section, showing the elongate cells of the envelope in their young form before their growth into spines. It will be seen that in this state their apices are obtuse. Compare with Fig. 11. (Author's Collection.) $\times 80$.

Fig. 11. *S. tubulatum*. Restoration of two spines in their mature state, showing their resemblance to those of *S. elegans*. The whole organism is, however, in this species spheroidal. $\times 1,000$ approx.

PLATE IX.

Fig. 12. *S. pachyderma*. Section through a conjoined group of individuals with a common tubular investment. One, which is cut medianly, shows a peculiar colonnade of radial cells, remarkably like that of *S. compactum*, inside the normal tubular envelope. A unique specimen. (U. C., London, Collection.) $\times 75$. See also Fig. 19.

Fig. 13. *S. pachyderma*. Part of the tubular investment shown in tangential section. The branching of the large thin-walled tubes composing the investment may be seen near the centre. (Author's Collection.) $\times 450$.

Fig. 14. *S. pachyderma*. Spore or juvenile individual with very slight investment, found in close association with a large group of the same species. (Author's Collection.) $\times 600$.]

Fig. 15. *S. pachyderma*. Median section with double-walled capsule. The envelope shows apparent orifices externally at A and a spine base at B. (Author's Collection.) $\times 450$.

Fig. 16. *S. cellulolum*. Radial section with large 'sorus' of spine bases. A small portion of the envelope is seen cut tangentially (A), showing the polygonal outline of the envelope units.

Fig. 17. *S. Oidospora*. Two individuals, apparently conjoined. The structure of the envelope is very like that of *S. compactum*. (U. C., London, Collection.) $\times 700$ approx.

PLATE X.

Fig. 18. *S. compactum*. Median section of a very well preserved specimen with an unshrunk capsule filled with sporoids and granular matter which appears to be residual plasma. U. C., London, Collection.) $\times 700$ approx.

Fig. 19. *S. pachyderma*. Portion of the envelope of the specimen shown in Fig. 12. It will be seen that the radial cells are prolonged at their distal ends into the tubes which form the envelope, the prolongation being in each case flexed in the same (clockwise) direction. $\times 200$ approx.

Fig. 20. *Traquairia ramex*. The type specimen of this species, which is here reproduced for comparison with the present genus. (U. C., London, Collection.) $\times 200$ approx.

9.

A

11.

18.

20.

19.

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