TWO NEW ECHINOIDEA, *AULECHINUS* AND *ECTINECHINUS*, AND AN ADULT PLATED HOLOTHURIAN, *EOTHURIA*, FROM THE UPPER ORDOVICIAN OF GIRVAN, SCOTLAND

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INTRODUCTION

This communication contains a description of species belonging to two genera of Echinoidea from the Upper Ordovician (Ashgillian) of Girvan, Scotland, namely, *Aulechinus* Bather and Spencer, and *Ectinechinus* n.g., together with a description of a new genus *Eothuria*, regarded as the first known holothurid, from the same locality.

Some notes are added on the Middle Ordovician echinoid *Myriastiches* and the Silurian genera *Palaeodiscus* and *Echinocystis*.

A short note upon one of the Ordovician genera, *Aulechinus*, was communicated by Spencer to the *Annals and Magazine of Natural History*, immediately after the death of Dr Bather. It contained facts which had been agreed upon by Dr Bather and Spencer, whilst working together. Dr Mortensen was anxious to include some account of the material in his new monograph, and the note was published to help him. At that time only fragments of the forms were known.

Since this note (partly as a consequence of it) very good additional material has been sent by Dr Currie of the Museum of the University of Glasgow. The Misses Gray also have discovered new material. Whole internal moulds are now available, and it is clear that the material formerly described as *Aulechinus* is really composed of two genera. In consequence, considerable modifications are necessary in the original description. The new material makes it possible to give much greater detail of structure, and the conclusions are more revolutionary than previously suspected.

This paper owes much to the careful collecting of the Misses Gray who are continuing the work commenced by their mother. The collections also sent us by Dr Currie, including that of Dr Lamont and of Mr Begg, also contain some very remarkable material.

We must thank Dr Mortensen for his careful criticisms and for early proofs of his new and valuable monograph. Mr L. Bairstow of the British Museum (Natural History) and Dr Brighton of the Sedgwick Museum, Cambridge, have also given important help.

The illustrations are paid for out of a grant from the Percy Sladen Fund, for which we are grateful. The drawings by Mr F. T. Jones show the same care as those which have clarified studies of the Palaeozoic Asterozoa.

Mr Herring, late of the British Museum, and Mr H. Stokes, of the Lowestoft Fisheries Research Station, have taken great pains with the photography.

A most satisfactory feature of these new fossils is the comparative abundance of their remains and their exceedingly good state of preservation. The material is very much easier to study than that from Leintwardine, the locality which previously had given us a very large part of our knowledge of pre-Devonian Echinoidea.

GENERAL

(*a*) Pre-Devonian Echinoidea

Palaeozoic Echinoidea, at any rate in recognizably large fragments, are rare fossils. The great majority of the genera and species are found in the Upper Devonian and Lower Carboniferous, and it is only a few special localities, mostly in Britain, which have yielded specimens from pre-Devonian rocks.

Previous to the discovery of the Girvan material the only pre-Devonian fossils recognized as echinoids were:

1. *Myriastiches* Sollas (1899) from the Llandeilo (Middle Ordovician) possibly of the Welsh Borderland.

One species, *M. gigas* Sollas. At first said by Sollas to be Lower Ludlow; locality unknown. A trilobite on the same slab enables Lake to say that the horizon is Llandeilo (see Bather and Spencer 1934).

2. *Bothriocidaris* Eichwald (1860) (Eichwald 1859, p. 654).

B. pahleni Fr. Schmidt (1874). Jewe beds (Middle Ordovician), Esthland.

Genotype, *B. globulus* Eichwald; *B. archaica* Jackson (1912): both Lyckholm beds (Upper Ordovician), Dago.

3. *Wrightia* Pomel (1869).

One species *W. phillipsiae* (Forbes) 1848. Jackson (1912) refers this to *Maccoya*. Hawkins and Hampton (1927) suggest *Echinocystis*, and give the age as Upper Valentian. Jackson gives the age as Llandovery.

4. *Koninckocidaris* Dollo and Buisseret (1888). The genotype, *K. cotteaui*, is from the Lower Carboniferous of Belgium, but *K. silurica* Jackson (1912) is from the base of the Rochester Shale, Middle Niagaran, Rochester (N.Y.).

5. *Lepidocentrus* ?, lantern only, Wenlock Limestone, Dudley. See Jackson (1912, p. 236).

6. *Echinocystis* (*Echinocystites*) Wyville Thomson (1861). Lower Ludlow (Upper Silurian), Leintwardine, Herefordshire.

One species, *E. pomum* Wyville Thomson.

7. *Palaeodiscus* Salter (1857) found with *Echinocystis*.

One species, *P. ferox* Salter.

To these must now be added:

8. *Aulechinus* Bather and Spencer. Drummuck Group, Ashgillian (= top of Lyckholm), Girvan, Ayrshire, Scotland.

One species, *A. grayae* Bather and Spencer.

9. *Ectinechinus* n.g. from the same beds.

One species, *Ect. lamonti* n.sp.

(*b*) Classification, including diagnosis of new genera

The great majority of authors have sharply distinguished the Palaeozoic Echinoidea from the later forms. M'Coy (1849) established the order Perischoechinoidea for all the then known Palaeozoic echinoids. Their characteristic was that they have more than two series (usually many series) of interambulacral plates, in contradistinction to the known later echinoids, in which the interambulacra consists of only two series of plates. The discovery of *Bothriocidaris* with its single series of interambulacrals necessitated a slight modification of this distinction, but as a whole it was accepted by Zittel who divided the echinoids into two subclasses, Palechinoidea and Euechinoidea.

This classification has been generally adopted. Jackson in his "Phylogeny" maintained it and derived both subclasses from *Bothriocidaris*. The Palechinoidea were the first to appear but they disappeared at the end of the Palaeozoic. The Euechinoidea, except for one genus *Miocidaris* (Lower Carboniferous and Permian), were unknown throughout the Palaeozoic but suddenly appeared in great numbers in the Secondary rocks.

Recently, Mortensen has vigorously attacked these views which, as he points out, divorce the Palaeozoic echinoids from the first Mesozoic echinoids, and compel the latter to hang mysteriously in the air, unconnected with their predecessors in Palaeozoic times. His attack is from two angles:

1. *Bothriocidaris* is not a true echinoid, but should be placed in a new subclass, the Pseudechinoidea.

2. There are several distinct lines of evolution amongst the true Palaeozoic Echinoidea. These lines are:

(*a*) Family Palaeechinidae M'Coy, all of which became extinct. This family Mortensen puts in a new order, the Melonechinoida.

(*b*) Family Archaeocidaridae, leading to the recent Cidaroidea.

(*c*) Family Lepidocentridae, leading to the remaining forms, and particularly nearly related to the Recent Echinothuridae. This relationship is so near that Mortensen unites the Lepidocentridae and the Echinothuridae into one new order, the Lepidocentroida.

We feel that at this stage it is not profitable to attempt any new classification of these extinct Echinoidea, and we have provisionally adopted Mortensen's definitions. We do recognize, however, that the three Ordovician Echinoidea—now known—*Aulechinus*, *Ectinechinus* and *Myriastiches*, differ amongst themselves very considerably in important characters, and that this diversity may later have to find some expression in classification. For the present we are placing the above three genera in the family Lepidocentridae.

ECHINOIDEA

Family **Lepidocentridae** Lovén (emend. Mortensen)

Test spheroidal or flattened. Two to twenty series of ambulacral plates, extending over the peristome to the mouth edge. Pore-pairs uniserial or multiserial. Interambulacra with plates arranged irregularly or in numerous (3–14, and exceptionally in 40) regular columns. Oculars exsert or inset, usually without distinct pores. Genitals with several pores. Spines simple, longitudinally striated. Tubercles noncrenulate. Lantern inclined. Gill notches absent.

From the Ordovician to the Permian of Europe and North America.

Genus **Aulechinus** Bather and Spencer

Generic Characters. Regular lepidocentrids with a pronounced per-radial groove furnished with specialized spines. Lantern frame small, teeth with deep pronounced grooves.

Contains one species, *Aulechinus grayae* Bather and Spencer. Upper Ordovician (Ashgillian) of Girvan, Ayrshire, Scotland. Holotype Brit. Mus. E. 31412.

Genus **Ectinechinus** n.g.

Generic Characters. Test distinctly elongate: mouth anterior: anus posterior, enclosed within apical system: posterior end of test higher than anterior: per-radial groove shallow without per-radial spines: lantern frame conspicuous, teeth with shallow grooves.

Contains one species, *Ectinechinus lamonti* n.sp., from the Starfish Bed of Girvan; Upper Ordovician (Ashgillian). Holotype Glasgow Univ. Hunterian Mus. H.M.E. 1218.

We propose a new order for *Eothuria*.

Order **MEGALOPODA** novum

Characters. Plated holothurians with circumoral valves. Ambulacral pores large, complex. No differentiation of the podia into buccal tentacles and walking feet. Contains one genus and species.

Family Eothuriidae

Characters as for the order.

Genus **Eothuria** n.g.

Characters as for the family.

Eothuria, the third genus from the Girvan rocks described here, is in some ways of even greater interest than the two Echinoidea. It has many features in common with the contemporary Echinoidea but the five teeth of the Echinoid lantern are replaced by a circle of ten circumoral "valves". Jaws if present were very small. With our present views on the classification of the Eleutherozoa it is easiest to regard it as a plated holothurian. Skeletal plates and circumoral valves are found in the young of *Cucumaria* and *Stichopus* and will probably be found in other young holothurids. Its discovery helps to confirm the long-suspected near relationship of the Echinoidea and the Holothuroidea. This form has some characters in common with those of the obscure group of fossil Echinodermata known as the Ophiocistia.

Eothuria beggi. Upper Ordovician (Ashgillian) of Girvan. Holotype. In coll. of Mr Begg, No. 31.

A comparison of the characters of the above three genera is given below.

Aulechinus	*Ectinechinus*	*Eothuria*
1. Test well rounded, base narrow, apex may be pointed.	1. Test superficially like that of a recent irregular heart-shaped sea-urchin; not flexible; elongated in the "primordial plane of von Übisch". Apical system posterior, mouth on the anterior pole.	1. Test elongated, probably shaped like that of *Ectinechinus*.
2. Apical system with only one interradial (genital 2, the madreporite): anus enclosed in the system, elongated and bordered by valvular plates.	2. As in *Aulechinus*.	2. Apical system as in *Aulechinus* except that there are no oculars.
3. Interambulacral plates numerous, in rather irregular columns, with evenly placed, fine, undifferentiated spines, but with no tubercles.	3. As in *Aulechinus*, except fewer spines, very occasionally differentiated.	3. As in *Aulechinus* except greater interspaces between spines.
4. Ambulacra of corona with a well-marked median groove near the apex with four solar curves and one contra-solar curve.	4. Ambulacra of corona without a groove, otherwise as in *Aulechinus*.	4. Ambulacra with per-radial groove slight or absent, as in *Ectinechinus*; with five pronounced, solar curves.
5. Ambulacrals with a row of prominent, larger spines disposed along the per-radius, and two rows of similar spines at each edge of groove.	5. No differentiated spines on the ambulacra.	5. As in *Aulechinus*, except differentiated spines less numerous.
6. Podial pores adjacent to the per-radius.	6. Podial pores often a little distant from the per-radius.	6. As in *Aulechinus*.
7. Podial pores large, incompletely divided, inner pore opens on adoral margin.	7. Podial pores sometimes double, sometimes incompletely divided as in *Aulechinus*; inner pore opens on adoral margin of plate.	7. Pores enclosed in plate, structure complex.
8. One row of ambulacrals around mouth, none on peristome. These ambulacrals seem to obey Lovén's Law.	8. At least three rows of ambulacrals on peristome.	8. A peristome with three rows of ambulacrals.
9. Jaws of lantern very small, teeth flat with deep grooves.	9. Jaws of lantern more elongate than in *Aulechinus*; teeth flat; grooves less distinct than on *Aulechinus*.	9. Jaws, reduced or absent. Mouth surrounded by a circlet of ten plates with ridges and grooves.
10. Inner views of test show upstanding hafts which enclose the radial water vessel.	10. As in *Aulechinus*.	10. Inner hafts reduced to tubercles.
11. Interior pores placed on the thickened shaft.	11. As in *Aulechinus*.	11. Interior pores placed on the tubercles.

(*c*) Conditions of deposit of the Starfish Bed, nature of material and mode of study

The Starfish Bed is a hard, greenish grey, finely grained sandstone, up to a foot and a half thick, containing, though only in the lower six inches, very abundant fossil remains. It seems to represent the material of a sea-bottom, the population of which was preserved in a singular state of completeness. A second thinner sandy layer with similar fauna occurs a few feet above the main Starfish Bed (Lamont 1934, pp. 170, 171). The isolation of beds such as these in a series of comparatively unfossiliferous rocks suggests that exceptional conditions caused the preservation of the fossil bed. It is possible, for example, that a sudden influx of fresh water altered the salinity so seriously as to make the conditions incompatible to the life of marine organisms, and the bed became buried in the mud conveyed by the same water which killed the animals.

Similar bottom-living faunas are being carefully studied by many workers at the present day. Petersen, who led the way in these studies, investigated the faunas of the Danish fiords. He showed that the food income of the bed was derived from the grass *Zostera* which was very abundant.

Both Hawkins and Hampton (1927) and Mortensen (1935) in their studies on Palaeozoic Echinoidea suggest that the echinoids are typical of lagoons. Mortensen (1935, p. 33), speaking of the Palaeechinids, says, "It is clear from their spheroidal form and from the small size of their spines that they cannot have been living in place with rough sea", and p. 49 "...the Lepidocentrids...must, like the Palaeechinids, be supposed to have been living in shallow, quiet lagoons with rich algal vegetation".

The old sea-bottom represented by the Starfish Bed is so crowded with forms that one must presume a very rich supply of food, probably a rich algal vegetation, as suggested by Mortensen. It is also probable that the bed was within a barrier such as described by Hawkins and Hampton (1927, p. 580) formed by "land, sandbank or coral reef, that excluded the disturbance of the open sea". Such isolated areas of "lagoon" water would be peculiarly susceptible to alterations in salinity such as suggested above, especially if situated near the mouth of rivers liable to flood periods.

An interesting feature of the fossils is that many seem to have been preserved in living postures. Thus one of us (Spencer 1919) has shown that several of the Ophiuroidea of the bed still have their arms flexed steeply upwards from the disk as they are flexed in *Amphiura*, when it digs itself into the bottom to-day. Again, some forms show direct adaptation to an environment of mud or fine sand. The small starfish *Girvanaster* had a disk modified for carrying on respiration whilst the animal remained buried in the mud, just as *Astropecten* and its allies live to-day. Observations such as these have encouraged us to endeavour to reconstruct the habits of the new forms described here (see pp. 100, 134).

After the animals were dead almost the whole of the calcium carbonate of their skeletons was leached out. It seems to have been redeposited in the matrix as a cement. We hence find nearly all the specimens as moulds in a hard matrix. This kind of matrix has many advantages, for the imprints can be studied conveniently by means of gutta-percha squeezes. The fine grain of the matrix does not obscure the original details of structure, and the wall of the mould remains firm when the gutta-percha is being withdrawn from an undercut, thus allowing many squeezes to be taken from the same imprint or mould. Should the matrix have been rendered fragile by continued leaching, it can be hardened by one or other of the usual processes. On the other hand, removal of some matrix after the first squeezes have been taken often allows an underlying (or overlying) structure to be studied from successive squeezes. Further, after the animal died, fine mud filled the hollows enclosed by plates. This infilling is left as hard strands which permit important anatomical conclusions to be drawn (see below, p. 114).

The following contractions are used:

All E. numbers are specimens in the British Museum (Natural History). The great majority were collected by Mrs Gray.

Numbers prefixed Gr. are from the collection of the Misses Gray, of Edinburgh, now presented to the British Museum (the Mrs Robert Gray memorial collection).

Numbers prefixed H.M.E. are in the Hunterian Museum of the University of Glasgow. They were collected by Dr Lamont.

Numbers prefixed J.L.B. are in the collection of Mr Begg of Shettleston, Glasgow.

In the following descriptions the main features of *Aulechinus* and *Ectinechinus* are kept together. This allows of a ready comparison and avoids much needless repetition.

DESCRIPTION OF *AULECHINUS GRAYAE* AND *ECTINECHINUS LAMONTI*

Aulechinus grayae

Material

Specimens almost Complete.

Gr. 12. A complete internal mould with the greater part of its counterpart. More than half of the internal mould is free from the matrix, allowing views both of the apical region and of the mouth. The mould is photographed (fig. 1, Pl. 10) and enlarged photographs of the apex are given (fig. 1, Pl. 13). A gutta-percha cast of the external impression is reproduced (fig. 2, Pl. 10). The reconstructions given of the form as a whole (fig. 1) and of the apical system (fig. 3) are based on this specimen.

Gr. 3 and *c*. An internal mould, which is only partially exposed, and a counterpart. The specimen is compressed laterally. Reproduced (fig. 5, Pl. 10).

Specimens showing the Upper Portion of the Test.

E. 31412 *a*, *b* (the holotype). Photographed (fig. 3, Pl. 10; fig. 1, Pl. 14).

Gr. 15. An internal mould, showing a pointed apex, photographed (fig. 4, Pl. 10).

H.M.E. 1200. A portion of an interior mould with a counterpart. The mould shows very well indeed one ambulacrum including the oculars. Photographed (fig. 2, Pl. 13). The counterpart gives very good views of the lateral spine-bunches. Photographed (fig. 3, Pl. 12).

J.L.B. 19. A good external impression, showing grooves and ornament. Photographed (fig. 2, Pl. 12).

H.M.E. 1201. Portions of an internal mould suggesting a pointed apex.

Gr. 1 and *c*. Extremely laterally compressed, external cast gives good views of groove (fig. 5 *C*).

Specimens showing the Basal Area of Test.

Gr. 10 and *c*, H.M.E. 1202 and *c*, H.M.E. 1203 and *c*. This last specimen gives very good views both of peristome and lantern almost in place. Photographs given (figs. 1 and 2, Pl. 15) and drawings (fig. 11).

H.M.E. 1202 and *c*. Has been subject to vertical compression, and in parts displaced. Portions, however, give good detail (figs. 3, 4, Pl. 15).

Specimens showing the Lateral Area of the Test.

E. 31410 *a*, *b*. External impression, cast photographed (fig. 6, Pl. 10) and a counterpart.

H.M.E. 1204. External impression, cast photographed (fig. 1, Pl. 12) drawn (fig. 5 D).

Other Fragments.

E. 31406 *a*, *b* (E. 31406 *a* photographed, fig. 2, Pl. 14), E. 31418 photographed (fig. 3, Pl. 14), E. 31407, E. 31415, E. 31416.

D. 216 and *c* (accompanied by the starfish *Cnemidactis*).

Gr. 4, 5, 6, 19, 20.

J.L.B. 18, 23, 27, 28.

H.M.E. 1205, 1206, 1208, 1211, 1212, 1213 and *c*, 1213 (internal mould used in making model, figs. 9 A), 1216, 1217.

Ectinechinus lamonti

Material

Specimens almost Complete.

H.M.E. 1218 (holotype). An excellent mould of the interior specially well preserved as regards detail on the dorsal surface; photographed (figs. 1, 2, Pl. 11); enlarged photograph of apical system (fig. 3, Pl. 13); also used as basis of reconstruction (fig. 2 A).

Specimens showing a Considerable Portion of the Upper Half of Test.

H.M.E. 1219. A distorted internal mould (larger specimen of two on same slab).

E. 31411 *a*, *b* (larger specimen of two on same slab).

H.M.E. 1220. An internal mould partially calcified; photographed (fig. 4, Pl. 13).

J.L.B. 26. Smallest specimen photographed (fig. 4, Pl. 11).

Specimens showing Lantern.

E. 31405. An external impression; casts from this photographed (fig. 8, Pl. 11); used in drawing fig. 6 and in the reconstruction (fig. 10 B).

E. 31408. An internal mould; photographed (fig. 6, Pl. 11).

E. 31414 *a*, *b*. A cast of the external impression; photographed (fig. 5, Pl. 12; fig. 5, Pl. 15).

H.M.E. 1219. Smaller specimen of two on same slab.
H.M.E. 1221. Used in making fig. 10 B.
J.L.B. 26.

Large Fragments.

E. 31411 *a*, *b*. Smaller specimen of two on same slab.

Gr. 11. The greater part of the internal mould of the base and its counterpart; photographed (fig. 3, Pl. 11).

H.M.E. 1223 *a*. Two internal moulds; photographed (fig. 7, Pl. 11). Its counterpart is H.M.E. 1223 *b*.

Other Fragments.

E. 12138.
E. 31403 *a*, *b*.
E. 31420.
E. 31421 *a*, *b*.
Gr. 2 and *c*, 8, 9, 14 and *c*, 17, 18.
J.L.B. 18, 21 (fig. 4, Pl. 12), 22 (fig. 6, Pl. 12), 23, 25, 29.

The shape of the test and mode of life

Aulechinus (fig. 1)

The only specimen preserved in its entirety is Gr. 12, which seems to be a complete internal mould, more than half of which is free from matrix. This specimen has a counterpart, a mould of the external surface. The internal mould is photographed (fig. 1, Pl. 10). A cast of the external impression is photographed (fig. 2, Pl. 10). The reconstruction given in fig. 1 is based on this specimen.

The photographs and figure show that *Aulechinus* is a regular echinoid with mouth and apex at opposite poles. It was well rounded, almost orange shaped, with narrow apical and oral poles. The apical pole here is flat, but pointed apices are shown both by Gr. 15 (fig. 4, Pl. 10) and A.L. 9. It would seem as if *Aulechinus* when alive could point its apex somewhat as starfish such as *Astropecten* can. In this starfish we know that this "pointing" is for respiratory purposes whilst the form is lying almost buried in the sand of the sea-bottom, but with a raised apical region exposed freely to the oxygen of the sea water. If we assume that *Aulechinus* also rested from time to time under the fine sand of the bottom it would help to explain this pointing of the apex seen in the fossil forms.

The habit may be due to dislike of light. It is not quite identical with the very definite habit of burrowing found in modern heart-urchins and possibly in *Ectinechinus* (p. 134) and *Eothuria* (p. 129).

The construction of a burrow requires that the animal should be able to make the walls firm by an agglutinating secretion (v. Uexkull, 1921, p. 97).

Gr. 12 has a height of 35 mm., a base of 15 mm. and a maximum distance between the per-radii of 24 mm.

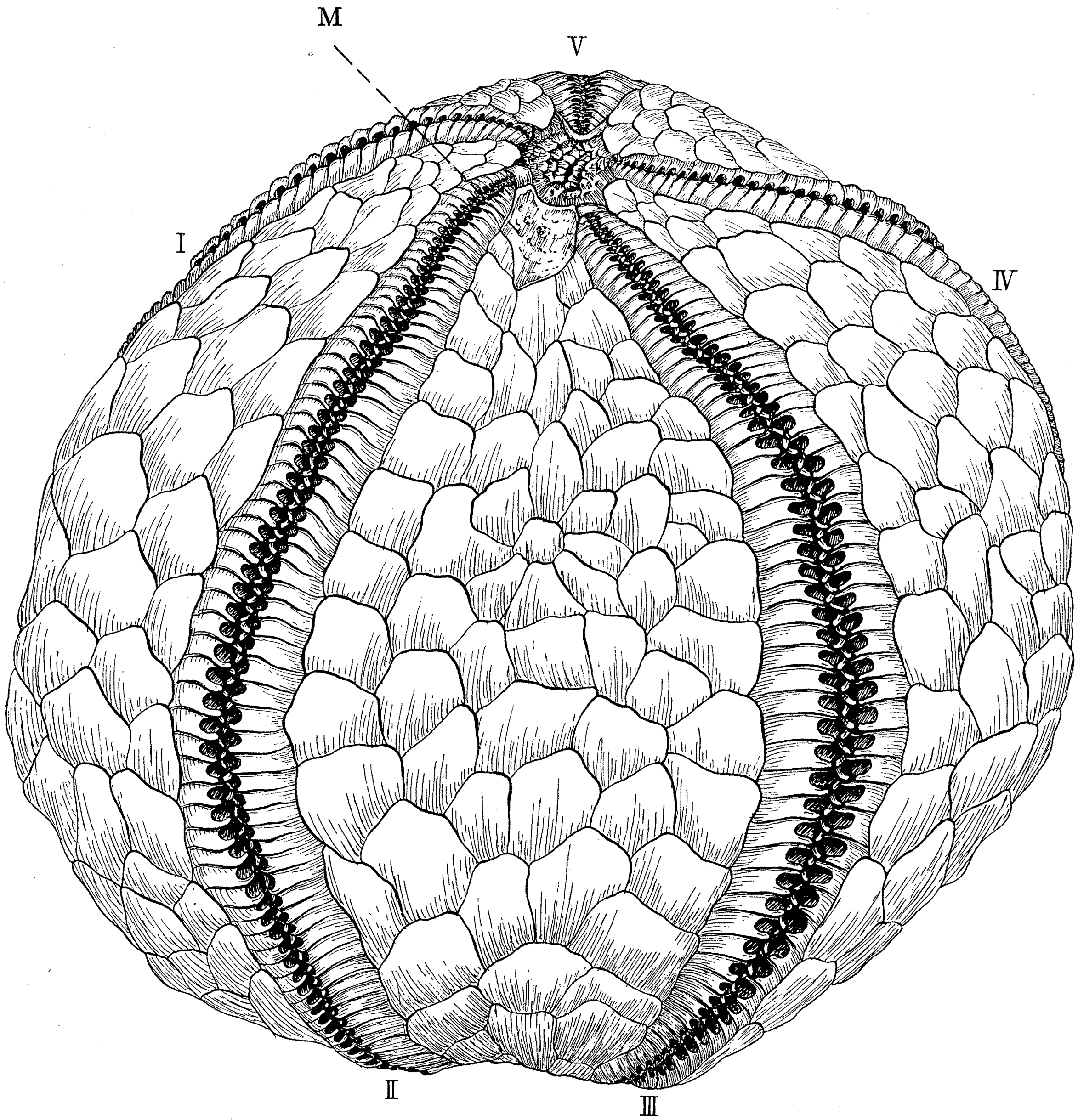

FIG. 1. *Aulechinus grayae.* Lateral view reconstructed. I–V, the ambulacra. (The recognized method of numbering the radii and interradii is to consider the madreporite as lying between radii II and III.) *M.* madreporite-genital. From Gr. 12, coll. the Misses Gray. ×4.

Ectinechinus (figs. 2 A, 2 B)

The test shape is of great interest.

1. The test is elongate with mouth and anus at opposite extremities. This is somewhat surprising. All previously known elongate urchins have been derived by pro-

found modification from regular sea-urchins. One would not have expected therefore the presence of elongate urchins at such an early period.

2. The plane of elongation is not in correspondence with Lovén's plane—the plane of elongation of Recent urchins.

There is no doubt that this is an elongate sea urchin. The remarkable mould photographed (figs. 1, 2, Pl. 11) and drawn (figs. 2A and 2B) shows this very clearly. In dorsal view it is approximately bilaterally symmetrical with the apex at one pole (posterior) and the mouth at the other (anterior pole). The posterior region is rounded and the anterior pointed. The base is flattened. In profile the maximum height is in the region of the apical system. Its dimensions are—maximum length 37 mm., maximum breadth 27 mm., maximum height 18 mm. The smallest specimen, J.L.B. 26 (fig. 4, Pl. 11), which is not quite perfect, seems to have been about half this size. The largest specimen, H.M.E. 1219, suggests a maximum length of 45 mm. The form is much more variable in size than *Aulechinus grayae*, probably indicating individuals of different ages.

Not only is the general form but also, at first sight, the disposition of the ambulacra, is like that of a Recent heart-urchin. From the apical system three ambulacra run forwards and two ambulacra backwards. There appears, therefore, to be a typical trivium and bivium. When, however, we come to analyse these rays we find that the bivium and trivium of *Ectinechinus* appear to differ profoundly from those of the Recent heart-urchin. Fortunately all the rays can be appropriately numbered from the known position of genital 2 (the madreporite-genital), and are lettered in the reconstruction (figs. 2A, 2B).

In *Echinocardium* the dorsal trivium is formed by II, III and IV. III is median, and II and IV lie almost symmetrically on each side of it. In *Ectinechinus* the dorsal trivium is formed by I, II, and III. II is median, and I and III on each side of it show considerable asymmetry in arrangement. Far more ambulacral plates can be seen of ambulacrum I than of ambulacrum III.

Turning to the ventral surface, in *Echinocardium* the trivium is formed by II, III and IV, that is, the same ambulacra which form the dorsal trivium. In *Ectinechinus* the trivium is formed by III, IV and V, that is, by quite different ambulacra to those which form the dorsal trivium. III and V are not symmetrically arranged about IV but much more of V is seen than of III.

Lovén's plane and the plane of elongation of *Ectinechinus** are illustrated diagrammatically (fig. 10).

The apical system of both genera (fig. 3)

The structure of the apical system is similar in both genera, and is of great importance. The individual ossicles are shown remarkably clearly, far more clearly than in the great majority of Palaeozoic Echinoidea. Their disposition is different

* It follows a plane called by von Übisch (1913, 1927) the primordial plane of symmetry.

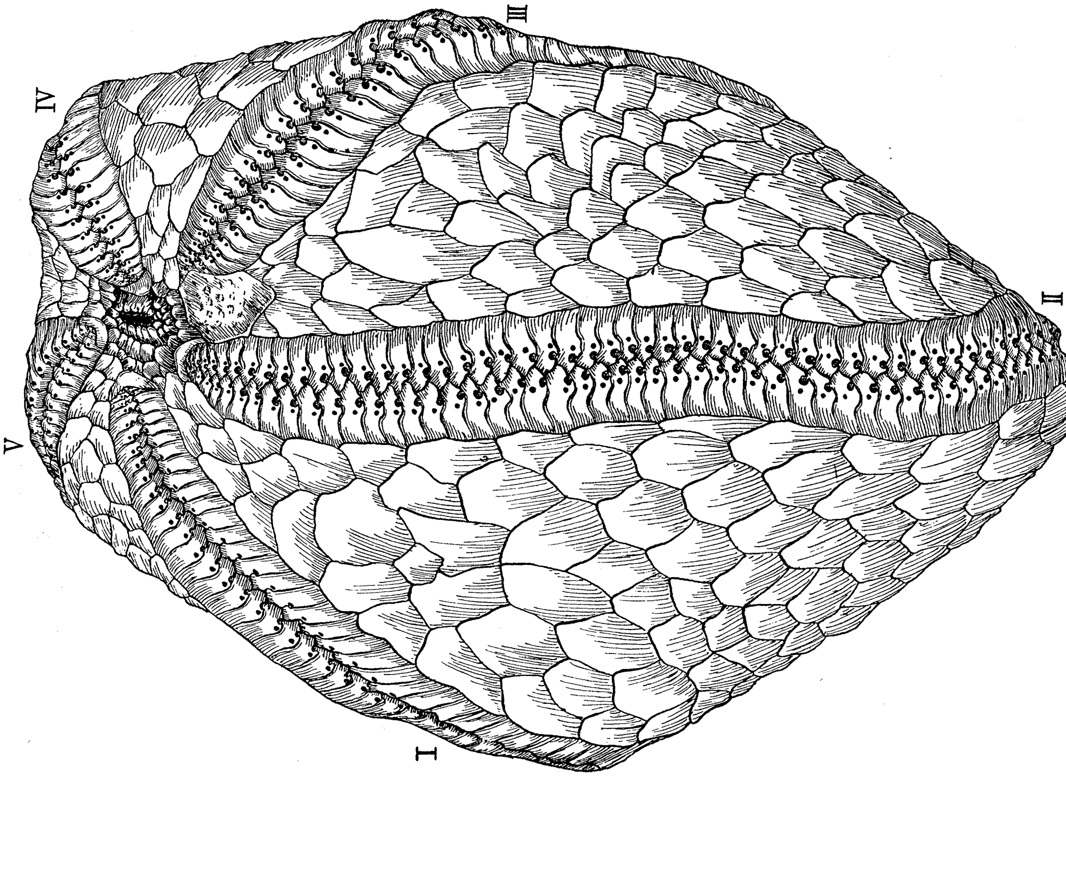

Fig. 2A. *Ectinechinus lamonti.* Dorsal view reconstructed, lettering as in fig. 1. From coll. Univ. Mus. Glasgow, coll. Lamont, A.L. 10. ×4.

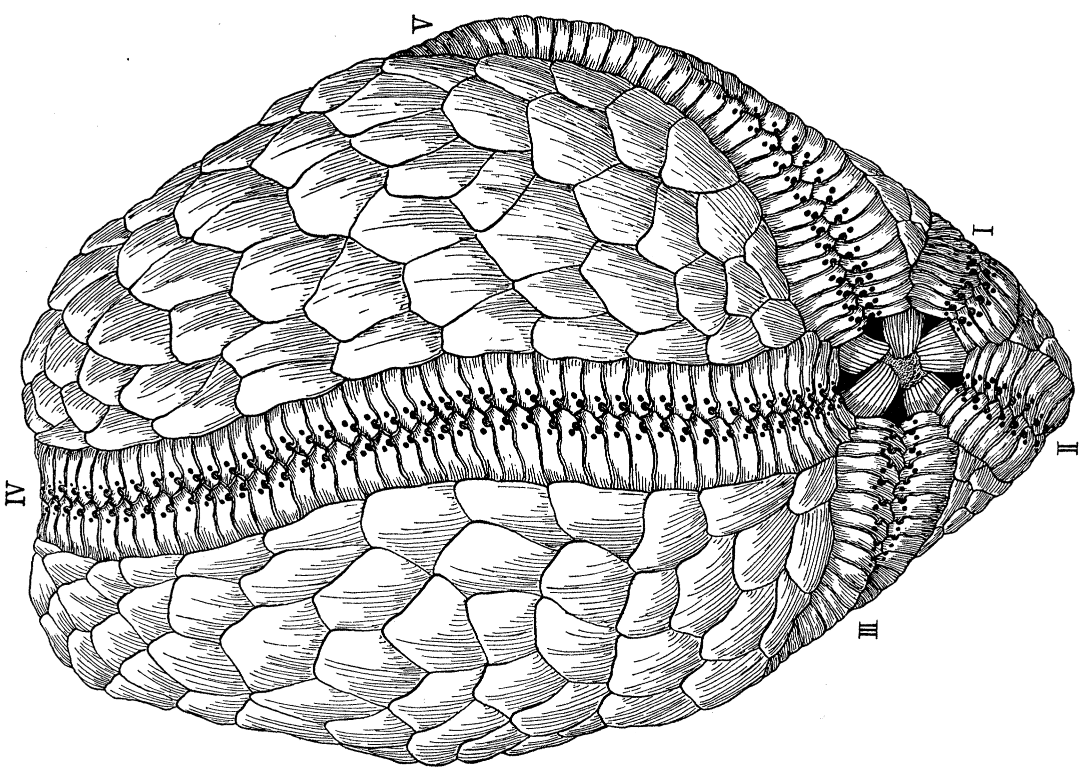

Fig. 2B. *Ectinechinus lamonti.* Ventral view reconstructed. From same specimen as in fig. 2A. ×4.

from that hitherto described in any echinoid, Recent or fossil, although it seems to be connected with unexplained features in the apical systems of the two other early Palaeozoic genera, namely the Silurian *Echinocystis* and *Palaeodiscus*. There is a very close resemblance to the apical system of *Eothuria*, the plated holothurian described later in this paper.

Altogether we must regard the system as being very primitive.

The important features are:

1. The large periproct with many plates.
2. The elongate, large anal pyramid surrounded by valvular plates.
3. The incomplete oculo-genital ring, which has only one differentiated interradial plate—the madreporite-genital.

Two specimens, one of *Aulechinus* and one of *Ectinechinus*, show the whole of the apical system very well indeed. The specimen of *Ectinechinus* (H.M.E. 1218, fig. 3, Pl. 13) is an internal mould which shows impressions of the whole of the plates in a very perfect state. That of *Aulechinus* (Gr. 12 *c*, fig. 1, Pl. 13) is not quite so well preserved, but the mould and counterpart studied together give additional detail of important plates. Other specimens show parts of the system. H.M.E. 1201 gives exceedingly good views of the ocular in relation to the water vessels (fig. 4).

The Periproct

The periproctal plates are numerous. They are smaller than the interambulacrals, and those of *Aulechinus* are also undoubtedly thinner. Evidence has been given already that in this genus the thin periproctal region was flexible, and could be either flattened or conical. Generally the plates are irregularly arranged except along a distinct mound. Here the plates are in rows, which are especially well marked in *Ectinechinus*. There can be no doubt that the periproct contains a distinct, elongated, anal pyramid with a valvular opening, placed somewhat excentrically.

At one time the ancestral condition in an echinoderm was supposed to be quite different from this. Young *Echinus* and young *Stronglyocentrus* show a single plate, the sur-anal, covering the entire periproct. Such a plate, surrounded by a complete oculo-genital ring, gave a radiately symmetrical system reminiscent of the crinoid calyx, and was supposed to be homologous with it. Mortensen has shown (1927, pp. 376–7) that, although in the very young stages of the cidaroids there was only a single sur-anal plate, very soon "several more plates appear, so that the periproct is from the first covered by 5 plates, of unequal size and not placed regularly in the corners between the five genital plates". Mortensen's figures also show an excentric anus, although as yet no developmental stages show exactly the same characters as those observable in *Aulechinus* and *Ectinechinus*.

The isolated anal pyramid is a new feature for Echinoidea, and it has additional significance since *Eothuria*, which we regard as a primitive holothurian, has a similar

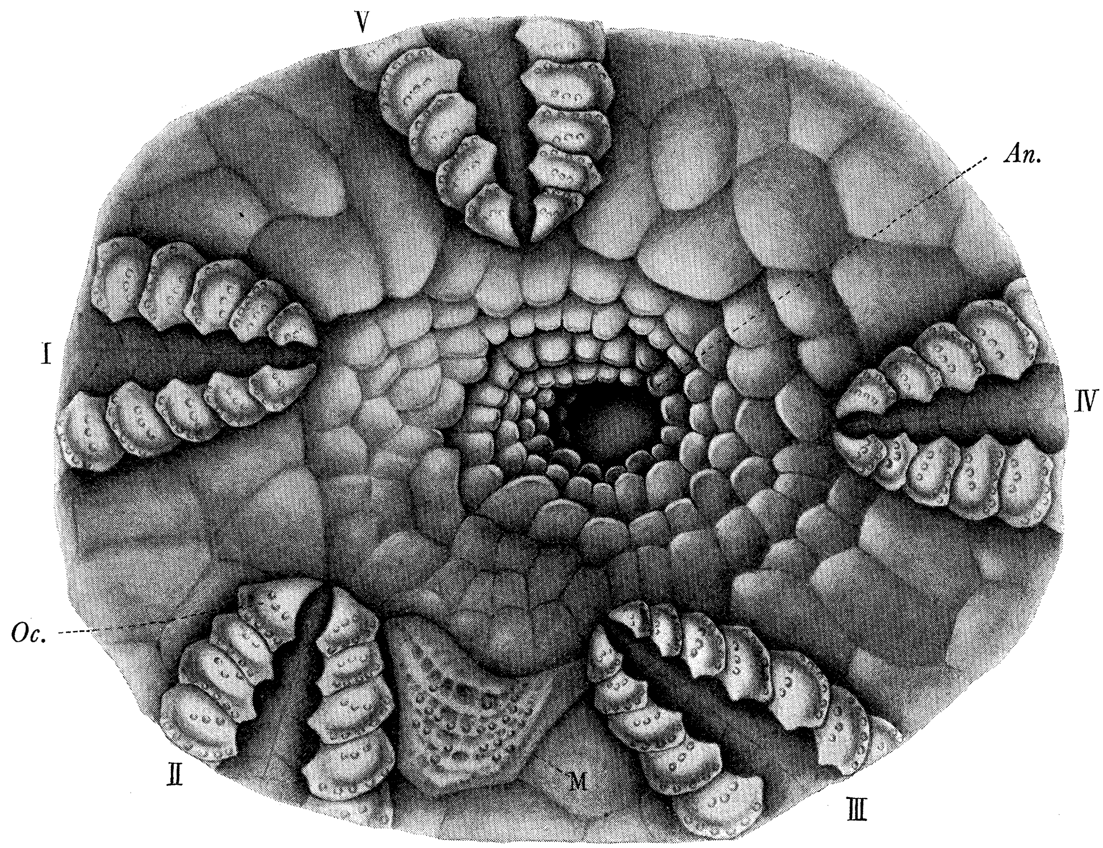

FIG. 3. *Aulechinus grayae*. Enlarged view of apical system slightly reconstructed from Gr. 12. × 12. *An.* = anus; *M.* madreporite-genital; *Oc.* ocular.

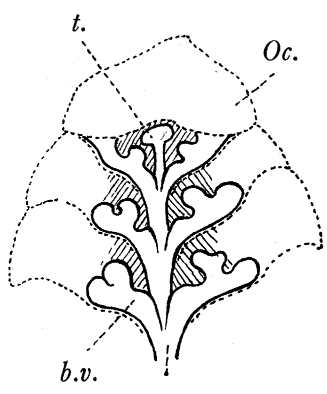

FIG. 4. *Aulechinus grayae*. Inner view of apical end of an ambulacral. The oculars and succeeding ambulacrals are dotted and the water vessels outlined in black. From coll. Glasgow Univ. Mus. No. H.M.E. 1200; *b.v.* branch water vessels; *Oc.* ocular; *r.v.* radial vessel; *t.* termination of radial vessel.

pyramid, with anal valves even larger and quite unmistakable in character. Such anal valves are known from the Cystidea, many groups having them very characteristically.

Amongst modern forms the closest parallel to this ancient periproctal structure is shown by *Echinocardium*. Miss Gordon (1926 *b*, p. 300) shows that "soon after metamorphosis a ring of plates (on an average 9–11 in number) is laid down around the anus and within the circle of five genital plates—no one plate corresponds to the suranal, for in the early stages all are of equal importance, and they appear practically simultaneously".

The narrow elongate plates shown to surround the anus in Miss Gordon's figures, e.g. fig. 15, are very similar indeed to those of *Ectinechinus*.

The oculo-genital ring and the madreporite-genital

The oculo-genital ring is incomplete. There are five oculars, but only one genital. This latter is large and readily distinguished from an interambulacral by its regular breast-plate-shaped form and by its shallow oblong pits arranged in rows. It is especially thick in *Ectinechinus* where internal moulds of the plate show a lobed pore (fig. 3, Pl. 13) representing the attachment of one or more ducts. Dr Mortensen, who has seen this material, suggested to us that the plate is really a madreporite-genital (genital 2). He has never seen in echinoids a true madreporite pore which was lobed. On this view the genital organs have not acquired the pentamerous symmetry characteristic of later Echinoidea, and the genital organs in that case are in the same condition as in recent holothurians; moreover, it is significant that *Eothuria* (see p. 129) has the same arrangement. The plates which fill in the remaining four spaces between the oculars are very similar in general form to those of the interambulacrals.

The oculars are semi-lunar plates. A very good internal impression of one is photographed (fig. 2, Pl. 13) and drawn (fig. 4). Both show the relationship of the ocular to the water system. The radial vessel seems to terminate almost abruptly at the edge of the ocular, where it can be seen giving off two side branches to the neighbouring pair of ambulacrals. It is of course possible that there was a terminal tentacle reaching beyond this abrupt ending since the strands representing the water vessel were only preserved where they pass through the plate. The greater part of the terminal tentacle would lie outside the plate and not be preserved. It is significant that the ocular, in exterior view, is seen to have a median groove.* It is well known that a similarly placed groove houses a terminal tentacle in starfish.

The only pre-Devonian echinoid whose apical system is at all definitely known is *Echinocystis*. The arrangement here, as figured by Hawkins and Hampton (1927), is very much as in *Aulechinus*. These authors could distinguish the oculars and one large

* Young *Echinus miliaris* and young *Echinus esculentus* have long, unpaired tentacles which afterwards become surrounded by the ocular plates, and are ultimately reduced to small ocular knobs.

interradial pustulose plate, the madreporite. They suggested "by analogy with comparable Perischoechinoids, the genitals may have been slender arcuate plates the non-detection of which is not surprising".

Neither *Aulechinus* nor *Ectinechinus* show any sign of such slender, arcuate plates, and there is no doubt that Hawkins and Hampton were considerably influenced in their view by their firm agreement with R. T. Jackson (1929, p. 500), who holds that it is typical of *Bothriocidaris* and most other Palaeozoic Echini (*Lovenechinus*, *Melonechinus*, *Perischocidaris et al.*), that oculars and genitals meet the periproct in a continuous ring of plates.

We are giving a photograph (fig. 5, Pl. 13) of a squeeze of a part of the apical system of *Echinocystis* from a specimen in the British Museum (Natural History). The detail, as can be seen, is quite good. The large madreporite-genital is very conspicuous. This was described by Hawkins and Hampton as follows:

"The madreporite is one of the most striking and anomalous features in *Echinocystis*. Apart from the pyramids, it is by far the most massive plate in the test. In shape it is a rounded hexagon, and its surface is abundantly papillate and spongy with pores. We cannot decide whether it is a complete ossicle in itself, or a local thickening of a plate with thinner edges; but concerning its position there is no question. All authors agree as to its interradial position, near the 'meeting' of the ambulacra. We find it to be within the ring indicated by the ocular plates (though projecting a little beyond it; and we see no reason to doubt that it is either on, or replacing, genital 2."

The "pores" described by these authors seem to be minute pits which, when the photograph is examined by a hand lens, are arranged in hexagonal patterns. Possibly the hexagon corresponds to the shallow pits seen on the madreporite-genital of *Aulechinus*. There is no trace of a large external pore. The single madreporite-genital is the only differentiated interradial plate near the ambulacral extremities. Everywhere else plates similar to interambulacrals, each plate with a conspicuous raised perforated tubercle, pass between the ambulacrals.

Miss Gordon (1926 *a*, *b*, and 1929) has succeeded in tracing the origin of the genitals in *Echinus*, *Arbacia*, *Echinocardium* and *Echinarachnius*. They do not all arise at once, and the order of succession is different in each species examined. Genital 2, however, arises very early. It is the first to appear in three of the genera and the second to appear in *Echinarachnius*. It is to be expected that an ossicle connected with the stone canal should appear at an early stage.

The excentric position of the apical system of *Ectinechinus* helps to elucidate certain peculiar appearances in *Palaeodiscus*. One of us some years ago (Spencer 1904, p. 34) pointed out that the anus of this genus was excentric and surrounded by a number of small plates. Hawkins and Hampton (1927, p. 593) state, "our opinion is that the structure is a true apical system enclosing the periproct, that it is definitely on the adapical surface, and that its polar position is indicated and excentricity not proved". Their drawing (fig. 6 B), however, is not like any apical system known. The facts seem to be that these authors are right in saying that the structure is on the adapical surface, but wrong in describing it either as a complete apical system or as polar in position. The small plates are probably only a part of the apical system analogous with the valve plates of *Ectinechinus* and *Aulechinus*. *Palaeodiscus* may have had the same "irregularity" as *Ectinechinus*.

The Corona of both Genera

The corona in both genera consists of relatively wide interambulacra and narrow ambulacra. The general imbrication agrees with that of other thin-walled Palaeozoic Echinoidea, that is, the interambulacrals overlap each other by their adapical and adradial margins, the ambulacrals by their adoral margins. It is of interest to note that Asterozoa with flexible skeletons obey the same rules. Laterally the interambulacrals, as is usual in the Lepidocentridae, overlap the ambulacrals.

The Ambulacra

External Features (fig. 5)

The ambulacra of both *Aulechinus* and *Ectinechinus* are simple, that is, they are composed of two rows of primary plates which meet alternately across the per-radial line. This always has been regarded as the most primitive arrangement among echinoids.

In addition, there are new features of great importance:

1. The ambulacrals are not fused along the per-radial line but are loosely joined and show marked overlap.

2. The pores are placed very near to the per-radial line in both genera.

3. The pores are undivided on all plates of *Aulechinus* and some plates of *Ectinechinus*.

4. Deep grooves are present along the per-radii of *Aulechinus*.

All these features are doubtless significant in echinoid ancestry. Other features include spaced groups of large differentiated spines bordering the groove and along the per-radii of *Aulechinus*, and the general shape of the ambulacrals of both genera.

1. *The Ambulacrals and the per-radial line.*

The two columns of plates in recent Echinoidea and in the great majority of fossil Echinoidea (including *Bothriocidaris*) are fused along the per-radial line to show a simple zig-zag suture. In *Aulechinus*, *Ectinechinus* (and *Eothuria*, see p. 130) there is no fusion. In its place there is a somewhat complicated overlap shown in figs. 5 A, B. Each ambulacral has contact with two of its opposing neighbours. For instance, an ambulacral on the left-hand side dips under the right-hand member lying aborally to it and overlaps its right-hand adoral neighbour.

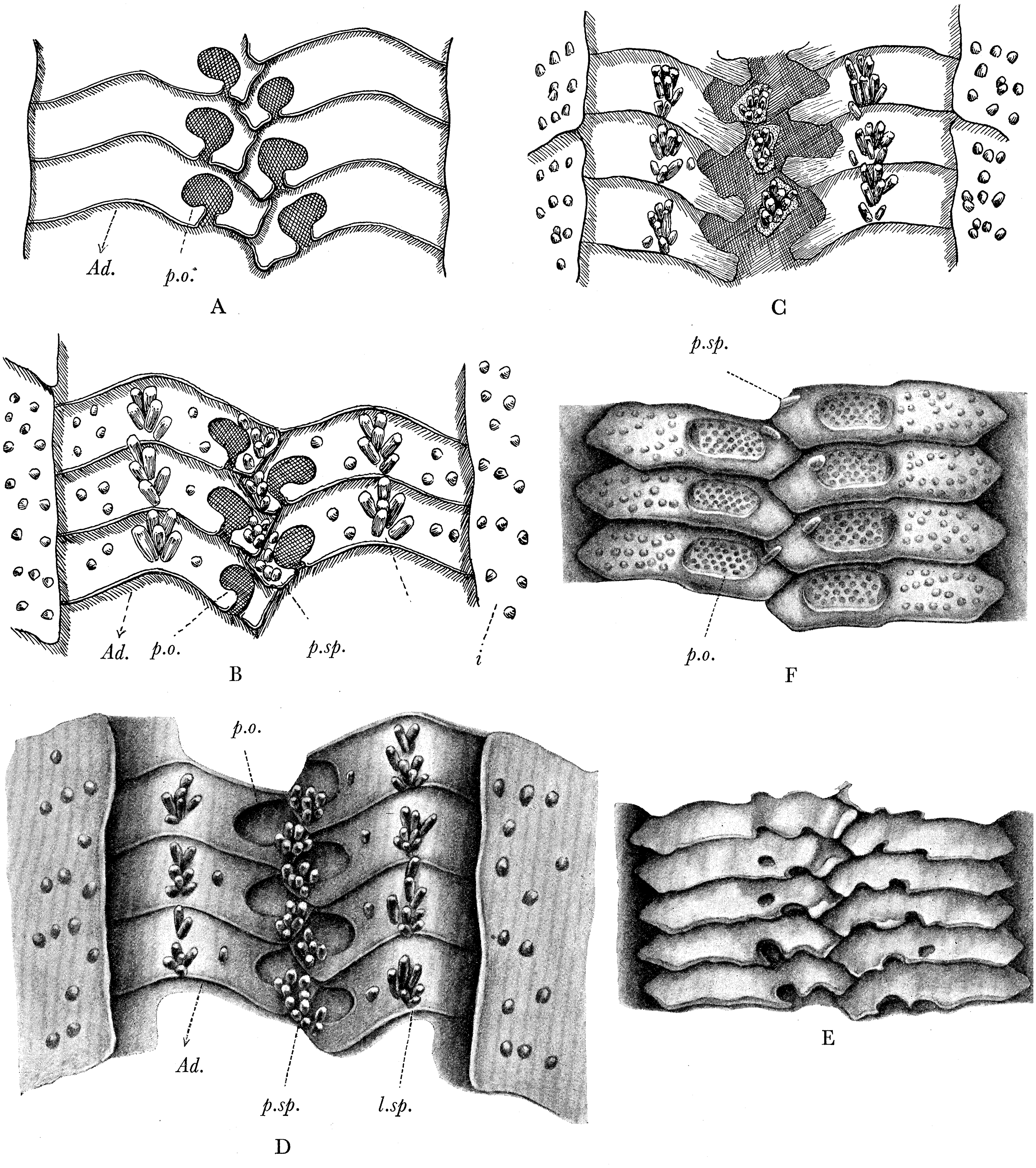

FIG. 5. External views of ambulacralia of *Aulechinus, Ectinechinus* and *Eothuria.* A, outline drawing from *Aulechinus* to show overlaps (× 16); B, outline drawings of *Aulechinus* to show details of ornament; C, outline drawing of ambulacrals of crushed *Aulechinus* to show per-radial edges of plates broken away and lying in series along the middle line (Gr. 1, × 16); D, wash drawing from *Aulechinus* to show ambulacrals and neighbouring interambulacrals (H.M.E. 1204, × 16); E, wash drawing of ambulacrals near peristome of *Ectinechinus* (E. 31405, × 12); F, wash drawing of ambulacrals of *Eothuria* (E. 27003, × 9); *Ad.* adoral overlap; *i.* interambulacral; *l.sp.* lateral spine groups; *p.sp.* per-radial spine groups; *p.o.* ambulacral pores.

We know from embryology that there was an open groove in the ancestral form and that such a groove was closed by growth from each side of the groove directed per-radially. The overlap is produced by these growths (see also *Eothuria*, p. 130). It may have been a device to combine strength with flexibility. In both sea-urchins and starfish overlap of plates rather than fusion of adjacent plates is used frequently in early forms, as a mode of giving strength to the skeleton.

A somewhat curious appearance of the ambulacrals is seen on some specimens of *Aulechinus* (fig. 5 C). The per-radius seems to be occupied by a single series of plates shaped somewhat like the ventro-lateralia of the Ophiuroidea. The explanation is quite simple. These are the per-radial edges which have broken away by compression after death, the large pores of *Aulechinus* making a line of weakness just exterior to the overlaps.

2. *Pore position.*

The pores of *Aulechinus* are very near to the per-radial lines. Those of *Ectinechinus* (fig. 5 E) are placed just at the edges of the groove but well within the inner half of the ambulacral. Jackson stated (1912, p. 57): "In all Palaeozoic types and most modern Echini, the pores lie either in the middle of the ambulacral plate, which is rare, or nearer the next adjacent interambulacrum than the middle of the plate, which is the usual position. In no Palaeozoic type do they lie nearer the median suture of the ambulacrum than the middle of the ambulacral plate." In 1927, however, Hawkins and Hampton (p. 595, fig. 7) figured the pores of *Palaeodiscus* at one-fifth of the width of the ambulacral from the per-radius, but made no comment on this. The position was already manifest in Sollas (1899, fig. 10). Jackson (1912, p. 251) said of *Palaeodiscus*, "The pore-pairs are about in the middle of the plates...as shown in my figures (Pl. 18, figs. 1–5)"; his figures, however, are not absolutely consistent on this point, and an apparent approach to the middle may be due to overlap by the interambulacrals as in Hawkins and Hampton (1927, fig. 7 A) which diminishes the apparent breadth of the ambulacrals. The true position of the pores of *Palaeodiscus* is re-figured here (fig. 7 F, p. 113).

3. *Pore shape.*

The pores of *Aulechinus* differ considerably from those of any other echinoid. Instead of the typical double pore separated by a distinct bridge there is one large pore enclosed except for an adorally situated narrow neck (fig. 5 A).

Some of the pores of *Ectinechinus* seem very similar, but the majority, especially those near the mouth, are distinctly divided by a bridge (fig. 5 E; fig. 5, Pl. 12).

Incompletely divided pores have not hitherto been described for adult echinoids, although they are found in young stages of plate development. Miss Gordon's figures (1926*a*, p. 289, Text-fig. 20, reproduced here, fig. 6) illustrate these stages. Her description of the first stages (figs. *a*, *b*) is as follows: "Each plate is laid down on the aboral side of a developing tube-foot, the latter being bounded adorally by the preceding plate. The pore which is at first simple, elongates obliquely, the plate meanwhile undergoing resorption to accommodate the enlarging tube foot." This may be said to represent the *Aulechinus* stage.

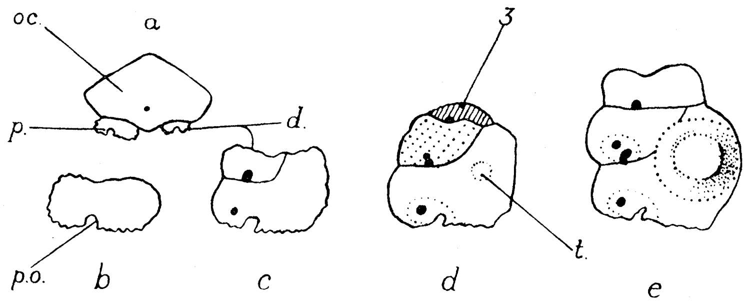

FIG. 6. The formation of an "Echinoid" triad. (*a*), inner view of an ocular plate (*oc.*) to show where the additional ambulacral plates are laid down. (*b*), an isolated primary plate the first of a triad. (*c*), the first primary together with the demiplate. (*d*), a triad just being completed, the third plate (3) is still very small. (*e*), a triad when completed. *p.* primary plate; *d.* demiplate; *p.o.* pore; *t.* first hint of the primary tubercle.

The double pore of *Ectinechinus* resembles the next stage in her developmental series (cf. figs. *c–e*). The pore is now set with its longer axis at a much more oblique angle to the per-radial line, the outer half is completely enclosed, and the inner half, corresponding to the neck of the *Aulechinus* pore, still opens on the adoral edge of the plate.

Miss Gordon's description is: "Soon calcareous processes grow out from either side cutting the single pore into two distinct pores. In course of time each pair so formed becomes surrounded by a definite peripodium and represents a single tube foot. The suture always passes through the lower border of the peripodium so that, when the triads are separated, the lower pore in the oral plate is incomplete." Hence in Miss Gordon's account the inner adoral pore may never be enclosed. Similar unenclosed adoral members are figured by her (1929, Text-figs. 6, 8) in the developing plates of *Arbacia*. It is obviously a frequent condition in Recent Echinoidea·

A similar incomplete condition of the inner pores on the ambulacrals of the adoral (not peristomial) region of *Palaeodiscus* was described by one of us (Spencer 1904, p. 34, fig. 2). The word "enclosed" in that passage was meant to imply only that the podium emerged within the limits of the plate and not between the ambulacrals, as had been maintained by Gregory (1897, p. 129, fig. 4). In this matter he was confirming Sollas (1899, p. 705), whose figs. 10 and 11 seem to indicate that the adoral pores of a pore-pair were incomplete or unenclosed.

The possibility that the early Echinoidea could have pores partially unenclosed by the plate has been regarded as being inconsistent with the theory of *Bothriocidaris* ancestry, and has been attacked. Hawkins and Hampton (1927, p. 594) disagree no less with Sollas and with Spencer than with Gregory. They maintain that all the numerous pores observed by them are double, and that when the area is radially stretched they are "Much farther away from the transverse sutures than in most Regular Euechinoids; they seem contiguous to, or coincide with, those sutures only when imbrication has telescoped the area".

We are afraid that we cannot see how any amount of telescoping could obscure a feature on the adoral margin of an ambulacral when seen from outside, since that margin would remain visible until the whole plate was covered. Hawkins and Hampton's fig. 7 B, which shows this result of imbrication, is an interior view. Dr Bather, in the notes prepared by him for this paper, remarks in respect of *Palaeodiscus* that he studied the specimens in the Oxford University Museum, and made drawings of various stages in the development of pores in *P. ferox*. These show a gradation from a slight scooping out of the margin, such as might have been seen by Gregory, through gradual increases of the scooping, up to a condition resembling that shown in Sollas's fig. 10; thence, through the rather more advanced stage in Sollas's fig. 11 and Spencer's fig. 2, up to a regular peripodium with a distinct septum.

Reasons for the transition from a single pore to a double pore are given on p. 118.

4. *Per-radial Groove.*

Along the greater part of each per-radius of *Aulechinus* is a marked groove shown very well in fig. 1, Pl. 10. The dip of the groove extends about half-way along the ambulacral plates. This feature is not to be seen to such an extent in any other Echinoid genus, although a slight groove has been noted in *Palaeodiscus* and *Echinocystis* (Hawkins and Hampton 1927, p. 587, fig. 4). The groove has large, flat spines along its middle and edges. They may have been ciliated, like fasciolar spines of Recent urchins which cause respiratory currents. If the flat spines of *Aulechinus* have the same function, we can understand also the function of the groove, for this latter would direct such respiratory streams over and around the tube feet and so would aid respiration during the time the animal was partially buried (see also p. 100).

5. *Ambulacral Shape.*

Another feature of the primitive echinoid ambulacral is shown very clearly by *Aulechinus*, namely, the shape of the individual ambulacrals (figs. 5 *a*, 5 *b*). Each is not a simple parallelogram, but is bent about the middle, so that the adoral margin is convex and the adapical margin concave. The sharpest bend of the curve is at the edge of the per-radial groove. The ambulacra of *Ectinechinus* and *Eothuria* are similarly shaped, although not quite so distinctly. Such a shape may persist as late as the Upper Silurian, for it is figured for *Palaeodiscus* both by Sollas (1899, p. 704, figs. 10, 11) and Hawkins and Hampton (1927, p. 595, fig. 7).

Internal Features

The inner features of both genera are very similar. Rubber impressions of the interiors show inner views of the plates noticeable for prominent internal ridges which run along the per-radii (figs. 1, 2, 3, 4, 6, 7, Pl. 14). The ridges can best be studied in combination with structures seen on the original mould. Attached to the moulds are natural casts of the soft structures which at one time occupied the per-radii. After the animal died, cavities in the plates, especially those which housed the water and adjacent systems, became filled in with mud. This mud hardened into tube-like casts. Later when the calcite of the plates was dissolved away the mud casts were left standing out from the surface of the mould as natural casts seen very clearly (fig. 2, Pl. 13). The ridges and moulds together give important details of structure of the water system. Similar hardened casts of the water vessels have been described by one of us (Spencer 1925, p. 246) from moulds of fossil Ophiuroidea.

1. *The Relationship of the Radial Water Vessels to the Plates.*

In a recent echinoid the radial water vessels lie free on the inner sides of the ambulacrals (fig. 8 A). In *Aulechinus* and *Ectinechinus* this was not so. The radial water vessels were enclosed within the walls of the test in inner ridges of the ambulacrals. These inner ridges roofed over the radial vessels separating them from the coelomic cavity (fig. 8 B), that is, the relationship of water vessel to ambulacral was as in the Asterozoa.

The evidence is quite clear, whether we examine the original moulds, or the rubber impressions. If we first examine a mould, e.g. that photographed (fig. 2, Pl. 13), we can see dark spaces along each side of the per-radial mud cast. These spaces represent the hollows left after the inner ridges of the original test had been dissolved away. If these inner ridges had enclosed the water tube the hollows should extend right under the casts and leave these casts suspended in the groove. Examination of the moulds shows this to be the case. In fact the per-radial casts, representing the main water vessel, are only kept in position by the lateral supporting casts, shown also in the photograph, representing the branch vessels to the tube feet.

It is now possible to understand the rubber impressions. If from natural causes the supports of the per-radial mud casts have disappeared, or if artificially we remove, by a needle, a portion of a mud cast, we get a rubber impression showing the entire depth of the internal ridge. The roofing is complete and the sutures extend right to the top of the ridge (fig. 7 A). If, however, we make a rubber impression, taking care not to press hard and so destroy the mud cast, we obtain at the summit of the ridge interruptions representing the impressions of the mud casts. The roof is flattened out and we see median hollows (fig. 7 B, fig 4, pl. 14), representing swellings in the original radial water system.

If now we examine these internal ridges afresh, following each ridge outwards and

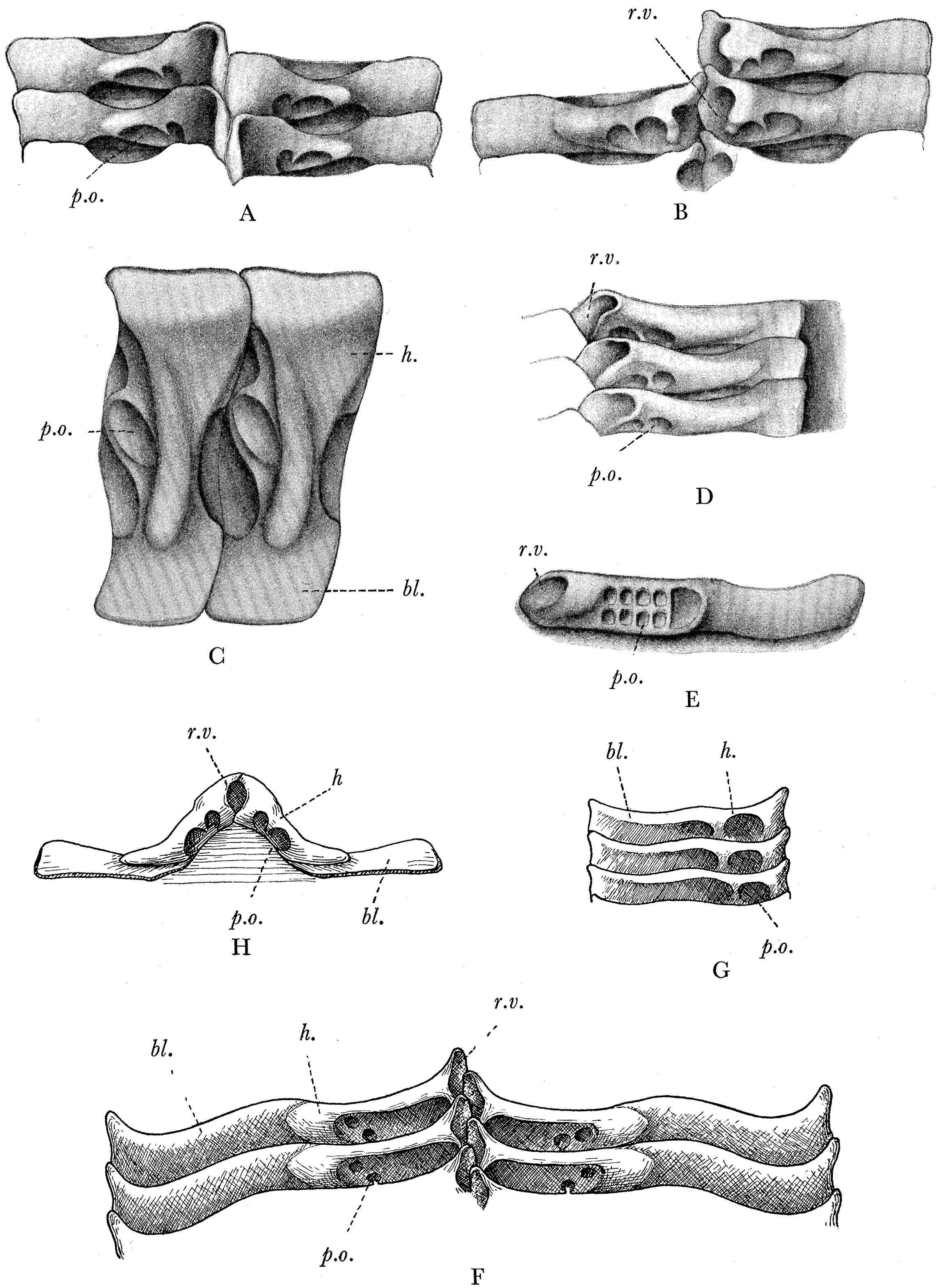

Fig. 7. Internal views of ambulacrals of *Aulechinus*, *Ectinechinus*, *Eothuria*, *Palaeodiscus*, and *Myriastiches*. A, upper view from *Aulechinus* with roof in place (E. 31412, × 20); B, upper view from *Aulechinus* with roof removed (E. 31412, × 20); C, lateral view from *Aulechinus* (E. 31412, × 32); D, upper view from *Ectinechinus* with roof removed (these have double pores) (Gr. 13, × 24); E, upper view from *Eothuria* (E. 27004, × 12); F, upper view from *Palaeodiscus* (Oxford Univ. Mus., × 24); G, upper view from *Myriastiches* (Oxford Univ. Mus., × 18); H, reconstructed cross-section of a pair of ambulacrals of *Aulechinus* (× 18). *bl.* blade; *h.* haft; *p.o.* pores; *r.v.* hollows for radial vessels.

downwards (i.e. in the direction of the plate's exterior), we see it continued as a shaft-like thickening, pierced by pores, which lie at a rather higher level than the outer mass of the plate (figs. 7 A–C). It is convenient to give names to these regions. For the roof plus the shaft we suggest the name ambulacral *hafts*, thus distinguishing them from the flat outer regions of the plates which may be termed ambulacral *blades*.

The hafts correspond to the second series of plates which Sollas (1899) and Spencer (1904) described as lying interior to the true ambulacrals in *Palaeodiscus* and supposed by them to represent vestiges of series homologous with the ambulacrals of the Asteroidea. The existence of such separate interior plates was denied by Jackson (1912, p. 251), who thought that those alleged structures were "the narrower ambulacral plates of the dorsal side brought into mechanical contact with the wider ventral plates by the (*post mortem*) flattening of the test".

Hawkins and Hampton (1927, pp. 594–5) admit the existence of thickened internal knobs in the region where Sollas and Spencer described plates. They regard the structure of the area as showing "exquisite adaptation to the needs of the radial water vessel in a form subject to much change in diameter and little in height", since "the internal knobs (which are grooved as if for the passage of the podial water-vessel) would keep the per-radii rigid, thus preventing complications in the radial vessel and associated nerves". The transverse margins "are so arranged that free imbrication could occur adradially, but be checked before the ampullae of the tube-feet were endangered". In their view, then, the knobs were merely secondary functional adaptation comparable to the secondary thickenings within the ambulacra of the recent *Clypeaster*. Their description (p. 594) is as follows: "On the inner surface a belt of thickening extends along the apicad transverse border, increasing in strength towards the per-radius, where (after the pore-pair is passed) it expands into a kind of knob covering the full height of the plate."

We have re-examined *Palaeodiscus*, and find these internal projections have a far more definite structure than can be explained by the suggestion that they are secondary functional adaptations. They can be recognized quite easily, and the relationship of haft and pore is similar to that in *Aulechinus* and *Ectinechinus* (fig. 7 F). The top of the roof enclosing the water vessel, however, has been lost, at any rate in certain areas, and is only represented by a groove as described by Hawkins and Hampton. We regard this as representing one stage in the progressive reduction of the hafts which occurs in later Echinoidea, and described below.

We have also re-examined *Myriastiches* and given new figures of interior views (fig. 6, Pl. 14, and fig. 7 G). These seem to us closely to resemble the inner structure seen in *Palaeodiscus* but we are deferring our redescription of *Myriastiches* to a later date.

2. *The significance of the ambulacral hafts.*

There can be no doubt that Jackson and Hawkins and Hampton were right in their view that there are no separate internal series of plates in these older Echinoidea.

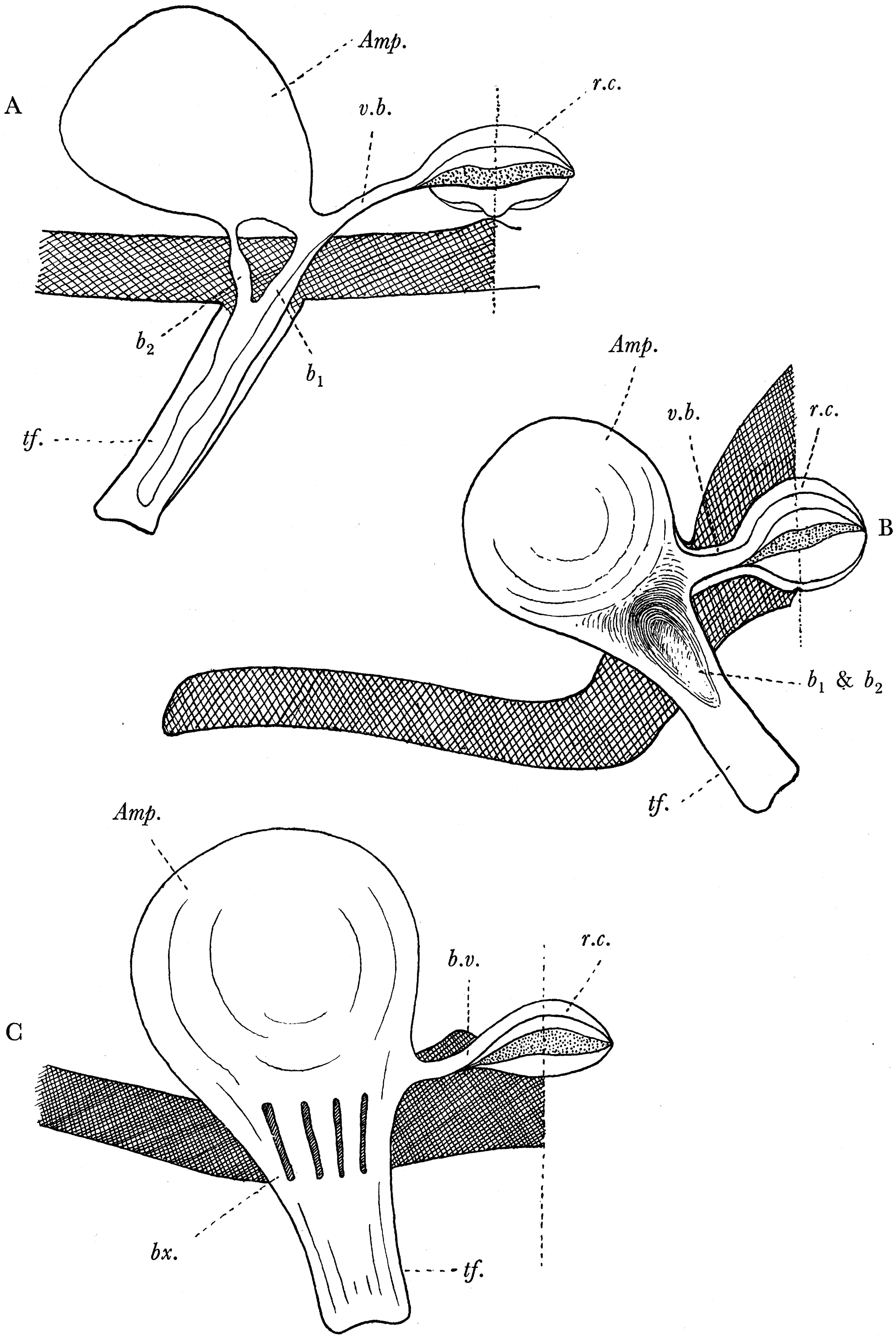

Fig. 8. A, *Echinus*. Diagram of a transverse section of an ambulacrum of a recent echinoid, showing the relation of the radial canal of the water-vascular system to the tube-feet and their ampullae. (From Chadwick, 1900, Text-fig. 29.) B, *Aulechinus*, corresponding diagram to A. C, *Eothuria*, corresponding diagram to A. *Amp.* ampulla; b_1 & b_2, the indented single branch of passage from ampulla to the tube foot. b_1, b_2, the two branches of passage from ampulla to tube-foot; *bx.* multiple branches of passage from ampulla to tube-foot; *r.c.* radial canal; *tf.* tube-foot; *b.v.* branch vessel from radial canal to tube-foot.

But we maintain that this does not disprove the original contention that the internal structure of the ambulacra suggests near relationship between the Echinoidea and the Asterozoa. Discussion upon this relationship is very much more possible now than it was thirty years ago. *Aulechinus* is a very much older echinoid than either *Palaeodiscus* and *Echinocystis*, and there is increasing knowledge of the structure of the Palaeozoic Asterozoa. These older asterozoan fauna allow newer interpretations. Such a fauna is found in the $D_{\gamma 1}$ (Lower Ordovician) rocks of Bohemia, and was described, in part, by Jaekel (1903, 1923). Before he died he handed over the material, with the consent of the authorities of the Prague Museum, to one of us (Spencer), who now has made detailed studies upon it. In general the fauna presents, as it were, an archaic survival from the Cambrian, a view which seems to be confirmed by the presence of nearly related forms at even lower horizons (Upper Cambrian and the lowest beds of the Arenig) in the south of France (Thoral 1935).

It is essential that this fauna should be described in detail before clear comparisons between the asterozoan and echinoid ambulacrals can be made. Spencer hopes shortly to be in a position to publish such a description. Meanwhile we can only state that these studies confirm us in our view that the asterozoan and echinoid ambulacrals have essential features in common.

3. *Disappearance of the internal ridges.*

There is no doubt that the hafts gradually disappear. They are retained to quite a recognizable extent in the later Silurian genera *Koninckocidaris*, *Palaeodiscus* and *Echinocystis*. In *Palaeodiscus* they have lost the roof of the radial canal. There has been further reduction in the Carboniferous genus *Hyattechinus* (Mortensen 1935, p. 60), where they are represented only by internal spine-like processes.

4. *The structure of the pore passages and the origin of the double pore in echinoids.*

Examination of the moulds of the interior of the test give further instructive information. The bilobed lateral mud casts, see e.g. fig. 2, Pl. 13, represent the hardened mud infillings of the pore passages through the ambulacrals. As the plates were thick, the passages show in considerable detail the structure of the vessel passing through the plate, that is, the passage from ampulla to podium. A careful wax model was made of these bilobed mud casts and drawings (fig. 9) are given from this model.

The models have also been used in the diagrammatic cross-section given (fig. 8 B). The following features can be noticed:

1. Each pore infilling sits almost at the top of the cast of the radial canal (*r.c.*), that is the branch to the tube-foot (*v.b.*) must have been very short.

2. The infilling is a single bilobed strand not a double strand. Such mud casts, if preserved in any known post-Ordovician Echinoidea, would show a double strand. Here the indentation (*i* of the figure) shows the beginnings of a slitting of a strand into two. In other words, the passage from the ampulla to the podium was not

double as is usual in Echinoidea but an indented single passage (compare figs. 8 A and B).

3. It is natural to suppose that at an even earlier stage still the passage from ampulla to podium was cylindrical in shape. If this were so the passage elongates and becomes indented at one and the same time. The next stage a division of the passage into two strands is already partially attained in the contemporary *Ectinechinus* (see p. 110). This is in line with the embryological studies of Miss Gordon (see p. 111).

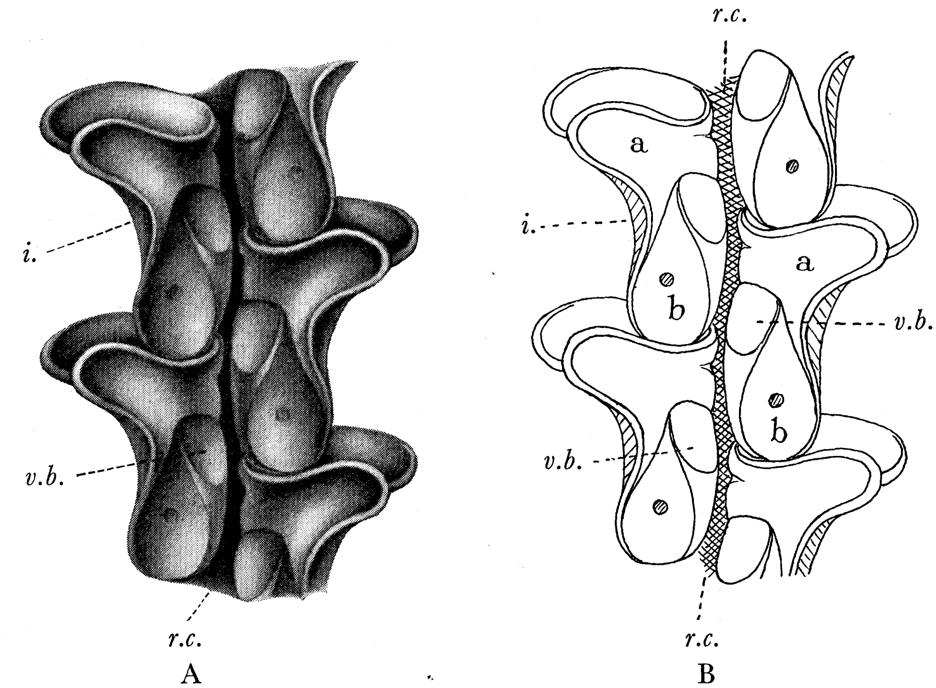

Fig. 9. A, *Aulechinus*. Wash drawing of wax model of mud strands representing the radial canal and the passage from ampulla to the tube-feet (H.M.E. 1200, × 40). B, Outline drawing to indicate the various structures shown in A. *i.* indentation, the beginning of the ingrowth which in later forms divides the passage into two parts; *r.c.* radial canal; *a.* the lateral branch of the passage; *b.* the longitudinal branch of the vessel; *v.b.* the branch vessel.

There can be no doubt that a division of the passage would help respiratory efficiency. The interior of the tube-feet is ciliated (MacBride 1906, p. 517), and Gislén (1924, p. 245) states "a rapid current runs inside them which enters the feet through one of the ambulacral pores and goes out through the other. Water inside the tube-feet aerated by means of absorption through the walls of the outer portions of the tube-feet would thus be rapidly conveyed to the ampulla and discharged through the ampullal wall into the coelom" (see also p. 130).

We can summarize much of the knowledge gained, by the diagrams given (fig. 8). They show the relationship of the water system and adjacent structures in *Aulechinus* (fig. 8 B) as compared with the same structures in a recent Echinoid (*Echinus*, fig. 8 A). The three features illustrated are: (1) the very short passage in *Aulechinus* of the branch vessel which passes from the radial vessel to the tube-foot; (2) the tube-feet pointing towards the per-radial line in *Aulechinus* and away from this line in *Echinus*; (3) the passage through the plate in two vessels in *Echinus* and in one indented vessel in *Aulechinus*.

The Interambulacral Plates (figs. 1, 2 A, 2 B)

The interambulacrals have the same general characters in both genera.

The plates very rarely have geometrical outlines, and it is difficult to distinguish definite columns. By reason of this and of the incomplete condition of the specimens it is difficult to state exactly the number of interambulacrals in the mid zone; it appears to have been between seven and nine. These numbers decrease adorally and adapically until only one plate is seen in each angle.

The number of columns appears to be similar to those of *Palaeodiscus* as drawn by Hawkins and Hampton (1927, fig. 5). This number contrasts very sharply with the very numerous (40) columns of interambulacral plates of *Myriastiches* (Sollas 1899).

The single plate in the basicoronal (adoral) row is regarded by Jackson (1896, 1912) as the primordial, or first-formed, interambulacral, in the single column of *Bothriocidaris*. It is found in the young stages of the developing echinoid (Lovén 1874, 1883) and in the adults of several Palaeozoic genera.

The spines are very numerous in *Aulechinus*, and rather sparse in *Ectinechinus*. They are housed in pits on the plates and there is no sign of tubercles.

The Peristome (fig. 10)

The peristome of *Aulechinus* has a structure corresponding to that in the first stages of the development of recent echinoids. The peristome of *Ectinechinus* has several rows of plates and leads towards the peristomes of *Echinocystis*, *Palaeodiscus* and other later Palaeozoic genera.

Aulechinus

Three specimens, Gr. 10, H.M.E. 1202 and H.M.E. 1203, give views of the peristome. All three give interesting details.

The most complete plan is that shown by H.M.E. 1203, drawn as fig. 10 A. It is that demanded by embryologists and comparative anatomists as the simplest possible. There is only one pair of plates oral to each odd inter-radial. These are the "primordial ambulacrals" of Lovén. They are not quite in the same line as the other ambulacrals but swing slightly outwards from the per-radial line to assume an apparently inter-radial position. There is a corresponding appearance in the development of the Recent *Echinus* (Gordon 1926 *a*, p. 265 and Text-fig. 3) where the buccal plates homologous with the primordial ambulacrals "are not, as one might anticipate,

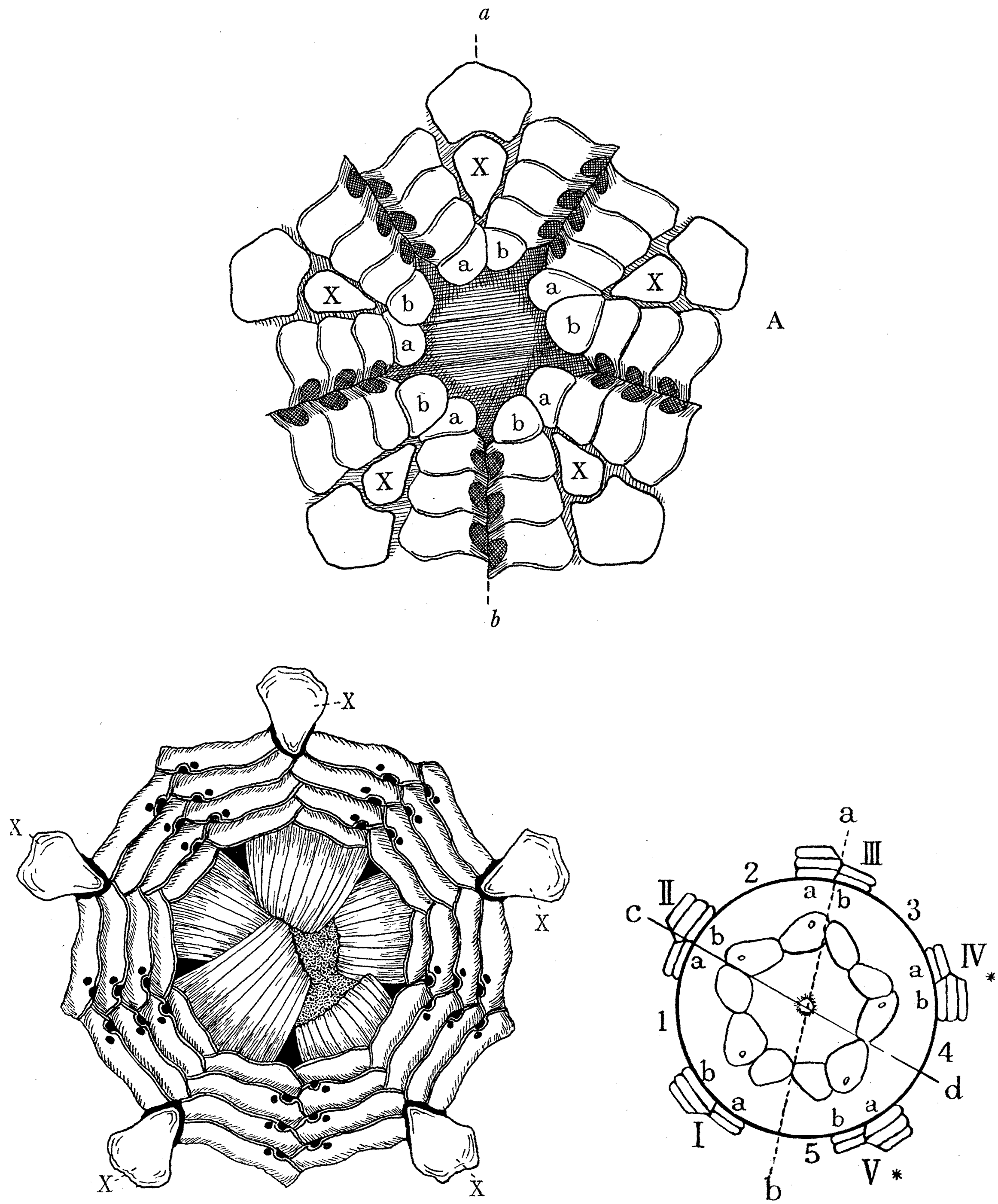

Fig. 10. The peristome. A, outline drawing of peristome of *Aulechinus* slightly diagrammatized (based on H.M.E. 1203), × 6. The arrangement according to Lovén's Law is shown by the letters *a* and *b*. B, outline drawing of peristome of *Ectinechinus* (based on H.M.E. 1221), × 12. *X*, first "odd" interambulacrals. C, Diagram to show the relationship of Lovén's plane (*ab*) to the plane of *Ectinechinus* (*cd*) and the relationship of the primordial ambulacral plates. *a*, *b*, primordial ambulacral plates. (Copied from Gordon 1929, Text-fig. 17.)

ambulacral but interambulacral in position, being situated opposite the two 'lateral' rays of the first formed interambulacral plates".

The peristome is so nearly perfect that we have felt justified in reconstructing it as if every angle obeyed Lovén's Law. In the four angles which are well preserved there is certainly that remarkable alternation in size of the primordial ambulacrals upon which the law is founded.

The inner edge of the peristome of Gr. 10 is not so flat as that of H.M.E. 1203. In consequence most of the "primordial ambulacrals" are seen slightly on edge. Otherwise the structure is exactly the same.

The peristome of A.L. 2 has been somewhat disturbed, but one angle is specially well preserved. This shows that the outer interradial portions of the "primordial ambulacrals" were very swollen and covered with short spines (fig. 4, Pl. 15). The swelling is more prominent on the larger plate than the smaller, suggesting that the inequality of Lovén's Law extends to characters other than mere size.

Ectinechinus

The peristome of *Ectinechinus* is seen in three specimens E. 31414 *b*, E. 31405, and H.M.E. 1221. It differs from that of *Aulechinus*. In place of the single ring of "primordial ambulacrals" which terminate the oral end of the ambulacrals of *Aulechinus* at least three rings of ambulacrals pass on to the peristome (fig. 10 B). Like the other ambulacrals they imbricate adorally. The peristomial ambulacrals closely touch, and there is no sign of any intercalated plates or of any interruption in the series.

This type of peristome is quite common in Palaeozoic Echinoidea and, as Mortensen has pointed out (1935, p. 92), has a parallel amongst the Recent Echinothuridae. Mortensen remarks on the origin of these plates in the Echinothuridae: "As to the way in which the peristomial plates, beyond the first pair, originate there is not the slightest doubt but they are coronal plates which became detached from the corona and pass on to the peristome. In the Cidarids this is easily effected through the resorption of the adoral part of the interambulacra, the proximal ambulacral plates thereby being loosened from the corona and coming to lie in the thus widened peristome. In the Echinothurids, where the primordial plate persists, the ambulacral plates must be pushed actively on to the peristome with the growth of the ambulacra."

The retention of the primary inter-radial plates in these early Palaeozoic Echinoidea shows that here there has been no resorption, and that the plates must have originated as in the echinothurids.

The lantern

Previous to the discovery of the Girvan Echinoidea, the earliest lantern known in detail is that belonging to *Palaeodiscus* (Sollas 1899; Hawkins and Hampton 1927).

This has the following characters, which are shared by Devonian and Carboniferous Echinoidea in general:

1. It is low, corresponding to early stages in the development of Recent Echinoidea.

2. The main constituents of the lantern, namely, jaw, teeth, rotulae, compasses and probably epiphyses are present.

3. There are no auricles.

The lanterns of *Aulechinus* and *Ectinechinus* are even simpler in build. The only constituents are the jaws and teeth; rotulae, compasses, and epiphyses all being absent. Further, the lantern frame of *Aulechinus* is the smallest known, its jaws can scarcely be distinguished from the ambulacral hafts, and the teeth have ridges and grooves similar to those possessed by the oral valves of *Eothuria*. It is suggested later (p. 125) that this simplicity of structure allows the lantern to be compared with the mouth-frame of the Asterozoa.

Aulechinus (figs. 11 A, 12 A, B)

The lantern is visible in four specimens, H.M.E. 1202*c*, H.M.E. 1203*c*, Gr. 10*c* and Gr. 12*c*.

The lantern frame is small. The jaws barely extend beyond the second ambulacrals, that is, for a distance of 3 mm. from the mouth centre. In the contemporaneous *Ectinechinus* the corresponding measurements are 5 mm., and in the Silurian genus *Palaeodiscus* 6 mm. The lantern not only covers a small superficial area, but it is also very shallow, as can be seen from the photograph reproduced (figs. 1, 2, Pl. 15).

The lantern frame also is simple. All the specimens show only the ten jaws (half-pyramids). We have been unable to trace any presence of braces or epiphyses. Further, as in all the early Palaeozoic echinoids, there is no trace of auriculae on the internal faces of the surrounding ambulacralia. The jaws are thin and elongate. Aborally each has a prominent knob, with a deep groove on its summit, and a shell-like blade. Along the shell-like blades there is a thin shelf (the tooth slide) for the lateral fitting of the tooth (H.M.E. 1202*c* photographed (fig. 3, Pl. 15; fig. 12)).

This lantern also suggests the true homologies of the echinoid jaws. An examination of the figures shows upstanding hafts for all ambulacrals from the second, third, fourth onwards. The first ambulacral has no haft, but the jaws lie over this ambulacral, and have a very strong general resemblance to the hafts on the other ambulacrals. The jaws, therefore, seem to be ambulacral hafts which are not fixed to their blades (the first ambulacrals).

The teeth have broad edges, and are laminate. Each lamina is composed of about seven ribs between which are grooves (fig. 2, Pl. 15; fig. 12 B). The broad edges and laminate character of these teeth suggest that they acted as scoops rather than biting teeth. They would serve for dredging loosely built and tender algae from the lagoon bottom (see p. 97). This is the way in which the teeth are used in *Echinarachnius* and

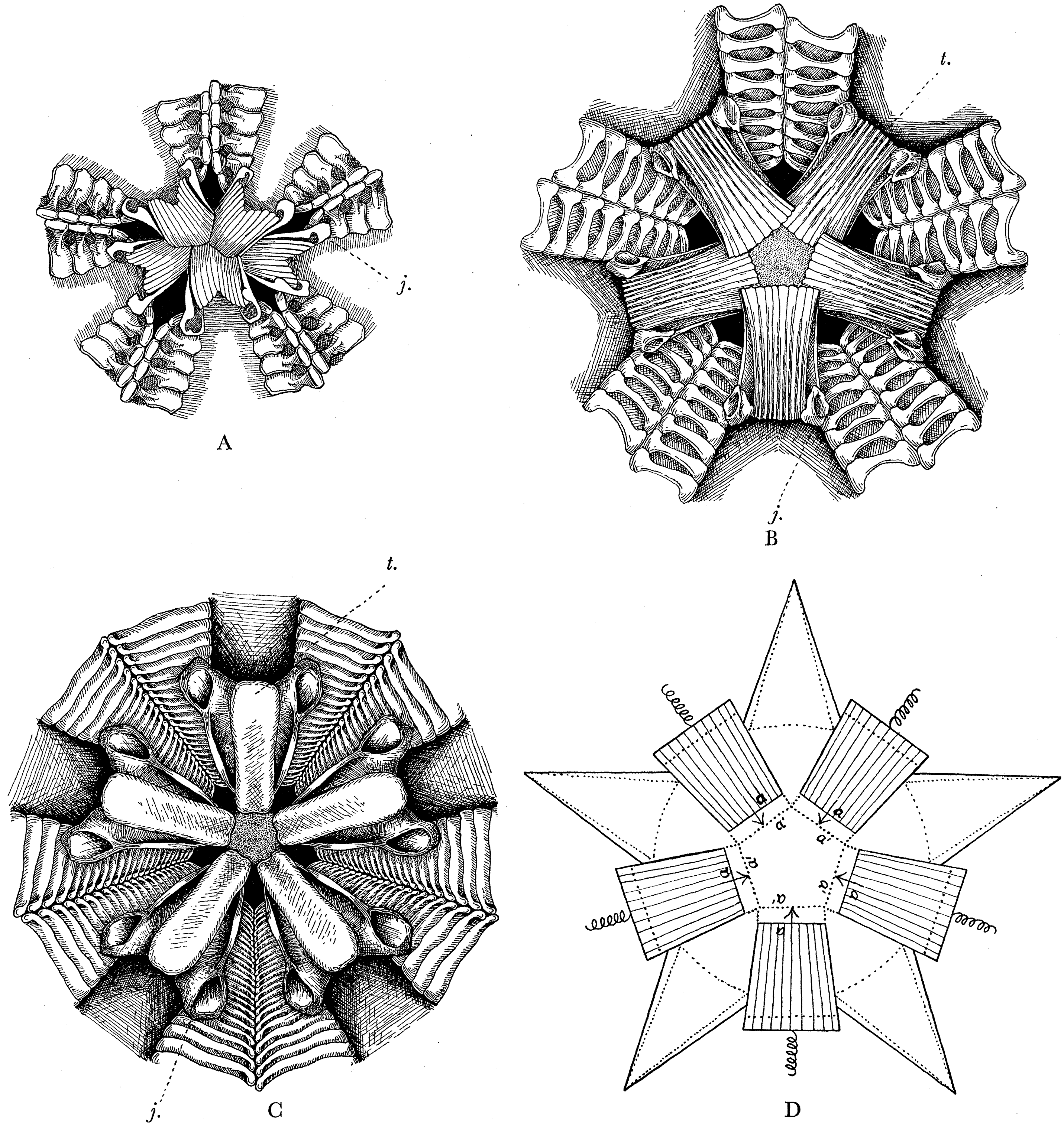

FIG. 11. Internal views of lantern. A, of *Aulechinus* (based on H.M.E. 1203), × 5. B, of *Ectinechinus* (based on H.M.E. 1221), × 5. C, of *Palaeodiscus*, the compasses and rotulae removed (based on No. 9774, Mus. Geol. Survey), × 5. D, Diagram to show the opening and closure of the lantern teeth. The firm lines indicate the position of the ossicles when the teeth are in an open position and the dotted lines when the teeth are closed. The arrows show the direction of movement and the springs indicate the tension which brings back the teeth to the open position. *j.* jaws; *t.* tooth; *a*, *a'*, adoral edge of tooth.

in *Clypeastroidea*. These have no rotulae. They use their teeth as is suggested for *Aulechinus*.

Ectinechinus (fig. 11 B)

The lantern can be seen to a greater or less extent in seven specimens: E. 31405, E. 31408, E. 31414*b*, Gr. 11*c*, H.M.E. 1219 (smaller specimen), H.M.E. 1221 and *c*, and J.L.B. 24. In all these cases, except E. 31414*b*, where it is slightly subcentral, the lantern is at the extreme hinder edge of the form. The best views are obtained from E. 31405 and from H.M.E. 1221 and its counterpart. The study of the posterior extremity of the test reconstructed in fig. 2 B is based largely on E. 31405, but the teeth have been added from H.M.E. 1221*c*. Fig. 11 B is based on H.M.E. 1221.

The jaws have the same essential structure as in *Aulechinus*, but they are longer, and extend back as far as the fifth ambulacral. The displacement is such as to destroy that connexion between the jaws and the first ambulacral, which is seen so well in *Aulechinus*. The teeth are grooved, but not so deeply as in *Aulechinus*. The grooves are much deeper on the outer side of the teeth than on the inner side.

The only other known echinoid with grooved teeth is *Meekechinus* from the Permian of Kansas. Here the teeth are said to be serrate. The published drawings of *Meekechinus* (Jackson 1912, Pl. 76, figs. 1, 7, 8) do not quite suggest the alternation of groove and swollen ridge so especially characteristic of *Aulechinus*.

Palaeodiscus

A drawing (fig. 11 C) of the lantern of *Palaeodiscus* is given. To allow a more ready comparison with *Aulechinus* and *Ectinechinus*, the rotulae of *Palaeodiscus* are omitted. It is seen that the jaws of *Palaeodiscus* are of exactly the same shape as those of the two Ordovician genera. The teeth are thicker, without grooves, and with blunt pointed ends. They are much more like true biting teeth. The jaws lie over a great number of ambulacrals. This backward extent of the frame is probably due to the greater development of the adult stomodaeum.

The rotulae (not drawn) are broad ossicles. Devanesen (1922, p. 471) compares an early stage in the development of the rotulae of *Echinus* to this broad rotula of *Palaeodiscus* which has been well described by Sollas (1899).

The Mechanism of the Lantern (fig. 11 D)

The lantern of the Recent regular echinoids consists of forty separate ossicles co-ordinated and controlled by sixty separate muscles. The lantern of *Aulechinus* and *Ectinechinus* is such an extreme simplication of this that it is necessary to add an explanation of the way in which a lantern of this kind could work. Von Uexküll's (1896, p. 473) observations help here. Von Uexküll greatly simplified previous accounts of the essential working of the lantern, and in particular the biting movements of the teeth. He showed that the muscles between the auricles and the lantern are accessory. They serve for protracting and retracting the jaws, and are not essential to the bite of the teeth.

The prime movers in the biting apparatus are the muscles between the jaws. These bring the jaws (and consequently the teeth) nearer to each other—the actual bite. The movement is exactly similar to the trap-like closure of the mouth frame of Asterozoa described by one of us (Spencer 1925) and is illustrated here (fig. 11D). The essential features of the origin of such a movement are the disposition of the skeleton surrounding the mouth in triangles, and the arising of muscles in the angles of the triangles. Contraction of the muscles narrows the triangles and brings the adoral ends of the triangle system nearer to each other (a bite or scoop movement).

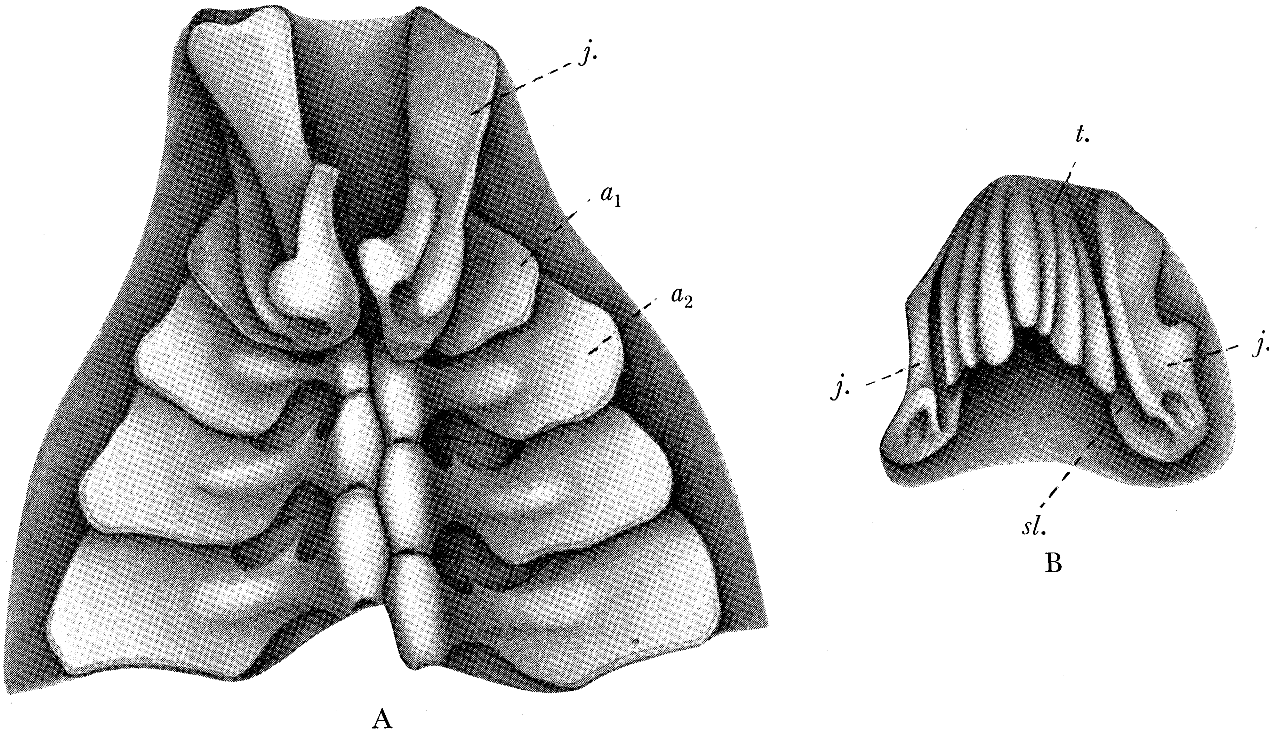

FIG. 12. A, jaws and anterior ambulacrals of *Aulechinus*, from H.M.E. 1202, ×25. B, teeth of *Aulechinus*, from H.M.E. 1202, ×15. a_1, first ambulacral; a_2, second ambulacral; *j.* jaws; *t.* tooth; *sl.* tooth slide.

There are no muscle antagonists to these prime movers, nor are they present in the more primitive Asterozoa. We must presume the antagonists to be the tensions set up by the primary movements. These are illustrated by a coiled spring in the diagram.

In later Asterozoa antagonistic muscles are developed. In the later Echinoidea, not only antagonistic muscles, but also a special ossicle is added—the rotula. Von Uexküll (1896) has given a clear account of this antagonistic mechanism. The antagonistic muscles are Lovén's internal and external *musculi rotulae* (overlooked in Lang's later account of the lantern). They acted by pulling the wedge-shaped rotula back into its original position after it had been displaced by the jaw closure.

It follows from this account that only broad homologies between the asterozoan and echinoid mouth frames are possible. Apparently much of the complicated jaw mechanism of later echinoids has been developed during the evolution of the echinoids themselves.

DESCRIPTION OF *EOTHURIA*

The broad ambulacra, with their strongly marked curvature, the large sieve-like pores and the ten grooved oral valves distinguish the animal from any other form known up to the present.

Material

Two specimens in the British Museum (Natural History). Both were broken during collection into a number of pieces which have been fitted together by Mr Bairstow. E. 27003 is a mould showing the greater part of the oral surface both in internal and external view (photographed, figs .6, 7, 8, 9, Pl. 15; fig. 4, Pl. 16). E. 27004 is the greater part of a specimen, a good deal of which is preserved in calcite and difficult to free from the matrix. A cast of a decalcified portion is photographed (fig. 4, Pl. 17).

Two specimens in the collection of Mr J. L. Begg. No. 31 (photographed, figs. 1, 2, Pl. 16) is the greater part of an internal mould, which has been indented at the side before preservation. This indentation forced a portion of the test towards the interior. In consequence both internal and external impressions of the test can be seen in this area. After death the specimen was considerably compressed. J.L.B. 30 is a fragment, very compressed.

Three specimens in the collection of the Misses Gray. H. 1: a considerable fragment, showing internal mould with encasings of external impressions, apparently compressed in a vertical plane (photographed, fig. 3, Pl. 16). H. 2: a considerable fragment of an internal mould with a portion of the encasing, compressed in a horizontal plane (photographed, figs. 3, 5, Pl. 17). H. 3: a fragment of an internal mould, compressed in horizontal plane.

One specimen in the collection of the Glasgow University Hunterian Museum, no. H.M.E. 1222 (photographed, figs. 1, 2, Pl. 17).

J.L.B. 31 is taken as the holotype and E. 27003 and H. 1 as paratypes.

The Form of the Test and the Ambulacral Paths (figs. 13, 14)

None of the specimens are quite complete, but there is good material for reconstruction. Such reconstruction leads to the conclusion that the form was very similar in shape and in the paths of its ambulacra to *Ectinechinus*.

The most important specimens, as evidence of this elongated form of test are H. 1 and E. 27003. H. 1, as stated already, is the greater part of an internal mould (only the apex is missing) together with much of the external casing. It is definitely elongate with the mouth at one extremity (fig. 4, Pl. 17). E. 27003 also has an elongate under-surface with the mouth at one extremity.

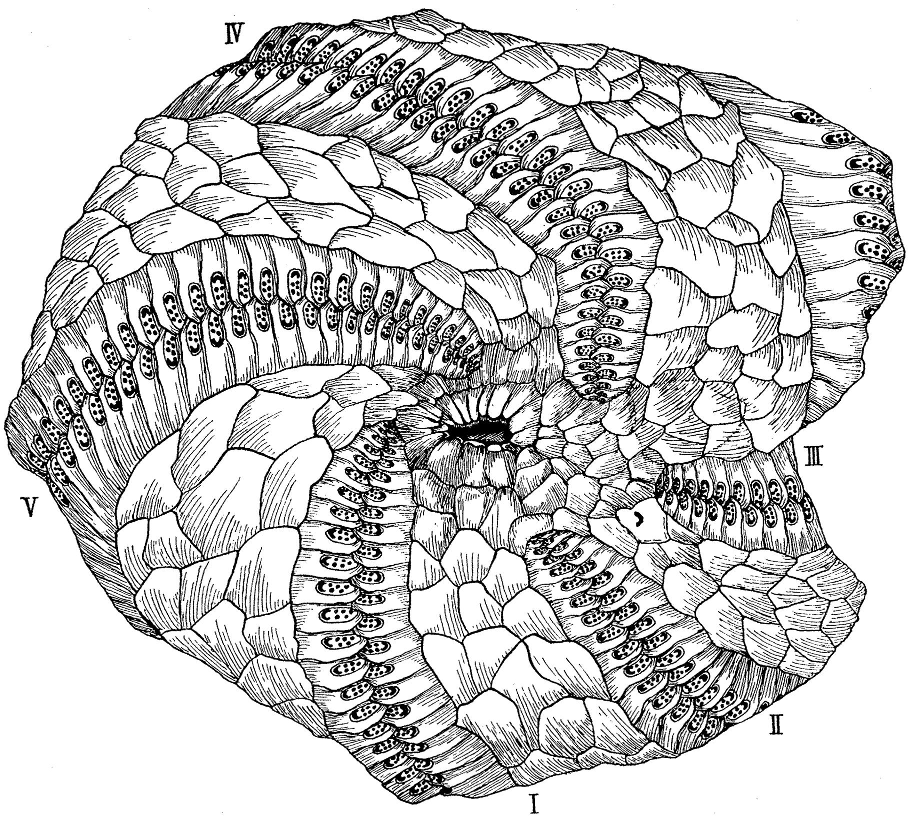

FIG. 13. *Eothuria.* Part of the apical surface reconstructed as an external view. × 3, from the holotype.

The holotype, which at first sight suggests a spherical form, has been somewhat distorted, but there is no doubt that here again the mouth is excentric.

We can deduce from the fossil remains two important facts: (1) that the test was thinner than in either *Aulechinus* or *Ectinechinus*; (2) that the test was elongate, with mouth and anus at opposite poles very much as in *Ectinechinus*.

The reconstructions (figs. 14 A, B) are based on the above deductions. Dorsally the form is made to resemble *Ectinechinus* except that the ambulacra have stronger curves and the valves of the anus are fewer and stouter.

Ventrally the reconstruction has one important difference from that of *Ectinechinus*. Both IV and V are well seen on the surface. The median line of symmetry is between IV and V, that is in inter-radius 4. This form therefore is built about a II–4 plane rather more than *Ectinechinus*.

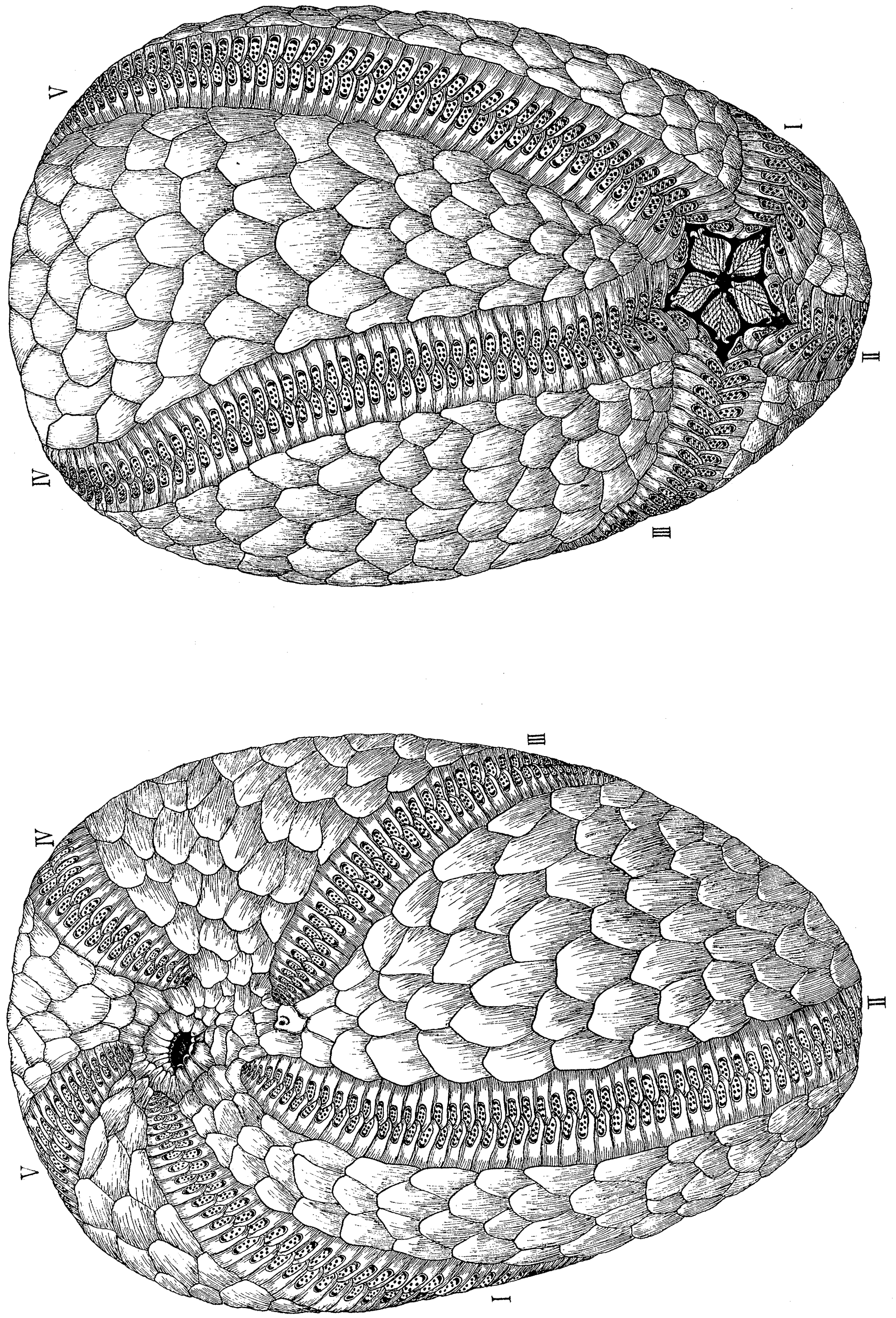

Fig. 14. *Eothuria.* A, reconstruction of dorsal surface; B, reconstruction of ventral surface. Lettering as in figs. 1, 2.

It also seems legitimate to suppose that the animal lived partially buried in mud, probably the same mud which encased the fossil. A large proportion of the specimens are nearly complete and have been little disturbed other than by compression since their death.

The Apical System

The apical system, in essential construction, is very similar indeed to that of *Aulechinus* and *Ectinechinus* except that there are no ocular plates. As in those forms, there is the same considerable area between the ambulacral extremities. This area is occupied by a valvular anus and other small plates. The anus, however, is considerably larger than in either of these echinoids. One of the plates of H. 1 has a trilobed pore between II and III (Fig. 14 A). Although this plate is not so large or so well differentiated as in *Ectinechinus* and *Aulechinus* there can be no doubt that it is the madreporite-genital. It is not readily identifiable in the holotype, where the central area has been broken and crushed.

The absence of oculars is shown by ambulacral extremities, seen in H. 1 and H.M.E. 1222. The ambulacral extremity in H.M.E. 1222 is photographed (figs. 1, 2, Pl. 17). The photograph shows that the ambulacral plates are continued as irregular pairs right to the fine point of the ambulacral extremity. There is no trace of the U-shaped ocular so well seen in *Aulechinus*. In contrast to their universal presence in echinoids, Recent holothurians have no ocular tentacles.

The Interambulacra

The interambulacra are very similar indeed to those both of *Aulechinus* and *Ectinechinus*. They have thin numerous plates which overlap, and are not regularly arranged in columns. The maximum number of plates about the ambitus would also seem to have been about the same as in the above genera.

The interambulacra have, however, an ornament which always distinguishes them from those of the above echinoids. The spines are evenly disposed but with somewhat wide interspaces. This ornament is very similar indeed to that found in the Ophiocistia.

The Ambulacra

The ambulacra are much more strongly curved than in *Aulechinus* and in *Ectinechinus*.

The plates are primaries, although here and there irregular growth suggests a primitive type of occlusion.

In external view the component plates are large as compared with those of *Aulechinus*. In the holotype they are roughly 1 mm. long and 4 mm. broad. Some specimens show them as large as 1·4 mm. long and 6 mm. broad. In consequence of this greater size they are less numerous than in *Aulechinus*.

Ambulacrals in External View (fig. 5 F, p. 109)

The ambulacrals in external view have many resemblances to those of the contemporaneous Echinoidea. They have the characteristic overlaps,* including those of the per-radial line. About the middle of the corona they show the same departure from a rectangular form, so specially noticeable in *Aulechinus*. Further, as in that form, there are here and there differentiated lateral and median spines.

The most remarkable feature is the pore. Each pore has not two, but many openings, and it is convenient to call the whole of these the pore complex. Although at first the structure seems to be quite different from the echinoid double pore, analysis strongly suggests that in essentials it is the same structure, that is, there are two main channels leading from an inner ampulla to an outer tube-foot. The channels are not equal in size, as they are in echinoids. The outer is the smaller and undivided, the inner is larger and much subdivided. The build of these pores is especially evident from the inside of the plates.

Ambulacrals in Internal View (fig. 7 E, p. 113)

The ambulacral hafts of *Eothuria* are not easy to recognize at first sight. The pore complex is so large that it has eaten into the ambulacral haft until that has almost disappeared. Careful examination shows that the plane of this pore complex is not parallel to the general surface of the plate, but tilted, and that a narrow but distinct band represents the hinder and highest region of the haft.

There are no roofs joining the hafts of opposite sides. Instead, there is a groove: that is *Eothuria* is in the *Palaeodiscus* stage rather than the *Aulechinus* stage. Not all these Echinoderms travel at the same pace along the same road.

The pore complex is seen to be even more markedly divided into two regions than it is in external view (fig. 7 E). The outer undivided pore region occupies more than a third of the whole, showing that in cross-section the channel through the ambulacral plate was distinctly wedge shaped, the inner end of the wedge being the thicker.

The inner divided pore area has small projecting masses very much like the teeth of a comb. Between the teeth are depressions, the small pores of the complex.

We can best understand the possible working of such a pore complex by a diagrammatic cross-section, adding as soft parts an ampulla with several branches to a tube-foot (fig. 8 C). The ampulla (*Amp.*) has water carried to it through the numerous small ciliated apertures of the internal pores, which because of their number will exchange the water rapidly as between ampulla and the tube-foot. The water, less the oxygen lost by the membranes of the ampulla to the fluids of the body cavity,

* One specimen, that photographed (fig. 9, Pl. 15), gives very good evidence that the ambulacral plates were only loosely joined along the per-radial line. The head of a Trilobite has been thrust through the test near the apex and this very slight pressure has produced a very considerable and regular spread of the ambulacral plates.

will be deflected by the slope of the outer pore towards the walk of the tube-foot. By these devices the water circulating in the tube-foot plus ampulla will have the maximum efficiency as a respiratory system.

The ridge of mud representing the infilling of the outer pore is well seen in the photograph of a mould of the interior of the form (fig. 3, Pl. 17).

The Peristome (fig. 15 A)

The peristome is fairly well preserved on E. 27003*d*. A cast from this is photographed (fig. 6, Pl. 15) and reconstructed (fig. 15 A). This specimen is an external mould. Impressions of the peristome are also seen on internal moulds of its counterpart E. 27003*b*, on the holotype and on H. 1. None of these specimens, however, gives the relationship of the plates so clearly as does E. 27003*d*.

There can be no doubt that this peristome is of a definitely echinoid type. There is the same odd interambulacral cut off from the mouth margin by ambulacrals. There seem to be three columns of two ambulacrals each adoral to the odd interradial. These apparently did not form a complete circlet around the mouth, but diverged in pairs from the per-radii, very much like the adoral ambulacrals of *Aulechinus*. There also is a suggestion that the ambulacral pairs nearest the mouth alternate in size, as if they obeyed Lovén's Law. The evidence for this however is slight, the ossicles being very disturbed except at one angle.

The Oral "Valves" (fig. 15 B)

The mouth is covered unmistakably by ten thin plates. These plates have ridges and grooves, and in this respect strongly resemble the teeth of *Ectinechinus* and *Aulechinus*. The plates are in pairs, each pair is lozenge shaped in outline and the grooves slope from the outer edges adorally towards the diagonal (figs. 15 A and figs. 7, 8, Pl. 15). There is no evidence however at all of any functional lantern apparatus although some views of the plates (fig. 15 B and fig. 8, Pl. 15) show a small distal ossicle *d* which may represent a small jaw component.

There is no convincing internal view of these plates although casts from the internal mould of H 2 show a part of a small circlet of plates somewhat similar to jaws.

The only other echinoderms which have a mouth covered by ten plates, at all comparable, are the Ophiocistia. In these the oral plates are very similar in general form to those of *Eothuria* but their surface is smooth, without any trace of ridges or grooves. It has been mentioned already that the ornament of the interambulacrals of the Ophiocistia and of *Eothuria* is very similar and other proofs of relationship will be given in a later paper.

A comparable feature in the young holothurian is the discovery made by one of us (MacBride 1914*a*), that in the young of the recent holothurian *Cucumaria* "the walls of the atrium, i.e. the larval stomodaeum, have split into five valves, and each valve is supported by a calcareous plate". This is true for *Stichopus* also (Mitsukuri 1897), and will probably be found to hold good for most primitive Holothuroidea. Each valve of the larva would therefore equal a fused pair of valves of *Eothuria*.

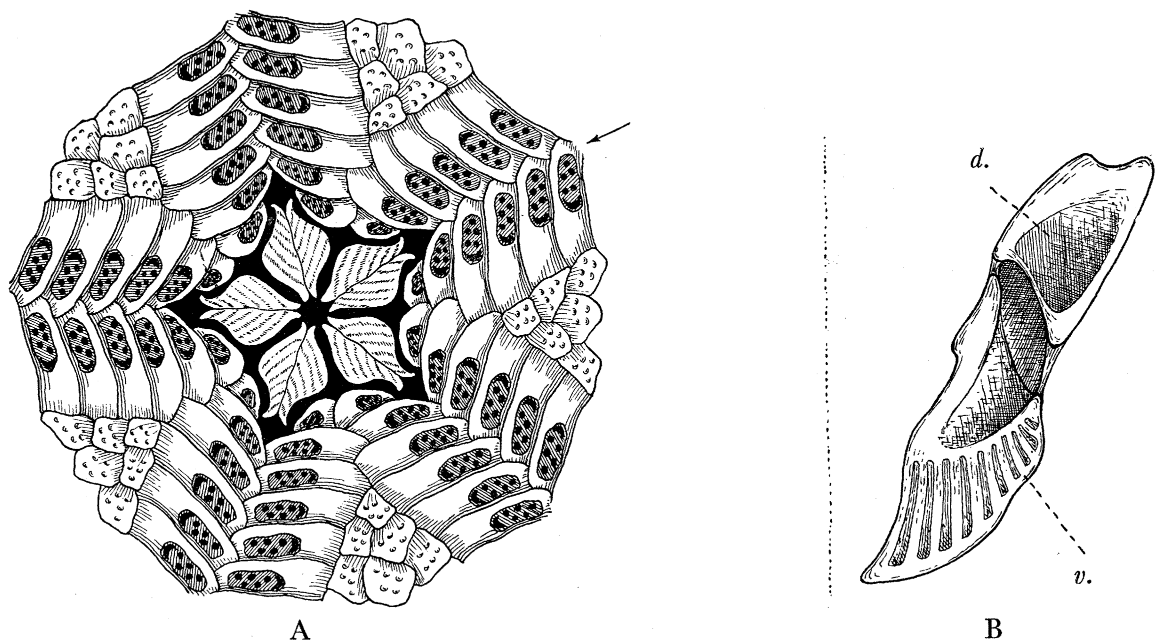

Fig. 15. *Eothuria*. A, reconstruction of peristome, × 4. B, drawing from the same specimen as is figured on fig. 7, Pl. 15, oral valve (*v.*) and distal ossicle (*d.*), × 12.

An interesting comparison can be made between these valves and the teeth of echinoids. Devanesen (1922, p. 473) showed that in origin the tooth is a paired structure, formed from a double row of lamellae. His figures (fig. 1, Pl. 11) show these lamellae sloping adorally towards the median line of the future tooth just as do the ridges and grooves of a pair of "valves" of *Eothuria*. This observation, together with the strong resemblance of the valves to the teeth of *Aulechinus*, would support a view that the valves are homologues of teeth whilst the distal processes are very possibly homologues of jaws.

SUMMARY AND CONCLUSIONS

A. *Aulechinus* and *Ectinechinus*

1. There are in the Upper Ordovician two new echinoids which, like almost all other Palaeozoic Echinoidea, have interambulacral areas composed of many rows of plates. Further, just as in the genera which immediately succeed them in the Silurian, these plates overlap to produce a flexible test. This structure is in strong contrast to the few plates and firm skeleton of the contemporary *Bothriocidaris* which previously has been assumed to be a representative of the ancestral stock of all echinoids.

2. The new echinoids show several features which can be reasonably regarded as being more primitive than those known for early Echinoidea:

(i) Neither have, as yet, acquired a perfect radiate symmetry as shown by the structure of the apical system.

(ii) Neither show fusion of ambulacrals along the per-radial line. The plates here merely overlap.

(iii) In *Aulechinus*, and to some extent in *Ectinechinus*, the passage from the internal ampulla to the tube-feet is notched but not completely divided.

(iv) The peristome of *Aulechinus* has only a single row of plates.

(v) The jaws of the lantern of *Aulechinus* are scarcely differentiated from the neighbouring skeleton.

3. Some of the above features can be directly associated with primitive features which can be deduced from the embryology of Recent forms:

(i) The apical system of the young urchin has incomplete radiate symmetry.

(ii) The unfused condition of the ambulacral junctions along the per-radial line would be an intermediate stage between a form which had an open groove to a stage in which the groove is completely sealed by overgrowth from opposite sides.

(iii) The single row of ambulacrals on the peristome corresponds to the primary ambulacrals of Lovén.

(iv) The jaws of the lantern in the young urchin are barely distinguishable from the rudiments of the ambulacrals.

4. There are internal projections on the ambulacrals. Our interpretatation is:

(i) That they are a primitive feature, inasmuch as they would form natural floors to the original open per-radial grooves, and thus preserve the continuity of the skeleton.

(ii) That they correspond in form to the ambulacrals of primitive starfish, which also had an open groove, exactly as in adult Recent starfish, primitive Ophiuroidea and the young of Recent Ophiuroidea.

5. *Aulechinus* in general shape is like the regular Echinoidea; but *Ectinechinus* is superficially like an irregular echinoid, inasmuch as it is elongated and has a mouth and anus at opposite extremities of an elongated flattened body. *Ectinechinus* presents features which show it to be in advance of *Aulechinus*, e.g. the structure of the jaws of the lantern, the peristome, and the condition of the ambulacral pores. But in *Ectinechinus* the apical portions of the ambulacra terminate in a ring round the anus, whereas in Recent irregular echinoids the anus is far removed from the apical pole, and is situated in an interradius so that the adaptation represented by *Ectinechinus* and modern irregular sea-urchins are widely different.

6. The presence of urchins in the Ordovician with such a considerable diversity

of form of test as is shown by *Aulechinus*, *Ectinechinus*, and *Myriastiches*, suggests that we must go lower in the rocks to obtain certain evidence of the exact structure of the most primitive echinoid.

B. *Eothuria*

1. A form, which in respect of the greater part of its characters resembles an elongated echinoid, is found in these same beds. But the form has a circlet of ten valve-like plates instead of five teeth.

2. Amongst modern forms the nearest approach to *Eothuria* is shown by the post-larval *Cucumaria* which, as was discovered by one of us (MacBride 1914*a*), has a test of loosely fitting plates and a circlet of valves around the mouth. There is a strong indication that a similar test exists in *Stichopus* (Mitsukuri) and, as the post-larval forms of Holothuroidea are very little known, a fruitful field here awaits the investigator.

3. The view that *Eothuria* is the first known adult plated holothurian is supported also by the absence of ocular plates, a characteristic difference between Echinoidea and Holothuroidea.

4. The suggested character, that *Eothuria* had only a single genital rachis, is also in accord with the structure of Recent Holothuroidea. It is noteworthy, however, that the same character must also be assumed for the two Girvan echinoids.

5. *Eothuria* has ambulacral pores unlike that of any known eleutherozoan.

Mode of Life

Some suggestions are made as to the mode of life of the forms. *Aulechinus* seems to have rested under sand, just as the Recent Astropectinidae, and therefore may be transitional to burrowing forms. *Eothuria* almost certainly burrowed, and it is possible that *Ectinechinus* was a burrowing form.

It is felt that, at this stage, it is inadvisable to attempt to build up the exact connexions between the various groups of echinoderms. One of us (Spencer) has in preparation an account of early starfish found at or near the base of the Ordovician, and an account also of various forms (including the Edrioasteroidea) allied to the cystids. When these accounts have been published we propose to attempt to place the forms in a general scheme of classification and to discuss further the homologies of the components of their skeletons.

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Description of Plates

Plate 10

Photographs of *Aulechinus grayae*

Fig. 1. Lateral view of an internal mould, $\times 4$; coll. the Misses Gray, No. Gr. 12.

Fig. 2. Cast of external mould of counterpart of the same specimen, $\times 2$.

Fig. 3. Lateral view of the apical portion of an internal mould, $\times 2\frac{1}{2}$; coll. Brit. Mus. (Nat. Hist.) E. 31412 (the holotype).

Fig. 4. Lateral view of the apical portion of an internal mould showing a pointed apex, $\times 2\frac{1}{2}$; coll. the Misses Gray, No. Gr. 15.

Fig. 5. Lateral view of a much compressed internal mould, $\times 2\frac{1}{2}$; coll. the Misses Gray, No. Gr. 3*c*.

Fig. 6. Cast of an external mould of the test showing a portion of an interambulacrum and of an ambulacrum, $\times 2\frac{1}{2}$; coll. Brit. Mus. (Nat. Hist.), No. E. 31410.

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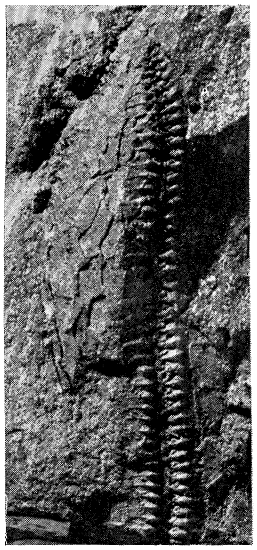

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Plate 11

Photographs of *Ectinechinus lamonti*

Fig. 1. Apical view of internal mould of holotype, $\times 4$; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1218.

Fig. 2. Profile view of same, nat. size.

Fig. 3. View of base of an internal mould, nat. size; coll. the Misses Gray, No. Gr. 11*c*.

Fig. 4. View of base of an external mould (the smallest specimen), nat. size; coll. Mr Begg, No. 26.

Fig. 5. Antero-lateral view of an internal mould, $\times 2\frac{1}{2}$; coll. the Misses Gray, No. Gr. 13.

Fig. 6. Cast of an internal mould, $\times 2\frac{1}{2}$; coll. Brit. Mus. (Nat. Hist.), No. E. 31408.

Fig. 7. Portions of two internal moulds embedded in the same block, $\times 2$; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1223*a*.

Fig. 8. Cast of external mould of a portion of an ambulacrum showing the double pores, $\times 8$; coll. Brit. Mus. (Nat. Hist.), No. E. 31405.

M. madreporite-genital; *o.* mouth; *p.o.* pores.

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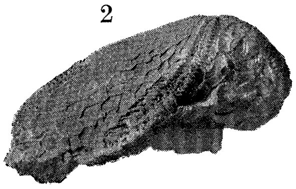

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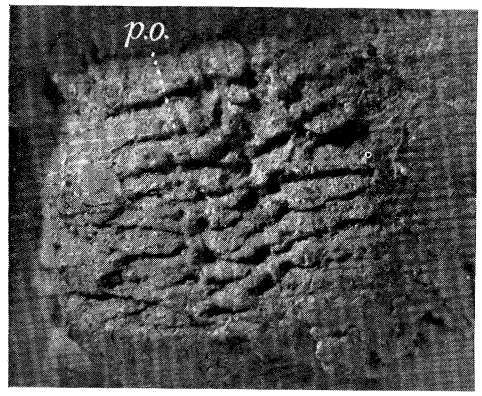

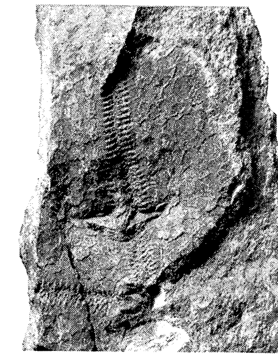

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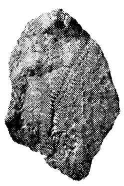

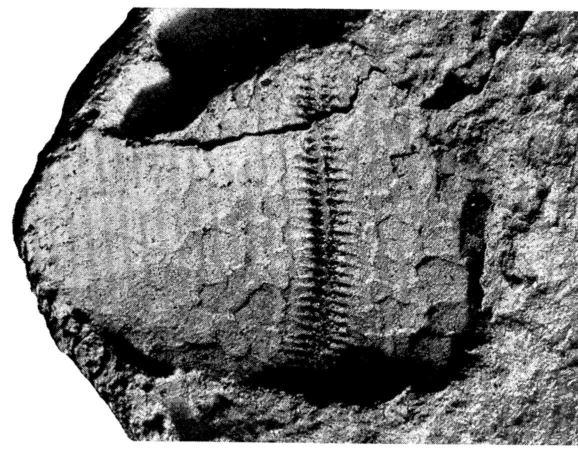

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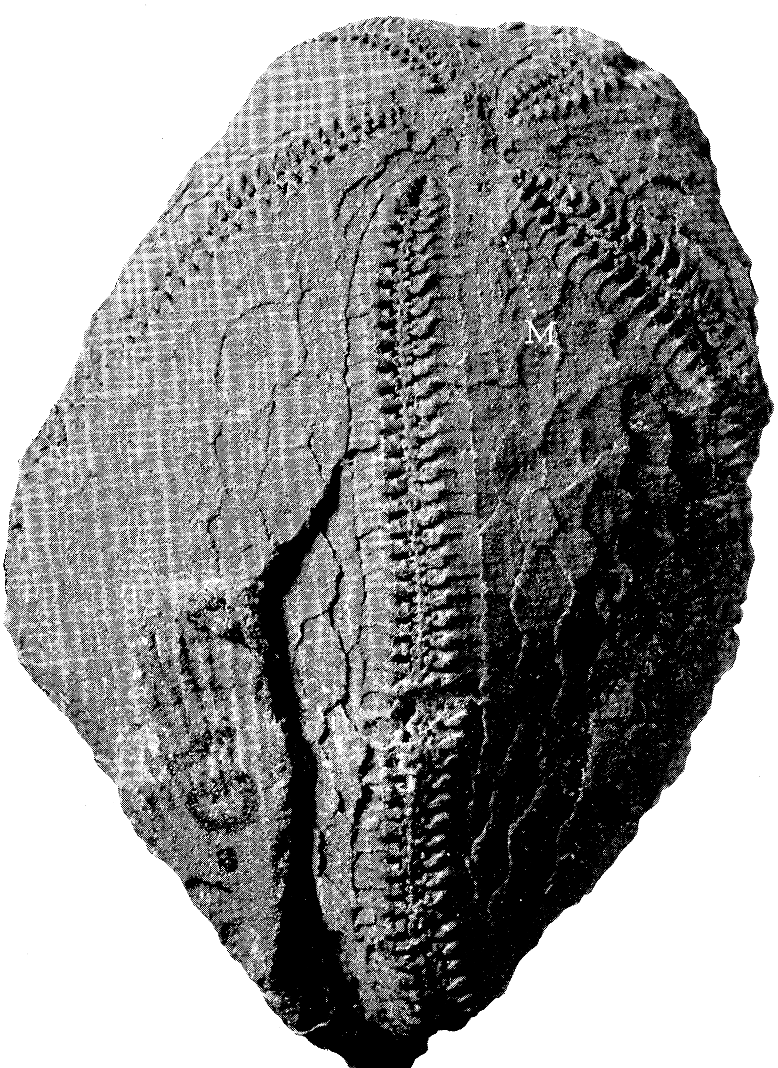

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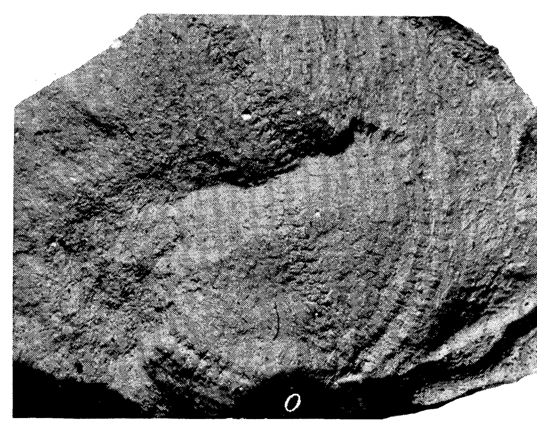

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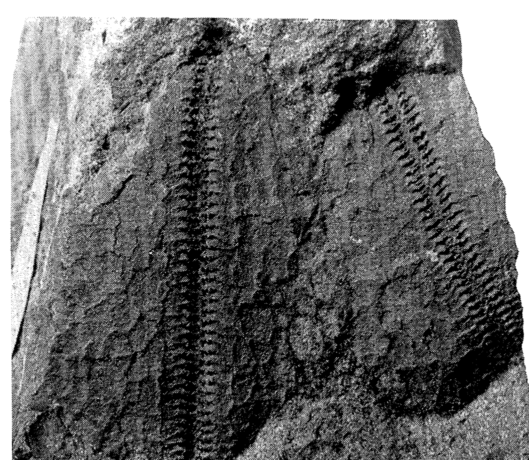

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PLATE 12

FIG. 1. *Aulechinus grayae*. Photograph of a portion of the ambulacrals and neighbouring interambulacrals, × 14; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1204.

FIG. 2. *Aulechinus grayae*. A photograph of a portion of the test taken with strong side lighting to show the depth of the groove, the overlap of the plates and the small numerous spines on the interambulacrals, × 8; coll. Mr Begg, No. 19.

FIG. 3. *Aulechinus grayae*. Photograph showing the lateral spine bunches magnified, × 14; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1200*c*.

FIG. 4. *Ectinechinus lamonti*. Photograph of a portion of the test showing the very slight perradial groove and the sparse spines on the interambulacrals, × 8; coll. Mr Begg, No. 21.

FIG. 5. *Ectinechinus lamonti*. Photograph of a portion of the test near the mouth to show the pores. The lower end of the photograph shows the jaws of the lantern, × 8; coll. Brit. Mus. Nat. Hist. No. E. 31414.

FIG. 6. *Ectinechinus lamonti*. Photograph of a small portion of the interambulacrals to show one larger centrally placed spine, × 8; coll. Mr Begg, No. 22.

i. jaw; *l.sp*. lateral spines of groove; *sp*. single spines on interambulacral; *p.o*. pores.

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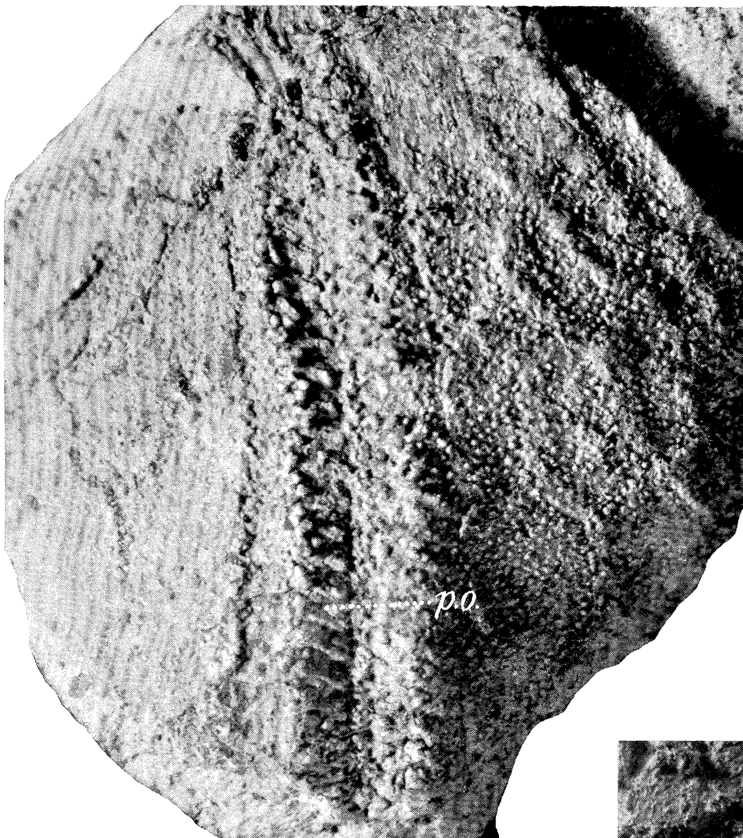

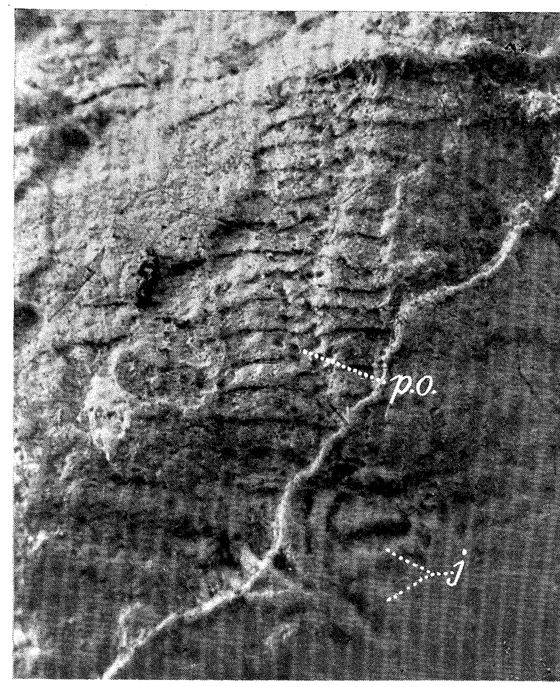

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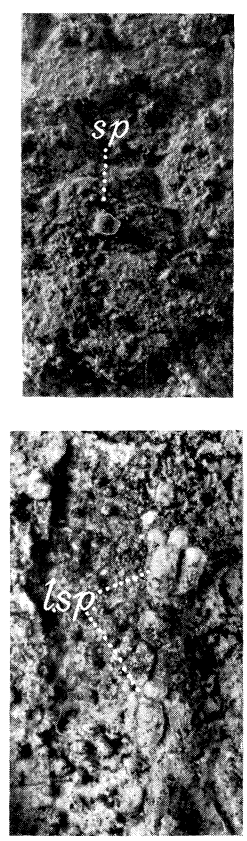

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Plate 13

Fig. 1. *Aulechinus grayae*. Photograph of an interior mould of the apical area of the same specimen as that figured (fig. 1, Pl. 10), × 8.

Fig. 2. *Aulechinus grayae*. Photograph of an interior mould of an extremity of an ambulacrum, × 12; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1200.

Fig. 3. *Ectinechinus lamonti*. Photograph of an interior mould of the apical area of the same specimen as that figured (fig. 1, Pl. 11), × 8.

Fig. 4. *Ectinechinus lamonti*. Photograph of an interior mould near the apex. (Calcite has not been entirely dissolved out of this specimen), × 2; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1220.

Fig. 5. *Echinocystis pomum*. Photograph of madreporite, initial and neighbouring plates, × 10; coll. Brit. Mus. (Nat. Hist.), No. 40158.

an. anal mound; *m*. madreporite-genital; *Oc*. ocular; *p.i*. strands filling pores.

The white line on fig. 2 indicates the strands filling radial vessel.

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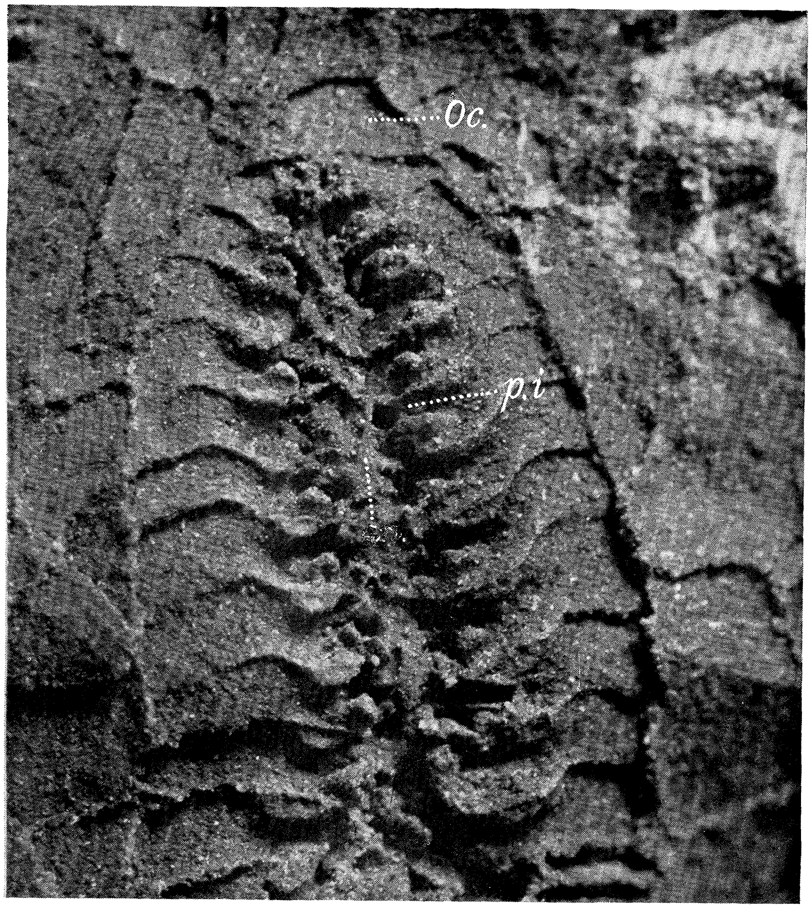

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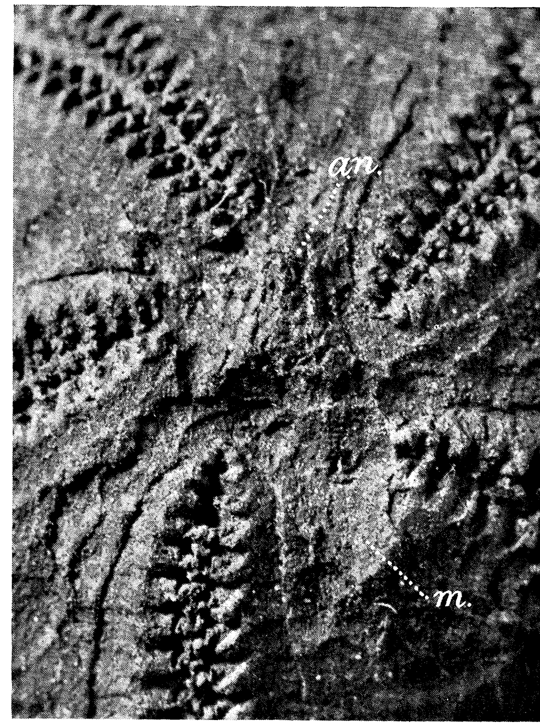

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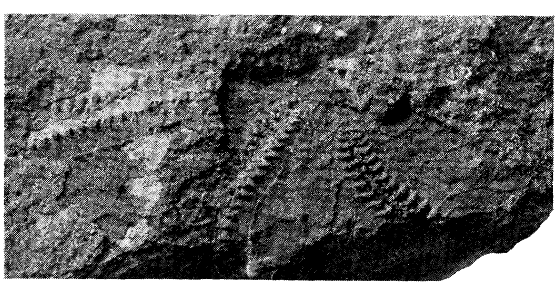

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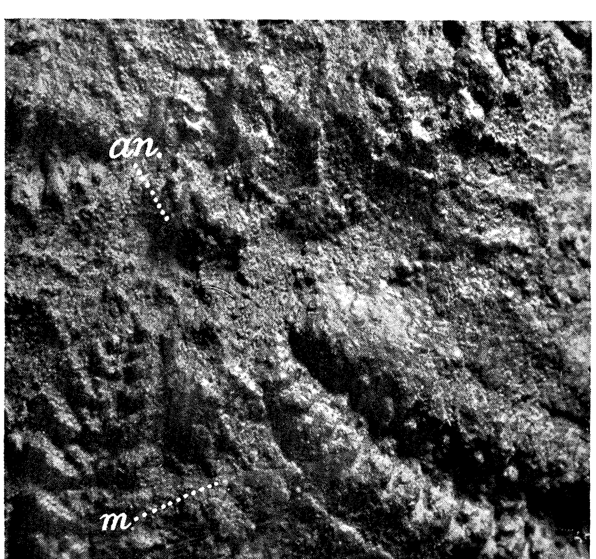

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PLATE 14

FIG. 1. *Aulechinus grayae*. Photograph of a portion of cast of an interior of a test showing two ambulacra (the holotype) and an intervening interambulacrum, $\times 2\frac{1}{2}$; coll. Brit. Mus. (Nat. Hist.), No. E. 31412.

FIG. 2. *Aulechinus grayae*. Photograph of a cast of a portion of an ambulacrum, $\times 4$; coll. Brit. Mus. (Nat. Hist.), No. E. 31406.

FIG. 3. *Aulechinus grayae*. Photograph of a cast showing displaced ambulacral plates, $\times 2\frac{1}{2}$; coll. Brit. Mus. (Nat. Hist.), No. E. 31418.

FIG. 4. *Ectinechinus lamonti*. Photograph of a cast showing a portion of an ambulacrum from within, $\times 12$; coll. the Misses Gray, No. Gr. 13.

FIG. 5. *Ectinechinus lamonti*. Photograph of the internal mould which gave the above cast. The strands representing the infillings of a double pore are seen clearly, $\times 12$.

FIG. 6. *Myriastiches gigas* Sollas. Photograph of a cast showing a portion of an ambulacrum from within, $\times 12$; coll. Oxford Univ. Mus.

FIG. 7. *Palaeodiscus ferox* Salter. Photograph of a cast showing a portion of an ambulacrum from within, $\times 12$; coll. Oxford Univ. Mus.

p.i. pore infillings; *r.v.* groove for radial vessels.

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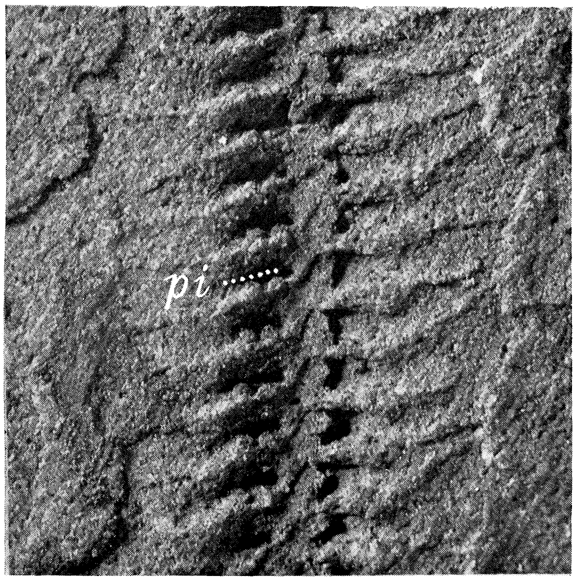


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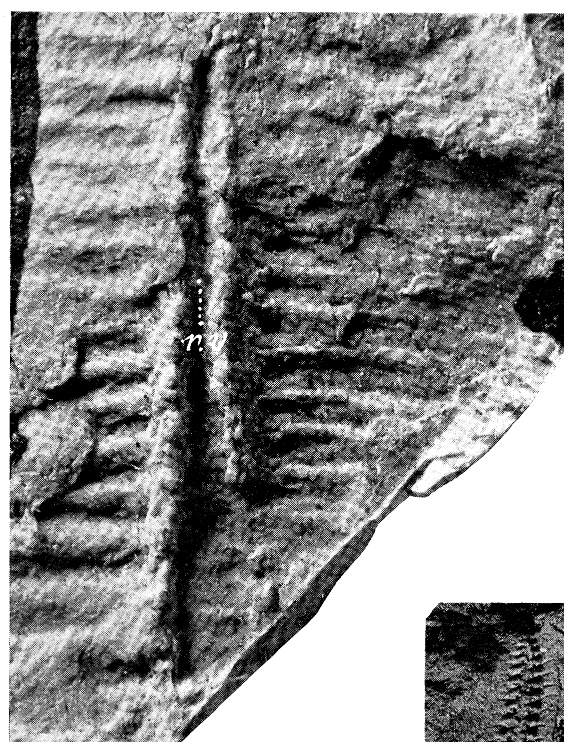

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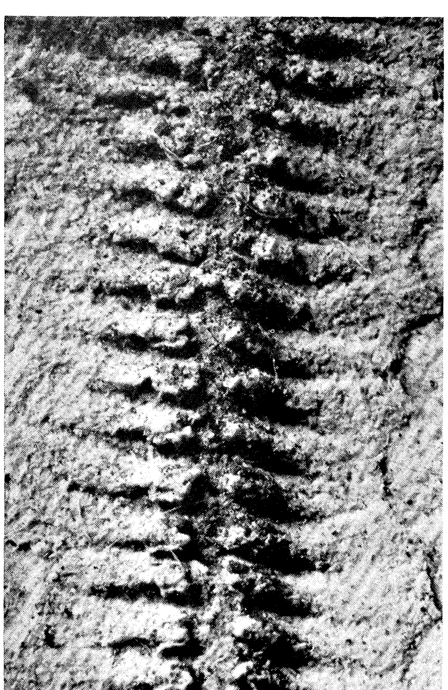

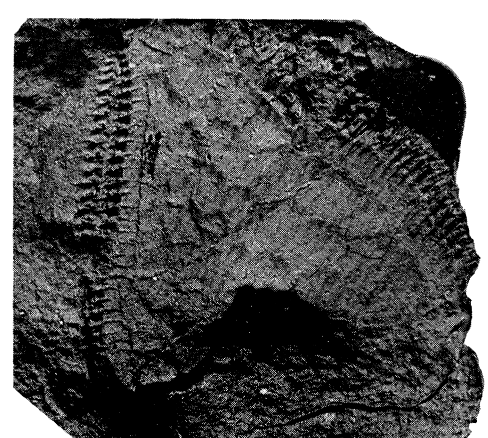
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Plate 15

Fig. 1. *Aulechinus grayae*. Photograph of a cast of the lantern seen from within the test, nat. size; coll. Glasgow Univ. Hunterian Mus. No. 1203*c*.

Fig. 2. *Aulechinus grayae*. Photograph of the same specimen further magnified. The original mould was cracked hence there is a ridge of gutta percha running across the cast almost north to south.

Fig. 3. *Aulechinus grayae*. Photograph of cast of a jaw as seen from within the test, × 12; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1202.

Fig. 4. *Aulechinus grayae*. Photograph of a cast of the bulbous primordial ambulacral plates (a_1) from counterpart of same specimen, × 12.

Fig. 5. *Ectinechinus lamonti*. Photograph of external cast of the oral region, × 3; coll. Brit. Mus. (Nat. Hist.), No. E. 31414.

Fig. 6. *Eothuria beggi*. Photograph of external cast of a portion of the oral surface including the mouth, × 2½; coll. Brit. Mus. (Nat. Hist.), No. E. 27003*d*.

Fig. 7. *Eothuria beggi*. Photographs of a pair of "valves" around the mouth of same specimen, × 14.

Fig. 8. *Eothuria beggi*. Another pair of valves from same specimen showing the distal ossicle(*d*).

Fig. 9. *Eothuria beggi*. Photograph of a portion of an internal mould showing a trilobite thrust through the test which is split along the per-radii, × 3; coll. Brit. Mus. (Nat. Hist.), No. E. 27003*b*.

a.i. swollen first ambulacral; *v.* oral valves; *d.* distal plates.

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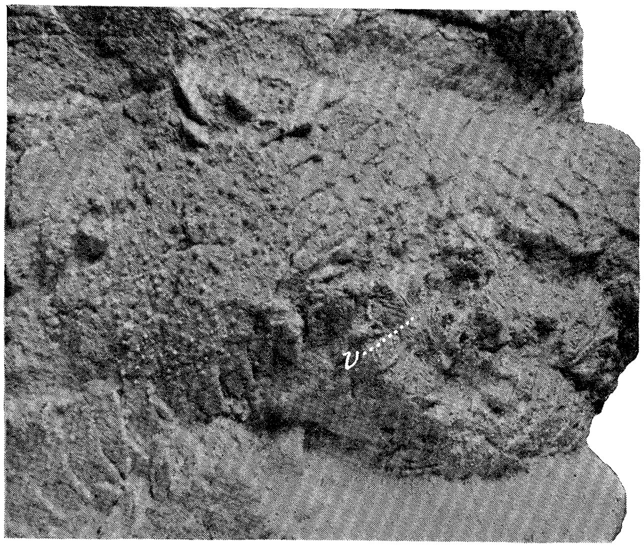

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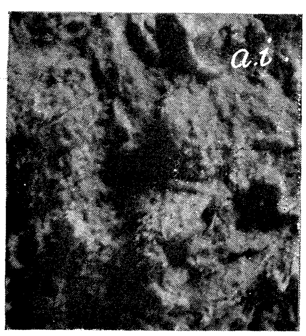

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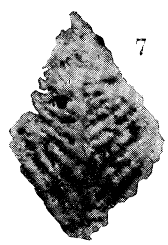

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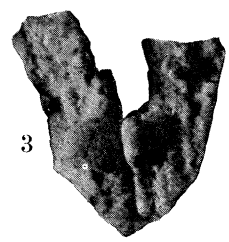

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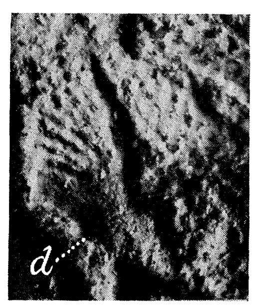

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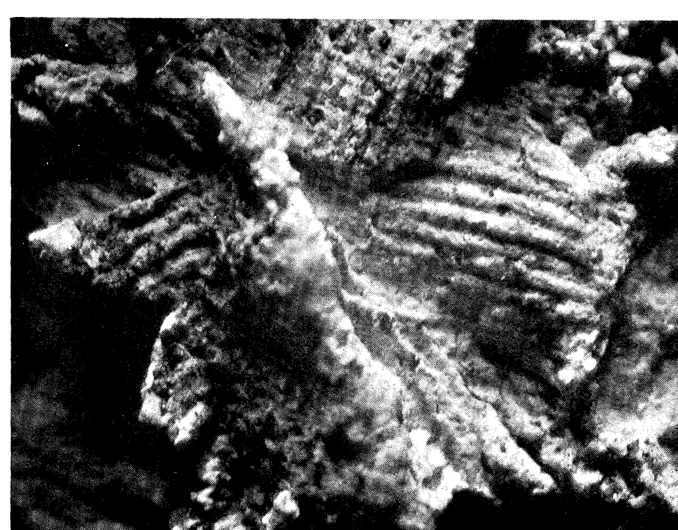

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PLATE 16

Photographs of *Eothuria beggi*

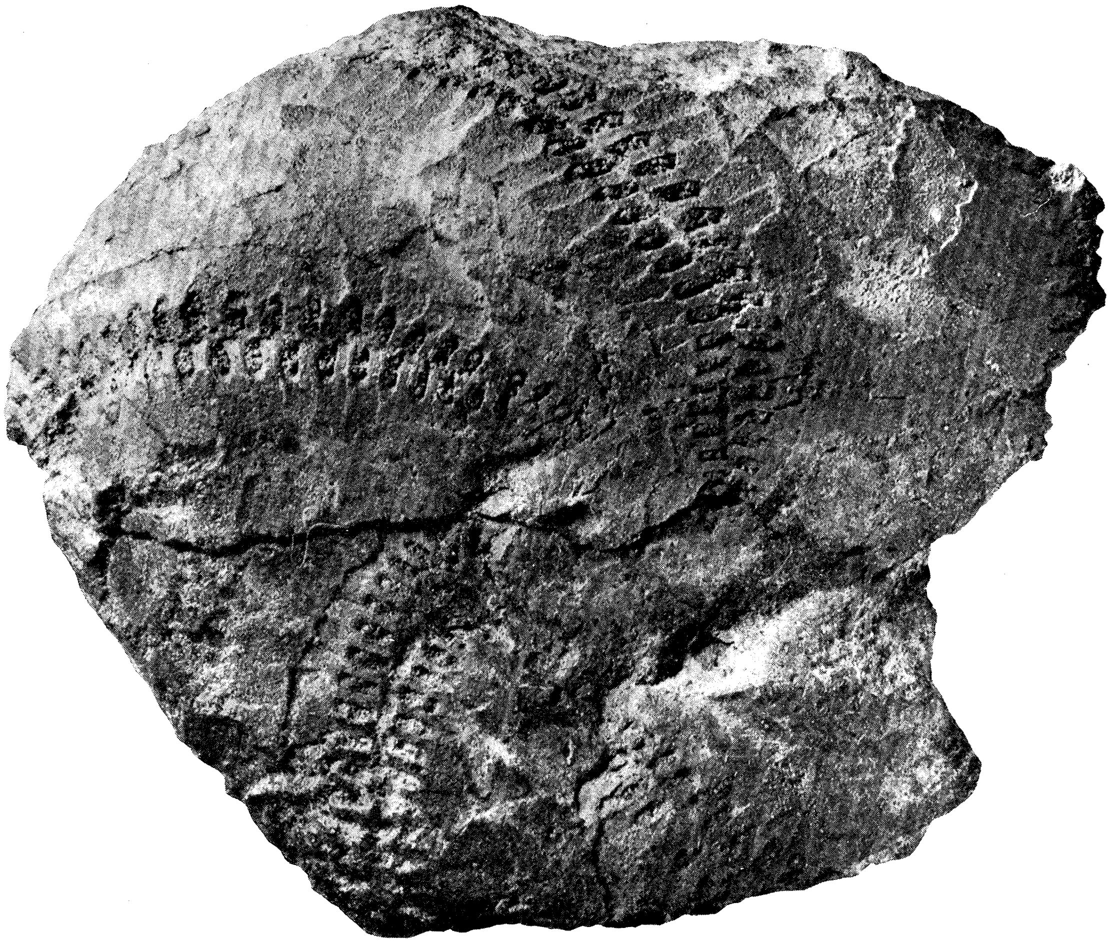
FIG. 1. Photograph of apical side of an internal mould (the holotype), nat. size; coll. Mr Begg, No. 31.

FIG. 2. Photograph of same specimen, × 4.

FIG. 3. Photograph of apical side of an internal mould of another specimen, nat. size; coll. the Misses Gray, No. H.1.

FIG. 4. Photograph of cast of a portion of an external mould showing ambulacrals, × 4; coll. Brit. Mus. (Nat. Hist.), No. E. 27003*c*.

FIG. 5. Photograph showing the same further magnified, × 12.



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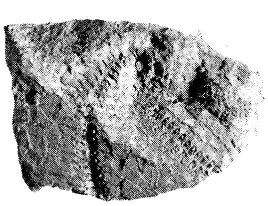

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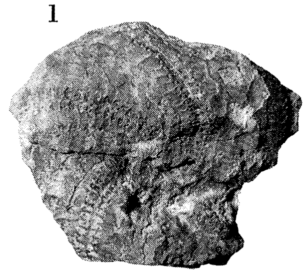

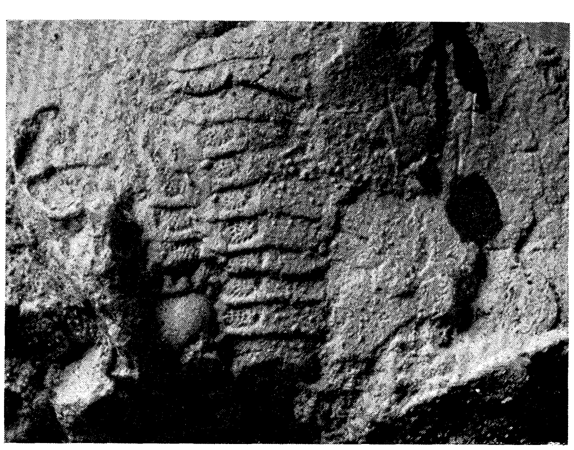

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Plate 17

Photographs of *Eothuria beggi*

Fig. 1. Photograph of an internal mould near the apical region, × 4; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1222.

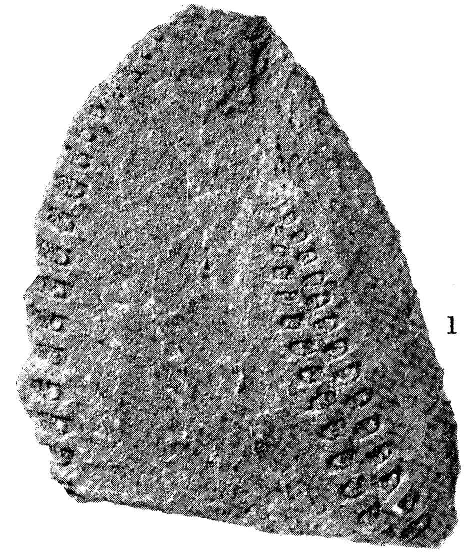
Fig. 2. Photograph of the right-hand ambulacral ray of the above mould further magnified, × 12.

Fig. 3. Photograph of a portion of a mould of an ambulacral ray, × 12; coll. the Misses Gray, No. H. 2.

Fig. 4. Photograph of cast of an internal mould showing the ambulacrals from within, × 12; coll. Brit. Mus. (Nat. Hist.), No. E. 27004*c*.

Fig. 5. Photograph of an interior mould showing the greater part of the oral surface, nat. size; coll. the Misses Gray, No. H 2.

o. mouth; p^1. outer infilling of pore; *t.a.* mould of terminal ambulacral plate.



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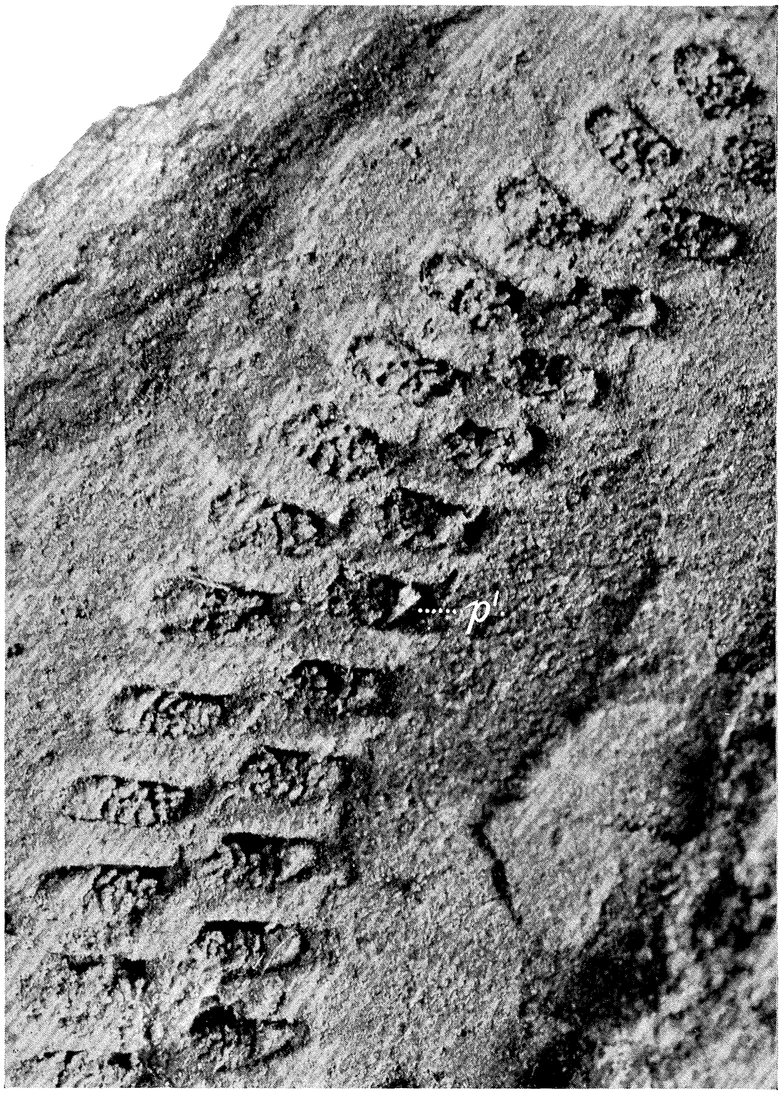

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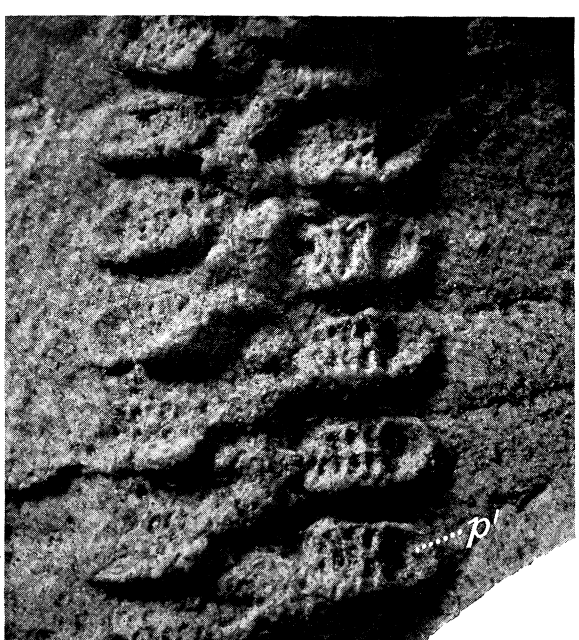

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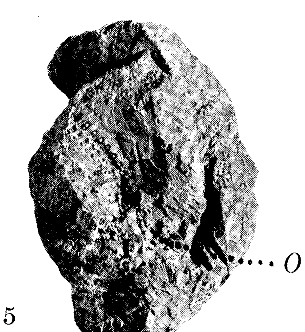

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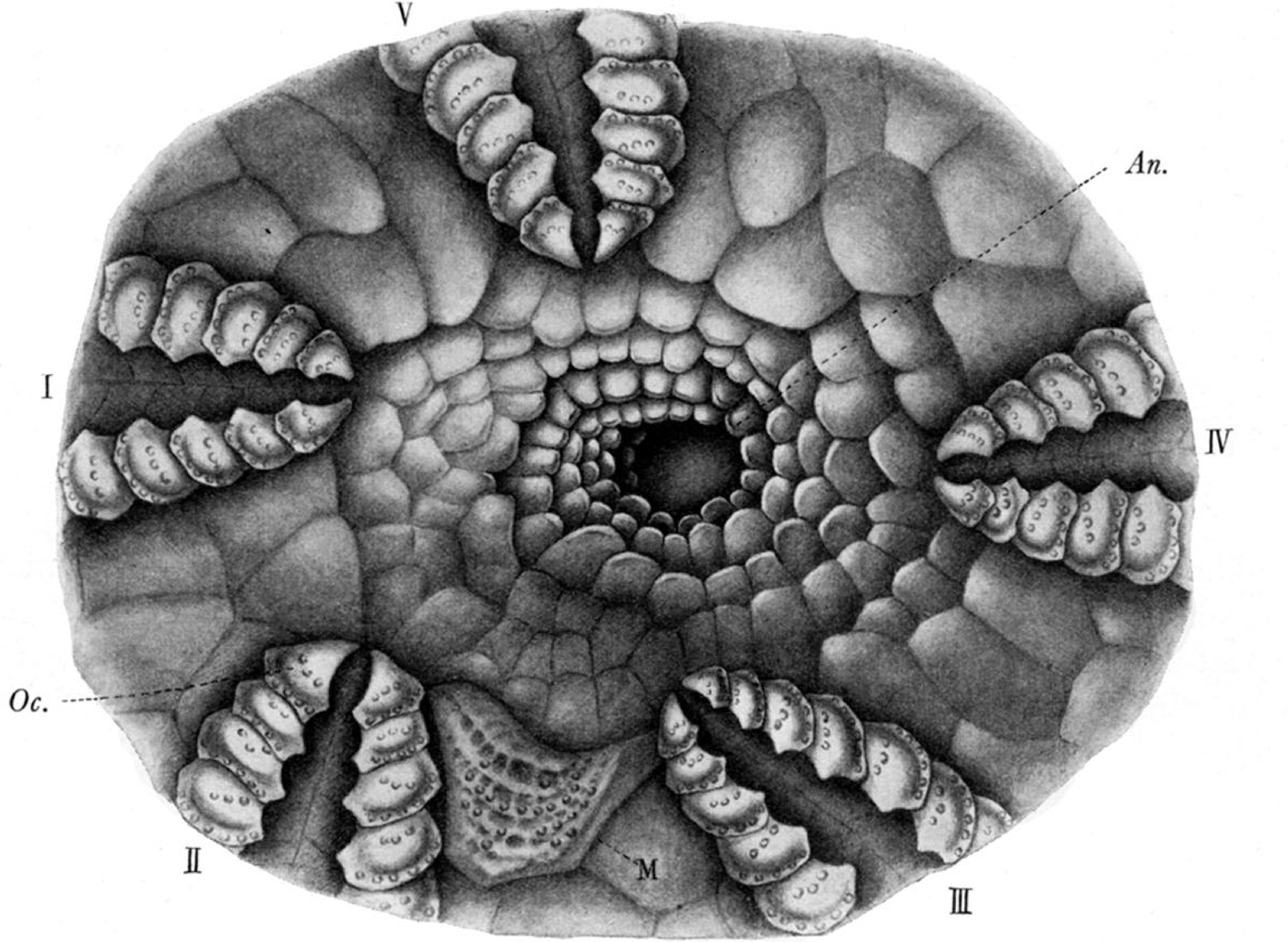


FIG. 3. *Aulechinus grayae*. Enlarged view of apical system slightly reconstructed from Gr. 12. ×12. *An.* = anus; *M.* madreporite-genital; *Oc.* ocular.

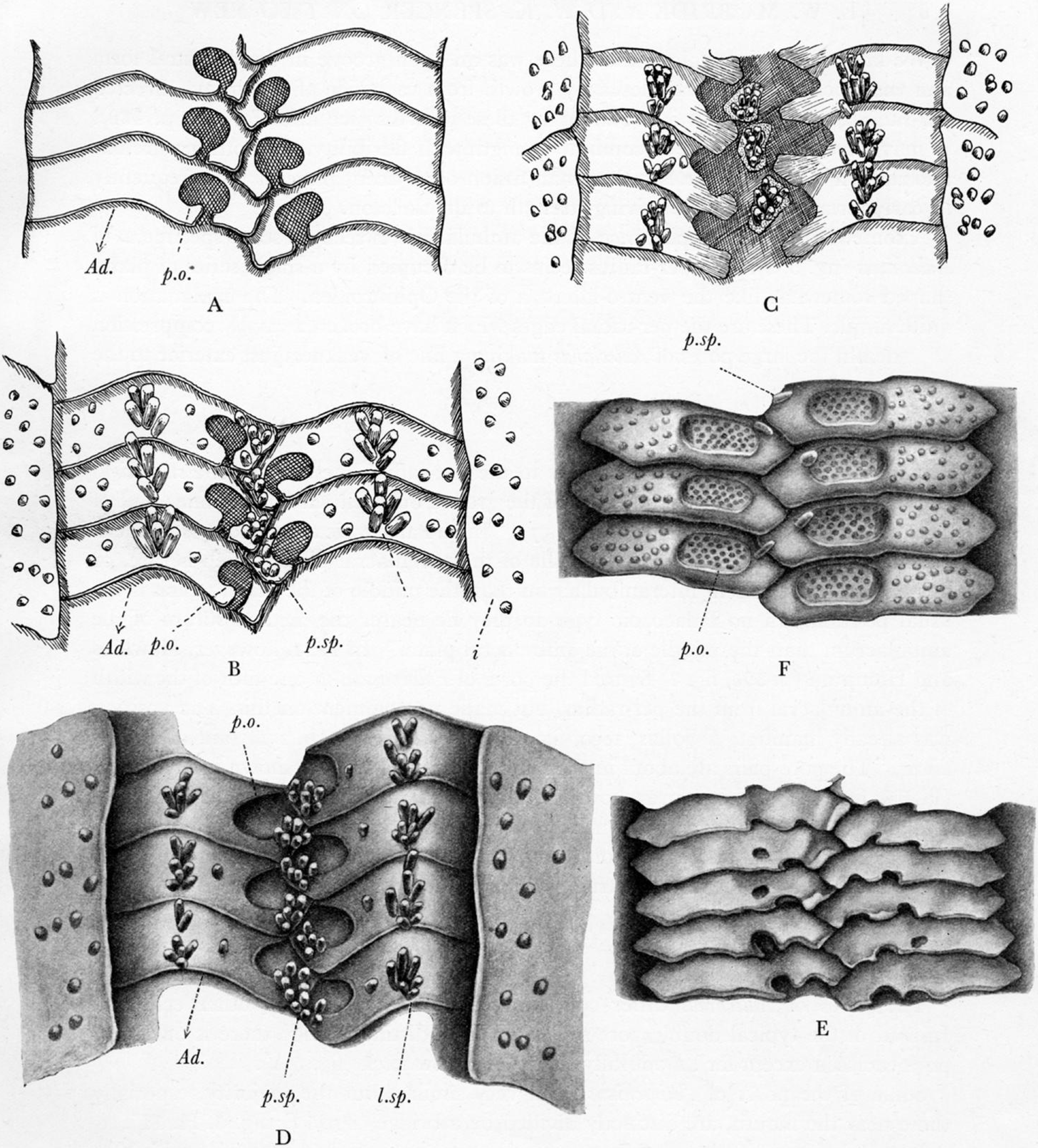


Fig. 5. External views of ambulacralia of *Aulechinus*, *Ectinechinus* and *Eothuria*. A, outline drawing from *Aulechinus* to show overlaps (×16); B, outline drawings of *Aulechinus* to show details of ornament; C, outline drawing of ambulacrals of crushed *Aulechinus* to show per-radial edges of plates broken away and lying in series along the middle line (Gr. 1, ×16); D, wash drawing from *Aulechinus* to show ambulacrals and neighbouring interambulacrals (H.M.E. 1204, ×16); E, wash drawing of ambulacrals near peristome of *Ectinechinus* (E. 31405, ×12); F, wash drawing of ambulacrals of *Eothuria* (E. 27003, ×9); *Ad.* adoral overlap; *i.* interambulacral; *l.sp.* lateral spine groups; *p.sp.* per-radial spine groups; *p.o.* ambulacral pores.

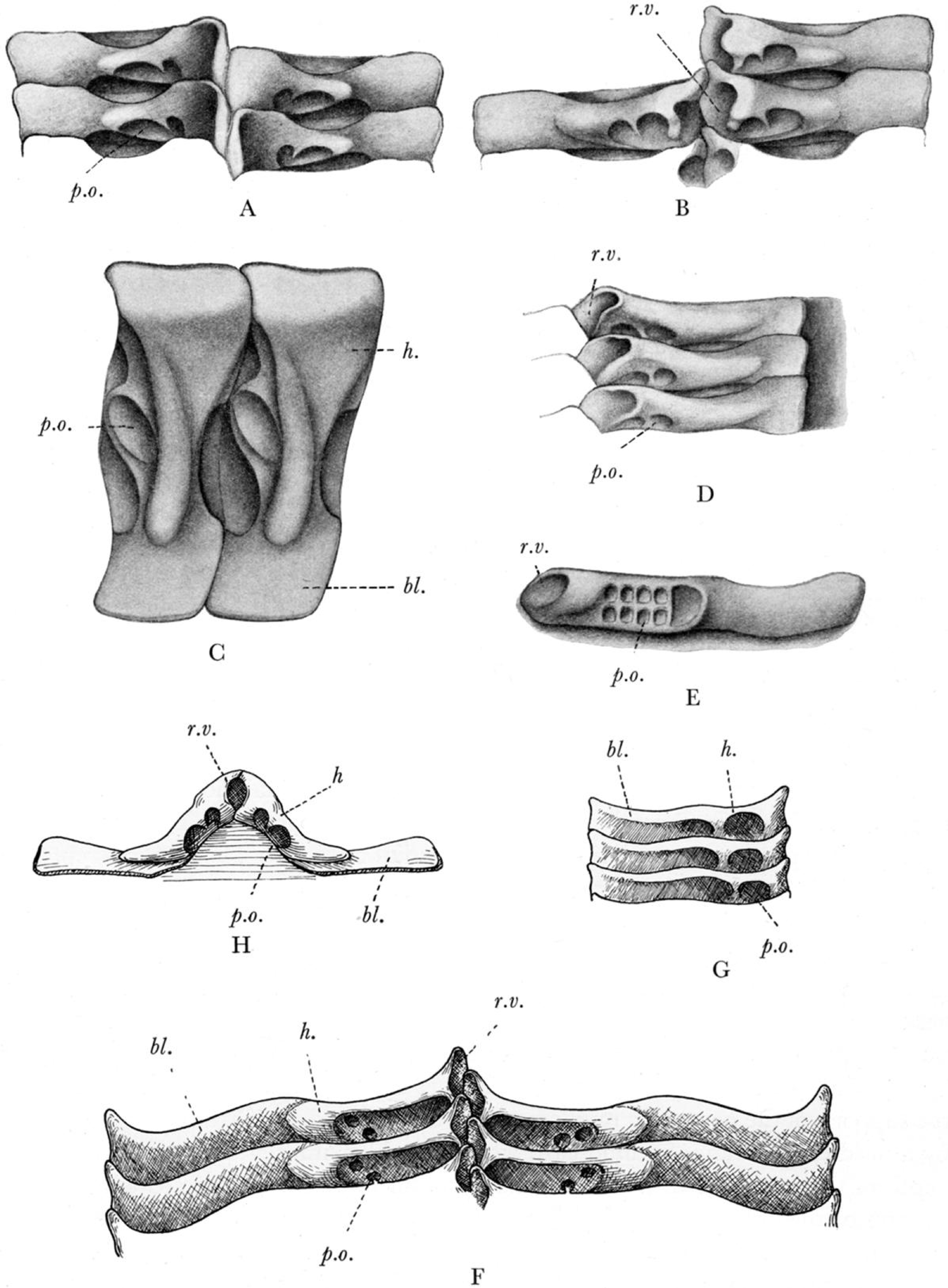
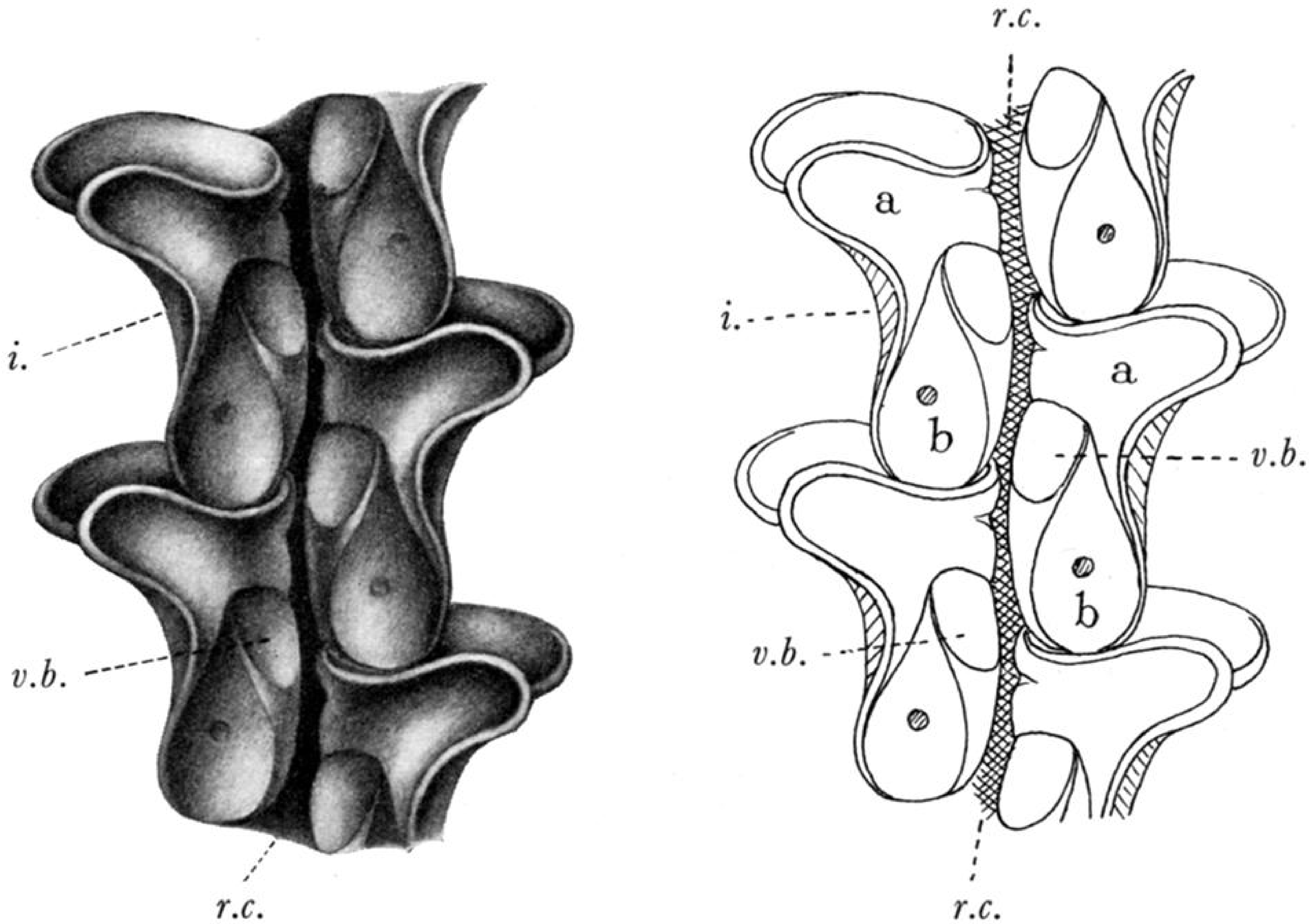


FIG. 7. Internal views of ambulacrals of *Aulechinus*, *Ectinechinus*, *Eothuria*, *Palaeodiscus*, and *Myriastiches*. A, upper view from *Aulechinus* with roof in place (E. 31412, × 20); B, upper view from *Aulechinus* with roof removed (E. 31412, × 20); C, lateral view from *Aulechinus* (E. 31412, × 32); D, upper view from *Ectinechinus* with roof removed (these have double pores) (Gr. 13, × 24); E, upper view from *Eothuria* (E. 27004, × 12); F, upper view from *Palaeodiscus* (Oxford Univ. Mus., × 24); G, upper view from *Myriastiches* (Oxford Univ. Mus., × 18); H, reconstructed cross-section of a pair of ambulacrals of *Aulechinus* (× 18). *bl.* blade; *h.* haft; *p.o.* pores; *r.v.* hollows for radial vessels.



A B

FIG. 9. A, *Aulechinus*. Wash drawing of wax model of mud strands representing the radial canal and the passage from ampulla to the tube-feet (H.M.E. 1200, × 40). B, Outline drawing to indicate the various structures shown in A. *i.* indentation, the beginning of the ingrowth which in later forms divides the passage into two parts; *r.c.* radial canal; *a.* the lateral branch of the passage; *b.* the longitudinal branch of the vessel; *v.b.* the branch vessel.

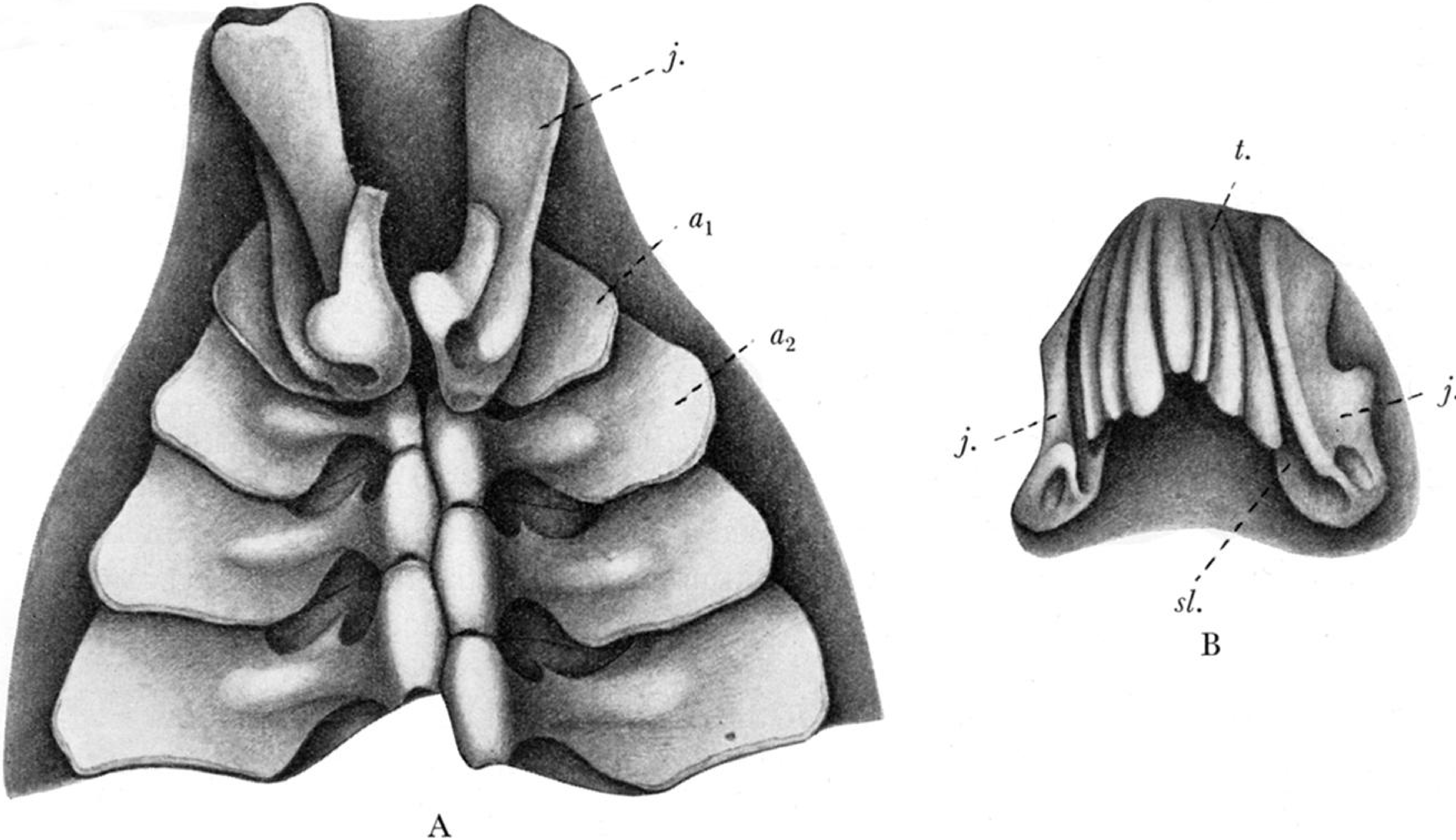
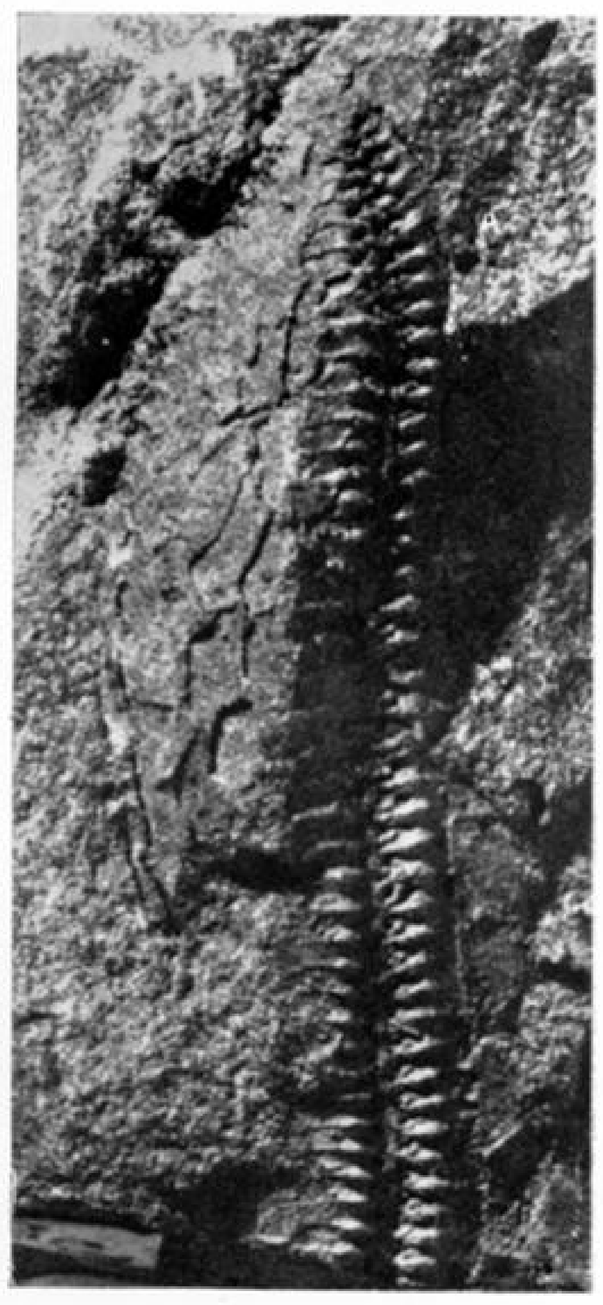


FIG. 12. A, jaws and anterior ambulacrals of *Aulechinus*, from H.M.E. 1202, ×25. B, teeth of *Aulechinus*, from H.M.E. 1202, ×15. a_1, first ambulacral; a_2, second ambulacral; *j.* jaws; *t.* tooth; *sl.* tooth slide.



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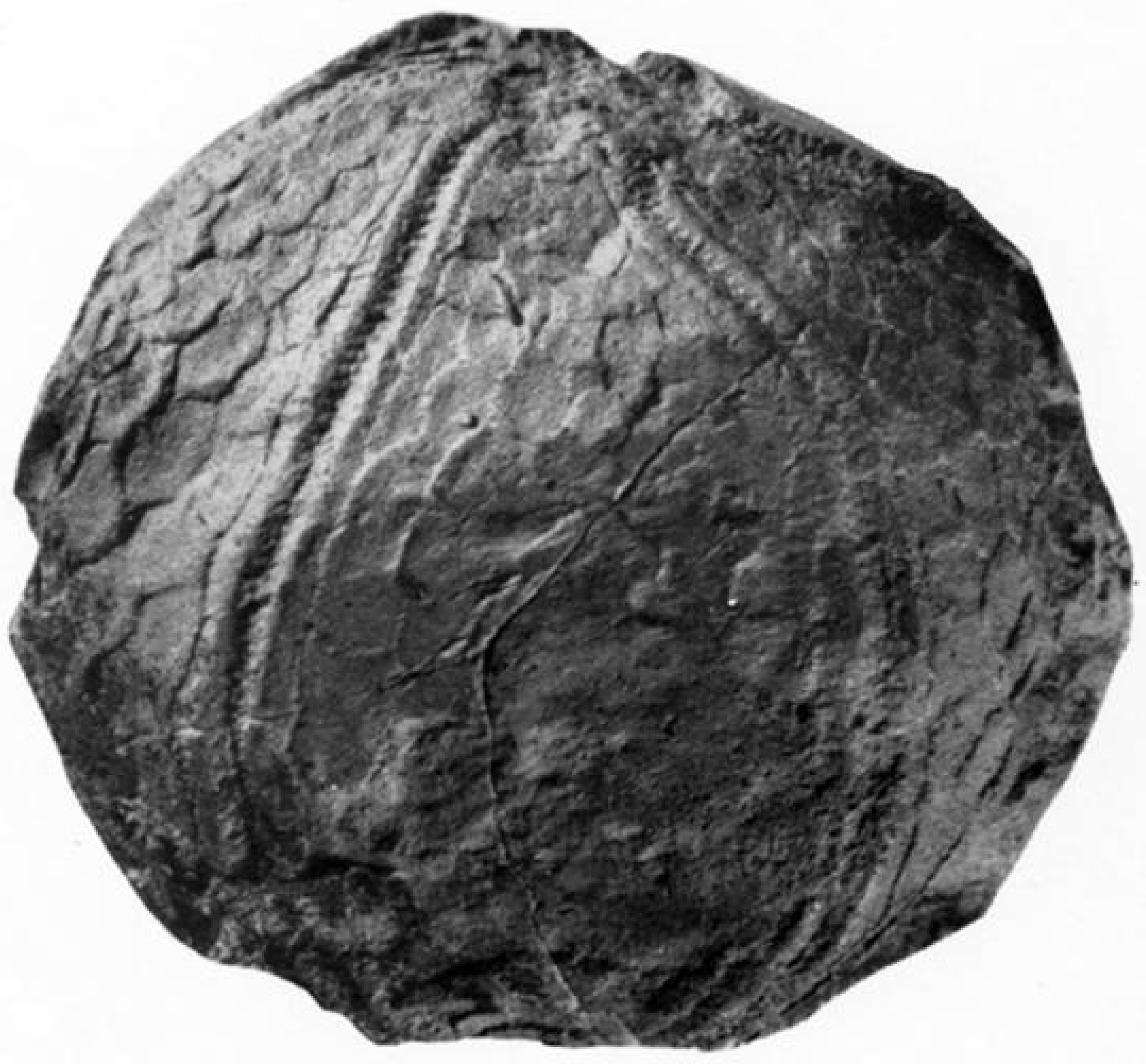

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PLATE 10

Photographs of *Aulechinus grayae*

FIG. 1. Lateral view of an internal mould, × 4; coll. the Misses Gray, No. Gr. 12.

FIG. 2. Cast of external mould of counterpart of the same specimen, × 2.

FIG. 3. Lateral view of the apical portion of an internal mould, × $2\frac{1}{2}$; coll. Brit. Mus. (Nat. Hist.) E. 31412 (the holotype).

FIG. 4. Lateral view of the apical portion of an internal mould showing a pointed apex, × $2\frac{1}{2}$; coll. the Misses Gray, No. Gr. 15.

FIG. 5. Lateral view of a much compressed internal mould, × $2\frac{1}{2}$; coll. the Misses Gray, No. Gr. 3*c*.

FIG. 6. Cast of an external mould of the test showing a portion of an interambulacrum and of an ambulacrum, × $2\frac{1}{2}$; coll. Brit. Mus. (Nat. Hist.), No. E. 31410.

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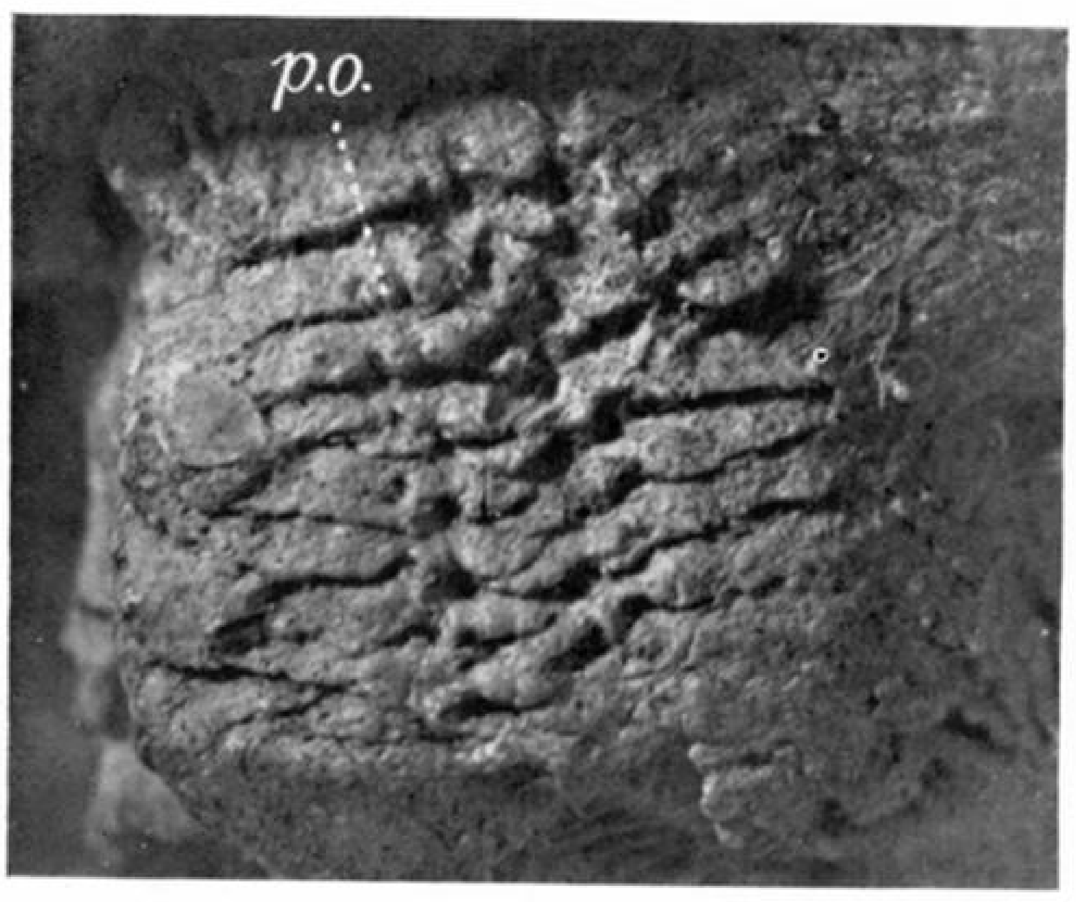

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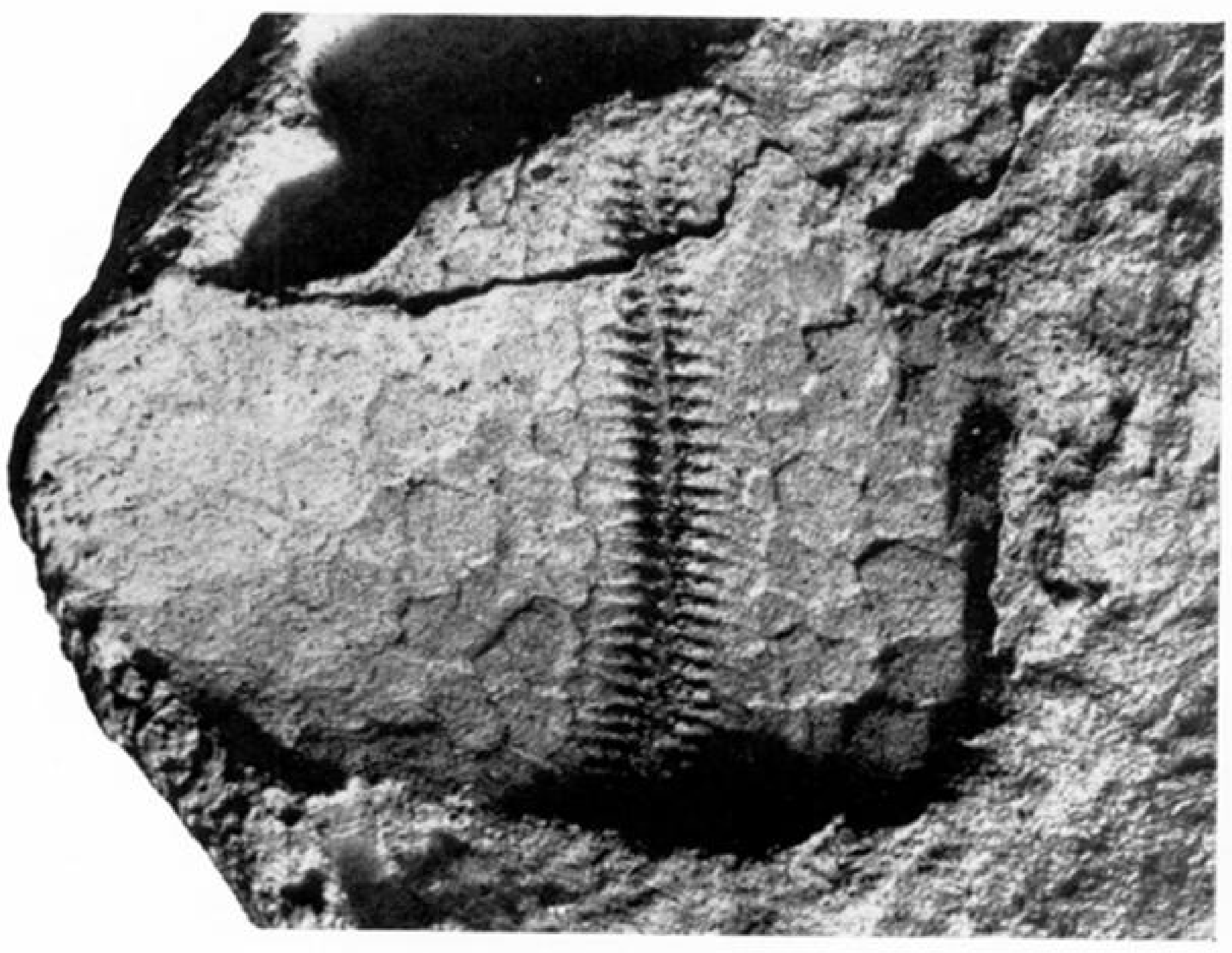

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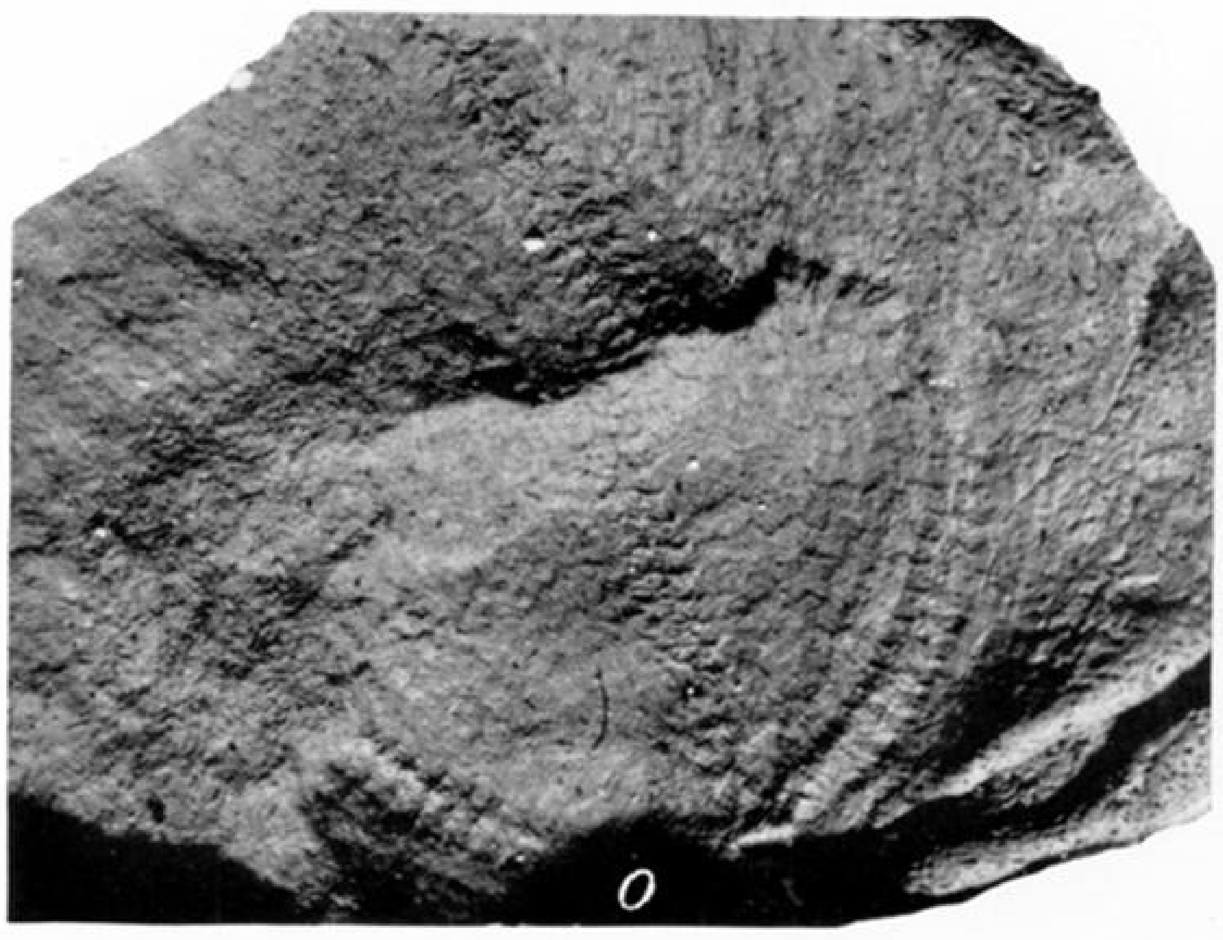

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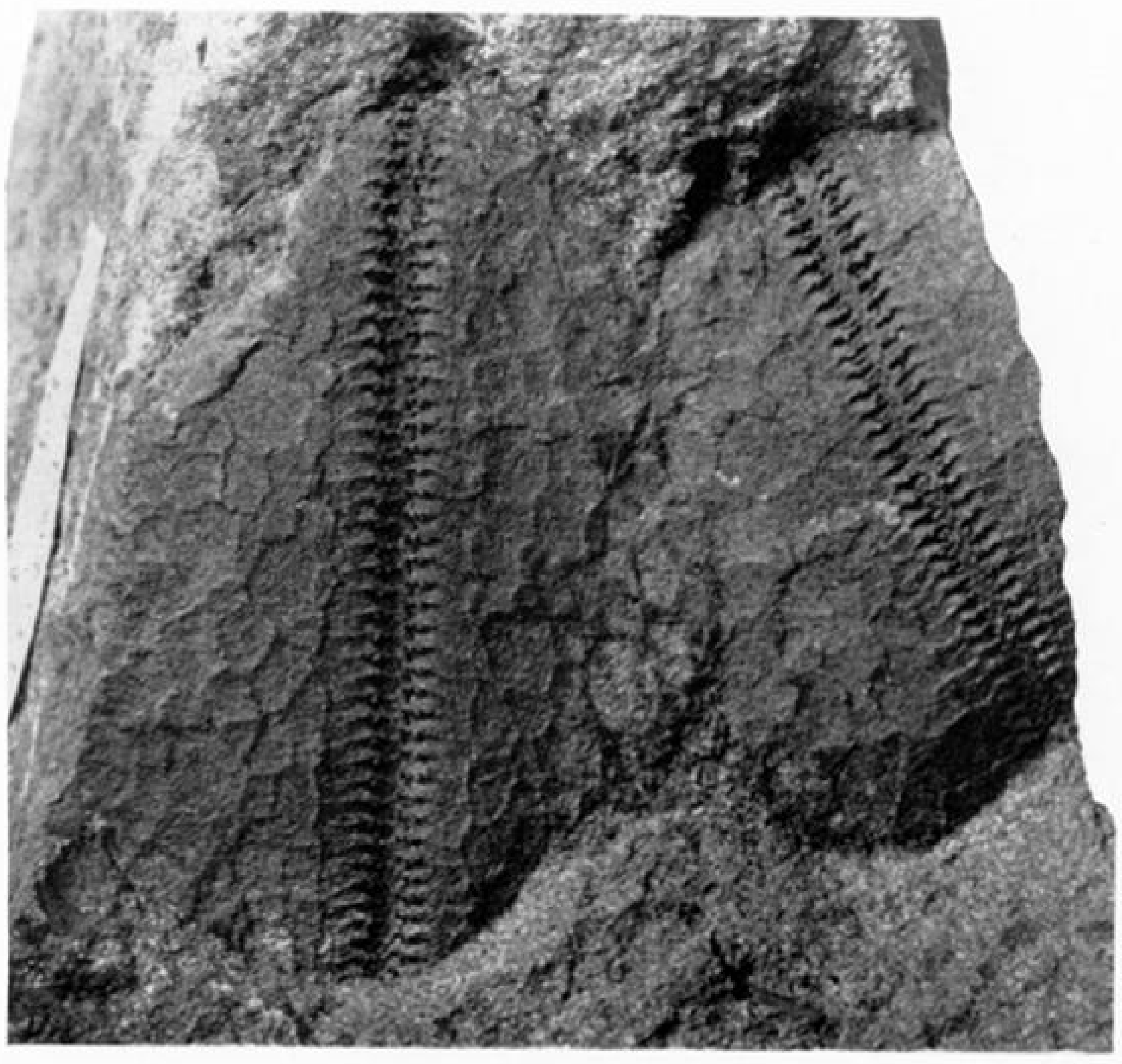

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PLATE 11

Photographs of *Ectinechinus lamonti*

FIG. 1. Apical view of internal mould of holotype, × 4; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1218.

FIG. 2. Profile view of same, nat. size.

FIG. 3. View of base of an internal mould, nat. size; coll. the Misses GRAY, No. Gr. 11*c*.

FIG. 4. View of base of an external mould (the smallest specimen), nat. size; coll. Mr Begg, No. 26.

FIG. 5. Antero-lateral view of an internal mould, × 2½; coll. the Misses Gray, No. Gr. 13.

FIG. 6. Cast of an internal mould, × 2½; coll. Brit. Mus. (Nat. Hist.), No. E. 31408.

FIG. 7. Portions of two internal moulds embedded in the same block, × 2; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1223*a*.

FIG. 8. Cast of external mould of a portion of an ambulacrum showing the double pores, × 8; coll. Brit. Mus. (Nat. Hist.), No. E. 31405.

M. madreporite-genital; *o.* mouth; *p.o.* pores.

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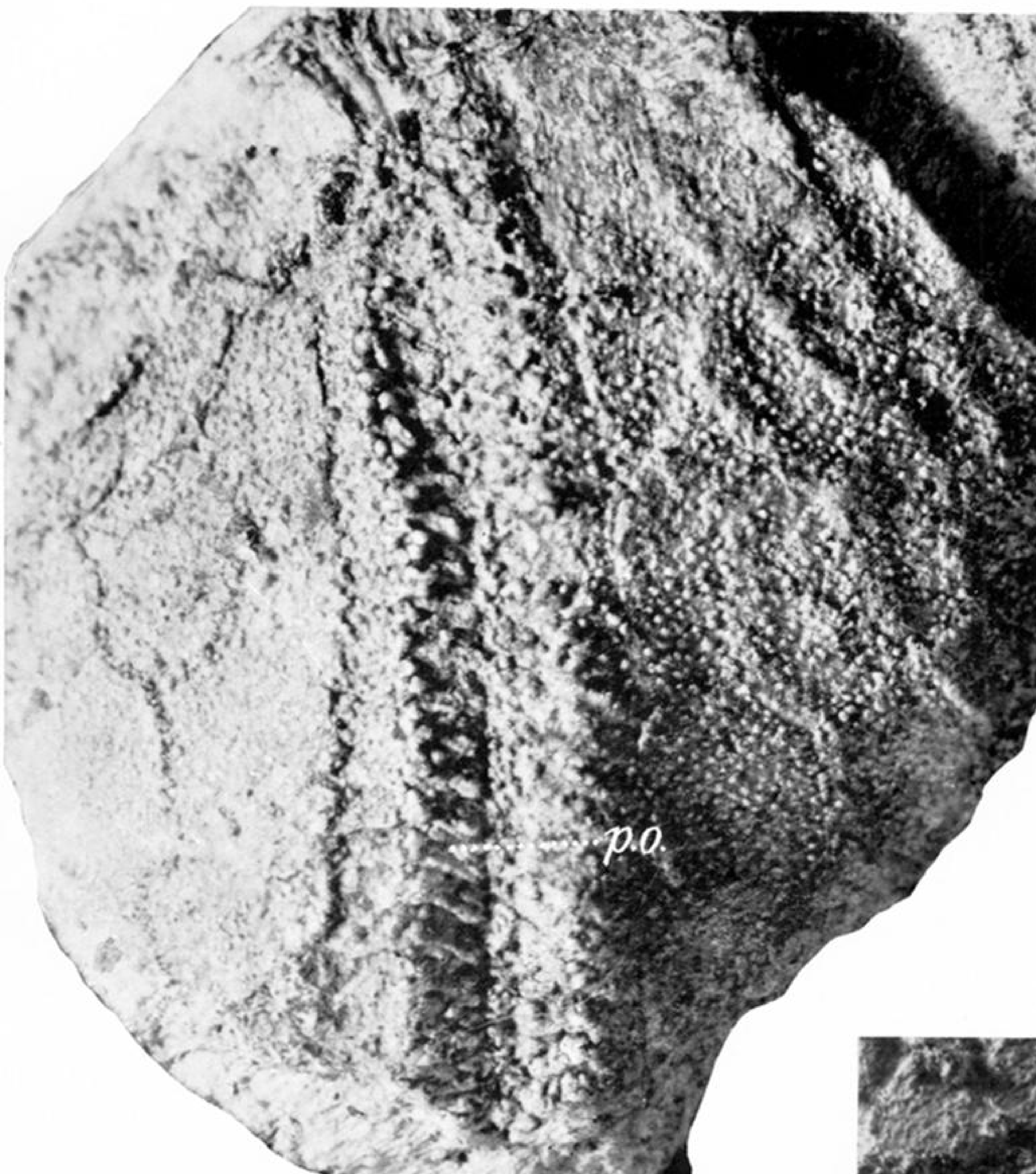

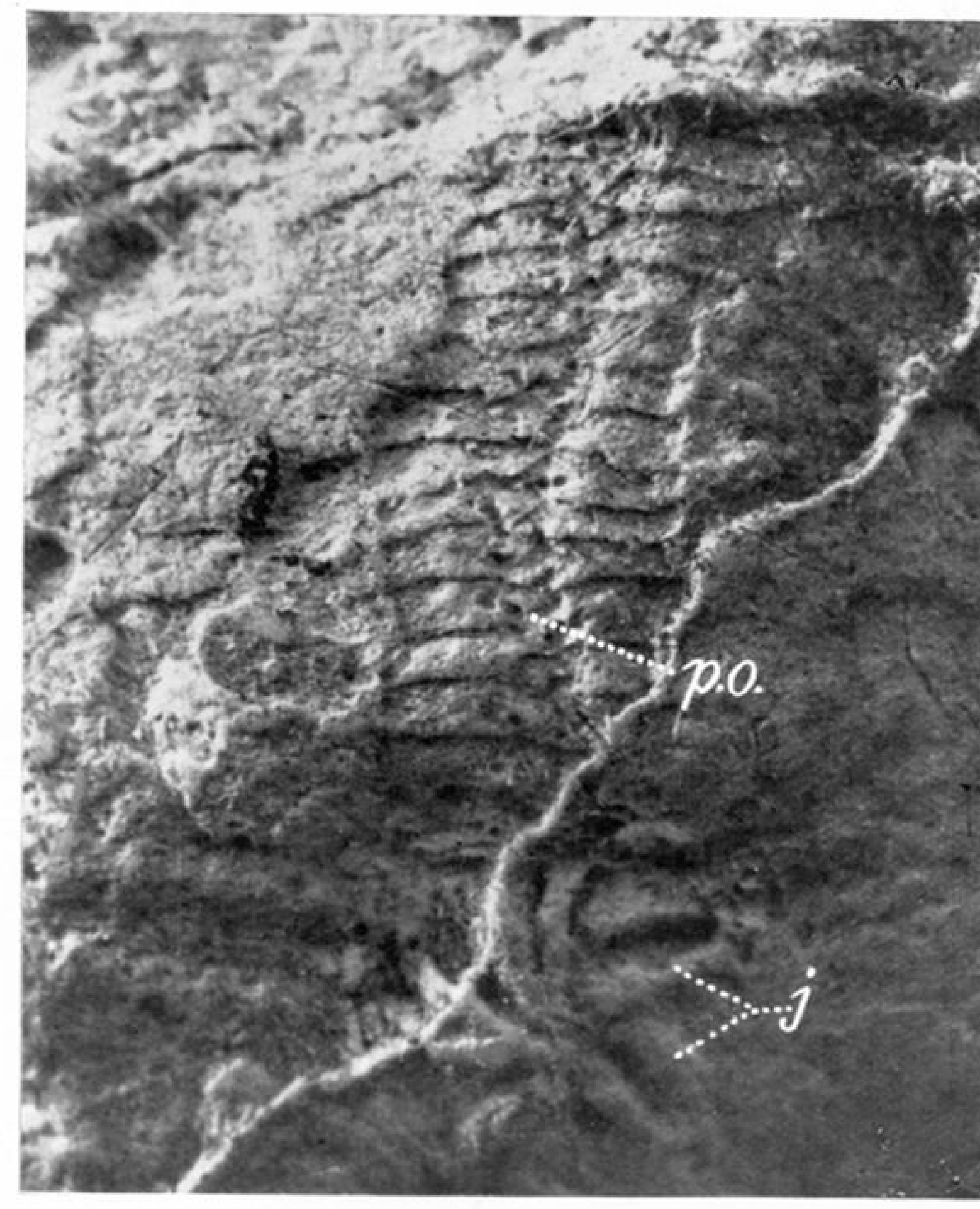

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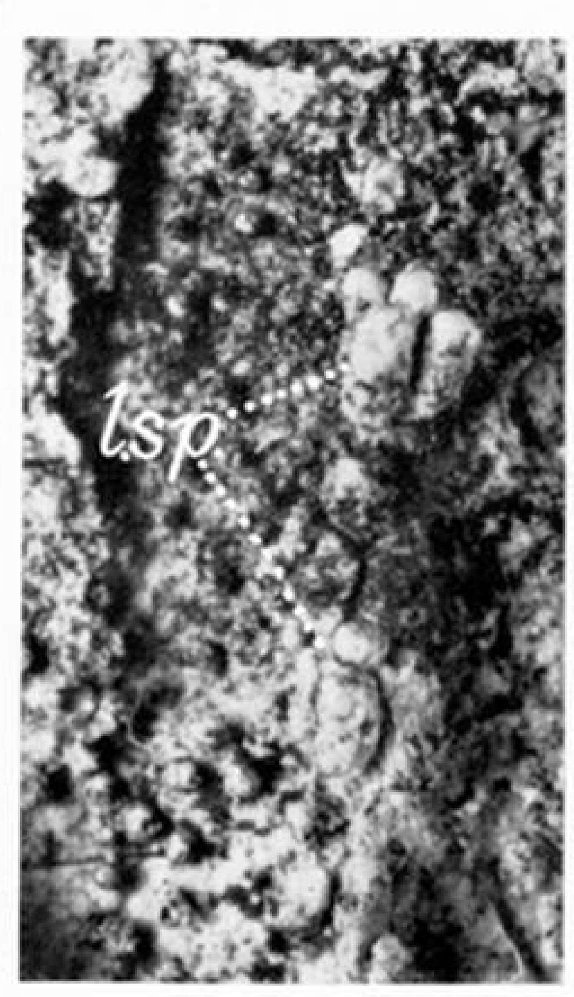

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PLATE 12

FIG. 1. *Aulechinus grayae.* Photograph of a portion of the ambulacrals and neighbouring interambulacrals, × 14; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1204.

FIG. 2. *Aulechinus grayae.* A photograph of a portion of the test taken with strong side lighting to show the depth of the groove, the overlap of the plates and the small numerous spines on the interambulacrals, × 8; coll. Mr Begg, No. 19.

FIG. 3. *Aulechinus grayae.* Photograph showing the lateral spine bunches magnified, × 14; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1200*c*.

FIG. 4. *Ectinechinus lamonti.* Photograph of a portion of the test showing the very slight perradial groove and the sparse spines on the interambulacrals, × 8; coll. Mr Begg, No. 21.

FIG. 5. *Ectinechinus lamonti.* Photograph of a portion of the test near the mouth to show the pores. The lower end of the photograph shows the jaws of the lantern, × 8; coll. Brit. Mus. Nat. Hist. No. E. 31414.

FIG. 6. *Ectinechinus lamonti.* Photograph of a small portion of the interambulacrals to show one larger centrally placed spine, × 8; coll. Mr Begg, No. 22.

i. jaw; *l.sp.* lateral spines of groove; *sp.* single spines on interambulacral; *p.o.* pores.

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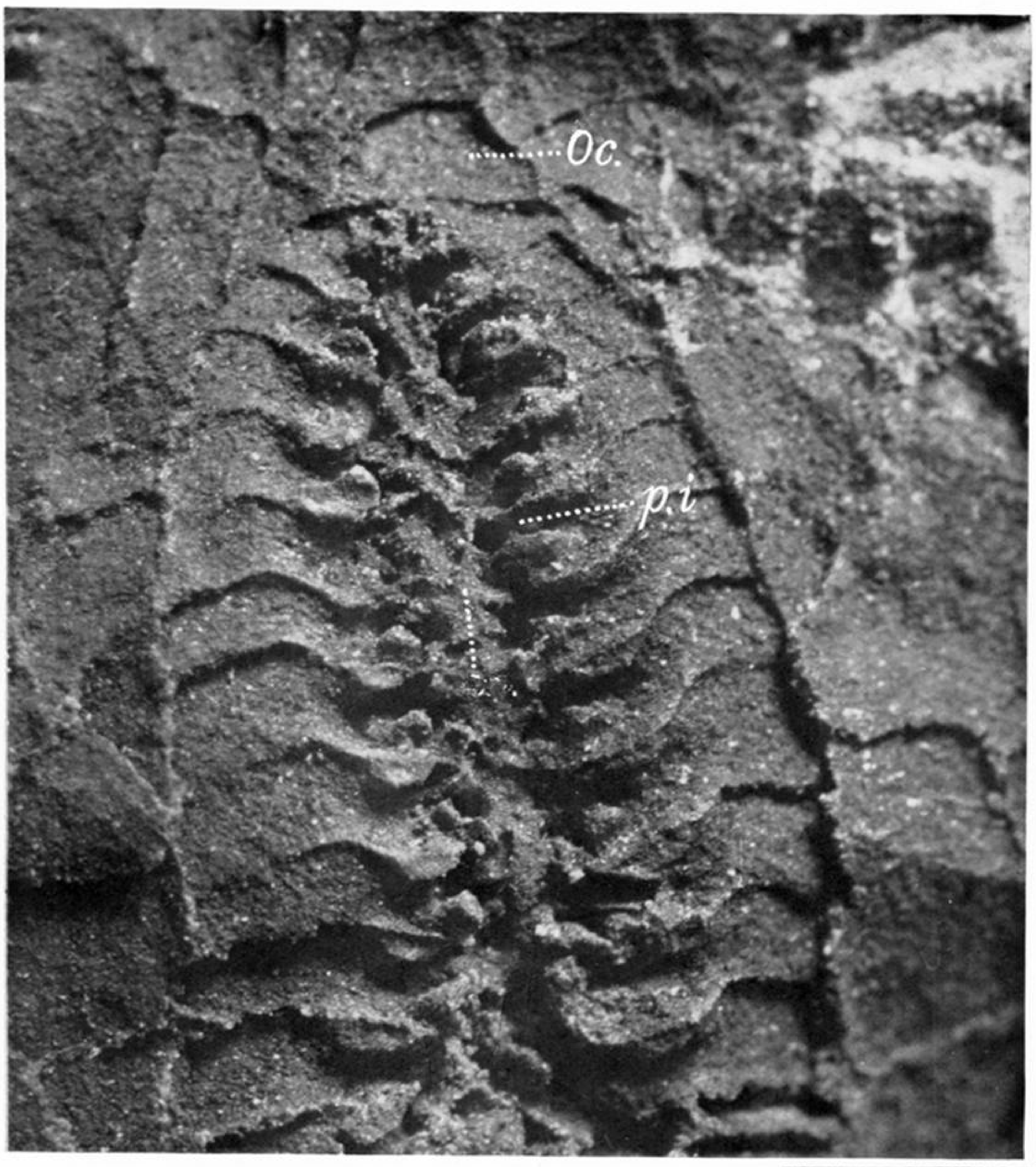

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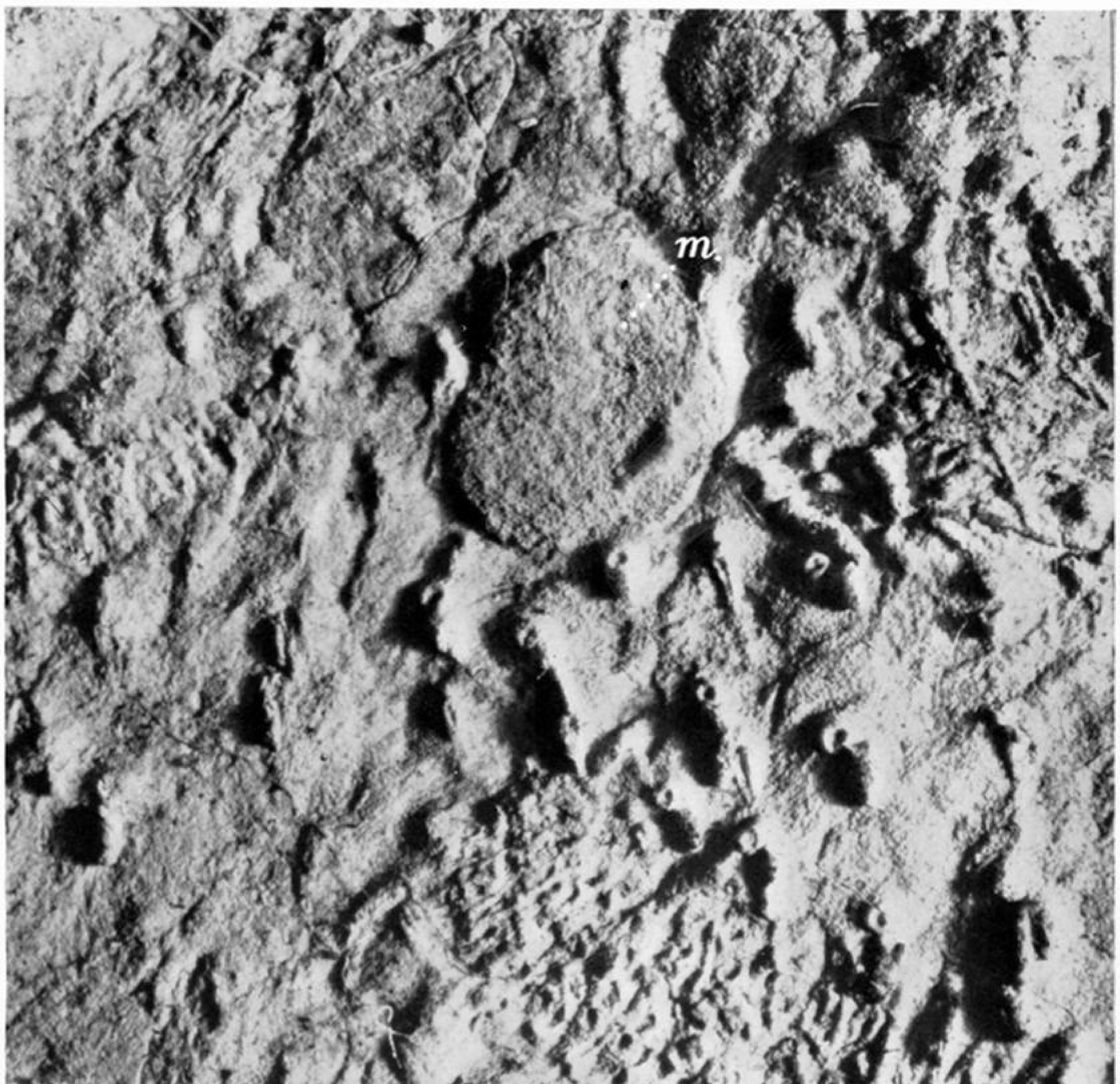

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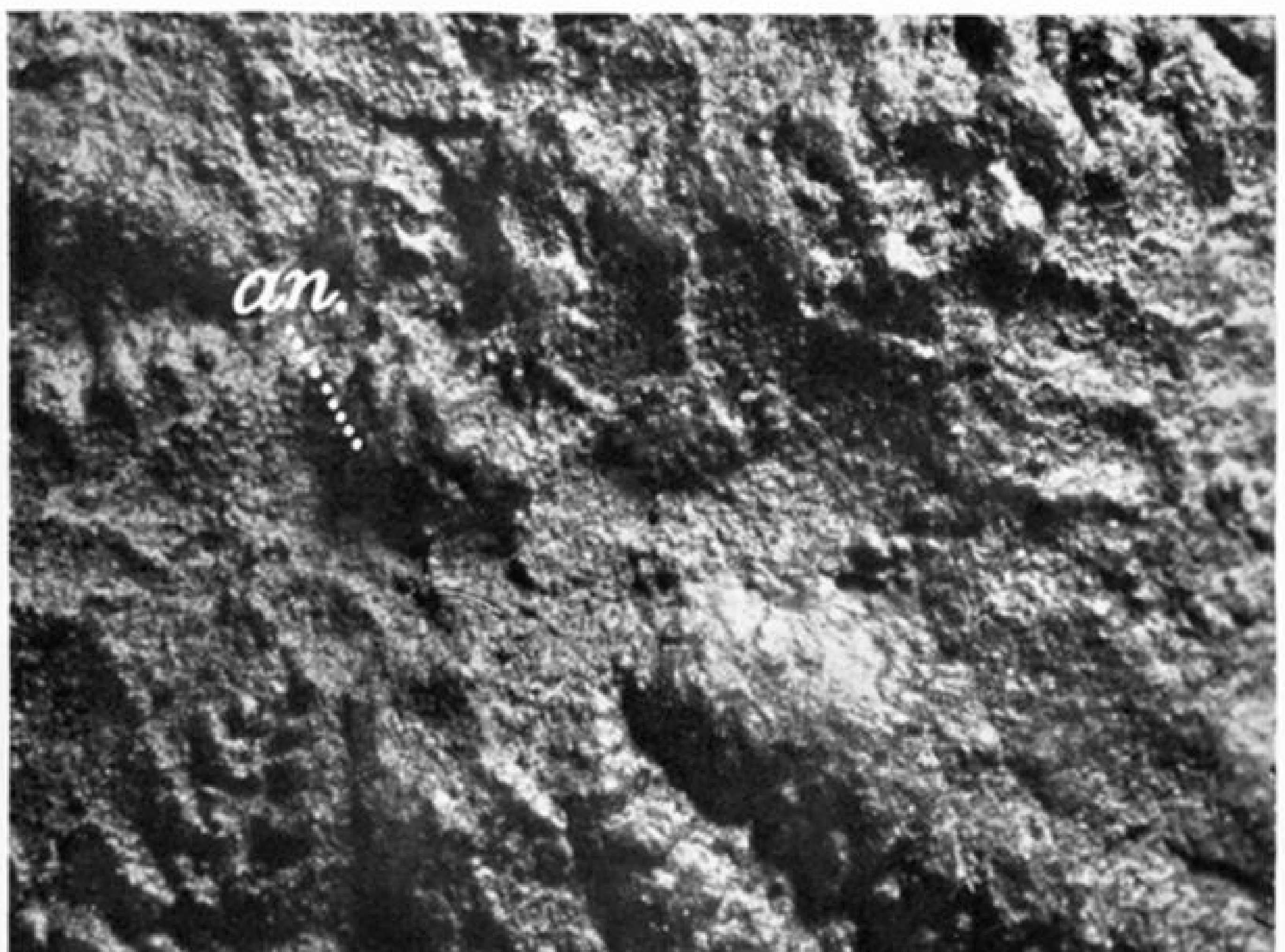

PLATE 13

FIG. 1. *Aulechinus grayae*. Photograph of an interior mould of the apical area of the same specimen as that figured (fig. 1, Pl. 10), ×8.

FIG. 2. *Aulechinus grayae*. Photograph of an interior mould of an extremity of an ambulacrum, ×12; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1200.

FIG. 3. *Ectinechinus lamonti*. Photograph of an interior mould of the apical area of the same specimen as that figured (fig. 1, Pl. 11), ×8.

FIG. 4. *Ectinechinus lamonti*. Photograph of an interior mould near the apex. (Calcite has not been entirely dissolved out of this specimen), ×2; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1220.

FIG. 5. *Echinocystis pomum*. Photograph of madreporite, initial and neighbouring plates, ×10; coll. Brit. Mus. (Nat. Hist.), No. 40158.

an. anal mound; *m.* madreporite-genital; *Oc.* ocular; *p.i.* strands filling pores. The white line on fig. 2 indicates the strands filling radial vessel.

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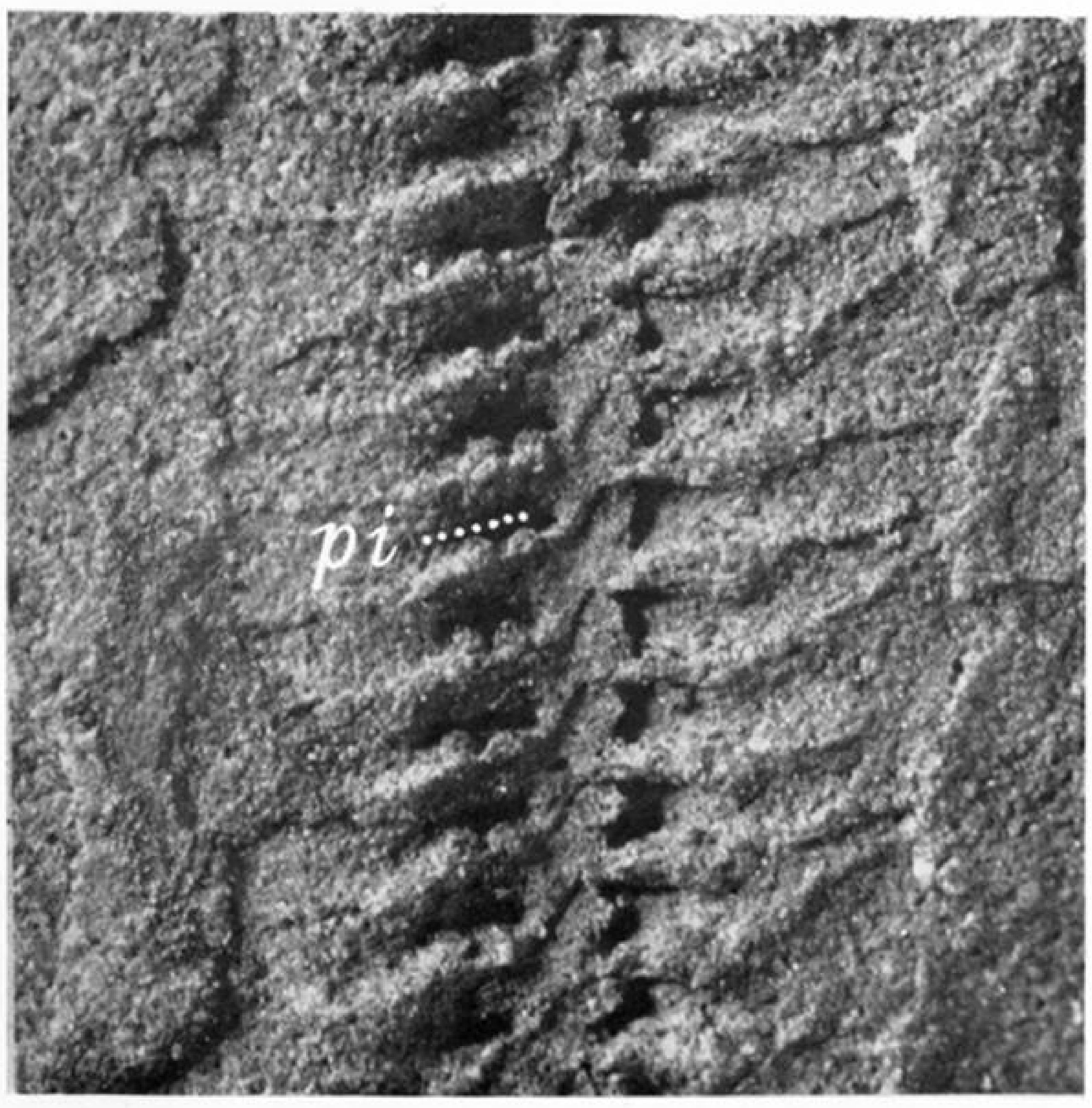

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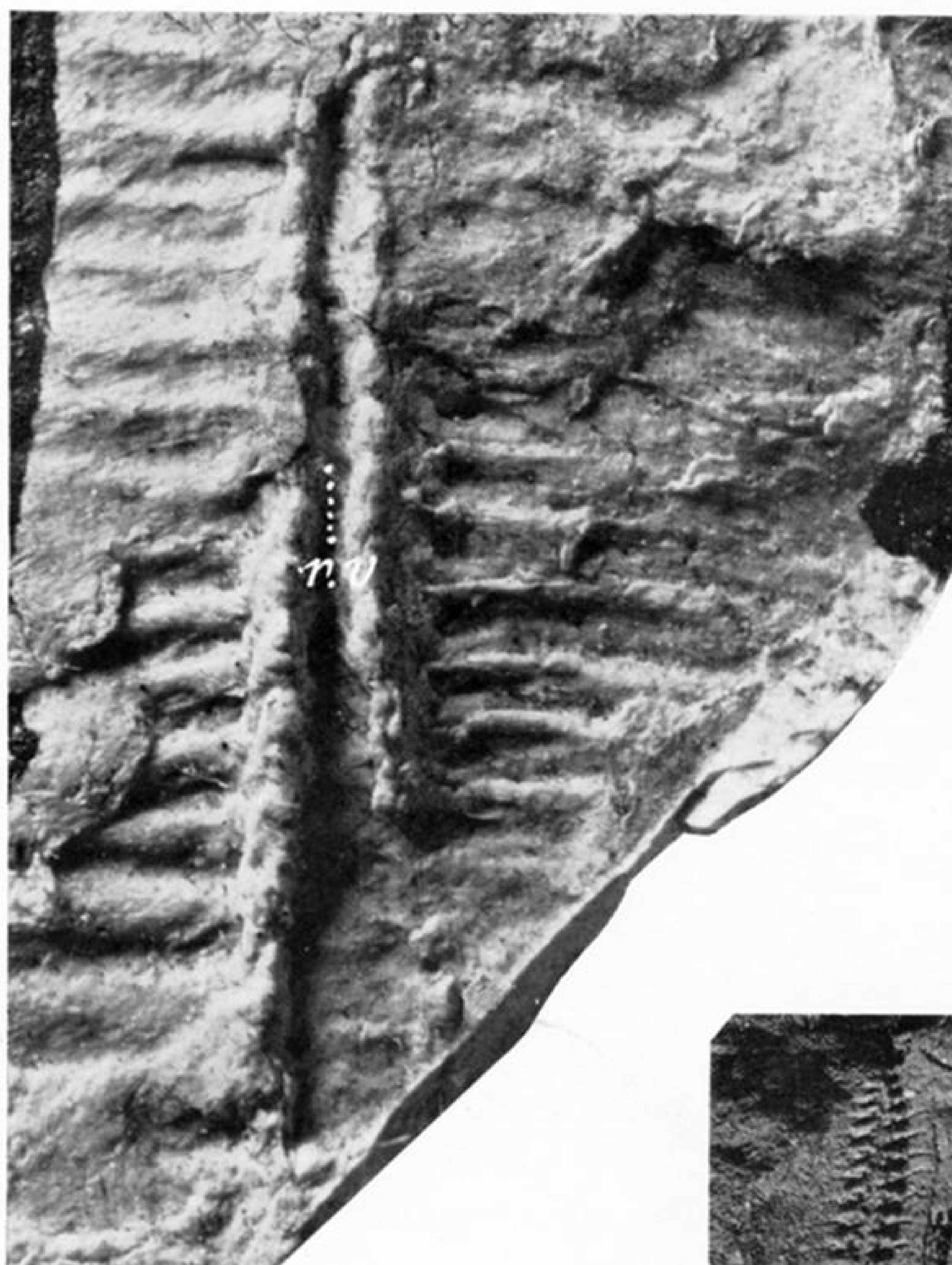

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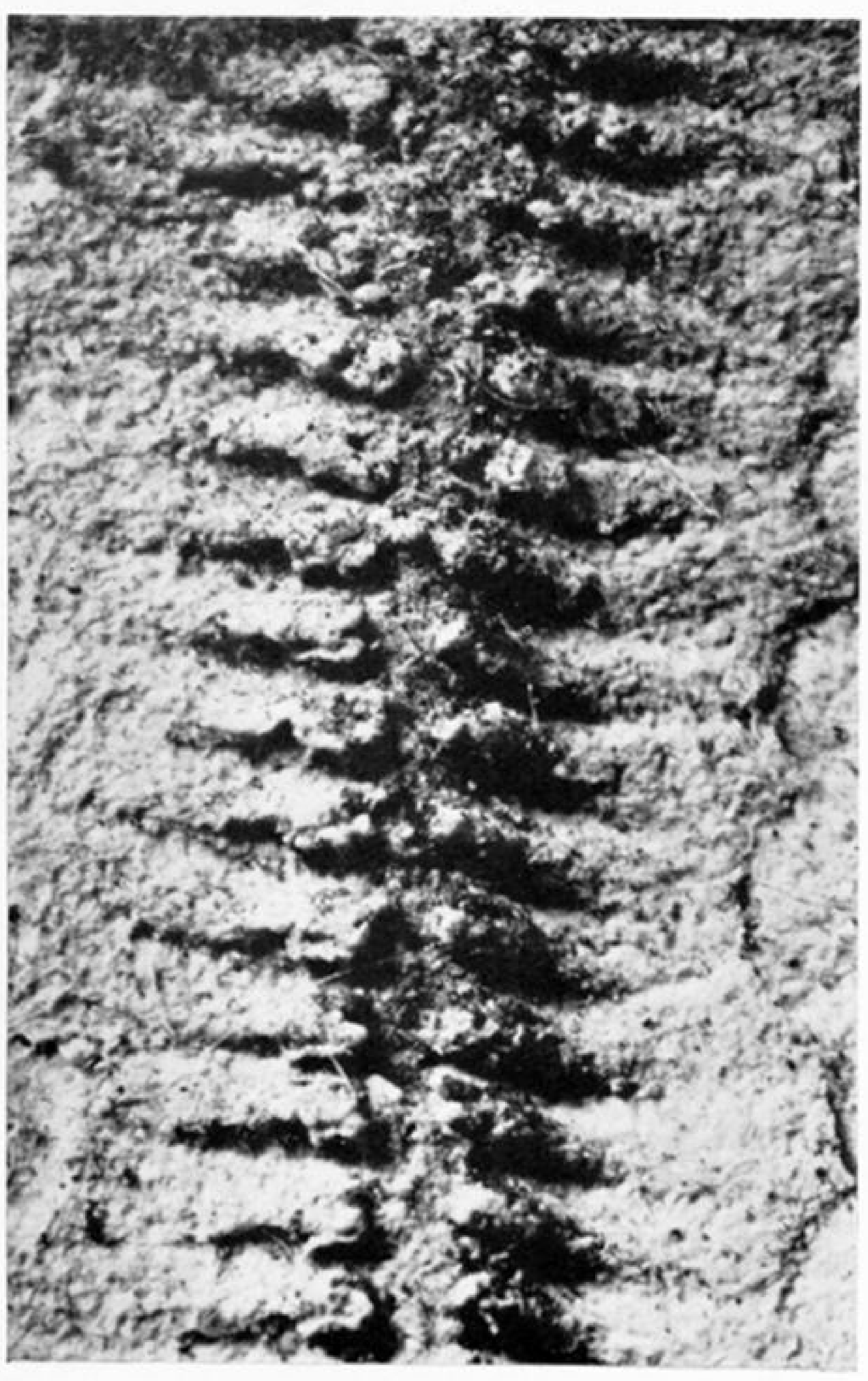

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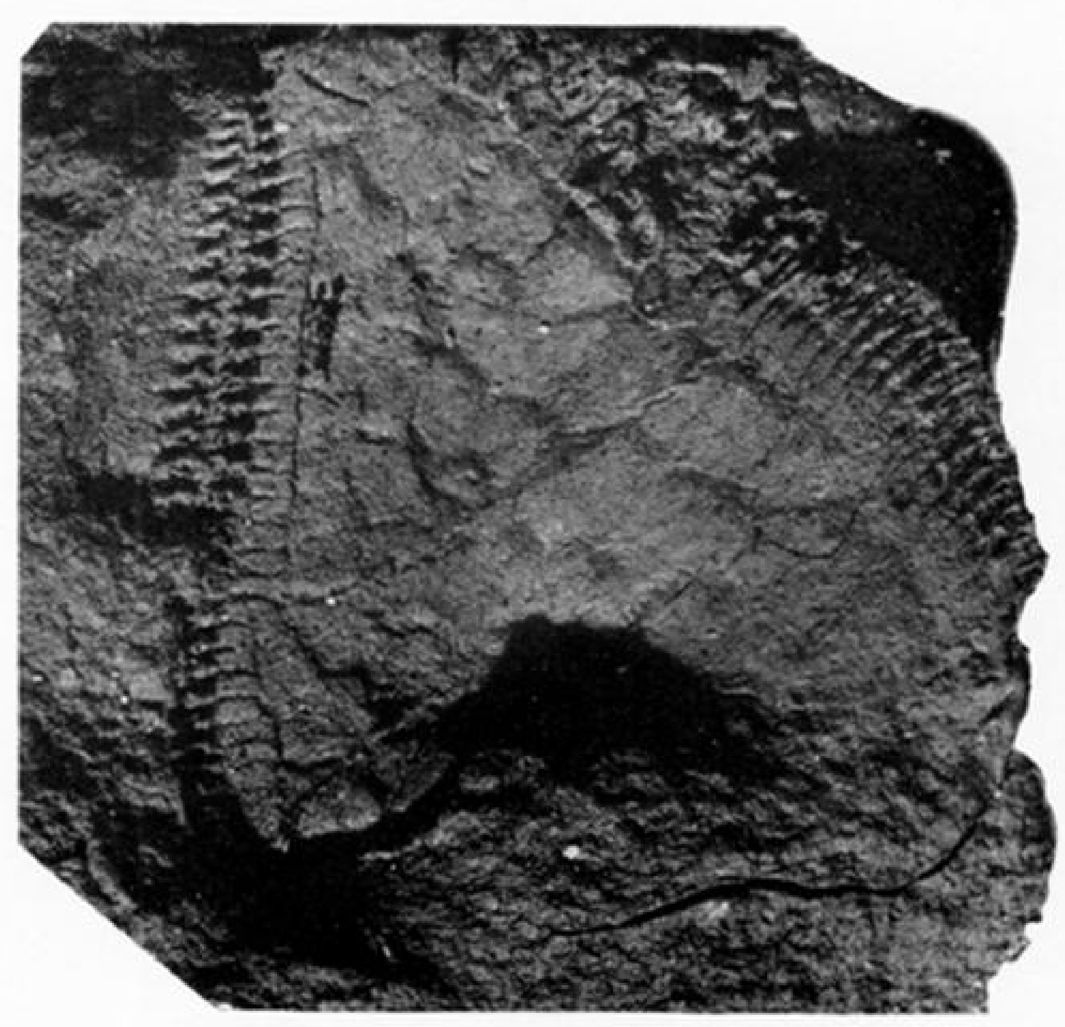

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PLATE 14

FIG. 1. *Aulechinus grayae*. Photograph of a portion of cast of an interior of a test showing two ambulacra (the holotype) and an intervening interambulacrum, $\times 2\frac{1}{2}$; coll. Brit. Mus. (Nat. Hist.), No. E. 31412.

FIG. 2. *Aulechinus grayae*. Photograph of a cast of a portion of an ambulacrum, $\times 4$; coll. Brit. Mus. (Nat. Hist.), No. E. 31406.

FIG. 3. *Aulechinus grayae*. Photograph of a cast showing displaced ambulacral plates, $\times 2\frac{1}{2}$; coll. Brit. Mus. (Nat. Hist.), No. E. 31418.

FIG. 4. *Ectinechinus lamonti*. Photograph of a cast showing a portion of an ambulacrum from within, $\times 12$; coll. the Misses Gray, No. Gr. 13.

FIG. 5. *Ectinechinus lamonti*. Photograph of the internal mould which gave the above cast. The strands representing the infillings of a double pore are seen clearly, $\times 12$.

FIG. 6. *Myriastiches gigas* Sollas. Photograph of a cast showing a portion of an ambulacrum from within, $\times 12$; coll. Oxford Univ. Mus.

FIG. 7. *Palaeodiscus ferox* Salter. Photograph of a cast showing a portion of an ambulacrum from within, $\times 12$; coll. Oxford Univ. Mus.

p.i. pore infillings; *r.v.* groove for radial vessels.

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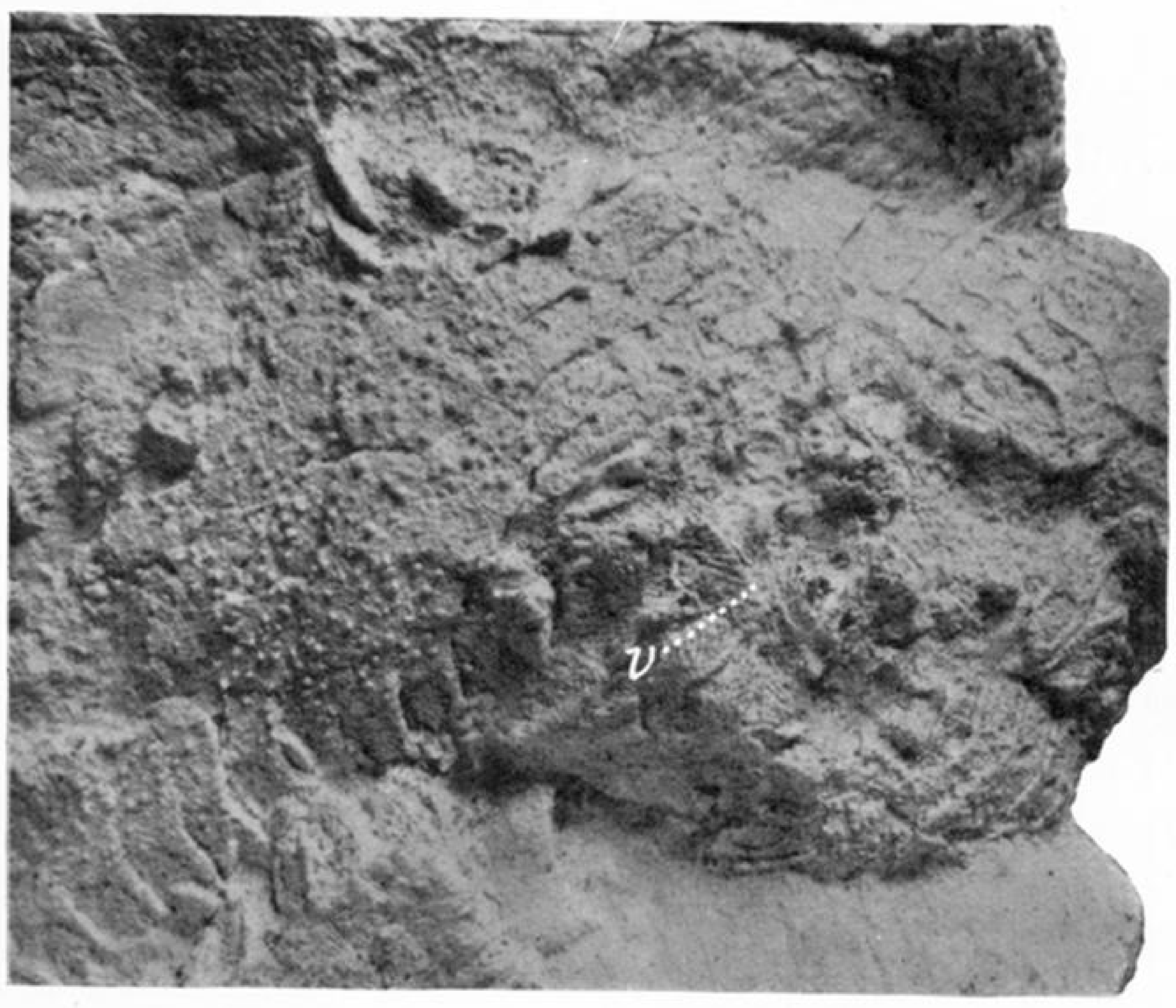

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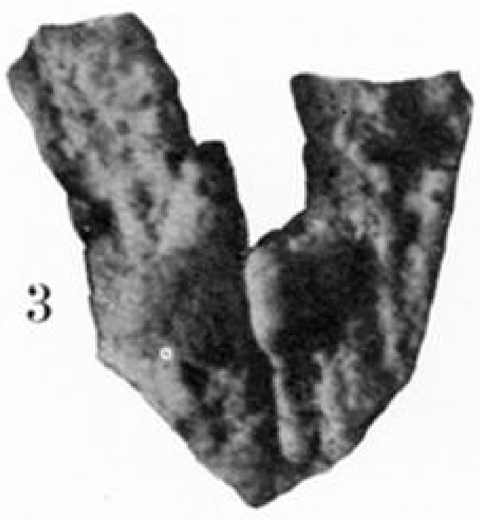

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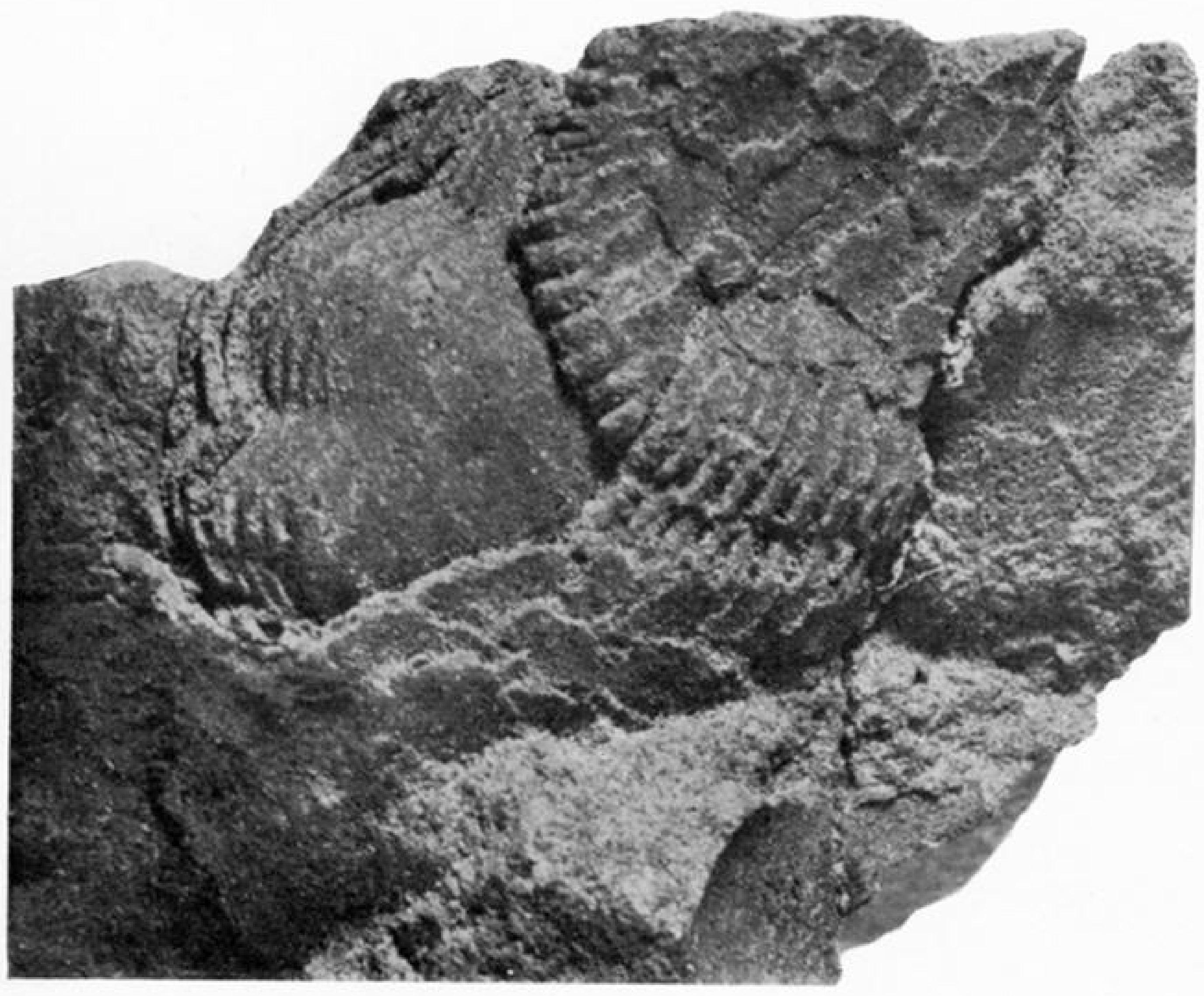

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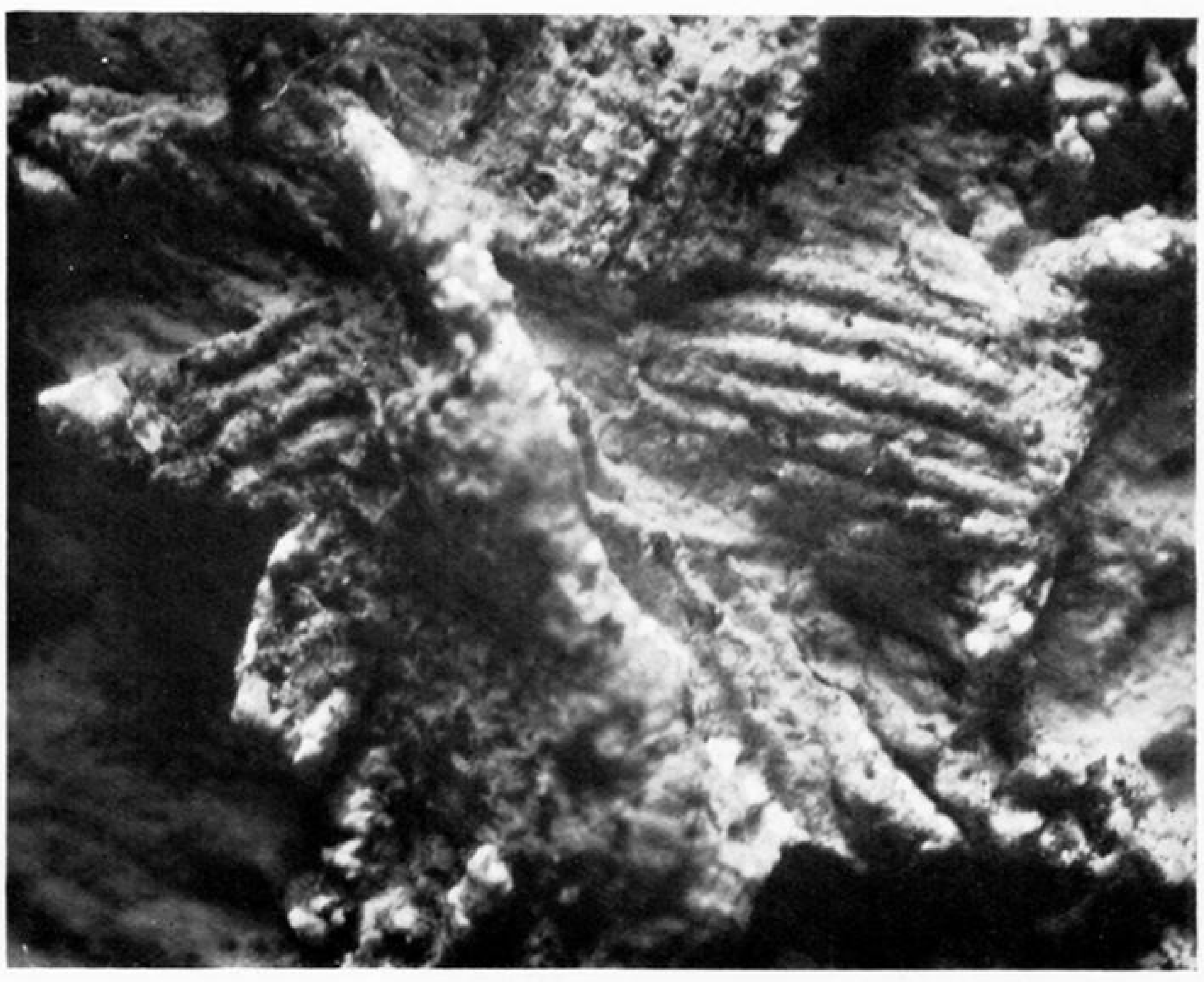

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PLATE 15

FIG. 1. *Aulechinus grayae*. Photograph of a cast of the lantern seen from within the test, nat. size; coll. Glasgow Univ. Hunterian Mus. No. 1203*c*.

FIG. 2. *Aulechinus grayae*. Photograph of the same specimen further magnified. The original mould was cracked hence there is a ridge of gutta percha running across the cast almost north to south.

FIG. 3. *Aulechinus grayae*. Photograph of cast of a jaw as seen from within the test, × 12; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1202.

FIG. 4. *Aulechinus grayae*. Photograph of a cast of the bulbous primordial ambulacral plates (a_1) from counterpart of same specimen, × 12.

FIG. 5. *Ectinechinus lamonti*. Photograph of external cast of the oral region, × 3; coll. Brit. Mus. (Nat. Hist.), No. E. 31414.

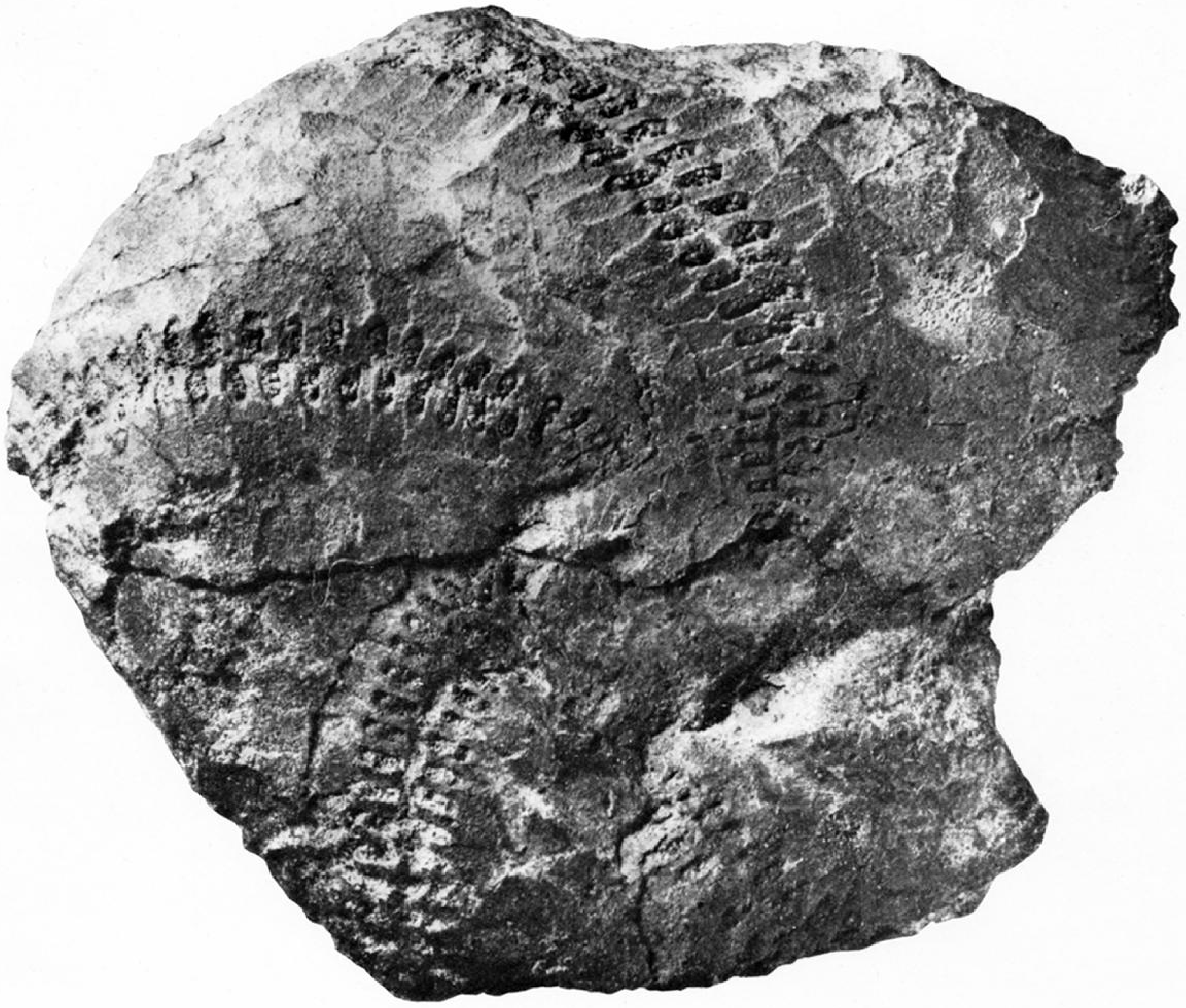
FIG. 6. *Eothuria beggi*. Photograph of external cast of a portion of the oral surface including the mouth, × 2½; coll. Brit. Mus. (Nat. Hist.), No. E. 27003*d*.

FIG. 7. *Eothuria beggi*. Photographs of a pair of "valves" around the mouth of same specimen, × 14.

FIG. 8. *Eothuria beggi*. Another pair of valves from same specimen showing the distal ossicle (*d*).

FIG. 9. *Eothuria beggi*. Photograph of a portion of an internal mould showing a trilobite thrust through the test which is split along the per-radii, × 3; coll. Brit. Mus. (Nat. Hist.), No. E. 27003*b*.

a.i. swollen first ambulacral; *v.* oral valves; *d.* distal plates.



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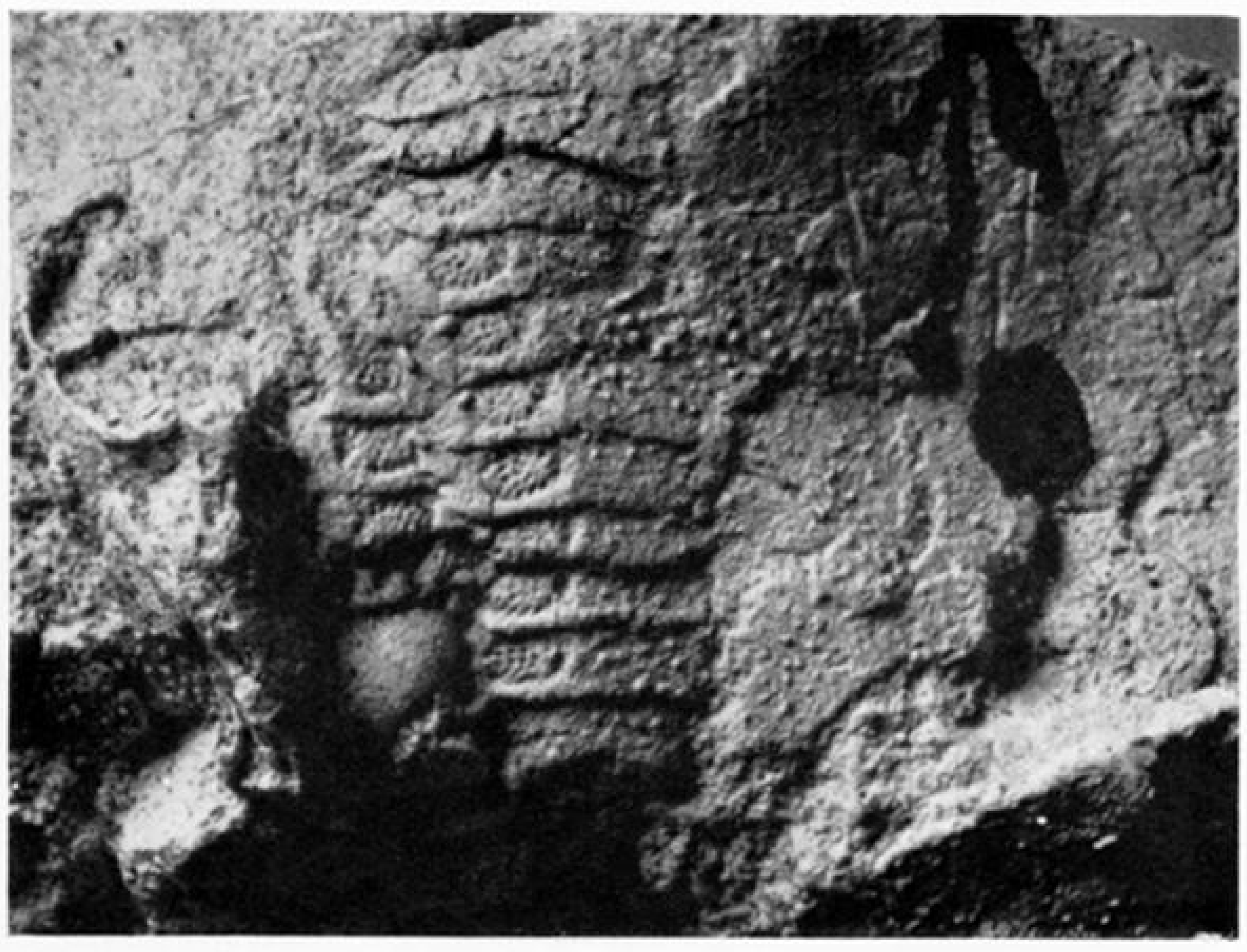

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PLATE 16

Photographs of *Eothuria beggi*

FIG. 1. Photograph of apical side of an internal mould (the holotype), nat. size; coll. Mr Begg, No. 31.

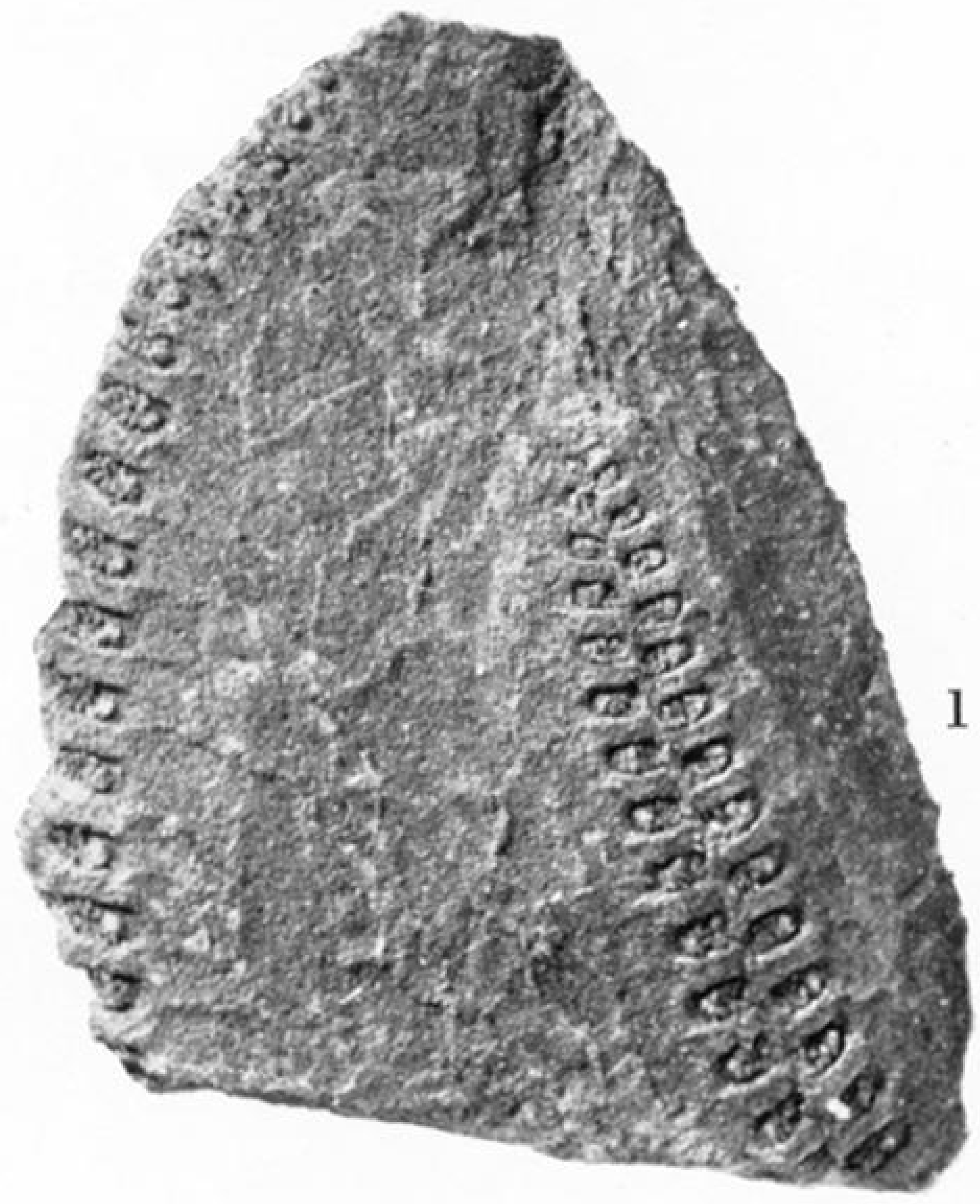
FIG. 2. Photograph of same specimen, ×4.

FIG. 3. Photograph of apical side of an internal mould of another specimen, nat. size; coll. the Misses Gray, No. H.1.

FIG. 4. Photograph of cast of a portion of an external mould showing ambulacrals, ×4; coll. Brit. Mus. (Nat. Hist.), No. E. 27003*c*.

FIG. 5. Photograph showing the same further magnified, ×12.

3



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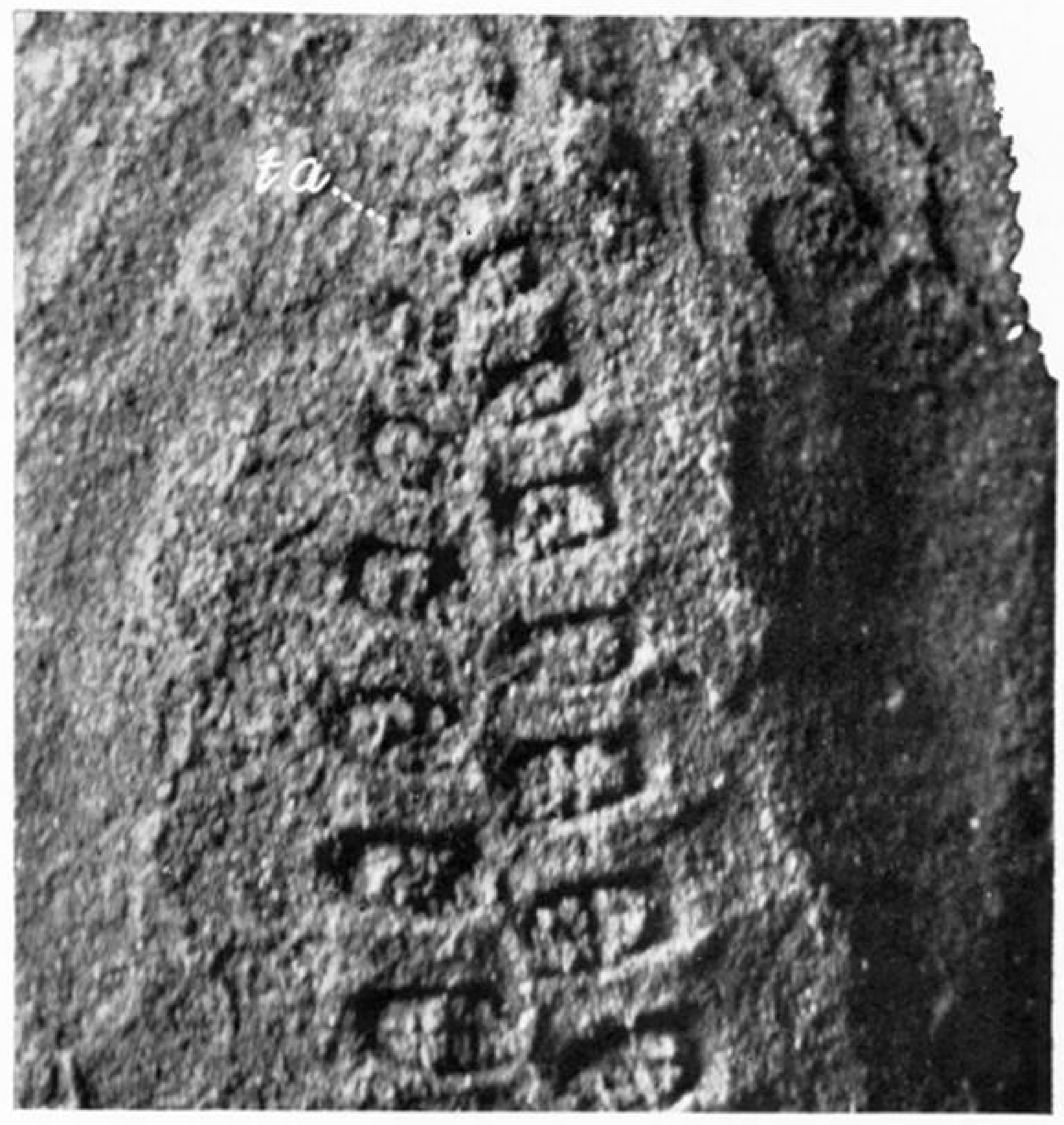

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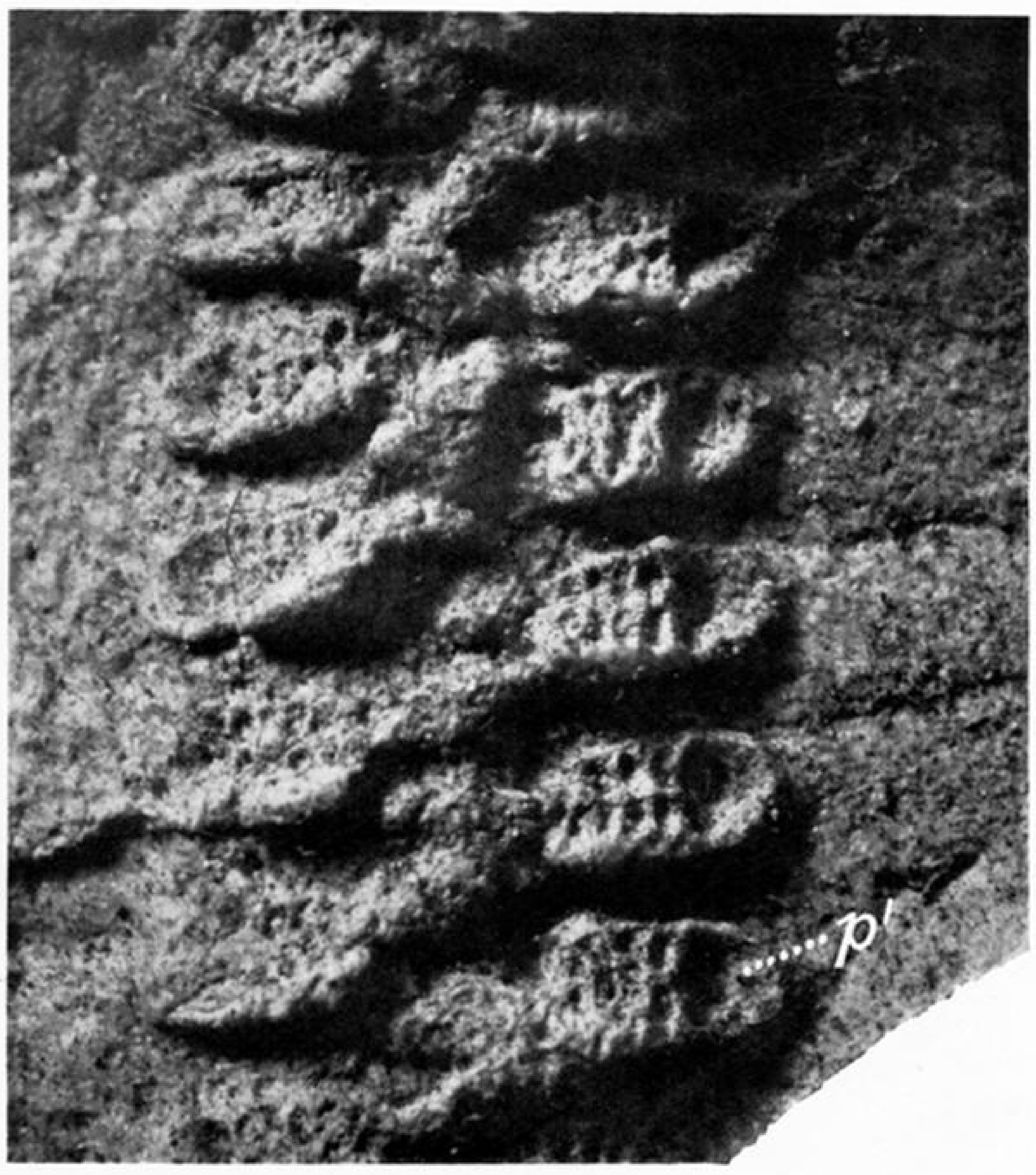

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PLATE 17

Photographs of *Eothuria beggi*

FIG. 1. Photograph of an internal mould near the apical region, ×4; coll. Glasgow Univ. Hunterian Mus. No. H.M.E. 1222.

FIG. 2. Photograph of the right-hand ambulacral ray of the above mould further magnified, ×12.

FIG. 3. Photograph of a portion of a mould of an ambulacral ray, ×12; coll. the Misses Gray, No. H. 2.

FIG. 4. Photograph of cast of an internal mould showing the ambulacrals from within, ×12; coll. Brit. Mus. (Nat. Hist.), No. E. 27004*c*.

FIG. 5. Photograph of an interior mould showing the greater part of the oral surface, nat. size; coll. the Misses Gray, No. H 2.

o. mouth; p^1. outer infilling of pore; *t.a.* mould of terminal ambulacral plate.