THE MORPHOLOGY, CLASSIFICATION AND EVOLUTION OF THE TRINUCLEIDAE (TRILOBITA)

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[Plates 1–10]

CONTENTS

The morphology of the trinucleid exoskeleton is reassessed and various new structures and terms defined. On the basis of new interpretations of cephalic morphology, particularly that of the fringe, of all known genera, a new subfamilial classification is proposed. Two new genera, *Deanaspis* and *Whittardolithus*, and the subfamily Reedolithinae are proposed, and the genus *Botrioides* Stetson resurrected. The existing subfamilies, Trinucleinae, Cryptolithinae and Marrolithinae are recast considerably and the Tretaspidinae, Novaspidinae and Incaiinae rejected. The Hanchungolithinae is left unmodified. Evolution within the family is discussed together with the distribution of genera in terms of recent palaeogeographic reconstructions. A review of the relations between phylogeny and ontogeny confirms the essentially recapitulative nature of trinucleid ontogenies. A list of current generic assignments of known species is given.

1. INTRODUCTION

Much of the copious literature on the Trinucleidae is concerned with the systematic descriptions of new species in biostratigraphic studies. A considerable proportion, however, is more directly concerned with the understanding of particular aspects of the group, for example, morphology, distribution and ontogeny. A very good account of much of the early work was given by Størmer (1930, pp. 7–8) in his classic work on the Trinucleidae of Scandinavia. Of particular note here are the works of Oehlert (1895), Salter (1847) and Reed (1912, 1914*b*, 1916) with their comments on the morphology of the exoskeleton, particularly the fringe. Subsequent to Størmer's work a vast amount of morphological, stratigraphical and ontogenetic information has accumulated, much of it due to workers such as Bancroft, Dean, Whittard, Whittington and Williams. Also, various of these authors, together with others, have considered problems of phylogeny and distribution, e.g. Stetson (1927), Stubblefield (1939) Whittington (1941*a*, 1966*b*), Dean (1960) and Lu (1963, 1964).

It has been suggested recently (Ingham 1970; Hughes 1971) that current interpretations of morphology and classification of the Trinucleidae need modification. The present study has materialized partly from the independent realization by the authors that Ingham's (1970) concept of an homologous innermost arc (I_n) in various species of *Tretaspis* could be widely applied in trinucleids. The discovery, in *Marrolithus* by Addison and, independently in *Onnia* by Ingham (1974), of an abrupt posterior truncation of the I_n arc by an adjacent *I* arc and also, of a pit grouping at the inner edge of the lateral part of the fringe (*F* pits) quite separate from the *I* arc series, has led us to a complete reassessment of trinucleid morphology and its bearing on generic and suprageneric classification. In order to do this we have considered all previously described trinucleid species. In the course of this many specific names now considered invalid, and thus not mentioned in the main body of this paper, have come to light. A table is given expressing the authors' opinion, based on the study of specimens in the majority of cases, as to the current generic assignment of all species originally described as trinucleids. The five-fold subfamilial classification that is proposed, while based on morphological criteria reflects, we believe, the phylogeny of the family. The species included in all genera are reassessed and the geographical and stratigraphical distribution of each genus given. This has led us to consider the evolution of the group with regard to its distribution, with particular reference to the various palaeogeographic models that have recently been proposed (Briden, Smith & Drewry 1973; McKerrow & Ziegler 1973; Whittington & Hughes 1972, 1973; Williams 1973).

It was felt that if this paper was to have the practical usefulness envisaged then specimens representative of as many trinucleid genera as possible would have to be figured. Some of the specimens selected for illustration have been figured previously in a large number of papers: rather than simply gather earlier figures together it was decided to provide new illustrations, mainly stereophotographs, in which the important morphological details are explicit. Almost half the photographs are of previously unfigured specimens.

Throughout this study the authors have received much help from colleagues throughout the world. In particular we thank Professors H. B. Whittington, F.R.S., and A. Williams, F.R.S. for advice and encouragement, and to Mrs Hilary Carlisle and Drs M. N. Chugaeva, B. A. J. Baldis, J. Destombes, J.-L. Henry and W. I. Mitchell for providing unpublished information regarding certain species. Thanks are also due to Drs D. L. Bruton, Paleontologisk Museum. Oslo; R. A. Fortey, British Museum, Natural History; R. E. Grant, United States National

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Throughout this work the new county names introduced in England and Wales on 1 April 1974 and the new names of the Scottish regions introduced on 1 April 1975 have been used with the old county names, where different, given in parentheses.

Prefixes to catalogue numbers refer to the following institutions:

Ar.	Riksmuseum, Stockholm
BM.	British Museum (Natural History), London
GSM.	Institute of Geological Sciences, London
HM.	Hunterian Museum, University of Glasgow
HU.	Hull University
NMI.	National Museum of Ireland, Dublin
NMW.	National Museum of Wales, Cardiff
PMO.	Paleontologisk Museum, Oslo
RSM.	Royal Scottish Museum, Edinburgh
SM.	Sedgwick Museum, University of Cambridge
UBA.	University of Buenos Aires
USNM.	United States National Museum, Washington, D.C.
VA.	Victoria University of Wellington, New Zealand

2. Morphology

(*a*) *Cephalic morphology*

(i) *Non-fringe features*

The basic elements of cephalic morphology are as shown in figure 1.

The glabella is a superficially simple structure in trinucleids, bounded by broad axial furrows and having variable convexity. Hanchungolithine genera usually have the simplest glabella type (figure 2*a*) with fairly evenly declined sides, no marked anterior expansion or differential convexities. The glabellar furrows are shallow and evenly spaced and the occipital ring may have a sharp posterior angulation which can be considered to represent an incipient occipital spine. In common with some early representatives of the Trinucleinae and Marrolithinae, hanchungolithines possess a gently convex preglabellar field between the shallow preglabellar furrow and the inner boundary of the upper lamella of the fringe. The trinucleines (figures 2*b–d*) are characterized by a glabella which reaches the fringe in most forms and develops a strong frontal convexity in the form of a variably swollen pseudofrontal lobe which encompasses the frontal and third lateral glabellar lobes. In some progressive trinucleines the pseudofrontal lobe is developed as an extremely swollen hemispherical structure separated from the remainder of the glabella by a transverse furrow. There may, however, still be traces of the 3p furrows on its sides. This type of glabella usually has apodemal pits deeply impressed in the 2p, 1p and occipital furrows (figure 2*c*). The 2p apodemal pits lie at the rear of the pseudofrontal lobe while the pits in the occipital and 1p furrows commonly define an independent posterior glabellar convexity referred to as the occiput (see §2(*c*)). Occasionally low composite 2–3p lateral

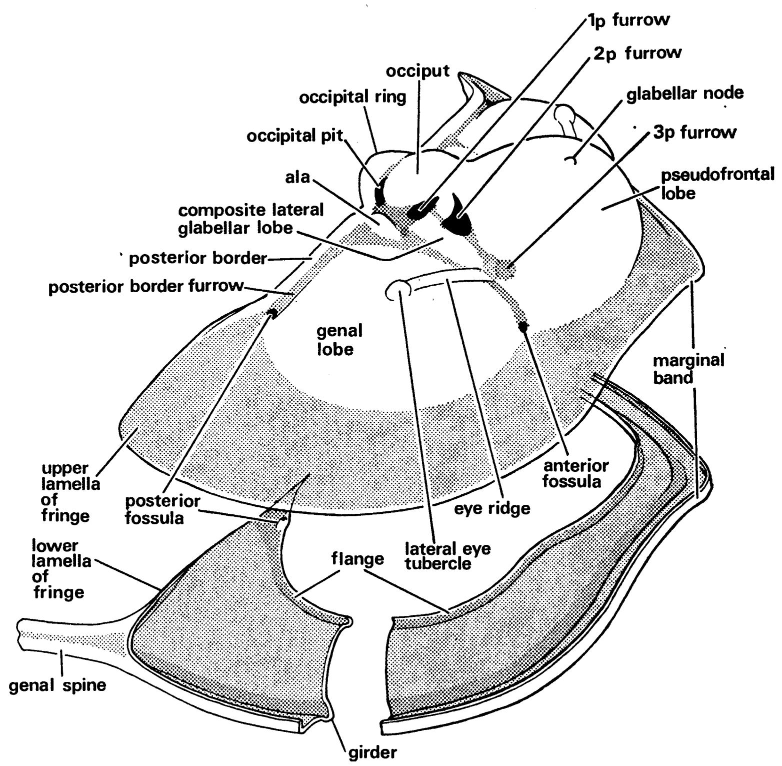


Figure 1. Basic morphology of the trincleid cephalon (fringe pitting omitted), seen in oblique view: lower lamella detached.

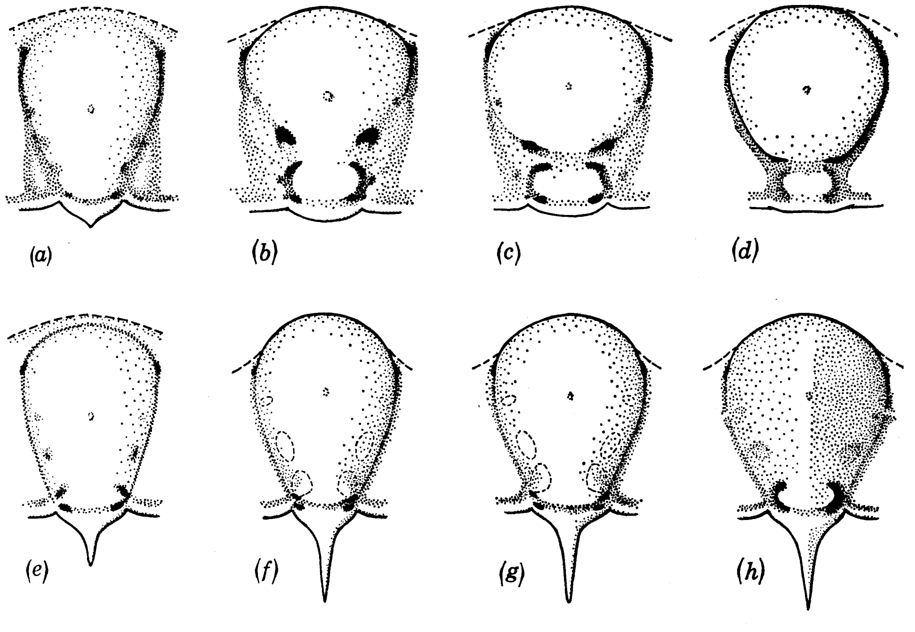


Figure 2. Trinucleid glabellar types (surface sculpture omitted). (*a*) *Hanchungolithus* (Hanchungolithinae). (*b*) *Bergamia*. (*c*) *Nankinolithus*. (*d*) *Novaspis* (Trinucleinae). (*e*) *Protolloydolithus*. (*f*) *Marrolithus* (Marrolithinae). (*g*) *Cryptolithus* (Cryptolithinae). (*h*) *Reedolithus* (Reedolithinae).

glabellar lobes are developed. Trinucleine glabellae are usually without occipital spines although a small elongated median tubercle on the anterior slope of the occipital ring is visible in some forms. In some, if not all trinucleines, two small pits are present in the axial furrows close to the base of the glabella; one, the larger, is just lateral and posterior to the 1p lateral glabellar furrows (see figures 26, 30, plate 2 and Hughes 1971, p. 123, pl. 1, fig. 3) and the other, generally very small, is close to the occipital pits (see figure 40, plate 3). The significance of these pits is not certain. Associated and immediately abaxial to them there is commonly a small, elongate swelling in the axial furrow which is a much reduced alar lobe. This structure is particularly clear in the silicified specimens of *Tretaspis sagenosus* studied by Whittington (1959, pl. 26, fig. 1), but is also discernible in other trinucleines (see plates 2–4, particularly figure 48, plate 4). One trinucleine genus, *Decordinaspis*, is unique within the family in possessing paired spines on the occipital ring.

Reedolithine genera possess high, carinate glabellae with a clavate outline (figure 2*h*). There is no marked independently convex occiput, although shallow glabellar furrows are usually visible on the steep lateral glabellar walls. In these forms the occipital and 1p furrows have their apodemal pits sufficiently deep to define slightly swollen basal glabellar lobes. Most reedolithines, like marrolithine and cryptolithine genera have stout occipital spines.

The glabella in the Marrolithinae and Cryptolithinae is, in mature individuals, clavate, commonly highly vaulted but non-carinate (figures 2*e*–*g*). The lateral glabellar furrows are almost completely effaced but are sometimes visible as faint muscle scars on the glabellar walls. However, a pair of small apodemal pits (representing the 1p furrows) and the occipital pits are very closely situated near the floor of the axial furrows. Small basal glabellar lobes are usually present.

In almost all trinucleids an apically situated glabellar node has been detected. Størmer's work on the detailed structure of this (1930, pp. 88–89) suggests that it is a median eye. Near the anterior ends of the axial furrows a pair of small pits, the anterior fossulae, is present, appearing on the ventral surface as apodemes which may have acted as a pivot for the hypostoma as in some other trilobites, e.g. Calymenidae. The hypostoma itself is poorly understood being known only from three specimens of *Cryptolithus tessellatus* (see Whittington 1959, p. 442). It appears to have had no sutural union with the inner margin of the lower lamella and it may well have been suspended entirely by the unsclerotized ventral cuticle. A small rectangular finely pitted area in front of the anterior fossula has been recorded in *Onnia* and *Broeggerolithus* (Dean 1960, pp. 106, 132). This area is well-displayed on specimens of *Onnia* recently collected from Salop (Shropshire) and it is seen to be entirely an internal mould feature representing a roughened area on the internal surface of the cranidial exoskeleton. A similar crescentic area is developed on the lateral parts of the genal lobes. These areas probably represent the sites of muscle attachment.

The genal lobes are very similar, quadrant-shaped structures in all trinucleids. Their convexity is variable, but only in the Hanchungolithinae and on immature cephala of other trinucleids, where known, is a distinct alar structure developed (see §2(*c*)). All reedolithines and some trinucleines have their genal lobes bearing a small lateral eye tubercle. Here, the shell is known to be thin (Størmer 1930, p. 91) and the tubercle may incorporate a single lens-like structure (Størmer 1930) which suggests that such tubercles were light receptors. Occasionally eye ridges are seen, particularly on ventral moulds, linking the eye tubercles to the glabella a little to the rear of the 3p furrows. In some, mostly immature trinucleines from the lower and middle Ordovician of the Anglo-Welsh area, and in the young of marrolithines, cryptolithines and hanchungolithines, there are short low eye ridges close to the glabella. It is not known if they terminated in any sensory structure.

(ii) *The fringe*

The fringe is a bilamellar structure in trinucleids such as that in the Harpidae and Dionididae, the upper lamella being contiguous with the glabella and genal lobes. There is an essentially marginal suture which passes around the fringe usually near the upper edge of the marginal band, becoming dorsal only around the genal angles, thence crossing the posterior margin of the fringe at an oblique angle to reach the inner edge of the lower lamella; thus the genal spine is an integral part of the lower lamella.

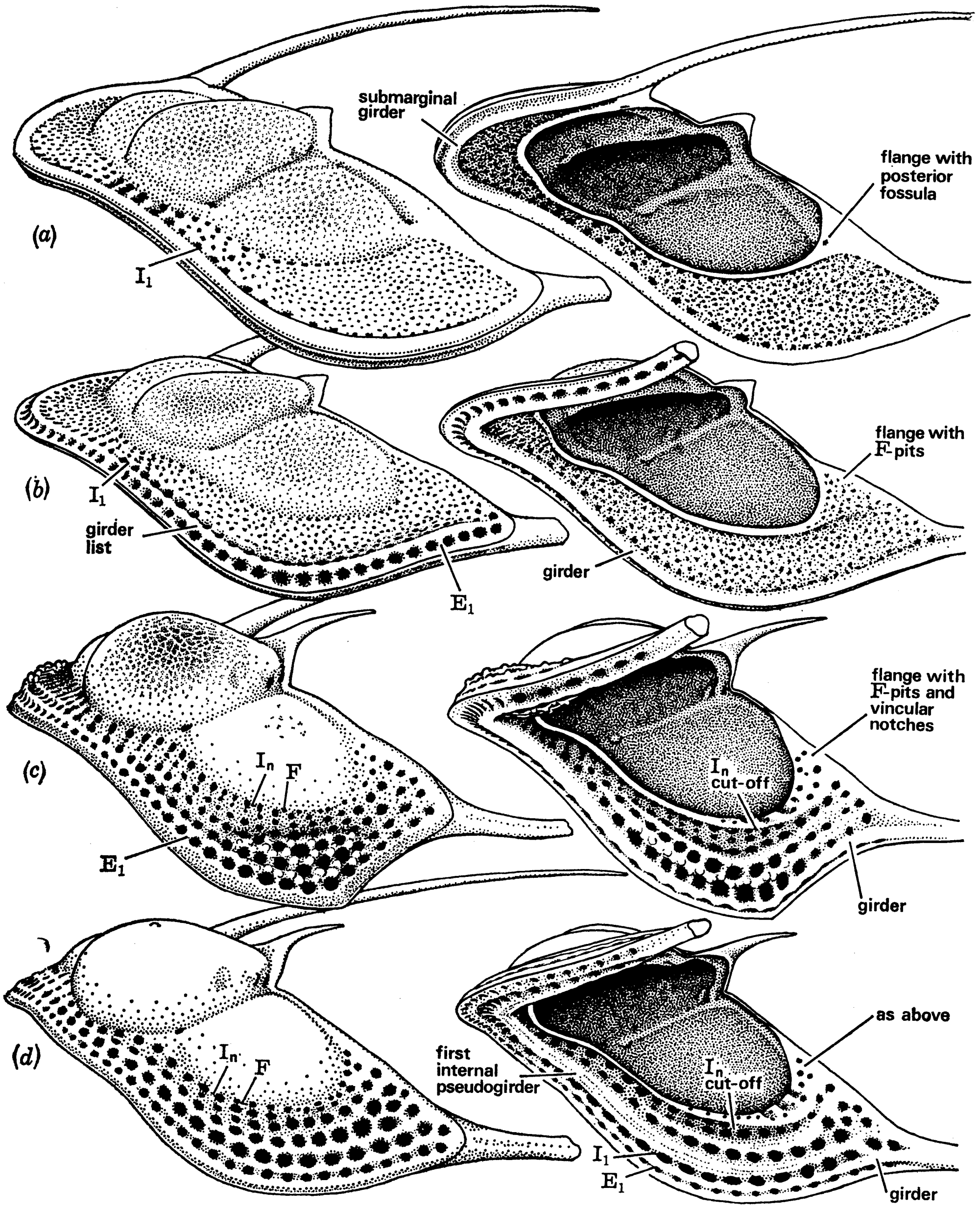


FIGURE 3. Cephala of selected trinucleid genera, illustrated in oblique dorsal and ventral views, to show comparative fringe morphology. (*a*) *Hanchungolithus* (Hanchungolithinae). (*b*) *Protolloydolithus*. (*c*) *Marrolithus*. (*d*) *Onnia* (Marrolithinae).

Trinucleid fringes are pierced by a variable number of narrow funnel-shaped pits, each dorsal pit having its ventral lower lamella counterpart. In the case of each pit, the combined structure thus formed resembles a hollow pillar, with the upper and lower halves having sutural separation (see Whittington 1959, pl. 20, fig. 8). The arrangement of these pits on the fringe is variable, but there is a basic framework whereby, on those fringes on which the pits have an organized arrangement, most of them are alined in radial *rows* and concentric *arcs* (Hughes 1970, p. 3).

The notation usually applied to the fringe pits is essentially that proposed by Bancroft (1929, pp. 69–72) although there have been elaborations and special modifications devised by

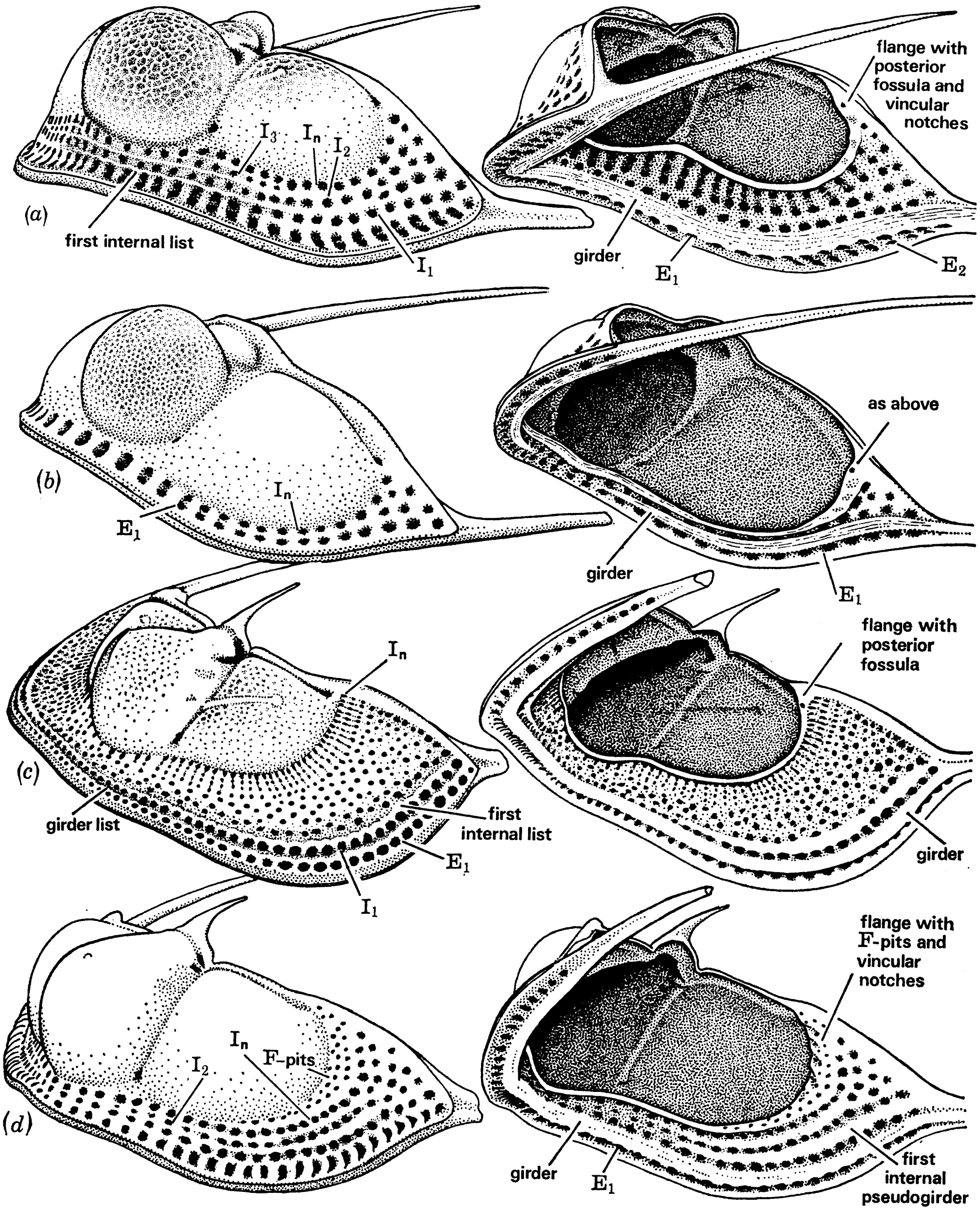


FIGURE 4. As for figure 3. (*a*) *Tretaspis* (*seticornis* group). (*b*) *Novaspis* (Trinucleinae). (*c*) *Reedolithus* (Reedolithinae). (*d*) *Cryptolithus* (Cryptolithinae).

Williams (1948, p. 49), Whittard (1955, p. 28) and Ingham (1970, pp. 40–41). In Bancroft's notation, a lower lamellar structure – the girder (figure 1) – is taken as a reference feature in the numbering of the arcs. The girder is a ventral concentric ridge confluent with a ridge on the genal spines. It is essential (Ingham 1970, p. 40) that the girder should be correctly identified from other concentric ventral ridges (pseudogirders) which occur in some forms, otherwise the notation loses its comparative usefulness.

We have found that the basic arc notation employed by Bancroft and most subsequent workers needs some reassessment, particularly at the inner fringe margins. The terms E_1, E_2, etc., for successive arcs external to the girder are left unchanged, but the internal 'I' arc notation has had to be modified in the light of recent observation. The Bancroft system of numbering successive I arcs inwards from the girder was adjusted by Ingham (1970) for the genus *Tretaspis*. His concept of a complete innermost arc (I_n) with incomplete I arcs successively inserted external to it solved the problem of homologous arc numbering in that genus. We have since found that the I_n concept has wide application within the family, and Addison's current study of silicified marrolithine young stages has shown that it is the I_n arc which is primary, i.e. it is the first arc to develop on the immature fringe with I_1 appearing next and successive I arcs being inserted between them. The recognition of this feature goes a long way towards rationalizing equivalent-arc numbering on most trinucleid fringes and it is the only arc numbering modification required for the trinucleines, reedolithines and hanchungolithines in which I_n is the innermost arc. In these three subfamilies an additional pit – the posterior fossula – is situated at the distal end of the posterior border furrow: it has its counterpart on the lower lamella, near the inner edge of the flange (see §2(*c*) and figures 1, 3*a*, 4*a–c*) and the posterior fossula is thus, strictly speaking, a fringe pit. In cryptolithines and marrolithines, however, there is no single posterior fossula: instead, a variable number of pits, all with their counterparts on the flange of the lower lamella, are developed internal to I_n. These pits we term flange- or F-pits. They rarely reach further forward than the mid-point of the genal lobe and usually they show only a rough arrangement into arcs. Posteriorly they are occasionally difficult to distinguish from adventitious pits inserted amongst the I series on the genal prolongation, for, on the lower lamella, the distal edge of the flange is sometimes unclear towards the rear; frontally, however, their position internal to I_n is usually very clear even on the upper lamella (figure 4*d*). In past studies of cryptolithine and marrolithine genera pits of the F series have been included and numbered consecutively with the I pits and this practice, together with the non-recognition of the I_n arc has meant that internal arc numbering has been highly subjective; demonstrably homologous arcs or pit groupings have previously received different numbers.

The Bancroft system of numbering pit rows outwards from the mid-line – R_0 (when present), R_1, R_2, etc., is continued, as is the inter-radial notation introduced by Whittard (1955), but only in those forms in which clear inter-radii are present, such as *Stapeleyella*. When complex radial relations are present, as in some species of *Tretaspis*, the use of aR and bR radii is advocated (see Ingham 1970, p. 40). It is sometimes useful to count pits along the posterior margin of the fringe (Størmer 1930) but this should be done with care: lack of precise pit alinement on this part of the fringe can make it a particularly subjective exercise.

Reference has already been made to the lower lamellar structures – girder and pseudogirders. The trinuceid upper lamella also frequently possesses inter-arc ridges but these 'lists' (see §2(*c*)) must not be confused with the lower lamellar features; the presence of a well-developed list on the upper lamella is no guarantee that the girder lies beneath it.

An additional feature is occasionally seen on the flange of the lower lamella in a variety of trinucleids. Besides bearing the posterior fossula or *F*-pits, the flange sometimes has a small number of concavities on its inner surface and indenting its margin. These are vincular notches: they received the tips of the thoracic segments during enrolment (figure 5). Their position is independent of any *F* pits the flange may bear.

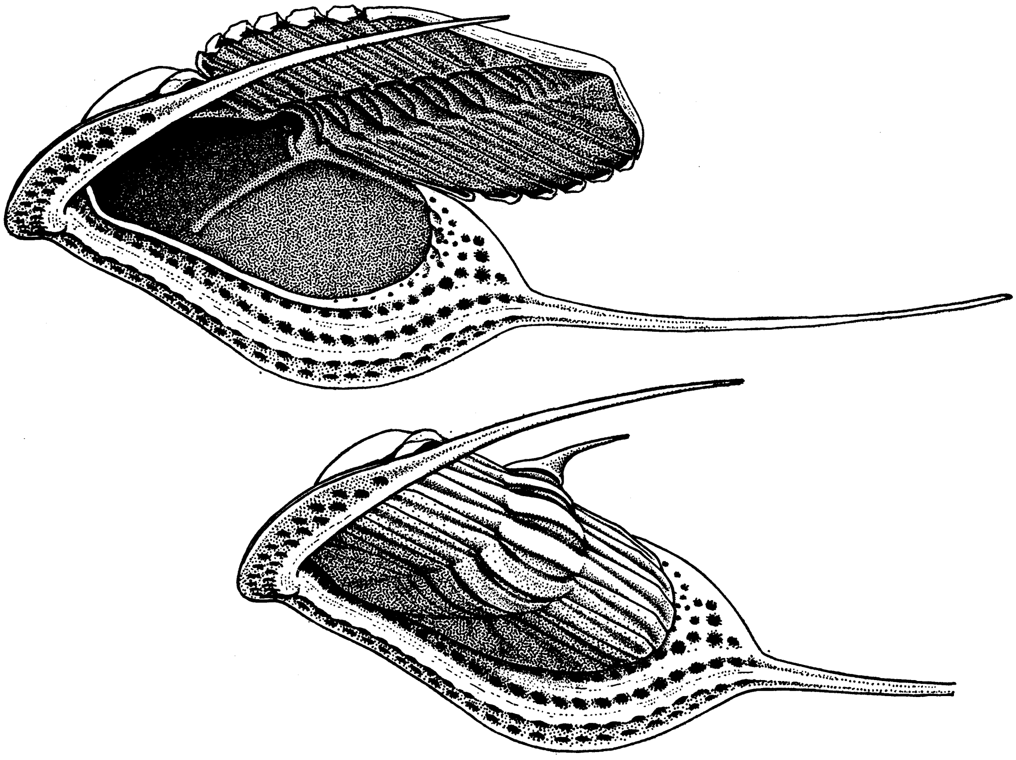


FIGURE 5. Trinucleid enrolment illustrated in *Broeggerolithus* (Cryptolithinae), to show the close fit of the tips of the thoracic segments into vincular notches on the flange of the lower lamella of the fringe.

The regular patterns of pit arrangement on the fringes of most trinucleids is surely a reflexion of the function of this elaborate structure. However, this must form an independent study.

(iii) *Surface sculpture*

External surface sculpture is virtually restricted to the cephalic regions. Apart from Dean's (1960, p. 85) reference to relic reticulation preserved on the thorax of *Reuscholithus reuschi*, the non-cephalic surface sculpture is almost entirely confined to the terrace lines of the deflected pygidial borders. The cephalic sculpture, when developed, is present on the glabella and genal lobes, tending to have its strongest development on the high points, e.g. along the crest of the glabella and over the postero-mesial portions of the genal lobes. The sides of the glabella and inner slopes of the genal lobes are commonly devoid of sculpture, even when it is well developed on other regions. There is a tendency for young individuals to possess a more pronounced sculpture than more mature individuals, e.g. *Bettonia* (see Hughes 1971), *Marrolithoides* (see Whittard 1966), *Smeathenia* (see Dean 1960), *Reuscholithus* (see Dean 1960) and *Tretaspis* (see Ingham 1970).

Three basic sculptural types may be recognized (figure 6). Rarely intermediates are found, particularly between types *b* and *c*, and the reticulate sculpture may range from coarse as in *Telaeomarrolithus* (figure 36, plate 3) to very fine as in *Novaspis* (figure 4*b*).

Very little comment appears to have been made regarding the possible function of external sculpture in trilobites. The positioning of the sculptured portions of the exoskeleton in the trinucleids usually on the topographical highs suggests that it possibly functioned as a camouflage from above, or in some way enabled changes in the water flow over the surface to be detected, possibly indicative of predator approach. The more pronounced development in immature individuals possibly reflects the greater need for protection or a slightly different mode of life. Further possible functions might involve the entrapment of gases for buoyancy purposes or simple strengthening of the exoskeleton.

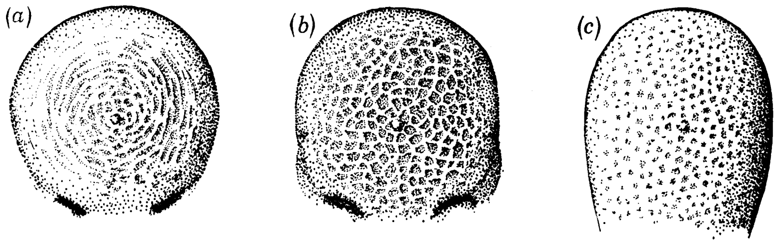


FIGURE 6. Types of surface sculpture. Part of the glabella of (*a*) *Botrioides*? (*bucculentus*), showing subconcentric ridges, (*b*) *Tretaspis*, showing reticulation and (*c*) *Bettonia*, showing pitting.

(iv) *Orientation*

The wide range of cephalic proportions in different trinucleid genera creates difficulties in selecting a consistent method of orienting specimens for comparative purposes and measurement. Few forms, when represented by uncrushed specimens, are sufficiently flat for them to be placed in an unequivocal horizontal position. Indeed, many genera have fringes so steeply declined that fringe details can only be seen in lateral, frontal or oblique views. Moreover, the margin of the fringe is never straight: anteriorly it is dorsally arched and laterally, although sometimes nearly straight, it is commonly curved ventro-laterally, depending on the degree of lateral fringe expansion. In life the resting position of trinucleids may well have been with the cephalon resting on the lateral margins of the fringe and the backwardly curving genal spines. This position is not readily usable for comparative purposes because it depends not only on the degree of curvature of the lateral fringe margin but also on the set of the genal spines, which is also widely variable and, in any event, the latter are rarely found in a complete and undistorted state. Of the non-fringe features we have considered, orientation of the glabella with the posterior and anterior margins placed in a horizontal position has been rejected because it is strongly influenced by the degree of anterior expansion and invasion of the fringe by its frontal part: in extreme cases – for example, the un-named reedolithine genus illustrated (figures 72–74, plate 6) – such an orientation gives rise to a marked rearward declination of the lateral fringe margin. The most useful orientation we have discovered is achieved by placing the anterior and posterior fossulae (or postero-mesial *F* pit) in a horizontal plane (see figure 7). This arrangement is influenced neither by variation in fringe proportions nor by glabellar convexity and we have found that when specimens are oriented in this manner their position approximates to the presumed resting posture.

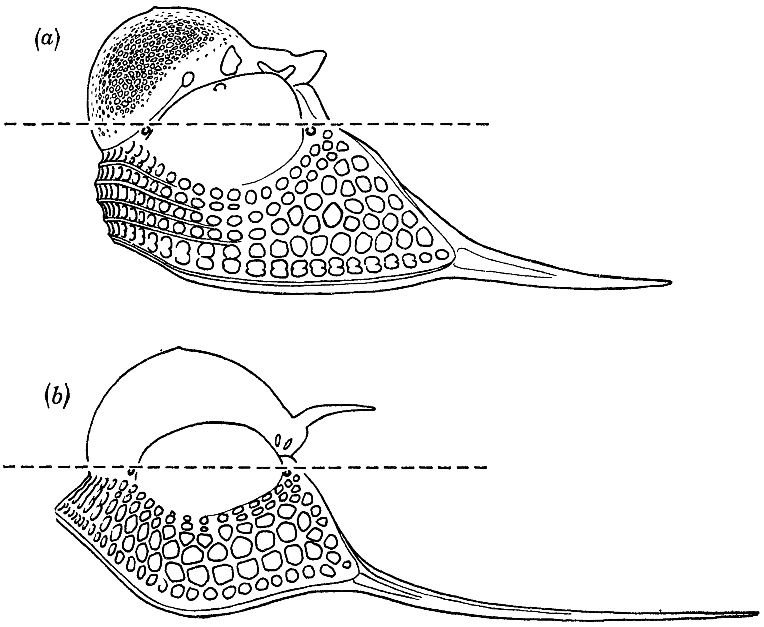


Figure 7. Suggested orientation of trinucleid cephala for measurement purposes (see text). (*a*) *Tretaspis*. (*b*) *Onnia*.

(*b*) *Thoracic and pygidial morphology*

There are six segments in the thorax of all mature trinucleids. Their detailed morphology is most clearly displayed by the silicified specimens of species of *Cryptolithus* and *Tretaspis* described by Whittington (1959). The axial region may occupy up to about one quarter of the total width of the thorax and although the axial furrows are shallow, the axis is nevertheless well-defined by the change in slope at its lateral margins. The axial rings are narrow (sag. and exsag.) and each may bear a transverse groove and narrow ridge. The latter may itself carry a row of very small tubercles, as in some species of *Tretaspis*, and a small, sagittally elongate tubercle is present on the anterior slope of the axial ring in a number of trinucleines. The articulating furrow is shallow but well-defined anteriorly: near its outer ends it contains a pair of deep, transverse apodemal pits which have ventral expression in short apodemes. In all but the first segment, the articulating half-ring is arched anteriorly and fits beneath a similarly shaped, transversely striated doublure under the adjacent axial ring. Whittington (1941*b*, p. 510; 1959, p. 443) stated that the first segment of *Cryptolithus* has no development of an articulating half-ring as does Hughes (1971, p. 126) with reference to *Trinucleus*, but, judging by Whittington's photographs (1959, pl. 21, figs 1–3, 8), the structure in front of the articulating furrow on the first segment is homologous with the articulating half-ring on other segments only it has a straight anterior edge and the posterior margin is rearwardly curved. Hughes (1971) mentions an additional pair of small apodemal pits in front of the main pair on the first segment of *Trinucleus fimbriatus*: similar, but shallow, depressions are also present in *Cryptolithus tessellatus* (see Whittington 1959, pl. 21, fig. 2). The large, originally integument-covered space produced between the occipital ring and the first half-ring during enrolment (Whittington 1941*b*, p. 510; 1959, pl. 20, fig. 5; Hughes 1971, p. 126) is partly a reflection of the modified form of the latter structure. Although a large part of the thoracic flexing took place between the first and second, and second and third segments (Hughes 1971, pp. 126–127), the close fit of the first segment against the inner face of the flange of the lower lamella (Whittington 1959, pl. 20, fig. 5) shows that even more flexing occurred between the cephalon and the first segment. Thus the space mentioned above was a reality in these trinucleids during life. A similar situation has been noted by us in material referable to *Onnia* from Morocco. The function of this vulnerable area is not known: in *Cryptolithus* and *Onnia* it is only partly protected by the occipital spine.

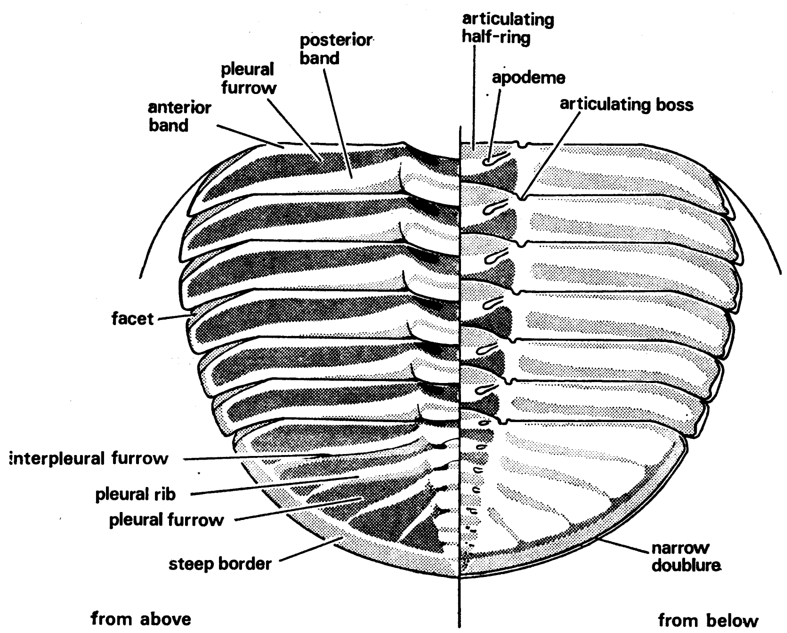


Figure 8. Basic morphology of the trinucleid thorax and pygidium, with posterior edge of cephalon indicated.

The pleural portions of the segments are long (tr.), narrow (sag.) and parallel-sided for most of their length. Distally, there is a fulcrum beyond which the pleura is deflected somewhat downwards and slightly rearwards. All but the anterior pleurae have blunt terminations, each consisting of a nearly vertical lateral border, below which is a very narrow recurved doublure. A pleural furrow begins at an apodemal pit in the articulating furrow and is directed either obliquely backwards as in *Cryptolithus* to terminate at a slightly raised rim above the lateral border, or it may become broad (exsag.) near the axial furrows to follow a path subparallel with the anterior and posterior margins of the pleura as in *Tretaspis*. There is thus a raised anterior and posterior band on each pleura: to the rear of the posterior pleural band is a very narrow, depressed border. The pleurae on the first thoracic segment have a modified shape to accommodate the form of the posterior edge of the cephalon, where the fulcral position is more proximal, and also to fit against the posterior part of the inner edge (flange) of the lower lamella of the fringe during enrolment (see above). In more posterior segments the narrow facet on the anterior edge of the distal part of each pleura was accommodated on enrolment, in a small notch in the terminal doublure at the rear of the adjacent segment. The main articulating mechanism between the thoracic segments, and with the cephalon and pygidium is in the vicinity of the axial furrows where, at the anterior margin of each segment, a deep antero-ventral notch between two small bosses accommodates a more prominent boss commonly flanked by two small notches on the posterior edge of the adjacent segment (see Whittington 1959, pl. 21, figs 1–6).

The pygidium in trinucleids is subsemicircular or subtriangular in shape with a steeply declined border. This is narrowest anterolaterally but becomes broader towards the rear: its ventral edge is commonly arched dorsally at the mid-line and is recurved to form a very narrow doublure (see, for example, Whittington 1959, p. 21, fig. 10). Fine terrace-lines are present on the deflected border and are subparallel to its ventral edge. The axis, which narrows appreciably towards the rear, has an articulating half-ring like those of the posterior thoracic segments. There are a variable number of axial rings separated by transverse furrows; a number of these on the anterior part of the axis contain a pair of apodemal pits (appendifers on the ventral surface) and commonly accompanying them is an anteriorly arched sharp furrow representing the frontal margin of a non-functional articulating half-ring. Towards the rear, the transverse furrows and apodemal pits become less well-defined and their place is taken by two sets of paired muscle scars, usually visible dorsally as very shallow depressions on the axis (see Whittington 1959, pp. 443, 452, pl. 21, fig. 11, pl. 24, figs 16–18). In many trinucleines, and at least some reedolithines and hanchungolithines, these axial structures continue onto the declined border: in most cryptolithines and marrolithines, however, they become very ill-defined before the border is reached or terminate at the border. The pleural lobes of the pygidium are usually rather flat and variably depressed below a rim forming the dorsal edge of the border. The lobes are usually crossed by a number of shallow, distally broadening pleural furrows which define the pleural ribs and the latter sometimes bear faint, narrow interpleural furrows. Commonly, the pleural ribs do not reach the border.

(*c*) *Explanation of terms*

Many of the morphological terms employed are in common usage in trilobite literature and are here used in accordance with the definitions given in Moore (1959, pp. 0117–0126). Other terms are either new or specifically refer to trinucleids and are defined below.

ala (pl. alae) (syn. alar lobes): most authors have used this term to refer to the small, low, generally elongate (exsag) and gently convex structure which lies adjacent to the posterior part of the glabella, bounded internally by the axial furrow and externally by the alar furrow, and this usage is followed here. Some authors, notably Whittard, have used the term for the structure referred to here as the composite lateral glabellar lobe (*q.v.*).

anterior fossula (syns. anterior pit, hypostomal pit, pseudo-antenary pit): small pit near anterior end of axial furrow.

arc: term proposed by Hughes (1970, p. 3) as a replacement for 'concentric row' applied to the concentrically arranged elements of the fringe.

brim: peripheral gently concave portion of upper lamella.

composite lateral lobe: lateral portion of glabella bounded externally by axial furrows and internally by 1p and 2p lateral glabellar furrows (see Reed 1914*b*, pp. 350–351). This structure tends to be accentuated in partially compressed specimens and has been referred to by some authors as an ala or alar lobe (e.g. Whittard 1956).

E pit: any pit situated externally to the girder (Bancroft 1929, p. 69).

flange (new term, see figures 1, 3, 4) (syn. 'integument attachment' of Stäuble 1953, p. 89, figure 1*c*): inner margin of lower lamella which may be expanded posteriorly.

F pit (new term, see figures 3, 4): pit developed on the inner face of the flange, occurring on the upper lamella as small pits at the inner edge of the fringe internal to arc I_n (*q.v.*).

genal flange: area of genal roll opposite posterior margin of genal regions, commonly occupied by irregularly distributed pits (see Whittard 1956, p. 29 and text-fig. 3*a*).

genal prolongation: that part of the fringe which extends posterior to the posterior margin of the genal region (see Moore 1959, p. 0112, figure 84).

genal roll: inner convex portion of the upper lamella of the fringe.

girder list (new term, see figures 3, 4): ridge on upper lamella of fringe corresponding in position to the girder of the lower lamella.

I_n: innermost arc of *I* pits (see Ingham 1970, p. 40).

I_n cut-off (new term, see figures 3, 4): point at which the I_n arc is terminated, i.e. 'cut-off', by the adjacent *I* arc as in the Marrolithinae.

I pit: any pit situated internally to the girder, but not including those on the flange.

inter-radial ridge/plate: ridge or plate separating adjacent rows of pits on both upper and lower lamellae, particularly prominent on sulcate fringes (see Hughes 1971, p. 117).

list: any concentric ridge on the upper lamella occurring between arcs.

occiput: independently convex posterior portion of glabella, bounded anteriorly by 1p lateral glabellar furrows and posteriorly by the occipital furrow (see Stäuble 1953, p. 87).

posterior fossula (syn. lateral pits of various authors e.g. Stäuble 1953): pit at lateral extremity of posterior border furrow opposed by a pit on the flange of the lower lamella.

pseudofrontal lobe: composite structure forming anterior part of glabella characteristically in the Trinucleinae, bounded posteriorly by the 2p lateral glabellar furrows and incorporating much reduced or absent 3p furrows (Reed 1914*b*, pp. 350–351).

pseudogirder (see figures 3, 4): any concentric ridge occurring between *E* or *I* arcs on the lower lamella.

rim: narrow peripheral ridge of either upper or lower lamella (cf. Whittinton 1950, text-fig. 1).

3. Generic and subfamilial criteria

Most modern work on the Trinucleidae has considered the structure of the cephalic fringe to be of primary importance in defining genera, and other morphological features, particularly those of the glabella and genal regions have been taken as of secondary value. Not all workers, however, have subscribed to this view in the past, for Reed in his series of papers on *Trinucleus* (1912, 1914*b*, 1916) placed particular emphasis on the glabellar structures, a concept that was followed essentially by Størmer (1930), who largely rejected Bancroft's (1929) new genera based on differing patterns of fringe pitting. Whittington (1940, 1941*a*) followed Bancroft and Størmer subsequently partially retracted his criticism (1945). Since that time most, if not all, authors, while not totally ignoring other features, have laid great emphasis on the fringe morphology both for specific and generic discrimination. Further, they have done so with very little discussion of the possible problems involved. Williams (1948) agreed with both Bancroft and Whittington, and Dean (1960), one of the few other authors to mention the problem, reviewed past practice but made little assessment of it. The present investigation has indicated that fringe characters such as the number and disposition of arcs developed, position and degree of development of girder, pseudogirders and lists, are important for generic discrimination, whereas what may be termed more basic fringe characters, i.e. presence of E arcs, presence or absence of F pits, and of I_n cut-off (see below), taken together with other cephalic characters as glabellar form are more important for discrimination at the subfamilial level.

Lu (1963) discussed the problem of deducing a satisfactory phylogenetic classification of the Trinucleidae in some detail, advocating the use of all cephalic morphological features; being in Chinese, however, has meant that it has been overlooked by most workers. The problem of what characters to use in attempting to deduce a phylogenetic classification has been discussed recently in detail for the trilobite family Calymenidae by Whittington (1971). In this group Whittington claimed that some features, for example, the papillate-buttress structure, which is present in a wide variety of forms over a range of time, were not obviously of adaptive value and thus considerable weight could be put on them in determining a classification. Other characters such as the form of the anterior border and the development of frontal extensions were more clearly adaptive and should thus carry less weight. Using these concepts he concluded that the pattern of evolution in the calymenids was one of 'shuffling and recombination of characters in an evolving plexus' similar to that he had previously demonstrated in the Odontopleuridae (Whittington 1956).

In some respects a similar situation is believed to exist in the Trinucleidae, and selection of characters upon which to base a supra-generic classification is not obvious at first sight, a fact reflected by the lack of any previous satisfactory attempt to erect a subfamilial classification. In the past a great deal of emphasis has been put on the pit distribution on the fringe, but with increasing knowledge of the variety of forms this has become progressively more unsatisfactory. Although the function of the pits and the fringe is unknown it is thought that the details, at least, of the pit distribution must in some way be adaptive.

However, in a group such as the Trinucleidae, ranging over a relatively short portion of geological time and showing little or no evidence of several distinct bursts of evolution, the only practical way of defining any classificatory units is in terms of hard-part morphology. The present study has shown that despite the apparent complexity of the evolution of the pattern of the distribution of the pits on the fringe, there are two major morphological features of the fringe that do appear to be consistent and of use in supra-generic classification, namely the presence/absence of a series of F pits, excluding the posterior fossula, and the relation between arc I_n and the other I arcs (either parallel or oblique, the latter causing I_n to be cut-off by the next I arc out). The apparent complexity of the evolution of the fringe is believed to be due to various combinations of adaptive features being superimposed on these two major features, much in the same way as Whittington showed for the calymenids and odontopleurids.

A further morphological feature that has proved of consistent value is the gross form of the glabella. Importance has been put on this feature by a few authors in the past, notably Reed (1912, 1914*b*) and Whittington (1941*a*). We consider that there are basic types of glabella, e.g. trinucleine, cryptolithine (figures 2*b*, *c*, *d*; *e*, *f*, *g*), which occur in a variety of forms throughout the family and that these can be used to help in deducing supra-generic affinities.

The subfamilial classification proposed here has been formulated by placing considerable weight on the two fringe features discussed above and on the gross glabellar form, with lesser stress placed on other cephalic features such as presence of a pre-glabellar field and lateral eye tubercles. Formal diagnoses of these subfamilial groups are given in the appropriate positions in §4, but for convenience of quick reference the more important characteristics of each subfamily, together with the known stratigraphic range are summarized in table 1.

It appears, if the classification proposed here is accepted, that although within each subfamilial group various combinations of characters, particularly of the details of the fringe, may occur, the major divisions in the Trinucleidae are more clear cut than is the case in some other trilobite groups, e.g. calymenids, where the reshuffling of characters tends to mask the major subdivisions to a greater extent.

Table 1

subfamily	*E* pits	*F* pits†	I_n cut-off	glabellar form	other features	range
Hanchungolithinae	absent	absent	no	clavate	*I* pits irregularly distributed	Arenig–Llandeilo
Trinucleinae	present or absent	absent	no	pseudofrontal lobe prominent	usually without occipital spine; may have lateral eye tubercles	Arenig–Ashgill
Reedolithinae	present	absent	no	high, clavate and carinate	usually with occipital spine; with lateral eye tubercles	Llandeilo–low Caradoc
Marrolithinae	present	present	yes	clavate	—	Llanvirn-Ashgill
Cryptolithinae	present	present	no	high, clavate	—	Caradoc-Ashgill

† Other than the posterior fossula.

We have taken the commonly accepted standpoint that a genus is a group of related species, of necessity including the designated type species, and the genera are diagnosed herein so as to embrace all the species included. However, there are bound to be some problems of generic assignment with the use of a hierarchical classification such as is currently favoured. An attempt is made to define all genera by using their characteristic cephalic morphological features in the main and also to deduce, as far as possible, relations between genera within each subfamily (see figure 120). These relations have been arrived at on morphological grounds, but the fact that, in general, stratigraphical and geographical occurrences are consistent with these relations lends weight to the argument that the proposed classification reflects natural relationships.

4. Systematic descriptions

(*a*) Family Trinucleidae, Hawle & Corda, 1847

Diagnosis. Trilobites with bilaminar cephalic fringe possessing numerous opposed pits on external surfaces. Facial suture marginal, becoming dorsal along posterior margin of fringe; genal spines on lower lamella. Thorax of six segments, with distal extremities of pleurae deflected strongly downwards. Pygidium triangular, posterior and lateral margins deflected nearly vertically downwards. Pygidial and thoracic doublure very narrow.

Distribution. Known throughout the Ordovician from all the major continental areas with the exception of the southern portion of Africa, where very little fossiliferous Ordovician rock is known, and Antarctica where no Ordovician trilobites have yet been discovered.

Discussion. The trinucleids, although clearly related to such families as the Raphiophoridae and Dionididae, are a very well-defined, and in many ways, uniform group of Ordovician trilobites. Divisions within the family as currently defined (Moore 1959, pp. 0420–0424) are no longer adequate in the light of modern knowledge and a new subfamilial classification is adopted here, based on a study of all currently accepted trinucleid genera.

(*b*) Subfamily Hanchungolithinae Lu, 1963

Diagnosis. Fringe nearly flat, with no E pits, or F pits, other than the posterior fossula. Girder marginal or submarginal. Considerable irregularity in pit distribution. Lateral eye tubercles and eye ridges present in juvenile forms, but hardly visible in adults.

Type genus. Hanchungolithus Lu, 1954.

Distribution. Lower Arenig of Wales, the Welsh Borderland, south-eastern Ireland and southern France; Llanvirn of central China; lower Llandeilo? of Argentina; undifferentiated middle Ordovician of Iran.

Discussion. The genera included in this subfamily form a compact early group from which all other trinucleid groups are likely to have descended. Lu (1963, 1964) drew attention to the similarities between cephala of adult hanchungolithines and immature individuals of a variety of later trinucleids and regarded this as evidence of recapitulation. Certainly the early marrolithine genus *Protolloydolithus* has many features in common with *Hanchungolithus* and *Ichangolithus*. *Myttonia* is here regarded as a hanchungolithine though it is in some characters intermediate between typical Hanchungolithinae and early Trinucleinae. *Ningkianolithus* and *Ceratolithus* exhibit some features such as pit enlargement and anterolateral fringe angulation which were subsequently developed independently in later marrolithines (see p. 569) and in a trinucleine (see pp. 556–557).

Genus **Hanchungolithus** Lu, 1954

figures 9, 10 plate 1; figures 2*a*, 3*a*

Diagnosis. Hanchungolithine with large pits of only I_1 and I_n developed in regular arrangement frontally.

Type species. Cryptolithus multiseriatus Endo, 1932. Original designation by Lu 1954 (not seen) (see also Lu 1963, 1964).

Other included forms:

H. primitivus (Born, 1921) (see also Whittard (1957) and Dean (1966)).

H. aff. *primitivus* of Brenchley *et al.* (1967).

Distribution. Lower Arenig of southern France and south-eastern Ireland; Llanvirn of central China.

Discussion. Although Lu (1964, p. 293) suggested that the two described species may be synonymous, Dean (1966, p. 282) indicated minor but consistent features which separate them. To Dean's points may be added the radial sulcation frontally in *H. primitivus* which is not present in *H. multiseriatus*.

Genus **Ichangolithus** Lu, 1963

Diagnosis. Like *Hanchungolithus* but with irregularly distributed small pits between I_1 and I_n extending in front of the glabella.

Type species. Ichangolithus ichangensis Lu, 1963. Original designation p. 320 (see also Lu 1964).

Other included form:

I. sp. (Dr B. A. J. Baldis 1972, private communication).

Distribution. Llanvirn of central China; lower Llandeilo of Argentina.

Discussion. Erected by Lu as a subgenus of *Hanchungolithus, Ichangolithus* is here regarded as being sufficiently distinctive to warrant full generic status.

Genus **Ningkianolithus** Lu, 1954

Diagnosis. Hanchungolithine with both lamellae of the fringe swollen laterally and anterolaterally and pits of the outer I arcs grossly enlarged, particularly those of I_1 around the periphery of the fringe.

Type species. Cryptolithus welleri Endo, 1932. Original designation by Lu 1954 (not seen) (see also Lu 1963, 1964).

Other included forms:

N. cf. *welleri* of Winsnes *in* Ruttner, Nabavi & Hajian (1968).

N. honghuayuanensis Chang (see Lu 1974).

Distribution. Llanvirn of central China; middle Ordovician of Iran; lower Ordovician of southwest China.

Discussion. The swollen fringe with its enlarged pits is reminiscent of *Marrolithus*, but in *Ningkianolithus* the basic fringe pattern is that of the Hanchungolithinae with a marginal girder, clavate glabella and no F pits.

Genus **Ceratolithus** Lu, 1963

Diagnosis. Hanchungolithine with a pair of stout spines present at the anterolateral angulations of the fringe. Lateral eye tubercles and eye ridges retained in adult.

Type species. Ceratolithus cornutus Lu, 1963. Original designation p. 320 (see also Lu 1964).

Distribution. Llanvirn of central China.

Discussion. Although Lu (1963, 1964) only tentatively regarded *Ceratolithus* as belonging to the Hanchungolithinae, its overall morphology and very close resemblance to immature individuals of *Ningkianolithus welleri* suggest that it is correctly placed, and that it may eventually prove to be best regarded as a synonym of *Ningkianolithus*.

Genus **Myttonia** Whittard, 1955

figures 11, 12, plate 1

Diagnosis. Radially alined I_1 and I_n present frontally with additional, rather irregular I arcs present laterally.

Type species. Myttonia confusa Whittard, 1955. Original designation p. 29.

DESCRIPTION OF PLATE 1

FIGURES 9, 10. *Hanchungolithus primitivus* (Born, 1921) Couches de Landeyran superieur (lower Arenig), near southern end of Landeyran valley, Hérault, France. 9, Latex peel from dorsal mould of incomplete cranidium, BM. It. 9694. 10, Latex peel from ventral mould of part of cephalon, BM. It. 11602, showing lower lamella with submarginal girder and a small posterior fossula on flange. (Magns × 6.)

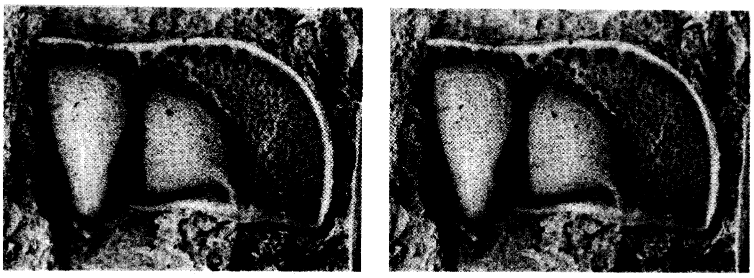
FIGURES 11, 12. *Myttonia fearnsidesi* Whittington, 1966*a*. Holotype. BM. It. 303. Henllan Ash (lower Arenig), east slopes of Moel Llyfnant, Gwynedd (Merionethshire) Wales. 11, Latex peel from dorsal mould. 12, Latex peel from ventral mould showing lower lamella. (Magns × 6.)

FIGURES 13, 14. *Famatinolithus noticus* Harrington & Leanza, 1957. Suri Formation (Llanvirn), Rio Cachiyuyo region, La Rioja Province, Famatino range of northwestern Argentina. 13, Latex peel from dorsal mould of incomplete cephalon UBA. 4216 (holotype) (magn. × 5). 14, Latex peel from ventral mould of cephalon UBA. 4215 (paratype) showing lower lamella with thick marginal girder (magn. × 4).

FIGURE 15. *Famatinolithus* sp. Undifferentiated Ordovician, Pantipampa, Tarija department, southern Bolivia. Oblique anterior view of cephalon retaining exoskeleton. USNM. 187757, (Branisa collection), showing well-defined preglabellar field (magn. × 4).

FIGURES 16–19. *Anebolithus simplicior* (Whittard, 1966). Mytton Flags (lower Arenig), near northeastern corner of Snailbeach Reservoir, Shelve Inlier, Salop (Shropshire), England. 16, Ventral mould of cranidium GSM. 102179 (magn. × 6). 17, Latex peel from dorsal mould (counterpart) showing sharply defined area of reticulate sculpture on genal lobes (magn. × 6). 18, Ventral view of internal mould of lower lamella GSM. 102419 (Paratype) (magn. × 8). 19, Latex peel from dorsal mould of holotype GSM. 102178a (magn. × 5).

All figures are stereophotographs.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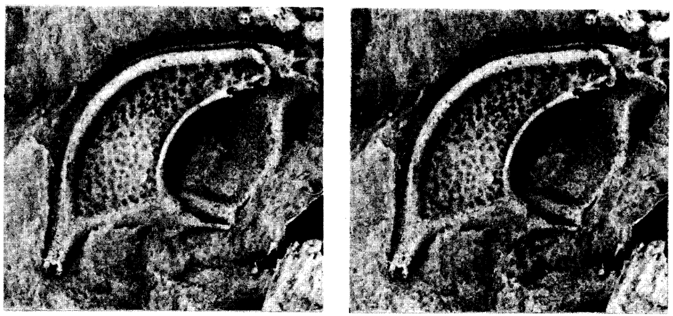
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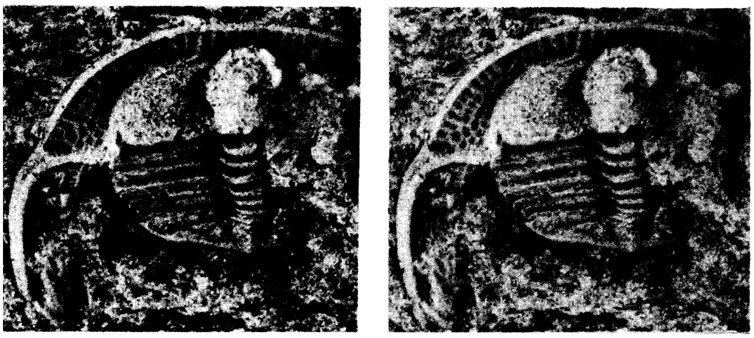
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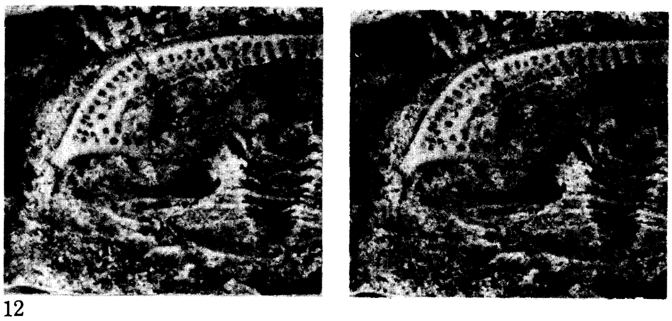
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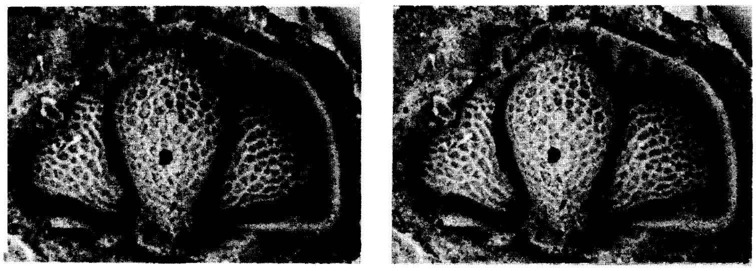
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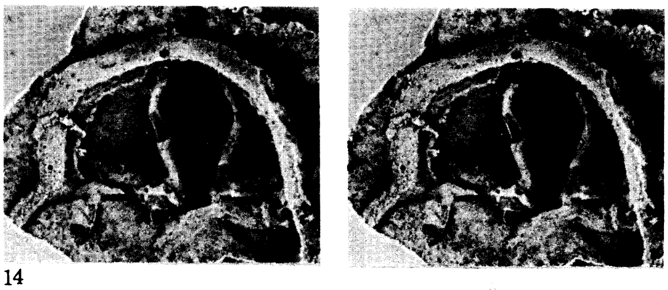
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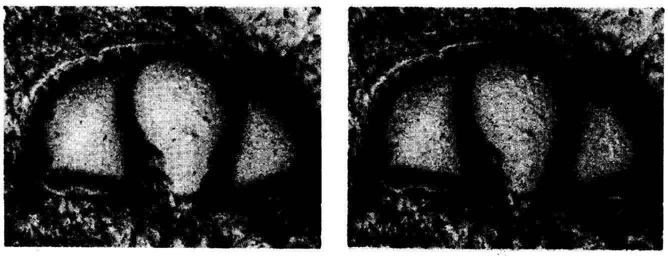
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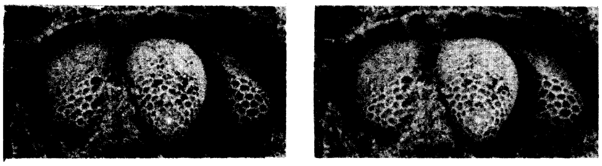
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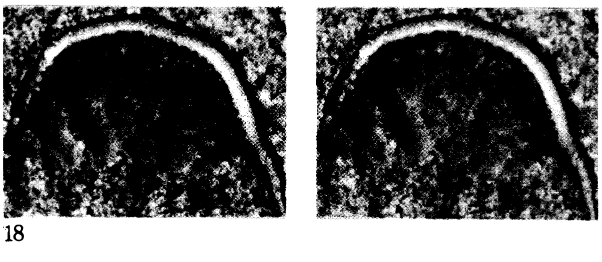
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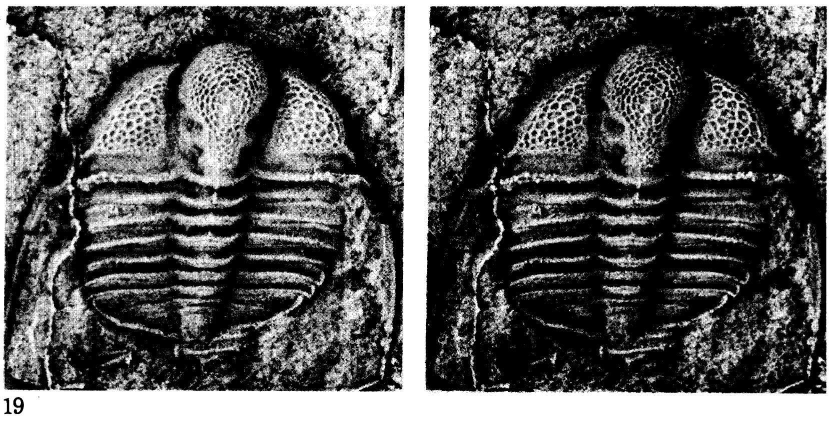
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FIGURES 9–19. For description see opposite.


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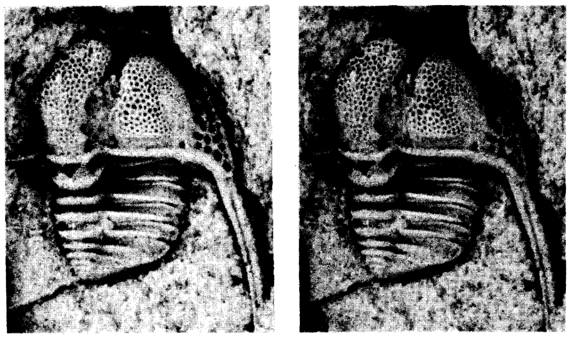
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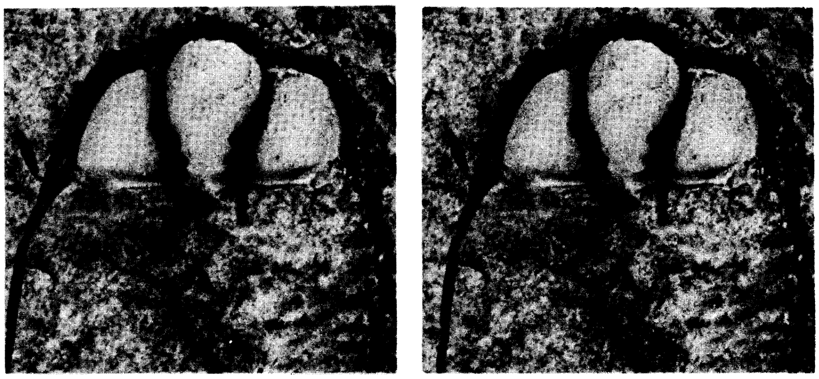
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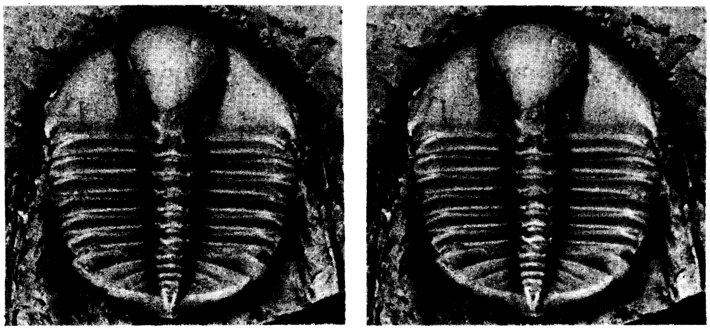
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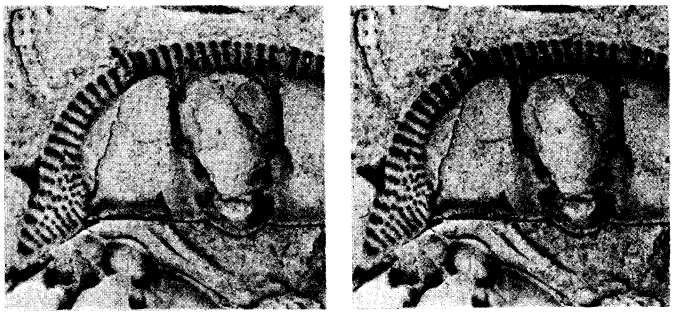
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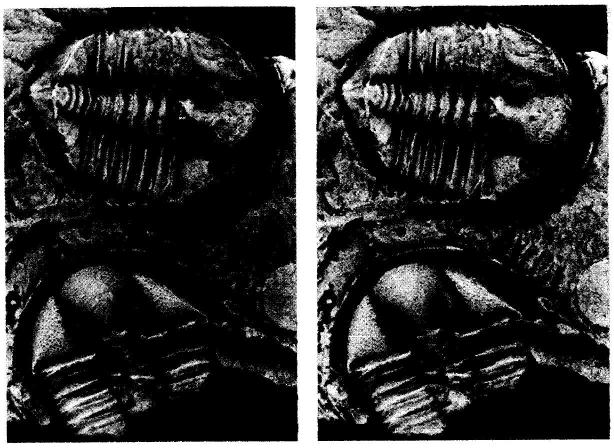
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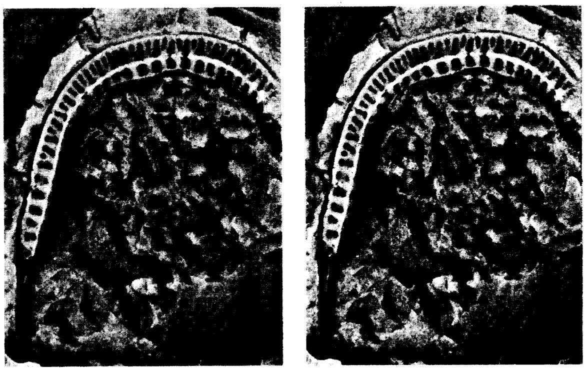
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FIGURES 20–31. For description see opposite.

Description of plate 2

Figure 20. *Incaia nordenskioeldi* (Bulman, 1931). Upper Llanvirn between Limpucuni and Itchubamba, southeastern Peru. Ventral mould of cranidium, Ar. 42446 (magn. × 6).

Figures 21, 22. *Incaia bishopi* Hughes & Wright, 1970. Golden Bay Group (middle to upper Llandeilo or lowest Caradoc—*N. gracilis* Zone), scree material, Paturau River, New Zealand. 21, Latex peel from replica of ventral mould of holotype lower lamella BM. It. 9302 (original VA.6a) (magn. × 6). 22, Latex peel from replica of dorsal mould of pygidium, BM. It. 9304 (original VA.9b) (magn. × 3).

Figures 23, 24. *Lordshillia confinalis* Whittard, 1966. Mytton Flags (lower Arenig), near northeastern corner of Snailbeach Reservoir, Shelve Inlier, Salop (Shropshire), England. 23, Latex peel from dorsal mould of imperfect individual, GSM. 102422 (paratype). 24, Ventral mould of cephalon showing ventral (external) mould of lower lamella, GSM. 102420 (holotype). (Magns × 6.)

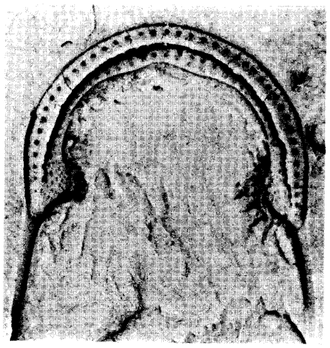
Figures 25, 27. *Bergamia prima* (Elles, 1940). *Glyptograptus teretiusculus* Shales (lower Llandeilo) respectively old quarry and stream section west of Maesgwynne, south of Llandrindod Wells, Powys (Radnorshire), Wales. 25, Ventral mould of complete individual, BM. It. 2753, showing faint, short eye ridges (magn. × 3). 27, Internal mould of lower lamella, BM. It. 2746, showing E_{1-2} twin pits (magn. × 5).

Figure 26. *Bergamia whittardi* Hughes, 1971. *Glyptograptus teretiusculus* Shales (lower Llandeilo) small quarry at southwestern end of Pen-cerig Lake, Powys (Radnorshire), Wales. Ventral mould of cranidium, BM. It. 2754 (paratype) (magn. × 4).

Figure 28. *Bergamia*? sp. Tal-y-tan Argillites (lower Llanvirn) of Penarfynydd, Aberdaron, Gwynedd (Caernarvonshire), Wales. Latex peel from ventral mould of lower lamella NMW. 27.110G 271b (C. J. Williams collection), showing an arrangement of pits in E_2 which suggests an intermediate stage between *Bergamia* and *Stapeleyella* (magn. × 1½).

Figures 29–31. *Stapeleyella inconstans* Whittard, 1955. 29, 31, Hope Shales (lower Llanvirn), path west of Brithdir, 1.6 km (1 mile) east-northeast of Old Church Stoke, Shelve Inlier, Salop (Shropshire), England. 30, Shales in Stapeley Volcanic Group (lower Llanvirn), Nind Quarry, also Shelve Inlier. 29, Two individuals, GSM. 92971 (syntypes), retaining some exoskeleton (magn. × 2). 30, Ventral moulds of two cranidia, GSM. 92972 (syntypes) (magn. × 3). 31, Internal mould of lower lamella, GSM. 92974 (syntype) (magn. × 3).

All figures except 20–22, 27, and 28 are stereophotographs.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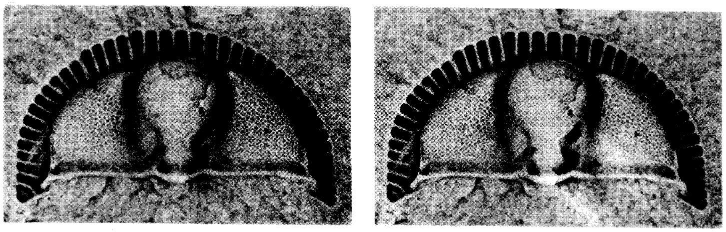
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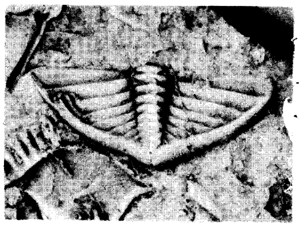
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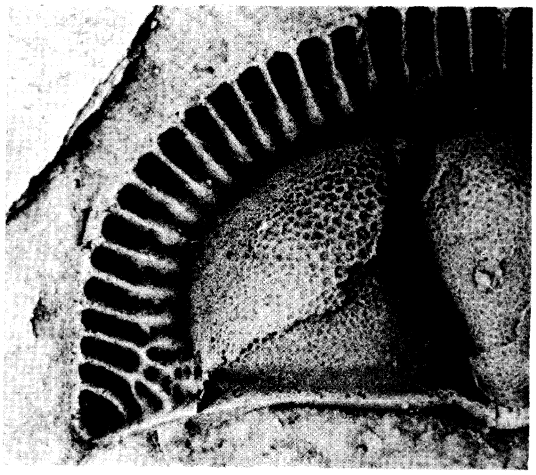
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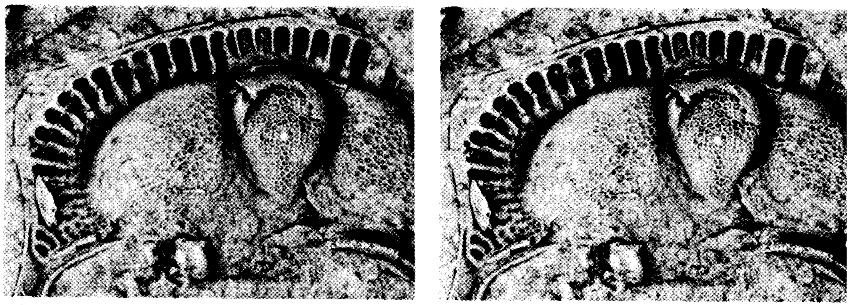
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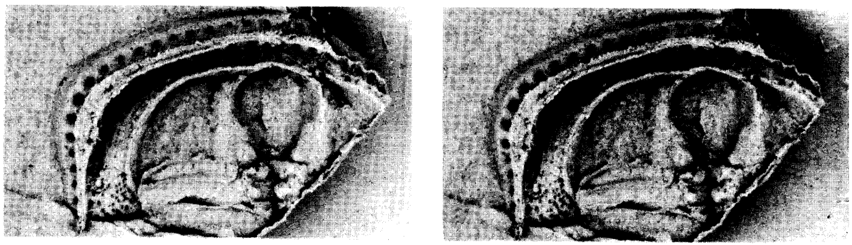
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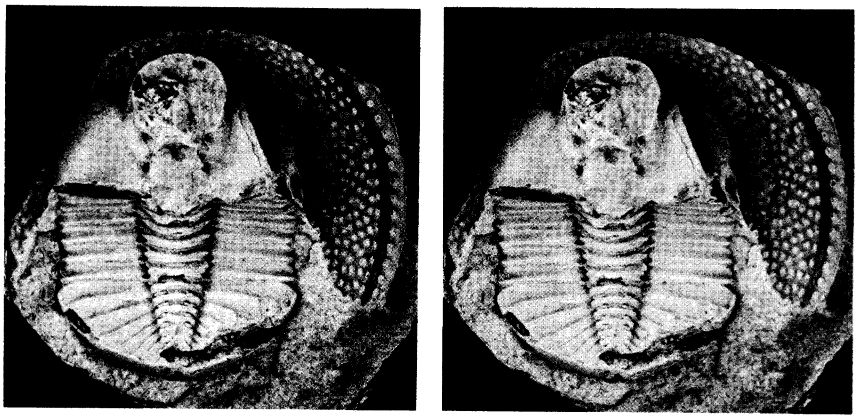
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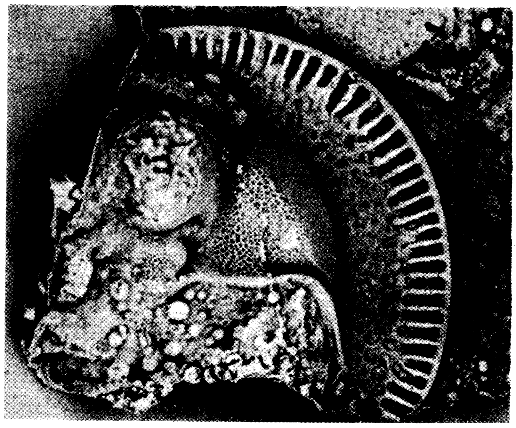
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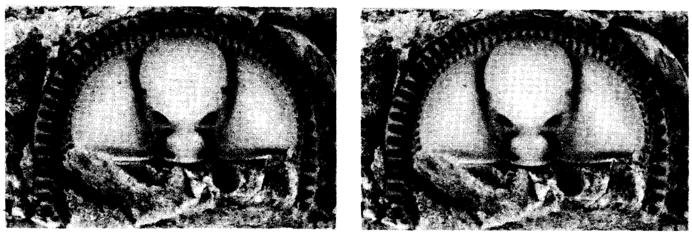
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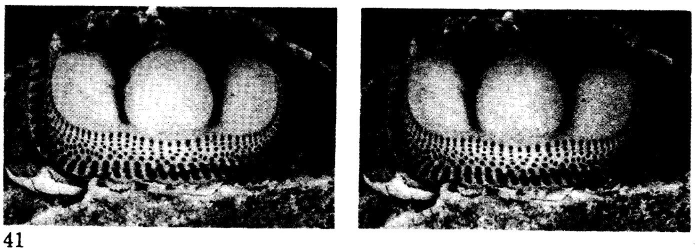
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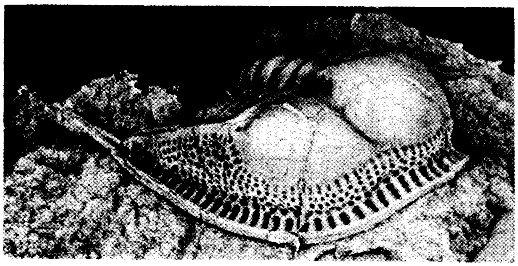
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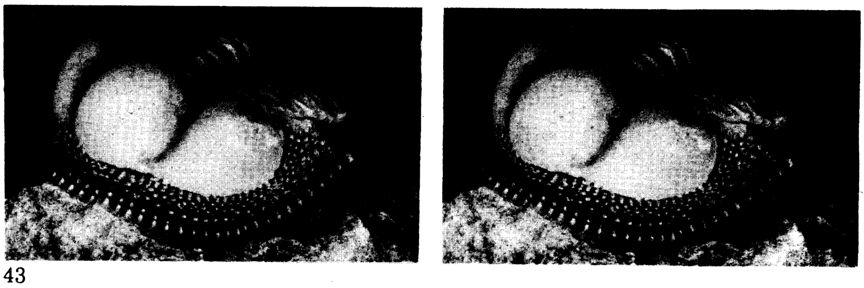
43

FIGURES 32–43. For description see opposite.

Other included forms:

M. fearnsidesi Whittington, 1966*a*.

M. multiplex Whittard, 1966.

Distribution. Low Arenig of Wales and the Welsh Borderland.

Discussion. Myttonia is clearly allied to *Hanchungolithus* but differs in that the irregular pits on the lateral portions of the fringe are fewer in number and are of similar size to the other pits. The fringe is also more steeply declined and the glabella more swollen anteriorly. In all these features *Myttonia* approaches the earliest true trinucleines such as *Incaia* and *Anebolithus* in which the fringe is steep with few, large, regularly positioned pits and the glabella pyriform, and the girder marginal.

(*c*) Subfamily TRINUCLEINAE Hawle & Corda, 1847

Diagnosis. Fringe with no F pits, other than the posterior fossula. Pits essentially radially alined. Glabella with prominent pseudofrontal lobe with three pairs of lateral glabellar furrows. Pits on upper lamella generally regularly arranged. Usually no occipital spine.

Type genus. Trinucleus Murchison, 1839.

Distribution. Arenig to Ashgill of Wales and the Welsh Borderland; Llanvirn to Ashgill of Central Europe; Llanvirn of South America; Llandeilo to Ashgill of North America; ?Llanvirn, Llandeilo to Ashgill of Norway and Sweden; high Llandeilo or low Caradoc of New Zealand; ?low Caradoc of Central Urals, Russia; highest Caradoc? and Ashgill of Scotland; Ashgill of Ireland; mid-Ordovician of central asiatic Russia; upper Ordovician of China.

Discussion. Whittington (1941 *a*, 1959) included only *Trinucleus* and *Paratrinucleus* in this subfamily. Whittard (1966) implied that *Myttonia, Incaia, Lordshillia, Cochliorrhoe, Bergamia* and possibly *Stapeleyella* were closely related. *Incaia* was separated into a separate subfamily by Hughes & Wright (1970) and Hughes (1971) placed *Bergamia* (including *Cochliorrhoe*), *Lordshillia* and *Stapeleyella* in the Trinucleinae together with *Anebolithus.*

The present authors believe that the subfamily should be enlarged further with the inclusion of genera previously placed by most authors in the Tretaspidinae, Novaspidinae and Incaiinae,

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DESCRIPTION OF PLATE 3

FIGURES 32–35. *Trinucleus fimbriatus* Murchison, 1839. *Nemagraptus gracilis* Shales (middle or upper Llandeilo), middle quarry, Llanfawr, Llandrindod Wells, Powys (Radnorshire), Wales. 32, Internal mould of lower lamella, BM. It. 2731 (magn. × 2). 33, Latex peel from dorsal mould of cranidium, BM. It. 2730 (magn. × 3). 34, Latex peel from dorsal mould of pygidium, BM. It. 2733 (magn. × 3). 35, Latex peel from dorsal mould of cranidium, HM. A10690b, showing arrangement of pits in sulci (magn. × 8).

FIGURES 36, 37. *Telaeomarrolithus intermedius* Hughes, 1971. Horizon and locality as figures 32–35. 36, Latex peel from dorsal mould of crushed cephalon, BM. It. 8800 (paratype) (magn. × 6). 37, Latex peel from ventral mould of cephalon, BM. It. 2790, showing lower lamella with pronounced girder and two E_2 pits on lateral fringe expansion (magn. × 3).

FIGURES 38, 39. *Declivolithus alfredi* (Želízko, 1906). Bohdalec Beds (Caradoc), respectively Steŕboholy and Hloubètín, near Prague. 38, Replica of almost complete individual BM. It. 220, (original National Museum, Prague CD. 2176), showing ventral (external) mould of part of lower lamella (magn. × 3). 39, Latex peel from dorsal mould of incomplete cephalon, BM. In. 58985 (magn. × 6).

FIGURES 40–43. *Nankinolithus* cf. *granulata* (Wahlenberg, 1818). Upper Drummuck Beds (Ashgill, high Rawtheyan Stage), Lady Burn, near Girvan, Kyle & Carrick, Strathclyde (Ayrshire), Scotland. Both specimens under same catalogue number R.S.M. 1889.91.8. 40, 41, Dorsal and anterodorsal views of ventral mould of cranidium. 42, 43, Oblique view of latex peel from dorsal mould of entire individual and oblique view of ventral mould of same specimen showing ventral (external) mould of lower lamella. (Magns × 1½.)

All figures except 32, 34, 35, 39 and 42 are stereophotographs.

together with *Famatinolithus* and *Telaeomarrolithus*. This is because no *F* pits are developed, the pits on the fringe are essentially radially alined and the glabella is swollen anteriorly and has three pairs of lateral glabellar furrows. The presence of lateral eye tubercles in some genera is not thought to warrant separation at the subfamily level.

Special difficulties arise with species exhibiting features characteristic of more than one genus (see discussion of *Bergamia* and *Botrioides*).

Genus **Trinucleus** Murchison, 1839
figures 32–35, plate 3

Diagnosis. E_1 and variable number of I arcs present. Pits on upper lamella set in radial sulci. No enlargement of pits or swelling of lamellae anterolaterally. Weak eye ridges present in juveniles.

Type species. Trinucleus fimbriatus Murchison, 1839. Subsequent designation by Vogdes 1890, p. 84 (see also Hughes 1971).

Other included forms:

T. acutofinalis Whittard, 1956.
T. cf. *acutofinalis* of Hughes, 1971.
T. abruptus Hughes, 1971.
T. sp. nov. (*Broeggerolithus nicholsoni* of Ancigin *in* Barganov *et al.* (1973)).

Distribution. Llanvirn and upper Llandeilo of Wales and the Welsh Borderland; ?low Caradoc of Central Urals, Russia.

Discussion. The early debate (Foerste, 1910; Raymond, 1913*a*, *b*) regarding the validity of *Trinucleus* and *Cryptolithus* has been discussed by Hughes (1971, pp. 121–122). In modern work both are considered valid and the genus *Edgellia* proposed by Shaw *in* Shaw & Stubblefield (1950) taken as redundant. (See also Stubblefield & Whittington 1956; I.C.Z.N. Opinion 505 (1958).)

The present study has had the effect of restricting the genus mainly to those forms from Britain; the Scandinavian species previously attributed being placed in '*Botrioides*' (*q.v.*).

A form recently described from the Bardimskiy complex, southwest of Sverdlovsk in the west central Urals from beds of low Caradoc age or slightly older by Ancigin (*in* Barganov *et al.* 1973, p. 81, pl. 9, figs 6–11) as *Broeggerolithus nicholsoni* is here placed in *Trinucleus*. It has the typical trinucleine glabella, sulcate upper lamella, lack of eye tubercles and apparently only one *E* arc. The genal prolongations, however, are much longer than in other *Trinucleus* species and in this respect it resembles *Declivolithus* (*q.v.*), a genus thought to be allied to, perhaps descended from *Trinucleus*. The relatively long pygidium is also similar to that of *Declivolithus*. The generic position of *Trinucleus wutangensis* Lu, 1962 is at present uncertain although Lu's (1965) fuller description suggests that it is probably some form of trinucleine.

Of other trinucleine genera, the most closely allied to *Trinucleus* are *Bergamia*, *Telaeomarrolithus* and probably *Declivolithus*.

Genus **Telaeomarrolithus** Williams, 1948
figures 36, 37, plate 3

Diagnosis. Fringe with anterolateral angulation and pits of E_1 enlarged anterolaterally on the lower lamella. Occasional pits of E_2 present and numerous I arcs developed laterally. Radial sulci suppressed laterally on inner portion of upper lamella.

Type species. Trinucleus radiatus Murchison, 1839. Original designation by Williams 1948, p. 83.

Other included forms:

T. intermedius Hughes, 1971.

T. cf. *intermedius* of Black, Bulman, Hey & Hughes, 1972.

T. sp. indet. of Whittard, 1956.

Distribution. Upper Llandeilo and/or lowest Caradoc of Wales and the Welsh Borderland.

Discussion. Hughes (1971) placed this genus in the Marrolithinae. However, with the recognition of the importance of F pits and the relation of I_n to the other I arcs it is clear that *Telaeomarrolithus* is a trinucleine. Its only abnormal characteristic is the possession of enlarged pits on the anterolateral portions of the lower lamella. The functional significance of swollen pits in this region is unknown, but it also occurs in *Ningkianolithus* (Hanchungolithinae) and *Marrolithus* (Marrolithinae) (*qq.v.*) and it is thought to have developed independently in all three cases.

Genus **Paratrinucleus** Whittington, 1941*a*

Diagnosis. Fringe narrow. E_{1-2}, I_n and I_1 complete; some extra E_2 pits present frontally. Upper lamella sulcate. Pygidium long with well-segmented axis and numerous pleural ribs.

Type species. Trinucleus acervulosus Raymond, 1920. Original designation by Whittington 1941 *a* p. 22.

Distribution. Upper Llandeilo or low Caradoc of eastern North America.

Discussion. This genus shows certain similarities to various early trinucleines from Europe, but is distinguished particularly by its relatively long, well-segmented pygidium. It is possible that the extra pits in E_2, if separated into distinct short sulci on the upper lamella, may cause a superficial cephalic likeness to *Stapeleyella.* However, none of the figured specimens show any indication of any intercalated sulci. Further it is the pits of E_2 and E_3 that are present in such sulci in *Stapeleyella* and only E_{1-2} are apparently developed in *Paratrinucleus.* The genus is currently being studied by Dr R. K. Bambach of the Virginia Polytechnic Institute.

The specimen figured by Stäuble (1952, fig. 11) as *Paratrinucleus* is here regarded as a *Stapeleyella* since the intercalated sulci are present laterally as well as frontally and clearly contain pits of two arcs.

Genus **Declivolithus** Přibyl & Vaněk, 1967

figures 38, 39, plate 3

Diagnosis. Fringe of 'harpiform' type with very long genal prolongations. E_1 only E arc, pits of which share radial sulci with I_1 and commonly I_2 on upper lamella, sulci separated by elevated radial plates. Pits internal to I_2 small, numerous and essentially randomly distributed, but innermost I pits show some regularity.

Type species. Trinucleus alfredi Želízko, 1906. Original designation of Přibyl & Vaněk 1967, p. 453 (see also Přibyl & Vaněk 1969; Chlupáč 1952 – as *Tretaspis nováki*).

Other included form:

D. sp. (J. Destombes 1972, private communication).

Distribution. Middle and upper Caradoc of Czechoslovakia: Caradoc of Morocco.

Discussion. This bizarre trinucleid with its superficial similarity of outline to the harpid trilobites possesses a number of features which ally it immediately with such trinucleines as *Trinucleus* and *Telaeomarrolithus.* Non-fringe features of importance are the form of the glabella, the absence of lateral eye tubercles and the well-segmented pygidium. On the fringe the radial sulci with intervening radial plates or ridges, although only peripheral, bear a striking resemblance to those of both *Trinucleus* and *Telaeomarrolithus*. In *Declivolithus*, however, the fringe is broader, with much longer genal prolongations and there is a wide band of irregularly disposed pits internal to the radially sulcate ones such as also occurs in *Nankinolithus*, *Decordinaspis* (Trinucleinae) and *Reedolithus* (Reedolithinae).

Genus **Bergamia** Whittard, 1955

figures 25–28 plate 2; figure 2*b*

Diagnosis. Fringe narrow, inner part steeply declined. E_1 complete, E_2 variably developed set very close to E_1. I_n complete, other I arcs variably developed. Pits on both lamellae in deep radial sulci with only a small number of irregularly arranged pits laterally in the centre of the genal prolongations. No eye ridges present. Pygidium short, axis extending onto posterior border.

Type species. Bergamia rhodesi Whittard, 1955. Original designation p. 31.

Other included forms:

B. gibbsi (Salter *in* Murchison, 1859).
B. prima (Elles, 1940).
B. inquilinium (Whittard, 1966).
B. matura Whittard, 1966.
B. whittardi Hughes, 1971.
B.? *sedgwicki* (Salter, 1866).
B.? *pamirica* (Balashova, 1966).
B.? sp. (*Trinucleus gibbsi* of Matley 1932, p. 262).
B.? sp. of Bates, 1968.

Distribution. Arenig, Llanvirn and lower Llandeilo of Wales; Arenig of Welsh Borderland. Mid-Ordovician of eastern Pamir, Russia.

Discussion. The decision by Hughes (1971) to consider *Cochliorrhoe* Whittard, 1966 a junior synonym of *Bergamia* is accepted. Also, although *B. inquilinium* and *B. matura* are listed separately above, it is thought likely that a full revision of these forms would show them to be conspecific (see Hughes 1971, p. 145). A form described as *Trinucleus gibbsi* by Matley (1932, p. 262) from the lower Llanvirn of the Lleyn peninsula, North Wales (see figure 28, plate 2) possesses a *Stapeleyella*-like feature in that some pits of E_1 are absent giving rise to short rows intercalated between the outer portion of complete rows. Unlike *Stapeleyella*, where pits of both E_2 and E_3 are present in these short rows, no E_3 pits are developed in Matley's specimen, which is tentatively assigned to *Bergamia*.

Genus **Nankinolithus** Lu, 1954

figures 40–43 plate 3; figure 2*c*

Diagnosis. Fringe with pits of the three outer arcs E_{1-2}, I_1 set in deep radial sulci on upper lamella, E_{1-2} becoming progressively closer posteriorly. Pits of inner I arcs also radially arranged but out of phase with the outer sulci and separated from them laterally and sometimes frontally by irregularly distributed pits of at least I_{2-3}. Eye ridges and tubercles absent.

Type species. Nankinolithus nankinensis Lu, 1954. Original designation by Lu 1954 (not seen) (see also Lu 1957).

Other included forms:

N. granulata (Wahlenberg, 1818) (see Kielan 1960).
N. jiantsaokouensis Lu (see Lu 1974).
N. portrainensis (Reed, 1897) (see also Lamont 1941).
N. praecedens (Klouček, 1916).
N. wanyuanensis Cheng & Jian, 1961.
N. sp. (*T. kiaeri* (*pars*) of Whittington 1968*b*).
N. sp. (*Tretaspis seticornis* of Malaise 1873).
N. sp. (*Tretaspis* aff. *granulata* of Apollonov 1974).
N.? sp. (M. N. Chugaeva 1971, private communication).

Distribution. Llandeilo and Ashgill of Czechoslovakia; highest Caradoc? and Ashgill of Scotland; Ashgill of Ireland, Wales, Norway, Sweden, Canada, Poland and Kazakhstan; upper Ordovician of China; upper Ordovician? of central asiatic Russia (Bukantau range, Uzbekistan).

Discussion. Ingham (1970, p. 44) excluded '*Tretaspis*' *granulata* and '*T.*' *portrainensis* from his two main groups of *Tretaspis*. The figures of the type species of *Nankinolithus* (Lu 1957, pl. 155, figs 11–13) show that '*T.*' *granulata* is very closely allied differing only in the pits of the inner *I* arcs not being in radial sulci frontally, in having the band of irregularly distributed pits developed all round the fringe and having larger genal prolongations with more pits posteriorly. *N. portrainensis* is not sufficiently well-known at present to show whether it is really significantly different from *N. granulata*. *Bergamia*? *praecedens* (Klouček, 1916) (see Přibyl & Vaněk 1969; Hughes 1971) is here transferred to *Nankinolithus* on account of the greater degree of irregularity in the outer *I* arcs laterally and posteriorly than is typical of *Bergamia* and because anterolaterally the pits of the inner *I* arcs lose their radial alinement with the sulci of the outer arcs. It is probable that *Bergamia* was the ancestor to *Nankinolithus* and *N. praecedens* forms a clear link. A band of irregularly distributed *I* pits around the fringe is seen in two other trinucleine genera, *Declivolithus* and *Decordinaspis* (*qq.v.*), but associated features suggest slightly different relationships. The only record of the genus in North America is that of Lespérance (1968, p. 813).

Genus **Stapeleyella** Whittard, 1955
figures 29–31, plate 2

Diagnosis. E_{1-3} generally complete, some pits of E_4 may be present. I_1, I_n complete, very close together frontally. Pits on upper lamella in radial sulci, many of the inter-radial ridges bifurcating external to E_1 to produce intercalated short sulci with E_2, E_3 and frontally E_4. Pygidium like *Bergamia*.

Type species. *Stapeleyella inconstans* Whittard, 1955. Original designation p. 36.

Other included forms:

S. murchisoni (Salter *in* Murchison, 1859).
S.? *etheridgei* (Hicks, 1875).
S.? *forosi* (Størmer, 1932).
S.? sp. (*Paratrinucleus* sp. of Stäuble, 1952).

Distribution. Lower Llanvirn of Wales and Welsh Borderland; Llanvirn? of Norway; Llanvirn of Czechoslovakia; lower Ordovician? of Quebec.

Discussion. Such a complete development of Y-shaped inter-radial ridges is unknown in any other trinucleid genus (although *Paratrinucleus* may possibly show this feature to a limited extent) yet this genus appears to be a trinucleine and it is believed to have developed from *Bergamia*, through forms such as the '*Trinucleus*' *gibbsi* of Matley (1932) (see discussion of *Bergamia*). *S.*? *forosi* (Størmer 1932), the only Scandinavian record of the genus, is based on a single rather compressed specimen, which has a *Stapeleyella*-like arrangement of short intercalated radial rows on the outer part of the fringe containing pits of E_2 and E_3. '*Trinucleus*' *etheridgei* Hicks, 1875 (see Whittard 1955) is here tentatively transferred to *Stapeleyella*. Hicks' original illustration clearly indicates the Y-shaped inter-radial ridges on the upper lamella and some topotypic material, probably conspecific (SM. A86135; A86136), indicates that E_{1-3} are developed.

Genus **Anebolithus** Hughes & Wright, 1970

figures 16–19, plate 1

Diagnosis. Fringe narrow with only I_1 and I_n developed; pits in radial sulci on upper lamella; genal prolongations present. No lateral eye tubercles or eye ridges.

Type species. Incaia simplicior Whittard, 1966. Original designation by Hughes & Wright (1970, p. 688).

Other included form:

A. sp. of Hughes (1971).

Distribution. Arenig and lower Llanvirn of Wales and Welsh Borderland.

Discussion. The current study has resulted in a revised interpretation of the fringe pits. Whittard originally believed I_{1-3} were developed, I_3 being represented by up to five pits posterolaterally. Hughes & Wright accepted this when they proposed the genus *Anebolithus*. We now believe that the correct interpretation is as follows: The outermost arc, i.e. I_1 of Whittard, remains as I_1; the innermost arc, made up of parts of I_2 and I_3 of Whittard, becomes I_n, and the remaining pits of Whittard's I_2 are best considered as genal flange pits to which no arc notation is applied.

Genus **Lordshillia** Whittard, 1966

Diagnosis. E_1 and I_n complete, and a few pits of I_1 present laterally. Radial sulci only developed frontally. No lateral eye tubercles or eye ridges.

Type species. Lordshillia confinalis Whittard, 1966. Original designation p. 277.

Distribution. Arenig of Welsh Borderland.

Discussion. This genus is one of two rather finely drawn genera erected by Whittard (1966) on very little material. The other, *Cochliorrhoe*, is here considered a junior synonym of *Bergamia*, and it might be argued that *Lordshillia*, with its single E arc should be considered as congeneric with *Trinucleus*. However, although it almost certainly gave rise to *Trinucleus*, we prefer to retain *Lordshillia* for those trinucleine species with a very simple fringe with only E_1 and one or two I arcs.

Genus **Famatinolithus** Harrington & Leanza, 1957

figures 13–15, plate 1

Diagnosis. Fringe narrow with broad marginal rim; no genal prolongations. Only I_1 and I_n complete; I_2 present anterolaterally. Preglabellar field developed. No lateral eye tubercles and eye ridges.

Type species. Famatinolithus noticus Harrington & Leanza, 1957. Original designation p. 199.

Other included forms:

F. sp. (undescribed specimens in the Branisa collection, U.S. National Museum, possibly the same as '*Trinucleus*' sp. of Branisa 1965, pl. 3, fig. 11).

F.? *kruegeri* (Hoek *in* Steinmann & Hoek, 1912).

F.? *bueyensis* (Rusconi, 1956).

F.? sp. (*Trinucleus*? *nordenskioeldi* of Newell & Tafur (1944)).

Distribution. Llanvirn of Argentina; undifferentiated lower Ordovician? of Argentina and Bolivia; upper Llanvirn? of Peru.

Discussion. Harrington & Leanza (1957, pp. 199–200) erroneously identified the well-developed inner flange of the lower lamella as the girder, thus they considered all pits to belong to the *E* series. It is clear, however, from latex peels kindly supplied by Dr B. A. J. Baldis, that the girder is submarginal, and that all pits belong to the *I* series. The genus is thus closely similar to *Incaia*, the main differences being the presence of large lateral eye tubercles and the absence of a preglabellar field. *Anebolithus* is also closely allied, but has no preglabellar field and posterolaterally the fringe is extended into a moderate genal prolongation. *Trinucleus bueyensis* Rusconi, 1956 from the lower Ordovician of the Mendoza region of Argentina is probably referable to *Famatinolithus* in that the figure and description of the holotype broadly conform to this genus. A paratype mentioned, but not figured, by Rusconi may be a different form allied to *Incaia* as it apparently possesses lateral eye tubercles. *Trinucleus kruegeri* is provisionally placed in this genus, although it appears to differ from the type species in having a complete I_2 arc, no preglabellar field and a ribbed pygidium. The lower lamella figured by Douglas (1932, pl. 29, fig. 8) as *Trinucleus* sp. from the Llanvirn of Peru could be a *Famatinolithus*, but equally it might be an *Incaia*. Specimens of *Trinucleus*? *nordenskioeldi* of Newell & Tafur (1944) kindly made available by Dr N. D. Newell, show this form has no lateral eye tubercles and is best considered as *Famatinolithus* sp., although it appears to lack any reticulate surface sculpture.

Genus **Incaia** Whittard, 1955

figures 20–22, plate 2

Diagnosis. Fringe narrow; only I_1 and I_n complete, occasional pits of I_2 present laterally; pits on upper lamella in radial sulci. Prominent lateral eye tubercles present.

Type species. Trinucleus nordenskioeldi Bulman, 1931. Original designation by Whittard (1955, p. 32).

Other included forms:

I. bishopi Hughes & Wright, 1970.

I.? sp. (*Trinucleus bueyensis pars.* of Rusconi, 1956. See discussion of *Famatinolithus*).

Distribution. Upper Llanvirn of southeastern Peru; upper Llandeilo or lowest Caradoc of New Zealand; lower Ordovician? of Argentina.

Discussion. Incaia is clearly related to both *Anebolithus* and *Famatinolithus*, and the differences between these genera have already been considered above.

Genus **Botrioides** Stetson, 1927

figures 44–51, plate 4; figure 6*a*

Diagnosis. Fringe narrow, declined. E_1 complete, E_2 may be present frontally; up to five *I* arcs present. Pits on upper lamella in deep radial sulci; no sulci on lower lamella. Genal prolongations poorly developed. Lateral eye tubercles present.

Type species. Trinucleus coscinorinus Angelin, 1854 (? = *B. bronnii* (Sars & Boeck *in* Boeck, 1838) (Størmer 1930, pp. 19, 30)). Original designation by Stetson (1927, p. 97).

Other included forms:

B.? *foveolatus* (Angelin, 1854 (= *T. efflorescens* Hadding, 1913; see Størmer (1930)).
B.? *foveolatus intermedius* (Størmer, 1930).
B.? *bucculentus* (Angelin, 1854).
B.? *hibernicus* (Reed, 1895).
B.? *hibernicus broeggeri* (Størmer, 1930).
B.? sp. (*Bergamia* sp. of Dean 1971*a*).
B.? sp. (D. L. Bruton 1971, private communication).
B.? sp. (?*Bergamia* sp. of Dean 1974).
B.? sp. (Trinucleid gen. et sp. indet of Sadler, 1974).

Distribution. Upper Llanvirn, Llandeilo and ?lowest Caradoc of Norway and Sweden; Llandeilo or lowest Caradoc of southeastern Ireland and central Newfoundland; Llandeilo of southwest England; ?Llandeilo of northeastern Newfoundland.

Discussion. The species tentatively placed within this genus form a closely-knit group morphologically, stratigraphically and geographically which parallels the superficially similar *Trinucleus* and *Bergamia* stocks endemic to the Welsh area.

Since the types of *T. coscinorinus* are lost and well preserved topotypic material is not known, it is impossible to check Størmer's (1930) synonymizing of this species with *T. bronnii*. There is thus a nomenclatural difficulty regarding the type species of this genus. With the exception of the type species, it is not possible at this stage to refer other forms unequivocally to Stetson's genus even though they are clearly related to one another and, judging from the original figures, to Angelin's species *coscinorinus*. Thus the generic name when used to refer to the whole group is here placed in inverted commas. While '*Botrioides*' and *Trinucleus* do resemble one another in having the upper lamellar pits in radial sulci, the sulcation in *Trinucleus* is more complex posteriorly in that short sulci are developed on the inner and outer regions set at slightly differing angles togethe1 with a third set along, and at right angles to, the posterior margin of the fringe. In addition, there is commonly a triangular area in the centre of the genal prolongation of irregularly positioned pits. Also, those species of '*Botrioides*' with more than one *I* arc show no lower lamellar sulcation such as is found in *Trinucleus* and *Bergamia*. Apically situated eye tubercles, invariably present on the genal lobes in '*Botrioides*', are never seen in any of the Anglo-Welsh genera of the *Trinucleus*/*Bergamia* stocks which possess, at the most, very short, faint eye ridges usually only in immature individuals.

B.? *bucculentus*, *B.*? *hibernicus*, *B.*? *hibernicus broeggeri* and *B.*? sp. (of Dean 1971*a*) differ from the other included forms in having a variable development of E_2 pits frontally with a corresponding increase in the length (sag.) of the outer band of the lower lamella and have previously been attributed to *Bergamia* (Dean 1971*a*; Hughes 1971). However, the present state of knowlege of this group makes it unwise to attempt a formal subdivision such as that accepted between *Bergamia* and *Trinucleus*, where the distinction has value as they are quite discrete early in their histories, producing separate stocks with different descendents.

Tretaspis is probably the closest ally of '*Botrioides*'; both almost certainly being descended from the same stock. *Tretaspis* possesses a well-developed pseudofrontal lobe and lateral eye tubercles, but has the upper lamellar sulcation of the pits restricted to the periphery of the fringe and the strict radial pattern, characteristic of '*Botrioides*', is sometimes broken down. A specimen (figure 48–51, plate 4), listed above as *B.*? sp., from the upper *Didymograptus* Shales (upper Llanvirn) of Hadeland, Norway, kindly lent by Dr D. L. Bruton, is probably very close to the common ancestor of '*Botrioides*' and *Tretaspis*. In any event if fills the morphological gap between them, and in view of its age its ancestral position appears reasonable. In this form, the fringe has what is probably E_1 as the outermost arc frontally where all the pits are in radial sulci on the upper lamella, as in other '*Botrioides*', but laterally the sulcation is peripheral and another short arc, probably E_2 is developed as in some species of *Tretaspis*.

The pygidia of some species of '*Botrioides*' also resemble those of *Tretaspis* species but in the Newfoundland form described by Dean (1971*a*) there is a strong resemblence to the pygidia of *Incaia* and *Novaspis*. The former South American and New Zealand genus also has prominent eye tubercles but these are close to the glabella. *Incaia*, with its marginal girder, could be a link between '*Botrioides*' and a hanchungolithine-like form in much the same way that *Anebolithus* links *Trinucleus* and *Bergamia* with the Hanchungolithinae, but in a different faunal realm.

Genus **Tretaspis** McCoy, 1849

figures 52–54, plate 4; figures 4*a*, 6*b*, 7*a*

Diagnosis. Up to two E arcs developed: where present E_2 pits share radial sulci with those of E_1 and I_1 on upper lamella. Pits of I_{2-n} radially alined but not normally in sulci. Lateral eye tubercles present.

Type species. *Asaphus seticornis* Hisinger, 1840. Subsequent designation by Bassler 1915, p. 1285.

Included forms. (Grouping modified after Ingham 1970.)

T. seticornis group:
- *T. seticornis* (Hisinger, 1840) (see Størmer 1930).
- *T.* sp. ?nov. of Ingham (1970, p. 41).
- *T. seticornis anderssoni* Størmer, 1945.
- *T.* sp. (*T. seticornis* of Lamont (1941)).
- *T. clarkei* Cooper *in* Schuchert & Cooper, 1930 (see also Bolton (1970) – as *T. ceriodes*).
- *T. hadelandica* Størmer, 1945 (see also Ingham 1970).
- *T. hadelandica brachystichus* Ingham, 1970
- *T. latilimbus* (Linnarsson, 1869) (see also Ingham 1970).
- *T. latilimbus distichus* Ingham, 1970.
- *T. sortita* Reed, 1935 (see also Ingham 1970).
- *T. convergens* Dean, 1961 (see also Ingham 1970).
- *T. persulcatus* Reed, 1935 (see also Ingham 1970).
- *T.* sp. indet. 1 of Dean (1971*b*).

T. moeldenensis group:
- *T. moeldenensis* Cave, 1960.
- *T.* cf. *moeldenensis* of Ingham (1970).
- *T. kiaeri* Størmer, 1930.
- *T.* aff. *kiaeri* (*T. kiaeri* (pars) of Whittington (1968*b*)).
- *T. calcaria* Dean, 1971*b*.
- *T.* sp. indet. 2 of Dean (1971*b*).
- *T. kiaeri* (*recte*) radialis Lamont, 1941.
- *T.* cf. *radialis* of Ingham (1970).
- *T. kiaeri duftonensis* Dean, 1961.
- *T. colliquia* Ingham, 1970.
- *T. ceriodes* (Angelin, 1854).

T. ceriodes angelini Størmer, 1930.
T. ceriodes donsi Størmer, 1945.
T. ceriodes favus Dean, 1963.
T. ceriodes alyta Ingham, 1970.
T. ceryx Lamont, 1940.
T. reticulata Ruedemann, 1901 (see also Stäuble 1953).
T. sagenosus Whittington, 1959.
T. canadensis Stäuble, 1953.
T. sp. (R. P. Tripp 1967, private communication).
T. sp. (M. Romano 1973, private communication.).

Distribution. Low Caradoc of eastern North America and Belgium; Caradoc and Ashgill of England, Ireland, Scotland, Wales and the Welsh Borderland, Norway and Sweden; Ashgill of Poland, Czechoslovakia and Quebec.

Discussion. In distinguishing two groups, typified by *T. seticornis* and *T. moldenensis* respectively, Ingham (1970, pp. 41–44) found difficulty in assigning a small number of *Tretaspis* species. Of these *T. granulata* and allied forms are here regarded as belonging to *Nankinolithus* (*q.v.*). This leaves *T. kiaeri*, the recently described allied forms *T. calcaria* and *T. persulcatus.* The latter species is difficult to place with the others because, although it has a narrow fringe with out-of-phase sulci like *T. seticornis* and related forms, arc E_2 is complete, as in the *T. moeldenensis* group, and an external pseudogirder is developed on the lower lamella such as occurs in no other *Tretaspis* species. Of the other two species, *T. kiaeri* and *T. calcaria* have fringes basically similar

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DESCRIPTION OF PLATE 4

FIGURE 44. *Botrioides*? *bronnii* (Sars & Boeck *in* Boeck, 1838). *Ogygia* Shale (Llandeilo), Asker, Norway. Latex peel from dorsal mould of cephalon with associated thoracic segment. PMO. H566 (magn. × 5).

FIGURES 45–47. *Botrioides*? *hibernicus* (Reed, 1895). Tramore Limestone Formation (high Llandeilo or lowest Caradoc), Newtown Glen, near Tramore, Co. Waterford, Ireland. 45, Latex peel from dorsal mould of cranidium BM. It. 13200 showing subconcentric sculpture (magn. × 3). 46, Ventral mould of same specimen showing eye tubercles and median glabellar node (magn. × 5). 47, Latex peel from external mould of enrolled specimen SM. A15942a (syntype), showing lower lamella together with most of thorax and pygidium (magn. × 4).

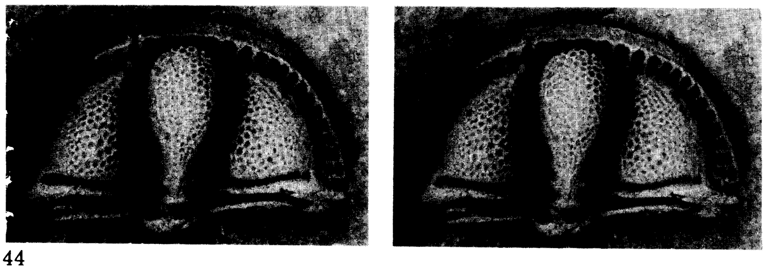
FIGURES 48–51. *Botrioides*? sp. Upper *Didymograptus* Shale, *c.* 16 m above the *Endoceras* Limestone (Upper Llanvirn), Hadeland, Norway. Dorsal, lateral, frontal and oblique views of cephalon retaining exoskeleton. PMO. 87252. (All magn. × 5.)

FIGURES 52, 53. *Tretaspis seticornis anderssoni* Størmer, 1945. *Tretaspis* Shale (Ashgill), Frognøy, Ringerike, Norway. Oblique and dorsal views of holotype cranidium, PMO. 65196 a ventral mould retaining little exoskeleton (magn. × 4 and × 3 respectively).

FIGURE 54. *Tretaspis sortita* (Reed, 1935). Starfish Beds, upper Drummuck Group (Ashgill, high Rawtheyan Stage), Lady Burn, near Girvan, Kyle & Carrick, Strathclyde (Ayrshire), Scotland. Latex peel from external mould of part of lower lamella of fringe, HM. A656, showing posterior fossula and vincular notches on flange (magn. × 4).

FIGURES 55–58. *Novaspis albida* (Reed, 1914*a*). Uppermost Whitehouse Beds (Ashgill), 55, 57, 58 from the Whitehouse shore, 56, from Myoch Bay, near Girvan, Kyle & Carrick, Strathclyde (Ayrshire), Scotland. 55, Latex peel from external mould of lower lamella of fringe, BM. In 56905a, showing genal spine and flange bearing posterior fossula and vincular notches (magn. × 4). 56, Lower lamella of fringe, HM. A6657, showing girder dying out frontally (magn. × 3). 57, Ventral mould of slightly crushed cranidium, HM. A6408 (magn. × 3). 58, Latex peel from dorsal mould of incomplete cranidium, HM. A6604, showing form of posterior part of glabella and very fine reticulation on pseudofrontal lobe (magn. × 4).

All figures except 54–58 are stereophotographs.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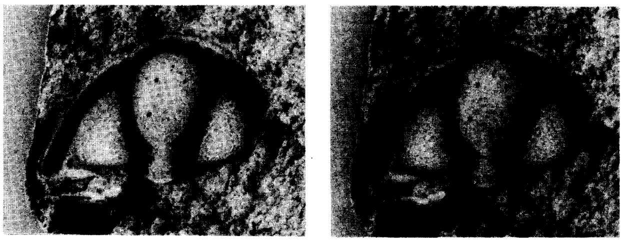
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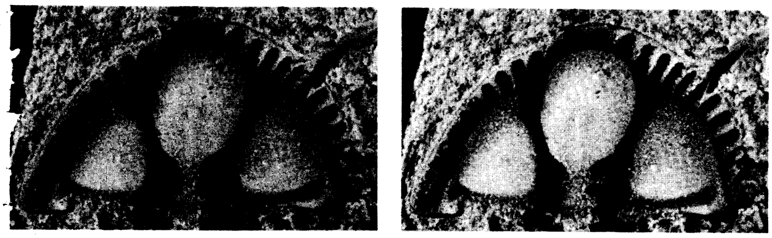
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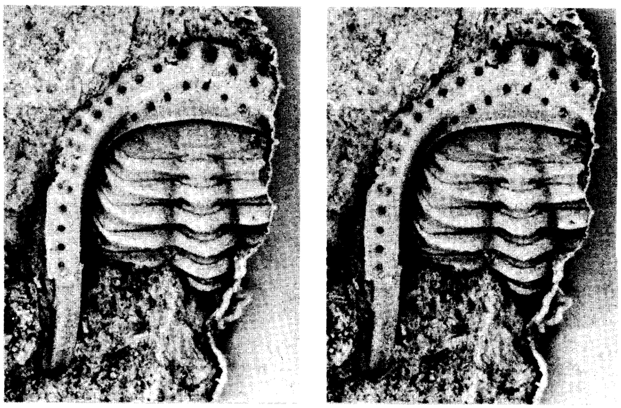
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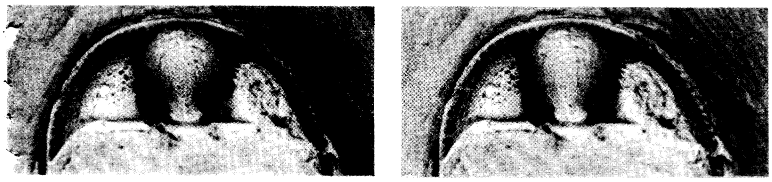
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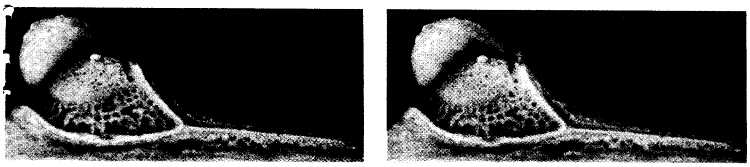
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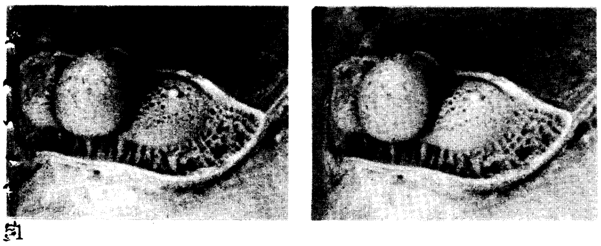
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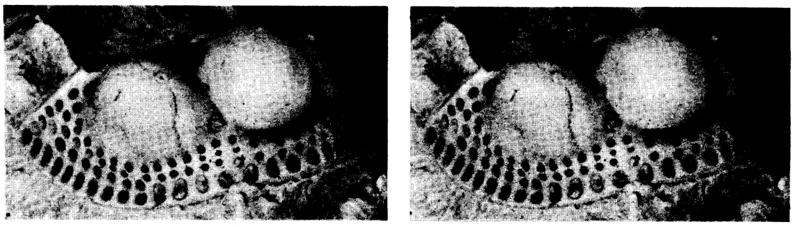
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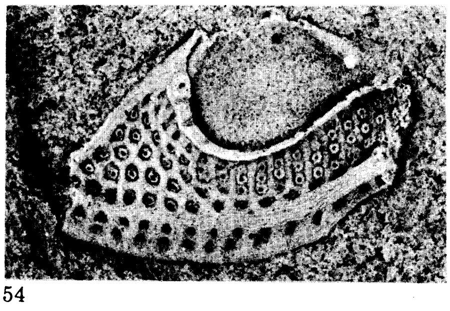
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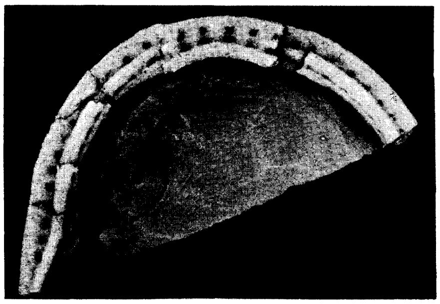
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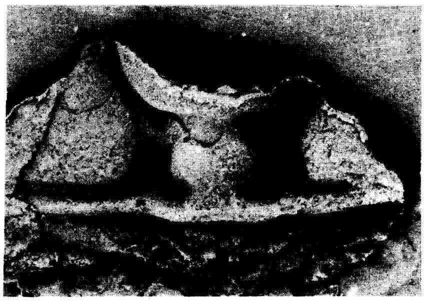
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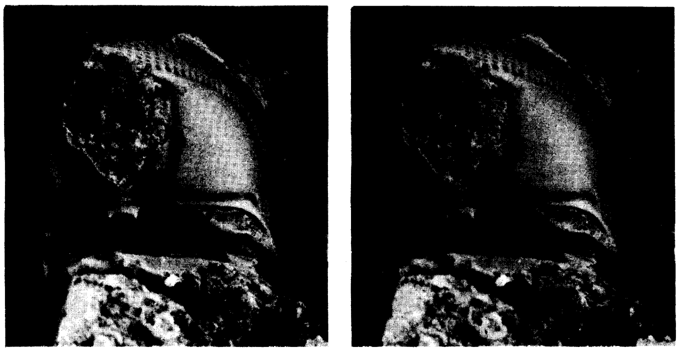
Figures 44–58. For description see opposite.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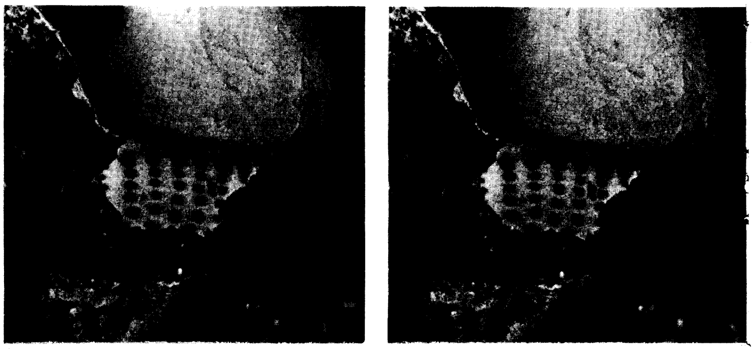
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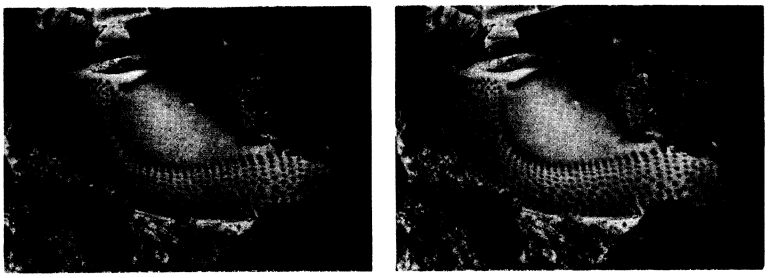
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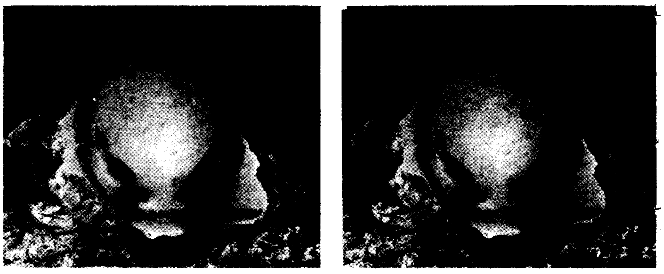
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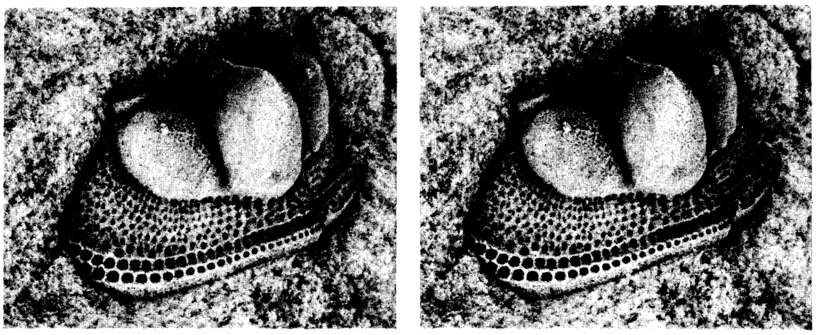
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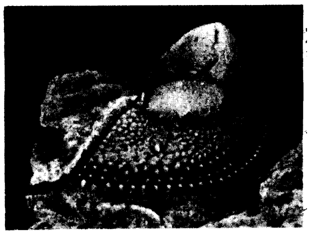
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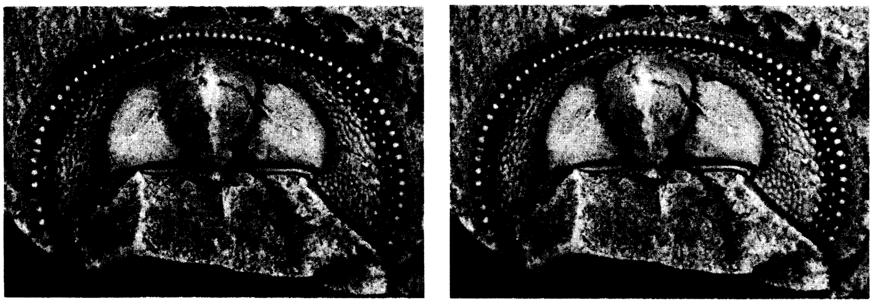
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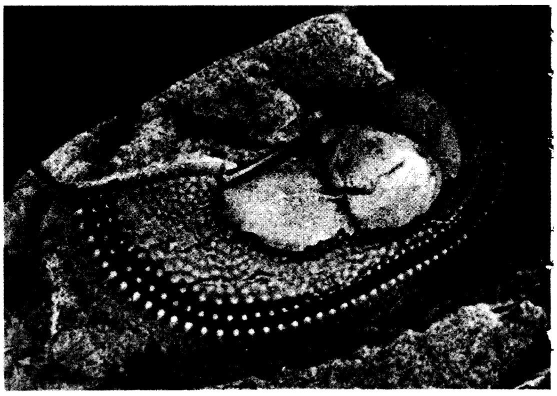
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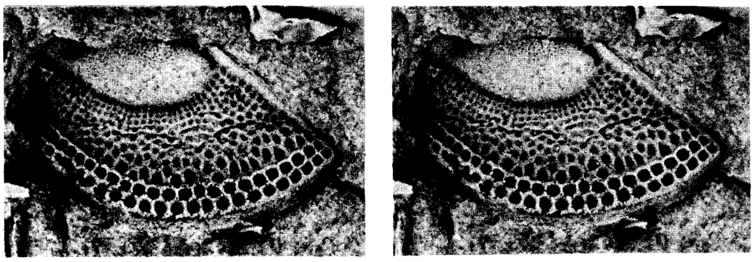
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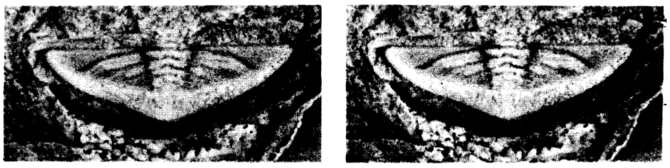
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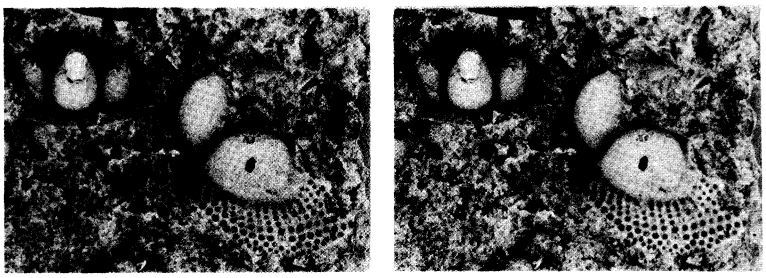
FIGURES 59–69. For description see opposite.

DESCRIPTION OF PLATE 5

FIGURES 59–63. *Decordinaspis bispinosa* Harper & Romano, 1967. Shales of low Caradoc age, near Grangegeeth, Co. Meath, Ireland. 59, 61, Dorsal and oblique views of ventral mould of damaged cranidium NMI. G. 104/1965 (holotype) (magns × 2). 60, 62, 63, Oblique frontal, dorsal and lateral views of a fragmentary cephalon on which the fringe is partly preserved as an internal mould and partly as a ventral (external) mould of the lower lamella. NMI. G. 105/1965 (paratype). 61, Girder and parts of three external arcs visible (magn. × 4). 62, 63, Form of glabella with composite lateral lobes and paired occipital spines shown (magns × 2).

FIGURES 64–69. *Reedolithus subradiatus* (Reed, 1903). Balclatchie Mudstones (low Caradoc), Dow Hill, near Girvan, Kyle and Carrick, Strathclyde (Ayrshire), Scotland. 64, Oblique view of latex peel from dorsal mould of incomplete cephalon, BM. In 20681b (syntype). 65–67, Lateral, dorsal, and oblique views of ventral mould of cephalon with fringe preserved as ventral (external) mould of lower lamella, BM. In 20685 (syntype). 68, Latex peel from dorsal mould of fragment of cranidium, BM. In 47974, showing lateral part of upper lamella of fringe. 69, Latex peel from dorsal mould of pygidium, BM. In 20687b (syntype). (Magns × 4 except figure 67 which is × 6.)

All figures except 63, 65, and 67 are stereophotographs.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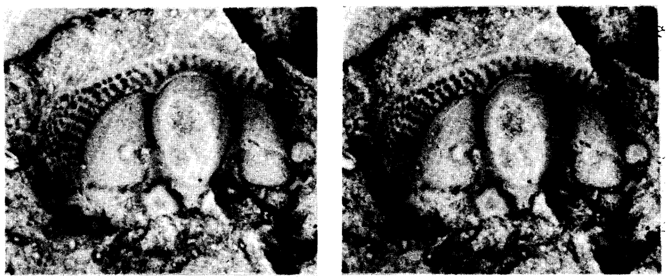
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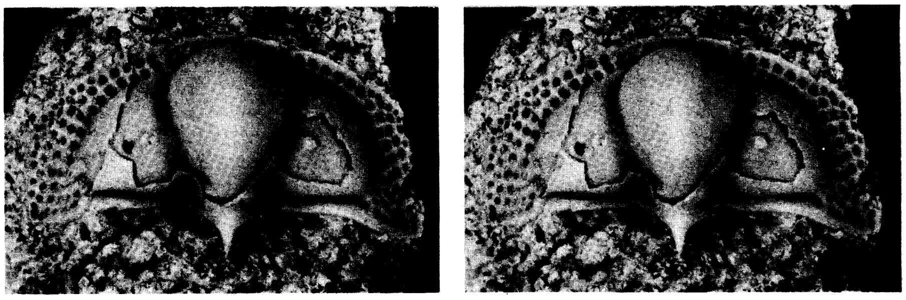
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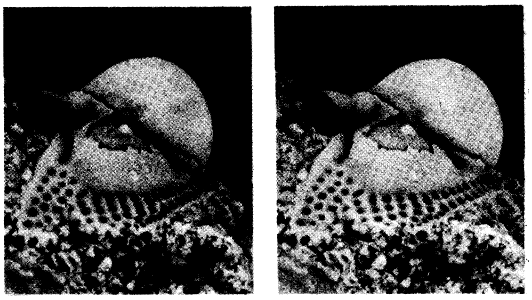
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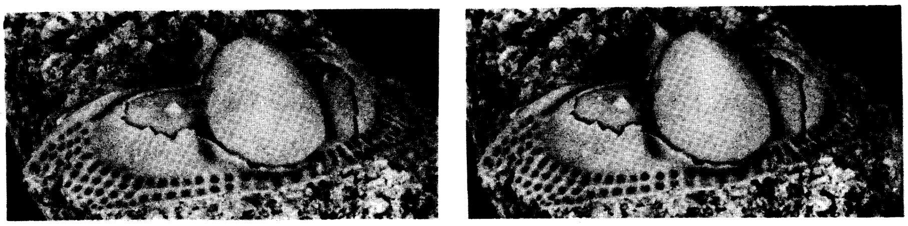
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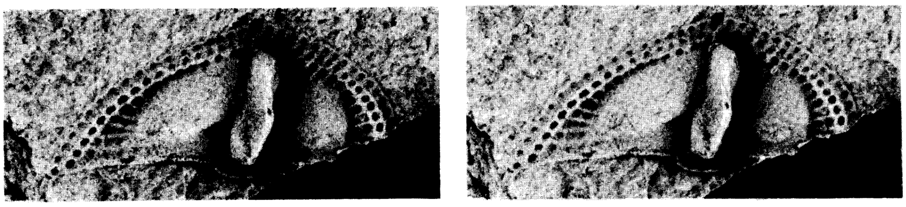
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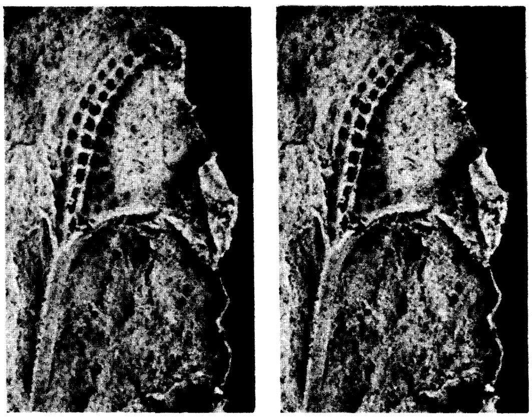
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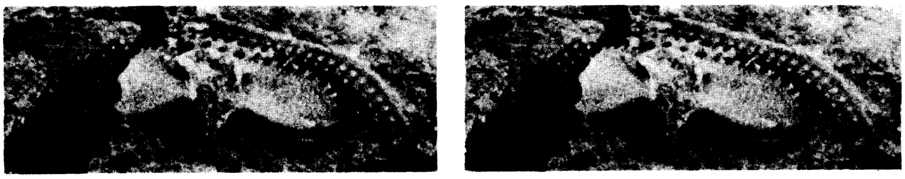
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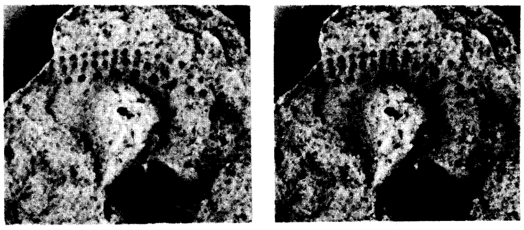
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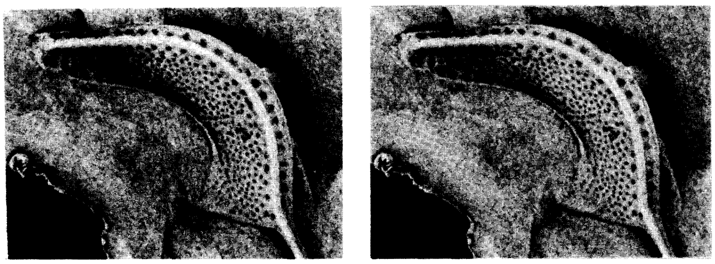
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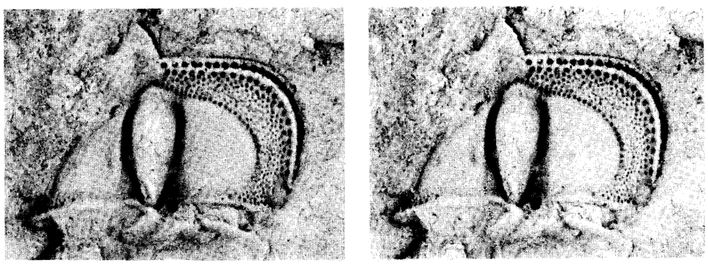
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FIGURES 70–80. For description see opposite.

to those of the *T. moldenensis* group, but they have their sulci out of phase with the other pits (Dean 1971*b*, p. 16). Two forms from the Ashgill of Cautley, described by Ingham as *T.* cf. *moeldenensis* and *T.* cf. *radialis*, are very closely allied but their differences, though small, are consistent and the two forms are extremely valuable stratigraphic indicators. The former, earliest form, differs in small detail from *T. moeldenensis* which Dean (1961, p. 125) regarded as synonymous with *T. radialis* (originally *T. kiaeri radialis*). However, it is suspected that it is the younger Cautley form which may prove to be synonymous with *T. radialis*. As indicated by Ingham (1970, p. 57) and Dean (1971*b*, p. 16) the best taxonomic treatment for these closely allied forms can only be assessed when *T. radialis* is redescribed from the type locality at Portrane in eastern Ireland.

A *Tretaspis* allied to the Appalachian *T. reticulata* and *T. sagenosus* occurs in the Caradoc of Grangegeeth in eastern Ireland (Dr M. Romano, private communication). A similar form has been collected by Mr R. P. Tripp from the Balclatchie Conglomerate and Mudstones of the Girvan district in southwest Scotland.

Genus **Paratretaspis** Dean, 1974

Diagnosis. Fringe broad; pits excluding E_2 radially arranged. I_{2-n} in sulci on both lamellae; E_1 and E_2 discrete laterally, crowded frontally. Pits of E_2 smaller and more numerous than those of E_1. Up to four I arcs frontally, pits of I_3 and I_n twinned. Pronounced eye tubercles and eye ridges present.

Type species. Paratretaspis terranovica Dean, 1974. Original designation p. 6.

Distribution. ?Llandeilo (see below) of New World Island, northeastern Newfoundland.

Discussion. Dean suggested that the genus provided a suitable ancestor for *Tretaspis*, but, in view of the multiplicity of pits in the outer E arc, it does not fulfill this function quite as well as the form described and figured here as *Botrioides*? sp. nov. (figures 48–51, plate 4) from the upper Llanvirn of Norway. *Paratretaspis* also shows some similarity to *Decordinaspis*. Although

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DESCRIPTION OF PLATE 6

FIGURES 70, 71. *Guandacolithus furquei* Harrington & Leanza, 1957. Las Plantas Shales (lower Caradoc), about 22 km southwest of Guandacol, San Juan Province, Precordillera of western Argentina. 70, Latex peel from slab with dorsal moulds of two incomplete cranidia, UBA. 4553a (magn. ×4). 71, Replica of cranidium retaining some exoskeleton, UBA. 4301 (holotype), showing suggestion of a broken occipital spine (magn. ×6).

FIGURES 72–74. Un-named reedolithine genus. Empozadense Beds, lower Ordovician, Mendoza western Argentina. Dorsal, lateral and oblique views of cranidium retaining some exoskeleton, SM. A88053 (magn. ×4).

FIGURES 75–78. *Eirelithus thersites* (Salter, 1853). Tramore Limestone Formation (high Llandeilo or lowest Caradoc), Newtown Glen, near Tramore, Co. Waterford, Ireland. 75, Latex peel from dorsal mould of slightly crushed cranidium, GSM. 26030 (syntype). 76, Latex peel from dorsal mould of fragment of cephalon, GSM. 26026 (syntype), showing lateral portion of upper lamella and form of genal spine. 77, Ventral mould of crushed cephalon in which a little of the fringe is preserved as an internal mould but the rest is seen as a ventral (external) mould of the lower lamella, GSM. 26031 (syntype). 78, Latex peel from dorsal mould of fragment of cranidium, GSM. 26032 (syntype), showing large I_n pits in front of glabella. (Magns ×8 except figure 75 which is ×6.)

FIGURES 79, 80. *Protolloydolithus neintianus* Whittard, 1956. Shales within the Stapeley Volcanic Group (lower Llanvirn), Nind Quarry, Shelve Inlier, Salop (Shropshire), England. 79, Latex peel from ventral (external) mould of lower lamella, HM. A10478b, showing flange with F pits. 80, Latex peel from dorsal mould of incomplete cranidium, HM. A10479b, showing pronounced girder list and preglabellar field. (Magns ×4.)

All figures are stereophotographs.

Dean argues in favour of a low Ordovician (Whiterock) age for *Paratretaspis*, we question this firstly because the other trinucleid recorded by Dean from the same horizon as ?*Bergamia* sp., we consider is better placed in the '*Botrioides*' group, typically Llandeilo or even lowest Caradoc in age, and secondly because a convincing Whiterock-type fauna is known from strata of Porterfield age (Llandeilo) at Girvan (Ross & Ingham 1970).

Genus **Decordinaspis** Harper & Romano, 1967

figures 59–63, plate 5

Diagnosis. Fringe broad and steep. Arcs I_{1-6}, I_n, and up to four E arcs present. Radial alinement of I pits good out to I_3, but arcs I_{1-2} with rather larger irregularly distributed pits. E_1 pits large; E_{2-3} pits smaller, a little more numerous and not all regularly alined with those of E_1; pits of E_4 small sporadically developed. Glabella trinucleine but with pseudofrontal lobe highest towards the rear and tapered posteriorly. Two short occipital spines present. Small lateral eye tubercles developed.

Type species. *Decordinaspis bispinosa* Harper & Romano, 1967. Original designation p. 305.

Distribution. Low Caradoc of eastern Ireland.

Discussion. The general cephalic proportions in *Decordinaspis* are typical of the Trinucleinae and the pit distribution resembles that of *Nankinolithus* in the large number of pits and irregularity in the outer I arcs. However the genus possesses unusual features. The glabella, although of general trinucleine form in having the pseudofrontal lobe poorly defined posteriorly, also recalls the glabellar form in reedolithine genera, although there is no carination. The presence of a pair of occipital spines is unique within the whole family: although a single occipital spine is usual in the Reedolithinae, Cryptolithinae and Marrolithinae; a small, very low occipital node is all that has ever been detected in any other trinucleine. Nevertheless, the gross cephalic morphology allies *Decordinaspis* with the Trinucleinae. It resembles *Tretaspis* and *Nankinolithus* more closely than any other genera, but its origins may be a little closer to the reedolithine stock.

Genus **Novaspis** Whittington, 1941*a*

figures 55–58, plate 4; figures 2*d*, 4*b*

Diagnosis. Fringe very narrow with E_1 and I_n only complete arcs, the pits of which share short radial sulci frontally on the upper lamella. Very short I_1 present posteriorly with small number of adventitious pits. Girder suppressed frontally leaving a few adjacent pits of E_1 and I_n close together. Flange of lower lamella with a pronounced thickening frontally. Pseudofrontal lobe of glabella sub-spherical and highly elevated. Lateral eye tubercles absent.

Type species. *Tretaspis elevata* Cooper & Kindle, 1936. Original designation by Whittington (1941*a*, p. 25).

Other included forms:

N. albida (Reed *a*, 1914).

N. aff. *albida* of Weir (1959) (see below).

N. sp. of Kielan (1960).

Distribution. Lowest Ashgill of Scotland, and similar levels in Ireland and Quebec; Ashgill of Wales (Gwynedd (Merionethshire)) and Poland.

Discussion. The cephalon of *Novaspis* bears a superficial resemblance to those of *Anebolithus*, *Incaia* and some species of '*Botrioides*' (*qq.v.*) in having an extremely narrow fringe. However, the first two of these much earlier genera possess a marginal girder and do not have the greatly swollen pseudofrontal lobe of *Novaspis*. Nevertheless, the pygidium of *Incaia* has a number of features in common with that of *Novaspis* and this could indicate a close relationship. On the other hand, like *Tretaspis*, *Novaspis* may derive from '*Botrioides*'-like forms. Some late species of this genus show progressive development of an enlarged pseudofrontal glabellar lobe, a narrowing of the fringe and reduction of the eye tubercles (Størmer 1930, p. 29) but these forms also develop an E_2 arc and have a continuous girder.

Welsh records of *Novaspis* (as *Trinucleus* cf. *albidus*) are those of Pugh (1923, 1928) and Jehu (1926) from the Abercwmeiddaw Formation ('Broad Vein'). They have been substantiated recently by Ingham and one specimen clearly shows that *Novaspis* has six thoracic segments (see Kielan (1960, p. 176) who stated there were five, although six were mentioned in her generic diagnosis (p. 175)).

It is clear from Weir's description (1959, p. 371) that not all his specimens from Co. Clare belong to *Novaspis*, although the lower lamella impression he figures (pl. 62, fig. 7) certainly does. Fragments of *Tretaspis* and/or *Nankinolithus* are probably represented in his material.

Whittington (1941 *a*, p. 25) created a separate subfamily, the Novasp(id)inae, to accommodate *Novaspis* on the basis of its swollen pseudofrontal lobe, narrow fringe and shallow glabellar furrows. The present writers, however, believe that the general features possessed by the cephalon of *Novaspis* are not greatly different from those of some other genera which are closely related to *Trinucleus* and that, therefore, a subfamilial separation of *Novaspis* is not warranted.

(*d*) Subfamily Reedolithinae subfam. nov.

Diagnosis. *E* and *I* arcs present; no *F* pits other than posterior fossula. More *I* and usually more *E* arcs laterally than frontally. Glabella high, clavate and carinate with three pairs of lateral glabellar furrows. Large lateral eye tubercles present; eye ridges and occipital spine generally so.

Type genus. *Reedolithus* Bancroft, 1929.

Distribution. Low Caradoc of Scotland; upper Llandeilo or low Caradoc of Ireland and Norway; middle Ordovician of Quebec; low Ordovician and Caradoc of Argentina; undifferentiated Ordovician of China?

Discussion. This subfamily is erected to accommodate a small number of allied genera which hitherto have not been satisfactorily placed subfamilially. There is a uniformity of glabellar and genal characters within the group and although the fringe shows considerable variation in the number of arcs present, the underlying pattern of pit distribution is similar in all genera.

The glabellar proportions and common presence of an occipital spine, suggest comparison with marrolithine and cryptolithine genera, as does the gross cephalic shape. On the other hand, the absence of an *F* pit series and the presence of lateral eye tubercles is a combination found in several trinucleines. Like the other trinucleid subfamilies, the Reedolithinae probably has its origins in the Hanchungolithinae, retaining such characters as overall fringe shape – narrow frontally, broad laterally – and the posterior fossula, while emphasizing others, e.g. the lateral eye tubercles and occipital spine. The gross similarity between *Reedolithus quebecensis* Stäuble, 1953 and such early American *Tretaspis* species as *T. canadansis* Stäuble, 1953 and *T. sagenosus* Whittington, 1959 in such features as eye position and fringe profile is thought to result from parallel development.

The subfamily has an interesting geographical and stratigraphical distribution which is not inconsistent with current ideas of Ordovician palaeogeography (Whittington & Hughes 1972).

Genus **Reedolithus** Bancroft, 1929

figures 64–69, plates 5; figure 2*h*, 4*c*

Diagnosis. Outermost arc E_1, and I_1 consist of large pits. I_n and a variable number of adjacent I arcs consist of relatively small pits radially alined. Inserted between these pits and I_1 are a variable number of rather irregularly disposed pits. The areal distribution of these pits progressively increases in width towards the genal prolongation. Girder narrow, but prominent; narrow first internal pseudogirder developed laterally. Occipital spine present. Lateral eye tubercles situated well away from the glabella and far back; narrow eye ridge present.

Type species. Trinucleus subradiatus Reed, 1903. Original designation by Bancroft 1929, p. 77.

Other included forms:

R. carinatus (Angelin, 1854).
R. quebecensis Stäuble, 1953.
R.? richthofeni (Kayser, 1883).

Distribution. Low Caradoc of Scotland; upper Llandeilo or low Caradoc of Norway; middle Ordovician of Quebec. Undifferentiated Ordovician of China?

Discussion. The inclusion of '*T.*' *richthofeni* Kayser, 1883 is tentative and follows Størmer (1930, p. 33).

Genus **Eirelithus** Lamont, 1941

figures 75–78, plate 6

Diagnosis. Fringe narrow, with only E_{1-2}, I_n well developed. E_1 elevated above other arcs, with relatively large pits. Sharp girder list present. Few I_1 pits and adventitious pits present posteriorly. E_3 sporadically developed anterolaterally. Girder strong. Glabella very high frontally. Lateral eye tubercles situated far from glabella and near posterior border furrow. Large triangular alar lobes present. No occipital spine.

Type species. Trinucleus thersites Salter, 1853. Original designation by Lamont 1941, p. 445.

Distribution. High Llandeilo or lowest Caradoc of southeastern Ireland.

Discussion. Although the fringe is narrow and, unlike *Reedolithus*, possesses an E_2 arc, there is some similarity in that E_1 is elevated. The glabellar characteristics of this genus taken together with the rearwardly placed eye tubercles and the presence of a posterior fossula suggest affinities with other reedolithines, despite the lack of an occipital spine. The differences suggest, however, that *Eirelithus* is not as closely allied to *Reedolithus* as are the other genera of the subfamily.

Current work by Mrs H. Carlisle to be submitted for a doctoral thesis at the Queen's University, Belfast includes a re-appraisal of *Eirelithus*. Mrs Carlisle states (1973, private communication):

> As noted by Lamont (1941, p. 446) E_3 is occasionally present laterally, one specimen showing this being figured. Study of further specimens in the Institute of Geological Sciences together with new material suggests that it is only the larger specimens that possess such pits: one fragment is known in which E_4 is represented anterolaterally.

This distribution of the outer E arcs is similar to the situation seen in *Guandacolithus*, but the position of the girder is not known in that genus.

A trinucleid reported to be 'close to *Eirelithus*' is present in siltstones of probable middle Ordovician age of Tasmania (Banks 1962), but it is insufficiently known to be assigned generically with any certainty.

Genus **Guandacolithus** Harrington & Leanza, 1957
figures 70, 71, plate 6

Diagnosis. E_1 fully developed, E_{2-3} present laterally as are some irregularly arranged E_4 pits. I_{1-2} and I_n complete, I_{3-4} present posterolaterally; pits of I arcs in shallow sulci on upper lamella. Lateral eye tubercles near glabella at mid-length of genal lobes.

Type species. Guandacolithus furquei Harrington & Leanza, 1957. Original designation p. 201.

Other included form:

G. verrucosa (Rusconi, 1956).

Distribution. Lower Ordovician and lower Caradoc of Argentina.

Discussion. The assignment of arcs in the above diagnosis is tentative because the position of the girder is not known in the type species. We have surmized that the outermost complete arc of large pits is E_1.

Our interpretation of the general morphology of *G. furquei* differs slightly from that of Harrington and Leanza in that latex peels of the type material, kindly supplied by Dr B. A. J. Baldis, fail to show the development of extra fossulae in the posterior border furrows as shown in their reconstruction. Further, one specimen shows what is possibly the base of an occipital spine (figure 71, plate 6).

Our inclusion of *Onnia verrucosa* Rusconi, 1956 in this genus is on the basis of the gross cephalic morphology and the presence of outer E arcs laterally.

We ally *Guandacolithus* with *Reedolithus* primarily because of the glabellar morphology and prominent lateral eye tubercles. The overall fringe proportions are similar, but there are marked differences in pit distribution. The two genera have probably evolved independently from an early date.

Un-named reedolithine genera
figures 72–74, plate 6

Discussion. Rusconi (1953, 1954) described two species, *Cryptolithus emposadensis* and *Cryptolithus stelarusconii* from the lower Ordovician of the Mendoza region of Argentina which possess reedolithine glabellae, an occipital spine and prominent lateral eye tubercles, although the latter are closer to the glabella than in *Reedolithus*. Rusconi's drawings and descriptions show that the fringe details are significantly different and the two forms may represent a new genus or genera. Another form also from the Mendoza district, horizon unknown, resembles the above species in glabellar, occipital and genal characters. In the only available specimen (figures 72–74, plate 6) kindly sent to Professor H. B. Whittington by Dr Rusconi, the fringe is narrow frontally and bears two complete arcs, here tentatively identified as E_1 and I_n, and a presumed I_1 present laterally with a short ?E_2, much as in *Guandacolithus*.

In view of the present lack of available material and stratigraphic information regarding these three forms, we feel it premature to erect any new formal taxa.

(*e*) Subfamily MARROLITHINAE Hughes, 1971

Diagnosis. E, I and F pits well developed. I_n usually cut-off laterally by adjacent I arc. One or more arcs, always including I_1 with some pit enlargement. Extreme pit enlargement commonly associated with fringe swellings. Glabella clavate with small deep basal lateral glabellar furrows and two further faint pairs of muscle impressions.

Type genus. Marrolithus Bancroft, 1929.

Distribution. Llanvirn to Caradoc of Wales and the Welsh Borderland; Llandeilo? and Caradoc of ?Spain; Llandeilo to Caradoc of ?Portugal; Llandeilo to Ashgill of Czechoslovakia and Morocco; Caradoc of Austria, France, asiatic Russia, Turkey and Venezuela; high Caradoc of northern England.

Discussion. Recent morphological discoveries have necessitated some expansion of this subfamily. However, two genera, previously included (Hughes 1971, p. 119), *Cryptolithoides* and *Telaeomarrolithus*, are now transferred to the Cryptolithinae (§4(*f*)) and Trinucleinae (§4(*c*)) respectively. The placing of *Marrolithus, Bettonia, Costonia, Deanaspis, Marrolithoides, Onnia* and *Reuscholithus* is unequivocal, all possessing among other common characters, a clearly cut-off I_n arc, although some species of *Onnia* require close examination. The position of *Protolloydolithus, Whittardolithus* and *Lloydolithus* is more equivocal since although they all show some marrolithine characters they also possess some features suggestive of links with either the Hanchungolithinae or the Cryptolithinae. *Protolloydolithus* closely resembles hanchungolithine genera in its general form and in the extensive development of irregular pitting, but it possesses an E_1 arc and an F pit series thus linking it to *Whittardolithus*. The latter genus forms a clear link between *Lloydolithus* and *Bettonia* (see figures 81–88, plate 7) and, as *Bettonia* has the characteristic I_n cut-off of the marrolithines clearly shown, it is preferred to include the three other genera in the same subfamily. I_n cut-off is commonly detectable in these genera but, because of the extensive pit irregularities on the posterior part of the fringe, there are occasional difficulties of I arc identification which do not arise in later marrolithine genera. These annectent genera possibly reflect stages in the development of a stock before the separation of more clearly defined cryptolithine and marrolithine paths.

Genus **Marrolithus** Bancroft, 1929

figures 89, plate7; figures 90–92, plate 8; figures 2*f*, 3*c*

Diagnosis. Fringe markedly subquadrate, predominantly biconvex with upper lamella almost flat or slightly concave in frontal cross-section. Variably developed anterolateral swellings, bearing enlarged pits affect lower and/or upper lamella and involve pits of E_1 and a variable number of I arcs. Girder most prominent anteriorly; internal pseudogirders usually only developed anterolaterally. Girder list only present anterolaterally in association with inflated areas. Glabella highly elevated.

Type species. Trinucleus ornatus var. *favus* Salter, 1848. Original designation by Bancroft 1929, p. 77.

Other included forms:

M. favus moderatus Williams, 1948.
M. ornatus (Sternberg, 1833).
M. ornatus paulisper Přibyl & Vaněk, 1969.
M. bureaui (Oehlert, 1895).
M. inflatus Williams, 1948.
M. inflatus incipiens Williams, 1948.
M. inflatus maturus Williams, 1948.
M. primus Williams, 1948.
M. arenarius Whittard, 1956.
M. bilinearis Whittard, 1956.
M. craticulatus Whittard, 1956.

M. inornatus Whittard, 1956.
M. scalpriformis Whittard, 1956.
M. ventriculatus Whittard, 1956.
M. lirellatus MacGregor, 1963.
M. magnificus MacGregor, 1963.
M. sp. of Hughes (1971).
M. spp. (J. Destombes 1972, private communication).
M.? sp. (*Onnia* sp. (sp. n.) of Přibyl & Vaněk (1969)).

Distribution. Upper Llanvirn to lower Caradoc (Costonian) of Wales and the Welsh Borderland; Llandeilo to ?lower Caradoc of Morocco; Llandeilo? to Caradoc of Czechoslovakia; Caradoc of France, Venezuela (undescribed form) and ?Spain.

Discussion. Many of the species included above are in need of revision and are currently under study by Addison. The fragments identified as *Onnia* sp. (sp. n.) by Přibyl & Vaněk (1969, p. 107, pl. 6, figs. 17–19), here tentatively included in *Marrolithus* could possibly belong to *Deanaspis* gen. nov., but their age (lower Llandeilo) suggests that they are unlikely to belong to *Onnia.*

Genus **Costonia** Whittard, 1956

figures 93, 94, plate 8

Diagnosis. Fringe subquadrate with slight anterolateral inflation which may affect both lamellae. E_1 outermost complete arc; I_{1-2} pits relatively large. Girder well-developed frontally and at genal angles; subdued laterally.

Type species. Marrolithus ultimus Bancroft, 1949. Original designation by Whittard 1956, p. 50.

Other included form:

C. elegans Dean, 1960.

Distribution. Low Caradoc (Costonian) of Wales and Welsh Borderland.

Discussion. The present revision has affected *Costonia* only in that the importance of the development of E_2 pits frontally is reduced in regard to the recognition of this genus. The irregularities which develop in the inner *I* arcs of *C. elegans* are worthy of note since they are possibly anticipatory of *Reuscholithus.*

Genus **Reuscholithus** Bancroft, 1929

figures 95, 96, plate 8

Diagnosis. Considerable irregularity in pit distribution in most arcs, but E_2, variably developed, contains numerous small pits and I_{1-2} have relatively large pits. Fringe subsemicircular to subquadrate.

Type species. Reuscholithus reuschi Bancroft, 1929. Original designation p. 78.

Other included form:

R. terryi (Leith, 1938).

Distribution. Lower Caradoc (Harnagian) of Welsh Borderland; Caradoc of Venezuela.

Discussion. The inclusion of '*Onnia*' *terryi* in this genus requires explanation. Although it is not entirely clear from the illustrations given of this species by Whittington (1954), new material to be described by Hughes, clearly shows only two *E* arcs developed, and that Whittington's identification of E_3 is in error. Further the shape of the lower lamella frontally and the distribution of E_2 pits is very similar to that in *R. reuschi* (see Dean 1960, pl. 14, fig. 9).

Genus **Marrolithoides** Williams, 1948

figures 97–99, plate 8

Diagnosis. Fringe narrow, essentially biconvex with sharp girder list defining relatively depressed inner part of upper lamella. Anterolateral fringe swellings may be developed on both lamellae. Girder sharp, better developed than internal pseudogirders. Glabella not highly elevated.

Type species. Marrolithus simplex Williams, 1948. Original designation p. 78.

Other included forms:

M. simplex elevata Williams, 1948.
M. anomalis Williams, 1948.
M. arcuatus Whittard, 1956.

Distribution. High lower and middle Llandeilo of Wales and the Welsh Borderland.

Discussion. There has in the past been some confusion between this genus and *Marrolithus*, especially in species with only slight development of anterolateral swellings. Much of this confusion has been due to the belief that the type species of *Marrolithoides* possessed no such swellings (see Williams 1948, pp. 78–79; Whittard 1956, pp. 49, 63). New, silicified material, collected by Addison, however, shows that slight swellings are developed in the type species. This being so, then the continued separation of *Marrolithoides* from *Marrolithus* needs justification. Comparison of the diagnoses given here show that the two genera, as understood by us, are differentiated on a number of counts in that, unlike *Marrolithus*, the fringe in *Marrolithoides* is very narrow with a well-developed girder list and an inner depressed region on the upper lamella

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Description of plate 7

Figures 81, 82. *Lloydolithus lloydii* (Murchison, 1839). Meadowtown Beds (lower Llandeilo). 81, From small quarry east of Betton Wood Farm. 82, From coppice northwest of Little Weston, Shelve Inlier, Salop (Shropshire), England. 81, Internal mould of lower lamella of fringe, GSM. 86811 (magn. × 8). 82, Ventral mould of almost complete individual lacking lower lamella, GSM. 86806 (magn. × 3).

Figure 83. *Whittardolithus inopinatus* (Whittard, 1958). Meadowtown Beds (lower Llandeilo), lane north of Meadowtown Chapel, Shelve Inlier, Salop (Shropshire), England. Holotype cranidium, GSM. 86792, showing form of glabella and fringe (magn. × 3).

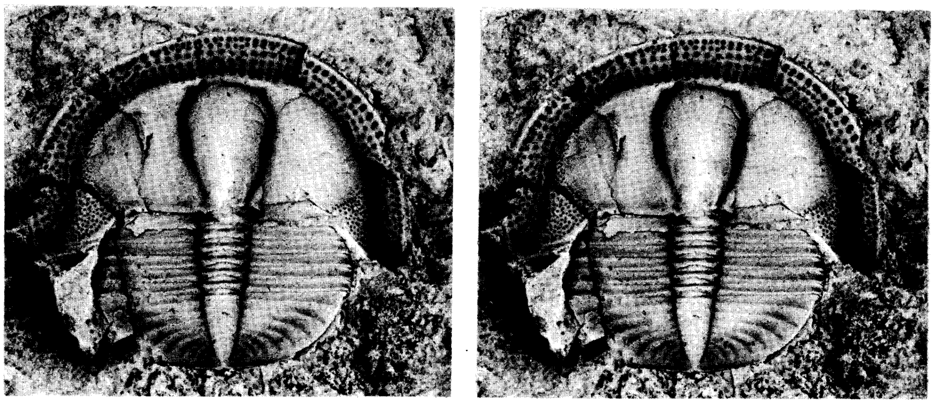
Figures 84, 85. *Whittardolithus instabilis* (Hughes, 1971). Shales of lower Llandeilo age, Dulas Brook, west of Maesgwynne, south of Llandrindod Wells, Powys (Radnorshire), Wales. 84, Latex peel from dorsal mould of holotype cranidium, BM. It. 2792b, showing first internal list on upper lamella (magn. × 4). 85, Latex peel from ventral (external) mould of lower lamella, BM. It. 2793 (paratype), showing girder and internal pseudogirders (magn. × 5).

Figures 86–88. *Bettonia chamberlaini* (Elles, 1940). 86, From Betton Beds (upper Llanvirn), below junction of Holywell and Whitehouse Brooks, Rorrington, Shelve Inlier, Salop (Shropshire), England. 87, From *Didymograptus bifidus* Shales (lower Llanvirn), Howey Brook, east-southeast of Carregwiber, near Llandrindod Wells, Powys (Radnorshire), Wales. 88, From Weston Beds (upper Llanvirn), southeast of road crossing Betton Dingle, Lyde, Shelve Inlier, Salop (Shropshire), England. 86, Ventral mould of damaged cranidium, GSM. 86785 (Holotype of *B. frontalis* Whittard, 1956), showing first internal pseudogirder and adventitious E_2 pits frontally (magn. × 4). 87, Latex peel from dorsal mould of cranidium, BM. It. 2818, showing occipital spine and sculpture on glabella and genal lobes (magn. × 6). 88, Latex peel from ventral (external) mould of part of lower lamella of fringe, GSM. 102434, showing pronounced first internal pseudogirder, I_n cut-off and F pits on flange (magn. × 4).

Figure 89. *Marrolithus craticulatus* Whittard, 1956. Probably topmost Betton Beds (upper Llanvirn), field southwest of well, by lane from Meadowtown to Castle Ring, Shelve Inlier, Salop (Shropshire), England. Latex peel from dorsal mould of holotype cephalon, GSM. 92990 (magn. × 4).

All figures except 81, 84, 87 and 88 are stereophotographs.


81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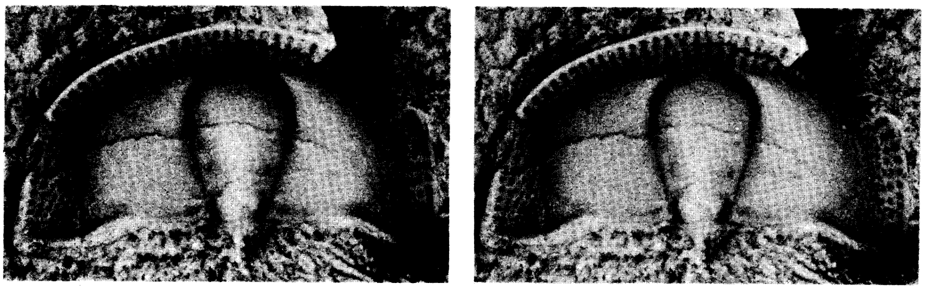
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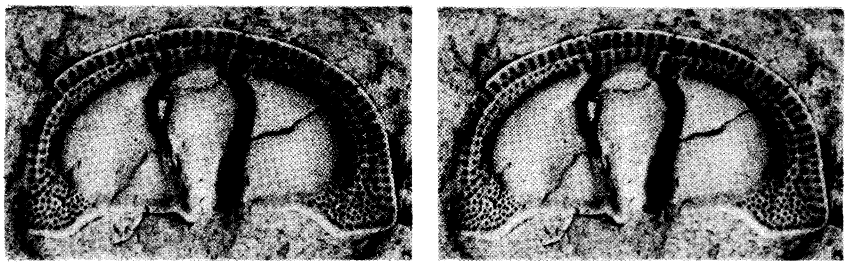
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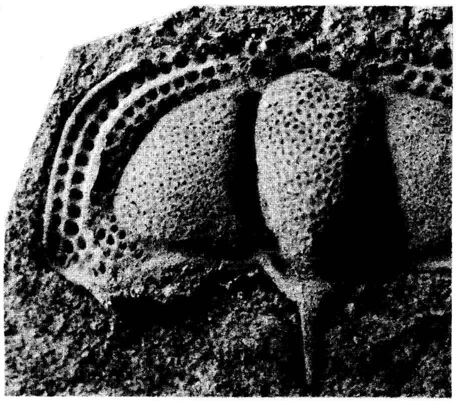
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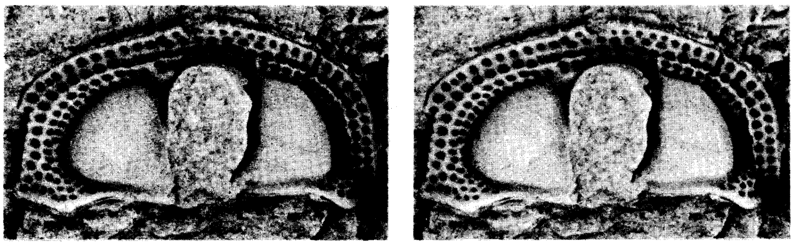
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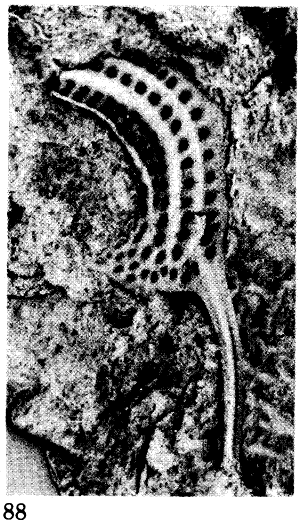
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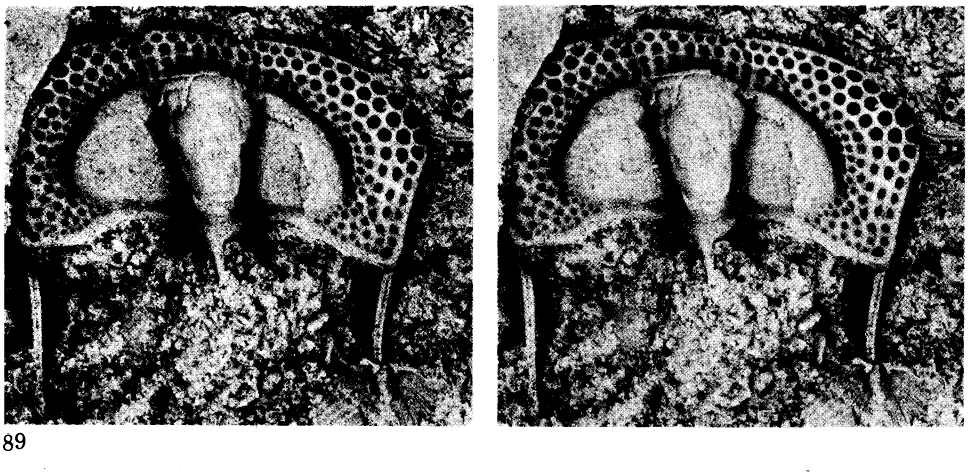
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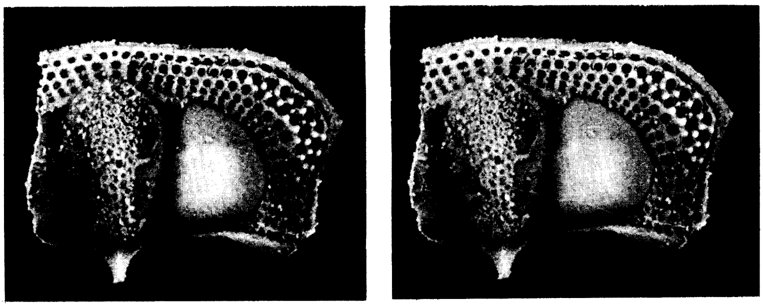
FIGURES 81–89. For description see opposite.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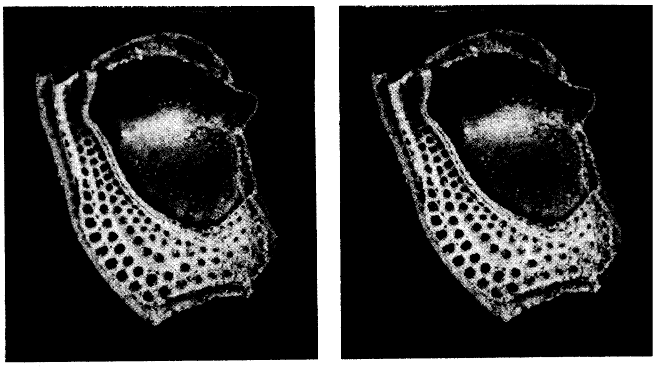
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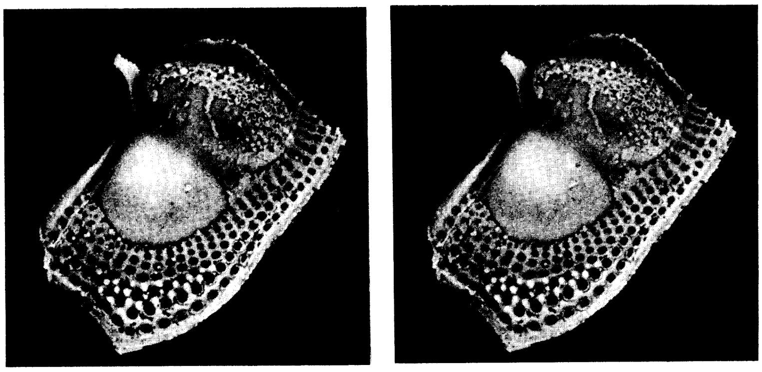
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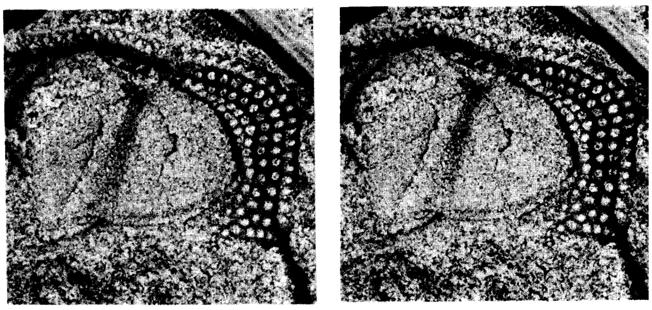
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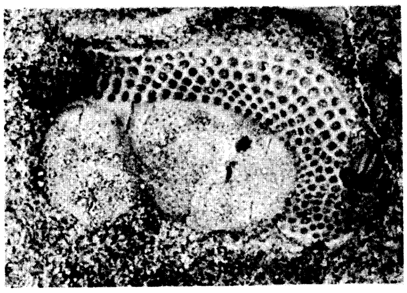
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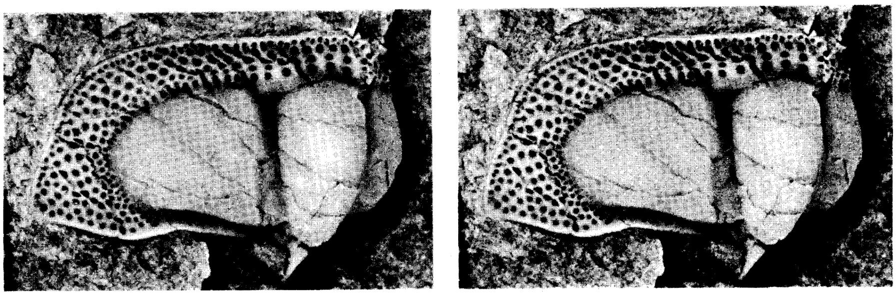
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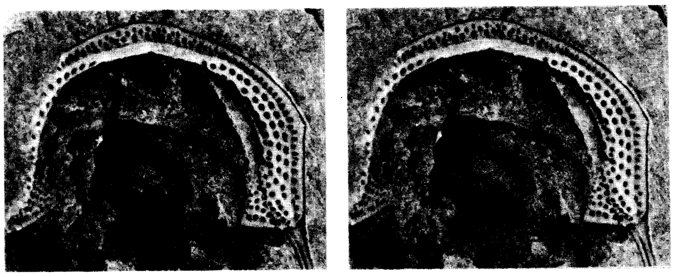
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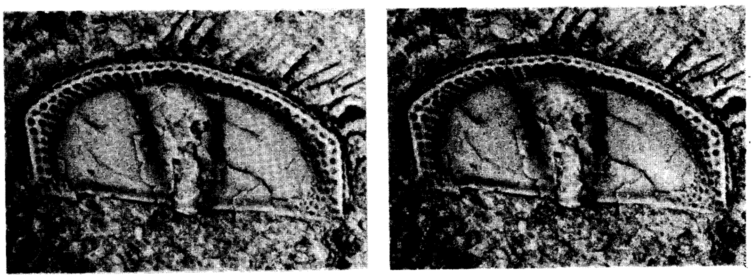
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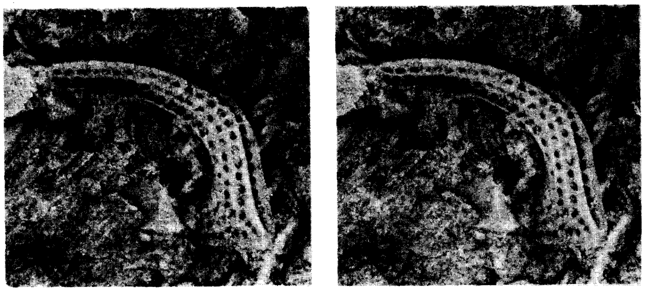
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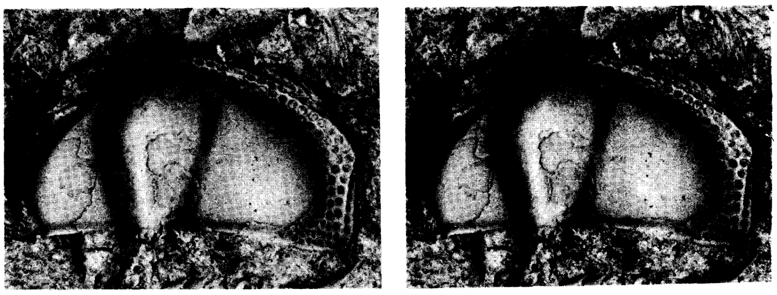
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FIGURES 90–99. For description see opposite.

DESCRIPTION OF PLATE 8

FIGURES 90–92. *Marrolithus* cf. *favus* (Salter, 1848). Limestone of upper Llandeilo age, old quarry north of Lower Court Farm, St Clears, Dyfed (Carmarthenshire), Wales. Dorsal, oblique ventral, and oblique dorsal views of incomplete silicified cephalon. BM. It. 9647 (magns ×6).

FIGURE 93. *Costonia ultima* (Bancroft, 1949). Hoar Edge Grit,—*C. ultima* Beds (Caradoc, Costonian Stage), old quarry south of Coston Farm, near Clunbury, Salop (Shropshire), England. Ventral mould of cephalon with fringe preserved as ventral (external) mould of lower lamella, HM. A10691, showing I_n cut-off, weak girder, except frontally, and adventitious E_2 pits in front of glabella (magn. ×3).

FIGURE 94. *Costonia elegans* Dean, 1960. Hoar Edge Grit,—*Harknessella subquadrata* Beds (Caradoc, Costonian Stage), old quarry in Round Nursery, south-southeast of Harnage Grange, Salop (Shropshire), England. Latex peel from dorsal mould of incomplete cranidium, HM. A10692, showing a few E_2 pits frontally and a larger number of more randomly arranged pits on the posterior part of the fringe than in *C. ultima* (magn. ×6).

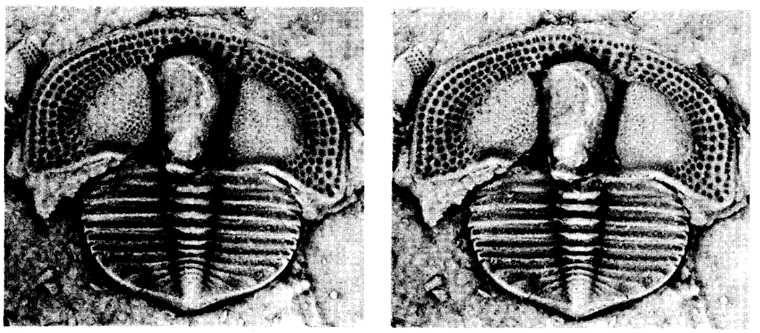
FIGURES 95, 96. *Reuscholithus reuschi* Bancroft, 1929. Harnage Shales (Caradoc, Harnagian Stage, *R. reuschi* Zone). 95, From Coundmoor Brook, southwest of Harnage Farm, near Acton Burnell, Salop (Shropshire), England. 96, From stream east of Gutter Farm, near Hope Bowdler, Salop (Shropshire). 95, Ventral mould of slightly crushed cranidium, HM. A10693a, showing extensive development of E_2 arc (magn. ×5). 96, Internal mould of lower lamella of fringe, BM. In. 49316, showing I_n cut-off and limited irregular distribution of E_2 arc (magn. ×3).

FIGURE 97. *Marrolithoides arcuatus* Whittard, 1956. Rorrington Beds (middle? Llandeilo), Holywell Brook, upstream from bridge, west of Rorrington Green, Shelve Inlier, Salop (Shropshire), England. Ventral mould of cranidium with a little exoskeleton preserved, GSM. 93013, showing pronounced girder list and narrow fringe (magn. ×4).

FIGURE 98. *Marrolithoides simplex* Williams, 1948. Lower part of Middle Llandeilo Flags (middle Llandeilo), lane northwest of Keeper's Lodge in Dynevor Park, Llandeilo, Dyfed (Carmarthenshire), Wales. Latex peel from ventral (external) mould of lower lamella of fringe, HM. A10694/1, showing sharp girder and weak pseudo-girders (magn. ×3).

FIGURE 99. *Marrolithoides anomalis* Williams, 1948. Middle Llandeilo Flags (middle Llandeilo), quarry, southeast of Bridge House, northeast of Llandeilo, Dyfed (Carmarthenshire), Wales. Holotype cranidium retaining exoskeleton on fringe and parts of glabella and genal lobes, GSM. 75203, showing pronounced girder list and slight anterolateral fringe swelling (magn. ×3).

All figures except 94 are stereophotographs.



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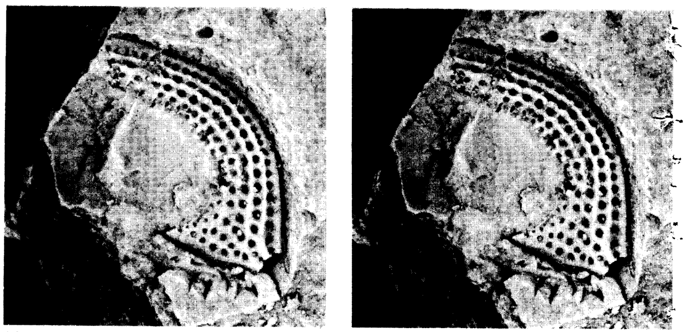

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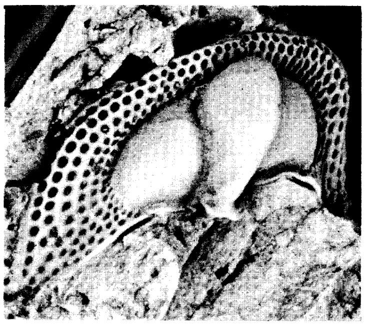

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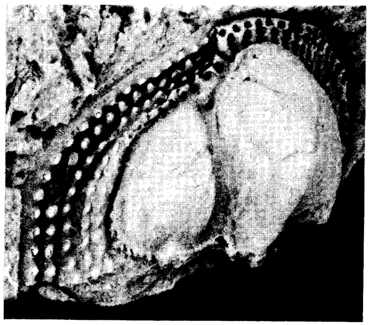

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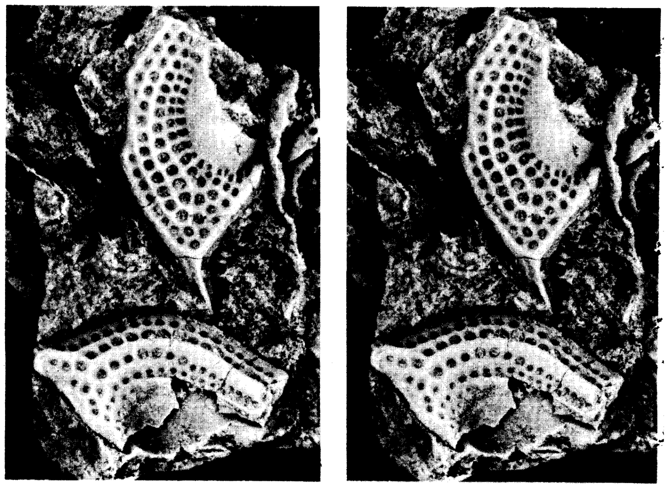

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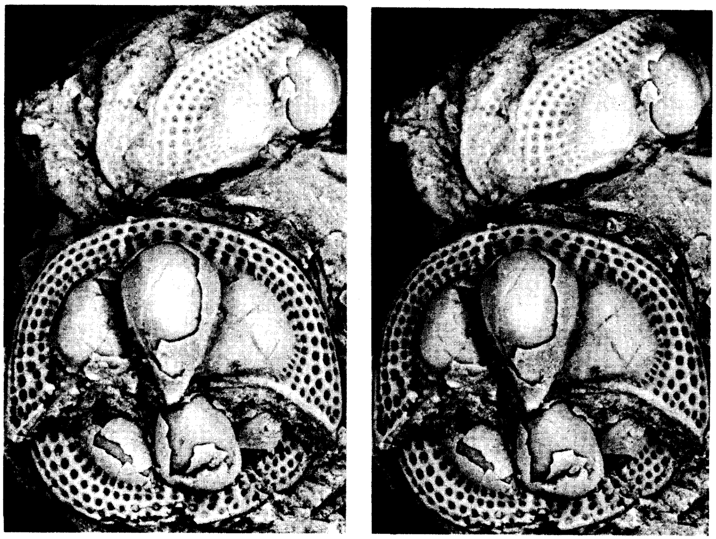

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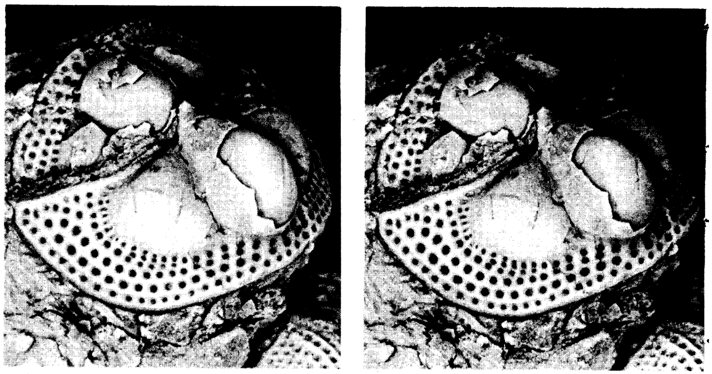

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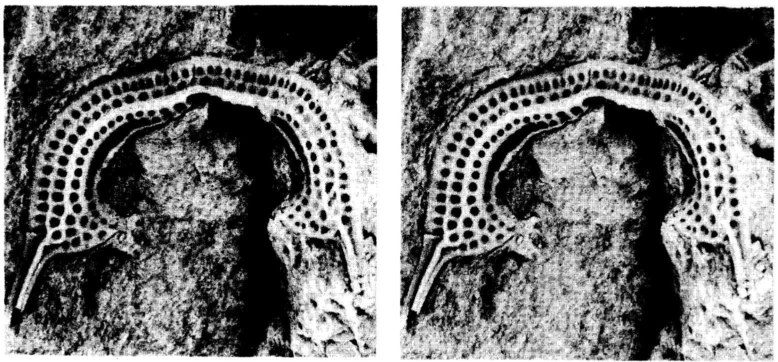

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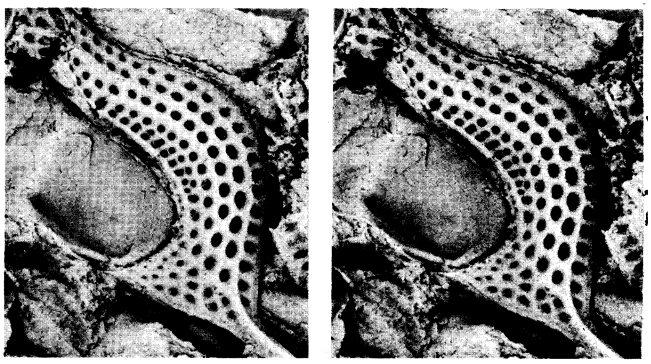


108

FIGURES 100–108. For description see opposite.

and a girder which is sharply developed throughout its length on the lower lamella. In addition, *Marrolithoides* has a less elevated glabella with a generally smaller occipital spine and relatively larger genal lobes.

M. anomalis Williams, 1948 is here returned to this genus, since Whittard's arguments (1956, pp. 49, 63) for placing it in *Marrolithus* no longer hold. The specimen assigned to *Marrolithoides arcuatus* from the upper Rorrington Beds of Shelve (Whittard 1956, pl. 9, fig. 2) almost certainly is a fairly juvenile *Marrolithus;* it is not a *Marrolithoides.* Similarly the *Marrolithoides* cf. *arcuatus* of MacGregor (1963, pp. 803–804, pl. 116, fig. 21), from the Llandeilo of the Berwyn Hills is placed in *Marrolithus,* and all forms referred to *Marrolithoides* from southeastern Turkey (Dean, 1967) are placed in *Deanaspis* gen. nov.

Genus **Deanaspis** gen. nov.

figures 100–103, plate 9

Diagnosis. Fringe subsemicircular to subquadrate. E_1 outermost arc with numerous pits; I_{1-2} pits relatively large. Girder list present; girder and first internal pseudogirder subequally developed; other pseudogirders slightly less well-developed.

Type species. Cryptolithus bedinanensis Dean, 1967.

Other included forms:

D. cf. *bedinanensis* (Dean, 1967).

D. senftenbergii (Hawle & Corda, 1847).

D. goldfussii (Barrande, 1846).

DESCRIPTION OF PLATE 9

FIGURES 100, 101. *Deanaspis bedinanensis* (Dean, 1967). Bedinan Formation (low Caradoc), southwest of Bedinan, Turkey. 100, Ventral mould of almost complete individual only lacking lower lamella of fringe, BM. It. 1210 (holotype) (magn. × 6). 101, Internal mould of lower lamella, BM. It. 715, showing sub-equal girder and first internal pseudogirder (magn. × 3).

FIGURES 102, 103. *Deanaspis* sp. Beds of low Caradoc age, Shakhriomon water-shed, western part of Zeravshanskiy region, Zeravshanskiy-Gissarskiy mountain range, southeast of Samarkand, Soviet central Asia. 102, Ventral mould of cephalon with fringe preserved as an internal mould, SM. A88054. 103, Ventral mould of cephalon with part of internal mould of fringe removed to reveal ventral (external) mould of lower lamella, SM. A88055. (Magns × 3.)

FIGURES 104–106. *Onnia cobboldi* (Bancroft, 1929). Onny Shales (Caradoc, Onnian Stage, *O. cobboldi* Zone), bed of River Onny, east of junction of Batch Gutter, Salop (Shropshire), England. 104, Fragments of two cephala, HM. A10695/1–2, illustrating relation between pit arcs on upper and lower lamellae. Lower lamella shows subdued girder, pronounced first internal pseudogirder, I_n cut-off (by I_3) and *F*-pits associated with vincular notches on flange. Upper lamellar fragment shows traces of healed damage (magn. × 3). 105, 106, Block with several cephala partially retaining exoskeleton, best preserved cephalon illustrated in dorsal and oblique views, BM. In. 49026, showing clearly relation between *F* pits and I_n cut-off on upper lamella (magn. × 2).

FIGURE 107. *Onnia superba* (Bancroft, 1929). Onny Shales (Caradoc, Onnian Stage, *O. superba* Zone), Cliff section. River Onny, Salop (Shropshire), England. Latex peel from ventral (external) mould of lower lamella of fringe, BM. In 52087, showing frontally pronounced first internal pseudogirder, I_n cut-off, *F* pits and vincular notches (magn. × 3).

FIGURE 108. *Onnia superba pusgillensis* Dean, 1961. Lower part of Cautley Mudstone (Caradoc, Onnian Stage, *O. superba* Zone), north-north-east of Foggygill Farm, Murthwaite Inlier, Cautley district, Cumbria (Westmorland), England. Latex peel from ventral mould of cephalon with ventral (external) mould of lower lamella HU. D.5.50a, showing typical *Onnia* features but with slightly more subdued first internal pseudogirder. I_n cut-off is by I_4 (magn. × 3).

All figures except 102 and 103 are stereophotographs.

D. inferus (Dean, 1967).
D. cf. *inferus* (Dean, 1967).
D. laticirrus (Dean, 1967).
D. orthogonius (Dean, 1967).
D. parviporus (Přibyl & Vaněk, 1969).
D. sp. (*Marrolithoides* sp. of Dean 1967, p. 101).
D. sp. (M. N. Chugaeva 1971, private communication).
D. spp. (J. Destombes 1972, private communication).
D. sp. (G. B. Vai 1974, private communication).

Distribution. Llandeilo to Caradoc of Czechoslovakia, Morocco, ?Spain and ?Portugal; Caradoc of Turkey, Sardinia and asiatic Russia (new undescribed form, M. N. Chugaeva, private communication).

Discussion. Previous generic assignments of many of the species included in this new genus have been unsatisfactory. Dean (1967) experienced particular difficulty with the generic placing of the Turkish specimens. Restudy of these and other forms in the light of the newly recognized morphological features of the fringe, shows them to constitute a distinct group of species allied to *Onnia*, to which they most likely gave rise. This is borne out by the stratigraphical distribution of a large series of allied forms from Morocco to be described by Ingham. The major morphological difference between the two genera is in the development of the girder and first internal pseudogirder, which are essentially subequally developed in *Deanaspis*, although the first internal pseudogirder is sometimes more prominently developed frontally.

Přibyl & Vaněk (1969, p. 120) considered *Tetrapsellium pulchrum* Hawle & Corda, 1847 to be based on a meraspis degree 4 of *Trinucleus senftenbergii*, but they gave no evidence to support their conclusion. In view of the uncertainty regarding the precise locality of Hawle & Corda's specimen and the lack of knowledge of the ontogenetic stages of most of the other trinucleids from Bohemia, it is preferred to restrict the use of *Tetrapsellium pulchrum* to the single specimen used by Hawle and Corda. Accepting this, then the generic name *Tetrapsellium* has no priority over the new name *Deanaspis* proposed here.

The form described as *Cryptolithus* sp. from Afghanistan (Pillet & de Lapparent 1969, p. 326, pls. 34, 35) shows some similarity to *Deanaspis*, but differs in that the first internal pseudogirder is less well developed than the girder.

Genus **Onnia** Bancroft, 1933

figures 104–108, plate 9; figures 3*d*, 7*b*

Diagnosis. Like *Deanaspis* but with girder list and internal lists only slightly developed: girder only weakly developed near genal angles; first internal pseudogirder very prominent, particularly frontally; second internal pseudogirder well marked laterally

Type species. Cryptolithus superbus Bancroft, 1929. Original designation by Bancroft 1933, p. 2.

Other included forms:

O. superba pusgillensis Dean, 1961.
O. pongerardi (Rouault, 1847).
O. grenieri (Bergeron, 1894).
O. suenesi (Kerforne, 1900).
O. gracilis (Bancroft, 1929).
O. cobboldi (Bancroft, 1929).

O. abducta (Přibyl & Vaněk, 1969).

O. spp. (J. Destombes 1972, private communication).

O.? ultima (Barrande, 1852).

O.? maladai (Oehlert, 1895).

Distribution. High Caradoc (Onnian) of Wales, the Welsh Borderland and northern England; Caradoc of northwestern France, Portugal and ?Spain; Caradoc to Ashgill of Czechoslovakia and Morocco.

Discussion. In the past the morphology of the fringe in this genus has been mis-interpreted. In the section on fringe morphology (§2(*b*)), the means of identifying the girder are stated, and it is clear that in *Onnia* the first internal pseudogirder has previously been mistaken for the girder (see figure 3*d*, and figures 104, 107, 108, plate 9). The genus is similar in many ways to *Deanaspis* gen. nov., but as noted above, in *Deanaspis* the girder and first internal pseudogirder are essentially subequally developed. In *Onnia* there is a tendency for I_n to be cut-off by the adjacent I arc at or near the most anterior F pit. This is particularly so in *O. cobboldi* (Bancroft, 1929), and it can give the impression on the upper lamella, of there being no cut-off of I_n, the more anterior F pits being misidentified as part of I_n. Study of the lower lamella, however, reveals the F pits and cut-off I_n clearly (figure 104, plate 9).

Latex peels of specimens, possibly including some of the type material, of *Trinucleus pongerardi* Rouault, 1847, kindly made available for study by Dr J.-L. Henry of Rennes, suggest an affinity to *O. seunesi* (see below), and so the species is provisionally placed here. The position of *Trinucleus ultimus* Barrande, 1852 is not entirely clear, since no adequate lower lamella has been available to us. However, from Barrande's illustrations (1852, pl. 29, figs. 18–20) and those of Přibyl & Vaněk (1969, pl. 10, figs 1–10) it appears to belong to either *Onnia* or *Deanaspis*. Although the occipital spine is present in most species of *Onnia*, in some specimens from Brittany, originally described as *Trinucleus seunesi* by Kerforne (1900), the occipital spine is absent as also in *O. pongerardi*; the significance of this is not yet entirely clear (Dr J.-L. Henry 1971, private communication). *Trinucleus maladai* Oehlert, 1895 (p. 334) is here tentatively and arbitrarily assigned to *Onnia*; it could equally well be a *Deanaspis*. The specimens, from the Sierra Morena of Spain, were originally described as *Trinucleus goldfussi* by Verneuil & Barrande (1855, p. 978, pl. 25, fig. 2). An *Onnia* similar to *O. seunesi* (with no occipital spine) occurs in the basal beds of the Grès de Loredo (Caradoc) of central Portugal (W. I. Mitchell 1974).

Genus **Bettonia** Whittard, 1956

figures 86–88, plate 7; figure 6*c*

Diagnosis. Fringe profile variable; posterior margin of fringe angulated. E_1 outermost complete arc, but a few pits of E_2 commonly developed frontally. I_1 pits and to a lesser extent, E_1 pits relatively enlarged but not elevated. First internal list broad, commonly clearly marked; girder list poorly developed. Girder prominent; first internal pseudogirder clear.

Type species. Bettonia frontalis Whittard, 1956. Original designation p. 66 (= *B. chamberlaini* (Elles, 1940), see Hughes 1971, p. 159).

Distribution. Llanvirn of Wales and the Welsh Borderland.

Discussion. B. chamberlaini and *B. superstes* were considered by Hughes (1971) as the only valid species within the genus. *B. superstes* Whittard, 1956 and *B.* aff. *superstes* of Hughes (1971) are here excluded from *Bettonia* since we believe them to be more closely allied to *Whittardolithus* gen. nov. (see below). Since the presence of E_2 pits frontally, the character used by Whittard originally to justify his 'species' from *Cryptolithus*, is now believed to be of minor importance in characterizing this genus, which is also now considered as mono-specific, the question as to the desirability of retaining *Bettonia* clearly arises. The angulation of the posterior margin of the fringe in *Bettonia* suggests a relationship with *Whittardolithus* on the one hand, and *Marrolithus craticulatus* Whittard, 1956 on the other. However, *Whittardolithus* and *Marrolithus* are clearly distinct morphologically and *Bettonia chamberlaini* forms a discrete intermediate stage of morphological development. It is thus proposed to retain *Bettonia* as a distinct genus.

Genus **Whittardolithus** gen. nov.

figures 83–85, plate 7

Diagnosis. Like *Bettonia* but with radial sulci variably developed frontally and anterolaterally on upper lamella, containing at least pits of E_1 and I_1. First internal list clear, cutting across sulci. Large area of irregularly distributed pits posteriorly, including F pits. Short preglabellar field.

Type species. *Cryptolithus instabilis* Hughes, 1971.

Other included forms:

- *W. superstes* (Whittard, 1956).
- *W.* aff. *superstes* of Hughes (1971).
- *W. inopinatus* (Whittard, 1958).
- *W.* cf. *inopinatus* of Whittard (1958).
- *W. intertextus* (Whittard, 1958).
- *W. radiatilis* (Whittard, 1958).
- *W.* cf. *radiatilis* of Whittard (1958).
- *W.* sp. (*Cryptolithus* sp. *A* of Hughes (1971)).
- *W.* sp. (*Cryptolithus* sp. *B* of Hughes (1971)).
- *W.* sp. (?*Cryptolithus* sp. *C* of Hughes (1971)).

Distribution. Upper Llanvirn to lower Llandeilo of Wales and the Welsh Borderland.

Discussion. Whittard (1958, p. 71), Dean (1967, p. 95) and Hughes (1971, p. 152) commented that the genus '*Cryptolithus*', as then understood, probably included representatives of at least two distinct groups. The present revision, with the recognition of I_n, I_n cut-off and F pits has indicated where and how the division of the genus may best be made. The Anglo-Welsh '*Cryptolithus*' spp. form a compact, distinct group, diagnosed as above, with marrolithine affinities, although also showing some affinities with cryptolithine genera (see below). The reasons for the inclusion of this genus within the Marrolithinae have already been discussed.

W. superstes (Whittard, 1956) and *W.* aff. *superstes* of Hughes, 1971 are assigned to this genus and not to *Bettonia*, because they possess a relatively large number of irregularly disposed pits on the genal prolongation. They are, however, clearly annectent with *Bettonia*.

Genus **Lloydolithus** Bancroft, 1933

figures 81, 82, plate 7

Diagnosis. Posterior margin less angulated than in *Whittardolithus*. E_2 extensively developed; incipient E_3 posteriorly. Pits of E_1 and I_1 slightly larger than remainder. Large area of irregularly developed pits posteriorly including numerous F pits. Pits arranged radially anteriorly and anterolaterally and in shallow sulci. Girder only clearly developed frontally and at genal angles. Preglabellar field short.

Type species. Trinucleus lloydi Murchison, 1839. Original designation by Bancroft 1933, p. 3.

Distribution. Lower Llandeilo of Wales and the Welsh Borderland.

Discussion. This genus, almost certainly derived from *Whittardolithus* presents the same problems regarding its subfamilial placing. In development of E arcs it shares common features with some later cryptolithines, such as *Broeggerolithus* and *Salterolithus*, but it is here placed in the Marrolithinae, together with the related *Protolloydolithus* and *Whittardolithus* for the reasons given (p. 570).

Genus **Protolloydolithus** Williams, 1948

figures 79, 80, plate 6; figures 2*e*, 3*b*

Diagnosis. Outer arc E_1; pits of E_1 and I_1 larger than other pits. I_n clearly developed at least anteriorly and anterolaterally; remainder of fringe consists of small irregularly positioned pits. F pits well developed. Girder prominent; girder list sharp. Preglabellar field present.

Type species. Trinucleus ramsayi Hicks, 1875. Original designation by Williams 1948, p. 66, type by monotypy.

Other included forms:

P. reticulatus (Elles, 1940).

P. neintianus Whittard, 1956.

Distribution. Lower Llanvirn to lower Llandeilo of Wales and the Welsh Borderland.

Discussion. This genus has obvious similarities with the hanchungolithines (see figures 3*b* and 79, 80, plate 6), but the well-developed F series and the presence of an external arc shows it to be annectent with *Lloydolithus* and *Whittardolithus*, which themselves retain significant areas of irregularly positioned small pits posterolaterally.

(*f*) Subfamily Cryptolithinae Angelin, 1854

Diagnosis. Fringe with E, I and F pits well developed. I_n not cut-off by outer I arcs. Glabella high, clavate, non-carinate with small basal lateral glabellar furrows and two further faint pairs. Occipital spine present.

Type genus. Cryptolithus Green, 1832*a*

Distribution. Caradoc of Norway, Sweden, Wales, Welsh Borderland and northern England, Caradoc and Ashgill of North America and Ireland; ?Caradoc, Ashgill of Scotland, Ashgill of Czechoslovakia? and Norway.

Discussion. Although in general cephalic form, nature of the glabella and presence of an occipital spine, the Cryptolithinae resemble the Marrolithinae, the cryptolithine genera can usually be readily distinguished in that there is no cut-off of I_n by the adjacent I arc and the girder is always well-defined in its entirety. Of the genera included in the Cryptolithinae, only the placing of *Cryptolithoides* is equivocal. This genus is allied to *Cryptolithus* (Whittington 1966*b*, text-fig. 3), but it exhibits a degree of irregular pit distribution laterally which frequently prevents positive I arc identification there, and in this respect it resembles early marrolithine genera such as *Lloydolithus* and *Whittardolithus*. The suggestion is that *Cryptolithoides* indicates possible early marrolithine or even hanchungolithine origins for the Cryptolithinae. It is also possible, in view of their different geographic distributions (see §5) that the Anglo-Welsh *Broeggerolithus–Salterolithus–Smeathenia* stock and the essentially North American *Cryptolithoides–Cryptolithus* stock have evolved independently, but along similar lines.

The F-pit series in cryptolithines commonly has the most postero-mesial pit slightly larger than the others (figure 109, plate 10). This is probably homologous with the posterior fossula in those trinucleids in which this is the only pit present on the flange of the lower lamella.

Genus **Cryptolithus** Green, 1832*a*

figures 109–112, plate 10; figures 2*g*, 4*d*

Diagnosis. Fringe narrow. Outermost arc, E_1 complete with radial ridges or plates between the outer pits, particularly laterally. I_1 and I_n complete with up to two other I arcs laterally. Pits radially alined frontally; laterally rows become deflected distally towards the front. Girder narrow, except frontally and prominent; internal pseudogirders poorly developed.

Type species. Cryptolithus tessellatus Green, 1832*a*. Original designation p. 73 (see also Whittington 1941*a*, 1968; Bertrand & Lespérance 1971).

Other included forms:

C. bellulus (Ulrich, 1878) (see also Whittington 1941*a*).

C. portlockii Salter, 1853.

C. portlockii girvanensis Lamont, 1935.

C. lorettensis Foerste, 1924 (see also Whittington, 1941*a*, 1968*a*; Bertrand & Lespérance, 1971).

DESCRIPTION OF PLATE 10

FIGURES 109–111. *Cryptolithus portlockii girvanensis* Lamont, 1935. Quarrel Hill Mudstones, lower Drummuck Group (Ashgill, probably Cautleyan Stage). 109, 110, From east brow of Quarrel Hill; 111, from Glenmard Quarry, near Dailly, Girvan, Kyle & Carrick, Strathclyde (Ayrshire), Scotland. 109, 110, Dorsal and oblique views of ventral mould of syntype cranidium, HM. A580, showing frontally incomplete I_2 arc and an extensive F-pit series inside I_n. 111, Internal mould of part of lower lamella of fringe, HM. A10696. (Magns × 3.)

FIGURE 112. *Cryptolithus lorettensis* Foerste, 1924. Lower Trenton limestones (Caradoc), Montmorency River, Quebec, Canada. Latex peel from ventral (external) mould of part of lower lamella of fringe, HM. A4318, showing well-defined girder, arcs E_1, I_{1-2}, I_n and, on the flange, the F-pit series (magn. × 6).

FIGURE 113. *Cryptolithoides ulrichi* Whittington, 1941*a*. Viola Limestone (Caradoc), 2 km (3 mile) north of Buckhorn, Oklahoma, U.S.A. Dorsal view of almost complete cranidium, HM. A4336, showing broad lateral part of fringe and irregularly distributed pits (magn. × 3).

FIGURE 114. *Cryptolithoides fittsi* (Ulrich & Whittington *in* Whittington, 1941*a*.) Viola Limestone (Caradoc), east of Highway 18, 0.7 km (1.1 mile) south of Sulphur, Oklahoma, U.S.A. Latex peel from ventral (external) mould of part of lower lamella of small individual, SM. A58255 (magn. × 8).

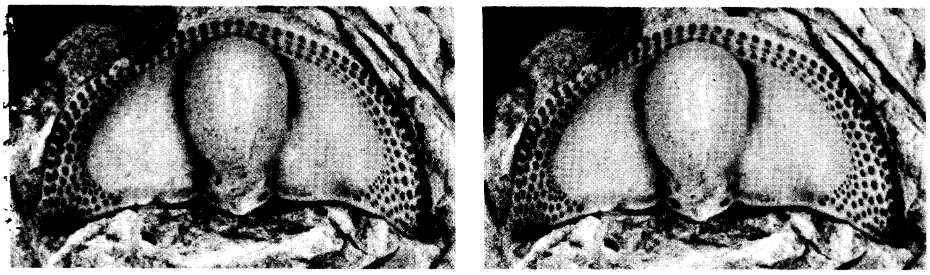
FIGURES 115, 116. *Broeggerolithus broeggeri* (Bancroft, 1929). Harnage Shales–Glenburrell Beds (Caradoc, Soudleyan Stage, *B. broeggeri* Zone) stream section at northeastern corner of Smeathen Wood, near Horderley, Salop (Shropshire), England. 115, Dorsal view of ventral mould of lectotype cranidium, BM. In 42077. 116, Internal mould of lower lamella of fringe, BM. In 50831, showing girder, two E arcs, two I arcs (I_1, I_n) and, on the flange, F pits and vincular notches (magns × 3).

FIGURE 117. *Salterolithus praecursor* Dean, 1960. Harnage Shales (Caradoc, Harnagian Stage, *R. reuschi* Zone), spring, east flank of Caer Caradoc, near Church Stretton, Salop (Shropshire), England. Ventral mould of cranidium HM. A10697, showing fringe with extensive F-pit series, two I arcs (I_1, I_n) and, frontally, three E arcs (magn. × 6).

FIGURE 118. A specimen currently difficult to place generically. Same horizon and locality as figure 117 where it is also associated with specimens referable to *Broeggerolithus harnagensis.* Latex peel from dorsal mould of incomplete cranidium, HM. A10698, showing anterolateral irregularity in distribution of outer pits suggestive of an incipient E_3 (magn. × 5). It is conceivable that a population study of lower Harnagian cryptolithines will show that *S. praecursor* and *B. harnagensis* are conspecific.

FIGURE 119. *Salterolithus caractaci* (Murchison, 1839). Same horizon and locality as figures 115, 116. Internal mould of part of lower lamella of fringe, BM. In 51193, showing up to four E arcs frontally (magn. × 4).

All figures except 110, 111, 116 and 119 are stereophotographs.



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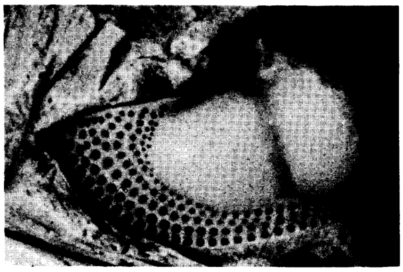

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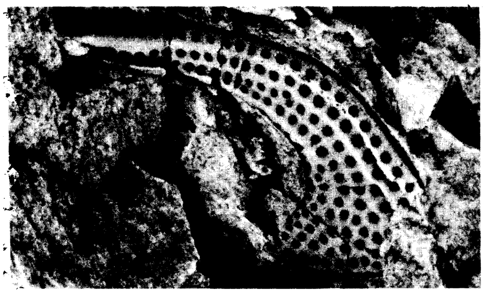

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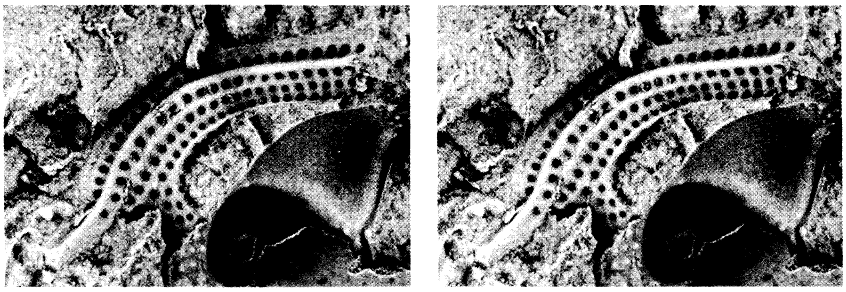

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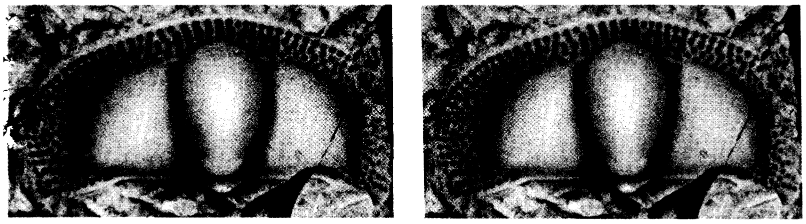

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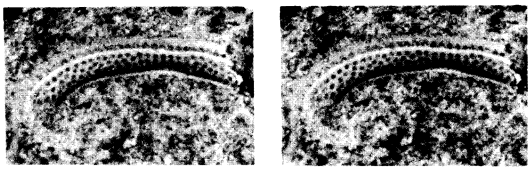

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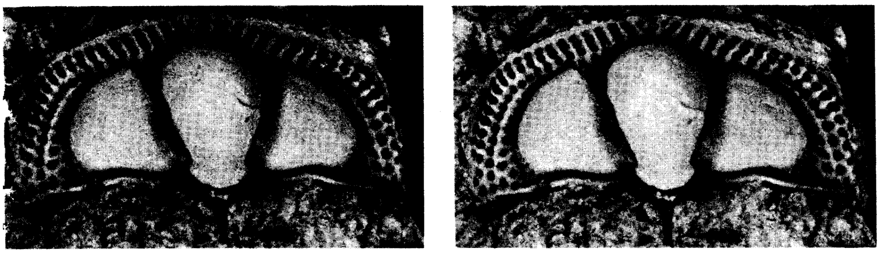

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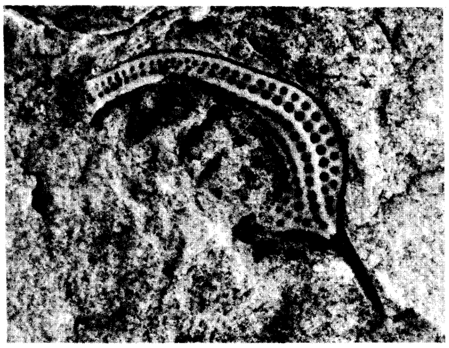

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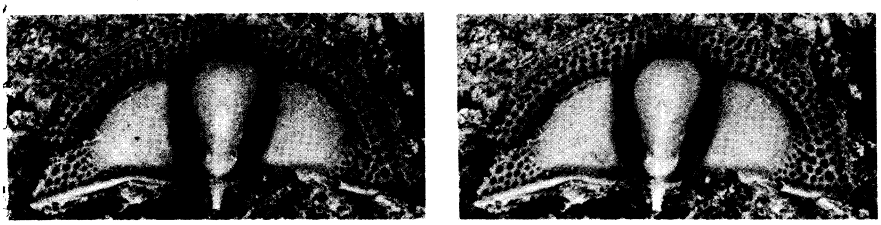

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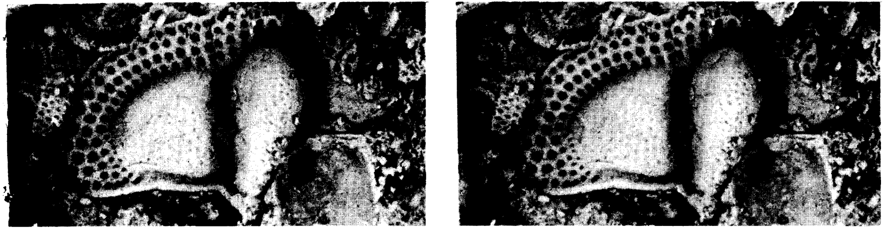

118

119

FIGURES 109–119. For description see opposite.

C. convexus Ulrich & Whittington *in* Whittington, 1941*a*.
C. praeterita (Reed, 1935).
C. n. sp. of Whittington (1941*a*).
C. sp. aff. *C. bellulus* of Bolton (1970).
C. sp. nov. (A. W. Owen, private communication).
C.? *kosoviensis* Marek, 1952 (see also Přibyl & Vaněk 1969).

Distribution. Caradoc and ?low Ashgill of North America; ?high Caradoc and Ashgill of Ireland (W. I. Mitchell, private communication); ?Caradoc and Ashgill of Scotland; Ashgill? of Czechoslovakia; Ashgill of Norway.

Discussion. Of the forms listed above, the closely related *C. tessellatus* and *C. lorettensis* have been subjected to population analysis by Whittington (1968*a*) and Bertrand & Lespérance (1971). The latter deduced that the two forms represented allopatric subspecies, whereas Whittington believed them to be two separate species with slightly different, though overlapping stratigraphic ranges. Neither study recognized the presence of *F* pits and the resultant re-allocation of the fringe pits suggests that two separate forms are present.

C. portlockii, from the Killey Bridge Beds of Co. Tyrone, Northern Ireland has long been in need of redescription and current work by Ingham & Mitchell should clarify its relationship with *C. portlockii girvanensis* from the lower Drummuck Beds of Girvan. The same studies have already made it clear that the latter form is not conspecific with the upper Drummuck *C. praeterita* as maintained by Lamont (1941, p. 450).

C.? *kosoviensis* from the Ashgill of Czechoslovakia is insufficiently known for an unequivocal generic assignment to be made. It could equally well be an *Onnia*. (See note added in proof, p. 597.)

Genus **Cryptolithoides** Whittington, 1941*a*

figures 113, 114, plate 10

Diagnosis. Like *Cryptolithus* but with a variable degree of irregularity in distribution of *I* pits, mainly on the lateral portions of the fringe.

Type species. Cryptolithoides ulrichi Whittington, 1941*a*. Original designation p. 24.

Other included forms:

C. fittsi (Ulrich & Whittington *in* Whittington, 1941*a*).
C. reticulatus Ross & Shaw, 1972.
C. sp. of Lenz & Churkin (1966).
C. sp. of Ross & Shaw (1972).
C.? *carinatus* (Ulrich & Whittington *in* Whittington, 1941*a*).

Distribution. Caradoc of central and western United States and ?Canada (British Columbia); Ashgill of Alaska.

Discussion. Ross & Shaw (1972), besides placing their new species in *Cryptolithoides*, also included three species previously referred to *Cryptolithus* by Whittington (1941*a*). Of these we concur with respect to *C. fittsi*, for although having a cephalon with a more *Cryptolithus*-like outline, there is a considerable amount of irregularity in pit distribution in this species and it therefore forms a morphological link between *Cryptolithus* and the more typical *Cryptolithoides* such as *C. ulrichi* and *C. reticulatus*. *C.*? *carinatus* shows some slight irregularity judging by Whittington's photographs, but its position is equivocal. *C. convexus* shows hardly any irregularity and is obviously closely allied to *Cryptolithus tessellatus* as noted by Whittington (1941*a*, p. 36). It is, therefore, placed in *Cryptolithus* here.

Although no occurrences of *Cryptolithoides* later than Caradoc age have been reported from central and western North America, the material described by Lenz & Churkin (1966) from Alaska (Yukon) seems satisfactorily dated as Ashgill.

Genus **Broeggerolithus** Lamont, 1935

(*pro Broeggeria* Bancroft, 1933, preoccupied Walcott, 1902)
figures 115, 116, plate 10; figure 5

Diagnosis. Only arcs E_1, E_2, I_1 and I_n present, all essentially complete. Pits generally radially arranged except that some forms have additional pits intercalated in E_2. Girder distinct; first internal pseudogirder weakly developed.

Type species. Cryptolithus broeggeri Bancroft, 1929. Original designation Bancroft 1933, p. 2.

Other included forms:

B. cf. *broeggeri* of Dean, 1960.
B. discors (Angelin, 1854).
B. nicholsoni (Reed, 1910).
B. globiceps (Bancroft, 1929).
B. harnagensis (Bancroft, 1929).
B. longiceps (Bancroft, 1929).
B. soudleyensis (Bancroft, 1929).
B. transiens (Bancroft, 1929).
B. ulrichi (Bancroft, 1949).
B. cf. *ulrichi* of Whittington (1966*c*).
B. constrictus Dean, 1960.
B. sp. (*Cryptolithus* sp. of Størmer (1930)).
B. sp. of Whittard (1958).

Distribution. Caradoc of Wales and the Welsh Borderland (Harnagian to Actonian), northern England (Longvillian to Marshbrookian) and Norway.

Discussion. The species of *Broeggerolithus* are in need of revision. We believe that some of the forms listed above have questionable validity and that a full taxonomic reassessment will result in a considerable reduction in the number of species. Some reduction has already taken place, for Dean (1962, p. 81) placed *B. simplex* Dean, 1960 in synonymy with *B. nicholsoni*, and Whittington (1966*c*, p. 87) considered *B.* sp. (?nov) of Dean, 1960 and *B. melmerbiensis* Dean, 1962 as best placed in synonymy with *B. nicholsoni* and (p. 88) that *B. longiceps* and *B. globiceps* may also belong there. We believe it may be necessary to go still further. We interpret the *B.* sp. of Dean (1960, p. 108) as an extreme individual of *B. harnagensis* and suggest that Dean's (1960) *B.* cf. *broeggeri* and *B. constrictus* be included in synonymy with *B. broeggeri.*

Although we have followed Dean (1960) in placing the early species *harnagensis* in *Broeggerolithus*, the considerable irregularity in pit distribution commonly present in E_2 makes it difficult to distinguish some specimens from *Salterolithus praecursor* Dean, 1960 (see below). The Norwegian form *B. discors* (see Størmer, 1930) has numerous adventitious pits in E_2 and exhibits some irregularity in this arc suggesting a comparison with the earlier *B. harnagensis*, and appears best placed in this genus.

Størmer figured a specimen (1930, pl. 6, fig. 14) as *Cryptolithus* sp. This specimen has recently been re-examined and, although it is not well-preserved, it is without doubt a *Broeggerolithus* and would not be out of place in Anglo-Welsh Caradoc rocks. Information on the horizon given by Størmer (Bryozoe layers of 'Fjicha', Dalarne, Sweden) has been kindly supplied by Dr Sven Laufeld of Lund. The 'Bryozolagret' [= Bryozoan Beds] (Törnquist 1883, p. 20) are about 10 m thick at Fjäcka. In more modern terms the horizon corresponds to the Macrourus Limestone which roughly correlates with Bergström's conodont zone of *Amorphognathus complicatus* and high in the *D. multidens* graptolite zone (see also Jaanusson & Martna 1948, p. 188; Martna 1955, pp. 229–256). This horizon falls well within the limits of *Broeggerolithus* in the Anglo-Welsh area.

The authorship of the genus has been variously quoted (see Whittington 1941*a*; Bancroft 1949; Moore 1959; Dean 1960; and Whittington 1966*c*). We prefer to follow Dean (1960).

Genus **Salterolithus** Bancroft, 1929

figures 118, 119, plate 10

Diagnosis. Like *Broeggerolithus* but with a broader fringe bearing three *E* arcs, E_3 commonly showing irregularity in pit distribution.

Type species. Trinucleus caractaci Murchison, 1839. Original designation Bancroft 1929, p. 78 (see also Cave 1957; Whittard 1958; Dean 1960).

Other included forms:

S. caractaci paucus Cave, 1957.

S. praecursor Dean, 1960.

Distribution. Low Caradoc (Harnagian to Soudleyan) of Wales and the Welsh Borderland.

Discussion. Although the two listed species are readily distinguished, some difficulty is often experienced in separating *S. praecursor* from its common associate *B. harnagensis* (see figures 117–119, plate 10). This difficulty is particularly evident when relatively small specimens are being considered, because few of these have E_3 well developed. In the variable irregularity of the pit distribution in E_2, some young of *S. praecursor* resemble more mature individuals of *B. harnagensis.* The problem is most acute when specimens referable to each species occur together, as in fact do the type specimens of both species (see Dean 1960, pp. 99, 107). The problem is purely a taxonomic one and results from the application of a devisive taxonomy to an evolving plexus in which, as in this case, two stocks are in the process of separation. At a higher stratigraphic level the separation is quite complete.

Genus **Smeathenia** Dean, 1960

Diagnosis. Similar to *Broeggerolithus* but with broader fringe having up to five *E* arcs present; E_{3-5} exhibiting varying degrees of irregularity.

Type species. Salterolithus smeathenensis Bancroft, 1949. Original designation Dean 1960, p. 100.

Distribution. Low Caradoc (Harnagian) of the Welsh Borderland.

Discussion. The difficulties experienced in the identification of some examples of *Broeggerolithus harnagensis* and *Salterolithus praecursor* (see above) apply also to *Smeathenia smeathenensis.* Although some immature specimens from the type locality have up to four *E* arcs present, other specimens do not, and could easily be placed in *Salterolithus.* Moreover, the variation in the number of pits external to E_1 is stated to range from 90 to 120 in *S. smeathenensis* by Dean (1960, p. 101), but a 14 mm wide cephalon is said to possess only 73 such pits – just within the range for *Salterolithus caractaci* (Dean 1960, p. 97, from Cave 1957, p. 285). The obvious very close relationship between all these forms throws some doubt on the value of their continued separation into discrete genera.

(*g*) Subfamily unassigned

Genus **Parkesolithus** Campbell & Durham, 1970

Diagnosis. E_{1-2} complete, E_3 may be present laterally; up to five I arcs, including I_n frontally. Pits in complete arcs approximately radially arranged but irregular arrangement present posterolaterally. Girder and first external pseudogirder prominent frontally, subdued laterally. First external list sharp. Glabella clavate with three pairs of lateral glabellar furrows. Prominent lateral eye tubercles close to glabella.

Type species. Parkesolithus gradyi Campbell & Durham, 1970. Original designation p. 573.

Other included form:

P. dictyotos Webby, 1974.

Distribution. Caradoc of New South Wales, Australia.

Discussion. Despite the lack of information regarding F pits, the combination of characters in *Parkesolithus* suggests a relationship both with the reedolithines and early marrolithines. Although there is no occipital spine, the large eye tubercles and general shape recall certain South American forms dealt with here as unassigned reedolithine genera (§4 (*d*)). Of the early marrolithines, *Lloydolithus* shares a number of features with *Parkesolithus* (Webby 1974). There are irregularly distributed pits on the genal prolongations, a similar distribution of E arcs and the girder becomes effaced laterally. In addition there is a resemblance in the development of internal pseudogirders, but the external list is not developed in *Lloydolithus*. The glabellar form is similar in the two genera but *Lloydolithus* has very reduced eye ridges in the adult and also has an occipital spine.

It is possible that *Parkesolithus* represents a separate stock with a probable hanchungolithine ancestry, developing along similar lines to the early marrolithine genera. (See note added in proof, p. 597).

5. Evolution and distribution

The primary aim of the present work, to reassess the classificatory position of trinucleid genera in the light of some new morphological observations, has had the incidental result of providing new insight into their evolution and distribution. It has been found that the subfamilial groupings, or suspected stocks within them, tend to reflect a geographic pattern which is particularly striking when plotted on some of the recent Lower Palaeozoic palaeogeographic reconstructions. This, we think, gives some credence to what we believe is an essentially phylogenetic classification.

The maps used for plotting subfamilial and generic distributions (figures 121–123) are primarily based on the work of Briden *et al.* (1973) but they incorporate some of the modifications proposed by Whittington & Hughes (1972, 1973) and McKerrow & Ziegler (1973). The latter authors followed Briden *et al.* in rotating the North American and Baltic plates westward relative to Gondwanaland for Silurian to Early Devonian times, partly because of the northern position of the European edge of Gondwanaland and a more southerly palaeolatitude suspected for North America during this period. However, because of the different pole positions, there are no such longitudinal constraints for Ordovician reconstructions, other than the purely geometrical ones of the general plate distribution indicated by Whittington & Hughes. The longitudinal position shown here for these northern plates relative to Gondwanaland must not, therefore, be regarded as in any way precise.

We have followed Whittington & Hughes in recognizing a mid-European separation between the Baltic plate and the central European region of Spain–France–Czechoslovakia – a divide subsequently to be the site of the Variscan suture – but there is, as yet, no evidence, other than faunal similarity, for the distance between these central European pieces and the southern parts of Europe and Gondwanaland. There is no clear indication here of the reality of an Ordovician proto-Tethyan divide; central as well as southern Europe may have formed part of Gondwanaland for much of the Lower Palaeozoic as already suggested by Burrett (1972,

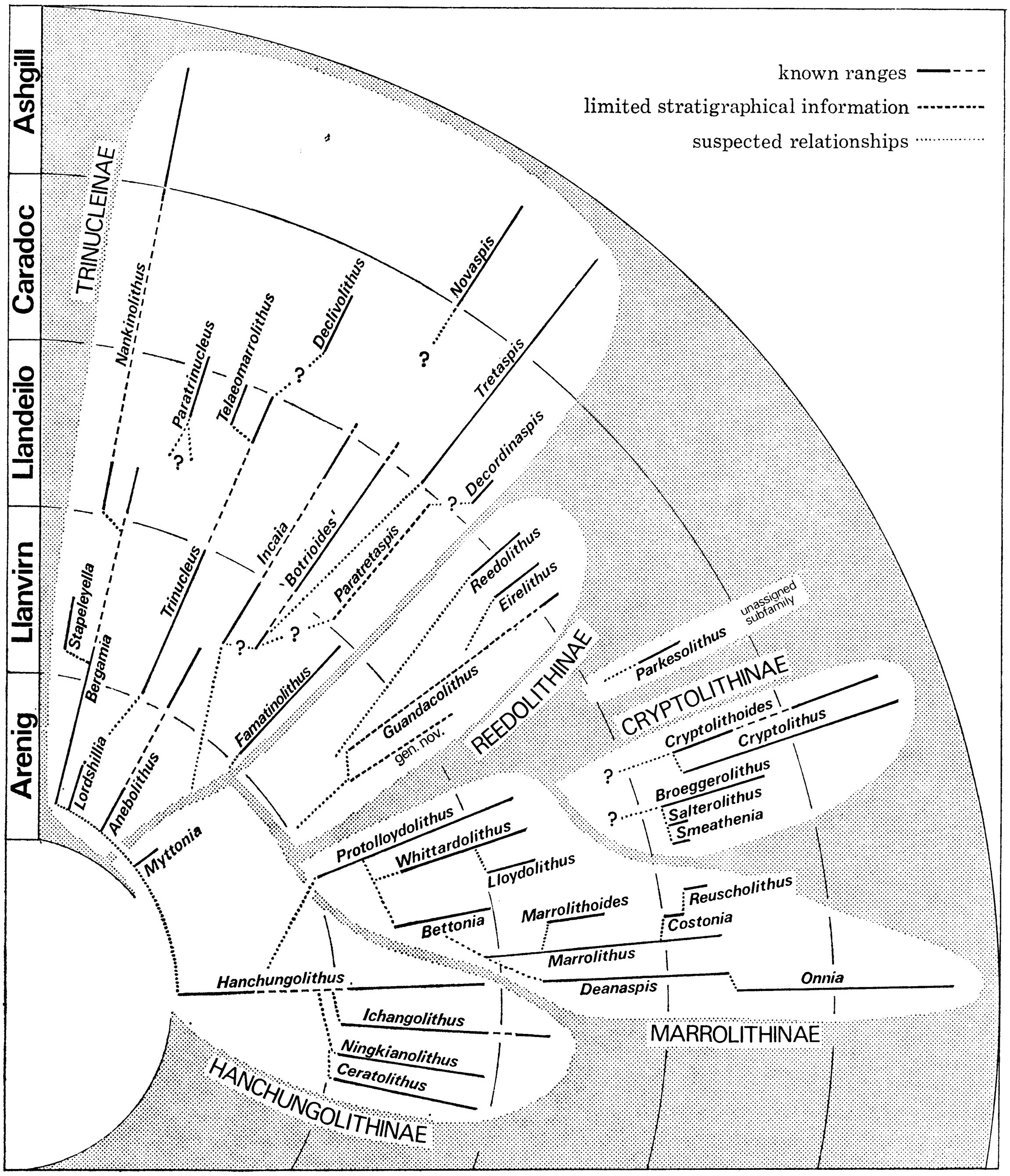

FIGURE 120. Suggested evolutionary relationships within the Trinucleidae. *Yinpanolithus* (unassigned subfamily) (see p. 597) not included.

1973). With regard to the position of southern Britain, we favour McKerrow & Ziegler's Silurian reconstruction (1973) in which it forms part of a volcanic island arc extending from the Baltic plate to include parts of Newfoundland, Nova Scotia and Maine, and not the isolated or central European positions shown by Whittington & Hughes (1972, 1973 respectively).

The orthographic projection used for the diagrams gives a clear impression of the plate positions and faunal distributions, but we have chosen to show only one hemisphere in each

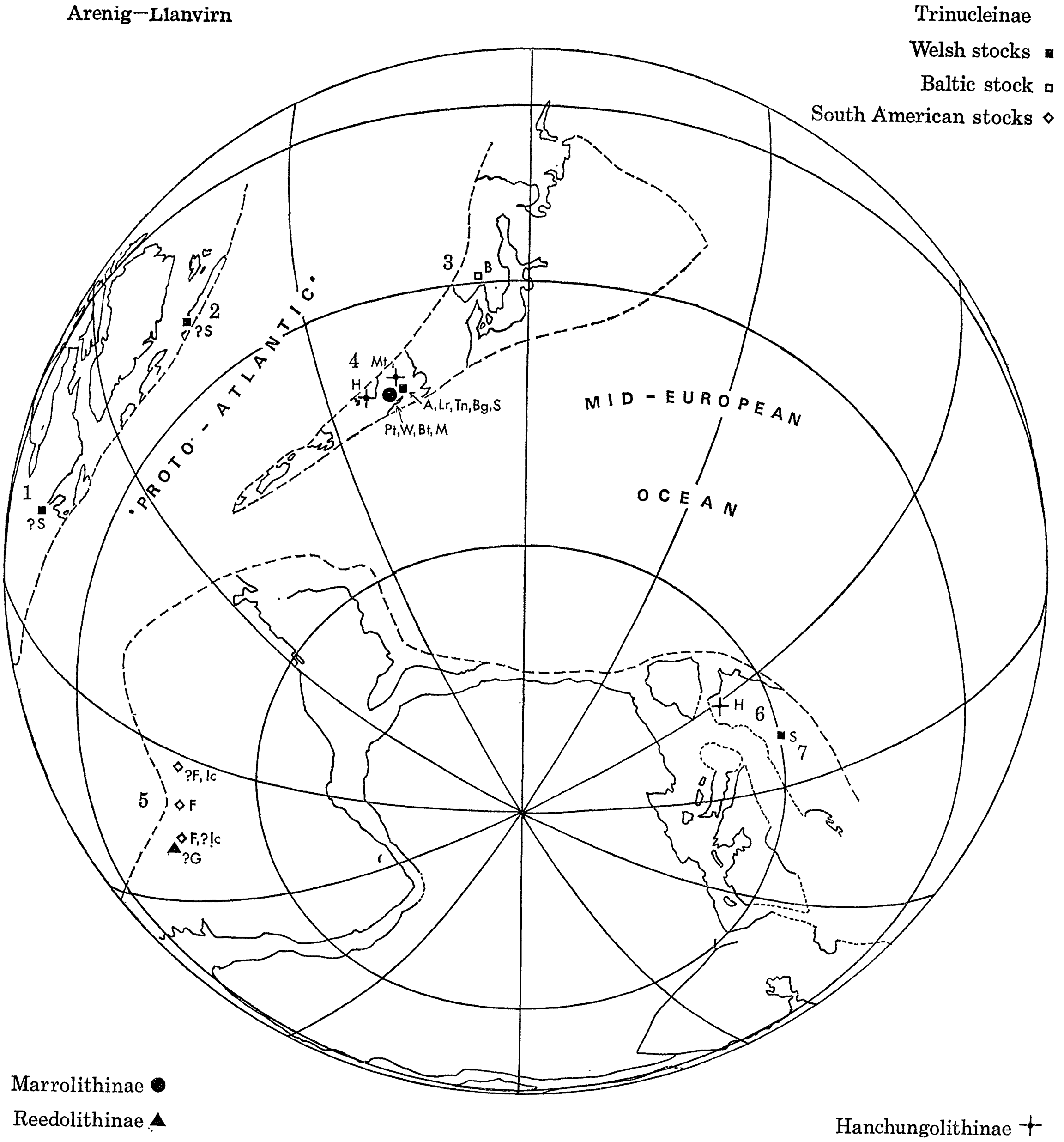

FIGURE 121. Trinucleid distribution 1 (see text). 1, Quebec. 2, Western Norway. 3, Southern Norway. 4, Anglo-Welsh area and southeastern Ireland. 5, Peru, Bolivia and northwestern Argentina. 6, Southern France. 7, Czechoslovakia. A, *Anebolithus;* B, '*Botrioides*' group; Bg, *Bergamia*; Bt, *Bettonia*; F, *Famatinolithus*; G, *Guandacolithus;* H, *Hanchungolithus*; Ic, *Incaia*; Lr, *Lordshillia*; M, *Marrolithus*; Mt, *Myttonia*; Pt, *Protolloydolithus*; S, *Stapeleyella*; Tn, *Trinucleus*; W, *Whittardolithus*. On the reverse hemisphere, not shown, are the Llanvirn hanchungolithine genera of central China.

diagram because of the small amount of current information with regard to the positions of the several Asiatic plates and also the limited distribution of trinucleids in the Australasian region. One important feature which emerges from the reconstructions is the suggestion that climatic control, as reflected by palaeolatitude, may have been as important a factor in influencing the distribution of various taxa as ocean currents and plate separation.

The ancestral trinucleid group, the Hanchungolithinae, has a scattered distribution (figure 121), *Hanchungolithus* being found in southern France, probably southern Ireland and, by Llanvirn times, in central China accompanied by a number of allied forms. One of them, *Ningkianolithus* is also known from Iran and another, *Ichangolithus*, apparently persisted into the Llandeilo, a probable occurrence being recorded at this level in Argentina. *Myttonia* seems to have been restricted to the Anglo-Welsh basin: there it gave rise to one of the two main stocks of the Trinucleinae, through *Anebolithus* (see figure 120). We believe that there were two branches to the Anglo-Welsh stock, one giving rise to *Trinucleus* and *Telaeomarrolithus* and the other to *Bergamia* and *Stapeleyella*, a grouping recognized by Whittington (1966*b*, text-fig. 3). Representatives of the latter branch are also known from central Europe (Bohemia) and *Trinucleus* has been recognized from the Urals. *Declivolithus* – a probable *Trinucleus* derivative – has a central European–north African distribution. It seems that the mainly upper Ordovician genus *Nankinolithus*, which is certainly a descendant of *Bergamia*, originated in this *Selenopeltis* faunal province (see Whittington & Hughes 1972) and that its wide occurrence from China to northern Britain and Canada reflects the late Ordovician cosmopolitan tendency in faunal distribution brought about it seems, at least as far as northern Europe is concerned, by the progressive closure of the proto-Atlantic. The occurrence of trinucleines apparently of Anglo-Welsh type in Virginia (*Paratrinucleus*) and Canada and western Norway (*Stapeleyella*?) remains problematical for the present.

The other trinucleine stock is not so well understood (see figure 120). The relationship, if any, between '*Botrioides*' and the South American and New Zealand genus *Incaia* is not clear, but both '*Botrioides*' and *Tretaspis* probably share a common ancestor and have their early evolutionary history in the slightly lower palaeolatitudes occupied by much of the Baltic and Appalachian regions. '*Botrioides*' may not have survived Llandeilo times: it has a distribution extending from Norway and Sweden along the volcanic island arc already mentioned to central Newfoundland, but excluding the Anglo-Welsh basin. This exclusion of '*Botrioides*' from Wales during Llandeilo times reflects local palaeogeographic conditions: at other times, Baltic elements are commonly present in the faunas particularly of North Wales, whereas in South Wales and the Welsh Borderland, central European elements occur together with endemic stocks (Williams 1973, pp. 252–253). *Tretaspis* has its known range entirely later than '*Botrioides*' but the earliest occurrences, of low Caradoc date, are confined to the Scoto-Appalachian region, and it was not until late Caradoc times that *Tretaspis* is known from the Baltic area and southern Britain, which suggests a closing proto-Atlantic control (but see below): by Ashgill times the genus had reached central Europe. The origins of *Novaspis* are not known although it shows some similarities to '*Botrioides*' and *Incaia*. Like most Ashgill trilobites it has a wide distribution. Similarly, *Famatinolithus* and *Decordinaspis*, found in South America and eastern Ireland respectively, have no known direct ancestors and may represent separate stocks, although *Decordinaspis* shows some resemblance to *Tretaspis* and the recently described *Paratretaspis* may provide the link.

Detailed relationships between the group of genera included by us in the Reedolithinae are

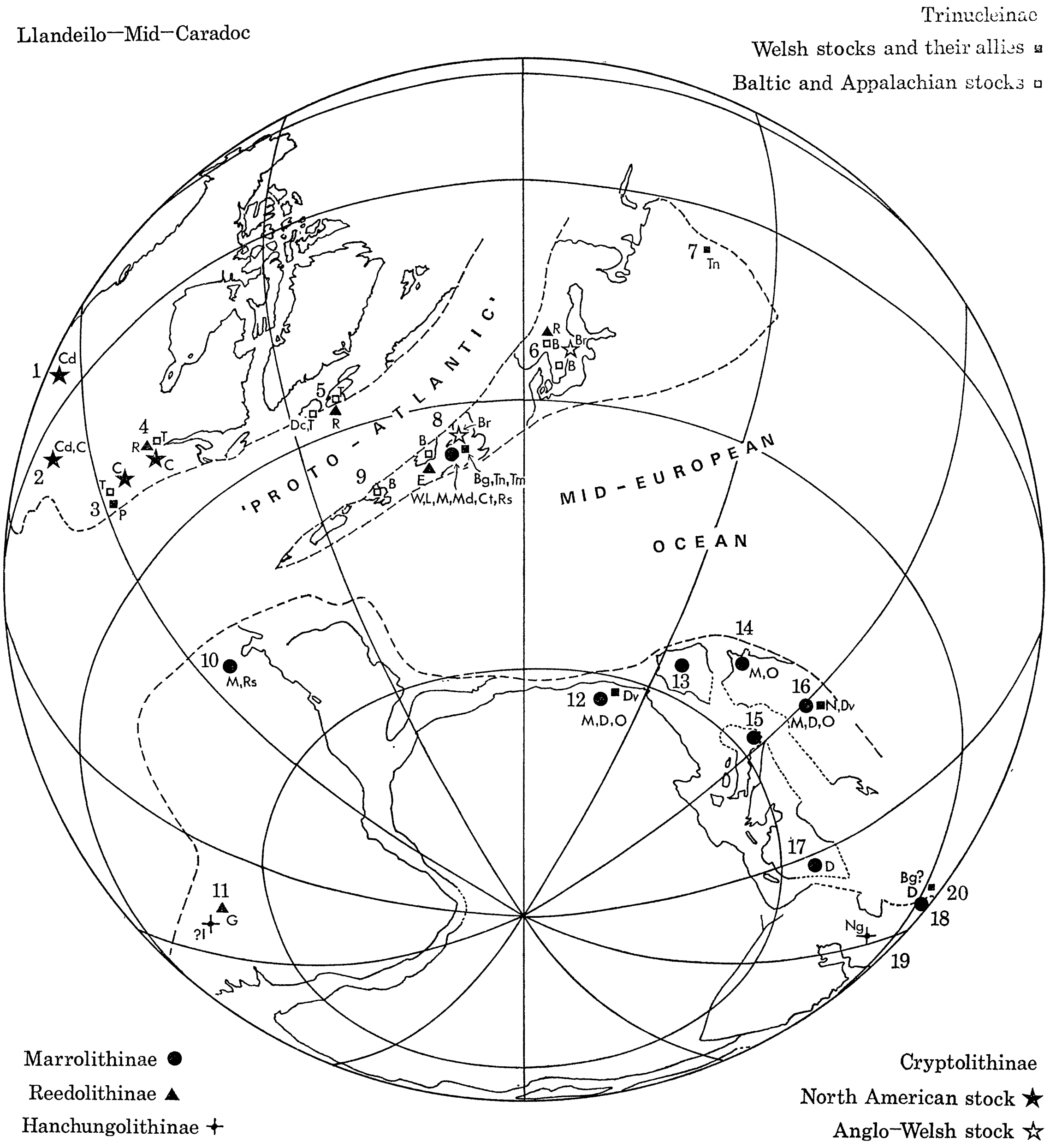

FIGURE 122. Trinucleid distribution 2 (see text). 1, Western U.S.A. 2, Central U.S.A. 3, Southern Appalachians. 4, Northern Appalachians. 5, Scotland and northwestern Ireland. 6, Southern Norway and Sweden. 7, West-central Urals. 8, Anglo-Welsh area and southeastern Ireland. 9, Central Newfoundland. 10, Venezuela. 11, Northwestern Argentina. 12, Morocco. 13, Iberian peninsula. 14, Northwestern France. 15, Carnic Alps. 16, Czechoslovakia. 17, Turkey. 18, Southern Soviet central Asia (Zeravshanskiy-Gissarskiy range). 19, Iran. 20, Eastern Pamir. 21, The occurrence of the marrolithine *Deanaspis* in Sardinia was inadvertently omitted on the figure. B, '*Botrioides*'; Bg, *Bergamia*; Br, *Broeggerolithus* and *Salterolithus*; C, *Cryptolithus*; Cd, *Cryptolithoides*; Ct, *Costonia*; D, *Deanaspis*; Dc, *Decordinaspis*; Dv, *Declivolithus*; E, *Eirelithus*; G, *Guandacolithus*; I, *Ichangolithus*; L, *Lloydolithus*; M, *Marrolithus*; Md, *Marrolithoides*; N, *Nankinolithus*; Ng, *Ningkianolithus*; O, *Onnia*; P, *Paratrinucleus*; R, *Reedolithus*; Rs, *Reuscholithus*; T, *Tretaspis*; Tn, *Trinucleus*; Tm, *Telaeomarrolithus*; W, *Whittardolithus*. On the reverse hemisphere, not shown, is *Incaia*, from the high Llandeilo or low Caradoc of New Zealand, and *Parkesolithus* from the Caradoc of Australia.

poorly known, although *Guandacolithus* is undoubtedly closely allied to other un-named lower Ordovician genera from South America mentioned in §4(*d*). There is also a strong possibility that these forms may relate in some way to the Llandeilo hanchungolithine *Ichangolithus*? recorded from Argentina. The late Llandeilo to early Caradoc *Reedolithus* is more distantly allied and has an interesting distribution for mid-Ordovician times as it bridges the Scoto-Appalachian and Baltic regions while the contemporaneous *Tretaspis* does not. This distribution of

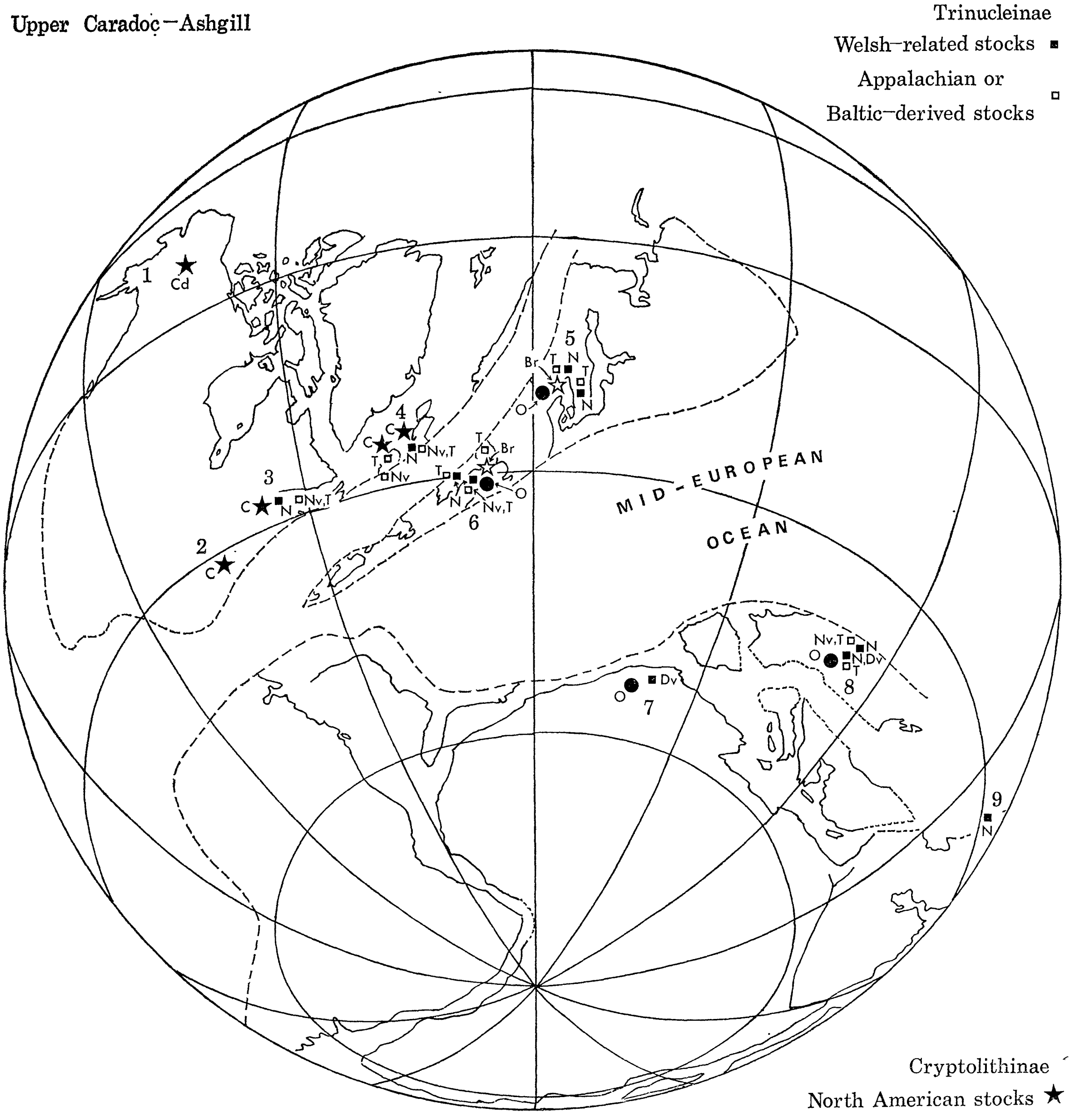

FIGURE 123. Trinucleid distribution 3 (see text). 1, Alaska. 2, Appalachians. 3, Quebec. 4, Scotland and north-western Ireland. 5, Southern Norway and Sweden. 6, Anglo-Welsh area and southeastern Ireland. 7, Morocco. 8, Czechoslovakia and Southern Poland. 9, South Soviet central Asia (Bukantau range, Uzbekistan) and Kazakhstan. Br, *Broeggerolithus;* C, *Cryptolithus*; Cd, *Cryptolithoides*; Dv, *Declivolithus*; N, *Nankinolithus*; Nv, *Novaspis*; O, *Onnia*; T, *Tretaspis*. On the reverse hemisphere, not shown, is *Nankinolithus* from the upper Ordovician of China and possibly Soviet Central Asia. The record of the marrolithine *Onnia* in Norway is erroneous; it should be the North American cryptolithine *Cryptolithus* (see p. 597).

Reedolithus may argue for a closer proximity between the North American plate together with the Baltic plate, and South America than is shown on the accompanying maps. This would require their further westward translation, at the same palaeolatitude, to a position similar to that advocated by McKerrow & Ziegler (1973) for the Silurian. *Eirelithus* is known with certainty only from southeastern Ireland where it occurs in a fauna containing a '*Botrioides*'-like form and other Baltic elements. There are no reedolithines in the *Selenopeltis* Province.

The distribution of the Marrolithinae is the most striking of all the trinucleid groups. For most of its history this subfamily was confined to the *Selenopeltis* Province which seems to have reflected a partly circum-polar cool climatic regime (see, for example, Spjeldnaes 1961, p. 57; Williams 1973, p. 261). The evolutionary picture we envisage for this group is similar in some respects to that shown by Whittington (1966*b*, text-fig. 3) but we include *Onnia* and exclude American and Anglo-Welsh cryptolithine stocks (see below). The early development of the Marrolithinae took place in the Anglo-Welsh basin but, by Llandeilo and early Caradoc times, marrolithine genera were widespread in central and southern Europe, Morocco, Turkey, Soviet central Asia and Venezuela where not only *Marrolithus* but also the presence of its derivative *Reuscholithus* argues for close links with the Anglo-Welsh basin during middle Ordovician times. *Deanaspis* (gen. nov.), which is also closely allied to *Marrolithus*, evolved outside the Anglo-Welsh basin and is known from Morocco to Soviet central Asia. In mid-Caradoc times progressive lower lamellar changes in *Deanaspis* eventually led to *Onnia*, a genus which then persisted in Morocco and perhaps Czechoslovakia well into Ashgill times. Only for a short period towards the end of the Caradoc epoch is *Onnia* found in the Anglo-Welsh area.

The cryptolithinae contains two, apparently independent stocks which have evolved along similar lines. The *Broeggerolithus–Salterolithus* stock, characterized by a fixed number of *I* arcs, is endemic to the Anglo-Welsh basin but its origins are obscure. *Broeggerolithus* had reached Sweden by mid-Caradoc times and persisted in Norway until the late Caradoc when the stock had virtually died out in southern Britain: its representatives have not been found elsewhere.

Cryptolithoides and *Cryptolithus*, however, with their single *E* arc, are essentially North American genera. The former genus is only known from the Caradoc of central and western North America and from the Ashgill of Alaska. It has already been noted (§4 (*f*)) that the irregularity of pit distribution suggests hanchungolithine origins. The closely allied *Cryptolithus* is an important element in the Caradoc of the Appalachian region and it persisted, at least in Scotland and Norway, until almost the end of Ashgill times. This cryptolithine stock was restricted for its entire range to the lower palaeolatitides. Its apparent link with a warmer climatic regime may explain its probable absence in the late Ordovician of central and southern Europe but it does not explain why its representatives have not been found in southern Britain or are so rare in the Baltic region at a time when Ordovician faunas generally were becoming more cosmopolitan.

6. Relation of ontogeny to phylogeny

Since Whittington's articles on the ontogeny of trilobites (1957; in Moore 1959) the main contributions on the subject have been in the form of morphological descriptions of young stages or complete ontogenetic suites (e.g. Whittington 1959; Palmer 1962; Chatterton 1971), although Kautsky (1962) has given a more general account of ontogeny in invertebrates, in which he included some trilobite information. Whittington's general conclusion (1957, p. 460) was that there was really insufficient evidence to make any general statements regarding the type of evolutionary patterns reflected in the trilobite ontogenies, and that many of the claimed cases of neoteny could not be substantiated. This statement still holds true for the great majority of trilobite groups.

In the Trinucleidae, early studies prior to Whittington (1957) consisted chiefly of the work of Barrande (1852, 1872), Bancroft (1929), Beecher (1895), Størmer (1930) and Whittington (1940, 1941 *b*). Subsequently, by far the most important work was that of Whittington (1959) with very full descriptions of the ontogenetic stages of *Cryptolithus tessellatus* and *Tretaspis sagenosus* based on silicified material. Lesser contributions have been made by various other authors (e.g. Whittard 1955, 1956, 1958; Dean 1960, 1966; Hughes 1971) chiefly by morphological descriptions of isolated occurrences of immature individuals of various species. One of us (R.A.), however, hopes shortly to publish nearly complete ontogenetic series of some marrolithines based on silicified material from South Wales. However, none of these published contributions gives any discussion of possible relations between ontogeny and the evolution and classification of the Trinucleidae. This is presumably due to the fact that there has been no real phylogenetic framework in which to discuss ontogenetic development. The one exception has been Lu (1963, 1964) who, although having an incomplete evolutionary framework in which to work, had a considerable amount of new information regarding the early primitive forms, the Hanchungolithinae. From this, and other available information, he concluded that trinucleids as a whole exhibited marked recapitulation, in particular quoting the meraspid features of *Reedolithus* and *Tretaspis* as being typical of mature hanchungolithine genera in many respects.

The present study does not attempt to add any new morphological information regarding the ontogeny of any trinucleid species, but it does allow the known ontogenetic information to be seen within an evolutionary framework. In all cases the evidence appears to support Lu's conclusions regarding recapitulation as being the main evolutionary trait.

The major changes during the ontogeny of non-hanchungolithine genera may be summarized as follows:

(1) Loss or reduction of eye ridges, and in many cases of lateral eye tubercles.
(2) Loss or reduction of alae.
(3) Gradual build up of arc elements of fringe, with girder being marginal initially.
(4) Loss of carination of glabella.

Some of these features also are true of hanchungolithine ontogenies, the only real exceptions being that the eye ridges are not lost, although they are considerably shorter in adult forms than in immature individuals, and the alae persist in the adult form. A further feature in some meraspid hanchungolithines is the presence of anterolateral spines, a feature also seen in the protaspis stages of both *Cryptolithus tessellatus* and *Tretaspis sagenosus*.

Each of the four points above is reflected to varying degrees in the several evolutionary lines of descent portrayed in the proposed phylogeny (figure 120). There are clearly other trends, for example changes in the convexity of both glabella and fringe and an increase in the orderliness of the pit distribution (figures 3, 4). The changing convexities of glabella and fringe are difficult to pick out in much ontogenetic material because of the preservation, but there are indications of the same type of changes (see Størmer 1930, p. 39 for *Reedolithus carinatus*; Whittington 1959, plates 20, 22, 23 for *Cryptolithus tessellatus*). Another feature seen in the ontogeny of nearly all trinucleids is a progressive change in the outline of the fringe posterolaterally. In early stages the posterior margin is directed forwards and this becomes less pronounced with increasing size, developing in many more mature individuals into pronounced genal prolongations. This is reflected phylogenetically by some later trinucleines (e.g. *Nankinolithus*, *Declivolithus* and some *Tretaspis*).

Since it appears that once a pit is formed during ontogeny it cannot under normal conditions of growth be removed, there is little opportunity for ontogeny to reflect the increase in orderliness apparent in the early phylogenetic development of the family. Apart from this difference there is a clear phylogenetic parallel in fringe development with (3) (above). In evolutionary terms the development of the trinucleid fringe must have been essentially as follows:

(*a*) Development of a bilaminar fringe by modification of the marginal areas and the ventral doublure and the introduction of irregularly distributed small pits internal to a marginal girder.

(*b*) Progressive ordering of the pits into radii and/or arcs (usually in the mesial region first) accompanied by an increase in pit size and marked reduction in their total number.

(*c*) Progressive increase (in many stocks) in the number of I arcs by intercalation between I_1 and I_n.

(*d*) Introduction of a separate pit series external to the girder.

(*e*) Development of F pits (in some forms only).

Points (*c*)–(*e*) are reflected ontogenetically in *Cryptolithus tessellatus* (Whittington 1959) and marrolithines currently being studied by one of us (R.A.). In the ontogeny of *C. tessellatus* it is clear that the F pits only develop after the other fringe elements are substantially complete. Points (*c*) and (*d*) are reflected in the ontogeny of *Tretaspis sagenosus* (Whittington 1959). This form, being a trinucleine, does not possess an F-pit series.

Thus Lu's deductions appear to be justified and the Trinucleidae possibly supply the only convincing example of recapitulation in the Trilobita. The demonstration of a clear relation between ontogeny and phylogeny in the Trinucleidae, highlights the need for similar studies in other groups. Although in the case of the trinucleids the study has not helped greatly with the problem of the ancestry of the family, it is predicted that subsequent studies of this kind linked to those on ontogenetic series will ultimately lead to a great increase in our understanding of the supra-familial relationships and general phylogeny of the trilobites.

7. Current generic assignments

Although the main emphasis of this study has been at the generic and subfamilial level, and not that of a monographic treatment of species, it has been necessary to examine many trinucleid species in considerable detail. The results of much of this appear in the lists of included forms in the various genera. It became apparent, however, that there are a considerable number of specific names that have been used in the literature that are now considered to be either junior synonyms of other trinucleid species, or to be forms no longer placed in the Trinucleidae. Such names do not occur in the lists of included forms. It is obviously impractical to attempt to deal with doubtfully or incorrectly identified species. The current generic assignments given below will, we hope, serve two functions; first as a form of index to species listed elsewhere in the paper under their appropriate genus, and secondly as a means of determining the current placing of obsolete specific names to be encountered in the trinucleid literature. Some of the assignments are new, for example, those to the new genera erected, and these are indicated by an asterisk. In other cases the present authors either agree with the most recent authoritative assignment or alternatively have no direct knowledge of the species with which to assess the placing. No attempt is made to distinguish between the various degrees of certainty, and the reader is asked to accept them as being the best the authors are able to give without a full specific revision. It should be noted, however, with reference to the Czechoslovakian species, that although published in 1970, the catalogue of type specimens in the National Museum, Prague (Horny & Bastl 1970) does not include reference to Přibyl & Vaněk's 1969 paper. The earlier paper is taken as the more authoritative. Species and subspecies are listed alphabetically and no segregation is made of those no longer considered to be trinucleids.

List of species and subspecies

abductus	*Cryptolithus abductus* Přibyl & Vaněk, 1969	*Onnia abducta**
abruptus	*Trinucleus abruptus* Hughes, 1971	*Trinucleus abruptus*
acervulosus	*Trinucleus acervulosus* Raymond, 1920	*Paratrinucleus acervulosus*
acutofinalis	*Trinucleus acutofinalis* Whittard, 1956	*Trinucleus acutofinalis*
affinis	*Trinucleus affinis* Angelin, 1854	? *Tretaspis seticornis*
albidus	*Trinucleus albidus* Reed, 1914*a*	*Novaspis albida*
alfredi	*Trinucleus alfredi* Želízko, 1906	*Declivolithus alfredi*
alyta	*Tretaspis ceriodes alyta* Ingham, 1970	*Tretaspis ceriodes alyta*
anderssoni	*Tretaspis seticornis* var. *anderssoni* Størmer, 1945	*Tretaspis seticornis anderssoni*
angelini	*Tretaspis cerioides* var. *angelini* Størmer, 1930	*Tretaspis ceriodes angelini*
anomalis	*Marrolithoides anomalis* Williams, 1948	*Marrolithoides anomalis*
arcuatus	*Trinucleus concentricus* var. *arcuatus* Fearnsides, Elles & Smith, 1907	*Cryptolithus portlockii*
arcuatus	*Marrolithoides arcuatus* Whittard, 1956	*Marrolithoides arcuatus*
arenarius	*Marrolithus arenarius* Whittard, 1956	*Marrolithus arenarius*
asaphoides	*Trinucleus? asaphoides* Murchison, 1839	*Ogygiocarella debuchii* (ogygiocaridinid)
barrandei	*Trinucleus barrandei* Hawle & Corda, 1847	*Deanaspis goldfussii**
bedinanensis	*Cryptolithus? bedinanensis* Dean, 1967	*Deanaspis bedinanensis**
bellulus	*Trinucleus bellulus* Ulrich, 1878	*Cryptolithus bellulus*
bigsbii	*Cryptolithus bigsbii* Green, 1832*b*	nomen oblitum
bilinearis	*Marrolithus bilinearis* Whittard, 1956	*Marrolithus bilinearis*
bishopi	*Incaia bishopi* Hughes & Wright, 1971	*Incaia bishopi*
bispinosa	*Decordinaspis bispinosa* Harper & Romano, 1967	*Decordinaspis bispinosa*
bohemicus	*Trinucleus bohemicus* Barrande	nomen nudum
boliviensis	*Trinucleus boliviensis* Lake, 1906	nomen dubium
brachystichus	*Tretaspis hadelandica brachystichus* Ingham, 1970	*Tretaspis hadelandica brachystichus*
brevis	*Trinucleus brevis* Murchison, 1845	nomen nudum
broeggeri	*Cryptolithus broeggeri* Bancroft, 1929	*Broeggerolithus broeggeri*
broeggeri	*Trinucleus hibernicus* var. *bröggeri* Størmer, 1930	*Botrioides? hibernicus broeggeri**

bronnii	*Trilobites bronnii* Boeck, 1838	*Botrioides? bronnii**
bucculentus	*Trinucleus bucculentus* Angelin, 1854	*Botrioides? bucculentus**
bucklandi	*Trinucleus bucklandi* Barrande, 1846	*Nankinolithus granulata**
bueyensis	*Trinucleus bueyensis* Rusconi, 1956	*Famatinolithus bueyensis**
bureaui	*Trinucleus bureaui* Oehlert, 1895	*Marrolithus bureaui*
calcaria	*Tretaspis calcaria* Dean, 1971	*Tretaspis calcaria*
canadensis	*Tretaspis canadensis* Stäuble, 1953	*Tretaspis canadensis*
caractaci	*Trinucleus caractaci* Murchison, 1839	*Salterolithus caractaci*
carinatus	*Cryptolithus carinatus* Ulrich & Whittington *in* Whittington, 1941*a*	*Cryptolithoides? carinatus*
carinatus	*Trinucleus carinatus* Angelin, 1854	*Reedolithus carinatus*
ceriodes	*Tretaspis ceriodes* Angelin, 1854	*Tretaspis ceriodes*
ceryx	*Tretaspis ceryx* Lamont, 1941	*Tretaspis ceryx*
chamberlaini	*Trinucleus chamberlaini* Elles, 1940	*Bettonia chamberlaini*
clarkei	*Tretaspis clarkei* Cooper *in* Schuchert & Cooper, 1930	*Tretaspis clarkei*
clarkii	*Trinucleus clarkii* Clarke, 1847	nomen nudum
cobboldi	*Cryptolithus cobboldi* Bancroft, 1929	*Onnia cobboldi*
colliquia	*Tretaspis colliquia* Ingham, 1970	*Tretaspis colliquia*
concentricua	*Nuttania concentrica* Eaton, 1832	*Cryptolithus tessellatus*
confinalis	*Lordshillia confinalis* Whittard, 1966	*Lordshillia confinalis*
confusa	*Myttonia confusa* Whittard, 1955	*Myttonia confusa*
constrictus	*Broeggerolithus constrictus* Bancroft, 1949	*Broeggerolithus constrictus*
convergens	*Tretaspis convergens* Dean, 1961	*Tretaspis convergens*
convexus	*Cryptolithus convexus* Ulrich & Whittington *in* Whittington, 1941*a*	*Cryptolithus convexus*
corndensis	*Trinucleus lloydii* var. *β corndensis* Salter, 1853	*Lloydolithus lloydii*
cornutus	*Ceratolithus cornutus* Lu, 1963	*Ceratolithus cornutus*
coscinorinus	*Trinucleus coscinorinus* Angelin, 1854	*Botrioides coscinorinus**
cosoviensis	see *kosoviensis*	
craticulatus	*Marrolithus craticulatus* Whittard, 1956	*Marrolithus craticulatus*
cribrosus	*Trinucleus cribrosus* Hawle & Corda, 1847	nomen dubium
cyllarus	*Asaphus cyllarus* Hisinger, 1840	*Tretaspis seticornis*
diademata	*Tretaspis diademata* Ruedemann, 1901	*Tretaspis reticulata*
discors	*Trinucleus discors* Angelin, 1854	*Broeggerolithus discors**
distichus	*Tretaspis latilimbus distichus* Ingham, 1970	*Tretaspis latilimbus distichus*
donsi	*Tretaspis ceriodes* var. *donsi* Størmer, 1945	*Tretaspis ceriodes donsi*
duftonensis	*Tretaspis kiaeri duftonensis* Dean, 1961	*Tretaspis kiaeri duftonensis*
efflorescens	*Trinucleus efflorescens* Hadding, 1913	*?Botrioides foveolatus**
elegans	*Costonia elegans* Dean, 1960	*Costonia elegans*
elegantulus	*Trinucleus elegantulus* Hawle & Corda, 1847	nomen dubium

elevata	*Marrolithoides simplex* var. *elevata* Williams, 1948	*Marrolithus simplex elevata*
elevata	*Tretaspis elevata* Cooper & Kindle, 1936	*Novaspis elevata*
ellipticus	*Trinucleus ellipticus* Münster, 1840	?harpid
elliptifrons	*Trinucleus elliptifrons* Olin, 1906	*Nankinolithus granulata**
elongatus	*Trinucleus elongatus* Portlock, 1843	?*Cryptolithus portlockii*
emposadensis	*Cryptolithus emposadensis* Rusconi, 1953	un-named reedolithine gen.
etheridgei	*Trinucleus etheridgei* Hicks, 1875	*Stapeleyella? etheridgei**
favus	*Tretaspis ceriodes favus* Dean, 1963	*Tretaspis ceriodes favus*
favus	*Trinucleus ornatus* var. *δ favus* Salter, 1847	*Marrolithus favus*
fearnsidesi	*Myttonia fearnsidesi* Whittington, 1966*a*	*Myttonia fearnsidesi*
fimbriatus	*Trinucleus fimbriatus* Murchison, 1839	*Trinucleus fimbriatus*
fittsi	*Cryptolithus fittsi* Ulrich & Whittington *in* Whittington, 1941*a*	*Cryptolithoides fittsi*
forosi	*Trinucleus forosi* Størmer, 1932	*Stapeleyella? forosi*
foveolatus	*Trinucleus foveolatus* Angelin, 1854	*Botrioides? foveolatus**
frontalis	*Bettonia frontalis* Whittard, 1956	*Bettonia chamberlaini*
furquei	*Guandacolithus furquei* Harrington & Leanza, 1957	*Guandacolithus furquei*
gibbifrons	*Trinucleus gibbifrons* M'Coy, 1849	nomen dubium
gibbosa	*Trinucleus* (*Cryptolithus*) *portlockii* var. *gibbosa* Reed, 1952	*Cryptolithus portlockii*
gibbosus	*Trinucleus* (*Cryptolithus*) *gibbosus* Elles, 1940	*Bettonia chamberlaini*
gibbosus	*Trinucleus? gibbosus* Münster, 1840	?odontopleurid
gibbsii	*Trinucleus gibbsii* Salter *in* Murchison, 1859	*Bergamia gibbsii*
girvanensis	*Cryptolithus portlockii* var. *girvanensis* Lamont, 1935	*Cryptolithus portlockii girvanensis*
globiceps	*Cryptolithus globiceps* Bancroft, 1929	*Broeggerolithus globiceps*
globosus	*Clavatellus globosus* Poletaeva *in* Egorova *et al.*, 1955	*Clavatellus globosus* (hapalopleurid)
goldfussii	*Trinucleus goldfussii* Barrande, 1846	*Deanaspis goldfussii**
gracilis	*Cryptolithus gracilis* Bancroft, 1929	*Onnia gracilis*
gracilis	*Trinucleus gracilis* Münster, 1840	?harpid
gradyi	*Parkesolithus gradyi* Campbell & Durham, 1970	*Parkesolithus gradyi*
granulatus	*Entomastracites granulatus* Wahlenberg, 1818	*Nankinolithus granulatus*
grenieri	*Trinucleus grenieri* Bergeron, 1893	*Onnia grenieri**
hadelandica	*Tretaspis seticornis* var. *hadelandica* Størmer, 1945	*Tretaspis hadelandica*
harnagensis	*Salterolithus harnagensis* Bancroft, 1929	*Broeggerolithus harnagensis*
hibernicus	*Trinucleus hibernicus* Reed, 1895	*Botrioides? hibernicus**
honghuayuanensis	*Ningkianolithus honghuayuanensis* Chang (see Lu 1974)	*Ningkianolithus honghuayuanensis*
ichangensis	*Hanchungolithus* (*Ichangolithus*) *ichangensis* Lu, 1963	*Ichangolithus ichangensis*

incipiens	*Marrolithus inflatus* var. *incipiens* Williams, 1948	*Marrolithus inflatus incipiens*
inconstans	*Stapeleyella inconstans* Whittard, 1955	*Stapeleyella inconstans*
inferus	*Cryptolithus? inferus* Dean, 1967	*Deanaspis inferus**
inflatus	*Marrolithus inflatus* Williams, 1948	*Marrolithus inflatus*
inopinatus	*Cryptolithus inopinatus* Whittard, 1958	*Whittardolithus inopinatus**
inornatus	*Marrolithus inornatus* Whittard, 1956	*Marrolithus inornatus*
inquilinium	*Cochliorrhoe inquilinium* Whittard, 1966	*Bergamia inquilinium*
instabilis	*Cryptolithus instabilis* Hughes, 1971	*Whittardolithus instabilis**
intermedius	*Trinucleus intermedius* Münster, 1842	?bronteid
intermedius	*Trinucleus intermedius* Wade, 1911	*Salterolithus caractaci*
intermedius	*Telaeomarrolithus intermedius* Hughes, 1971	*Telaeomarrolithus intermedius*
intermedius	*Trinucleus foveolatus* var. *intermedius* Størmer, 1930	*Botrioides? foveolatus intermedius**
intertextus	*Cryptolithus intertextus* Whittard, 1958	*Whittardolithus intertextus**
irregularis	*Bettonia irregularis* Whittard, 1956	*Bettonia chamberlaini*
issedon	*Trinucleus issedon* Eichwald, 1857	'*Harpes*' *issedon* (?harpid)
jiantsaokouensis	*Nankinolithus jiantsaokouensis* Lu (see Lu 1974)	*Nankinolithus jiantsaokouensis*
kiaeri	*Tretaspis kiaeri* Størmer, 1930	*Tretaspis kiaeri*
kruegeri	*Trinucleus kruegeri* Hoek *in* Steinmann & Hoek, 1912	*Famatinolithus? kruegeri**
kosoviensis	*Cryptolithus kosoviensis* Marek, 1952	*Cryptolithus? kosoviensis*
laevis	*Trinucleus laevis* Münster, 1840	?harpid
laticirrus	*Marrolithoides laticirrus* Dean, 1967	*Deanaspis laticirrus**
latilimbus	*Trinucleus latilimbus* Linnarsson, 1869	*Tretaspis latilimbus*
latus	*Trinucleus latus* Portlock, 1843	?*Cryptolithus portlockii*
lirellatus	*Marrolithus lirellatus* MacGregor, 1963	*Marrolithus lirellatus*
lloydii	*Trinucleus lloydii* Murchison, 1839	*Lloydolithus lloydii*
longiceps	*Cryptolithus longiceps* Bancroft, 1929	*Broeggerolithus longiceps*
lorettensis	*Cryptolithus lorettensis* Foerste, 1924	*Cryptolithus lorettensis*
lorrainensis	*Cryptolithus lorrainensis* Ruedemann, 1926	*Cryptolithus bellulus*
macconochiei	*Ampyx? macconochiei* Etheridge & Nicholson, 1879 also as *Trinucleus? macconochiei* Reed, 1903	*Raymondella macconochiei* (raphiophorid)
magnificus	*Marrolithus magnificus* MacGregor, 1963	*Marrolithus magnificus*
maladai	*Trinucleus maladai* Oehlert, 1895	*Onnia? maladai**
matura	*Bergamia matura* Whittard, 1966	*Bergamia matura*
maturus	*Marrolithus inflatus* var. *maturus* Williams, 1948	*Marrolithus inflatus maturus*
melmerbiensis	*Broeggerolithus melmerbiensis* Dean, 1962	*Broeggerolithus melmerbiensis*
minor	*Trinucleus minor* Hawle & Corda, 1847	nomen dubium
moeldenensis	*Tretaspis moeldenensis* Cave, 1960	*Tretaspis moeldenensis*
moderatus	*Marrolithus favus* var. *moderatus* Williams, 1948	*Marrolithus favus moderatus*

multiplex	*Myttonia multiplex* Whittard, 1966	*Myttonia multiplex*
multiseriatus	*Cryptolithus multiseriatus* Endo, 1932	*Hanchungolithus multiseriatus*
murchisonii	*Trinucleus murchisonii* Salter *in* Murchison, 1859	*Stapeleyella murchisonii*
nankinensis	*Nankinolithus nankinensis* Lu, 1954	*Nankinolithus nankinensis*
neintianus	*Protolloydolithus neintianus* Whittard, 1956	*Protolloydolithus neintianus*
nicholsoni	*Trinucleus nicholsoni* Reed, 1910	*Broeggerolithus nicholsoni*
nilsoni	*Trinucleus*? *nilsoni* Münster, 1840	?bronteid
nordenskioeldi	*Trinucleus nordenskiöldi* Bulman, 1931	*Incaia nordenskioeldi*
noticus	*Famatinolithus noticus* Harrington & Leanza, 1957	*Famatinolithus noticus*
novaki	*Tretaspis nováki* Chlupáč, 1952	*Declivolithus alfredi*
nudus	*Trinucleus nudus* Murchison, 1839	*Cnemidopyge nuda* (raphiophorid)
ornatus	*Trilobites ornatus* Sternberg, 1833	*Marrolithus ornatus*
orthogonius	*Marrolithoides orthogonius* Dean, 1967	*Deanaspis orthogonius**
otarion	*Trinucleus*? *otarion* Münster, 1840	?bronteid
pamiricus	*Trinucleus pamiricus* Balashova, 1966	*Bergamia*? *pamirica**
parviporus	*Marrolithus ornatus parviporus* Přibyl & Vaněk, 1969	*Deanaspis parviporus**
parvulus	*Collis parvulus* Koroleva, 1959	*Collis parvulus* (? raphiophorid)
paucipuncta	*Bettonia paucipuncta* Whittard, 1956	*Bettonia chamberlaini*
paucus	*Salterolithus caractaci* var. *paucus* Cave, 1957	*Salterolithus caractaci paucus*
paulisper	*Marrolithus ornatus paulisper* Přibyl & Vaněk, 1969	*Marrolithus ornatus paulisper*
pedemontanus	*Tetraspis pedemontanus* Rusconi, 1953	non-trinucleid
persulcatus	*Trinucleus* (*Tretaspis*) *persulcatus* Reed, 1935	*Tretaspis persulcatus*
pongerardi	*Trinucleus pongerardi* Rouault, 1847	*Onnia pongerardi**
portlockii	*Trinucleus concentricus* var. *ε portlockii* Salter, 1853	*Cryptolithus portlockii*
portrainensis	*Trinucleus seticornis* var. *portrainensis* Reed, 1897	*Nankinolithus portrainensis**
praecedens	*Trinucleus bucklandi* mut. *praecedens* Klouček, 1919	*Nankinolithus praecedens**
praecursor	*Salterolithus praecursor* Dean, 1960	*Salterolithus praecursor*
praeterita	*Trinucleus* (*Cryptolithus*) *gibbifrons* var. *praeterita* Reed, 1935	*Cryptolithus praeterita*
pragensis	*Trinucleus pragensis* Hawle & Corda, 1847	nomen dubium
primitivus	*Trinucleus primitivus* Born, 1921	*Hanchungolithus primitivus*
primus	*Marrolithus primus* Williams, 1948	*Marrolithus primus*
primus	*Trinucleus fimbriatus* mut. *primus* Elles, 1940	*Bergamia prima*
pulchrum	*Tetrapsellium pulchrum* Hawle & Corda, 1847	nomen dubium
pusgillensis	*Onnia superba pusgillensis* Dean, 1961	*Onnia superba pusgillensis*

quadrilineus	*Cryptolithus tessellatus* var. *quadrilineus* Whittington, 1941*a*	*Cryptolithus lorettensis*
quatuor-lineatus	see bibliographic appendix	
quatuor-spinus	see bibliographic appendix	
quebecensis	*Reedolithus quebecensis* Stäuble, 1953	*Reedolithus quebecensis*
radialis	*Tretaspis kjaeri* mut. *radialis* Lamont, 1941	*Tretaspis radialis*
radiatilis	*Cryptolithus radiatilis* Whittard, 1958	*Whittardolithus radiatilis**
radiatus	*Trinucleus radiatus* Murchison, 1839	*Telaeomarrolithus radiatus*
ramsayi	*Trinucleus ramsayi* Hicks, 1875	*Protolloydolithus ramsayi*
recurvus	*Cryptolithus recurvus* Ulrich *in* Bassler, 1919	*Cryptolithus bellulus*
reticulatus	*Tretaspis reticulatus* Ruedemann, 1901	*Tretaspis reticulata*
reticulatus	*Cryptolithoides reticulatus* Ross & Shaw, 1972	*Cryptolithoides reticulatus*
reticulatus	*Trinucleoides reticulatus* Elles, 1940	*Protolloydolithus reticulatus*
reuschi	*Reuscholithus reuschi* Bancroft, 1929	*Reuscholithus reuschi*
reussi	*Trinucleus reussi* Barrande, 1872	*Trinucleoides reussi*
rhodesi	*Bergamia rhodesi* Whittard, 1955	*Bergamia rhodesi*
richthofeni	*Trinucleus richthofeni* Kayser, 1883	*Reedolithus? richthofeni*
sagenosus	*Tretaspis sagenosus* Whittington, 1959	*Tretaspis sagenosus*
salteri	*Trinucleoides salteri* Elles, 1940	*Trinucleus fimbriatus*
scalpriformis	*Marrolithus scalpriformis* Whittard, 1956	*Marrolithus scalpriformis*
sedgwicki	*Trinucleus sedgwicki* Salter, 1866	*Bergamia? sedgwicki*
senftenbergii	*Trinucleus senftenbergii* Hawle & Corda, 1847	*Deanaspis senftenbergii**
seticornis	*Asaphus seticornis* Hisinger, 1840	*Tretaspis seticornis*
seunesi	*Trinucleus seunesi* Kerforne, 1900	*Onnia seunesi**
simplex	*Broeggerolithus simplex* Dean, 1960	*Broeggerolithus nicholsoni*
simplex	*Marrolithoides simplex* Williams, 1948	*Marrolithoides simplex*
simplicior	*Incaia simplicior* Whittard, 1966	*Anebolithus simplicior*
smeathenensis	*Salterolithus smeathenensis* Bancroft, 1949	*Smeathenia smeathenensis*
sortita	*Trinucleus* (*Tretaspis*) *cerioides* var. *sortita* Reed, 1935	*Tretaspis sortita*
soudleyensis	*Cryptolithus soudleyensis* Bancroft, 1929	*Broeggerolithus soudleyensis*
sparkskii	see *spaskii*	
sparsa	*Nuttania sparsa* Eaton, 1832	?non-trinucleid
spaskii	*Trinucleus spaskii* Eichwald, 1840	?'*Harpes*' *spaskii*
stelarusconii	*Cryptolithus stelarusconii* Rusconi, 1954	un-named reedolithine gen.
sternbergii	*Trinucleus ornatus* var. *α sternbergii* Salter, 1847	*Deanaspis goldfussii**
subradiatus	*Trinucleus subradiatus* Reed, 1903	*Reedolithus subradiatus*
sulcifera	*Trinucleus* (*Cryptolithus*) *portlockii* var. *sulcifera* Reed, 1952	*Cryptolithus portlockii**
superbus	*Cryptolithus superbus* Bancroft, 1929	*Onnia superba*
superstes	*Bettonia superstes* Whittard, 1956	*Whittardolithus superstes**

terranovica	*Paratretaspis terranovica* Dean, 1974	*Paratretaspis terranovica*
terryi	*Cryptolithus terryi* Leith, 1938	*Reuscholithus terryi**
tessellatus	*Cryptolithus tessellatus* Green, 1832*a*	*Cryptolithus tessellatus*
thersites	*Trinucleus thersites* Salter, 1853	*Eirelithus thersites*
transiens	*Cryptolithus transiens* Bancroft, 1929	*Broeggerolithus transiens*
trinucleum	*Trinucleus trinucleum* Boeck, 1828	nomen dubium
ulrichi	*Salterolithus* (*Ulricholithus*) *ulrichi* Bancroft, 1949	*Broeggerolithus ulrichi*
ulrichi	*Cryptolithoides ulrichi* Whittington, 1941*a*	*Cryptolithoides ulrichi*
ultimus	*Marrolithus ultimus* Bancroft, 1949	*Costonia ultima*
ultimus	*Trinucleus fimbriatus* mut. *ultimus* Elles, 1940	*Trinucleus fimbriatus*
ultimus	*Trinucleus ultimus* Barrande, 1852	*Onnia ultima*
ventriculatus	*Marrolithus ventriculatus* Whittard, 1956	*Marrolithus ventriculatus*
verrucosa	*Onnia verrucosa* Rusconi, 1956	*Guandacolithus verrucosa**
wahlenbergi	*Trinucleus wahlenbergi* Rouault, 1849	*Nankinolithus granulata**
wanyuanensis	*Nankinolithus wanyuanensis* Cheng & Jian, 1961	*Nankinolithus wanyuanensis*
welleri	*Cryptolithus welleri* Endo, 1932	*Ningkianolithus welleri*
whittardi	*Bergamia whittardi* Hughes, 1971	*Bergamia whittardi*
wilkensii	*Trinucleus wilkensii* Münster, 1840	?harpid
wutangensis	*Trinucleus wutangensis* Lu, 1962	generic placing uncertain
yinpanensis	*Yinpanolithus yinpanensis* Lu, 1974	*Yinpanolithus yinpanensis*

(*Note added in proof* 9 *August* 1975). Since this paper went to Press, the following information has become available regarding *Yinpanolithus* (p. 582) and *Cryptolithus* (p. 579).

Subfamily unassigned

Genus **Yinpanolithus** Lu, 1974

Diagnosis. Glabella clavate, with small glabellar node. E_1 and I_n complete; I_1 present except frontally; E_{1-3} present laterally but only two E arcs developed posterolaterally. Pits arranged in radial rows except anterolaterally.

Type species. Yinpanolithus yinpanensis Lu, 1974

Distribution. Lower Ordovician (upper part of Yinpan Group) of Szechuan and (Tawan Group), Hupeh, China.

Discussion. Until it is known whether F pits are developed or whether I_n is cut-off by I_1 the subfamilial placing of this genus must remain uncertain. The glabellar characters and the development of E arcs could indicate marrolithine or cryptolithine affinities, although the increase in the number of E arcs anterolaterally is reminiscent of many reedolithines.

The *Cryptolithus* confr. *portlockii* of Størmer (1930, p. 43, pl. 6, fig. 13) from the 'Upper Chasmops Zone' of the Oslo region, which Dean (1960, p. 138) thought was referable to *Onnia*, is, in fact a new species of *Cryptolithus* (A. W. Owen 1975, private communication). In view of Størmer's stratigraphical comments (1930, p. 78) in which Brøgger's 'Upper Chasmops Zone' was equated with the 'Gastropod Limestone', it is apparent that the horizon is '5a' and therefore Ashgill in age. A. W. Owen has confirmed this and has collected additional material.

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Bibliographic appendix

In the course of the necessary bibliographic searches required for this work, one or two problems have arisen about which it is thought worth while to comment rather than to leave them as unsatisfactory, and in a few cases, unchecked, entries in the references. For this reason the following notes are given regarding certain references.

Angelin, N. P. (1838). Bigsby (1868) in his *Thesaurus Siluricus* attributes the species *Cryptolithus quatuor-lineatus* and *Cryptolithus quatuor-spinus* to Angelin. He gives no date, but does mention among papers by Angelin that he consulted 'Museum Palaeontologicum Suecicum? Prof. Kröyer's Nat.-Hist. Review, 1838'. Investigations by Dr V. Jaanusson have revealed that this refers to what is essentially an advertisement by Angelin which appeared on the inside cover of *Naturhistorisk Tidskrift* (ed. H. Kröyer) 1838–1839, 2 (2).

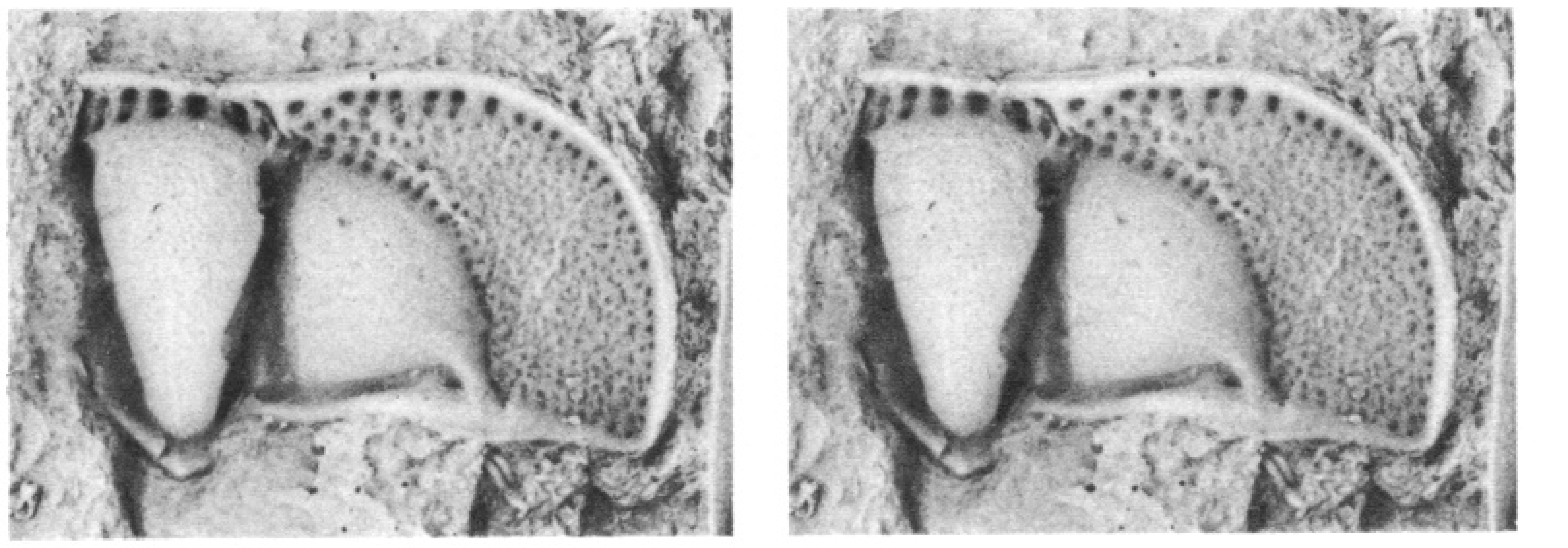
Clarke, W. B. (1847). This paper is quoted for the authorship of '*Trinucleus*' *clarkii*, although there is some doubt here. With reference to this species Clarke states: 'Mr Macleay has done me the honour of naming etc...', which sounds as if the species may have been published elsewhere by Macleay, possibly in the *Launceston Examiner*, though it has not been possible to confirm this.

Fearnsides, W. G., Elles, E. & Smith, B. (1907). Authorship of trilobite species in this paper have been commonly attributed to Smith. However, since the palaeontological appendix was clearly actually written by Fearnsides and is written in the pleural, it is believed more accurate to attribute the authorship jointly.

Green, J. (1832*a*, *b*). The genus *Cryptolithus* has been variously attributed to these two papers of Green. There appears also to have been some doubt in the past as to which of the two papers appeared first. However, the genus should be attributed to his Synopsis of the trilobites of North American in *Monthly Am. J. Sci.*, which was the earlier of the two publications.

Lu, Yen-hao (1954, 1962). Neither of these papers is currently available in China (Professor Yin 1973, private communication). Attempts to locate copies in Europe, North America, Russia and Japan have also proved unsuccessful.

Wahlenberg, G. (1818). This paper is generally quoted as being published in 1818, but the serial was not published until 1821. Bassett & Cocks (1974, p. 40) have recently put forward evidence to suggest that the date of publication of the main body of this work is 1818. Their conclusion is further supported by the fact that the paper is listed as having been received in *Handl. K. vet. Acad.* for 1819, thus was probably published in the previous year.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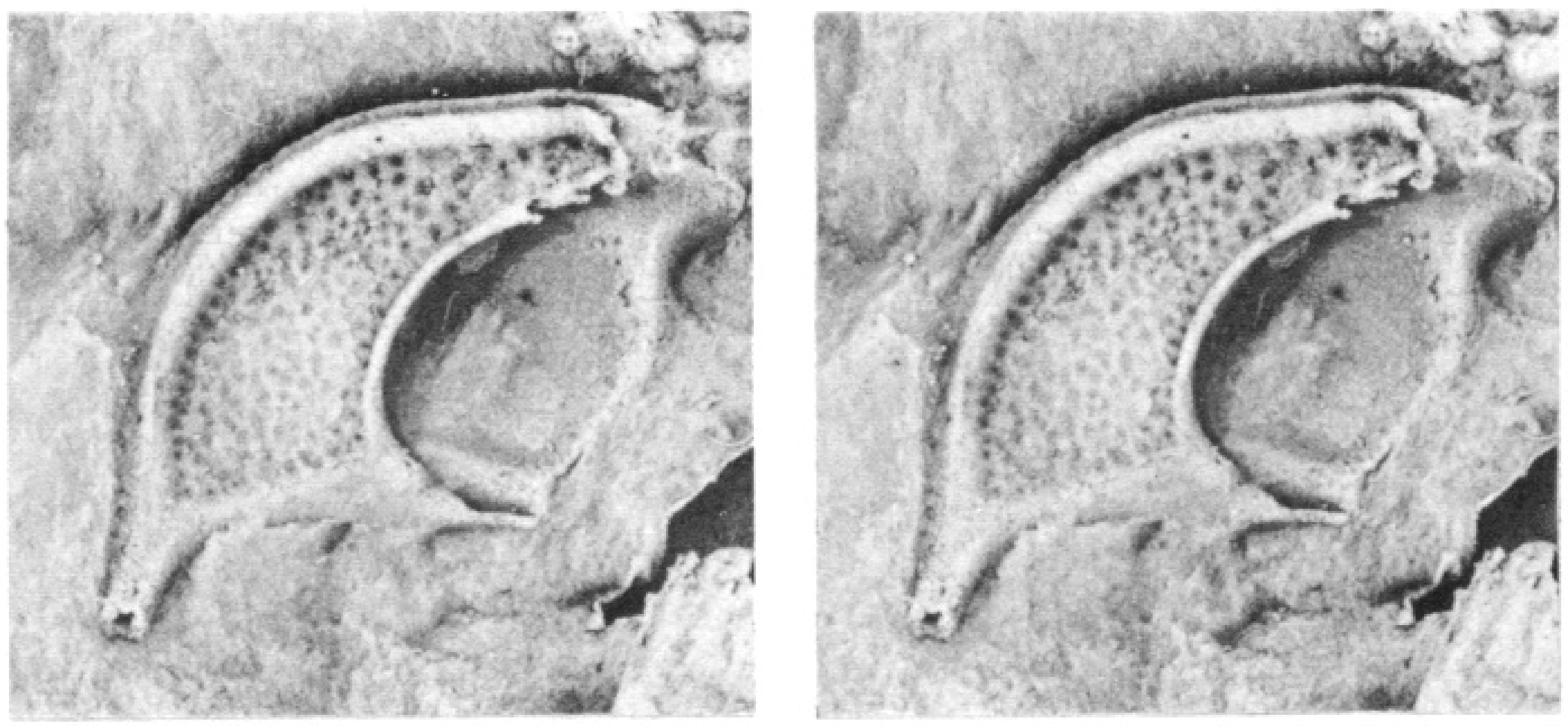
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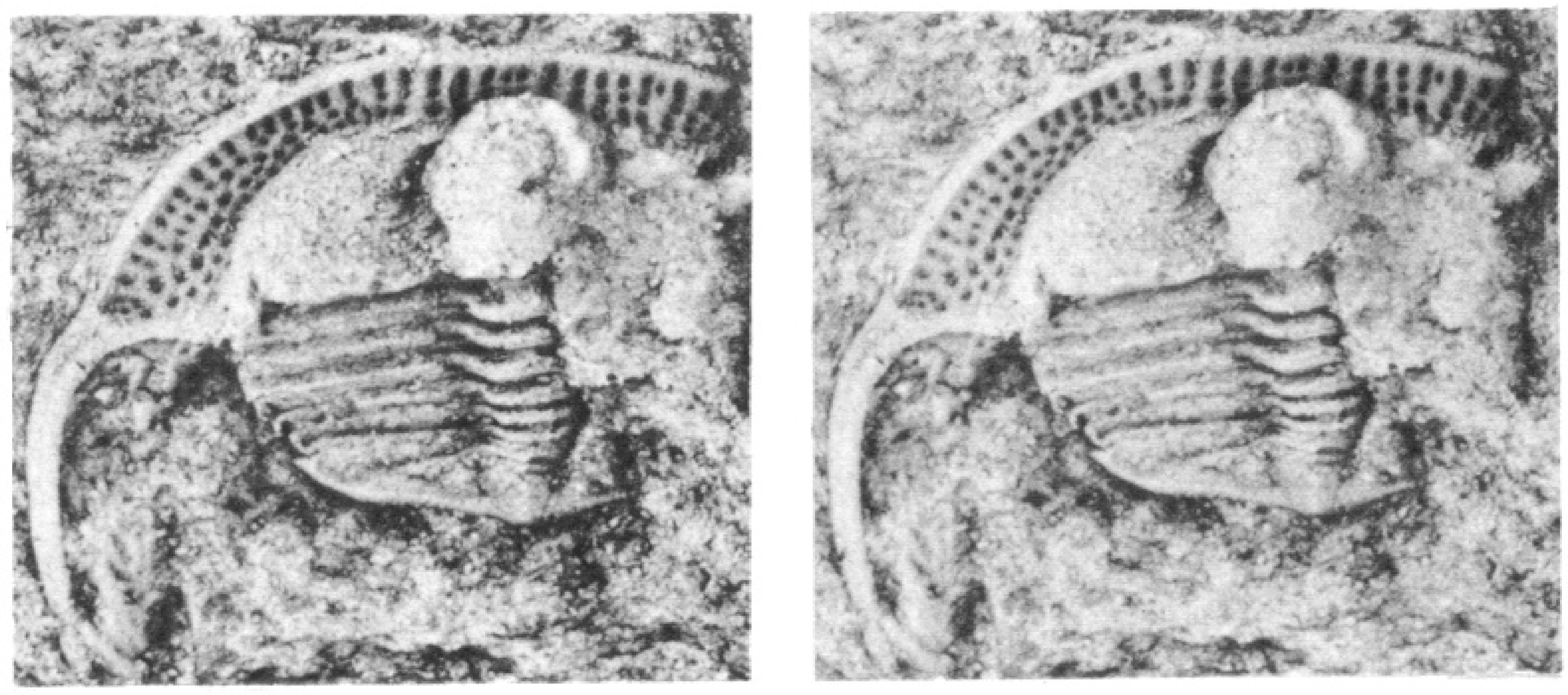
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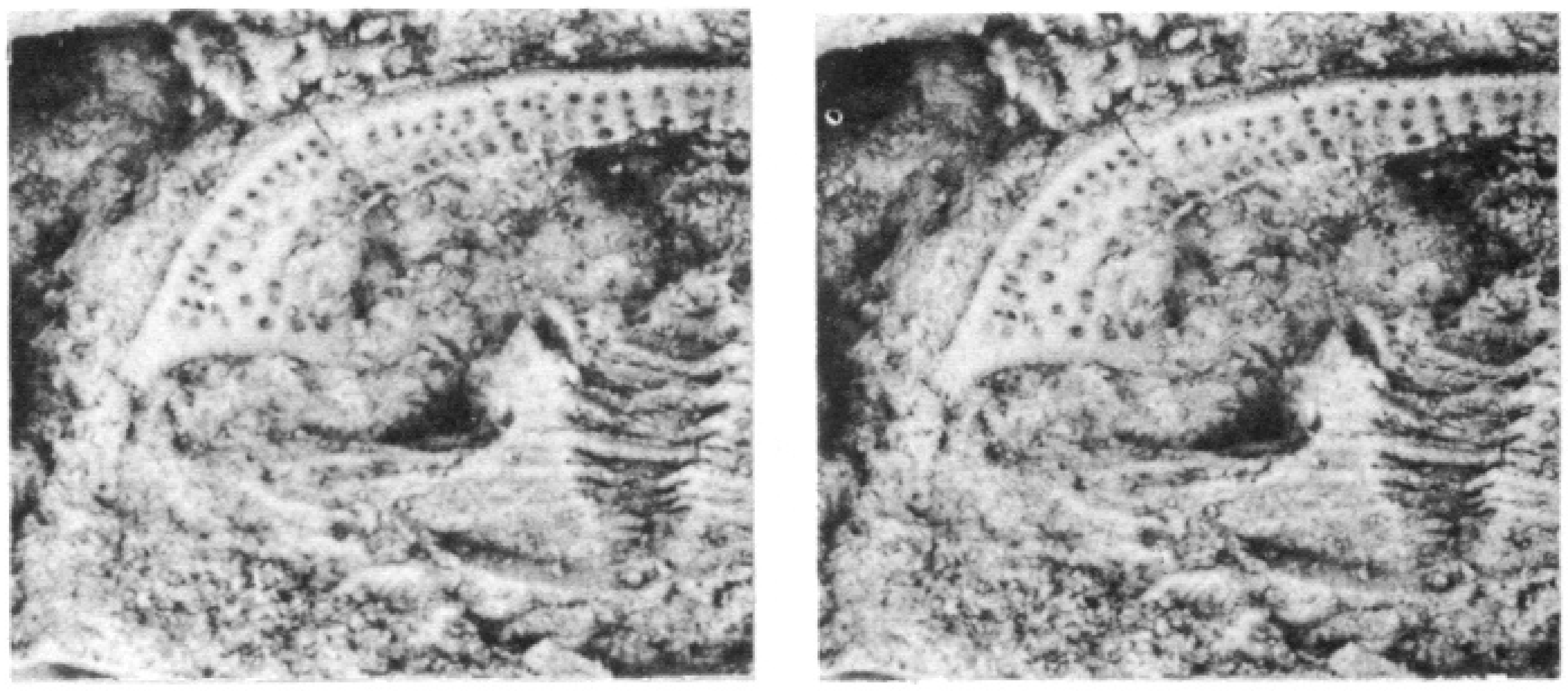
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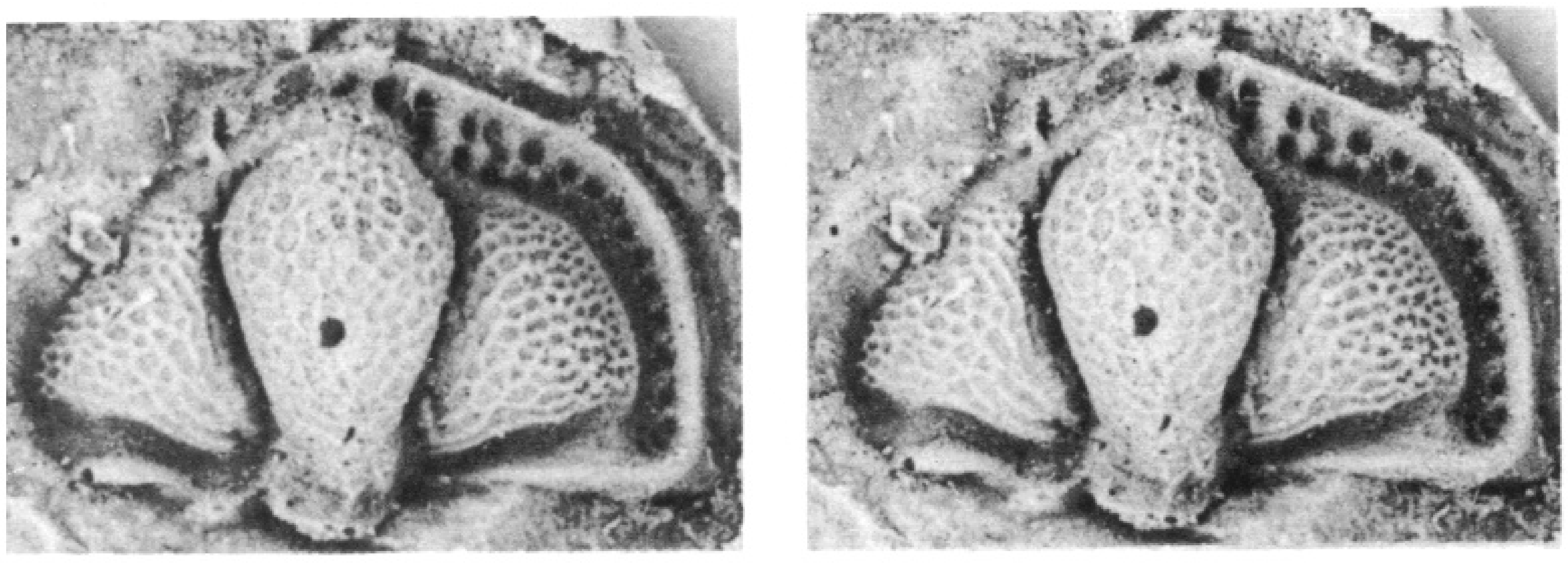
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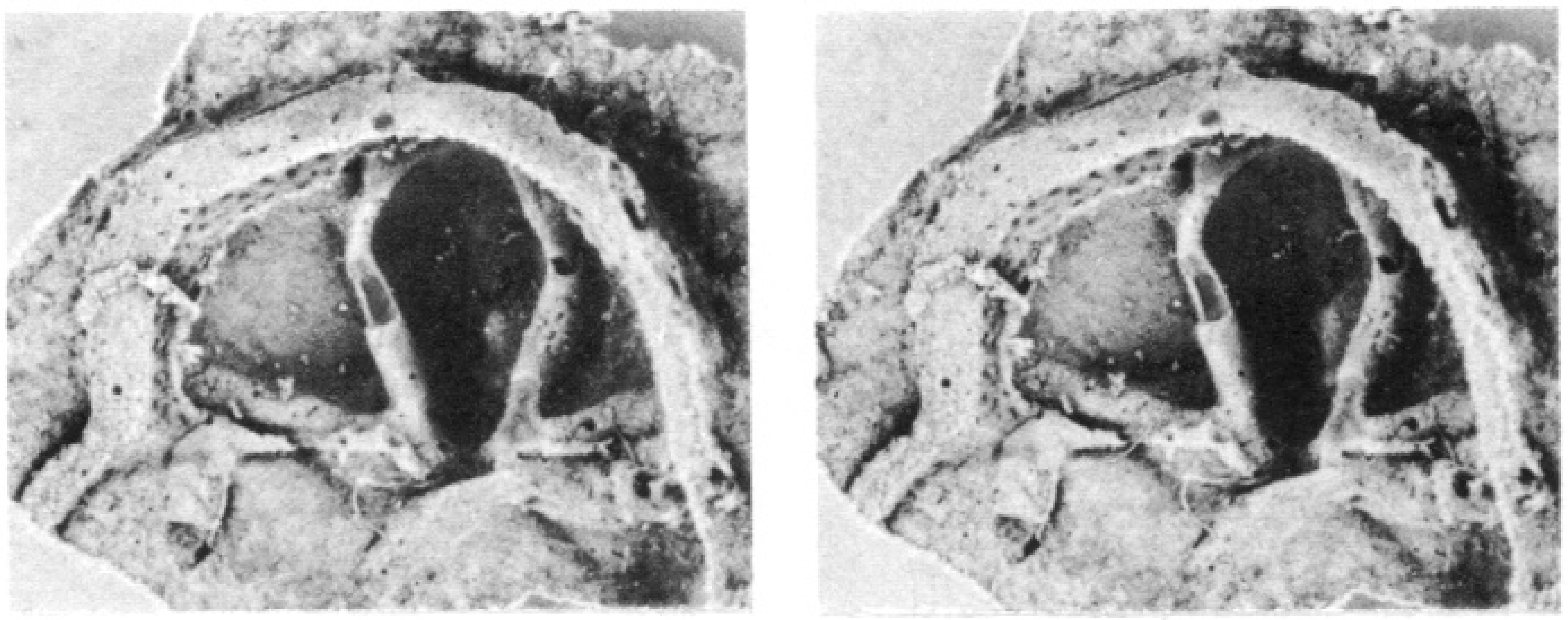
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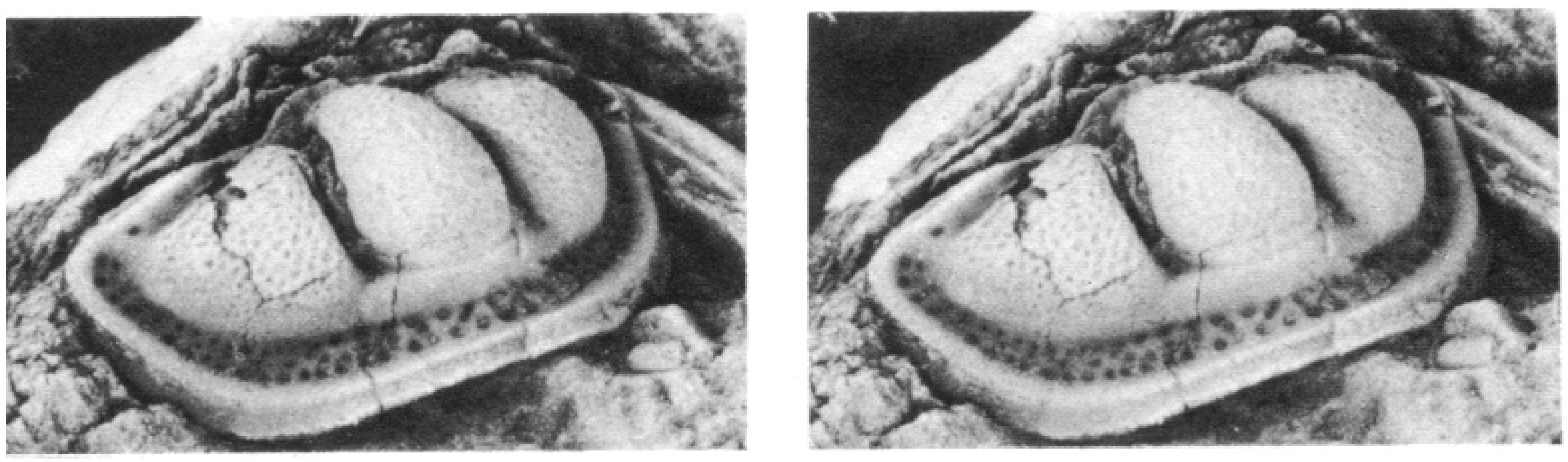
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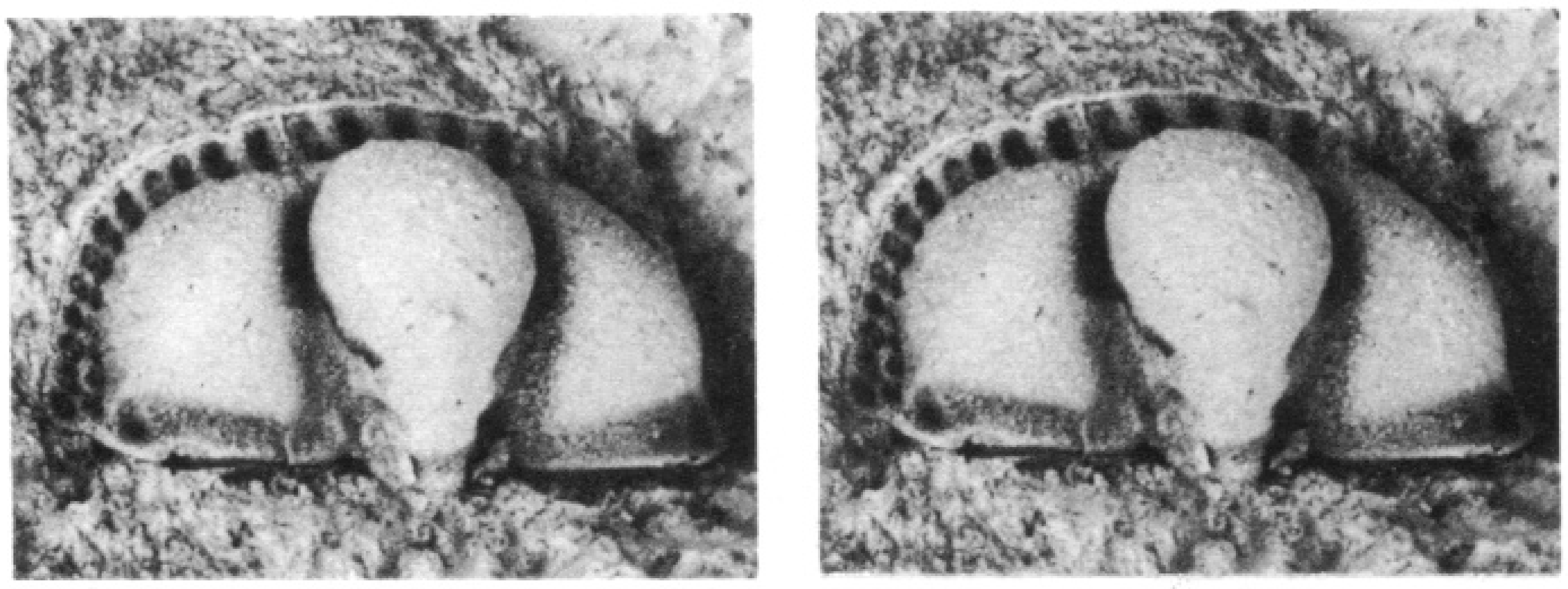
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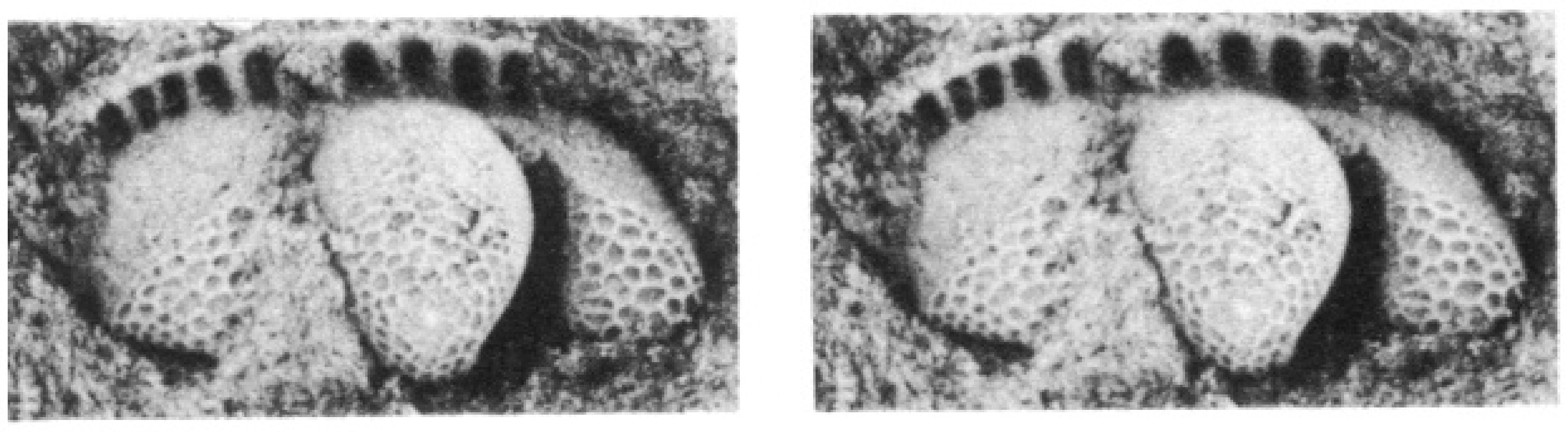
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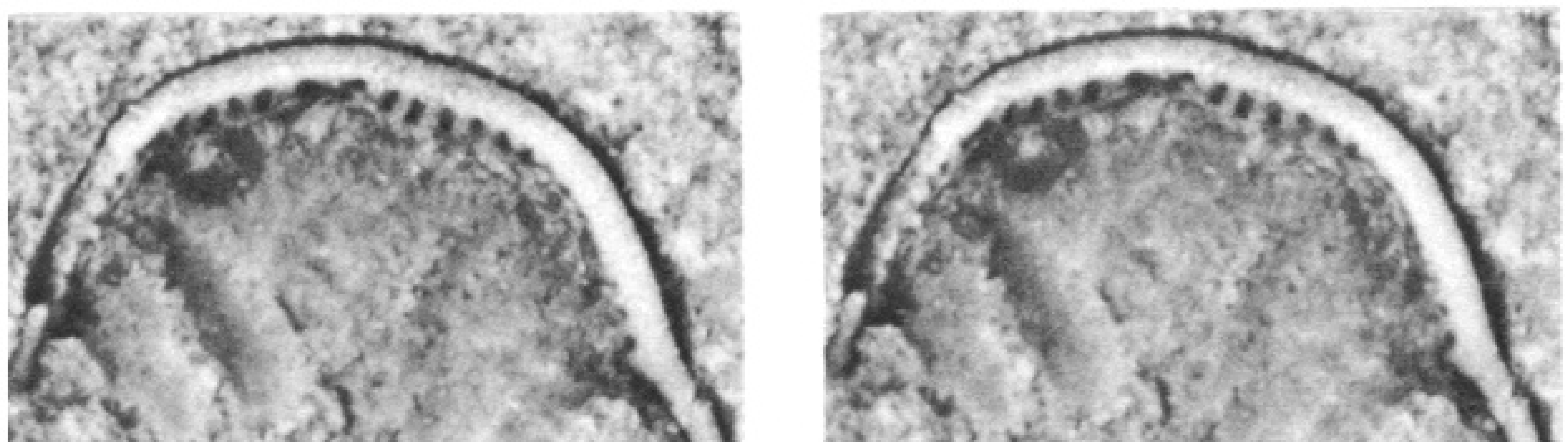
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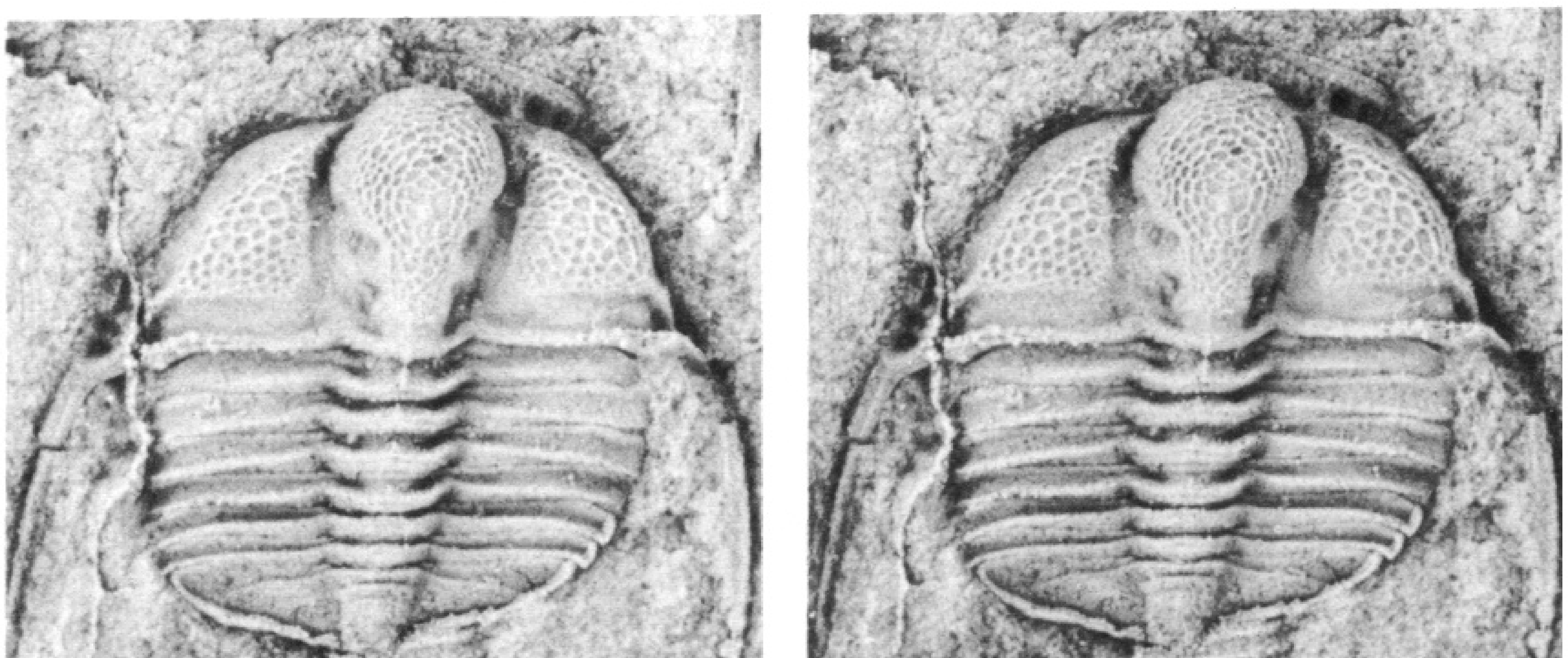
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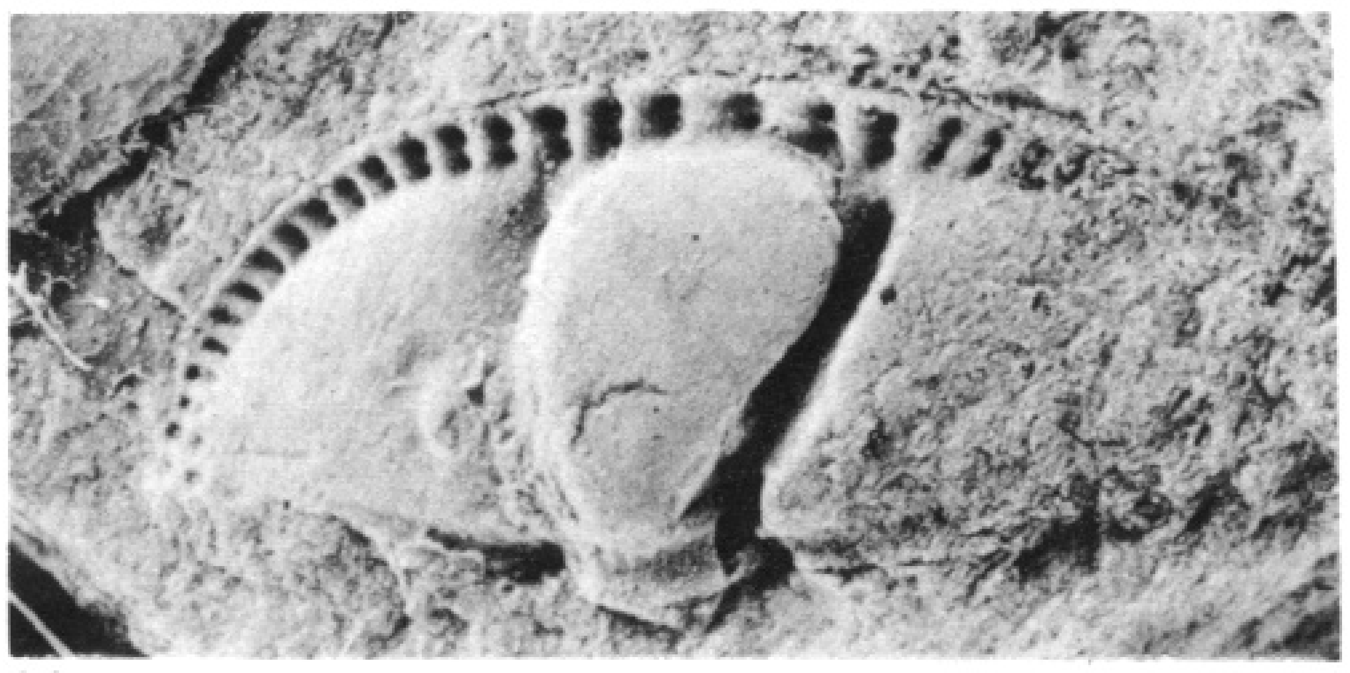
FIGURES 9–19. For description see opposite.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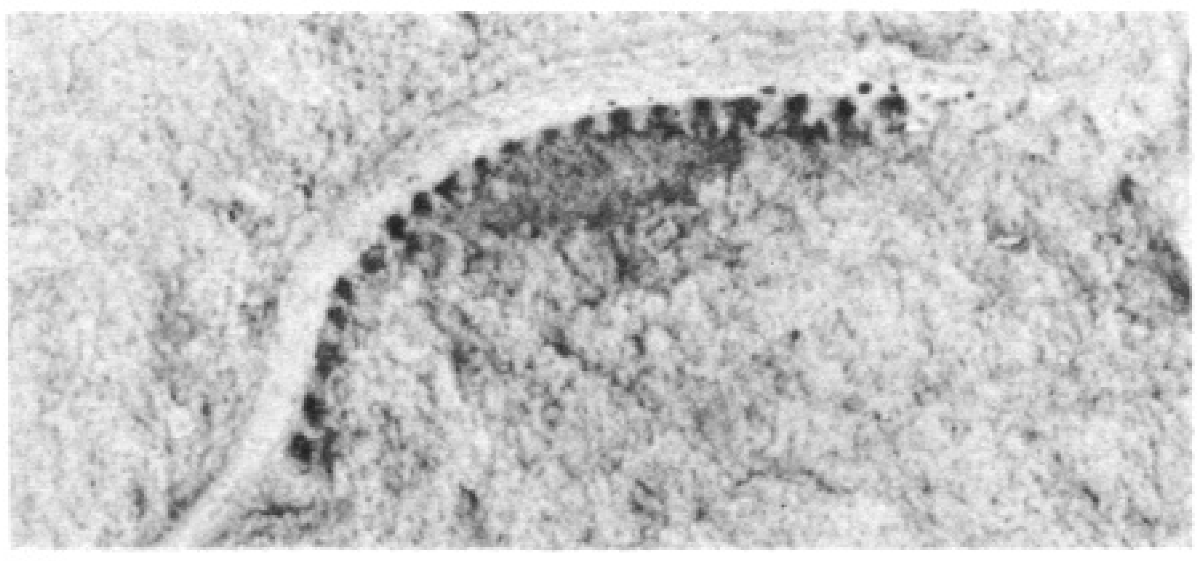
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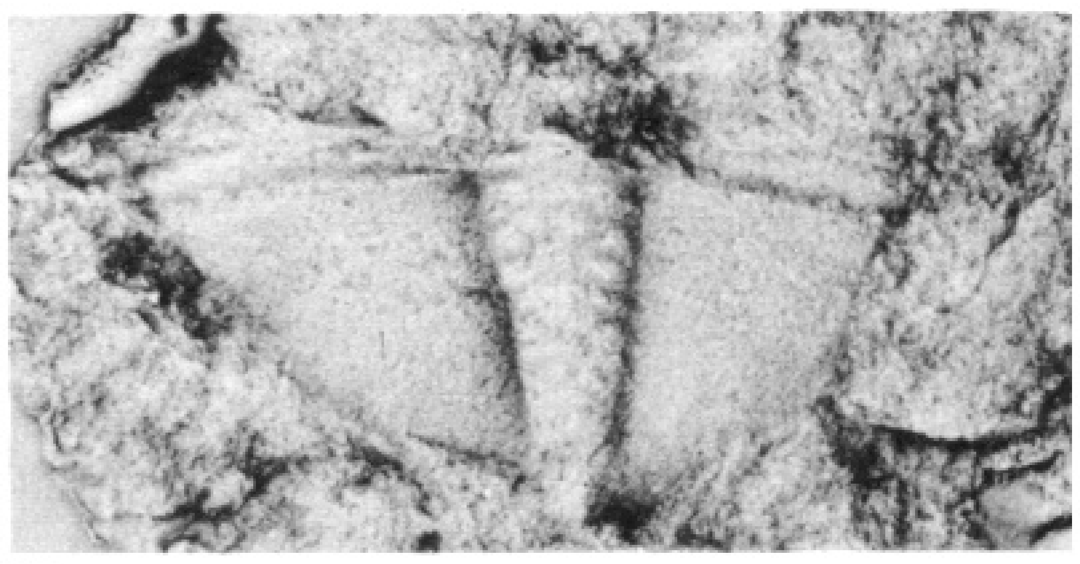
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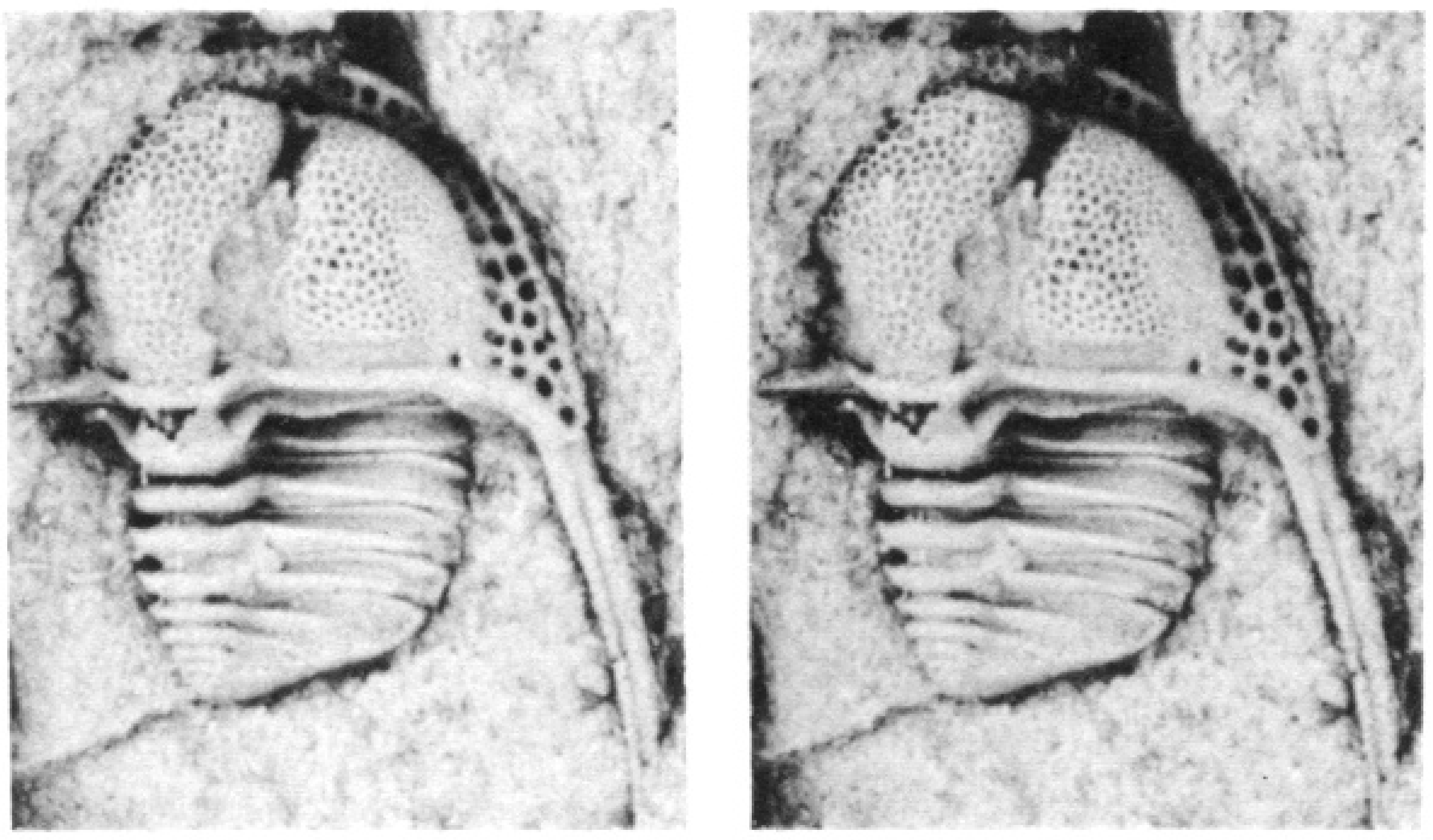
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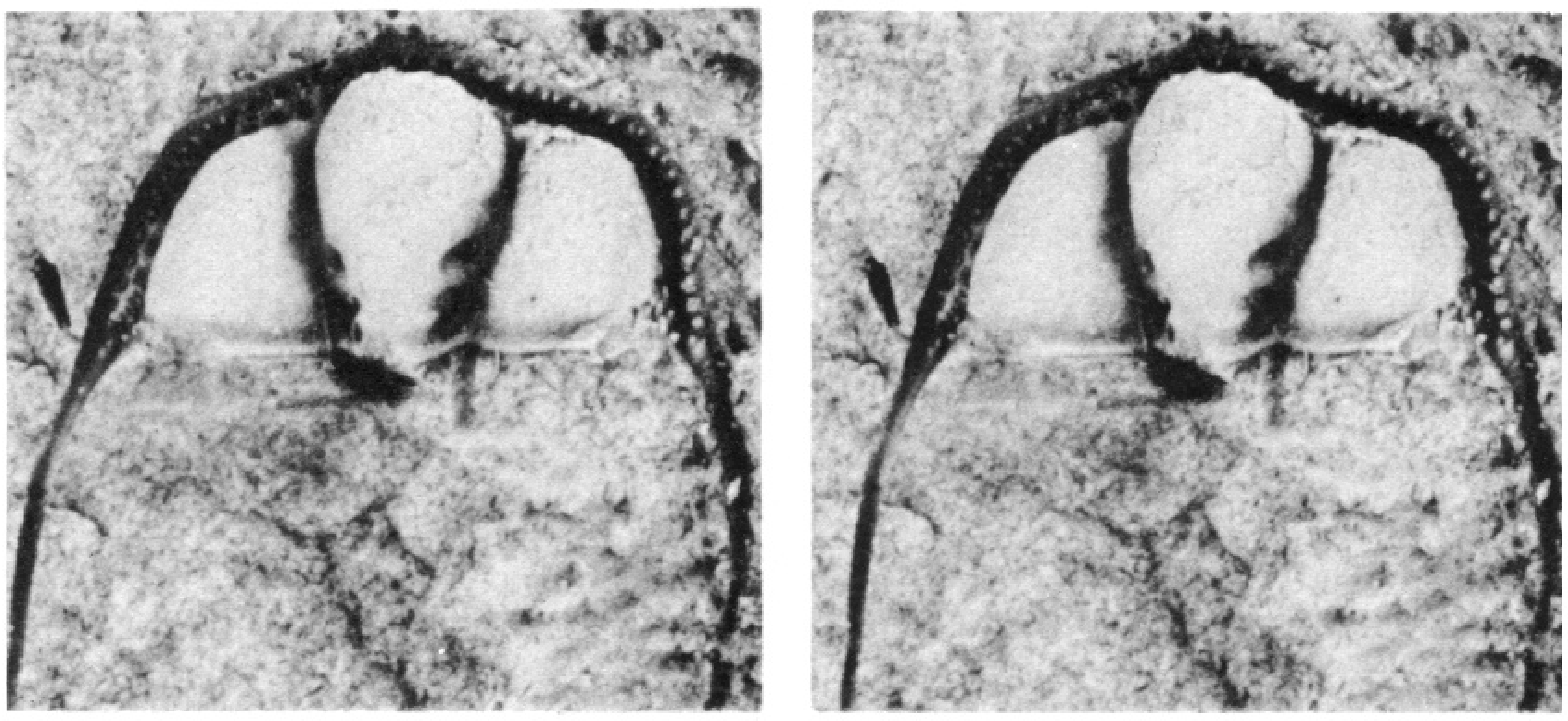
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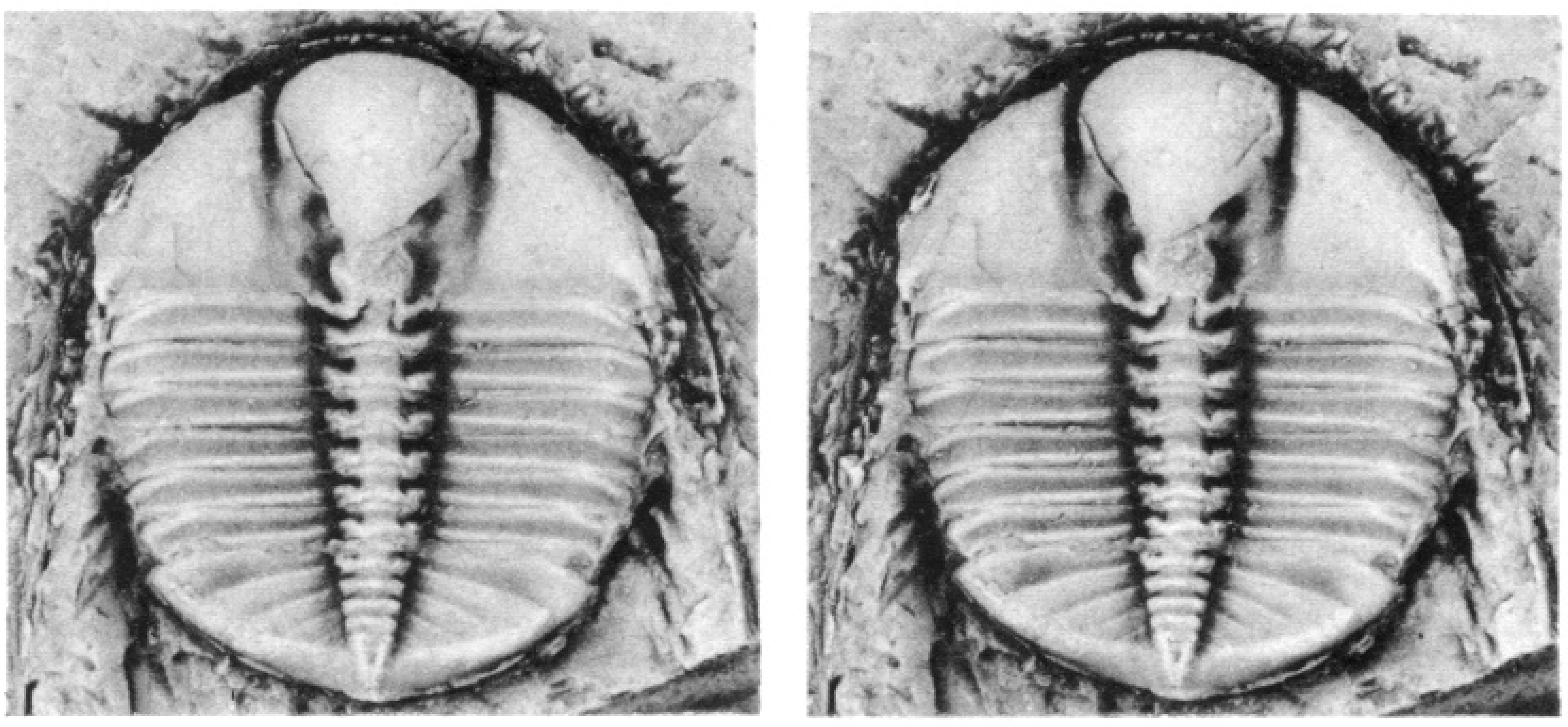
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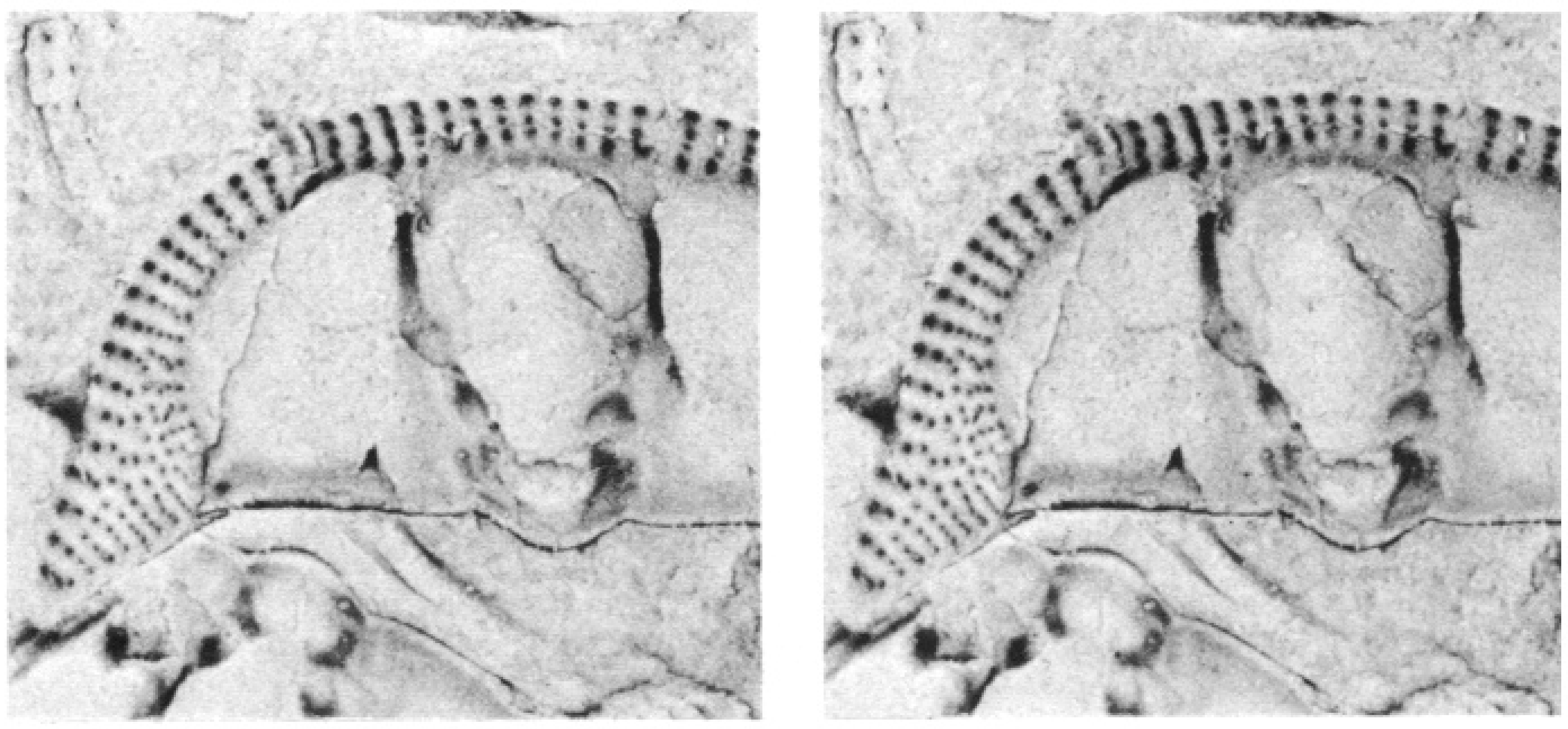
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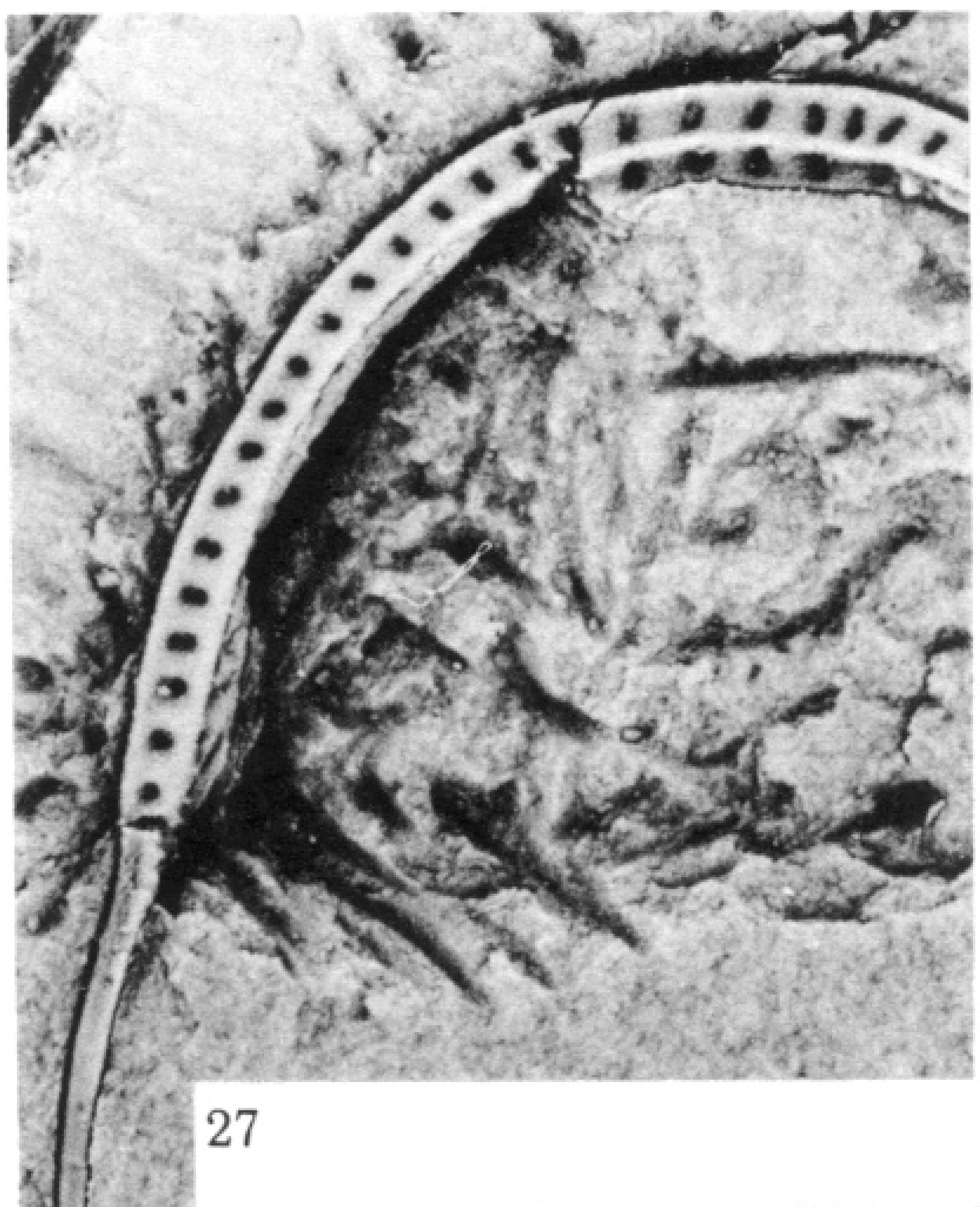
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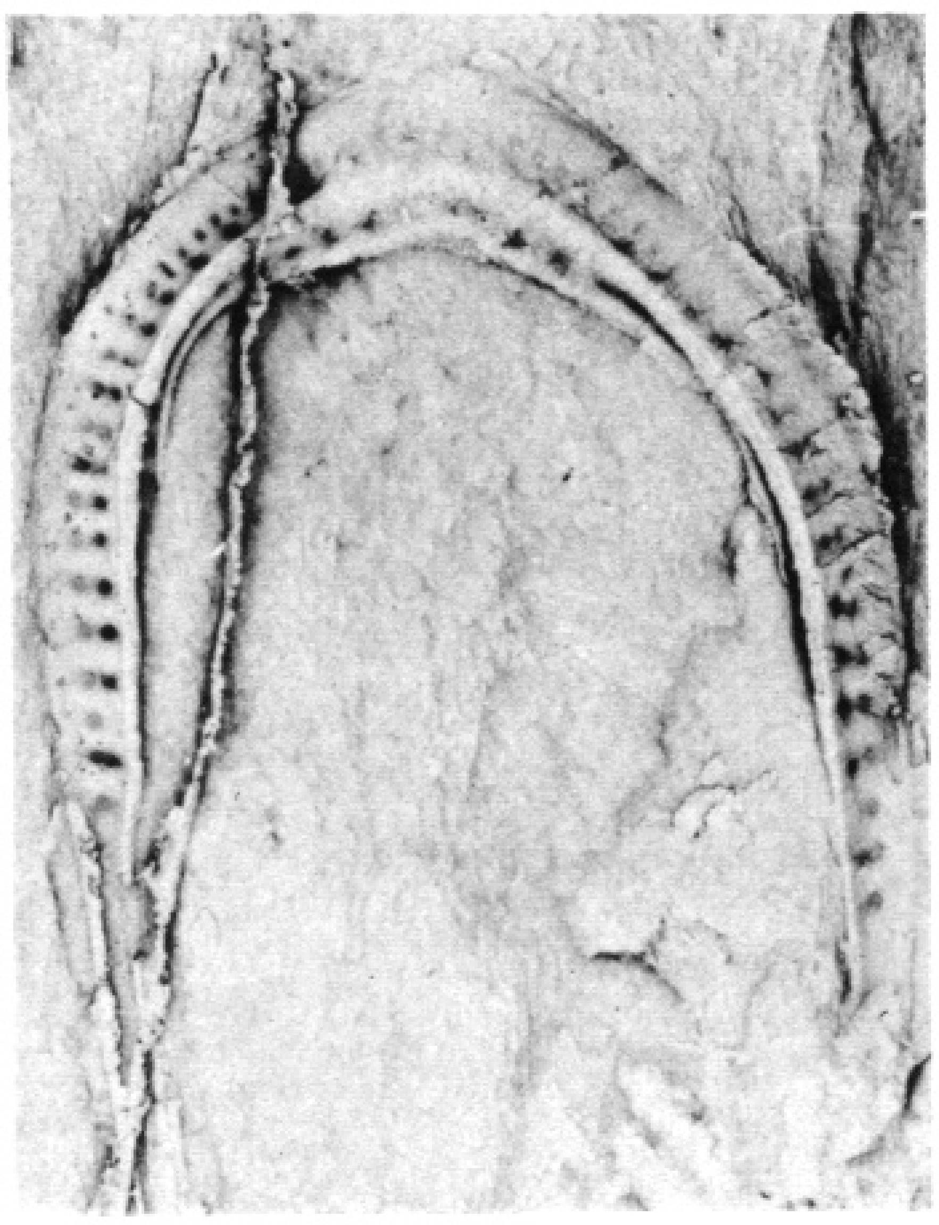
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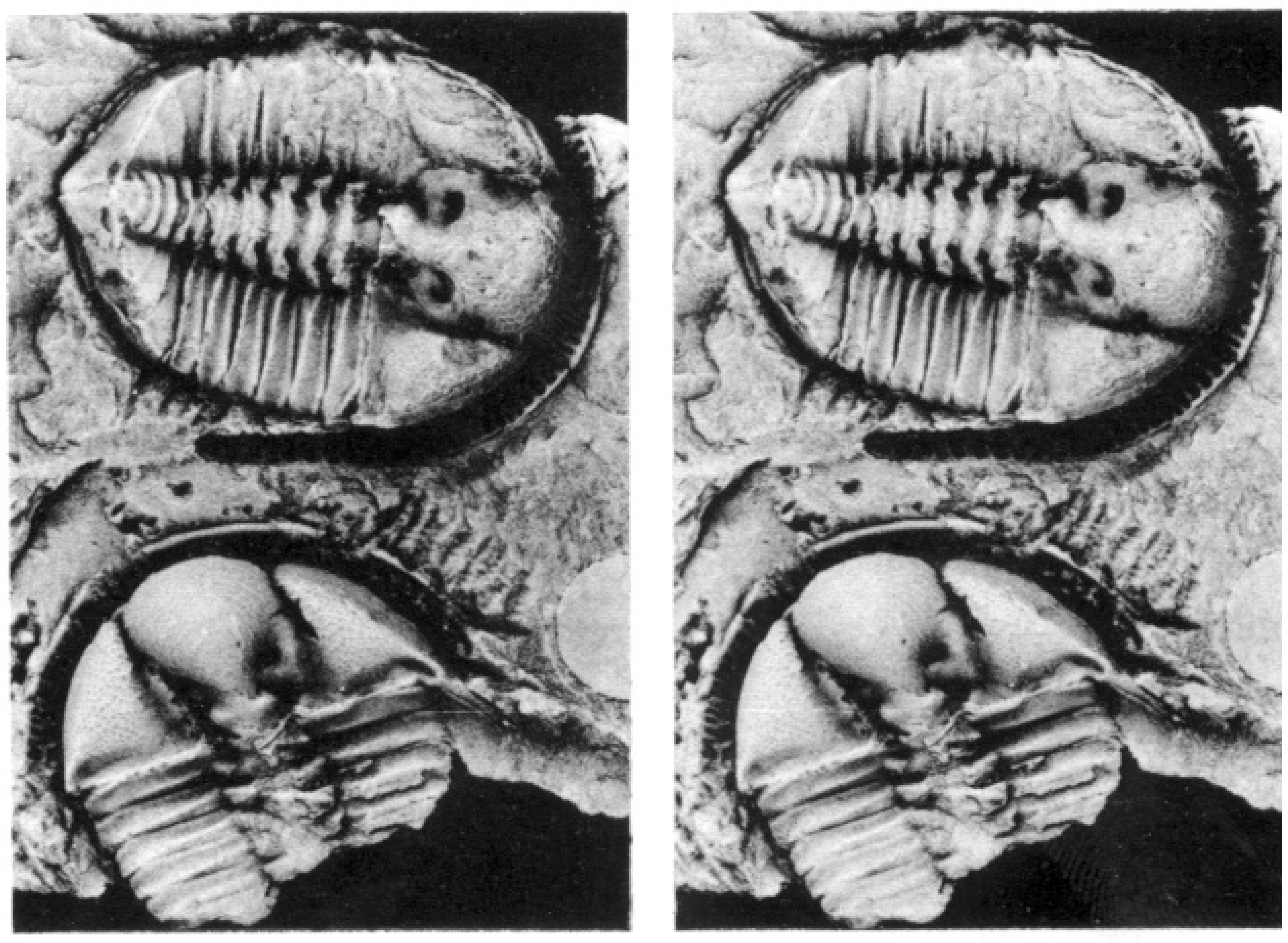
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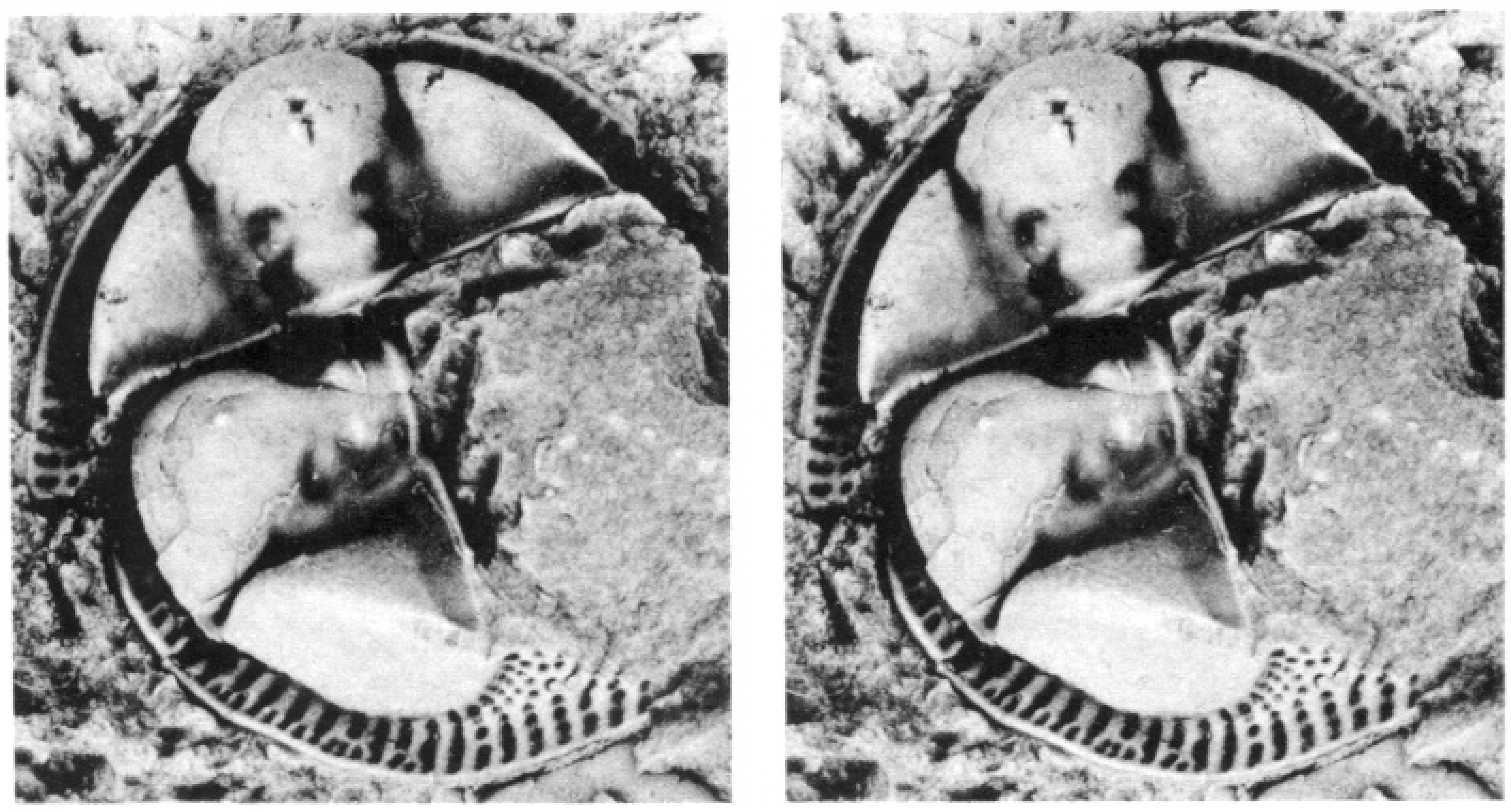
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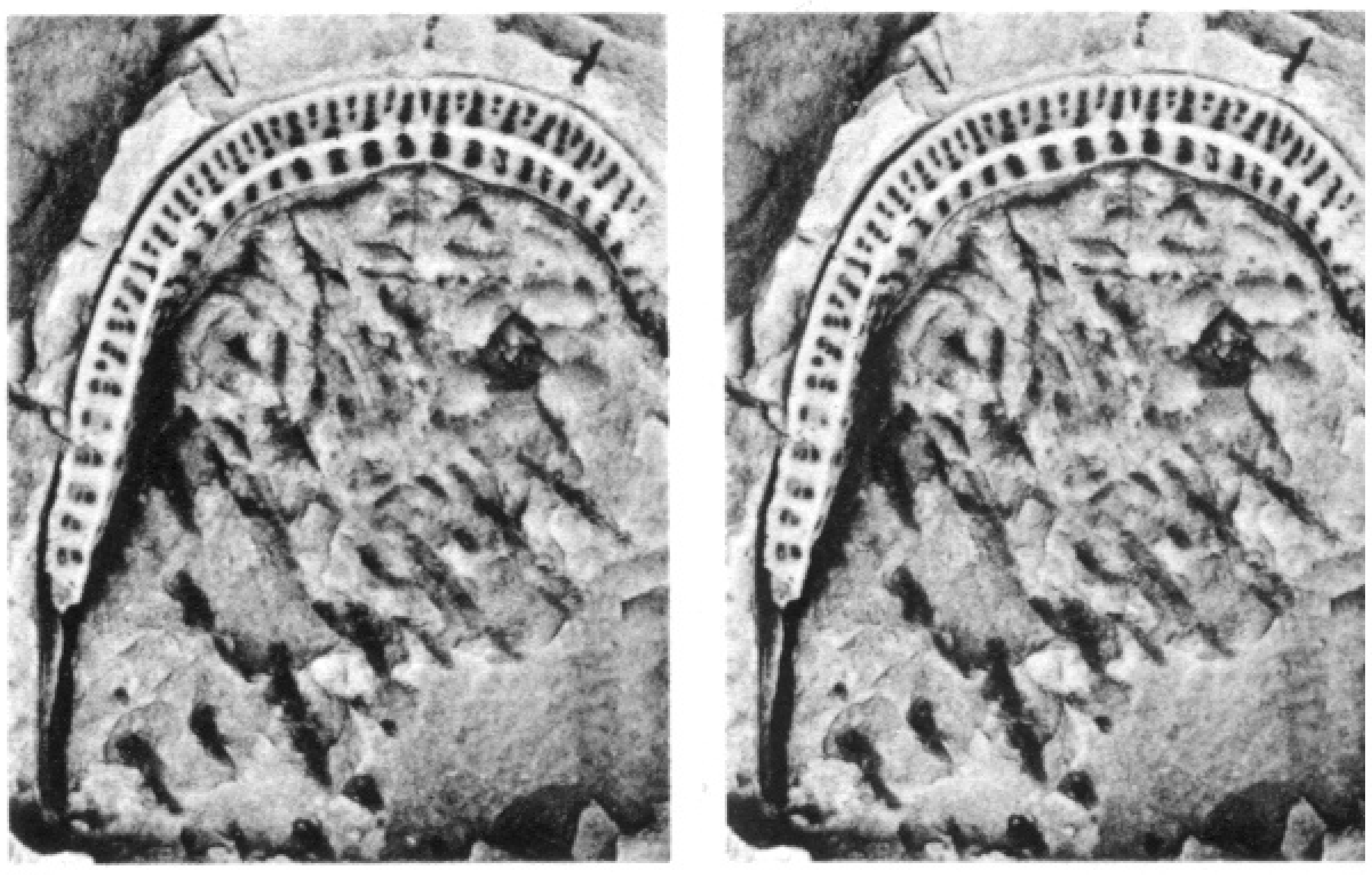
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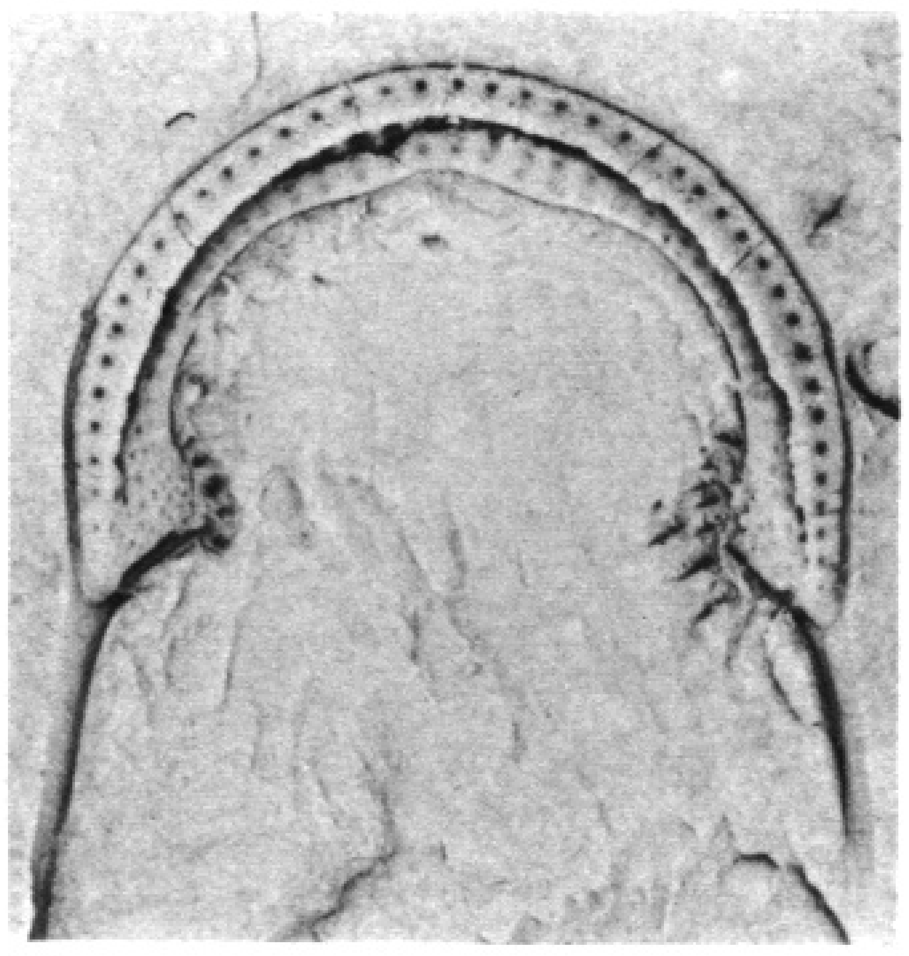
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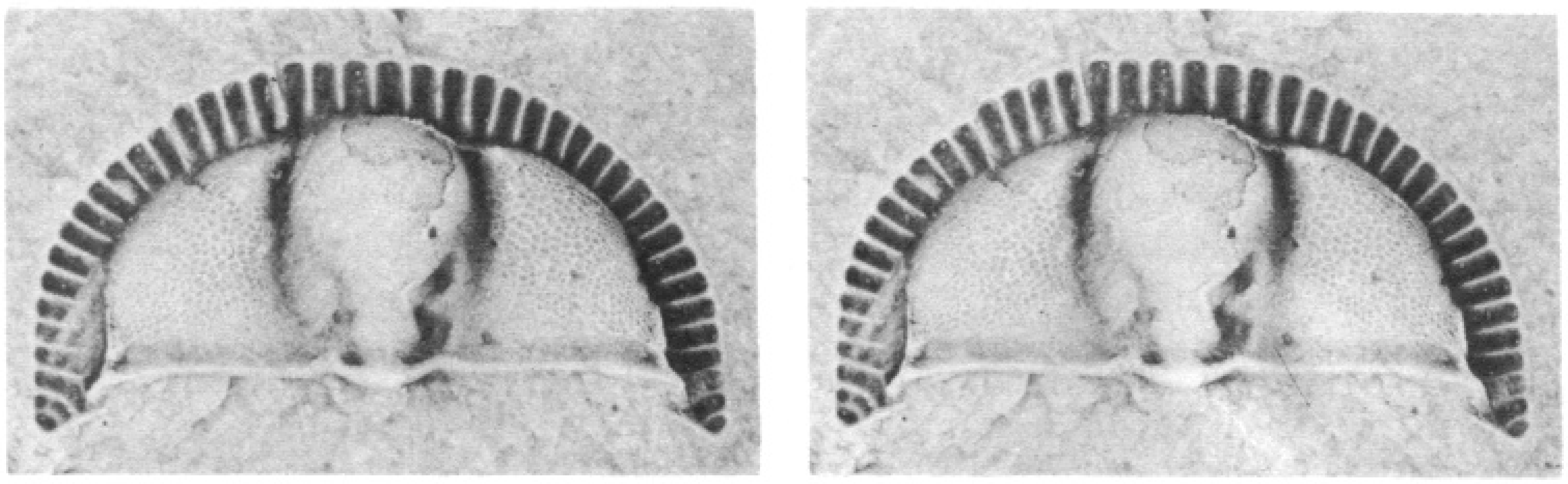
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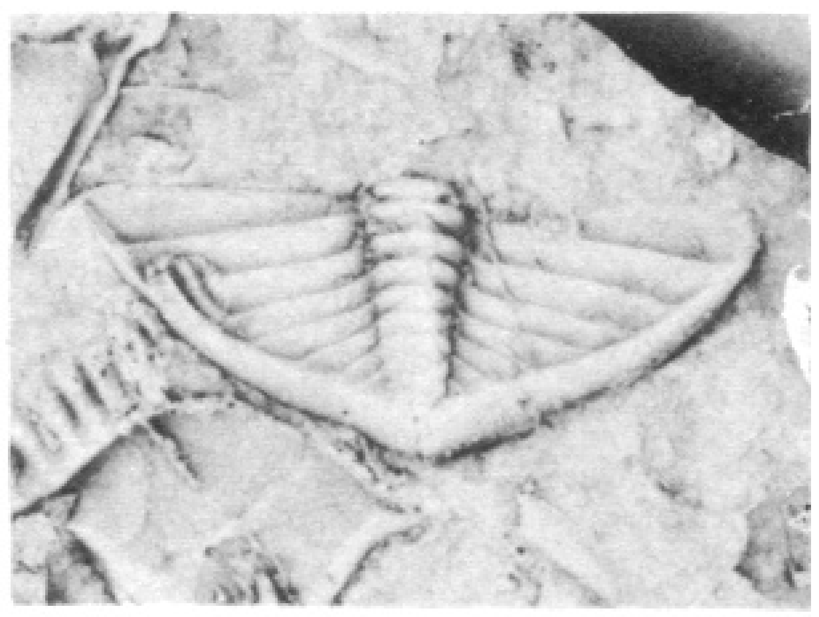
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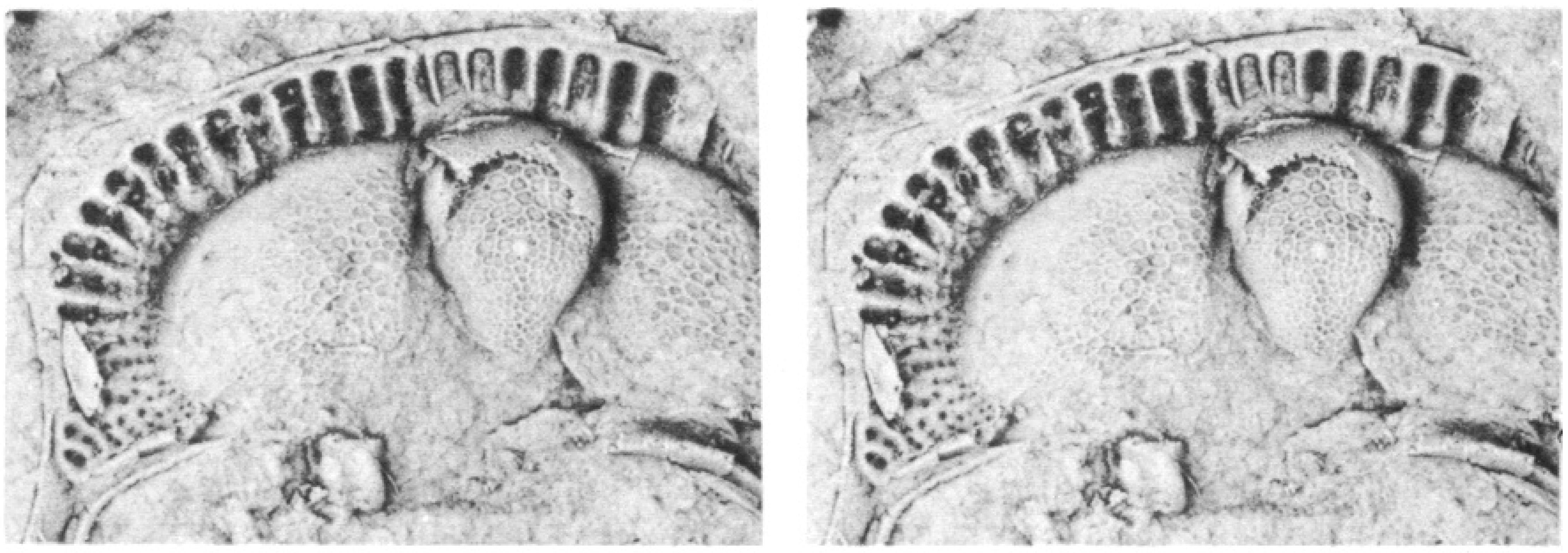
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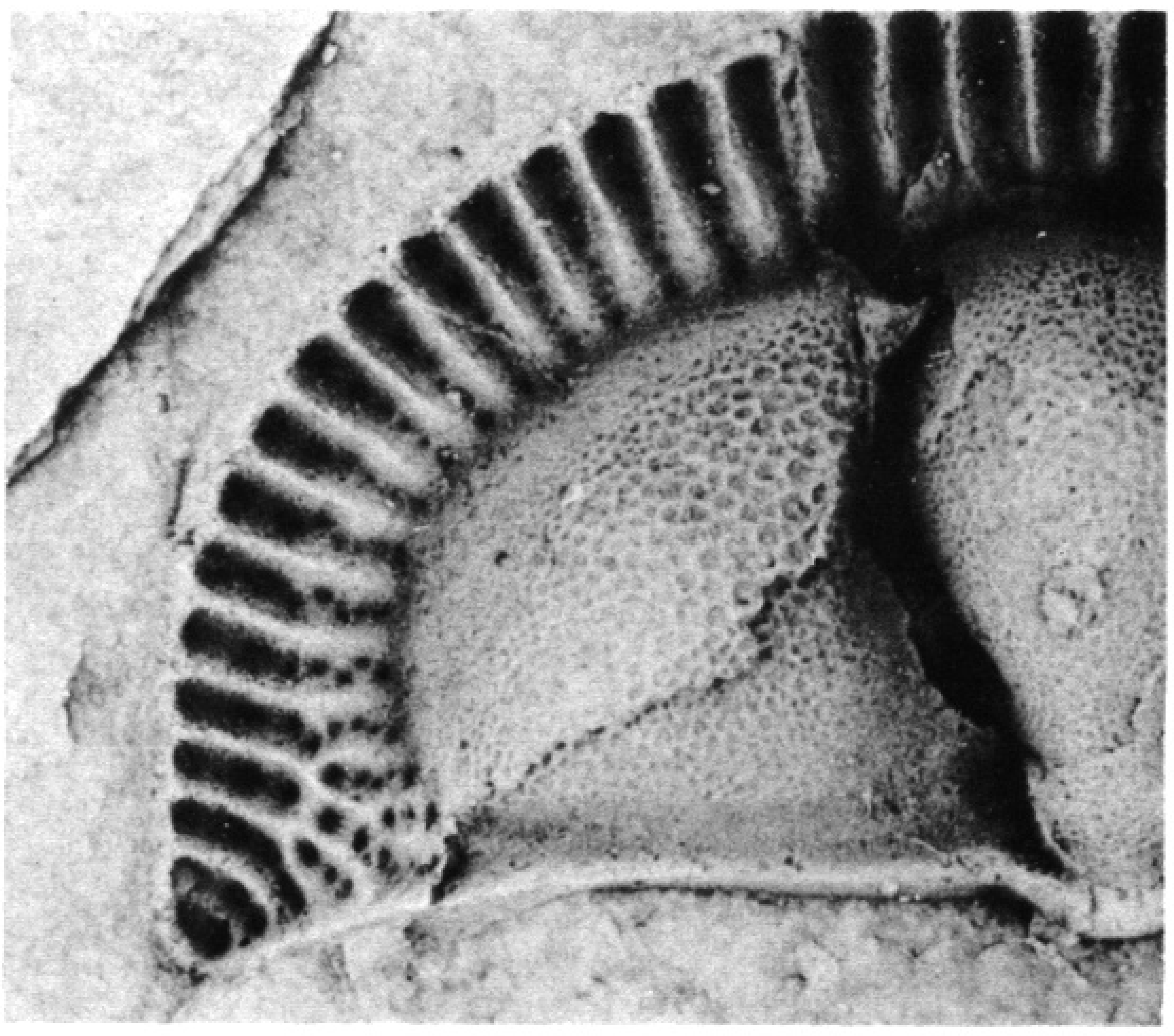
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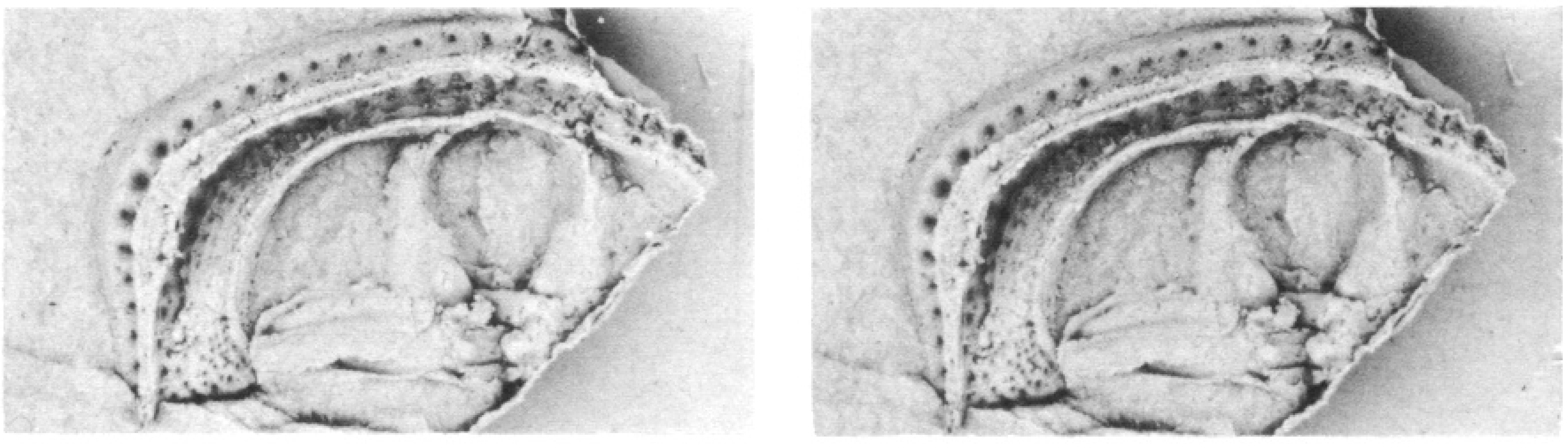
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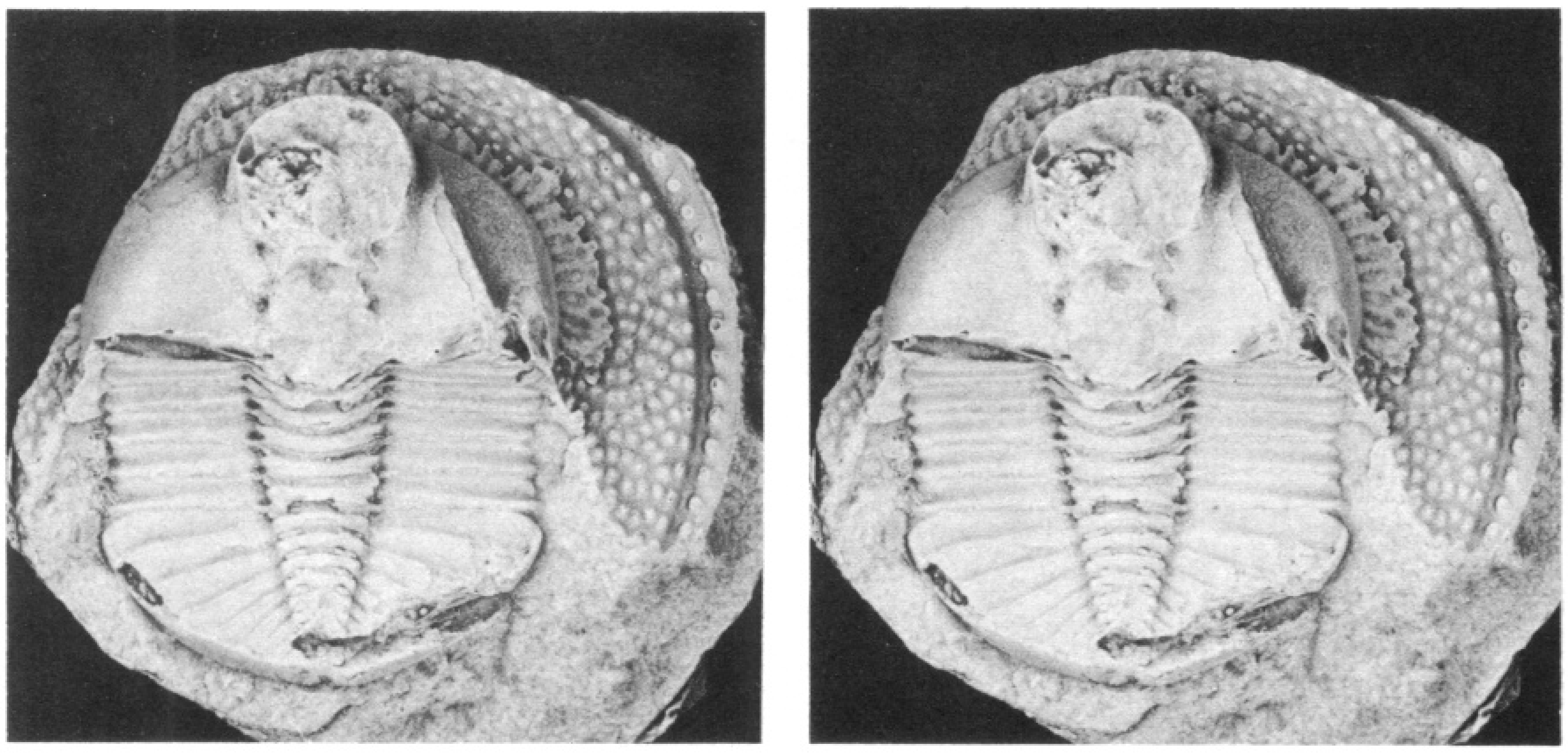
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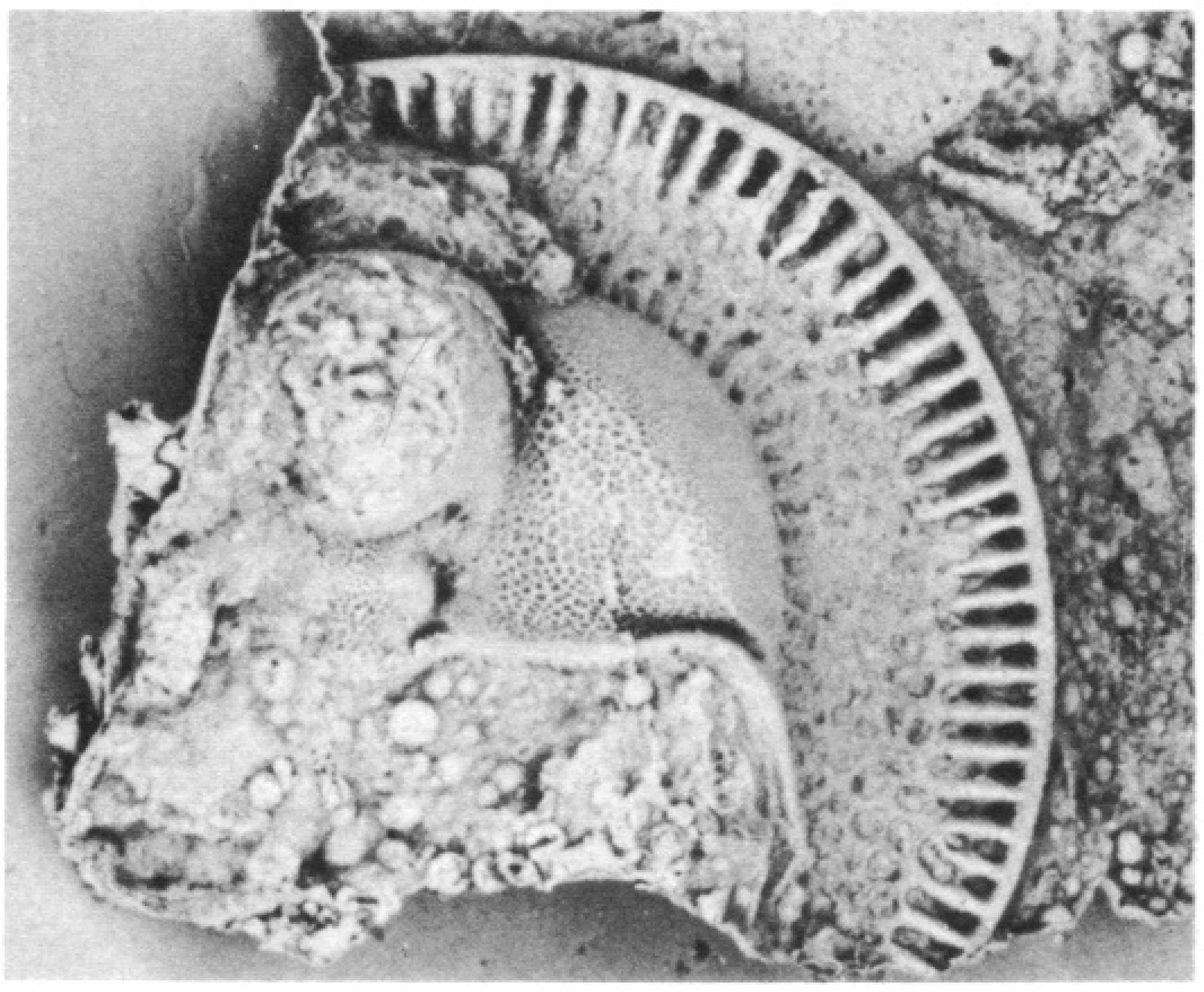
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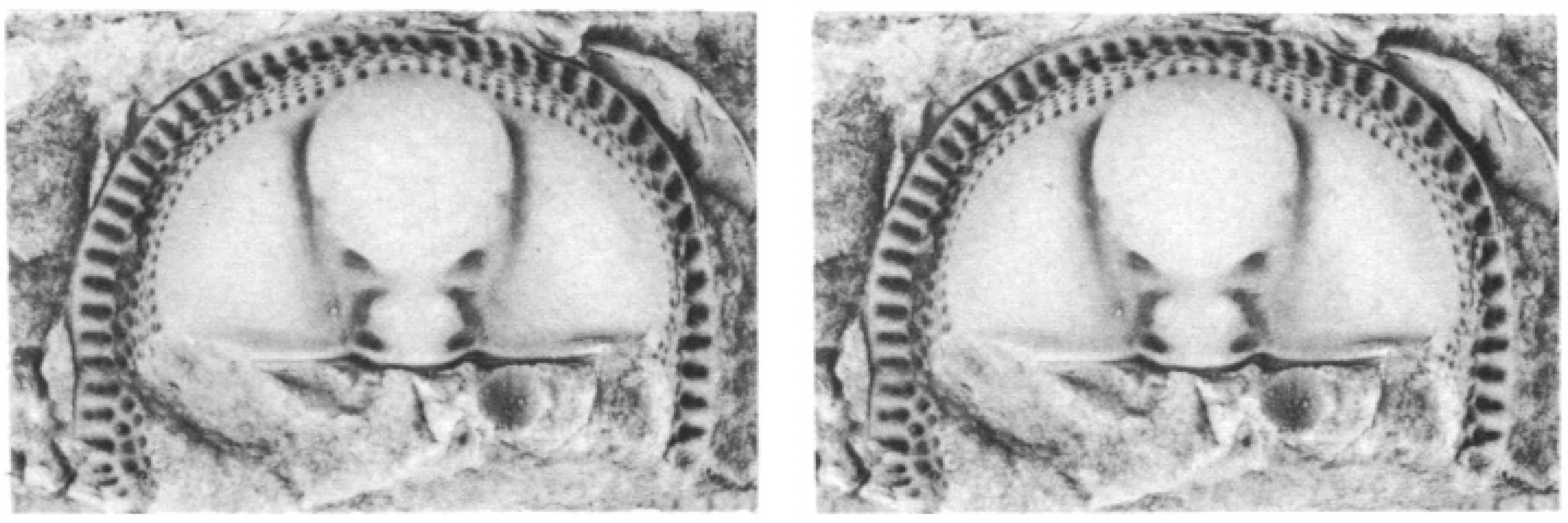
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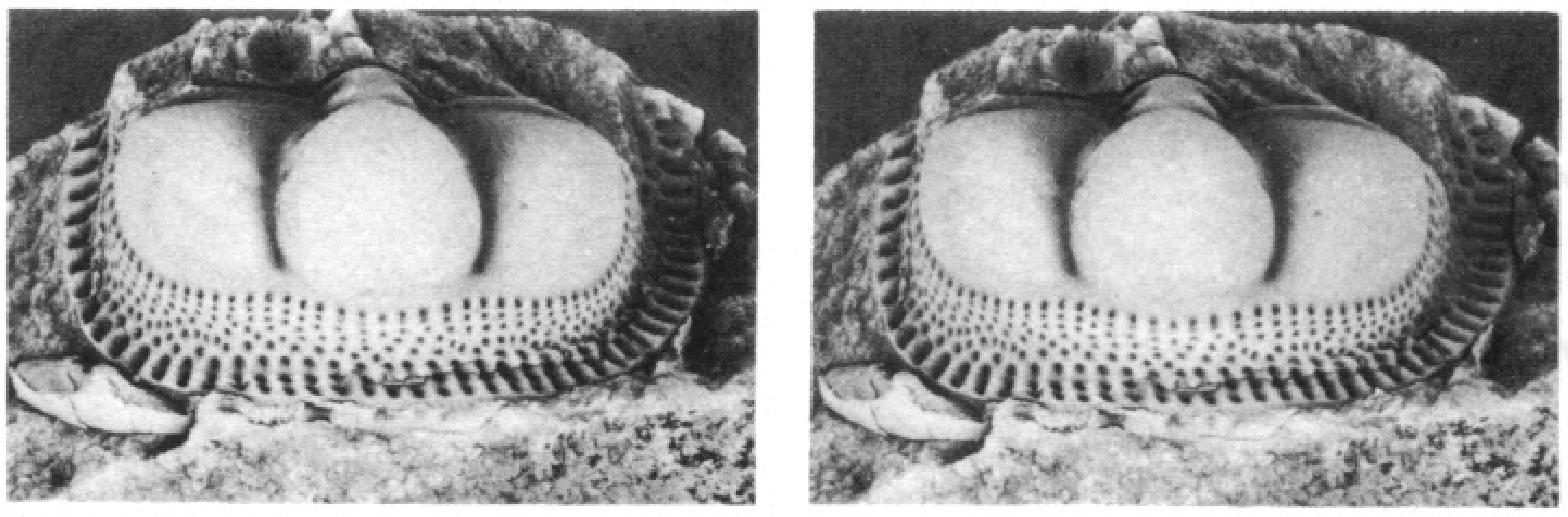
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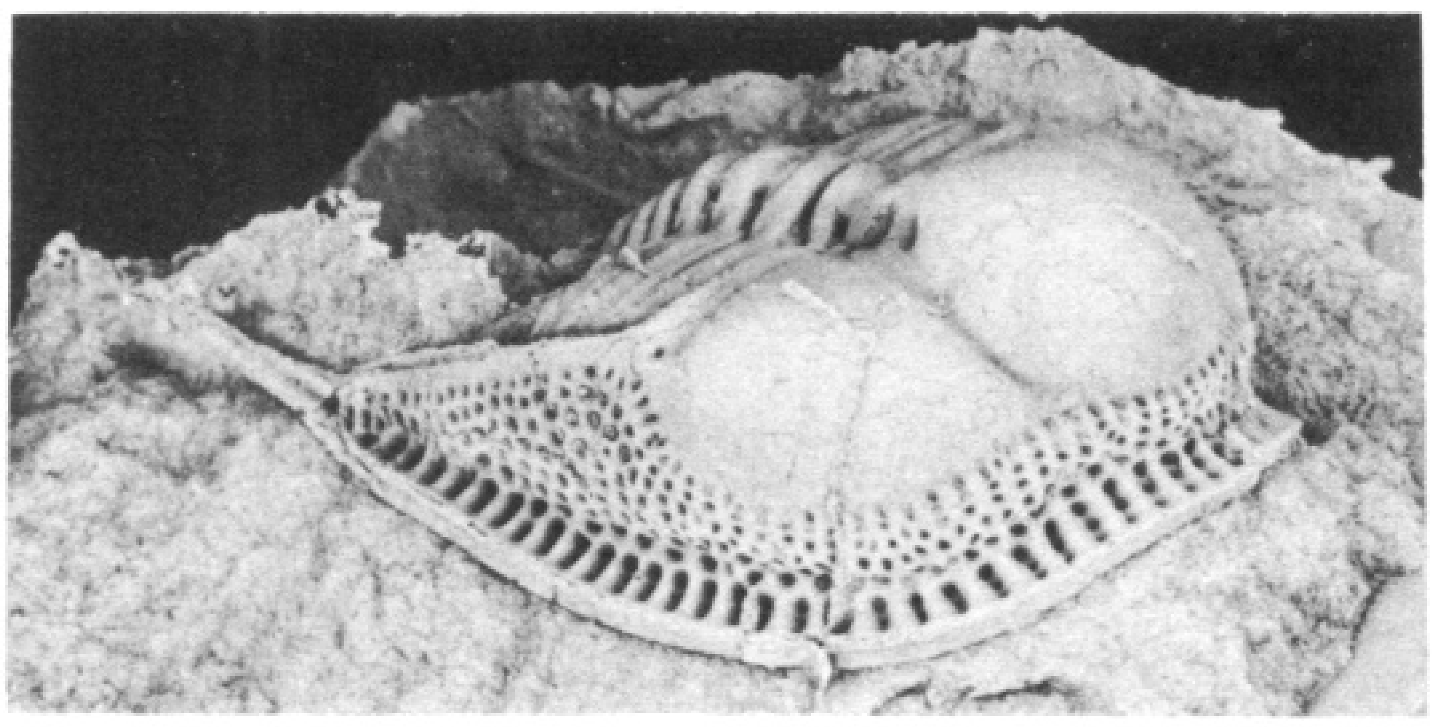
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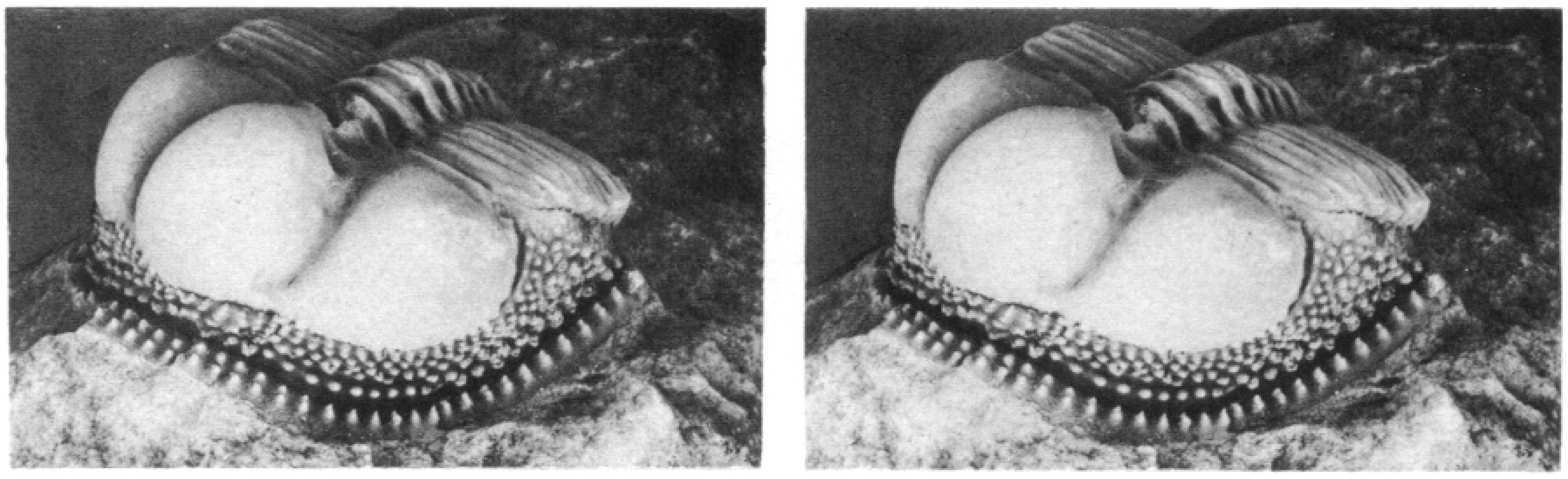
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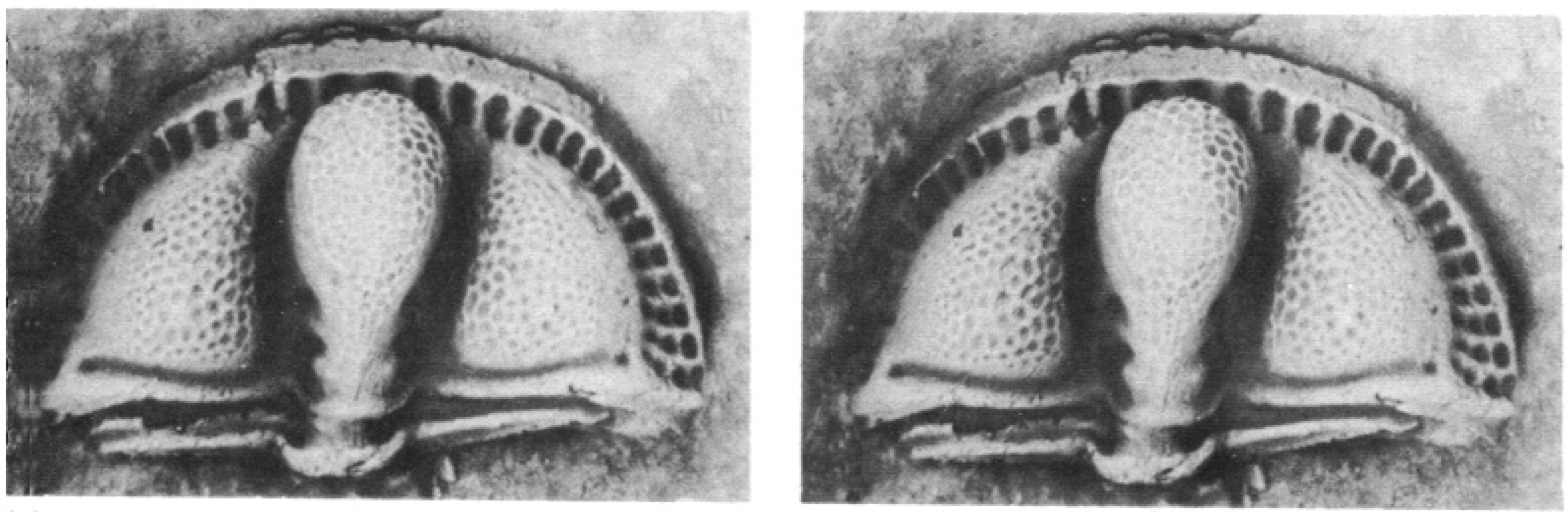
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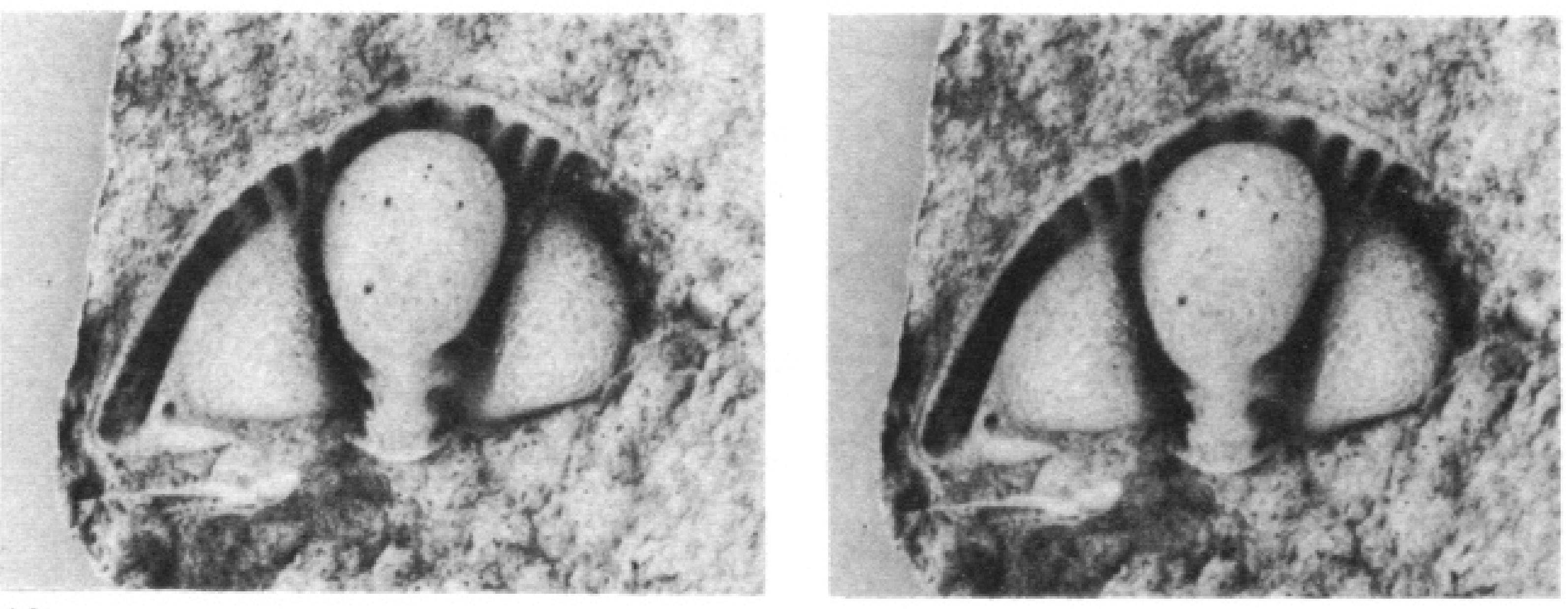
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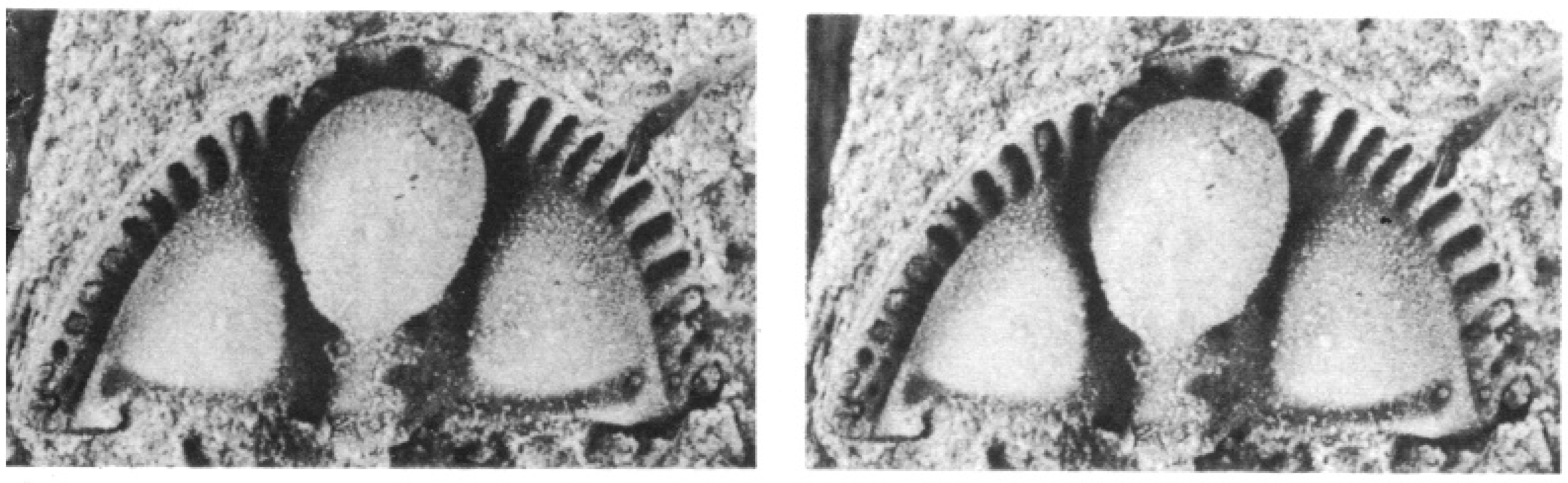
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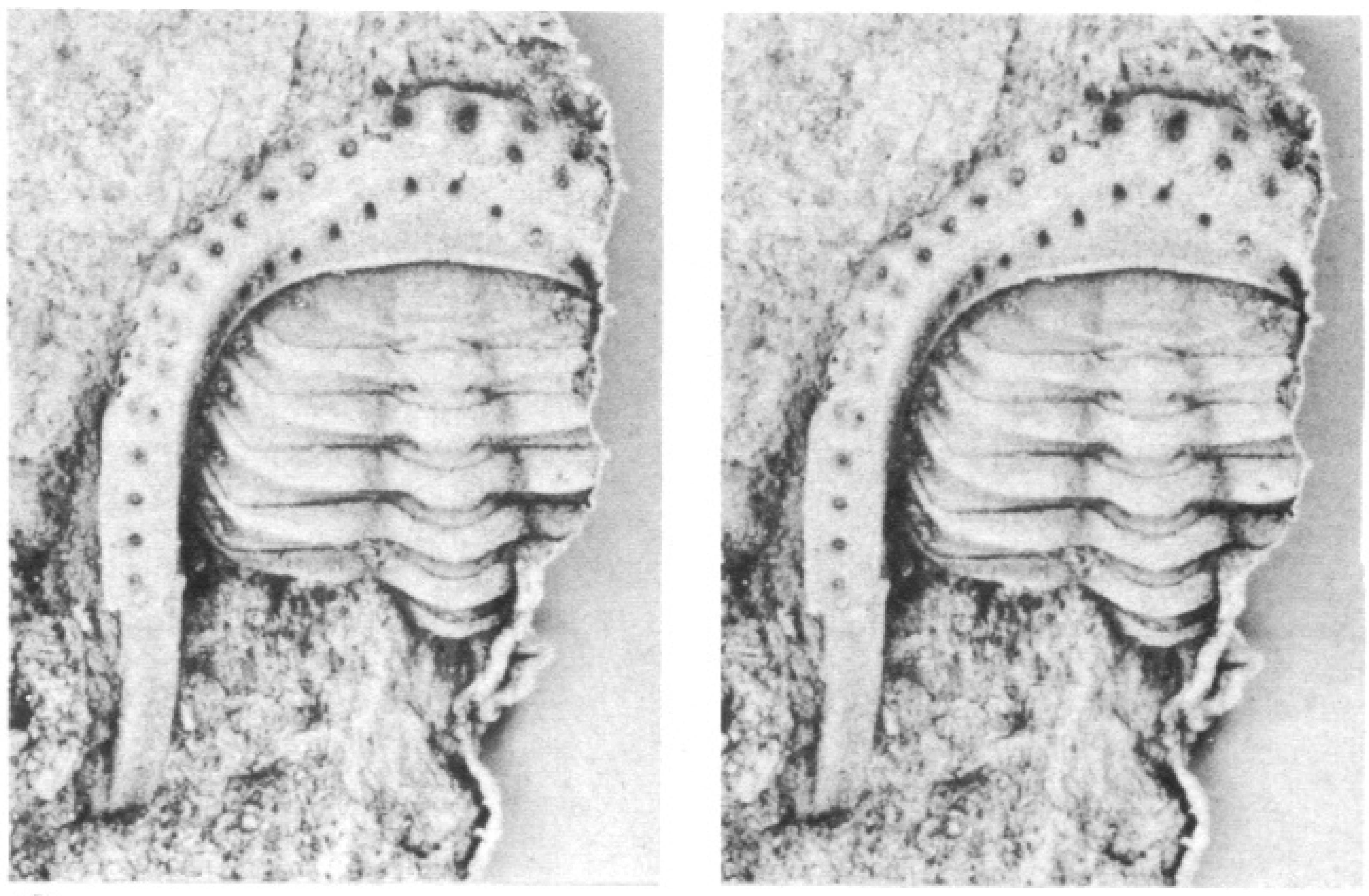
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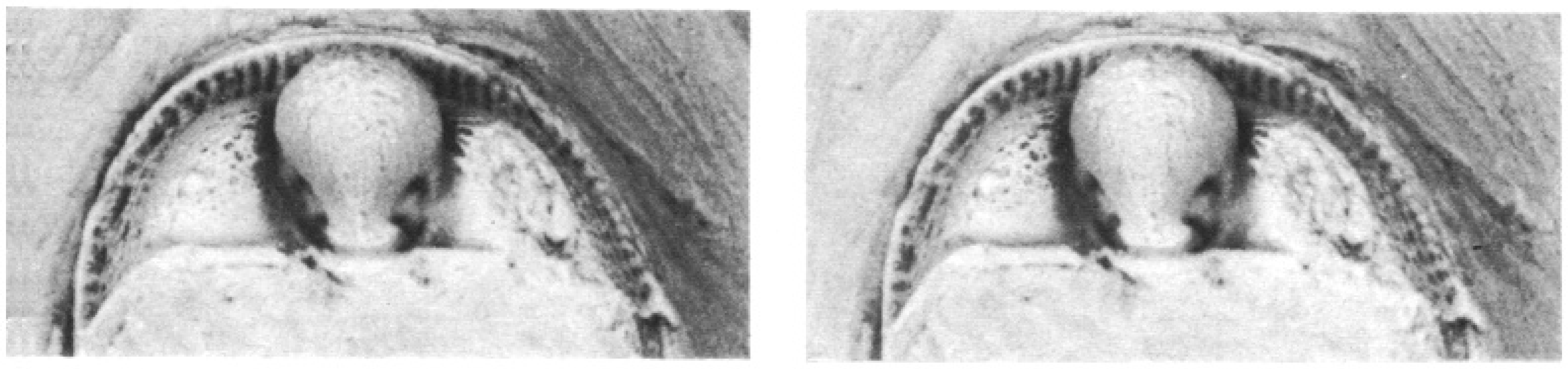
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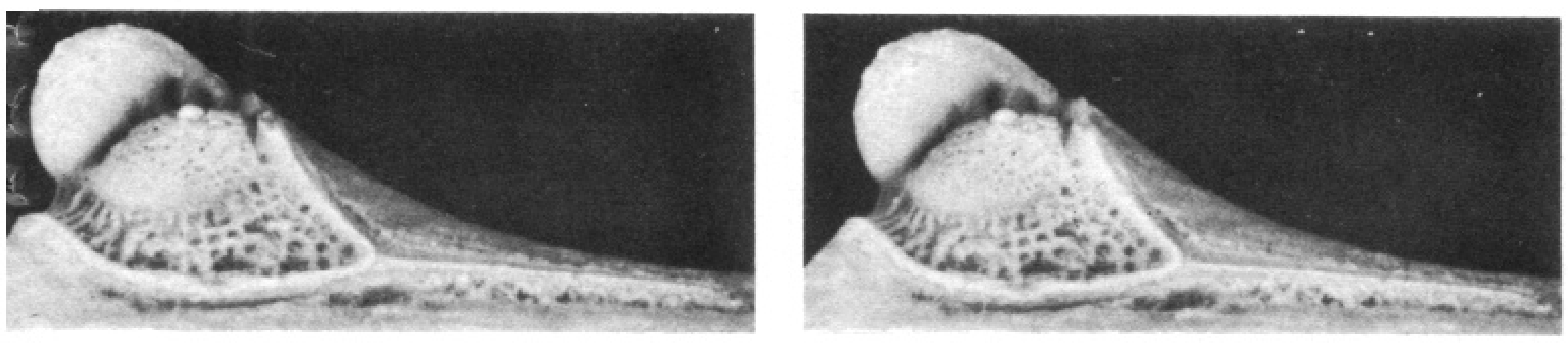
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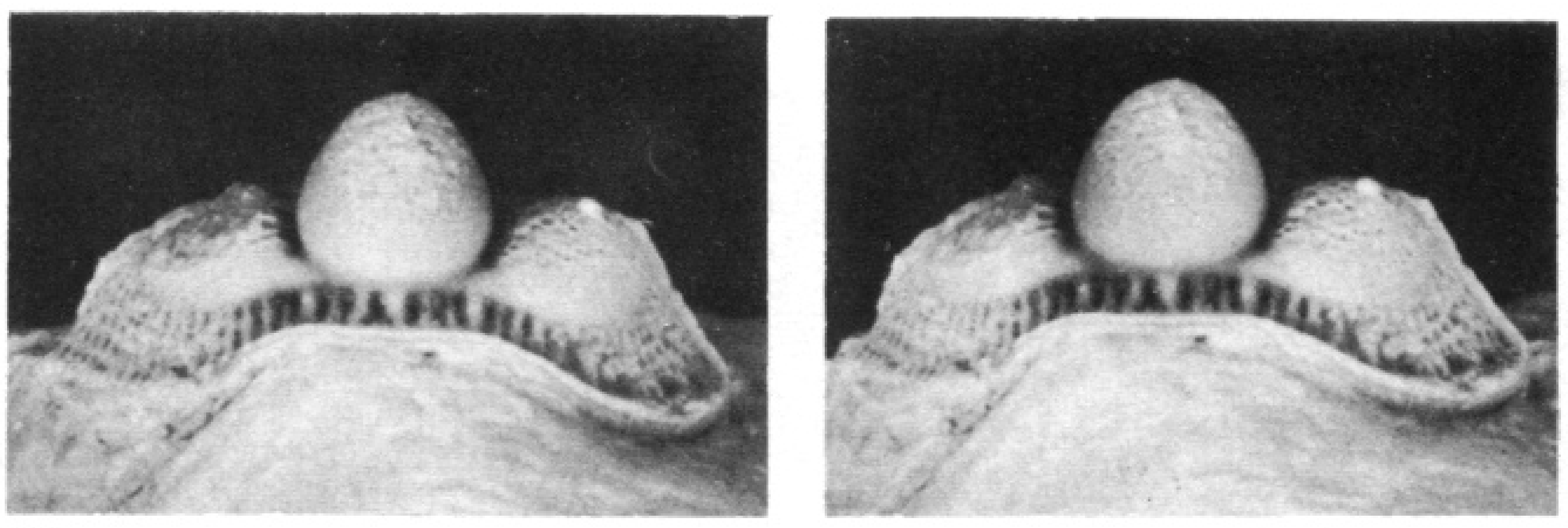
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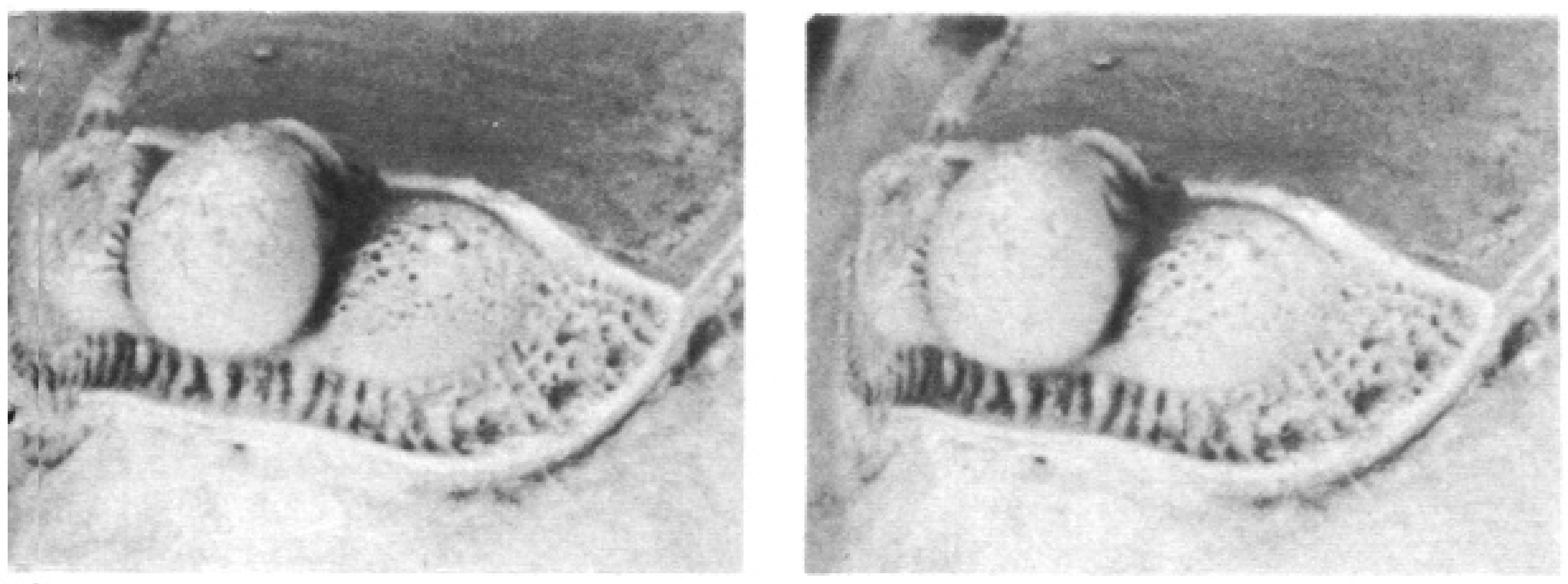
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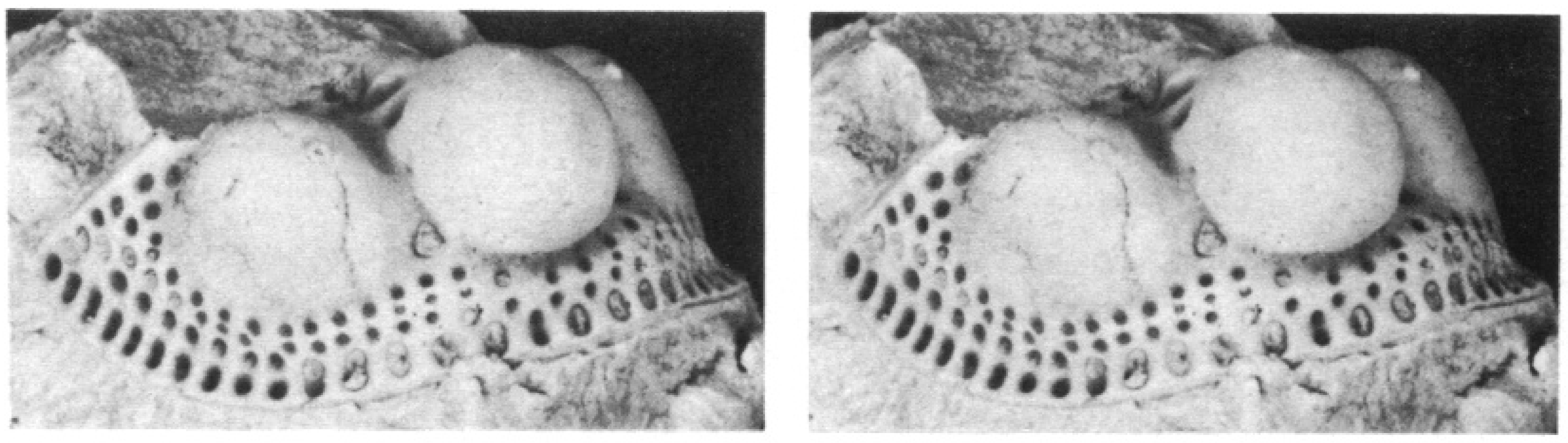
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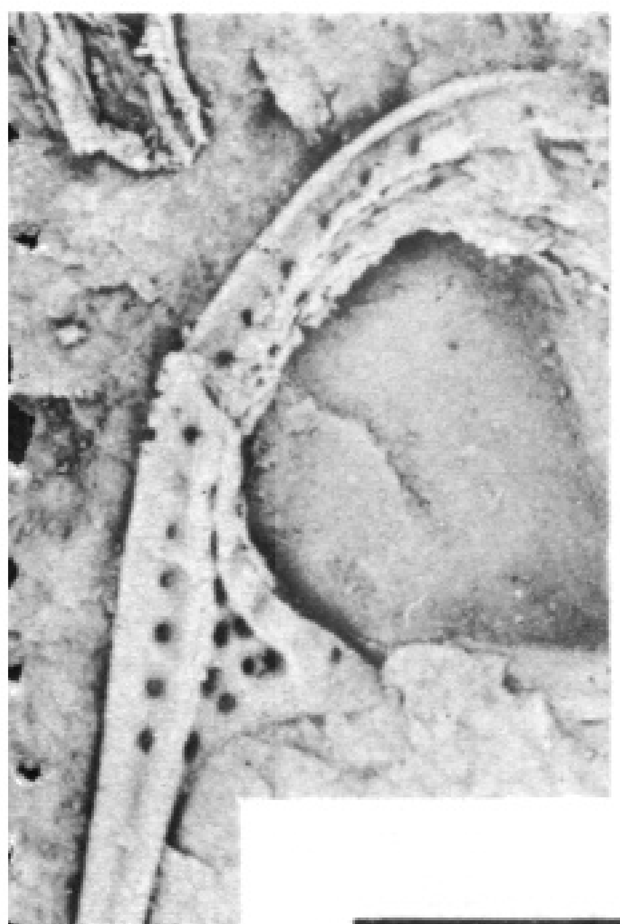
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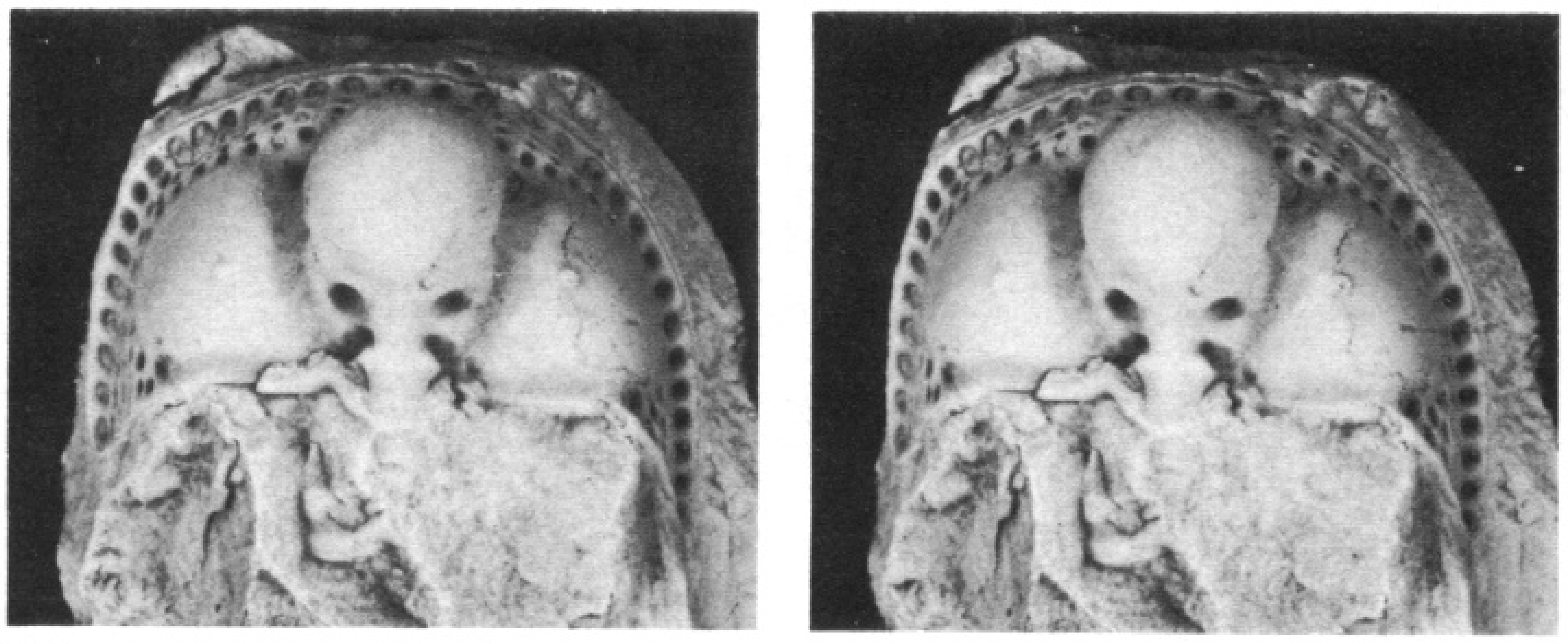
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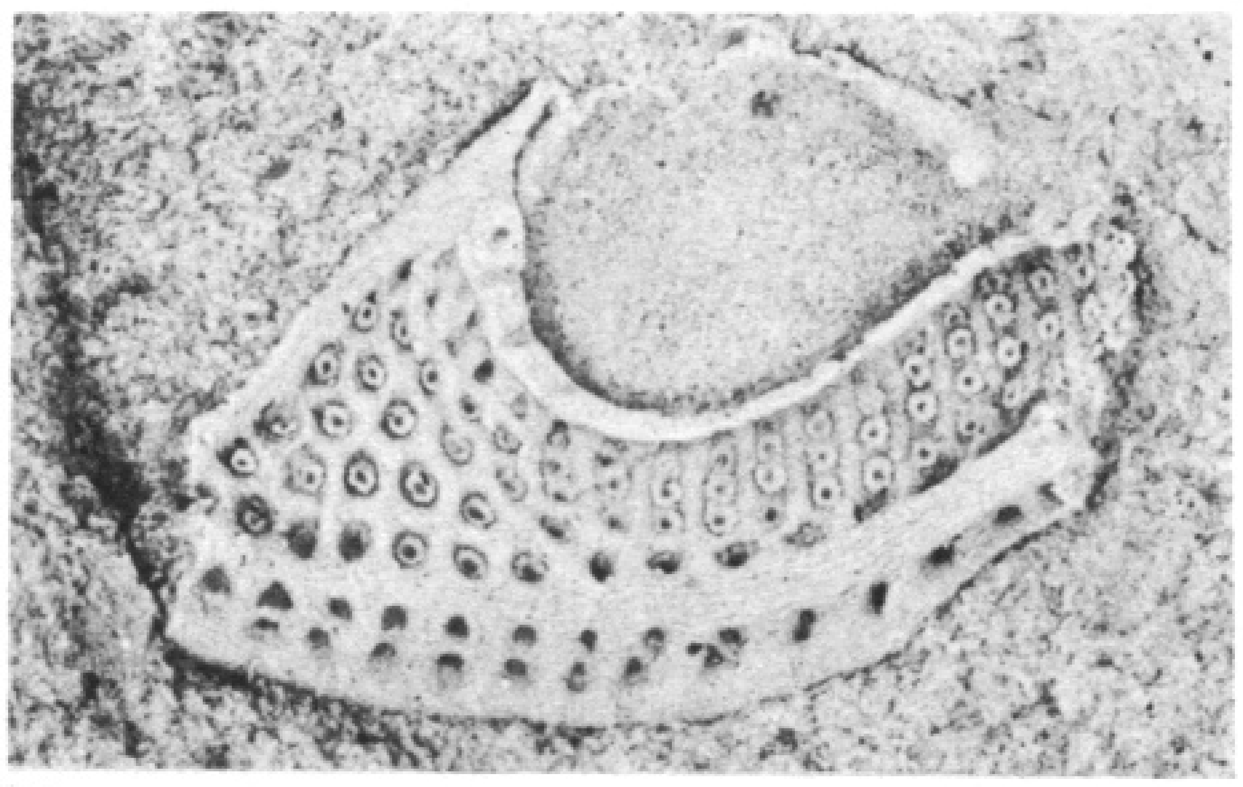
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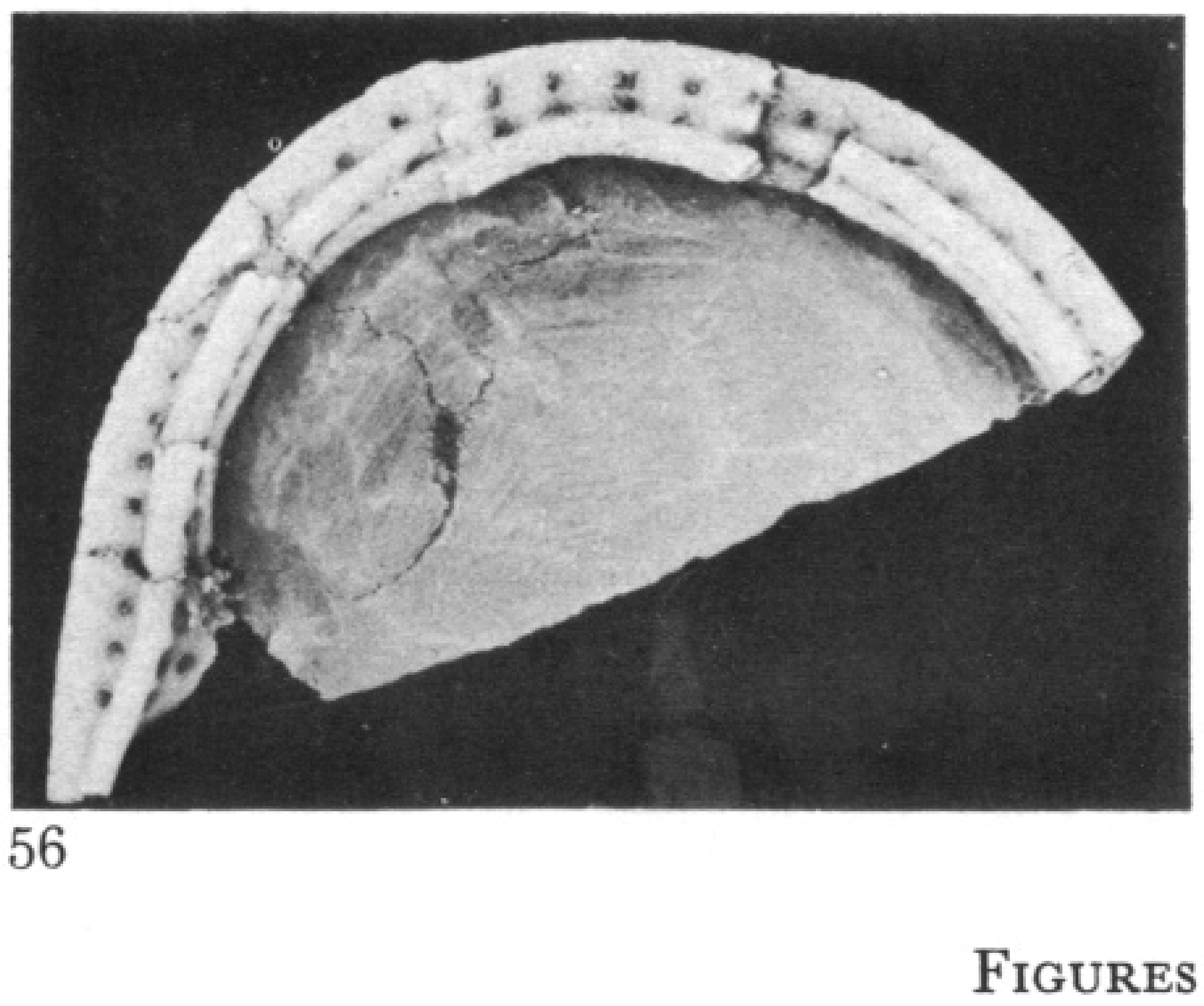
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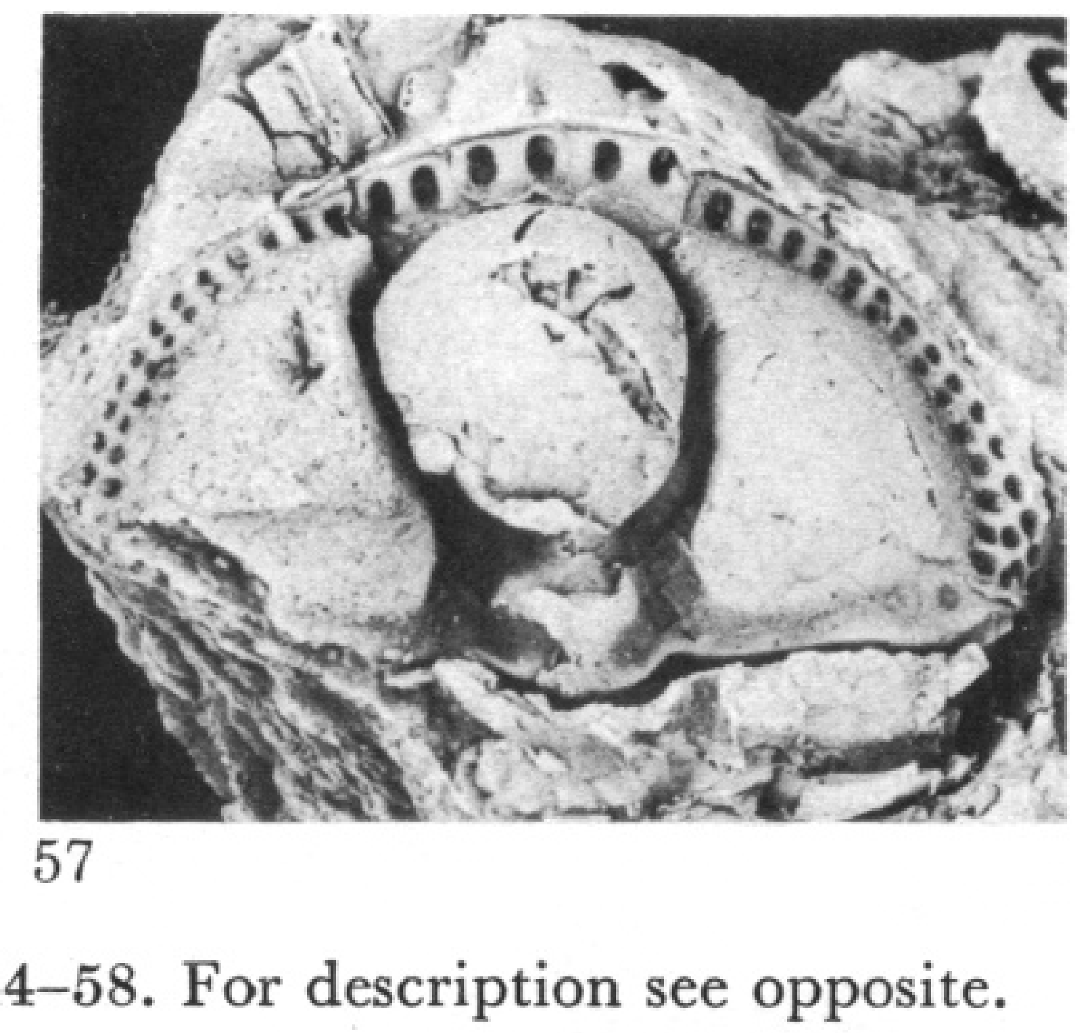
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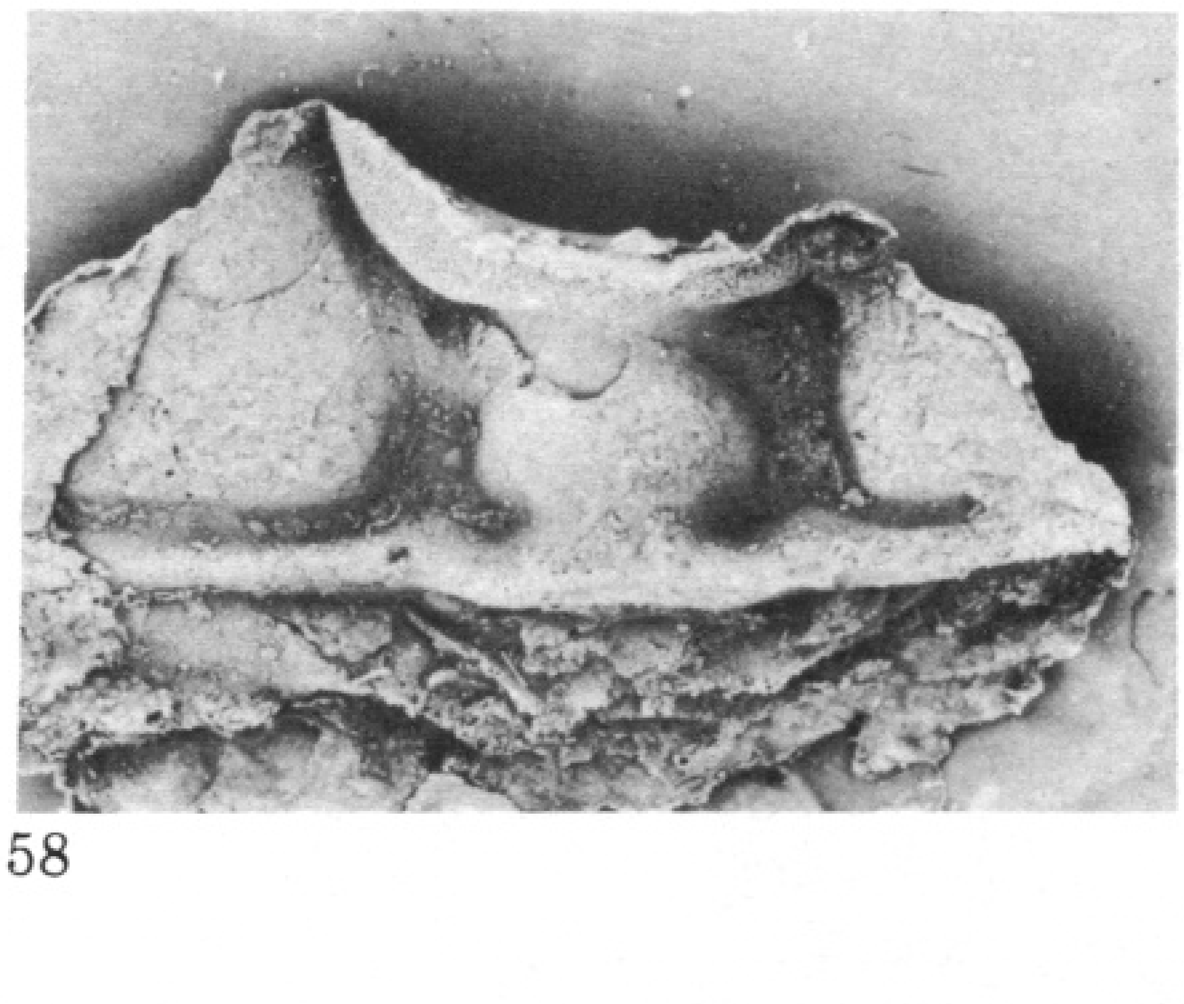
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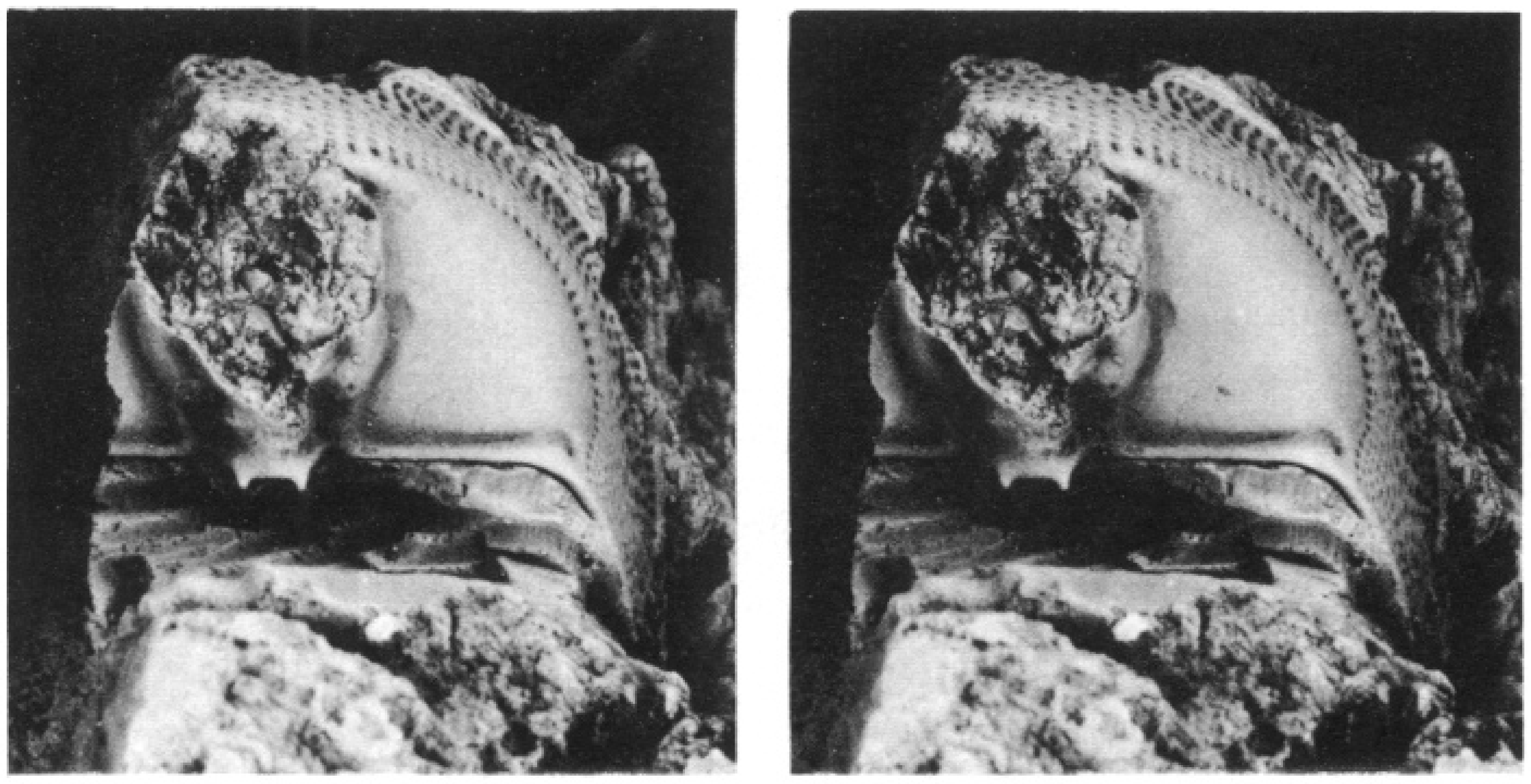
Figures 44–58. For description see opposite.



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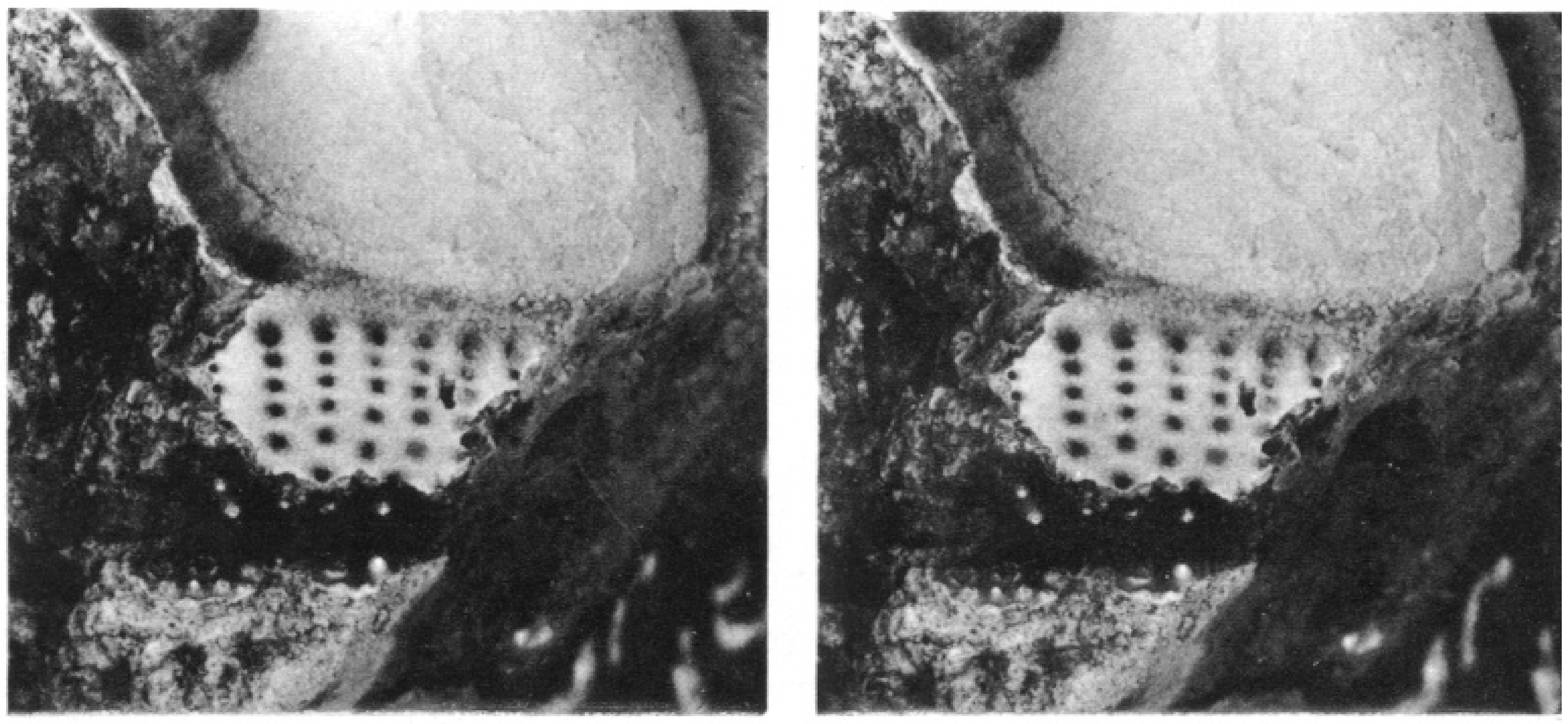

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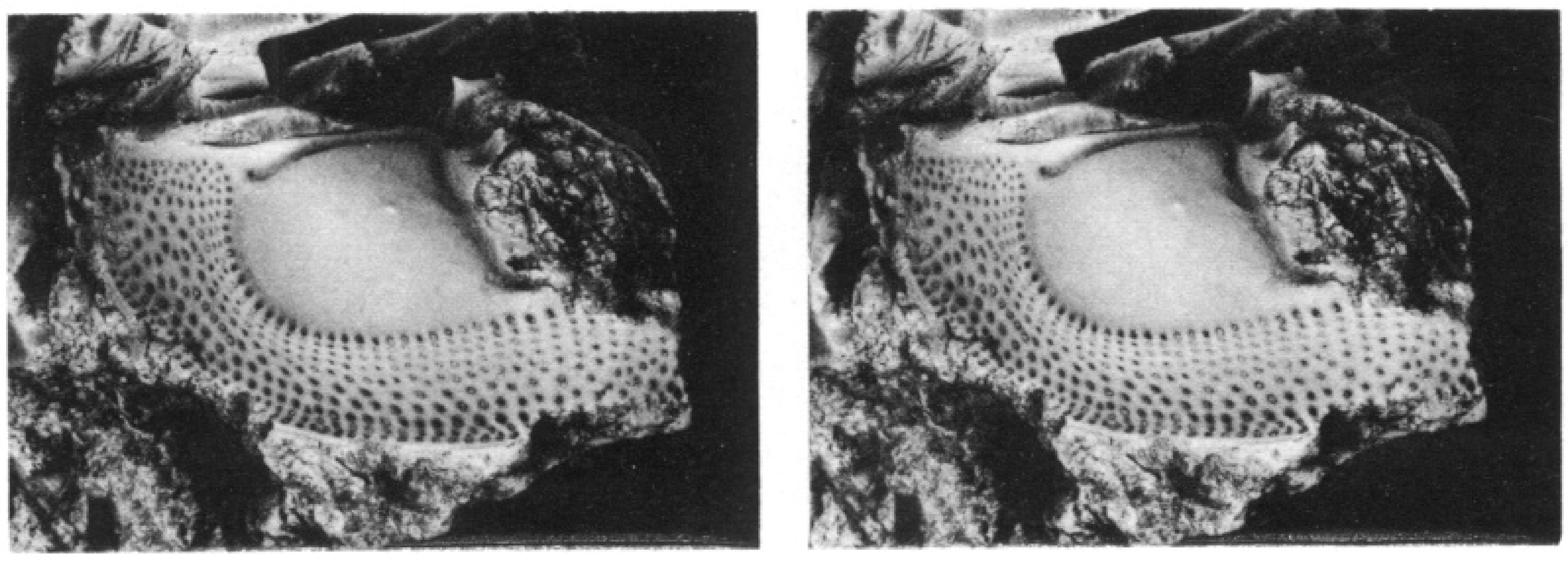

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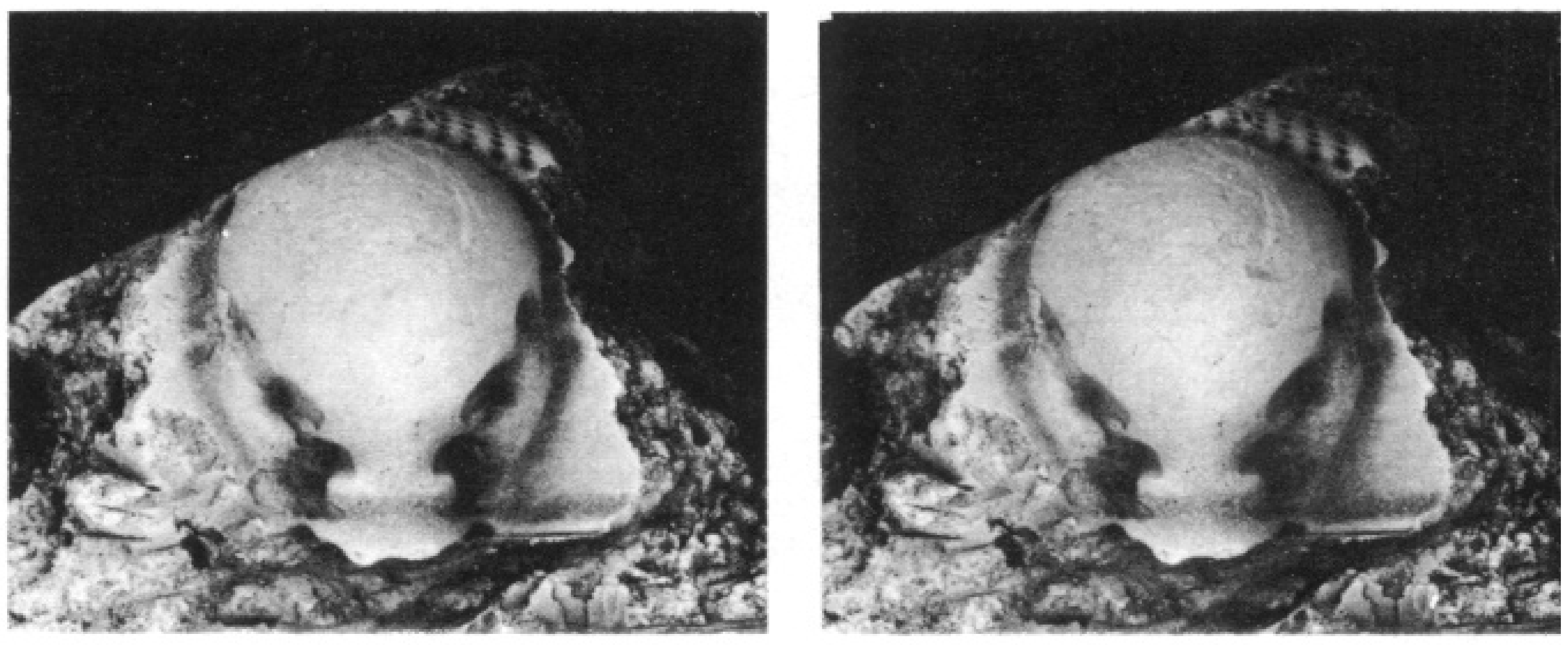

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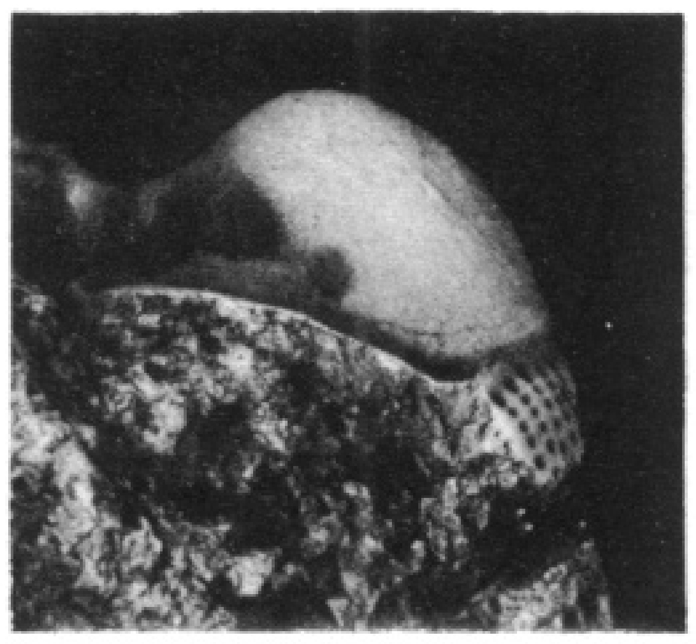

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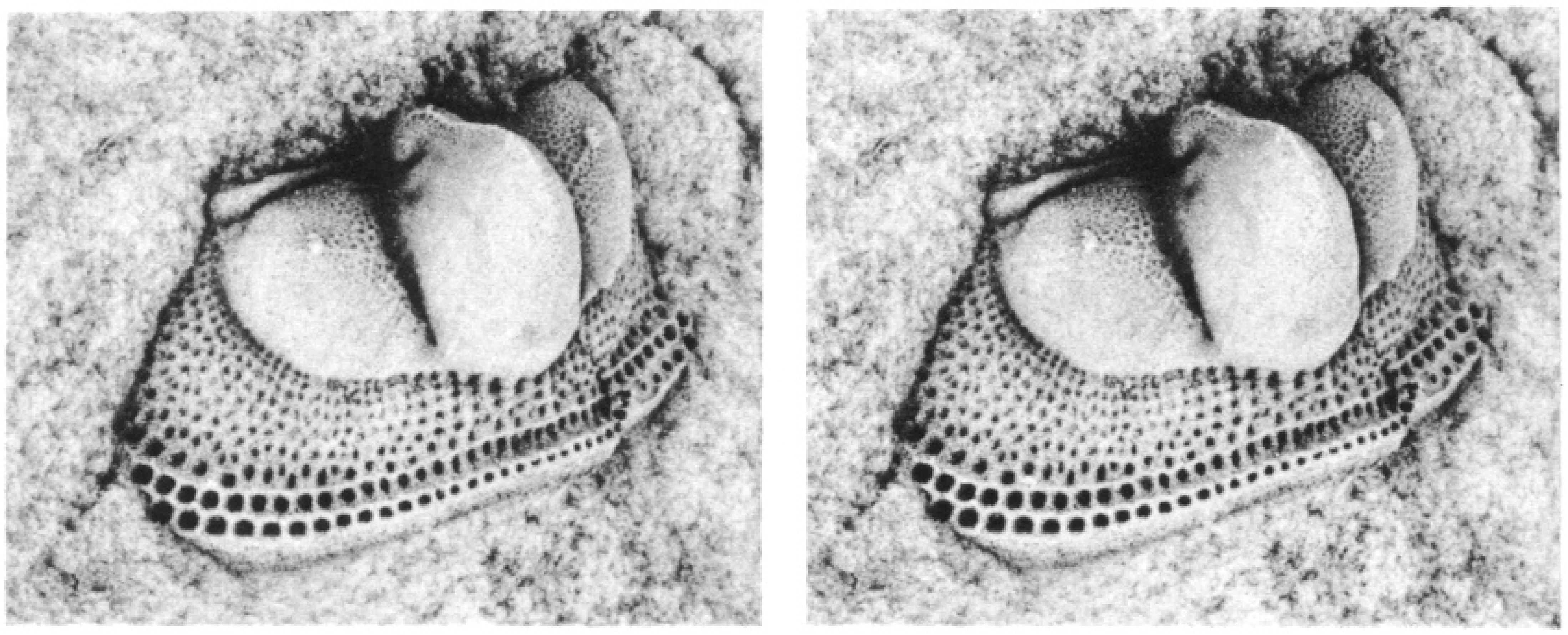

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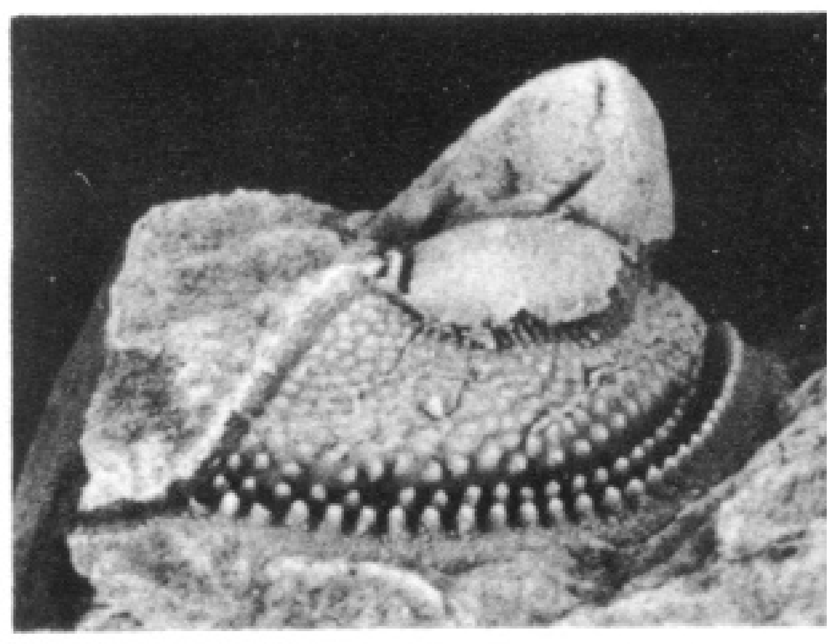

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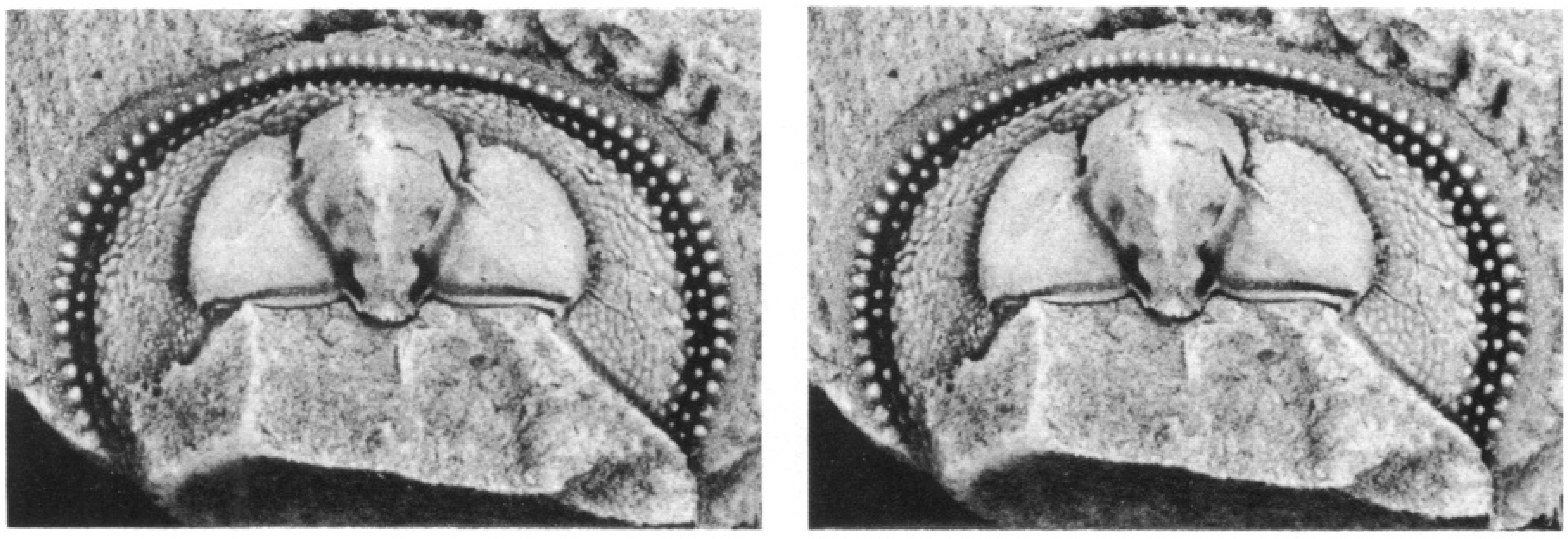

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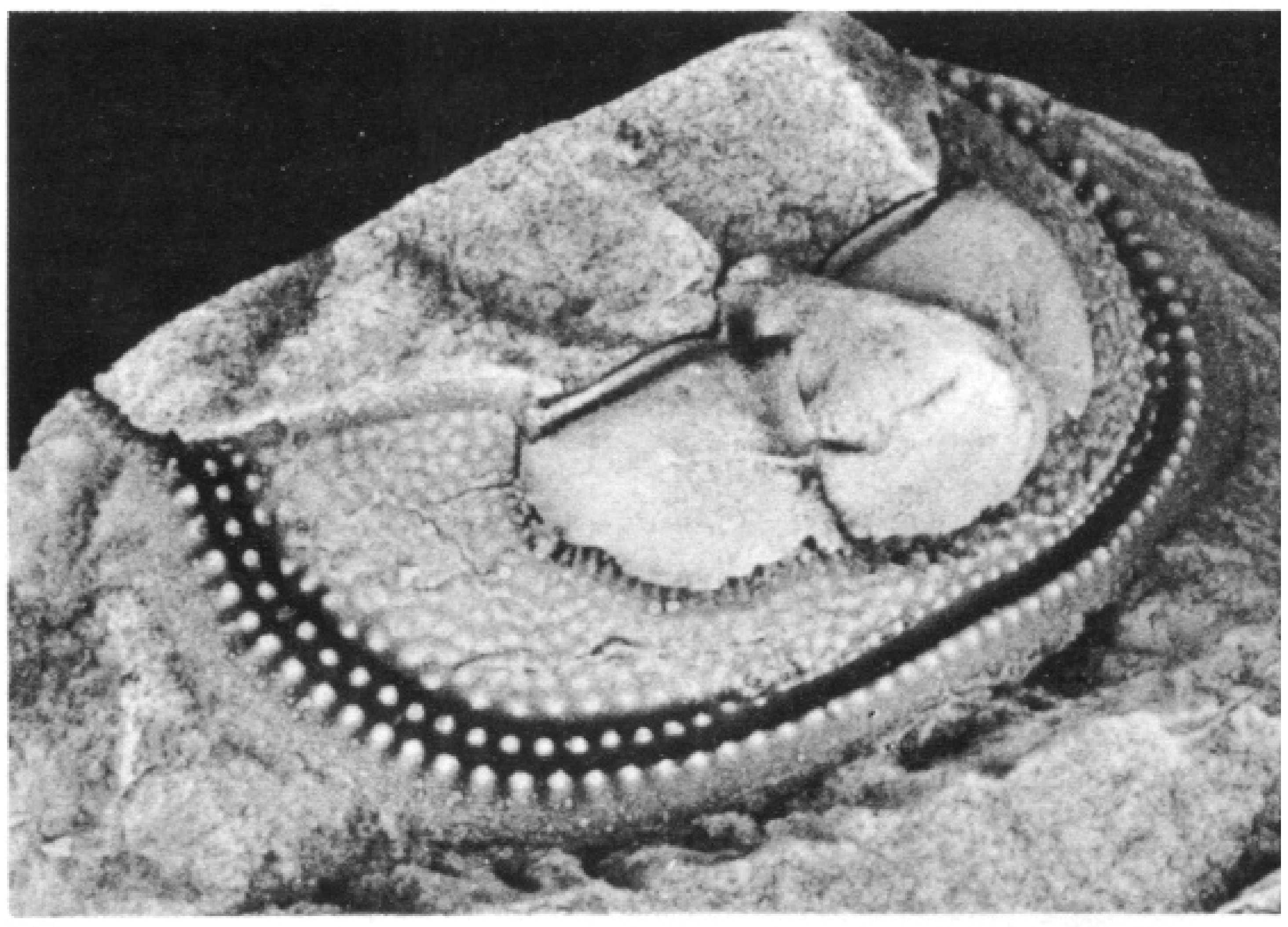

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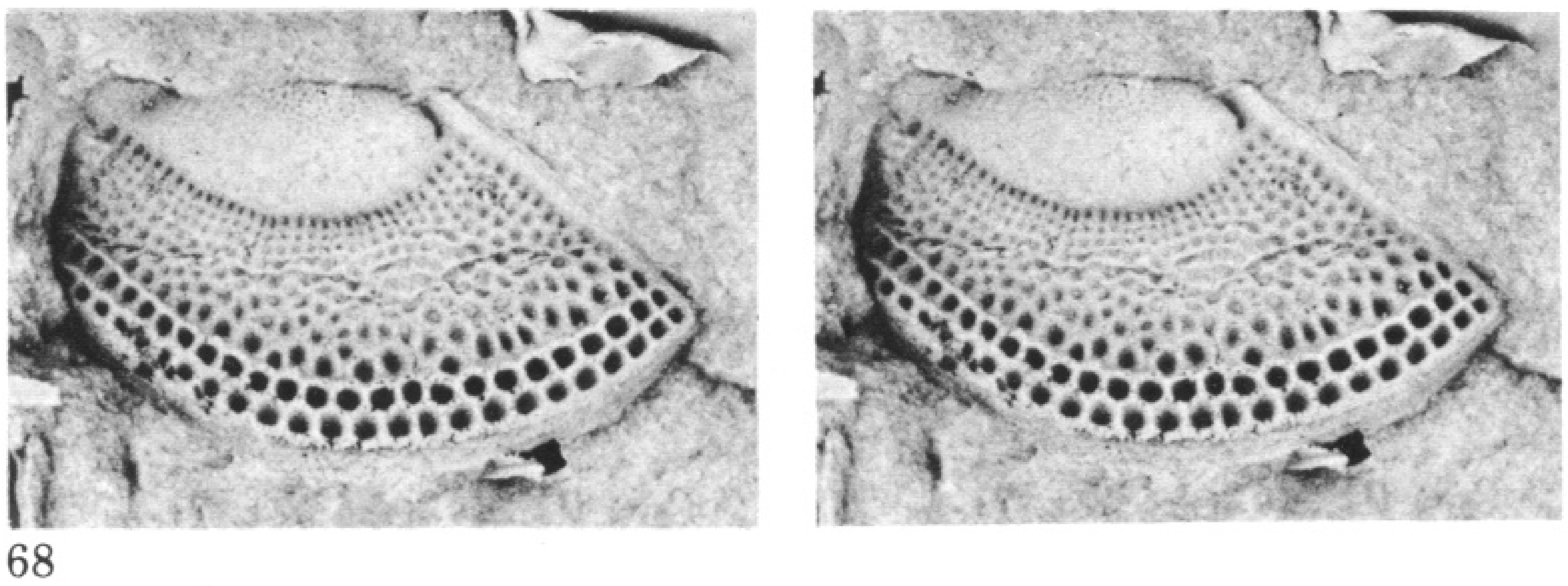

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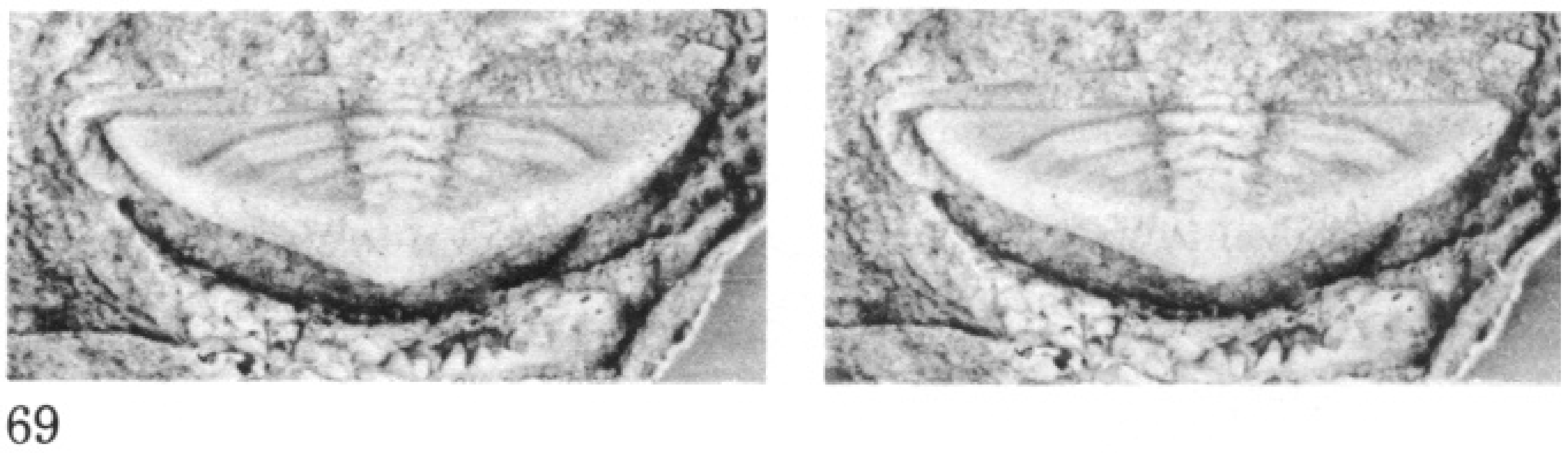

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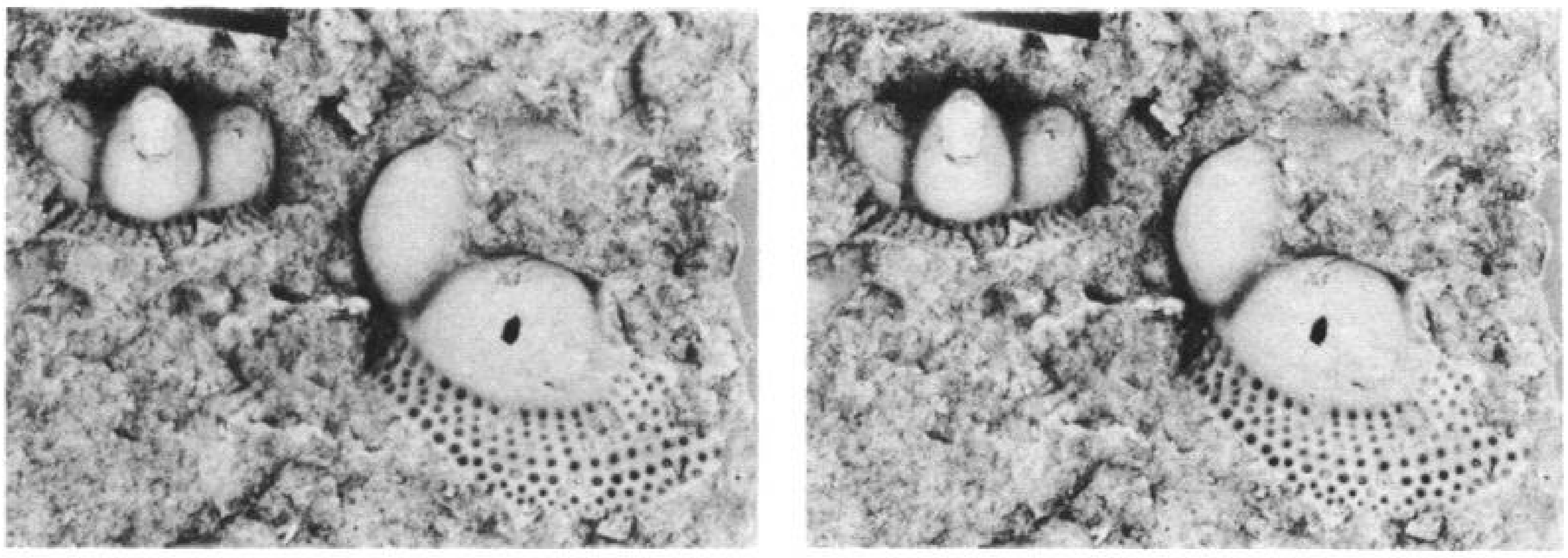
FIGURES 59–69. For description see opposite.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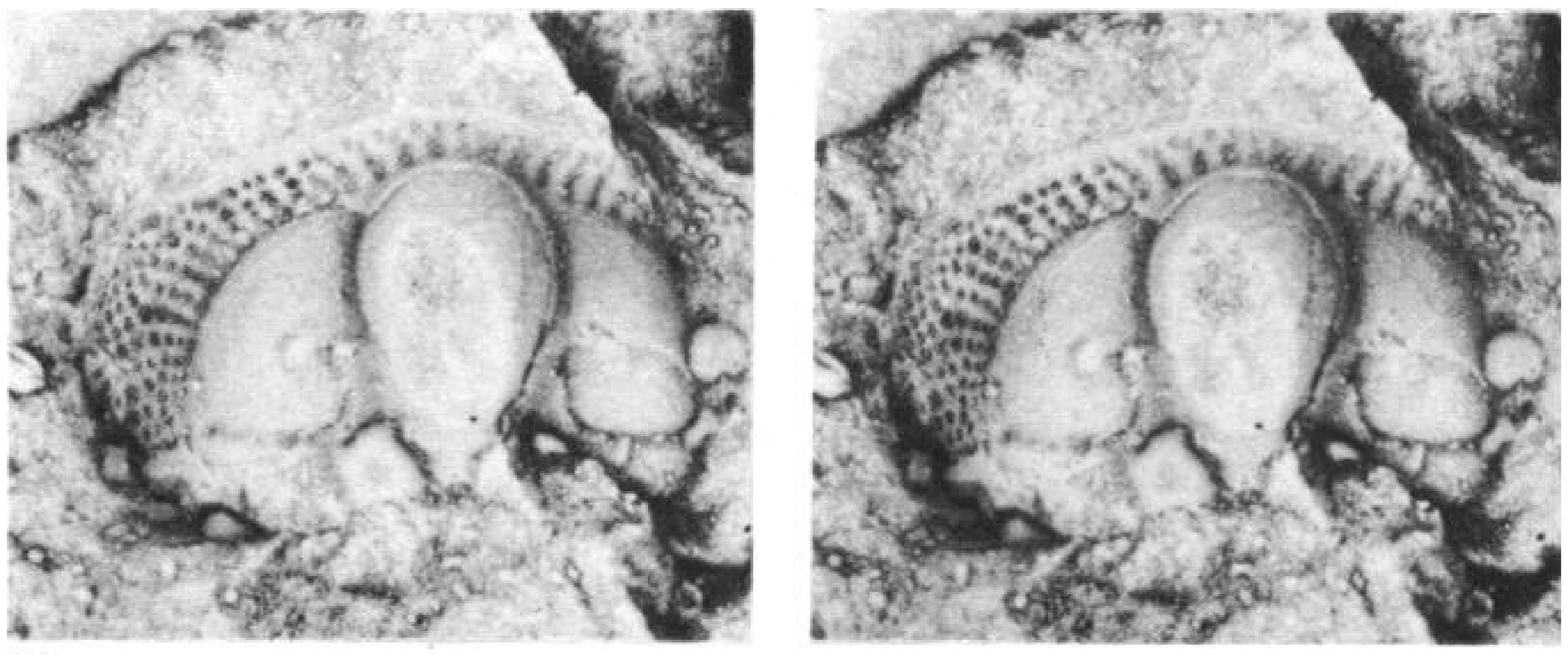
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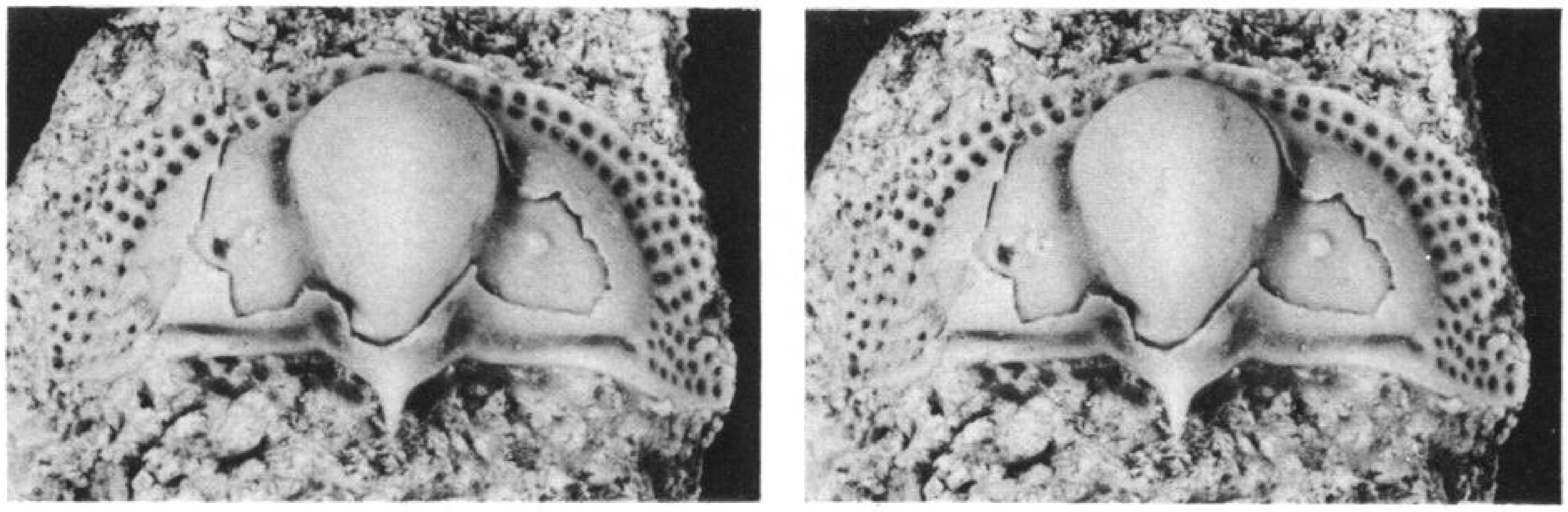
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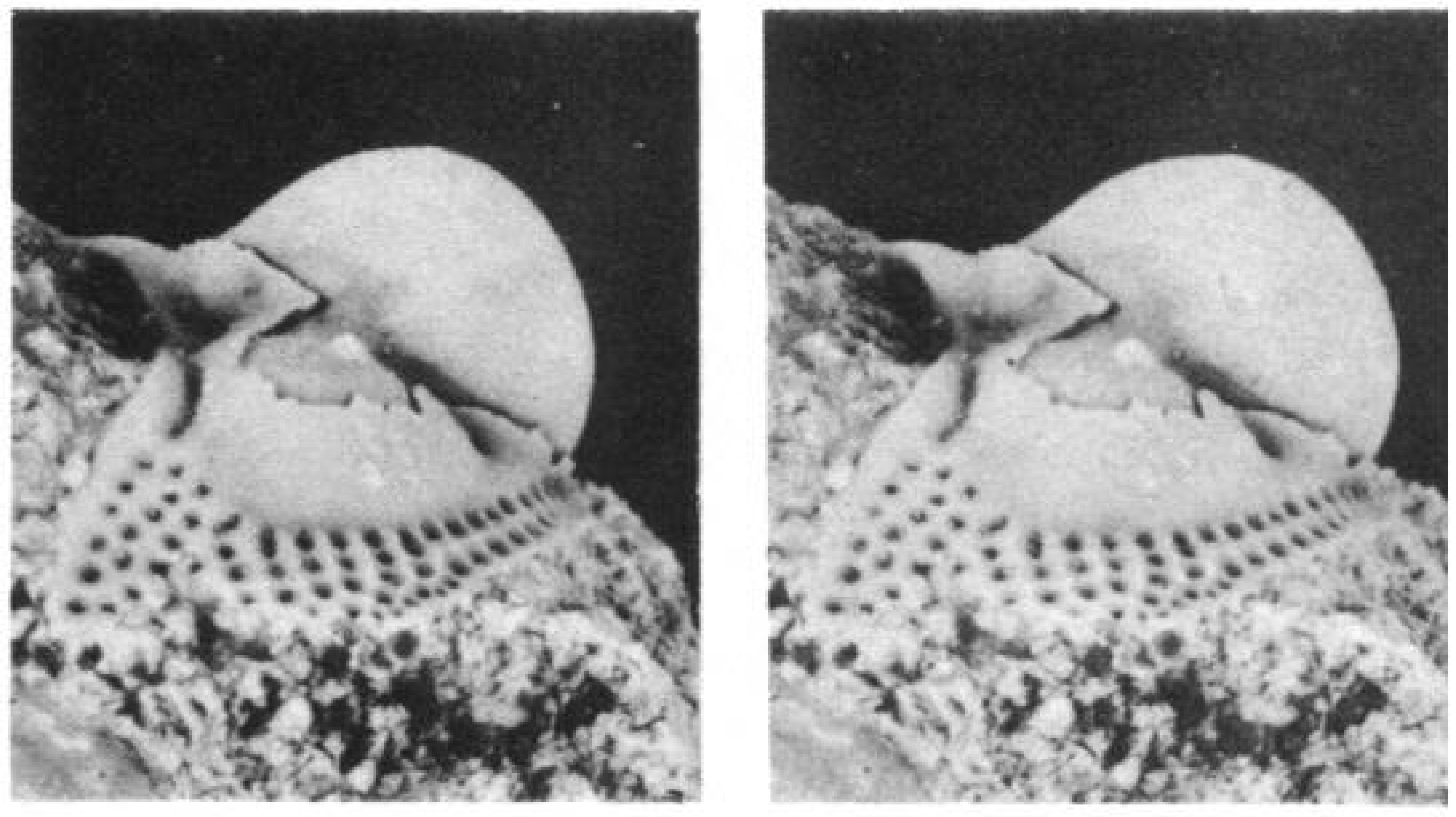
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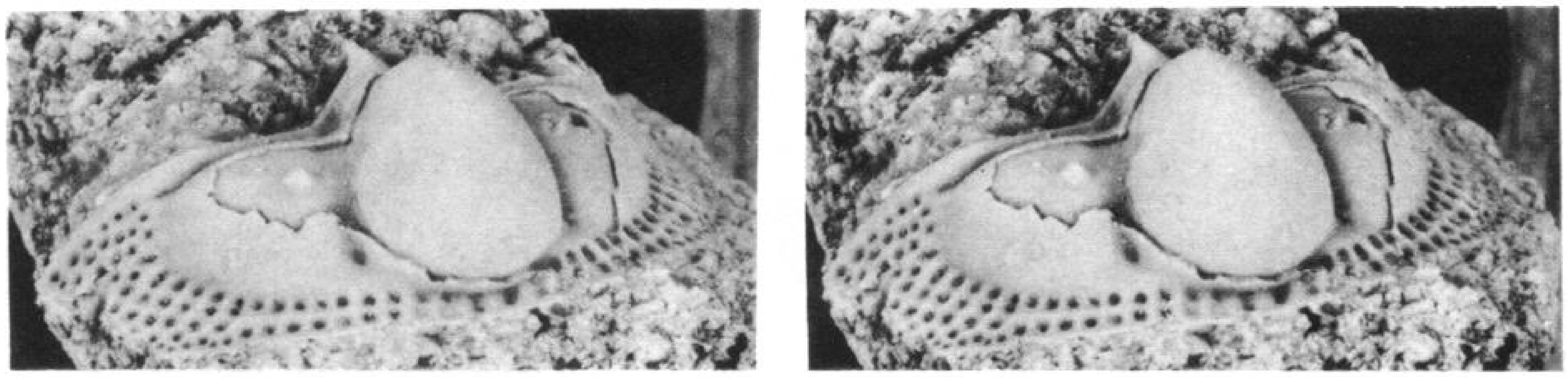
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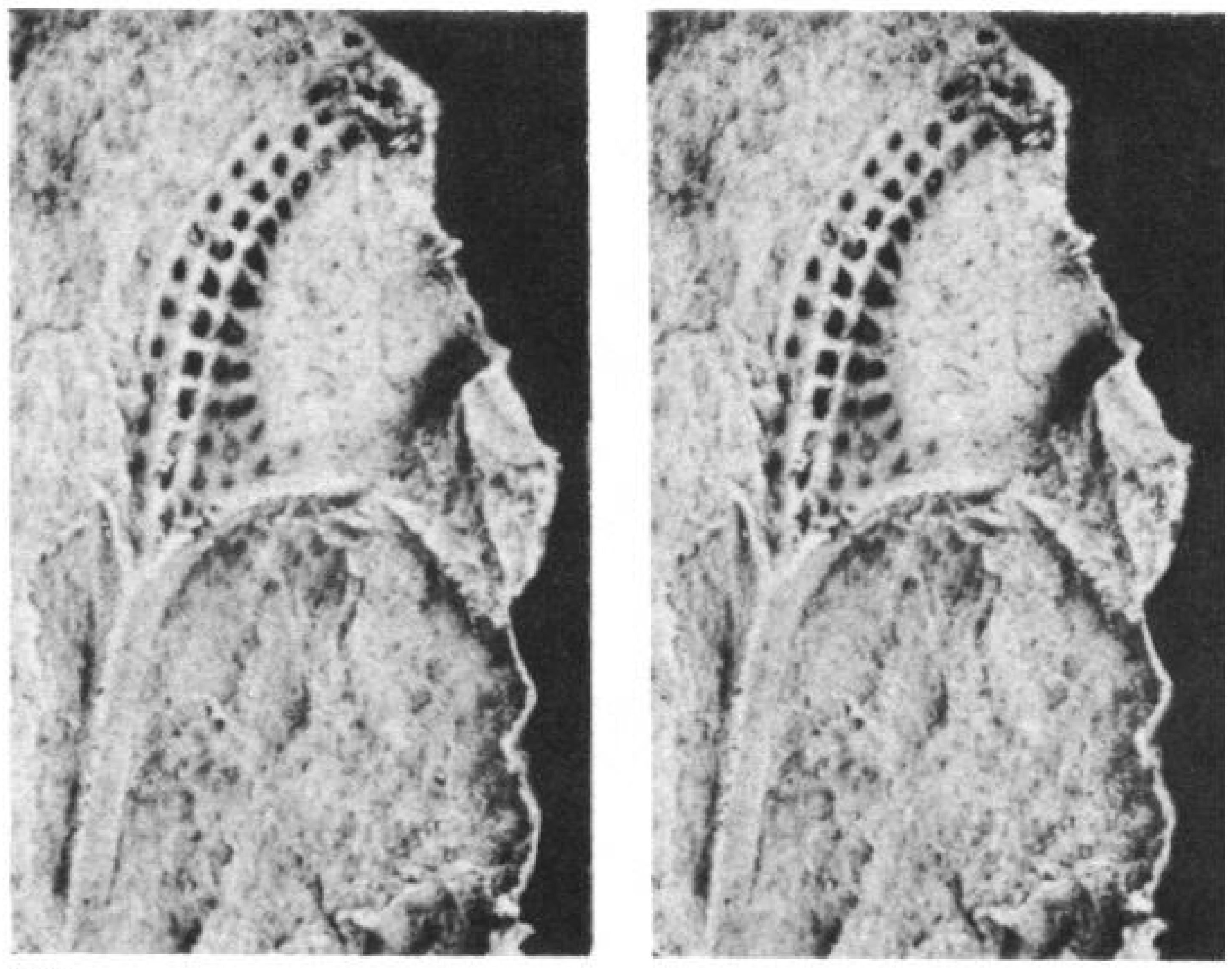
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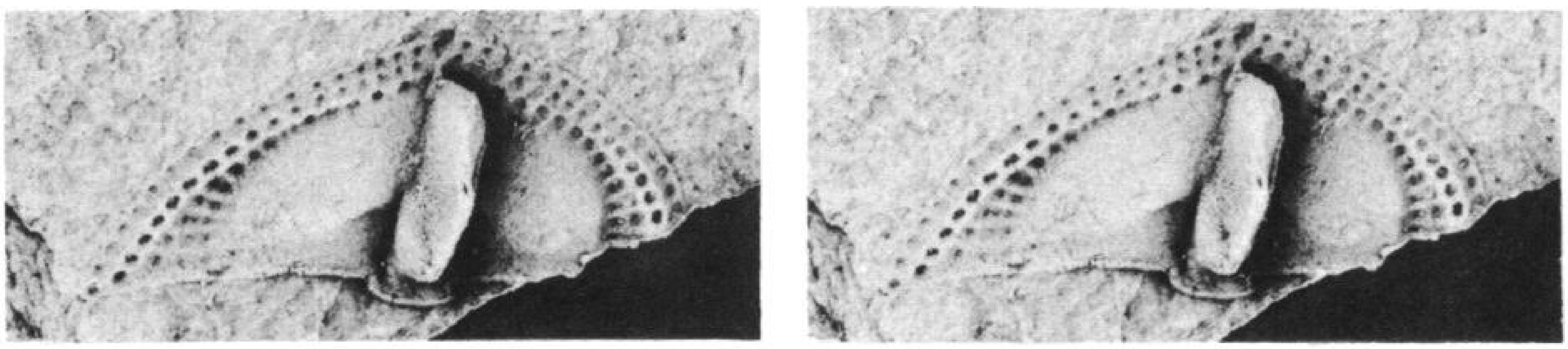
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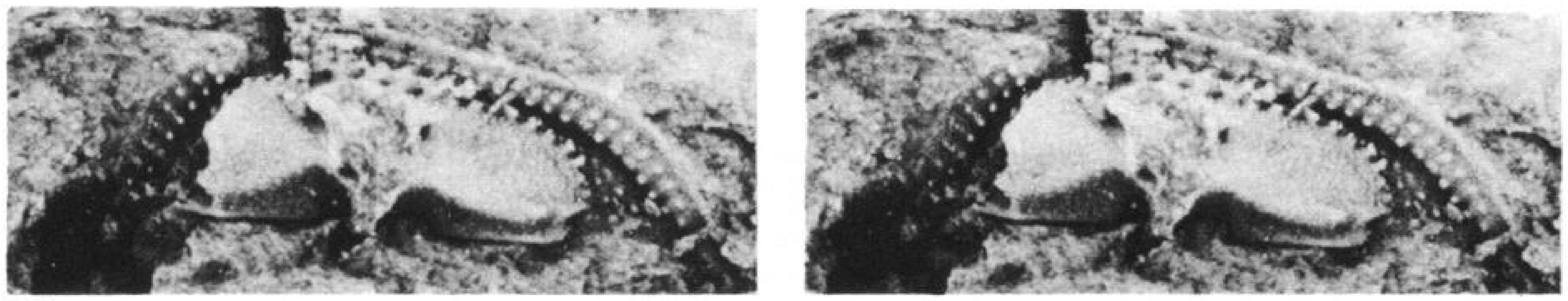
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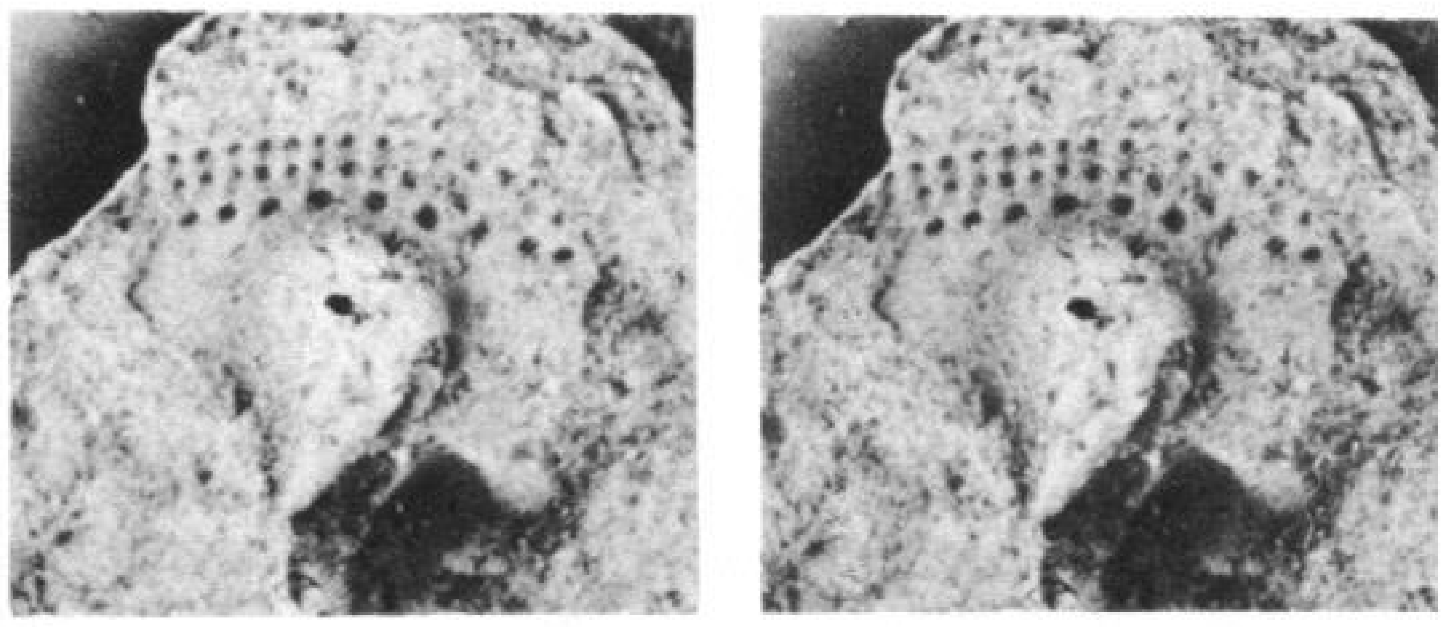
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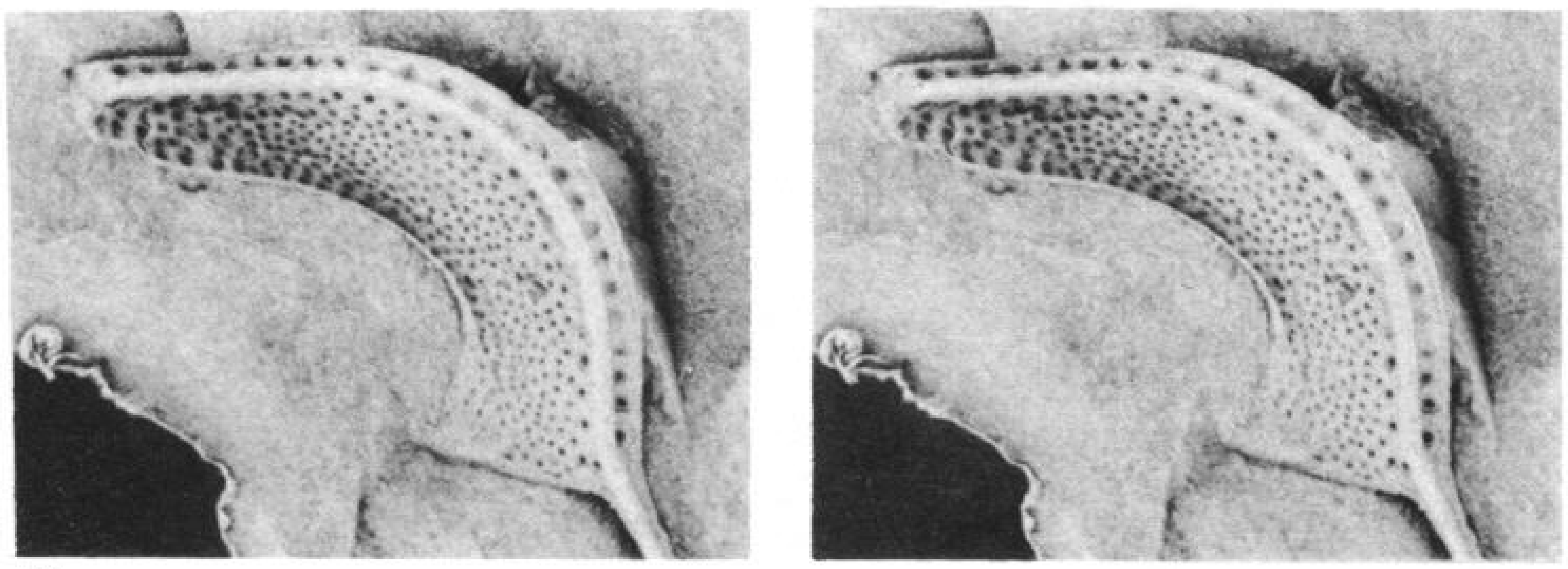
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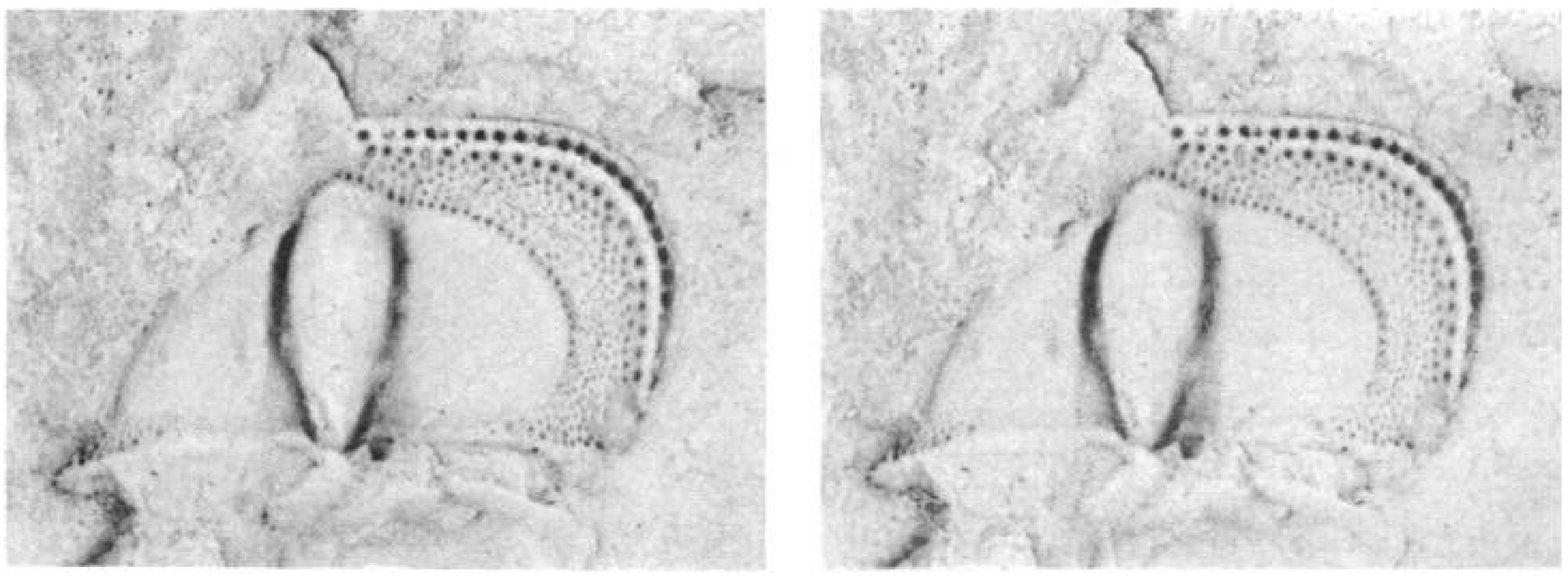
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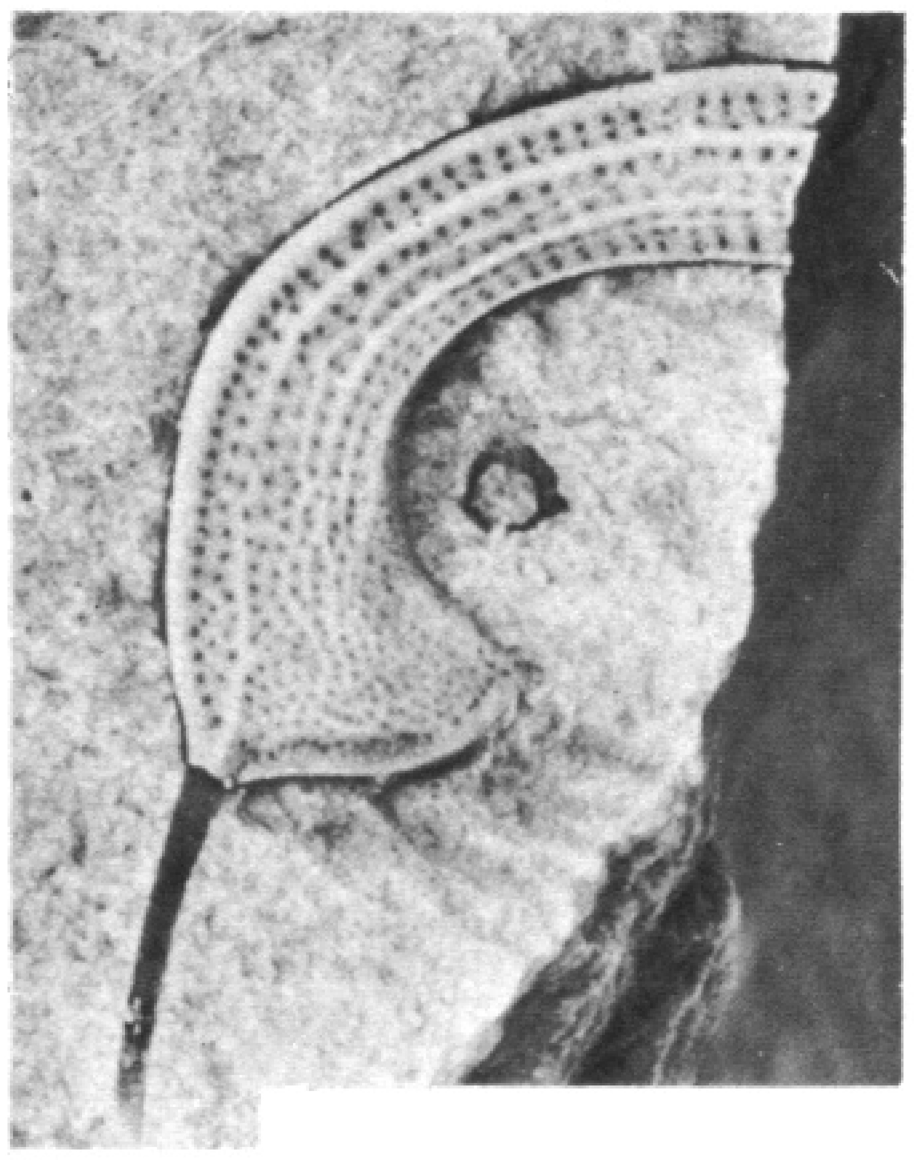
FIGURES 70–80. For description see opposite.



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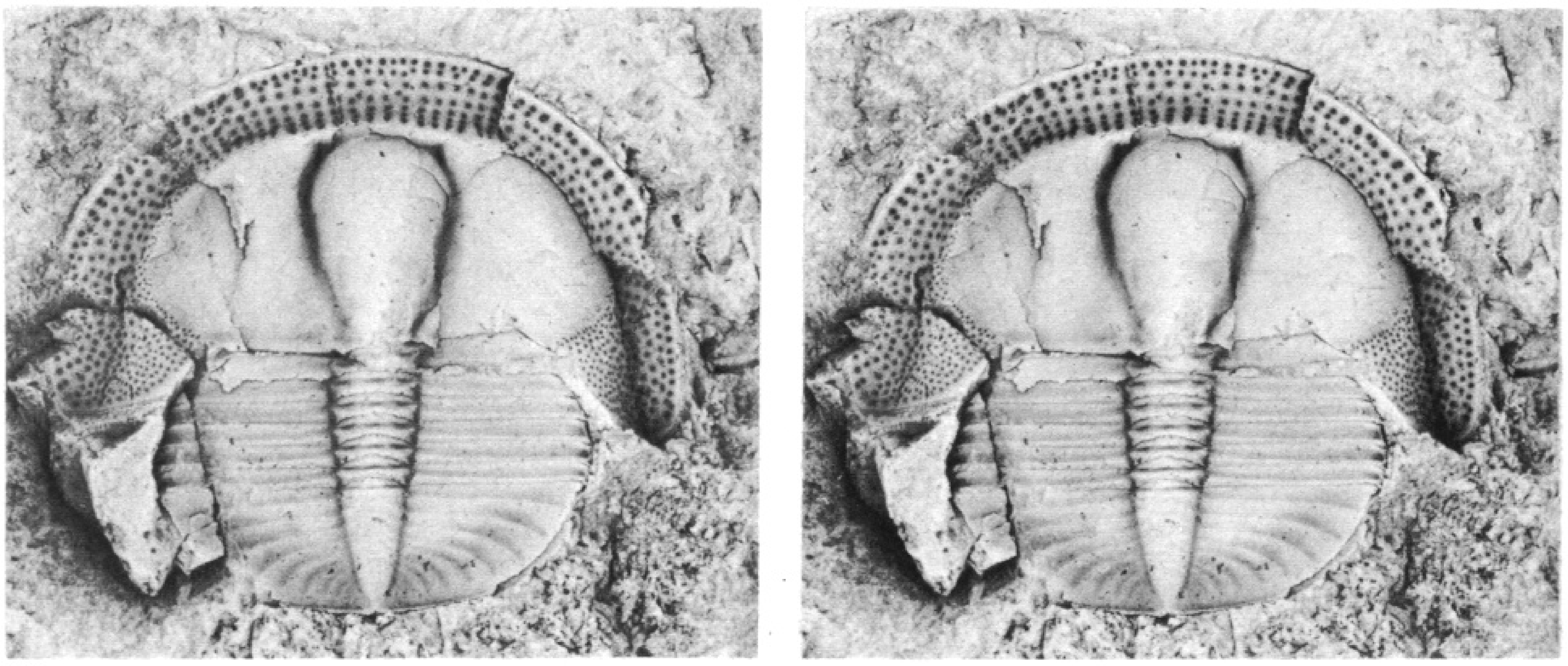

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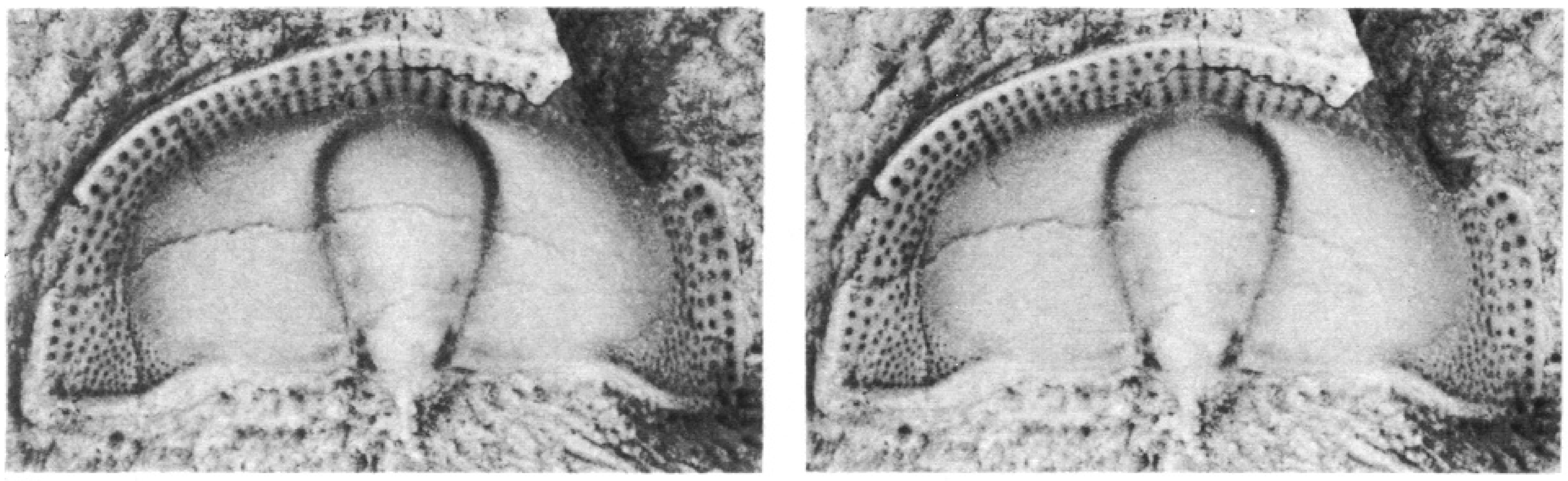

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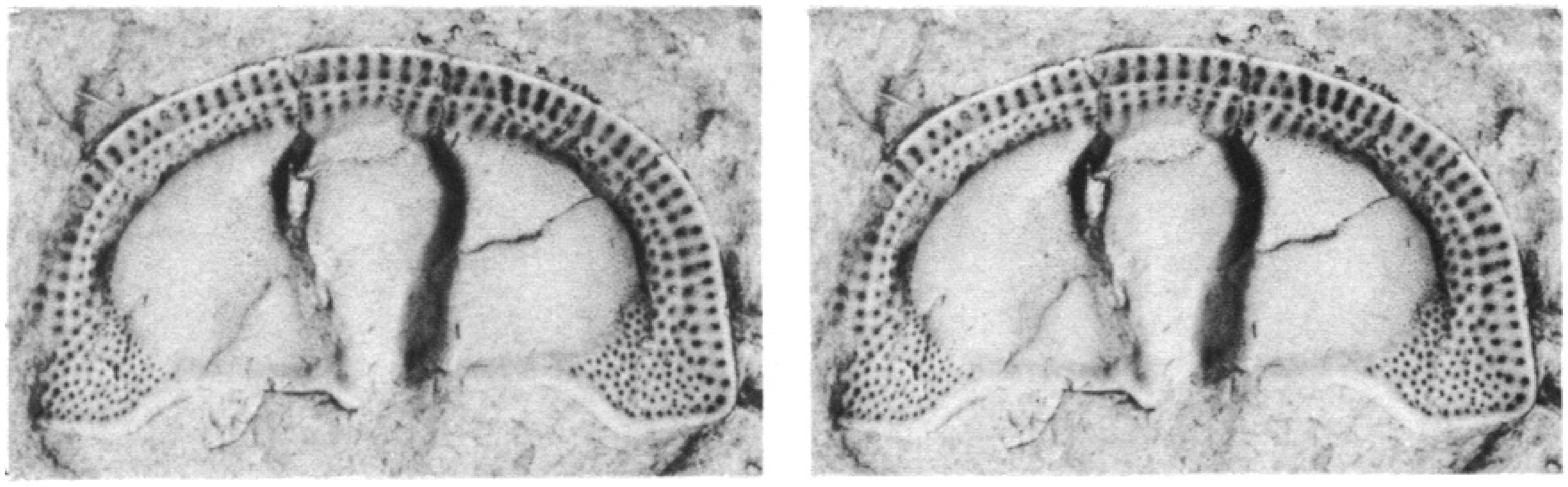

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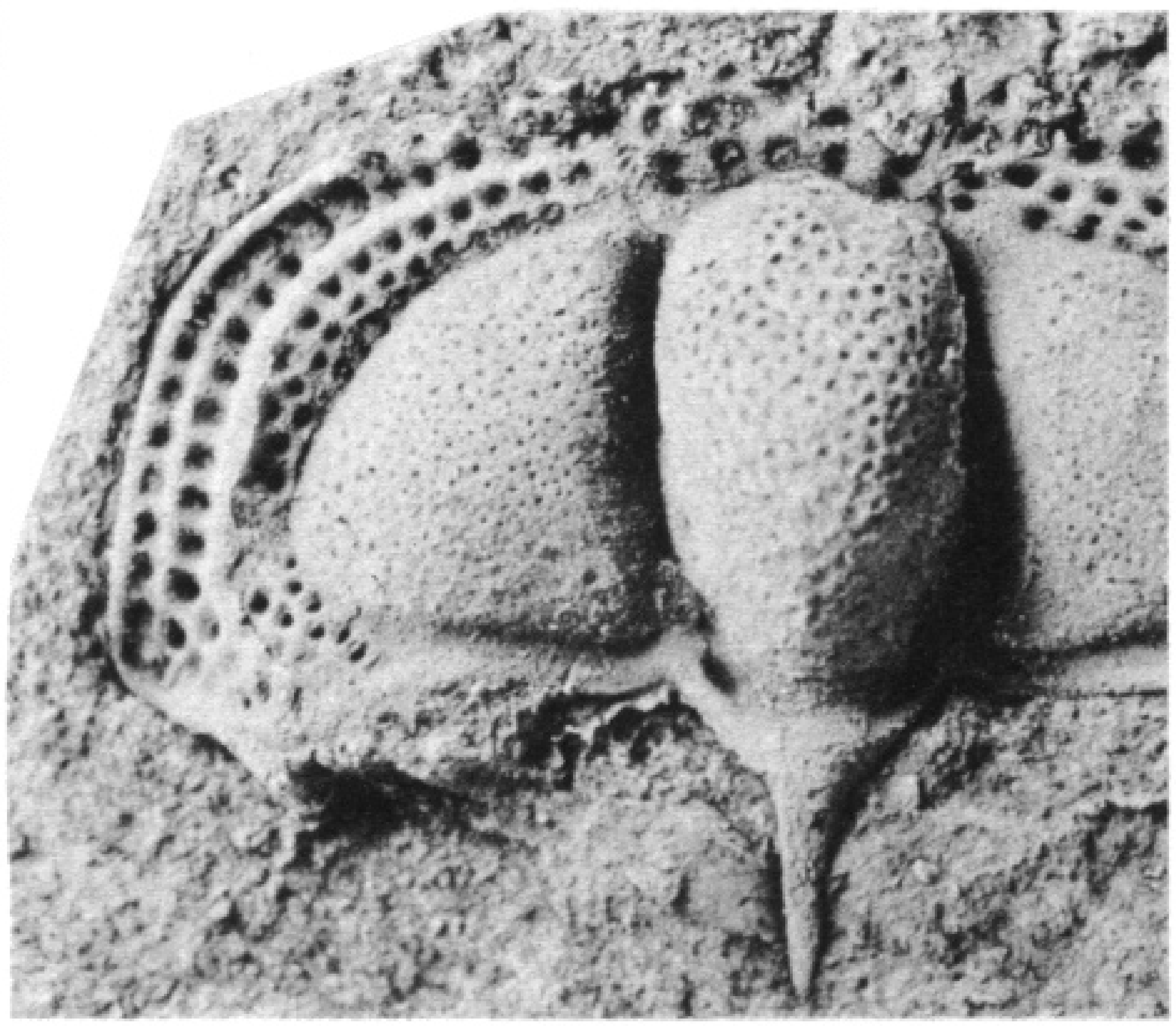

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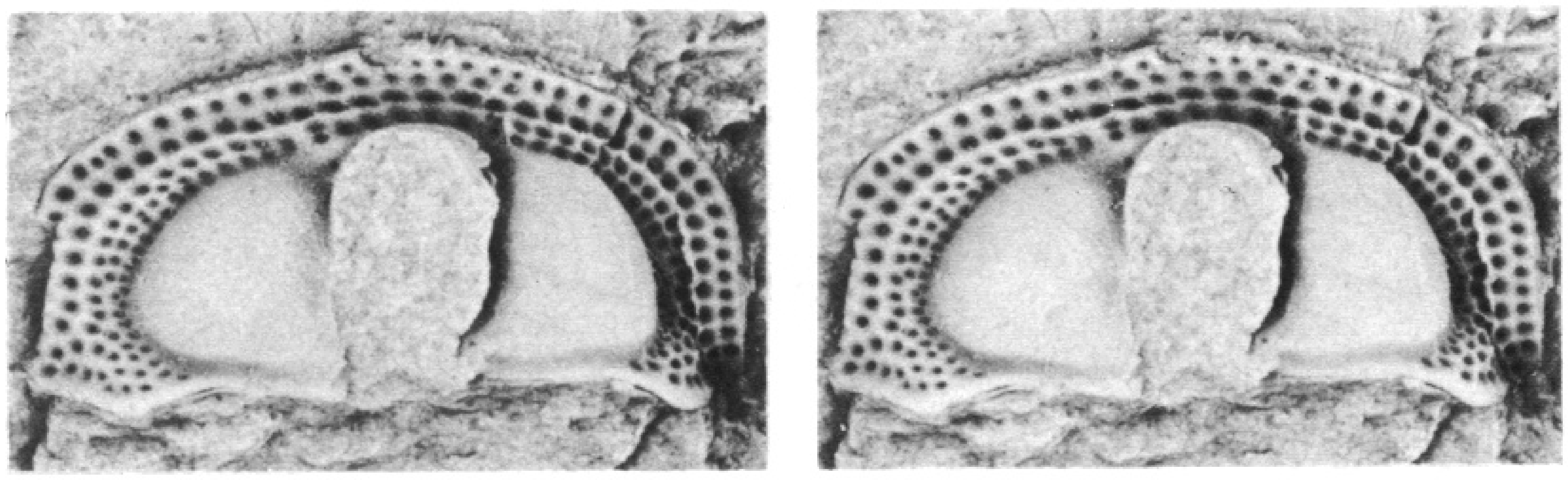

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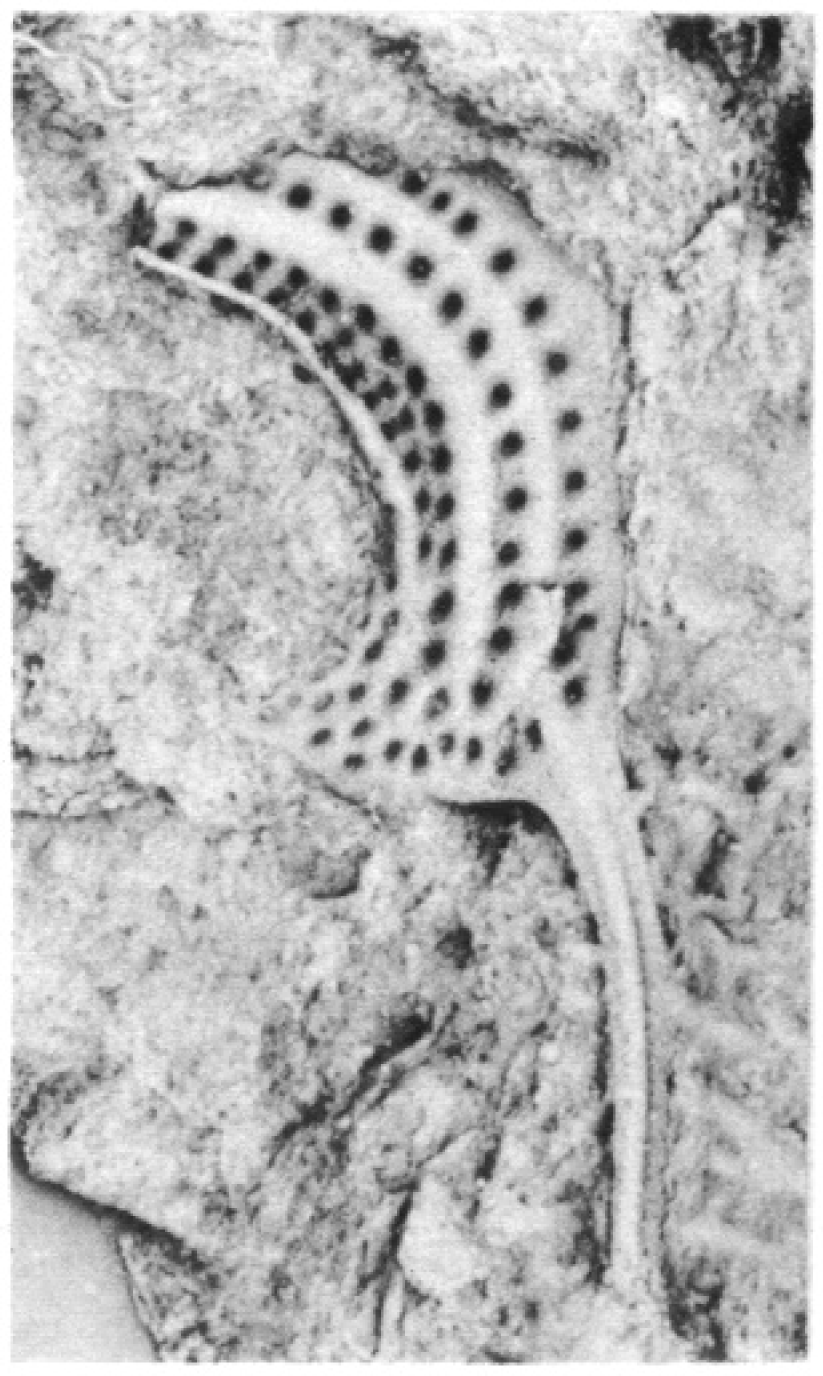

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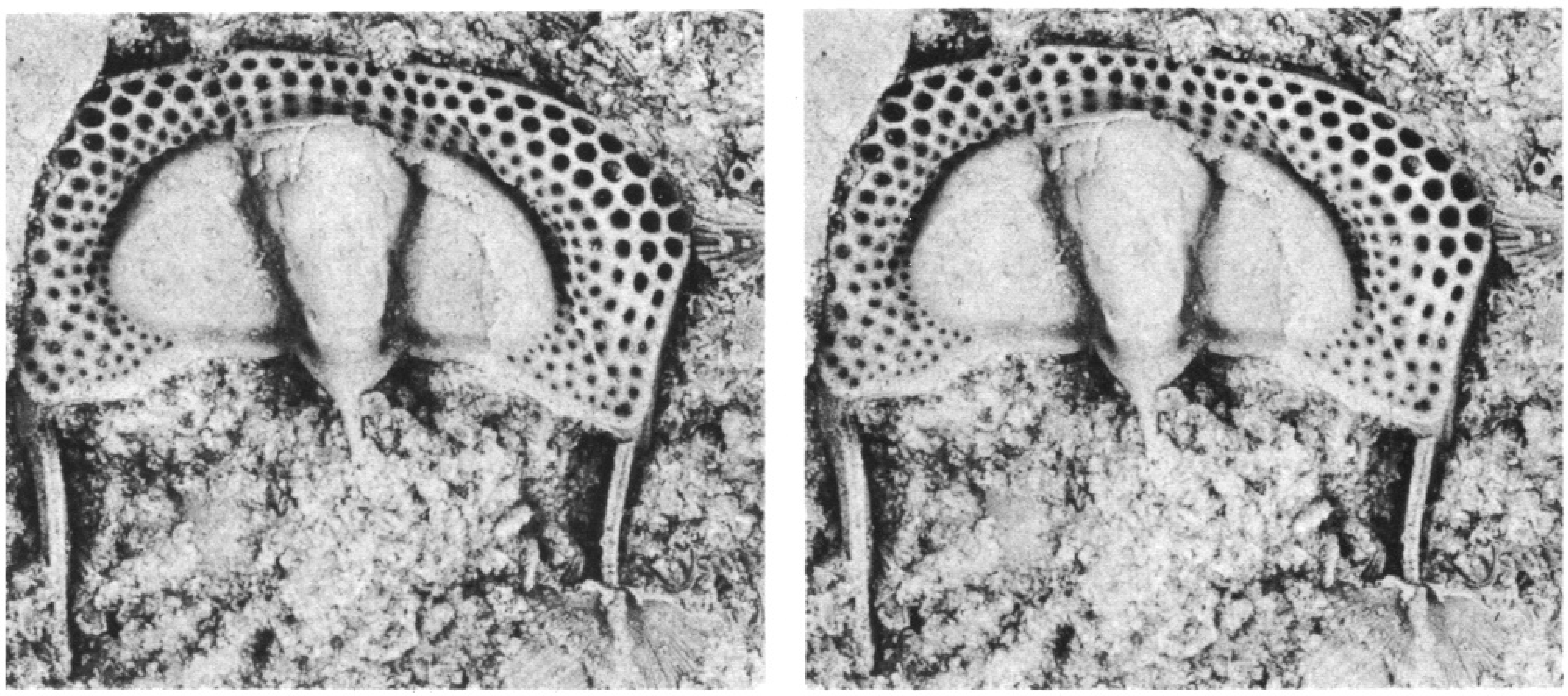

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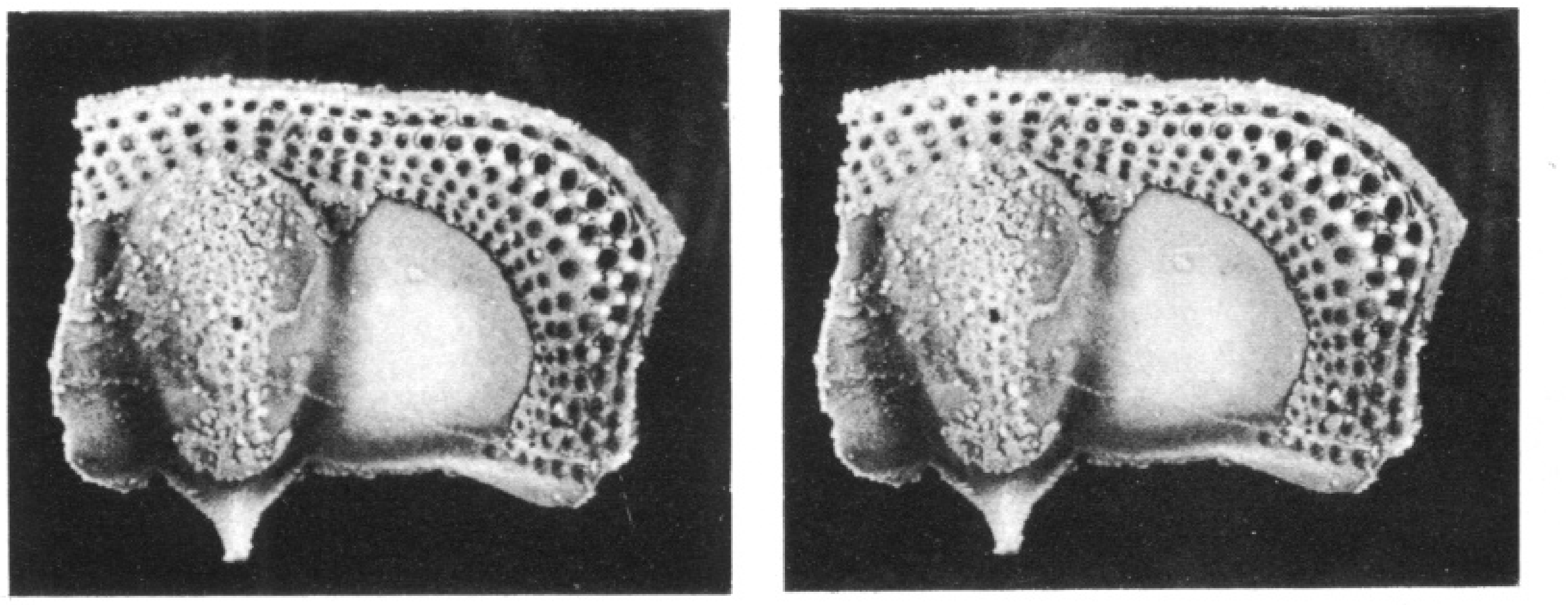
FIGURES 81–89. For description see opposite.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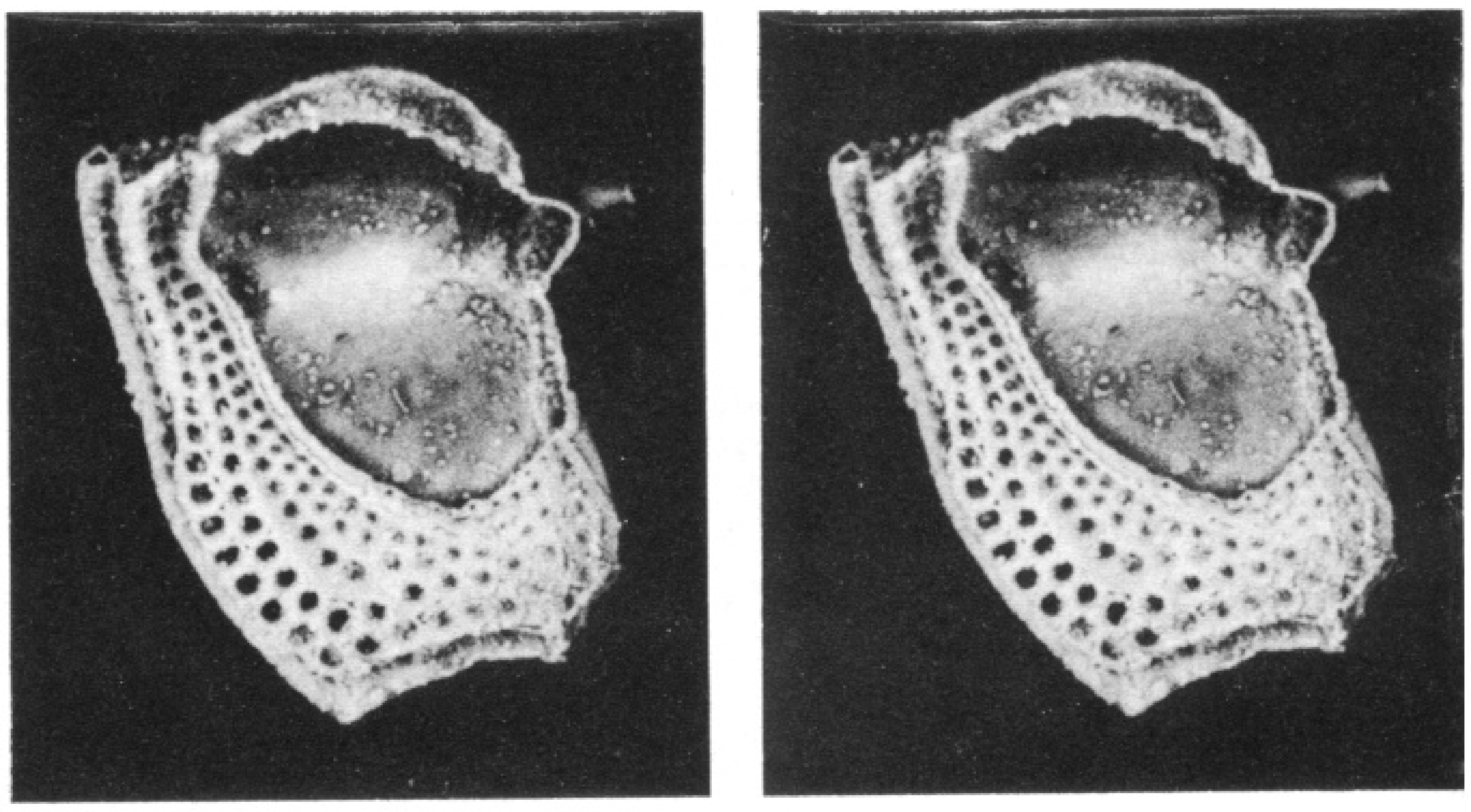
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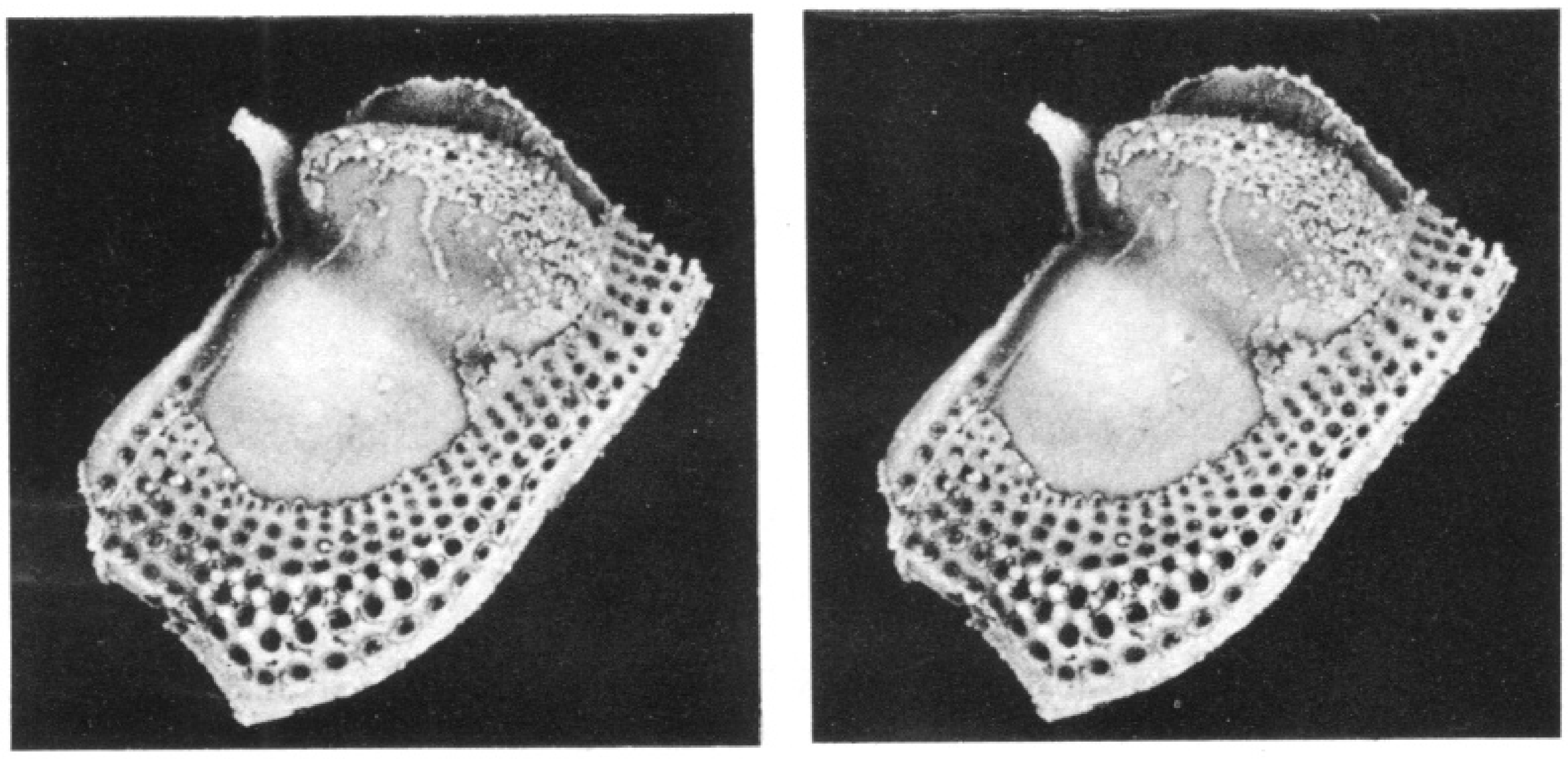
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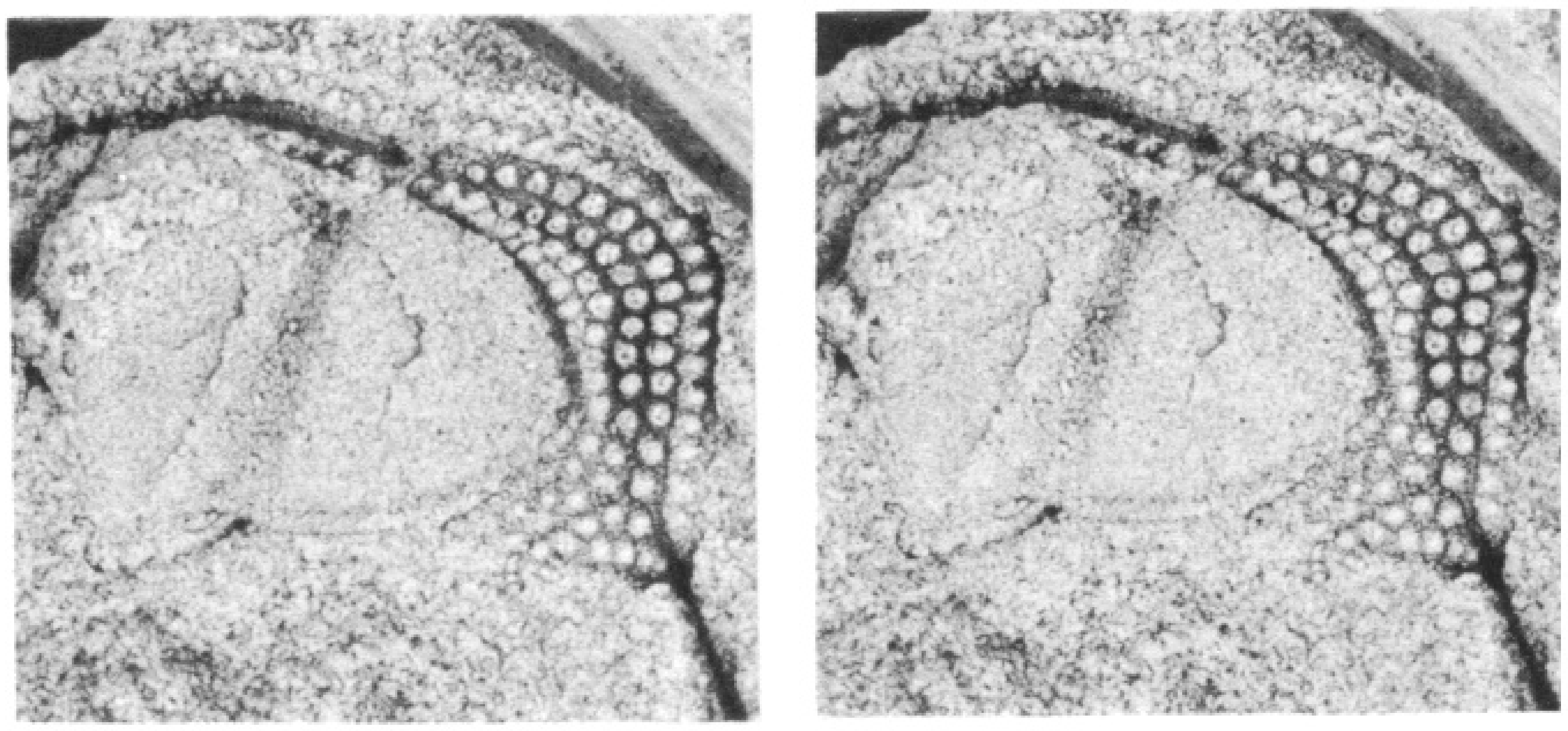
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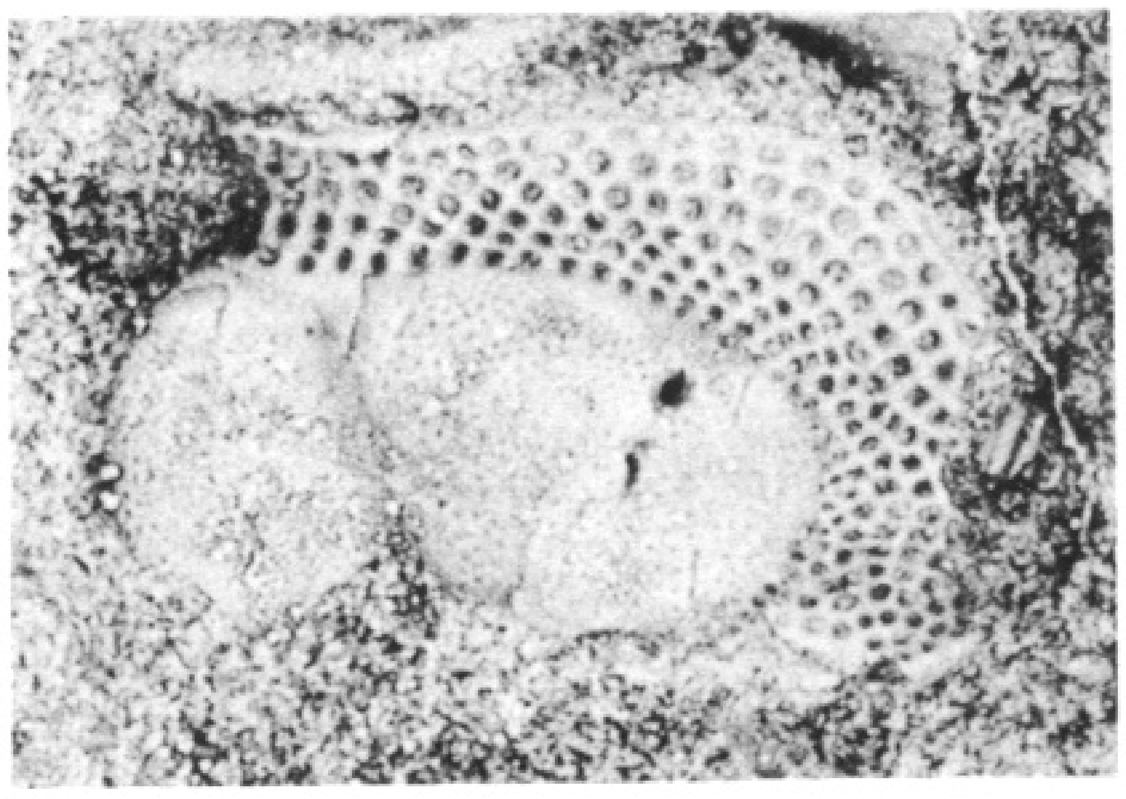
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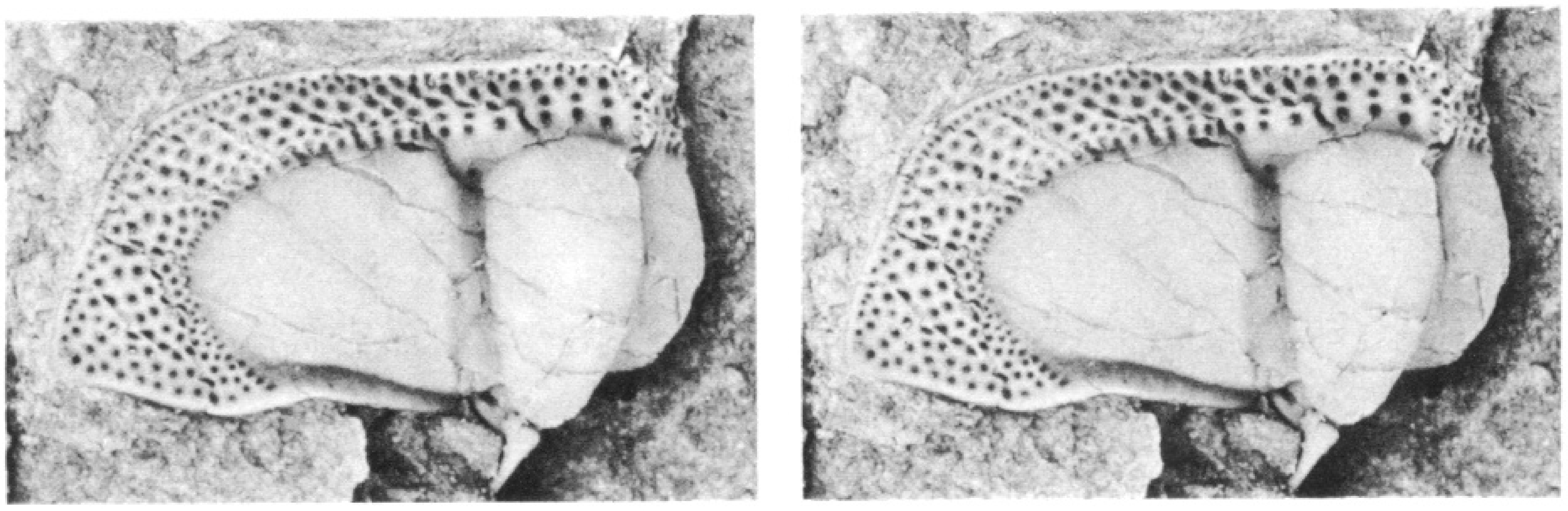
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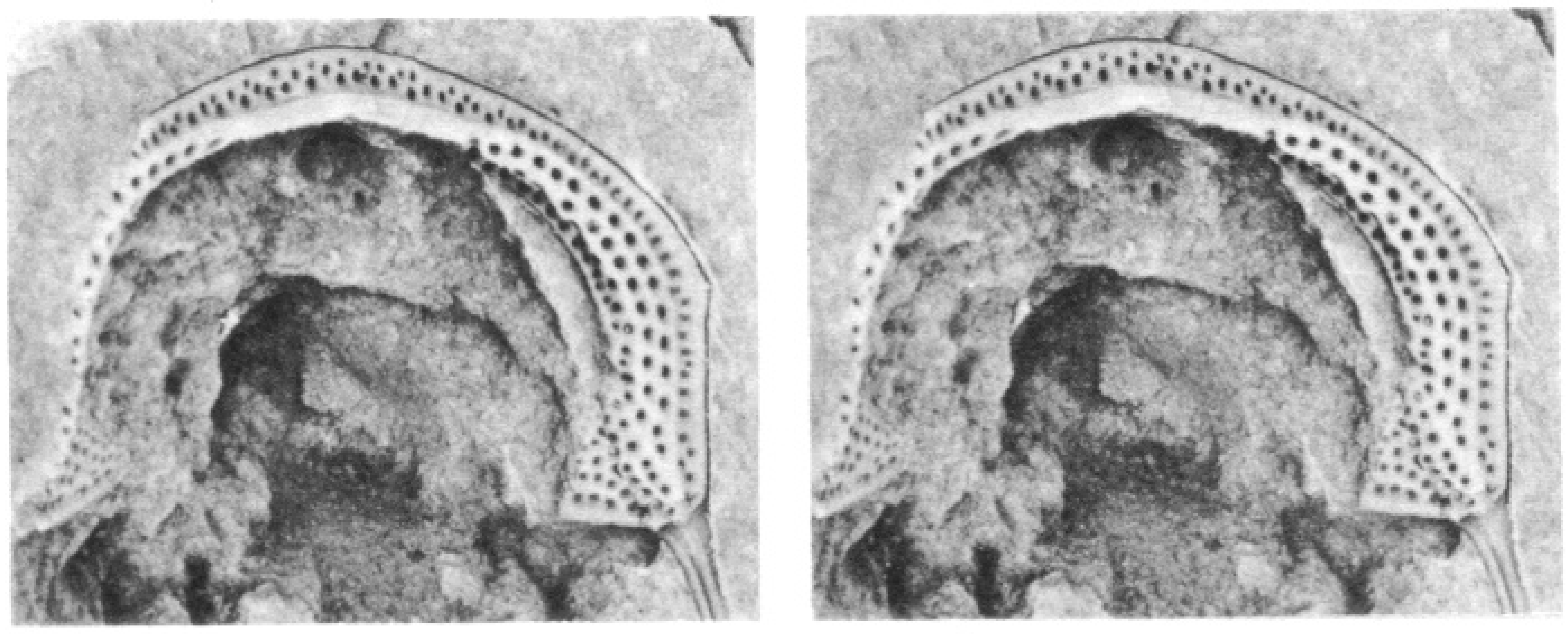
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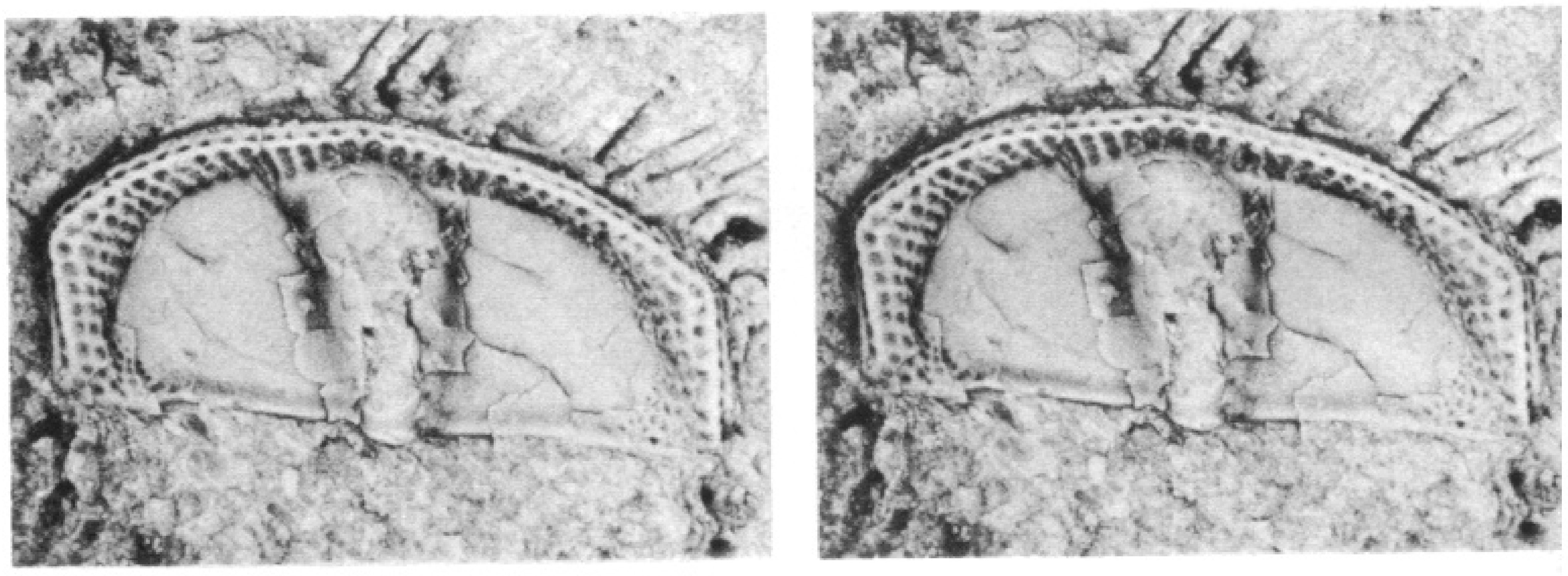
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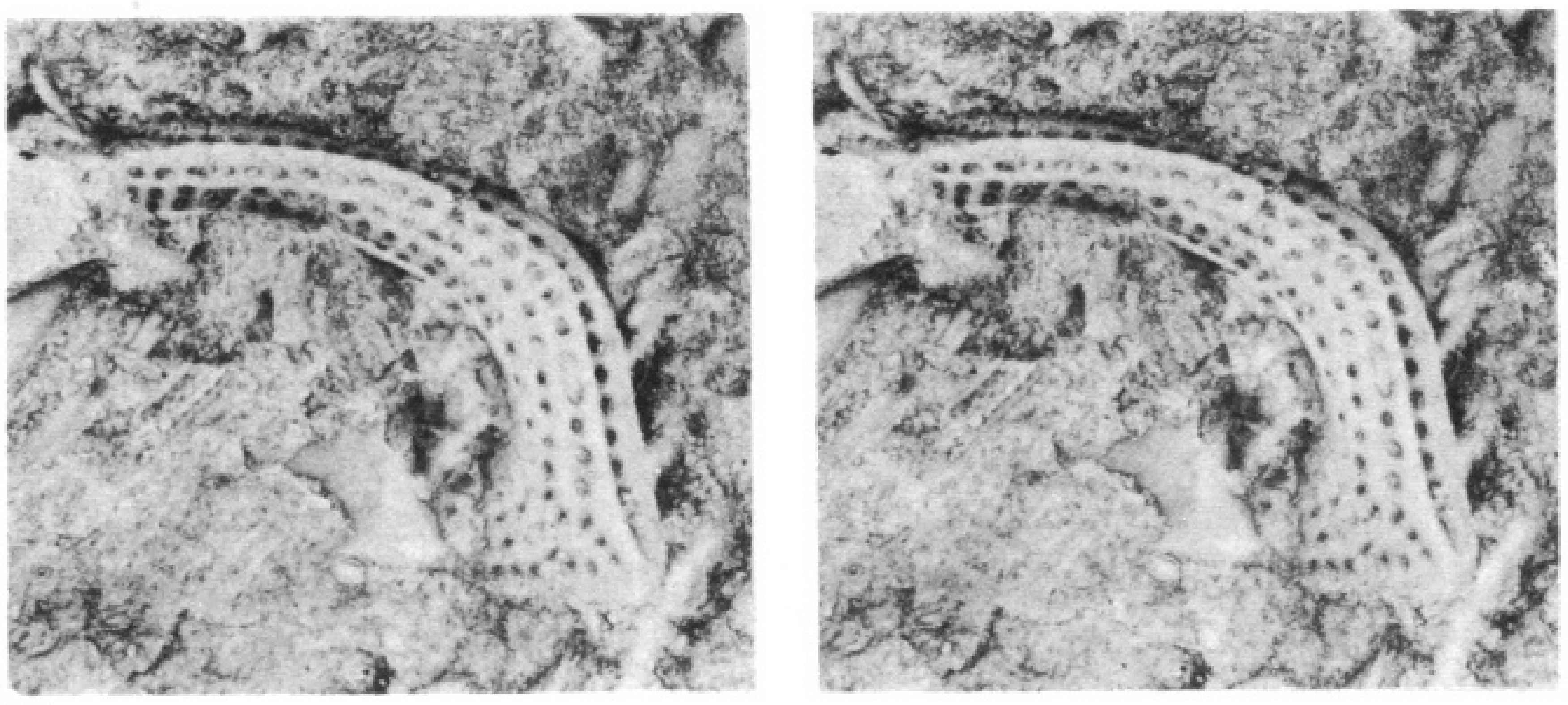
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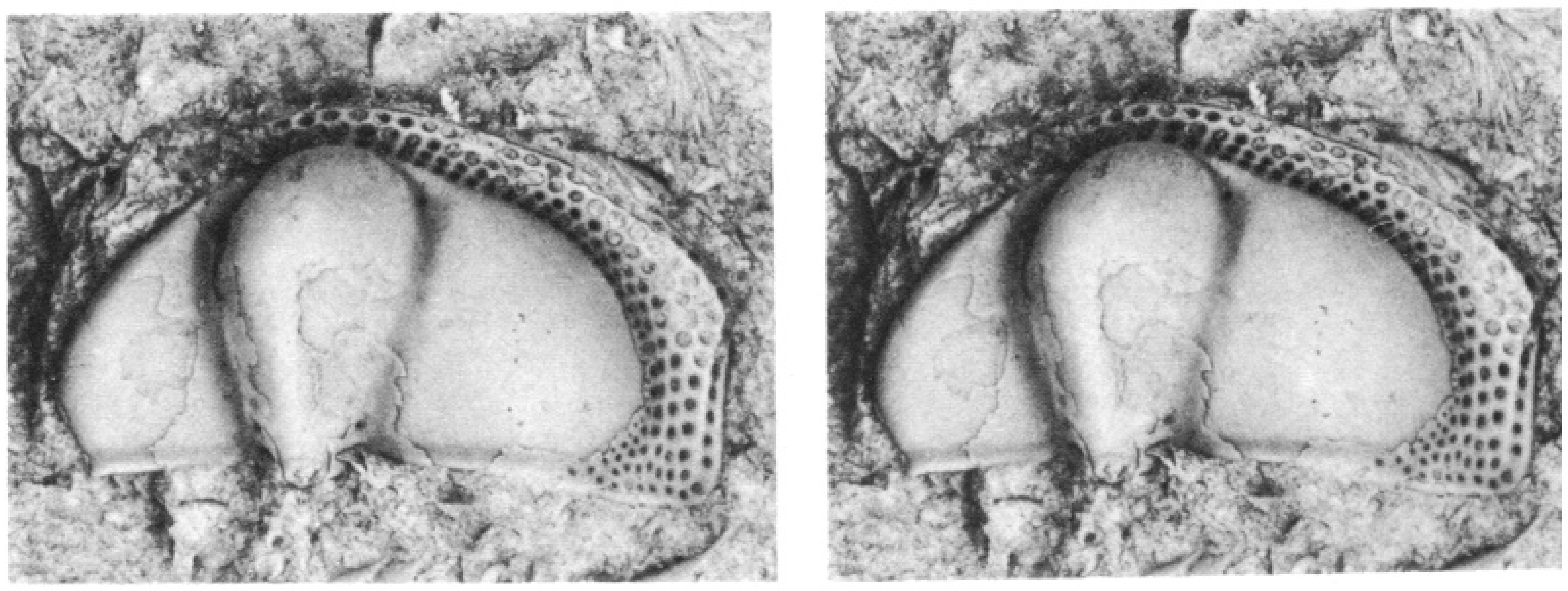
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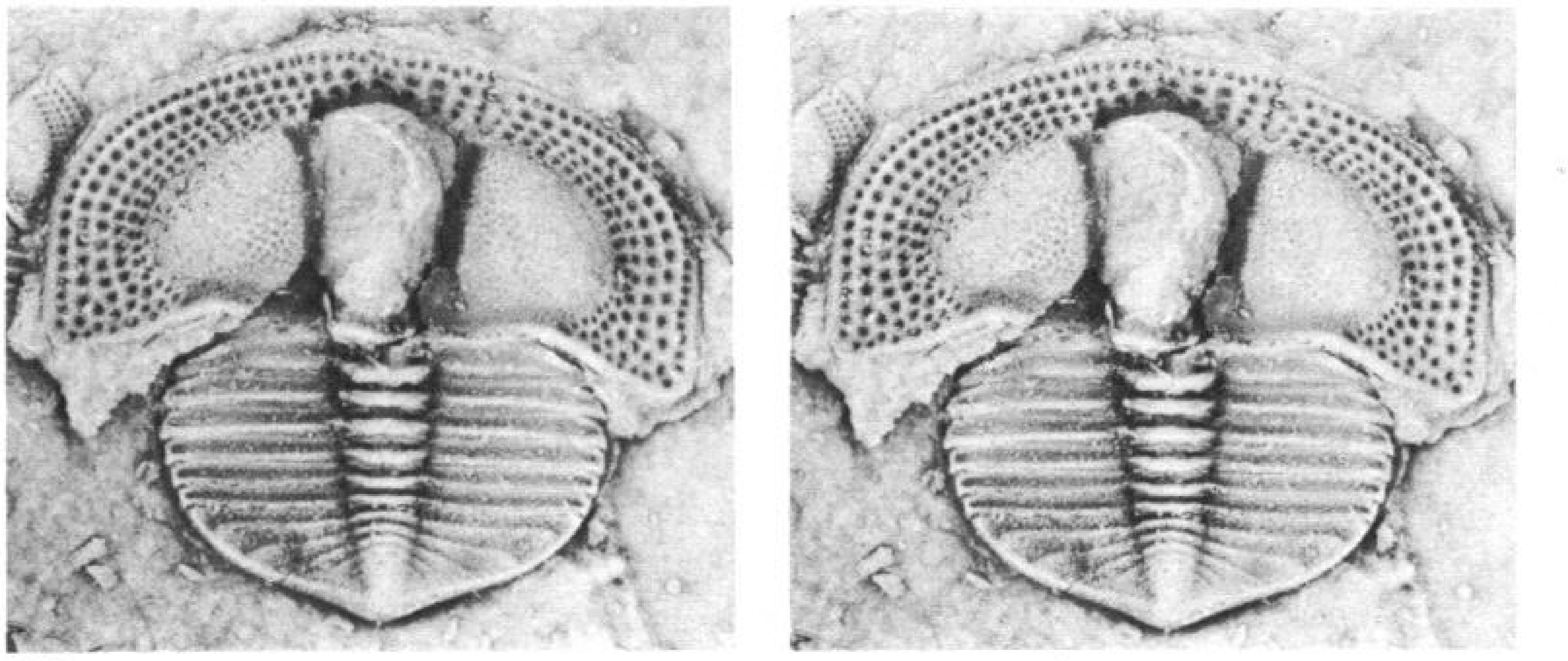
Figures 90–99. For description see opposite.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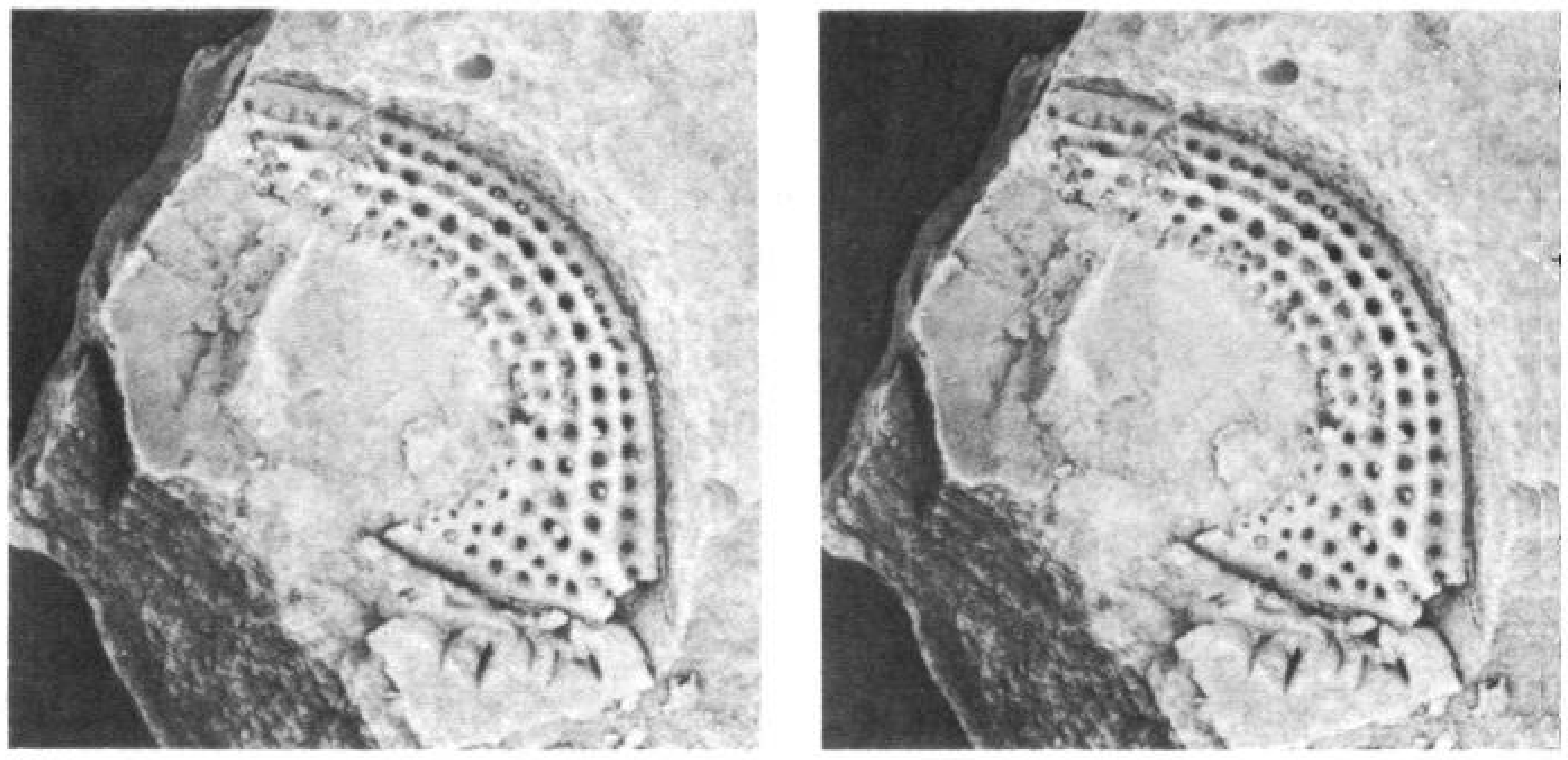
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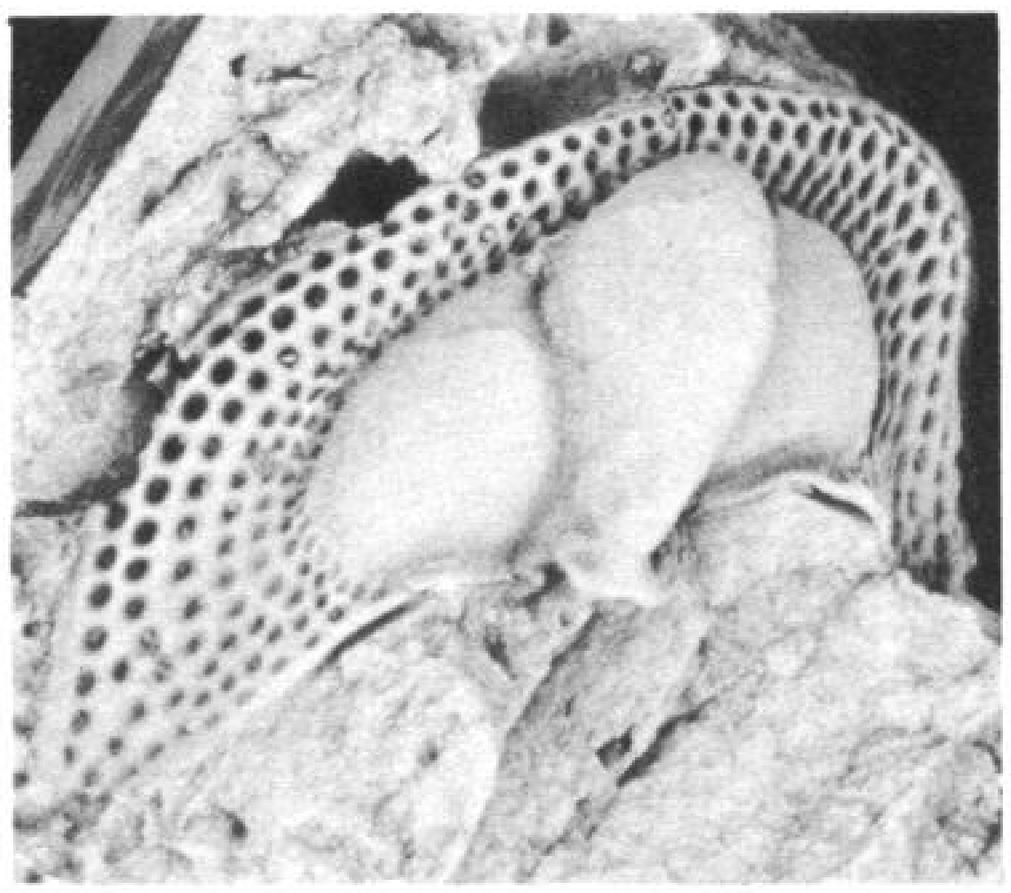
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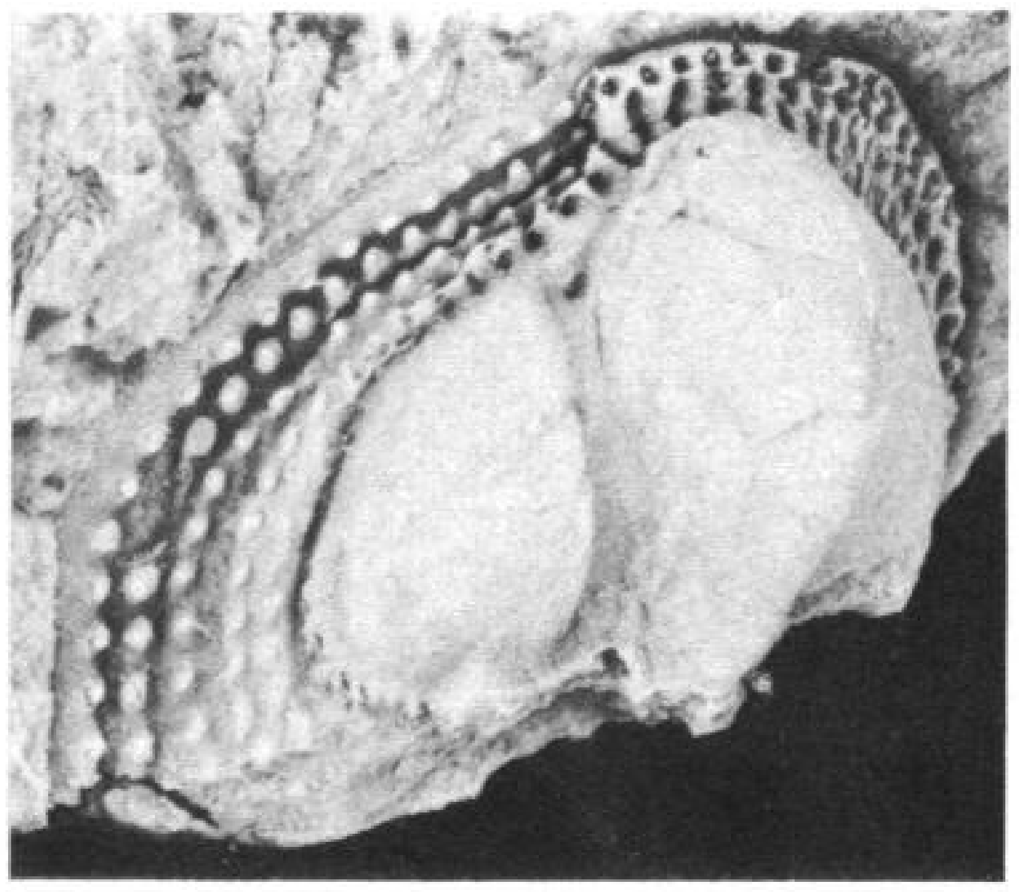
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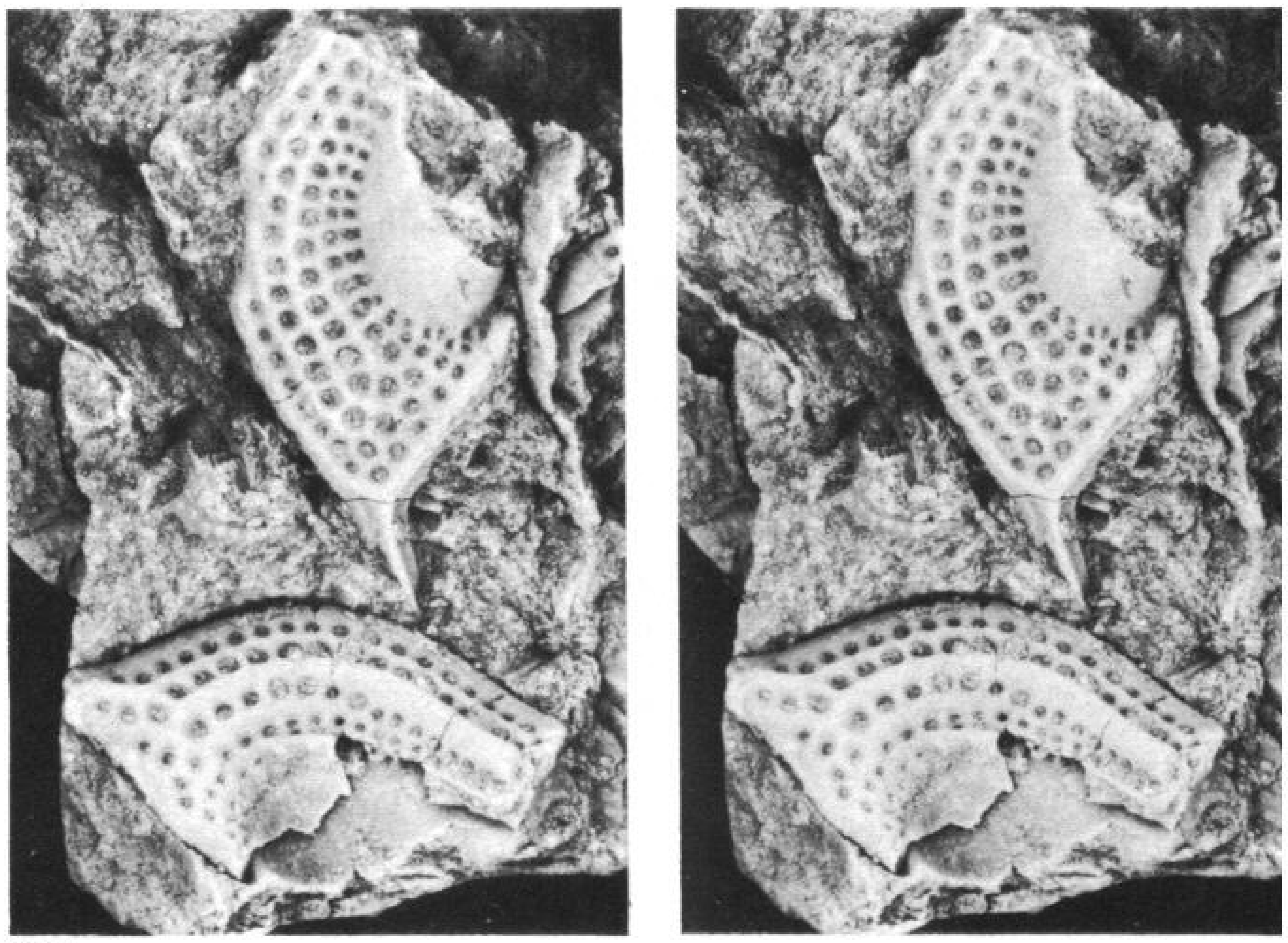
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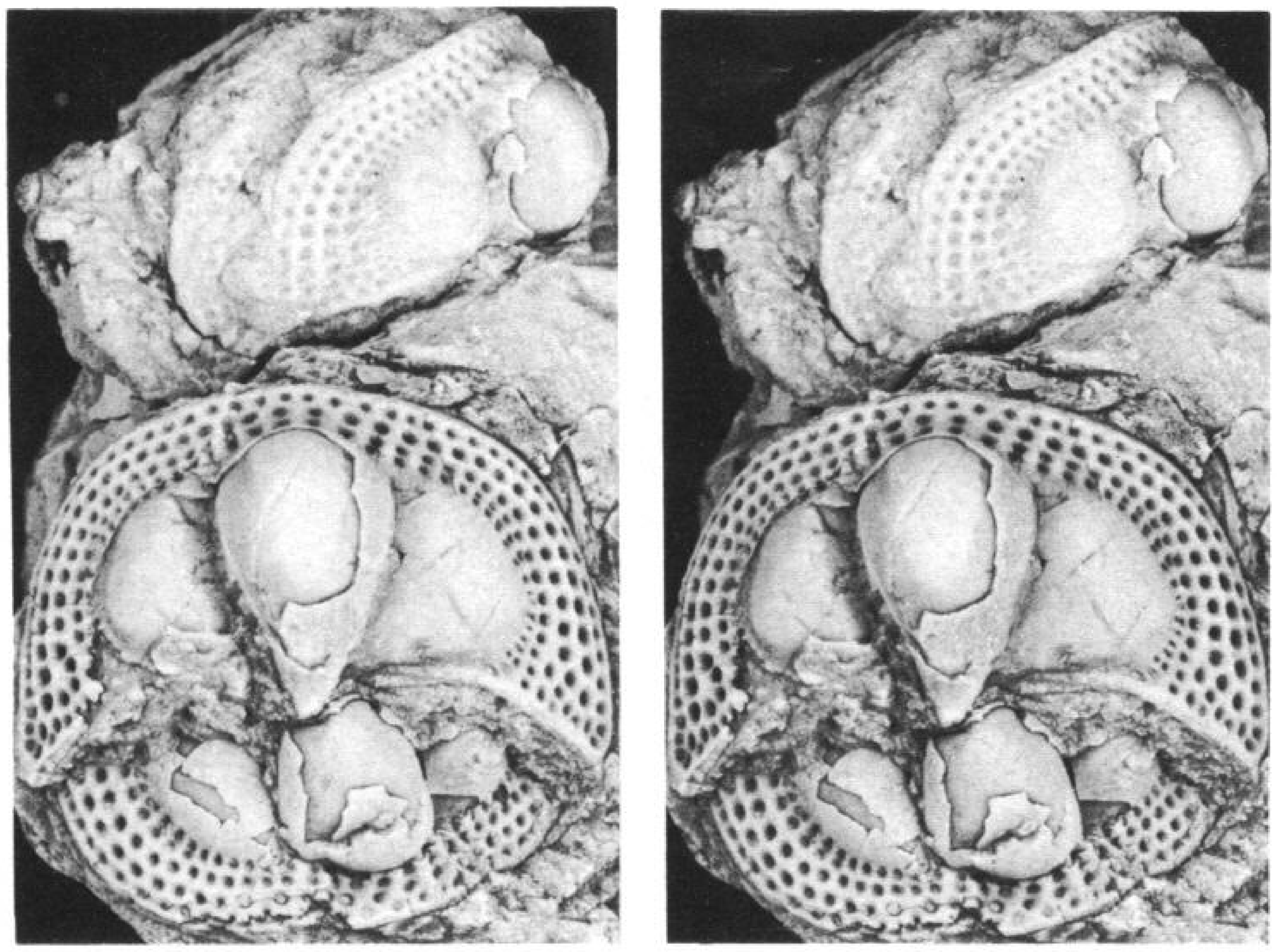
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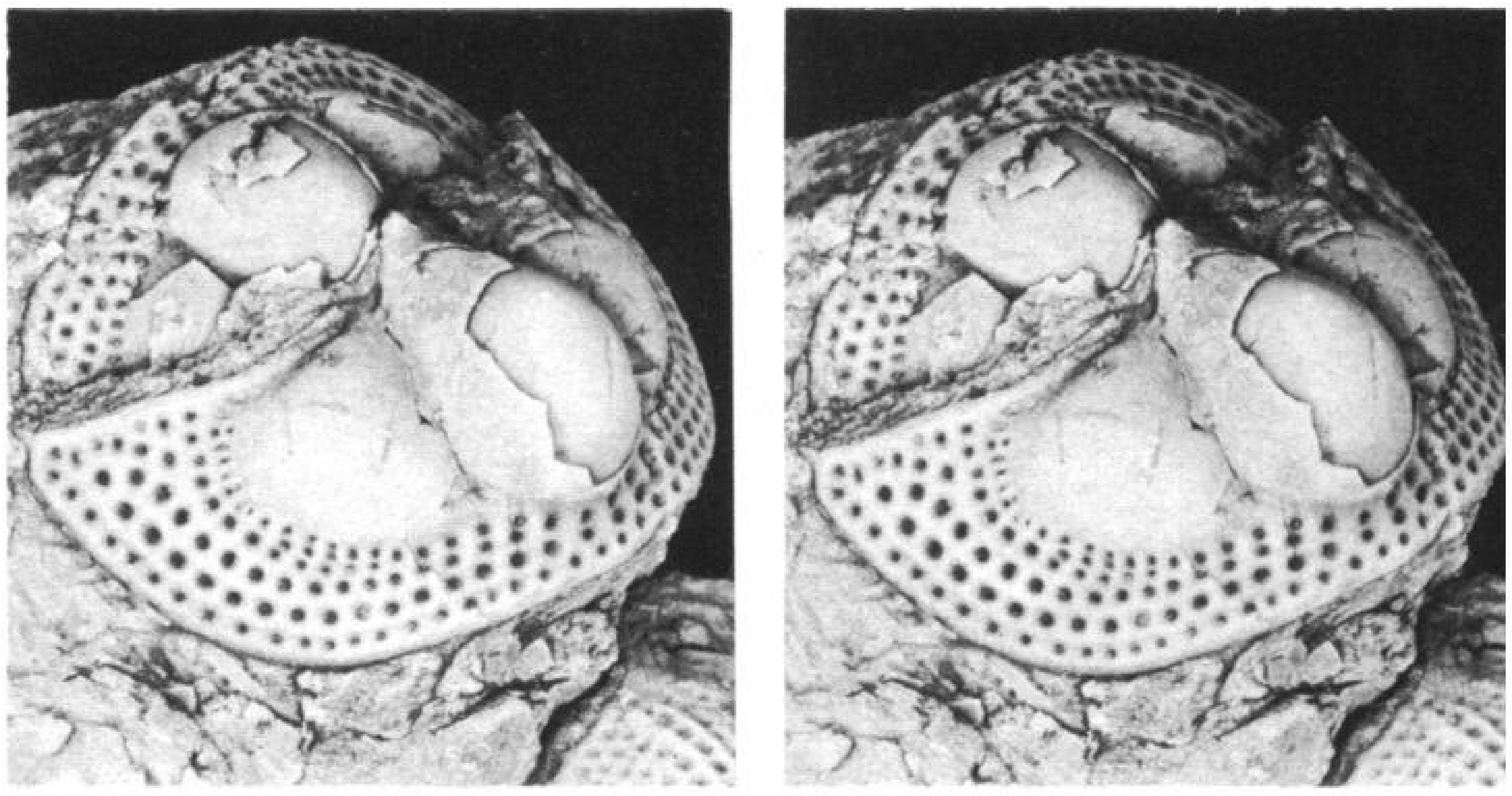
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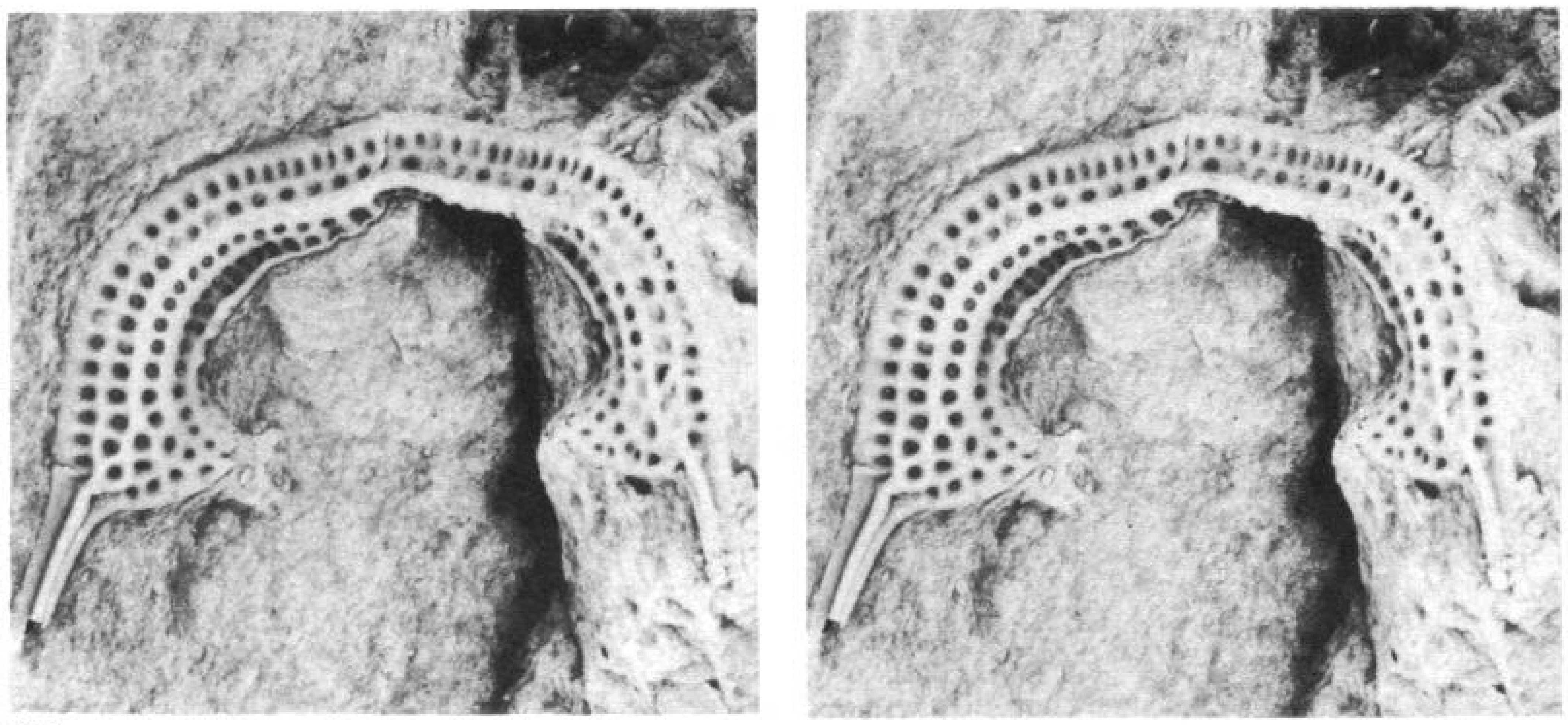
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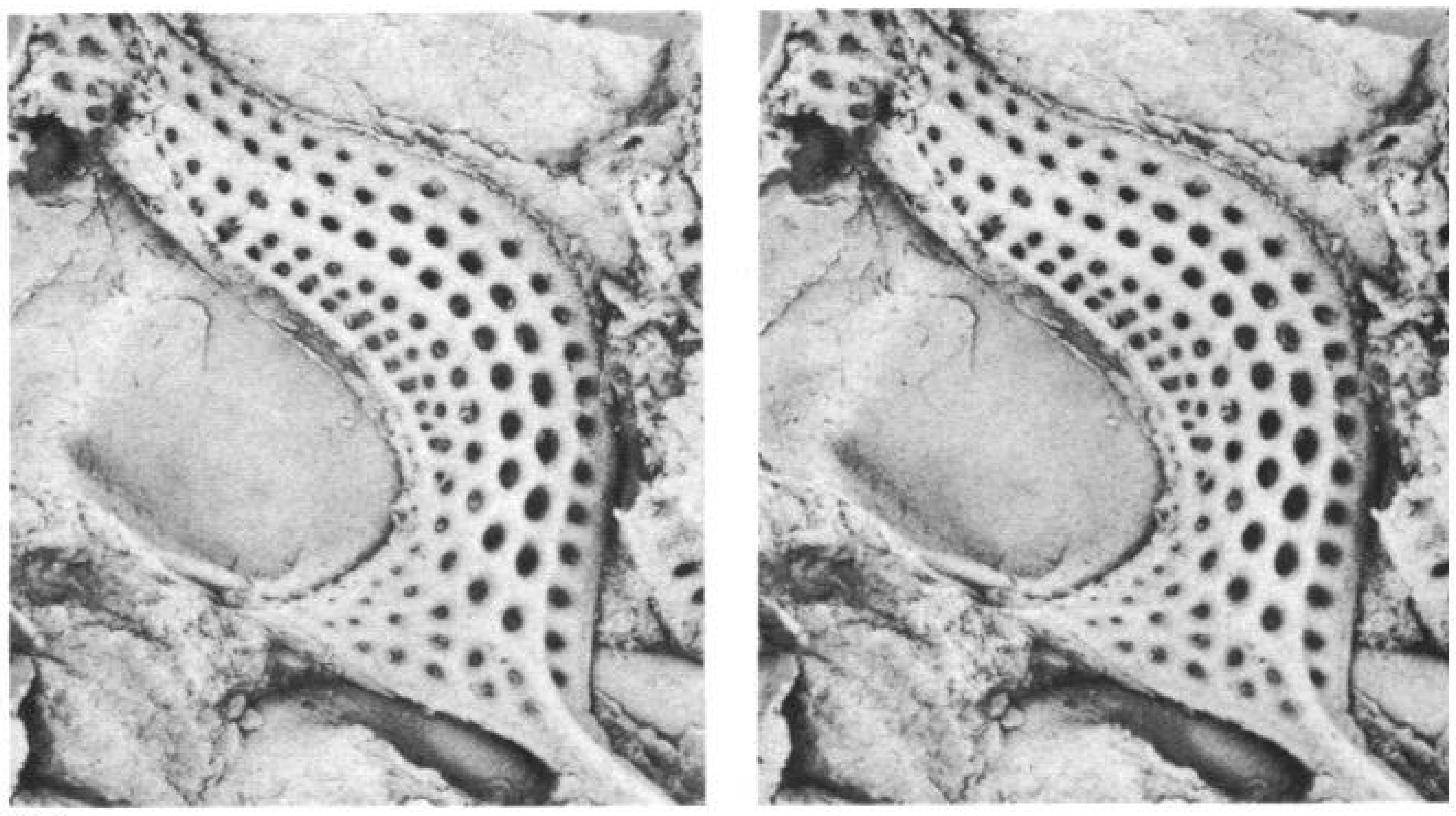
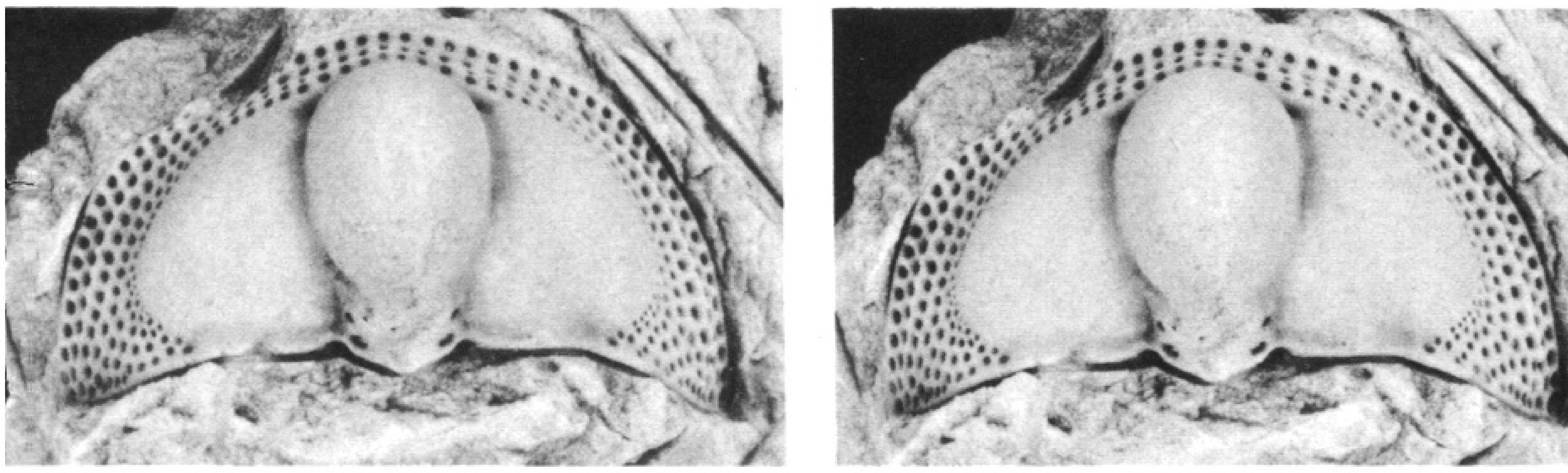

108

Figures 100–108. For description see opposite.



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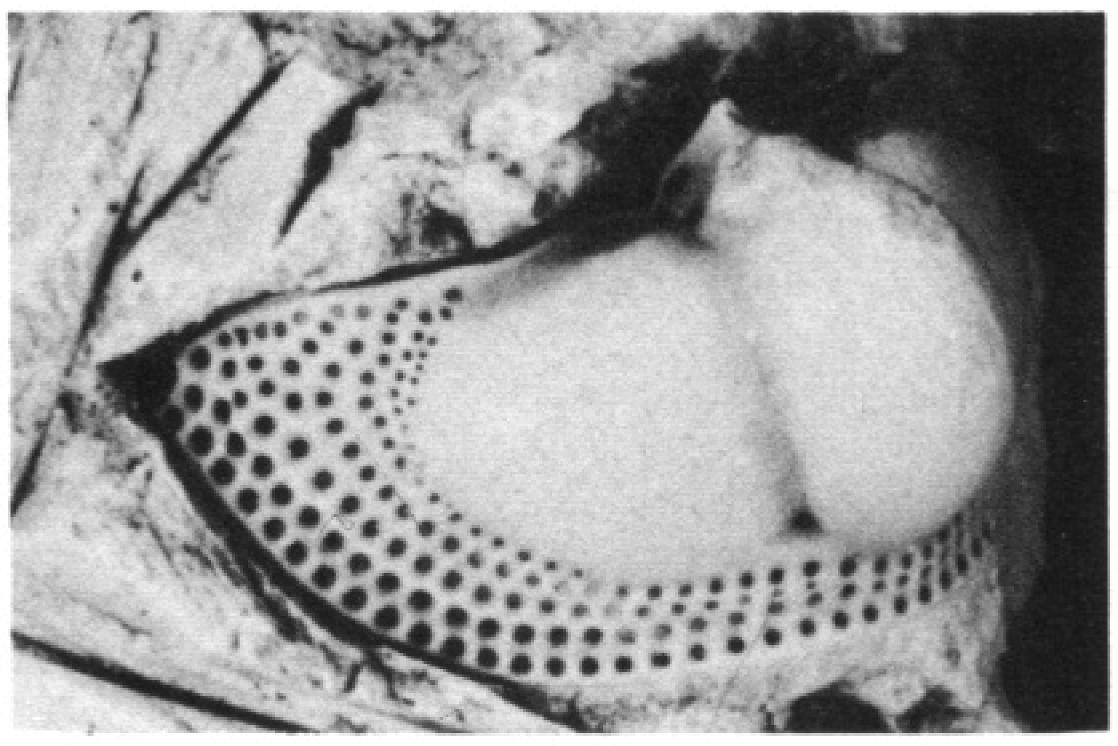

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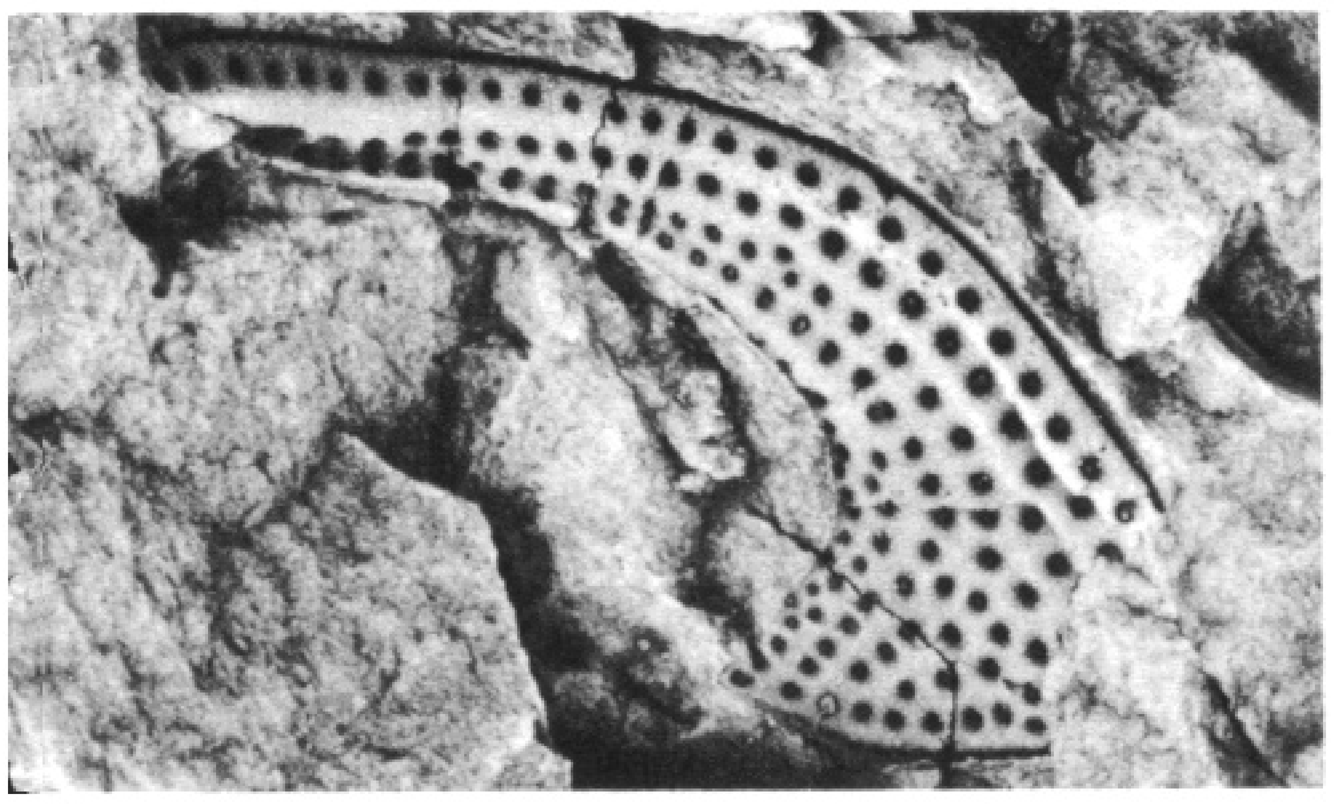

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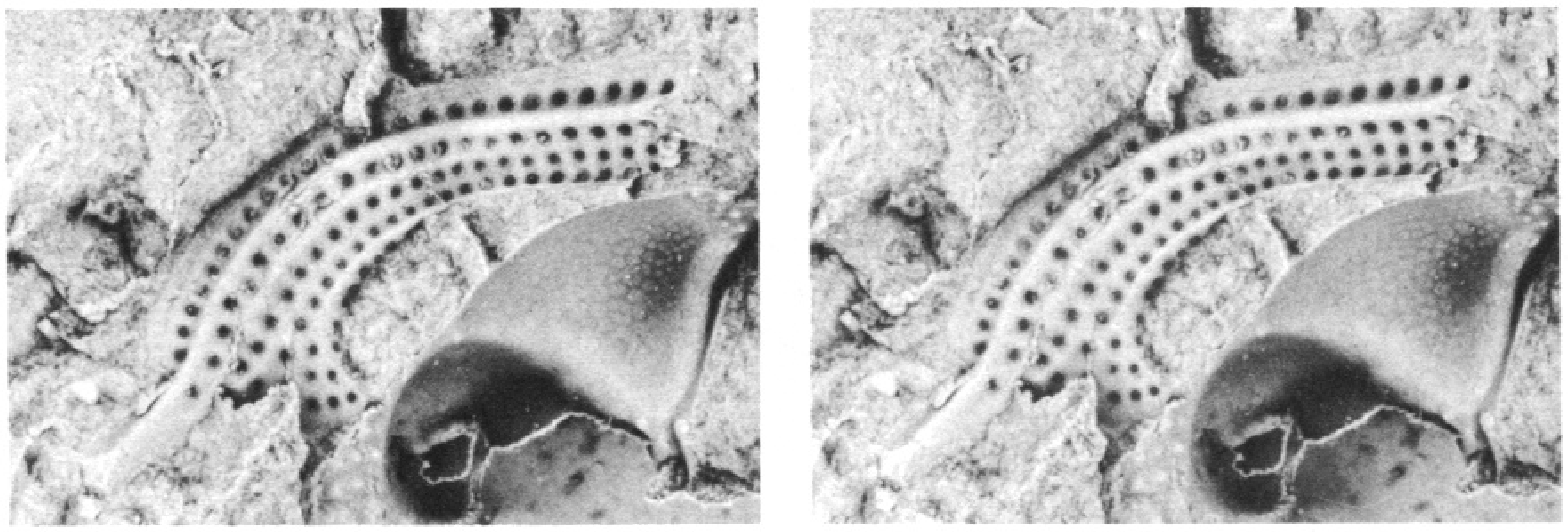

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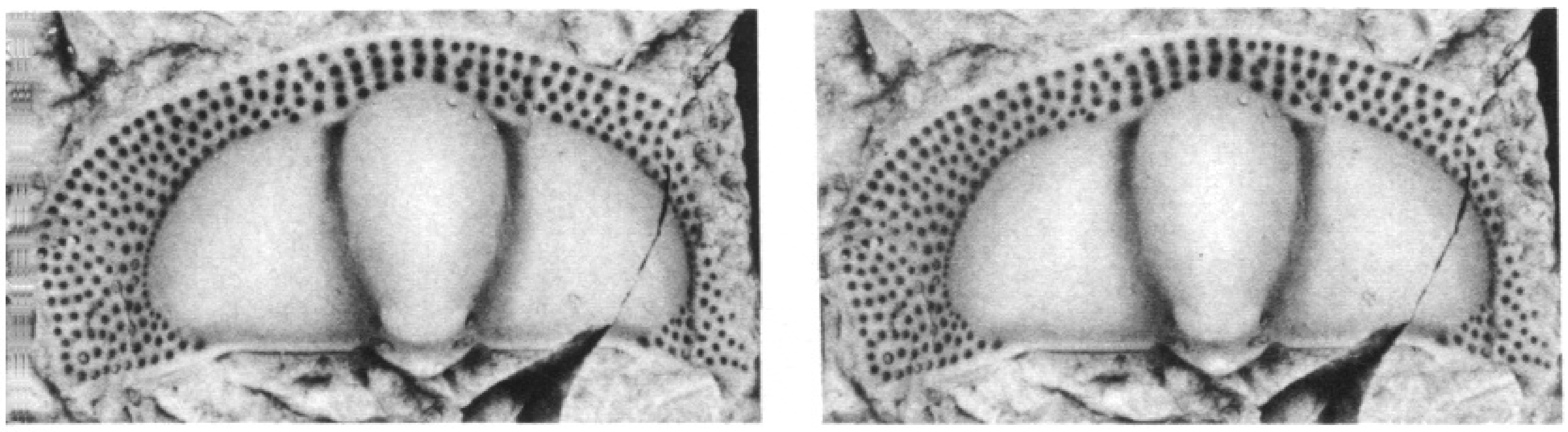

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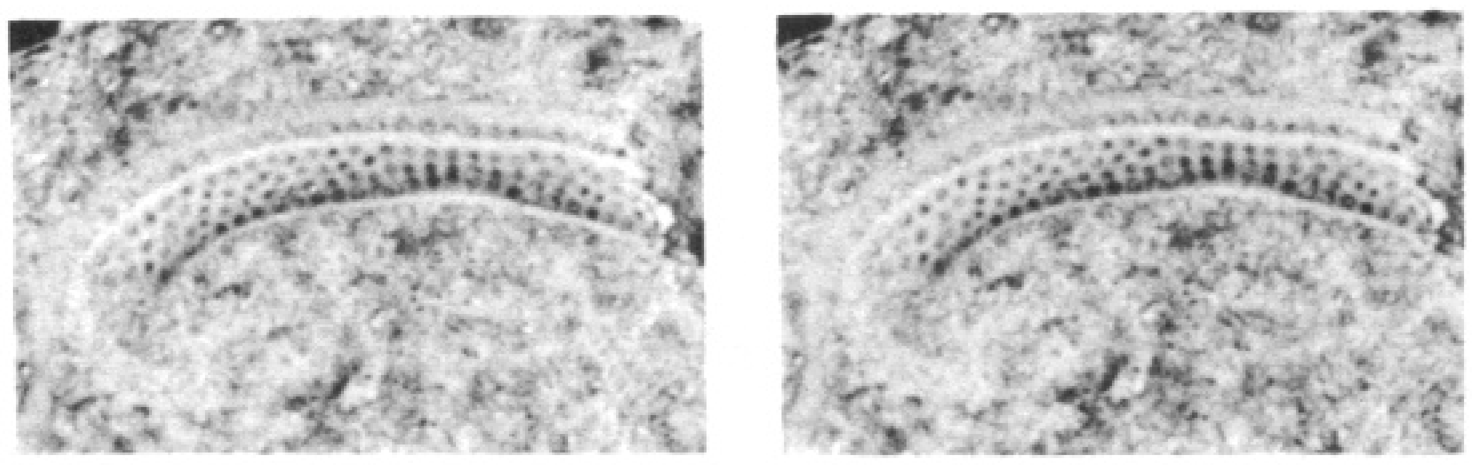

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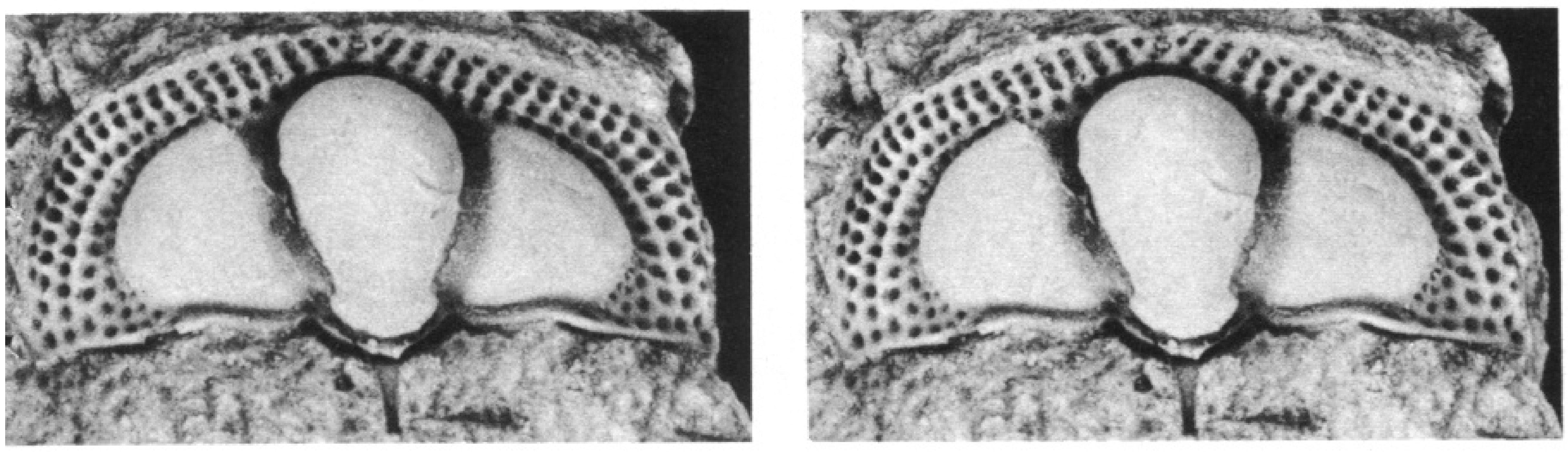

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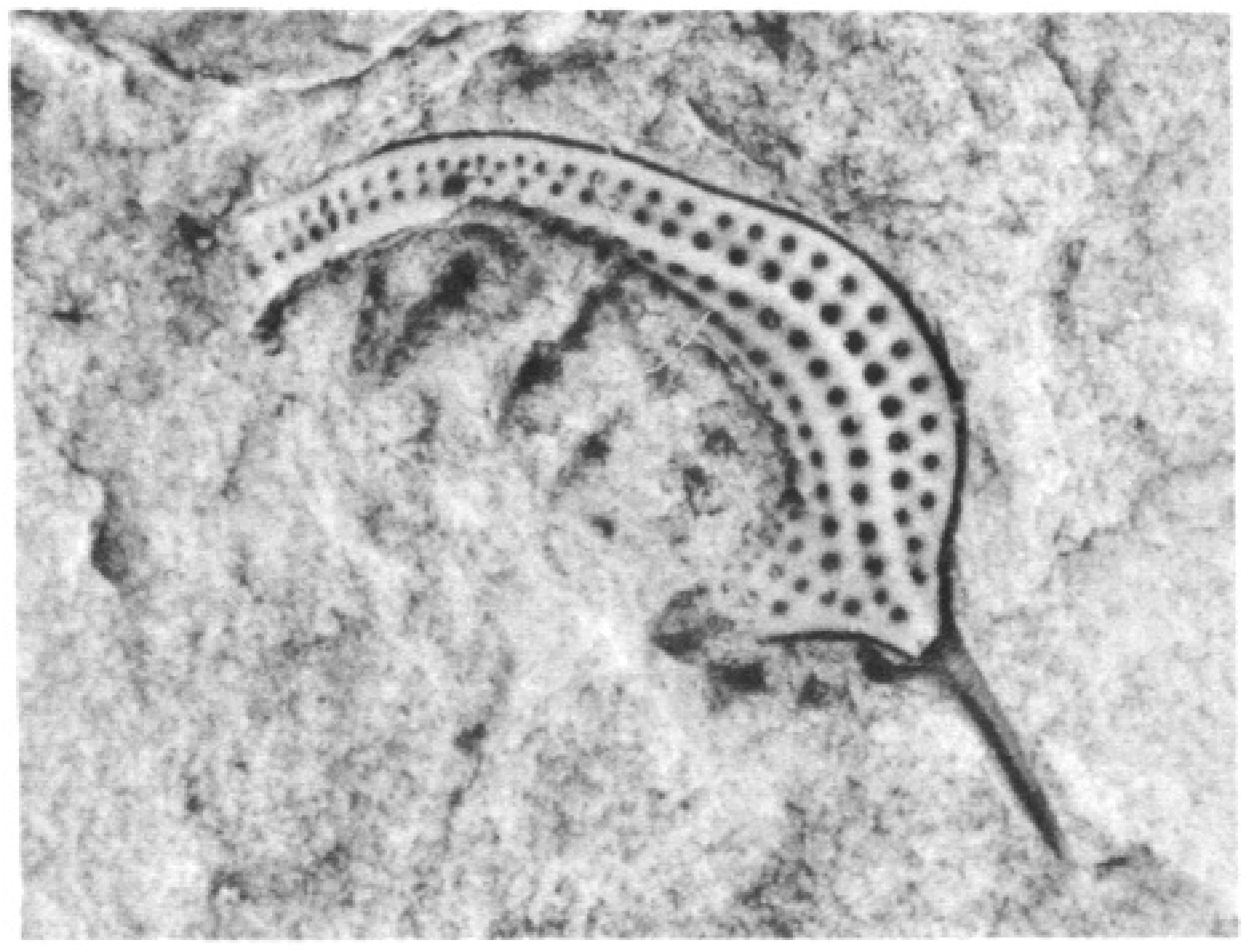

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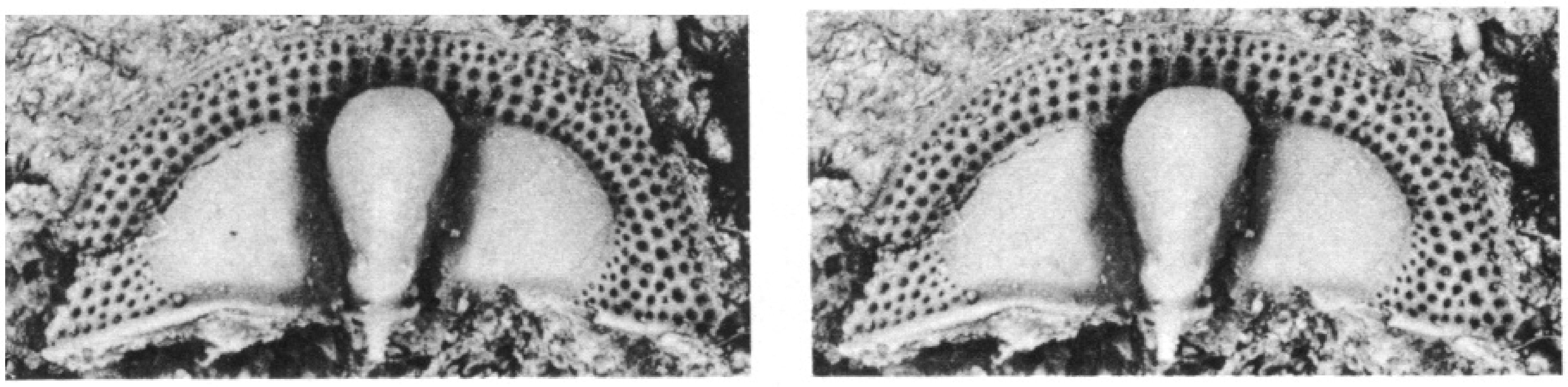

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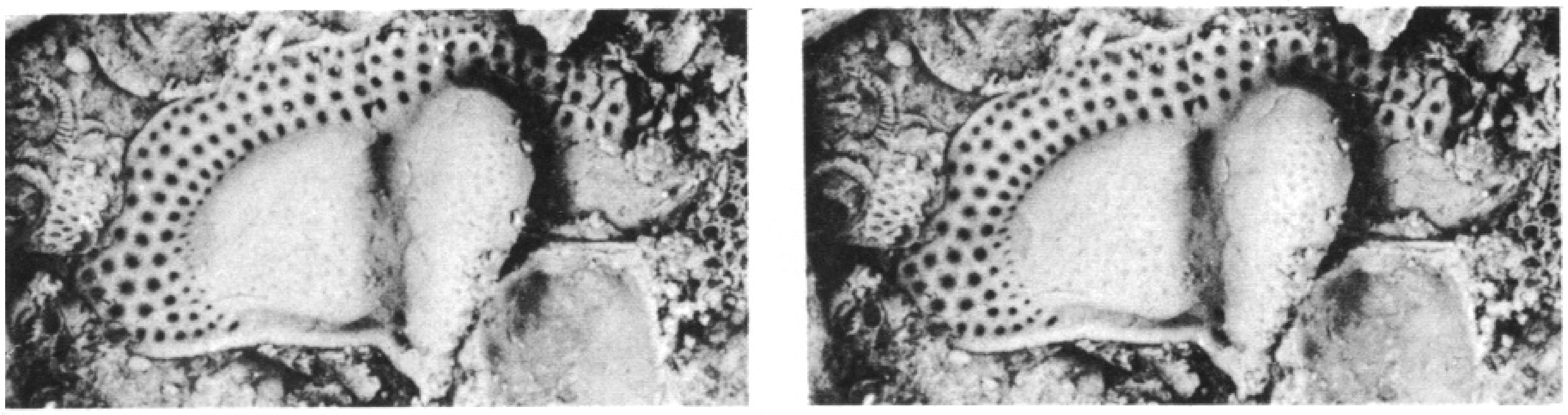

118

119

FIGURES 109–119. For description see opposite.