EARLY PALAEOZOIC STARFISH

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[Plates 2 to 8]

CONTENTS

Subclass Ophiuroidea (Cont.)

The fossil starfish described here are mainly from the Lower Ordovician (including the Tremadocian). Only brief descriptions of these starfish have been given previously. They are the earliest starfish known, and arrived in a series of transgressions which began in the Tremadocian and persisted throughout the immediately succeeding beds. Each of the transgressions brought in new faunas. Cephalopods arrived in the Tremadocian and locally graptolites in the basal Arenig.

The grouping of the starfish adopted here is based upon the activities of the arms, especially during feeding. Three groups of starfish are recognized. Two of these groups are recognizable as Asteroidea and Ophiuroidea. In both these groups the arms are functional, but the arm activities have different mechanisms.

The asteroid arm from the beginning is adapted for a carnivorous diet of large food, whilst the arm of the primitive ophiuroid is adapted for feeding on the small food present in or near the sea bottom. It is suggested that the primitive Ophiuroidea, like the recent *Amphiura*, had a 'burrowing habit'.

The third group had no functional arms. The forms belonging to this group appear slightly earlier (Tremadocian) than do either the Asteroidea (Lower Arenig) or the Ophiuroidea (basal Arenig). The tube feet are placed in position by changes in body shape. They seem to have lived on small food either from the planktonic shower (*Villebrunaster* n.g.) or from that in the upper layers of the bottom (*Archegonaster*). Their skeleton shows many primitive characters. The name Somasteroidea n.subclass is suggested for this third group. Its members show the first stages in the differentiation of a starfish.

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It is noticeable that these first stages show no sign of an ambulacral groove, a character which previously has been regarded as primitive and used to link starfish with certain non-crinoid Pelmatozoa (Edrioasteroidea Bather; Thecoidea Jaekel).

The view held (Spencer 1905) that the asteroid groove was present in early Echinoidea must also be abandoned.

Early representatives of all these groups have characters which link them with a common ancestral structure. Each tube foot is housed on two ambulacralia in all Asteroidea (living and fossil), in the Somasteroidea and in the extinct primitive Ophiuroidea. Some groups of Ophiuroidea retain this character throughout the early Palaeozoic, whilst other groups acquired 'vertebrae'. Each vertebra, a modified ambulacral, acquires its own tube foot. All early representatives have a mouth frame with radial V's. It is suggested that the presence of the V's is associated with a primitive oral opening, the stomodaeum, which had radial slits, the buccal slits.*

The Somasteroidea have an aboral skeleton composed of ossicles which are little more than spicules radiating from a number of centres. The arrangement can be compared to that in the early stages of the skeletal components of recent forms. No other fossil echinoderm is known with ossicle components in a condition as primitive as this.

It would seem that starfish arose at a very early stage in the development of echinoderm stocks.

INTRODUCTION AND HISTORICAL

The interrelationship of the two great groups of starfish, the Asteroidea and the Ophiuroidea, was firmly established by Ludwig many years ago. Applying the principles of comparative anatomy he showed that both were built to a common plan, and turning to embryology he found an asteroid stage during the development of the ophiurid.

The prestige of Ludwig and the clarity of his observations have profoundly influenced palaeontologists. Schuchert, who wrote the first clear account of the evolution of the Palaeozoic Asteroidea, found an archetype to both groups in the primitive asteroid *Hudsonaster*, which (1915, p. 34) he held to 'be very near the radicle that gave rise through modification and inheritance to all subsequent Stelleroidea'. His diagrams show that he regarded the arrangement of the plates of the dorsal surface of the disk as closely resembling those of a crinoid.

Both Jaekel and Bather looked for the asteroid ancestry in another Pelmatozoan group, the Edrioasteroidea of Bather, the Thecoidea of Jaekel. The asteroid character regarded as primitive was the open ambulacral groove with its floor of double plates and its wall of cover plates (adambulacralia) (see p. 121). An endeavour was also made (Spencer 1904) to apply this 'groove' theory to the establishment of the relationship between Asteroidea and Echinoidea.

The observations given below throw suspicion upon the above views. They are based largely upon new material from the south of France, which was shortly described by Thoral (1935) in his comprehensive survey of the fossil fauna found in the Tremadocian and basal Arenig in the neighbourhood of St Chinian. Several groups of animals, including the starfish, make their first appearance in the European rocks during this period, and no earlier starfish have been found anywhere.

Dr Stubblefield put me in touch with Professor Thoral, who on learning of my interest in the starfish, proceeded to give me every help. He lent me material and gave me facilities to work in his Department in the University of Montpellier. I am very grateful to him for this and for much pleasant companionship.

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* For definition see Glossary, p. 124.

My second source of material for studies upon early starfish is a large collection from the Upper Arenig of Bohemia. This fauna was thoroughly examined by Jaekel, who published two short papers. Neither described the genera in detail, but the latter paper stated his general views upon the place the genera should occupy in classification. It was later arranged that he and I should collaborate in a full description, but his untimely death prevented this. The manuscript notes forwarded to me elaborate his views and give accurate descriptions, with illustrations of many of the genera. I am not following Jaekel's viewpoint exactly. I feel that he himself would have modified it if he had been acquainted with the earlier French fauna. This material has been in my hands rather a long time, and the patience of those who control the Narodni Museum, Prague, must have been somewhat tried. Without it my work would have been seriously hampered, for it has taken me several years and much study to understand the implications of the fauna.

It now seems possible to draw some general conclusions which are briefly:

(1) That the earliest known starfish are found in Western Europe. They arrived in a series of floodings which brought in the Tremadocian and Lower Arenig faunas.

(2) That starfish unmistakably, like recent Asteroidea and Ophiuroidea, arrived in the Lower Arenig. Both show certain primitive characters. Those possessed by the Ophiuroidea are of special interest, for they show the arm structure prior to the modification of the ambulacralia into vertebrae.

(3) That these early faunas contain a third group, called here the Somasteroidea n.subclass. In this group the arms are in an early stage of differentiation. This group arrived in the first, Tremadocian, floodings. The manner of differentiation is not in accordance with the view that a 'groove' structure is of importance in an assessment of ancestral characters.

I am greatly indebted to Dr Barnard for the facilities afforded me at the South African Museum and to Mrs Mary Maytham Kidd for her clear illustrations. The completion of this communication would have been very difficult without their help. I am also indebted to Dr C. J. Stubblefield for assistance in the preparation of the manuscript, to Professor Day of the University of Cape Town, to Lady Rutherford for rescuing both material and drawings which in 1941 had to be abandoned in France and to the British Museum (Nat. Hist.), Geological Department, for assistance at all times.

Material

The starfish, both in the French and Bohemian beds, are found by splitting rounded flint-like nodules which are often found loose in weathered soil. I accompanied Professor Thoral on some of his collecting expeditions. In particular, we visited vineyards where the soil, kept in a constant state of cultivation, was a source of much material. Usually the owner of the vineyard had put aside a heap of nodules exposed during his cultivation. Other nodules were found during the visit by stirring the soil with a suitable geological hammer. A very large proportion of the nodules when split showed that the 'flint' had formed around an animal nucleus.

Starfish form only a very small proportion of the fossils collected in this way, and the material available for study is the result of collection over many years. The part played by the individuals who were interested in collecting for its own sake cannot be overestimated.

All the fossils are preserved as moulds. It is usual to find only portions of the body of the starfish within the nodule, but these portions are very perfect. Casts from the mould show fine details, spines, joints and facets for the accompanying musculature, grooves for vessels, in fact all the information which can be obtained from a well-preserved endoskeleton.

The explanation which seems to fit the observations on the material is that the portions preserved were within the mud of the sea-bottom at the time of death, and that chemical interaction between the animal matter and the surrounding mud caused the enclosure of the remains in a 'flint' casing. During this interaction the calcite of the skeleton was gradually dissolved away. Possibly compounds of iron entered into this reaction. Usually the hollow of the moulds is filled in with a ferric oxide or carbonate, sometimes so hard that it has to be removed by a needle before a cast is made.

The proportion of the original animal preserved varies considerably according to its build. Generally speaking, we can say that the central parts are often preserved in their entirety, whilst the projecting parts, the arms, are often missing. It is suggested later that some, if not all of these starfish, had a burrowing habit. The parts of the starfish which were well preserved were those in the deeper parts of the burrow. The portions badly preserved or absent were thrust upwards into the top layers of the bottom mud, to feed from the layers richest in organic remains.

The following studies endeavour to interrelate studies of preservation with studies of the structure of the individual ossicles. Such studies seem to make possible a reconstruction of the habits and trends of evolution of these early starfish.

Feeding habit

Hunt (1925) suggested the following classification of feeding habit:

A. *Suspension-feeders* appertaining to animals 'either permanently sedentary in habit or at least remaining in one place when feeding....They feed by creating currents of water over parts specialized to strain or select from the water its contained small floating particles and organisms.'

B. *Deposit-feeders*. These include *selective feeders*, animals which pick out organic material from the substratum by a variety of prehensile devices.

C. *Carivores*. Animals which specialize in the capture of prey, other living animals, or in some cases carrion.

Respiration

Gemmill (1915) showed that respiratory ciliary currents, both ectodermal and endodermal, washed large areas of the parts of the asteroid body, and that the path of these currents could be traced by examination of the body surfaces.

Respiration in the Ophiuroidea is confined to limited areas, respiratory pouches (sometimes called genital bursae). These pouches are formed during body outgrowths (the ophiuroid disk).

Classification

The classification adopted is linked with the above observations on habit. It seems to satisfy studies upon the palaeontological material, whilst offering the least disturbance to groupings familiar in literature.

Subclass Somasteroidea nov. (diagnostic characters, see below)

This new subclass includes a number of very early starfish in which the arms are just beginning to be differentiated. There is evidence that at least one form, *Villebrunaster* n.g., was a suspension-feeder. This mode of feeding connects with a probably ciliary feeding pelmatozoan ancestor.

Subclass Asteroidea (diagnostic characters, p. 121)

Carnivorous starfish with well-developed stout arms. The structure of the skeleton of the arms is linked with the habit of engulfing its food in an everted stomach.

Respiration both ectodermal and endodermal. Many forms have external gills (papulae).

Subclass Ophiuroidea (diagnostic characters, p. 106)

The primitive Ophiuroidea, like many of the recent forms, were selective deposit-feeders. Both the long thin arms and the modification of the proximal tube into buccal tentacles are well adapted for this mode of feeding. Carnivorous Ophiuroidea evolve later. Their very mobile arm, used in the capture of food, is highly specialized.

Respiration from the outset was by means of respiratory pouches developed between the edge of the disk and the arms. This method of respiration is peculiar to the Ophiuroidea.

Subclass SOMASTEROIDEA n.subclass

Diagnostic characters

The central part of the body is large and the 'arms' are merely differentiated portions of its oral surface. In the earliest genera the skeleton of this surface has only two types of ossicles: (1) ambulacralia, arranged in a double alternating row which stretches from the central opening to an arm extremity, and (2) interambulacralia, rod-shaped ossicles placed in linear series at an angle to the ambulacralia. In the Upper Arenig genus *Archegonaster* marginalia and adambulacralia are differentiated as end-members of these interambulacral rows. In still later genera the interambulacral skeleton is entirely wanting.

The aboral skeleton, when present, has ossicles with a small centre from which radiate slender branches. The whole forms a net with a wide mesh.

This subclass contains only a few genera, but they are important as they include the earliest known starfish and show peculiarities of skeletal build which do not find a parallel in either Asteroidea or Ophiuroidea. The general plan of such a skeleton is well shown in figure 1, founded upon well-preserved specimens of *Villebrunaster* n.g.

The interambulacralia are especially characteristic. The rods are walls of shallow channels. Such ossicles are only found in members of this subclass. They are called virgalia* in the following descriptions.

The ambulacralia are also characteristic. They form a stout radial skeleton and are developed as a sheath to the radial water vessel. Similar ambulacralia are found in the primitive Ophiuroidea.

The interambulacral areas are interpreted as collecting organs for small food which, by centrifugal currents, was carried to tube feet placed in basins on the ambulacralia. There the

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* For definition see Glossary, p. 124.

small food was picked out from the currents and transported, partially by ciliary action and partially by the tube feet, to the receiving organ placed in the centre of the body. This receiving organ is placed within a frame of ossicles, the mouth frame. Radially the frame has five deep V's formed from divergent ambulacralia. The open angle of the V is continuous with the central opening. I am calling the spaces in the angles of the V's 'buccal slits', and interpreting the central opening, continuous with the slits, as a stomodaeum. The disposition of the tube feet within the frame can be inferred from the position of their basins. These

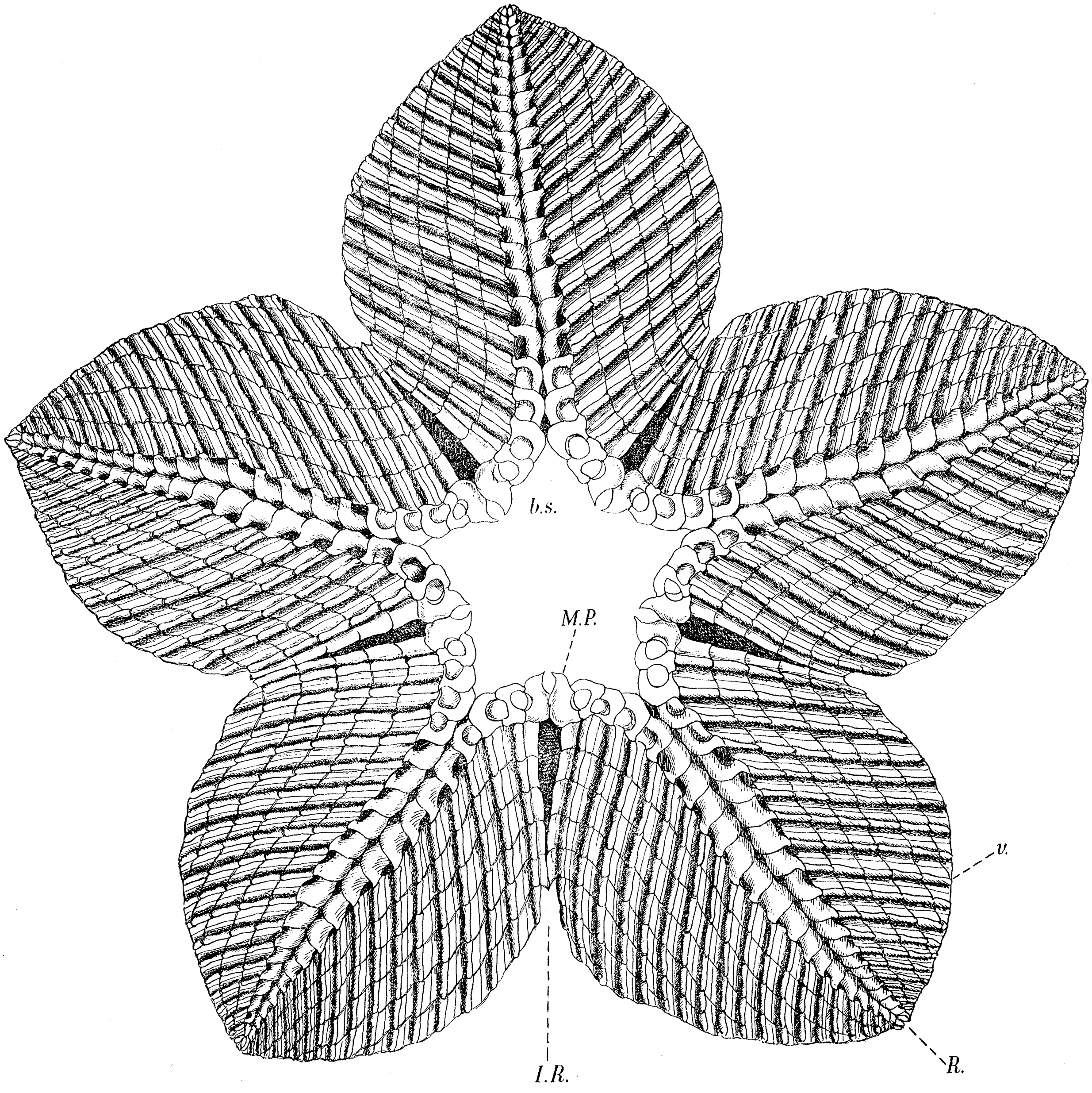


FIGURE 1. *Villebrunaster thorali* n.g. n.sp. Reconstruction of the oral surface based mainly on the specimen photographed on the left of figure 29, plate 2. *b.s.*, buccal slits; *I.R.*, interradius; *R.*, radius; *M.P.*, mouth-angle plate; *v.*, virgalia. The double row of ossicles along the radius are the ambulacralia with basins for the tube feet along their outer edges. Near the central opening the ambulacralia diverge to form V's of the mouth frame. The spaces between the ambulacralia are filled in by rod-shaped interambulacralia (virgalia). The mouth-angle plates are in the interradii and adjoin the central opening.

suggest that the food was finally sorted by tube feet alined alongside the slits before entry into the slits and the farther passage to the stomodaeum (p. 97).

In all these starfish the interambulacral skeleton, except for the marginal frame of *Archegonaster*, is slightly built. Such a skeleton offers slight resistance to the very considerable changes in body shape which can be observed possibly associated with a burrowing habit (see p. 97). At one time the body is strongly compressed, at another the body of the same species is well rounded. Such changes are brought about in recent animals by well-developed longitudinal and circular muscles which bring about alternate thickening and narrowing of the body.

A well-known example is that of the earthworm.

Von Uexküll (1921, p. 96) has pointed out that such movements provide a pressure which hardens the walls of the burrow and allows free passage of respiratory gases. *Sipunculus* employs the same method, whilst the heart urchin hardens the wall by pressure from suitably placed spines. All these animals add to the strength of the walls by some form of secretion; in the heart urchin it is mucus.

Mucus is a common secretion in Echinodermata and may well have been employed by these primitive starfish. Unfortunately, we have no confirmatory information upon the method employed in burrowing by those recent Ophiuroidea which adopt this mode oflife. We also lack information upon the same habit of the Dendrochirote holothuroids, *Cucumaria* and *Thyone*. Hunt (1925, p. 570) stated: 'Both the above are burrowing forms. When feeding, the anterior end of the animal protudes from the burrow and the crown of tentacles is widely extended.' It is difficult to understand the anal respiration of these animals unless 'new' water can freely circulate within the burrow. The anus is placed within the burrow.

This interrelation of the change of body form form and burrowing habit is also discussed in reference to the structure of the disk of the primitive Ophiuroidea (see p. 109).

Order GONIACTINIDA n.ord.

I am placing all the forms in one order Goniactinida nov. with the same characters as those of the subclass.

The following families can be recognized:

Family Chinianasteridae nov., with the interambulacral skeleton occupying the whole of the interradii.

Family Archegonasteridae nov., interambulacral skeleton confined to the outer angles of a pentagonal frame.

Family Archophiactinidae Spencer, with no interambulacral skeleton.

The progressive loss of skeleton in the history of the subclass may be due to the interference of the skeleton with the muscular activities associated with 'burrowing'.

Family CHINIANASTERIDAE n.fam.

There are two genera, *Chinianaster* Thoral and *Villebrunaster* n.g.

Villebrunaster n.g.

Synonymy

Chinianaster pars Thoral, 1935, p. 127, plate x, figure 4.

Diagnosis

A chinianasterid with small ambulacral basins which served for the insertion of the bases of the tube feet arranged, except near the mouth, along the sides of a tube which is closed along the mid-radius.

Type species

V. thorali n.nom. for *Chinianaster levyi* Thoral pars 1935, plate x, figure 4, found in the Upper Tremadoc or basal Arenig in the neighbourhood of St Chinian, Dept. Hérault, south France.

Material

The fossil was found as impressions preserved in two nodules. The larger nodule was split into several fragments which apparently show five specimens in close association. The second nodule, only half of an original nodule, shows the oral surface of another specimen.

One portion of the larger nodule shows two specimens lying side by side. Casts of these are photographed (figure 29, plate 2). The specimen on the left shows the body compressed in a vertical plane, with all the interambulacral areas in the horizontal plane. In the second, the specimen on the right, the body is elongated in the vertical plane, and the interambulacral areas are placed at a steep angle to the horizontal plane. These different appearances are interpreted in terms of the condition of the body musculature at the time of internment. The first specimen had these muscles relaxed and the second had the muscles in a condition of tension. It is possible that the latter shows the customary shape of the body. The interambulacral areas are in position to face the food in the surrounding sea water, possibly a descending planktonic shower.

The specimen with relaxed musculature affords the greater detail and is chosen as the holotype; the remaining material as paratypes. All these are preserved in the Villebrun collection of the University of Montpellier, France.

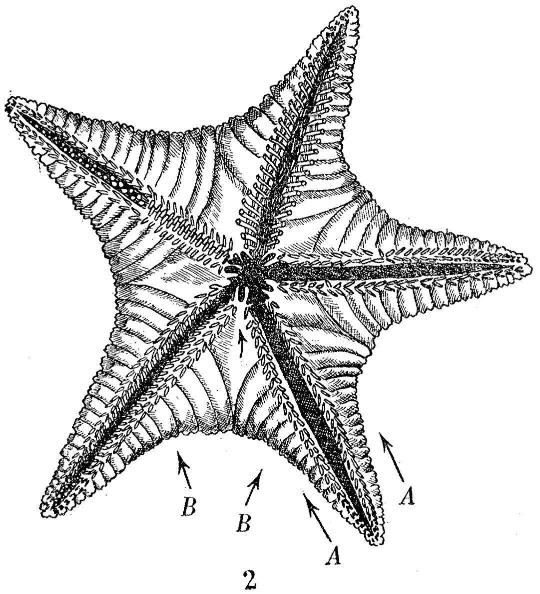
Description of holotype

The oral surface possesses three kinds of ossicles: (1) half-cylinders—the ambulacralia—placed along the radii; (2) virgalia often carrying a small keel, the skeleton of the interambulacral areas; (3) mouth-angle plates, a pair of plates placed at each of the interradial angles and projecting into the central opening. The groove, characteristic of the typical Asteroidea, is absent as also are adambulacralia (see p. 89).

The half-cylinders are stoutly built ossicles which project strongly from the general level of the oral plane (figure 4). They are arranged alternately to enclose a cylindrical hollow which housed the radial water vessel. Ambulacralia with these same characters are found in the primitive Ophiuroidea (see p. 109). Their surface is excavated into small basin-like hollows which served for the insertion of the bases of tube feet. At the extremity of the arm the excavations are placed towards the upper (aboral) edge of the half-cylinders, but they gradually approach the oral plane as the radius is followed towards the mouth. The exact structure of the basins is given below in the description of the nearly related genus *Chinianaster*, where they are larger and more fully exposed.

The ambulacralia near the mouth form a frame around the central opening. The frame is not circular but is prolonged into V's along each radius. The broadened end of the V's open into the cavity of the frame. The interradial angles are joined together by a pair of mouth-angle plates; short, broad ossicles, almost spade-like in outline.

The virgalia are in line and form continuous walls between which are shallow channels. The channels run in curved paths from the outer edge of the starfish towards the middle of the arm. The floor of the channels seems to have been devoid of calcifications. Small areas in the interradial angles (shaded dark in the figures) are also devoid of skeleton.



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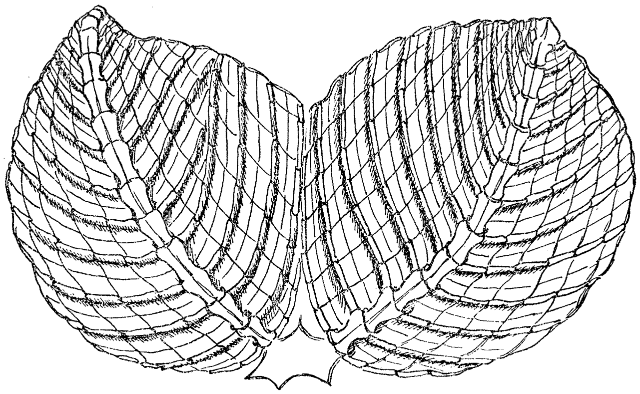

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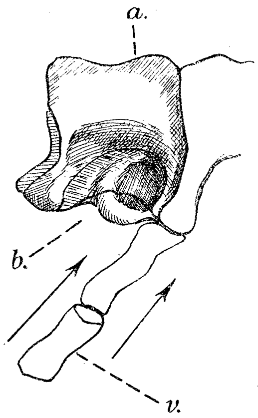

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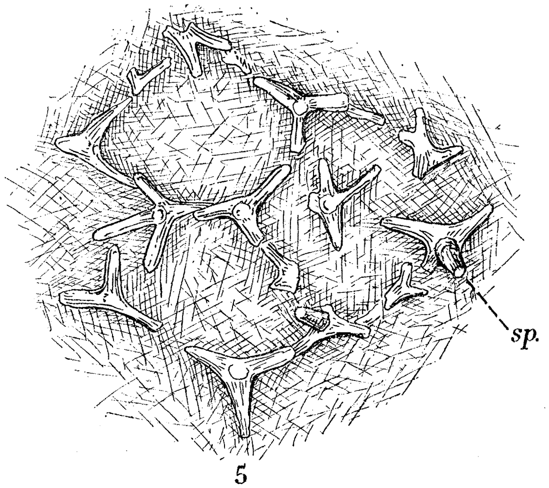

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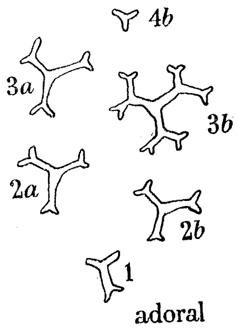

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FIGURE 2. Oral surface of *Porania* reproduced from Gemmill (1915, plate 1, figure 1). The arrows indicate the direction of the currents. *A*, radial currents; *B*, interradial currents.

FIGURE 3. *Villebrunaster thorali* n.g. et n.sp. Profile view with body flexed. The food-collecting areas face upwards. Based on the specimen photographed to the right in figure 29, plate 2.

FIGURE 4. *Villebrunaster thorali.* Lateral view of the high ambulacralia with adjoining virgalia, *a.*, ambulacralia; *b.*, basin for a tube foot; *v.*, virgalia. The arrows indicate the direction of the incoming current.

FIGURE 5. *Sturzaster marstoni* (Salter). Ossicle of network of aboral surface reproduced from Spencer (1940, text-figure 334). The aboral network of *Chinianaster* is closely similar.

FIGURE 6. Early stages in the development of the plate of an echinoid; reproduced from Gordon (1926, *B* of figure 1, p. 261).

The whole of the aboral surface is covered with triradiate spicules which collectively form a net of wide mesh. Impressions of the net are seen in the photographs (figures **30**, **31**, plate 2). A similar net for *Sturtzaster* is drawn (figure 5).

A collapse of the skeleton after death brought about slight irregularity in the disposition of the mesh. It is probable that originally the mesh was regular in pattern with hexagonal interspaces. It would then present the same appearance on a macroscopic scale, as is so well shown on a microscopic scale during the development of the echinoderm skeleton (figure 6).

This is a very primitive skeleton which finds some parallel with that of a sponge. It forms the background of the aboral skeleton of all later starfish.

Interpretation of the structure of Villebrunaster *in relation to function*

The various oral areas are interpreted as follows:

(1) Food collecting area—the interradii.
(2) Food carriage area—the ambulacralia.
(3) Food reception area—the space between the V's of the mouth frame interpreted as buccal slits.

Much of this interpretation is based upon Gemmill's investigation (1915) into ciliary nutrition in the Asteroidea. Gemmill, when investigating the development of the recent starfish *Asterias rubens*, 'was struck by the constancy and functional importance of the ciliation on the various surfaces (epidermal, endodermal and enterocoelic) of the larva'. As the larval ciliation was continued at metamorphosis into that of the adult he made extensive investigation into the role played by ciliary activity in the adult life.

Several species of starfish were kept in tanks and deprived of solid food. The only food they could obtain was from a continuous current of sea water which had to pass through a hair cloth of fine mesh. Under these conditions the starfish *Porania* had not lost any weight after a period of 4½ months, the period from the end of February to the middle of July, during which microscopic material was most abundant in the tanks.

Gemmill (1915, p. 11) notes several structural or functional peculiarities of *Porania* which, taken as a complex, seemed direct adaptations for ciliary nutrition (figure 2).

(1) The cilia all over the oral surface (in ambulacral grooves, around bases of spines bordering these grooves, on the oral interradii, on buccal membrane, and on denticles) act in such a way that streams of particles are continually converging on the mouth opening.

(2) The general shape of the starfish with its large interradial areas ensures that there is an extensive circumoral ciliated field, adapted for food-gathering purposes.

Food collecting in Villebrunaster

Villebrunaster has similar large interradial areas which would ensure an extensive circumoral ciliated field. The shallow channels between the virgalia follow a precisely similar course to those mapped for the ciliary currents of *Porania* (see Gemmill's diagram).

These currents can be described as adradial. They lie at an angle to the radial currents which flow over the surface of the ambulacralia directly towards the mouth.

Food sorting and food carriage

All animals which collect food by ciliary fields bring together, at the outset, both nutritive particles and debris. In a large number of cases the sorting of these two components is brought about by 'physical' methods. Such methods could have been used by *Villebrunaster*, but it seems probable that more use was made of the discriminatory powers of the tube feet.

A first 'physical' sorting would be brought about by the loss of velocity when the adradial currents from opposite side meet, change their direction through an angle, and then flow towards the mouth. There would be a further loss of velocity because the adradial currents impinge upon the steep walls of the ambulacralia (figure 4). Because of the loss of velocity the heavier debris falls to a lower level. This debris would be conducted along the base of the ambulacral walls to find an outlet at the interradial angles already noted as being devoid of skeleton. Gemmill (1915, p. 3) has noted that there are outgoing currents in *Porania* within these angles (see unlettered arrow in figure 2).

A further and more effective sorting would take place during the radial passage of the food by the use of the discriminatory powers of the tube feet. All tube feet have a well-developed sensory system which is associated with the motor nerve supply of the muscles of the tube feet (see, for example, Smith 1937). The reaction of the tube feet to the presence of food has been described by several observers.

I have quoted in full (Appendix p. 124) the observations of Gislén upon the feeding of *Antedon.* These show that the tube feet not only notice the presence of food but take action to throw it into the ciliary produced stream which is flowing towards the mouth. Von Uexküll (Appendix, p. 126) quotes observations which show that the tube feet of *Ophiothrix* can take similar action, and observes that the food is passed from tube foot to tube foot along a zigzag path, a natural path for a starfish with alternating ambulacralia. Gislén also discusses the possible narcotic effects of secretions from glands along this path. Such a possibility has also been suggested by Blegvad (Appendix, p. 125) as an aid to the opening of a bivalve during the feeding of the Asteroidea.

Food reception

The structure of the ambulacralia bordering the buccal slits suggests that the slits were the food-reception areas. The basins upon the ambulacralia are lifted into the oral plane, and the tube feet attached to these basins are in position to throw the food into the floor of the slits, whence it would pass to the central body opening. It is possible that here was a final selection of food material. Observations upon the evolution of the Ophiuroidea (see p. 110) show a differentiation of the proximal tube feet, perhaps for this same purpose.

The significance of change of the body shape

The second body shape is that photographed in figure 29, plate 2, and drawn in figure 3.

The body is elongate in the vertical plane, with its food-collecting areas thrust upwards. This body shape is in accordance with its presumed mode of ciliary feeding.

The body if compressed in the vertical plane would have its food-collecting surface facing downwards. In this position the ciliary channels would tend to choke. This would be the more likely if, as seems possible, the starfish lived partially under the bottom mud. The thrust upwards presented the collecting areas to a medium as free from debris as possible. A parallel amongst recent echinoderms is given by *Cucumaria*, which Hunt (1925) describes as living buried in the mud with its food-collecting surface (the buccal tentacles) projecting into the clear water above the bottom.

Chinianaster Thoral

Synonymy

Chinianaster pars Thoral, 1935, p. 127, plate ix, figures 1*a*, 1*b*; plate viii, figure 1; *non* plate x, figure 4.

Diagnosis

A chinanasterid with large ambulacral basins placed on the oral surface and separated by a mid-radial open channel.

Type species (by original designation)

Chinianaster levyi Thoral.

Material

Four specimens; the first, the original of Thoral, 1935, plate ix, figure 1*a*, 1*b*, is here chosen as the lectotype, it was found by Villebrun and is either of Tremadoc or Lower Arenig age; the second, the original of Thoral, plate viii, figure 1, was found by Thoral and is of Upper Tremadoc age; the remaining two specimens were collected subsequent to 1935 by Thoral. All came from the neighbourhood of St Chinian, Dept. Hérault, south France.

Description of the lectotype (figure 7 and figures 35, 36, plate 3)

Oral surface. A few of the ambulacralia at the arm extremity are similar to those of *Villebrunaster*. There the ossicles are small and narrow, the basins for the tube feet face outwards and the channel between the ambulacralia almost enclosed. Proximal to these there is a considerable stretch of arm with broad ambulacralia which have a deep channel running along the midradius, open on its oral surface.

This channel, the ambulacral channel (Spencer 1914), is found in the later related genus *Archegonaster* and in all Asteroidea.

The basins for the tube feet in this portion of the arm are large and placed almost in the oral plane. The build of these basins appears to be primitive since it is similar in all Somasteroidea; palaeozoic Asteroidea and primitive Ophiuroidea. The hollow of the basins indicates a rounded seating of the tube feet (possibly an external ampulla, see p. 103). The floor of the basin is elongate in the direction of the arm and is shared unequally by two ambulacralia. The narrower portion of the floor is on the hinder part of the proximal ossicle, and here the edge of the basin rises steeply. The distal portion of the basin is large and the edge gently sloping. The branch which leaves the radial water vessel to proceed to the tube feet passes in a gap placed on the proximal inner edge of the basin. It thus appears that the tube foot, although seated on the distal portion of a basin, really belongs in origin to the more proximal of the pair of ambulacralia. This feature is of importance when considering the evolution of the ophiuroid vertebrae (see p. 118).

There are three ambulacralia on each side of a buccal slit. The basins within the slits are slightly tilted inwards, but there is no tilt forwards such as is noticeable in *Archegonaster* and the Ophiuroidea. The general arrangement of the basins for the tube feet finds a close parallel amongst the Asteroidea found in the early Palaeozoic.

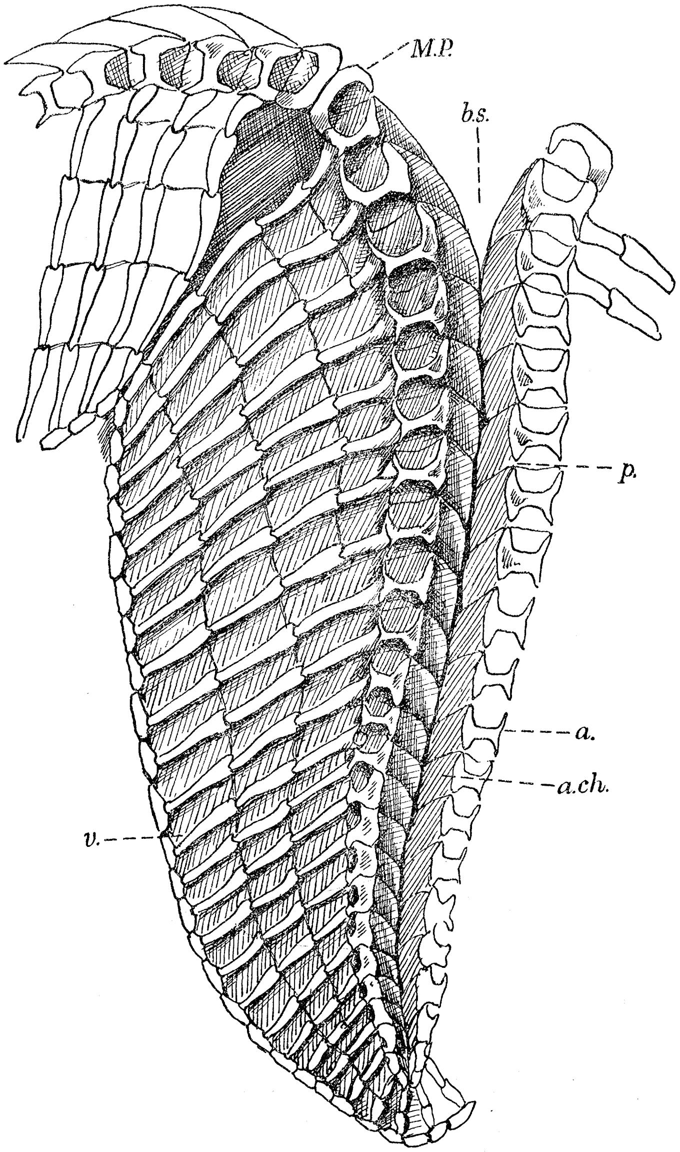


FIGURE 7. *Chinianaster levyi* Thoral. Reconstruction of one arm. *a.*, ambulacral; *a.ch.*, ambulacral channel; *b.s.*, buccal slit; *M.P.*, mouth-angle plate; *v.*, virgalia. The interradial area, behind the mouth-angle plates, without skeleton is deeply shaded (see p. 97).

The structure of the interradial areas is much as in *Villebrunaster*, except that the outline of the margin is not so distinctively petaloid. The ossicles at the edge of the disk are closely set, apparently to add to the strength of these edges.

A madreporite is present in one of the oral interradial angles. It is difficult to decide whether this was its original position or whether it has fallen from a more aboral position.

Aboral surface (figure 36, plate 3). The skeleton extends only over the centre of the body and the arm bases. The greater part of the arm appears to be without skeleton.

There seems to be little doubt that the central area was considerably swollen, the majority of the ossicles here have collapsed into a heap. At the outer edges of the heap there are areas where the typical net appears to be undisturbed. The same net can be seen from the oral side within the cavity of the central opening (see the photographs reproduced in figures 35 and 36).

The restriction of the skeleton allows good views of the aboral surfaces of the majority of the ambulacralia. They are slightly tumid, closely touching, without any sign of joints or of interskeletal musculature.

Description of the remaining syntype and the two small specimens

In these specimens the mouth frame apparently is much enlarged. Each V has at least seven ambulacralia, and the ambulacralia which touch one another along the midradii are much reduced in number (figure 8 and figures 32, 33, plate 2).

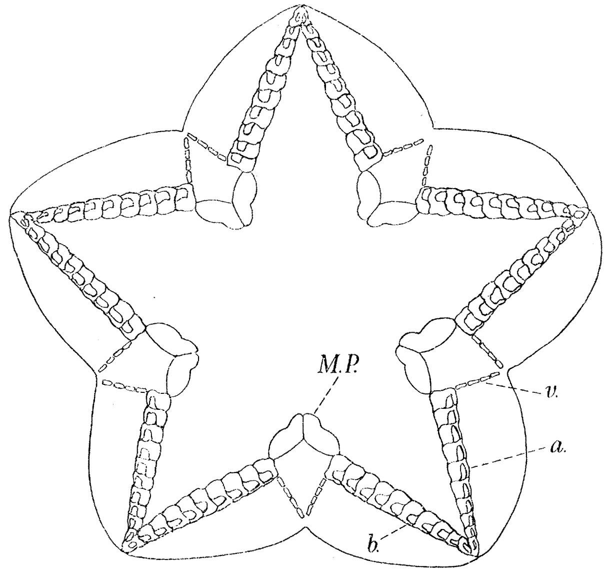


FIGURE 8. *Chinianaster levyi* Thoral. A reconstruction of the mouth frame as seen in a small specimen. *a.*, ambulacral; *b.*, basin for tube foot; *M.P.*, mouth-angle plate; *v.*, virgalia.

The explanation appears to be that the V's have become enlarged by a split along the midradial line due to a relaxation (possibly post-mortem) of the musculature which normally held them together. The ambulacralia within the V's have in consequence assumed an abnormal tilt which makes their basins slope outwards and not in position to facilitate the handing by tube feet of food into the mouth. The musculature which could bring the basins into a feeding position, that is, with their basins tilted inwards, is a ventral cross-musculature which on tightening would bring the inner edges of the ambulacralia nearer to the middle of a radius and at the same time swing their outer edges into the oral place. A similar musculature is found in the Asteroidea.

Mode of life

The specimens give little information as to the mode of life. The basins for large tube feet placed in the oral plane find a parallel in *Archegonaster*.

Family ARCHEGONASTERIDAE n.fam.

Diagnosis

Somasteroidea with bodies bounded by a stout marginal frame, approximately pentagonal in outline, rows of virgalia confined to wedge-shaped area within the outer angles of the pentagon, proximal tube feet were buccal tentacles. Adambulacralia present.

Remarks

The family contains one genus, *Archegonaster* Jaekel. This is found in the Dγ_1 (Upper Arenig) of Bohemia.

The relationship of this genus to the early French starfish is shown by the presence of rows of virgalia. These, however, do not occupy the whole of the interambulacralia but are confined to limited outer areas. It is suggested that they no longer serve as the main organ in nutrition but are retained as an aid in respiration.

The orientation of the proximal tube feet suggests that the main method of feeding was by pushing selected bottom material into the mouth by means of the tube feet. This method appears to be similar to that adopted in the Ophiuroidea from the time of their appearance and onwards (see p. 110).

Both the marginalia and adambulacralia arise as a differentiation of the inner and outer members of rows of virgalia. The marginalia are very similar indeed to those found in *Petraster* Billings [*Uranaster* Gregory], the earliest known asteroid, which appears in the Lower Arenig. The adambulacralia are cover-plates like those of the Ophiuroidea and quite unlike the adambulacralia of Asteroidea.

It is difficult to recognize with certainty any skeletal elements on the aboral surface, except the madreporite.

Archegonaster Jaekel emend.n.

Synonymy

Archegonaster Jaekel, 1923, p. 344.

Diagnosis

As for family.

Type species

I adopt Jaekel's unpublished MS. name for the only known species, *A. pentagonus* n.sp.

Material

A considerable number of specimens have been collected from the Upper Arenig Dγ_1 beds of Osek, Bohemia, and are now preserved in the Narodni Museum, Prague. The specimen illustrated here in figures 39 and 40, plate 4, is chosen as the holotype. Jaekel (1923) gave a very short description. His manuscript notes, however, are very full, but my account differs in interpretation largely because I have the earlier French material (unknown to Jaekel) for comparison. The abundant material not only allows study of the skeletal units, but the changes in the disposition of the units during the muscle contractions which brought about important arm flexures.

The general characters of the form are shown in figure 9.

Description

The ambulacralia are built on the same general plan as are those of *Chinianaster*, but they are lighter in construction and show a marked approach to those of the early Asteroidea. The large hollow which occupies the midradius in *Chinianaster* is replaced in *Archegonaster* by a shallow channel. The ambulacralia however are placed alternately as in *Chinianaster* not opposite as in all Asteroidea.

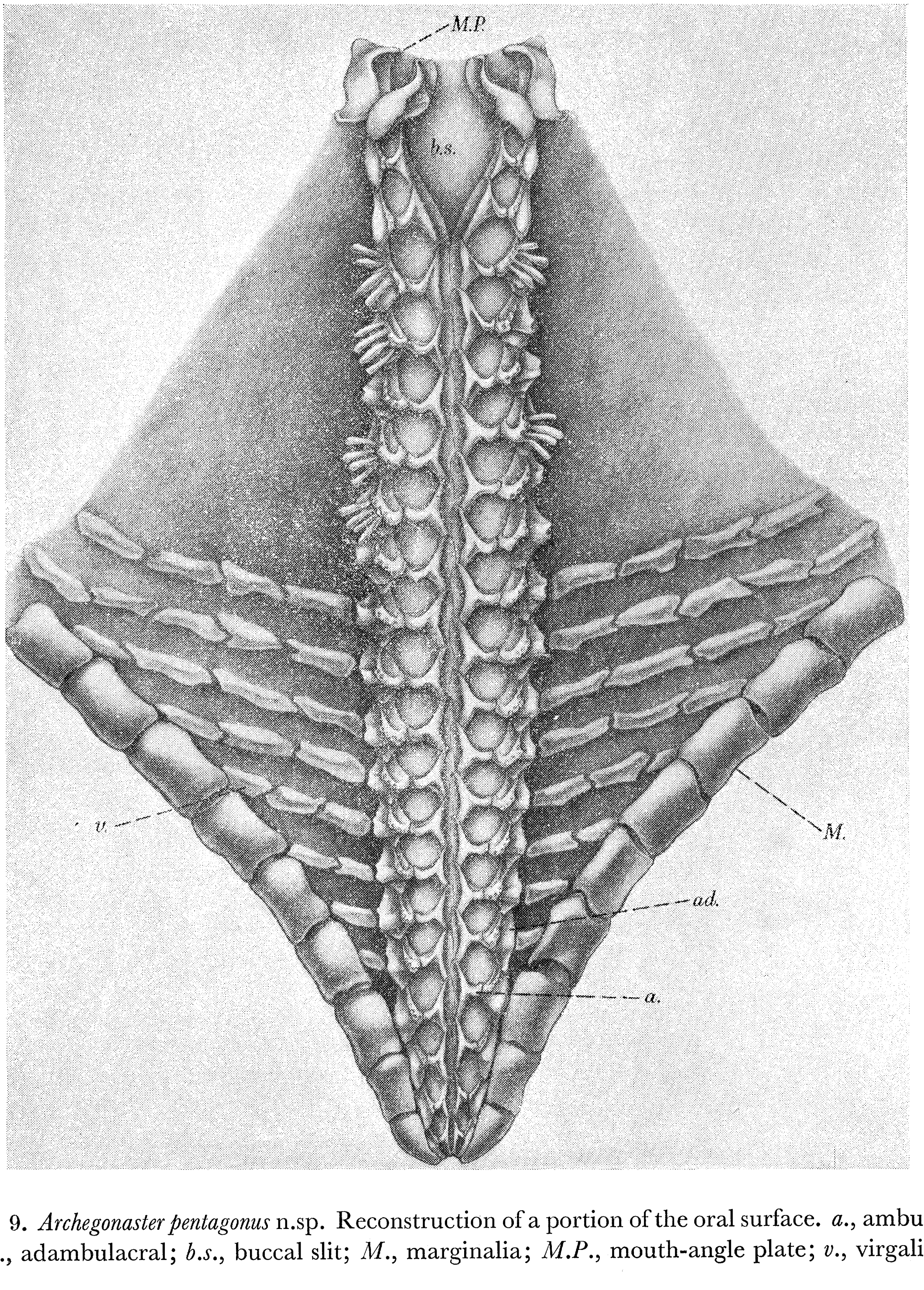


FIGURE 9. *Archegonaster pentagonus* n.sp. Reconstruction of a portion of the oral surface. *a.*, ambulacral; *ad.*, adambulacral; *b.s.*, buccal slit; *M.*, marginalia; *M.P.*, mouth-angle plate; *v.*, virgalia.

The floor of the channel has tongue-shaped projections which overlap proximally (figure 10). Similar tongue-shaped projections have been figured for several Palaeozoic Asteroidea. They can be seen in the following genera all figured by Schuchert (1915: *Hudsonaster*, plate 5, figure 1; *Promopalaeaster*, plate 20, figure 2 and plate 23, figure 2; *Urasterella*, plate 27, figure 7 and plate 30, figure 3). I have also figured them for *Schuchertia* (Spencer 1919, p. 183). The tongues are important hinges during arm flexion.

The basins are large and deep, and it is difficult to see more than their upper edges. The tube feet must have been large. Jaekel in his manuscript notes makes a suggestion that the deep hollows between the basins were occupied by basal extensions of the tube feet which he called external ampullae, to distinguish them from the internal ampullae of the recent Asteroidea which lie within the body cavity. A similar deep basin is seen in the primitive ophiuroid *Eophiura* (figures 19 and 20, pp. 114, 115). It is also seen in Palaeozoic Asteroidea. No Palaeozoic asteroid shows the pore between the ambulacralia marking the passage to an interior ampulla.

A comparison of figures 10 and 11 suggests that the pore area of a recent Asteroid corresponds to the ambulacral basin of these early starfish and that the ampulla has migrated inwards during evolution.

The lack of skeleton allows good views of the upper surfaces of the ambulacralia (figure 13). Where they meet along a midradius they look like overlapping tiles. Laterally they are prolonged into wings with interspaces. If they are compared with a corresponding view of the ambulacralia of the primitive ophiuroid *Palaeura* (figure 26*A*, p. 120), many points of resemblance can be noted.

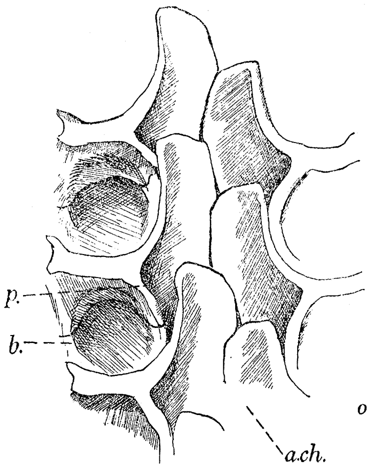
In *Palaeura* there are well-developed midradial balls and sockets and lateral facets for the insertion of longitudinal muscles connecting one ossicle with its neighbour. The corresponding structures are seen in *Archegonaster*, but in a more rudimentary stage of development. Nevertheless, they functioned to flex the arm dorsally, as in *Palaeura*. This was the position of the arm in both forms during feeding.

The adambulacralia (figure 12 and figure 54, plate 8) are pear-shaped. The broad end of the pear has a thickening upon its oral surface which carried a row of spines. These rows are at right angles to the arm axis, and the spines appear to be arranged as a fan. The stalk of the pear appears to be short in figure 12, and long in the photograph of figure 54.

The apparent increase in length is due to a different placing of the pear relative to the tube feet. The extreme end of the stalk is a hinge joint which articulates with the lateral extremity of an ambulacral. If the stalk is long the adambulacralia have swung outwards to allow full extrusion of the tube feet. If the stalk appears short the adambulacralia have swung inwards to shelter the tube feet. The adambulacralia therefore are hinged cover-plates. Movement is facilitated by the narrow sutures between successive ossicles.

These adambulacralia differ in two important respects from the adambulacralia of the Asteroidea. There they are rectangular in outline with broad interossicular sutures. Between the sutures are broad muscle bands, the longitudinal adambulacral muscles, which play an important part in maintaining the characteristic asteroid posture (see p. 122). In *Archegonaster*, if any longitudinal musculature was present, it was only feebly developed.

The second important difference lies in the character of the joint which links the ambulacral with the adambulacral. The asteroid adambulacral lies upon a large flat excavation



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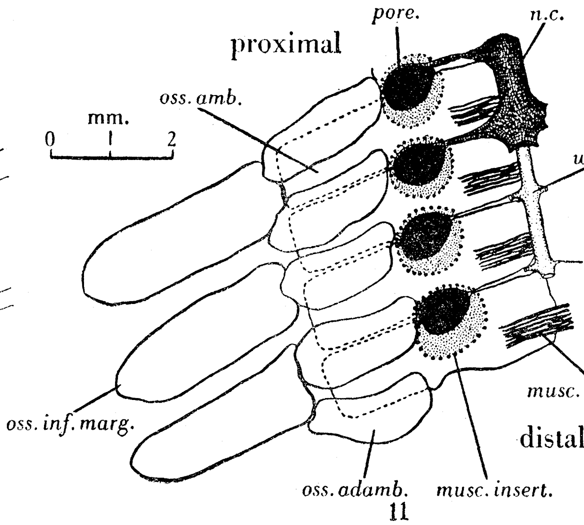

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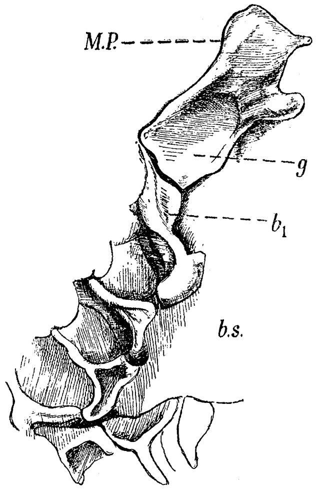

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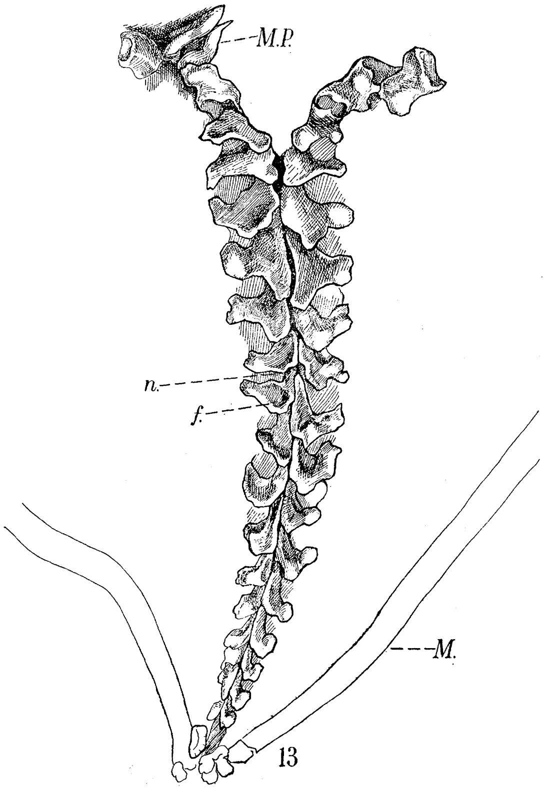

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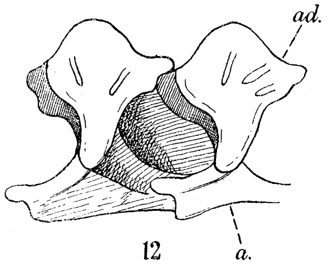

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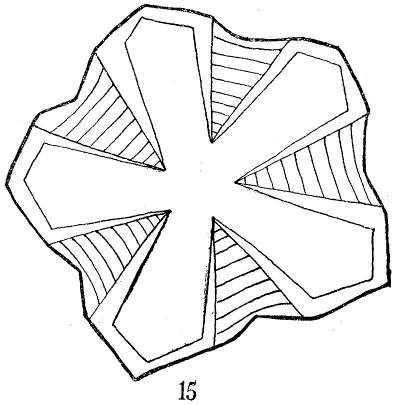

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FIGURE 10. *Archegonaster pentagonus* n.sp. Ambulacralia enlarged. *a.ch.*, ambulacral channel; *b.*, basin for the tube foot; *p.*, passage for branch vessel (from E.H. 7).

FIGURE 11. Reproduced from Smith (1946, figure 2, p. 285). Diagram to show the structures visible on one side of a portion of the ambulacrum of *Astropecten irregularis* after removal of the tube feet and adambulacral and infra-marginal spines. Parts of the radial nerve cord and of the radial water vessel have been removed to expose the underlying structures. *musc.inf.trans.*, inferior transverse muscle; *musc.insert.*, insertion of the tube-foot musculature on the ambulacral ossicle,

placed on the oral surface of the ambulacralia (figure 11). The corresponding articular surface in *Archegonaster* is narrow and lateral, a character seen also in the primitive Ophiuroidea (see figure 20, p. 115).

As noted above complete rows of virgalia are present only towards the arm extremities. The median members of these rows are long narrow plates as in the Chinianasteridae. The inner members of the rows, however, are broadened and differentiated as adambulacralia. The outer members also have been broadened and differentiated to form portions of the marginal frame. The presence of adambulacralia and marginalia in the interambulacral region, otherwise devoid of skeleton, suggests that rows of virgalia occupied the whole of the interambulacral areas in the *Archegonaster* ancestor. A loss of skeleton is carried even further in the later representatives of these primitive starfish.

The marginalia are thick and triangular in cross-section. They are covered with minute granules giving them a roughened surface. Between the separate components there are hollows for the insertion of interconnecting muscles or ligaments. There is evidence (see below) that the frame acted as an antagonist to the prime-moving muscles during arm flexure.

The madreporite opens on the aboral surface. It is flat with shallow channels. The lack of calcification in the interambulacral areas allows in one specimen (figure 37, plate 3) a good view of its interior face. In the centre is a U-shaped furrow for the attachment of the stone canal, resembling a similar furrow in recent Asteroidea. Near it is a group of very small ossicles, the scattered small components of the wall of the stone canal.

The arrangement of the tube feet within the buccal slits is somewhat different from that in the Chinianasteridae. There all the tube feet bordering the slits pointed inwards towards a midradius. In *Archegonaster* the more distal tube feet pointed inwards, but the first two tube feet pointed forward, towards the central body opening. A view of the proximal ossicles of the slit area is given in figure 14; it is similar to a view of the same ossicles in the primitive ophiuroid *Eophiura* (figure 23), where there is a similar disposition. In both cases the mouth-angle plates have a hollow groove which shows the forward angle of protrusion of the podium of the first tube foot. The base of the tube foot is housed in a small basin (b_1, figure 14) at right angles to this.

It is suggested below (p. 118) that the specialization of the proximal tube feet into buccal tentacles is associated with deposit feeding.

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n.c., radial nerve cord; *oss.adamb.*, adambulacral ossicle; *oss.amb.*, ambulacral ossicle; *oss.inf.marg.*, infra-marginal ossicle; *pore.*, pore between successive ambulacral ossicles; *w.v.l.*, lateral water vessel; *w.v.r.*, radial water vessel.

FIGURE 12. *Archegonaster pentagonus* n.sp. Ambulacral-adambulacral fitting. *a.*, ambulacral; *ad.*, adambulacral (from E.H. 11).

FIGURE 13. *Archegonaster pentagonus* n.sp. Ambulacralia and portion of mouth frame as seen from above, *f.*, facets for the insertion of dorsal longitudinal muscle; *n.*, nose fitting (incipient ball and socket joint;) *M.P.*, mouth-angle plate; *M.*, outline of marginal frame (from E.H. 36).

FIGURE 14. *Archegonaster pentagonus* n.sp. Buccal slit seen from within. *b.s.*, space occupied by buccal slit; b_1, basin for first tube foot; *g.*, groove for channel of emergence of first tube foot. *M.P.*, mouth-angle plate (from E.H. 25).

FIGURE 15. *Archegonaster pentagonus* n.sp. Diagrammatic drawing showing the arm wedge flexed over the aboral surface (see also figure 34, plate 2).

Arm-flexure feeding and respiration

Specimens which show the animal as a complete pentagon are comparatively rare. Most of the specimens show the arm flexed upwards. The manner in which this flexure is brought about can be followed from a study of specimens which show stages in the flexure.

In the first stage the arc of the marginal frame is drawn sharply inwards and wedges appear in the angles of the pentagon. The photograph (figure 38, plate 3) shows the formation of a wedge. The frame is drawn inwards towards the central opening. It is clear that the pull which brought this about is by musculature placed in the uncalcified portions of the oral surface. The marginal frame would be under tension during this muscular contraction and 'by inertia' controls the forces and directs them.

In the next stage the wedges are flexed upwards and lie evenly spaced facing upwards (figure 34, plate 2, and figure 15).

The dorsal flexure is possible because of the musculature noted above as inserted on the dorsal surfaces of the ambulacralia. The dorsal median ball and socket and the ventral overlap of the oral surface keep the ambulacralia in place during this upward arm swing.

This dorsal arm flexure raises the arm wedges, with their rows of virgalia, to face the superficial layers of the bottom mud.

The distal tube feet now face upwards, exactly as in the Palaeozoic Ophiuroidea described later. Their ability to protrude and reach well out would enable them to search the top layers of the bottom mud, then pull the food downwards into positions where it could be pushed by other tube feet towards the mouth (compare feeding of Atelostomata, p. 125).

This reconstruction makes *Archegonaster*, like the primitive Ophiuroidea, a burrowing starfish. Animals with such a habit have difficulties with respiration. Later it is suggested that the Ophiuroidea meets this difficulty by the provision of respiratory pouches (see p. 107). There is no evidence that pouches occur in *Archegonaster*. On the other hand, the ciliary currents created within the rows of virgalia placed near the arm extremity would bring along 'new' water. This 'new' water passing along the ambulacral channel would enter the mouth and provide for endodermal breathing.

Subclass OPHIUROIDEA

Diagnosis

The arms are long and narrow. Their musculature is not in the body walls but inserted upon the proximal and distal faces of the ambulacralia where ball and socket joints are developed.

The ossicles which border the arm in early forms are hinged (in later forms they are fixed) upon narrow facets on the outer lateral edges of the ambulacralia.

The centre of the body is occupied by a 'disk' which has a scale (or granular) skeleton. The disk structure is associated with respiratory pouches placed between the oral surface of the disk and the arm.

The tube feet act usually as individuals and not collectively.

The relationship between structure and function in the primitive Ophiuroidea is discussed below.

There is evidence that some of the more important characters of the Ophiuroidea are associated with a 'burrowing' habit. Such evidence is provided by (1) the state of the fossil remains, (2) a reconstruction of the mechanisms concerned in respiration.

The state of the fossil remains

The body of a starfish readily disintegrates after death and the skeleton is usually scattered. If the skeleton is found with its bones in position there were special conditions at the time of death, which favoured preservation. A favourable condition would be a 'burrowing' habit, for the starfish died in the grave which it had already dug during its life.

The fossil Ophiuroidea described below show not only the whole or considerable portions of their skeleton in place but also indications of the structure and position of the soft parts. Decay after death must have been very gradual. Mud infiltrated into the hollow of the vessels and hardened. The original course of the radial and branch vessels of the water-tube system are well shown in this way, especially in large Ophiuroidea such as *Eophiura* (figure 57, plate 8).

When only portions of the skeleton are preserved they are those which lie deepest in the burrow. The majority of the fossil ophiurids, *Pradesura* n.g., *Eophiura* Jaekel emend. Schuchert and *Palaeura* Jaekel emend. Schuchert show only the disk and the arm bases. The distal arm regions have been lost. Aquarium observations give the reasons for this. *Amphiura* is an example. After it has burrowed it lives with its arm flexed steeply to the disk. The arm extremities project above the sea-bottom and busy themselves with the capture of the rich supply of food available there (Hunt 1925). It is these exposed arm regions which tend to be lost.

The descriptions of the Ophiuroidea given below detail the characteristics of preservation in relation to the presumed burrowing habit.

Respiratory mechanisms

The respiratory organs are enclosed gills (respiratory pouches often called 'genital bursae') These pouches are lined with cilia, and their walls project into the cavity of the disk.

Two mechanisms are concerned with the change of water within the pouches, (1) ciliary activity and (2) changes in the pressures on the walls of the pouch brought about by pulsations of the walls of the disk.

Ciliary activity is the normal method. The activities of the disk arise only when the ciliary activity weakens. The weakening of ciliary activities has been investigated by Gray (1928). It is brought about when the water immediately surrounding the cilia is impoverished of oxygen and enriched in carbonic acid, that is, under forced respiration.

The mechanisms which occur during forced respiration have been described by MacBride (1906, p. 485). There are ten radial shields placed on the aboral surface. Each articulates with a bar ('genital' bar). Muscles placed on each side of the articulation allow the movement of the shield upon the bar. MacBride's observations on *Ophiothrix* show that in this species the articulations allow the radial shields to be raised or lowered.

When they are raised, the centre of the disk is lifted into a cone and water is sucked into the pouches, whereas when they are lowered the pouches are compressed and water is expelled. He adds in a footnote that he has also observed this in *Ophiura ciliaris* and *Amphiura squamata*.

The disk of the early Ophiuroidea has no radial shields or 'genital bars'. The upper part of the disk is swollen. The scales there fit together loosely whilst at the base they form a firm mosaic skeleton. A squeeze of muscles within the body wall would bring about a rise and fall of the upper loosely built skeleton. The firm base would not give and the pressure would be exerted on the walls of the pouches arranged around the base.

The Palaeozoic genera belonging to the Euzonosomatidae (Spencer, 1930, p. 405) have the base of the disk further strengthened by a marginal frame.

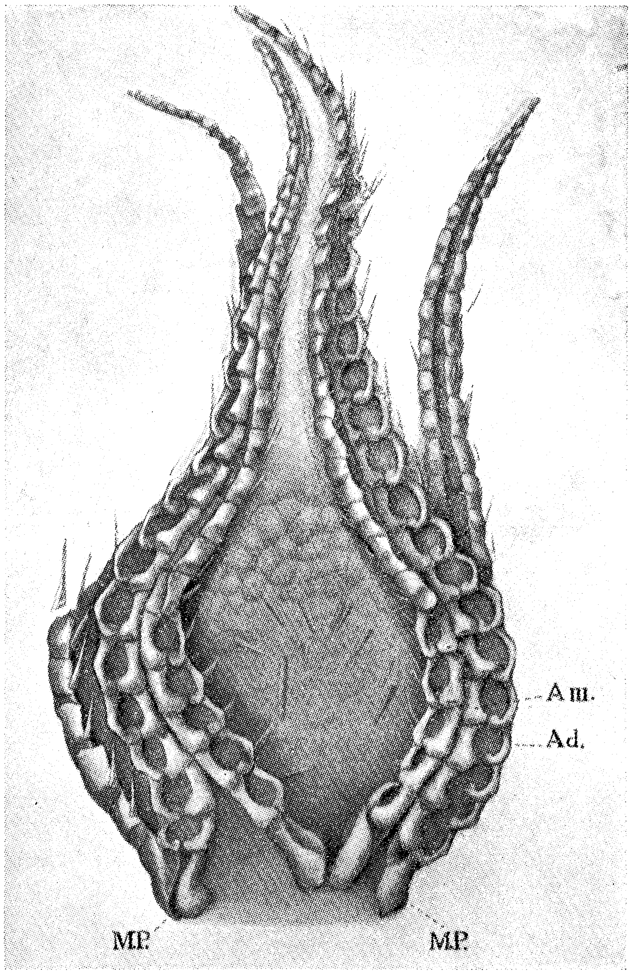


FIGURE 16. *Taeniaster spinosus* (Billings). A small specimen showing the arms flexed steeply over a swollen disk (copied from Spencer 1922, text-figure 140). *Ad.*, lateral; *Am.*, ambulacral; *M.P.*, mouth-angle plate.

Other activities of the Ophiuroidea within the burrow

I have not seen any observations upon recent burrowing Ophiuroidea which describe the burrow itself or deal with the difficulties of respiration and transport of food associated with the burrowing habit. Examination of the fossil material suggests the methods which were employed by the early Palaeozoic forms to meet the problems.

The transport of small food to the mouth, placed as it is at the bottom of the burrow, could only be effective if the surrounding sand or mud be excluded from the food channel.

A tunnel through the mud is provided by the ossicles (lateralia) at the edge of the arms. These carry a border of long spines. The lateralia with their spines can swing over and form the walls and roof of such a tunnel. A specimen of *Eophiura* (see p. 117) shows such a tunnel.

It is probable that an ophiuroid can harden the walls of the burrow and thus provide space between the animal and the surrounding mud for free circulation of 'new' water. This problem has been considered by von Uexküll (see p. 93). In all the cases quoted the animal exerts pressure upon the surrounding medium to form a wall and then cements the particles of the wall by mucus or similar material.

In the case of the ophiuroid, pressure to form the wall would arise from alternate narrowing and widening of the disk as described above. Such movements would become more active in forced respiration, that is, when a supply of 'new' water was in process of being cut off. In this way lack of new water would automatically bring into being new pressures to form the wall.

The Ophiuroidea and the primitive echinoderm stock

The ambulacralia

The early Ophiuroidea have characters which suggest that they are near to a primitive echinoderm stock.

The ambulacralia are very similar to those of *Villebrunaster*, a starfish which shows the beginnings of skeletal differentiation. In both the ossicles are developed within the sheaths enclosing the radial water vessel, and their tubular cross-section shows no sign of any mid-radial groove, which in the Asteroidea houses the broad thick radial nerve cord. Smith's investigations show this nerve to possess definite cable-like tracts providing paths for the rapid conduction of impulses from the sensory elements of the ectoderm to the circum-oral nerve ring, the centre responsible for the maintenance of co-ordinated movement of the tube feet and arms.

The absence or presence of a well-developed radial nerve cord is linked with the methods of feeding. In the Asteroidea (see p. 122) feeding is a result of the co-ordination of tube feet and arms.

In the Ophiuroidea there is no such co-ordination. In an account of the suggested method of feeding of *Villebrunaster* (see p. 97) I drew comparisons between the possible method employed by the primitive starfish and the accounts given of the capture of small food by the recent crinoid *Antedon* and by *Ophiothrix*. In each form every tube foot acts as an autonomous agent. It recognizes a food particle, places itself adjacent and then pushes the particle into the food channel. There it is recognized by an adjacent tube foot and pushed farther along. Eventually the proximal tube feet push it into the mouth. During feeding on small food the arms, both of the Crinoidea and of the Ophiuroidea, act merely as supports of the tube feet during the period in which the tube feet are engaged in food capture and transport. In the asteroid both arms and feet work together in the feeding activities to bring the food nearer the mouth.

Upon the evidence available it would seem that the condition in the Crinoidea and the Ophiuroidea where the tube feet act as isolated elements is more primitive than that in the Asteroidea which have acquired an equipment of association elements within the sensory system.

The aboral skeleton

The scales of the aboral surface of *Pradesura* and some other early Palaeozoic Ophiuroidea (figure 18) have a radiate cap. The disposition of the branches of the caps recalls the radiate spicules of *Villebrunaster*, and suggests that the scale has been formed by shallow infillings between the branches. Support is given to this view by the structure of the aboral ossicles of *Sturtzaster*. This Silurian ophiuroid has a high swollen disk with ossicles which have reverted to the *Villebrunaster* type (figure 5, p. 95).

The mouth frame

The mouth frame in the Arenig Ophiuroidea has deep radial V's, a character also found in the Somasteroidea (see p. 92) and in the early Asteroidea (see p. 123). The interpretation suggested is that the V's represent the marginal skeleton of buccal slits which in the common echinoderm ancestor opened into a central stomodaeum.

The stone canal

A stone canal is present in recent Asteroidea but not in recent Ophiuroidea. It is present in the early Ophiuroidea (see p. 116) and in the Somasteroidea (see p. 105).

The buccal tentacles

A characteristic of recent Ophiuroidea is that the first two pairs of tube feet are enlarged and placed in position to reach into the stomach. In origin they are the proximal elements of the tube feet placed within the buccal slits where, it was suggested (see p. 92), the selection of nutritive from non-nutritive material mainly occurred. These buccal tentacles can be regarded as making the final decision upon the material passed into the stomach. The orientation of these tube feet is an important factor in the evolution of the ophiuroid 'jaw'.

The first stage in the orientation brings the mouth-angle plates into alinement with the first ambulacralia. In the early Ophiuroidea only the first pairs of tube feet are buccal tentacles. Food selection in this way does not occur in the Asteroidea which never have buccal tentacles.

Classification

I am dividing the Ophiuroidea into:

Order Stenurida n.ord. The ambulacralia have not become vertebrae. The arm is capable only of limited movements.

Order Ophiurida n.ord. The ambulacralia have become vertebrae. The arm is capable of snake-like movements.

Order STENURIDA n.ord.

All the Arenig Ophiuroidea, with the exception of *Hallaster* known from one solitary specimen, belong to this order. The genera described here are *Pradesura* n.g. (Basal Arenig), *Eophiura* Jaekel emend. Schuchert and *Palaeura* Jaekel emend. Schuchert (Upper Arenig).

All have

(1) Ambulacralia formed in a sheath which enclosed the radial vessels. Each tube foot was placed in a basin shared by two ambulacralia.

(2) A clearly defined disk with a 'scale' skeleton.

(3) A mouth frame with radial V's. The ossicles within the V's are fused, and each arm of the V acts as a unit during the opening of the frame.

(4) The ossicles bordering the arm (lateralia) are hinged to the ambulacralia and act as covering plates to the groove. They correspond in position to the side-shields of the Ophiurida, but these latter are fixed not hinged.

The lateralia usually can be recognized as a double series. In a previous publication (Spencer 1940) I called the members of the double series outer and inner lateralia. Jaekel uses the terms lateralia and sublateralia for these same two series, and his terms prove to be more suitable for the purposes of description.

Classification of Stenurida

1. Superfamily Eophiuricae n.superfam.

   Stenurida with the basins for the tube feet placed subequally on two ambulacralia.

   (*a*) Family Stenasteridae Schuchert 1915 emend.n. Lateralia broad, each carrying several rows of spines.

   Stenaster Billings.

   (*b*) Family Eophiuridae n.fam. Outer lateralia broad with a single row of spines placed parallel to the arm axis.

   Eophiura Jaekel emend. Schuchert, *Rhopalocoma* Salter, *Ptilonaster* Hall.

   (*c*) Family Pradesuridae n.fam. Outer lateralia broad with a single row of spines placed at an angle to the arm axis.

   Pradesura n.g., *Sturtzaster* R. Etheridge junr.

   (*d*) Family Phragmactidae n.fam. Outer lateralia narrow, spines in single row at right angles to arm axis.

   Phragmactis Spencer, *Bdellacoma* Salter.

2. Superfamily Palaeuricae n.superfam. Stenurida with the basins for the tube feet placed almost entirely on one ambulacral.

   Family Palaeuridae n.fam. *Palaeura* Jaekel emend. Schuchert.

Pradesura n.g.

Synonymy

Palaeura Thoral, 1935, p. 123 *non* Jaekel, 1903.

Diagnosis

A stenurid of the family Pradesuridae with a well-plated disk and spines on the lateralia placed upon a ridge which runs at an angle to the arm's length. Ambulacral basins shared subequally by two ambulacralia.

Type and early known species

Palaeura jacobi Thoral (1935, p. 123, plate ix, figures 2–5). Basal Arenig, Prades sur Vernazobres, near St Chinian, Hérault, South France and near localities.

Material

The collections of the University of Montpellier contain seven specimens, three with counterparts. The central parts of the starfish are well preserved, but none of the specimens shows the distal parts of the arm.

Lectotype

The specimen figured by Thoral (1935, plate ix, figure 2 (here figure 41, plate 5)).

Remarks

Pradesura is the first ophiuroid to appear.

Its nearest relation is *Sturzaster* from the Silurian. This has a disk which is very swollen and devoid of scales.

The two characters which differentiate the genus from *Palaeura* are (1) the spines on the lateralia; in *Palaeura* parallel to the arm's length; (2) the basins for the tube feet, shared subequally by two ambulacralia in *Pradesura*, almost entirely upon one ossicle in *Palaeura*.

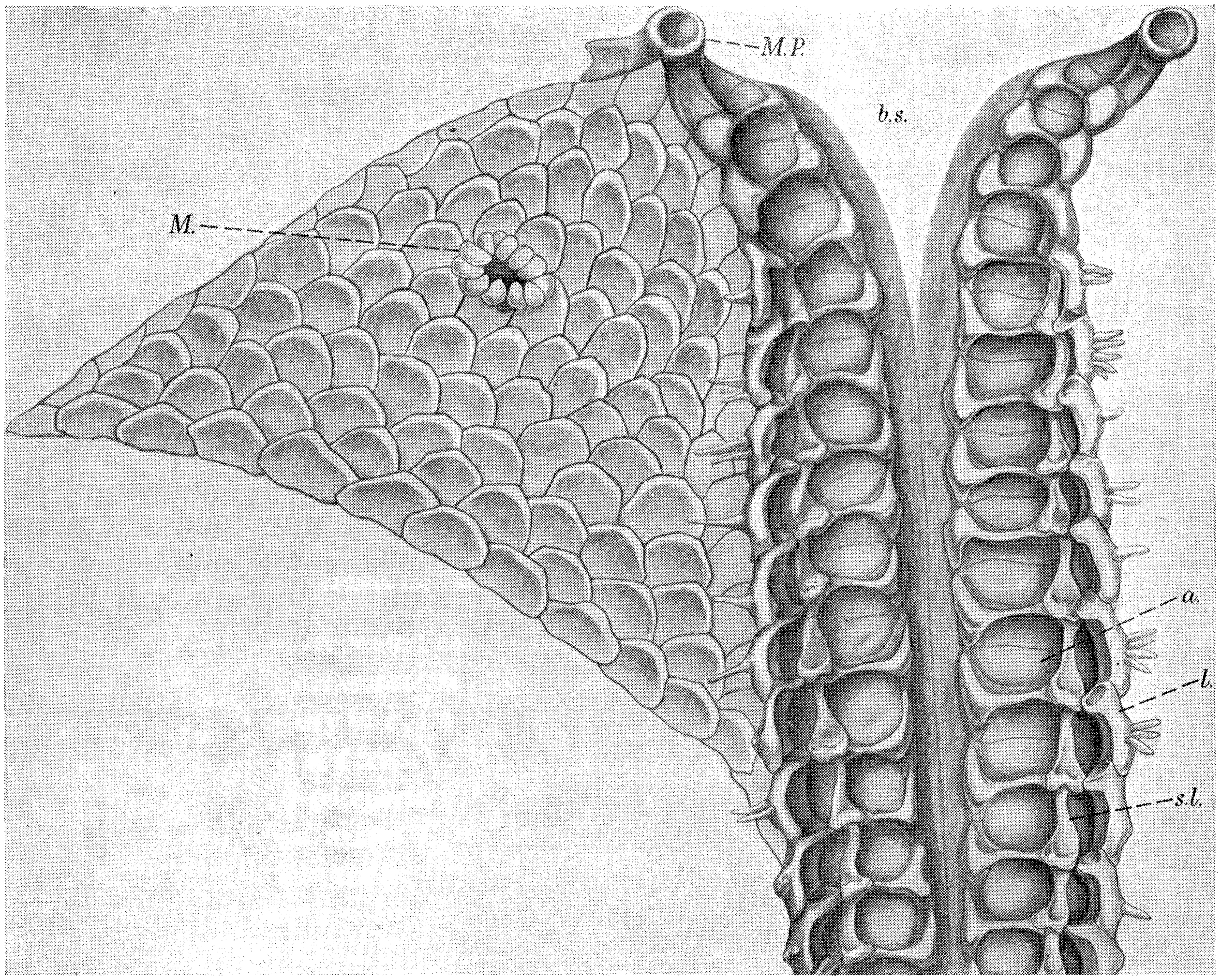


FIGURE 17. *Pradesura jacobi* (Thoral). Oral view of a portion of the disk and the neighbouring arms. *a.*, ambulacral; *b.s.*, buccal slit; *l.*, lateral; *s.l.*, sublateral; *M.*, madreporite; *M.P.*, mouth-angle plate.

Description

The arms (figure 17) have a thick central core of stoutly built ambulacralia and a narrow edging of lightly built lateralia. Although they are typically ophiuroid they have features which link the genus with the Chinianasteridae. The ambulacralia, in particular, have marked resemblances to those of *Villebrunaster*. They are placed alternately on each side of the arm, and collectively form a thick sheath to the radial water vessel. The basins for the tube feet throughout the greater part of the arm are excavated on the lateral margins of the sheath and the floor of each basin is shared by two neighbouring ambulacralia.

Some specimens, because of the collapse of the aboral covering of scales, allow views of the ambulacralia from above. The best of these views is given by No. Px. coll. Marty 1937, figured here (figure 44, plate 5). It shows ball and socket joints and facets for the insertion of the dorsal longitudinal muscles, similar, but less well developed, to those figured for *Palaeura* (figure 26*A*, p. 120).

The proximal ambulacralia form a mouth frame with radial V's similar to that of *Villebrunaster* in the number of ambulacralia (3×2) in each V. This is a smaller number than those present in the radial V's of *Palaeura* and *Eophiura.*

The disposition of the ambulacral basins within the frame follows that described above, p. 110. The first tube feet only are 'buccal tentacles'. The mouth-angle plates are very similar indeed to those of *Sturzaster* (Spencer 1940, text-fig. 337).

Both lateralia and sublateralia are present. The lateralia carry a row of spines placed on a slight ridge set almost at right angles to the arm length. The ridge passes over the entire width of the slightly swollen oral surface and then on to the lateral surface. The spines project outwards from the arm. Usually they are not well preserved, and in the specimen drawn (figure 17) they are only represented by their bases.

Specimen no. 140 shows impressions of long thin spines very similar to those of *Sturtzaster* (Spencer 1940, figure 33, p. 519).

The sublateralia, as is usual, carry no spines. They are long, narrow and thickened at their distal edge and lie alongside the ambulacralia with their greatest length along the arm radius. There are slight displacements here and there which suggest that the lateralia and sublateralia had not fused.

They could swing to shelter the tube feet. The specimen photographed in figure 43, plate 5, shows the lateralia in such a position.

The scales of the disk differ somewhat in form and disposition upon the two surfaces. On the oral surface they form a firm skeleton. Their rather irregular rows show no trace of association with the ambulacral skeleton noticeable in the Somasteroidea. The disk margins are straight or concave, not rounded as is usual in recent Ophiuroidea. One specimen (figure 42, plate 5) shows long thin spines on the scales near the margin.

On the aboral surface the scales fitted more loosely (figure 44, plate 5) and occasionally they have collapsed in heaps as if they had fallen from a tumid surface. Many show the radiate cap described above, p. 110. Specimen no. 137 shows that each cap carried a long spine similar to that carried by *Taeniaster* (Spencer 1934, text-fig. 292).

The madreporite is a small rounded thick ossicle with comparatively few surface channels. It is placed slightly to the left of a mid-interradius and near the interradial angle (figure 17).

Eophiura Jaekel, 1903 emend. Schuchert, 1915

Synonymy

Eophiura Jaekel, 1903, p. 107; *Eophiura* Schuchert, 1915, p. 222; *Eophiura* Jaekel, 1923, p. 347.

Diagnosis

A stenurid of the family Eophiuridae with a well-plated disk with small overlapping scales, spines set parallel to the arm's length; ambulacral basins shared subequally by two ambulacralia; ambulacral axis broad and stiff; paired mouth-angle plates broadly notched proximally.

Type (and only known) species

E. bohemica Schuchert, 1915 (=*E. pelaloides* Jaekel, 1923) from the Upper Arenig, $D\gamma_1$, of Osek, Bohemia.

Material

The original specimen illustrated by Jaekel (1903, text-figure 4) is here chosen as the lectotype of *E. bohemica*. That author gave two figures together with a short description.

Both are of the oral surface. One figure was drawn from the lectotype and the other from the specimen, here illustrated as figure 56, plate 8. The lectotype, like so many ophiuroids from the Arenig, shows only the disk and the arm bases. The second specimen gives an oral view of the distal arm regions flexed over the disk in a position I am interpreting as that adopted for feeding (see p. 117). Three other specimens show portions of the middle of the arms flexed steeply to the disk as in figure 57, plate 8.

Jaekel made further observations in 1923, but gave only a diagrammatic figure, the basis for my figure 19. His views are further elaborated in his manuscript. I have found that I could add little from my own observations, but, at times, I differ somewhat in interpretation.

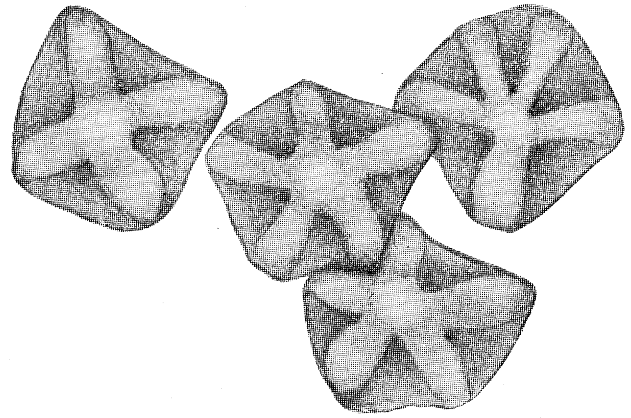


FIGURE 18. *Encrinaster grayae* Spencer. Scales from the aboral surface (copied from Spencer 1930, text-figure 260, p. 406).

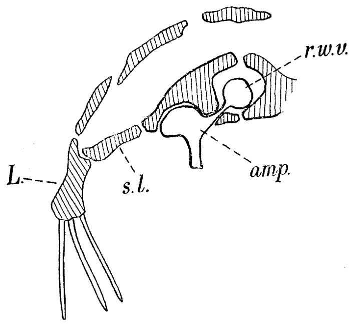


FIGURE 19. *Eophiura bohemica* Schuchert. Diagrammatic cross-section of arm, after Jaekel. *amp.*, external ampulla; *L.*, lateralia; *s.l.*, sublateralia; *r.w.v.*, radial water vessel.

Description

The ambulacralia resemble those of *Pradesurae* in that the basins for the tube feet are shared almost equally by two ambulacralia. They differ in two characters, the basins are nearer the oral surface, and the hollow between the ambulacralia housed a large radial vessel (figure 57, plate 8).

The basins are deep, and Jaekel in his MS. notes suggests that, as in *Archegonaster*, they were occupied by external ampullae. Towards the end of the arm (figure 20) they are oval but broaden laterally as they are followed towards the mouth. The anterior and posterior edges of the basins show a distinct groove (figure 48, plate 6) which probably was occupied by a lateral branch of the perihaemal canal surrounding the tube feet.

There are slight roughenings on the floor of some of the basins which may indicate the positions of attachment of the bases of the tube feet.

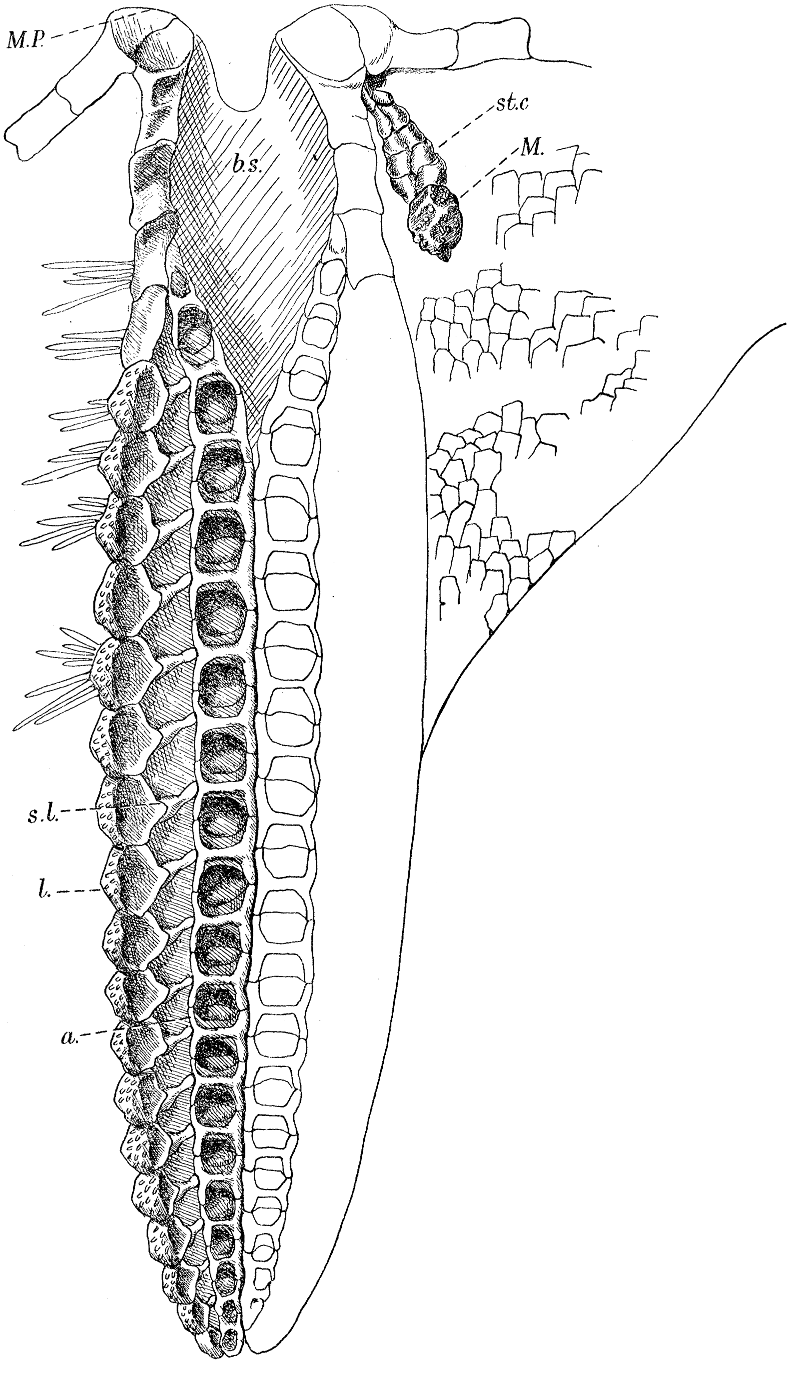


FIGURE 20. *Eophiura bohemica* Schuchert. Oral view of the arm and a portion of the disk. *a.*, ambulacral; *b.s.*, buccal slit; *l.*, lateral; *s.l.*, sublateral; *M.*, madreporite; *M.P.*, mouth-angle plate; *st.c.*, stone canal (based on E.H. 94 and E.H. 101).

The sides of the basins are thickened along their radial edges to form a series of longitudinal ridges which meet across the middle line. These ridges usually hide the large hollow between the opposite ambulacralia. Occasionally, however, the ambulacralia have fallen apart exposing the hollow in full depth. This is very similar to the hollow in *Chinianaster*. Some casts also show a tear where the side branch to a tube foot left the radial vessel. This tear is always immediately behind the cross-ridge, the thickened edge which separates two basins (figure 50, plate 7).

The tear always points backwards, and the branch vessel therefore followed the same path as that in a recent asteroid (figure 11, p. 104).

At the extreme outer edge of a basin is a small shallow depression which housed the muscle connecting an ambulacral with a sublateral.

The ambulacralia are well exposed from above in several specimens. They are rectangular in outline and convexly curved, so that they appear almost cylindrical in cross-section. They fit closely, but here and there are signs of the former presence of dorsal muscles (figure 22). This drawing shows the ossicles slightly dislocated with an overlap upon a slightly curved fitting. The overlap brings the outer upper edge of one ambulacral over its predecessor.

Both lateralia and sublateralia are present. They articulate by means of well-developed ball and socket joints. The effect of this articulation is to impart a wide swing to the movements of the lateralia.

The lateralia, when the swing outwards is at a maximum, show large flat surfaces, which, at their extreme outer edges, carry spines placed in a row parallel to the arm length. Near the arm extremities this single row is replaced by spines scattered irregularly on the faces of the ossicles (figure 52, plate 7).

The sublateralia are slightly twisted rods. Their outer ends are broad, and where they meet the lateralia ball and socket joints are well developed. Their inner ends are pointed and rest upon small hollows placed on the outer edges of the ambulacralia.

The buccal slits were deep and the proximal ambulacralia bordering them tightly joined together. Each arm of the V extends forward to form an alinement with a mouth-angle plate. Between a pair of mouth-angle plates there is a proximal deep cut in the ossicles. This housed a muscle which could thrust the frame by the V's widely open. The mechanism of this movement was dealt with in an earlier communication (Spencer 1925, p. 264).

The only distinction between the structure in *Eophiura* and that in the later Ophiuroidea described in that communication is that the V here is made from a number of ambulacralia, whilst in the later Ophiuroidea it is built from the enlarged first pair of ambulacralia only.

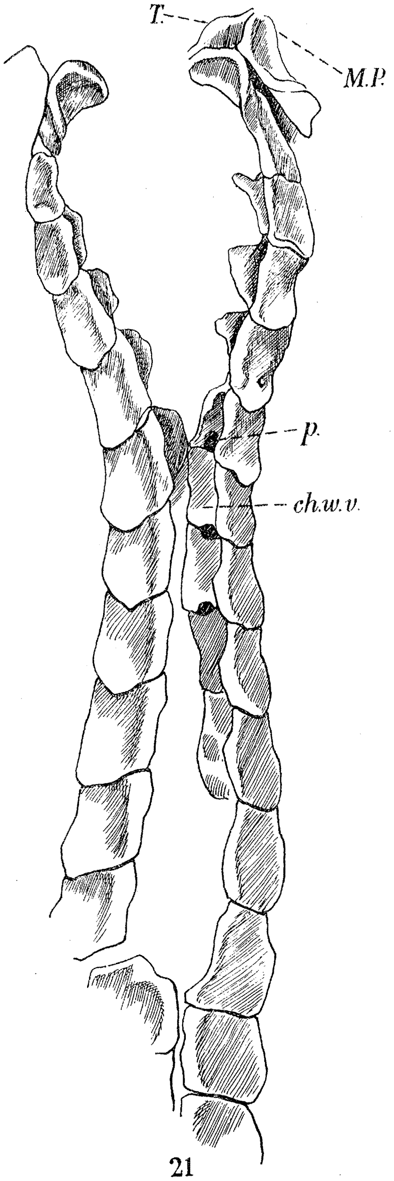
The positions of the basins for the first tube foot are as in *Archegonaster* (see p. 105). The first pair of tube feet could project as 'buccal tentacles' into the central opening.

In one of the buccal slits of the specimen, E.H. 94, there is a displaced torus. It is a narrow and thin plate and is furnished with a row of long spines set along the length of the plate.

The specimens show a well-ossified stone canal (figure 47, plate 6). The greater part of the length of the canal is shown by the specimen in figure 20, p. 115. This is the stretch between the madreporite and the lower edge of the mouth frame. The part of the canal attached to the central 'ring' is shown in E.H. 105, where the mouth frame is exposed from above.

Mode of feeding

The state of preservation of the fossils suggests that the animal lay buried in the mud with the more distal parts of the arms flexed upwards and then brought parallel to the upper layers of the sea-bottom (figure 56, plate 8). The mud, rich in detritus, would be scooped by the upwardly projecting tube feet and pushed along the arm to the mouth. Specimen E.H. 100 shows the lateralia swung inwards at the edges of the buccal slits, with their



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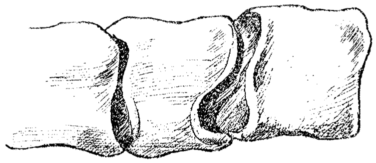

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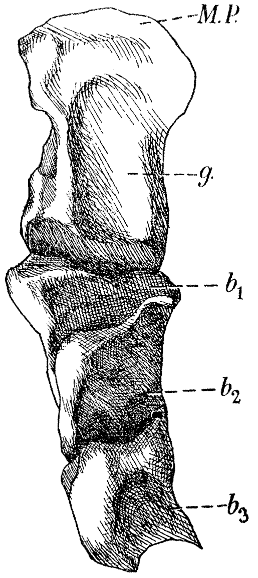

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FIGURE 21. *Eophiura bohemica* Schuchert. Mouth frame and ambulacralia seen from above. *M.P.*, mouth-angle plate; *p.*, pore for passage of branch water vessel; *ch.w.v.*, channel for radial water vessel; *T.* torus (from E.H. 105).

FIGURE 22. *Eophiura bohemica* Schuchert. Aboral surface of slightly displaced ambulacralia showing the articulations between them (from E.H. 105).

FIGURE 23. *Eophiura bohemica* Schuchert. An angle of the mouth frame seen in side view. b_1, basin for first tube foot; b_2, basin for second tube foot; b_3, basins for the third tube foot; *g.*, groove for first tube foot; *M.P.*, mouth-angle plate (from E.H. 105).

spines completely roofing over the ambulacral groove. Through the tunnel thus formed the food would be passed to the mouth. Some selection of food from debris was probably made by the buccal tentacles.

Palaeura Jaekel, 1903, emend. Schuchert, 1915

Synonymy

Palaeura Jaekel, 1903, p. 110; *Palaeura* Schuchert 1915, p. 223.

Diagnosis

A stenurid of the family Palaeuridae with a well-plated skeleton and with ambulacral basins seated almost entirely on one ambulacral.

Type (and only known)species

P. neglecta Schuchert, 1915. From the Upper Arenig, Dγ_1 of Osek, Bohemia.

Material

There are many specimens. The majority, like those of *Pradesura*, show only the disk and the arm bases, that is, the arm extremities were washed away before preservation. Five specimens, however, show one or more complete arms. These are always found with their arms bent backwards over the disk with their oral surface uppermost (figure 60, plate 8). This is a position comparable to that found in *Eophiura* (figure 56, plate 8). The tube feet are in position to feed from the superficial layers of the sea-bottom. A further specimen shows a profile view which can be compared to that shown by the lower half of the specimen drawn in figure 16, p. 108). It is photographed in figure 59, plate 8. The disk is tumid and the bases of the arms are flexed to wrap around it. A comparable view is presented by a specimen of *Eophiura* (figure 57, plate 8).

Remarks

A short description of this genus with a very diagrammatic text-figure was given by Jaekel in 1903. The MS. notes of Jaekel are almost entirely devoid of further description.

Palaeura has a considerable general resemblance to *Pradesura*. The special features of interest are:

(1) The state of preservation of the material. This supports the views already advanced of the mode of life of these primitive Ophiuroidea.

(2) The ambulacral basins which show a marked advance towards the basins prevalent in the Ophiurida, that is Ophiuroidea which have their ambulacralia constructed as 'vertebrae'.

Description

Palaeura is the earliest known ophiuroid to show the marked change in the seating of the tube feet which accompanies the completion of the formation of 'vertebrae'. In all the starfish described in the previous pages the floor of each ambulacral basin was shared subequally by two ambulacralia, the larger portion of the seating being upon the distal member of the pair. In *Palaeura* (figure 24) the basin is still shared by two ambulacralia, but by far the larger portion of its floor is upon the proximal member of the pair. Only a very small portion of the basin is on the distal ambulacral.

This change in seating has taken place by an elongation of one ossicle which has captured the seating from its more distal neighbour. Ludwig (1881) many years ago pointed out that such a capture must have taken place during evolution. He arrived at this conclusion after observations on the early developmental stages of the ophiuroid vertebra. The 'anlage' of a vertebra is a triradiate spicule with a definite orientation. The branches of the spicule are subequal each with a definite orientation. Two are directed adoralwards, one along the length of the arm, the other at an angle to it (figure 27*C*). The third branch, also along the length of the arm, is directed aboralwards. In the next stage the spicule is still triradiate, but the aboral branch has elongated (figure 27*D*). These proportions are retained during the further growth of the vertebra.

Ludwig compared this growth of the ophiuroid spicule with an imaginary Asteroid 'anlage', and came to the conclusion that the tube feet in the ophiuroid moved forward relatively to the ambulacralia. The tube foot, e.g. of the twelfth vertebra of an ophiuroid, corresponded to the tube foot placed between the twelfth and thirteenth ambulacral of an asteroid.

The comparable evidence afforded by embryology and palaeontology can be best illustrated from figures which show the strong ridges marking the boundaries of the basin in which the tube foot is seated. These ridges have the same form as the spicular 'anlage'. Figure 27*A* shows them in *Eophiura*, where the basin is shared subequally by two ambulacralia. The disposition of the ridges is exactly as in the first stage in the ophiuroid development, all the branches being subequal. The next stage is shown by *Palaeura* (figure 27*B*), where the aboral branch has elongated.

The new growth takes place immediately behind the branch vessel to the tube foot. Several specimens of *Palaeura* are preserved with this branch filled in with hardened mud, and the casts show that the vessel entered the basin just behind the cross-ridge which separated the basins from each other (*p.* of figures 27*A* and *B*). This is the same position as in both *Eophiura* (figure 50, plate 7) and the Asteroidea (figure 11, p. 104). The position of the branch vessel has not altered, and the new growths are confined to the regions behind the vessel. In later evolution the branch vessel itself must have been caught up in the new growth. Otherwise it is difficult to explain the tortuous course of this vessel (see, for example, Ludwig 1878).

Order OPHIURIDA n.ord.

Diagnosis

Ophiuroidea with ambulacralia changed into vertebrae.

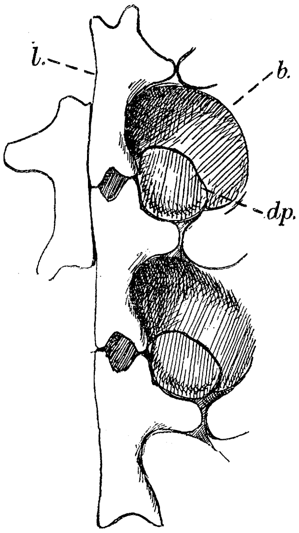
A drawing (figure 25) from a mid-Ordovician ophiurid (*Taeniaster*) shows the completion of the 'vertebral' structure. The basin is on one ambulacral, and there are pits for the insertion of the two ventral muscles.

Suborder OEGOPHIURINA (subclass Oegophiuroida Matsumoto)

Diagnosis

Ophiurida with an open ambulacral groove.

Superfamily Lysophiuricae (order Lysophiurae Gregory) with ambulacralia alternating contains families Protasteridae Spencer, Euzonosomatidae Spencer and Cheiropterasteridae Spencer.



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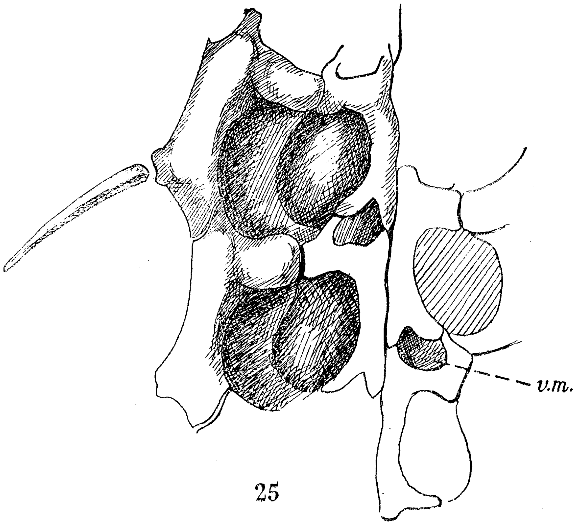

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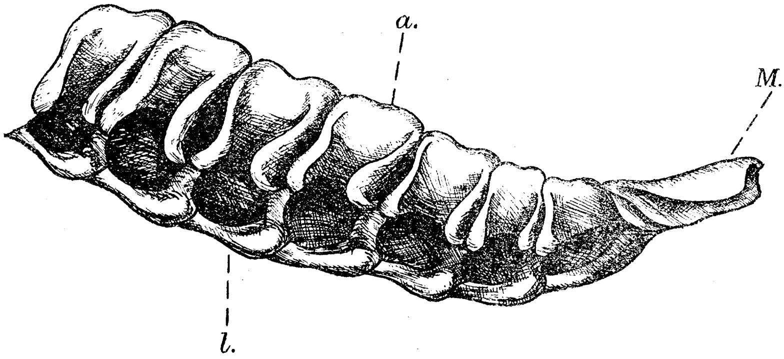

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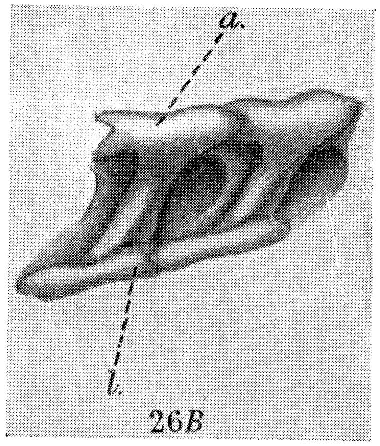

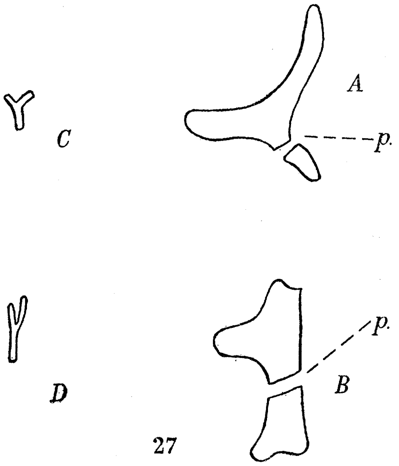

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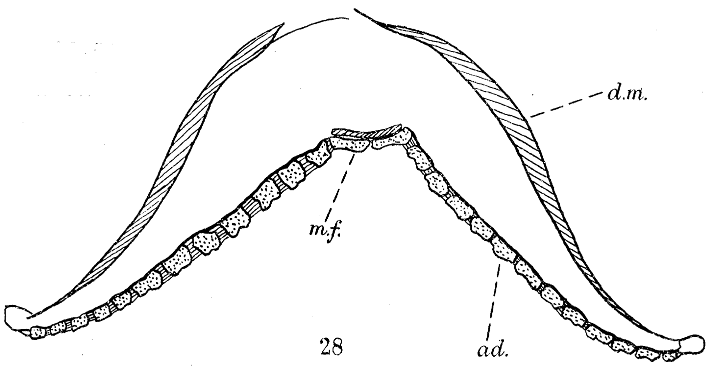

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Figure 24. *Palaeura neglecta* Schuchert. Drawing of ambulacralia in oral view. Main portion of ambulacral basin. *b.*, large proximal portion of basin; *dp.*, hollow in sole of boot, the small remains of the distal portions of the basin. *l.*, leg of ambulacral boot.

Figure 25. *Taeniaster.* Portion of an arm to show the basin for the tube foot placed on one ambulacral only and the large pit *v.m.*, for the housing of the ventral longitudinal muscle.

Figure 26*A*. *Palaeura neglecta* Schuchert. Side view of the aboral surface of the arm. *a.*, ambulacral; *l.*, lateral; *M.P.*, mouth-angle plate.

Figure 26*B*. Similar view of *Drepanaster* (copied from Spencer 1940, text-fig. 325*C*), showing interambulacral joints; *a.*, ambulacral; *l.*, lateral.

Figure 27. Outline of edges of basin in *A*, *Eophiura*. *B*, *Palaeura* compared with the first stages in the growth of a vertebra. *C*, first stage; *D*, second stage (after Ludwig 1882); *p.*, pore for passage of tube foot.

Figure 28. Diagrammatic arm section of an asteroid during feeding. *ad.*, adambulacral chain; *d.m.*, dorsal muscle; *m.f.*, mouth-frame.

Superfamily Zeugophiuricae (order Zeugophiuroidea Matsumoto) with ambulacralia opposite contains families Hallasteridae Spencer, Furcasteridae Spencer, Klasmuridae Spencer and Onychasteridae Miller.

Notes

The only Arenig ophiurid is a small specimen of *Hallaster* (*Hypophiura* Jaekel).

Suborder MYOPHIURINA (subclass Myophiuroida Matsumoto)

Diagnosis

Ophiurida with an enclosed ambulacral groove. Palaeozoic family Agaпasteridae.

Subclass ASTEROIDEA

Diagnosis

Asterozoa possessing arms with thick muscular walls and a well-knit skeleton on their under surface. Usually the spines are abundant and well distributed orally and aborally.

The characteristic underarm skeleton has long been recognized. Ludwig calls it 'the ambulacral skeleton', and so differentiates it from the remaining skeleton which he calls (following Sladen) the ambital skeleton. It is formed around a well-marked ventral groove (the ambulacral groove). The floor of the groove is occupied by ambulacralia which are elongate laterally and walled by stoutly built ossicles (adambulacralia). These latter are placed in linear series upon shelves formed on the outer extensions of the ambulacralia (figure 11, p. 104).

Significance of the ambulacral skeleton

Mechanisms associated with both the floor of the groove and the walls play an important part in the arm activities. Those associated with the floor of the groove have been thoroughly investigated by Smith (1937, 1946). These include:

(1) The tube feet. Each tube foot is an antonomous organ, 'and as such, must possess its own sensory-motor reflexes. In its normal functioning, however, a podium does not react independently of its fellows, and there is in the starfish a degree of co-ordination of movement sufficient for the performance, in conjunction with muscle action within the body of the animal, of the complicated movements necessary for the righting reaction or for the more normal actions of the animal in its every day life' (Smith 1937, p. 130).

(2) Nerve elements, including a well-developed sensory system (ectoneural) present on the tips of the tube feet and the floor of the groove, including the radial cord; a motor system hyponeural (Lange's nerve) and association ganglia lying in cable-like tracts within the radial cord communicating with a central nerve ring, the directing centre of the animal's activities.

(3) Muscle elements, transverse muscles uniting the ambulacralia of opposite sides of the arm and serving to widen or narrow the groove. These movements are associated with the protrusion and retraction of the tube feet.

It is the association of these elements which allows combined movements of groups of tube feet and arm musculature (see observations of Jennings quoted p. 126).

The following suggestion is made upon the ossicles of the walls of the groove. These seem to be arranged as a resistant to disruptive forces such as may occur when feeding upon mollusca (the favourite food).

Figure 28 gives a diagrammatic cross-section to illustrate the forces involved. The starfish has raised the middle of its body to place itself over its prey. The structure then is approximately that of a dome. The tensions produced by the pull of the tube feet, during the opening of the bivalve shell, are very considerable. Unless they were resisted the dome would collapse. The resistants on the lower-arm surface are longitudinal muscles, short muscles placed between the adambulacralia, a combination of tension elements with compression elements as used in reinforced concrete which together form 'adambulacral chains'. The resistants on the upper-arm surface are the dorsal muscle bands. These are firmly attached to each other in the centre of the roof of the dome. A further resistant is the ring of ossicles around the mouth (the mouth frame), which serves for the attachment of the adambulacral chains. It seems probable that the above muscles contain elements capable of resisting muscle fatigue.

The ambulacral skeleton and classification

The Palaeozoic Asteroidea can be classified according to the various characters shown by the components of the ambulacral skeleton and the neighbouring buttressing skeleton (arm axils plus marginal frame).

Order PLATYASTERIDA nov.

The adambulacralia and ambulacralia are almost in one plane and the adambulacralia fail to form a well-defined wall to the groove. The oral surface of the arm is broad and flat. There is one family, Platanasteridae Spencer.

Order HEMIZONIDA nov.

The adambulacralia form a defined wall. The buttressing skeleton is confined mainly to the arm axils and the ambulacral skeleton is the main arm skeleton. There are two sub-orders.

Suborder GNATHASTERINA nov.

With conspicuous mouth-angle plates with the families Taeniactinidae Spencer, Palasterinidae Gregory and Schuchertiidae Schuchert.

Suborder URASTERINA nov.

With inconspicuous mouth-angle plates, with families Cnemidactinidae Spencer, Urasterellidae Schuchert and Arthrasteridae Spencer.

Order PHANEROZONIDA (Phanerozonata of Sladen).

The adambulacralia form a well-defined wall. The buttressing skeleton is very conspicuous and tends to dominate the ambulacral skeleton.

Suborder PUSTULOSA nov.

With undifferentiated spines placed on pustules. With the families Petrasteridae nov., Hudsonasteridae Schuchert, Promopalaeasteridae Schuchert, Palaeasteridae Schuchert and Xenasteridae Schöndorf.

Notes

1. The earliest known asteroid is *Petraster* [*Uranaster*] *ramseyensis* Hicks (described Spencer 1918). It is from the Lower Arenig of Ramsey Island, south Wales. A near relative occurs in the Upper Arenig of Osek. Other Osek asteroids include a '*Hudsonaster*' and two small asteroids, possibly *Palasterina* and *Urasterella.*

2. Comparative studies show that supero-marginalia arise independently of the infero-marginalia, and that these latter are the true buttressing frame in the early forms. The beginning of the differentiation of the supero-marginalia from the skeleton of the aboral surface is well shown by *Petraster.*

3. Mouth frames with deep radial V's are well shown by members of the Platyasterida and Gnathasterina. The mouth frame of early Phanerozonida, e.g. *Petraster* and *Siluraster*, shows a V, but only between the first pair of proximal ambulacralia.

4. A calcified madreporite is often absent in the fossils. When present it is placed on the oral surface near the edge of the body both in the Platyasterida and the Gnathasterina, and then is a very large flat plate. I am unacquainted with any observations upon recent starfish which would explain the anomalous position and size.

In the two remaining orders the madreporite is in an aboral interradius. In the Phanerozonida it is associated with a ring of five primary interradialia, exactly as is customary in recent Asteroidea (either in developmental stages or in the adult).

5. One genus, *Petraster* Billings [*Uranaster* Gregory], is placed in the Petrasteridae, and the Palasterinidae is confined to one genus, *Palasterina* McCoy.

Characters associated with burrowing

Paxillary spines

Many fossil Asteroidea appear to have lived under the sea bottom. Evidence for this is afforded by the presence of paxillae or an epiproctal cone.

Gemmill (1915) has shown that centrifugal currents created on the surface of spines keep the epidermis free from debris, an operation necessary for epidermal respiration. The arrangement of the aboral spines of *Astropecten* is specially adapted for respiration when the starfish retires under the sea-bottom. The spines, placed on shafts, form an extensive paxillary umbrella which protects the aboral surface from the overlying mud.

Respiratory currents circulate under the umbrella which can be compared to the walls of a burrow. The channels under the umbrella represent the space within the burrow between the animal and the walls of the burrow. *Astropecten* may be said to carry the walls of its burrow upon its back. It has far greater freedom to roam in search of food than have animals which must build a new 'house' every time they change their headquarters.

Many early Asteroidea belonging to widely different groups carry a paxillary umbrella. It is found in the Platanasteridae, Schuchertiidae and the Urasterellidae. In the last group it is almost universal.

Epiproctal cone

Some recent starfish have the centre of the aboral surface raised as an epiproctal cone. MacBride (1906, p. 496) observed that *Astropecten* could raise the centre temporarily above the surface of the sea-bottom. MacBride regarded the movement as respiratory. It may, however, be associated with evacuation of the considerable volume of water often taken by recent starfish, possibly during endodermal respiration (see Gemmill 1915, p. 12). Examples of epiproctal structures have been given by me, especially for the early Palaeozoic Asteroidea, the Hudsonasteridae (Spencer 1916).

Glossary of new terms

Virgalia. Rod-shaped ossicles present in the oral interradii of the very early starfish, the Somasteroidea.

Lateralia and sublateralia. A double series of ossicles present in the primitive Ophiuroidea in approximately the same position as are the side-shields of recent Ophiuroidea.

Buccal slits. The slits presumed to be present in the soft tissues between the radial V's of the mouth frames which led into the central opening.

Appendix. Observations upon feeding habits of recent Echinodermata

(*a*) T. Gislén, 'Echinoderm Studies', *Zool. Bidrag. Uppsala*, 1924, **9**, 273–275.

'A hungry *Antedon*, when not irritated, sits immovably fastened to the substratum with outstretched arms, slightly curved upwards. The pinnules are spread out from the arms almost at right angles, and the tentacles, arranged in groups of three on the pinnules, are stiffly stretched out. If a plankton sample or a few grains of carmine with some crab-liver is put into the water of the aquarium, the arms and pinnules at once become very active. The tentacles all beat rapidly in towards the ambulacral furrow. This, the margins of which generally lie pressed tightly together, opens as soon as any grains fall upon it, with a wavy movement proceeding towards or away from the mouth. The mouth, only a narrow slit before, opens to its widest extent, and becomes rounded (cf. figs. 333, 336). After some time the tentacles straighten themselves again, but now and then, when tiny grains fasten on the papillae, the tentacles are whipped with rapid, nervous movements towards the ambulacral groove, and then again straighten out as quick as lightning. Some of the groups opposite each other usually whip in at the same time towards the furrow, but one cannot observe any flexing in of the pinnules proceeding along the arms. As Reichensperger (1908*c*) has shown, unicellular mucous glands open on the papillae of the tentacles. Small particles are fastened to the tentacles by their secretion, and with rapid motions of the tentacles are cast into the ambulacral groove, where the ciliary current takes hold of them and carries them to the mouth.

'Sensory hairs are found on the tentacles too, and it has been supposed therefore that these serve as sensory organs. The function of the tentacles is probably in reality manifold: first, they are certainly of considerable importance for the respiration; secondly, the mucous secretion, as is pointed out above, serves to fasten the falling grains of plankton or detritus upon the tentacles temporarily; thirdly, the sensory cilia serve presumably as some kind of organ for taste and feeling. When I dropped picric acid upon them, the arms were flexed and relaxed violently; when I added a few drops of sublimate the arms were also rapidly bent and twisted; the pinnules were stretched out and the animal made swimming motions, as if to escape. On a third occasion quinine sulphate + a few grains of carmine were added; the arms were waved actively to and fro, the pinnules were flexed into the sides of the arms, or rubbed against each other, or laid over the place where the drops had fallen, the arms were turned upside down, with the evident intention of getting rid of the unpleasant matter (cf. Graber's statements, 1889). When old putrefying crab liver was added to the fluid containing the grains of carmine, the pinnules were flexed in towards the sides of the arms. This seems to indicate that a sense of taste is present which, presumably, may be considered as localized in the sensory hairs of the tentacles' papillae.

'I cannot decide with certainty whether Reichensperger's assumption is correct that the secretion of the papillae of the tentacles is poisonous, and these papillae, like the cnidoblasts in *Cnidaria*, are partly defensive organs. I allowed living pinnules to lie in contact with freshly caught plankton (Ephyrae, Peridineans, Diatoms and Plutei). Nevertheless, I was not able to ascertain that any rapid unconsciousness or poisonous action took place. A small *Cladonema* seemed to make motions of escaping when touched by a tentacle, but usually the tentacle bent away from the irritating object. In the intestine of *Heliometra eschrichti* (see below) I have found quantities of copepods. The copepods have a tolerably strong power of motion of their own, and it is very probable that in this case the secretion of the papillae of the tentacles in some way paralyses the prey. Otherwise, it is difficult to imagine how the relatively weak ciliary currents can transport the captured prey to the mouth. (N.B. however, the rudimentary combs on the proximal pinnules (cp. p. 287)).'

(*b*) Extracts from Blegvad. Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea-bottom in Danish waters. *Report of the Danish Biological Station*, **22**, 1914 (publ. 1915):

P. 61: 'Animals feeding by means of ambulacral feet (tube feet):

'(1) Those without arms and living buried in the bottom, Echinoidea irregularia without masticatory organs (Atelostomata), includes *Brissopsis*, *Echinocardium* and *Spatangus*. All these are typical detritus eaters, feeding directly on the upper layer of the bottom, without any previous sorting of the detritus. As the aquarium observations have shown, they live buried in the bottom, maintaining communication with the surface by means of vertical tubes, and drawing their food by means of the far reaching ambulacral feet. As already mentioned, the *Echinocardium cordatum* frequently devours, together with the bottom detritus, numbers of quite small young bivalves.

'(2) Very mobile arms, living buried in the bottom *Amphiura*. Two species.

'The *Amphiura* species live, as I have frequently observed in aquaria, buried deep down in the bottom, only the extremities of some of the arms reaching up over it. These extremities are in constant movement, feeling about over all the small particles in the vicinity, and now and again coiling round and grasping some few of them, the food being then drawn down beneath the surface of the bottom to the mouth....Having noticed that *Amphiura* in aquaria would allow themselves to be fed with small pieces of meat I was for some time inclined to believe that they might, occasionally at any rate, be carnivorous; I have, however, examined several hundreds of specimens taken at different times and seasons, without ever finding anything in their stomachs beyond more or less finely sorted bottom detritus, with the micro-organisms and skeletal parts therein contained.'

P. 63: 'It would seem most probable that both poison and mechanical suction are applied when a starfish attempts to draw out a large bivalve or gastropod.'

P. 64: '*Astropecten mülleri* lived for the most part on molluscs. Small forms and young specimens especially are attacked by this voracious animal.'

(*c*) Jennings, H. S. 'Behaviour of starfish.' *Univ. Calif. Publ. Zool.* 1907, **4**, no. 2, pp. 153–185, 19 text-figures.

P. 93: 'There are two main methods of conveying food to the mouth. Large objects are usually carried by the active bending of the ray beneath the body, till the object is applied to the mouth, as described above in our account of the capture of a crab. Small pieces of flesh are transported in a somewhat different manner. After being carried to the ventral side of the ray, near its tip, perhaps the ray bends downward and under at precisely the point where the food body touches it, as to bring the food into contact with a point on the lower surface of the ray nearer the disk. The tube feet of this nearer point then seize the flesh while the more distal ones release it. Now the point at present bearing the food bends downward, applying it to a new region, while the point first bent straightens out. Thus the food is passed from one set of tube feet to another, slowly along the under side of the ray till it reaches the mouth.

When the stomach is passed out of the mouth in feeding, it usually appears as five yellowish lobes or sacs. These fold about the prey, partly envelop it, and insert themselves into its cavities and angles. But the prey is never, so far as I have observed, actually within a sac formed by the stomach; it merely has these lobes closely applied to it.'

(*d*) von Uexküll, J. *Umwelt und Innenwelt der Tiere,* 1921. Berlin: J. Springer.

'Die Schlangensterne' (*Ophiothrix*).

'Die Armmuskulatur beteiligt sich gar nicht am Erfassen der Beute, sondern die bei ihr besonders ausgebildeten Tentakel (siehe Hamann) schieben sich gegenseitig die kleinen Nahrungsbrocken zu, die im Zickzack von der Armspitze zum Mittelkörper wandern.'

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Description of plates 2 to 8

Plate 2

Figure 29. *Villebrunaster thorali*, n.g. et n.sp. Holotype. Photograph of a cast showing two individuals lying side by side (magn. × 2). The photograph to the left (the holotype) shows five arms lying in one plane (see figure 1); that to the right two arms flexed upwards (see figure 3). Coll. Villebrun, Univ. Montpellier.

Figure 30. *Villebrunaster thorali*. Photograph of an original mould showing impressions of the arm in aboral view and, to the right, impressions of the spicules (magn. × 6). The mesh between the spicules, on the left of the photograph, is irregular. Adjacent are impressions of the rows of virgalia.

Figure 31. *Villebrunaster thorali*. Photograph of another portion of a mould showing the spicular impressions (magn. × 10). The mesh, in the lower part of the photograph, has hexagonal outlines.

Figure 32. *Chinianaster levyi* Thoral. Photograph of a cast of the oral surface of a small specimen (magn. × 3). Coll. Thoral.

Figure 33. *Chinianaster levyi* Thoral. Photograph of a cast of one angle (magn. × 2). Coll. Univ. Montpellier. Rows of virgalia are seen to the upper left of the angle.

Figure 34. *Archegonaster pentagonus* n.sp., with arms flexed upwards (magn. × 1·5). Coll. Mus. Rokitzan.

Plate 3

Figure 35. *Chinianaster levyi* Thoral. Lectotype. Photograph of a cast of the oral surface (magn. × 1·75). Coll. Villebrun, Univ. Montpellier. The structure of an interradius is seen lower right.

Figure 36. *Chinianaster levyi* Thoral. Photograph of a cast of the aboral surface of the same specimen (magn. × 1·75). A spicular net covers the centre of the body, exposed ambulacralia are seen in the lower arm.

Figure 37. *Archegonaster pentagonus* n.sp. Photograph of a cast of the oral surface (magn. × 1·75). Coll. Narodni, Mus. Prague, E.H. 30. The virgalia are confined to the distal arm regions. The rounded ossicle with a central depression seen in the lower left interradius is the madreporite. Above it are seen the dislocated ossicles of the stone canal.

Figure 38. *Archegonaster pentagonus*. Aboral surface (about nat. size). Specimen E.H. 36. The marginal frame is drawn inwards slightly (lower right) and sharply (upper left).

Plate 4

Figure 39. *Archegonaster pentagonus* n.sp. Holotype. Photograph of a portion of the oral surface (magn. × 4). Coll. Narodni, Mus. Prague, E.H. 7. The adambulacralia on the right arm carry tufts of spines. They have swung outwards exposing the wide ambulacral channel and the basins for the tube feet. (See also figure 54, plate 8 and figure 10, p. 104.)

Figure 40. *Archegonaster pentagonus*. Photograph of the counterpart of the same specimen showing the aboral surface (magn. × 4). The upper surfaces of the ambulacralia are well exposed. (See also figure 13, p. 104.)

Plate 5

Figure 41. *Pradesura jacobi* (Thoral). Lectotype. Oral surface of the disk and the arm bases (magn. × 2·6). Coll. Univ. Montpellier, no. 139 (mould of this specimen figured, Thoral, plate ix, figure 2).

Figure 42. *Pradesura jacobi* (Thoral). The same view of a second specimen (magn. × 3·5). Same collection, no. 138 (mould figured, Thoral, plate ix, figure 3*a*). Spines are seen near the disk margins in the upper left-hand interradius.

Figure 43. *Pradesura jacobi* (Thoral). The same view of a third specimen (magn. × 1·75). Same collection, Px. The lateralia have revolved inwards and partially closed the groove.

Figure 44. *Pradesura jacobi* (Thoral). Aboral surface of same specimen Px (magn. × 1·75). The aboral surfaces of the exposed ambulacralia show small ball and socket joints.

Figure 45. *Pradesura jacobi* (Thoral). Aboral surface of another specimen (magn. × 1·75). Same collection, no. 137. The mouth frame is widely open and crushed through the aboral covering.

Plate 6

Figure 46. *Eophiura bohemica* Schuchert. Lectotype. Oral surface of the disk and the arm bases (magn. × 2). The madreporite is in the upper right-hand interradius lying alongside the mouth frame. Coll. Narodni Mus. Prague, no. E.H. 94.

Figure 47. *Eophiura bohemica* Schuchert. Madreporite and stone canal of same specimen (magn. × 9).

Figure 48. *Eophiura bohemica* Schuchert. Ambulacral basins at the base of the buccal slits from same specimen (magn. × 6). The upper ossicle shows a groove at the distal end of the basin, the second ossicle a groove at the proximal end of the basin.

Figure 49. *Eophiura bohemica* Schuchert. Aboral surface showing exposed ambulacralia and buccal slits, defined by a light wash, natural size. Same collection, E.H. 105.

Plate 7

Figure 50. *Eophiura bohemica* Schuchert. Photograph of a cast of ambulacralia showing the tears in the cast by the hardened infillings of the branch vessels (magn. × 6). Coll. Narodni Mus. Prague, E.H. 98. The tears between the ambulacralia to the left are shown clearly.

Figure 51. *Eophiura bohemica* Schuchert. Oral surface of the distal extremity of an arm (magn. × 10). Specimen no. E.H. 97. Sub-lateralia are seen to the lower left.

Figure 52. *Eophiura bohemica* Schuchert. Lateralia showing spine attachments and spines (magn. × 10). Specimen no. E.H. 110.

Figure 53. *Eophiura bohemica* Schuchert. Scales of the oral surface of the disk (magn. × 6). Specimen no. E.H. 94.

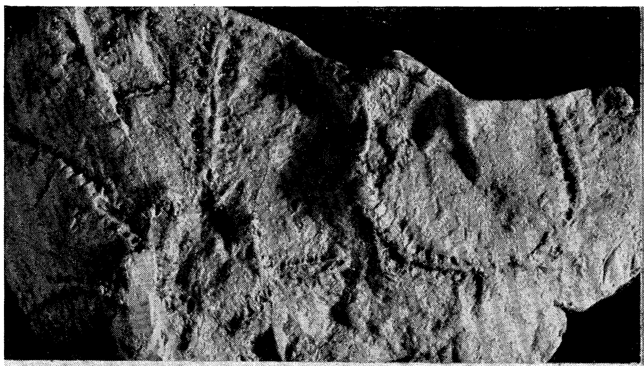
Plate 8

Figure 54. *Archegonaster pentagonus* n.sp. Ambulacralia (right) and adambulacralia (left) (magn. × 6). Coll. Narodni Mus. Prague, E.H. 11. The adambulacralia have swung open. Their stalks and the ambulacral-adambulacral narrow joints are seen upper left.

Figure 55. *Archegonaster pentagonus* n.sp. With arms flexed over disk (magn. × 1·5). Another photograph of the specimen shown in figure 34.

Figure 56. *Eophiura bohemica* Schuchert. Three arms flexed over the aboral surface (magn. × 1·5). Coll. Narodni Mus. Prague, E.H. 101. The oral surfaces of the arms are exposed and the tube feet were in position to feed from the contents of the overlying mud.

Figure 57. *Eophiura bohemica* Schuchert. The mould of two arms flexed steeply to the disk with the water vessels infilled with hardened mud. The infilling of the radial vessel is along the middle of the arm and on each side are the infillings of the short branch vessels and the round bases of the tube feet (magn. × 1·5). Specimens no. E.H. 100.



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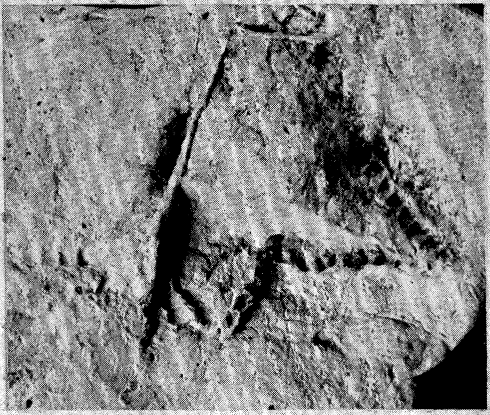

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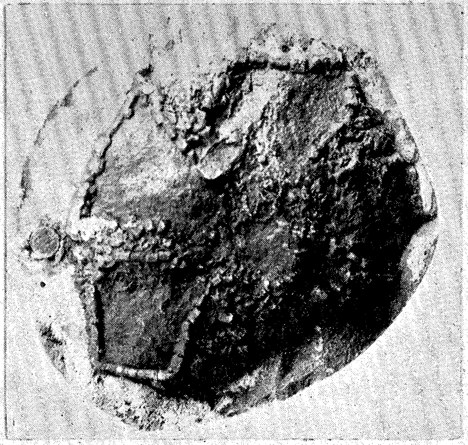

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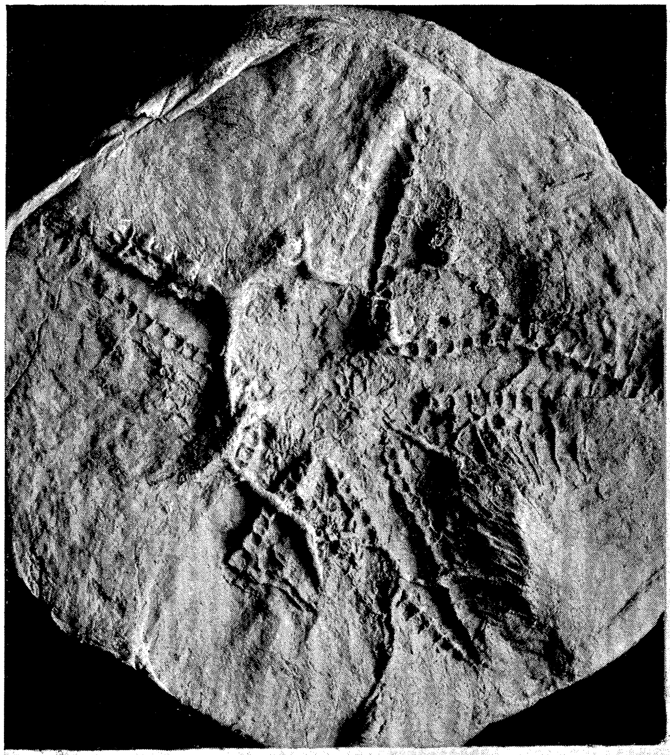

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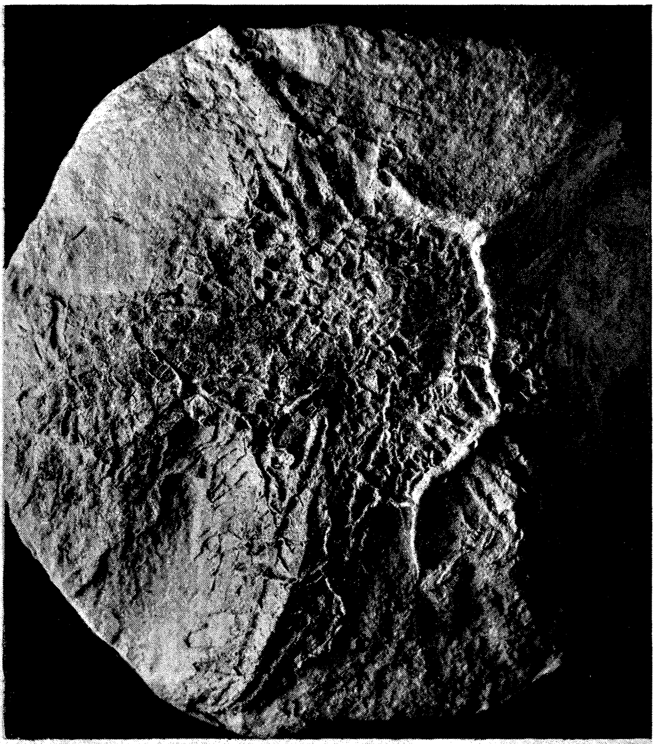

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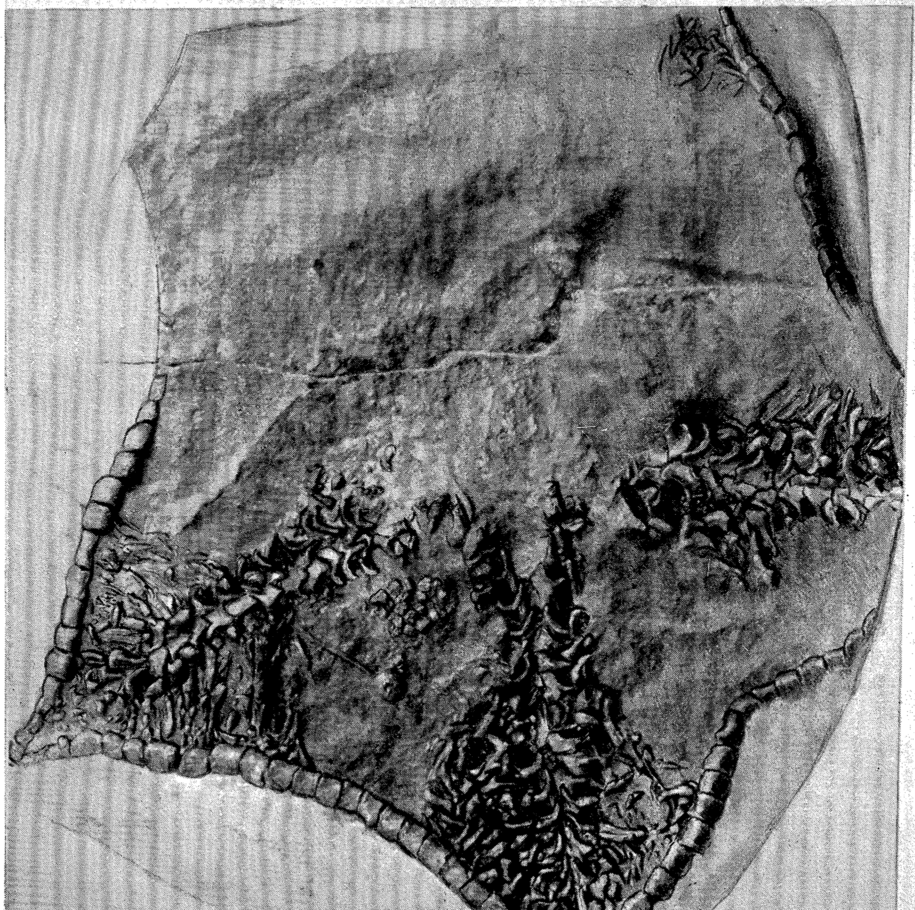

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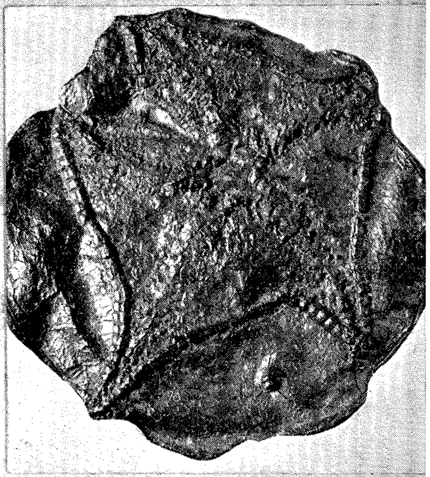

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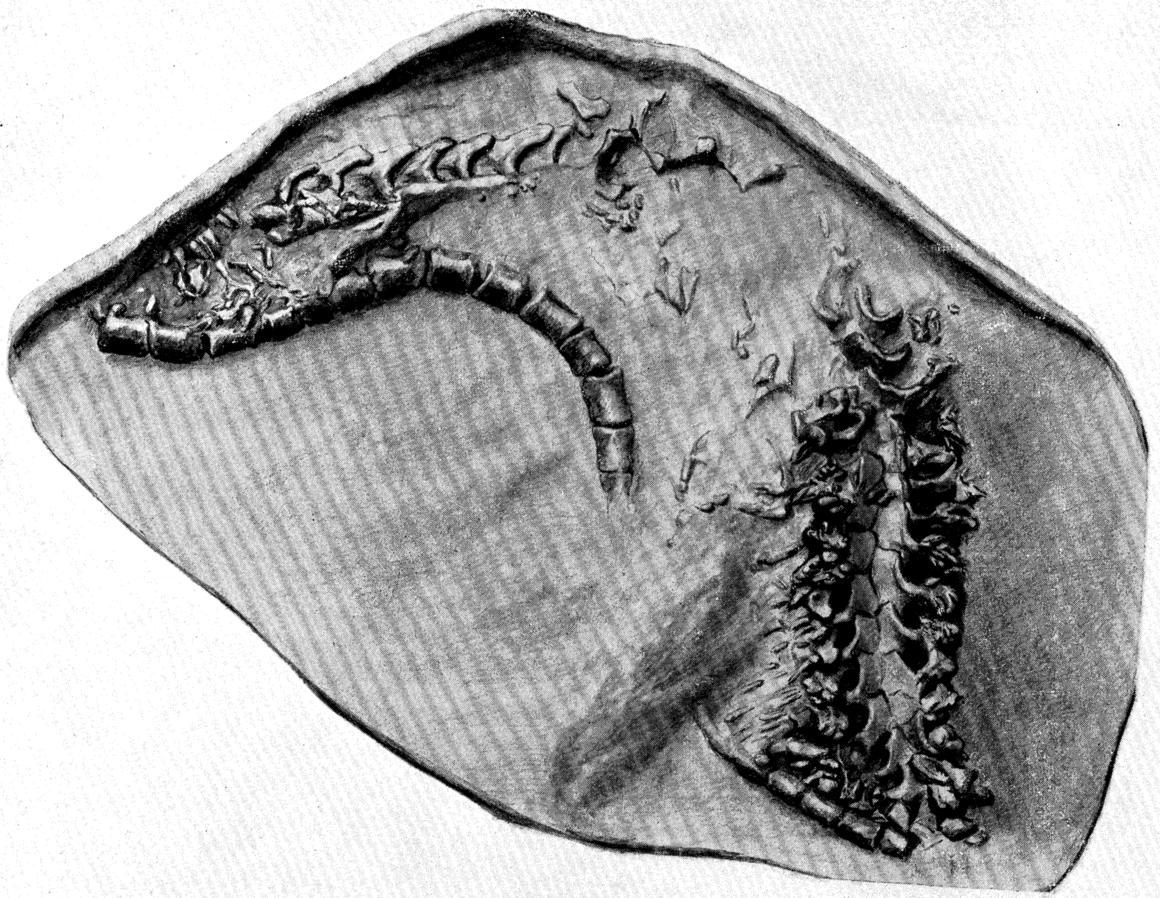

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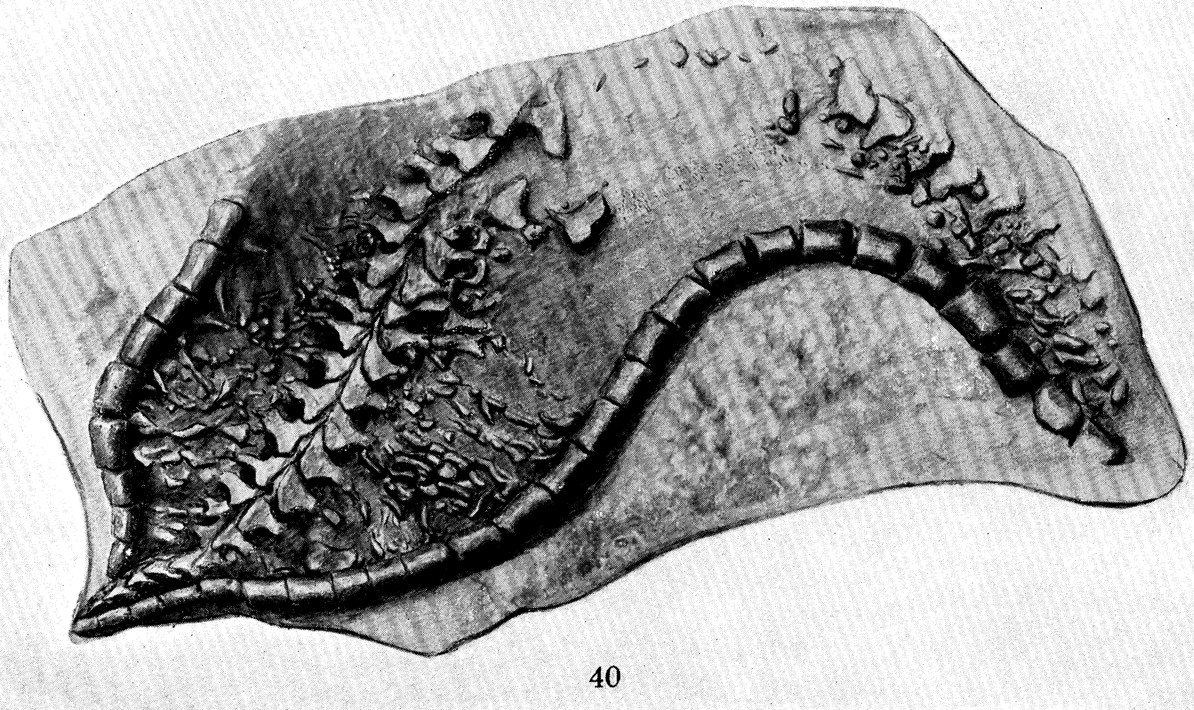

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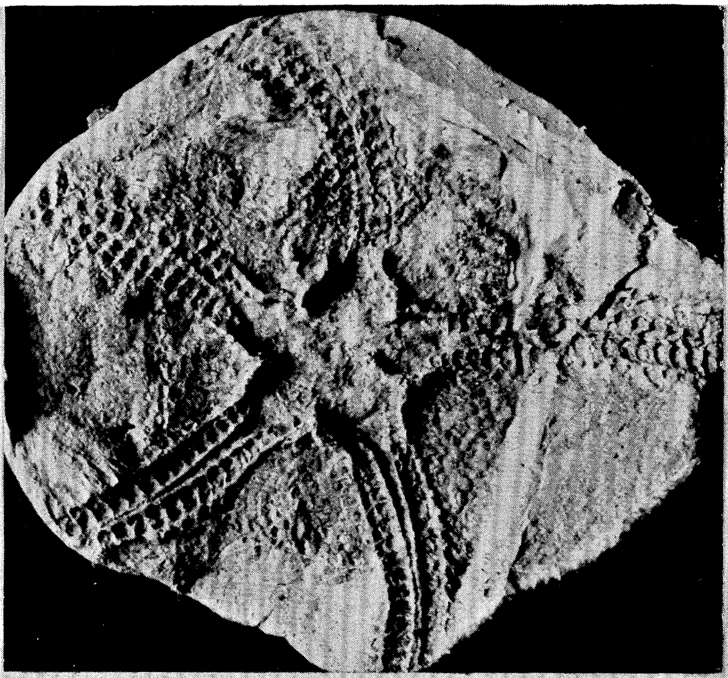

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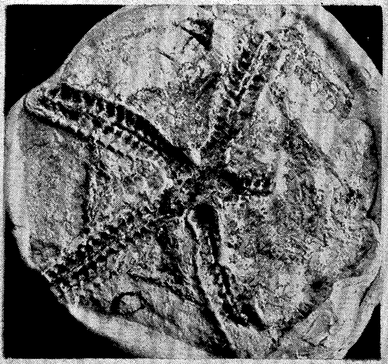

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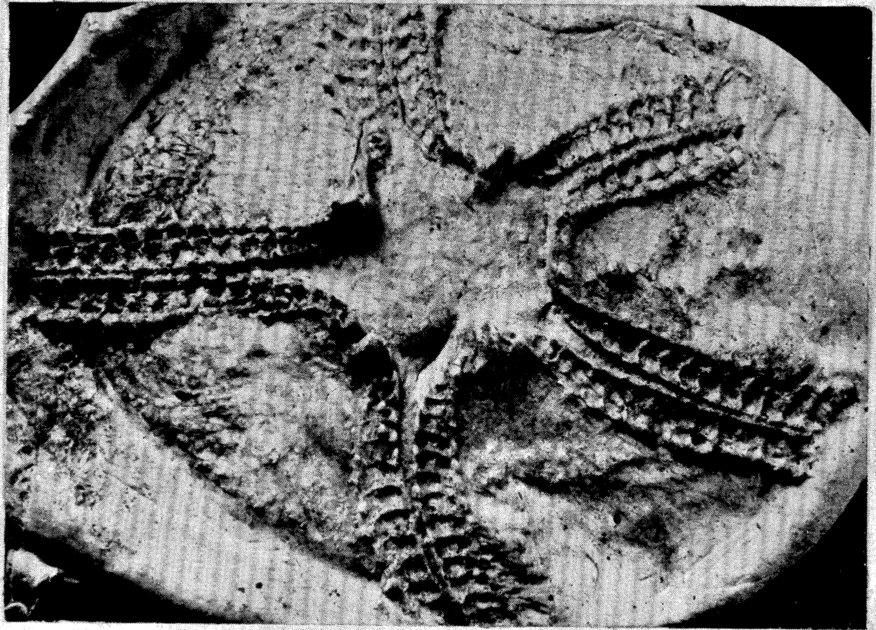

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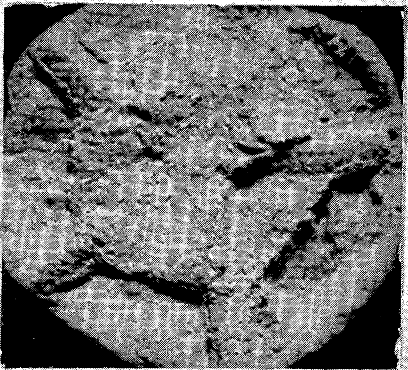

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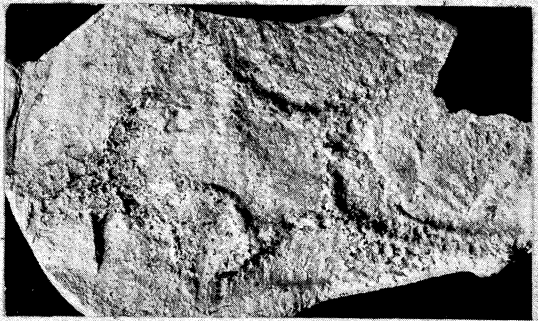

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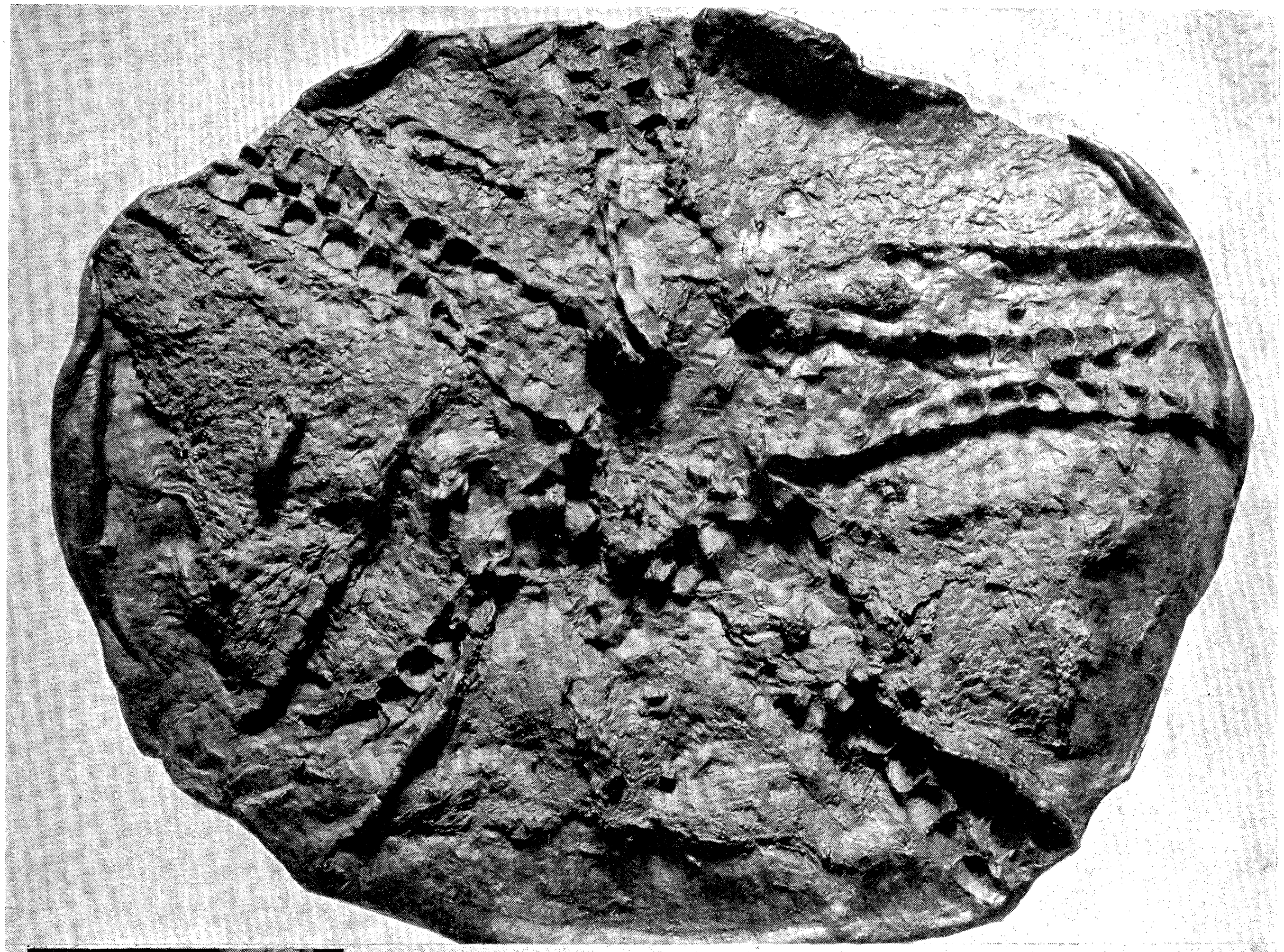

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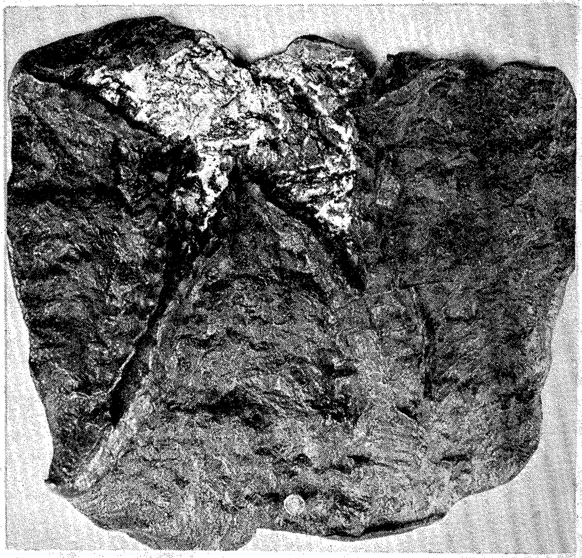

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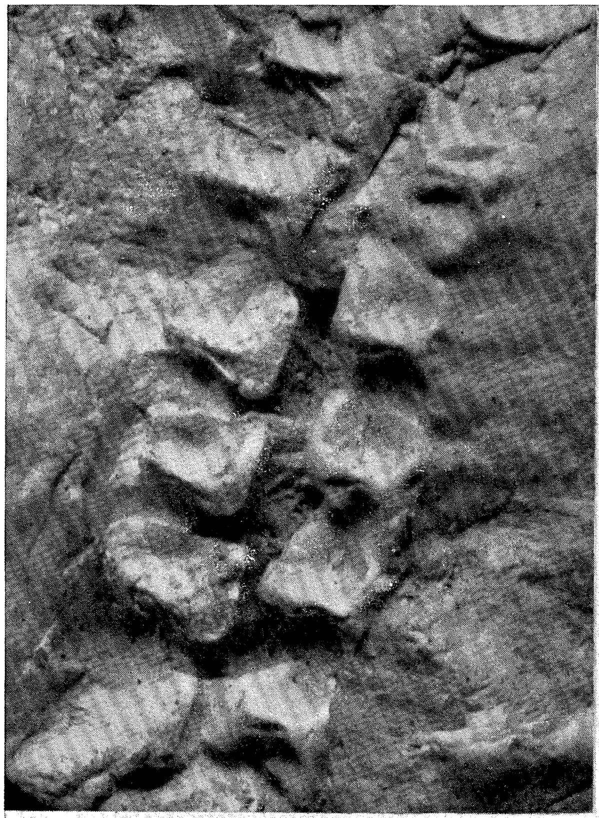

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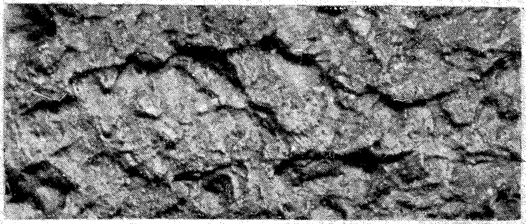

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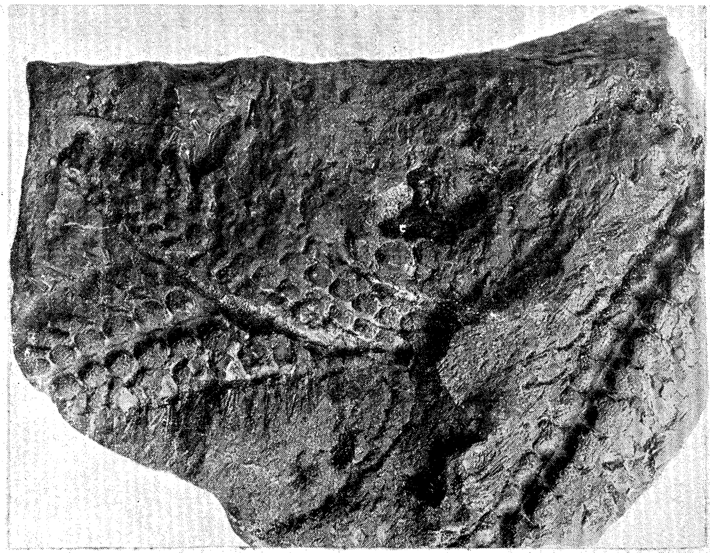

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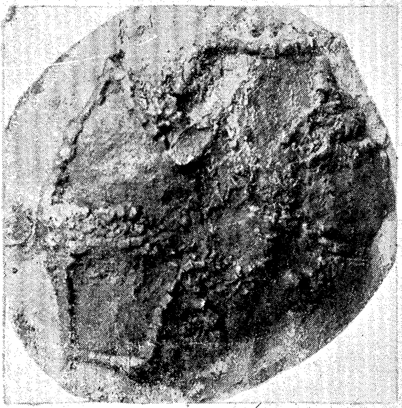

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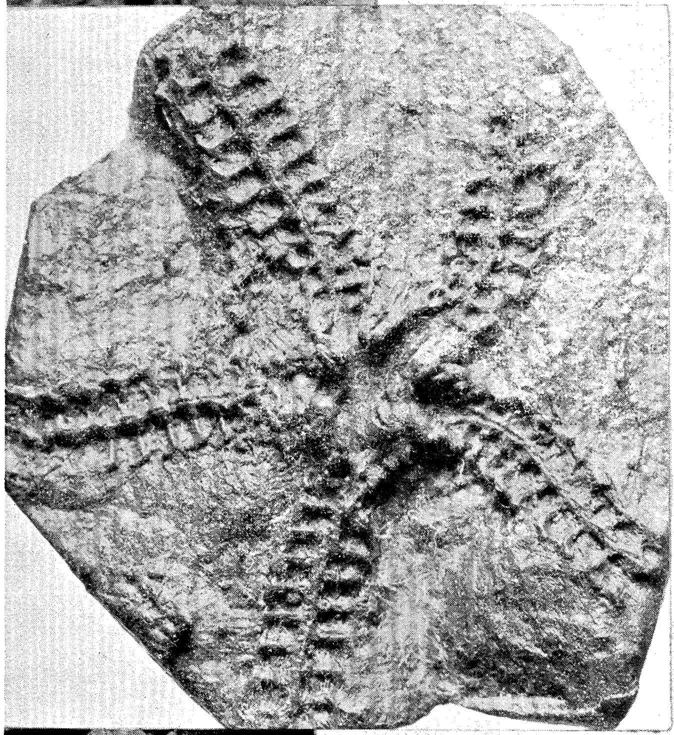

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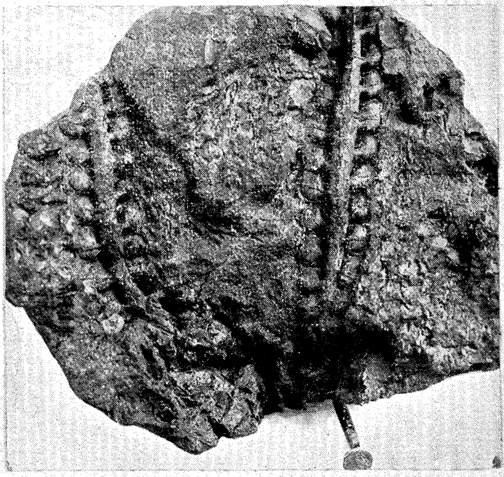

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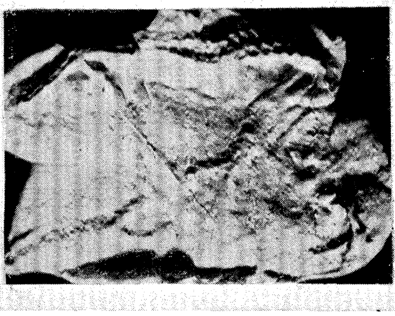

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Figure 58. *Palaeura neglecta* Schuchert. Oral view of the disk and the arm bases (magn. × 3). Coll. Narodni Mus. Prague, no. 141.

Figure 59. *Palaeura neglecta* Schuchert. Profile view of the disk and the arm bases (nat. size). Specimen no. 135. The arms are flexed in much the same position as in figure 16, p. 108.

Figure 60. *Palaeura neglecta* Schuchert. Disk in aboral view with one arm flexed and lying over the disk (nat. size). Specimen no. 155. The oral surface of the arm is exposed as in figure 56 above.

Figure 61. *Palaeura neglecta* Schuchert. Disk in aboral view with mouth frame crushed through the surface (nat. size). Specimen no. E.H. 136. The buccal slits are well exposed from above as in figure 49, plate 6.

I am indebted to the Parliamentary Grant-in-Aid for Scientific Publication, administered by the Council of the Royal Society, for financial assistance towards the cost of the preparation of the illustrations.

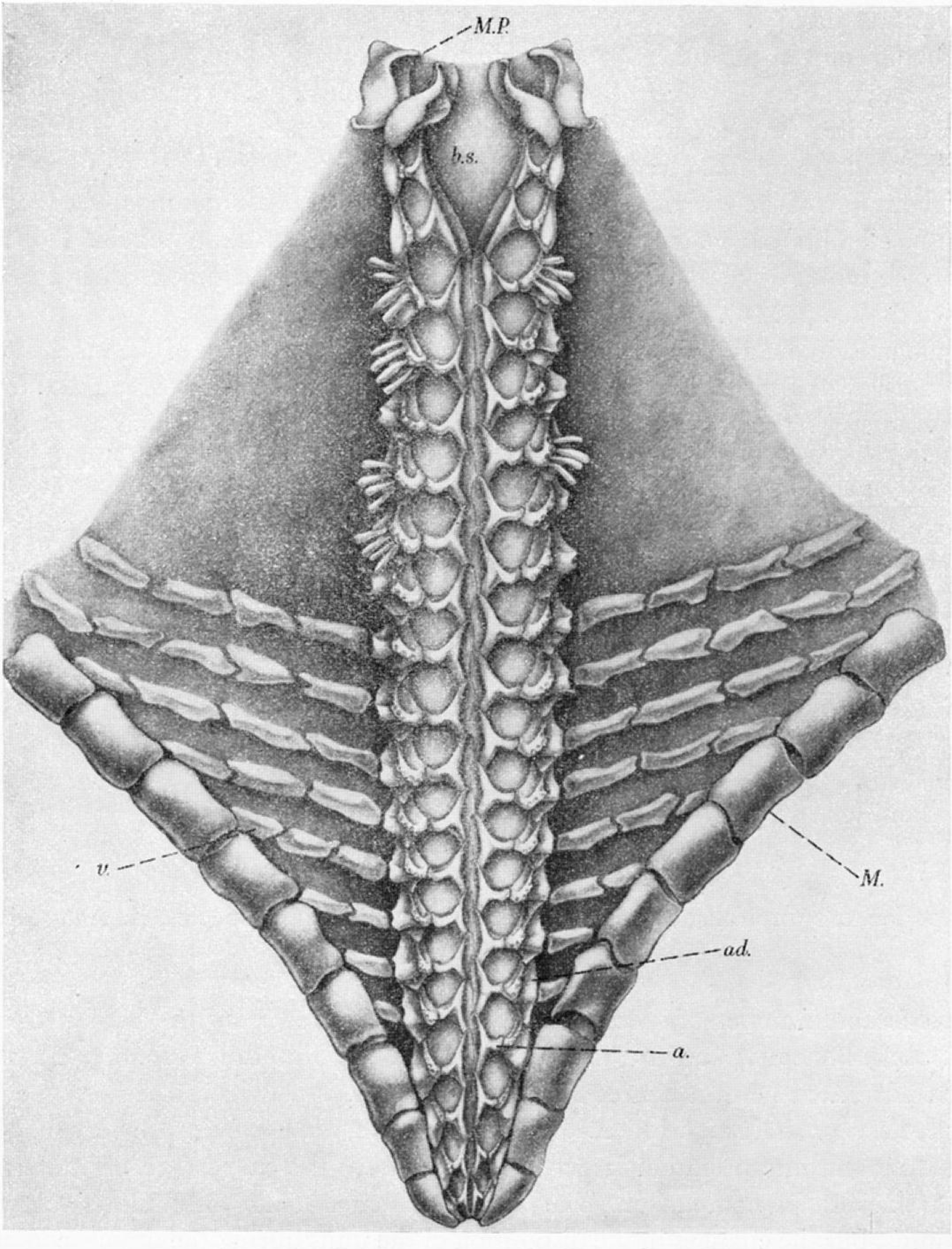


FIGURE 9. *Archegonaster pentagonus* n.sp. Reconstruction of a portion of the oral surface. *a.*, ambulacral; *ad.*, adambulacral; *b.s.*, buccal slit; *M.*, marginalia; *M.P.*, mouth-angle plate; *v.*, virgalia.

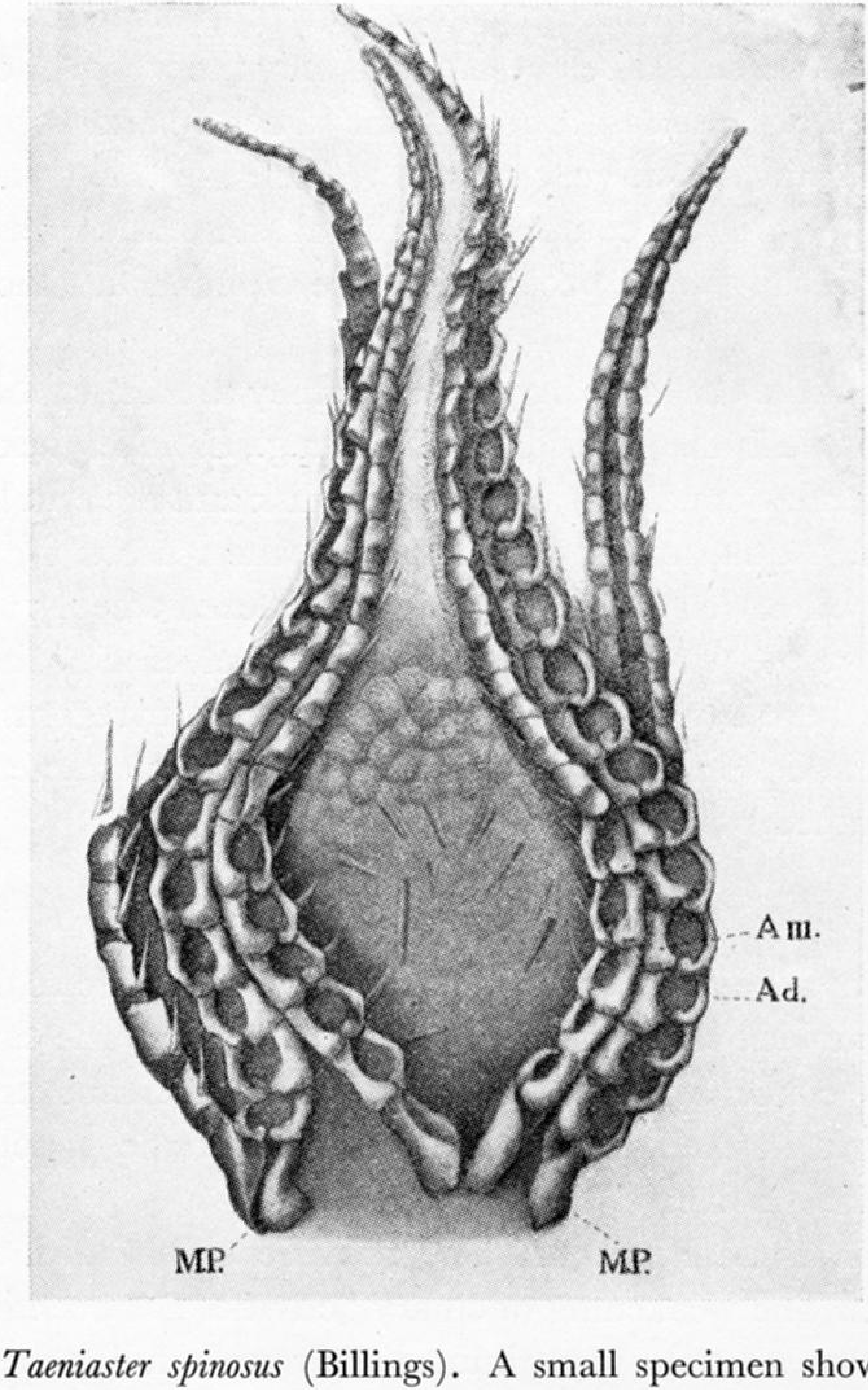


FIGURE 16. *Taeniaster spinosus* (Billings). A small specimen showing the arms flexed steeply over a swollen disk (copied from Spencer 1922, text-figure 140). *Ad.*, lateral; *Am.*, ambulacral; *M.P.*, mouth-angle plate.

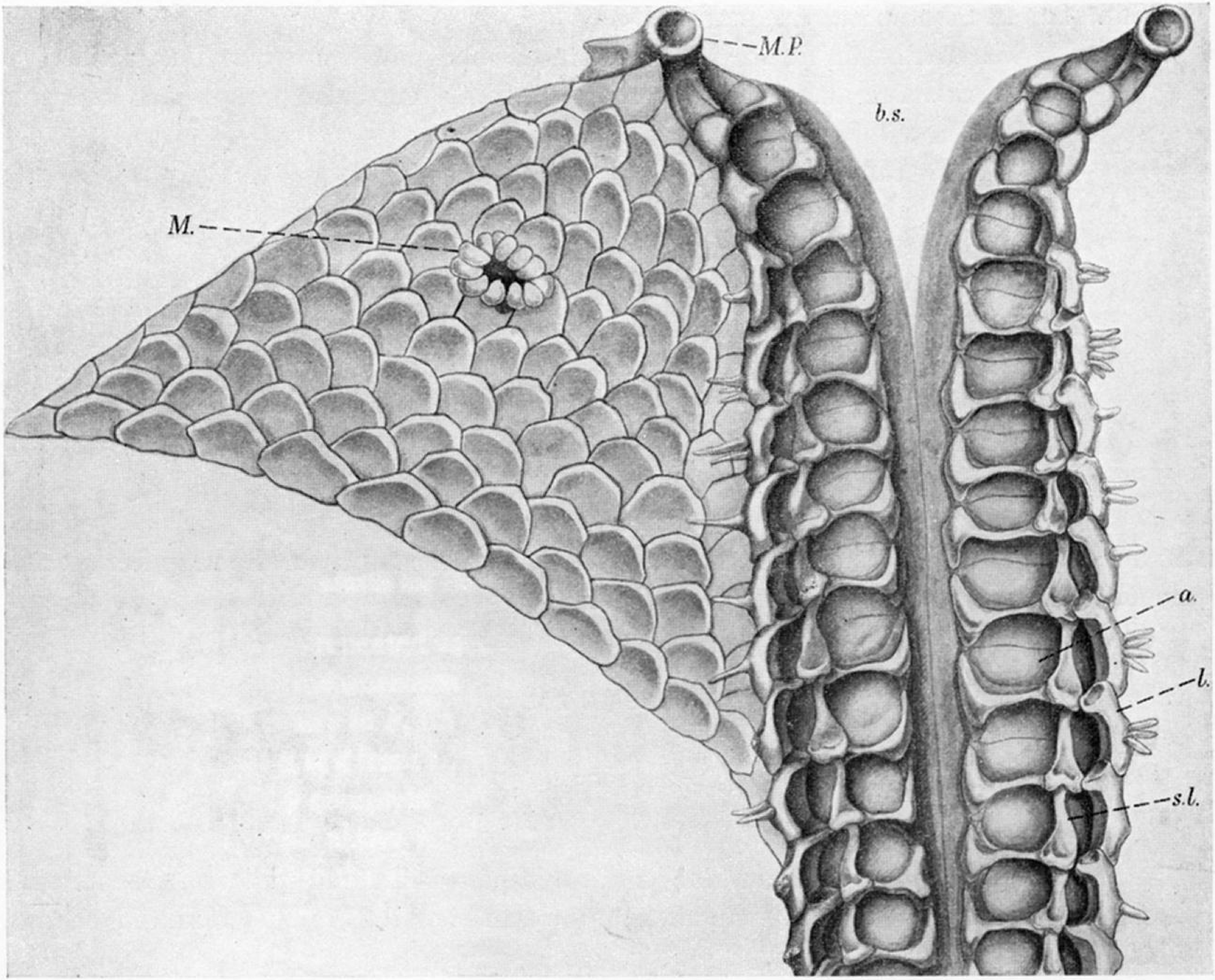


FIGURE 17. *Pradesura jacobi* (Thoral). Oral view of a portion of the disk and the neighbouring arms. *a.*, ambulacral; *b.s.*, buccal slit; *l.*, lateral; *s.l.*, sublateral; *M.*, madreporite; *M.P.*, mouth-angle plate.

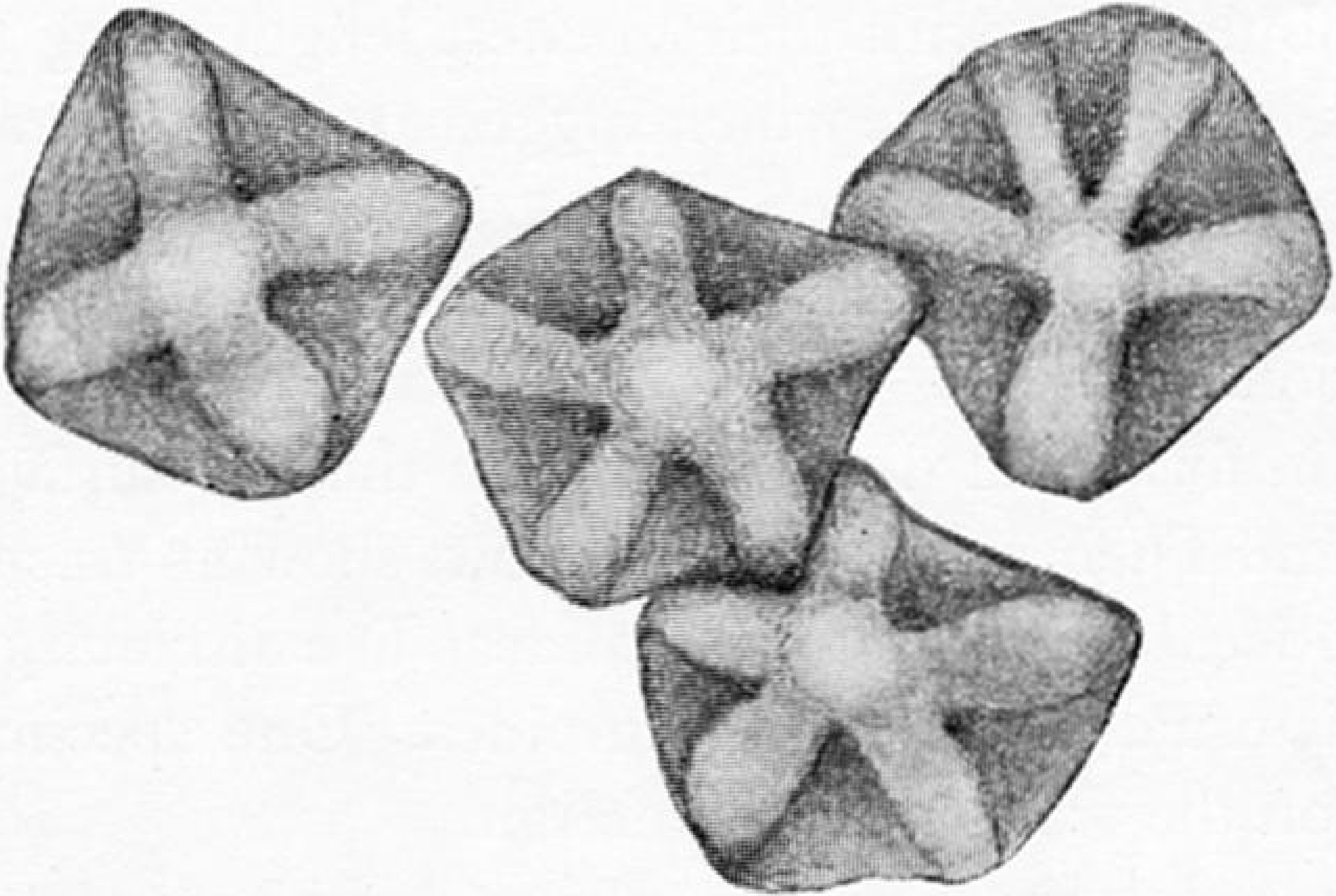
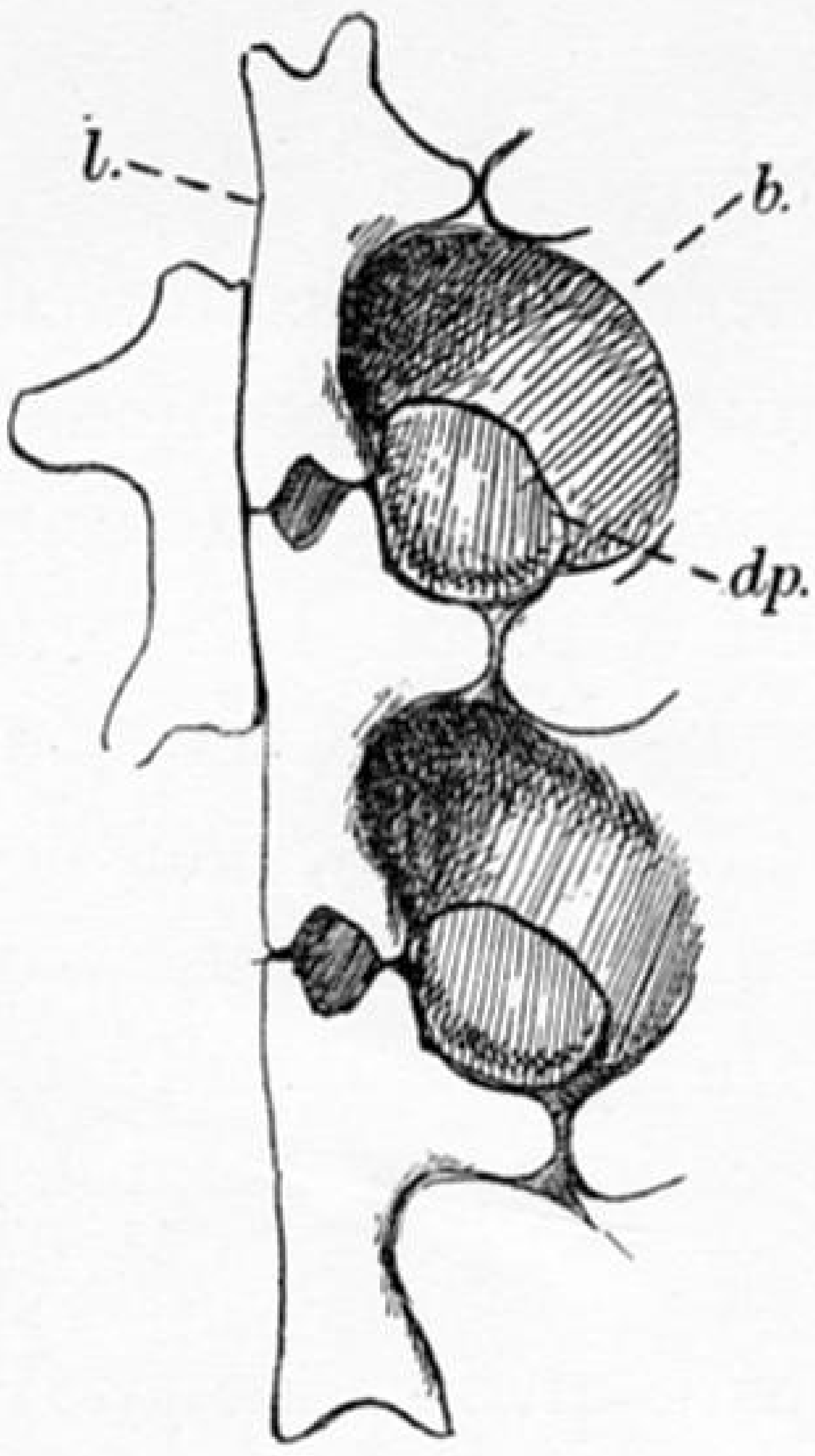


FIGURE 18. *Encrinaster grayae* Spencer. Scales from the aboral surface (copied from Spencer 1930, text-figure 260, p. 406).



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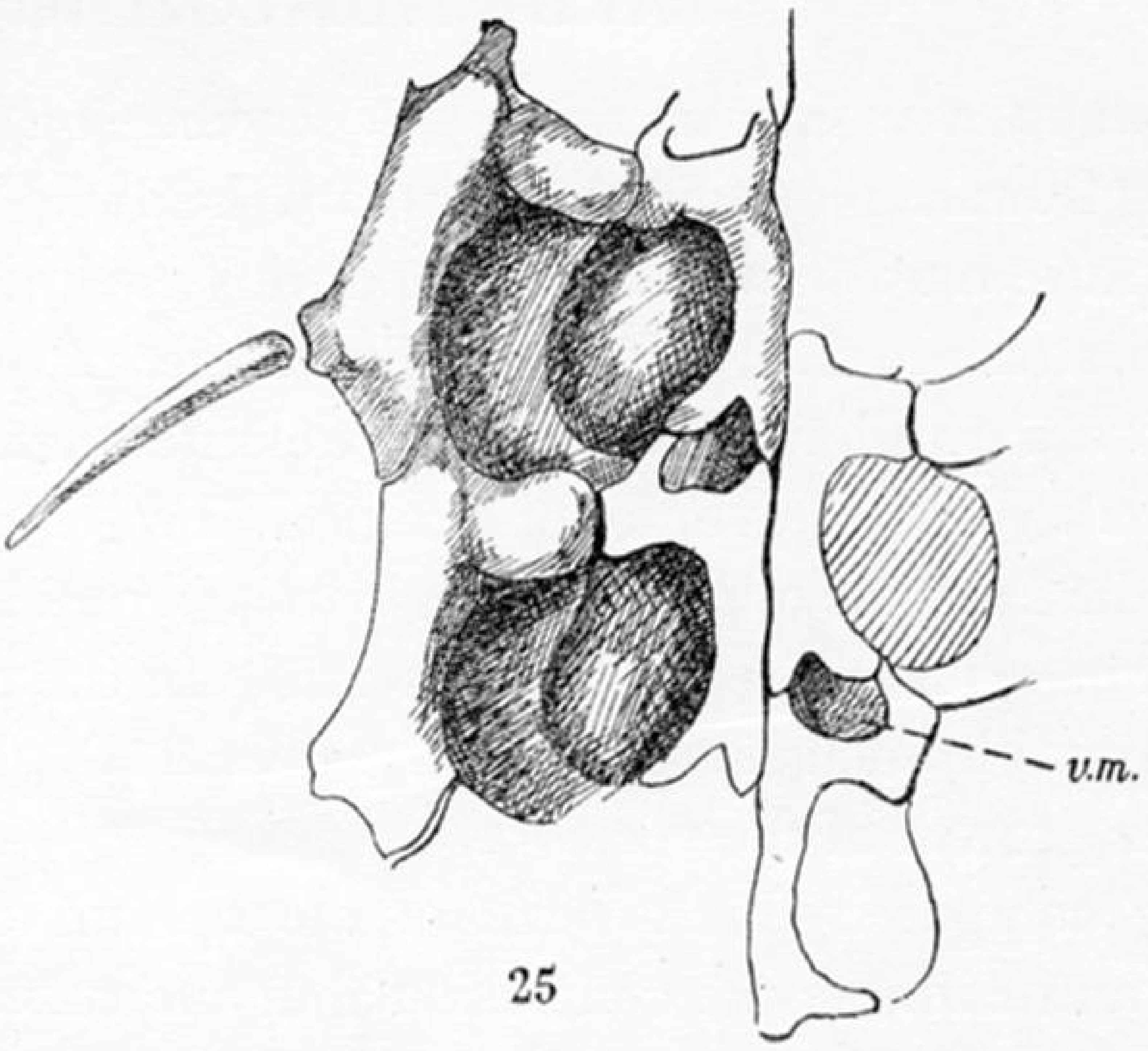

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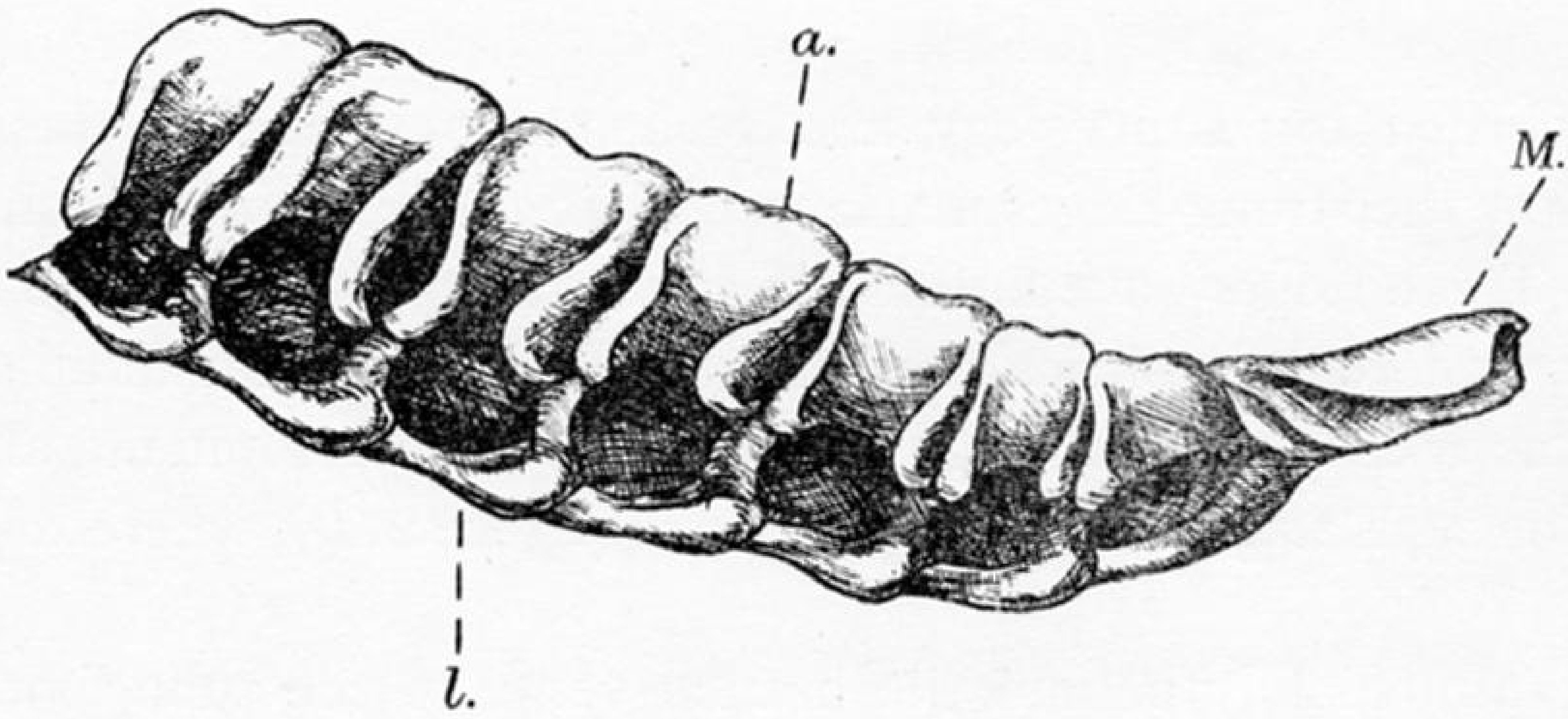

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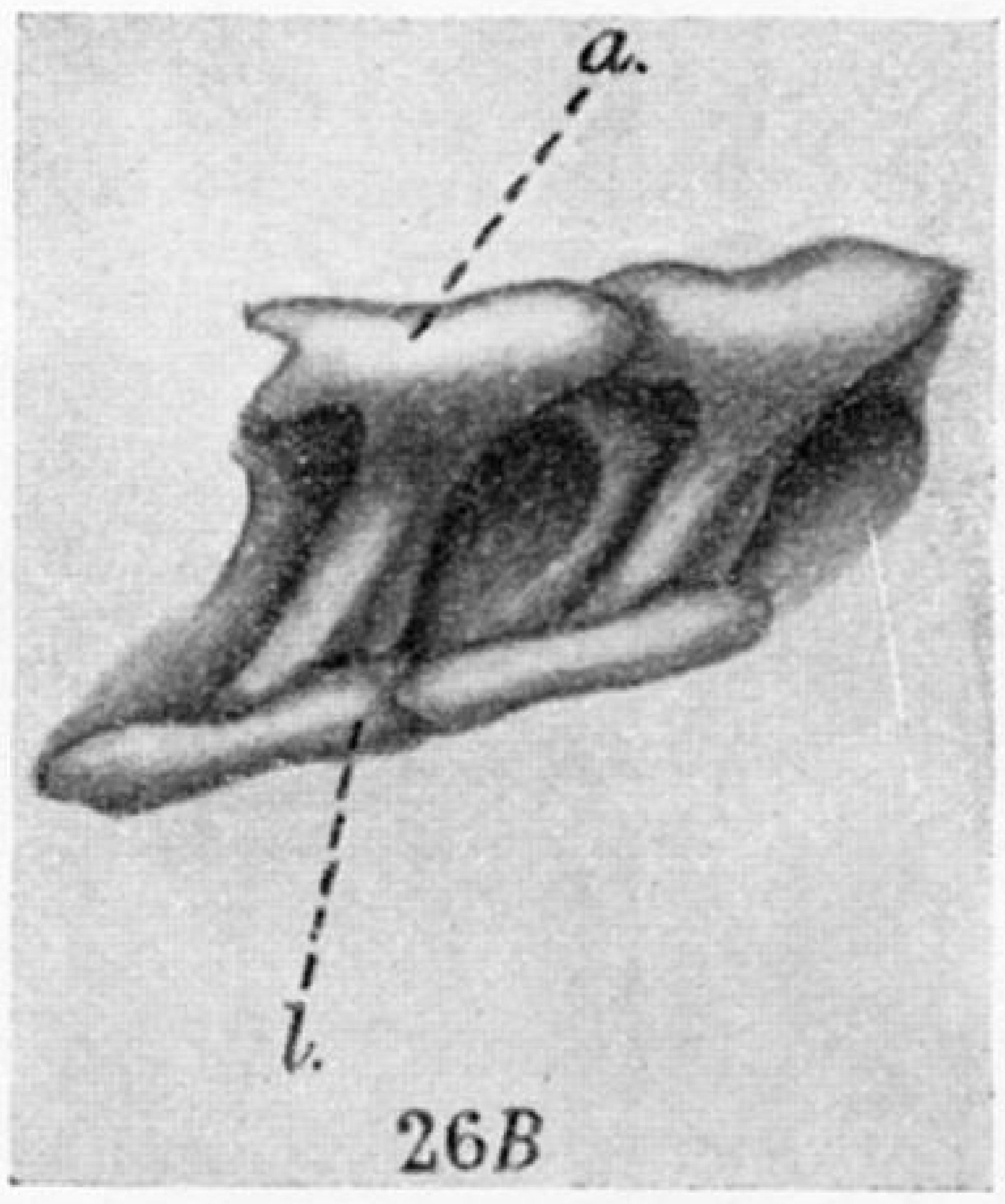

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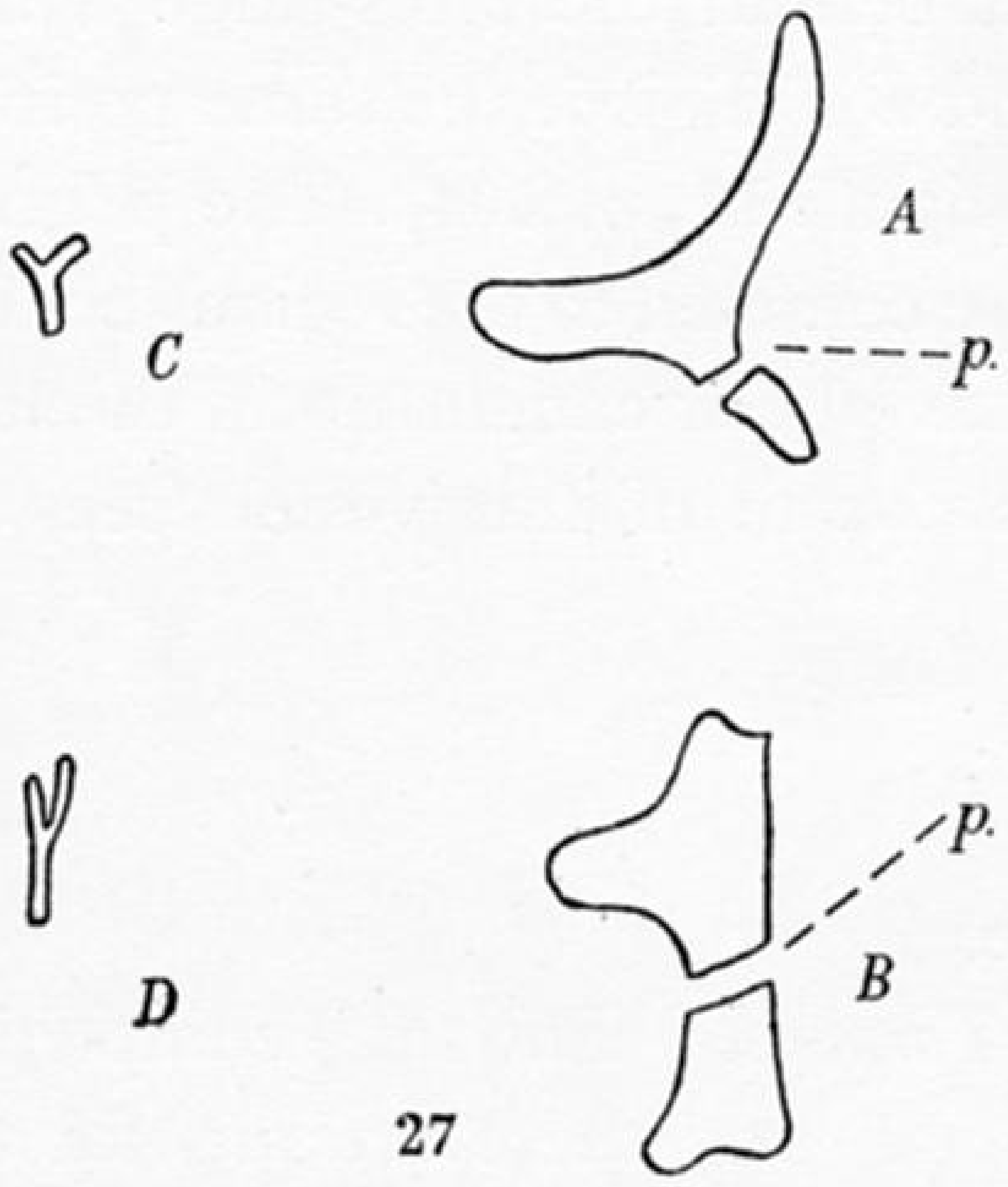

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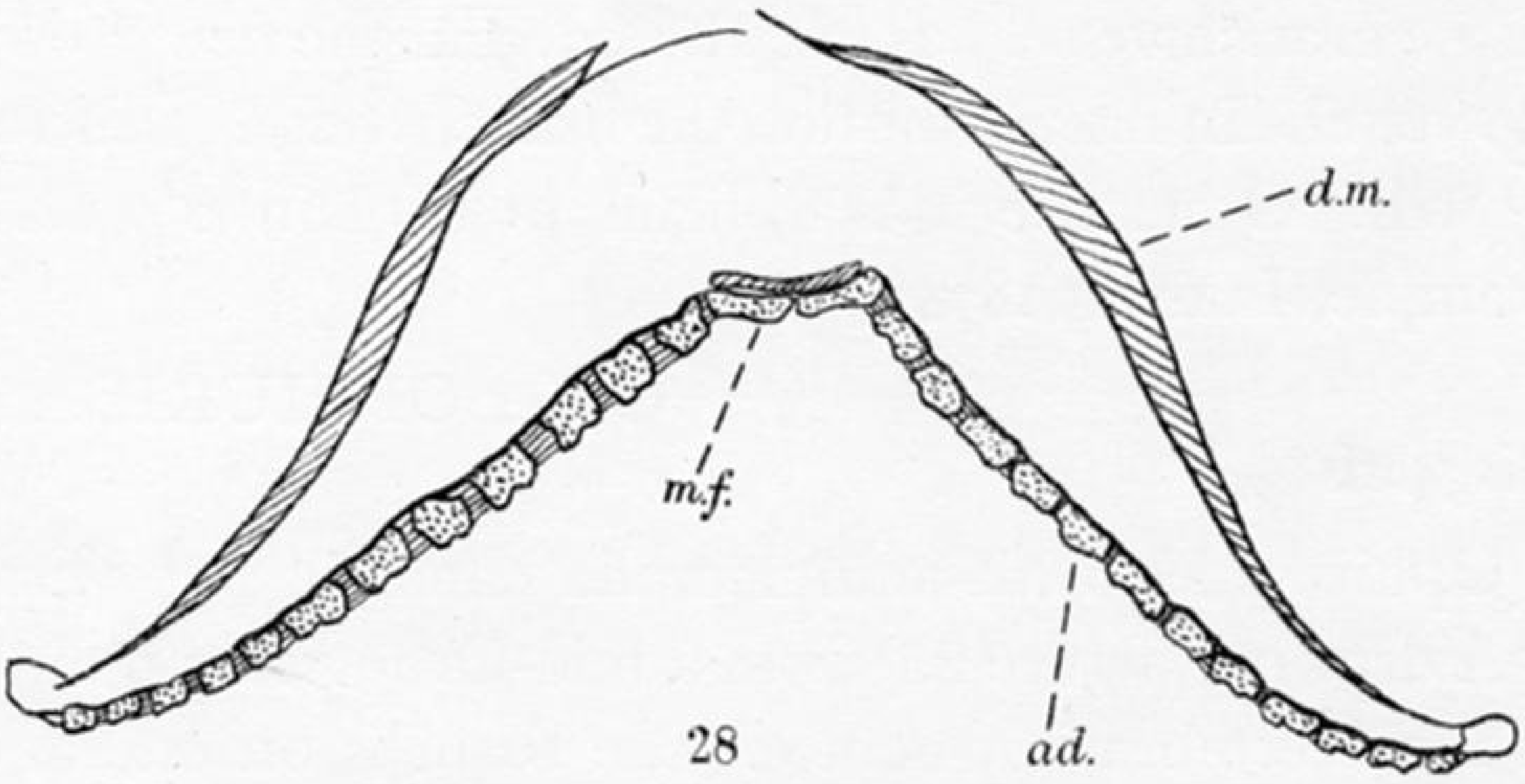

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Figure 24. *Palaeura neglecta* Schuchert. Drawing of ambulacralia in oral view. Main portion of ambulacral basin. *b.*, large proximal portion of basin; *dp.*, hollow in sole of boot, the small remains of the distal portions of the basin. *l.*, leg of ambulacral boot.

Figure 25. *Taeniaster*. Portion of an arm to show the basin for the tube foot placed on one ambulacral only and the large pit *v.m.*, for the housing of the ventral longitudinal muscle.

Figure 26*A*. *Palaeura neglecta* Schuchert. Side view of the aboral surface of the arm. *a.*, ambulacral; *l.*, lateral; *M.P.*, mouth-angle plate.

Figure 26*B*. Similar view of *Drepanaster* (copied from Spencer 1940, text-fig. 325*C*), showing interambulacral joints; *a.*, ambulacral; *l.*, lateral.

Figure 27. Outline of edges of basin in *A*, *Eophiura*. *B*, *Palaeura* compared with the first stages in the growth of a vertebra. *C*, first stage; *D*, second stage (after Ludwig 1882); *p.*, pore for passage of tube foot.

Figure 28. Diagrammatic arm section of an asteroid during feeding. *ad.*, adambulacral chain; *d.m.*, dorsal muscle; *m.f.*, mouth-frame.

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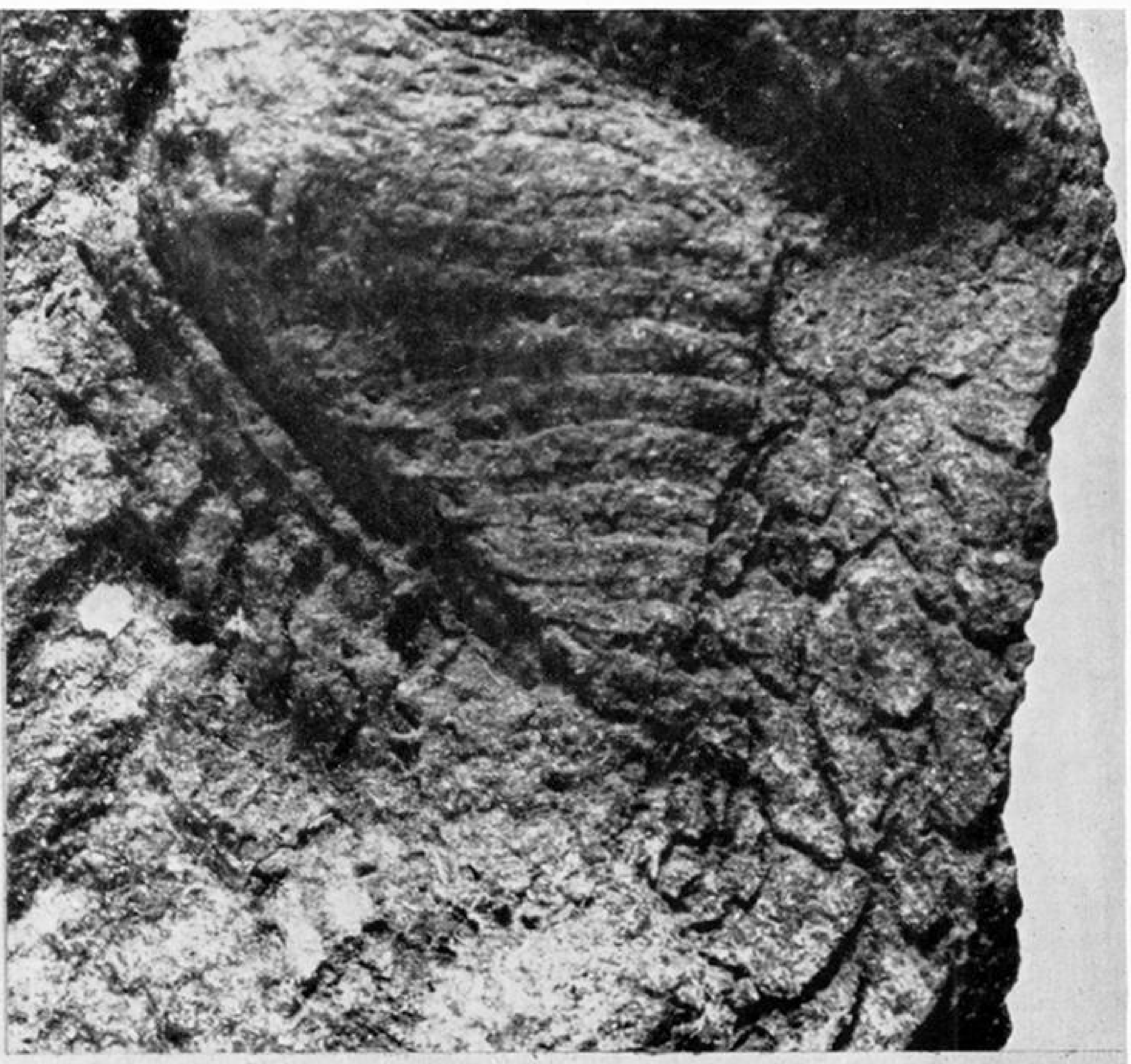

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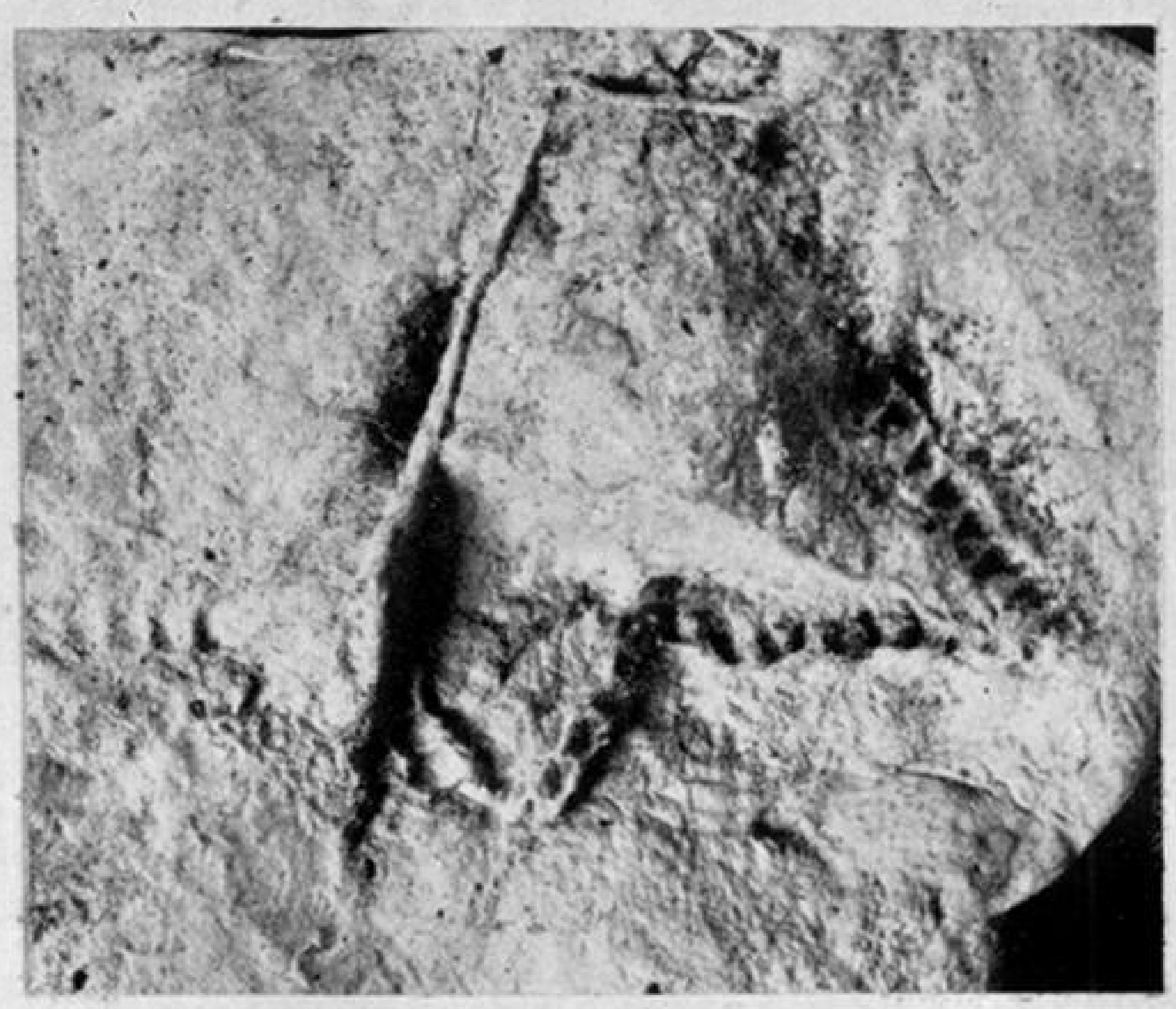

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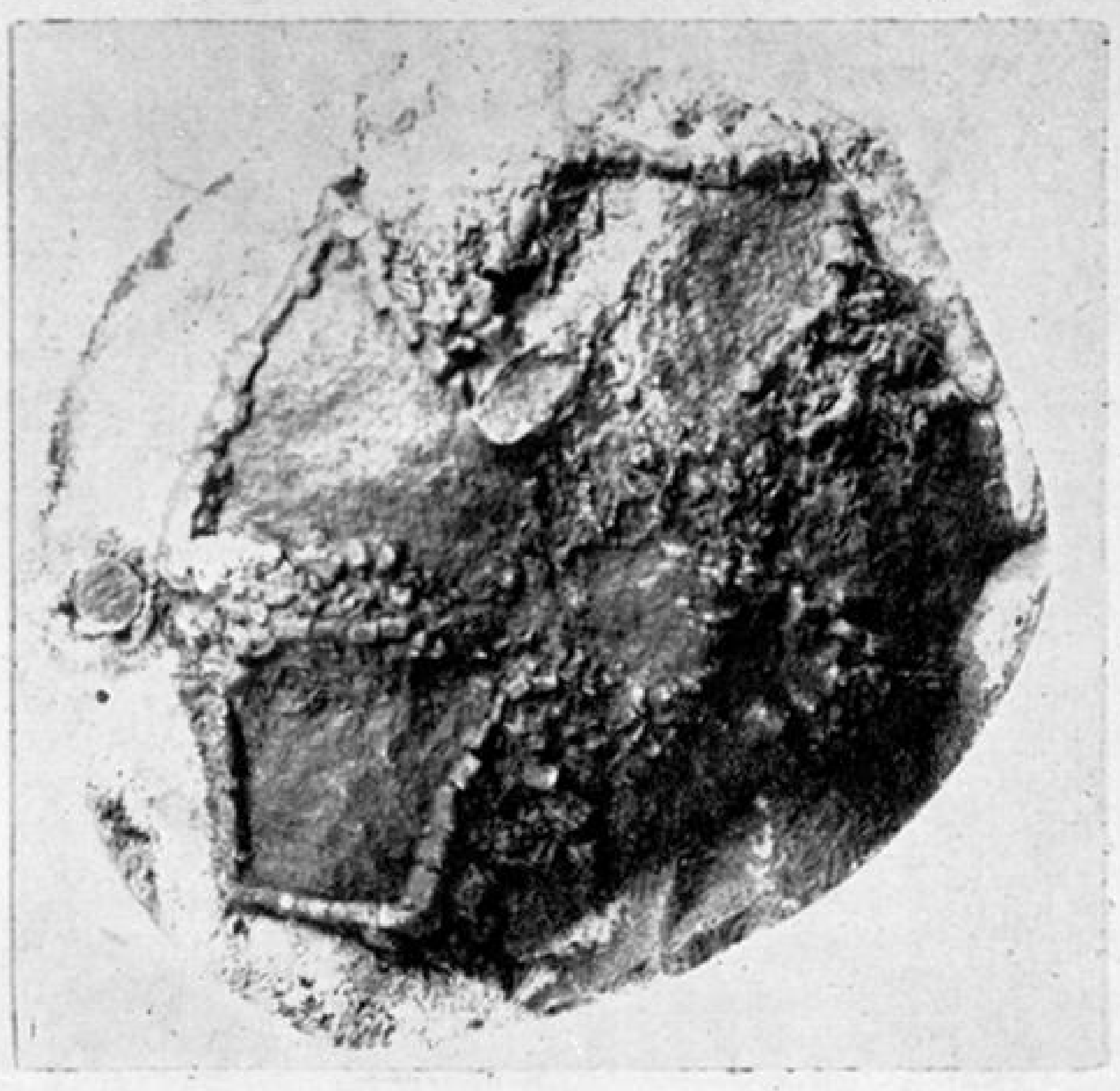

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Plate 2

Figure 29. *Villebrunaster thorali*, n.g. et n.sp. Holotype. Photograph of a cast showing two individuals lying side by side (magn. × 2). The photograph to the left (the holotype) shows five arms lying in one plane (see figure 1); that to the right two arms flexed upwards (see figure 3). Coll. Villebrun, Univ. Montpellier.

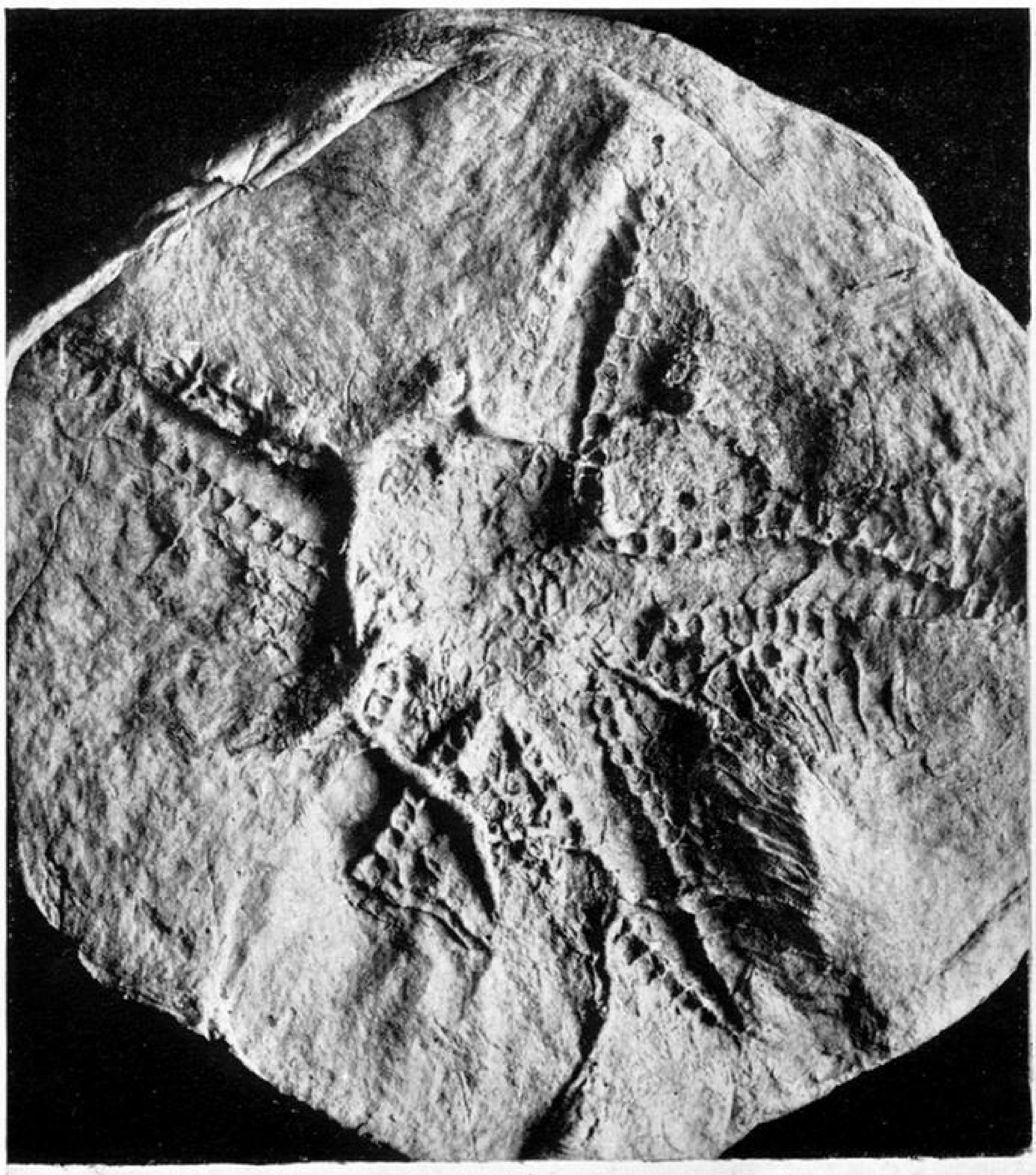
Figure 30. *Villebrunaster thorali*. Photograph of an original mould showing impressions of the arm in aboral view and, to the right, impressions of the spicules (magn. × 6). The mesh between the spicules, on the left of the photograph, is irregular. Adjacent are impressions of the rows of virgalia.

Figure 31. *Villebrunaster thorali*. Photograph of another portion of a mould showing the spicular impressions (magn. × 10). The mesh, in the lower part of the photograph, has hexagonal outlines.

Figure 32. *Chinianaster levyi* Thoral. Photograph of a cast of the oral surface of a small specimen (magn. × 3). Coll. Thoral.

Figure 33. *Chinianaster levyi* Thoral. Photograph of a cast of one angle (magn. × 2). Coll. Univ. Montpellier. Rows of virgalia are seen to the upper left of the angle.

Figure 34. *Archegonaster pentagonus* n.sp., with arms flexed upwards (magn. × 1·5). Coll. Mus. Rokitzan.



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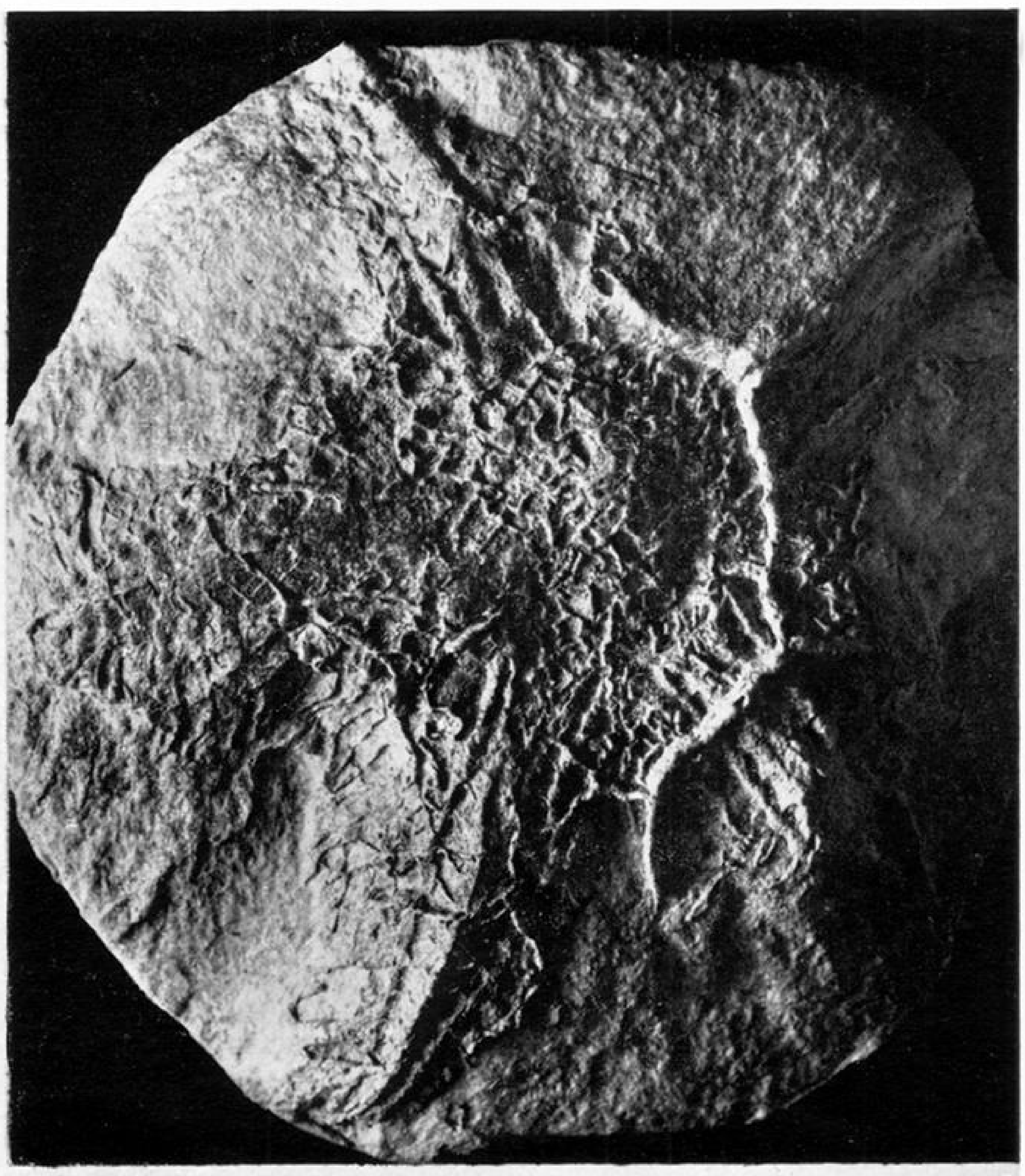

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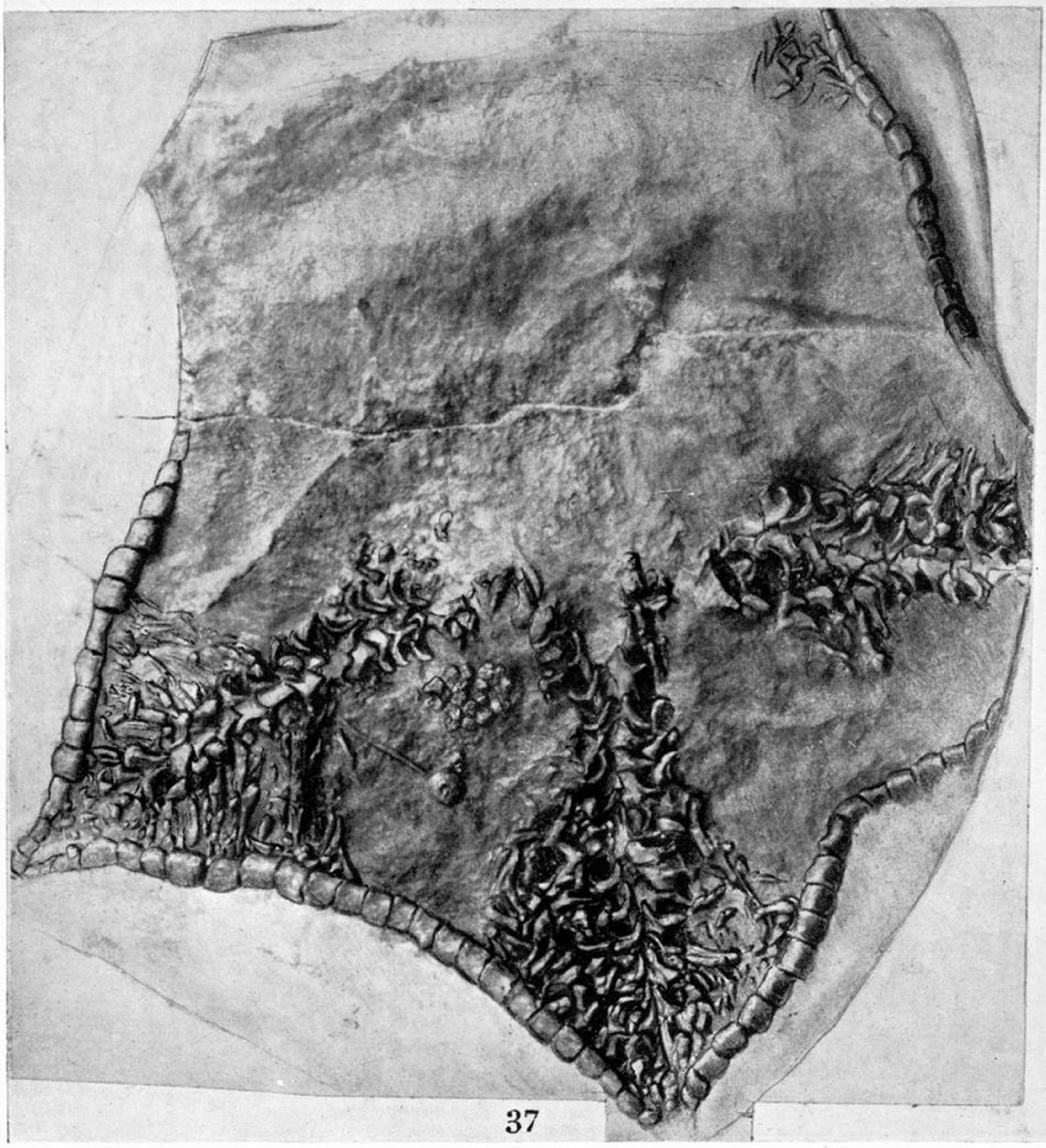

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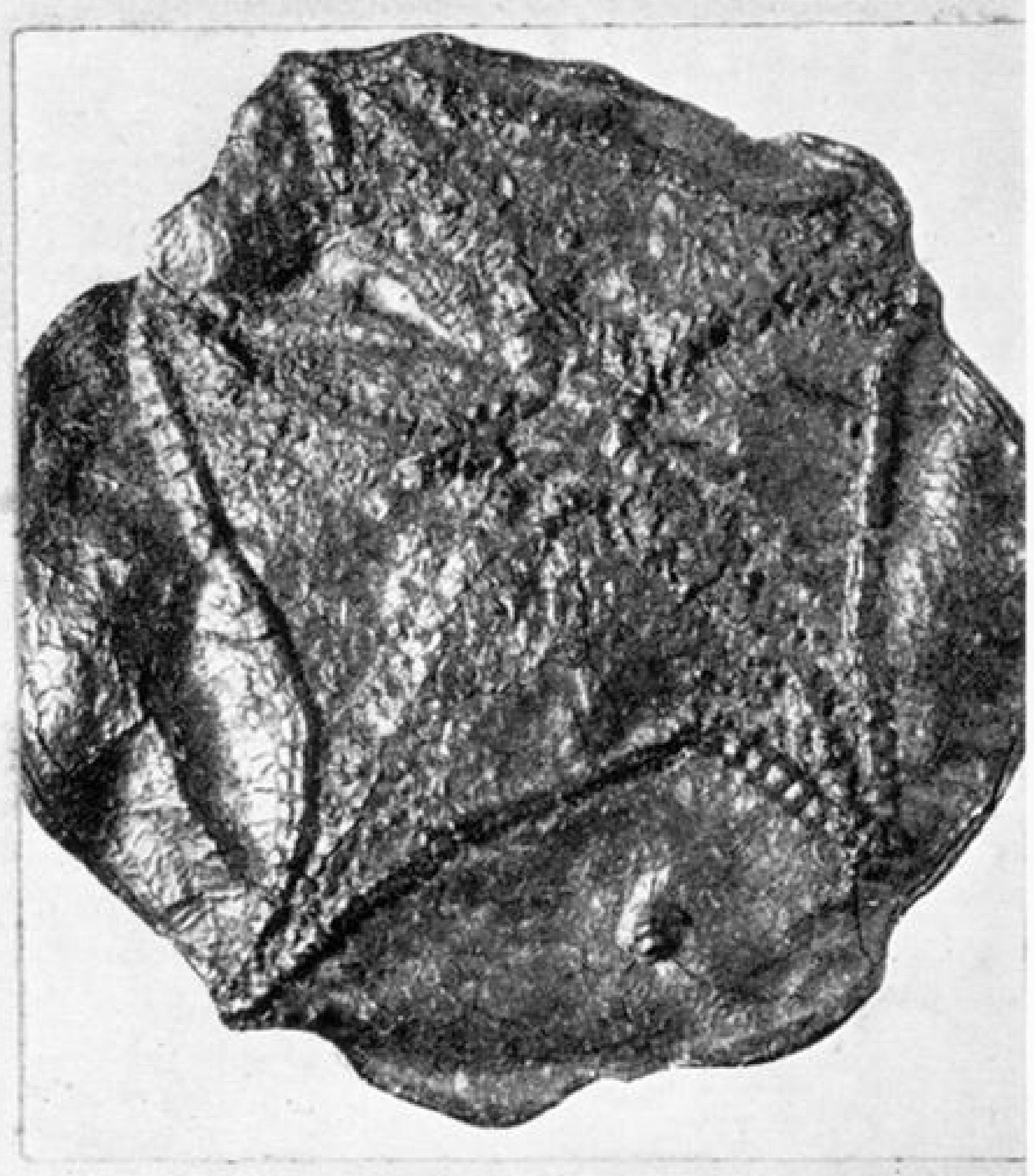

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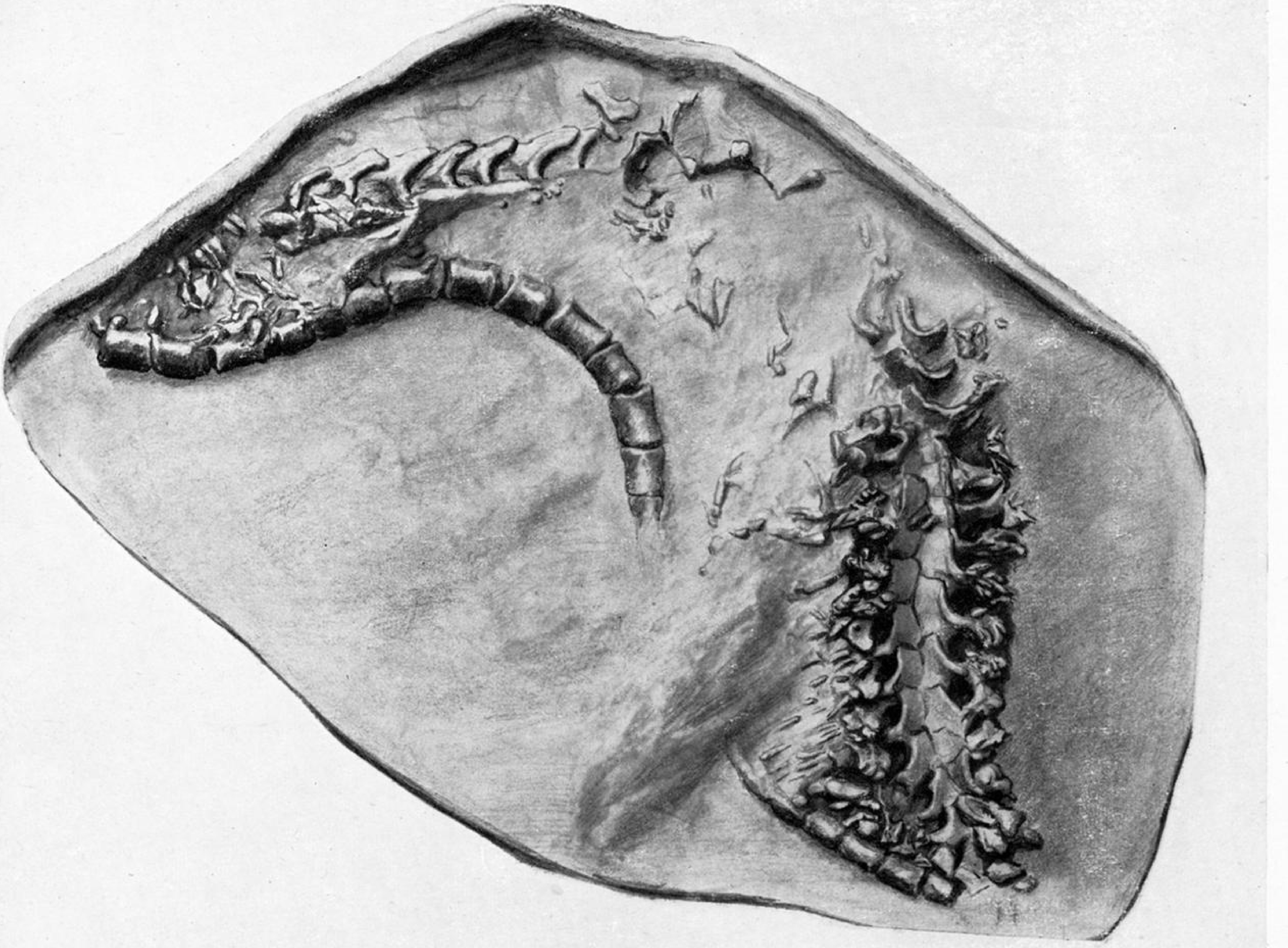
PLATE 3

FIGURE 35. *Chinianaster levyi* Thoral. Lectotype. Photograph of a cast of the oral surface (magn. × 1·75). Coll. Villebrun, Univ. Montpellier. The structure of an interradius is seen lower right.

FIGURE 36. *Chinianaster levyi* Thoral. Photograph of a cast of the aboral surface of the same specimen (magn. × 1·75). A spicular net covers the centre of the body, exposed ambulacralia are seen in the lower arm.

FIGURE 37. *Archegonaster pentagonus* n.sp. Photograph of a cast of the oral surface (magn. × 1·75). Coll. Narodni, Mus. Prague, E.H. 30. The virgalia are confined to the distal arm regions. The rounded ossicle with a central depression seen in the lower left interradius is the madreporite. Above it are seen the dislocated ossicles of the stone canal.

FIGURE 38. *Archegonaster pentagonus*. Aboral surface (about nat. size). Specimen E.H. 36. The marginal frame is drawn inwards slightly (lower right) and sharply (upper left).



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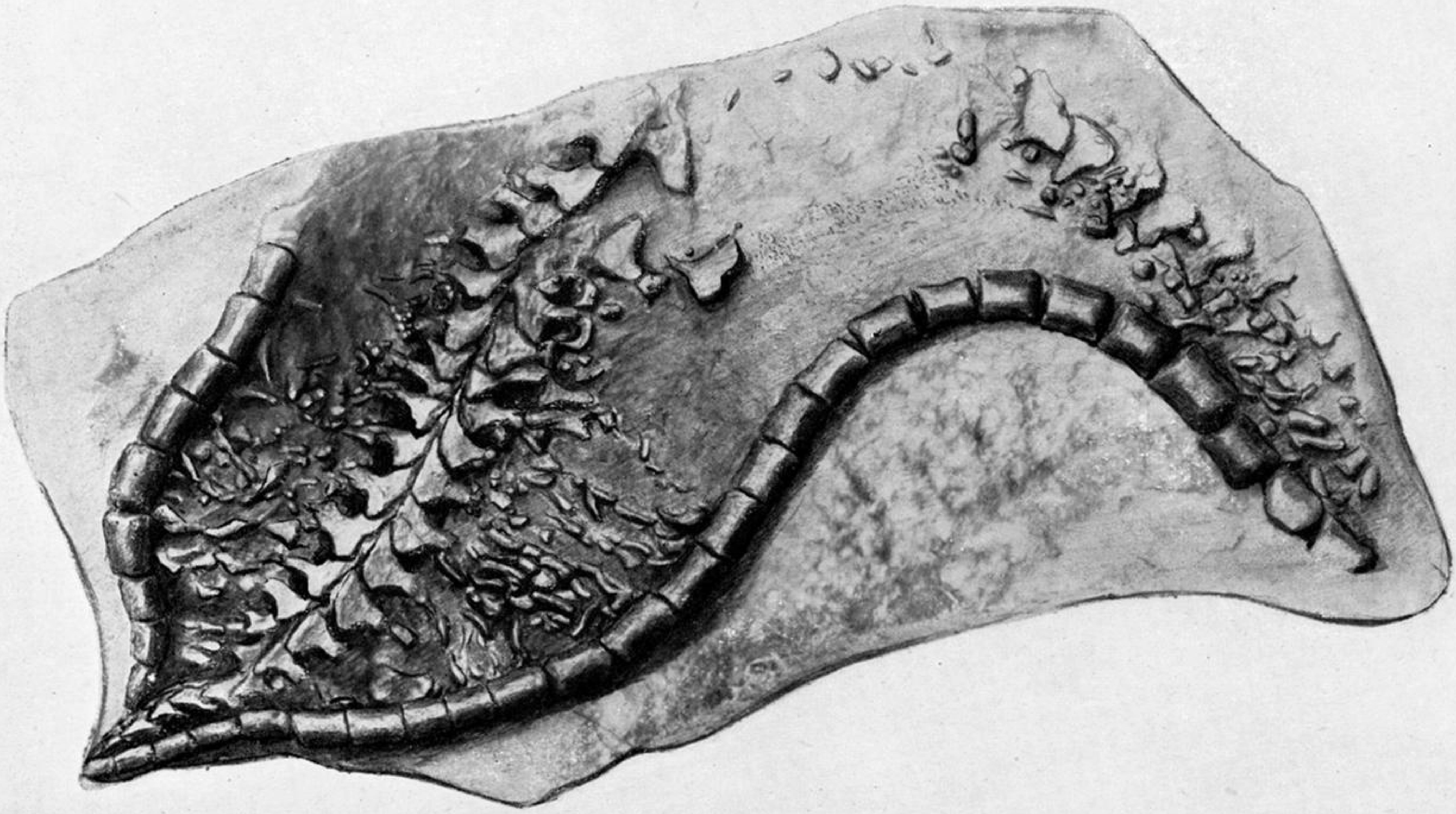

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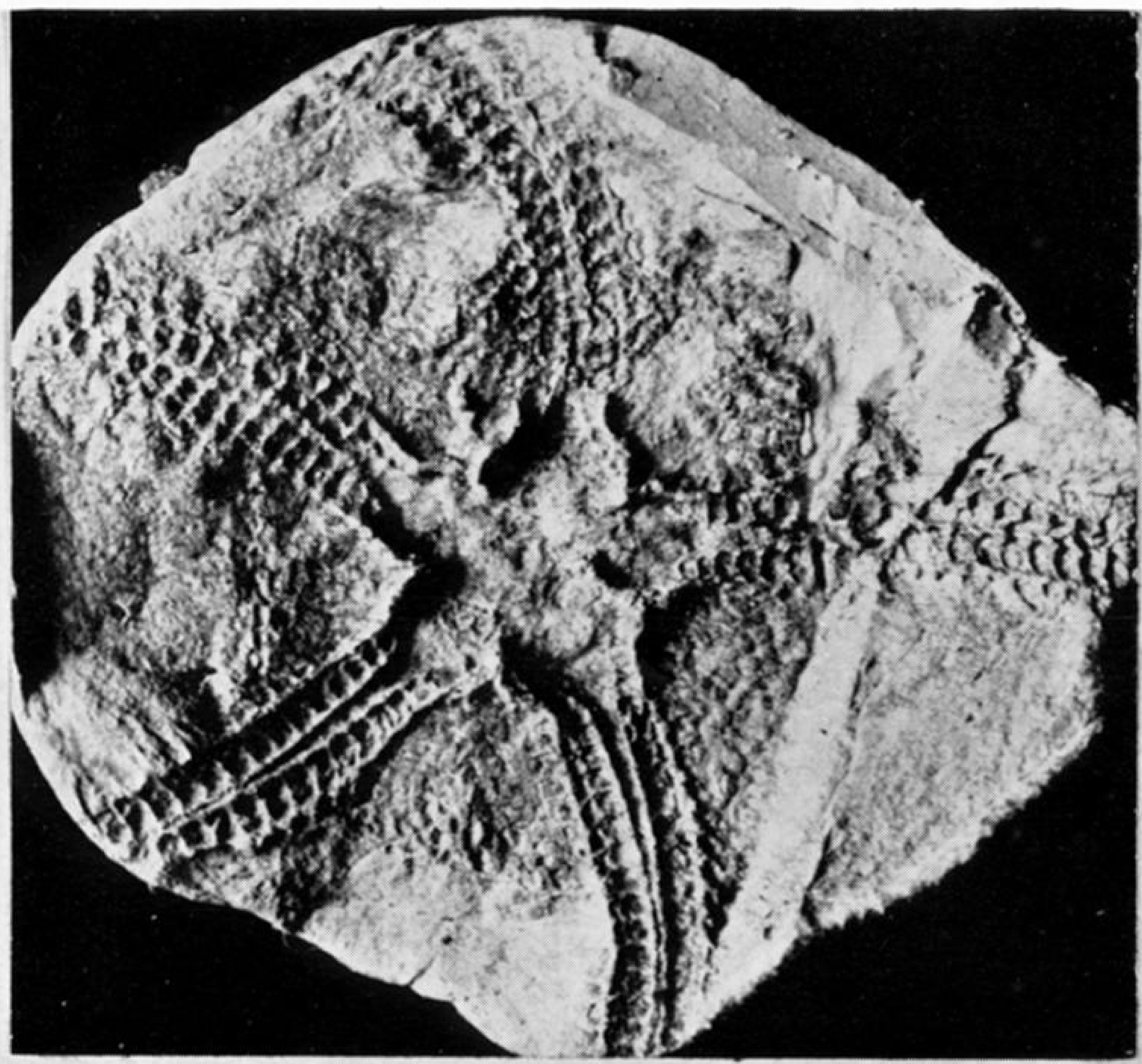
Plate 4

Figure 39. *Archegonaster pentagonus* n.sp. Holotype. Photograph of a portion of the oral surface (magn. × 4). Coll. Narodni, Mus. Prague, E.H. 7. The adambulacralia on the right arm carry tufts of spines. They have swung outwards exposing the wide ambulacral channel and the basins for the tube feet. (See also figure 54, plate 8 and figure 10, p. 104.)

Figure 40. *Archegonaster pentagonus*. Photograph of the counterpart of the same specimen showing the aboral surface (magn. × 4). The upper surfaces of the ambulacralia are well exposed. (See also figure 13, p. 104.)



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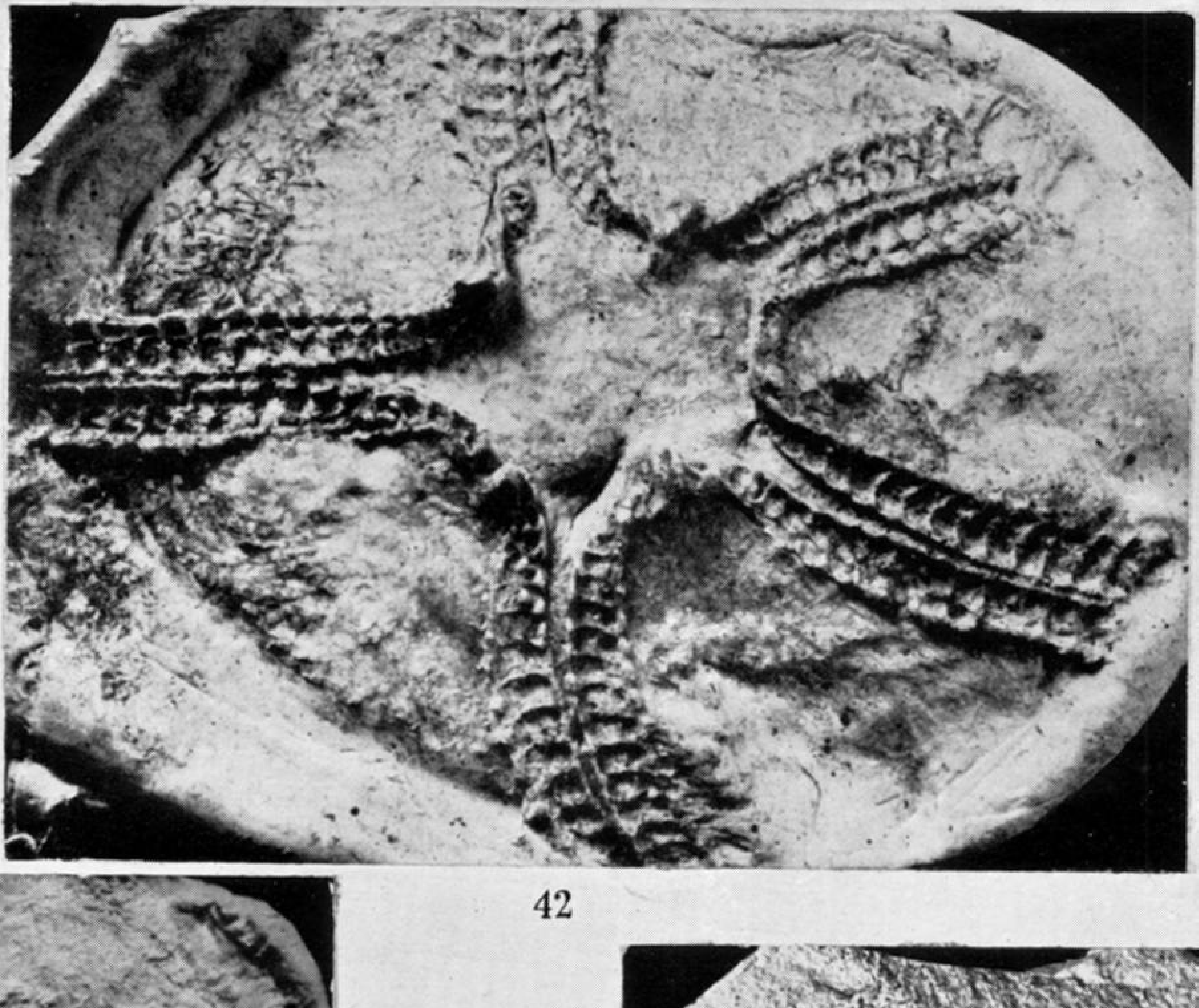

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PLATE 5

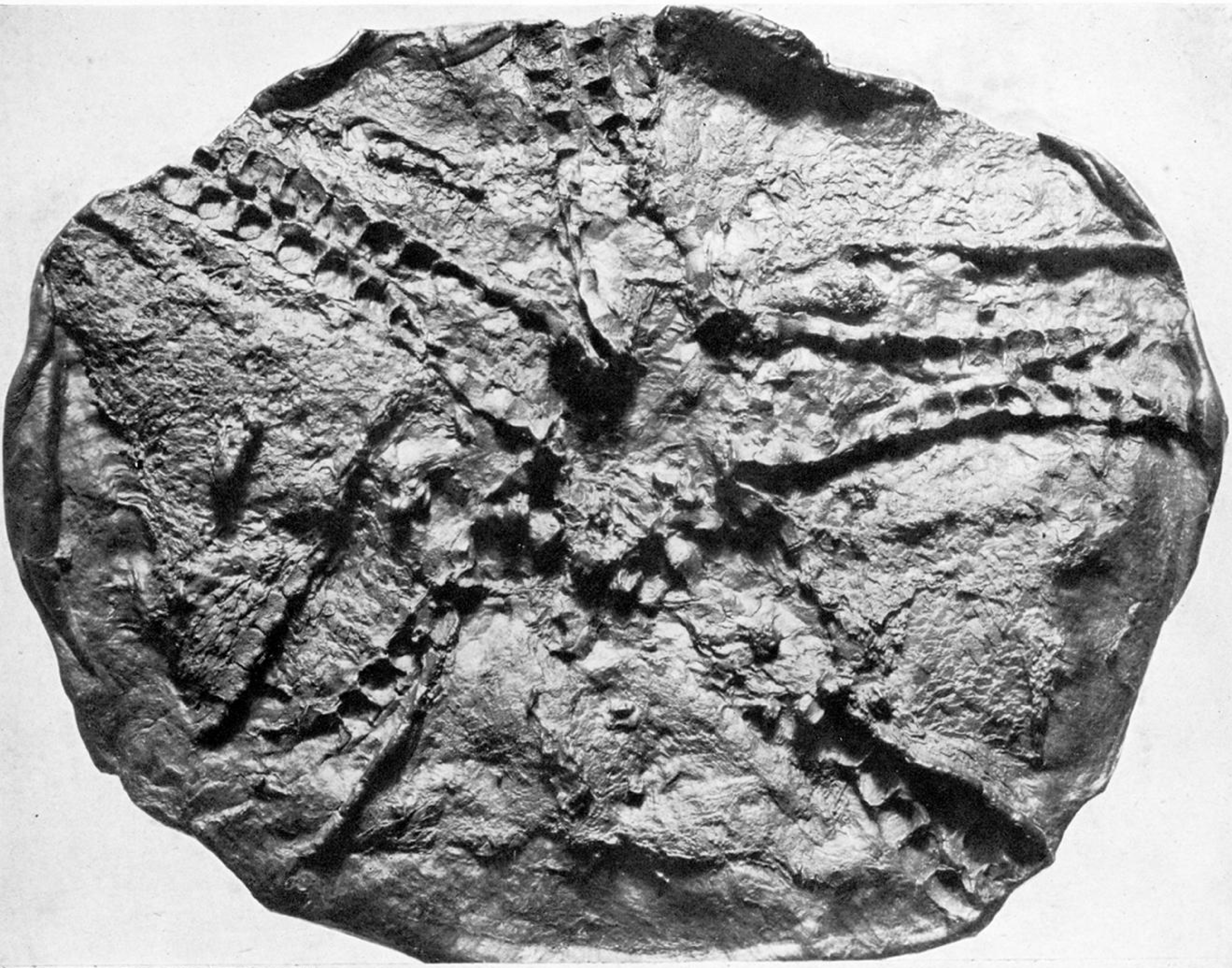
FIGURE 41. *Pradesura jacobi* (Thoral). Lectotype. Oral surface of the disk and the arm bases (magn. × 2·6). Coll. Univ. Montpellier, no. 139 (mould of this specimen figured, Thoral, plate ix, figure 2).

FIGURE 42. *Pradesura jacobi* (Thoral). The same view of a second specimen (magn. × 3·5). Same collection, no. 138 (mould figured, Thoral, plate ix, figure 3*a*). Spines are seen near the disk margins in the upper left-hand interradius.

FIGURE 43. *Pradesura jacobi* (Thoral). The same view of a third specimen (magn. × 1·75). Same collection, Px. The lateralia have revolved inwards and partially closed the groove.

FIGURE 44. *Pradesura jacobi* (Thoral). Aboral surface of same specimen Px (magn. × 1·75). The aboral surfaces of the exposed ambulacralia show small ball and socket joints.

FIGURE 45. *Pradesura jacobi* (Thoral). Aboral surface of another specimen (magn. × 1·75). Same collection, no. 137. The mouth frame is widely open and crushed through the aboral covering.



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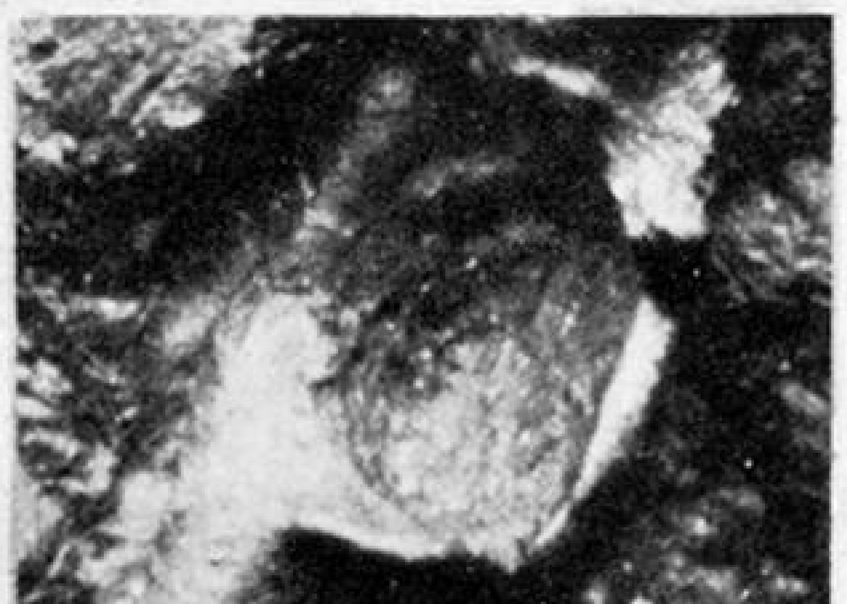

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Plate 6

Figure 46. *Eophiura bohemica* Schuchert. Lectotype. Oral surface of the disk and the arm bases (magn. × 2). The madreporite is in the upper right-hand interradius lying alongside the mouth frame. Coll. Narodni Mus. Prague, no. E.H. 94.

Figure 47. *Eophiura bohemica* Schuchert. Madreporite and stone canal of same specimen (magn. × 9).

Figure 48. *Eophiura bohemica* Schuchert. Ambulacral basins at the base of the buccal slits from same specimen (magn. × 6). The upper ossicle shows a groove at the distal end of the basin, the second ossicle a groove at the proximal end of the basin.

Figure 49. *Eophiura bohemica* Schuchert. Aboral surface showing exposed ambulacralia and buccal slits, defined by a light wash, natural size. Same collection, E.H. 105.

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PLATE 7

FIGURE 50. *Eophiura bohemica* Schuchert. Photograph of a cast of ambulacralia showing the tears in the cast by the hardened infillings of the branch vessels (magn. × 6). Coll. Narodni Mus. Prague, E.H. 98. The tears between the ambulacralia to the left are shown clearly.

FIGURE 51. *Eophiura bohemica* Schuchert. Oral surface of the distal extremity of an arm (magn. × 10). Specimen no. E.H. 97. Sub-lateralia are seen to the lower left.

FIGURE 52. *Eophiura bohemica* Schuchert. Lateralia showing spine attachments and spines (magn. × 10). Specimen no. E.H. 110.

FIGURE 53. *Eophiura bohemica* Schuchert. Scales of the oral surface of the disk (magn. × 6). Specimen no. E.H. 94.


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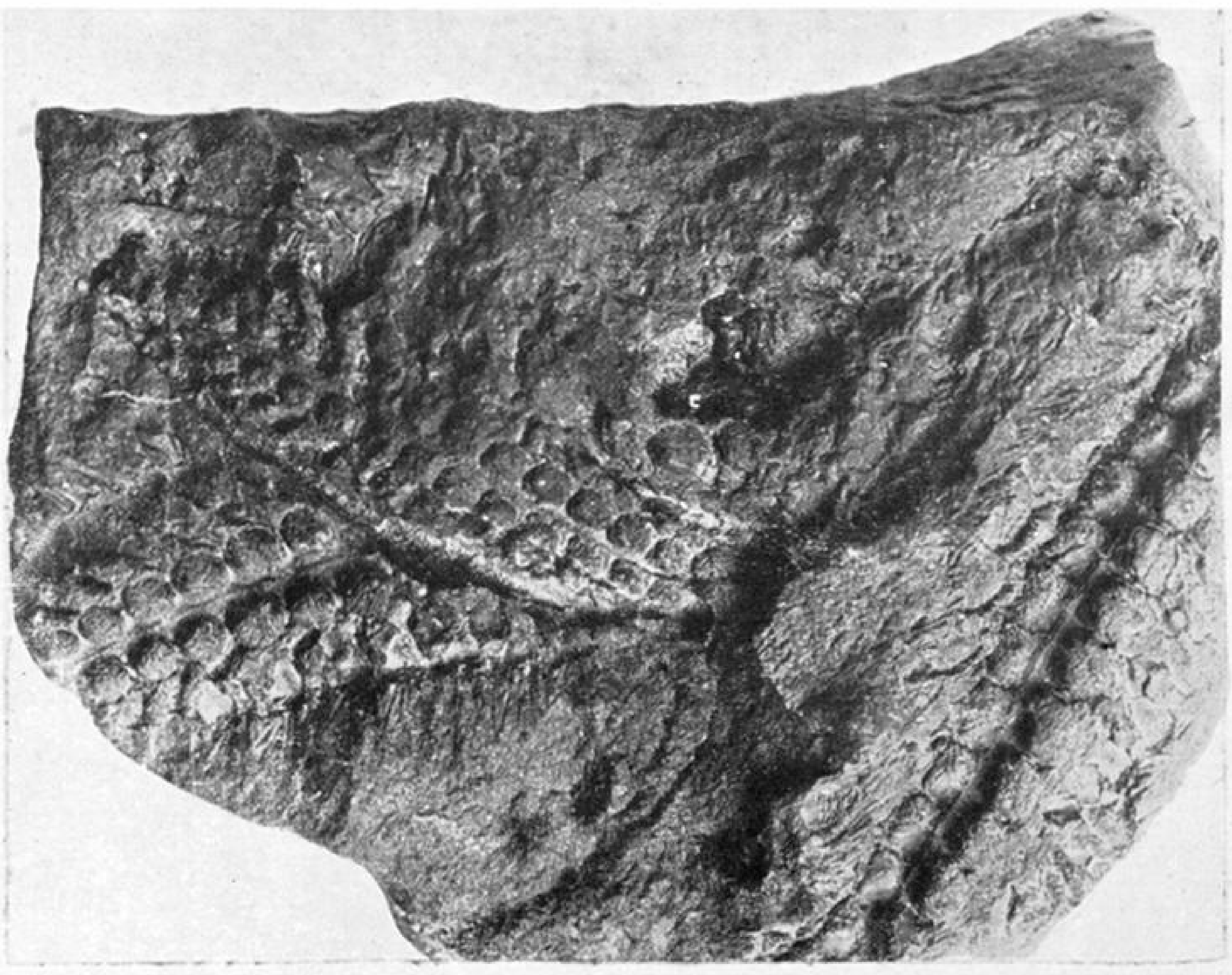
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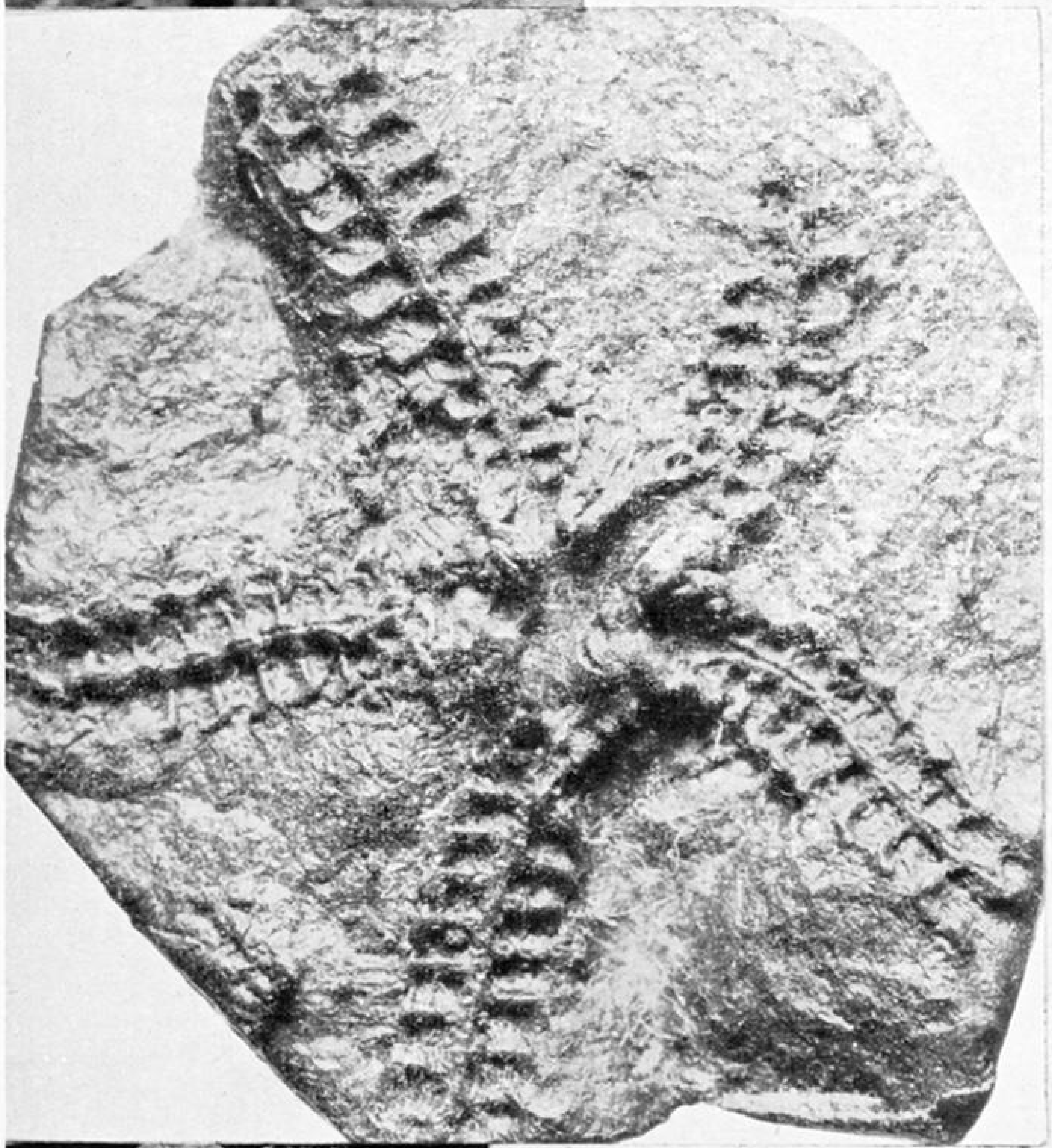
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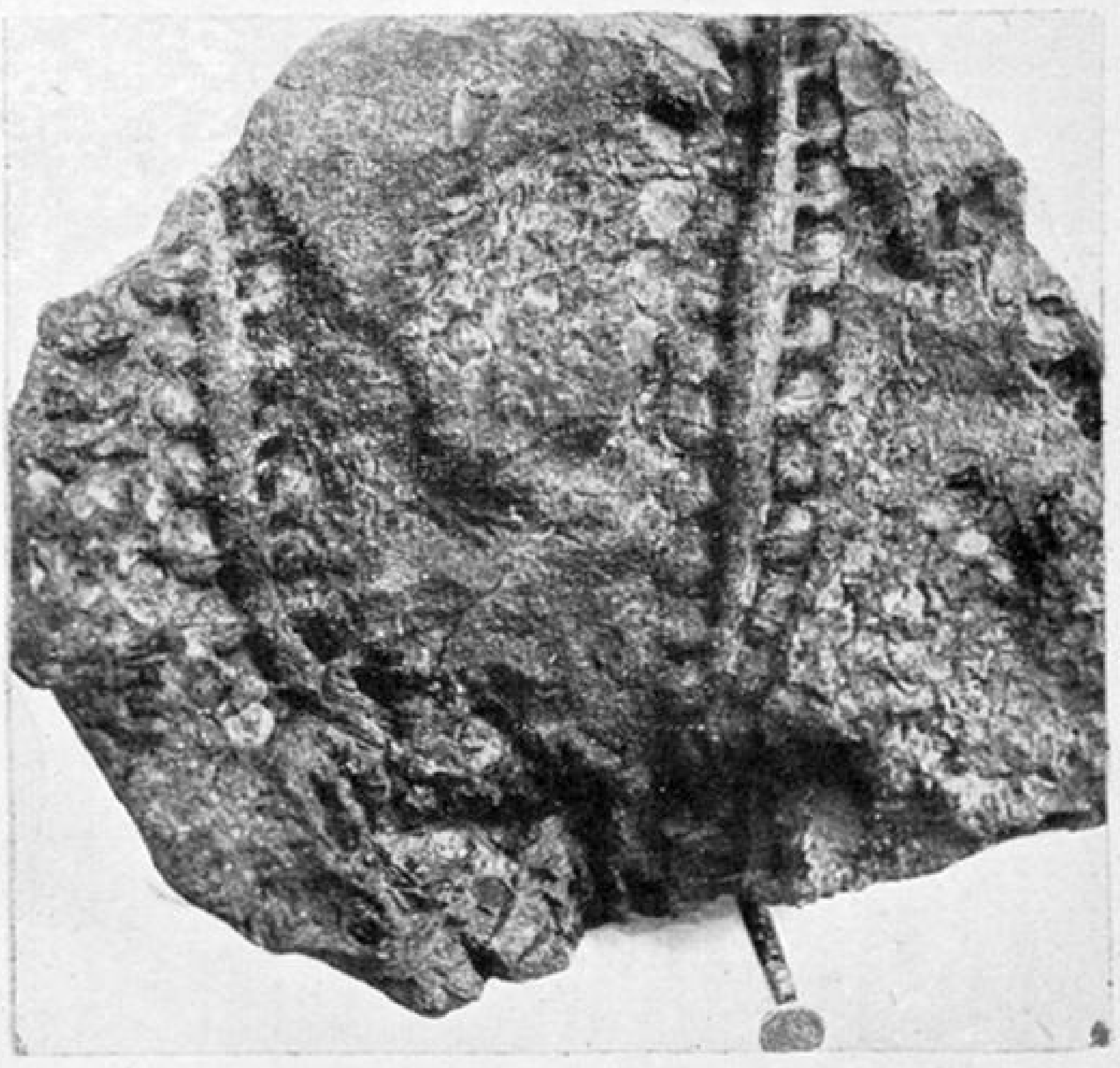
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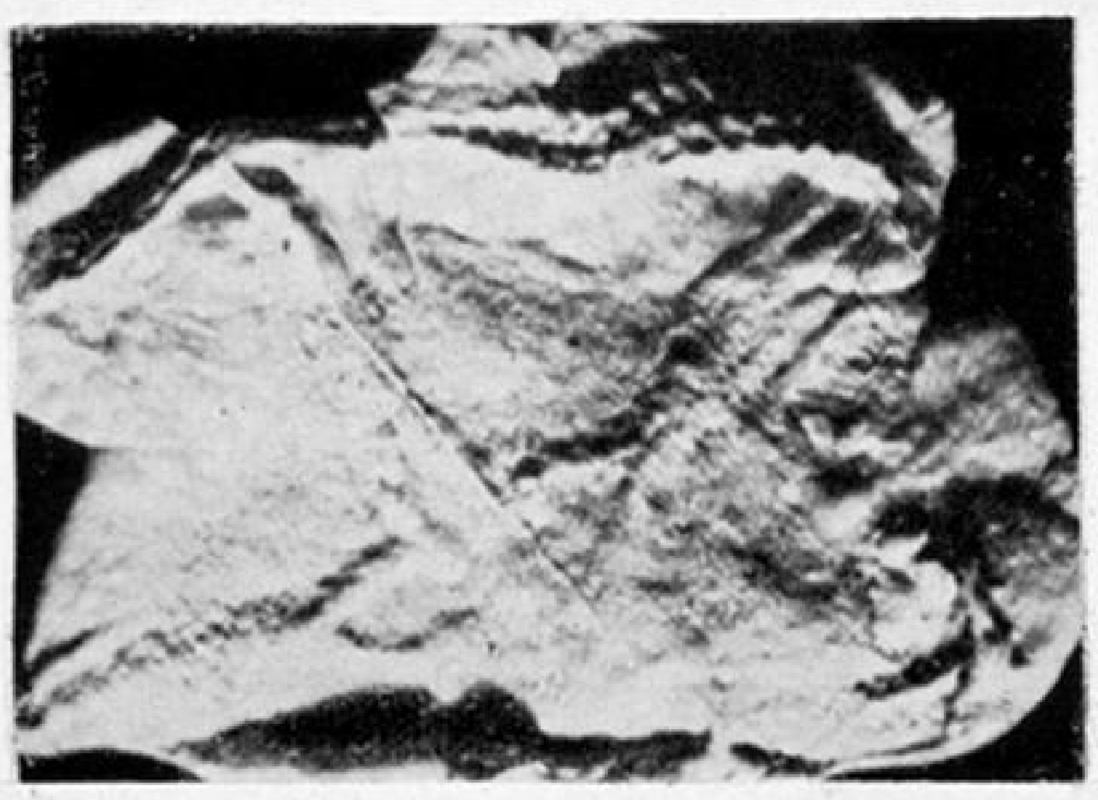
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PLATE 8

FIGURE 54. *Archegonaster pentagonus* n.sp. Ambulacralia (right) and adambulacralia (left) (magn. × 6). Coll. Narodni Mus. Prague, E.H. 11. The adambulacralia have swung open. Their stalks and the ambulacral-adambulacral narrow joints are seen upper left.

FIGURE 55. *Archegonaster pentagonus* n.sp. With arms flexed over disk (magn. × 1·5). Another photograph of the specimen shown in figure 34.

FIGURE 56. *Eophiura bohemica* Schuchert. Three arms flexed over the aboral surface (magn. × 1·5). Coll. Narodni Mus. Prague, E.H. 101. The oral surfaces of the arms are exposed and the tube feet were in position to feed from the contents of the overlying mud.

FIGURE 57. *Eophiura bohemica* Schuchert. The mould of two arms flexed steeply to the disk with the water vessels infilled with hardened mud. The infilling of the radial vessel is along the middle of the arm and on each side are the infillings of the short branch vessels and the round bases of the tube feet (magn. × 1·5). Specimens no. E.H. 100.

FIGURE 58. *Palaeura neglecta* Schuchert. Oral view of the disk and the arm bases (magn. × 3). Coll. Narodni Mus. Prague, no. 141.

FIGURE 59. *Palaeura neglecta* Schuchert. Profile view of the disk and the arm bases (nat. size). Specimen no. 135. The arms are flexed in much the same position as in figure 16, p. 108.

FIGURE 60. *Palaeura neglecta* Schuchert. Disk in aboral view with one arm flexed and lying over the disk (nat. size). Specimen no. 155. The oral surface of the arm is exposed as in figure 56 above.

FIGURE 61. *Palaeura neglecta* Schuchert. Disk in aboral view with mouth frame crushed through the surface (nat. size). Specimen no. E.H. 136. The buccal slits are well exposed from above as in figure 49, plate 6.