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Art. X.—*The Lagenid Foraminifera and Their Relationships.*

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Abstract.

The writer reviews the opinions currently held as to the position of the lagenid foraminifera and submits evidence to show the close relationship of the genera *Lagena, Oolina* (with *Entosolenia* as a synonym), *Fissurina,* and the hooded forms usually referred by authors to the genus *Ellipsolagena.* He regards *Ellipsolagena* as identical with *Fissurina* and erects a new genus, *Parafissurina,* for the reception of the hooded forms.

From the evidence, the writer concludes that, instead of the lagenid foraminifera being a polyphyletic group of end forms derived from multilocular genera belonging to several families, they are not end forms and that all belong to the same family. He also does not consider them, as was believed by Brady, to be ancestral to the multilocular forms of the Nodosariidae and the Polymorphinidae, but suggests that the lagenid forms and the multilocular forms had a common ancestor. The family Lagenidae is proposed for the unilocular forms, with the Nodosariidae restricted to the multilocular forms usually placed in this family.

Introduction.

During work on the foraminifera extending over more than twenty years, the writer has met with from 200 to 300 species of lagenid foraminifera, and their identification has led to a consideration of the value of the genera erected by authors for the reception of these forms. In submitting the results of these investigations, it should be said at the outset that a full understanding of the lagenid foraminifera cannot be obtained until well-preserved foraminiferal faunas from the Jurassic and also from the Palaeozoic have been studied, as it is in deposits of these ages that we must look for the progenitors of the present day genera. It is however hoped that the evidence now to be presented will be sufficient to show that the views which are currently held with regard to the status and relationships of some of the lagenid foraminifera should be revised.

Until the publication of Dr. J. A. Cushman's outline of a re-classification of the foraminifera in 1927, authors had, with few exceptions, been content to follow the late Dr. H. B. Brady in refering all of the single-chambered hyaline foraminifera to the genus *Lagena* Walker and Boys. Cushman limited the use of *Lagena* to those species in which the test was either with or without a neck and the aperture was radiate (rarely), rounded, elliptical, or slit-like and terminal. He included within the definition of *Lagena* such genera as *Oolina* d'Orbigny, *Amphorina* d'Orbigny *Fissurina* Reuss, *Trigonulina* Seguenza, and other genera which are now generally accepted as synonymous with *Lagena.* For those species with a rounded test and an internal tube, free at the inner end, and with the aperture centrally situated at the end of the test and elliptical or circular in shape, Cushman revived Williamson's genus *Entosolenia,* which he transferred from the family Lagenidae to the Buliminidae. The third group of lagenid foraminifera recognized by Cushman was referred by him to the genus *Ellipsolagena* A. Silvestri, which he placed in the family Ellipsoidinidae. In this the test has an internal tube at one side of the aperture, which is elongate, subterminal, curved, with one side raised into a protecting hood.

Several years after the appearance of Cushman's work, Dr. J. J. Galloway (1933) published his book, "A Manual of Foraminifera", in which a different treatment of the lagenid foraminifera was proposed. He recognized eight genera, of which *Balanulina* Rzehak is now known to be a cirripede, and *Obliquina* Seguenza, as an abnormal form with apparently only a single record, need not be considered here. The remaining genera were divided among three families, viz.—

Genus.	Family.
(1) *Oolina* d'Orbigny (with *Entosolenia* as a synonym)	NODOSARIIDAE (= Lagenidae of Cushman)
(2) *Lagena* Walker and Boys	,,
(3) *Amphorina* d'Orbigny	,,
(4) *Fissurina* Reuss	,,
(5) *Trigonulina* Seguenza	UVIGERINIDAE
(6) *Ellipsolagena* A. Silvestri	PLEUROSTOMELLIDAE (= Ellipsoidinidae of Cushman)

The four genera used by Galloway and not by Cushman are *Oolina, Amphorina, Fissurina*, and *Trigonulina*. *Oolina* has, however, *Entosolenia* as a synonym.

Chapman and the present writer, in their classification of the foraminifera (1936), recognized only two genera, *Lagena* and *Ellipsolagena*, the former being placed in the Nodosariidae and the latter in the Pleurostomellidae. *Lagena* was used in the same sense as by Cushman with the addition of *Entosolenia* as a synonym, as it was considered *Entosolenia* could not be satisfactorily distinguished from *Lagena*.

Here, it may be convenient to give in some detail the published views of the authors named on the origin and relationships of the various genera. Cushman, in the third edition of his Classification (1940) states on page 195 (under the family Lagenidae) :—

"It is rather evident that the forms included under *Lagena* have probably been derived from various sources, and perhaps but a few of them really belong to the family Lagenidae".

P. 203. "It is very doubtful if many of the forms classed as *Lagena* really belong to this genus of this family" (*i.e.* the Lagenidae).

and on p. 238 (under the family Buliminidae) :—

"*Entosolenia* with its *Bulimina*-like aperture and internal tube probably developed into numerous species now usually called *Lagena*."

P. 238. "*Angulogerina* with its sharply triangular test is triserial, and from it came *Trifarina* which is uniserial in the adult. From this were probably derived those angled "Lagenas" sometimes called *Trigonulina* and *Tetragonulina*."

In every case, Cushman regards the unilocular forms as having evolved from multilocular ones.

Galloway (1933, p. 230 *et seq.*), in his account of the Nodosariidae, discusses at length the relationships of the unilocular foraminifera placed by him in this family. His views are too long to quote in full, but to summarize them, he regards these unilocular genera as end forms derived from multilocular forms. On p. 233, he gives reasons why they should be regarded as neither simple nor ancestral to the multilocular genera of the Nodosariidae, contrary to the belief of Brady and others. *Lagena* and *Amphorina* are considered to be derived from *Dentalina* and *Nodosaria*, while *Fissurina* is regarded as having evolved from *Lingulina*. *Oolina* is considered to have *Glandulina* as an ancestral form.

On p. 372, he states :—

"*Trigonulina* seems to be the end stage from *Dentalinopsis* or from *Trifarina*, and since it is usually monothalamous has heretofore been considered as a synonym of *Lagena*. *Lagena*, as ordinarily defined is a highly polyphyletic group, the end member of several lines of evolution. It may also be that the three-sided forms of single-chambered foraminifera, here referred to *Trigonulina*, were derived from several different families, but if so there is as yet no known way of separating the isomorphs."

On p. 380, Galloway remarks :—

"In *Ellipsolagena*, the internal chambers have been accelerated out or resorbed much as in the case of *Orbulina*. Whether *Ellipsolagena* was derived from *Ellipsoidina*, which it most nearly resembles, or from *Ellipsobulimina*, or from *Ellipsolingulina*, is not clear. The carinate edge of the test, and particularly the compressed form of some species indicate that *Ellipsolingulina* was the ancestor of *Ellipsolagena*. It may be that *Ellipsolagena*, as now understood, embraces the end members of all three genera of the family mentioned as possible ancestors."

Chapman and Parr (1936) and Glaessner (1945) have also treated the lagenid foraminifera as having evolved from multilocular forms, belonging to more than one family.

Discussion of the Lagenid Foraminiferal Genera.

Lagena Walker and Boys, *Testacea minuta rariora*, etc., 1784, p. 2.

Type species: *Lagena sulcata* Walker and Jacob = *Serpula* (*Lagena*) *sulcata* Walker and Jacob, 1798 = *Serpula* (*Lagena*) *striata sulcata rotunda* Walker and Boys, 1784. Designated by Parker and Jones, 1859.

In its typical form, as represented by the genotype, *L. sulcata* (Plate VI., fig. 1), the test consists of a single almost globular chamber, with the apertural end drawn out into a moderately long neck at the end of which is the circular aperture. There is no entosolenian tube.

The wall in species of *Lagena* does not appear to show the variety of ornamentation seen in *Oolina* and *Fissurina*, being either smooth, as in *L. clavata* (d'Orbigny), variously costate, as in *L. sulcata* (W. & J.), *L. curvilineata* Balkwill and Wright, and other species, or hispid, aculeate, or beaded (as in *L. distoma-margaritifera* Parker and Jones). The reticulate ornament and double wall found in some species of *Oolina* and *Fissurina* are not represented, but the neck shows a variety of ornamentation not seen in these two genera, being at times longitudinally or spirally costate or annulated.

Amphorina d'Orbigny, "*Foraminifères*", in: *Dictionnaire universel d'histoire naturelle*. Paris, 1849, vol. 5, p. 666.

Type species: No species named by d'Orbigny. *Amphorina gracilis* Costa, 1856, designated by Cushman, 1928.

This genus was erected by d'Orbigny for the reception of those lagenid foraminifera with a fusiform body chamber one end of which is drawn out into a long neck terminating in the circular aperture. The genotype, designated by Cushman, is *A. gracilis* Costa (Plate VI., fig. 3), but better-known examples of this generic type are *Lagena distoma* Parker and Jones and *L. distoma-margaritifera* Parker and Jones. The genus differs only from *Lagena* in having the aboral end tapering to a point instead of having the end rounded as in *Lagenae* of the *L. sulcata* group. The forms with rounded tests intergrade with those of the *Amphorina* type to such an extent that it is not possible to draw a dividing line between

the two. Structurally the two genera cannot therefore be separated and the writer accordingly agrees with Cushman that the *Amphorina* forms should be included under *Lagena.*

Oolina d'Orbigny, *Voyage dans l'Amérique méridionale; Foraminifères.* Strasbourg, Levrault, 1839, vol. 5, pt. 5, p. 18.

Type species: *Oolina laevigata* d'Orbigny 1839. Designated by Galloway and Wissler, 1927.

For some unknown reason, the genus *Lagena* was never used by d'Orbigny, although it had been recognized by two other French authors, Defrance and Deshayes, before the genus *Oolina* was erected. *Oolina,* as described by d'Orbigny, includes forms of *Lagena, Fissurina,* and *Oolina,* as now understood. The genotype of *Oolina, O. laevigata* d'Orbigny (Plate VI., fig. 5), was first designated by Galloway and Wissler in 1927. Although d'Orbigny states that the test of this species is very transparent, he makes no reference to an internal tube, which, if present, should have been readily recognizable. As it is not visible in his figure, the position of *Oolina* would be doubtful but for the information given by Heron-Allen and Earland in their work on the foraminifera of the Ice Free Area of the Falkland Islands and Adjacent Seas (1932, p. 361, pl. 10, fig. 4). They did not find the type specimen of *O. laevigata* from the Falkland Islands, but record that there is another specimen from the same area in d'Orbigny's collection labelled *Oolina laevigata.* This they consider to be the same as *Lagena globosa* (Montagu). Another specimen from their own material from the Falklands is figured by them and is very similar to d'Orbigny's type figure. As the entosolenian tube is visible in their figure, there appears no doubt that *O. laevigata* belongs to the group of lagenid foraminifera for which Williamson later proposed the name of *Entosolenia. Oolina* is accordingly regarded as a valid genus, with *Entosolenia* as a synonym.

The test of *Oolina* in most species is spherical or ovoid and the wall may be smooth, as in *O. laevigata* d'Orbigny, costate, as in *O. costata* (Williamson), or reticulated, as in *O. hexagona* (Williamson) and *O. squamosa* (Montagu). In one species, *O. hertwigiana* (Brady), the wall is double, and on both the outside and inside surfaces of the test it is conspicuously perforated.

The aperture in *Oolina* is typically a centrally-placed, rounded, terminal orifice which opens internally into an entosolenian tube. In the genotype, *O. laevigata,* it is at the end of a very short neck. In one species, *O. globosa* (Montagu), it may be rounded, ovate, slit-like, tri-radiate, cruciform, or radiate (*vide* Brady, 1884, p. 441, text-figs 11*a-g*), but such variation is not typical of *O. globosa* as it usually occurs. The aperture in this species is generally a rounded opening but is not infrequently stellate. The stellate aperture is found in fossil examples of *O. globosa* from the Miocene of Victoria and may occur earlier. With the exception of *O. globosa,* all species of *Oolina* have, in the writer's experience, constantly a rounded aperture.

Another feature which is found in *O. globosa* and its costate variant, *O. lineata* (Williamson) is the occasional development of an ectosolenian tube. This is not an extension of the body chamber of the same character as the neck of *Lagena sulcata,* but is merely a prolongation of the outer end of the internal tube. It has been well figured by Wiesner (1931, pl. 18, fig. 215) from the Antarctic, where the writer has met with similar examples. Brady (*loc. supra cit.*) has also figured several examples of *O. globosa* from the Irish Sea showing the same form of structure. The

ectosolenian tube is rather irregular in form and in one of the specimens figured by Brady (Plate VI., fig. 4), the outer end of the tube is bifurcated. Balkwill and Wright (1885, p. 336) note that *O. lineata* frequently bears an external tube which is often bent and irregular in shape. They figure (*loc. cit.*, pl. 14, fig. 14) a specimen showing a straight annulated tube.

In one species of *Oolina*, Brady's *Lagena hertwigiana*, there is a short internal tube and a delicate ectosolenian neck. The shape of the neck, its diameter which is the same as that of the internal tube, and the abrupt manner in which it rises from the apex of the test, suggest that it is merely an extension of the internal tube of the same nature as that seen in *O. globosa* and *O. lineata*.

One species of *Oolina*, Cushman's *Lagena collaris* (Plate VI., fig 6), from the North Pacific, has an apertural chamberlet, from the base of which and not from the exterior opening the internal tube commences. Sidebottom (1912, p. 380, pl. 14, figs. 7, 8), in his paper on the Lagenae of the South-West Pacific, has figured under the name of *Lagena globosa* (Montagu) bilocular forms, two specimens which have a very small second chamber. In fig. 7, the entosolenian tube is, as in *L. collaris*, found only in the initial chamber, but in fig. 8 each chamber has an entosolenian tube. Mr. Arthur Earland has sent me a slide containing three specimens of the same form as Sidebottom's and in each of these the entosolenian tube is developed only in the first chamber. While an apertural chamberlet is commonly found in the multilocular forms of the Nodosariidae and in the Polymorphinidae, the records now given appear to be the only evidence of a somewhat similar structure in the lagenid foraminifera.

There are several described species which are probably referable to *Oolina* although the apertural end of the test is drawn out to form a neck resembling that seen in *Lagena*. Two of these, Brady's *Lagena stelligera* and Heron-Allen and Earland's *L. scotti*, are Recent forms, and two others are the Tertiary species figured by Silvestri (1912, p. 153, text-figs. 18-22) under the names of *L. strumosa* Reuss var. *schlichti* Silvestri and *L. hystrix* Reuss (Plate VI., fig. 7). These four forms all have an internal tube. The writer has also met with a smooth entosolenian species like *O. globosa* with, however, a short neck, in the Upper Cretaceous of Dandarragan, Western Australia. Another fossil species with a produced neck in addition to a probably entosolenian tube is described by Macfadyen (1941, p. 63, pl. 4, fig. 63) under the name of *Lagena davoei* from the uppermost beds of the Lower Lias of England. Macfadyen was not able to satisfy himself beyond doubt of the presence of the internal tube, but it is not unlikely that the Mesozoic species showing the external characters of the genus *Lagena* include a number in which the entosolenian tube is also present. As will be seen later, the apertural end of the test in many species of *Fissurina* is similarly extended and the same development is to be expected in *Oolina*, which differs only from *Fissurina* in having the test rounded in transverse section instead of being compressed.

Entosolenia Williamson, Ann. Mag. Nat. Hist., ser. 2, vol. 1, 1848, p. 5.

Type species: *Entosolenia lineata* Williamson, 1848.

This genus is regarded as a synonym of *Oolina* d'Orbigny 1839 (*q.v.*).

Fissurina Reuss, Denkschr. k. Akad. Wiss. Wien, Math.—Nat. Cl., vol. 1, 1850, p. 366.

Type species: *Fissurina laevigata* Reuss, 1850 (Plate VI., fig. 8). Monotypic.

The characteristics of this genus in its typical form are a compressed, subglobular test, with a terminal fissure-like cavity which is deepest at the centre where is situated the rounded aperture. Internally the aperture is extended into a straight, tubular process directed into the centre of the body cavity. Apart from the variations in the nature of the surface ornament and the amount of inflation of the test, the apertural end in many species tends to be drawn out into a neck and the outer margin of the aperture then loses its slit-like shape, becoming oval or even circular in outline. These forms constitute Seguenza's "subgenus" "Produttine" (*vide* Seguenza, 1862, p. 53). A well-known species exemplifying the *Fissurinae* with a short apertural neck and oval aperture is Brady's *Lagena clathrata*. Representatives of those species of *Fissurina* with an elongated neck and circular aperture are Williamson's *Entosolenia lagenoides* (Plate VI., fig. 15), and the forms figured by Brady in the "Challenger" Report under the name of *Lagena formosa* Schwager. In one species of *Fissurina*, Hada's *Lagena curta* (Plate VI., fig. 14), the aperture is radiate.

The species of *Fissurina* have received closer attention from Seguenza (1862) than any other author. In addition to the "Produttine" already mentioned, he recognizes two other groups, "Fissurine" and "Tubuline". The "Fissurine" and "Produttine" comprise respectively the forms with the typical aperture of *Fissurina* and those with the apertural end extended into a neck, in none of which he had observed the presence of an internal tube. Those forms with an internal tube were referred by him to the "Tubuline" which embraces species with the external apertural characters of both his "Fissurine" and his "Produttine". Despite this division of the genus into species with an internal tube and those without it, the writer has never met with a species of *Fissurina* in which the internal tube was not present. Individual specimens may occur from which, for some unknown reason, the tube is missing, but they are always associated with other specimens of the same species showing the typical characters of *Fissurina*. The tube in some species, e.g. *F. clathrata* (Brady), is very short, but generally it extends well down the centre of the body chamber. Although usually straight, it may, as in *F. bispinosa* (Hada), and other species, be curved back towards the margin of the chamber, and is occasionally S-shaped or twisted like a corkscrew towards one side of the test.

In other species, e.g., the form figured by Brady (1884, pl. 59, figs. 8-11) as *Lagena staphyllearia* (Schwager), the tube, instead of being centrally placed, is directed to one side, following the curve of the chamber wall along a line midway between the margins of the test. This departure from the usual position of the entosolenian tube is considered to be the first step in the transition from *Fissurina* to *Parafissurina*, in which the tube typically occupies this position. Mr. Earland has pointed out to me that, in forms in which the tube occupies this position, it is frequently attached to the wall of the chamber and is then semi-circular in section, the chamber wall forming the flat side. This has been described by Sidebottom (1912, p. 406). In the species recorded by Brady (*loc. supra cit.*) as *Lagena staphyllearia* (Schwager), the tube is free and circular in section at first, then becoming attached and semicircular in section in its later half (Plate VII., fig. 3).

Another direction in which *Fissurina* varies is in the shape of the body chamber. The amount of compression may be so slight, as in *F. stewartii* (J. Wright), that the test is oval in transverse section, but in most species the test is compressed to such an extent that it is distinctly

carinate. Up to as many as seven or more marginal keels may be developed, and in some species, e.g., *F. formosa* (Schwager), the keel may be tubulated. The surface of the chamber may be smooth, e.g., *F. laevigata* Reuss; longitudinally costate, e.g., *F. clathrata* (Brady); beaded, e.g., *F. castrensis* (Schwager); pitted, e.g., *F. lacunata* (Burrows and Holland); reticulate, e.g., *F. squamoso-sulcata* (Parker and Jones); or with costae (Mr. Earland informs me these are actually tubules in the wall) radiating from a more or less central point, e.g., *F. radiato-marginata* (Parker and Jones) (Plate VI., fig. 11).

Species of *Fissurina,* e.g., *F. pulchella* (Brady), *F. orbignyana* Seguenza (Plate VI., figs. 12, 13), and *F. lagenoides* (Williamson), show a tendency to develop trigonal and tetragonal forms, some of which have been figured and described as new species by Balkwill and Millett (1884) in their paper on the foraminifera of Galway. In a later paper Balkwill and Wright (1885, p. 341) abandoned this view as to the status of these forms, remarking that trigonal examples of nearly all the British depressed Lagenae had been found by them. Seguenza's genus *Trigonulina* is clearly based on trigonal forms of this nature. While these trigonal and tetragonal forms are generally associated with the normal form and are therefore not true species, there is one species in which the trigonal form is almost constant. This is the Antarctic species described by Wiesner (1931, p. 121, pl. 19, fig. 230) under the name of *Lagena texta* (Plate VII., fig. 2). It has the most highly developed test of all the *Fissurinae.* Quoting Earland's excellent description of the wall structure (Earland, 1934, p. 165), "The three facial surfaces are slightly convex and double walled, the stout internal wall being covered by low ramifying costae, over which is a delicate and hyaline outer shell. The spaces between the costae form cellules, irregularly fusiform in shape, like the pulp cells of an orange." No other species of *Fissurina* known to me has a double wall. Neither Wiesner nor Earland records the presence of an internal tube, although it should be noted that Wiesner placed the species in the sub-genus *Entosolenia.* However, on breaking open specimens, the writer found that the species has an internal tube. The tube, which is straight, slender, and slightly bell-mouthed at the inner end, extends centrally into the chamber cavity for about one quarter of the length of the latter.

Several other species may be referred to here. Three of these, *Lagena cymbula* Heron-Allen and Earland (Plate VII., fig. 1), *L. cymbaeformis* Millett, and *L. depressa* Chaster, all have a depressed oval test, with an internal tube which passes down the median line of one of the longer sides of the test. The aperture is either round or oval. Like Joseph Wright's *Lagena stewartii,* these species all connect *Oolina* with *Fissurina,* but in view of the slight lateral compression of the test and the position of the internal tube, they are perhaps best referred to *Fissurina,* although they are far from typical of this genus. The other form, *Lagena stelligera* Brady var. *nelsoni,* described by Heron-Allen and Earland (1922, p. 148, pl. 5, figs. 20-22) from the Antarctic, is one of the most abnormal of all of the lagenid foraminifera. The aperture is directed to one side of the irregular compressed oval test and there is a long S-shaped internal tube extending almost to the base of the test, which is encircled by a collar-like keel. While the form might be regarded as an asymmetrical *Oolina,* it is probably nearer Brady's *Lagena fimbriata* than to any other species and is accordingly here referred to *Fissurina.* Very similar forms not yet described occur in the Early Tertiary of Victoria.

While *Fissurina* has been neglected by most authors, it appears to be the most important of all of the lagenid genera, its variety of forms and ornamentation showing a greater development than any other genus of the foraminifera. It is also represented by a larger number of well-defined species than any other lagenid genus.

Trigonulina Seguenza, *Dei terreni Terziarii del distretto di Messina; Parte II.—Descrizione dei foraminiferi monotalamici delle marne mioceniche del distretto di Messina.* Messina, 1862, p. 74.

Type species: Not designated. *Trigonulina oblonga* Seguenza, 1862, first species, designated by Cushman, 1928 (Plate VI., fig. 16).

This genus is regarded as a synonym of *Fissurina, q.v.*

Ellipsolagena A. Silvestri, Mem. Pont. Acc. Romana Nuovi Lincei, ser. 2, vol. 6. 1923, pp. 265, 268.

Type species: *Ellipsolagena acutissima* (Fornasini) = *Lagena acutissima* Fornasini, 1890 (Plate VII., fig. 5). Monotypic.

The characters of *Ellipsolagena*, as it is understood by most authors, are a monothalamous test, with an internal tube directed backwards from the aperture which is elongate, subterminal, curved, with one side raised into a protecting hood. While *Lagena ventricosa* Silvestri was designated the genotype by Cushman (1928, p. 265) and this was accepted by Galloway, it was apparently overlooked by both authors that Silvestri, in the paper in which he named *Ellipsolagena*, had referred *Lagena acutissima* Fornasini to the genus. No description of the genus was given by Silvestri in the body of the paper, but on page 268, in his explanation of the plate, he describes Fig. 13 as follows:—

"*Lagena acutissima* Fornasini (1890, Mem. R. Acc. Sci. Bologna, ser. 4A, vol. X, page 466, tavola, fig. 2, 2A) = *Ellipsolagena acutissima* (Fornasini). . . . ."

As *L. acutissima* is the only species mentioned, it is necessarily the genotype and its characters determine those of the genus. Unfortunately Silvestri had not copied Fornasini's figure of the aperture of *L. acutissima* correctly, as he shows it to be slightly arcuate, while in Fornasini's drawing it is an elongated oval. Fornasini's figures in the 1890 paper (Plate VII., fig. 5) (he figured only the front view of what is unquestionably the same form in his original description of *L. acutissima* and in neither case described the aperture) show the species to be a *Fissurina*-like form without any sign of the hooded aperture found in *Ellipsolagena*, as this genus is usually understood. The absence of any reference in Silvestri's paper to his own earlier species, *Lagena ventricosa* (text-fig. 1) and *Fissurina schlichti* (Plate VII., fig. 6), both of which have a hooded aperture, suggests that he may not have considered them to be *Ellipsolagenae*. It will also be noted that the genera included by him in the family Ellipsoidinidae (*vide* p. 265 of the paper) do not include *Pleurostomella* or any other genera with hooded apertures. This probably gives the reason why he omitted mentioning *Lagena ventricosa* and *Fissurina schlichti*. In the circumstances, there appears to be no alternative but to regard *Ellipsolagena* as a synonym of *Fissurina* and to erect a new genus for the hooded lagenid forms. For this genus, the name of *Parafissurina* is proposed.

PARAFISSURINA, gen. nov.

Test calcareous, perforate, consisting of a single, usually compressed, chamber, with an internal tube directed backwards from the sub-terminal aperture, which is an arched or crescentic opening facing the front under a hood-like extension of the ventral wall of the test

Type species: *Lagena ventricosa* A. Silvestri, 1904 (text-fig. 1).

Both Cushman and Galloway, and in this they were followed by Chapman and Parr, regard the hooded lagenid species as being unrelated to the nodosarian forms and group *Ellipsolagena* with *Ellipsoidina, Pleurostomella,* and similar genera, of which they consider it an end form. In the writer's view, based on the examination of examples of a large number of species, this is incorrect, and he regards the hooded forms as a development from *Fissurina.*

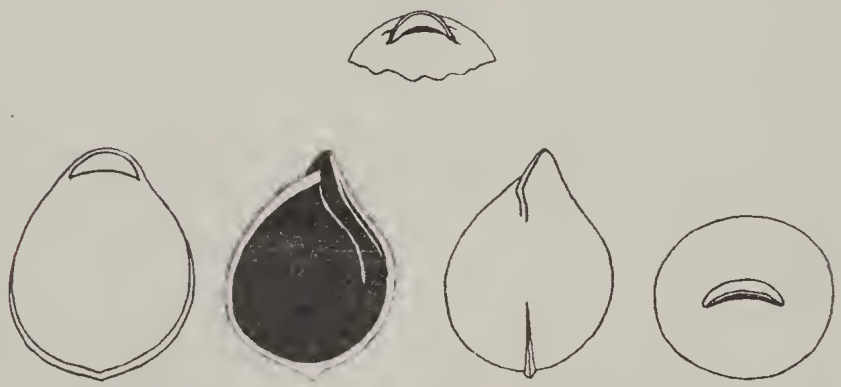

FIG. 1.—*Parafissurina ventricosa* (A. Silvestri). Genotype of *Parafissurina*, gen. nov. After type figures.

As has already been pointed out, the first indication of the development of *Parafissurina* from *Fissurina* is the alteration of the position of the entosolenian tube from the centre of the body chamber to a point midway between the margins of the test along one side of the test. When this is observed, the aperture should be examined from the side, when it will be found that in some specimens, particularly of the species figured by Brady (1884, pl. 59, figs. 8-11) under the name of *Lagena staphyllearia* (Schwager), the apertural margin on the side of the test under which the internal tube extends is slightly higher than the opposite edge to the aperture (Plate VII., fig. 3). *Ellipsolagena mauricensis* Howe and Roberts (Plate VII., fig. 4) also shows this structure. The difference in height between the two edges is sometimes so slight as to be barely perceptible. In these forms, the aperture is a straight fissure, but in others, e.g., *Fissurina biconica* Silvestri (Plate VII., fig. 8) and *F. obtusa* Egger, there is apparently no difference in the height of the rim to the aperture, but the aperture itself is arcuate in shape. From this point the apertural characters develop along several lines. The margin of the aperture on what may now be referred to as the ventral side of the test increases in height and inclines forward till it forms a pronounced hood which may, as in Wright's *Lagena marginata* (Walker and Boys) var. *inaequilateralis* (Plate VII., fig. 7) and Chaster's *L. millettii* (Plate VII., fig. 9), completely surround the aperture. The aperture itself becomes crescentic (as in *Lagena ventricosa* Silvestri), when seen from above, and then develops into an arched opening (*Ellipsolagena dorbignyana* Wiesner and other species), finally becoming circular, as in *Lagena millettii* Chaster. Where the hooded opening is large, as in *Ellipsolagena marginata* Wiesner, a plate is developed which nearly fills the opening, leaving the aperture a curved fissure between the plate and the overhanging hood. The description of the aperture as so far given refers to the external appearance of the apertural cavity (the Mündungsniche of Wiesner).

The aperture itself, like that of *Fissurina,* is situated at the base of the cavity and is a rounded opening from which the entosolenian tube extends into the interior of the test.

Except that the entosolenian tube in *Parafissurina* is curved to conform to the shape of the side of the test on which it rests, it is exactly similar to that found in *Oolina* and most species of *Fissurina,* viz., a narrow tube of even diameter throughout, usually becoming somewhat bell-shaped at the lower end. No structure of this form is found in any genus of the Ellipsoidinidae or in any families other than the Nodosariidae and the Polymorphinidae and there accordingly appears to be no doubt that the relationships of *Parafissurina* are with *Oolina* and *Fissurina,* and not elsewhere.

The test in species of *Parafissurina* does not develop the variety of ornamentation seen in *Fissurina.* Most species have a single encircling keel, but an undescribed species from the Tertiary of Victoria has two keels, and in Wiesner's *Ellipsolagena dorbignyana,* from the Antarctic, there are three. In *P. lateralis* (Cushman), *P. cor* (Wiesner), and some other species, the test is compressed but the margins are rounded. Species with costate, pitted, beaded, or reticulated faces, which occur in *Fissurina,* do not appear to have been recorded if we except the costate *Ellipsolagena sculpturata* Cushman and Bermudez, the generic position of which is doubtful.

Apart from the Eocene species, *Ellipsolagena mauricensis* Howe and Roberts, which is not a typical *Parafissurina,* the earliest satisfactory published records of the genus are from the Miocene. The writer has, however, met with a species of the normal hooded type in the Upper Middle Eocene (Bortonian) of New Zealand, and several species occur in beds of Upper Eocene or Lower Oligocene age in Victoria.

As there are several anomalous lagenid foraminifera which are considered to be species of *Parafissurina,* it may be desirable to give a list of the forms now referred to the genus. This comprises only those known to the writer and is therefore probably incomplete. The forms, using the generic, specific, and varietal names under which they were originally described, are *Ellipsolagena bidens* Cushman, *E. ovata* Wiesner, *E. marginata* Wiesner, *E. inversa* Wiesner, *E. fusiformis* Wiesner, *E. lata* Wiesner, *E. cor* Wiesner, *E. dorbignyana* Wiesner, *E. fijiensis* Cushman, *E. cucullata* Chapman and Parr, *E.* (?) *mauricensis* Howe and Roberts, *Fissurina schlichti* A. Silvestri, *F. biconica* A. Silvestri, *F. obtusa* Egger, *Lagena ventricosa* A. Silvestri, *L. lateralis* Cushman, *L. marginata* (Walker and Boys) var. *armata* Sidebottom, *L. marginata* (Walker and Boys) var. *inaequilateralis* J. Wright, *L. inaequilateralis* Wright var. *seminarginata* Sidebottom, *L. millettii* Chaster, *L. elcockiana* Millett (Plate VII., figs. 10, 11) *L. invaginata* Sidebottom, *L. irregularis* Sidebottom, *L. reniformis* Sidebottom, and its variety *spinigera* Sidebottom, and *L. unguis* Heron-Allen and Earland. Reference to Sidebottom's papers on the Lagenae of the South-West Pacific (1912, 1913) will show that he figured a number of other hooded forms but identified them with previously-described species in which the aperture is typically fissurine. These hooded forms require describing as new species.

To sum up the conclusions so far reached, the writer recognizes *Lagena, Oolina,* and *Fissurina* as valid genera. *Entosolenia* is regarded as a synonym of *Oolina,* and *Ellipsolagena* of *Fissurina.* A new genus, *Parafissurina,* is erected for the reception of the hooded lagenid species hitherto referred to *Ellipsolagena.*

The Relationships of the Genera.

The earliest true lagenid foraminifera appear in the Jurassic, in which they are of comparatively rare occurrence. From the Lias of Germany, Franke (1936) has recorded a number of species under the names of *Lagena vulgaris* Will., *L. globosa* Walker, *L. stutzeri* Franke, *L. clavata* d'Orb., *L. ovata* (Terquem), *L. urnula* Franke, *L. mucronata* Terq. and Berthelin, *L. oxystoma* Reuss, and *L. tenuicostata* Franke. Terquem and Berthelin (1875) have recorded *L. ovata* Terq., *L. acicularis* Terq., *L. simplex* Terq., *L. vulgaris* Will., *L. clavata* Reuss, *L. mucronata* Terq. and Berth., *L. hispida* Reuss, *L. aspera* Reuss, and *L. laticosta* Terq. and Berth., from the Middle Lias of France. With the exception of *L. stutzeri* (Plate VI., fig. 9), which is compressed and without an apertural neck, these species are all forms in which the test is circular in transverse section. They include typical *Lagenae,* a number of which are of the amphorine type, and apparently also species of *Oolina,* although it is not stated that an internal tube has been recognized in any of the specimens. Undoubted *Oolinae* are, however, known to occur in the Jurassic, as Haeusler (1887, p. 181) records and figures under the name of *Lagena globosa* Montagu specimens showing the internal tube from the Upper Lias of Switzerland.

The presence of true *Fissurinae* in the Jurassic is not so well established, as, while *Lagena stutzeri* Franke and *L. compressula* Gümbel (Plate VI., fig. 10) have the external characters of *Fissurina,* no statement of the existence of an internal tube in these species has been made. When we come to the Lower Cretaceous, the species of lagenid foraminifera are in general form much like those from the Jurassic, although more varied. Haeusler (1887, pl. 4, fig. 53) has figured under the name of *Lagena marginata* Montagu a compressed, carinate form from the Neocomian of Switzerland which in external features is a typical species of *Fissurina.* Chapman (1893, pl. 8, figs. 1-16), in his work on the Gault of Folkestone, figures from the Albian a number of species which include true *Lagenae,* as well as what may be forms of *Oolina* and *Fissurina* (recorded as *Lagena marginata* Walker and Boys). The internal characters of these species are not however described, and it is not until the Upper Cretaceous that one finds undoubted *Fissurinae* of similar types to those which are so common in Tertiary and Recent deposits. As has already been stated in the notes on *Parafissurina,* this genus makes its appearance in the Eocene. All four genera occur in many forms in the Tertiary and have a world-wide distribution in Recent seas in which they reach their greatest development. In the Tertiary of Victoria they are exceptionally well represented, over one hundred species occurring at one locality, Balcombe Bay, in beds of Miocene age.

From the evidence available, there can be no doubt that *Lagena* and *Oolina* both appear at least as far back as the Lias and that forms with the external characters of *Fissurina* are also present in the early Jurassic. It also appears probably that *Fissurina* came from *Oolina* in the Jurassic by the compression of the test and the consequent development of an aperture adapted to the requirements of a test of this shape. For reasons which are given in the notes on *Parafissurina,* it is considered that the hooded lagenid forms were derived from *Fissurina* and that they have no relationship to the Pleurostomellidae. It is however more difficult to demonstrate satisfactorily the relationship between these entosolenian genera and *Lagena.* There is some evidence which may indicate that the entosolenian forms belong to the same family as *Lagena.* In several genera of the Nodosariidae and also of the Polymorphinidae, multicamerate forms occur which have

developed the internal tube. Brady (1884, p. 443) records its presence in Recent species which he identifies as *Nodosaria calomorpha* Reuss, *Polymorphina angusta* Egger, and *P. lanceolata* Reuss, and the writer has also observed an internal tube in the genera *Glandulina* and *Sigmomorphina.* There are also the peculiar minute forms with a fissurine aperture and entosolenian tube described under the names of *Frondicularia translucens* Heron-Allen and Earland, *Lingulina armata* Sidebottom, *L. carinata* d'Orbigny, var. *biloculi* J. Wright, *L. falcata* Heron-Allen and Earland, *L. quadrata* Heron-Allen and Earland, and *L. translucida* Heron-Allen and Earland. A slit-like aperture, resembling that of *Fissurina,* but without the internal tube, is found in typical species of *Lingulina,* in *Gonatosphaera,* and in an undescribed Victorian early Tertiary species otherwise like *Globulina,* and Dr. M. F. Glaessner has a species from the Pliocene of Papua resembling in form *Guttulina* but with a slit-like aperture.

It might be suggested that none of these species or genera belongs to the Nodosariidae or the Polymorphinidae, although, on their general form, it would be difficult to place them elsewhere. On the other hand, structures comparable with the fissurine apertures and the internal tube are not known in any other family of the foraminifera. It is true that in some species of *Siphogenerina* there is an internal tube, but this is of a different type from that seen in the entosolenian forms under discussion, being much wider and extending from the top to the bottom of each chamber, while the short phialine apertural neck of this genus is unlike any aperture found in the Nodosariidae or the Polymorphinidae.

As apertural characters of the types found in *Lagena, Oolina,* and *Fissurina* all occur in species of the multicamerate genera of the Nodosariidae, there can be little doubt of the relationship of *Oolina* and *Fissurina,* and also *Parafissurina,* to *Lagena* and to the polythalamous Nodosariidae.

Whether the lagenid genera should be regarded as end forms derived from the multilocular genera of the Nodosariidae now needs to be considered. While it has been stated by authors that the lageniform foraminifera are end forms developed from polythalamous genera, there is, in the writer's view, nothing to support this. If this were correct, one would expect that, among the hundreds of species of lagenid foraminifera, microspheric examples would have occurred showing more than one chamber. No one has, however, to the writer's knowledge, ever recorded a microspheric specimen of any of these species. It might be suggested that they have been found and referred to one of the multilocular genera, but this is unlikely as the external characters of most species of the lagenid genera are sufficiently distinct to enable the microspheric form, even if multilocular, to be associated with the megalospheric form. There is, of course, the possibility that, as in some other genera of the foraminifera, microspheric forms apparently do not occur in the lagenid foraminifera. However, in the absence of microspheric multilocular specimens, there is no direct evidence that these single-chambered forms were derived from multilocular forms, the view that the latter were ancestral to the former being based on apparent similarities in form, ornament, and apertural characters. The writer considers it more likely that the lagenid foraminifera, while undoubtedly closely related to the polythalamous genera of the Nodosariidae and the Polymorphinidae, have not evolved from them, but had a single-chambered ancestor. What this ancestor was is unknown but it may have been either a chitinous form or, perhaps, the Palaeozoic genus *Archaelagena* Howchin, which in many respects is close to *Lagena.* Whether the multilocular Nodosariidae were derived from *Lagena, Oolina,* and *Fissurina,* or came directly from the same ancestor as these genera cannot be stated in

our existing state of knowledge. Although well-developed multilocular genera of the Nodosariidae occur in the Permian, there does not appear to be any satisfactory record of *Lagena*, *Oolina*, or *Fissurina* from the Palaeozoic. *Archaelagena* is known from the Carboniferous, and Chapman (1900) has recorded from the Upper Cambrian of England under the name of *Lagena* a single-chambered foraminifer the wall structure of which is uncertain, but which is possibly chitinous.

The exact relationship of the lagenid foraminifera to the polythalamous Nodosariidae is therefore uncertain, but the high degree of ornamentation found in the older genera, particularly *Oolina* and *Fissurina*, which is in advance of anything seen in the multilocular forms, as well as the specialized apertures, best developed in *Fissurina* and *Parafissurina*, indicate a different line of development. It is accordingly suggested that the four genera which have been described should be grouped in a separate family, the Lagenidae, and that the family Nodosariidae should comprise only those polythalamous forms which have hitherto formed only part of this family. The superfamily Lagenidea recently proposed by Glaessner (1945, p. 126) will then embrace those two families and the Polymorphinidae. A description of the Lagenidae, with a key to the genera of the family, follows:—

> Family Lagenidae.—Test calcareous, perforate, consisting of a single rounded or compressed chamber with or without an apertural neck; aperture terminal or sub-terminal, variously formed, rounded, stellate, radiate, elliptical, slit-like, or an arched opening directed to one side under an overhanging hood.

Key to Family Lagenidae.

I. Test with terminal aperture—

- A. With apertural neck and without entosolenian tube .. *Lagena.*
- B. With entosolenian tube and without or with apertural neck—
  - (1) Test circular in transverse section .. *Oolina.*
  - (2) Test compressed .. .. .. *Fissurina.*

II. Test with sub-terminal aperture and entosolenian tube .. *Parafissurina.*

In conclusion, the writer realizes that the genera he has recognized could justifiably be subdivided into a larger number of genera. Mr. Earland has pointed out to me that the double wall seen in some species, e.g., Wiesner's *Lagena texta*, Brady's *L. hertwigiana*, and Heron-Allen and Earland's *L. scotti;* the marginal tubes in species such as Williamson's *Entosolenia lagenoides* and *E. marginata* var. *ornata*, and Schwager's *Lagena formosa;* and the development of horizontal tubules on the surface, as in Parker and Jones' *L. radiato-marginata*, are all much more radical differences from the presumably original form, a simple globose test, than the differences on which *Oolina*, *Lagena*, *Fissurina* and *Parafissurina* are separated. The purpose of these notes has, however, been to deal with the status, and more particularly, the relationships of known genera, leaving the description of new genera to other workers.

Acknowledgments.

The writer gratefully acknowledges his obligation to his friends, Mr. Arthur Earland, F.R.M.S., and Dr. Martin F. Glaessner, who have both read the manuscript and whose criticism has been largely responsible for the final form of this paper. To Mr. Earland, whose experience of the lagenid foraminifera is unequalled, he is still further indebted for a slide

of over 1,000 specimens of these forms, selected by him from the material he has examined during work on the foraminifera extending over a period of nearly sixty years. Mr. Earland has also kindly sent another slide of specimens from the South-West Pacific mounted by the late Mr. W. Blundell Thornhill, whose main collection of these forms from the same area was described by Henry Sidebottom in the Journal of the Quekett Microscopical Club for 1912 and 1913.

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Explanation of the Plates.

Plate VI.

Fig. 1.—*Lagena sulcata* (Walker and Jacob). Genotype of *Lagena*. After type figure.

Fig. 2.—*Lagena laevis* (Montagu). After Fornasini, 1890.

Fig. 3.—*Lagena gracilis* (Costa). Genotype of *Amphorina*. After type figure.

Fig. 4.—*Oolina globosa* (Montagu). Section of specimen showing bifurcated tubular extension of aperture. After Brady, 1884.

Fig. 5.—*Oolina laevigata* d'Orbigny. Genotype of *Oolina*. After Heron-Allen and Earland, 1932.

Fig. 6.—*Oolina collaris* (Cushman). After Cushman, 1913.

Fig. 7.—*Oolina hystrix* (Reuss). After A. Silvestri, 1912.

Fig. 8a, b.—*Fissurina laevigata* Reuss. Genotype of *Fissurina*. After type figures.

Fig. 9a-c.—*Fissurina stutzeri* (Franke). After type figures.

Fig. 10a-c.—*Fissurina compressula* (Gümbel). After type figures.

Fig. 11a, b.—*Fissurina radiato-marginata* (Parker and Jones). After Brady, 1884.

Fig. 12a, b.—*Fissurina orbignyana* Seguenza. After type figures.

Fig. 13a, b.—*Fissurina orbignyana* Seguenza. Trigonal form = *Lagena trigono-orbignyana* Balkwill and Millett, 1884. After Balkwill and Millett.

Fig. 14a, b.—*Fissurina curta* (Hada). After type figures.

Fig. 15.—*Fissurina lagenoides* (Williamson). After Williamson.

Fig. 16a, b.—*Fissurina oblonga* (Seguenza). Genotype of *Trigonulina*. After type figures.

Plate VII.

Fig. 1a-c.—*Fissurina cymbula* (Heron-Allen and Earland). After type figures.

Fig. 2.—*Fissurina texta* (Wiesner). After Earland, 1934.

Fig. 3.—*Fissurina staphylleria* (Brady-*non* Schwager). Section through specimen showing transition to *Parafissurina*. Original. Recent, Kerguelen, 20-30 metres.

Fig. 4a, b.—*Parafissurina mauricensis* (Howe and Wallace). After type figures.

Fig. 5a, b.—*Fissurina acutissima* (Fornasini). Genotype of *Elipsolagena*. After Fornasini, 1890.

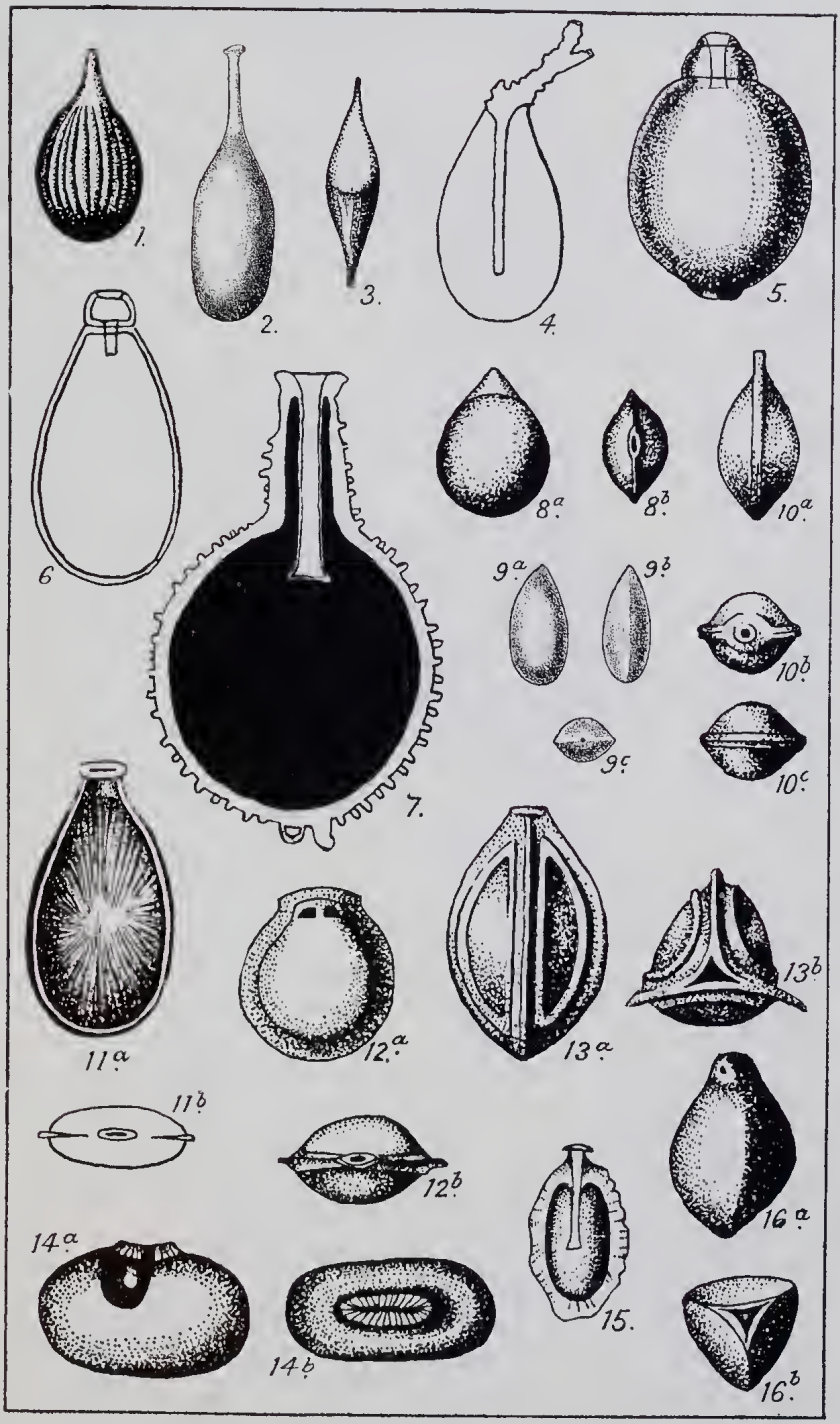
Fig. 6a-c.—*Parafissurina schlichti* (A. Silvestri). After type figures.

Fig. 7a-c.—*Parafissurina inaequilaterulis* (J. Wright). After type figures.

Fig. 8a-c.—*Parafissurina biconica* (A. Silvestri). After type figures.

Fig. 9a, b.—*Parafissurina millettii* (Chaster). After type figures.

Fig. 10a-c, 11.—*Parafissurina elcockiana* (Millett). After type figures.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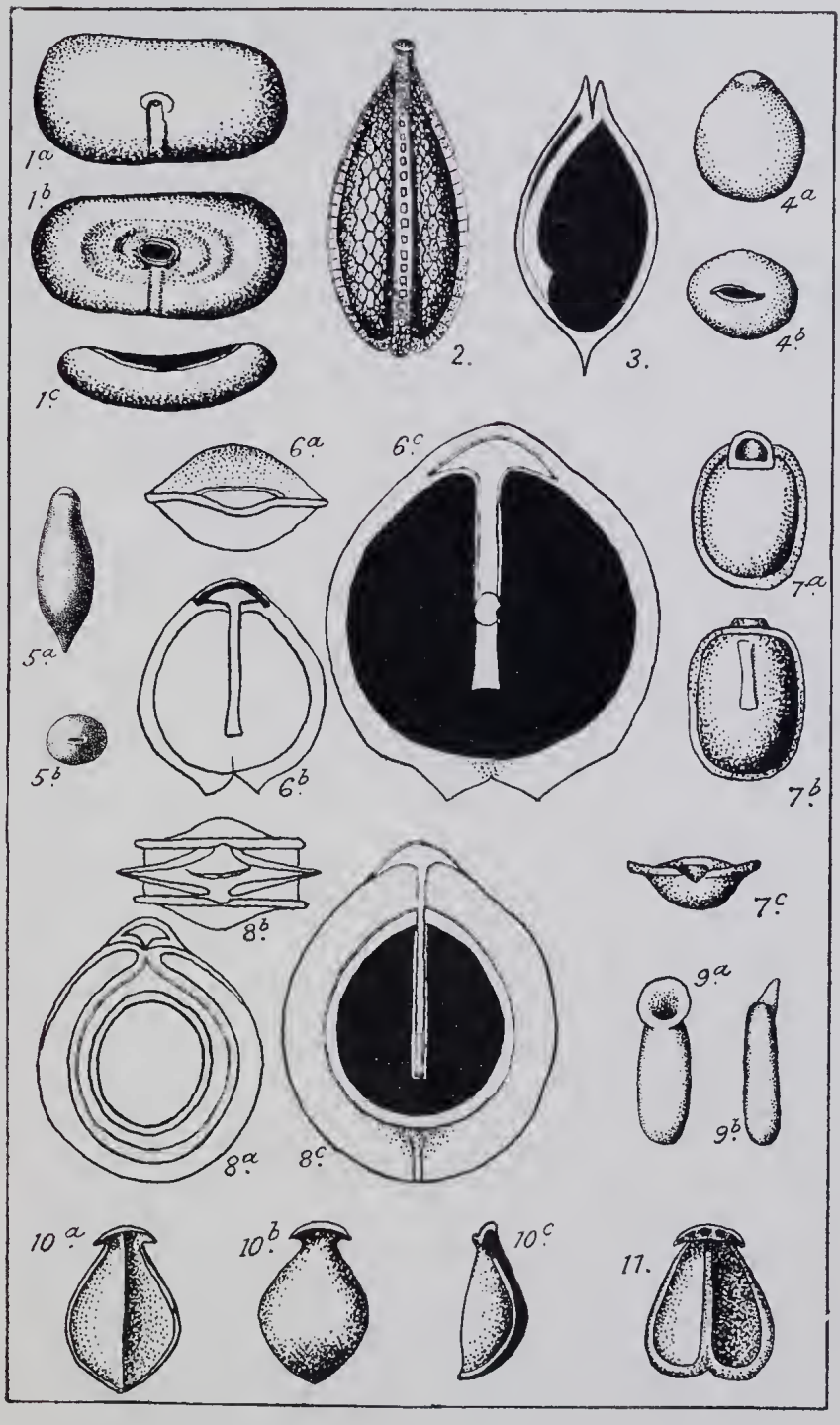
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