THE

AMERICAN JOURNAL OF SCIENCE

[FOURTH SERIES.]

ART. XX. — *Development of Fenestella*; by EDGAR ROSCOE CUMINGS, Ph.D. (With Plates V, VI, and VII.)

Introduction.

DURING the past two years, the writer's studies of the development of Paleozoic Bryozoa* have brought out some very interesting points bearing upon the earliest stages of *Fenestella*. The present paper deals with the development (astogeny) and morphology of *Fenestella*, and is based entirely upon calcified material from the Hamilton formation of Thedford, Ontario.† This material consists of numerous bases of *Fenestella* colonies. In these, the minutest details of internal structure are preserved with remarkable fidelity. The method of study has been the preparation of both thin and serial sections. The latter were obtained by slowly grinding down the bases and accurately drawing each stage as seen by reflected or in some cases by transmitted light. The specimens studied are in various stages of growth. Some represent the bases of adult colonies from which the adult (ephebastic) portion has been lost; others are minute bases, which in their growth never proceeded farther than the nepiastic stage. In these nepiastic

* In a former paper, a classification of the growth stages of the bryozoan colony was given, together with a general classification of the growth stages of any colony belonging to any group of organisms. The terms applicable to the growth stages of any colony are: *Nepiastic*, *neaniastic*, *ephebastic*, and *gerontastic*, corresponding to the well-known terms *nepionic*, *neanic*, *ephebic*, and *gerontic*, applicable to the growth stages of the individual. Dr. Ruedemann has recently proposed the term *astogenetic* with reference to the colony, as the term parallel with *ontogenetic* with reference to the individual. The *astogenetic* stage of a colony, therefore, corresponds with the *ontogenetic* stage of an individual.

† This *Fenestella* is probably the form listed by Grabau as *Semicoscinium labiatum*.

colonies, the zoœcia emerge upon the surface; but in the older ones, the apertures of the zoœcia in the basal portion are submerged in a copious deposit of punctate sclerenchyma. In all cases, however, there has been no resorption of the earlier zoœcia, so that sections of the bases of ephebastic or gerontastic zoaria reveal the morphology of the earliest stages as faithfully as sections of a nepiastic colony. As an aid to the elucidation of the astogeny of *Fenestella*, the writer studied the astogeny of *Retepora phœnicea*, a recent bryozoan morphologically very similar to the ancient Fenestellas and Polyporas.

In the writer's former paper on the development of Paleozoic Bryozoa, the term *protœcium* was introduced as designating the primary individual of the colony. In this sense, it would have the same signification as the term *ancestrula* of Jullien or *primary cell* of Hincks. In the Cyclostomata, as is well known, the first zoœcium surmounts a hemispherical base (*basal disc*), which serves as the point of attachment of the young colony to the substratum. This basal disc has been shown to be the calcified wall of the metamorphosed and histolyzed embryo (Barrois and others). It is believed by the present writer that the persistence of this structure (kathembryonic stage) in the ancient order of Cyclostomata is not without significance, especially in view of the fact, to be shown presently, that it is a conspicuous feature in the development of the ancient Cryptostomata and possibly of the Trepostomata (*Phylloporina corticosa*). The basal disc is probably the *true* first zoœcium. In the present paper, therefore, the term *protœcium* is restricted to the basal disc or its equivalent, and the superjacent portion of the primary cell is designated the *ancestrula*. In many recent Chilostomata, there seems to be no distinction of protœcium and ancestrula. This may mean that the extreme acceleration of these modern types has practically eliminated the protœcium from the ontogeny. In the ancient Cryptostomata, on the other hand, the protœcium greatly predominates over the ancestrula, which is often little more than an exaggerated aperture to the former. In any case, the ontogenetic stage of which the protœcium is the index is always present throughout the Ectoprocta, for by a degenerative metamorphosis they all give rise to a hemispherical kathembryo, from which the adult polypide arises by a sort of budding process. Furthermore, this kathembryo becomes invested with a calcareous or chitinous ectocyst, which is the first skeletal structure of the developing individual. The protœcium is therefore very closely analogous to the protegulum of brachiopods, the protoconch of cephalopods, etc.

Development of Fenestella.

The Protœcium.

Many well-preserved *Fenestella* bases show a minute circular pit on their basal surface. This can be seen only in colonies that were attached to a substratum which disappeared in the process of fossilization, leaving the basal surface of the colony free from all extraneous matter. Where the colony is still attached to the substratum, frequently the frond of another bryozoan, the circular pit can always be demonstrated by means of thin sections. This pit is the protœcium. As will be seen from the longitudinal sections (figs. 20, 36, 37, 59), the protœcium is separated from the substratum by a thin basal membrane. In such sections, this pit appears as a semicircular object in the proximal portion of the colony. In transverse sections, it appears as a dark ring surrounded by concentric zones of punctate secondary sclerenchyma. That the protœcium has its own proper wall, similar to that of ordinary zoœcia, is shown by numerous sections (figs. 36–38, and 59). The diameter of the protœcium is from $0{\cdot}4-0{\cdot}6^{mm}$, or about three or four times that of the ordinary zoœcia. In form and position it corresponds precisely to the basal disc of Cyclostomata, and there can be little doubt that it has the same morphological and developmental significance.

The Ancestrula.

The protœcium is surmounted by a tubular structure arising from the center of its distal surface. This is the ancestrula. In some of the earlier sections prepared by the writer, one of the primary buds was mistaken for the ancestrula, and its size and shape were therefore thought to be different from what was shown in later sections. It is considerably smaller than the primary buds, being both shorter and of less diameter. It seems altogether likely that the primary polypide never permanently ascended into the ancestrula as in the Cyclostomata. On the other hand, the ancestrula of *Fenestella* is far from being the homologue of the vestibule of ephebastic zoœcia. It is not built up of secondary deposits, but is composed of the same thin non-punctate substance as the proper wall of the protœcium and other zoœcia. The homology of the ancestrula of *Fenestella* is with the tubular primary zoœcium of the Cyclostomata. Figures 59 and 60 indicate the shape and appearance of the ancestrula as seen in the majority of properly orientated longitudinal sections,* and figures 10–13, 24, 43, and 54 in transverse sections.

* The zoœcium marked *I*, in figures 19 and 20, was at first thought to be the ancestrula, since it communicates freely with the protœcium. A careful study of the appearances possible in a series of longitudinal sections with

The Primary Buds.

Two lateral primary buds arise from the primary zoœcium (figs. 3–7, 21–23, 40–43). There is still some question as to whether these buds arise from the protœcium or from the ancestrula. The sections figured reveal all that can be expected. The question becomes one of interpretation and of analogy with recent Bryozoa. The proximal ends of the primary buds are in contact with the protœcium and are separated from its cavity by a very thin calcareous wall, which is frequently broken away (figs. 19 and 20). The appearance of this wall is well shown in figure 36. Figures 3–7 and 38–40, 42 show the intimate relation of the primary buds to the protœcium. From the analogy of recent Bryozoa, on the other hand, these buds might be expected to originate from the ancestrula. A median primary bud is not indicated by any of the sections. If it existed, it certainly arose from the ancestrula.

The size, shape, and position of the primary buds is beautifully shown in figures 38 and 39, and in the transverse sections. These buds are long and tubular, and diverge but slightly from the axis of the zoarium. There is no long vestibule as in ephebastic zoœcia, but the whole aspect of the buds is that of a simple tubular zoœcium, quite similar to that of the Cyclostomata. There is also no indication of hemisepta or any other structures within the zoœcium.

Secondary Buds.

All buds of the second generation from the protœcium are designated secondary buds. The series of sections (figs. 1–16) seems to indicate that each of the primary buds produces a lateral and a median bud. The lateral buds are very clearly shown in such a position that they could have originated from no other source than from the primary buds (see especially figs. 5, 41, and 42). The median buds belong to the second tier of zoœcia. They are designated II_{21} and II_{31} in figure 13. The shape of the secondary buds is quite similar to that of the primary ones (figs. 37, 45, 59, and 60). Figure 50 is a drawing

different assumed orientation has convinced the writer that the zoœcium in question is a primary bud. To test this, four different bases in which the protœcium and primary buds could be seen on the basal surface (in some cases only after slight etching) were sectioned in the direction $j - j$, figure 48, which had been determined by previous inspection of the basal surface, and marked by carefully drawing a fine line through the center of the protœcium and as nearly as possible between the primary buds. Every one of these sections has the appearance shown in figures 59, 60, and 45. It is therefore unlikely that figures 19 and 20 (which were orientated at random) represent the ancestrula. It is needless to state that only a very small proportion of the many sections prepared in this study are figured.

of a secondary bud, and may be compared with figure 53, which is a drawing of two zoœcia of *Protocrisina* (after Ulrich), a cyclostomatous bryozoan from the Trenton. The resemblance is too striking to need further emphasis. No internal zoœcial structures have been observed in the secondary buds.

Tertiary and Later Buds.

One bud of the third generation from the ancestrula occupies a position in the first tier of zoœcia, diametrically opposite the ancestrula (*III*, figs. 6–13, 24, 26, 43, 54–58). The shape of this bud is well shown in figures 37, 45, 59, and 60. There is no means of telling from which of the two secondary buds this tertiary one is derived. It may have originated now from one, now from the other. In figure 43, it is rather more intimately associated with *32*, which was in turn derived from the right lateral primary bud. Figure 13 indicates that each of the secondary buds gives rise to a median bud lying in the second tier of zoœcia.

Ascending the axis of the zoarium (figs. 17–20, 36–39), there is exhibited a series of zoœcia very symmetrically arranged about the axis. In transverse sections, above the level of *y*, figure 17, these present a peculiar star-shaped appearance seen in figures 15, 16, and 58, as well as in figure 61 of the writer's former paper. The order of budding of these later zoœcia cannot be determined, although the writer has devoted a large amount of time and study to this point. It is probable that the order of budding in these later generations is without significance. An important point shown by the sections, however, is the shape and size of these zoœcia. This is best seen in figures 17 and 38. The zoœcia are tubular, but somewhat less elongate than the earlier ones. It is not until the zoarium begins to expand into its characteristic infundibular form that the zoœcia assume the shape normal to *Fenestella*. Figure 51 shows a row of zoœcia from the neanastic region (base of the cone) of the specimen represented in figure 38. For comparison with this is inserted figure 52, showing a specimen of *Fenestella acmea* from the Waldron shale of Tarr Hole, Indiana. The resemblance is striking. The adult zoœcia of the Thedford *Fenestella* are shown in figure 49.

Discussion and Conclusions.

The morphological element of the bryozoan colony which corresponds to the primitive integument of Mollusca, Brachiopoda, etc. (that is, to the protoconch, protegulum, etc.), is the *protœcium*, or basal disc, of the primary individual of the colony. The protœcium is the calcareous or chitinous wall of

the kathembryo. In *Fenestella* it is very large and in every way similar to the protœcium (basal disc) of the Cyclostomata. The ancestrula is the tubular superstructure of the primary individual. It is a simple, undifferentiated, tubular zoœcium. The earlier formed zoœcia (nepiastic zoœcia) of the *Fenestella* colony differ markedly in shape and size from later formed (neanastic and ephebastic) zoœcia. In every feature in which they depart from the ephebastic zoœcia of *Fenestella* they approach the ephebastic zoœcia of the Cyclostomata.

From these observations, it may be reasonably concluded that *Fenestella* as well as the entire order of Cryptostomata is derived from the Cyclostomata. Certain other general conclusions, more or less speculative, are suggested by a consideration of the probable significance of the protœcium and ancestrula.

The meaning of the degenerative metamorphosis of Bryozoa has always been a puzzle to students of this class. The striking analogy of this metamorphosis to the degeneration of an ordinary polypide and production of a brown body, together with the nearly identical life history of the regenerating polypide or of ordinary buds and the primitive polypide issuing from the kathembryo, have more than once led to the suggestion that the primitive polypide is in the true sense a bud. The writer is inclined to hold this view. Assuming, therefore, that the primitive polypide is a bud, the following suggestions may be made in regard to the significance of the metamorphosis and of the resulting protœcium:

1. In the primitive bryozoan, there was no histolysis of the larval organs. The development was direct and resulted in a primitive zoœcium and polypide.

2. This primitive zoœcium was hemispherical in shape and possessed a simple aperture in the center of its upper surface. Some ancient types of Cyclostomata retain nearly such a form of zoœcium (*Stomatopora* of the Trenton, especially *S. turgida*).

3. This primitive zoœcium might now give rise to a linear adnate series of zoœcia, as in *Stomatopora*, or to a series of superposed zoœcia, as in the Trepostomata. By variations of zoarial habit based upon one or the other of these fundamental plans of budding all existing types of Bryozoa could have been produced.

4. In accordance with the law of tachygenesis, later in the history of the bryozoan group a tendency toward concentration of the early stages in development would arise. In any colony the tendency to degenerate may be supposed to have applied to the primitive polypide as well as to later ones, and finally to have become an invariable part of its life history. By the continued operation of the law of tachygenesis, the life history of the first polypide became so abbreviated as to be

represented only by its degenerative stage, that is, by its latest growth stage, all the earlier growth stages having been crowded out or back into the larval stage.

In accordance with this interpretation of bryozoan development, the large size of the protœcium in ancient types is explicable and is thought to be due to a less degree of acceleration, the calcification of the zoœcial wall of the primitive individual being allowed to proceed nearly to completion before the second zoœcium was superposed upon it. The probability that the first polypide remains in the protœcium in *Fenestella*, instead of ascending into the ancestrula as in modern Cyclostomata, may indicate a still more primitive condition. The relations of the protœcium and ancestrula in the Cyclostomata and in *Fenestella* suggest the normal relation of superposition of the zoœcia in the Trepostomata. It is not without interest to find evidence, in the development of Paleozoic Bryozoa, of the fundamental relationship of these great groups. Ulrich (Geol. Surv. Illinois, vol. viii) has already suggested such a relationship on the ground of the resemblances of such types as the early Fenestellas, *Phylloporina* and *Protocrisina*. The evidence presented by these adult types is greatly strengthened by the striking parallelism of the nepiastic stages of *Fenestella* with the series of adult types named above.

Paleontological Laboratory, Indiana University,
June, 1905.

EXPLANATION OF PLATES.

*Description of Figures.**

Letters having the same meaning for all the figures:—

a, *b*, *c*, *d*, *e*, primary carinæ (except figs. 17, 24, 47, and 48).
f, fenestrule.
k, carina.
o, protœcium.
s, substratum of bryozoan colony.
z, *z'*, etc., zoœcia of generations later than the primary zoœcia.
A, ancestrula.
I, primary bud.
II, bud of second generation, that is, derived from a primary bud.
III, bud of third generation.
2, left lateral bud.
3, right lateral bud.
23, right lateral bud of the second generation, derived from a left lateral primary bud.
32, left lateral bud of the second generation, derived from a right lateral primary bud.

* All drawings except figures 1–16 were made with the camera lucida. Figures 30–32 are after Barrois, and figure 53 is after Ulrich. All the specimens of *Fenestella* are from Thedford, Ontario.

PLATE V.

FIGURES 1-16.—Transverse serial sections of a *Fenestella* base. These sixteen sections represent 1^{mm} thickness of rock.

FIGURES 1, 2.—Protœcium (cf. figs. 40, 41, 31-35).

FIGURE 3.—Section in the plane of *a–a*, figure 47, cutting the proximal ends of the primary buds and the buds of the second generation (secondary buds) (cf. fig. 42).

FIGURES 4, 5.—Successively higher sections.

FIGURE 6.—Section in plane of *a′–a′*, figure 47, cutting the proximal end of the tertiary bud (cf. fig. 43).

FIGURES 7-12.—Successively higher sections between the planes of *a′–a′* and *c–c*, figure 47, showing the development of the initial buds. Figures 10-12 cut the aperture of the ancestrula (cf. fig. 24, with fig. 12).

FIGURE 13.—Section cutting the proximal ends of buds of the second tier (II_{21}, II_{31}, *IIIb*, and *IIIc*) (cf. fig. 26).

FIGURE 14.—Section just cutting the distal end of the aperture of the ancestrula.

FIGURES 15, 16.—Assumption of the star-shaped arrangement of zoœcia, characteristic of the paranepiastic stage of *Fenestella*.

PLATE VI.

FIGURE 17.—Longitudinal section of a *Fenestella* base cutting in the plane of *e–e*, figure 47, and *a–a*, figure 48. This section passes through the edge of the protœcium and misses the ancestrula entirely. *b*, *b′*, buds of the second tier. At *z* and *z′* the zoœcia are vertically above each other; at *z″*, *z‴* they alternate, and at the top of the figure they lie side by side. × 17.

FIGURE 18.—Longitudinal section cutting still more excentrically than that shown in figure 17, probably in the plane of *b–b*, figure 48. This misses the protœcium and ancestrula entirely, but their relative position is shown at *o* and *A*. The vertical alignment of zoœcia is shown at *z–z′* and the ordinary arrangement, on either side of the carina, at *z″*. The bifurcation of a primary branch is shown at *g–h* (between *z″* and *g*, *h*). In each new branch, the zoœcia first alternate and later lie side by side. Normal arrangement shown at *k′* *k″*. × 17.

FIGURE 19.—Longitudinal section cutting in the plane of *c–c*, figure 48. The section cuts a row of zoœcia (*z′–z″*) nearly longitudinally. × 17.

FIGURE 20.—Section in nearly the same plane as in figure 19 (*d–d*, figure 48). This section was orientated by polishing and etching the basal surface of the colony and marking the position of the protœcium and primary buds. The section was then ground as nearly as possible in the marked direction. A primary bud is very clearly shown (*I*). × 17.

FIGURE 21.—Transverse section in the plane of *a–a*, figure 47. The primary buds are very distinct. × 17.

FIGURE 22.—Similar section of another specimen, cutting the proximal end of the ancestrula. × 17.

FIGURE 23.—Transverse section of a very slender base. Section in about the same plane as 22. × 17.

FIGURE 24.—Section in the plane of *b–b*, figure 47. Ancestrula very distinct. × 17.

FIGURE 25.—Longitudinal section of a base from which the substratum was absent. × 17.

FIGURE 26.—Transverse section in the plane of *d–d*, figure 47, showing the proximal ends of two buds of the second tier (*z*, *z′*) (cf. fig. 13). × 17.

FIGURE 27.—Protœcium and ancestrula of *Retepora phœnicea* from St. Vincent's Gulf, Australia. × 27.

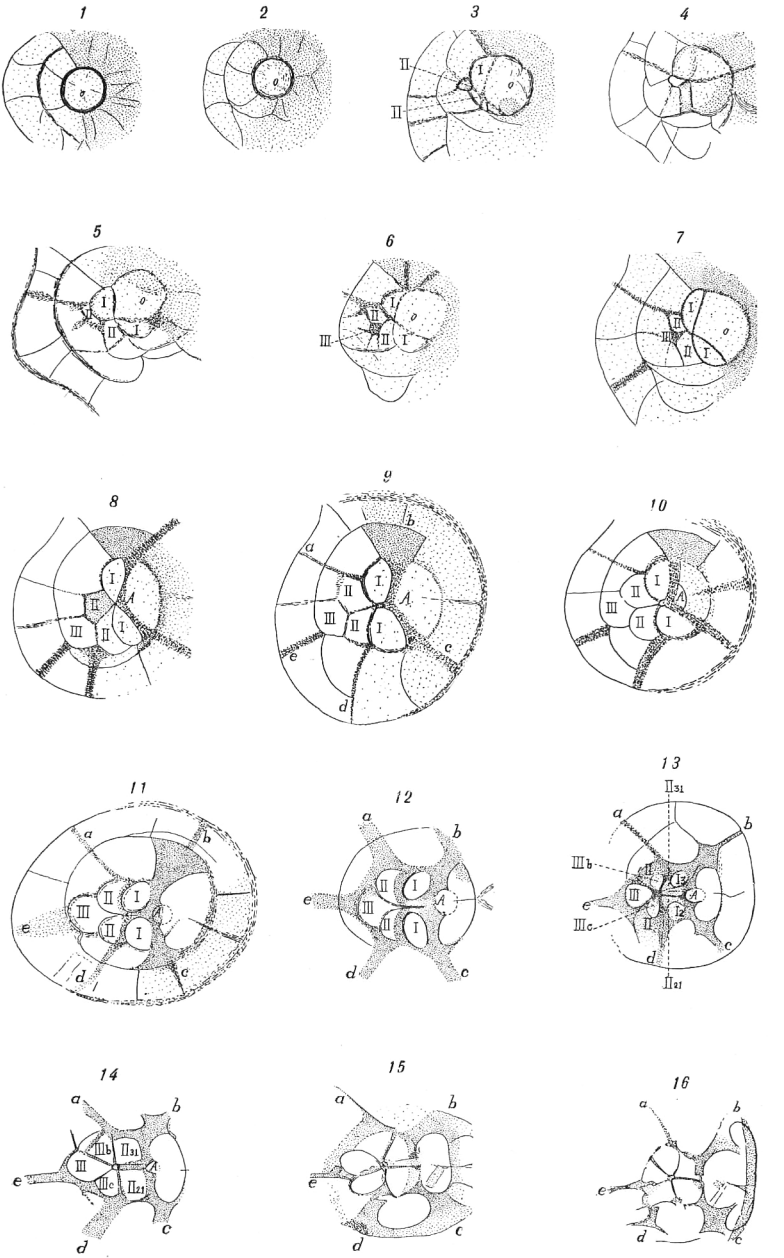
FIGURE 28.—Ancestrula and three primary buds (*1*, *2*, *3*) of *Retepora phœnicea*. × 29.

FIGURE 29.—Profile view of protœcium and ancestrula of another specimen of *Retepora phœnicea*. × 27.

FIGURE 30.—Protœcium, ancestrula, and primary bud of *Tubulipora*. After Barrois. ×27.
FIGURE 31.—Same; seen from the under surface. ×27.
FIGURE 32.—Ancestrula and primary bud of *Schizoporella*. ×33.
FIGURE 33.—Protœcium and primary zoœcia of *Phylloporina corticosa* from Cannon Falls, Minnesota. ×17.
FIGURE 34.—Protœcium of *Polypora* from the Lower Helderberg of Indian Ladder, New York. ×28.
FIGURE 35.—Protœcium of *Thamniscus* from the Upper Coal Measures of Kansas. ×17.

PLATE VII.

FIGURE 36.—Longitudinal section of *Fenestella*, in the plane of *f–f*, figure 48. ×17.
FIGURE 37.—Longitudinal section in the plane of *g–g*, figure 48. ×17.
FIGURE 38.—Longitudinal section in the plane of *h–h*, figure 48. This section shows remarkably well the shape of the nepiastic zoœcia. ×17.
FIGURE 39.—Longitudinal section in the plane of *i–i*, figure 48. ×17.
FIGURE 40.—Transverse section in the plane of *a–a*, figure 47. Shows the primary buds (*2*, *3*). ×17.
FIGURE 41.—Transverse section of another specimen in which the primary and secondary buds have a rather unusual arrangement. ×17.
FIGURE 42.—Transverse section in the plane of *a′–a′*, figure 47 (cf. fig. 5). Same specimen as figures 54–58. ×17.
FIGURE 43.—Transverse section in the plane of *b–b*, figure 47. Shows the proximal end of the tertiary bud (cf. fig. 10). ×17.
FIGURE 44.—Probable interpretation of figure 39. Section in the plane of *i–i*, figure 48.
FIGURE 45.—Semidiagrammatic drawing of a longitudinal section (in the plane of *j–j*, fig. 48) of a specimen showing the ancestrula and two zoœcia, probably one of the secondary buds and a tertiary bud (*II*, *III*). ×17.
FIGURE 46.—Semidiagrammatic drawing of a longitudinal section (in the plane of *k–k*, fig. 48) of the ancestrula and protœcium of another specimen. ×17.
FIGURE 47.—Semidiagrammatic drawing from figure 37, to show the position of transverse sections.
FIGURE 48.—Semidiagrammatic drawing from figure 43, to show the position of longitudinal sections.
FIGURE 49.—Ephebastic zoœcia of *Fenestella*. Specimen from Thedford, Ontario. ×17.
FIGURE 50.—Nepiastic zoœcium of *Fenestella*. Specimen from Thedford, Ontario. ×17.
FIGURE 51.—Neanastic zoœcia of *Fenestella*. From the proximal portion of the cone of the same specimen as that shown in figure 38. ×17.
FIGURE 52.—Ephebastic zoœcia of *Fenestella acmea* from the Waldron shale of Tarr Hole, Indiana (cf. fig. 51). ×17.
FIGURE 53.—Ephebastic zoœcia of *Protocrisina exigua* Ulr. from the Trenton limestone of Montreal, Canada (cf. fig. 50). After Ulrich. ×18.
FIGURES 54–58.—Serial sections of a *Fenestella* base. Same specimen as that shown in figure 42, figure 54 being the next section above. Figures 55–58 are successively higher sections. ×17.
FIGURE 59.—Longitudinal section (in the plane of *j–j*, fig. 48) of a *Fenestella* base, showing the shape of the ancestrula most often seen, and three nepiastic zoœcia (*II*, *III*, *z″*). ×17.
FIGURE 60.—Semidiagrammatic drawing from figure 59.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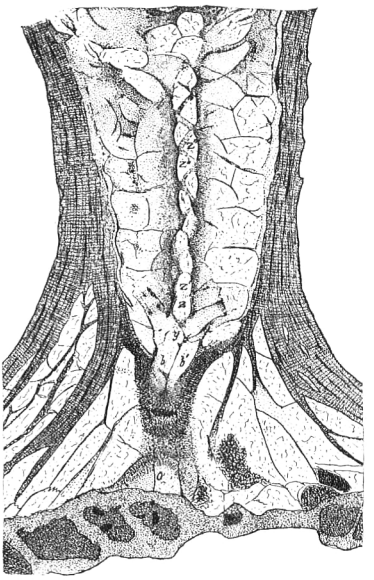

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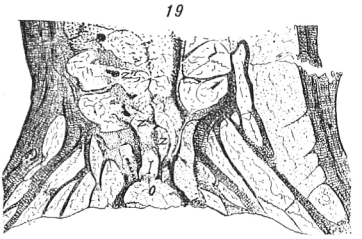

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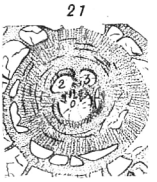

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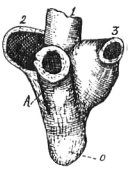

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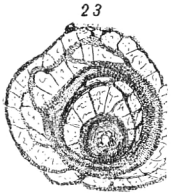

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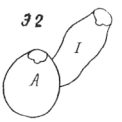

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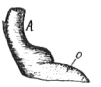

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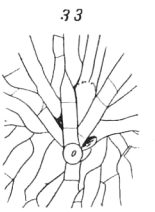

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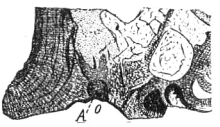

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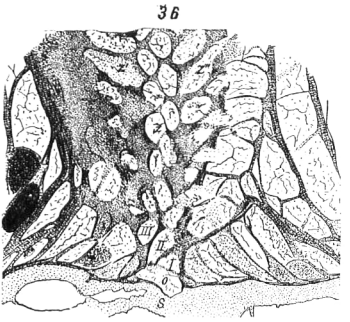
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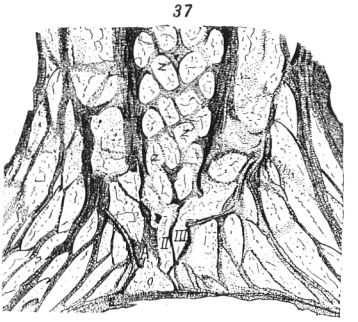
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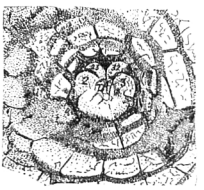
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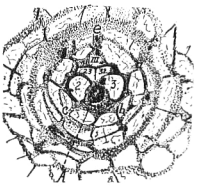
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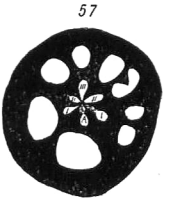
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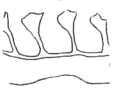
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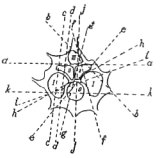
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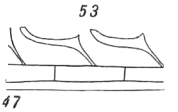
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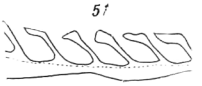
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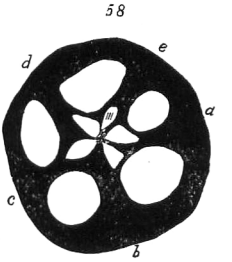
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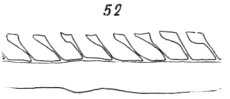
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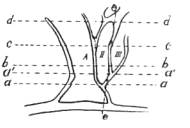
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