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The Lantern and Girdle of Some Recent and Fossil Echinoidea

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XIV. *The Lantern and Girdle of Some Recent and Fossil Echinoidea*

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(*Communicated by* F. A. Bather, *F.R.S.*)

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I. Introduction

Two centuries ago Klein (1734) proposed a classification of the Echinoidea based upon the position and character of the "mouth." The clumsy terms "Emmesostomi" and "Apomesostomi" that he applied to the two main sections of the class have fortunately lapsed; but the situation of the peristome has been recognized as fundamental in all subsequent schemes of classification. Like Klein's collateral scheme based on the position of the periproct, this principle has the advantage of being applied with equal ease to recent and fossil forms.

In a general way, a central position of the peristome may be taken to imply the presence of jaws, while an eccentric position implies their absence. Thus a classification on that basis divides the Echinoids into two sections which have very different habits. The types that have jaws live in the open, scrambling among rocks, while those without jaws shuffle over silt or may burrow into it. The gnathostomatous condition precedes the atelostomatous both in palæontology and ontogeny, although both conditions are abundantly represented in the modern fauna.

The three living orders of gnathostomatous Echinoids, the Cidaroida, Centrechinoida (Diademoida) and Clypeastroida, are separable by the marked differences in the construction of their jaws and associated structures. Within the limits of the several orders, there is little variation in this respect among the Cidaroida, and scarcely more among the Clypeastroida; but among the Centrechinoida there are important diversities. Modern schemes of classification of the Centrechinoida are based mainly on differences in the construction of the lantern and teeth. Jackson's (1912) division of the Centrechinoida into three sub-orders, Aulodonta, Stirodonta, and Camarodonta, seems the simplest, most practicable, and most natural classification yet devised; but it demands knowledge that is difficult to acquire for fossil forms. The nature of the jaws, and even of the perignathic girdle, is entirely unknown in the great majority of fossil Centrechinoid genera.

During the past twenty-four years I have collected some evidence on the buccal structure in a number of fossil Echinoids; and I publish my results in the hope that they will establish the taxonomic position of a few genera, and encourage other workers to continue the search for this important evidence in the host of types that are still "*incertæ sedis*." The lantern is preserved in fossil Echinoids more often than might be supposed; but its presence usually remains undetected unless the specimens are mutilated. Even when found, it is very difficult to extract, for the infilling of a test is often concretionary and sometimes crystalline. The perignathic girdle is usually more accessible, but as often as not it has been broken before fossilization.

In this paper I describe the buccal apparatus of Mesozoic Centrechinoids and Holectypoids only, except for purposes of comparison. I have excavated the lantern and girdle in many fossil Cidaroids and Clypeastroids, but the variations of structure that I have observed in them seem to have merely generic significance. Most of the

Holectypoids have already been described by me in a series of papers (1910–1918); but I am able to make corrections and additions to the previous accounts in the light of new preparations.

The nature of the jaws is known in only eight of the twenty fossil genera here discussed. This is sufficient testimony to the need for further research, especially when it is realized that the acquisition of these few data has involved the destruction of many scores of specimens during nearly twenty-five years' work.

II. The Anatomy of the Lantern

The structure of this wonderful apparatus, consisting (in regular Echinoids) of forty separate ossicles co-ordinated and controlled by sixty separate muscles, has been described so fully by Lovén (1892) and Jackson (1912) that a bare summary of its nature will here suffice. The only addition that I am able to make to published accounts is concerned with the crystallographic relations of the parts of the pyramids.

Briefly enumerated, the constituents of the lantern are: five teeth (interradial in position), five pyramids (each consisting of two symphysially united maxillæ crowned by epiphyses) which support the teeth and appear to be interradial, five rotulæ situated radially between the pyramids, and (in Regular Echinoids) five compasses (each in two parts) superposed on the rotulæ. Ten protractor, ten retractor, and ten radial

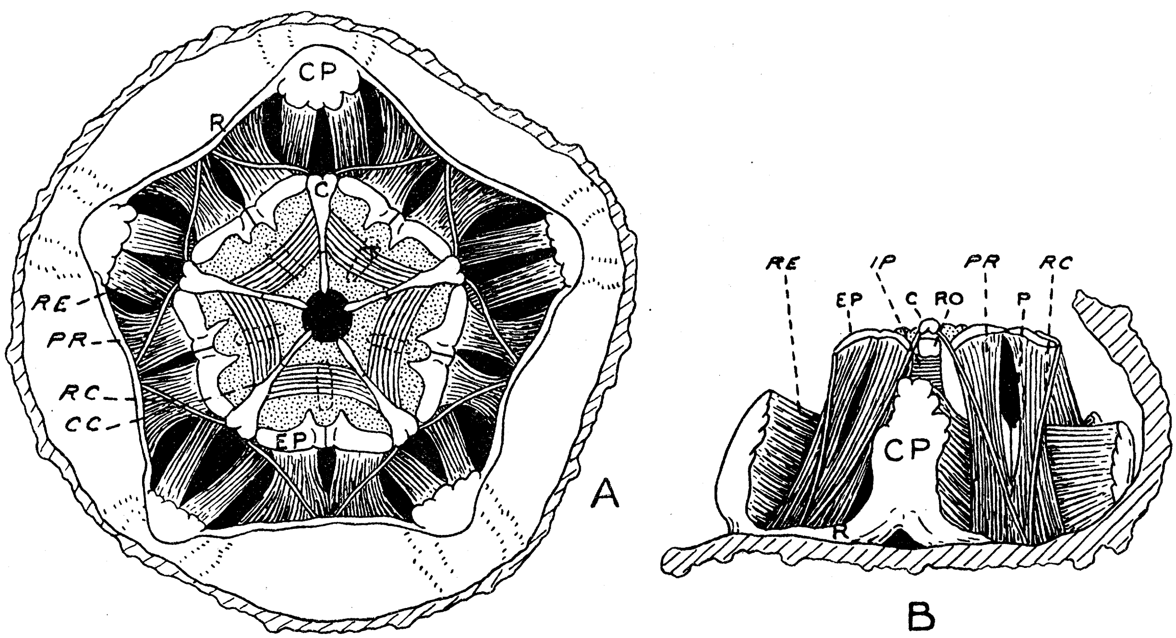

Fig. 1.—Top and side views of the lantern and girdle of *Echinometra lucunter* (Linn.). (See also figs. 27 and 28, Pl. 68.) Slightly diagrammatic.

Skeletal parts:—C, compass; CP, capped process; EP, epiphysial arch; P, pyramid; R, ridge; RO, rotula; T, tooth.

Muscles:—*CC*, circular compass; *IP*, interpyramidal; *PR*, protractor; *RC*, radial compass; *RE*, retractor.

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compass-muscles pass from the lantern to the corona; five interpyramidal muscles (radially situated) unite the pyramids; five circular compass-muscles form a ring binding the compasses together; and twenty small muscles connect the rotulæ with the epiphyses.

JACKSON (1912, pp. 189–190) expressed the opinion that the whole of the lantern (excepting only the teeth) might be regarded as built of radially situated elements. Thus he considered the two maxillæ that are held together by an interpyramidal muscle to be a unit, rather than the pair that, by symphysis, constitute a pyramid. This view receives strong support from the crystallographic orientation of the ossicles concerned. A small specimen of *Cidaris cidaris* (LINN.) was impregnated with, and embedded in, Canada Balsam, and then sectioned (hard and soft parts together) by petrological methods. The section was made at about the mid-level of the lantern. Examination between crossed nicols shows the effect diagrammatically represented in fig. 2. The calcite of the two half-pyramids connected by an interpyramidal muscle is

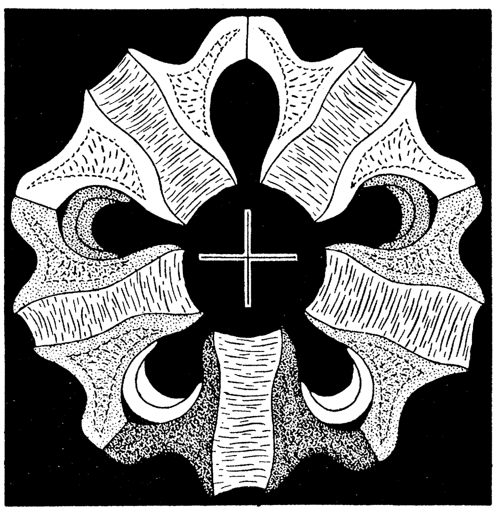

FIG. 2.—Transverse section of the lantern of a young *Cidaris cidaris* (LINN.) cut at about the mid-level. Viewed between crossed nicols; showing orientation of the calcite in the maxillæ and teeth.

seen to be in one orientation, while that of the two halves of a single pyramid shows two different qualities of interference. It is interesting to observe that the orientation of the substance of a tooth is exactly opposite to that of the pyramids, so that it is the tooth on the opposite side of the lantern from an extinguished pair of maxillæ that is itself extinguished. It seems clear, therefore, that the maxillæ of adjacent pyramids are cognate, while those of a single pyramid are independent.

The chief variations in the constitution of the lantern can be expressed in a morphogenetic scheme.

(*a*) The whole *lantern* may be inclined or upright. It is inclined in Palæozoic forms (and in the Echinothuriidæ) and in the early post-larval stages of most later types. It is virtually upright in the Cidaroida, and scarcely less so in most of the Centrechinoida

("Diademoida"). It becomes progressively more inclined through the series of the Holectypoida, and is almost recumbent in the Clypeastroida.

(*b*) The *symphysis* between the maxillæ of a pyramid may extend for almost their entire height, or may be restricted to their lower parts. In the latter condition the gape between the upper parts of the maxillæ is known as the foramen, which may be open or closed. The foramen is deep and open in Palæozoic forms, but it scarcely exists in the Cidaroida. It is usually about half the length of the pyramid in the Centrechinoida. In the Holectypoida it is relatively shallow (but the evidence is limited); and in the Clypeastroida it almost disappears on account of the peculiar shape of the pyramids.

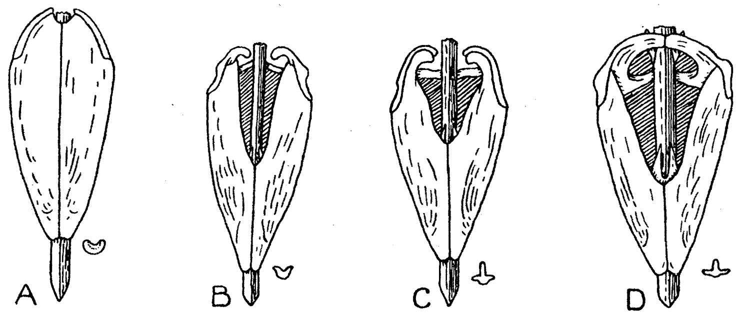

FIG. 3.—Outer views of representative types of pyramids. A, Cidaroid (*Eucidaris*); B, Aulodont (*Centrechinus*); C, Stirodont (*Arbacia*); D, Camarodont (*Tripneustes*). After JACKSON (1912), p. 184.

(*c*) The *epiphyses* may be small and disjunct, or large and united by suture into arches at the tops of the pyramids, completing the closure of the foramina. The latter condition is restricted to the Camarodont section of the Centrechinoida, but some tendency towards it is often found in other sections.

(*d*) The *sutural face* where the epiphyses fit on to the maxillæ may be smooth or pitted. A pitted surface is characteristic of the Centrechinoida (and possibly of the Holectypoida), while a smooth surface is normal in all other gnathostomatous groups.

(*e*) The *teeth* may be grooved or carinate. All Palæozoic types, all Cidaroida, and the Aulodont section of the Centrechinoida, have grooved teeth; all the other Centrechinoida, as also the Holectypoida and Clypeastroida, have carinate teeth. On the whole, the teeth are broadest in the early types, and become progressively narrower, until in the Clypeastroida there is little left but the keel.

(*f*) *Compasses* may be present or absent. They are present in all Regular Echinoida, Palæozoic forms included; they are certainly absent in the Clypeastroida. They occur in the vestigial lantern of *Echinonëus*, and so may be assumed to have existed in the Mesozoic Holectypoida, but their presence there has not been proved.

III. THE ANATOMY OF THE PERIGNATHIC GIRDLE

The girdle consists of ingrowths from, or internal additions to, the proximal coronal plates, designed to give attachment for the distal ends of the protractor retractor, and radial compass-muscles of the lantern. It is not known to have existed in the Palæozoic Echinoidea; but in some guise it occurs in all later gnathostomatous groups; and it may persist in a reduced state in forms that are edentulous when adult. In the Cidaroida it consists exclusively of ingrowths from the proximal interambulacral plates (ridges), but in all other Regular Echinoidea, and in the Holectypoida, it is built of ambulacrally situated processes in addition to the ridges or even in lieu of them. While the ridges are actually parts of otherwise normal coronal plates, the processes are separate ossicles planted upon one or many of the proximal ambulacrals.

The girdle may be *discontinuous* (when a gap occurs at each ambulacrum) or *continuous* (when the ambulacra are bridged by the meeting of the upper extremities of the bordering structures). The girdle of the Cidaroida is normally discontinuous, but very occasionally the ridges may meet in an arch. In the Centrechinoid girdle the processes often meet, but even in that group discontinuity seems the commonest condition. In the Holectypoida and Clypeastroida the girdle is always discontinuous.

An additional feature is found in the girdles of many Centrechinoida, where secondary growths from both ingredients may increase the height of the structure. This " capping " is shown in such diverse cases as *Centrechinus* (" *Diadema* ") and *Echinometra*, but it seems not to have more than a generic significance. Most of the near allies of *Centrechinus* have wholly uncapped girdles ; while *Colobocentrotus*, an advanced Echinometrid, is quite without caps. " Capping " has long been recognized as a phenomenon affecting the processes ; but I have found that it is quite as common a development on the ridges. The " caps " are in crystalline continuity with the girdle elements to which

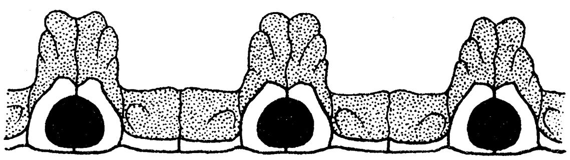

FIG. 4.—Plan of girdle of *Centrechinus setosus* (LESKE), showing the true girdle (plain) and the secondary capping (stippled). A continuous girdle amplified by capping.

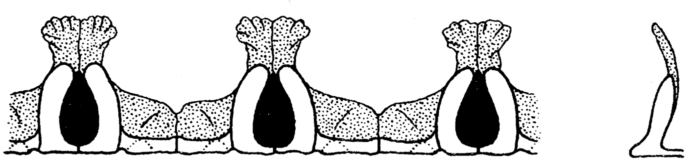

FIG. 5.—Plan of girdle of *Echinometra lucunter* (LINN.) (convention as in fig. 4). A discontinuous girdle made continuous by capping.

they are attached, but they are made of a much looser stereo-mesh than the main structures. It is possible for capping to transform a discontinuous girdle into a continuous one by exaggerating the height and expanse of the processes.

(1) *The interambulacral ridge*

Unlike the ambulacral process, which is always a separate ossicle suturally attached to the ambulacral plates, the interambulacral ridge is a mere ingrowth of the proximal coronal plates. It may be developed in very varying degree. It is consistently large, and the only element of the girdle, in the Cidaroida; while among the Centrechinoida it may form a high collar around the peristome (as in *Salmacis* and *Centrechinus*) or it may be a barely noticeable thickening of the edges of the plates (as in *Strongylocentrotus*). In the Holectypoida it is reduced to a mere "button" in the Pygasteridæ; but it assumes great importance in the girdle of the Discoidiidæ. In the Clypeastroida it is lacking, although its site may be usurped by migrated processes. Whenever they exist, the ridges afford attachment for the protractor and radial compass-muscles; in the Cidaroida they support the retractor muscles as well.

Although the ridges are ingrowths of the interambulacral plates, modification has often gone far enough to obliterate all outward signs of their coronal nature. Sometimes even the median interradial suture disappears near the free edge of a ridge, and it is exceptional for any sutures to be visible on the "front" (*i.e.*, peristomial) surface. That surface is normally sculptured by muscle-scars and warty processes that bespeak a secondary growth of stereom forming a veneer over any sutures that may have existed. It is only by study of the "back" of a ridge that its plate-composition can be detected. Even there a kind of syzygy often develops, amounting to amalgamation of the plates; so that the ridge may appear to be a single structure seemingly as distinct from the corona as an ambulacral process.

In this connexion it is important to realize the significance of the obliteration of sutures. Echinoid plates are modified during life, whether in accretion or resorption, by virtue of the activity of a film of living sutural tissue that surrounds them. If and when this film is destroyed (by the intimate coalescence of two plates), the resulting compound ossicle is stereotyped; it may still increase or decrease in thickness or at its margins, but not within itself. Such a compound offers inert resistance to any pressure exerted upon it by neighbouring plates, and will compel those plates to undergo all of the necessary adjustment instead of sharing it with them. This principle, which applies typically to the production of ambulacral complexity, is well illustrated in the "back-view" of many perignathic ridges. An excellent example is seen in *Tripneustes*, fig. 6, where the bulk of the ridge consists of a pair of large plates which may or

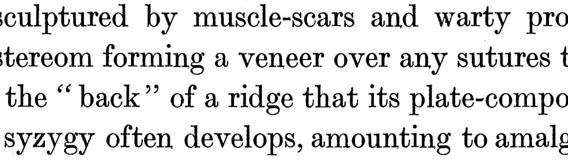

FIG. 6.—The ridge of *Tripneustes esculentus* (LESKE) seen from behind. Successive interambulacral plates, though crushed and resorbed, are invading the ridge near the median line.

may not have been originally simple, while the contiguous plates, which form the foundation of the ridge, are in various stages of resorption. This condition resembles that seen in the ambital parts of the interambulacra of *Linopneustes* and *Lovenia* (HAWKINS, 1916), where the enlarged plates of the adoral surface act as buffers against which the others are telescoped.

A very curious condition occurs in the ridge of *Eucidaris tribuloides* (LAMARCK), fig. 7. The back of the ridge in this species is deeply hollowed at the foundation, and a zigzag interradial suture is plainly visible. But the ridge itself is built of a succession of ingrowths from two or three of the coronal plates plastered against one another. The

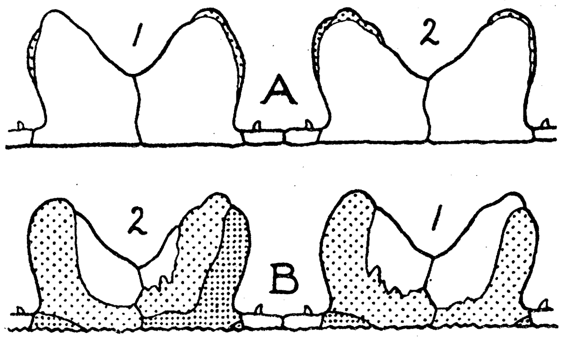

FIG. 7.—The ridge of *Eucidaris tribuloides* (LAMARCK). A, front view ; B, back view. Successive inter-ambulacral plates are plastered on to the back of the main ridge-plates.

hindmost plate involved (second or third as the case may be) grows up as a kind of frame along the back of the adambulacral margin of the ridge. Hence, while the median part of the ridge is only one plate thick, the marginal part may be two or three layers thick. The effect of this can be readily seen by varying grades of translucency if the ridge is moistened and held up to a light. The mechanical advantage of this arrangement is obvious ; but I have not found anything like it in any non-Cidaroid types. LOVÉN (1892) found the same feature in *Cidaris cidaris* (LINN.) and explained it as a precaution against peristomial resorption.

Although there are great differences in the proportionate development of the ridges in the Centrechinoida, there does not seem to be much important variation in their construction. In some forms (*e.g.*, *Centrechinus*, fig. 8) the high capped ridge is made

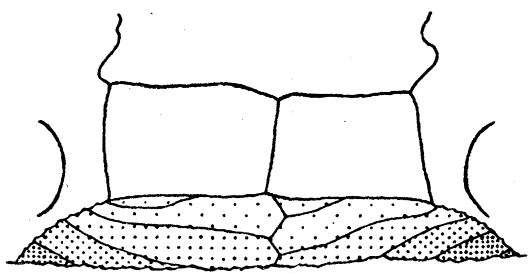

FIG. 8.—The ridge of *Centrechinus setosus* (LESKE) seen from behind. The ridge-plates have obstructed the advance of the coronal plates, which are crushed and resorbed against them.

wholly of the two proximal interambulacrals, while in others (*e.g.*, *Tripneustes*, fig. 6) two or three plates in each column are invaginated to form the ridge. In either form, examination of the back of the ridge shows that the obstruction caused by enlargement and specialization of the main ridge-plates has induced crushing and resorption of the others. This is especially marked in *Centrechinus*. There the ridge-plates are heavily capped, so that their original height is increased sixfold, fig. 4. The ridges of *Echinometra*, fig. 5, and *Heterocentrotus* are similarly exaggerated by capping.

(2) *The ambulacral processes*

These ossicles are attached to the proximal parts of the ambulacra (actually in the line of the pore-fields) in all of the Centrechinoida and Holectypoida. They are unknown in Palæozoic forms, certainly absent in the Cidaroida, and may occasionally migrate on to the proximal interambulacrals in some Clypeastroida. Their main purpose is to give attachment for the retractor muscles of the lantern. They may rise almost vertically from the peristomial margin, or may be inclined away from it at varying angles.

The distal ends of the processes are usually expanded so as to give broader muscle-attachment, and this expansion is most strongly developed on the perradial side. When the expanded crests meet, they form an arch over the ambulacrum, and thus produce a continuous girdle. Evidently the presence of the arch is a sign of specialization ; it appears late in the ontogeny of the forms that acquire it, and they are only a relatively small series of the Centrechinoida.

Capping is developed on the processes of many diverse types, and may occur on connected or disconnected processes. In the former case the caps form a crest rising above the normal crown of the arch (*e.g.*, *Centrechinus*, fig. 4) ; in the latter they may, on occasion, transform a discontinuous girdle into a continuous one (*e.g.*, *Echinometra*, fig. 5). It is, I believe, important to distinguish between continuity achieved by the processes proper and that induced by the expansion of their caps. For instance, *Colobocentrotus*, which is in most respects an extreme form of the Echinometridæ, appears utterly unlike its nearest relatives in the structure of its girdle. It is, at first sight, difficult to reconcile the towering battlemented arches of *Echinometra* or *Heterocentrotus* and the feeble, sometimes discontinuous, processes of *Colobocentrotus* with any conception of their near affinity. But, stripped of the secondary capping, the girdle of *Echinometra* is reduced to a condition virtually identical with that of *Colobocentrotus* (see fig. 5). It is still surprising that two such closely allied forms should display extremes of difference in respect of capping ; but the difference is in a secondary growth, and not so fundamental as might be supposed.

IV. The Lantern and Girdle in Some Fossil Centrechinoida

In this section, as much of the buccal apparatus as is available in thirteen Mesozoic Centrechinoid genera is described, with a view to placing these genera in their true position in modern classification. In four of them only is it possible to give a tolerably complete account of the lantern ; but these four genera are fortunately characteristic members of well-marked families, so that a much wider range of related forms can be classified with some confidence. With one exception, the genera are considered in stratigraphical order, to avoid premature assumption of their affinities.

(1) Diademopsis bowerbanki (WRIGHT). *Lower Lias* (fig. 9),
WRIGHT, 1857, p. 145 ; pl. ix, fig. 2 (*Hemipedina*).*

Material.—Specimens of this species, one of the earliest British Euechinoids, occur in some abundance in the Lower Lias of Dorsetshire, usually in clusters of tests with the radioles attached. They must have been smothered by a sudden influx of silty clay, and securely buried before decay could dissipate their detachable parts. Unfortunately the tests received scarcely any infilling, and they have collapsed during conversion of their matrix into shale. Only the solidity of their jaws has prevented them from being completely flattened.

In all of the specimens that I have opened the perignathic girdle has been smashed by the maxillæ. BATHER (1909, p. 116) found that the processes were " very slightly developed " ; and the broken stumps that I have found are consistent with that statement.

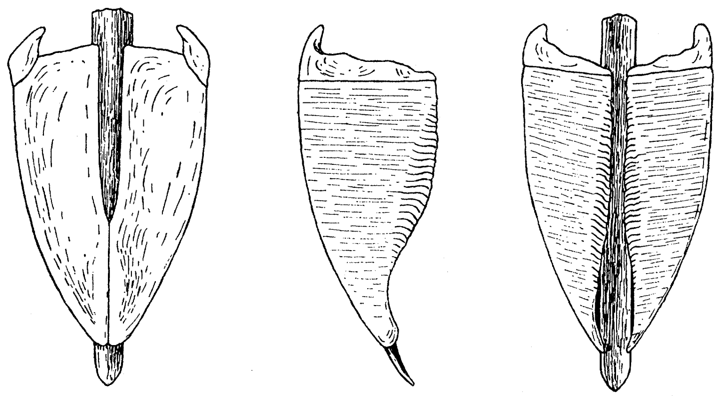

FIG. 9.—*Diademopsis bowerbanki* (FORBES). E. 678. Outer, side, and inner views of a pyramid. (The maxillæ are slightly dislocated in the original.) Considerably enlarged.

My impression is that the ridges must have been proportionately feeble, if indeed they were developed at all ; but the evidence is unconvincing.

It has proved possible to extract two almost undamaged pyramids (complete with epiphyses and teeth) from one specimen (No. E. 678).† I have not succeeded in separating rotulæ or compasses (although I have seen traces of both), for in all cases they were welded to, and mixed with, the plates and radioles of the adapical part of the corona.

Description.—The maxillæ are 5·4 mm in total length. They are symphysially united for less than half their length, the foramen being almost 3·0 mm deep. Actually the foramen is a narrow slit, almost parallel-sided and not more than 0·5 mm broad. The whole pyramid is about 3·7 mm across at the top. The maxillæ make a considerable angle with one another at the symphysis, so that the pyramid appears strongly carinate in its middle part. The proximal tips of the maxillæ are strongly incurved.

The outer surface of each maxilla is very deeply hollowed ; its excavation is made

* References given under each species indicate adequate figures of the test, not necessarily the first introduction of the name.

† Registered number in the Geological Museum, University of Reading.

the more conspicuous by the median carina and a flange-like splay of the interpyramidal edge. The interpyramidal surface is 2·75 mm wide at the epiphysial margin, and maintains most of this width until the incurved part is reached, when it is sharply cut away to leave a passage for the tooth. The transverse striations of interpyramidal muscle-attachment are very delicate over most of the surface; but they become suddenly coarse and deep in the middle part bordering the inner (free) edge.

The epiphyses are narrow; their attachments to the maxillæ are 2·75 mm long and quite straight, and their free upper surfaces are almost parallel to this suture except at the outer ends, which rise into prominent spines slightly curving towards each other over the tops of the pyramids.

The teeth are remarkably wide, and profoundly grooved. As preserved they taper abruptly to a blunt point.

Notes.—Diademopsis is clearly an Aulodont; but its jaws show some peculiarities. The great length of the foramen (exceeding that of the symphysis) can be matched only in advanced Camarodont lanterns, while its extreme narrowness compares with the proportions of the very short foramen of the Cidaroida. The square top of the pyramid, cornered by thorn-like projections of the epiphyses, is exceptional; it bears a slight resemblance to the condition in *Cidaris*, and is probably the result of the narrowness of the foramen in both cases. The great width of the teeth can be matched in the Perischoechinoida and in the Echinothuriidæ. The lantern therefore shows a blend of Palæozoic, Cidaroid, Aulodont, and post-Aulodont characters that conforms very well to its occurrence at an horizon when most of the critical modifications of Euechinoid structure were taking place.

It is interesting to compare the lantern of *Diademopsis* with that of its virtual contemporary *Eodiadema* as described by MORTENSEN (1933, p. 437). That form is also Aulodont, and its tooth is fairly broad. But the depth of the foramen in *Eodiadema* is rather less than half the total height of the pyramid, and its open end is widely splayed. Indeed, the pyramid of *Eodiadema* invites close comparison with that of the Perischœchinoida, and for that reason is quite unlike that of the Cidaroida. Apparently *Diademopsis* and *Eodiadema* represent independent lines of development, in spite of the baffling similarity of their tests.

(2) Pedina salteri (DE LORIOL). *Bajocian* (fig. 10).

WRIGHT, 1858, p. 173; pl. 13, fig. 1 (*Pedina rotata*).

Material.—Only the perignathic girdle has been found in the two specimens of this species that have been excavated. The more complete of these (E.12) is the basis of the following description. The test is 19·8 mm in diameter, and 11·0 mm in height.

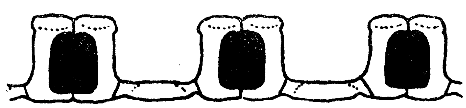

FIG. 10.—Plan of girdle of *Pedina salteri*. DE LORIOL. E. 12.

Description.—The processes are slightly set back from the peristomial margin, but they are almost upright. They are narrow, and very thin. The paired shafts are almost parallel for most of their height, and expand distally to meet in a substantial arch, the complete " auricle " being almost square. The outer (peristomial) faces of the crests show a slight thickening, which causes the arch to appear as if leaning towards the lantern. The height of the crest of the arch is 2·0 mm from the peristome-margin, or rather less than one-fifth of the height of the test.

The ridges are very feeble, scarcely projecting inwards above the level of the internal coronal surface. They are, by contrast with the processes, decidedly oblique, splaying outwards on both sides of a small interradial thickening, and returning to the vertical where they join the processes.

Notes.—For what the comparison is worth, it may be noted that the girdle of *Pedina* shows some resemblance to those of *Stomechinus*, *Pseudodiadema*, and *Acrosalenia* described below, and differs considerably from those of the other genera here described. As far as I am aware, *Pedina* shows the chronologically oldest example yet known of a continuous girdle.

(3) Stomechinus

It is unfortunate that there is not yet available any evidence as to the lantern of this genus, probably owing to the large size of the peristome. Mortensen (1933, p. 439) refers to the importance of the type, and for the present the perignathic girdle is all that can be invoked as a contribution to the problem of its place in classification. I have succeeded in excavating the girdle in two species, representative of early and late members of the genus.

(i) Stomechinus bigranularis (Lamarck). *Bathonian.*

Wright, 1858. Pal. Soc., p. 210 ; pl. 14, fig. 3.

The specimen (E.14) of this well-known species from the " Upper Inferior Oolite " that I have prepared shows the girdle to be essentially similar to that of the next species (wherein it has been possible to display it much more completely) ; and I refer to it here merely to illustrate the constancy of girdle-structure within the limits of a genus when traced through many stratigraphical stages.

(ii) Stomechinus robinaldinus (Cotteau). *Corallian* (fig. 29, Plate 68 ; fig. 11).

Cotteau, 1853, p. 271 ; pl. 22 (*Echinus*).

Material.—A specimen of this species (E.196) from Saul (Meurthe et Moselle) invited excavation on account of the softness of its infilling ; and, although the peristomial region was somewhat broken, a sufficient expanse of the girdle was found to be intact. The approximate dimensions of the test are—diameter 45 mm, height 29 mm.

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Description.—The processes rise directly from the peristomial margin, and are, in fact, based on promontories of the ambulacra which project into the peristomial circle beyond its average circumference. The shafts are stout at their roots, and almost carinate along the sides of the arch. They are very slightly splayed outwards, but almost vertical. Distally they become very thin, but remain broad, and at the free edge they expand radially to meet in an arch. The top rim of the arch is feebly thickened, but I have not been able to decide whether this is a " cap " or merely an eave. The top of an arch is 5·5 mm high, a little more than one-fifth of the height of the test.

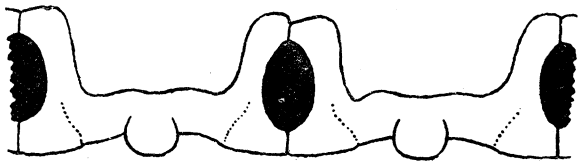

FIG. 11.—Plan of girdle of *Stomechinus robinaldinus* (COTTEAU). E. 196.

The ridges rise to almost exactly half the height of the processes, and their character is modified by the deep and approximated indentations of the branchial incisions. They maintain a fairly constant height, but show a very slight maximum behind each branchial incision, where also they are inclined away from the peristome at a considerable angle. Their most notable feature is a median knob that projects into the peristome, and is so well differentiated from the rest of the ridge that it seems as if it were suturally separate. This I believe to be a deceptive appearance, due to the sharpness of the re-entrant angle between the " branchial " and " interbranchial " portions. The knob seems to be at least as prominent in *S. bigranularis*. Its exaggerated development is partly due to the depth and proximity of the branchial incisions ; but when this is discounted it still remains proportionately larger than its homologue in other types. Above it the ridge rises vertically to a sharp edge.

Notes.—This well-developed girdle corresponds in most respects with those of *Pedina*, *Acrosalenia*, and *Pseudodiadema*, and is especially like that of the last named.

(4) Acrosalenia pustulata (FORBES). *Callovian* (figs. 12–13).

WRIGHT, 1858, p. 242 ; pl. 16, fig. 2.

Material.—This species occurs in the Cornbrash, and may sometimes be found in clusters matted together with the radioles still in place. Under those circumstances the lanterns are almost always present ; and, although the matrix is usually very hard, it is not difficult to separate the light-coloured ossicles from the dark infilling. It is a strange coincidence that in most of those specimens that I have dissected (to the number of eight) where the lantern was visibly projecting through the peristome, the teeth were missing, suggesting that their attachment to the maxillæ was weak. Fortunately, there is one specimen (E. 101) in which the lantern had split and fallen backwards into the test-cavity, and in this the teeth are in position. The presence of the jaws in this specimen was not suspected until they had been partly scraped away during exposure of the perignathic girdle; but the series of transverse sections unwittingly produced could not have been better devised for display of the structures.

For the purpose of this description four specimens were used. One of these (E. 103) is a complete lantern extracted bodily from its test. A second (E. 252) shows a more or less disjointed series of lantern ossicles, mixed up with numerous peristomial plates, lying in the cavity of the test: MORTENSEN (1933, p. 433) has already recorded the fact that this specimen proves the Stirodont nature of the lantern. The third (E. 251) affords evidence of the nature of the rotula, and shows the interpyramidal faces of the maxillæ very well. The fourth (E. 101) has been referred to above.

Description.—The pyramids, fig. 12A, are short and relatively wide; in E. 103 the full height of the pyramid is 7·3 mm, and its width at the epiphysis is 4·9 mm. The open foramen is 3·5 mm deep (practically equal to the symphysis) and very widely splayed distally. The epiphyses appear as small corner-pieces rising into short spines when seen from the outside—there is very little tendency to convergence across the foramen. The interpyramidal face, fig. 12C, is very flat and rather coarsely striated;

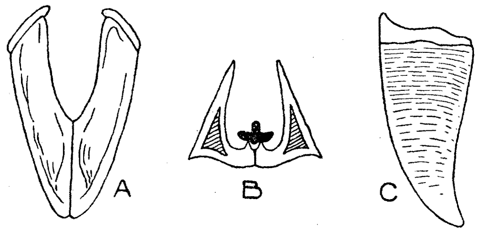

FIG. 12.—*Acrosalenia pustulata* FORBES. A, outer view of pyramid, E. 103. B, transverse section, E. 101. C, side view, E. 251.

it is 4 mm wide at the epiphysial suture. A curious feature of the muscle-striations is their curvature with upward convexity. When seen in section at about the level of the base of the foramen, fig. 12B, the maxillæ appear to be hollow. Possibly this may be an imperfection of preservation, owing to disappearance of the delicate stereo-mesh that usually occurs in the interior of maxillæ; but there is no visible reason for doubting the original existence of the cavity. I have found comparable (but much smaller) cavities in the maxillæ of *Strongylocentrotus*. The feature, if a genuine one, takes on a special interest in view of the condition found in the maxillæ of *Hemicidaris* (*q.v.*).

The tooth is strongly keeled, and the spine-like sections of the sides of the dental slide show that groove to have been much narrower than the tooth itself. There is a small counter-keel on the outer surface of the tooth, and it is along the sides of this that the edges of the dental slide fit.

The perignathic girdle, fig. 13, is continuous, but very simply constructed. The processes rise almost vertically. They are relatively wide, but very thin, and turn

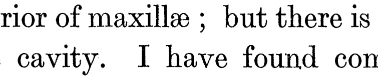

FIG. 13.—Plan of girdle of *Acrosalenia pustulata*. FORBES. E. 101.

towards one another to meet in a rounded arch without any diminution in width, enclosing an elliptical space. The crest of the arch is 2·7 mm high in E. 101, where the test has a height of 12 mm. The ridges are very feeble, even the usual median thickening being scarcely discernible.

Notes.—There can be no question as to the Stirodont character of the lantern of *Acrosalenia*, and the small development of the epiphyses indicates a lack of specialization.

(5) Pseudodiadema pseudodiadema (LAMARCK), *Corallian* (fig. 30, Plate 68; fig. 14).

WRIGHT, 1857, p. 127; pl. 8, fig. 1 (*P. hemisphaericum*).

Material.—The typically stirodont lantern of this species has recently been described by MORTENSEN (1933, p. 435). It is very similar to that of *Hemicidaris*, particularly in the curvature of the tops of the maxillæ and epiphyses.

I have been able to expose the complete perignathic girdle of a specimen from Malton (E. 197), where the soft oolitic infilling was not, as usual, recrystallized. The evidence given by this specimen has been confirmed in several others. The test is 45·5 mm in diameter; unfortunately its height was not recorded.

Description.—The girdle is continuous. The processes have substantial bases, but become fairly thin, and very narrow, when they rise above the level of the ridges. They tend to lean a little apart before turning almost horizontally to meet in a flat arch 3·8 mm high. As a result, the lumen of the "auricle" is pyriform with the

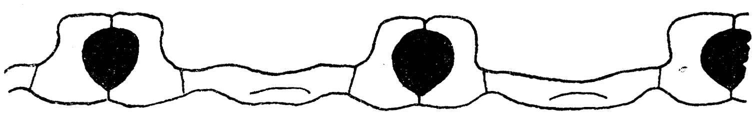

FIG. 14.—Plan of girdle of *Pseudodiadema pseudodiadema*. (LAMARCK.) E. 197.

pointed end downwards. The five arches meet in sutures of varying strength, but such irregularity is common in uncapped girdles. The ridges are low, and deeply entrenched by the branchial incisions. Seen from the peristome they are inconspicuous, but seen from behind they rise as rather blunt rims definitely above the coronal level. There is no appreciable median prominence.

Notes.—The girdles of the four types just described (*Pedina*, *Stomechinus*, *Acrosalenia*, and *Pseudodiadema*) show certain points of resemblance that may be significant. They are all continuous and apparently uncapped; and their processes rise very nearly vertically from their junction with the ridges, so that the span of the arches is virtually that of their foundations. This makes the lumen of the "auricles" rectangular, elliptical, or invertedly pyriform. This is quite different from the condition found in the continuous girdles described later. Although it would be rash to claim any very close affinity for the four genera on a single character of such doubtful importance, it is perhaps permissible to assume that they all belong to the same suborder. If such a contention is justified, *Pedina* and *Stomechinus* are probably Stirodonta, since *Acrosalenia* and *Pseudodiadema* certainly belong to that group.

(6) Phymopedina marchamensis (WRIGHT). *Corallian* (fig. 15).

WRIGHT, 1858, p. 161; pl. 9, fig. 1 (*Hemipedina*).

Material.—I was fortunate in obtaining a broken specimen of this very rare species from the Lower Calcareous Grit of the type-locality (E. 198); and in view of its imperfection I was emboldened to excavate its interior. The coarse, compact gritty infilling was not a promising medium from which to disengage delicate and friable structures; and I am not prepared to state that the girdle as I have exposed it is necessarily complete. I am fairly certain, however, that the girdle was undamaged in the process of extraction; but it may have been broken before fossilization. Naturally no "control" dissections are available.

Description.—The girdle is widely discontinuous. The processes rise abruptly, almost vertically, and converge very slightly at their extremities. They are lath-like (scarcely thicker than stiff paper) and slender. The tallest of the three exposed rises to a height of 5·8 mm. The test must have been about 48 mm in diameter, but its height cannot be determined. The ridge is prominent, although it is less than half as high as the processes. It rises to a knife-edge (comparable with the margins of the processes); but no details of sculpture on its surface can be seen.

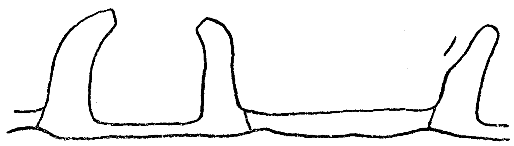

FIG. 15.—Plan of girdle of *Phymopedina marchamensis.* (WRIGHT.) E. 198.

Notes.—*Phymopedina* is usually considered to be a late and specialized descendant of the *Hemipedina* series. If this be so, specialization seems not to have affected the girdle very much; and the indications would point to an even greater simplicity of the girdle in the Lower Jurassic Hemipedinas. The nature of the teeth of *Hemipedina* is not yet known. Analogy with *Diademopsis* would suggest that they were Aulodont, in view of the close similarity between the two genera in coronal character. *Phymopedina* gives no direct clue to the solution of this problem, but the nature of its girdle may be significant. In many respects the proportions of the processes in *Phymopedina* resemble those of the Pygasteridæ. In Aalenian times, the resemblance between the tests of small species of *Hemipedina* and immature specimens of *Plesiechinus* (the forerunner of *Pygaster*) was so close that the young of *P. ornatus* were described by Wright as "*Hemipedina bonei*" (vide BATHER, 1909, p. 106). Hence the similarity of the girdles of the two groups is consistent with their evident affinity.

But the argument cannot be left there; for it must be assumed that the teeth were keeled in the Pygasteridæ, since they are known to be keeled in all of the Holectypoida in which they have been seen. This would imply that *Hemipedina* was a Stirodont, and so quite distinct from *Diademopsis*. The recent *Coenopedina* appears to be a Stirodont; but I am not satisfied as to its relationship with the true Jurassic *Hemipedina*.

It is greatly to be hoped that direct evidence of the structure of the lantern of a true *Hemipedina* may be discovered.

(7) Hemicidaris intermedia (Fleming). *Corallian* (figs. 16–17).

Forbes, 1850, Dec. iii, pl. 4.

Material.—This familiar species, which is doubtfully distinct from the genotype *H. crenularis* (Lamarck), was at one time found in great abundance and complete preservation at Calne, in a quarry which is now the playground of St. Mary's School. Slabs of marly oolite covered with tests and radioles were obtained there, and are now preserved in most museums. My experience has shown that the lantern is still within all of the tests that occurred under those conditions, so that it is strange that its nature has been unknown until recently. It is true that a good deal of crystalline calcite occupies the test-cavities (which seem to have been but incompletely filled by silt), but there is always a fair proportion of the infilling that can be removed with water and a brush. Mortensen (1933, p. 433) has already referred to my best specimen of the lantern (E. 193), and has noted that it is typically Stirodont in construction. This specimen was found after the test had been bisected with a saw, and was itself cut in half almost at the level of the base of the foramen. Both halves of the lantern have been cleaned, and the saw-cut is an advantage rather than otherwise. The top of the lantern was, as is usual, much involved in crystalline calcite (probably owing to the impermeability of the membranes to silt), so that the rotulæ and compasses were not clearly extractable, although it was possible to preserve and expose the curved plume of a tooth.

Description.—The pyramid, fig. 16, A, may be shortly described as being very like

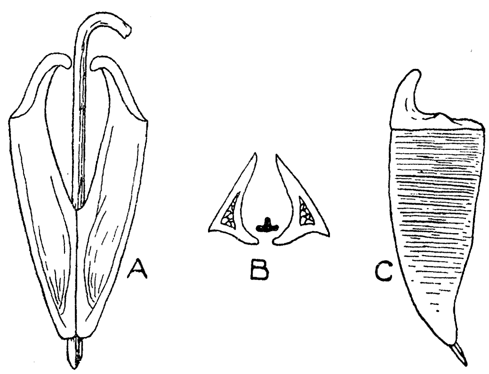

Fig. 16.—*Hemicidaris intermedia* (Fleming). E. 193. A, outer view of pyramid. B, transverse section. C, side view.

that of the recent *Arbacia,* but proportionately narrower. The length of the pyramid is about 18·0 mm, the depth of the foramen about 10·0 mm, and the greatest width 7·4 mm. The epiphyses are sigmoid when viewed from without, and rise as curved epaulettes to a height of 5·0 mm above their bases. They are narrow, and sufficiently incurved at the top to touch the tooth on either side. The upper parts of the maxillæ follow the epiphyses for most of their height, ending in points where the incurved tips of the epiphyses transgress them.

The interpyramidal surface, fig. 16, C, is 5·3 mm wide at the epiphysial suture, and maintains this width with scarcely any reduction for more than half its length. The striations are very fine and directly transverse.

The maxillæ are thin, as seen in section just above the base of the foramen, fig. 16, B, and they include a cavernous space that is crossed by an open network of stereom-strands. In *Acrosalenia* (p. 630) this core of the maxilla appears to be actually empty; but it is possible that a similar mesh may once have occupied the cavity in that specimen also.

The tooth is very narrow, and strongly keeled. The plume (growing end) is disposed exactly as in modern types.

The rotula was massive and almost square in transverse section, but I have not been able to expose its surface. Such traces of the compasses as I have seen did not show any notable features.

The perignathic girdle, fig. 17, is extraordinarily feeble. In view of the huge size of the peristome, and the robust development of the lantern, it is strange that the greatest

FIG. 17.—Plan of girdle of *Hemicidaris intermedia* (FLEMING). E. 132.

height of the girdle should be scarcely more than a tenth part of that of the test. In a specimen that is about 30 mm high, the height of the tallest process is only 3·5 mm. The processes are stout, and they incline towards one another across the ambulacra from their roots upwards. Even so, they very rarely meet, so that the girdle is usually discontinuous. The ridges, which are indistinguishable from the edge of the test behind the branchial incisions, expand interradially into a low parapet with a slight median protuberance.

Notes.—Although the processes of *Gymnocidaris* are even lower in proportion, and the ridges of *Acrosalenia* are practically negligible, the ridges and processes of those two genera are respectively well developed; so that the girdle of *Hemicidaris* proves to be, on the average, the feeblest that I have seen in any fossil Centrechinoid.

(8) Gymnocidaris pustulosa (AGASSIZ). *Bathonian* (fig. 18).

WRIGHT, 1857, p. 73; pl. 3, fig. 1 (*Hemicidaris*).

Description.—It is only to be expected that the girdle of this genus should resemble that of *Hemicidaris*, for the two types are very closely allied. But although the resemblance is unmistakable, the differences are manifest. In the only specimen that I have been able to dissect, the girdle is continuous, although the contact between the processes may be very slight. Except for their meeting, the processes are essentially like those of *Hemicidaris*; they seem to be even lower in proportion (but the true height of the test cannot be determined in my specimen). The ridges are much more strongly developed than in *Hemicidaris*. They are low behind the branchial incisions (near their meeting with the processes); but they rise sharply to form a parapet that is almost as high as the tops of the "auricular" arches. A pronounced knob occurs near the top of the front surface of the ridge; presumably this was for attachment of the radial compass-muscle.

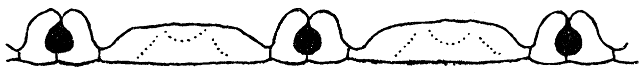

FIG. 18.—Plan of girdle of *Gymnocidaris pustulosa* (AGASSIZ). E. 301.

The whole girdle is very inconspicuous. The diameter of the test is about 34 mm, and the greatest height reached by a process is 2·8 mm, while the ridges are 2·3 mm high. As in *Hemicidaris*, the peristome is very wide.

Notes.—Although the *Hemicidaridæ* are regarded as closely akin to the modern *Arbaciidæ*, their perignathic girdles do not appear (at first sight) to be similar. The stiffly upright processes of *Arbacia* or *Tetrapygus* contrast strongly with the convergently curved processes of *Gymnocidaris* and *Hemicidaris*. When the processes meet in the Arbaciidæ, they do so by virtue of an extra development of the transverse rims at their tips; while those of the Hemicidaridæ are so disposed that they are bound to meet if they are long enough. It is, however, interesting to find that in both families an exceptionally wide peristome is associated with a very feeble girdle.

The chronological sequence of the types is significant. In respect of the girdle-character, the Bathonian *Gymnocidaris* (with a continuous girdle) may be assumed to have led, by degeneration, to the Corallian *Hemicidaris* (where continuity is very exceptional and incomplete), and thence to the Arbaciidæ with sub-parallel upright processes whose meeting (when it occurs) is achieved by obviously secondary growth.

(9) Hyposalenia wrighti, DESOR, *Aptian* (fig. 19).

WRIGHT, 1871, p. 150; pl. 30, figs. 1–2 (*Peltastes*).

Material.—A fully-grown specimen of this common species from Faringdon (E. 55) reveals the surprising fact that the girdle of *Hyposalenia* is quite continuous. The girdle of recent members of the Saleniidæ is definitely discontinuous; perhaps this is another example of degeneracy comparable with that just indicated for the Arbaciidæ. The evidence of E. 55 has been confirmed in very many specimens of varying size, and even in the smallest the continuity of the girdle was found to be complete.

Description.—The processes are very broad, and they lean against one another, meeting in a long suture. The top of the arch is widened by lateral expansions of the

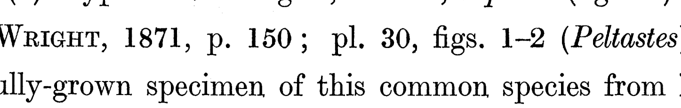

FIG. 19.—Plan of girdle of *Hyposalenia wrighti* (DESOR). E. 55.

processes which begin to spread at about the level of the top of the lumen. Owing to the breadth of the processes the lumen is narrow ; it may be elliptical or ovoid, but it is always small. The ridges are scarcely recognizable, but a slight interradial knob occurs on the peristomial margin. The specimen figured is 9·4 mm in height, and the top of the process is 1·7 mm from its base. The girdle is thus rather less than one-fifth of the height of the test-cavity, but it is a robust and prominent feature.

Notes.—I have found several keeled teeth, and other lantern fragments, in washings of the Faringdon Greensand, and many of these may have belonged to *Hyposalenia*. Since species of *Tetragramma* also occur in the deposit, it is not possible to be certain on this point, but it may be assumed that *Hyposalenia*, like *Salenia*, was one of the Stirodonta.

In this connexion, it is interesting to find that the girdle of the reputed "*Salenia*" from the Faringdon Greensand is exactly like that of *H. wrighti*. This fact seems to support the suggestion that I have made previously (1923, p. 211) that the rare specimens with saleniform periprocts that are associated with the abundant Hyposalenias in this deposit may be variants of that species, and not generically distinct. Certainly, if the disconnected girdle of such a recent species as *Salenia pattersoni* A. Ag., represents the typical condition in the genus *Salenia*, the forms from Faringdon cannot belong to that genus in spite of the radial displacement of their periprocts.

(10) Tetragramma brongniarti (Agassiz). *Cenomanian* (fig. 31, Plate 68; fig. 20).

Wright, 1868, p. 111; pl. 21*a*, fig. 2 (*Pseudodiadema*).

Description.—The girdle of this species (and that of its near ally *T. variolaris* (Brongniart) is much more like that of a modern *Echinus* than any Mesozoic type that I have seen. It is continuous, but the contact between a pair of processes is so slight that it is difficult to extract an arch unbroken. The processes are set back somewhat from the margin of the peristome, but they rise almost vertically. They are substantial at the base, but they become exceedingly thin when free of the ridges. They are inclined towards one another, and expand distally. Their top rim is very

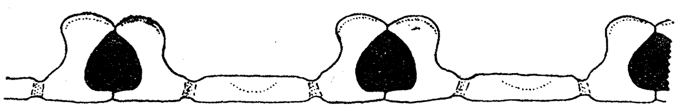

Fig. 20.—Plan of girdle of *Tetragramma brongniarti* (Agassiz). E. 135.

slightly thickened ; it overhangs as a feeble eave towards the peristome. The lumen of the arch is acutely pyriform, sometimes almost triangular. In a specimen whose full height is 16·5 mm (diameter 44 mm) the processes are 4·5 mm high. In view of the invagination of the apical surface, this implies that the girdle rises through more than a quarter of the height of the cavity.

The ridges are well developed ; they appear as if cut off from the processes by deep grooves, which are the inward extension of the branchial incisions. The parts of the ridges between these grooves slope away from the peristome margin so that their free edges can coalesce with the sides of the set-back processes. The outer face of a ridge shows very little sculpture apart from the branchial grooves.

Notes.—*Tetragramma* was originally involved in the medley of types called "*Pseudodiadema*," and its girdle, though rather differently proportioned, shows nothing inconsistent with its association with *Pseudodiadema sens. str*. By a remarkable coincidence, the girdle of *T. brongniarti* is almost exactly an *inverted* copy of that of *P. pseudodiadema* (*cf*. figs. 20 and 14) with a slight exaggeration of the depth of the branchial grooves.

(11) Allomma normanniæ (Cotteau). *Cenomanian* (fig. 32, Plate 68; fig. 21).
Cotteau, 1865, p. 468; pl. 612 (*Pseudodiadema*).

Material.—A broken example of this very rare monotypic genus from the Lower Chalk of Folkestone (E. 326) enabled me to excavate the girdle. Although this species was originally classed with "*Pseudodiadema*," its coronal characters justified Pomel's diagnosis of a separate genus for its reception; the girdle now described emphatically endorses his action, for it is unique in many ways.

Description.—Allomma has a relatively narrow peristome, and the girdle forms a continuous high wall inside it. The highest point of the girdle reaches up to 7·5 mm (the test being 24 mm high), nearly one-third of the height of the test-cavity; while the lowest part of a ridge is no less than 5·3 mm high, being proportionately much higher than the arches of most Echinoids.

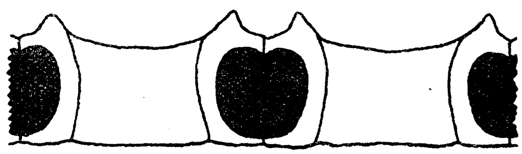

Fig. 21.—Plan of girdle of *Allomma normanniæ* (Cotteau). E. 326.

The processes are narrow and slightly arcuate, rising to prominent spines and meeting in a cross-bar constructed of projections springing from a point below the spines. These bars are inclined slightly downwards, so that the lumen of the arch is more or less cordiform. This peculiar quality of the processes is almost insignificant when the remarkable development of the ridges is considered. These are notably smooth, and their free edges are approximately at the level of the meeting of the arches.

Notes.—The only girdle with which it seems possible to compare this enormous erection is that of *Salmacis*, but the high collar of that genus (associated, as in *Allomma*, with a very small peristome) is proportionately inferior. Until the nature of the lantern is known, discussion of the affinities of *Allomma* is useless; it remains a strangely isolated type. It would be particularly interesting to discover the girdle of such a form as *Codiopsis* or *Cottaldia*; their small peristomes and some of their coronal features suggest that some internal correspondence might be found.

(12) Gauthieria spatulifera (FORBES). *Lower Senonian* (fig. 22).
WRIGHT, 1870–1871, p. 141 ; pl. 28 (*Cyphosoma*).

Material.—This small species (once classed with *Phymosomal*) is fairly common in the zone of *Holaster planus*. Its infilling is usually concretionary, but abundant material has made it possible to ascertain the structure of the girdle.

Description.—The girdle is as uncompromisingly discontinuous as any that I have seen. The processes rise vertically from a base set back a little from the margin of the peristome, and they are straight and practically parallel throughout their height. A slight constriction near the top of each process seems to mark the oncoming of a

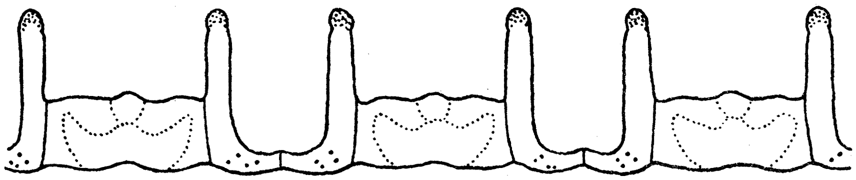

FIG. 22.—Plan of girdle of *Gauthieria spatulifera* (FORBES). E. 661. The stippled parts are believed to be secondary caps.

small secondary "cap." In the specimen figured (E. 661) the test is 10·5 mm high, and the processes rise to 2·8 mm, a little more than a quarter of the height of the cavity. The ridges are a trifle less than half as high as the processes ; the two elements meet abruptly, almost at right angles. They are deeply sculptured, with a prominent knob near the middle of the free edge, and a strong thickening of curious shape extending to, and reinforcing, the margin of the peristome.

Notes.—This girdle is essentially like that of *Phymosoma*, although it appears very different at first sight. The most important resemblance is in the capping ; *Gauthieria* is the earliest example of this feature yet known. But the straightness of the processes in *Gauthieria*, contrasted with the curvature of those of *Phymosoma*, would be a sufficient criterion for their generic separation even if other characters were not available.

(13) Phymosoma koenigi (MANTELL). *Upper Senonian* (fig. 33, Plate 68 ; figs. 23, 24).
WRIGHT, 1870, p. 131 ; pl. 24 (*Cyphosoma*).

Material.—There are three specimens available for the description of the lantern of this familiar species ; in one of them (E. 269) the ossicles have been extracted so that they can be studied almost as fully as those of a recent form. More than twenty girdles have been exposed in specimens of varying size.

Description.—The pyramid (readjusted in fig. 23, A) is narrow and strongly carinate along the symphysis. The maxillæ (*i.e.*, the pyramids without tooth or epiphyses) have an all-over length of 11·5 mm in all of the three lanterns studied ; their greatest width (at the epiphysial suture) is 6·7 mm. The foramen is relatively shallow, extending for only 3 mm below the distal points of the maxillæ, which are 4 mm apart.

The outer surface of the pyramid is very evenly curved, figs. 23, B and D. Its most striking feature is the median keel, which expands into massive prominences at the proximal tip, giving reinforcement to the issuing tooth at a point where the symphysis has tapered away, fig. 23, D.

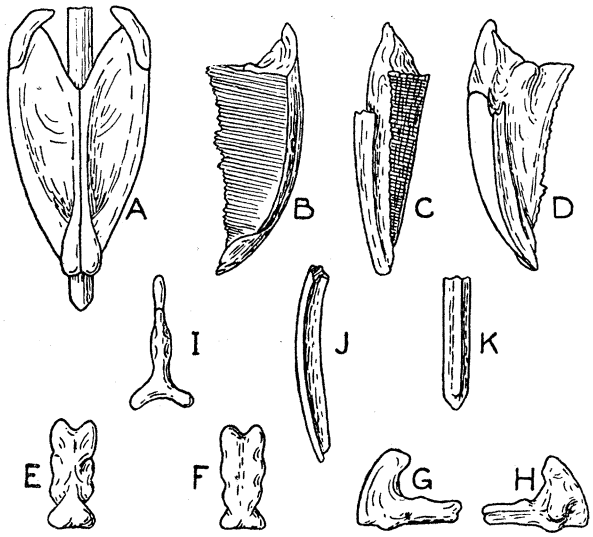

Fig. 23.—*Phymosoma koenigi* (Mantell). Parts of the lantern. A (E. 394), Outer view of pyramid (parts replaced). B–K (E. 269). B, Side view of pyramid. C, Œsophageal view. D, Inner view. E, F, Lower and upper views of rotulæ. G, H, Outer and inner views of epiphyses. I, Upper view of compass (the proximal ossicle replaced). J, K, Side and inner views of teeth.

The epiphyses, as seen from the outer surface of the pyramid, are like epaulettes, and their spinose distal points project a little above the tops of the maxillæ and are slightly incurved. They are, however, very far from meeting. The sutural surface between an epiphysis and its maxilla is deeply pitted.

The interpyramidal and other aspects of the maxillæ call for no special comment ; but it is interesting to have been able to preserve traces of the pectinate inner edge. Similarly, the other lantern-ossicles are of standard pattern, and their nature is sufficiently displayed in the figures. The very strong bifurcation of the compass is perhaps worth noting, and also the extreme shortness of its inner element.

The teeth, fig. 23, J and K, are gently curved and their points are rather blunt. The keel is very stout, and seems to be at its maximum strength about midway along the tooth. This may be due to incipient attrition towards the biting end ; the keel stops suddenly just where the tooth begins to taper to its point.

The perignathic girdle, fig. 24, is low, but fairly elaborate. The processes are

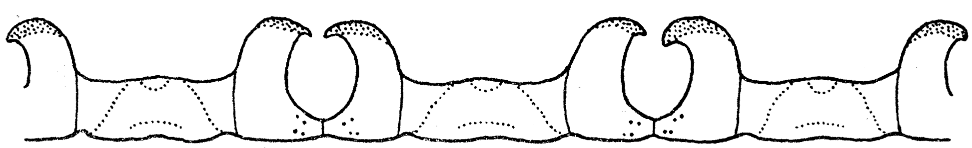

Fig. 24.—Plan of girdle of *Phymosoma koenigi* (Mantell). E. 653. The stippled parts are believed to be secondary caps.

inclined away from the peristome, and at their distal ends turn sharply towards one another without actually meeting. (In one specimen seen actual contact was made, but this is the only one out of about a hundred where it does not occur.) The strong eaves at the tops of the processes seem to be definite "caps." In a test with a height of 12·5 mm, the greatest length of a process is 2·0 mm; and since the processes are far from upright, their effective height is less than this small figure. The ridges are rather more than half as high as the processes; at their adradial sides they curve up to conform to the slope of the processes, thus appearing far less distinct than those of *Gauthieria*. The median part of each ridge is thickened, with a knob above and a bar below, while the lateral parts are thin and smooth.

Notes.—Apart from the exaggerated development of the median "tooth-buttresses" on the outer surfaces of the pyramids, there is nothing peculiar in the lantern of *Phymosoma*. It is a fully-developed, and absolutely typical, Stirodont lantern.

V. The Lantern and Girdle in some Fossil Holectypoida

A special interest attaches to the jaws and associated structures in this order, for two reasons. One series of the Holectypoida may be expected to show the earlier stages of transition from the relatively upright girdle of the Regular Echinoids to the recumbent one of the Clypeastroids; while another must witness to the gradual disuse and abandonment of biting organs by forms destined to become atelostomatous. While it is true that some edentulous Echinoids (including probably the Spatangoida) lost their buccal armature early in the Mesozoic era, others (the Cassiduloida) seem to have remained gnathostomatous until the approach of the Cainozoic era. However that may be, we can trace in some of the groups classed with the Holectypoida a slow degeneration of the buccal structures that may be assumed to show in a modified form the manner of its disappearance in less retarded lineages. Indeed, in *Echinonëus*, which is now generally regarded as a surviving member of the Holectypoida, it is possible in a sense to watch the process carried through in ontogeny, since the discovery by Agassiz (1909) of a vestigial lantern and girdle in young stages.

Duncan (1885) and Lovén (1888) and 1892) initiated the description of Holectypoid jaws and girdles. At various intervals since 1909 I have described the structures in several genera; but there yet remain serious lacunæ in our knowledge. In the following account only new material is discussed at length; it is gratifying to be able to describe the girdles of two genera (*Holectypus* and *Pyrina*) which were scarcely known previously; although it is a matter for regret that the true nature of the lantern is as yet known only in the Discoidiidæ.

(1) Plesiechinus ornatus (Buckman). *Aalenian* (fig. 25, D, and fig. 34, Plate 69).

Wright, 1858, p. 275; pl. 19, fig. 1 (*Pygaster semisulcatus*).

Excavation of several additional girdles since I published an account of that in specimen E. 924 (Hawkins, 1917, *a*) has served to confirm generally the previous description. There are, however, certain modifications to be made. In the restored figure given (*loc. cit.*, p. 344) of the girdle of E. 924, all of the processes are represented as divergent. More complete specimens (Nos. E. 349 and 923) show that the processes are quite as liable to be parallel or slightly convergent, and that all three conditions may occur (apparently fortuitously) in a single girdle.

The inclination of the processes, measured in relation to the average plane of the base of the test, is considerable, often reaching 45° ; but it is necessary to take into account the peristomial invagination. In relation to the plane of the base from which a process springs it is virtually perpendicular. This condition, which applies also in *Holectypus*, may perhaps have a bearing on the problem of the origin of the Clypeastroid lantern. Peristomial invagination is typical of almost all the Holectypoida except some of the Echinonëidæ ; so that, unless the processes of the girdle were inclined towards the peristome, a splaying effect would be inevitable. The only example of an attempt to counteract undue obliquity is found in *Pseudodiscoidea*. Hence a " flaring " of the lantern must have been developed which might readily lead to the recumbent state. Some Clypeastroida (*e.g.*, *Clypeaster*) have strong peristomial invagination, while others (*e.g.*, *Scutella*) have practically none ; but the attitude of the lantern in either type may be a result of invagination in an ancestral stage.

A second feature of the disposition of the processes that seems prophetic of the Clypeastroid plan is seen in their departure from concentric arrangement. Each process rises from the side of a branchial incision, so that its flat surface makes a sharp angle with the circumference of the peristome as a whole. This angle may be as much as 45°, when the alignment of the processes is as much radial as concentric. In *Clypeaster* the processes are radially aligned, so that the Pygasteridæ may be considered to represent a stage midway between the Clypeastroida and the Centrechinoida in this respect.

The third feature of the girdle of *Plesiechinus* that must be emphasized is the buttress which supports each process. The general nature of the buttress was shown in my earlier figure (1917, *a*, p. 344) ; but better preparations reveal that it is shorter and stouter than in the figure. LOVÉN (1888, pl. 2) gave a more accurate representation of it. In a specimen of a *Plesiechinus* that is probably specifically different from *P. ornatus* (apparently from some Bathonian deposit), the buttress is a massive block at the back of the process, and is so sharply truncated that it leaves scarcely any carina behind it (fig. 25 D). Elongated and carinate buttresses support the processes of *Pygaster* and *Holectypus*, but short blocky ones are characteristic of *Plesiechinus*.

Consideration of these three characters of the girdle of *Plesiechinus* makes it fairly certain that the lantern must have been definitely inclined (" flaring "). The retractor muscles will have been attached to the oblique sides of the processes, and they can only have maintained a direct course if the place of their attachment to the maxilla was well removed from the middle of the peristome. Further, the strong buttressing of the processes may imply that the lantern actually leaned against them in some positions, as it does permanently in the Clypeastroida.

(2) Pygaster cf. semisulcatus (Phillips). *Corallian* (fig. 25, A–C, and fig. 35, Plate 69).

Wright, 1858, p. 282 ; pl. 20, fig. 2 (*P. umbrella*).

Encouraged by the apparent softness of its infilling, I sacrificed a large specimen of a *Pygaster* from the Corallian of Headington (E. 372). The appearance proved illusory, but it was possible to expose most of the girdle. The species is a broad and flat one, perhaps more rightly called *P. dilatatus* than *P. semisulcatus*, but the two species are certainly congeneric.

The processes are slender laths disposed much like those of *Plesiechinus*, but yet more unevenly developed. Some pairs almost meet into an arch, although their situation back to back on the sides of the branchial incisions prevents actual contact. They are often considerably broader at the distal end than at the base.

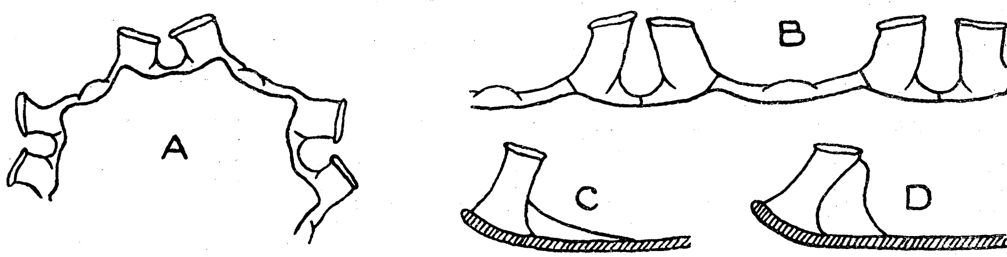

Fig. 25.—A–C, *Pygaster* cf. *semisulcatus* (Phillips). E. 372. A, The girdle seen from above ; B, Plan as seen from the peristome ; C, Side view of a process and its buttress.
D, *Plesiechinus* cf. *ornatus* (Buckman). E. 923. Side view of a process and its buttress.

The quality of the buttresses was wrongly inferred in my previous paper (1917, *a*, p. 349) ; they are steeply sloping carinæ that are definitely longer (not shorter) than those of *Plesiechinus* ; but they are much lower in *Pygaster*, for the processes are free for almost half their height. This condition is more like that found in *Holectypus*.

(3) Holectypus hemisphæricus (Agassiz). *Bathonian* (fig. 26, A–C, fig. 36, Plate 69).

Wright, 1858, p. 264 ; pl. 18, fig. 2.

After innumerable failures, I have at length succeeded in exposing the girdle in a well-grown specimen (E. 71) of this species from the Upper Inferior Oolite of Dorsetshire.

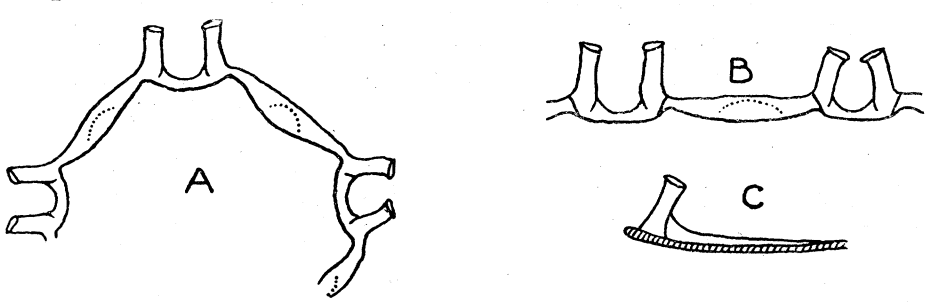

Fig. 26.—*Holectypus hemisphæricus* (Agassiz). E. 71. A, The girdle seen from above. B, Plan of girdle as seen from the peristome. C, Side view of a process and its buttress.

The test is scarcely thicker than paper, and the elements of the girdle are proportionately delicate.

The girdle is much like that of the Pygasteridæ, but it has a far more definite ridge. The processes are narrow, slender laths set on the sides of the branchial incisions, and buttressed by carinæ which pass from a point about half-way up the process to taper very gradually into the test-surface, disappearing about midway between the girdle and the ambitus. Presumably these carinæ, which are extended representatives of those of *Pygaster*, are the forerunners of the radiating septa of *Discoidea*, and it is an interesting speculation that the elaborate calcifications of the interior of a Clypeastroid may have originated as supports for perignathic processes that had been weakened by peristomial invagination in a remote ancestor.

The ridges, which have the usual knob in the middle, are low, sharp-edged parapets linking the processes, and showing more clearly from the back than from the peristome. Their shadows betray them in the photograph, fig. 36, Plate 69. In this point also *Holectypus* proves to be intermediate between *Pygaster* and *Discoidea*, for in the last-named genus the ridge is quite an important part of the girdle, albeit masked by the secondary thickening of the interambulacral plates behind it.

The lantern of *Holectypus* is known to exist, but I have been unable to obtain a specimen for dissection. From various figures that show it protruding from the peristome it may be judged to have been quite like that of *Pseudodiscoidea*.

(4) Pseudodiscoidea cylindrica (LAMARCK). *Cenomanian* (fig. 37, Plate 69 and figs. 38, 39, Plate 70). WRIGHT, 1874, p. 204; pl. 44 (*Discoidea*).

I have little to add to the accounts of the perignathic and lantern characters of this beautiful form that have been given by DUNCAN (1885) and DUNCAN and SLADEN (1889), LOVÉN (1888 and 1892) and myself (1909 and 1917, *b*). I have excavated about a dozen specimens, and have never failed to find some parts of the lantern within, together with perfectly preserved girdles. The small size of the peristome and periproct doubtless accounts for this fortunate condition. No trace of any ossicle that could have formed part of a compass has been seen in any of the specimens, so that it is possible that compasses were absent, as they are in the Clypeastroida; but I do not feel justified in denying their existence, for they are delicate structures and the infilling of the specimens is very hard.

The girdle has been adequately described already, but it is important to realize that its inclination is at least at 45° to the plane of the base of the test; indeed, in many specimens it seems to be almost as oblique to the peristomial margin, whose sharp invagination may thus make the angle between the ridges and the floor of the test extremely acute. The free ends of the processes often bend up from the oblique direction of their fixed parts; and, as the retractor muscles will have been attached there, the relative uprightness of the lantern will have been thus compensated.

The small knob-like thickening of the perradial part of the girdle (between the processes) is a curious feature; perhaps it represents the constantly developed excrescence in the same position in the Clypeastroida.

The increase in importance of the ridges in this type, while consistent with the sequence *Plesiechinus* → *Holectypus* → *Pseudodiscoidea*, is contrary to any tendency towards the Clypeastroida, where ridges are wholly absent. It may be assumed that *Pseudodiscoidea* represents a side-line from the main lineage.

(5) Discoidea dixoni (FORBES). *Turonian.*

WRIGHT, 1874, p. 212; pl. 43, figs. 2–3.

Excavation of this small and fragile form, usually filled with intensely hard concretionary chalk, is far from easy; but, fortunately, specimens are common. I have succeeded in preparing a specimen (E. 321) from the *R. cuvieri* zone, in which the internal structure of the test and two pyramids are clearly shown. The pyramids seem to be exactly like those of *P. cylindrica* (except for their minute size); but the girdle and adoral surface show some differences. The low ridges are much more like those of *Holectypus* than those of *Pseudodiscoidea*, and although the carinate buttresses reach to the ambitus, they do not rise high on the processes. There is scarcely any interambulacral thickening behind the ridges. Most of these characters are evidently connected with the smallness and delicacy of the test; but in their effect they show *Discoidea* to be a much more likely ancestor than *Pseudodiscoidea* for such Clypeastroida as *Echinocyamus*. Discovery of the internal structure of the Upper Cretaceous forms ascribed to *Fibularia* would be very interesting.

(6) Conulus albogalerus (LESKE). *Senonian* (figs. 40, 41, Plate 70).

WRIGHT, 1874, p. 221; pl. 50 (*Echinoconus conicus*).

The vexed question as to the presence or absence of a lantern in this species is still unsolved. The mysterious bunch of keeled teeth that I described in 1911 from a specimen of *C. subrotundus* is the only positive evidence; and the absence of any traces of maxillæ for their support tends to discount even that clue. The buccal plates of *C. albogalerus*, fig. 41, Plate 70, with their extraordinary capacity for fitting into the hollows of the perignathic ridges, still retain their mystery. The girdle of *C. subrotundus* is essentially like that of *C. albogalerus* (making allowance for the thinness of the test); but no sign of thickened buccal plates has been found in the earlier species. If negative evidence (based on careful emptying of several score of tests) is allowed to count, *C. albogalerus* had no calcified lantern when adult. The object that I figured (1917, *c*, pl. 28, fig. 4) as a possible fragment of a maxilla seems, on further examination, more likely to be a chip of a *Plicatula* or other Pelecypod. It is unfortunate that all of the really young specimens available for study are filled with flint. Discussion of the problem of *Conulus* is deferred to the end of the next section.

(7) Pyrina desmoulinsi (D'ARCHIAC). *Cenomanian* (fig. 42, Plate 70).

WRIGHT, 1875, p. 236; pl. 54, fig. 2.

The systematic confusion that surrounds the group represented by this species is profound. This bewilderment can only be resolved by investigation of the internal structure of all the species involved in the mélange that starts with *Pseudodesorella* and ends in *Echinonëus*. *P. desmoulinsi* is a *Pseudopyrina* for M. Lambert; but since his genus includes most of the forms usually regarded as typical Pyrinas, it may be taken as representing the Cenomanian state of the group. The test is fragile, and the calcareous sandstone which fills specimens from the Western Cenomanian in this country is most intractable. But at the expense of many cherished examples, I have succeeded in excavating one completely (E. 280). The result is disconcerting. *P. desmoulinsi* has a perignathic girdle precisely similar, in every detail, to that of a *Conulus* with a test of the same thickness. The marked obliquity of the peristome seems scarcely to affect the girdle. It is beyond question that *Pyrina* (as represented by this species) and *Conulus* are very closely akin.

In some ways, the discovery of this perignathic girdle intensifies the systematic confusion; for generic distinction between *Pyrina* and *Conulus* (never very satisfactory) is now scarcely tenable. Such Cenomanian forms as *C. castanea* are Pyriniform in shape, and the passage of the periproct of *Conulus* from a supramarginal to an inframarginal position can be traced morphogenetically through the zones of the Chalk and ontogenetically in individual species. VALETTE (1908) figured a very small *Conulus* "*subconicus*" with an inframarginal periproct; but in my experience this is abnormal: I have examined many young forms that were evidently *C. albogalerus*, and in every one the periproct was supramarginal, as it is in "*Globator*" or *Pyrina*.

Nevertheless, the presence of a fully-developed girdle in *Pyrina* simplifies the phylogenetic problem. The relation between *Conulus* and *Pyrina* was difficult to explain, so long as the latter was supposed to be atelostomatous, in the light of the stratigraphical succession. Now it appears to me that *Conulus* must be a direct descendant of *Pyrina*, showing reversionary tendencies in respect of symmetry. While the through line from *Pyrina* culminates in *Echinonëus* (with a very probable branch to *Pygaulus* and beyond), the *Conulus* branch revived the tradition of "roundness" without ever attaining true circularity of contour.

I conclude that *Pyrina*, like *Echinonëus*, had a vestigial lantern (the girdle persisting in the former and disappearing in the latter); and this would imply that in *Conulus* also the lantern will have been vestigial. The persistent girdles of *Pyrina* and *Conulus*, deprived, at an early stage in ontogeny, of the lantern for whose service they were designed, would naturally assume strange characters and new functions—among them, I am once more convinced, the accommodation of the peristomial plates when these were retracted.

VI. Summary and Conclusions

(1) *General*

Optical investigation of a transverse section of the lantern of *Cidaris* shows that the calcite of the pair of maxillæ united by an interpyramidal muscle is in one orientation, while that of the pair that constitutes a pyramid is not. This fact gives strong support to the view that the maxillæ are paired radial structures, and that their association into interradially situated pyramids is a secondary feature. The teeth (which seem to be crystallographic units) are thus the only truly interradial parts of the lantern.

Secondary additions to the perignathic girdle (capping) are found to occur on the interambulacral ridges as well as on the ambulacral processes in many of the Centrechinoida. The secondary growth can be detected in thin section by its looser stereomesh. When well developed on the processes, it is liable to transform a discontinuous girdle into a continuous one by completing the " auricular arch."

(2) *Centrechinoida*

(i) *The Lantern*—Details of the construction of the lantern and teeth are described in four Mesozoic genera: *Diademopsis*, *Acrosalenia*, *Hemicidaris*, and *Phymosoma*. Of these, *Diademopsis* proves to be an Aulodont, and the peculiar proportions of its maxillæ are in some ways intermediate between those of normal Aulodonta and of the Cidaroida. This discovery is interesting in view of the similarity between *Diademopsis* and *Hemipedina*. The jaws of the latter are not yet known, but all the indirect evidence suggests that they must have been Stirodont rather than Aulodont.

The other three genera belong definitely to the Stirodonta, and their lanterns show no important differences from those of modern members of the order. *Pseudodiadema* is known to be Stirodont, so that the four great families of Mesozoic Centrechinoids named after these genera definitely belong to the Stirodonta (assuming that they are homogeneous). The Acrosaleniidæ and Hemicidaridæ seem nearly allied to one another and to the modern Arbaciidæ. The affinity of the Pseudodiadematidæ with modern types is less evident. The Phymosomatidæ are also somewhat isolated; they may perhaps be considered as the Stirodont equivalents of the Camarodont Echinometridæ.

(ii) *The Girdle*—The two main variants in the perignathic girdles of the genera investigated are the continuity or discontinuity of the " auricular arches " and the proportionate height of the processes and ridges. *Pedina* shows that continuity had been attained in Bajocian times; continuity seems to have been at least as common a condition in Mesozoic genera as in later types. The continuous girdle of *Hyposalenia* is curious in view of the discontinuity of that of the modern Saleniidæ.

In the matter of proportionate development of the girdle, the strangest case is that of *Allomma*, where the whole structure is very high, and the ridges form a continuous collar scarcely less tall than the processes. A comparable, but less extreme, condition obtains in the recent genus *Salmacis*; it is significant that the peristome is very small in both genera. On the other hand, the girdle of *Hemicidaris* (which has a very large peristome) is extremely low and feeble, somewhat like that of its probable descendant *Arbacia*. It would be natural to suppose that a form with a wide periproct would require stronger muscles (and muscle-supports) than one with a narrow peristome; but the reverse is found. Perhaps it may be correlated with the potential gape of the mouth, for less force would be required to snap together teeth that were wide apart than to close a set that was scarcely open. On the other hand, it may be argued that an increase in height of the girdle involves an increase in fragility, and so a diminution of the muscular strain supportable. Such a view would imply the development of an elaborate structure for the achievement of inefficiency, and seems inherently improbable. There may be other functions of the girdle in addition to giving support to the lantern muscles; but their nature is problematical.

(3) *Holectypoida*

Preparation of further examples of the Pygasteridæ has led to correction and amplification of the accounts of the girdle previously published. In particular, the relation between the angle of setting of the processes and that of the peristomial invagination seems significant. In *Plesiechinus* and *Pygaster* the projection of the processes in a direction normal to the floor of the test actually results in an obliquity of as much as 45° to the vertical axis of the body. Unless the retractor muscles were extraordinarily long, this must have involved a "flaring" attitude of the lantern. The massive buttresses that support the processes may have strengthened them to bear the weight of the maxillæ when the jaws were closed; such a condition would lead easily to the recumbent attitude of the pyramids in the Clypeastroida. These buttresses are longer in *Holectypus*, and in the Discoidiidæ they form carinæ that radiate across the adoral surface and extend some way up the sides. The carinæ of the primitive Clypeastroid *Echinocyamus* are similar, so that the short buttresses of *Plesiechinus* may be the forerunners of the elaborate calcification of the Clypeastroid interior.

In *Pseudodiscoidea* the obliquity of the processes is counteracted by an inward bending of their tips. The lantern of this genus is well known, but no others are available for comparison.

Pyrina is found to have a perignathic girdle exactly similar to that of *Conulus*, so that the two genera are less easy to distinguish than before. There seems no reason to doubt the close affinity of *Pyrina* with *Echinonëus*; perhaps *Conulus* is a reversionary offshoot from that lineage. The relation between this series and the rest of the Holectypoida remains obscure.

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VIII. EXPLANATION OF PLATES

PLATE 68.

FIGS. 27 and 28.—Top and side views of the lantern, girdle, and associated muscles of *Echinometra lucunter* (LINN.) (see p. 619).

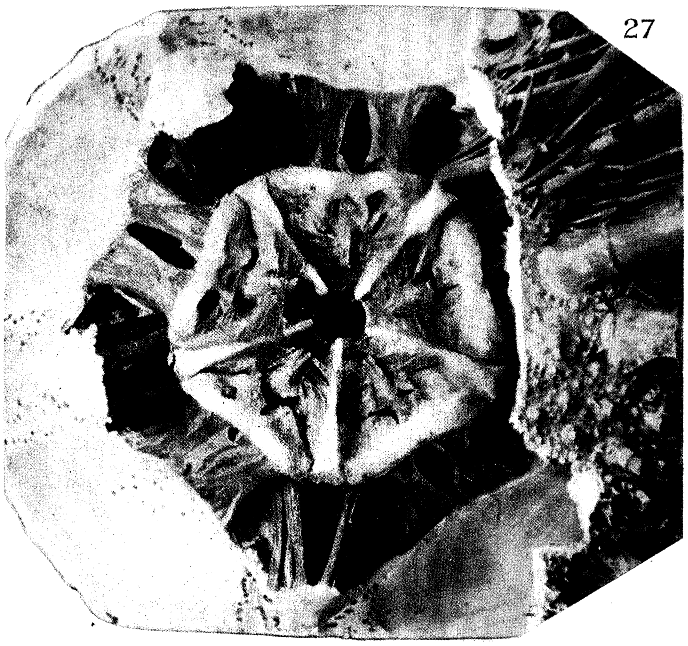
FIG. 29.—Perignathic girdle of *Stomechinus robinaldinus* (COTTEAU) (E. 196) (see p. 628).

FIG. 30.—Perignathic girdle of *Pseudodiadema pseudodiadema* (LAMARCK) (E. 197) (see p. 631).

FIG. 31.—Perignathic girdle of *Tetragramma brongniarti* (AGASSIZ) (E. 135) (see p. 636).

FIG. 32.—Perignathic girdle of *Allomma normanniæ* (COTTEAU) (E. 326) (see p. 637).

FIG. 33.—Associated lantern-ossicles of *Phymosoma koenigi* (MANTELL) (E. 269) (see p. 638).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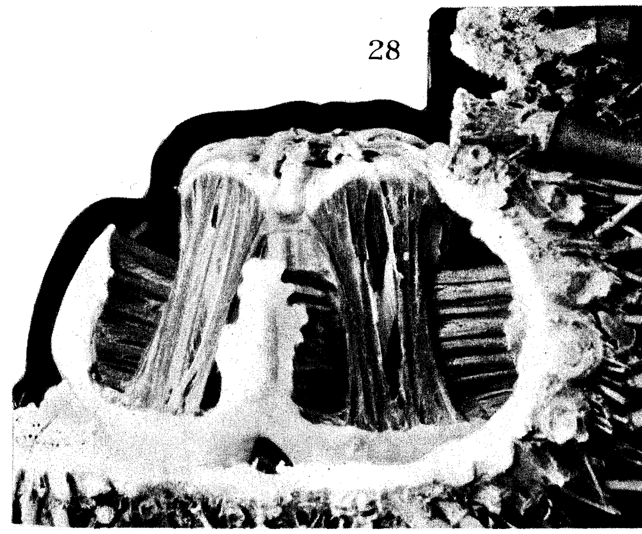
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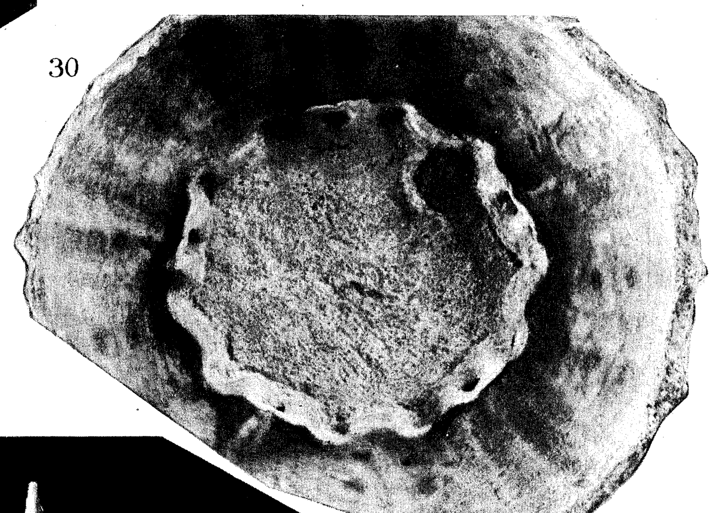
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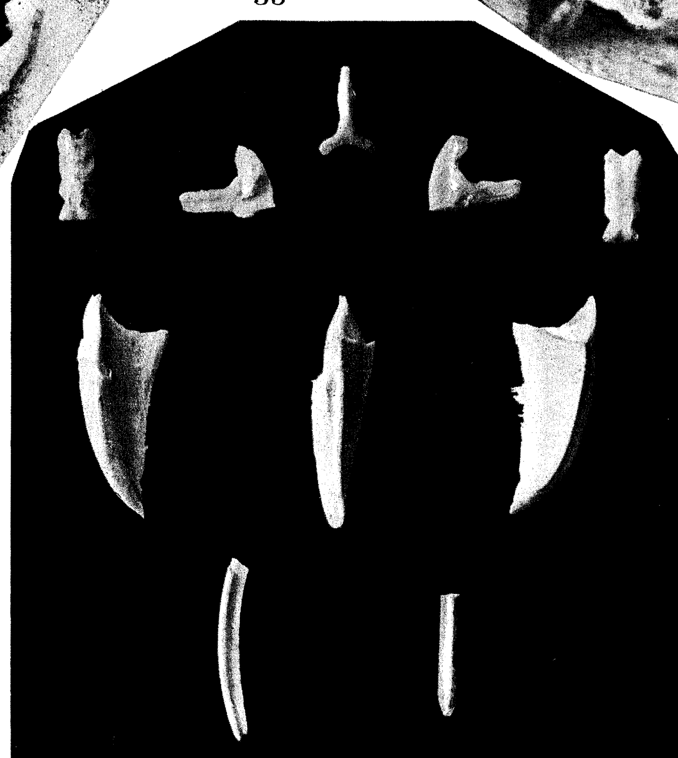


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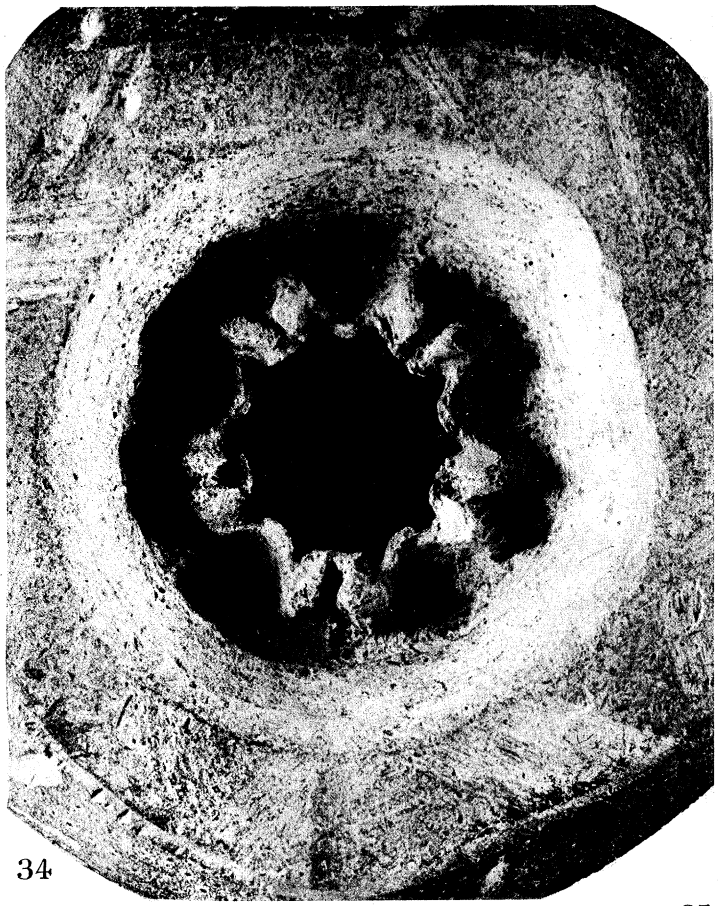

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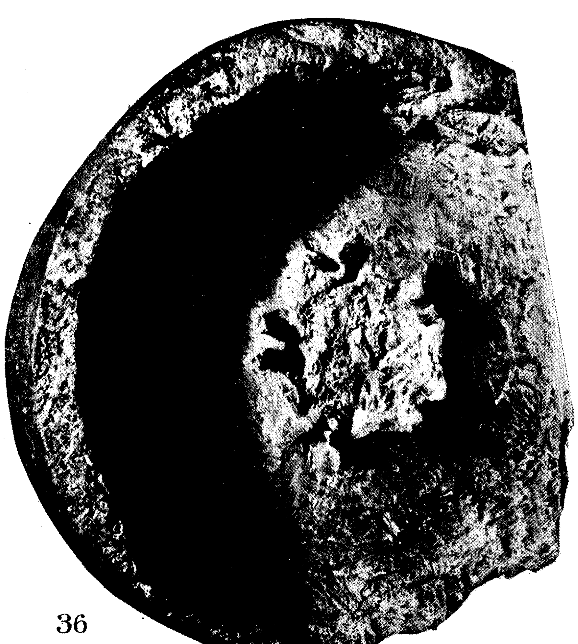

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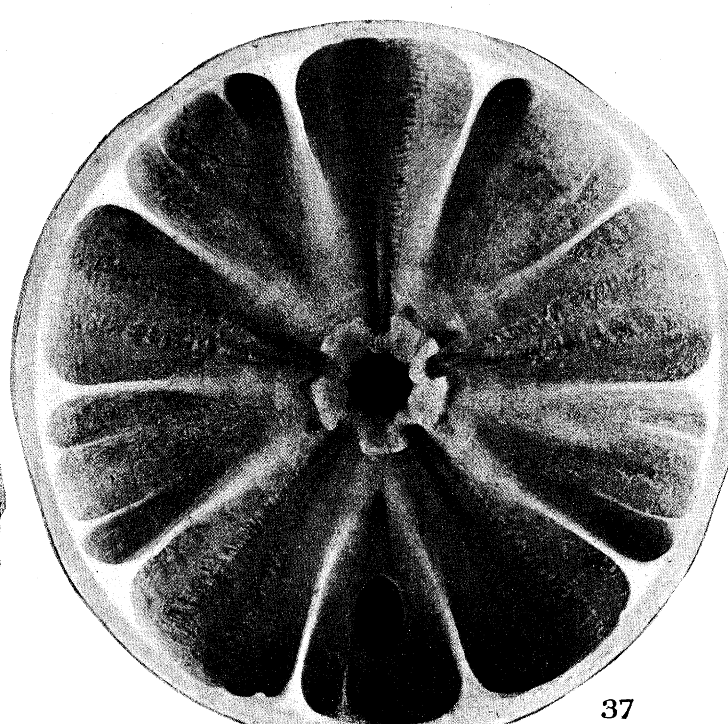

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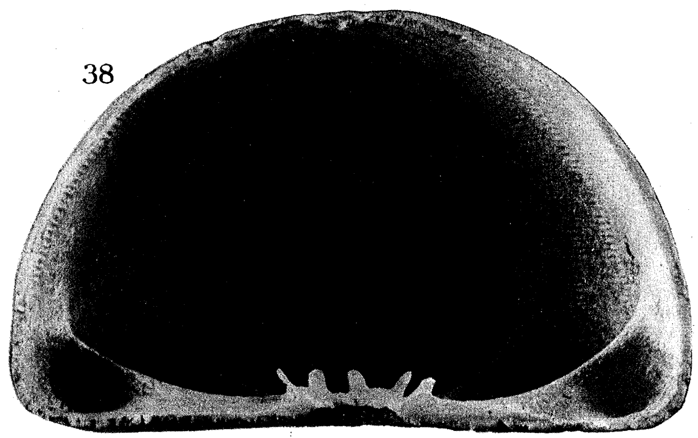

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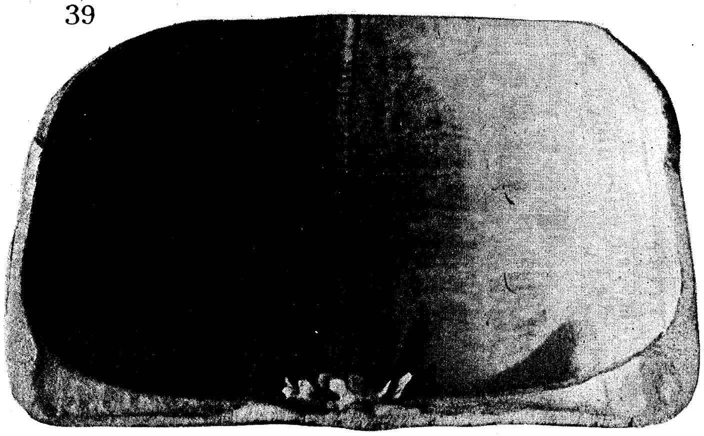

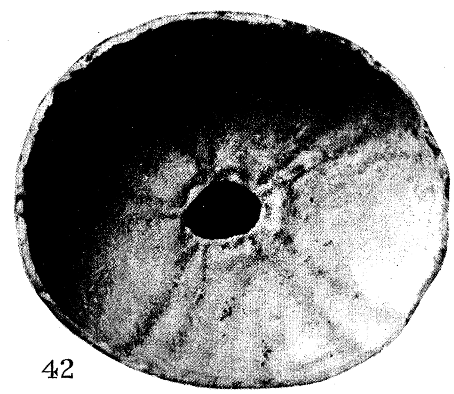

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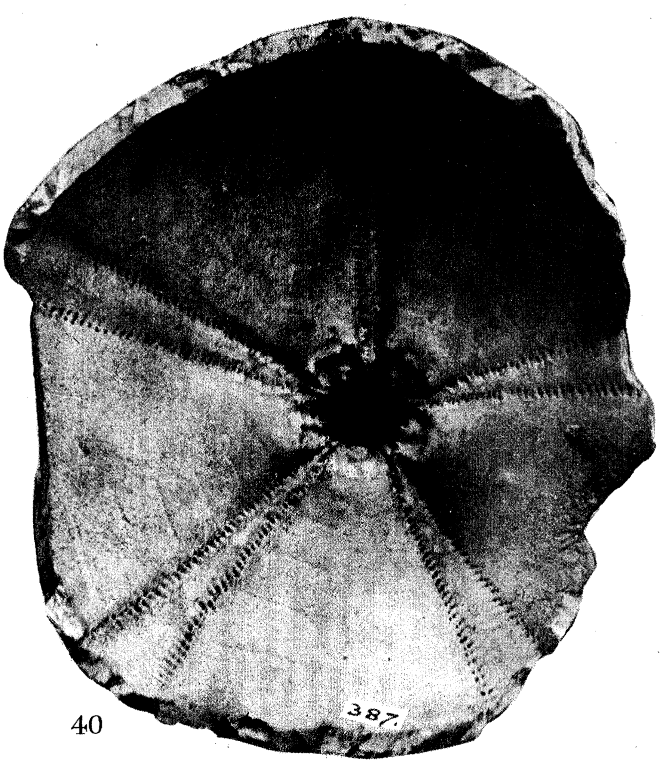

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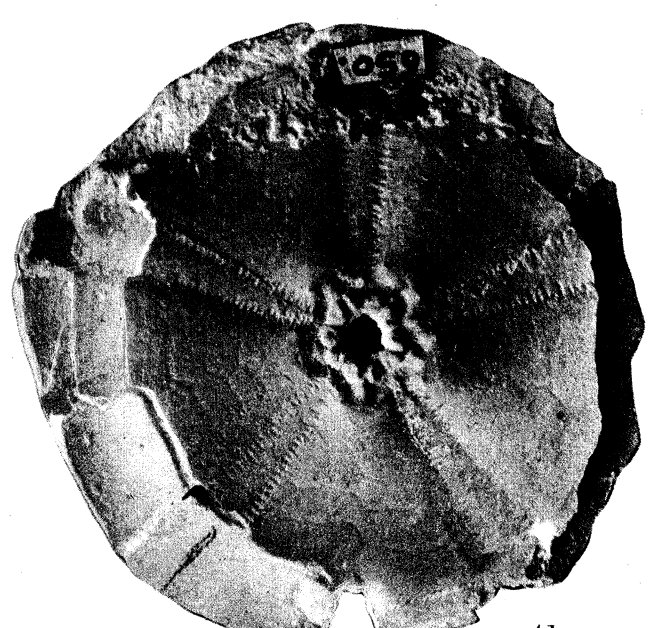

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PLATE 69.

FIG. 34.—Perignathic girdle of *Plesiechinus ornatus* (BUCKMAN) (E. 349) (see p. 640).

FIG. 35.—Perignathic girdle of *Pygaster* cf. *semisulcatus* (PHILLIPS) (E. 372) (see p. 642).

FIG. 36.—Perignathic girdle of *Holectypus hemisphæricus* (AGASSIZ) (E. 71) (see p. 642).

FIG. 37.—Interior of the adoral surface of *Pseudodiscoidea cylindrica* (LAMARCK) (hemispherical form) (E. 70) (see p. 643).

PLATE 70.

FIG. 38.—Longitudinal section of *P. cylindrica* (LAMARCK) (hemispherical form) (E. 204).

FIG. 39.—Sagittal section of *P. cylindrica* (LAMARCK) (cylindrical form) (E. 644).

FIG. 40.—Perignathic girdle of *Conulus albogalerus* (LESKE) (E. 387) (see p. 644).

FIG. 41.—Perignathic girdle of *C. albogalerus* (LESKE) with the peristomial plates in situ (E. 650).

FIG. 42.—Perignathic girdle of *Pyrina desmoulinsi* (D'ARCHIAC) (E. 280) (see p. 645).

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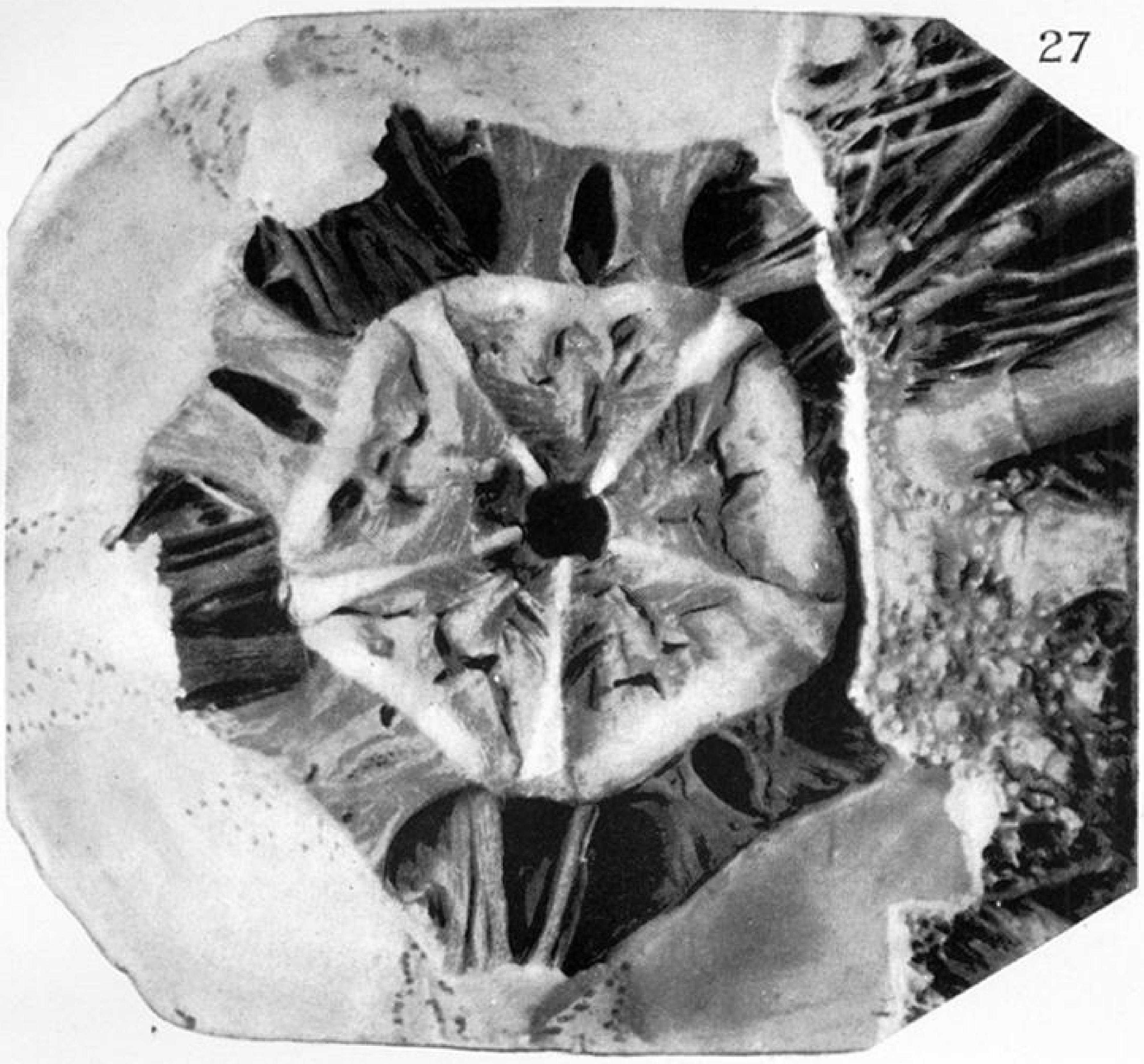

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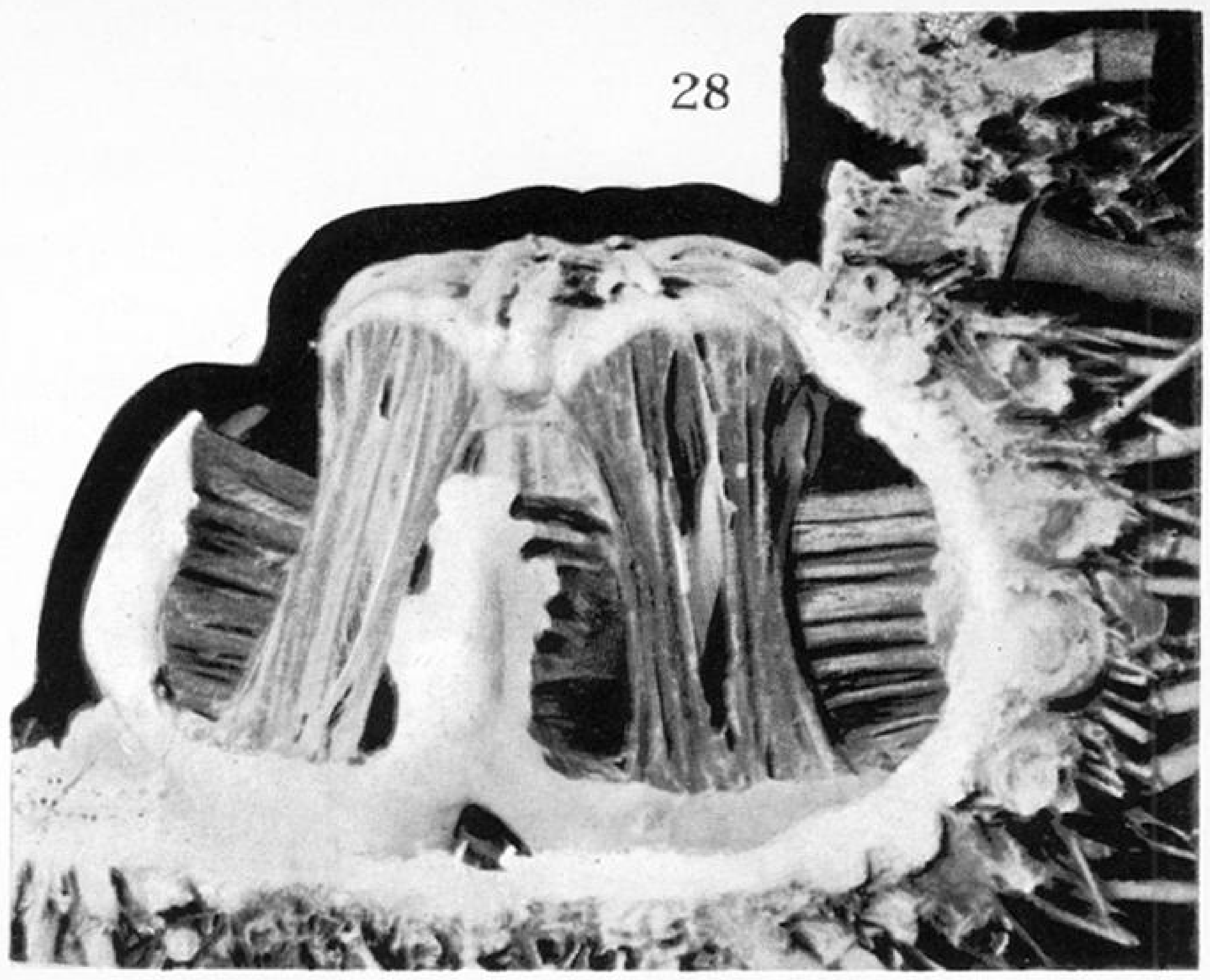

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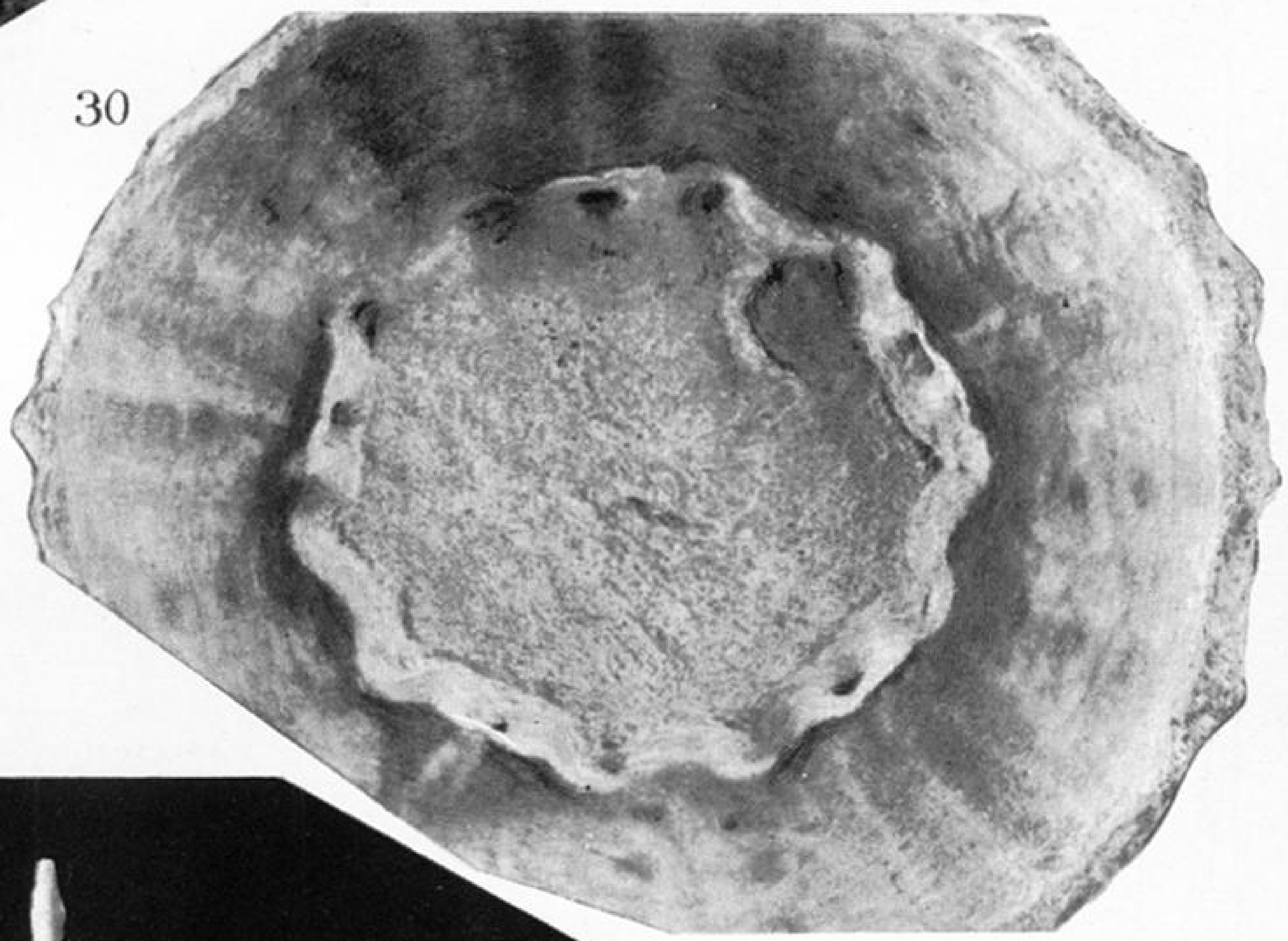

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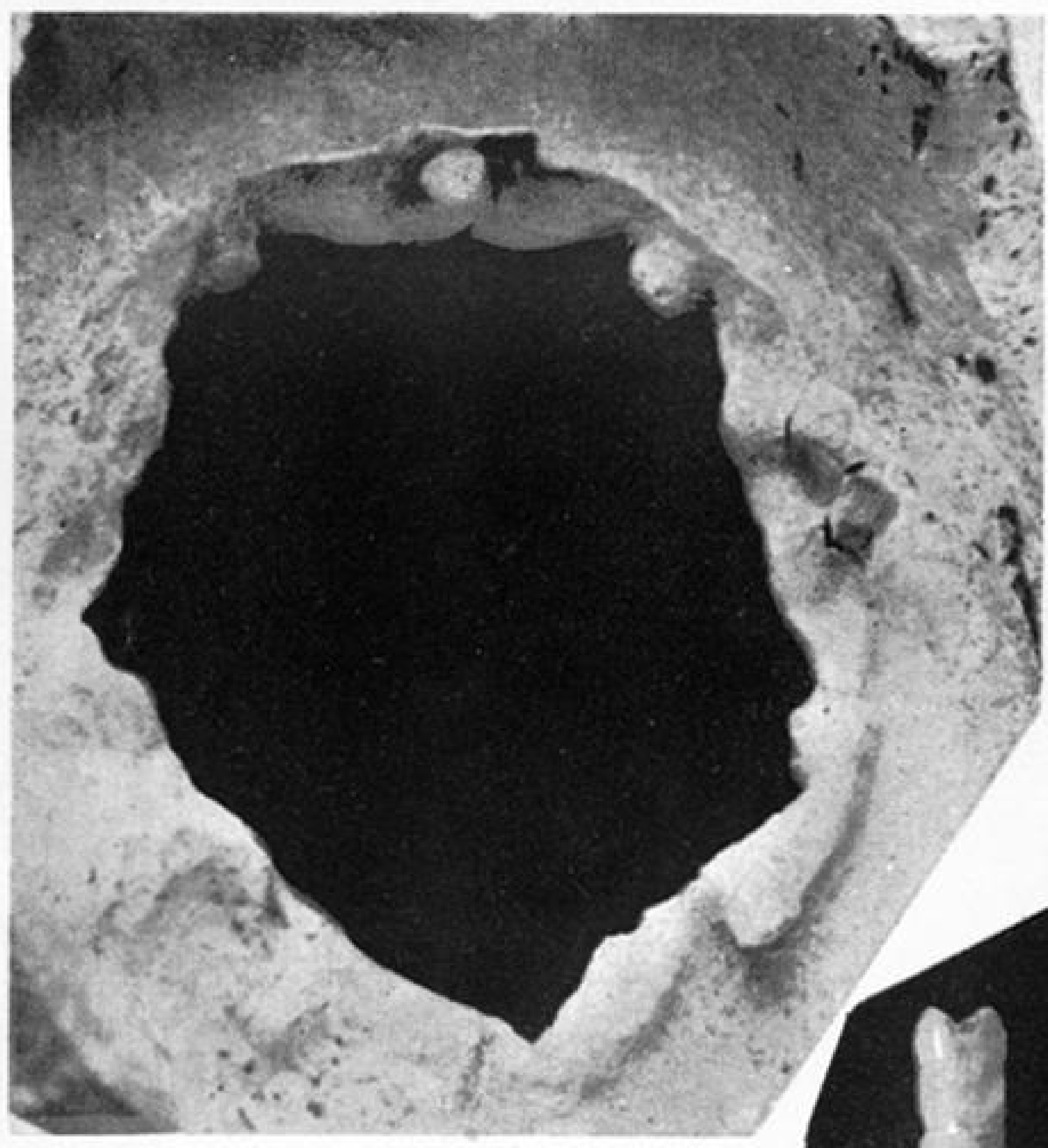

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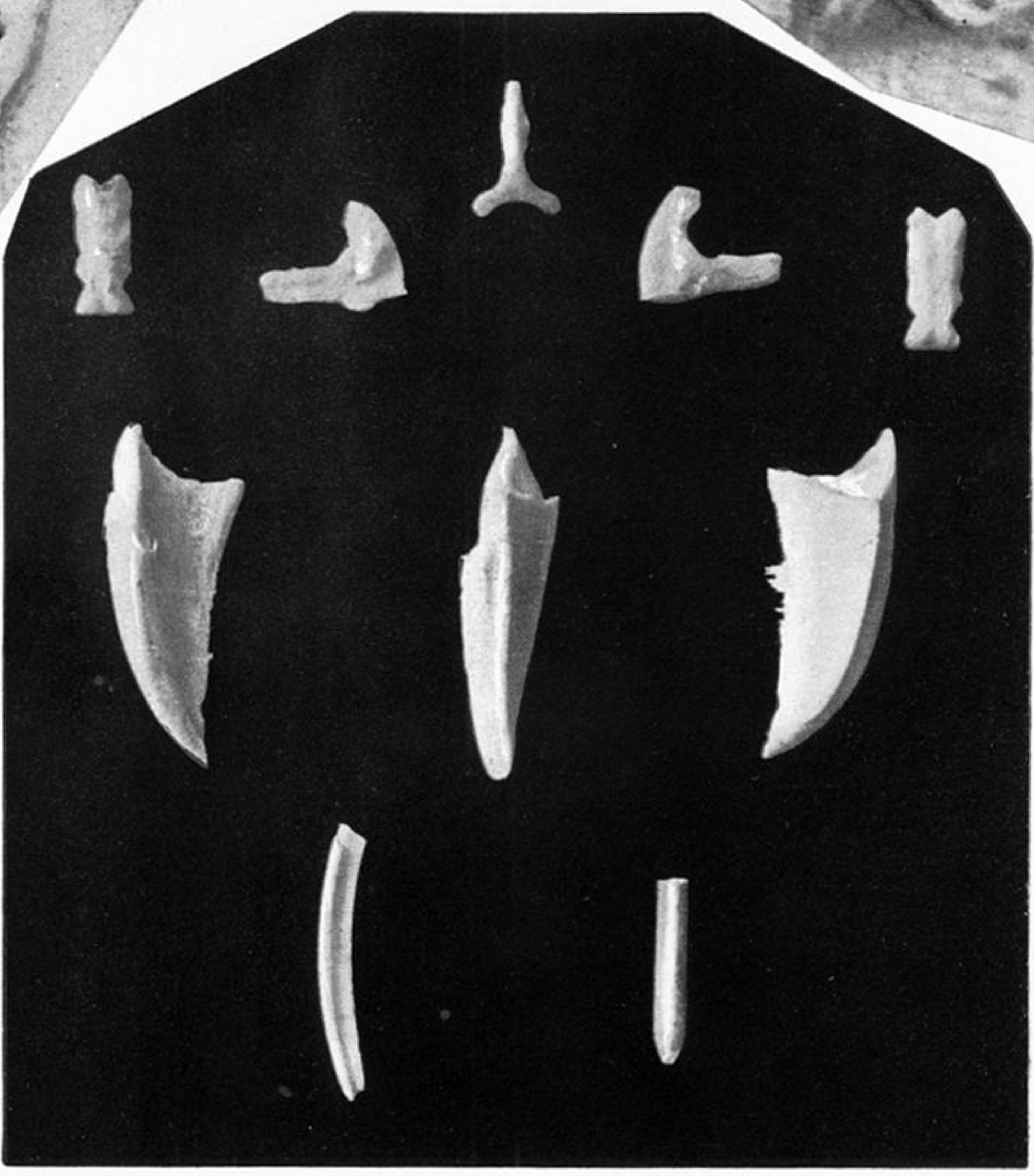

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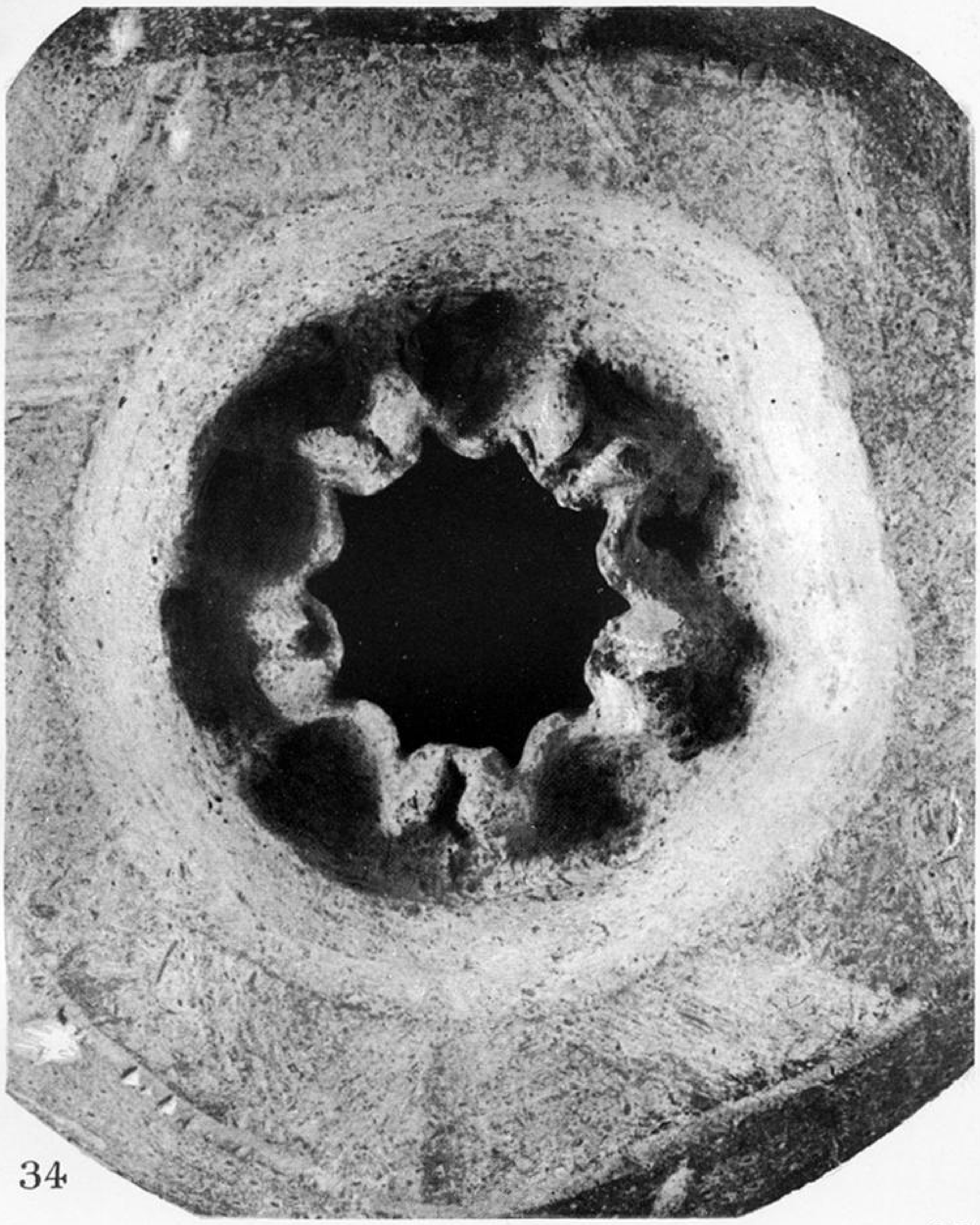

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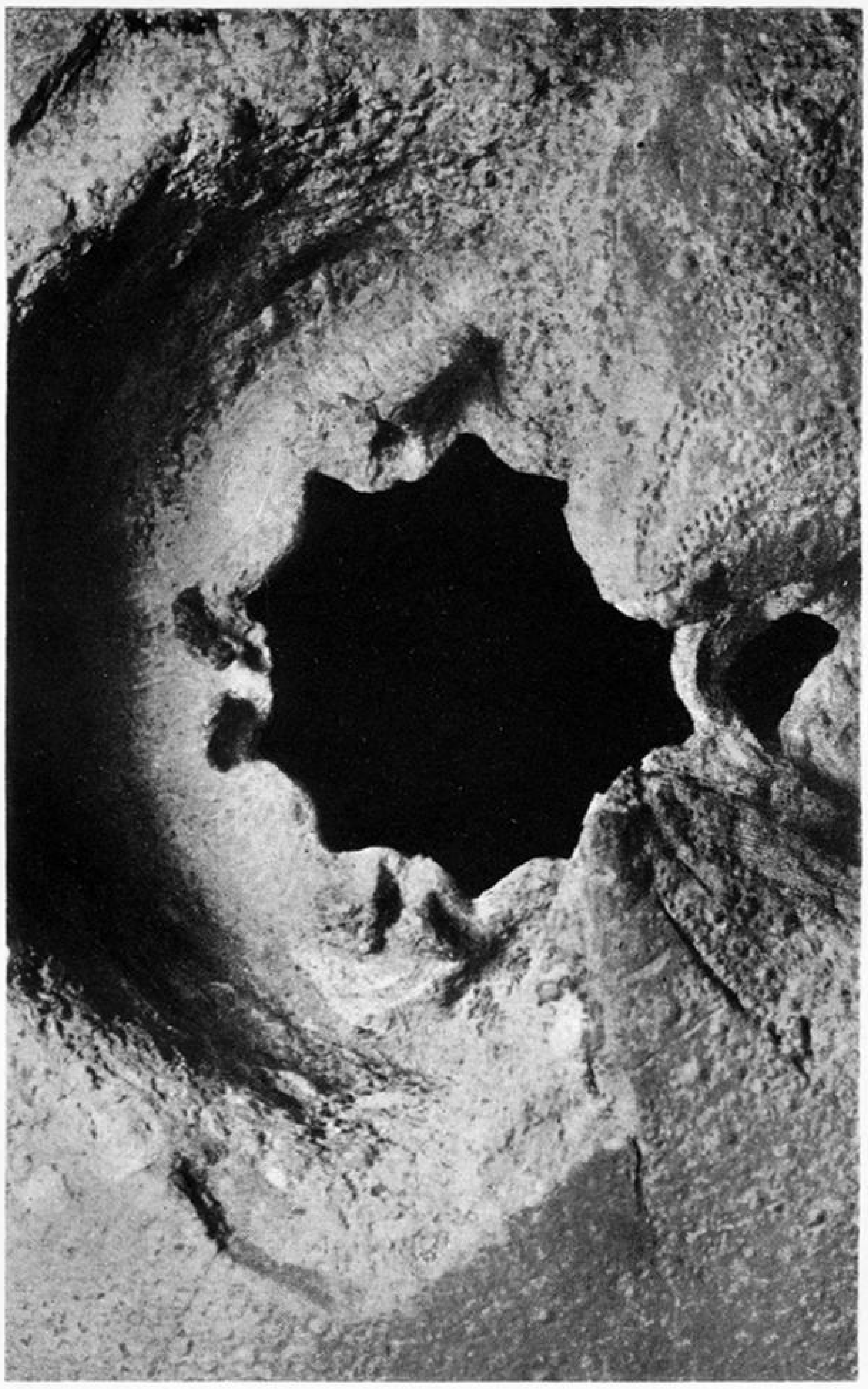

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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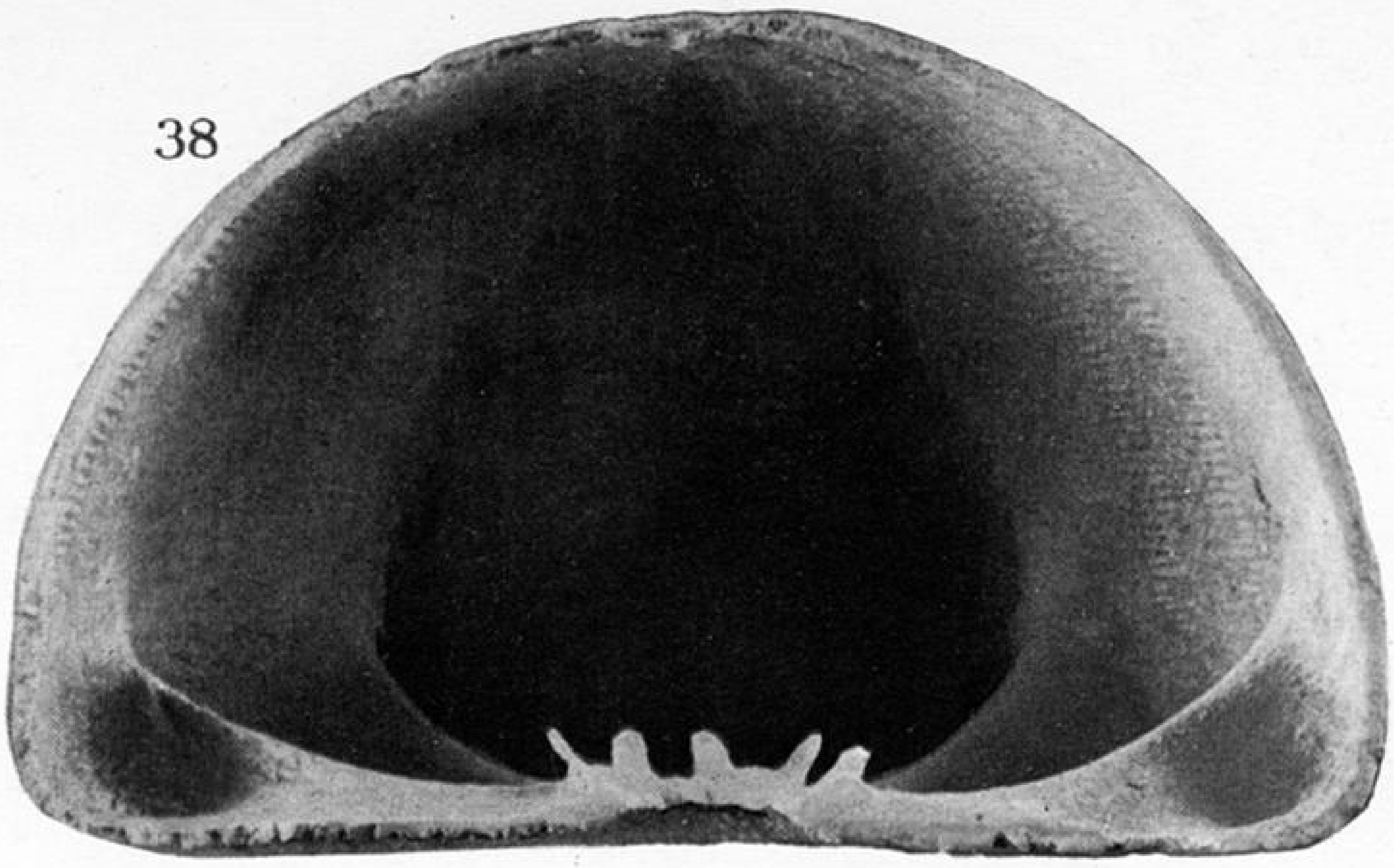

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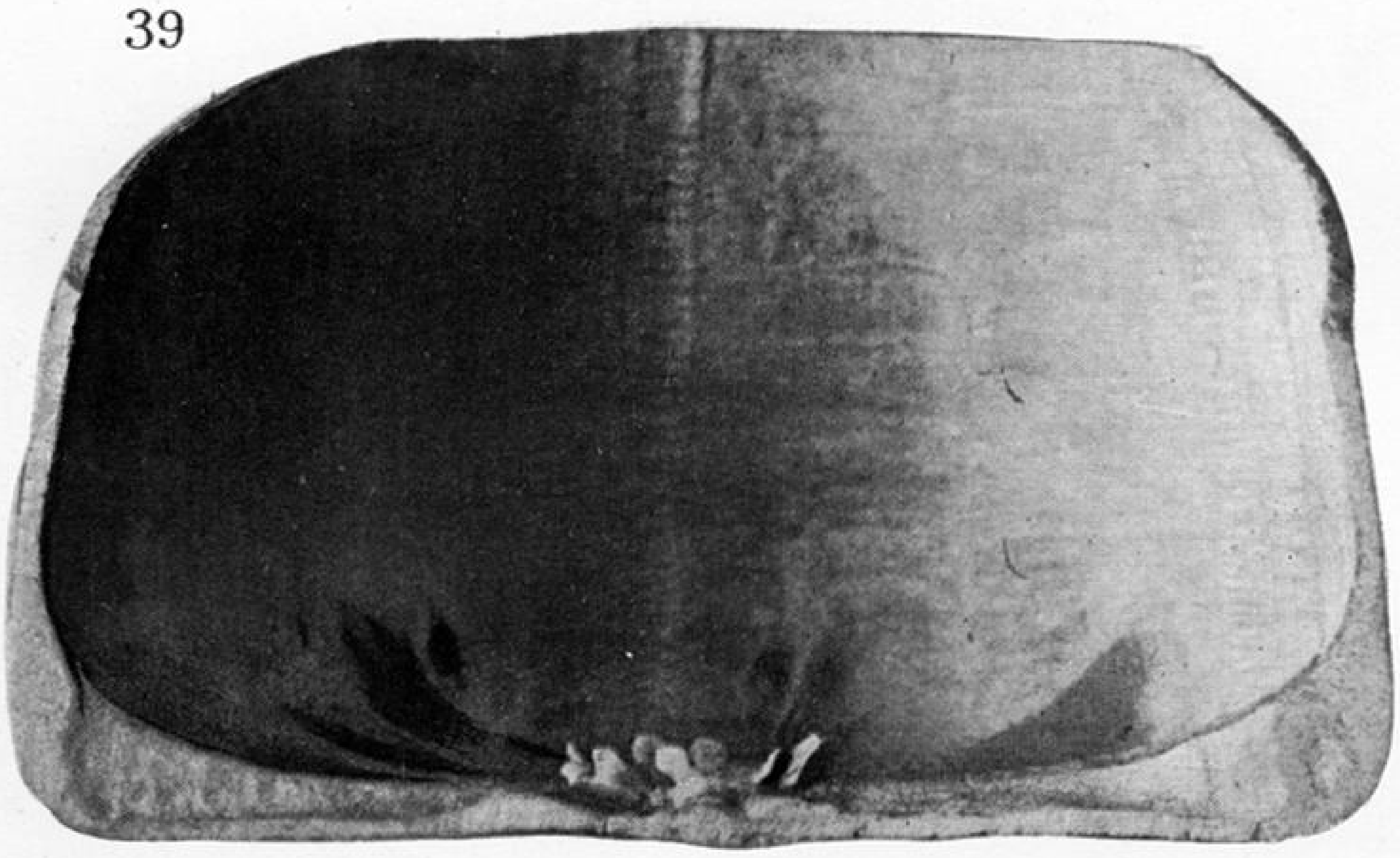

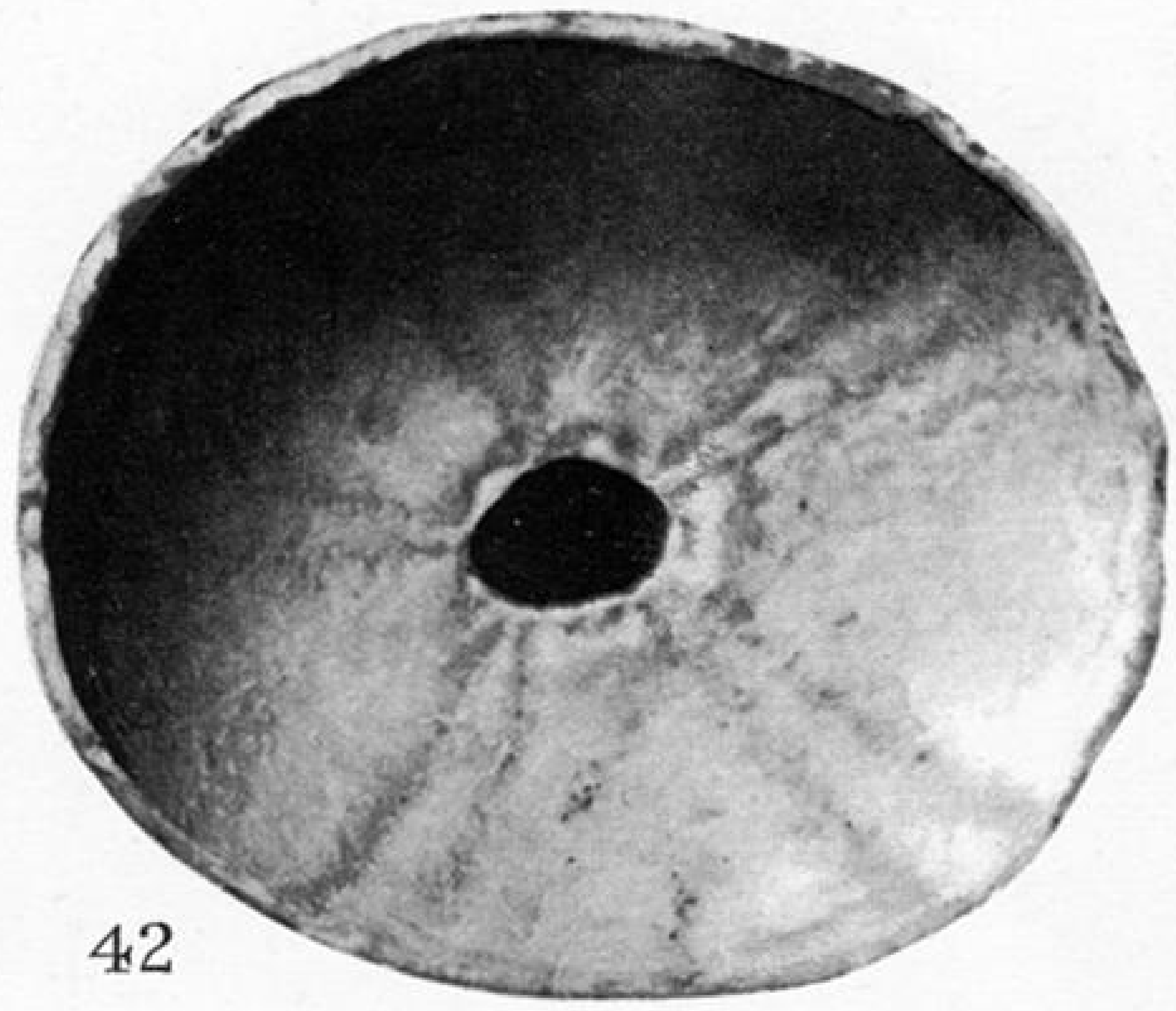

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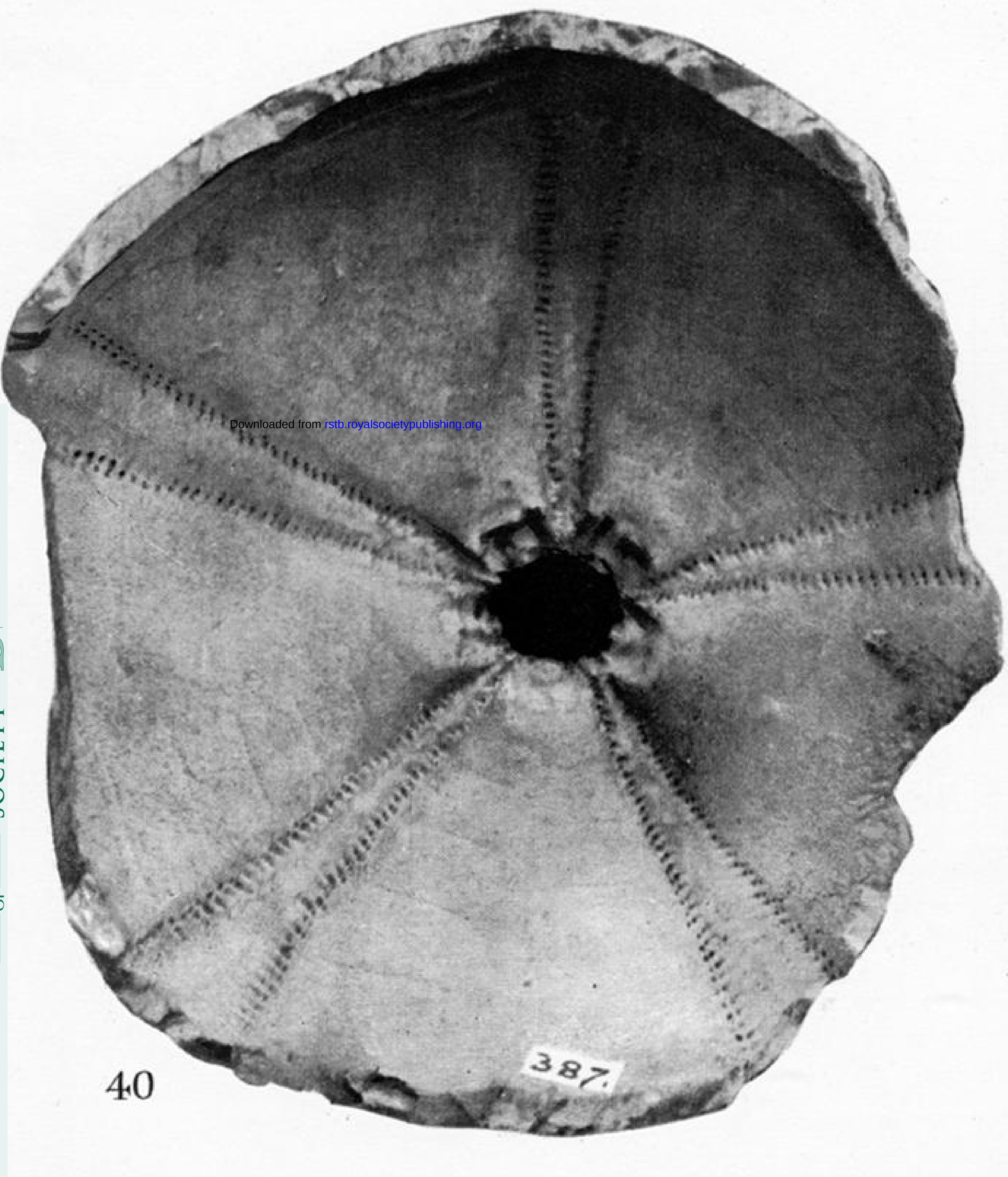

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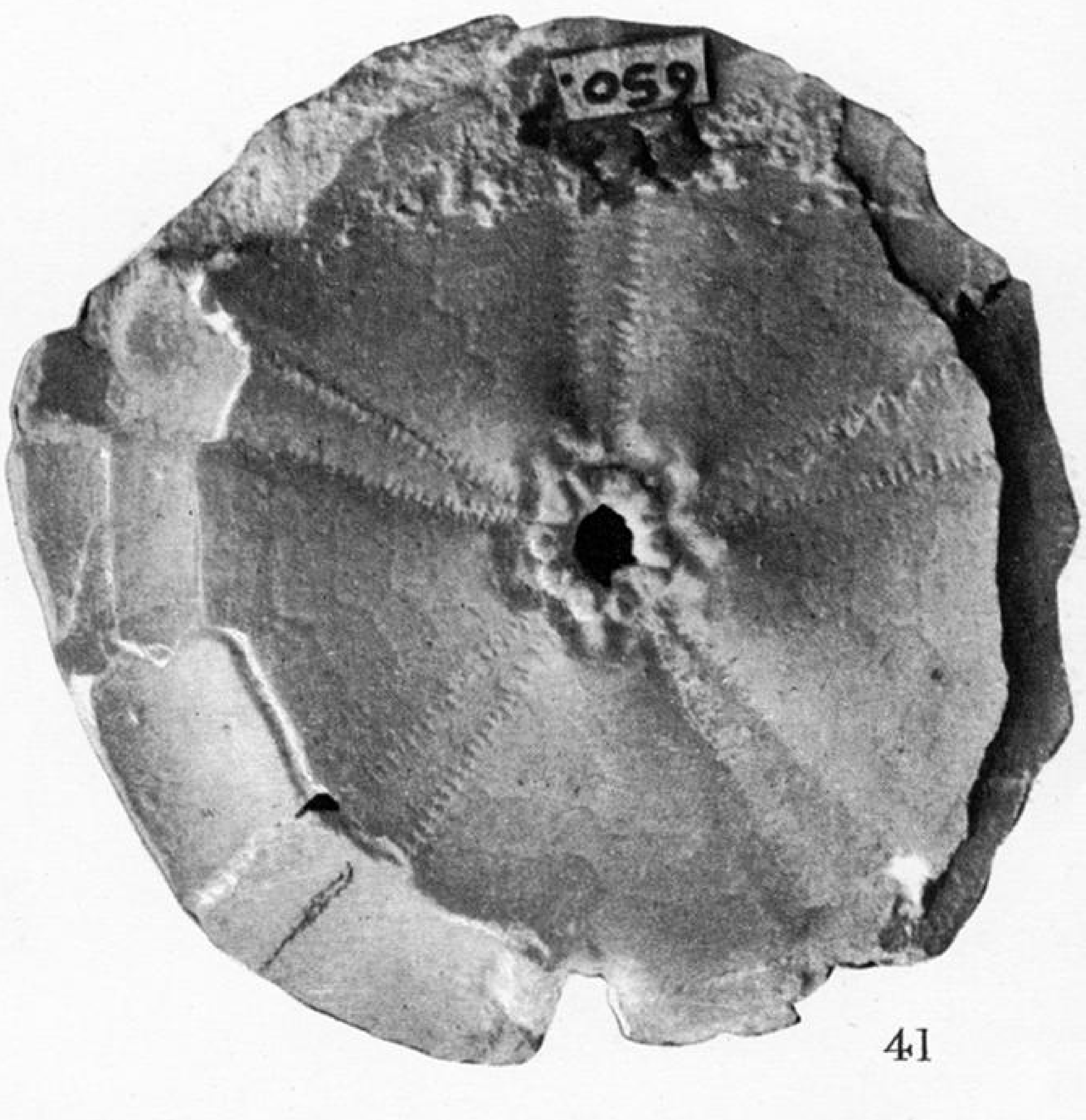

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