VIII. Contributions to the Life-History of the Foraminifera.

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[Plates 6-9.]

#### Introduction.

In the preface to his classical work, 'Über den Organismus der Polythalamien,' published in 1854, Max Schultze acknowledged with regret the incompleteness of the account which he was able to give of the reproductive processes of the Foraminifera, and pointed out that a rich field here lay open for future investigation.

In the years that followed Schultze himself made further contributions to our knowledge on this head, but, important as they were, they only went a short way towards solving the problem.

Of late Munier-Chalmas and Schlumberger have contributed an essential factor in demonstrating the existence of dimorphism in many and widely separated species of Foraminifera. It has been shown in many cases that the individuals of a species fall into two distinct sets. In one, the first formed chamber is very minute, while in the other it is large. Differences in the size attained by the adult shell, in the plan of symmetry on which the chambers are arranged, and, as I have to show, in the nuclei may also be present. Munier-Chalmas and Schlumberger distinguish the two groups as Form A, with a megasphere, and Form B, with a microsphere. I have ventured to modify one of these terms, and refer to the forms as megalospheric (with a large central chamber), and microspheric (with a small central chamber) respectively.

What is the relation existing between these two forms of a species? Do they represent two sexes, or do they belong to different generations? I believe them to belong to different generations.

In what follows I have attempted to collect the more important evidence which bears on the life-history, and have given an account of my own observations, which deal mainly with two species:—Polystomella crispa (Linn.), belonging to the Perforate division of the group, and Orbitolites complanata, Lamk., a representative of the Imperforata.

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The evidence will be presented under the following heads:—

- 1. Previous contributions to the life-history of the Foraminifera.
  - a. Observations on Reproduction and Dimorphism.
  - b. The relation of Orbulina and Globigerina.
  - c. Observations on Nuclei.
- 2. Observations on:
  - a. Polystomella crispa (Linn.).
  - b. Orbitolites complanata, Lamk.
  - c. Rotalia beccarii (Linn.).
  - d. Truncatulina, D'Orb.
  - e. Calcarina hispida, Brady.
  - f. Cycloclypeus Carpenteri, Brady.
- 3. Concluding Remarks.

#### 1. Previous Contributions to the Life-History of the Foraminifera.

#### (a.) Observations on Reproduction and Dimorphism.

In the year 1847, GERVAIS (12) brought before the Académie des Sciences, an observation on some Triloculine *Miliolidæ*, which he had kept in sea water. Young individuals, consisting of a single large chamber, with their shells already formed and capable of sending out pseudopodia had appeared, in number about 100, grouped about the orifice of a parent shell. He also states that prior to the production of the young, individuals presenting differences in the form and size of shell, had come together in pairs on the side of the vessel. These individuals, he suggests, were male and female.

In 1854, Max Schultze published his work 'Über den Organismus der Polythalamien' (38). In it he described and figured young individuals of Miliolidæ and Rotalidæ. Examples of young Miliolidæ, consisting only of a spherical central chamber and tubular second chamber, are figured, and others in various stages of growth. He was struck by the marked difference in size of the central chamber presented by examples of the former group. From the figures it appears that the long diameter of the central chamber was in some cases  $170 \,\mu$ , and in others  $35 \,\mu$ . As will be shown below, these figures correspond approximately with the diameters of the central chambers in the megalospheric and microspheric forms of Biloculina depressa, D'Orb, one of the Miliolidæ (woodcut p. 405). Schultze, however, did not recognise the existence of dimorphism, and referred the individuals to different species.

In 1856, Schultze made a further contribution (39) to the life-history of the Foraminifera. On May 15th, an example of the genus *Triloculina* which had been kept in sea-water, after remaining stationary on the wall of the vessel from 8 to 14

days, produced some 40 young. They were composed of colourless protoplasm contained in a shell consisting of a central chamber, having a diameter of  $54\,\mu$ , and a tubular second chamber coiled about it. These gradually crawled away over the glass by means of pseudopodia. On breaking open the chambers of the parent shell, only a little granular material was found, and Schultze concludes that all or nearly all the contents had been fashioned into the young. It is stated that the parent of the young Triloculinas was conspicuous by its larger size, among the other examples present.

In the same paper, Schultze described a form with a siliceous shell, which he provisionally called *Nonionina silicea*, in which numbers of spheres with siliceous coats, having a diameter of about  $97 \mu$ , were present in the chambers. The evidence, as to the nature of these bodies which he took for the young, appears however to be less convincing.

In 1860, M. Schultze described (40) the production of young in a species of Rotalina, closely allied to R. nitida, Williamson, which had been kept for about a year-and-a-half in an aquarium. The young consisted of three chambers of which the first was the largest, measuring  $25-34\mu$ . He states that the central chamber of the parent shell was of the same size as that of the young.

In 1861, Strethill Wright (45) recorded his observation of two large specimens of *Spirillina vivipara*, Ehrb., surrounded by multitudes of very small ones; and within one of the large ones three small living *Spirillina* existed. Ehrenberg (11) had previously described and figured a specimen of this species containing two young shells near the mouth. In his figure, the central part of the coil of the young is represented of the same size as that of the parent. In the same paper, Wright described a specimen of *Gromia*, partly filled with a "milky matter," which was found to consist of "large active molecules, like spermatozoa, in which there was no mistaking the characteristic movement."

In the same year, Carter (10) called attention to the existence of spherules in the shells of fossil Foraminifera belonging to the following forms: Nummulites, Orbitoides, Orbitolites mantelli, Orbitolina lenticularis, and Alveolina elliptica. He considered that there could be "no reasonable doubt" that they were "propagative agents."

In 1865, Semper (43) sent home a short notice of a specimen collected on the reefs of the Pelew Islands, and referred by him to the genus Nummulites. As BUTSCHLI points out ((6), p. 141), and as Semper's figures clearly show, the specimen was not a Nummulite, but one of the simple forms of the genus Orbitolites. The peripheral chambers are described as larger than those in the interior of the disc, and each contained a young individual invested by a shell, and consisting of a central chamber, and a second chamber surrounding it.

In 1875, Schlumberger (32) described two specimens of the shells of *Miliolidæ* containing young ones. In one several chambers contained young shells, consisting of a nearly spherical chamber and a canal-like second chamber. In the second

specimen two young ones, similar to those contained in the other specimen, lay in the terminal chamber.

In 1878, Schneider (37) described reproductive processes of different kinds in the genus *Miliola*.

In one species he found the protoplasm broken up within the shell into bodies of two sizes, of which the smaller were compared with spermatozoa and the larger with ova. Different stages of the development of the "ova" into young Miliolas were found. These became free when invested by a spherical shell. This phase of reproduction was observed in September and October.

After the winter Miliolas were again found giving rise to young, but now the process appeared to be asexual, none of the spermatozoa-like bodies being found.

A species of Miliola from Heligoland was kept in vessels of sea-water. After some weeks rounded heaps some 2 millims in diameter were found at the bottom of the vessel. These were invested by a firm wall covered with sand, and contained several alveolar spaces. In some examples the spaces contained numbers of bodies resembling Euglena in their shape and movement, though no flagellum was observed. In other cases the alveoli contained undivided protoplasm, or they were empty, or they contained young shells, one to each alveolus, which presented some resemblance to young Miliola shells. The further development of these shells was, however, not observed. Schneider's observations require confirmation before they can be accepted.

In 1879, Lankester (20) described a number of "egg-like bodies" in the protoplasm of  $Haliphysema\ tumanowiczii$ , Bowerbank, having a diameter varying from  $\frac{1}{500}$  to  $\frac{1}{1500}$  inch (51–17 $\mu$ ). The larger masses were nucleated, but the smaller were said to be devoid of a nucleus. It was conjectured that these bodies are in some way concerned with reproduction.

In the following year, 1880, Munier-Chalmas (24) stated as the result of the investigations of four fossil species of Nummulites and two of the allied genus Assilina, his conclusion that these species were dimorphic, and that probably the phenomenon of dimorphism was general. This conclusion was based on the fact that Nummulites occurring in the same strata, and having identical external characters, fall into two groups. These differ from one another, first, in the size of the whole disc; second in the size of the central chamber. On breaking them open it is found that the small ones have a large central chamber, and the large ones a small central chamber. Intermediate forms, it was stated, do not occur. Although the superficial markings are alike in the two forms, they had hitherto been reckoned as distinct species.

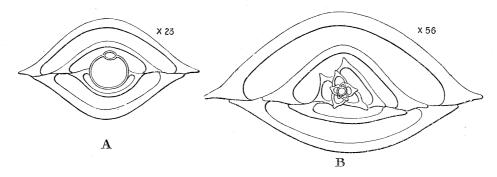
Relying on the fact that only large examples of the forms with small central chambers had been found, Munier-Chalmas concluded that each species consisted of two sets of individuals; first, those with a large central chamber, which attained a small size, and whose development was arrested at this stage; second, those in which the size was increased by the addition of chambers at the end of the spiral, while the large central chamber was replaced by a prolongation of the spire of chambers to the centre of the shell.

D'Archiac and Haime (1) had described the two kinds of arrangement of the central chambers in this family, and pointed out the corresponding difference in the size of the whole shell. These characters are referred to (pp. 63, 64, and 77) as indicative of different species, though this view is not consistently followed throughout.

The view stated by Munier-Chalmas, that the two types represent different forms of the same species, had been previously expressed, though less definitely, by Parker and Jones (27a). These authors, in commenting on d'Archiac and Haime's 'Monographie,' refuse to recognize the mode of arrangement of the central chambers as a character on which to separate natural groups, and state their opinion that the forms of small size, with a large central chamber are "free growing individuals soon arriving at their limit of growth."

The existence of the two closely associated forms had also been previously recognized by DE HANTKEN and DE LA HARPE. DE LA HARPE, in a letter to Professor Rupert Jones, dated Oct. 1, 1879 (19a, p. 91), states a "general law of the distribution of Nummulites, according to which the characteristic species of a bed are always two of the same zoologic group, of which the larger has no central chamber" (distinguishable by a lens) "and the smaller always has one." In illustration eight pairs of species thus associated are given.

In 1881, DE LA HARPE (15), expressing his own views and those of DE HANTKEN, commented on Munier-Chalmas' paper. While agreeing that the two forms constituting a "pair" resemble one another in the external sculpturing, he points out that examples intermediate in size between them do occur, and also small examples with a small central chamber. It is also shown that the two forms differ in the characters of the chambers which make up the inner whorls as well as in the size of the central chambers. While the view that one form results from the modification of the other is thus shown to be untenable, it is suggested that they might with more reason be regarded as representing two sexes of a species. The authors, however, do not definitely abandon the old idea of the specific distinctness of the two forms.



Biloculina depressa, D'ORB. Sections of the shell-

A. Of the megalospheric form. (Megalosphere 200-400  $\mu$ .)

B. Of the microspheric form. (Microsphere  $20 \mu$ .) The two terminal chambers are omitted in B. (Munier-Chalmas and Schlumberger, 25.)

In 1883, Munier-Chalmas and Schlumberger (25) communicated to the Académie des Sciences the fact that the phenomenon of dimorphism occurs also in several species of the Miliolidæ. Thus, in Biloculina depressa, D'Orb, there are two forms (see wood-cut, p. 405): A, with a large central chamber  $200-400 \,\mu$  in diameter, and with an outside diameter of the shell of 2·10 millim.; and B, with a small central chamber  $20 \,\mu$  in diameter, and an outside diameter varying from 1·5 millim. to 2·64 millim. The interesting fact was also brought forward, that in this group there is a very marked difference in the mode of growth of the two forms. While in the form A, the arrangement of the chambers following the central one is biloculine from the first, in the form B the chambers following the minute central chamber are arranged at first on the quinqueloculine plan, the biloculine arrangement not being attained, in B. depressa, until the eleventh chamber is formed.

A similar dimorphism is stated to exist in the genera Dillina, Lacazina, Fabularia, Triloculina, Trillina, Quinqueloculina, Pentellina, Heterillina, and Alveolina among the Imperforata, and among the Perforata in the genera Nodosaria, Dentalina, Siphogenerina, Rotalina, and Amphistegina.

In the same year Schacke (29) described a dry specimen of *Peneroplis proteus*, D'Orb., many of whose chambers contained numbers of young shells. These consisted of an eval central chamber measuring some  $35 \mu$  in long diameter, and a canallike second chamber. The central and second chambers of the parent shell are represented as exactly resembling in size and shape those of the young.

In 1884, Brady's magnificent monograph (1a) on the Foraminifera appeared in the "Challenger" Reports. The work deals mainly with the classification and distribution of the Foraminifera, their life-history being little noticed. There are, however, two records in it which bear upon the matter.

A specimen of Cristellaria crepidula (Fight. and Moll. sp.) is described and figured (Plate 68, figs. 1 and 2), which contained young shells in three of the terminal chambers. The parent shell is megalospheric, the megalosphere being pear-shaped, and measuring  $110 \times 84 \,\mu$ . The young shells consist of a spherical or somewhat triangular chamber varying in size from 60 to 30  $\mu$ , to which in some cases a second smaller chamber is added.

In the description of Cymbalopora (Tretomphalus) bulloides, D'Orb., in which the shell of small chambers, arranged in an irregular spiral, is completed by an enormously inflated terminal chamber, it is stated, on the authority of Dr. John Murray (p. 639), that in every specimen from the surface which was examined, "the shell was filled with minute monadiform bodies."

In a paper (26) published in 1885, MUNIER-CHALMAS and SCHLUMBERGER introduced the terms *Mégasphère* and *Microsphère* for the central chambers of the two forms of a species.

In October, 1888, Brady (2) described specimens of *Orbitolites complanata*, Lamk., var. *laciniata*, Brady, collected in Fiji, whose large peripheral chambers were crowded

with young megalospheric individuals. Such specimens had been previously recorded by W. K. PARKER.

In Brady's specimens the parent form was microspheric. Vertical and horizontal sections of the shell are figured, showing the small chambers continued to the centre. It is pointed out that these shells differ from those whose centre is occupied by a primitive disc (the megalospheric forms, cf. fig. 45), not only in the absence of the primitive disc, but in the fact that the thickness of the shell at the centre is only one-third of that of the megalospheric form. However, in alluding to the question of dimorphism, Brady considered that the evidence of Orbitolites supported the view suggested by Munier-Chalmas that the microspheric form was a modification of the megalospheric.

In 1890, Schlumberger (35) described Adelosina polygonia, a new species of the Miliolidæ. From the figures it appears that the dimensions of the megalosphere and microsphere of this species are, in particular instances, 216  $\mu$  and 25  $\times$  18  $\mu$  respectively. The plans of growth of the two forms are different throughout, the megalospheric forms having the chambers arranged (in 99 cases out of 100) in a tri angular, while the microspheric forms have them arranged in a quadrangular figure.

Among the specimens examined the frequency of occurrence of the megalospheric and microspheric forms was as 8 to 1. In fully-formed shells the microspheric form is slightly smaller than the megalospheric (microspheric form 1.4 mm., megalospheric form 1.5 mm. in diameter). Young specimens of the microspheric form occur. It is pointed out that in this case the view suggested by Munier Chalmas, and adopted by the author, that the microspheric is a development of the megalospheric form, is clearly untenable.

In May, 1893, VAN DEN BROECK (5) published his "Étude sur le dimorphisme des Foraminifères," in which the relationship of the two forms is discussed.

In this work the author reviews the evidence on the subject of dimorphism, and the reasons for regarding the two forms as distinct from their origin are urged with much force. It is shown that the difference in the size of the central chamber indicates a difference in the reproductive processes by which the two forms originate.

In speculating as to the nature of this difference VAN DEN BROECK puts forward the view, which, as is stated, had previously been suggested by Dollfus ('Annuaire Géologique,' 1890, p. 1099), that the megalospheric young are the result of "endogenous gemmation," and the microspheric young of "ectogenous fission." Both processes it is conceived might be going on simultaneously in one individual. The author has unfortunately revived, in support of his hypothesis, the old idea of the individual distinctness of the contents of the different chambers of the foraminiferan shell. Apart from this, however, the view as to the mode of origin of the two forms of young cannot be accepted as correct. For, as will be shown below, in the cases in which the origin of the megalospheric young has been traced (*Polystomella*, *Rotalia*), they have arisen by the multiple fission of the whole of the protoplasm of

the parent. The exact origin of the microspheric form is still unknown, but the zoospores from which it is probably in some way derived, are also produced (in *Polystomella*) by the multiple fission of the parent protoplasm.

## (b.) The Relation of Orbulina and Globigerina.

The features presented by *Orbulina* have been much discussed (cf. Bütschli (6), pp. 68-70), and as they have been supposed to exemplify the phenomenon of dimorphism, the subject claims our notice here.

Pourtales (28) first drew attention, in 1858, to the fact that a spirally arranged group of chambers, resembling the complete shell of a *Globigerina*, is often found within the spherical shell of *Orbulina* (cf. wood-cut, p. 409). This he considered to be the young of *Orbulina*, and he suggested that *Globigerina* and *Orbulina* might be alternate generations in the life-history of one species.

In 1868, Major Owen (27) stated his opinion that the *Orbulina* shell "may be regarded as a wild-growing closing-in chamber" of the *Globigerina*.

In 1883, Schacko (29) described specimens of Orbulina, both recent and fossil. He showed that the Orbulina shell is sometimes double; that the contained Globigerina shell is most fully developed when the Orbulina shell is small, and that in large (dry) specimens a heap of thin-walled fragments is often all that remains of it. He considers that the Globigerina shell is gradually absorbed, and ultimately disappears. With regard to the contained Globigerina shell it was shown that, as in free living Globigerina, its terminal chambers are frequently covered with spines, and that these reach to the Orbulina shell and fuse with it; they are, however, exceedingly slender. The chambers composing it may be as many as thirteen. The diameter of the apical chamber varies from 16 to 23  $\mu$ .

Schacko found some small bodies "resembling in shape and size" the first two chambers of the *Globigerina*, especially abundant in the terminal chamber of the latter. These he regarded as young.

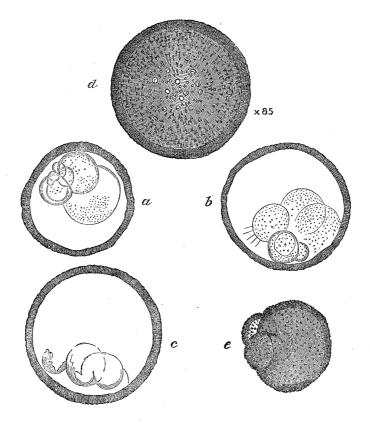
In April, 1884, Schlumberger (34) presented a note to the Académie des Sciences in which he urged the view that the empty Orbulina shell and that with Globigerina-like contents, were dimorphic forms of the same species, comparable to the forms which had been shown to exist in the species of Nummulites and Miliolids. After reviewing the evidence he proceeds as follows (p. 1004):—"La loge unique de l'Orbulina est l'homologue de la loge initiale des autres Foraminifères: lorsqu'elle reste vide, elle est de la forme A; avec la série de loges internes elle est de la forme B."

Schlumberger concludes with the remark that the case of Orbulina is in favour of the view that the forms A and B are distinct from their origin.

The ascertained facts appear to be as follows:—

In a sample of the shells of Orbulina many of the individuals are simple empty

spheres varying in size, and the largest shells of the sample are of this character. In others, the interior of the sphere is more or less completely occupied by a spire of chambers closely resembling a free Globigerina shell. This is firmly attached to the wall of the investing spherical chamber. In rare instances (e, wood-cut) the Orbulina chamber does not completely enclose the Globigerina chambers, and in that case the outer spherical surface of the Orbulina is interrupted by the prominences formed by the terminal chambers of the Globigerina. Usually the Globigerina shell is remark-



Orbulina universa, bottom specimens, Brady Collection, Globigerina-Orbulina series. × 170.

- a-c. Orbulinas with contained Globigerina chambers (represented in optical section). These are seen in different stages of absorption. The spines are only seen in b.
- d. An empty Orbulina shell.
- e. A specimen in which the Orbulina shell does not completely enclose the Globigerina chambers.

able for the extreme tenuity of its walls and spines, but when portions of it are not enclosed by the *Orbulina* shell, they are found, as Schlumberger points out, to be thick walled, while the enclosed portions are thin (e).

The Globigerina chambers are usually most perfect when the investing chamber is small, the larger this chamber is the less perfect are the contained chambers. In dead specimens these are frequently represented by a mass of broken fragments. In the largest Orbulinas no trace of contained chambers is found.

A small chamber whose diameter varies, according to Schacko, from 16 to  $23\mu$  is frequently found at the apex of the spire of chambers.

While the *Globigerina* chambers are perforated by small apertures of uniform size, the pores of the *Orbulina* are of two sizes.

It not unfrequently occurs that the *Orbulina* shell is double or even treble, the spheres being contained one within the other, and unattached, as in a Chinese carving.

Before discussing the evidence, it will be well to recall the mode of life of Orbulina.

In common with the rest of the family Globigerinidæ, and species of the genus Pulvinulina among the Rotalidæ, Orbulina is frequently found leading a pelagic existence at or near the surface of the sea. When taken in the tow-net, it is often beset with long spines which may be more than three times the diameter of the shell in length. When the protoplasm is extended a thick vacuolated layer invests the shell and the bases of the spines.

The fact that all transitional stages are found between small *Orbulina* shells containing a perfect spire of chambers, and large ones which are empty, appears to point to the conclusion that the empty *Orbulina* shells when small contained such chambers.

What is the relation between the *Orbulina* shell and the contained chambers? The suggestion that these constitute a young individual about to be set free is incompatible with the facts (1) that they are attached to and sometimes involved in the *Orbulina* shell; (2) that they are often seen in stages of degeneration; and (3) that the largest *Orbulina* shells are empty and complete.

According to Major Owen's view, the outer sphere may be regarded as a "wild growing closing-in chamber," and it appears probable that this is the correct interpretation. The Globigerina chambers, with their radiating spines, are probably invested with vacuolated protoplasm before the Orbulina chamber is formed, as the Orbulina shell is afterwards. When the growth of the shell has reached a certain stage by the addition of chamber to chamber on a spiral plan, a spherical chamber is formed concentric with the surface of the investing protoplasm. This may completely enclose the chambers already formed, or parts of these may, in rare instances, project beyond it. At a later stage a second and a third shell may be added while the contained chambers are absorbed. [Rhumbler has recently published a preliminary account of his investigations of Orbulina, in which he arrives at the same conclusion with regard to the relation of the Orbulina shell to the contained chambers. 'Zool. Anzeiger,' vol. 17, May 28, 1894, p. 196. (March 13, 1895.)]

The formation of such a large terminal chamber, as Major Owen pointed out, is not peculiar to this form. As mentioned above, in specimens of *Cymbalopora* taken at the surface, the spire of small chambers is completed by a large inflated chamber far exceeding in volume the rest of the chambers taken together.

If this view of the relation of the Orbulina shell to the enclosed chambers is

correct, it is clear that the idea that the empty Orbulina shell, and that enclosing the Globigerina chambers, correspond respectively to the megalosphere and microsphere of other Foraminifera, is untenable. As M. Schlumberger has done so much to show, it is to the first formed chambers that we must look for the characters which distinguish the two forms, and the first formed chambers are surely those, as in all other cases, which occupy the apex of the spire. It follows that, unless it is shown that other characters distinguish the forms, only those specimens of Orbulina in which the contained chambers are complete can furnish evidence of dimorphism.

With regard to the relationship of the free Globigerina shell to Orbulina, I have very little evidence to offer. The first chamber of the free Globigerina is about the same size as that of the Globigerina chambers included in Orbulina. In 63 surface specimens of Globigerina mounted in balsam, in the Brady Collection, the mean diameter of this chamber varies from 7 to 20  $\mu$ , the most frequent diameters being 14 and 17  $\mu$ . Schacko gives the diameter of the first chamber of the Globigerina enclosed in the Orbulina shell as 16 to 23  $\mu$ . So far as this rather scanty evidence goes, then, it appears that there is no evidence of dimorphism in the central chambers of these forms.

It will be shown below that in the species which I have examined the two forms are as sharply distinguished by the character of their nuclei as by the size of the central chambers. The only evidence on this head with which I am acquainted is that of one specimen of a free *Globigerina bulloides* with eight chambers, described by R. Hertwig (17), in which a single large nucleus was present. From analogy it would appear that this specimen was megalospheric.

Further evidence on the nature of the nuclei of *Orbulina* and *Globigerina* would no doubt throw light on the question of their relationship.

# (c.) Nuclei.

Our knowledge of the nuclei of Foraminifera is mainly derived from the descriptions of R. Hertwig, F. E. Schulze, and O. Bütschli.

The evidence is for the most part of a fragmentary character, but it may be convenient to bring it together. The observations which I have met with are here arranged under the names of the families.

- I. Gromida.—In Gromia, MAX SCHULTZE ((38), p. 22) found a single nucleus in young specimens, and from two to sixty in old ones.
- II. Miliolidæ.—In Quinqueloculina fusca, F. E. Schulze ((41), p. 136) described an oval body which he took for the nucleus.

In a species resembling *Spiroloculina hyalina*, F. E. Schulze, R. Hertwig ((16), p. 46) found a single nucleus in young specimens, and as many as seven in one with four chambers.

Among the *Peneroplina*, Bütschli ((7), p. 80) found a single nucleus in two specimens of *Peneroplis pertusus*, Forsk., but in a third specimen as many as four

were present. The central chambers of the specimens (which appear to have had a mean diameter of 29 to  $34 \mu$ ) are considerably larger than those which succeed them, and are of the same size as that of Schacko's specimen described above (p. 406). It is probable therefore that they belonged to the megalospheric form.

In an example of the type of *Peneroplis planatus*, F. and M., whose central chamber measured about 27  $\mu$  in diameter, and hence would appear to have belonged to the same form, some eighteen to twenty nuclei were distributed through the protoplasm.

In Orbitolites complanata, Lamk., Bütschli ((7), pp. 80-82) described numbers of small round or oval or irregular nuclei in which a reticular structure could be detected. They were most numerous in the peripheral chambers, and might be absent from the central chambers. As will appear below, this description differs considerably from what I have found to be the usual condition either in the megalospheric or microspheric form of this species.

III. Astrorhizidæ.—In Dendrophrya radiata, WRIGHT, MÖBIUS ((23), p. 13) found a single large nucleus, 66  $\mu$  in diameter.

IV. Lituolida.—No record.

V. Textularidæ.

BÜTSCHLI ((7), p. 83) described two specimens of this genus whose central chambers appear to have measured about 12  $\mu$  in diameter, and which, therefore, may have belonged to the microspheric form. In one, which was young (nine chambers are represented), a single nucleus was present; in the other, which had fourteen chambers, at least three were present.

R. Herrwig ((16), p. 50) found a single nucleus situated in the first formed chamber in a specimen of this genus with five chambers, and in another specimen, with thirteen chambers, one nucleus was also present.

VI. Chilostomellidæ.—No record.

VII. Lagenidæ.—A single round nucleus is described in species of the genus Lagena, by M. Schultze ((38), p. 56), F. E. Schulze ((42), p. 14), Gruber ((14), p. 501), and Bütschli ((7), p. 83). In Bütschli's figure a coarse nuclear reticulum and rounded nucleoli are represented.

VIII. Globigerinidæ.—A single large nucleus containing granules, is described by R. Hertwig ((17), p. 345) in a specimen of Globigerina bulloides, D'Orb.

IX. Rotalidæ.—In Spirillina vivipara, Ehrb., Bütschli ((7), p. 84) described numbers of minute stained bodies distributed through the protoplasm. Some of these he considered to be nuclei, while others were regarded as stained portions of food material.

In *Discorbina*, sp., numbers of bodies regarded by this author as probably nuclear in nature, were found in the protoplasm ((7), p. 86).

In a species belonging to the Rotalidæ, R. Hertwig ((16), p. 49) found a single nucleus in individuals whose chambers numbered from 1 to 3. The central chambers in these specimens measured from 27 to 35  $\mu$  in diameter. In examples with four

chambers, from one to four nuclei were present. The size of the central chamber is not stated in these cases, but from the figures it appears that its diameter was about the same as in the examples mentioned above.

F. E. Schulze mentions ((42), p. 20) the occurrence of a single nucleus quite similar to that of *Polystomella* (see below) in *Rotalina*, sp.

In Calcarina Spengleri (LINN.), BÜTSCHLI ((7), p. 85) described and figured a single large nucleus, with a clearly-marked reticulum. Nucleoli were present in the peripheral zone, in three cases out of four. In some the nucleoli are said to have a fine reticular structure.

X. Nummulinidæ.—In Amphistegina Lessonii, D'Orb., Bütschli ((7), p. 86) also found a single large nucleus in one of the inner chambers. Some small bodies in the later chambers are also mentioned, which it is suggested may have been of the nature of nuclei.

Polystomella striatopunctata, F. and M. Schulze's account ((42), p. 18) of the nucleus of this species is the most complete that has yet been given. It is described as a round body having, in some cases, a diameter of 56  $\mu$ , and surrounded by a conspicuous membrane of considerable thickness. Highly refracting nucleoli, lying in a clear and apparently fluid substance, occupy the interior. In quite young specimens only one nucleolus was found, but they may number as many as twenty or more in advanced specimens. The nucleus occupies a position in the middle third of the series of chambers, and often lies partly in one of the narrow canals connecting the chambers, being preserved in its progress from one chamber to another. Schulze points out that the position of the nucleus is thus dependent on the total number of chambers.

Sometimes two, and in one instance three, nuclei were present, and in this case they occupied adjoining, or at least neighbouring, chambers.

Verworn ((46), p. 462) has made a very interesting observation on the nucleus of *Polystomella*. On breaking an individual into pieces, he finds that, while many of the larger pieces remain alive, as shown by their extended pseudopodia, only the fragment containing the nucleus possesses the power of secreting fresh material to repair the broken shell.

HOFER ((19), p. 149) objected to Verworn's experiment on the ground that, in the Polystomellas investigated by him, by far the greater number of specimens had many nuclei, so that when a shell is broken it would be improbable that any considerable fragment would be free from nuclei. I can only say that Hofer's experience is very different from mine, as will appear later.

At first sight much of the evidence here collected appears contradictory.

It will be shown below that in *Polystomella* the megalospheric form has a single nucleus during the greater part of its existence, and the microspheric form numbers of comparatively small nuclei.

Some of the apparently contradictory statements may probably thus be reconciled.

Thus, in *Textularia*, while Max Schultze and Bütschli find two, three, or more nuclei, R. Hertwig finds a single one. From Bütschli's figures it appears that he was dealing with microspheric forms.

The frequent occurrence of a single nucleus in the genera which have been examined is in harmony with the fact that the megalospheric form usually far outnumbers the microspheric. It is probable, however, that the nuclear history differs to some extent in different groups of Foraminifera. It may also be observed that, as I shall show presently in the case of *Polystomella*, bodies which I believe to be formed in the elaboration of the food may possess staining properties and be thus readily mistaken for nuclei.

In Rotalina and Globigerina, Herrwig describes the nuclei as consisting of two parts, of which one is granular and takes the stain, and the other is clear and homogeneous. Schulze, however, states that the nucleus of Rotalina, as seen by him, resembles that of Polystomella, and this is also true of Rotalina Beccarii (figs. 39 and 40). In Polystomella, an appearance somewhat resembling that which Herrwig describes is sometimes presented when a vacuolar space, probably resulting from the action of the reagents, lies alongside the nucleus.

At the conclusion of his paper, Herrwig says that the Foraminifera, with one or few nuclei, would doubtless at the time of reproduction become many-nucleated. Relying on the analogy of the Radiolaria, with whose life history he had recently dealt (18), Herrwig concluded that it is improbable that the multiplication of the nuclei should take place by simple fission, and that a process similar to that which he had found in *Thalassicola*, in which the originally single nucleus becomes divided into minute particles, which are distributed through the protoplasm, was more to be expected.

How correct Hertwig's surmise appears to have been will be seen in the sequel.

2.

## (a.) Polystomella crispa (Linn.). Figs. 1-3 and 5-32.

In the hope of throwing light upon the life-history of Foraminifera, I have examined a large number of specimens of *Polystomella crispa* (Linn.), a species of almost cosmopolitan distribution in shallow water, and abundant in the pools of our own shores.

Methods.—In collecting material I have used a large horsehair sieve with bolting cloth fastened beneath it. The sieve is set in a shallow pool, and handfuls of seaweed are torn from the rocks and shaken in the water standing in the sieve. The small creatures which live amongst the weed, including the Foraminifera, fall through the meshes of the sieve and are caught by the bolting cloth.

I have tried several reagents for killing the specimens, and have obtained fairly satisfactory results with warm saturated solution of corrosive sublimate and glacial

acetic acid, in proportions about 4 to 1. The advantage of this reagent is that the walls of the chambers of the peripheral whorl are rapidly dissolved by the acid, so that it is not long before the protoplasm is killed.

After thoroughly washing in water, the specimens were stained for some hours in picro-carmine. By this means the nuclei are stained bright red, and the protoplasm pale yellow.

Many specimens have been examined by means of sections, but the majority have been mounted whole.

As has been shown to be the case in so many other Foraminifera, this species is dimorphic. Externally the two forms are, so far as I am aware, undistinguishable; but, on examining decalcified and stained specimens, they may be at once referred either to the megalospheric or microspheric form.

These differ from one another in respect of the size and shape of the central chambers, and in respect of their nuclei.

The megalospheric form (fig. 13) has a large central chamber, a second chamber of a characteristic shape, and, during the greater part of its existence, a single large nucleus.

The microspheric form (figs. 6a and b) has a small central chamber, and a number of small nuclei distributed through the protoplasm.

As in other species, the two forms differ greatly in the frequency of their occurrence. Out of 1812 specimens which I had examined up to January 12th, 1894, 52 were microspheric, giving a proportion of megalospheric to microspheric forms of about 34 to 1. The relative proportion of the two forms varies, however, at different seasons.

Among the microspheric forms I have met with several young ones, which are far inferior in size and the number of their chambers to the large megalospheric individuals. (Cf. Figs. 6a, 7, and 13, which are all magnified 170 times.)

Before describing the characters of the two forms, certain features common to both may be mentioned.

The Structure of the Protoplasm in Preserved Specimens.—When a live specimen of Polystomella is crushed under a coverslip, and examined under a high power, the protoplasm appears as a colourless mass, containing granules, but not vacuolated.

In sections of specimens killed with osmic vapour, or any of the other reagents usually employed, the protoplasm is found to present an appearance which resembles that of bread, the granular solid portions forming walls and strands between rounded vacuolar spaces, which communicate with one another to a greater or less extent. This structure, for want of a better name, may be referred to as a reticulum.

In examining decalcified and preserved specimens as a whole, it is often seen that the protoplasm of one chamber protrudes into the next through the canals which connect the chambers together. These protrusions are marked by the lines of the reticulum. In the parts of the chambers away from the connecting canals the reticular structure is obscurely seen, but in the regions where such protrusions have occurred the strands of the reticulum are seen to be drawn out parallel with one another in the canal, and, in the chamber beyond, to be disposed concentrically around the aperture by which the protoplasm has entered (fig. 1). These protrusions are frequently repeated through successive chambers.

The movement of the protoplasm to which this effect is due occurred, no doubt, solely as the result of the action of the reagent used in killing it.

In many cases the nucleus is involved in one of these movements of the protoplasm, a portion of it being carried through into the succeeding chamber, where it is seen drawn out, and, like the protoplasm which surrounds it, disposed concentrically to the aperture by which it entered. Portions may thus be carried through as many as three chambers from that in which the main body of the nucleus lies (fig. 1).

Bodies other than the Nuclei contained in the Protoplasm.—In Polystomellas collected in summer there are present, in about one specimen in five or six of the megalospheric form, and also in specimens of the microspheric form, small bodies of a rounded shape, which take a red stain with picro-carmine (fig. 2). They are most abundant in the terminal chambers, becoming fewer and fewer as the series of chambers is followed backwards. In some cases they also increase in size towards the terminal chambers. The size may vary from 8  $\mu$  in diameter to 1  $\mu$  and under, and in any specimen, though frequently uniform, they may present considerable variations in size. Sometimes they are so abundant as to form a prominent feature in a stained specimen (fig. 2); in other cases they are sparsely scattered through the protoplasm, and, as stated above, they are absent altogether in the majority of specimens. These statements hold true of examples killed and stained in a batch, so that the differences cannot be dependent on different modes of treatment.

Though generally spherical, they sometimes present an elongated shape, and they may be excavated by deep concave indentations (fig. 3), which may be so extensive as to reduce the body to a hollow shell of stained material.

While they are generally uniformly stained, in some cases stained and unstained regions, variously distributed, may be detected. In sections of specimens stained with picro-carmine, and afterwards with methylene blue, they retain the red stain, while the surrounding protoplasm is stained blue.

They are at least as frequently met with, and in that case they are as abundant, in young individuals as in old ones.

In a batch of specimens of *Polystomella* collected in October, and kept in dishes of sea-water for some months, these bodies are found, after the usual preparation, to be almost entirely absent. The water in which the Polystomellas were kept contained numbers of Infusoria, and some small clumps of brown algae, which may have served as food. Although the protoplasmic contents of the shell may have shrunk during

the period that they were submitted to these conditions, and their nuclei, as will be shown later, underwent a very marked diminution in size, few or none of the specimens died. Out of 116 examples only four showed any indication of the bodies under consideration. Some of the specimens were killed in January (after three months' captivity), and the remainder in March (after five months); and, with the second set, examples freshly collected from the sea were killed and stained, using the same solutions for all. In those fresh from the sea the stained spheres were more abundant, though fewer than in specimens collected in summer.

How are these bodies to be regarded?

It appears probable that they are either of nuclear nature, or that they are food material in some stage of metabolism.

In favour of their nuclear nature is the fact that with the reagents which I have used they have the same staining reactions as the nuclear elements.

On the other hand against their nuclear nature many considerations may be urged. They are generally (at least in four cases out of five) absent altogether from specimens in which the large nuclear elements are well stained, and their presence or absence appears to be entirely independent of any change which may be seen in these nuclei. They may occur in both microspheric and megalospheric forms, whose large nuclear elements are so strongly contrasted, and in both young and old specimens.

In favour of the view that they are food stuff are the facts that they are always most abundant in the terminal chambers, through which the greater part of the food taken in must pass before it is elaborated into protoplasm, and that, as above stated, they are to a large extent absent from specimens kept under conditions unfavourable to nutrition.

In the Infusorian Balantidium entozoon (Ehr.), which inhabits the rectum of the frog, bodies which appear to be of a similar nature are often present (fig. 4, a and b). In preparations (made in March) killed with osmic vapour, and stained with picrocarmine, the macro-nucleus is deeply stained, and what appears to be the micro-nucleus may generally be detected lying in a depression in it. In some specimens no other stained bodies are present, but in most cases numbers of round bodies with a deep red stain are thickly scattered through the protoplasm. They vary in size from 1 to 5  $\mu$  or more in diameter, and while many are uniformly stained, in others darkly stained bodies are seen to lie in a clear or granular matrix (fig. 4 b).

Considering the quiescent condition of the macro-nucleus and the micro-nucleus in these specimens, the inconstant occurrence of the bodies, and the variety in size and constitution which they present, it appears impossible to entertain the view that they are nuclear, while the hypothesis that they are formed in the elaboration of the food material presents no difficulty, and is in accordance with other observations.

Miss Greenwood (13) has described in the endoderm cells of *Hydra* certain "nutritive spheres," which take a pink stain with picro-carmine, and which, as the MDCCCXCV.—B.

name given to them implies, there is good reason to believe are formed in the metabolism of the food materials.

On these grounds I regard the stained bodies in question met with in *Polystomella* as nutritive in nature, formed, that is to say, in the elaboration of the food.

It must, however, be stated, that I am unable by the methods which I have hitherto employed to distinguish them from the small nuclei which are found in the protoplasm in the later stages of the megalospheric form.

Besides these bodies which are stained by picro-carmine, several others are commonly present in the protoplasm. Among these may be mentioned:—

- (1) Clear transparent globules which swell in water, and give the appearance of concentric light and dark bands with transmitted light; they are 3 to  $4 \mu$  in diameter, and do not stain violet with iodine.
- (2) Dark yellowish-brown globules, having a diameter of  $4 \mu$  and under. They are sometimes present in large numbers (fig. 5).
- (3) Pale yellow bodies of the same diameter, but less highly refracting than the last.

Radial arrangement of the Reticulum about the Nuclei.—In many cases, both in the megalospheric and microspheric forms the strands of the protoplasm are set in radiating lines about the nuclei (figs. 10 and 23). On examining whole specimens of the megalospheric form after decalcification, it is often seen that the outline of a chamber is indented opposite the nucleus. This effect must be due to the shrinkage of the nucleus after the wall of the shell is dissolved, the shrinkage of the nucleus having been greater than that of the protoplasm as a whole. The effect of this shrinking must be to produce a radial arrangement of the strand of the reticulum about the nucleus. It appears impossible in preserved specimens to distinguish such an artificially produced arrangement from any slightly-marked radiating disposition of the protoplasm which may exist naturally.

The Microspheric Form (figs. 6-12). The *Microsphere* is a nearly spherical chamber, whose diameter varies in different specimens from 6.5 to 13  $\mu$ . The average of the mean diameters in twenty-seven cases is 9.6  $\mu$ .

The second chamber is of the shape of a somewhat curved cone, and is applied to the microsphere by its concave side, communicating with it by a short canal at or near its apex. In some cases there is an indication of a globular swelling near the apex of the cone, and this might be considered to be the second chamber, the remainder of the cone being the third. The succeeding chambers gradually increase in size, but the cog-like "retral processes" (see fig. 13) characteristic of the genus do not appear for some distance along the series of chambers.

The spire in which the first few chambers are disposed is often not flat, as in the succeeding chambers, but helicoid. When this is the case, the direction of the spire is sometimes dextrotropic and sometimes levotropic.

Though the size attained is not larger than that of the megalospheric form, the number of chambers in specimens of the two forms of equal size is greater in the microspheric. This is owing to the fact that in this form the central region is occupied by small chambers which gradually diminish in size to the microsphere, while in the megalospheric form, a single large chamber, the megalosphere, occupies the centre.

The smallest specimen I have seen (fig. 7) has twenty chambers, and measures 230  $\mu$  across the short diameter of the spire of chambers; one of the largest has forty-seven chambers, and measures 800  $\mu$ .

Nuclei.—Microspheric individuals have many nuclei. They are distributed through many chambers, beginning at one of the internal chambers, and extending some distance beyond the middle of the series, counting from the microsphere to the terminal chamber. Thus, in a specimen with twenty-nine chambers there are twenty-eight nuclei extending from the fourth to the twenty-third. In one with forty-two chambers, there are forty-four nuclei extending from the thirteenth to the thirty-first.

There may be one, two, or as many as six nuclei present in one chamber, and on the other hand a chamber may be free from nuclei while the adjoining chambers contain them. I have never seen the nuclei extending into the terminal chambers.

The nuclei are generally of a round or oval shape. In nearly every case they are small in the inner chambers, and gradually increase in size as they are situated further along the series. Thus, in one specimen, the innermost nucleus measures  $30 \times 20 \mu$ , and the outermost  $48 \times 38 \mu$ .

Structure of the Nuclei.—In sections the nuclei appear to consist of a homogeneous substance which stains moderately deeply with picro-carmine, with deeply stained nucleoli, round or oval, embedded in it. The nucleoli vary much in size and number, and when large may contain round vacuolar spaces with clear unstained contents (figs. 8 and 9). The large nuclei contain larger nucleoli than the small ones. Externally the homogeneous inter-nucleolar substance does not appear to be limited by a membrane or wall of any kind, but terminates sharply against the coarse reticulum of the surrounding protoplasm.

Division of the Nuclei.—Very often the nuclei are disposed in pairs in the protoplasm, and in some cases the opposed surfaces are flat and corresponding, as though marking a plane of division (figs. 9 and 10).

In a specimen of one of the microspheric individuals which was cut into sections, a nucleus in process of division is seen (fig. 11, a-c) in three consecutive sections. It so happens that the plane of the sections passes nearly at right angles to the plane of division of the nucleus. In the first section both divisions of the nucleus (which I will distinguish as right and left) are seen united by a constricted portion, and the right division appears larger than the left. In the next section a similar appearance is presented, but now the left is larger than the right. In the third section the left half alone appears. The nucleoli and the inter-nucleolar substance present exactly the same appearance as in nuclei which are not undergoing division.

It may, I think, be taken as a fact that the nuclei of the microspheric form increase in number during the earlier stages of growth by simple division.

Dispersal of Nuclear Substance.—Besides the round or oval nuclei, there are very generally present in the protoplasm irregular strands of red-stained substance. These may be small and few in number, or they may be so large and abundant that the chambers containing them appear under a low power red with the irregular deeply stained masses. In sections these strands are frequently seen to be continuous with the nuclei (fig. 12).

In some specimens (fig. 6,  $\alpha$  and b) the nuclei furthest removed from the centre present the rounded shape above described, several of them being disposed in pairs as though recently divided, but as the series of chambers is followed toward the centre the nuclei assume an irregular shape, and the red-stained strands appear in the protoplasm about them; gradually the nuclei become more and more irregular, until in the innermost chambers no nucleus of the rounded form is seen, but in their stead there are the irregular deeply stained strands. In one large specimen, with forty-seven chambers, no rounded nuclei are visible, and the whole of the stained matter appears to consist of the irregular strands.

It has been stated that the rounded nuclei have not been observed in the terminal chambers, but this is not the case with the strands. Though in the majority of cases these are most abundant in the chambers in which the rounded nuclei lie, in others they are found in the terminal chambers, and in one specimen they are seen to be closely massed in the terminal chamber.

To repeat, the facts which the preparations show are these:—

- 1. The irregular strands may be seen continuous with the rounded nuclei.
- 2. In a single specimen all transitions are found between the rounded nuclei and the irregular strands.
- 3. While in some specimens, and especially young ones, only rounded nuclei are present and no strands, in others the reverse is the case, only strands being present and no nuclei.

It appears probable that while in young specimens the nuclear material is in the form of rounded bodies multiplying by simple division, it is gradually dispersed through the protoplasm in the form of these irregular strands.

[Since this was written I have examined specimens of the microspheric form in the reproductive stage which is briefly described in Postscript 2, at the end of this Paper.

At the beginning of the process there described, before the protoplasm has emerged from the shell, numbers of nuclei as well as stained strands are present. The nuclei resemble in size and distribution those of a rounded form found in the vegetative phase, but they appear homogeneous, the nucleoli being very indistinct, or altogether absent. In view of the presence of these nuclei in the early reproductive phase, it appears doubtful whether, as above implied, and as stated in the preliminary Paper published in the 'Proc. Roy. Soc.,' vol. 56, p. 156, the

whole of the nuclear material becomes distributed through the protoplasm in the previous stage.

I have no evidence as to the nature of the stained strands, and the part they play in the economy of the organism. I have simply attempted to describe the very remarkable condition which these microspheric forms present.—March 13, 1895.]

THE MEGALOSPHERIC FORM (figs. 13-32).—The Megalosphere, which occupies the centre of individuals of this form, is a globular chamber varying considerably in size. Among eighty-nine examples, taken consecutively as they were collected, the diameter of the megalosphere lay between 60  $\mu$  and 100  $\mu$  in seventy cases. The greatest diameter among the eighty-nine cases was 165  $\mu$ , and the smallest 35  $\mu$ , and this is the smallest megalosphere that I have seen in any example of this species which I have examined.

The relations of the second and succeeding chambers to the megalosphere are shown in fig. 13. The second chamber is applied to the megalosphere for its whole length; at one end it is pointed, and at the other it abuts against the third chamber. The short canal by which it communicates with the megalosphere is usually situated near the middle of the concave side.

Nucleus.—A single large nucleus is present in the great majority of cases in the megalospheric form. When the nucleus lies completely in one chamber it is usually round or oval. In many cases, however, it is found to send one or more diverticula into the succeeding chamber, as though fixed in the act of passing from one chamber to another (figs. 13, 15, and 23).

Position of the Nucleus.—As Schulze has shown (42), the nucleus usually lies in or somewhere near the chamber which is numerically in the middle of the series from the megalosphere to the terminal chamber. There is some evidence to show that its position depends, in part at least, on the disposition of the bulk of the protoplasm. This is most clearly seen in young specimens. It has been pointed out above that the megalosphere varies considerably in size in different specimens. Now in specimens with few chambers the megalosphere, being considerably larger than the chambers which immediately succeed it, contains a considerable quantity of the whole bulk of the protoplasm. If in a young specimen the megalosphere is large, the nucleus is found to be less advanced along the series of chambers than in those in which the megalosphere is small. In such specimens it appears that the nucleus tends to lie near the centre of the protoplasm.

In specimens with twenty to thirty chambers, however, the nucleus is generally found, as above stated, near the middle of the series, and as the chambers which follow the megalosphere successively increase in size, it is clear that its position is some distance behind the centre of the whole of the protoplasm.

As will appear below, in dealing with other species whose growth is spiral (Rotalia, Calcarina, Truncatulina) the nucleus in like manner moves on from

chamber to chamber as the number of chambers increases. In *Orbitolites* and *Cycloclypeus*, on the other hand, whose growth is cyclical, the nucleus in the megalospheric form remains in or close to the first formed chamber, which, owing to the mode of growth, is at the centre of the protoplasm.

The Size of the Nucleus.—The nucleus increases in size as the protoplasm grows. The truth of this statement may be realised by inspecting the accompanying diagram (p. 423), in which the results of the measurement of a number of examples are given. The abscissæ indicate the diameter of the nucleus in  $\mu$ 's, and the ordinates give the number of chambers (containing protoplasm) of the different examples whose nuclei were measured.

It must be observed, however, that these measures only roughly indicate either the size of the nucleus or the bulk of the protoplasm. The nucleus is generally an oval body, and the "diameter" here given is the mean between the long and short diameters as it presented itself in the specimen. In many cases the nucleus would be seen endwise, hence the measure of size here given is in many cases too small." Again, the number of chambers is only a rough indication of the bulk of the protoplasm, for it takes no account of the size of the varying megalosphere, or of the fact that in many specimens the terminal chambers are empty, a condition due either to their contents having been extended in the form of pseudopodia, and hence torn off when the specimen was collected, or to other causes.

In the diagram two curves are given. The upper one embodies the results obtained with 118 specimens preserved fresh from the sea in the months of May and June. The lower gives the results obtained from specimens kept in dishes in the laboratory for three months, October to January. The dots indicate the average size of the nuclei of the individuals having the same number of chambers, the number placed by each indicating the number of individuals from which the average is taken. It will be seen that on the whole the direction of the curves is upwards and to the right. In other words, as the protoplasm increases in bulk the nucleus undergoes a corresponding increase.

In the specimens which had been kept alive in dishes the nuclei are much smaller than in those killed fresh from the sea. In these specimens so many of the terminal chambers were empty that it appears probable that the protoplasm had shrunk considerably as the result of the scanty food supply. As I had no means of measuring the extent of the shrinkage, the individuals are tabulated according to the actual number of chambers which contained protoplasm when they where mounted. The case is therefore rather understated, but the distance between the curves is sufficient to show the marked diminution in the size of the nucleus under the conditions in which the animals were kept.

Structure of the Nucleus.—In a section through the nucleus, which has been stained in picro-carmine, and in hæmatoxylin (fig. 14) or methylene blue, so as to give a contrast in colour between the nucleus and the surrounding protoplasm, the outline of the nucleus is generally sharp for the greater part of the periphery. It is

not unfrequently the case however, that there are regions where the sharpness of the separation is lost. This appearance I believe to be due to the fact that the plane of the section here cuts the nucleus obliquely.

Although, as F. E. Schulze states, the nucleus often appears to be surrounded by a definite membrane when seen in the whole specimen, and in sections has a well-marked limit (figs. 14 and 16), I have failed, in examining sections, to see a clear indication of a nuclear wall which is distinct from the protoplasm on the one hand, and the contents of the nucleus on the other.

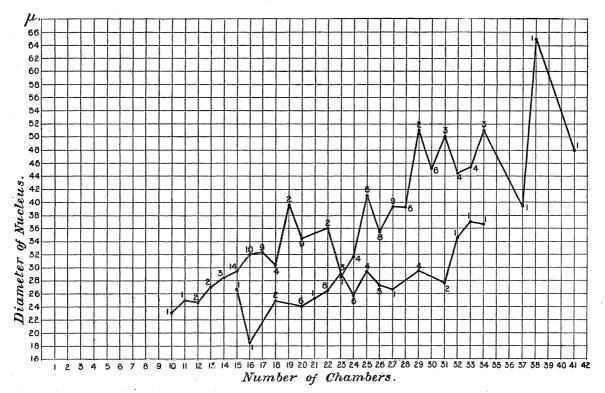


Table showing the increase in size of the nucleus accompanying the growth of the organism.

The abscissæ indicate the diameter of the nucleus, and the ordinates the number of chambers containing protoplasm of the specimens whose nuclei are measured.

The figure placed by each dot shows the number of specimens having a given number of chambers, the average diameter of whose nuclei is here given.

The upper curve refers to specimens preserved fresh from the sea, the lower to specimens kept for three months with scanty food supply.

The curves overlap at one point, but do not cross.

Three elements are to be distinguished in the nucleus: the nucleoli, the reticulum, and the intermediate substance.

The nucleoli appear to be invested by the substance which forms the reticulum, and the strands of the latter spring from this investment (figs. 14 and 16). They are round or oval bodies, staining readily with picro-carmine. They present great differences in different individuals. Their size in a given nucleus may be nearly uniform,

or it may vary widely. If large, they generally contain one or more cavities (figs. 14, 18, &c.). Sometimes the nucleoli are compound *morula* like masses, whose appearance suggests that a large nucleolus is breaking up into a number of small ones (figs. 17 to 19), and frequently their disposition suggests that they have recently been set free by the breaking up of such a compound nucleolus (fig. 21). Young specimens always have large nucleoli, and it appears probable that the nucleoli become smaller as development advances.

The reticulum varies much in the closeness of its meshes. In some cases (fig. 16) it forms an open network, while in others its communications are so intricate and minute as to give the appearance of an almost homogeneous substance. This is especially the case in the shrunken nuclei of the specimens kept for some months in dishes.

Separation of portions of the Nucleus.—Very commonly in the chambers which lie towards the centre of the shell from that which the nucleus occupies—in the chambers, that is to say, through which the nucleus has passed as it has moved on with the growth of the individual—there are present fragments which take a pale reddish stain with picro-carmine, and hence are readily seen as they lie in the yellow stained protoplasm (fig. 24). The contour of these fragments is generally indistinct, and in sections it is seen that they are more or less homogeneous granular bodies, while at their periphery they gradually acquire the reticular structure of the surrounding protoplasm. In some cases sections of the fragments show them to contain globular bodies, staining bright red with picro-carmine, which appear to be precisely similar to the nucleoli of the nucleus (fig. 25). In most cases, however, no such bodies are to be seen. These fragments lie as has been said in the track of the nucleus, and never extend far beyond it. In a few cases a prominence is seen in the profile of the nucleus as though a portion were being separated off (fig. 24)

From the appearance of these bodies, their position in the track of the nucleus, and from the fact that they may contain bodies like nucleoli, it seems probable that they are indeed fragments of the nucleus which have been given off into the protoplasm as it has moved on from chamber to chamber. It is to be observed that though these fragments sometimes contain nucleoli, the reticular structure is not seen in them.

Not unfrequently after treatment with picro-carmine, certain portions of the protoplasm present a generally diffused flush. In many cases this flush cannot be seen, either by examination of the whole specimen or of sections, to depend on the presence of stained particles, though these may exist and be so small as to escape detection; the appearance is that the protoplasm in these regions has a general stain. Frequently the flushed region either extends from the central chamber to a little beyond the nucleus, or is limited to the chambers in the immediate neighbourhood of the nucleus. In the specimen from which fig. 23 is drawn the flush is present only in part of the chamber in which the nucleus lies, and here minute stained particles can be detected in the flushed region. Such an appearance suggests that minute portions of nuclear substance are being given off into the protoplasm. Apparent Degeneration of the Nucleus.—In some cases the nucleus presents a different appearance from what has been described. Instead of possessing a rounded shape it may have the appearance of being partially collapsed, or it may be quite irregular, extending through several chambers, and sending rounded offsets into the protoplasm (fig. 26). This appearance is quite distinct from that produced by the change in shape which the nucleus undergoes when it is involved in a protrusion of the protoplasm, such as has been described above (cf. fig. 1).

Associated with this loss of its rounded shape is the absence or scarcity of nucleoli, and a general paleness, so that the characteristic red colour is only faintly indicated at the profile of the nucleus, the peripheral parts alone retaining their staining power, and this in a diminished degree. Such nuclei appear to be undergoing degeneration, having lost their shape, and, to a large extent, their nucleoli and their staining power.

Multiple Nuclei.—I have met with twenty-one cases in which more than one large nucleus is present in a megalospheric form. Sometimes this condition is associated with irregular growth; thus, in one example, where the inner chambers are very irregular in size and shape, there are seven nuclei. Three are present in another irregularly-grown specimen. In a case where there are two nuclei, the shape of the megalosphere suggests that it was formed of two equal and incompletely fused or possibly incompletely separated spheres, to which apparently the nuclei correspond. In one specimen with seventeen chambers the nucleus is represented by seven pieces, distributed through the first seven chambers; in this case the megalosphere is very large ( $160 \times 134 \,\mu$ ). There is no irregularity or peculiarity of growth in the remaining seventeen specimens. In two of them three nuclei are present, and two in the remainder.

The nuclei, when more than one are present, are generally about equal in size, and usually, though not always, situated in the same or adjoining chambers. The size of their nucleoli may be about the same, or the nuclei may present a marked difference in this respect. Thus, in one case in which two nuclei are present in one chamber, one contains vacuolated nucleoli, of 3  $\mu$  diameter, the other is crowded with minute nucleoli of a diameter of 1  $\mu$ . Two other cases presented a similar contrast.

The significance of the presence of more than one large nucleus in a megalospheric form will be discussed below.

Reproductive Phase. Formation of Zoospores.—Among Polystomellas collected between the end of March and the end of May, 1893, specimens are not uncommon in which the large nucleus is absent altogether. As an indication of the frequency with which these specimens occur, I may mention that among thirty-eight examples of megalospheric forms, collected on April 30, and stained and mounted without any selection, eight have no large nucleus.

These specimens generally present another conspicuous feature, namely, that the megalosphere in many cases communicates by broad channels with the adjacent

chambers of the inner whorl, in addition to the usual communication between successive chambers. In the same way communications are found between the peripheral parts of the chambers of the inner whorl and those of the outer (fig. 32,  $\alpha$ ).

When treated with picro-carmine such specimens frequently stain a more or less deep pink colour throughout, though in some cases they remain pale.

Sections of these specimens generally show minute nuclei scattered through the protoplasm of the terminal chambers. These are sometimes uniformly distributed, sometimes disposed in groups (fig. 30). In some cases these nuclei appear as compact, nearly uniformly stained bodies, in others they contain many round vacuoles (fig. 31). It may be observed that all the nuclei in such a specimen appear to be vacuolated to the same degree, whether it be much or little.

Two examples of the megalospheric form in which the large nucleus has disappeared (collected on May 31) present different conditions.

In one of these (fig. 27), which is composed of eighteen chambers, the whole protoplasm except that of the last two chambers is broken up into small spherical masses, 3 to 4  $\mu$  in diameter, the centre of each of which is occupied by a nucleus. The nuclei are in the phase of karyokinetic division (fig. 28), in which the chromatin elements have separated from one another, and present in profile the appearance of two distinct parallel bands, 1.5  $\mu$  in length, separated by achromatic substance. From what is seen in the specimen next described it appears that the spherical masses are about to divide to form spores. In the two terminal chambers numbers of nuclei are present, but they are not in process of division, and the protoplasm though much vacuolated is not broken up into spheres. I am not able to account for this condition of the terminal chambers.

In the second specimen (fig. 32, a) which is composed of seventeen chambers, the whole of the protoplasm is divided up into spherical masses 3 to 3.5  $\mu$  in diameter. Each contains a nucleus, and a trabecular structure of the protoplasm can be seen in the interior. Between adjacent spheres a delicate network is seen, and in the terminal chambers a curved strand of this reticulum may here and there be detected, having the appearance of a flagellum (fig. 32, b).

Four days after this specimen was collected (June 4), I happened to be examining a partially empty shell under the microscope, and saw at one point through a transparent region of the wall of one of the chambers, an active movement in the interior. I crushed the specimen under a coverslip, and numbers of actively moving spherical spores were set free in the water, while numbers of bodies, similar in all respects except their activity, remained among the broken fragments of the shell. On staining these with acid gentian violet indications of two flagella were made out, but the spores were too darkly stained for the nuclei to be detected. The spores were approximately of uniform size (4 to 6  $\mu$  in diameter), and, except for certain dark yellow masses, and some brown granules, constituted the whole of the contents of the shell.

It appears most probable that these actively moving spores are identical with the

spherical masses seen in the preserved specimen last described. The difference in size may be accounted for by the difference in the modes of preparation.

It will be noticed that while the masses in which the dividing nuclei lie have a diameter of 3 to 4  $\mu$ , the spores, which it appears are produced by the division of these masses, have an almost equal diameter (3 to 3.5  $\mu$ ). It is probable that the spores owe their large diameter to the more vacuolated condition of their protoplasm.

On another occasion I again saw the production of actively moving bodies, but these were of a different character from those just described.

On examining a large specimen only partly filled with protoplasm, in a watch-glass, numbers of small bodies were seen circling about the terminal chamber, while additions were frequently made to their number from the interior of the shell. On putting the shell under a coverslip with a little water, this was soon alive with small actively moving bodies which came out from the interior.

These bodies were of two kinds (fig. 33):—(a) large globular transparent cells which executed a rapid rotating movement. They were 10 to 11  $\mu$  in diameter, and contained highly refracting bodies (1  $\mu$  in diameter), and also, in most cases, a large globular brown body (4  $\mu$ ). Now and then a glimpse of a flagellum could be detected, but I was unable to see it clearly. (b) There were present, in much greater numbers, small actively moving cells, whose size varied from 6 to 1  $\mu$  in diameter. They were globular or oval, and like the large cells, contained small highly refracting bodies. On killing with osmic vapour, two flagella, one longer than the other, rising close together from the body of the cell, could be detected.

On crushing the shell more of the spores were liberated, and a considerable quantity of undivided protoplasm, with what appeared to be fat globules, and some brown granules were seen.

I have no evidence to show whether this specimen belonged to the megalospheric or microspheric form.

[I was at first inclined to regard these bodies as reproductive elements of Polystomella, comparable with the anisospores of Radiolaria, and as I was not then aware of the mode of reproduction of the microspheric form, it seemed possible that they were produced by it. Now that the mode of reproduction of the microspheric form is known (see Postscript 2) this view becomes untenable, unless it is supposed that the bodies in question belong to yet another phase in the life-history. The more probable view appears to be that they were not the spores of Polystomella at all, but were the products of some other organism which had entered the shell of the Polystomella. This is supported by the fact that a considerable amount of protoplasm occupied the central chambers of the specimen and showed no indication of being divided up into spores.—March 13, 1895.]

The evidence afforded by the investigation of *Polystomella* may now be reviewed.

The Microspheric form occurs in various phases of development, both young and old specimens having been found (figs. 6 and 7). Numbers of small nuclei are present, scattered through the protoplasm, but not extending into the terminal chambers. Those in the inner chambers are smaller than those situated further on. The nuclei contain nucleoli of different sizes lying in an apparently homogeneous inter-nucleolar substance. The nuclei increase in number by simple division, and it appears probable that they are so derived from a single nucleus. After maintaining their rounded form for a certain time, the nuclei give off portions of their substance, which become dispersed in the surrounding protoplasm.

Of the further history of the microspheric form of this species my preparations yield no evidence.\*

The Megalospheric form, during the greater part—the vegetative period,—of its life, has a single large nucleus, which grows in size with the growth of the protoplasm, and passes on from chamber to chamber; moving towards the centre of the bulk of the protoplasm, though lagging some distance short of it. It contains a nuclear reticulum, nucleoli, which occupy the nodes of the reticulum, and a substance occupying the meshes. The nucleoli appear to increase in number and diminish in size with the advance of the organism. There is reason to believe that, as the nucleus moves on through the chambers, portions of its substance are given off into the protoplasm. It appears that this may occur either by the separation of considerable portions (figs. 24 and 25), sometimes containing several nucleoli, which lie strewn along the track it has followed, or by the dispersal of minute fragments into the surrounding protoplasm, causing a flush in the neighbourhood of the nucleus in the stained specimens (fig. 23).

What is the fate of the large nucleus? It might be supposed that it divides up by binary fission, and so gives rise to the small nuclei which are found later. As stated above, I have met with twenty-one cases in which more than one large nucleus is present, and in two there are as many as seven nuclei. Do these represent stages at the beginning of the process?

If there are twenty-one cases in which binary fission has begun and the segments into which the nucleus has divided are still large and few in number, the cases in which, by this process, many nuclei of smaller size have been produced, ought to be abundant. The fact is, that amongst the 1760 examples of the megalospheric form which have been examined (up to January 12, 1894), including a large number in some stage of the reproductive phase, not one has presented itself which showed an intermediate condition between that with seven comparatively large nuclei and those with multitudes of minute nuclei of minimal size.

Although the conclusion is founded on negative evidence, it seems clear that the view that the small nuclei of the later stage are derived from the large nucleus by binary fission is untenable.

<sup>\*</sup> The mode of reproduction of the microspheric form is briefly described in Postscript 2.

It seems not impossible that the presence of more than one large nucleus in the megalospheric form may be due to an accidental division having occurred in the process of passing from one chamber to another. The nucleus, which is a very plastic body, is often found with two or more processes extending into the chamber adjoining that in which the body of it lies, through the connecting canals. In the ordinary course, the nucleus must eventually take to one canal, any processes which may have extended into other canals being withdrawn, but it might occur if the forces propelling it onward were evenly balanced that a separation into two halves should take place. However this may be, I am inclined to think that the condition with multiple nuclei is not a necessary stage in the life-history, and may therefore to that extent be regarded as abnormal.

It appears probable that an indication of the fate of the large nucleus as an entity is given by those cases in which the nucleoli have decreased in number, its shape has become irregular, and its staining properties diminished (fig. 26). In such cases a large part of the substance of the nucleus appears to have passed into the protoplasm, while the remainder is in process of dissolution.

In what manner the nuclear material dispersed in the protoplasm becomes fashioned into the small nuclei of the later stage I have no evidence to show.

[Rhumbler has recently published an account (28, b) of his investigation of Saccammina spharica (M. Sars), in which he has obtained a much more complete history of some of the nuclear changes than I have succeeded in doing.

Rhumbler shows that the large solitary nucleus of this species is gradually altered during its growth. The Binnenkörper, the nucleoli of other authors, which in young specimens are few, large and frequently compound, after increasing in numbers at first, become in the later stages fewer or disappear altogether. Meanwhile chromatin granules appear in the nucleus, and increase in numbers, becoming embedded in linin fibres. In the course of development, the substance between the Binnenkörper, which is at first homogeneous, becomes vacuolated and then formed into a well-marked reticulum (Wabenwerk) which appears first at the centre, and gradually extends to the periphery of the nucleus. Finally, the nuclear wall, which has been very distinct in previous stages, disappears, and the linin fibres with the chromatin grains are dispersed in the protoplasm.

It is suggested that the last stage of this process is preparatory to reproduction.

There are clearly several points of resemblance between the nuclear changes of Saccammina and those of the megalospheric form of Polystomella. I find, on referring to my specimens, that minute granules are frequently present in the reticulum, which may very possibly be grains of chromatin, though they are not seen so distinctly as in the very large nuclei described by Rhumbler. On the other hand, the nucleoli of Polystomella stain more readily with picro-carmine, and appear to retain their large size for a longer period than those of Saccammina.

Saccammina belongs to the family Astrorhizide, and builds a test which is

generally single chambered and is composed of foreign particles cemented together. This, as Rhumbler clearly shows, is expanded to accommodate the growth of the contained protoplasm. Hence, the evidence of dimorphism, which is afforded by the first formed chambers of the shell in many multiloculate Foraminifera, cannot be present here. But it does not appear that there is evidence of dimorphism to be derived from the nuclei, whose condition in *Polystomella* and in the species described below, is so different in the two forms. Out of the 286 specimens examined by Rhumbler, a single nucleus was present in all but one (which had two nuclei, and was regarded as pathological), and the phases presented by the nuclei fall into a continuous series.

It is, of course, possible, though not probable, that Rhumbler did not happen to meet with the microspheric form, which is always the rarer, or that this form is in *Saccammina* so different from the megalospheric, that the two forms are not regarded as belonging to the same species. As the evidence stands however, it appears that we have in *Saccammina* a species in which the differentiation into microspheric and megalospheric forms has not occurred. Its nucleus would not, therefore, be strictly comparable with the nucleus of the megalospheric form of a dimorphic species, such as *Polystomella crispa* (Linn).—March 13, 1895.]

In the second, or reproductive phase, minute nuclei (1 to  $2 \mu$ ) are at first found scattered irregularly through the protoplasm in varying numbers (fig. 30), and broad channels of communication become opened up between the inner and outer chambers. The little nuclei are sometimes found as compact bodies, sometimes excavated by vacuoles, and the changes of which these conditions are the expression appear to be simultaneous throughout the animal.

It appears that, while the nuclei are sometimes readily stained by picro-carmine, they may pass through a phase in which they do not react to this stain, for specimens are not unfrequently met with in which the large nucleus has disappeared, and the direct communications between the chambers have become established, and which, therefore, appear to be in the reproductive phase, but in which no stained bodies of any kind are recognisable.

Ultimately the nuclei become evenly dispersed throughout the chambers and divide by karyokinesis, the protoplasm becoming aggregated about them in spherical masses (3.5  $\mu$  in diameter), each of which contains a dividing nucleus (figs. 27 and 28). At a later stage each nucleus, presumably the daughter nucleus of this division, becomes the centre of a flagellated zoospore (fig. 32,  $\alpha$  and b). These are of approximately equal size. Their diameter in the specimens killed in corrosive sublimate and acetic acid is  $4 \mu$ .

A simultaneous division of nuclei by karyokinesis immediately before the formation of the reproductive elements, such as occurs in the megalospheric form of *Polystomella*, is a phenomenon of very general occurrence.

Among the Mycetozoa it was shown by Strasburger (44) to occur in Trichia

fallax in the developing sporangium, and later researches (21) have shown that it takes place immediately before the formation of the spores in this and ten other species belonging to eight genera. In three of these (Craterium, Didymium, Badhamia), as in Polystomella, the protoplasm becomes aggregated about the dividing nuclei in rounded masses before the ultimate division into spores.

It appears probable that the phenomenon is akin to the division of the micro-nucleus which precedes conjugation in the *Infusoria*, and to the division of nuclei which occurs in the maturation of the reproductive elements in the higher forms of animals and plants.

## (b.) Orbitolites complanata. Lamk. Figs. 41-51.

My specimens of this species were collected from the reef at Nukualofa, in Tonga, where it is very abundant. They were preserved in 95 per cent. spirit, and have been examined by means of section.

I have also examined the fine series from Fiji in the Brady Collection, the property of the University of Cambridge, and a collection, in spirit, kindly placed at my disposal by Dr. S. J. HICKSON, and obtained by him from the reef at Talisse Island, to the north of Celebes.

Before I left England my attention was called by the late Mr. H. B. Brady to this species, which he had obtained from the reefs of the Fiji Islands, and especially to the desirability of preserving specimens, with a view to following out their nuclear history. The observations recorded in this paper are the outcome of Brady's suggestion.

The species is not, however, a good one for throwing light on the history of the nucleus, as it is so large that each specimen must be examined by means of sections; moreover, the parasitic organisms that it harbours, and the abundance of large food particles contained in the protoplasm, often make it a difficulty to distinguish the nuclear elements proper to the organism itself.

As shown by Brady (2), the phenomenon of dimorphism is also presented by this species. The individuals fall into two groups, (1) those whose centre is occupied by a "primitive disc" (fig. 45), which consists of the large "primordial chamber" (megalosphere), together with the second or "circumambient" chamber, and (2) those in which the small chambers or chamberlets, as they are called by Carpenter, are continued to the centre. These evidently correspond with the megalospheric and microspheric forms of *Polystomella* and other Foraminifera.

It will be convenient to deal with the Tongan and Fijian specimens first, and with those from Celebes afterwards.

In the Fijian and Tongan specimens that I have examined there is a marked difference in size between the two forms, the microspheric attaining a much larger size than the megalospheric. Thus, among my thirty-three largest specimens of the megalospheric form from Tonga, the number of rings of small chambers is under thirty

in all cases except one, in which it is thirty-eight; among thirteen specimens from Fiji, the greatest number is thirty-three. In the specimens of the microspheric form, on the other hand, the number of rings of chambers varies from 79 to 110, as they are seen in sections of five specimens in the Brady Collection, and I have many examples from Tonga which are equally large.

The shells of this species, as is well known, are bi-concave, being thin at the centre and thick at the margin. As Brady points out, the central part of the microspheric form, composed, as above stated, of small chambers, is not more than one-third the thickness of the primitive disc which occupies the centre of the megalospheric form.

As the microspheric form increases in size, it frequently happens that the edge of the disc becomes double, so that a radial section at right angles to the plane of the disc is  $\gamma$ -shaped (fig. 43).

The shells whose margins present this character, and which have only been obtained from Fiji and Tonga, have been separated as a distinct variety, named "laciniata" (Brady). So far as I have seen they are all microspheric.

I may further recall the fact that the peripheral annuli of the full grown disc of this form are often found to be not divided up into small cubical or columnar chambers, as are those lying nearer the centre, but are composed of spacious chambers extending vertically through the whole thickness of the disc, and circumferentially round a considerable portion of its circuit. These may be called the *brood chambers* (fig. 43). In specimens which Brady obtained from the reefs of Fiji these chambers contained multitudes of young shells, consisting of the "primitive discs" of the megalospheric form.

I have now to give the results of my examination of preserved specimens.

MICROSPHERIC FORM.—All the examples of this form which I have examined, were full grown or nearly so. As above stated, the central part of the shell is occupied by small chambers. I have not been able to distinguish the central chamber (microsphere) from those which surround it, in the preparations I have seen.

Before the young are formed, the protoplasm fills all the chambers of the disc, with the exception of the brood chambers, which contain only a thin lining of protoplasm. This may in part be due to the withdrawal of the protoplasm as the result of the action of the spirit.

In the specimens of which I have cut sections (fourteen), numbers of small rounded nuclei are thickly scattered through the protoplasm, so that two or more often appear in the section of a single chamber (fig. 41). The great majority of these are about 6 to 10  $\mu$  in diameter, but some reach 20  $\mu$ .

A reticular structure may often be seen in the nuclei, and small darkly-stained masses, which appear to be nucleoli, are seen near the peripheral parts of the nucleus. The smaller nuclei are very often disposed in pairs in the protoplasm, and in some cases the pairs may be seen to be united by a constricted band, being killed in process

of division (fig. 41). The nucleoli in such dividing nuclei are as distinctly seen as in those which are single.

There appear to be all intermediate forms between the small nuclei and the larger ones. In the latter the reticulum is more clearly seen, and the nucleoli are less conspicuous. They are, moreover, not disposed in pairs, but solitary (fig. 42).

There are generally numbers of stained particles present in the protoplasm, some of which appear to be food material. It is possible that others may be of nuclear nature, but I have not recognised in these specimens anything of the nature of the stained strands met with in the microspheric form of *Polystomella*.

Reproductive Phase.—I have met with thirteen specimens among my preserved material, in which the brood chambers contained young. In those which have been decalcified (seven), the part of the disc internal to the brood chambers contained no protoplasm. It is clear that the protoplasm has been withdrawn from the small chambers of the disc and massed in the brood chambers, where it has been divided up into the young. In such specimens this central part is quite transparent, and consists of the organic basis of the walls of the chambers, together with the larger parasitic algae which are contained in them (fig. 43).

In marked contrast to the central region are the brood chambers at the periphery, closely packed with the young (figs. 43 and 44). In all my specimens the young are fully developed, and in all they belong to the megalospheric form. They consist of the primordial and circumambient chambers, invested by the darkly staining basis of the thin shell, from which the calcareous salts have been dissolved. The protoplasm of the primordial chamber is generally denser, and takes a darker stain than that in the circumambient chamber, and an oval nucleus measuring about  $20 \times 15 \,\mu$  lies in it. Even in this young condition the small parasitic algae are present in the protoplasm.

As in Brady's specimens, the young shells are set in the brood chambers, with their plane at right angles to that of the portion of the disc which contains them. Fig. 43 represents a vertical radial section through a disc containing young, and fig. 44 a vertical tangential section of such a disc. It will be seen that a considerable amount of protoplasm is present in the brood chambers, filling in the interstices between the young shells. This generally contains great numbers of the small alge, but I have failed to find any nuclei in it. It is, no doubt, continuous through the pores of the shells with the protoplasm of the young.

When the central region of the disc is thus left empty, the large parasitic algae contained in it, which are too large to pass through the channels connecting the chamberlets with one another, are found in active division, their reproductive phase following that of their host.

This species is often found attached to the green ovate leaves of a plant which grows in the shallow water on the reef. On one occasion when I had brought in some large specimens and put them with the leaves in a dish of water, in the course

of a few hours I found numbers of the megalospheric young which had escaped from a shell and lay scattered over the leaves and the surface of the parent, whose large brood chambers were empty.

The large shells lie flat on the leaves, but the young ones with few rings of chamberlets or none, often cruise about on the edge of the disc, which is thus directed vertically to the supporting object. Sometimes, when the specimens were kept in dishes, the young shells were found floating at the surface of the water with a film of pseudopodia extended about them, in the same manner as pond snails often float supported by a raft of mucus.

The Megalospheric Form.—As stated above, the megalospheric form begins its existence with a single nucleus situated in the primordial chamber (figs. 46–48). This nucleus maintains its position during a greater part of the period of growth. Thus among thirty-one examples of the megalospheric form in which the rings of chamberlets numbered from seventeen to thirty-eight, there are eighteen whose primordial chamber still contains a single nucleus. The nucleus measures about  $24 \times 14 \,\mu$ , it is of a round or oval shape, and a close reticulum can be detected in the interior. I have not seen definite nucleoli, but the central region of the nucleus often appears, in sections, to be separated from the peripheral region by a ring of more deeply stained particles (figs. 47 and 48).

In one specimen, with twenty-two rings of chamberlets, two rounded nuclei are present in the primordial chamber. In several others (fig. 49) no nucleus of the form above described is to be seen, but in its place, numbers of compact bodies of different sizes, and often of irregular shape, are present. These are not confined to the primordial chamber, but extend into the circumambient chamber and surrounding chamberlets. It would appear that in the megalospheric form of this species, after the individual has nearly completed its growth, the nucleus breaks up into a number of fragments, which become dispersed among the chambers.

Dr. Hickson's collection from Celebes consisted of 117 specimens. They were obtained from the reef at Talisse Island, to the north of the main island. Although, in this species, the central chambers are not covered by those that are added later, they are frequently obscured by a calcareous deposit on the surface. By dissolving the superficial parts of the shell, the central chambers may be exposed and their character recognised. In some cases, however, the central chambers are empty, and their character can then only be observed by examining the delicate organic basis of their walls. I failed to recognise the character of the central chambers in two cases, but of the remaining specimens only one belonged to the microspheric form, the others being megalospheric. The size attained by shells of the megalospheric form is much larger than in those which I have seen from Fiji or Tonga. In one case there are as many as sixty-six rings of chamberlets between the primitive disc and the

periphery. In sections of these specimens numbers of rounded bodies, which appear to be nuclei, can be detected in the protoplasm.

In three examples of the megalospheric form, while the central chambers of the shell are empty, those at the periphery have the form of brood chambers, and are crowded with young "primitive discs," similar to that whose empty chambers occupy the centre of the parent shell (figs. 50 and 51).

The young are disposed in the brood chambers in the same way as in the microspheric forms from Tonga and Fiji, above described, except that, owing to the thinness of the margin of the disc, as compared with these specimens, the young in each annulus are in a single row. I have failed to recognise a nucleus in the young form, probably owing to the imperfect preservation. The specimens containing young belong to a batch collected in the month of November.

We are here then brought face to face with the fact that in this species megalo-spheric young are produced by megalospheric parents, while it is no less certain that (in Fijian specimens, as described by Brady, and in Tongan specimens, as I have shown), megalospheric young are produced by microspheric parents. The relation of the two forms to one another will be discussed at the end of this paper.\*

It may be pointed out here that, in the Tongan specimens, the nuclear characters of the two forms agree fairly well with those of *Polystomella*.

In the microspheric form numbers of rounded nuclei are found scattered through the protoplasm, and they may be found in process of simple division. I have not, however, recognised anything like the giving off of deeply staining strands, which is so marked a feature in *Polystomella*.

In the megalospheric form, a single nucleus is found during a large part of the growth of the individual, and ultimately it appears to break up into a number of fragments.

In *Polystomella*, as we have seen, the nucleus of the megalospheric form increases in size with the growth of the protoplasm. In *Orbitolites*, however, the nucleus in the primordial chamber is hardly larger in the examples with many rings of chambers than in those with few.

The Celebean specimens are in a phase of growth to which I have found no analogy in *Polystomella*.

The account of the nuclei of *Orbitolites* here given differs from that of Professor BÜTSCHLI in which numbers of minute and irregular nuclei are described scattered through the protoplasm. Possibly his examination was confined to such later stages of megalospheric specimens as those which I obtained from Tonga, in which, as above described, the nuclei are found in this condition.

## (c.) Rotalia Beccarii (Linn.). Fig. 38-40.

Among seven examples of this species, six were megalospheric, and one microspheric.

MICROSPHERIC FORM. In the representative of this form there are thirty-two chambers. The microsphere measures 13  $\mu$  in diameter (fig. 38). Some twenty-four nuclei are present, irregularly distributed through chambers 10 to 25. As in *Polystomella*, the nuclei increase in size from within outwards. I see no "stained strands," but the protoplasm in the immediate neighbourhood of some of the nuclei has taken a diffused flush.\*

MEGALOSPHERIC FORM (fig. 39). The mean diameter of the megalosphere varies between 37 and 65  $\mu$ , having an average of 54.6  $\mu$ . In the four cases in which the protoplasm is preserved, a single large nucleus is present, situated some distance behind the middle point of the protoplasm. In one case it is drawn out into the succeeding chamber, in the other three whose nuclei are round or oval, the mean diameter of the nucleus varies between 27.5 and 33  $\mu$ . In each case fairly large nucleoli are present (fig. 40).

# (d.) Truncatulina lobatula (W. and J.).

When the shells of this species are decalcified, a brown and apparently chitinous element remains, which retains the size and shape of the chambers. This is present in the walls of the inner chambers of many species, but is particularly well developed in this.

In a single example of the *Microspheric* form, the microsphere measures  $11 \times 10 \mu$ , and at least seven nuclei are present.

In twelve examples of the Megalospheric form, the mean diameter of the megalosphere varies between 35.5 and 15  $\mu$ , and has an average of 28  $\mu$ . In the three cases in which the protoplasmic contents are preserved (including the example with the megalosphere of 15  $\mu$  diameter), a single large nucleus is present.

Eight examples from Tonga appear to belong to Brady's species, T. tenuimargo. They are all of the megalospheric form, the mean diameter of the megalosphere varying between 24 and 14.5  $\mu$ , and having an average of 20.8  $\mu$ . In five specimens which contain protoplasm (including that with the megalosphere of 14.5  $\mu$ ) a single large nucleus is present.

Thus, in *Truncatulina*, the diameter of the megalosphere, though often considerable, may be so small as to approach that of the microsphere. In these cases, if the size of the central chamber were the only character on which to rely, it would be doubtful to which form the specimen should be referred. It appears, however,

<sup>\*</sup> As stated in Postscript 2, I have observed the production of megalospheric young by a microspheric parent in this species.

that this is indicated by the character of the nuclei. In the example of the microspheric form, whose central chamber measures  $11 \times 10 \,\mu$ , at least seven nuclei are present, while the specimen of the megalospheric form whose central chamber is smallest  $(14.5 \,\mu)$  has a single large nucleus measuring  $20 \times 15 \,\mu$ .

#### (e.) Calcarina hispida, Brady. Figs. 34-37.

Some examples of this species were contained in sand collected with corals from a depth of from 20 to 40 fathoms off the Tonga Islands. They were preserved in spirit of about 70 per cent. Of these, twenty-two belong to the megalospheric form, and two to the microspheric. In this species also there is a considerable quantity of the chitinous element in the walls of the chambers, which remains after the lime has been dissolved. Owing to the presence of this substance the walls of the chambers of specimens which are mounted in Canada balsam are generally to some extent shrivelled; hence the measurements of the chambers fall rather short of their proper size.

The average mean diameter of the megalosphere in twelve specimens is  $49 \mu$ , the extremes being 58.5 and 38.5  $\mu$  (fig. 34).

The microspheres in the two microspheric examples measure  $15 \times 12.5 \mu$  and  $13 \times 11 \mu$  (fig. 35).

In the thirteen examples of the megalospheric forms in which the preservation is sufficiently good to show the nuclear characters, a single large nucleus is present (fig. 34).

In one of the microspheric forms at least five small nuclei can be seen, and probably others are present, but the preservation is not sufficiently good to allow the nuclei to be well seen.

In the other microspheric specimen, while the inner chambers are empty, several of the terminal chambers contain numbers of large protoplasmic bodies, in number about 140 (figs. 36 and 37). At first these bodies are flattened against one another, but as the series of chambers is followed they assume a more perfectly oval shape. In seven examples the mean of the long and short diameters is  $58.3 \,\mu$ . A round nucleus may be detected in many of them.

It appears probable that these bodies are young megalospheric individuals which have not yet acquired a shell.

#### (f.) Cycloclypeus Carpenteri, Brady. Figs. 52-54.

I obtained a few examples of this rare species to the south-east of Nomuka, in the Tonga Islands, at a depth of from 20 to 40 fathoms.

On decalcifying them two were found to have been preserved with the protoplasm contained in the shell. One of these, which measured about 1 centim. in diameter, was mounted whole, after staining with picro-carmine, and sections were cut of the other (which was smaller) parallel to the plane of the disc.

In both specimens large chambers, resembling to some extent the primitive disc of Orbitolites complanata, LAMK., occupy the centre of the shell (fig. 52). These consist of: (1) A somewhat oval chamber which appears to be the megalosphere, measuring  $300 \times 205 \,\mu$ . (Owing to the shrivelled condition of the walls of the inner chambers, which consist of a thin apparently chitinous layer, these numbers are only approximately correct.) (2) A very large crescent-shaped chamber, in the concave side of which the megalosphere lies. The length in a straight line is  $610 \,\mu$ , and the greatest breadth  $310 \,\mu$ . In the sections a single short canal can be detected passing from the megalosphere to the second chamber, at about the middle of the concave side. (3) Another somewhat crescent-shaped chamber, enclosing the other side of the megalosphere; while its length is about equal to that of the second chamber, its breadth is very much less (under  $100 \,\mu$ ). This chamber appears to be intermediate in character between the large chambers and the small ones making up the surrounding annuli.

The two crescent-shaped chambers thus surround the megalosphere. Their ends are in apposition, the third chamber somewhat overlapping the second on the outer side, and they communicate at either end by short canals passing from one chamber to another.

The first ring of chambers surrounds these three, communicating with the crescentic chambers by several short canals, and the others follow in concentric rings, but the innermost ring is less completely divided up into cubical chambers than those which follow.

As in the megalospheric forms described above, a large nucleus is present. In the large specimen it lies in the second chamber (fig. 52), and is nearly spherical, measuring about 85  $\mu$  in diameter. In the other, of which sections were cut, it lies in the megalosphere, and has an oval shape, measuring 60  $\times$  40  $\mu$ . In section (fig. 54) it presents the appearance of a close reticulum with dark masses of different sizes embedded in it, and is surrounded by a dark line which clearly separates the nucleus from the coarse reticulum of the protoplasm. This obscure structure of the nucleus is no doubt due to the imperfect preservation.

#### 3. Concluding Remarks.

From the evidence now presented, it appears that the following statements relating to the life-history of the Foraminifera may be accepted.

1. The species of Foraminifera are in a great number of cases dimorphic. Relying on the difference in size of the central chambers of the shells, the dimorphism has been stated to exist in four out of the ten families into which Brady divided the group. This is shown in the following table:—

Family.	Authority.	Reference. (The numbers refer to the works named at the end.)
I. Gromidæ. II. Miliolidæ. Sub-Fam. Miliolinæ. Biloculina Dillina Fabularia Lacazina Triloculina Trillina Quinqueloculina Pentellina Heterillina Spiroloculina Adelosina Sub-Fam. Peneroplidinæ. Orbitolites Sub-Fam. Alveolininæ. Alveolina III. Astrorhizidæ. IV. Lituolidæ.	Munier-Chalmas and Schlumberger  Schlumberger	25 36 35 2 33
V. Textularidæ. VI. Chilostomellidæ. VII. Lagenidæ. Sub-Fam. Lageninæ.		
Nodosaria	Schlumberger	33
Siphogenerina	SCHLUMBERGER	33
Sub-Fam. Rotalinæ.  Rotalia	Schlumberger; L.* L. L.	33
Polystomella Sub-Fam. Nummulilinæ. $Amphistegina$ $Nummulites$	L. SCHLUMBERGER MUNIER-CHALMAS	33 24

- 2. The two forms differ from one another in the following features:—
- (a.) The size of the central chamber.

From their difference in this respect the two forms are distinguished as *Megalospheric* and *Microspheric*. The contrast in size between the megalosphere and microsphere is much greater in some species than in others.

In Biloculina depressa, D'ORB., according to Schlumberger, the diameter of the

<sup>\*</sup> The observation is my own.

megalosphere is between 200 and 400  $\mu$ , while the mean diameter of the microsphere is 20  $\mu$ .

In Polystomella crispa (Linn.), the megalosphere varies, in the specimens in which I have measured it, from 165 to 35  $\mu$  in diameter, and the microsphere from 13 to 6.5  $\mu$ .

In Rotalia Beccarii (Linn.), the difference is less. Among five examples of the megalospheric form the diameter of the megalosphere varied from 65 to 37  $\mu$ ; the diameter of the microsphere in one individual was 13  $\mu$ .

In the allied form, Calcarina hispida, Brady, among the twelve examples the diameter of the megalosphere varied from 58 to 42  $\mu$ , and that of the microsphere in two examples from 14 to 12  $\mu$ .\*

In the description above given of *Truncatulina*, it was shown that, while the megalosphere is usually considerably larger than the microsphere, it may approach it closely in size. Possibly there are genera of Foraminifera in which the central chambers of the two forms are of the same size. In such cases, analogy with the types above described would lead us to look for differences in the nuclei by which they might be distinguished. It cannot however be assumed that all forms of Foraminifera are dimorphic.

(b.) The shape and mode of growth of the chambers succeeding the megalosphere and microsphere.

SCHLUMBERGER has called attention to the very interesting fact, that in many species among the Miliolidæ the chambers immediately succeeding the central one are arranged on the biloculine plan in the megalospheric form, and on the quinqueloculine plan in the microspheric form (woodcut, p. 405.)

In several species the second chamber of the megalospheric form is peculiar. Thus, in *Orbitolites*, it forms the large circumambient chamber (Carpenter) which almost surrounds the primordial chamber (megalosphere); in *Cycloclypeus* the second chamber has a similar relation to the megalosphere. In *Polystomella* it is not so large in proportion as in these forms, but it is applied to the megalosphere for the whole of its length. In other species the second chamber differs little in shape from those which follow it.

The size attained by the complete shell is, in some species, markedly different in the two forms, while in other species this difference does not exist.

In Nummulites the microspheric form grows to a much larger size than the megalospheric. In Polystomella, however, the two forms attain about the same size.

Among the Miliolidæ, according to Schlumberger, the microspheric form is usually the larger, but in *Adelosina polygonia*, Schlumberger, the megalospheric form attains a rather larger size than the microspheric (1.5 to 1.4 millim.)

\* The numbers given are not strictly comparable in the different species, for while, in *Biloculina*, the measurements are taken from sections of the shell, in the others they are from decalcified and mounted, and hence somewhat shrunken, specimens.

#### (c.) The character of the nuclei.

In Polystomella crispa (Linn.) it has been shown that in the megalospheric form a single large nucleus is present during the greater part of the life of the individual, while in the microspheric form numbers of smaller nuclei are found. How far this contrast in the nuclei in the two forms is of general occurrence among the Foraminifera remains to be seen. In Rotalia Beccarii (Linn.), and Calcarina hispida (Brady), in which I have seen the nuclei of both forms, the condition was similar to that found in Polystomella, the megalospheric form having a single large nucleus, the microspheric form several small ones.

In *Cycloclypeus*, in which I have only seen two megalospheric forms, a single large nucleus was present.

In *Orbitolites* the conditions of the nuclei found in the two forms are, on the whole, similar, but a phase is here presented, the production of megalospheric young by megalospheric parents, of which I have no evidence in *Polystomella*.

3. The two forms differ in the frequency of their occurrence, the megalospheric form being much more abundant than the microspheric.

In Polystomella crispa (Linn.), among the examples that I have seen, the proportion of the megalospheric forms to microspheric is as 34 to 1.\* In Adelosina polygonia, Schlumberger gives the relative proportions of the two forms as 8 to 1.

4. The megalospheric form arises as a young individual already invested by a shell, which may be found lying in or about the peripheral chambers of the parent. Such megalospheric young have been seen in—

Miliolina, by Gervais (12), M. Schultze (38), Schlumberger (32) and Schneider (37).

Peneroplis proteus, D'ORB., by SCHACKO (29).

Orbitolites, simple form, by SEMPER (43).

,, complanata, Lamk., by Lister.

,, complanata, var. laciniata, Brady, by Parker, Carpenter, Brady (2), and Lister.

Spirillina vivipara, Ehrb., by Ehrenberg (11), and Strethill Wright (45).

Cristellaria crepidula (FICHTEL and MOLL), by BRADY (1).

Rotalina, sp., by M. Schultze (40).

Calcarina hispida, Brady, by Lister.

Megalospheric young may be produced both by microspheric and megalospheric parents.

In the specimens of *Orbitolites complanata*, var. *laciniata*, described by Brady, and in those which I have examined, the parents of such young are microspheric.

In MAX SCHULTZE's account of the production of young by one of the Miliolidæ, it is stated that the parent was distinguished from other individuals in the aquarium by

\* Among specimens collected in July and August, 1894, the microspheric forms were, however, more abundant than here indicated.

its large size. As it is generally the case in this family that the microspheric form attains a larger size than the megalospheric, it is probable that in this case also the parent was microspheric.

The specimen of *Calcarina hispida*, Brady, described above, was microspheric, and here, too, the young were probably megalospheric.\*

On the other hand the production of megalospheric young by megalospheric parents has been seen in several instances.

In the specimens of *Orbitolites complanata*, Lamk., from Celebes, described above (figs. 50 and 51), megalospheric parents are giving rise to megalospheric young.

In Schacko's specimen of *Peneroplis proteus*, d'Orb., the central chambers of the young and of the parent were of the same size, measuring about  $35 \,\mu$  in long diameter. It seems probable that they were both megalospheric.

MAX SCHULTZE'S Rotalia is said to have had a central chamber of the same size as those of the young which it produced. The diameters of these varied from 25 to 34  $\mu$ . Judging by the size of the megalosphere (37–65  $\mu$ ) and microsphere (13  $\mu$ ) in R. beccarii (Linn.), it appears probable that this was a megalospheric individual producing megalospheric young.

Again, in the specimen of Cristellaria crepidula (Ficht. und Moll.) figured by Brady, the first chamber of the parent shell measured 110  $\mu$  × 84  $\mu$ , while those of the contained young varied from 60 to 30  $\mu$ . It seems clear that the parent, at any rate, was megalospheric; the nature of the young shells is less evident, but the range of variation between the size of the parent shell and that of the smallest young is not greater than that recorded above in the size of the megalosphere among different examples of Polystomella, so that it is not impossible to regard them as megalospheric also.

5. Under certain circumstances active zoospores are produced by Foraminifera.

These have been recorded by STRETHILL WRIGHT in *Gromia*, and by MURRAY in *Cymbalopora* (in specimens with the large inflated chambers).

A specimen of the megalospheric form of *Polystomella crispa* (Linn.) is described above whose protoplasm was broken up into small round spores of uniform size, and I have seen such uniform spores escape from the broken shell of a specimen. The *Euglena*-like bodies, described by Schneider (37), may possibly have been of the same nature.

I have also observed in *Polystomella* macrospores and microspores escaping in large numbers from an unbroken shell.<sup>†</sup> Such bodies have also been described by Schneider in one of the Miliolidæ, although they were not seen in the active condition.

<sup>\*</sup> To these instances have now to be added *Polystomella crispa* (Linn.) and *Rotalia beccarii* (Linn.), as recorded in Postscript 2.

<sup>†</sup> As stated in the added note on p. 427, I am now inclined to think that these bodies were produced by some other organism.

When the existence of dimorphism in the species of Foraminifera was brought forward by Munier-Chalmas, it was, as we have seen, supposed that the microspheric form was a modification of the megalospheric. It was suggested that when the megalospheric form attained a certain size an absorption of the central chamber occurred in some individuals, the space which it had occupied being then filled in by small chambers, while additional chambers were added at the outside of the shell. Small megalospheric forms would thus be converted into the large microspheric forms.

DE HANTKEN and DE LA HARPE (15), and more recently, VAN DEN BROECK (5), have brought forward strong reasons for rejecting the hypothesis that the microspheric form is produced by modification of the megalospheric.

In the genus Biloculina among the Miliolide, as Schlumberger has shown, the plan of growth of the chambers immediately succeeding the central chamber differs entirely in the two forms (cf. the woodcut on p. 405), and this difference produces an effect on the form of the ultimate chambers. As in the case of the two forms of the Nummulites cited by De Hantken and De la Harpe the hypothesis would imply a remodelling of the whole shell. Again, in the bi-concave discs of Orbitolites the centre of a megalospheric individual is three times as thick as that of a microspheric. Hence to convert the megalospheric form into the microspheric, not only the primitive disc but many of the inner rings of chamberlets must be absorbed and replaced by fresh ones.

If such a process were to occur, the replacement of the chambers would not take place very rapidly, and various stages should be found. Such stages are, however, not found.

While the megalospheric form is not found in process of transition into the microspheric, it has been found either with the protoplasm broken up into zoospores (*Polystomella*), or containing megalospheric young in the peripheral chambers, while the central chambers are empty (*Orbitolites*, &c.). In both cases the megalosphere remains unabsorbed at the centre of the shell.

The microspheric form is met with in the young stage (fig. 7), though such specimens are necessarily rare, owing to the small numbers of the microspheric form as compared with the megalospheric.

The nuclear characters of the two forms are, in the species at any rate which I have examined, quite distinct.

It appears that we may safely conclude that the microspheric and megalospheric forms are distinct from their origin.

What then is their relationship?

When two forms of a species are met with in animals or plants they generally either belong to different sexes or they are members of a cycle of recurring generations.

The hypothesis that the two forms of the Foraminifera represent the two sexes appears to be disproved by the fact that in *Orbitolites complanata*, Lamk., both megalospheric and microspheric forms are found with the young of the megalospheric form (primitive discs) in their broad chambers. Other genera furnish analogous, though less complete evidence. Hence it is impossible to regard either form as male.

We turn then to the other hypothesis, namely, that the two forms are members of a recurring cycle of generations.

[This view receives further support from the facts that in the reproduction of the microspheric form (Postscript 2) the whole of the protoplasm of the parent is divided into the young, and that these all belong to one form, the megalospheric. On the hypothesis that the two forms represent different sexes, we should expect to find both megalospheric and microspheric young produced by the microspheric parent.

Adopting this view, the individuals of the microspheric generation of *Polystomella* give rise asexually, by a process of multiple fission, to young megalospheric forms, and these in their turn produce, also by that multiple fission, the flagellate zoospores.

In *Orbitolites* the microspheric form gives rise to megalospheric young, but in this genus, as in *Peneroplis* and *Rotalia*, the megalospheric form may repeat itself for one or more generations, though ultimately it may be assumed by analogy with *Polystomella*, that a megalospheric form is produced which gives rise to zoospores.

How is the gap in the life-history between the liberation of the zoospores and the formation of the microsphere filled in?

Schaudinn has recently described (Sitz-Ber. Gesellsch. Naturforsch. Freunde, Berlin, Jahrg. 1894. Abstract in 'Zool. Centralblatt,' I., p. 519) the production of zoospores of approximately uniform size, in Hyalopus (Gromia dujardinii, M. Sch.) and their subsequent conjugation.

It appears not improbable that a similar process may occur in *Polystomella* and the other dimorphic species, the initial chamber of the microspheric form being the result of the conjugation of zoospores of the megalospheric form. The sizes of the zoospores and microsphere in *Polystomella* (about 4  $\mu$  and 6–13  $\mu$ , respectively) accord fairly well with this view; and the comparative scarcity of the microspheric form may be understood on the supposition that the union of two separate organisms is required for its production.

If this is the case, the two forms of the Foraminifera must be regarded as sexual and asexual generations, of which the sexual generation retains the power in some genera (Orbitolites and others) of reproducing asexually.

It must, however, be borne in mind that while there seems good reason to regard the two forms of Foraminifera as belonging to different generations, the view above suggested of the sexual nature of the zoospores of the megalospheric form is at present insecure. There is no direct evidence of the conjugation of zoospores or the mode of origin of the microspheric form in a dimorphic species.—March 13, 1895.]

#### Postscript 1.

In reviewing the previous work on the life-history and nuclei of the Foraminifera, I have confined myself to a rather limited range of forms. I have done so because it appeared best to select the evidence of such forms as are most obviously related to those which I had to describe.

Schaudinn has recently published (31) a preliminary account of his researches into the reproduction and mode of increase of the nuclei in the Foraminifera. This I did not see until after my paper was written. Many of the observations appear to be of the highest interest, but no mention is made of the important fact of the existence of dimorphism. Polystomella crispa (Linn.) is described as usually having one or four nuclei, but is said to become many-nucleated during reproduction; a form of reproduction is also described in which the whole of the protoplasm leaves the shell and divides up into numbers of young individuals which assume the characteristic shape of the species. Schaudinn has, however, apparently failed to recognise what is undoubtedly the fact, that in this species one in every thirty to forty individuals is microspheric and possesses nuclei of a quite different character from that of the megalospheric form.

In his account of the changes which the nuclei of the Foraminifera undergo preparatory to reproduction, Schaudinn describes a breaking up of the nucleus into fragments which are dispersed through the protoplasm; in this general result, my observations on the nucleus of the megalospheric form of *Polystomella*, so far as they go, agree with his, but I am quite unable to recognise the remarkable phases of the process which he describes in those that I have seen.

#### Postscript 2. August 3, 1894.

It is stated above that I had no evidence as to the fate of the microspheric form of *Polystomella crispa* (Linn.).

I have since made further observations on living Foraminifera (chiefly *Polysto-mella*), and have seen in some hundreds of cases the mode of reproduction mentioned by Schaudinn.

The specimen of Polystomella, as seen attached to the glass walls of a vessel, becomes surrounded by a halo of closely-set radiating pseudopodia. After some hours the protoplasm is withdrawn from the shell, emerging into the area covered by the halo. Here, after involved streaming movements, it gradually separates into distinct spherical masses, which, in the case of the specimens in my jars, usually had a diameter of 50 to 60  $\mu$ .

In a short time these masses secrete a shell, and, some four or five hours after they first became distinct, they throw out long pseudopodia, and rapidly draw apart from

one another and from the empty parent shell. In the course of a few hours the wall of a second chamber is formed, a third and fourth being added by the second day after separation occurred. In this stage they are readily recognized as young megalospheric individuals.

After the protoplasm has left the central part of the shell there is no direct evidence, in decalcified specimens, as to the nature of the parent; but in specimens (some fifty or more) killed and decalcified at earlier stages of the reproductive process it is seen that the parent is in every case microspheric.

The fate of the microspheric form of *Polystomella crispa* (Linn.) is, then, to give rise to megalospheric young.

In two examples of *Rotalia Beccarii* (LINN.) the same process occurred. The parent in each case was microspheric.

The fact that the whole of the protoplasm of the parent is used in the production of the young, and that these are all of one form, supports the view that the two forms of the Foraminifera belong to different generations.

A fuller account of the process of reproduction, with what I am able to make out of the nuclear changes, will be reserved for another paper.

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#### DESCRIPTION OF PLATES.

#### List of Reference Letters.

- b. Brown bodies.
- c. Spiral canal in the umbilical region of the shell.
- f. Foreign particles.
- M. Megalosphere.
- m. Microsphere.
- N. Nucleus.
- s. Bodies in the protoplasm, staining red with picro-carmine, and here regarded as nutritive in nature.
- st. Stained strands.
- v. Vacuole.
- Figs. 1 to 33, with the exception of 4,  $\alpha$  and b, relate to Polystomella crispa (Linn.).
- Fig. 1.  $\times$  230. Part of a megalospheric specimen in which the nucleus has been involved in a movement of the protoplasm, probably the effect of the reagent. N. The main mass of the nucleus. N'. Portions of the nucleus carried on by a movement of the protoplasm. Sublimate and picrocarmine.
- Fig. 2.  $\times$  250. Example of a megalospheric individual in which the protoplasm contains numbers of spherical bodies (s), probably nutritive, which take a red stain in picro-carmine.
- Fig. 3.  $\times$  523. End of one of the chambers of a similar specimen.
- Fig. 4a. × 690. Balantidium entozoon (EHR.). Specimen containing numbers of darkly staining spherical bodies, probably nutritive.
- Fig. 4b.  $\times$  1460. One of the spherical bodies from another specimen of *Balantidium* entozoon. Osmic vapour, picro-carmine.
- Fig. 5. × 1047. End of a chamber of a specimen containing brown bodies (b).

  MDCCCXCV.—B. 3 M

#### Microspheric form.

- Fig. 6α. × 170. Complete specimen, with forty-two\* chambers. As the series of chambers is followed towards the centre, the nuclei lose their rounded shape, and strands of nuclear substance are seen scattered through the protoplasm.
- Fig. 6b.  $\times$  690. The inner chambers of this specimen. The microsphere measures  $11 \mu \times 9 \mu$ .
- Fig. 7.  $\times$  170. A young specimen of the microspheric form. The microsphere measures 10  $\mu$ . f. Foreign particles collected at the mouth of the shell.
- Fig. 8, a and b.  $\times$  980. Sections of two nuclei. In 8a the nucleoli are vacuolated.
- Fig. 9. × 690. A pair of nuclei, with nucleoli of different sizes. One of the larger nucleoli is vacuolated.
- Fig. 10. × 307. A pair of nuclei with their opposed surfaces flat, as though they had recently separated.
- Fig. 11.  $\times$  730. Three consecutive sections through a dividing nucleus.
  - In (a) the two parts of the nucleus are united by a constricted band; the right-hand part is larger than the left.
    - In (b) the left-hand part is larger than the right.
    - In (c) the left-hand part alone is seen.
- Fig. 12. × 690. A section through three chambers, showing irregular stained strands continuous with the substance of the nuclei.

#### Megalospheric form.

- Fig. 13.  $\times$  170. Specimen with thirty-nine chambers. Megalosphere 85  $\mu$   $\times$  80  $\mu$ ; nucleus 98  $\mu$   $\times$  43  $\mu$ . Picro-carmine.
- Fig. 14.  $\times$  1275. Section through the nucleus of a specimen with thirty-two chambers. It measures 65  $\mu$   $\times$  40  $\mu$ . A large vacuolated nucleolus (18  $\mu$   $\times$  14  $\mu$ ) lies in the middle. The other nucleoli vary in size up to 4  $\mu$ . Picro-carmine, hæmatoxylin.
- Fig. 15. × 700. Section of the nucleus of a specimen with twenty-three chambers. It sends a process through a canal leading to another chamber. The nucleoli are seen to be drawn out as the result of the stress to which they are subjected. Picro-carmine, eosine, methylene-blue.
- Fig. 16.  $\times$  700. Section of nucleus. The reticulum is here coarser than in the nucleus shown in fig. 15. The nucleoli vary in size up to  $2 \mu$ . FLEMMING's fluid, safranin.
- \* This is the number of chambers of whose presence there are indications in the decalcified specimen. It frequently occurs that in the live state one or more of the terminal chambers contain little or no protoplasm, and hence might not be represented after decalcification. The same remark applies to the other descriptions in which the number of chambers is given.

Figs. 17-19. × 710. Nuclei in optical section. Many of the nucleoli are compound. Piero-carmine.

In fig. 18 a large nucleolus is represented, having a vacuole in the centre, and its walls composed of bodies similar to the small simple nucleoli which lie in the reticulum. Smaller compound masses are also present.

- Fig. 20. × 460. Nucleus with many small vacuolated nucleoli. Optical section. Picro-carmine.
- Fig. 21. × 690. Nucleus with thin-walled vacuolated nucleoli. Their disposition suggests that they have been set free by the breaking up of a compound nucleus. Optical section. Picro-carmine.
- Fig. 22. × 1460. Part of a section of a nucleus whose nucleoli contain many vacuoles.
- Fig. 23. × 250. Specimen with a "flushed" region of the protoplasm at one end of the nucleus, due to the presence of minute stained particles. Piero-carmine.
- Fig. 24. × 250. Specimen showing "fragments" lying in the chambers through which the nucleus has passed, and in those immediately beyond it. In this figure the fragments have been somewhat over-emphasized, they are generally much less conspicuous.
- Fig. 25.  $\times$  1460. Sections through such fragments as those shown in fig. 24. In this case they contain nucleoli. a and b are consecutive sections of the same fragment. Picro-carmine, hæmatoxylin.
- Fig. 26.  $\times$  230. A nucleus which has lost its rounded form.
- Fig. 27.  $\times$  250. The whole of the protoplasm, except that occupying the last two chambers, has broken up into small nucleated spheres, having a diameter of 2.5 to 3  $\mu$ . At c, a portion of the spiral canal, which lies in the umbilical region, is seen filled with similar spheres. Picro-carmine.
- Fig. 28. × 1275. Part of a section of the same specimen as that in fig. 27. The nuclei which lie in the spheres are seen to be in process of karyokinetic division. Picro-carmine and hæmatoxylin.
- Fig. 29. × 487. Section of nucleus with few and irregularly outlined nucleoli. FLEMMING's fluid. Safranin.
- Fig. 30.  $\times$  730. Section of the terminal chamber of a specimen of the megalospheric form, in which the large nucleus has disappeared, and numbers of small nuclei 1 to 1.5  $\mu$  in diameter, are distributed in groups through the protoplasm. Picro-carmine and hæmatoxylin.
- Fig. 31. Part of a section through a specimen of the megalospheric form, in which the large nucleus has disappeared and numbers of small vacuolated nuclei are distributed through the protoplasm. The structure of the protoplasm is not represented. Zeiss 1/15 oil.
- Fig. 32a.  $\times$  460. Section of a specimen of the megalospheric form in which the whole protoplasm is broken up into zoospores, having a diameter of 3 to 4  $\mu$ . A broad communication is seen to connect chambers 2 and 10.

- Fig. 32b. × 1460. Groups of zoospores in the terminal chambers; indications of flagella are seen. In the left-hand group of the nuclei of the zoospores have not taken the stain.
- Fig. 33a and b.  $\times$  1200. Actively moving bodies which emerged from a specimen of *Polystomella crispa*. Probably they belonged to another organism.

#### Calcarina hispida, Brady.

- Fig. 34. × 250. The inner chambers of a specimen of the megalospheric form with seventeen chambers. The nucleus is seen in the fourth chamber, sending a process into the fifth.
- Fig. 35.  $\times$  250. Inner part of a specimen of the microspheric form with thirty-nine chambers. The microsphere is 13  $\mu \times$  11  $\mu$  in diameter. The specimen is ill-preserved, but indications of five nuclei can be detected in some of the chambers which follow those here represented.
- Fig. 36.  $\times$  56. Another specimen of the microspheric form. The inner chambers are not represented. The microsphere measured about 15  $\mu \times$  12·5  $\mu$ . The later chambers contain numbers of young, presumably megalospheric, forms.
- Fig. 37. × 250. Part of one of the chambers of the specimen shown in fig. 36, with its contents.

#### Rotalina Beccarii, LINN.

- Fig. 38.  $\times$  170. Microspheric form. Thirty-three chambers are present. The microsphere is 13  $\mu$  in diameter. Many nuclei are contained in the inner chambers.
- Fig. 39.  $\times$  170. Megalospheric form. Twenty-four chambers are present. The megalosphere measures 45  $\mu \times$  40  $\mu$ . A single large nucleus is contained in the eighth chamber.
- Fig. 40.  $\times$  460. The nucleus of another megalospheric specimen.

#### Orbitolites complanata, LAMK.

#### Microspheric form.

- Fig. 41. × 760. Section through the contents of a "chamberlet." Four rounded nuclei are seen to be disposed in pairs. A nucleus is in process of division, the two halves being connected by a constricted band. Alcohol, picrocarmine.
- Fig. 42. × 760. Three of the larger nuclei of this form. The nuclear reticulum is distinctly seen. Alcohol, picro-carmine.
- Fig. 43. × 38. Vertical radial section through the margin of the disc of a fully-grown specimen. As is usually the case in the microspheric form of the

variety *laciniata*, the margin is double, hence the section is Y-shaped. The more central part of the disc is represented only by the organic basis of the walls of the chamberlets. In the peripheral portions the large *brood-chambers* are seen crowded with young. Alcohol, hæmatoxylin.

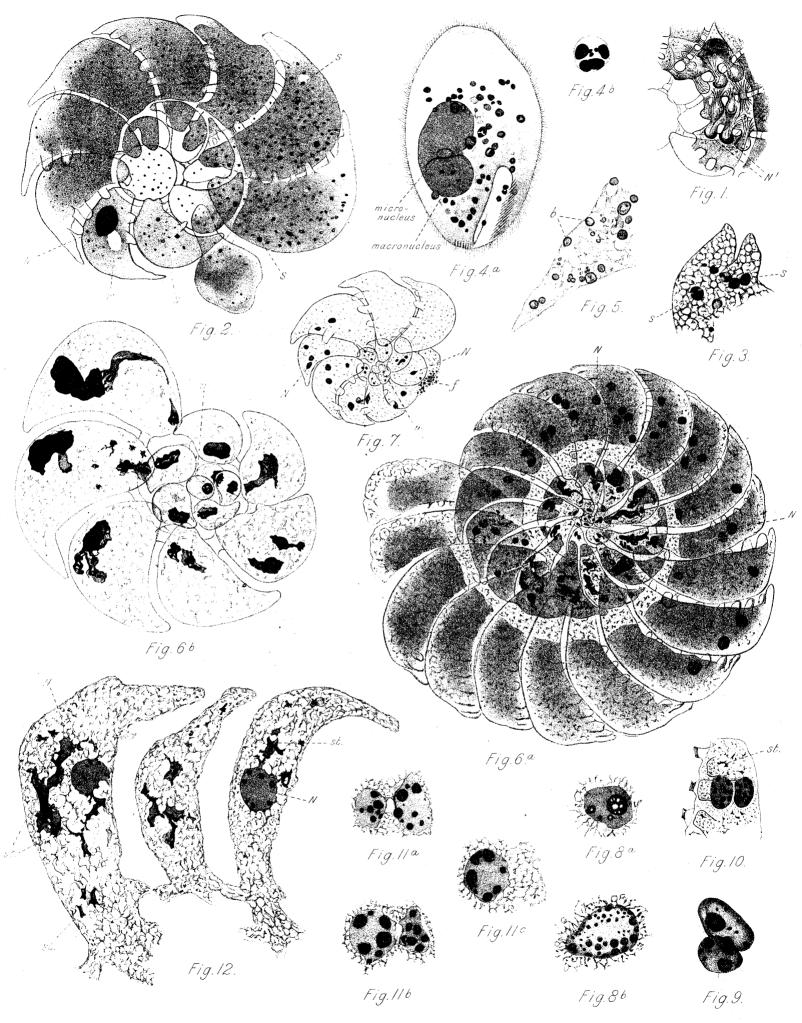
Fig. 44. × 56. Vertical tangential section through the margin of a disc whose brood-chambers contain young. Alcohol, hæmatoxylin.

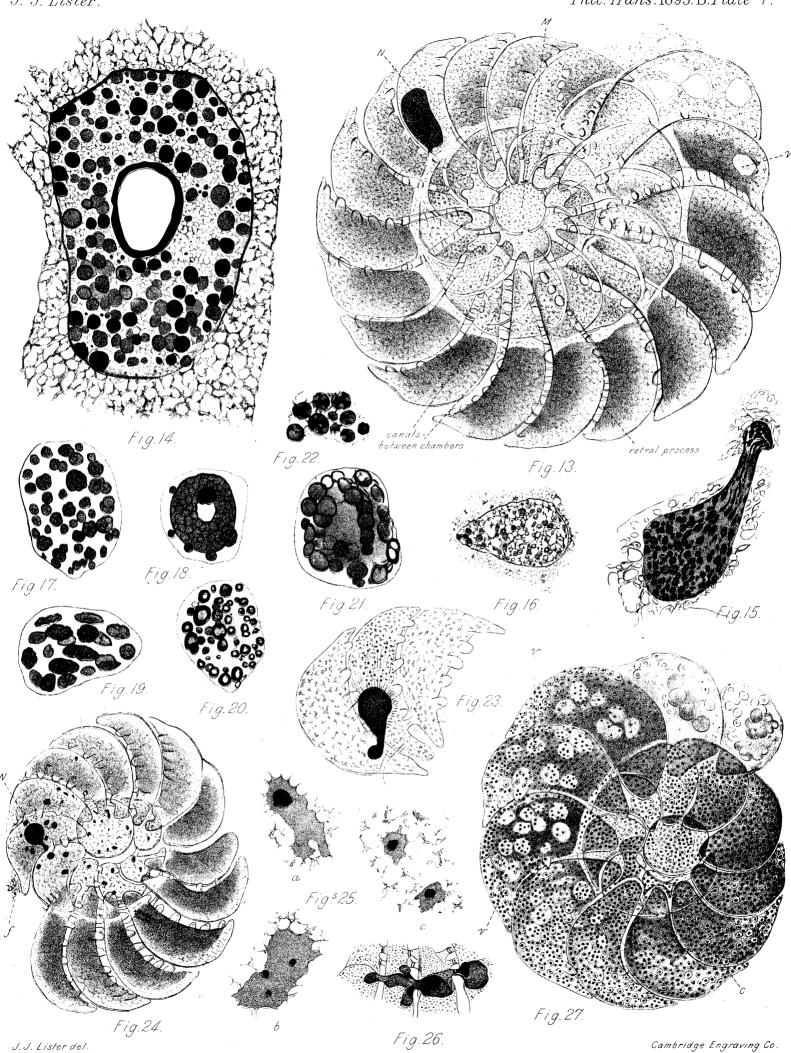
#### Megalospheric Form.

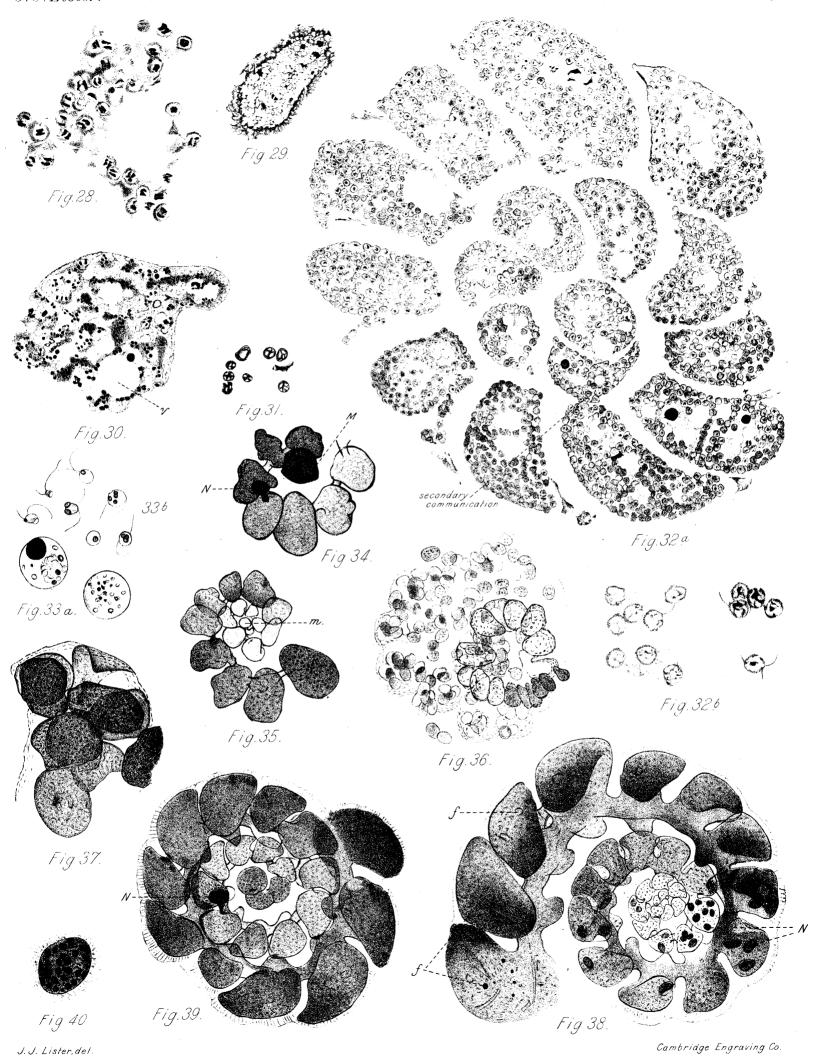
- Fig. 45. × 120. Young specimen, decalcified. The centre is occupied by the "primitive disc," consisting of the "primordial chamber" (megalosphere) and the "circumambient chamber." Some six rings of chamberlets have been formed.
- Fig. 46. × 540. Section of the nucleus of a very young specimen recently liberated from the brood-chambers of the parent. Hæmatoxylin.
- Fig. 47. × 760. Section of nucleus of a specimen with about twenty-six rings of chamberlets. Hæmatoxylin.
- Fig. 48. × 760. Section of the primordial chamber of a specimen with about thirty rings of chamberlets, showing the nucleus. Small algae and starch grains are contained in the protoplasm. Hæmatoxylin.
- Fig. 49. × 415. Section of the primordial chamber of a specimen in which the nucleus appears to have broken up into irregular fragments. About twenty-five rings of chamberlets had been formed. Picro-carmine.
- Fig. 50.  $\times$  6. Part of the disc of a specimen bearing young in its brood-chambers. Decalcified. P.d. (primitive disc.) The protoplasm has left the part of the disc internal to the brood-chambers.
- Fig.  $51a. \times 38$ . The young contained in the brood-chambers of the same specimen.
- Fig. 51b.  $\times$  38. One of the young removed from the brood-chambers. The spaces from which the shell has been dissolved are seen dividing the protoplasm.
- Fig. 51c.  $\times$  38. The empty primitive disc of the parent shell. The walls have shrunk owing to the action of the reagents.

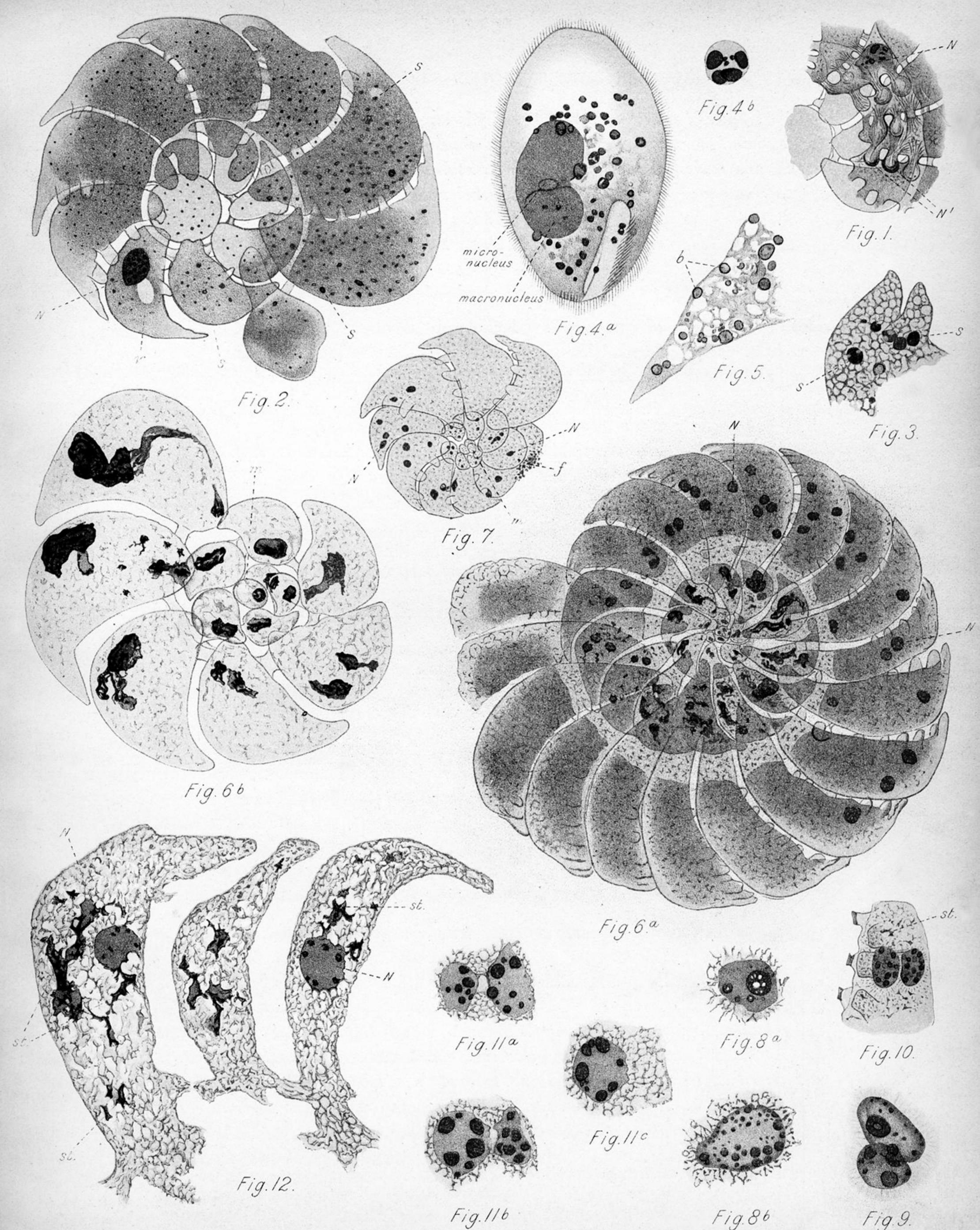
#### Cycloclypeus Carpenteri, Brady.

- Fig. 52.  $\times$  56. The chambers occupying the centre of a specimen measuring about 1 centim. in diameter: M. the megalosphere; (2) the large second chamber containing, in this instance, the nucleus. The nucleus measures 85  $\mu$  in diameter.
- Fig. 53. Some of the chambers of a decalcified specimen, showing the somewhat irregular arrangement of the connecting canals.
- Fig. 54.  $\times$  460. Section of the nucleus of another specimen. In this case the nucleus was in the megalosphere. It measures 60  $\mu$   $\times$  40  $\mu$ .







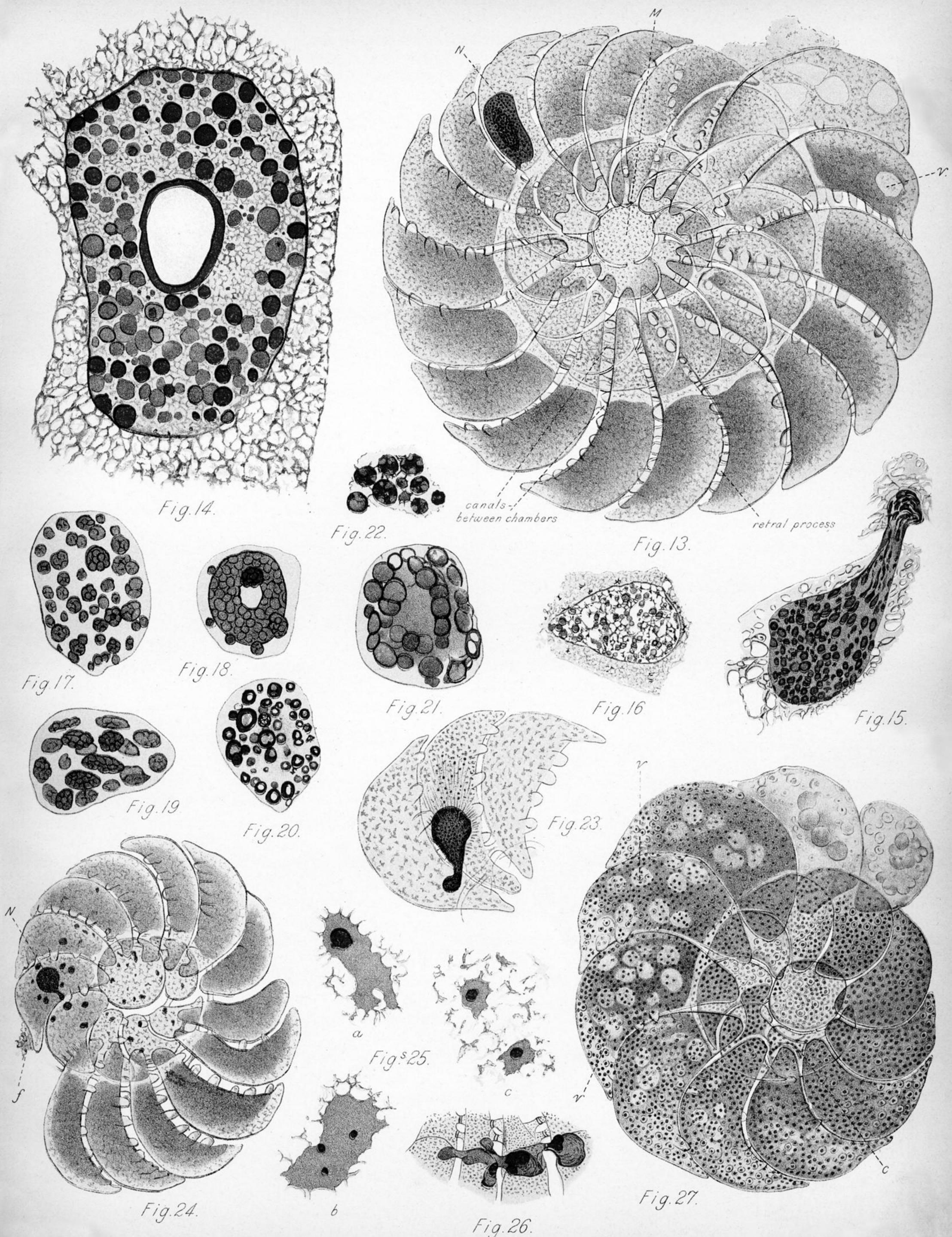


× 230. Part of a megalospheric specimen in which the nucleus has been involved in a movement of the protoplasm, probably the effect of the reagent. N. The main mass of the nucleus. N. Portions of the nucleus carried on by a movement of the protoplasm. Sublimate and picrocarmine.

- × 250. Example of a megalospheric individual in which the protoplasm Fig. 2. contains numbers of spherical bodies (s), probably nutritive, which take a red stain in picro-carmine.
- Fig. 3. '× 523. End of one of the chambers of a similar specimen.
- $\times$  690. Balantidium entozoon (Ehr.). Specimen containing numbers of darkly staining spherical bodies, probably nutritive.
- $\times$  1460. One of the spherical bodies from another specimen of Balantidium entozoon. Osmic vapour, picro-carmine.
- Fig. 5.  $\times$  1047. End of a chamber of a specimen containing brown bodies (b).

### Microspheric form.

- Fig. 6a.  $\times$  170. Complete specimen, with forty-two\* chambers. As the series of chambers is followed towards the centre, the nuclei lose their rounded shape, and strands of nuclear substance are seen scattered through the protoplasm.
- Fig. 6b.  $\times$  690. The inner chambers of this specimen. The microsphere measures  $11 \mu \times 9 \mu$ .
- Fig. 7. × 170. A young specimen of the microspheric form. The microsphere measures 10  $\mu$ . f. Foreign particles collected at the mouth of the shell.
- Fig. 8,  $\alpha$  and b.  $\times$  980. Sections of two nuclei. In 8 $\alpha$  the nucleoli are vacuolated.
- Fig. 9. × 690. A pair of nuclei, with nucleoli of different sizes. One of the larger nucleoli is vacuolated.
- Fig. 10. × 307. A pair of nuclei with their opposed surfaces flat, as though they had recently separated.
- Fig. 11. × 730. Three consecutive sections through a dividing nucleus.
  - In (a) the two parts of the nucleus are united by a constricted band; the right-hand part is larger than the left.
  - - In (b) the left-hand part is larger than the right. In (c) the left-hand part alone is seen.
- × 690. A section through three chambers, showing irregular stained strands continuous with the substance of the nuclei.



Megalospheric form.

- $\times$  170. Specimen with thirty-nine chambers. Megalosphere 85  $\mu$   $\times$  80  $\mu$ ; nucleus 98  $\mu \times 43 \mu$ . Picro-carmine.
- × 1275. Section through the nucleus of a specimen with thirty-two chambers. It measures 65  $\mu$  × 40  $\mu$ . A large vacuolated nucleolus (18  $\mu$  × 14  $\mu$ ) lies in the middle. The other nucleoli vary in size up to 4  $\mu$ . Picro-carmine, hæmatoxylin.
- Fig. 15.  $\times$  700. Section of the nucleus of a specimen with twenty-three chambers. It sends a process through a canal leading to another chamber. The nucleoli are seen to be drawn out as the result of the stress to which they are subjected. Picro-carmine, eosine, methylene-blue.
- × 700. Section of nucleus. The reticulum is here coarser than in the nucleus shown in fig. 15. The nucleoli vary in size up to  $2 \mu$ . FLEMMING's fluid, safranin.
- Figs. 17-19. × 710. Nuclei in optical section. Many of the nucleoli are compound. Picro-carmine.

In fig. 18 a large nucleolus is represented, having a vacuole in the centre, and its walls composed of bodies similar to the small simple nucleoli which lie in the reticulum. Smaller compound masses are also present.

- × 460. Nucleus with many small vacuolated nucleoli. Optical section. Picro-carmine.
- × 690. Nucleus with thin-walled vacuolated nucleoli. Their disposition suggests that they have been set free by the breaking up of a compound nucleus. Optical section. Picro-carmine.
- × 1460. Part of a section of a nucleus whose nucleoli contain many vacuoles. Fig. 22.
- × 250. Specimen with a "flushed" region of the protoplasm at one end of the Fig. 23. nucleus, due to the presence of minute stained particles. Picro-carmine.
- × 250. Specimen showing "fragments" lying in the chambers through which the nucleus has passed, and in those immediately beyond it. In this figure the fragments have been somewhat over-emphasized, they are generally much less conspicuous.
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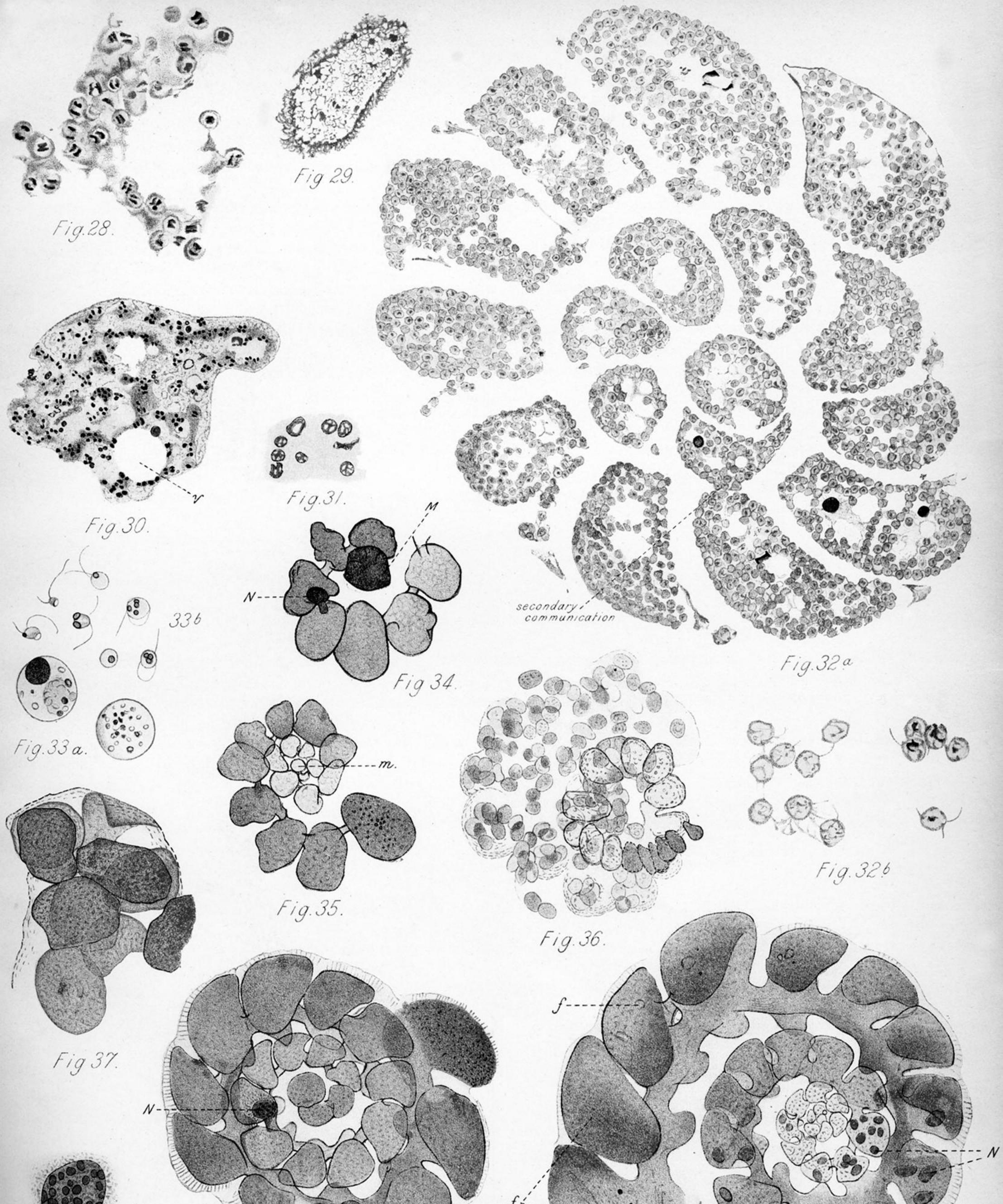


Fig. 28. × 1275. Part of a section of the same specimen as that in fig. 27. The nuclei which lie in the spheres are seen to be in process of karyokinetic division. Picro-carmine and hæmatoxylin.

Fig 38.

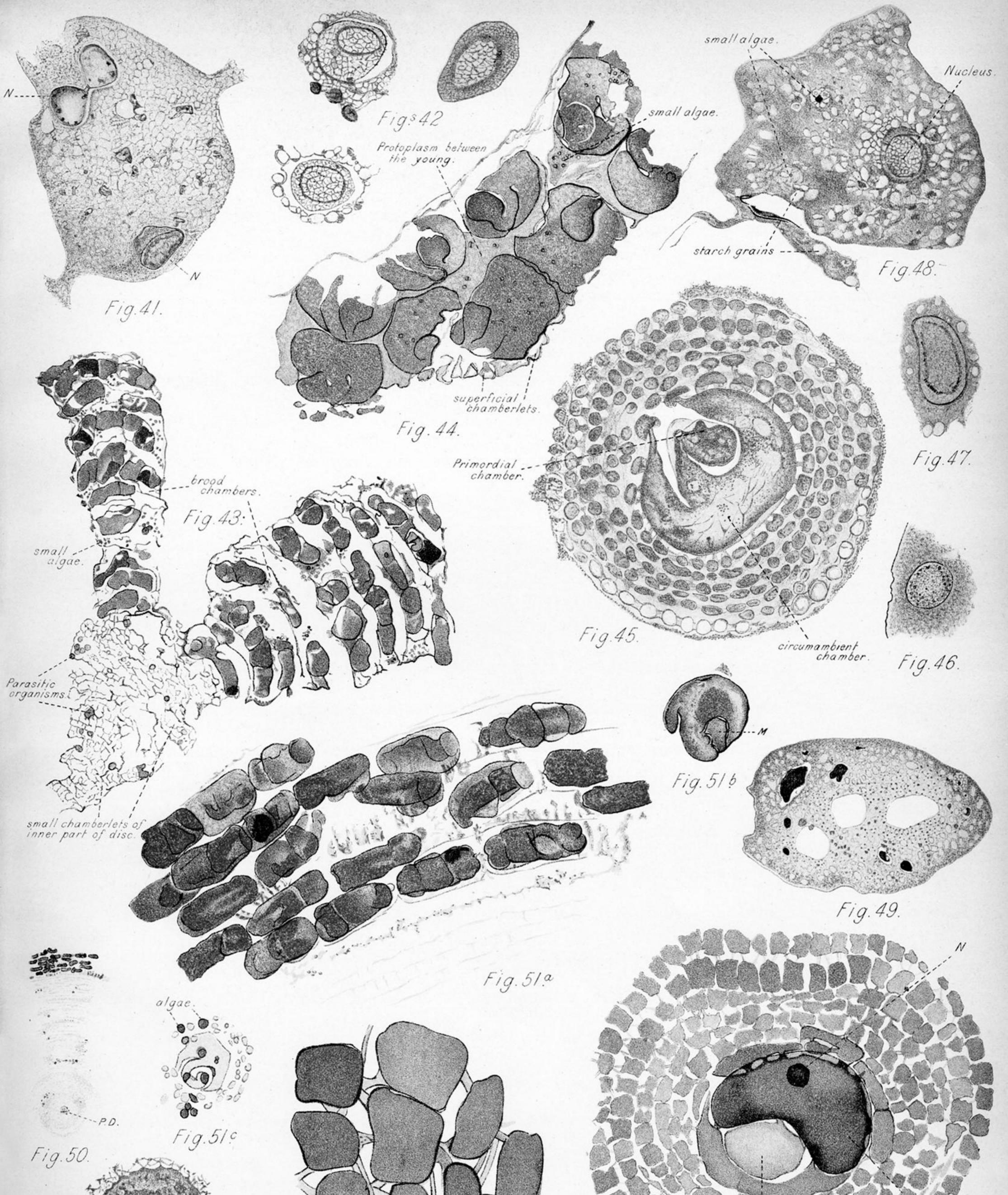
Fig. 39.

- Fig. 29. × 487. Section of nucleus with few and irregularly outlined nucleoli. FLEMMING's fluid. Safranin.
- Fig. 30.  $\times$  730. Section of the terminal chamber of a specimen of the megalospheric form, in which the large nucleus has disappeared, and numbers of small nuclei 1 to 1.5  $\mu$  in diameter, are distributed in groups through the protoplasm. Picro-carmine and hæmatoxylin.
- Fig. 31. Part of a section through a specimen of the megalospheric form, in which the large nucleus has disappeared and numbers of small vacuolated nuclei are distributed through the protoplasm. The structure of the protoplasm is not represented. Zeiss 15 oil.
- Fig. 32a.  $\times$  460. Section of a specimen of the megalospheric form in which the whole protoplasm is broken up into zoospores, having a diameter of 3 to 4  $\mu$ . A broad communication is seen to connect chambers 2 and 10.
- Fig. 32b. × 1460. Groups of zoospores in the terminal chambers; indications of flagella are seen. In the left-hand group of the nuclei of the zoospores have not taken the stain.
- Fig. 33a and b.  $\times$  1200. Actively moving bodies which emerged from a specimen of Polystomella crispa. Probably they belonged to another organism.

### Calcarina hispida, Brady.

- Fig. 34. × 250. The inner chambers of a specimen of the megalospheric form with seventeen chambers. The nucleus is seen in the fourth chamber, sending a process into the fifth.
- Fig. 35. × 250. Inner part of a specimen of the microspheric form with thirty-nine chambers. The microsphere is 13 μ × 11 μ in diameter. The specimen is ill-preserved, but indications of five nuclei can be detected in some of the chambers which follow those here represented.
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- Fig. 36.  $\times$  56. Another specimen of the microspheric form. The inner chambers are not represented. The microsphere measured about 15  $\mu$  × 12·5  $\mu$ . The later chambers contain numbers of young, presumably megalospheric, forms.
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- in the eighth chamber.

  Fig. 40. × 460. The nucleus of another megalospheric specimen.



Orbitolites complanata, Lamk.

Fig. 53.

Fig. 52

Fig. 54.

## Microspheric form.

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- Fig. 42. × 760. Three of the larger nuclei of this form. The nuclear reticulum is distinctly seen. Alcohol, picro-carmine.
- Fig. 43. × 38. Vertical radial section through the margin of the disc of a fully-grown specimen. As is usually the case in the microspheric form of the variety laciniata, the margin is double, hence the section is Y-shaped. The more central part of the disc is represented only by the organic basis of the walls of the chamberlets. In the peripheral portions the large brood-chambers are seen crowded with young. Alcohol, hæmatoxylin.
- Fig. 44. × 56. Vertical tangential section through the margin of a disc whose brood-chambers contain young. Alcohol, hæmatoxylin.

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- Fig. 45. × 120. Young specimen, decalcified. The centre is occupied by the "primitive disc," consisting of the "primordial chamber" (megalosphere) and the "circumambient chamber." Some six rings of chamberlets have been formed.
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- from the brood-chambers of the parent. Hæmatoxylin.

  Fig. 47. × 760. Section of nucleus of a specimen with about twenty-six rings of
- chamberlets. Hæmatoxylin.

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- thirty rings of chamberlets, showing the nucleus. Small algæ and starch grains are contained in the protoplasm. Hæmatoxylin.

  Fig. 49. × 415. Section of the primordial chamber of a specimen in which the
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- Decalcified. P.d. (primitive disc.) The protoplasm has left the part of the disc internal to the brood-chambers.
- Fig. 51a.  $\times$  38. The young contained in the brood-chambers of the same specimen. Fig. 51b.  $\times$  38. One of the young removed from the brood-chambers. The spaces

from which the shell has been dissolved are seen dividing the protoplasm.

- Fig. 51c. × 38. The empty primitive disc of the parent shell. The walls have shrunk owing to the action of the reagents.
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- about 1 centim. in diameter: M. the megalosphere; (2) the large second chamber containing, in this instance, the nucleus. The nucleus measures 85  $\mu$  in diameter.
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