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CLASSIFICATION AND PHYLOGENY OF THE TRILOBITE ORDER LICHIDA

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[Plates 1–16]

CONTENTS

The Lichida (informal lichide) comprises two families: the Lichidae (informal lichid) and Lichakephalidae (= Eoacidaspididae). A new interpretation of lichide glabellar morphology is given, based on ontogenetic data and comparative morphology of holaspides. No occipital lobe is developed but, in front of the occipital ring, L1 is divided into subsidiary lobes L1a and L1b. The large (bullar) lobe typically lying anterior to L1b originates from L2 fairly early in ontogeny and later expands forwards, apparently incorporating more anterior parts of the glabella as it does so. L1a, L1b and the bullar lobes may be variously fused with each other or with the fixigena. The Lichakephalidae certainly includes 4 genera, 2 further genera (1 new)

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being included there with reservation, whereas 43 genera and subgenera (5 new) are recognized within the five subfamilies of the Lichidae. New diagnoses are given for all these taxa with a summary of their geographical and stratigraphical distribution and lists of the species included in each genus. The phylogeny of the Lichida is discussed and cladograms summarize the relationships of genera within each subfamily. The Lichida may be related to the Odontopleurida and may also have more distant affinities with the Scutelluina.

1. INTRODUCTION

Lichida are among the most distinctive of trilobites because of their unusual glabellar morphology, their typically tuberculate and spinose exoskeleton, and the considerable size attained by certain species. This distinctive morphology has perhaps been overweighted in adducing relationships and has thus exaggerated their degree of taxonomic isolation from other trilobites; the group being accorded ordinal status by Moore (1959) and this ascription has been followed by subsequent authors. Particular taxonomic difficulties arise because not only does convergence seem to have been an important process in lichide evolution but many species are rare and occur in only a fragmentary condition. The majority of type species, moreover, have not been described since the 19th century and have a limited geographical distribution; these factors increase the problems involved in studying the group.

The account that follows is intended as the basis for a revision of the Lichida for the second edition of the *Treatise on invertebrate paleontology*. We hope that its publication here will stimulate informed criticism and thereby will lead to improvements in our proposed classification. Our revision is based mainly on examination of the type material of type species, where this has been available, and a study of the literature. We have only in a minority of cases been able to refer to type or topotype material of other species.

Terminology employed here is essentially that of Harrington *et al.* (in Moore 1959, p. O117). In contrast to their views, however, we take the glabella to include the occipital ring. The glabellar structure of lichides is complex and fully discussed separately in §4. Where appropriate, glabellar lobes and furrows are identified by L1, S1, etc., numbering forwards from the back of the glabella. The term 'longitudinal furrow' is used entirely descriptively to refer to any exsagittal furrow on the glabella without implication as to its origin. In certain places the term 'lateral glabellar lobe' is used for brevity and descriptive convenience in the text. This term may refer to a variety of lobes and should not be taken to imply any particular homology. Our interpretation of lobation in individual subfamilies and genera is given in the diagnosis of those taxa (also see figure 2). 'Subgenal notch' is used to describe the incurved section of the cephalic margin which lies behind the genal spine in such genera as *Radiolichas* (figure 287†). Greek letters are used to signify various positions along the facial suture (figure 2), following the system described by Richter & Richter (1949).

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† Figures 3–358 appear on plates 1–16.

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2. History of classification

The concept of a separate family to include lichid trilobites was introduced by Hawle & Corda (1847), who considered their Lichades to consist of *Lichas* itself and four newly erected genera. Before this, Burmeister (1843) and Emmrich (1844) had placed *Arges* (= *Ceratarges*) in the same family as *Odontopleura*. Although Hawle & Corda did not list *Arges* as belonging to their family, they indicated that some of the species included in that genus by Beyrich (1846) belonged in their view to *Corydocephalus*. The latter also included the species for which Beyrich (1845) erected *Trochurus*, but Hawle & Corda did not regard this genus as a lichid at all, because they erroneously believed that the type species was based not on the pygidium illustrated by Beyrich, but on the cephalon that he associated with it. This cephalon actually belongs to *Staurocephalus murchisoni*. The only other lichid genus mentioned by Hawle & Corda was *Metopias* (= *Metopolichas*) which they regarded as a synonym of *Lichas*. McCoy (1849) apparently considered that Hawle & Corda had overestimated the taxonomic differences between lichids and other trilobites, as he assigned *Lichas* (which he divided into the two subgenera *Trochurus* and *Acanthopyge*) to the subfamily 'Ogyginae', with five other non-lichid genera.

Barrande (1852) accepted Hawle & Corda's family as a 'natural' one, although, as he designated families only by numbers, he did not use their name for the taxon. He assigned all members of the family to *Lichas*, which he divided into three groups. The first group comprised species having pygidia with flattened anterior and posterior pleural bands, the second comprised species with convex posterior pleural bands, and the last group included forms in which only the cephalon was known. The first group was further subdivided according to the presence or absence of a third pair of marginal spines.

Angelin (1854) corrected the name of the family to Lichidae and used the form of the glabellar lobation to classify the Swedish species of *Lichas*, in which he recognized six unnamed subgroups, and the newly erected genus *Platymetopus* (= *Amphilichas*). *Metopias* was considered by Angelin to be a synonym of *Lichas*. In a preliminary classification in the introduction to his unfinished monograph of British trilobites, Salter (1864) listed *Lichas* as the only member of the family Lichadae.

Schmidt (1885) followed Barrande in considering all members of the family to belong to *Lichas*, but among the east Baltic Ordovician species he recognized eight subgenera including *Metopias* (in which he included the type species of *Lichas*) and the newly proposed *Leiolichas*, *Homolichas* and *Oncholichas* (the last having the same type species as the earlier-named *Arctinurus*). The subgenera were defined mainly on glabellar lobation and pygidial characters. *Hoplolichas*, *Conolichas* and *Homolichas* were considered by Schmidt possibly to have been derived from *Metopias* (which included the oldest species known to him), but he regarded it as unlikely that the other subgenera were derived from the same ancestor. Using the same characters as Schmidt, Clarke (1894) classified the North American lichids into *Arges*, *Platynotus* (= *Arctinurus*), *Platymetopus*, *Ceratolichas*, *Terataspis*, *Hoplolichas* and *Conolichas*, all of which were regarded as subgenera of *Lichas*.

A more comprehensive classification than any previously attempted for the lichids was proposed by Gürich (1901). He recognized the genera *Lichas* and *Arges*, which he assigned to the monotypic subfamilies Lichinae and Argetinae, although the name *Lichas* was also used in a broader sense to include both genera. He distinguished *Arges* from *Lichas* (in his narrower sense) mainly on pygidial characters, including the strongly convex posterior pleural bands, the well-defined axial terminus, and the raised postaxial ridge. On the basis of glabellar lobation, *Lichas* and *Arges* were divided into subgenera; many of these were designated by new names but only *Platylichas*, *Echinolichas*, *Hemiarges* and *Craspedarges* represented taxa not previously proposed by other authors. Gürich was the first author to discuss the evolutionary relationships of lichids in any detail. Within his Lichinae, he considered that *Metopolichas* and *Platopolichas* (= *Uralichas*) had evolved from the same ancestor, probably of Cambrian age, whereas *Leiolichas*, *Homolichas* and *Platymetopus* (= *Amphilichas*) had their origins in another common ancestor; these two ancestral forms had in turn been derived from the same root stock. *Platylichas* was regarded as a probable descendent of *Platopolichas*, and a form intermediate between these genera was considered to have given rise to the Argetinae in the early Ordovician. Gürich seems to have been uncertain about the phylogenetic position of *Craspedarges*.

Table 1. Summary of the history of classification of the Lichida

Hawle & Corda		Barrande		Angelin	Schmidt		Gürich
Lichades		Famille VII		Lichidae	Lichidae		Lichidae
Lichas		Group 1		Group 1	*L.* (*Arges*)		Lichinae
				Group 2	*L.* (*Platymetopus*)		
Acanthopyge					*L.* (*Metopolichas*)	*Lichas*	14 subgenera
				Group 3	*L.* (*Hoplolichas*)		
Corydocephalus	*Lichas*	Group 2	*Lichas*	Group 4	*L.* (*Conolichas*)		Argetinae
					L. (*Leiolichas*)		
Dicranogmus				Group 5	*L.* (*Homolichas*)	*Arges*	6 subgenera
				Group 6	*L.* (*Oncholichas*)		
Dicranopetis		Group 3		*Platymetopus*			

Reed	Phleger	Warburg	Tripp
Lichadidae	Lichadacea	Lichidae	Lichida
	Lichadinae (5 genera)	*Lichas*	Lichidae
Deuterolichas	Echinolichadinae (7 genera)	*Conolichas*	
(8 subgenera)	Homolichadinae (8 genera)	*Hoplolichas*	Lichinae (10 genera)
	Tetralichadinae (6 genera)	*Platylichas*	Homolichinae (3 genera)
	Trochuridae	*Dicranopeltis*	
	Trochurinae (8 genera)	*Leiolichas*	Tetralichinae (2 genera)
Protolichas	Euarginae (7 genera)	*Amphilichas*	Ceratarginae (9 genera)
(8 subgenera)	Dicranopeltinae (3 genera)	*Trochurus*	
	Platylichadinae (4 genera)	*Dicranogmus*	Lichakephalidae

Reed (1902) recognized two major groups of lichids, the first having a glabella with a bicomposite lobe in front of L1 (although he considered L1 to be secondarily lost in some forms), and the second with a tricomposite lobe formed by the fusion of the bullar lobe with L1 (see §4 for discussion of glabellar terminology). He accorded these groups generic status, proposing for them the names *Protolichas* and *Deuterolichas* respectively. These were each divided into eight sections or subgenera, two (*Metalichas* and *Paralichas*) being new; the type species of *Lichas* was assigned to *Metopolichas*, following Schmidt and Gürich. Reed's genera *Protolichas* and *Deuterolichas* have not been recognized by later workers and their identity is uncertain because a type species has not been designated for either of them. Reed (1923) did not use these names himself, but referred all of the subgenera he had previously recognized, together with ten additional ones, to *Lichas*. In this paper he also removed the type species of *Lichas* from *Metopolichas* and placed it instead in the newly erected subgenus *Autolichas*, giving as his reason for doing so the view of Foerste (1920) that *Lichas* and *Metopolichas* are distinct.

In reviewing the American Ordovician lichids, Foerste (1920) recognized 15 genera but did not discuss their evolutionary relationships. He commented on the resemblance between cranidia of *Acrolichas* and *Amphilichas* (which are now regarded as synonymous), and between pygidia of *Acrolichas*, *Metalichas* and *Platopolichas*, considering these similarities to be due to convergent evolution. He concluded from this that the form of both cranidia and pygidia must be taken into account in defining lichid genera.

An extensive revision of the classification and evolutionary relationships of the lichids was done by Phleger (1936, 1937*a*, *b*, *c*) who recognized 48 genera, 19 of them new. Many of these new genera were based on trivial features, such as the development of spines or processes on the glabella and anterior cephalic border. Phleger considered the lichids to constitute a superfamily consisting of the families Lichadidae and Trochuridae, distinguished by S1 being complete in the latter but obsolete or absent in the former. The subfamilies of the Lichadidae were defined by the bullar lobes being completely or only partly fused with L1, and the presence or absence of L1a. The Lichadinae was considered to have given rise to the other subfamilies, the Homolichadinae and Tetralichadinae having their origins in *Metopolichas*, and the Echinolichadinae in *Lichas*. Within the Trochuridae Phleger diagnosed subfamilies on the structure of the pygidium, the presence or absence of L1a, and on whether or not L1 is confluent with the fixigena. These subfamilies were all considered to have been independently derived from a common ancestor, which had also given rise to the Lichadidae. Phleger's classification has not been widely accepted but the same arrangement of suprageneric taxa was followed by Hupé (1953, 1955) and Balashova (in Chernysheva 1960*a*), both of whom placed in synonymy many of the genera recognized by Phleger.

Warburg (1939, p. 7) reviewed the history of classification of the Lichidae, repeating her earlier (1925, p. 254) observation that many of the taxa recognized by previous authors as subgenera of *Lichas* are at least as distinct morphologically as separate genera in other groups of trilobites. It was in her view both impractical and unnatural to continue to group the lichids together in one genus. She was highly critical of Phleger's revision of the lichids, believing that his interpretation of the glabellar structure was incorrect, and that many of his genera were based on characters undeserving of recognition at that taxonomic level. She recognized nine lichid genera in the Ordovician and Lower Silurian of Sweden and placed many other names in synonymy with these. Warburg did not discuss the evolutionary relationships of the genera, nor did she recognize any subfamilies within the Lichidae.

Tripp (1957; in Moore 1959) divided the Lichidae into subfamilies primarily on the structure of the hypostome. He considered the Tetralichinae and Ceratarginae to be derived from a common ancestor, and possibly also the Lichinae and Homolichinae from another, although this is not clear from his text-fig. 7 (1957). The family Lichakephalidae was erected to include only *Lichakephalus*; this family was united with the Lichidae in the superfamily Lichacea (Tripp 1957) and in the order Lichida Moore, 1959. Tripp agreed with Warburg's (1939) broad concept of the genera, except that he regarded *Metopolichas* as distinct from *Lichas*. He considered the arrangement of the glabellar lobes and furrows to be the principal guide in distinguishing genera but also placed importance on the form of the librigena and, in some genera, the pygidium. Features he considered to be of little taxonomic importance include spines, protuberances or swellings on the cephalon or pygidium, and the presence of an extra segment at the front of the pygidium.

3. Taxonomic characters

In revising the Lichida we have attempted to consider all the characters of the exoskeleton, some of them subsequently being weighted for use in our diagnoses. The lichide glabella, with its anteriorly expanding median lobe and distinctive arrangement of lateral lobes (§4) is the most important unifying character of the order, though furrow effacement and lobe fusion do obscure the pattern in some genera. The rostral plate of lichides is wide and short and this may prove to be an important character uniting lichides, odontopleurides and the Scutelluina (§6). More information on the ventral morphology of other trilobites, particularly Cambrian forms, is needed to assess this possibility further. Lichides are opisthoparian and tend to be isopygous. We do not place great weight on these characters, however, especially because the former one is primitive for trilobites as a whole.

Our recognition of two families within the order is provisional. Some of the characters used to distinguish the Lichakephalidae (see §5*h*) are probably primitive features that could not properly justify familial separation. If our association of lichakephalid cranidia and pygidia is correct, however, at least one important contrast emerges. The obvious furrows on lichakephalid pygidia are all pleural furrows, interpleural furrows being weakly developed at best (e.g. figures 343, 348, 357 and 358). This is in sharp contrast to the situation in most lichids where the interpleural furrows are distinct and bound the spinose pleural ribs (e.g. figure 5).

Details of glabellar structure remain constant within most lichid subfamilies. The Lichinae, for instance, generally have the bullar lobe fused with L1b, and L1a is circumscribed, whereas tetralichines are characterized by the more or less complete fusion of the lateral lobes. Similarly, the number of spinose pygidial pleurae, the shape of the marginal spines in cross section (rounded or flattened), the relative size and degree of inflation of the anterior and posterior pleural bands all provide useful characters. Like Tripp, we have placed particular weight on hypostomal morphology in recognizing subfamilies (figure 2). Variation in hypostomal morphology does occur, in the Homolichinae for instance. Some obvious variations, such as the relative elongation of the hypostome in certain species of the homolichine *Platylichas* (q.v.), are easily explained by reference to morphological modifications of the cephalon. Only in the Echinolichinae are there quite striking contrasts in hypostomal morphology in the two genera in which that structure is known (see discussion of *Teratapsis*). These differences may relate largely to effacement of the hypostome in *Terataspis*. In tentatively assigning *Metopolichas* to the Homolichinae, rather than to the related subfamily Lichinae, we have weighted its hypostomal characters above its cranidial ones.

The importance of the convergent acquisition of similar structures in various parts of the lichid exoskeleton has been noted previously (Tripp 1957, p. 112) and is re-emphasized here. For instance, the glabellar morphology of *Dicranopeltis* (figure 41) closely resembles that of *Trochurus* (figure 109), particularly as regards the configuration of the lateral lobes. Nevertheless, the two are easily distinguished in other respects and their hypostomal and pygidial morphology indicates that they should be assigned to different subfamilies.

Particularly because of the problems of convergence, it is important to diagnose genera by using several characters from different parts of the exoskeleton. Unfortunately, the ease with which the lichide exoskeleton seems to have become disassociated after death or ecdysis causes difficulties in this context. The unverified attribution of exoskeletal parts to individual species has caused much confusion in the past, especially because sculptural similarities may occur in only distantly related forms and several species of Lichida may be recorded from the same locality. Articulated specimens of species belonging to many of the genera dealt with here are known, but there are still some in which the association of cranidia and pygidia is unproven.

We have diagnosed the genera on more detailed variations of the themes defined by the cranidial and pygidial characters used to recognize subfamilies, also taking into account the relative size, orientation and degree of inflation of the glabellar lobes, relative size of the pygidial axis and presence or absence of a border. Like Warburg and Tripp we do not consider the presence of spines or other protuberances on the crandium to be especially important taxonomically, as these structures are developed sporadically in some of the species-groups defined on the cranidial and pygidial characters outlined above.

In *Acanthopyge* and *Platylichas* we have found groups of species united by a similar cranidial morphology, but which may be distinguished from each other on the characters of the pygidium. In these instances we have weighted cephalic characters in diagnosing genera and emphasized pygidial morphology in dividing these into subgenera.

Both Warburg and Tripp considered lichid genera in broad terms, in this contrasting strongly with Phleger who erected many new genera mostly based on only a single, often comparatively trivial, morphological character. We have circumscribed the genera more finely than Warburg and Tripp and generic names coined by Phleger are available for many of the species-groups so recognized. That we utilize several of Phleger's names reflects this circumstance rather than any confidence on our part in his revision.

4. GLABELLAR STRUCTURE

All earlier authors have considered that the lobes developed in the axial region of the lichide cranidium are entirely of glabellar origin and we agree with this interpretation. It would be possible, however, to suggest that the median lobe is homologous with the entire glabella of other trilobites and that the lateral lobes have their origins in the fixigenae: that is, that they are bacculae or modified bacculae. Such structures are found in various groups of trilobites: endymioniines (Fortey 1975, pl. 32, figs 9, 6, 13), telephinids (Fortey 1975, pl. 36, figs 15, 13, 12) and certain asaphids (Fortey & Shergold 1984, pl. 41, fig. 2), for instance. In the early ontogeny of some lichids the structure termed the bulla (see discussion below) occupies an almost central position within the axial furrow (e.g. *Acanthopyge* (*Jasperia*) *bifida*, see Chatterton 1971, pl. 7, figs 6a, b), so that it is impossible to determine with certainty whether it is derived from the glabella or from the cheek. In other cases, however, the bulla is obviously initiated on the glabella (e.g. *Amphilichas conradi*, see Chatterton 1980, pl. 18, figs 12, 15, 16), being marked anteriorly by an inwardly and backwardly directed furrow (S2). On this evidence, we make the assumption that the lateral lobes are of glabellar origin in all lichides. This assumption facilitates a plausible interpretation of the cranidial axis in the early lichakephalid *Acidaspidella* (Bruton 1983, pl. 88, figs 16, 19) (figure 346 herein) where there is little doubt as to the position of the axial furrow. In the account that follows we firstly summarize previous discussions of lichide glabellar structure (figure 1), and then offer our own interpretation (figure 2).

In such lichids as *Amphilichas* (figure 246) the pre-occipital part of the glabella is of superfically simple construction, consisting of a pair of exsagitally elongated lateral lobes flanking the median lobe. By comparison with other trilobites such a morphology is clearly derived and must result from fusion or differential growth or both of several lateral glabellar lobes. Other Lichida may have up to three pairs of lateral glabellar lobes and there has been considerable discussion concerning the interpretation of these and their likely homology.

The early workers (including Gürich (1901)) seem to have generally accepted that the three pairs of lateral glabellar lobes found in certain Lichida were homologous with those found in many other trilobite groups. Reed (1902, p. 64), however, pointed to the disproportionately large size of the most anterior lateral lobe and to the presence in a number of species of a weak furrow or adaxial notch near its mid-length (e.g. figures 174 and 327). These features suggested to Reed that the anterolateral lobe was bicomposite in nature, comprising fused L2 and L3. Reed further hypothesized that behind the bicomposite lobe lay the homologue of L1 (sometimes fused anteriorly to produce a tricomposite lobe) with an occipital lobe still farther posteriorly. The latter had previously been generally regarded as L1 but Reed (1902, p. 65) argued for its occipital nature partly on comparative morphological grounds. He also emphasized that, in certain Ordovician species particularly, this lobe is anteriorly bounded by a furrow which extends without deflection from the median part of the occipital furrow. In his view, the interpretation of the occipital lobe as L1 was based on more highly modified forms in which enlargement of the lobe had occurred, producing deflection of the surrounding furrows. Foerste (1920, p. 260) did not evaluate these suggestions, instead following Gürich (see figure 1). Both Reed (1923) and Warburg (1925, p. 245), however, followed Reed's (1902) interpretation.

Phleger (1936, p. 593) discussed both Reed's and Foerste's views in some detail. He concluded that the most posterior of the lateral lobes represented L1, no occipital lobe being developed. Like Foerste, he regarded the next most anterior lobe as homologous with L2 of other trilobites. He followed Reed, however, in interpreting the larger anterior lobe as being bicomposite in nature, and considered it to be composed of L3 and L4. Warburg (1939, pp. 7, 9) dismissed Foerste's and Phleger's suggestions. She, like Tripp (1957, p. 106) and most subsequent authors, accepted the substance of Reed's interpretation, although expressing some reservations concerning details of the arguments which had originally been used to support it.

Öpik (1937) followed the early workers in regarding the posteriormost lateral lobe as L1 and the anteriormost as L3. He seems to have been uncertain, however, concerning the identity of L2, and even about which parts of the cranidium belong to the glabella. In certain *Metopolichas*

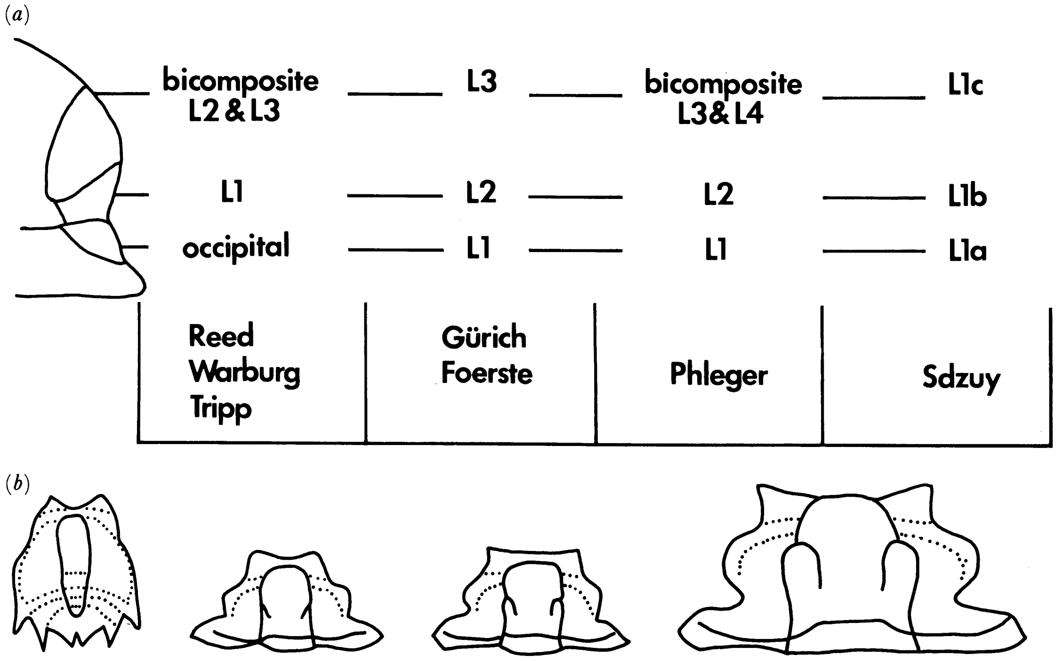

FIGURE 1. (*a*) Some previous interpretations of glabellar structure in the Lichida, as applied to *Dicranopeltis*. (*b*) Ontogenetic stages of *Amphilichas*. From left, these are metaprotaspis, lacking fine cheeks, small meraspid cranidium, meraspid cranidium, larger meraspid cranidium, magn. × 25. Sculpture and spines omitted in all cases. (Redrawn from Chatterton 1980, figs 12A, E, D, C, p. 54.)

species he described, for instance, Öpik seems to have regarded the portion of fixigena lying medial to the palpebral lobe as L2, although he correctly identified the furrow lying adaxial to this portion as the axial furrow.

Vaněk (1959), although making no reference to previous interpretations of glabellar lobation in lichids, agreed with Reed that the large anterior lobe consisted of L2 and L3 fused together, but considered the posteriormost lobe to be L1 rather than occipital. The structure between the anterior and posterior lobes was regarded by Vaněk as part of the median glabellar lobe that had expanded laterally and displaced L1 and L2 so as to lie between them. Sdzuy (1979) redescribed the cranidium of the Tremadoc genus *Lichakephalus* on the basis of new material and offered a radical new interpretation of lichide glabellar lobation, arguing that all the lateral lobes represent subdivisions of L1 (figure 1).

Before the late 1960s virtually no data were available concerning lichid ontogenies and arguments concerning glabellar homology were therefore based entirely on study of holaspid morphology. The ontogenetic development of several lichine, tetralichine and trochurine species – ranging from Ordovician to Devonian in age – is now known (Temple 1969, 1972; Chatterton 1971, 1980; Tripp & Evitt 1981). These studies provide the basis for a more reliable interpretation of lichid glabellar structure when taken together with comparative morphology of holaspides.

The lichid protaspis possesses an almost parallel-sided glabella, slightly waisted at its mid-length, and the occipital ring is a broad oval in shape (Whittington 1956, text-fig. 1A). Short, weakly incised lateral furrows may be present (see, for example, Tripp & Evitt 1981, pl. 1, fig. 3) (figure 1*b* herein) and L1 is defined in the metaprotaspis of *Acanthopyge* (*Jasperia*) *bifida* (see Chatterton 1971, text-fig. 9B, p. 35). In *Hemiarges turneri rasettii* (Tripp & Evitt 1981, text-fig. 1.3a, p. 668) L1 is circumscribed early in the meraspid period and, a little later, L2 appears in front of it. In *Amphilichas* species (figure 1*b*) the first lobe to form is in the same position as L2 in *H. t. rasettii* (Chatterton 1980, text-fig. 12H, p. 54; Tripp & Evitt 1981, text-fig. 1.8, p. 668). This is the lobe for which Temple (1972) coined the term 'bulla'. In *Lichas laciniatus* (see Temple 1969) he noted the formation of a large anterolateral (i.e. bullar) lobe by the rapid forward differential growth of the bulla during ontogeny. The same process of differential bullar growth seems to be of general application in the group (see, for example, Tripp & Evitt 1981, text-fig. 4).

Chatterton (1971, p. 34; 1980, p. 53) discussed the regularly arranged spines found on the glabella of lichid protaspides and argued for their segmental nature. During the ontogeny of *Acanthopyge* (*Jasperia*) *bifida* the bulla grows forward relative to these segmental spines. It therefore seems that the bullar lobe, although having its origin in L2, may come to incorporate material homologous with L3 and L4 in other trilobites. In *A.* (*J.*) *bifida*, *Amphilichas conradi* and *Hemiarges turneri* it is clear that the bulla does not incorporate cheek material as it grows, for it displaces laterally the prominent tubercles A2 and D which lie adjacent to it on the fixigena. The bullar lobe therefore appears to be entirely glabellar in origin and the longitudinal furrow which adaxially bounds the lobe is not simply an extended S4 as Reed (1902) proposed.

Tripp & Evitt (1981, p. 674) showed that the small posterior lateral glabellar lobe that was interpreted by Reed (1902)as an occipital lobe develops in the meraspid stage of *H. turneri rasettii* from the posterior part of L1, and not from the occipital ring. Occipital lobes in other trilobites develop in a quite different fashion from this (see, for example, *Proetus talenti*; Chatterton 1971, pl. 14, figs 2, 4, pl. 16, figs 4, 5). In *Amphilichas* the posterior part of the lateral glabellar lobe, which presumably is fused with the homologue of the posterior lateral lobe in such forms as *Hemiarges* and *Dicranopeltis*, also develops from L1 rather than from the occipital ring (Chatterton 1980, pl. 18, figs 4, 8). It seems therefore that occipital lobes are absent in lichids. In such genera as *Dicranopeltis* (see Thomas 1981, pl. 18, fig. 4c) (figure 41 herein) three pairs of lateral glabellar lobes are defined, of which the most anterior is the largest and presumably the bullar lobe. Because the bullar lobe is initially derived from L2, the two more posterior lateral lobes must represent subdivisions of L1, and it seems appropriate to use Sdzuy's terms L1a and L1b for these structures (figure 2).

L1a is independently inflated and surrounded by a furrow in most Lichida. In such genera as *Platylichas* and *Apatolichas*, however, L1b is not independently inflated and the axial furrow is locally effaced so that this lobe merges abaxially with the fixigena. In most trochurines the axial furrow is also effaced alongside L1b (or alongside the whole of L1 in genera in which L1a is not developed), but it is weakly defined in *Uripes scutalis* (see Thomas 1981, pl. 21, figs 1b, 4b, 8) (figures 338 and 339 herein) and in some specimens of *Hemiarges turneri* (see Chatterton & Ludvigsen 1976, pl. 19, figs 5, 16). In both of these species the axial furrow is deflected strongly inwards in front of L1a, and in *H. turneri* it curves around the adaxial side of tubercle A1 on the fixigena. There is no doubt that this is the axial furrow because its course can be traced throughout the ontogeny of *H. turneri turneri* (Chatterton 1980) and *H. t. rasettii* (Tripp & Evitt 1981). In contrast to this, the posterolateral cranidial lobe of *Acanthopyge* (*Jasperia*) *bifidia* expands laterally throughout the meraspid stage so as to enclose A1, and thus incorporates cheek material as well as part of L1 (Chatterton 1971). The same process must also have occurred in *Trochurus* (figure 120), the prominent tubercle or spine that is commonly present at the summit of the posterolateral cranidial lobe presumably being A1. In this case,

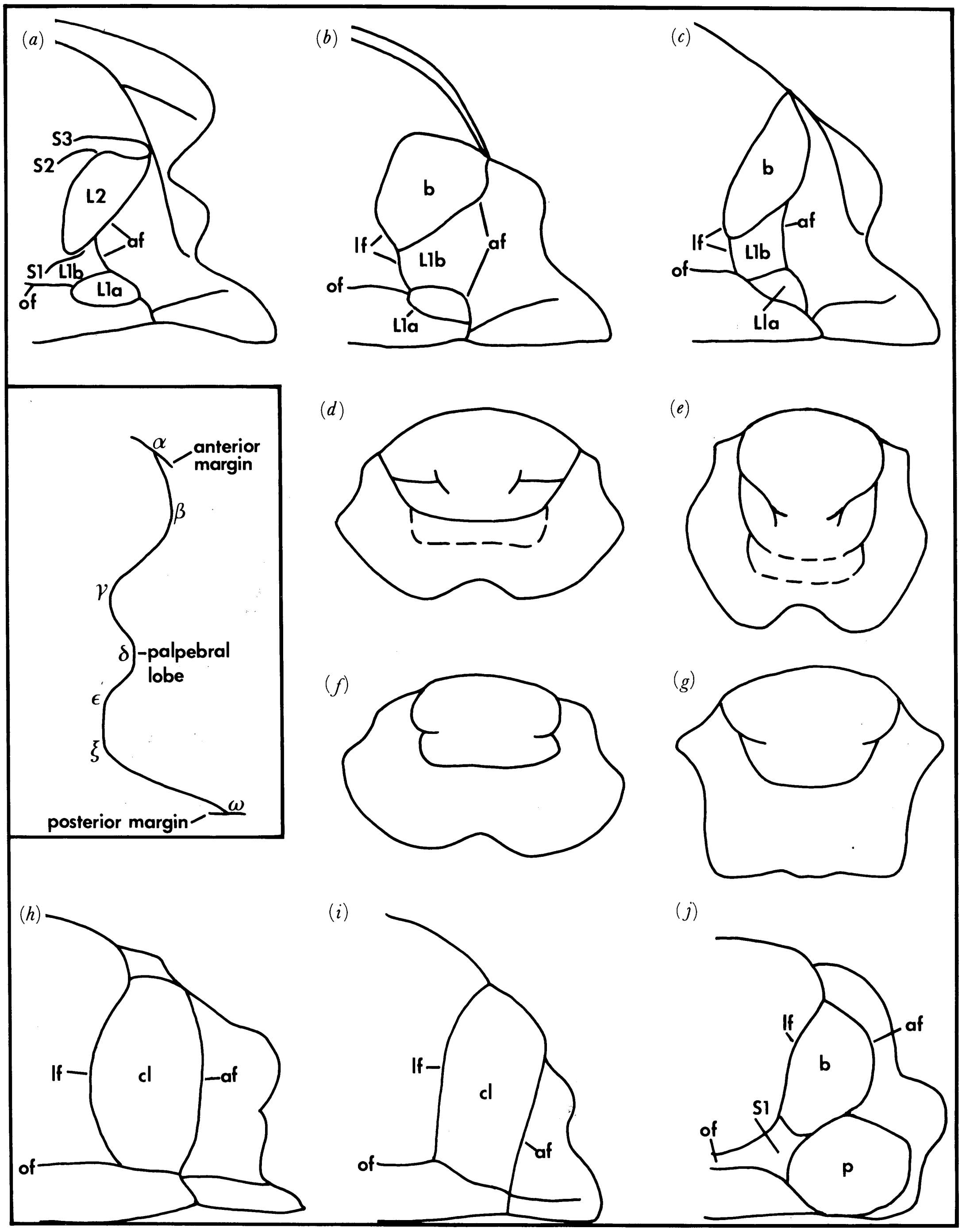

FIGURE 2. Cranidial and hypostomal morphology of Lichida. (*a*) *Lichakephalus* (after Sdzuy 1979, fig. 2A); (*b*) *Platylichas* (*Platylichas*) (after Warburg 1939, pl. 11, fig. 1c); (*c*) *Dicranopeltis* (lobation after Thomas 1981, pl. 18, fig. 4c); (*d*) *Platylichas* (*Rontrippia*) (after figure 187 herein); (*e*) *Dicranopeltis* (after figure 28 herein); (*f*) *Amphilichas* (after figure 250 herein); (*g*) *Acanthopyge* (*Acanthopyge*) (after figure 275 herein); (*h*) *Echinolichas* (after figure 128 herein); (*i*) *Amphilichas* (after figure 246 herein); (*j*) *Acanthopyge* (*Jasperia*) (after Chatterton 1971, p. 32, fig. 8). Inset to left shows the terminology applied to various points along the facial suture (Richter & Richter 1949, p. 68). S1, S2, S3, L2 used in conventional terms; see text for explanation of L1a and L1b. Other abbreviations: af, axial furrow; b, bullar lobe; cl, composite lateral lobe (compound lobe formed by fusion of bullar lobes with L1b and sometimes L1a); lf, longitudinal furrow; of, occipital furrow; p, posterolateral cranidial lobe.


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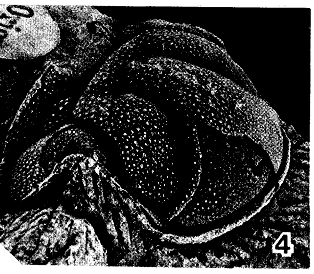
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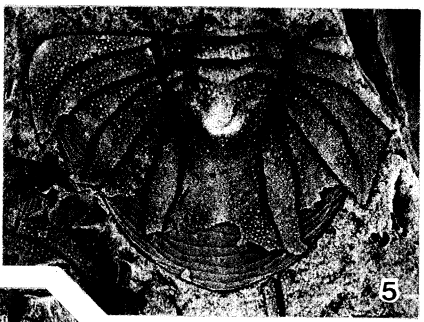
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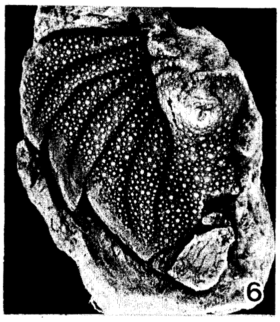
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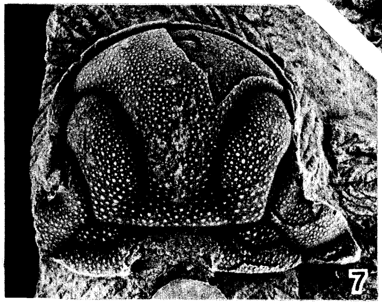
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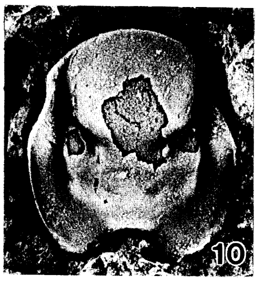
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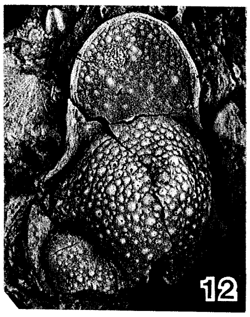
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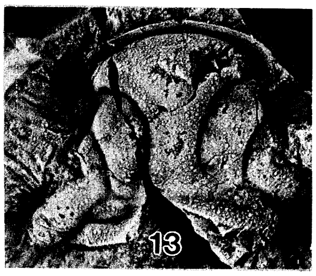
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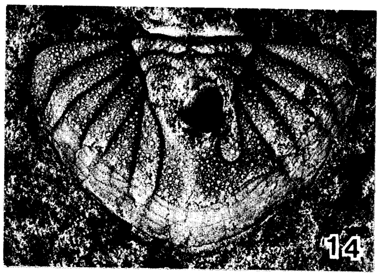
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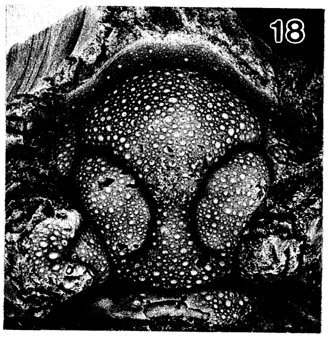
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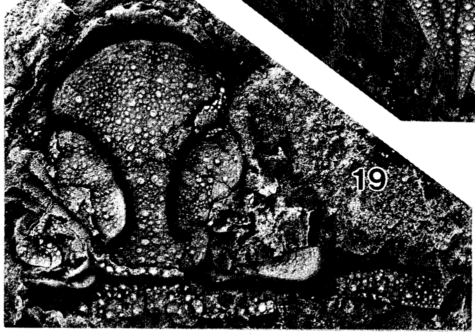
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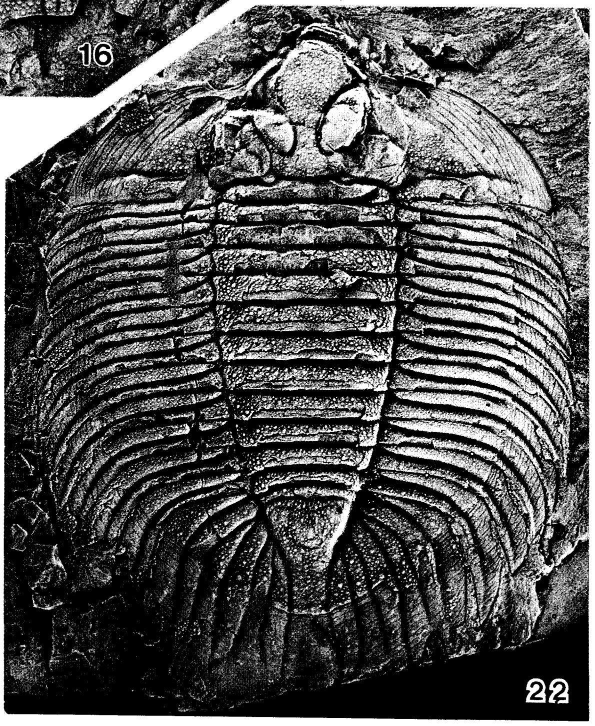
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DESCRIPTION OF PLATE 1

FIGURES 3, 4, 7, 8 AND 15. *Lichas affinis* Angelin, 1854, Dalmanitina Beds (Ashgill), Borenshult, Östergötland, Sweden. Figures 3, 4 and 7, neotype cranidium, RM Ar6078, figured Warburg (1939, pl. 9, fig. 13a, b); lateral, oblique and palpebral views, magn. × 2. 8, Pygidium, RM Ar6082, figured Warburg (1939, pl. 9, fig. 15); dorsal view, magn. × 1.5. Figure 15, pygidium, RM Ar2440, figured Warburg (1939, pl. 9, fig. 14); dorsal view, magn. × 1.5.

FIGURES 5, 6 AND 10. *Lichas laciniatus* (Wahlenberg, 1818), Dalmanitina Beds (Ashgill), Sweden. Figure 5, Holotype pygidium, UM Vg2, figured Wahlenberg (1818, pl. 2, fig. 2*), Warburg (1925, fig. 20; 1939, pl. 9, fig. 1), Temple (1969, pl. 3, fig. 5); dorsal view, magn. × 2. Bestorp, Mösseberg, Västergötland. Figure 6, pygidium, RM Ar6080, figured Warburg (1939, pl. 9, fig. 4); dorsal view, magn. × 2.5. Borenshult, Östergötland. Figure 10, hypostome, RM Ar6107, figured Warburg (1939, pl. 9, fig. 8); ventral view, magn. × 2.5. Borenshult, Östergötland.

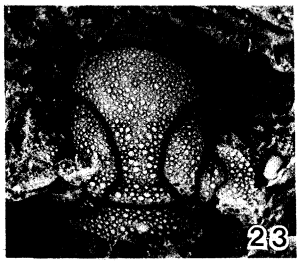
FIGURES 9, 13 AND 14. *Lichas ferrisi* (Weller, 1907), Kankakee Dolomite (Llandovery), near Channahon, Illinois. (UC = University of Chicago collections, stored at FMNH). Figure 9, syntype crandidium, UC 10737C, figured Weller (1907, pl. 22, fig. 12); dorsal view, magn. × 1.75. Figure 13, syntype cranidium, UC 10737A; dorsal view, magn. × 1.75. Figure 14, syntype pygidium, UC 10737B, figured Weller (1907, pl. 22, fig. 13); dorsal view, magn. × 1.75.

FIGURE 11. *Lichas? truncatus* (Kobayashi & Hamada, 1974), Lower Ludlow, Kôchi Prefecture, Shikoku, Japan. Plaster replica of paratype pygidium, KM 16087, figured Kobayashi & Hamada (1974, pl. 8, fig. 10); dorsal view, magn. × 1.

FIGURES 12, 16 AND 17. *Arctinurus occidentalis* (Hall, 1963*a*), Waldron Shale (Wenlock), Waldron, Indiana. Figure 12, plaster replica of cranidium, USNM 298958; dorsal view, magn. × 1.5. Figure 16, plaster replica of pygidium, USNM 298959; dorsal view, magn. × 1. Figure 17, plaster replica of hypostome, USNM 41050; ventral view, magn. × 1.25.

FIGURE 18. *Arctinurus clairensis* Thomas, 1929, St. Clair Limestone (Wenlock), Batesville district, Arkansas. Cranidium, USNM 298960; dorsal view, magn. × 2.25.

FIGURES 19–22. *Arctinurus boltoni* (Bigsby, 1825), Rochester Shale (Wenlock), Lockport, New York. Figure 19, cranidium, AMNH 31074, figured Hall (1852, pl. 70, fig. 1f); dorsal view, magn. × 1.25. Figure 20, cranidium, AMNH 31073, figured Hall (1852, pl. 70, fig. 1d); ventral view, magn. × 1.25. Figure 21, pygidium, AMNH 31075, figured Hall (1852, pl. 70, fig. 1g); dorsal view, magn. × 1.25. Figure 22, latex cast of dorsal exoskeleton, AMNH 31071, figured Hall (1852, pl. 69, fig. 1); dorsal view, magn. × 0.5.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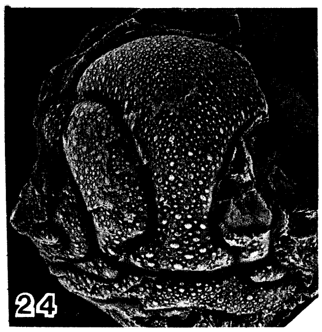
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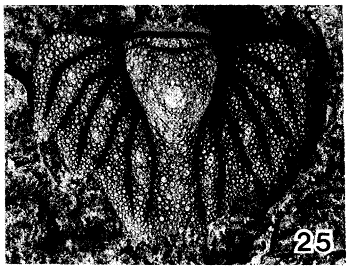
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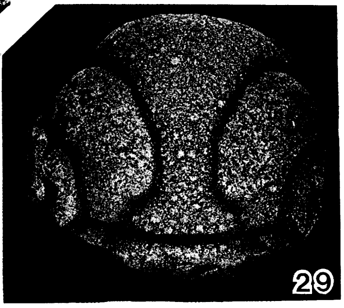
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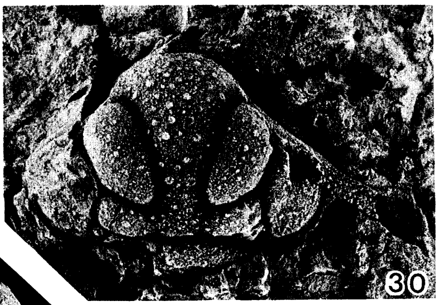
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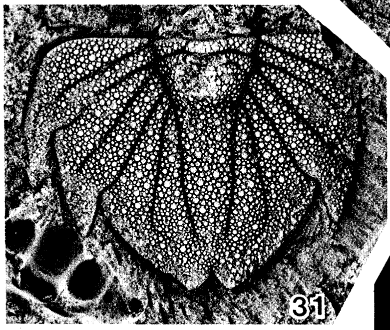
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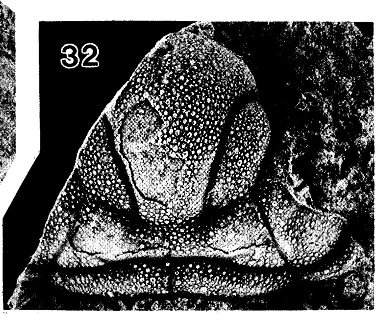
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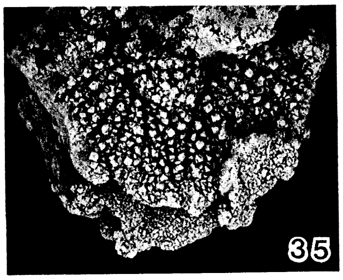
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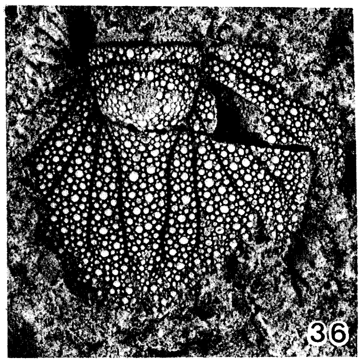
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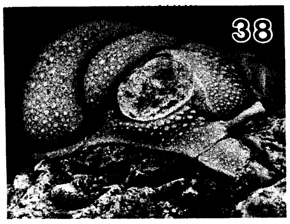
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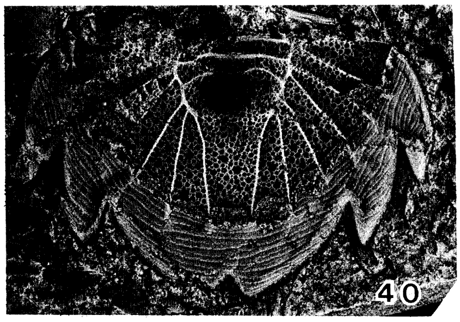
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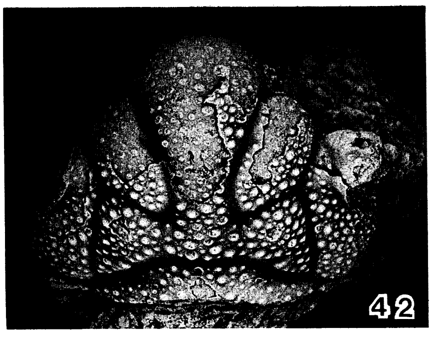
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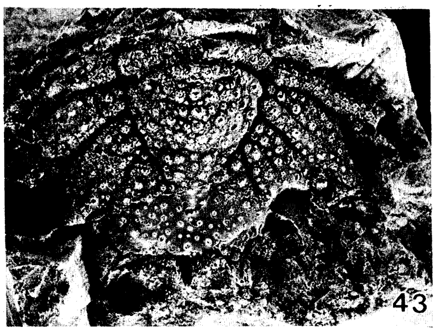
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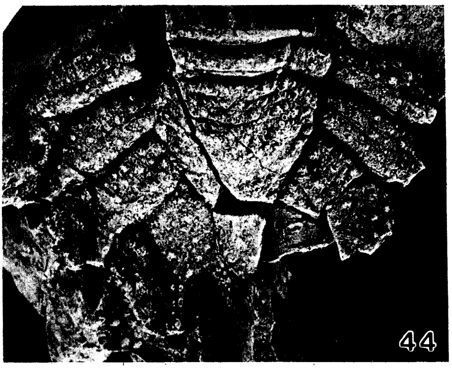
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DESCRIPTION OF PLATE 2

FIGURES 23–27. *Arctinurus? norvegicus* (Angelin,1854), Solvik Formation (Llandovery), Malmøy, Norway. Figure 23, cranidium, PMO (Paleontologisk Museum, Oslo) 88786; palpebral view, magn. ×4. Figure 24, cranidium, PMO 2570, figured Warburg (1937, fig. 2); dorsal view, magn. ×1.25. Figure 25, pygidium, PMO specimen; dorsal view, magn. ×2.5. Figure 26, pygidium, PMO H2577, figured Warburg (1937, fig. 3); dorsal view, magn. ×0.75. Figure 27, hypostome, PMO 44795; ventral view, magn. ×2.

FIGURES 28, 31, 32, 34, 36 AND 40. *Dicranopeltis scabra* (Beyrich, 1845), Liteň Formation (Wenlock), Prague district, Czechoslovakia. Figure 28, hypostome, BM 42419; ventral view, magn. ×2.5. Sedlec. Figure 31, pygidium, BM 42420; dorsal view, magn. ×1.75. Svatý Jan pod Skalou. Figures 32 and 34, cranidium, BM 42419; dorsal and lateral views, magn. ×2. Sedlec. Figure 36, holotype pygidium, HUB k159, figured Beyrich (1845, fig. 16; 1846, pl. 1, fig. 4b); dorsal view, magn. ×2. Svatý Jan pod Skalou. Figure 40, pygidium, BM 42420; ventral view, magn. ×1.75. Svatý Jan pod Skalou.

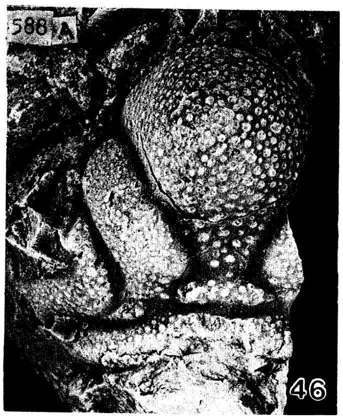
FIGURE 29. *Arctinurus? obvius* (Hall, 1870), Llandovery or Wenlock, Lyons, Iowa. Holotype cranidium, AMNH 2154, figured Hall (1870, pl. 25, fig. 19); palpebral view, magn. ×1.5.

FIGURES 30, 33 AND 35. *Dicranopeltis decipiens* (Winchell & Marcy, 1865), Niagaran dolomites (Silurian), Illinois. (UC = University of Chicago collections, stored at FMNH). Figures 30 and 33, cephalon, UC 9876, figured Weller (1907, pl. 22, fig. 10); palpebral and lateral views, magn. ×1.75. Near Lemont. Figure 35, pygidium, UC 8610, figured Weller (1907, pl. 22, fig. 11); dorsal view, magn. ×2. Hawthorn.

FIGURES 37, 38 AND 41. *Dicranopeltis* sp. nov. 1, St. Clair Limestone (Wenlock), Batesville district, Arkansas. Cephalon, USNM 298961, oblique, lateral and occipital views, magn. ×4.

FIGURES 39, 42 AND 45. *Dicranopeltis* sp. nov. 2, St. Clair Limestone (Wenlock), Batesville district, Arkansas. Figures 39 and 42, cranidium, USNM 298962; lateral and occipital views, magn. ×2.5. Figure 45, pygidium, USNM 298963; dorsal view, magn. ×2.

FIGURES 43 AND 44. *Nonix sauroter* Lane, 1984, Wenlock of Hall Land, north Greenland. Figure 43, paratype pygidium, MGUH 16.336, figured Lane (1984, pl. 3, fig. 12); dorsal view, magn. ×1.5. Figure 44, holotype pygidium, MGUH 16.338, figured Lane (1984, pl. 3, fig. 14); dorsal view, magn. ×2.



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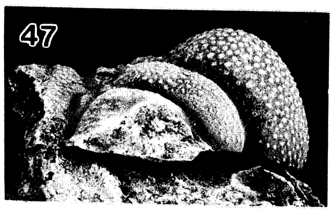
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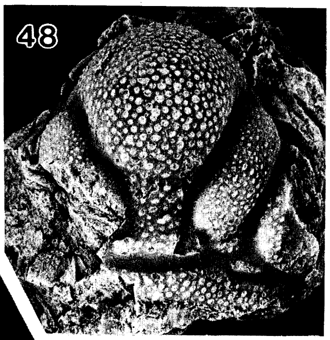
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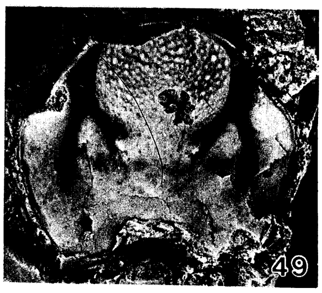
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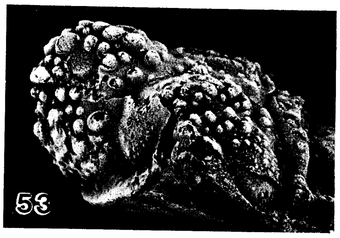
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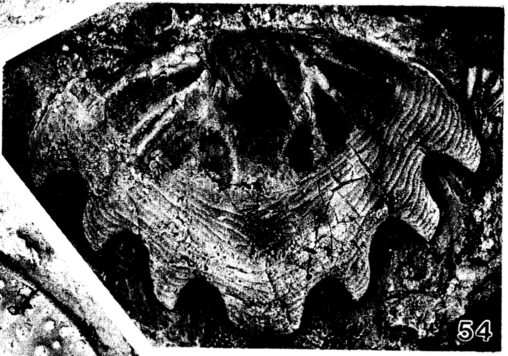
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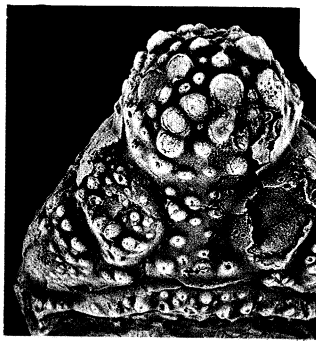
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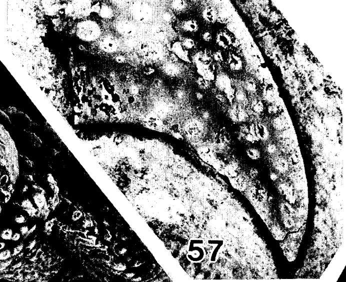
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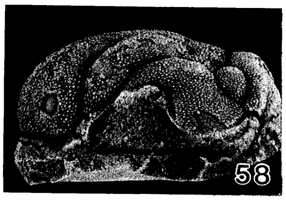
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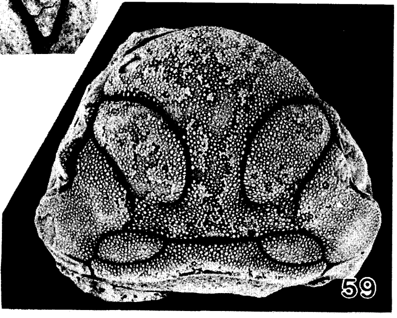
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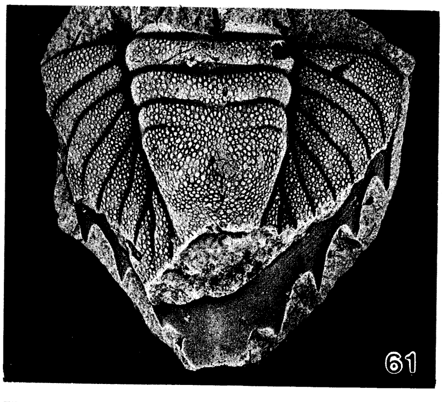
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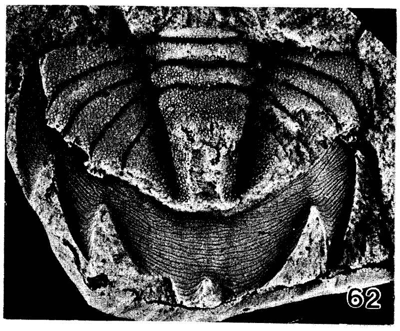
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DESCRIPTION OF PLATE 3

FIGURES 46–49 AND 51. *Oinochoe bigsbyi* (Hall, 1859), Lower Helderberg Group (Gedinnian), New York. Figure 46, syntype cranidium, AMNH 34588A, figured Campbell (1977, pl. 39, figs. 2A, B); occipital view, magn. × 1.25. Albany County. Figures 47 and 48, syntype cranidium, AMNH 2610, figured Hall (1861, pl. 77, fig. 4); lateral and occipital views, magns × 1.25. Albany County. Figure 49, syntype hypostome, AMNH 34586, figured Hall (1861, pl. 77, fig. 7), Campbell (1977, pl. 39, fig. 8); ventral view, magn. × 1.5. Hudson, Columbia County. Figure 51, syntype pygidium, AMNH 34587, figured Hall (1861, pl. 77, fig. 8), Campbell (1977, pl. 39, fig. 6); dorsal view, magn. × 1. Albany County.

FIGURES 50, 52–57, 60 AND 63. *Oinochoe pustulosa* (Hall, 1859), New Scotland Limestone (Gedinnian), New York. Figures 50 and 52, syntype cranidium, NYSM 4558, figured Hall (1861, pl. 77, figs 9, 10); lateral and occipital views, magn. × 1.25. Schoharie. Figures 53 and 56, cranidium, NYSM 15062; lateral and occipital views, magn. × 1.25. Schoharie. Figure 54, syntype teratological pygidium with posterior spine pair fused, NYSM 4529, figured Hall (1861, pl. 78, fig. 7), Hall & Clarke (1888, pl. 19, fig. 9); ventral view, magn. × 1. Schoharie. Figure 55, cranidium, NYSM 15061; occipital view, magn. × 1.5. Clarksville. Figure 57, librigena, NYSM 4568, figured Hall & Clarke (1888, pl. 19, fig. 11); dorsal view, magn. × 1.25. Schoharie. Figure 60, syntype pygidium, NYSM 4563, figured Hall (1861, pl. 78, fig. 5); ventral view, magn. × 0.75. Schoharie. Figure 63, syntype pygidium, NYSM 4562, figured Hall (1861, pl. 78, fig. 4); dorsal view, magn. × 0.75,

FIGURES 58, 59 AND 62. *Uralichas? incola* (Barrande, 1872) Šárka Formation (Llanvirn), Osek near Rokycany, Czechoslovakia. Figures 58 and 59, plaster replica of cranidium, NMP IT1254, figured Barrande (1872, pl. 10, figs 8, 9), Vaněk (1959, pl. 3, fig. 4); lateral and dorsal views, magn. × 1.5. Figure 62, plaster replica of pygidium, NMP IT1259, figured Barrande (1872, pl. 10, fig. 17) as *Lichas avus*; dorsal view, magn. × 1.5.

FIGURES 61, 64, 65. *Uralichas avus* (Barrande, 1872), Šárka Formation (Llanvirn), Osek near Rokycany, Czechoslovakia. Figure 61, plaster replica of pygidium, NMP 29032, figured Holub (1909, pl. 1, fig. 9a–b); dorsal view, magn. × 0.9. Figures 64 and 65, plaster replica of lectotype cephalon, NMP IT1256, figured Barrande (1872, pl. 10, figs 12–15), Vaněk (1959, pl. 2, figs 4–5), palpebral and lateral views, magn. × 0.9.


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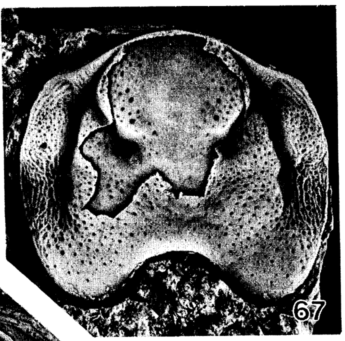
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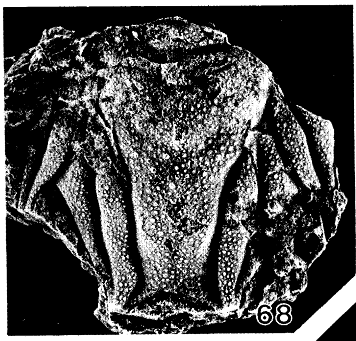
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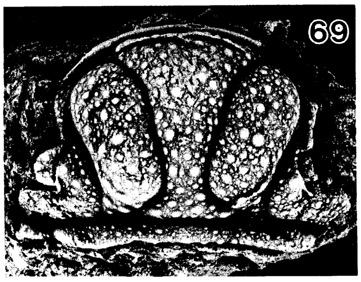
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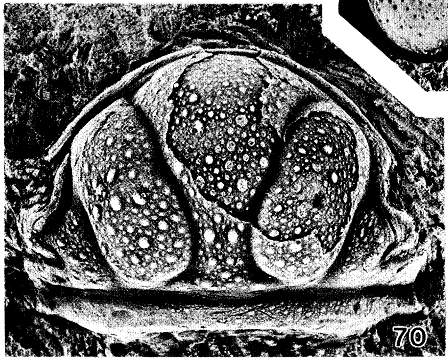
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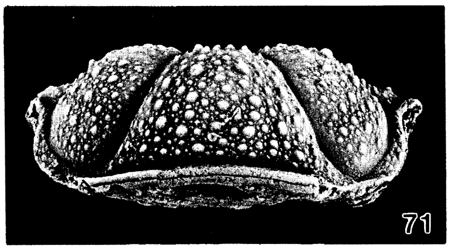
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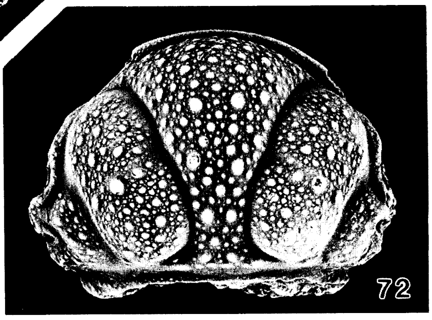
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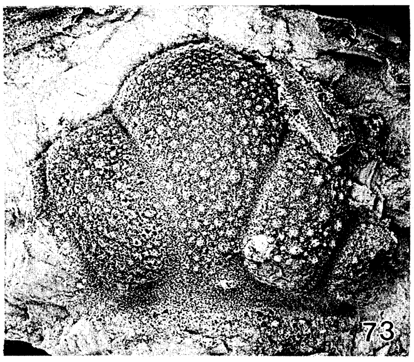
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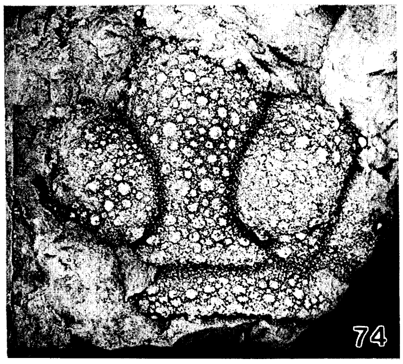
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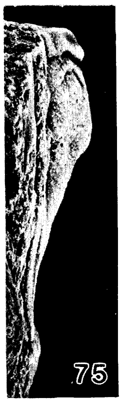
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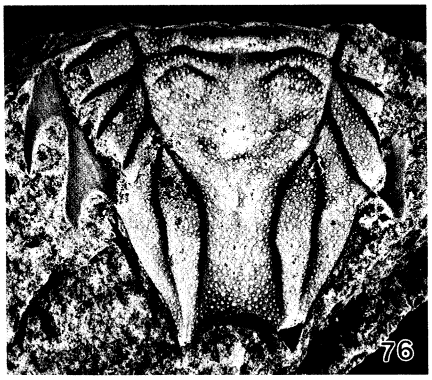
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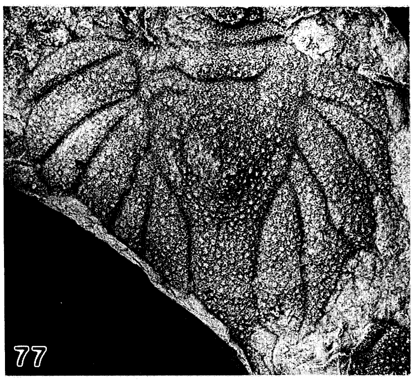
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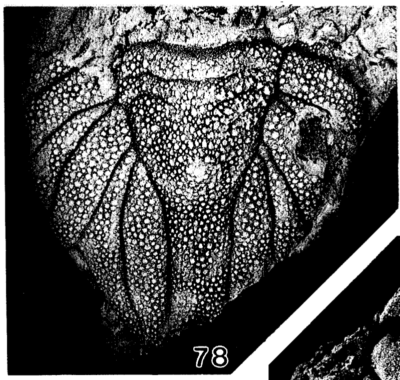
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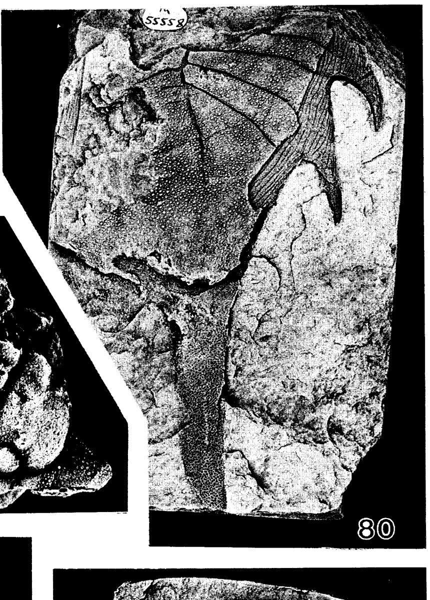

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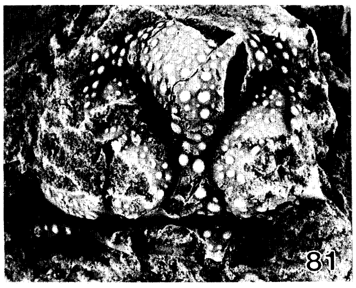
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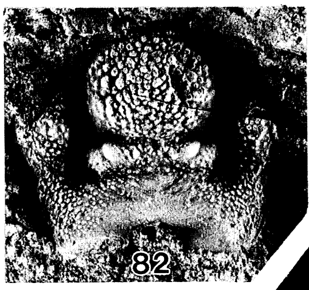
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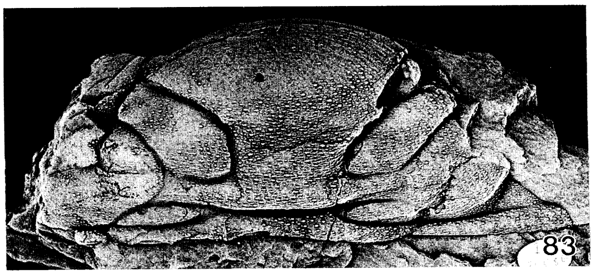
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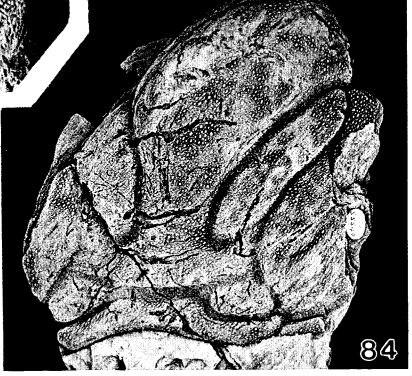
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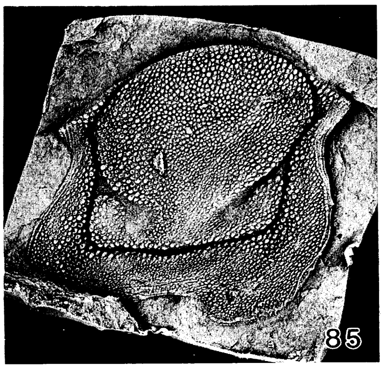
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DESCRIPTION OF PLATE 4

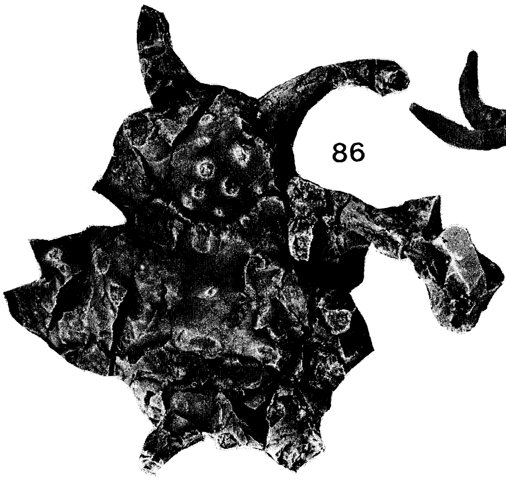
FIGURES 66–72, 75 AND 76. *Pseudotupolichas ornatus* (Angelin, 1854), Wenlock of Gotland, Sweden. Figures 66 and 70, cranidium, RM Ar2375; lateral and dorsal views, magn. × 1.5. ?Högklint Beds; Hangvars Kanal, Hangvar Parish. Figure 67, hypostome, RM Ar2467, figured Lindström (1901, pl. 4, figs 44–46); ventral view, magn. × 1.5. Högklint Beds; Visby Parish. Figure 68, pygidium, RM Ar5032a; dorsal view, magn. × 1.5. Slite Beds; Larbro Parish. Figure 69, cranidium, RM Ar5148; dorsal view, magn. × 2. Högklint Beds; Vattenfallsprofilen 1, Visby Parish. Figures 71 and 72, cranidium, RM Ar2396; anterior and dorsal views, magn. × 1.5. Slite Beds; Lansa, Faro Parish. Figures 75 and 76, pygidium, RM Ar2390, figured Lindström (1885, pl. 15, fig. 13); lateral and dorsal views, magn. × 1.5. ?Slite Beds; Lansa, Faro Parish.

FIGURES 73, 74, 77 AND 78. *Pseudotupolichas chicagoensis* (Weller, 1907), Niagaran dolomites (Silurian), Hawthorn, Illinois. (UC = University of Chicago collections, stored at FMNH). Figure 73, latex cast of syntype cranidium, UC 9860; dorsal view, magn. × 1.5. Figure 74, plaster replica of syntype cranidium, UC 9860A; dorsal view, magn. × 1.75. Figure 77, latex cast of syntype pygidium, UC 9860; dorsal view, magn. × 1. Figure 78, Plaster replica of syntype pygidium, UC 9860A; dorsal view, magn. × 0.75.

FIGURE 79. *Uralichas hispanicus* (Verneuil & Barrande, 1855), Llandeilo of Puente de las Ovejas, near Ciudad Real, Spain. Holotype cranidium, T182, figured Verneuil & Barrande (1855, pl. 24, fig. 1); dorsal view, magn. × 1.

FIGURES 80 AND 83–85. *Uralichas ribeiroi* (Delgado, 1892), Valongo Formation (Llandeilo), Portugal. Figure 80, pygidium, BM In55558; dorsal view, magn. × 0.6. Valongo. Figure 83, cranidium, BM In 55556; dorsal view, magn. × 0.75. Valongo. Figure 84, cranidium, BM In55540; dorsal view, magn. × 0.4. Covelo. Figure 85, latex cast of hypostome, BM In48930; ventral view, magn. × 1. Covelo, Gondomar.

FIGURES 81 AND 82. *Echinolichas bellamicus* (Clarke, 1907), Grande Grève Formation (Siegenian), Gaspé Peninsula, Quebec. Figure 81, syntype cranidium, NYSM 9777, figure Clarke (1908, pl. 3, fig. 6); palpebral view, magn. × 2. Grande Grève. Figure 82, syntype hypostome, NYSM 9778, figured Clarke (1908, pl. 3, fig. 5); ventral view, magn. × 5. Indian Cove.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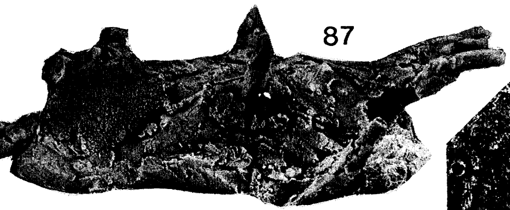
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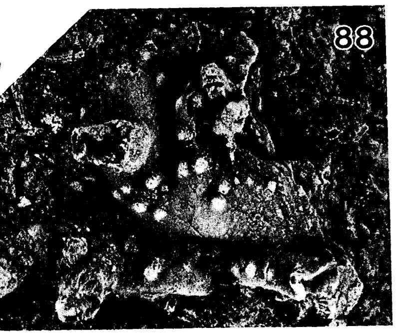
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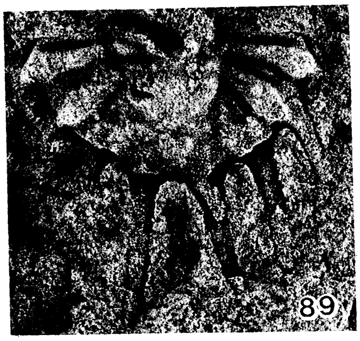
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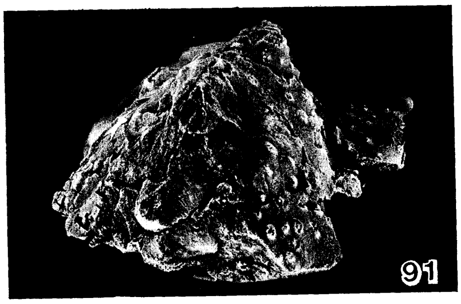
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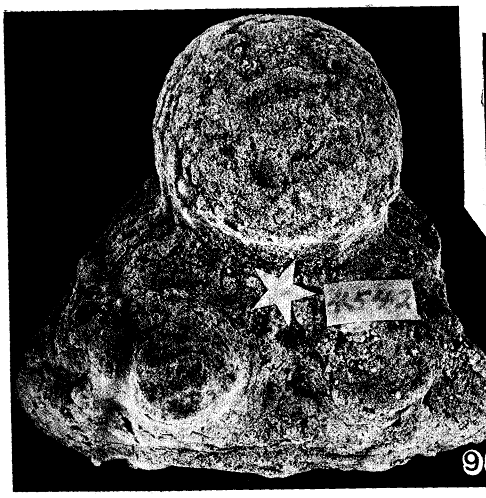
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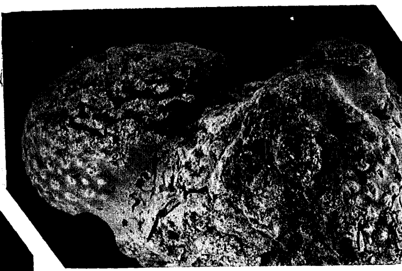
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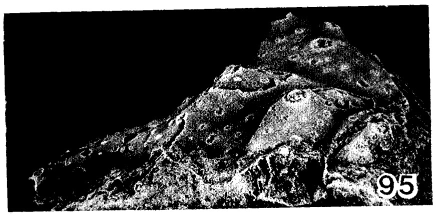
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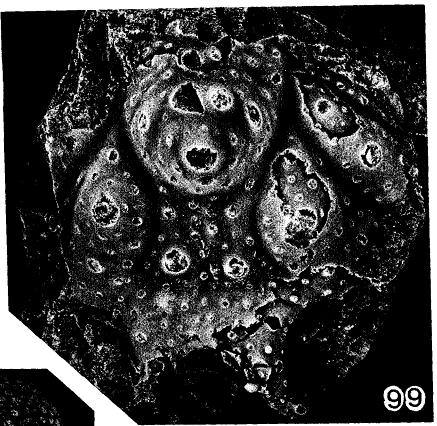
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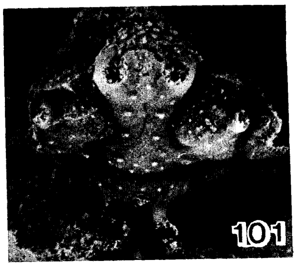
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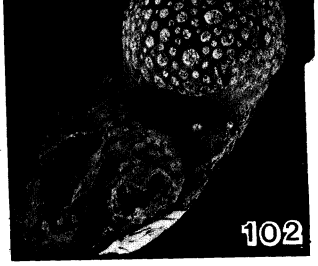
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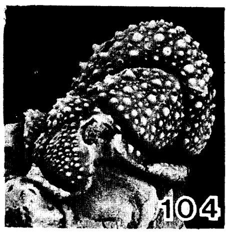
103

DESCRIPTION OF PLATE 5

FIGURES 86–88 AND 90. *Gaspelichas forillonia* (Clarke, 1907), Grande Grève Formation (Siegenian), Gaspé Peninsula, Quebec. Figure 86, syntype cranidium, NYSM 9742, figured Clarke (1908, pl. 3, fig. 1); dorsal view, magn. ×1. Grande Grève. Figures 87 and 90, syntype cranidium, NYSM 9740, figured Clarke (1907, unnumbered fig., p. 168; 1908, pl. 2, figs 1, 2); lateral and dorsal views, magn. ×1.25. Note that upwardly directed spines are reconstructed. Figure 88, latex cast of syntype, right fixigena and part of occipital ring. NYSM 9743, figured Clarke (1908, pl. 3, fig. 2); dorsal view, magn. ×2. Dolbel Brook.

FIGURES 89, 91–95, 98, 99, 102 AND 103. *Terataspis grandis* (Hall, 1863*b*), Schoharie Formation (Emsian), New York. Figure 89, pygidium, NYSM 4546, figured Hall & Clarke (1888, pl. 19, fig. 4); dorsal view, magn. ×2.25. Near Clarksville. Figures 91 and 92, holotype cranidium, NYSM 4543, figured Hall (1876, pl. 17, figs 4, 5), Hall & Clarke (1888, pl. 17, figs 4, 5); lateral and occipital views, magn. ×0.75. Schoharie. Figures 93 and 94, cranidium, NYSM 4542, figured Hall & Clarke (1888, pl. 17, figs 1, 2); dorsal and lateral views, magn. ×1. Schoharie. Figure 98, latex cast of pygidial spines, NYSM 4544, figured Hall & Clarke (1888, pl. 19, fig. 1); dorsal view, magn. ×1. Near Clarksville. Figures 102 and 103, cranidium, NYSM 4547, figured Hall & Clarke (1888, pl. 19, fig. 5); occipital and lateral views, magn. ×1.5. Schoharie. Onondaga Formation (Eifelian), New York. Figures 95 and 99, pygidium, NYSM 15063; lateral and dorsal views, magn. ×0.7. Schoharie.

FIGURES 96, 97, 100 AND 101. *Ceratolichas gryps* (Hall & Clarke, 1888), Onondaga Formation (Eifelian), New York. 96, 97, Syntype cranidium, NYSM 4550, figured Hall & Clarke (1888, pl. 19B, figs 7, 8); palpebral and lateral views, magn. ×3. Schoharie. 100, 101, Syntype cranidium, NYSM 4551, figured Hall & Clarke (1888, pl. 19B, figs 9–11); lateral and palpebral views, magn. ×4. Canandaigua.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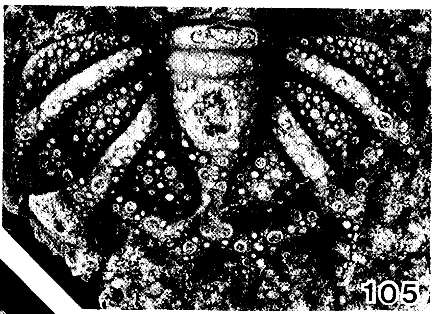
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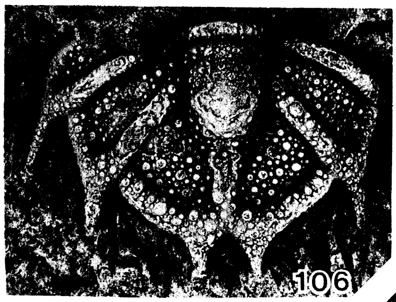
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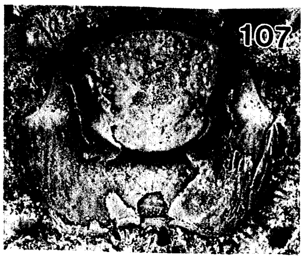
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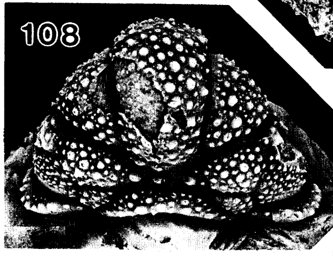
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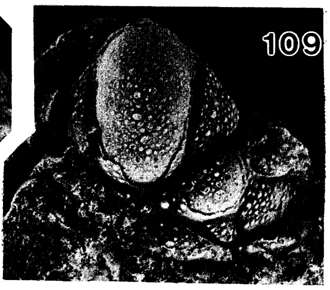
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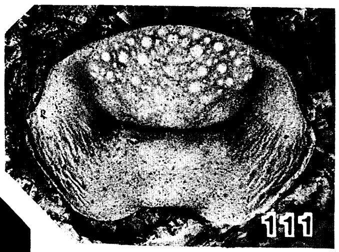
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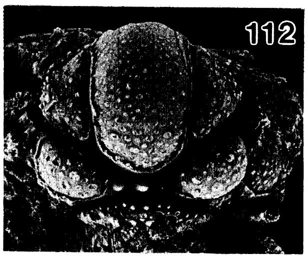
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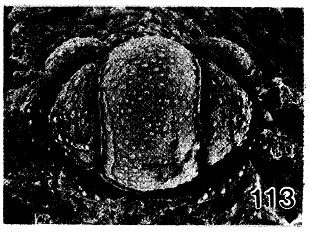
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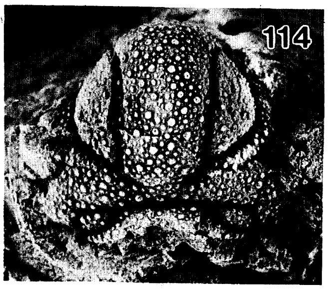
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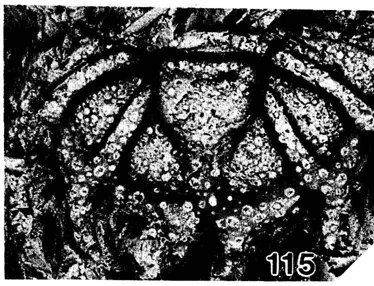
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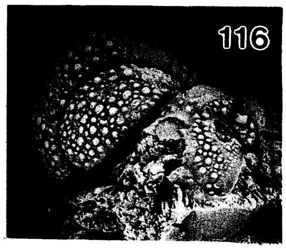
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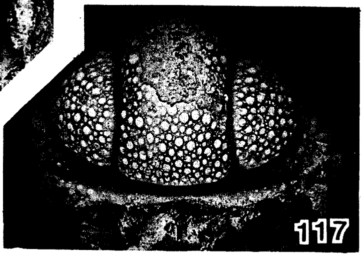
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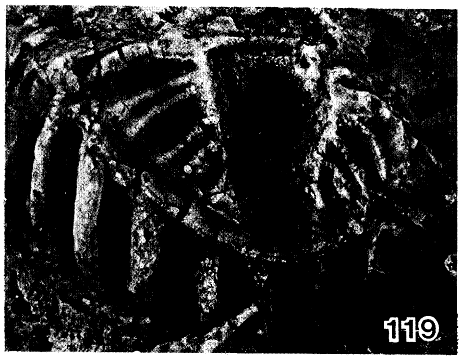
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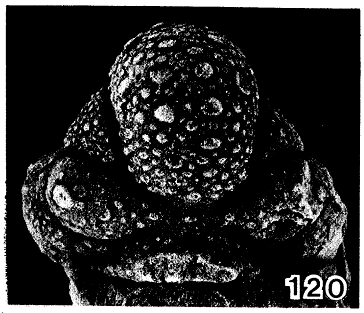
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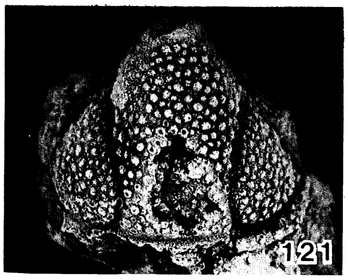
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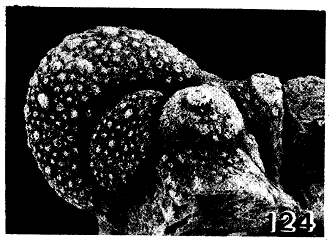
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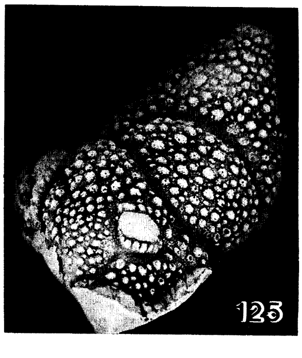
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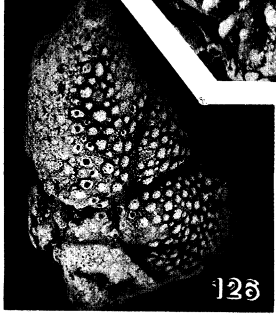
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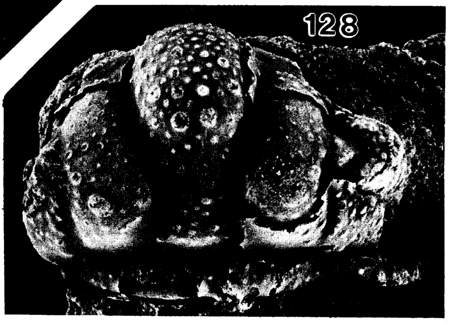
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DESCRIPTION OF PLATE 6

FIGURES 104 AND 108. *Trochurus halli* Foerste, 1917, Rochester Shale (Wenlock), near Albion, New York. Holotype cranidium, AMNH 1826, figured Hall (1852, pl. 70, figs 2A–C), Weller (1917, pl. 12, figs 4A–D); lateral and occipital views, magn. × 2.25.

FIGURES 105–107, 109, 112 AND 113. *Trochurus speciosus* Beyrich, 1845, Liteň Formation (Wenlock), Prague district, Czechoslovakia. Figure 105, lectotype pygidium, HUB k162, figured Beyrich (1845, pl. 1, fig. 14; 1846, pl. 1, fig. 1c), Přibyl & Vaněk (1975, pl. 1, fig. 7); dorsal view, magn. × 3. Svatý Jan pod Skalou. Figure 106, pygidium, SM A49251; dorsal view, magn. × 2.5. Svatý Jan pod Skalou. Figure 107, hypostome, BM In49625; ventral view, magn. × 2.5. Sedlec. Figure 109, cranidium, BM 42419; dorsal view, magn. × 2. Sedlec. Figures 112 and 113, cranidium, BM 42419; occipital and anterior views, magn. × 2. Sedlec.

FIGURES 110, 111 AND 115–117. *Trochurus depauperatus* (Van Ingen, 1901), St. Clair Limestone (Wenlock), Batesville district, Arkansas. Figures 110, 116 and 117, cranidium, USNM 298964; occipital, lateral and anterior views, magn. × 3. Figure 111, hypostome, USNM 298965; ventral view, magn. × 5. 115, Pygidium, USNM 298966; dorsal view, magn. × 4.

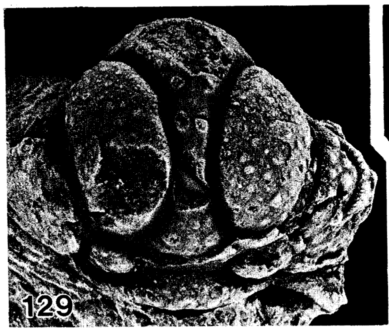
FIGURE 114. *Trochurus bartonensis* (Fletcher, 1950), Rosyth Limestone (Late Llandovery–Wenlock), Borenore district, New South Wales. Holotype cranidium, AMS F42932, figured Fletcher (1950, pl. 15, fig. 8); occipital view, magn. × 3.

FIGURE 118. *Echinolichas hispidus* (Hall & Clarke, 1888). Schoharie Formation (Emsian), Schoharie, New York. Holotype pygidium, NYSM 4553, figured Hall & Clark (1888, pl. 19A, figs 14, 17); dorsal view, magn. × 3.

FIGURES 119, 122, 123, 127 AND 128. *Echinolichas eriopis* (Hall, 1863*b*), Onondaga Formation (Eifelian), New York. Figure 119, pygidium, NYSM 4540, figured Hall & Clarke (1888, pl. 19A, fig. 11); ventral view, magn. × 2. Schoharie. Figure 122, librigena, NYSM 4538, figured Hall & Clarke (1888, pl. 19A, fig. 8); dorsal view, magn. × 4. Canandaigua. Figure 123, syntype pygidium, NYSM 4539, figured Hall (1876, pl. 19, fig. 10), Hall & Clarke (1888, pl. 19A, fig. 9); dorsal view, magn. × 2.5. Schoharie. Figures 127 and 128, syntype cranidium, NYSM 4537, figured Hall (1876, pl. 19, figs 4–7), Hall & Clarke (1888, pl. 19A, figs 2–5); lateral and occipital views, magn. × 2.25. Schoharie.

FIGURES 120 AND 124. *Trochurus hanoverensis* (Miller & Gurley, 1893), Laurel Limestone (Wenlock), Hanover, Indiana. (UC = University of Chicago collections, stored at FMNH). Holotype cranidium, UC 6141, figured Miller & Gurley (1893, pl. 8, figs. 6, 7), Foerste (1917, pl. 12, figs. 2A–D); occipital and lateral views, magn. × 1.75.

FIGURES 121, 125 AND 126. *Trochurus nasutus* (Weller, 1907), Niagaran dolomites (Silurian), Racine (not Milwaukee as stated by Weller 1907, p. 241), Wisconsin. Figure 121, plaster replica of syntype cranidium, USNM 96657, figured Weller (1907, pl. 22, fig. 7); anterior view, magn. × 2. Figures 125 and 126, plaster replica of syntype cephalon, USNM 96657, figured Weller (1907, pl. 22, figs 5, 6); lateral and occipital views, magn. × 2.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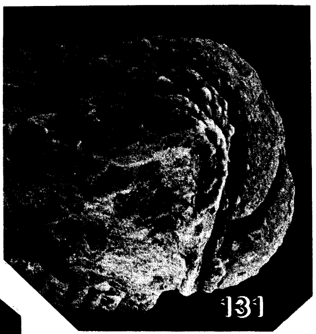
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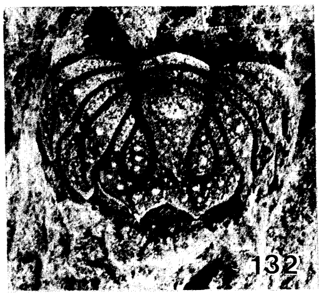
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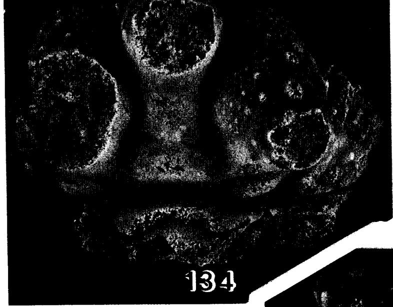
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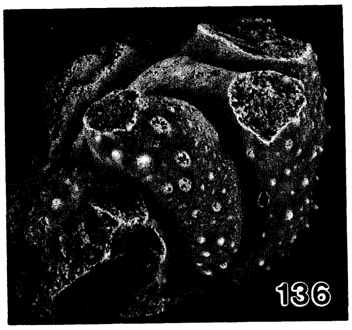
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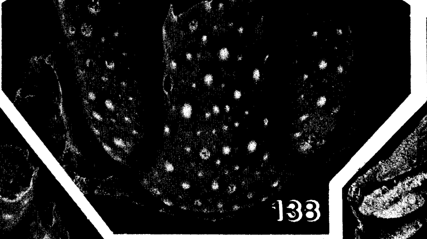
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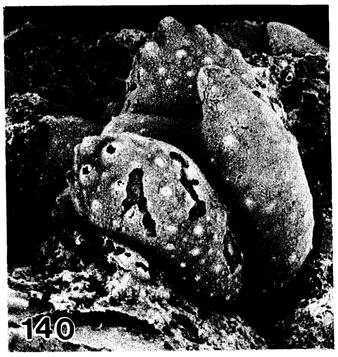
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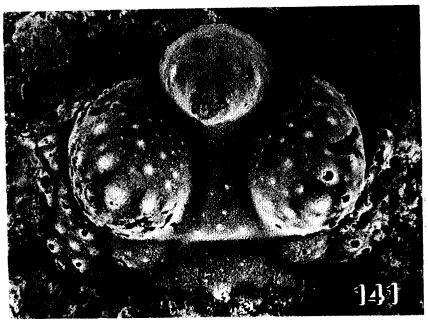
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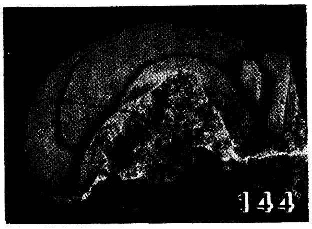
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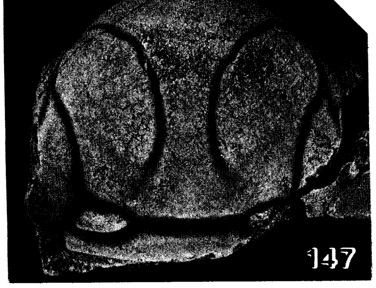
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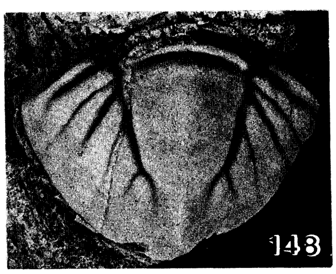
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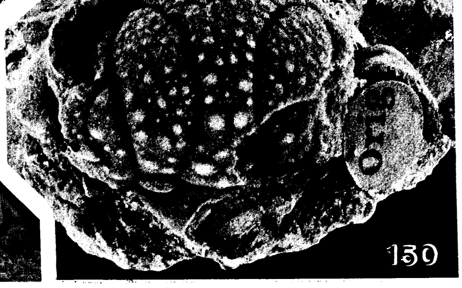
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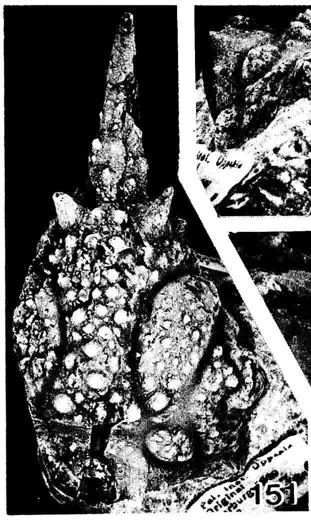
DESCRIPTION OF PLATE 7

FIGURES 129–133, 135. *Conolichas deflexus* (Angelin, 1854), Erratic boulders of Macrourus Limestone (Caradoc), Öland. Figures 129, 130, 131 and 133, cranidium, RM Ar22149, figured Warburg (1939, pl. 6, figs 2a, b); palpebral, anterior, lateral and occipital views, magn. × 1.25. Eriksöre. Figure 132, pygidium, RM Ar5097, figured Warburg (1939, pl. 6, fig. 5); dorsal view, magn. × 3. Hulterstad. Figure 135, pygidium, RM Ar2210, figured Warburg (1939, pl. 6, fig. 6); dorsal view, magn. × 2. Eriksöre.

FIGURES 134, 136–138, 140–142 AND 146. *Conolichas triconicus* (Dames, 1877), Ordovician erratics, Backsteinkalk (Caradoc), Germany. Figures 134, 136, 137, 138 and 142, syntype cranidium, HUB k217, figured Dames (1877, pl. 13, fig. 7); palpebral, oblique anterolateral, occipital, anterior and lateral views, magn. × 1.75. Angermünde. Figures 140, 141 and 146, syntype cranidium, HUB T698, figured Dames (1877, pl. 14, figs 1a–c); oblique anterolateral, palpebral and oblique anterior views, magn. × 2.5. Berlin.

FIGURES 139, 143 AND 150. *Hoplolichoides curvifrons* (Warburg, 1939), Erratic of Chiron or Lower Chasmops Limestone (Llandeilo-Caradoc), Vätö, Uppland. Holotype disarticulated specimen, RM Ar2189, figured Warburg (1939, pl. 7, figs. 1a–c); oblique anterior (cranidium), dorsal (pygidium) and palpebral views, magn. × 2.

FIGURES 144, 145 AND 147–149. *Leiolichas illaenoides* Nieszkowski, 1857, Caradoc erratics, Eberswalde, N. Germany. Figures 144, 145 and 147, Cranidium HUB T1510.1 figured Neben & Krueger (1973, pl. 60, fig. 3); lateral, oblique anterolateral and palpebral views, magn. × 1.5. Locality given as Niederfinow by Neben & Krueger. Figures 148 and 149, Pygidium, HUB T1510.2, magn. × 1.5.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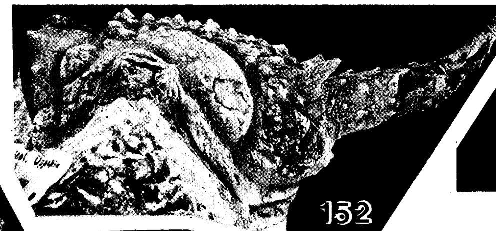
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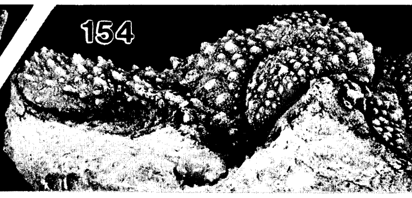
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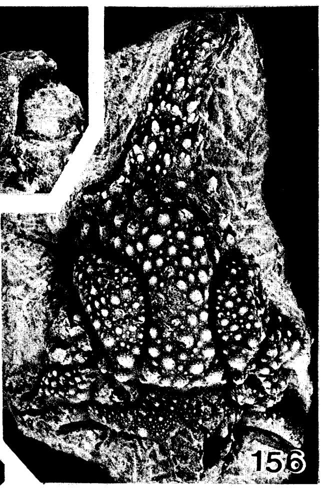
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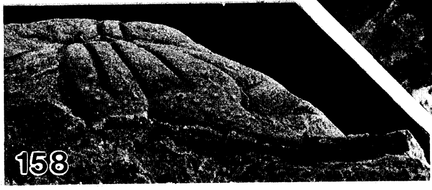
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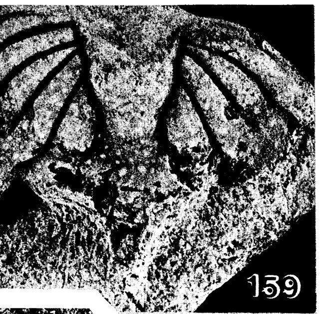
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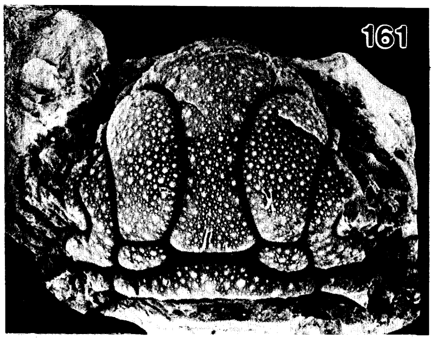
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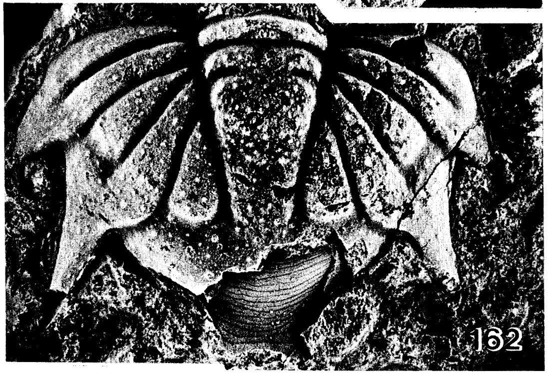
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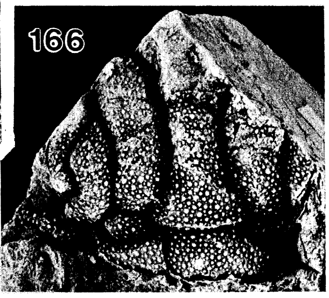
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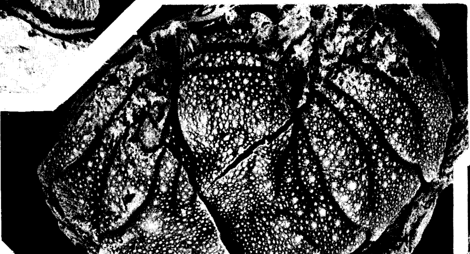
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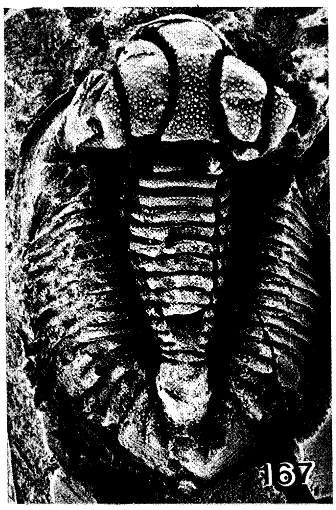
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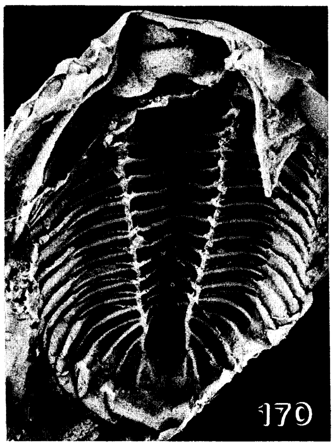
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DESCRIPTION OF PLATE 8

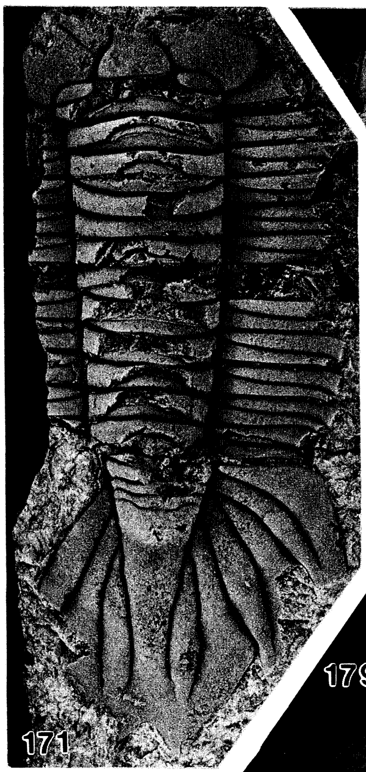
FIGURES 151, 152, 154 AND 156. *Hoplolichas proboscideus proboscideus* Dames, 1877, Erratics of Chiron or Lower Chasmops Limestone (Llandeilo–Caradoc), Sweden. Figures 151 and 152, cranidium, UM B179/80, figured Warburg (1939, pl. 8, figs 8a, b); palpebral and lateral views, magn. × 1.25. Haraldsbyholme, Åland. Figures 154 and 156, cranidium, UM B178, figured Warburg (1939, pl. 8, fig. 6); lateral and palpebral views, magn. × 1. Kragsta, Uppland.

FIGURES 153 AND 155. *Hoplolichas tricuspidatus* (Beyrich, 1846), Ordovician erratic, Sorau, north Germany. Holotype cranidium, HUB k179, figured Beyrich (1846, pl. 1, figs 7a, b); lateral and palpebral view, magn. × 2.

FIGURES 157–159 AND 162. *Hoplolichas dissidens* (Beyrich, 1845). Erratic of Chiron or Upper Chasmops Limestone (Llandeilo–Caradoc), Visby, Gotland. Figures 157 and 158, pygidium RM Ar2191, figured Warburg (1939, pl. 8, fig. 4); dorsal and lateral views, magn. × 1. Figure 159, pygidium, RM Ar2190, figured Warburg (1939, pl. 8, fig. 5); dorsal view, magn. × 1. Ordovican erratic, Sorau, north Germany. 162, Holotype pygidium, HUB k161, figured Beyrich (1845, unnumbered plate, figure 18); dorsal view, magn. × 1.5.

FIGURES 160, 161, 164 AND 165. *Otarozoum eichwaldi*; (Nieszkowski, 1857), Caradoc erratic, Wisenberg, Germany. Figures 160, 161 and 164, cranidium, BM I498, oblique anterolateral, occipital and lateral views, magn. × 2. Figure 165, pygidium, BM I498; dorsal view, magn. × 2.

FIGURES 163, 166 AND 167–70. *Otarozoum melmerbiensis* (Reed, 1907), Dufton Shales (Caradoc), Alston Road cutting, Melmerby, Cross Fell Inlier, northern England. Figure 163, paralectotype pygidium, SM A29642a, figured Reed (1907, pl. 17, fig. 6), Dean (1962, pl. 18, fig. 2); dorsal view, magn. × 2. Figure 166, paralectotype cranidium, SM A29640, figured Reed (1907, pl. 17, fig. 4); palpebral view, magn. × 2.5. Figure 167, lectotype articulated specimen, SM A29638, figured Reed (1907, pl. 17, fig. 2), Dean (1962, pl. 18, figs 3, 4); dorsal view, magn. × 2.25. Figure 168, paralectotype articulated specimen, SM A29637, figured Reed (1907, pl. 17, fig. 1), Dean (1962, pl. 18, fig. 1); dorsal view, magn. × 2.25. Figures 169 and 170, latex casts from paralectotype articulated specimen, SM A29639a, b, figured Reed (1907, pl. 17, figs 3, 3a); dorsal and ventral views, magn. × 2.5.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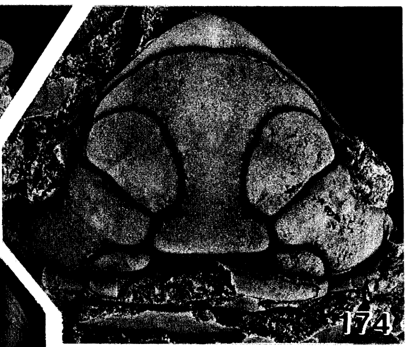
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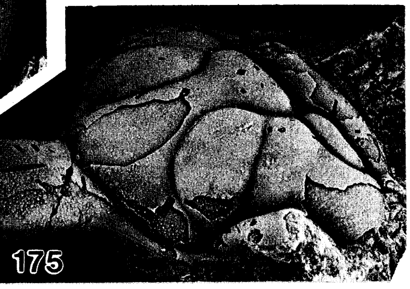
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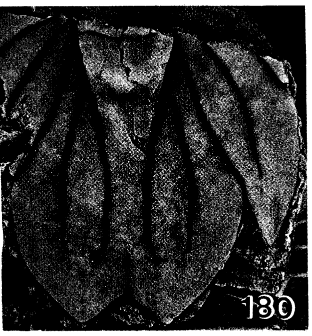
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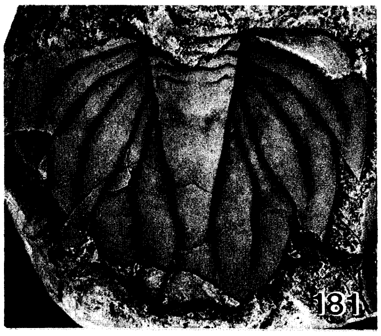
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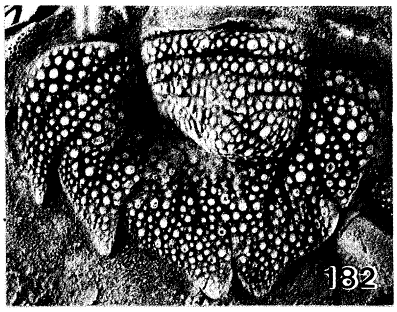
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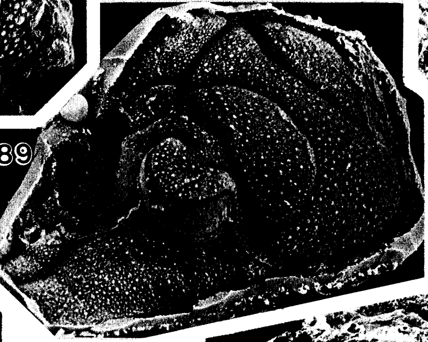
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Description of plate 9

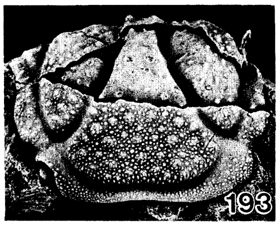
Figures 171, 175, 178, 179 and 183. *Platylichas* (*P.*) *lingua* Warburg, 1939, Kullsberg Limestone (Ashgill), Kullsberg, Dalarne, Sweden. Figure 171, paratype articulated specimen, UM D282, figured Warburg (1939, pl. 9, fig. 11); dorsal view, magn. × 1. Figures 175, 178, 179 and 183, paratype cranidium, UM D298, figured Warburg (1939, pl. 13, figs 10a, b); oblique anterolateral, ventral, occipital and lateral views, magn. × 1.25.

Figures 172–174, 176, 177, 180 and 181. *Platylichas* (P.) *nasutus* (Wigand, 1888), Kullsberg Limestone (Ashgill), Amtjarn, Dalarne, Sweden. Figures 172, 174 and 176, cranidium, UM D295, figured Warburg (1939, pl. 13, fig. 4); lateral, palpebral and oblique anterolateral views, magn. × 1.5. Figure 173, hypostome, UM D293, figured Warburg (1939, pl. 13, fig. 2); ventral view, magn. × 1.5. Figures 177 and 181, pygidium (latex cast from counterpart and part respectively), UM D292a, b, figured Warburg (1939, pl. 13, fig. 1); dorsal views, magn. × 1.25. Figure 180, pygidium figured Warburg (1939, pl. 13, fig. 3); dorsal view, magn. × 1.5.

Figures 182, 184 and 187. *Platylichas* (*Rontrippia*) *grayii* (Fletcher, 1850), Much Wenlock Limestone Formation (Homerian), England. Figure 182, pygidium, BU 2059, figured Thomas (1981, pl. 21, fig. 19); dorsal view, magn. × 3. Dudley. Figure 184, cranidium, BGS 19521, figured Salter (1848, pl. 8, fig. 8), Thomas (1981, pl. 21, figs 10a, b); palpebral view, magn. × 3. Ledbury. Figure 187, hypostome, BU 2056, figured Thomas (1981, pl. 21, fig. 15); ventral view, magn. × 4. Dudley.

Figures 185 and 188–192. *Autoloxolichas nodulosus* (McCoy, 1851), Caradoc, field exposure 600 ft (540 m) W of Ty'n-y-bryn, $4\frac{1}{2}$ miles (7.2 km) west–northwest Corwen, North Wales. Figure 185, pygidium, BU 1809, figured Whittington (1968, pl. 31, fig. 14); dorsal view, magn. × 2. Figures 188, 189 and 191, latex cast of cephalon, BU 1808, figured Whittington (1968, pl. 31, figs 8–11); palpebral, oblique anterolateral and anterior views, magn. × 3. Horizon 100 ft (90 m) above base of Gelli-grîn Group, section in Ffrîdd Bâch, south of Maes meillion, Bala district, North Wales. Figure 190, latex cast of cranidium BU 787, figured Whittington (1962, pl. 7, figs 4, 5); dorsal view, magn. × 3. ?Gelli-grîn Group, Pont-y-Glyn diffwys, Denbighshire, North Wales. Figure 192, latex cast of holotype pygidium, SM A41346, figured McCoy (1851, pl. 1F, fig. 16), Whittington (1962, pl. 6, fig. 12); dorsal view, magn. × 4.

Figure 186. *Autoloxolichas glenos* (Whittington, 1962), Rhiwlas Limestone (Ashgill), southern tip of central Rhiwlas outlier, on Creigiau bychain, Bala district, North Wales. Holotype articulated specimen, BU 796, figured Whittington (1962, pl. 8, figs 1, 2, 8); dorsal view, magn. × 1.5.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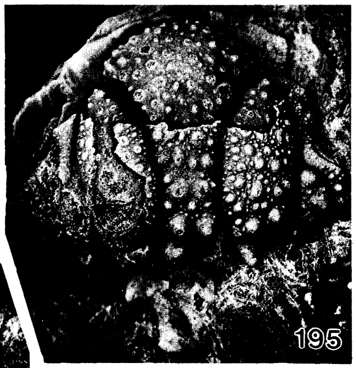
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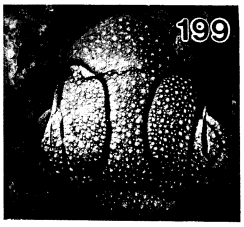
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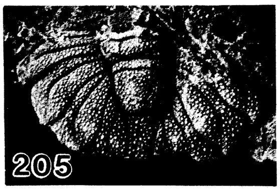
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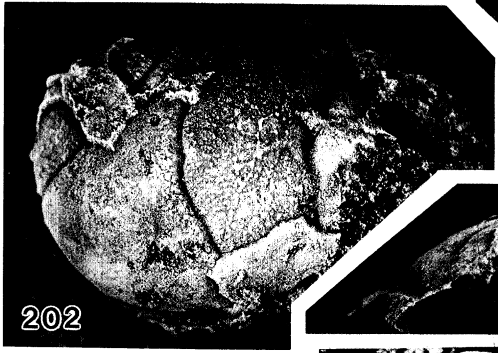
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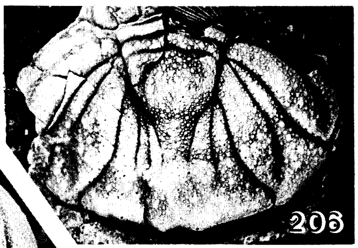
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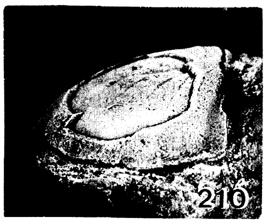
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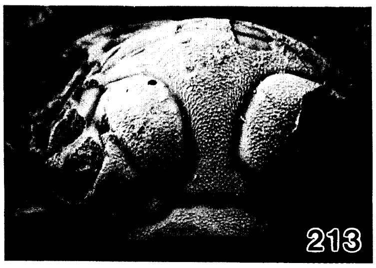
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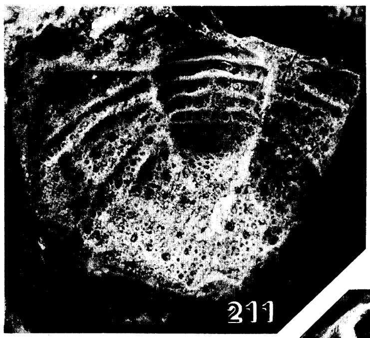
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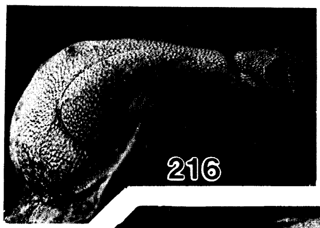
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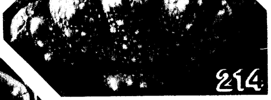
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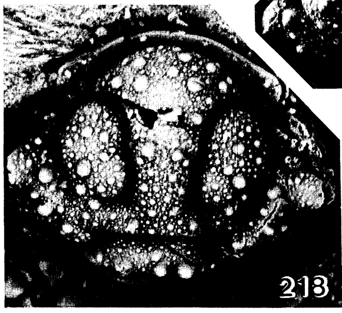
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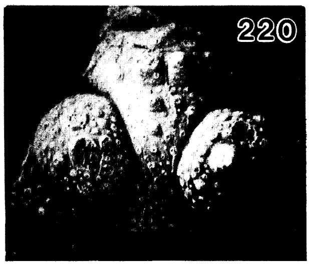
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Description of plate 10

(Photographs kindly supplied by Dr R. Männil)

Figures 193–197. *Hoplolichas conicotuberculatus* (Nieszkowski, 1859), Kukruse stage (Caradoc), Estonia. Figures 193 and 194, cranidium, GIE Tr2962, oblique anterior and palpebral views, magn. × 2. Kukruse. Figure 195, ?syntype cranidium, GIE Tr2099, ?figured Nieszkowski (1859, pl. 1, figs 7, 8); palpebral view, magn. × 2. Erra. Figure 196, syntype hypostome, GIE Tr2109, figured Nieszkowski (1859, pl. 1, fig. 10), Schmidt (1885, pl. 3, figs 22a, b); ventral view, magn. × 1.5. Erra. Figure 197, cranidium GIE Tr1590; palpebral view, magn. × 2. Ubja.

Figures 198–200, 203, 205 and 206. *Otarozoum eichwaldi* (Nieszkowski, 1857), Rakvere Stage (Caradoc) Estonia. Figure 198, librigena, GIE Tr29636; exterior view, magn. × 1.5. Rakvere. Figure 199, syntype cranidium, GIE Tr2136, figured Nieszkowski (1857, pl. 1, fig. 16); palpebral view, magn. × 1.5. Rakvere. Figure 200, cranidium, GIE Tr2139; palpebral view, magn. × 3. Rakvere. Figure 203, cranidium, GIE Tr2963a; palpebral view, magn. × 2. Rakvere. Figure 205, syntype pygidium, GIE Tr2137, figured Nieszkowski (1857, pl. 1, fig. 17); dorsal view, magn. × 3. Rakvere. Figure 206, pygidium, GIE Tr1589a, dorsal view, magn. × 1.5. Rägavere.

Figures 201, 202, 204 and 207–210. *Leiolichas illaenoides* (Nieszkowski, 1857), Keila Stage (Caradoc), Estonia. Figure 201, pygidium, GIE Tr2108b; dorsal view, magn. × 1.5. Erratic, Rakvere. Figure 202 and 204, cranidium, GIE Tr2961; oblique anterolateral and lateral views, magn. × 1.5. Jälgimäe. Figure 207, lectotype cranidium, GIE Tr2108a, figured Nieszkowski (1857, pl. 3, figs 3, 5); palpebral view, magn. × 1.5. Figures 208 and 210, paralectotype pygidium, GIE Tr2107, figured Nieszkowski (1857, pl. 3, fig. 4), Schmidt (1885, pl. fig. 29); dorsal and lateral views, magn. × 1.5. Erratic, Rakvere. Figure 209, cranidium, GIE Tr2966; palpebral view, magn. × 2. Tammiku.

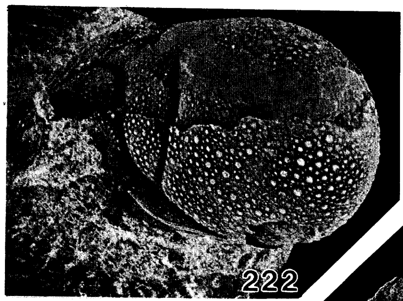
Figures 211, 215 and 220. '*Trochurus*' *mastocephalus* Öpik, 1937, Porkuni Stage (Caradoc), Porkuni, Estonia. Figures 211 and 215, syntype counterpart external mould and pygidium, GIE Tr2262, 2264, figured Öpik (1937, pl. 26, fig.2, pl. 28, fig. 2); ventral and dorsal views, magn. × 2. Figure 220, syntype cranidium, GIE Tr2261, figured Öpik (1937, pl. 23, fig. 4); dorsal view, magn. × 5.

Figures 212 and 213. *Autoloxolichas sanctamathiae* (Schmidt, 1885), Johvi Stage (Caradoc), Estonia. Figure 212, cranidium, GIE Tr2254, figured Öpik (1937, pl. 22, fig. 2); palpebral view, magn. × 2. Figure 213, cranidium, GIE Tr1956; palpebral view, magn. × 2. Alliku.

Figures 214, 218 and 219. *Hemiarges wesenbergensis* (Schmidt, 1885), Rakvere Limestone (Caradoc), Estonia, Figure 214, cranidium, GIE Tr2260a, figured Öpik (1937, text-fig. 18, pl. 22, fig. 7); palpebral view, magn. × 5. Rägavere. Figure 218, cranidium, GIE Tr2967; palpebral view, magn. × 5. Figure 219, pygidium, GIE Tr2260b; dorsal view, magn. × 5. Rägavere.

Figures 216 and 221. *Platylichas margaritifer* (Nieszkowski, 1857), Porkuni Stage (Caradoc), Porkuni, Estonia. Cranidium, GIE Tr2253; lateral and palpebral views, magn. × 3.

Figure 217. '*Amphilichas*' *hexadactylus* (Nieszkowski, 1859), Johvi Stage (Caradoc), Puhalepa, Estonia. Holotype pygidium, GIE Tr2252, figured Nieszkowski (1859, pl. 1, fig. 14), Öpik (1937, pl. 6, fig. 4); dorsal view, magn. × 3.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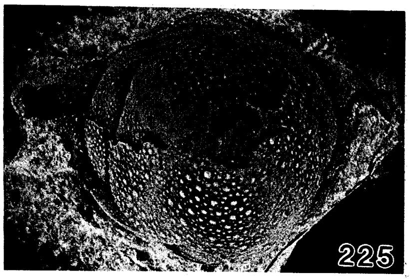
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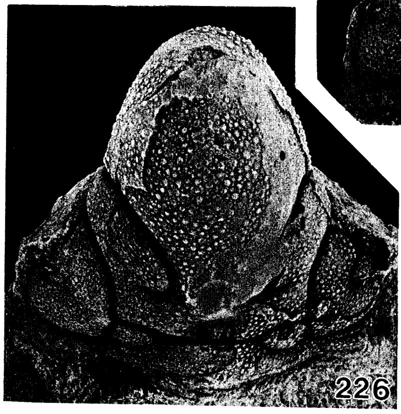
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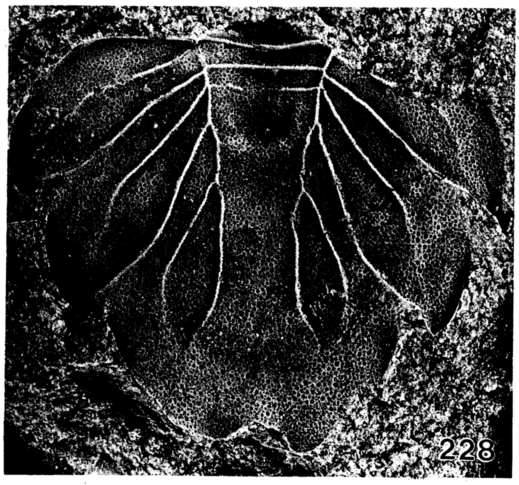
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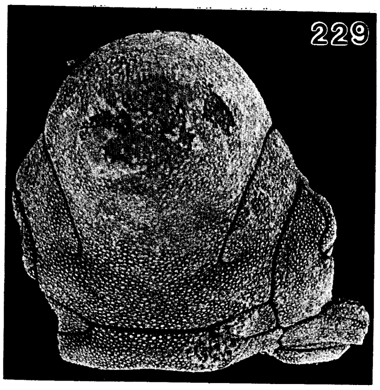
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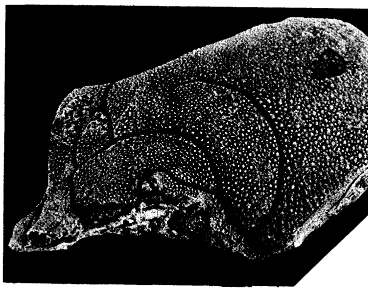
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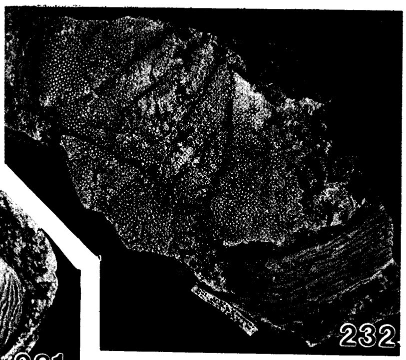
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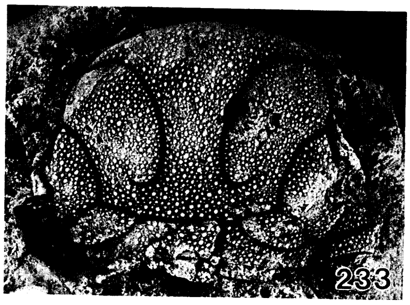
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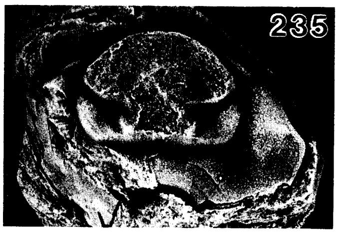
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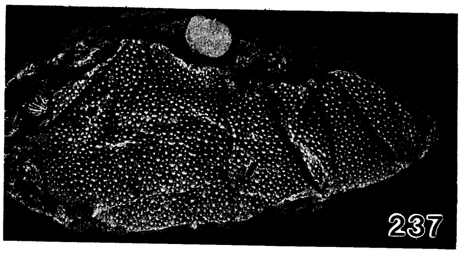
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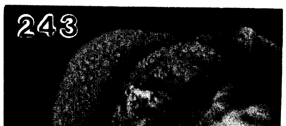
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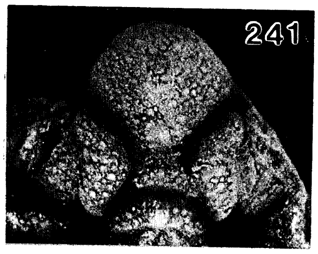
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DESCRIPTION OF PLATE 11

FIGURES 222–228. *Metopolichas celorrhin* (Angelin, 1854), Asaphus Limestone (Arenig), Sweden. Figures 222–226, cranidium, RM Ar2249, figured Warburg (1939, pl. 1, figs 3a–c); oblique anterolateral, occipital, lateral, anterior and palpebral views, magn. × 1.25. Humlenäs, Småland. Figure 227, paralectotype hypostome, RM Ar2256, figured Angelin (1854, pl. 35, fig. 16), Warburg (1939, pl. 2, fig. 3); ventral view, magn. × 1. Humlenäs, Småland. Figure 228, external mould of pygidium, RM Ar2253a, figured Warburg (1939, pl. 2, fig. 5); ventral view, magn. × 1. Enerum stranden. Öland.

FIGURES 229–232. *Metopolichas pachyrhinus* (Dalman, 1827), Asaphus Limestone (Arenig), Sweden. Figures 229, 230 and 231, holotype cranidium with *in situ* hypostome, RM Ar2246, figured Lovén (1845, pl. 1, figs 6a–d), Warburg (1939, pl. 4, figs 1a–c); palpebral, lateral and ventral views, magn. × 1.25. Hysbyfjöl at Skarpåsen, Östergötland. Figure 232, pygidium, UM D384a, figured Warburg (1939, pl. 4, figs 3a, b); dorsal view, magn. × 0.8. Rattvik, Dalarne.

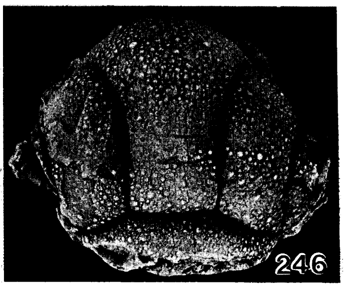
FIGURES 233, 235 AND 237. *Metopolichas patriarchus* (Wyatt-Edgell, 1866), Ffairfach Group (Upper Llanvirn), Pont Ladies Quarry. Llandeilo, South Wales. Figure 233, lectotype cranidium, BGS 35243, figured Wyatt-Edgell (1866, fig. 1), Whittard (1961, pl. 25, figs 14–16); dorsal view, magn. × 2.5. Figure 235, paralectotype hypostome, BGS 35245, figured Wyatt-Edgell (1866, fig. 3); ventral view, magn. × 2. Figure 237, paralectotype pygidium, BGS 35244, figured Wyatt-Edgell (1866, fig. 2); dorsal view, magn. × 1.75.

FIGURES 234 AND 238. *Metopolichas contractus* MacGregor, 1963, Upper Llandeilo, Berwyn Hills, North Wales. Figure 234, holotype cranidium, SM A46894, figured MacGregor (1963, pl. 118, figs 8–10); palpebral view, magn. × 2.5. Pen-y-graig, Plas-yn-glyn, Llanrhaiadr-ym-Mochnant. Figure 238, paratype pygidium (latex cast), SM A53031b, figured MacGregor (1963, pl. 118, figs 16, 17). 80 yards (72 m) north of Nant, 1 mile (1.6 km) north of Llanrhaiadar-ym-Mochnant.

FIGURES 236, 239 AND 240. *Metopolichas? klouceki* (Růžička, 1926), Třenice Formation, (Tremadoc), Ouzký, near Holoubkov, Czechoslovakia. Figure 236, plaster cast of paralectotype hypostome, NMP specimen, figured Růžička (1926, pl. 3, figs 5a, b); ventral view, magn. × 4. Figure 239, lectotype pygidium (latex cast), NMP Br684/58, figured Růžička (1926, pl. 3, figs 3a, b), Vaněk (1959, pl. 1, fig. 3); dorsal view, magn. × 7. Figure 240, plaster cast of paralectotype cranidium, NMP specimen, figured Růžička (1926, pl. 3, figs 4a–b); dorsal view, magn. × 8.

FIGURES 241, 242 AND 243. *Amphilichas? periformis* Warburg, 1925, Boda Limestone (Ashgill), Kallholn, Dalarne, Sweden. Syntype cranidium, UM Ar189 (D105), figured Warburg (1925, pl. 7, figs 32, 33); occipital, anterior and lateral views, magn. × 7.

FIGURES 244 AND 245. *Amphilichas* sp., Glyn Gower Group (Ashgill), crags 1100 ft (990 m) east 40° N of summit of Moel y Garnedd. Hypostome, BU 794, figured Whittington (1962, pl. 7, figs 17, 18); lateral and ventral views, magn. × 3.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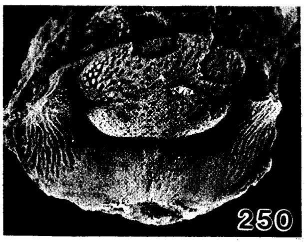
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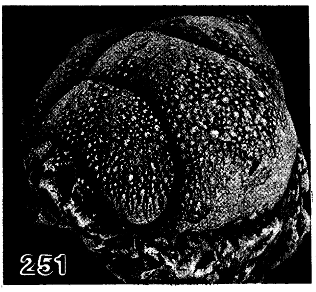
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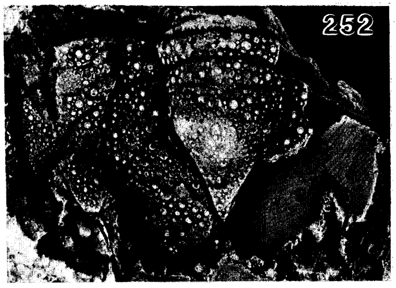
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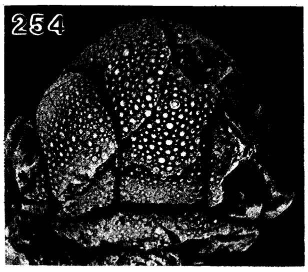
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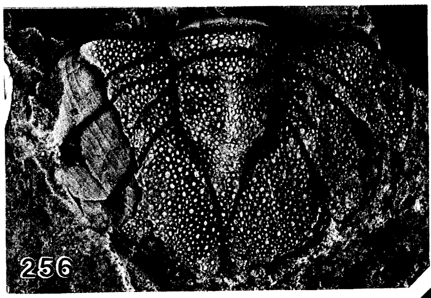
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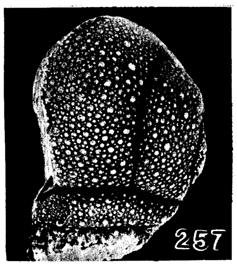
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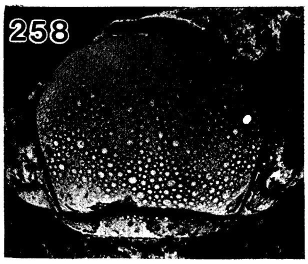
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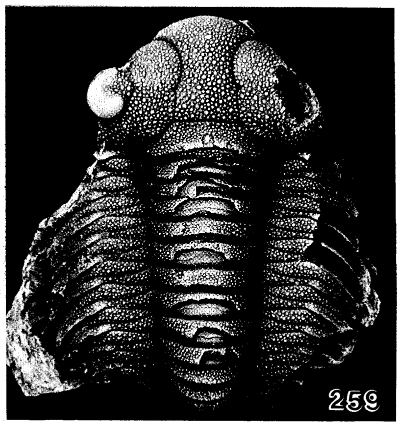
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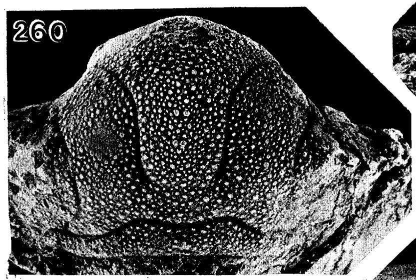
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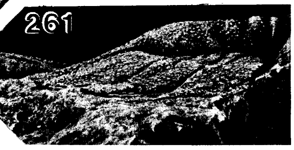
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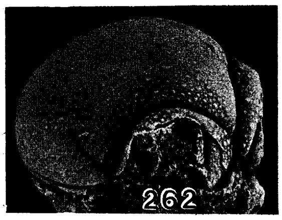
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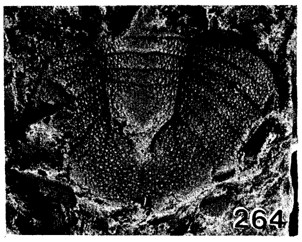
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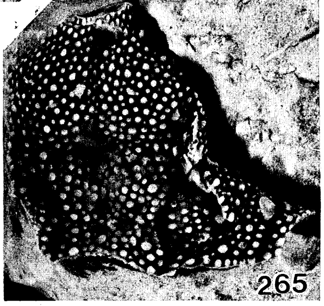
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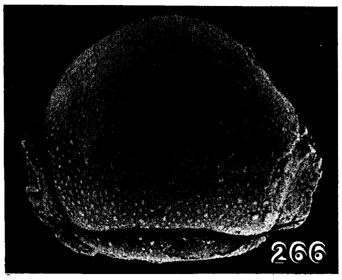
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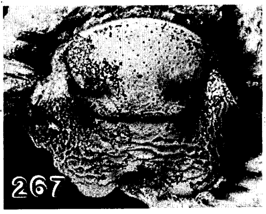
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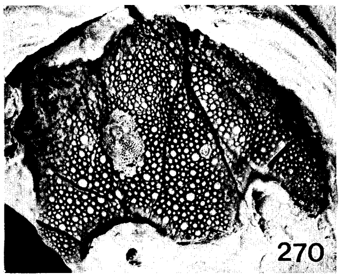
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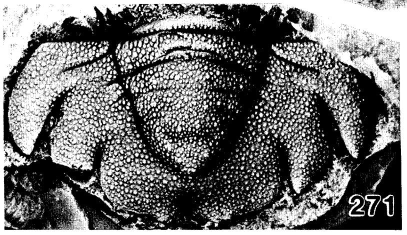
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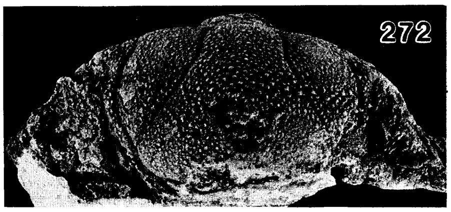
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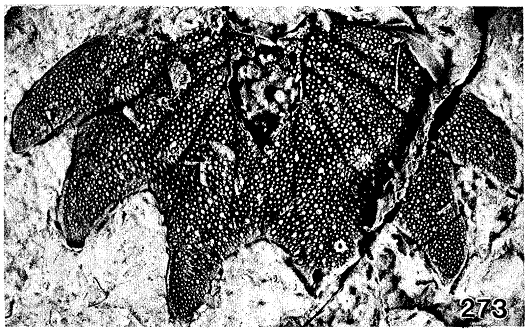
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DESCRIPTION OF PLATE 12

FIGURES 246–254 AND 257. *Amphilichas wahlenbergi* Warburg, 1925, Boda Limestone (Ashgill), Kallholn, Dalarne, Sweden. Figure 246 and 251, lectotype cranidium, UM D120, figured Warburg (1925, pl. 8, figs 33, 34); palpebral and oblique anterolateral views, magn. × 1.5. Figure 247, 248 and 253, paralectotype cranidium, UM D116, figured Warburg (1925, pl. 8, figs 27–29); palpebral, lateral and anterior views, magn. × 2.25. Figure 249, paralectotype librigena, UM D119, figured Warburg (1925, pl. 8, fig. 32); dorsal view, magn. × 2.5. Figure 252, pygidium, UM D115, figured Warburg (1925, pl. 8, fig. 26); dorsal view, × 2. Figure 254, paralectotype cranidium, UM D117, figured Warburg (1925, pl. 8, fig. 30); dorsal view, × 2.25. Figure 257, paralectotype cranidium, UM D118, figured Warburg (1925, pl. 8, fig. 31); palpebral view, magn. × 2.25. Chair of Kildare Limestone (Ashgill), Irish Republic. Figure 250, hypostome, BM It2041; ventral view, magn. × 3.

FIGURE 255. *Amphilichas rhinoceros* Slocum, 1913, Ordovician (Lower Maquoketa), Elgin, Iowa, U.S.A. Holotype cranidium, FMNH P11181, figured Slocum (1913, pl. 15, figs 5, 6); ventral view, magn. × 1.

FIGURES 256 AND 261. *Amphilichas hibernicus* (Portlock, 1843), Balclatchie Group (Caradoc), Ardmillan, Girvan district, Scotland. Pygidium, BM In22810, figured Reed (1914, pl. 5, fig. 2); dorsal and lateral views, magn. × 1.5.

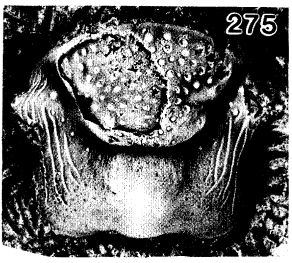
FIGURES 258, 262 AND 266. *Amphilichas lineatus* (Angelin, 1854), Boda Limestone, Dalarne, Sweden. Figure 258, cranidium, UM D123, figured Warburg (1925, pl. 8, fig. 40); palpebral view, magn. × 2.25. Kallholn. Figures 262 and 266, lectotype cranidium, RM Ar6040, figured Angelin (1854, pl. 38, figs 12, 12a); lateral and palpebral views, magn. × 2.25. Osmundsberget.

FIGURES 259, 263, 267 AND 271. *Apatolichas jukesi* (Billings, 1865), Allochthonous boulder in Cow Head Breccia (Arenig – lower Llanvirn), Lower Head, western Newfoundland. Figure 259 and 263, articulated specimen, GSC 16300, figured Whittington (1963, pl. 32, figs 6, 7, 8); occipital and lateral views, magn. × 4. Figure 267, hypostome, GSC 16303, figured Whittington (1963, pl. 33, figs 3, 4); ventral view, magn. × 5. Figure 271, pygidium, GSC 16301, figured Whittington (1963, pl. 32, figs 9–11); dorsal view, magn. × 4.

FIGURES 260, 264, 268, 269 AND 272. *Lyralichas bronnikovi* (Weber, 1932), Ordovician, Karatan Range, Tamdy River, Turkestan, U.S.S.R. Syntypes, all numbered 349, from Central Museum (VSEGEI) Leningrad. Figures 260, 268 and 272, cranidium, figured Weber (1932, pl. 4, figs 46, 47); occipital, lateral and anterior views, magn. × 2. Figure 264, pygidium, figured Weber (1932, pl. 4, fig. 48); dorsal view, magn. × 2. Figure 269, hypostome, figured Weber (1932, pl. 4, fig. 49); ventral view, magn. × 2.

FIGURES 265, 270 AND 273. *Probolichas*? sp., Pooleville Member, Bromide Formation (Blackriverian), Criner Hills, Carter Co., Oklahoma. Specimens from J. Page Collection. Figure 265, cranidium; dorsal view, magn. × 1.75. Figure 270, pygidium; dorsal view, magn. × 1. Figure 273, pygidium; dorsal view, magn. × 1.


274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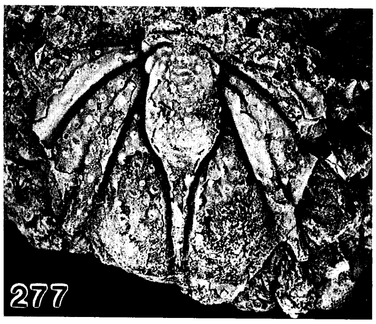
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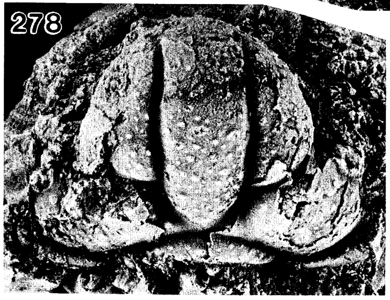
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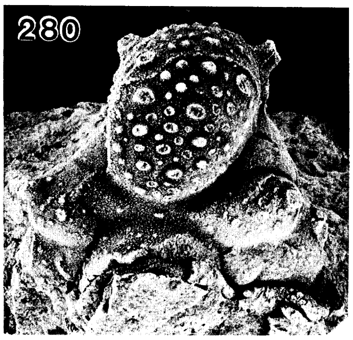
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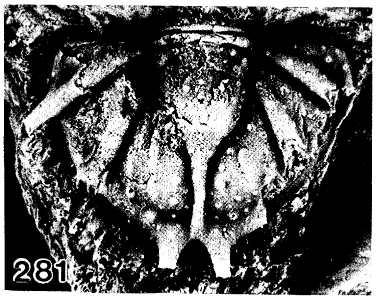
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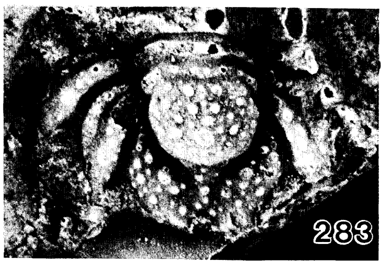
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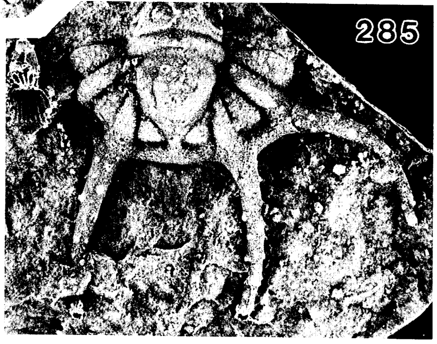
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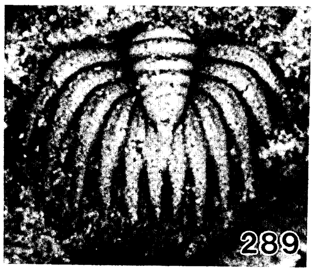
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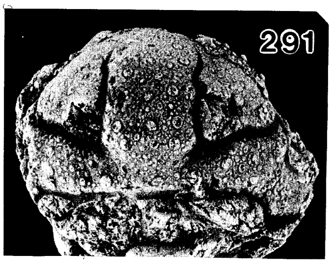
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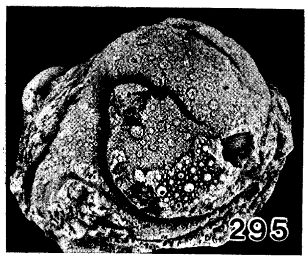
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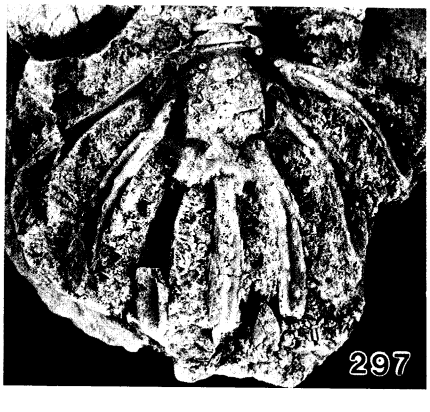
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Description of plate 13

Figures 274–279 and 281. *Acanthopyge* (*Acanthopyge*) *haueri* (Barrande, 1846), Acanthopyge Limestone (Eifelian), Koněprusy, Czechoslovakia. Figure 274, cranidium, SM H7716; occipital view, magn. ×2.5. Figure 275, hypostome, BM 42421; ventral view, magn. ×2.5. Figure 276, pygidium SM H7712; dorsal view, magn. ×2.25. Figure 277, pygidium, SM H7711; dorsal view, magn. ×1. Figures 278 and 279, cranidium, SM H7713; occipital view, magn. ×1.75; lateral view, magn. ×1.5. Figures 281, pygidium, SM H7716; dorsal view, magn. ×2.5.

Figures 280 and 285. *Trochurus? welleri* Foerste, 1917, Racine Dolomite (Late Wenlock-Ludlow), near Lemont, Illinois. (UC = University of Chicago collection, stored at FMNH). Figure 280, syntype cranidium, UC 10741, figured Weller (1907, pl. 22, fig. 1); occipital view, magn. ×1.5. Figure 285, latex cast of syntype pygidium, UC 10743A, figured Weller (1907, pl. 22, fig. 2); dorsal view, magn. ×1.5.

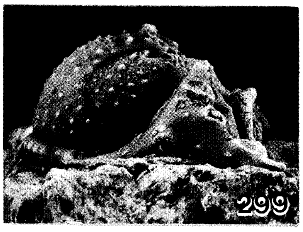
Figures 282 and 283. *Acanthopyge* (*Lobopyge*) *branikensis* (Barrande, 1872), Dvorce-Prokop Limestone (Pragian), Braník, Prague, Czechoslovakia. Figure 282, plaster replica of hypostome, NMP IT1380, figured Barrande (1872, pl. 16, fig. 33); ventral view, magn. ×7. Figure 283, plaster replica of lectotype pygidium, NMP IT1378, figured Barrande (1872, pl. 16, fig. 31), Přibyl & Erben (1952, pl. 11, fig. 6), Vaněk (1959, pl. 7, fig. 10); dorsal view, magn. ×7.

Figures 284, 286–288, 293, 294, 297 and 298. *Radiolichas aranea* (Holzapfel, 1895), Massenkalk Limestone (Givetian), western Germany. All specimens are syntypes in RTHA collections. Figures 284, 287 and 288, cephalon; lateral, occipital and oblique views, magn. ×3. Frettermuhle or Fretterthal. Figure 286, cephalon, figured Holzapfel (1895, pl. 13, fig. 1, 1a); occipital view, magn. ×2.5. Frettermuhle. Figure 293, pygidium, figured Holzapfel (1895, pl. 13, fig. 2); dorsal view, magn. ×3. Frettermuhle. Figure 294, hypostome, figured Holzapfel (1895, pl. 13, fig. 16); ventral view, magn. ×2.75. Frettermuhle. Figure 297, pygidium; dorsal view, magn. ×2.5. Fretterthal or Frettermuhle. Figure 298, pygidium, figured Holzapfel (1895, pl. 13, fig. 3); dorsal view, magn. ×3.5.

Figure 289. *Acanthopgye* (*Perunaspis*) *longispina* (Přibyl, 1949), Trebotov Limestone (Eifelian), Holyne near Prague, Czechoslovakia. Plaster replica of holotype meraspide transitory pygidium, NMP L6345, figured Přibyl (1949, pl. 1, figs 5, 6), Horný & Bastl (1970, pl. 18, fig. 6); dorsal view, magn. ×15.

Figures 290, 291 and 295. *Dicranogmus pustulatus* Hawle & Corda, 1847, Kopanina Formation (Ludlow), Koledník, Czechoslovakia. Plaster replica of holotype cranidium, NMP L11413, figured Hawle & Corda (1847, pl. 7, figs 77a, b), Šnajdr (1984*b*, pl. 7, fig. 10); lateral, occipital and oblique views, magn. ×1.75.

Figures 292 and 296. *Radiolichas devonianus* (Whidborne, 1889), Givetian (*terebratum* Biozone), Lummaton, Devonshire, England. Syntype cranidium, BM In25872, figured Morris & Fortey (1985, pl. 5, fig. 6); lateral and dorsal views, magn. ×2.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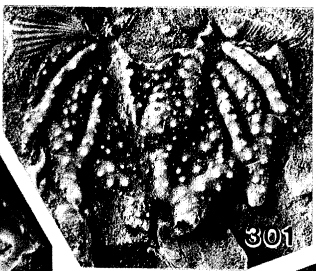
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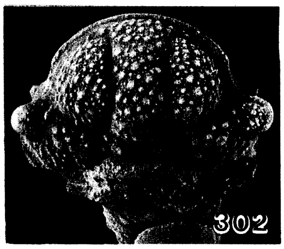
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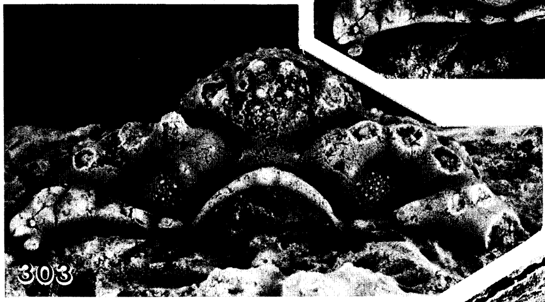
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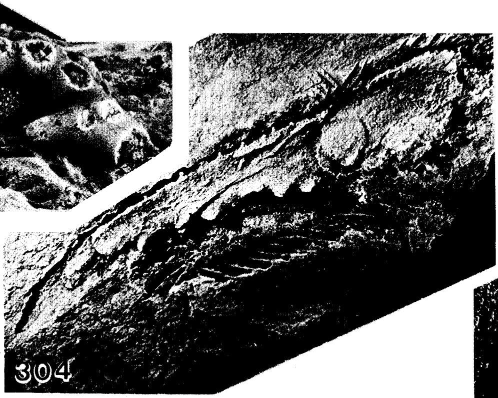
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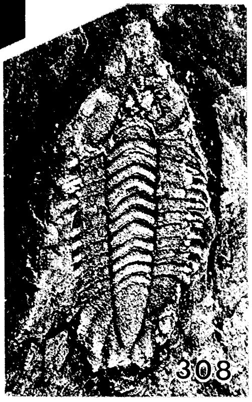
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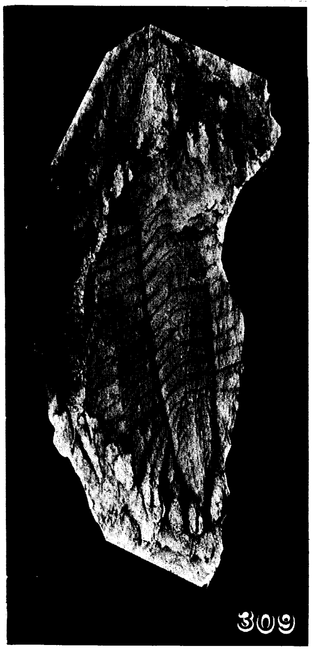
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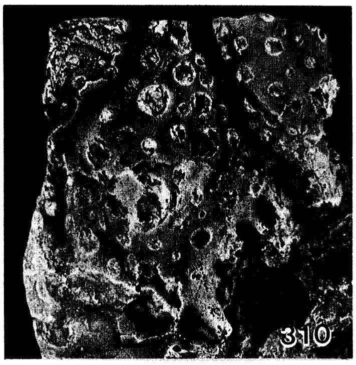
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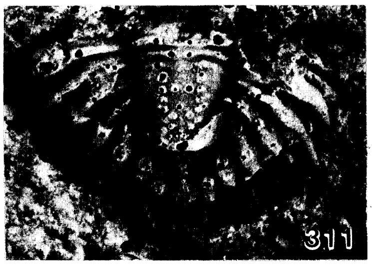
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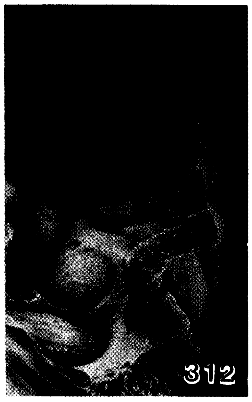
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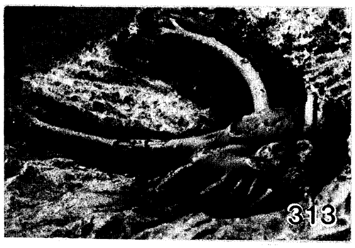
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Description of plate 14

Figures 299, 300 and 303. *Akantharges* sp., Eifelian, Erfoud, Morocco. Cranidium, BM It18686; lateral, occipital and posterodorsal views, magn. ×2.5.

Figures 301 and 302. *Acanthopyge* (*Lobopyge*) *hirsuta* (Fletcher, 1850). Much Wenlock Limestone Formation (Wenlock), Dudley, West Midlands, England. Figure 301, paralectotype pygidium, SM A3474, figured Fletcher (1850, pl. 27, figs 6, 6a), Thomas (1981, pl. 20, fig. 17); dorsal view, magn. ×3. Figure 302, cranidium, BM 44203, figured Fletcher (1850, pl. 27, figs 1a, b), Thomas (1981, pl. 20, figs 2a–c); dorsal view, magn. ×3.

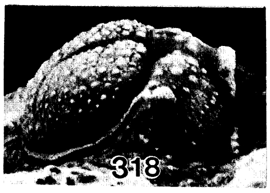
Figures 304, 305 and 307–309. *Akantharges gourdoni* (Barrois, 1886), 'schistes à trilobites de Cathervielle' (Eifelian), central Pyrenees, France. All specimens are syntypes in Museum d'Histoire Naturelle, Nantes. Photographs courtesy of Dr R. Feist. Figure 304, cephalon, CB 160, figured Barrois (1886, pl. 2, fig. 1d); dorsal view, magn. ×1.4. Figure 305, cranidium, CB 158, figured Barrois (1886, pl. 2, fig. 1a); dorsal view, magn. ×1.8. Figure 307, incomplete thorax and pygidium, CB 156, figured Barrois (1886, pl. 2, fig. 1c); dorsal view, magn. ×1.25. Figure 308, dorsal exoskeleton, CB 155, figured Barrois (1886, pl. 2, fig. 1g); dorsal view, magn. ×3.35. Figure 309, dorsal exoskeleton, CB 154, figured Barrois (1886, pl. 2, fig. 1f); dorsal view, magn. ×1.25.

Figure 306. *Terranovia nalivkini* Maksimova, 1977, Valnev Horizon (Pragian), Novaya Zemlya, U.S.S.R. Plaster replica of holotype pygidial mould, TSNIGR 10466, figured Maksimova (1977, pl. 5, fig. 1), Yolkin & Ormiston (1985, fig. 5.11); dorsal view, magn. ×0.75.

Figure 310. *Terranovia radugini* (Weber, 1949), Malobatchat Horizon (Pragian), Salairka River, Salair, U.S.S.R. Plaster replica of syntype, right posterior part of pygidium, TSNIGR (Central Museum, Leningrad) 6253, figured Weber (1949, pl. 3, fig. 3); dorsal view, magn. ×1.25.

Figure 311. *Eifliarges caudimirus* (Richter & Richter, 1917), Upper Calceola Beds (Eifelian), Gees, near Gerolstein, Eifel district, western Germany. Plaster replica of syntype pygidium, SMF X178c, figured Richter & Richter (1917, fig. 1e, pl. 5, fig. 2); dorsal view, magn. ×5.

Figures 312–317. *Ceratarges armatus* (Goldfuss, 1839), Eifelian, near Gerolstein, Eifel district, western Germany. Figures 312 and 315–317, composite specimen (cephalon added on to incomplete thorax and pygidium), RM Ar53131; lateral view of cephalon, magn. ×3; dorsal view of complete specimen, magn. ×2; anterior and posterior views of cephalon, magn. ×3. Upper Calceola Beds, Gees. Figures 313 and 314, pygidium, BM I16012; lateral and dorsal views, magn. ×2. Middle Calceola Beds, Salmerweg.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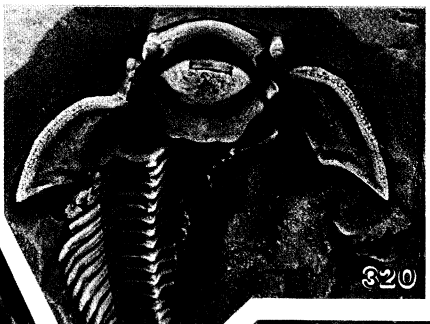
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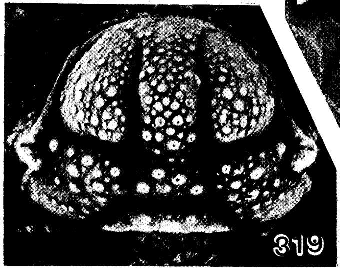
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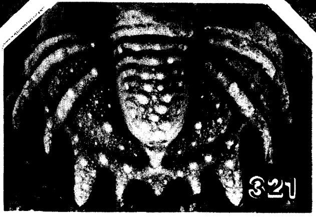
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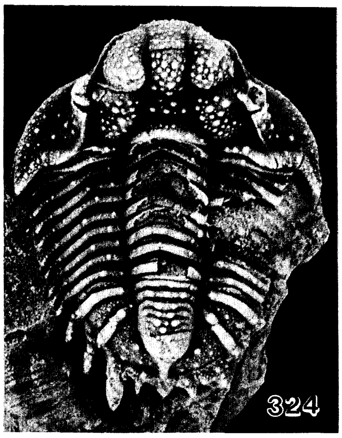
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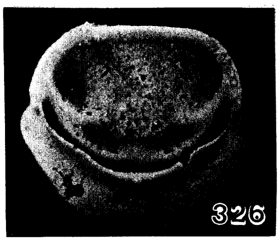
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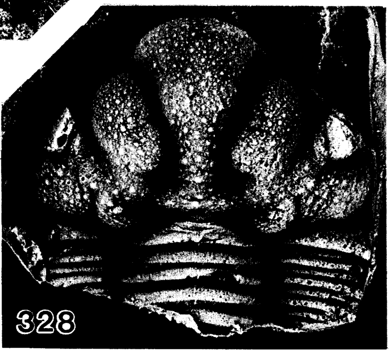
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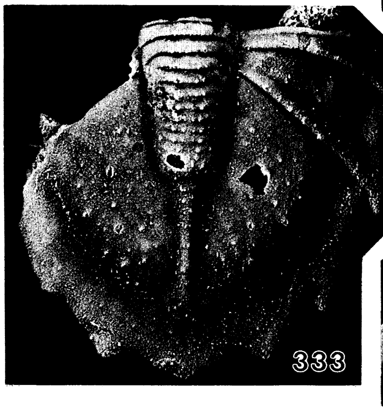
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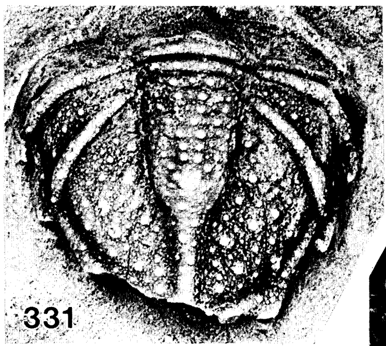
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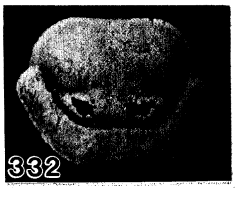
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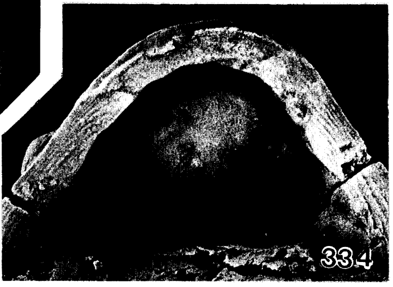
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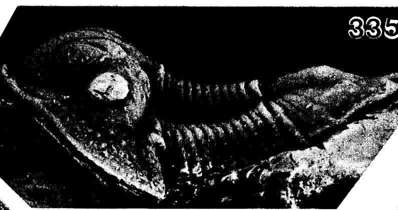
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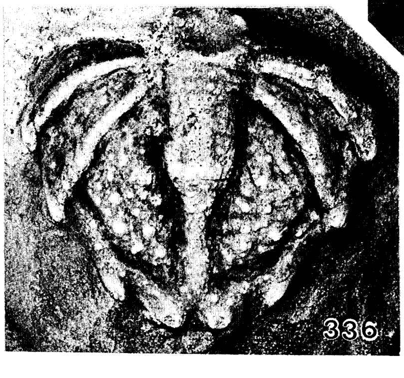
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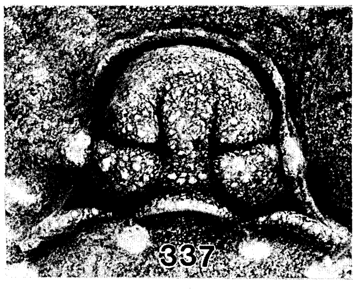
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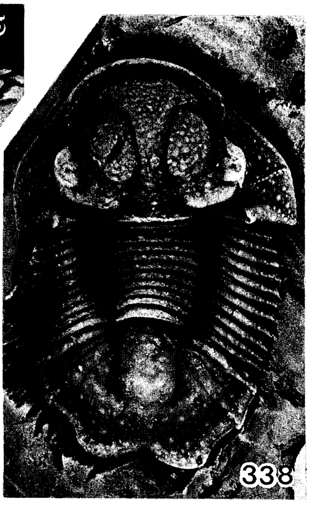
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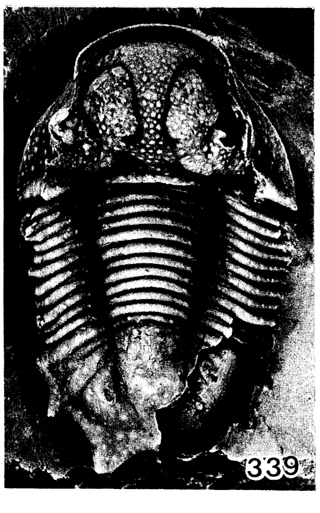
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DESCRIPTION OF PLATE 15

FIGURES 318–321 AND 324. *Richterarges bucklandii* (Milne Edwards, 1840), Much Wenlock Limestone Formation (late Wenlock), Dudley, West Midlands, England. Figures 318 and 319, cranidium, SM A3470, figured Fletcher (1850, pl. 27, fig. 2); lateral and dorsal views, magn. ×3.5. Figure 320, incomplete exoskeleton, SM A3486, figured Thomas (1981, pl. 20, fig. 19); ventral view, magn. ×3. Figure 321, pygidium, SM A28294, figured Thomas (1981, pl. 20, fig. 24); dorsal view, magn. ×4. Figure 324, dorsal exoskeleton, SM A3472, figured Fletcher (1850, pl. 27bis, figs 1, 1a); dorsal view, magn. ×3.5.

FIGURES 322, 323 AND 327. *Hemiarges maccullochi* (Reed, 1914), Starfish bed, Drummuck Group (Ashgill), Thraive Glen, Girvan, Ayrshire, Scotland. Figure 322, lectotype dorsal exoskeleton (see Morris & Tripp 1986, p. 174), BM In22744, figured Reed (1914, pl. 4, fig. 9); dorsal view, magn. ×2.5. Figure 323, latex cast of dorsal exoskeleton, BM In41240; dorsal view, magn. ×3. Figure 327, latex cast of dorsal exoskeleton, BM In41245; dorsal view, magn. ×2.5.

FIGURES 325, 326, 330, 332 AND 333. *Richterarges aquilonius* (Whittington, 1961), Read Bay Formation, member C (middle Ludlow), near Cape Hotham, Cornwallis Island, arctic Canada. All paratype specimens; GSC, Geological Survey of Canada. Figure 325, rostral plate, GSC 15263, figured Whittington (1961, pl. 57, figs 2, 3); ventral view, magn. ×15. Figure 326, hypostome, GSC 15261, figured Whittington (1961, pl. 57, figs 8, 9); dorsal view, magn. ×15. Figure 330, crandidium and librigena, GSC 15250, librigena figured Whittington (1961, pl. 56, fig. 19); dorsal views, magn. ×7.5. Figure 332, hypostome, now lost, figured Whittington (1961, pl. 57, figs 4, 5); ventral view, magn. ×15. Figure 333, pygidium, GSC 15255, figured Whittington (1961, pl. 56, fig. 25); dorsal view, magn. ×4.

FIGURES 328 AND 329. *Uripes geikei* (Etheridge & Nicholson in Nicholson & Etheridge, 1879), Drummuck Group (Ashgill), Thraive Glen, Girvan, Ayrshire, Scotland. Latex cast of cephalon and incomplete thorax, BM In22704, figured Reed (1914, pl. 13, figs 14, 14a); dorsal and oblique views, magn. ×3.

FIGURES 331, 336 AND 337. *Richterarges ptyonurus* (Hall & Clarke, 1888), Cobleskill Limestone (upper Přídolí), Schoharie, New York. Figure 331, paralectotype pygidium, NYSM 4556, figured Hall & Clarke (1888, pl. 19B, fig. 20), Whittington (1961, pl. 55, figs 8, 9, 11); dorsal view, magn. ×3.5. Figure 336, Paralectotype pygidium, NYSM 4557, figured Hall & Clarke (1888, pl. 19B, fig. 21), Whittington (1961, pl. 55, figs 5–7); dorsal view, magn. ×4. Figure 337, lectotype cranidium, NYSM 4555, figured Hall & Clarke (1888, pl. 19B, fig. 19), Whittington (1961, pl. 55, figs 1–4); dorsal view, magn. ×4.

FIGURES 334, 335, 338 AND 339. *Uripes scutalis* (Salter, 1873), Coalbrookdale Formation (Wenlock), Malvern, England. Figure 334, complete exoskeleton, SM A3484, figured Reed (1901, pl. 1, figs 2, 3,.4 (*pars*)), Thomas (1981, pl. 21, figs 4a, b); cephalon in ventral view showing hypostome, magn. ×3. Figures 335 and 338, dorsal exoskeleton, BGS 19531, figured Thomas (1981, pl. 21, fig. 2); lateral and dorsal views, magn. ×2. Figure 339, dorsal exoskeleton, BM 58998; dorsal view, magn. ×2.


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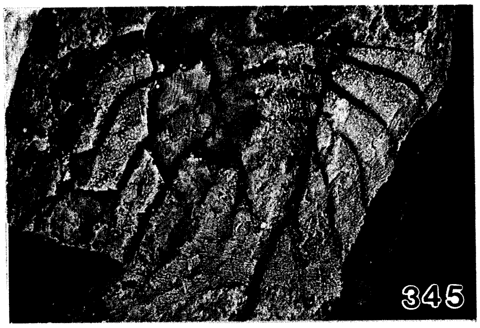
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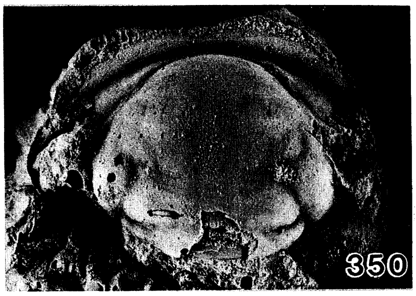
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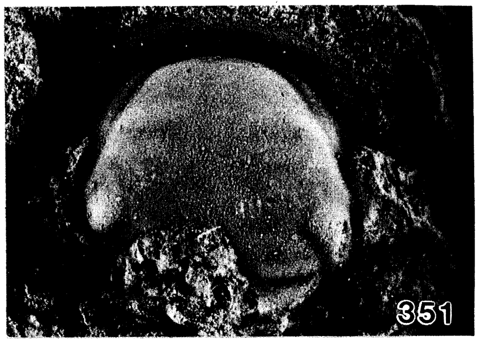
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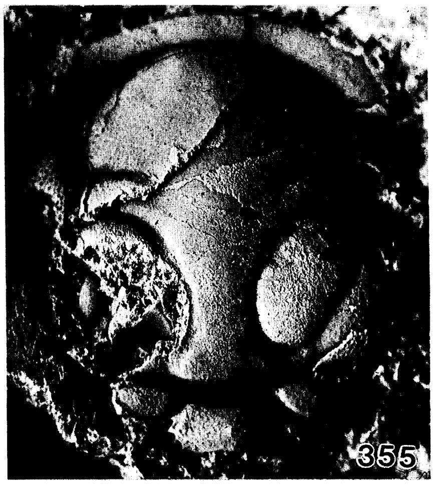
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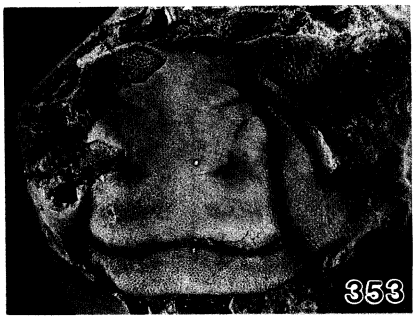
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the shallow exsagittal furrow bounding the posterolateral cranidial lobe abaxially cannot be the axial furrow, although it has previously been interpreted as such (see, for example, Phleger 1936; Tripp in Moore 1959).

The pattern of glabellar lobation seen in *Lichakephalus* is broadly similar to that of *Platylichas*, except that the axial furrow is present abaxial to L1b, and there is a lateral glabellar furrow developed a short distance in front of the bullar lobe. Assuming that the bullar lobe in *Lichakephalus* is composed of L2 alone – a reasonable assumption in a primitive form – this furrow is best interpreted as S3.

5. Systematic palaeontology

(*a*) Order LICHIDA Moore, 1959

Diagnosis. Glabella typically widest across occipital ring and extending forwards to anterior margin or almost so; no preglabellar field. Median glabellar lobe expanding (tr.) anteriorly and flanked by L1a and L1b and bullar lobes; L1a indenting front of occipital ring abaxially. Lateral lobes may be variously fused and their bounding furrows effaced. Facial suture

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Description of plate 16

Figures 340–345. *Lichakephalus erbeni* Sdzuy, 1955, Leimitz Shales (Tremadoc), sunken road ('Hohlweg') north of Leimitz, near Hof, Germany. Figure 340, plaster replica of cranidium, SMF 28775a, figured Sdzuy (1979, figs 5E–F); dorsal view, magn. ×1.5. Figure 341, plaster replica of holotype cranidium, SMF 1812a, figured Sdzuy (1955, pl. 5, fig. 5); dorsal view, magn. ×4. Figure 342, plaster replica of cranidium, SMF 11779, figured Sdzuy (1970, pl. 2, figs 7a, b); dorsal view, magn. ×3. Figure 343, plaster replica of paratype pygidium, SMF 1812c, figured Sdzuy (1955, pl. 5, fig. 31); dorsal view, magn. ×4.5. Figure 344, plaster replica of cranidium, SMF 28774a, figured Sdzuy (1979, figs 5A–D); dorsal view, magn. ×4.5. Leimitz Shales (Tremadoc), Leimitz. Figure 345, plaster replica of paratype pygidium, SMF 1812e, figured Sduzy (1955, pl. 5, figs 33, 33a), dorsal view, magn. ×1.25.

Figure 346. *Acidaspidella limita* Rozova, 1963, Upper Cambrian, northwest Siberian Platform. Plaster replica of cranidium, NMV (Museum of Victoria) P71058, ?figured Rozova (1963, pl. 1, fig. 4); palpebral view, magn. ×13.

Figures 347 and 348. *Eoacidaspis amplicauda* Lazarenko, 1968*a*, Upper Cambrian, northwest Siberian Platform. Figure 347, plaster replica of paratype cranidium, NMV P72564, figured Lazarenko (1968*a*, pl. 18, fig. 11; 1968b, pl. 12, fig. 14), Bruton (1983, pl. 18, figs 3, 4); palpebral view, magn. ×2.5. Figure 348, plaster replica of paratype pygidium, NMV P72565, figured Lazarenko (1968*a*, pl. 18, fig. 12); dorsal view, magn. ×2.5.

Figure 349, *Eoacidaspis? cyclica* Rozova, 1964, Upper Cambrian, northwest Siberian Platform. Plaster replica of cranidium, NMV P71053; palpebral view, magn. ×3.5.

Figure 350. *Eoacidaspis? calva* Chernysheva in Poletaeva, 1956, Middle Cambrian, northwest Siberian Platform. Plaster replica of holotype cranidium, NMV P72435, figured Chernysheva in Poletaeva (1956, pl. 32, fig. 10), Bruton (1983, pl. 83, figs 1, 2); palpebral view, magn. ×2.5.

Figure 351. *Eoacidaspis? aliquantula* Rozova, 1964, Middle Cambrian, northwest Siberian Platform. Plaster replica of cranidium, NMV P70999, figured Rozova (1964, pl. 4, fig. 21); palpebral view, magn. ×8.

Figure 352. *Acidaspides precurrens* Lermontova, 1951, Upper Cambrian, Kazakhstan. Plaster replica of paralectotype pygidium, NMV P72638, figured Lermontova (1951, pl. 6, fig. 9); dorsal view, magn. ×5.

Figures 353, 354, 356 and 357. *Acidaspidina plana* Lazarenko, 1960, Upper Cambrian, north Siberian Platform. Figure 353, plaster replica of cranidium, NMV P72580, figured Lazarenko (1960, pl. 4, figs 9, 10; 1968*b*, pl. 11, fig. 12), Bruton (1983, pl. 88, fig. 13); palpebral view, magn. ×2.5. Figure 354, plaster replica of cranidium, NMV P72582, figured Lazarenko (1960, pl. 4, fig. 13); palpebral view, magn. ×4.5. Figure 356, plaster replica of cranidium NMV P71110, figured Rozova (1968, pl. 3, fig. 16); palpebral view, magn. ×3. Figure 357, plaster replica of pygidium, NMV P72581, figured Lazarenko (1960, pl. 4, figs 11, 12; 1968*b*, pl. 11, fig. 13); dorsal view, magn. ×2.5.

Figures 355 and 358. *Lichakephalina schilikta* Antcygin in Varganov, 1973, Lower Arenig, Middle Urals. UGS specimens; photographs courtesy of Dr V. A. Antcygin. Figure 355, cranidium; dorsal view, magn. ×3. Figure 358, paratype pygidium, figured Antcygin in Varganov (1973, pl. 19, fig. 16); dorsal view, magn. ×1.5.

opisthoparian. Rostral plate wide and short (except in species with anterior prolongation), laterally defined by connective sutures which converge backwards, at least initially. Rostral suture marginal or almost so. Thorax of 10–11 segments with simple spinose tips. Pygidium often similar in size to cranidium, with 2–6 pairs of furrowed pleurae (most commonly 2 or 3). Exoskeleton frequently spinose and densely granulate.

Stratigraphical range ? Middle Cambrian, Upper Cambrian–Givetian.

Remarks. The order comprises the Lichidae, containing five subfamilies, and the Lichakephalidae, within which we recognize no subfamilial groups. Those genera included in the Lichakephalidae are only known from fragmentary material and they do not form a demonstrably monophyletic group. The family is provisionally circumscribed here, pending improved understanding of the relationships between its constituent genera. Relationships between these various family-group taxa are discussed in detail below (§6).

(*b*) Family LICHIDAE Hawle & Corda, 1847

[*nom. correct.* Angelin 1854 ex Lichades Hawle & Corda, 1847]

Diagnosis. Lichida typically with L1a, L1b and bullar lobes defined, but these lobes may be partly or completely fused with each other or with adjacent parts of the fixigena. No lateral glabellar furrows impressed anterior to bullar lobe. Anterior sections of facial suture parallel or converging forwards. Eye ridge typically absent.

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

[*nom. transl.* Gürich 1901 ex Lichades Hawle & Corda, 1847]

Diagnosis. Lichidae with glabella as wide or wider at occipital ring than at bullar lobe, but markedly constricted in between; longitudinal furrow terminating at base of bullar lobe or extending to occipital furrow; S1 incomplete abaxially or absent, except in *Dicranopeltis*; L1a may be present. Hypostome subhexagonal in outline (excluding posterior notch) and approximately as wide as long, with shoulders situated at about midlength; middle furrow strongly oblique, bifurcating adaxially around slightly inflated maculae; posterior border furrow commonly poorly defined. Pygidium with three pairs of pleural furrows (except in some species of *Uralichas*) and 1–4 axial rings; anterior and posterior pleural bands flattened; pleural margin with 2–4 (or possibly more in some *Uralichas* species) pairs of flattened spines.

Genera included. Lichas Dalman, 1827; *Arctinurus* Castelnau, 1843; *Dicranopeltis* Hawle & Corda, 1847; *Nonix* Lane, 1984; *Oinochoe* gen.nov.; *Pseudotupolichas* Phleger, 1936; *Trimerolichas* Phleger, 1936; *Uralichas* Delgado, 1892.

Stratigraphical range. Llanvirn–Gedinnian.

Genus *Lichas* Dalman, 1827

[Subjective synonyms: *Autolichas* Reed, 1923;
?*Apolichas* Kobayashi & Hamada, 1974]
Figures 3–10, 13–15 and ?11, plate 1.

Type species. Original designation; *Entomostracites laciniatus* Wahlenberg, 1818, p. 34, from the Dalmanitina Beds (Ashgill), Sweden. Holotype: internal mould of pygidium, UM Vg2; figured Wahlenberg (1818, pl. 2, fig. 2*), Warburg (1925, fig. 20; 1939, pl. 9, fig. 1), Temple (1969, pl. 3, fig. 5) (figure 5 herein).

Other species. L. affinis Angelin, 1854; *L. breviceps breviceps* Hall, 1863*a*; *L. breviceps clintonensis*

Foerste, 1895; *L. ferrisi* (Weller, 1907); *L. keisleyensis* Reed, 1896; *L. marocanus* Destombes, 1968; *L. pugnax* Winchell & Marcy, 1865; *L. silvestris* Reed, 1925; *L. subpropinquus* McCoy, 1851; *L? truncatus* (Kobayashi & Hamada, 1974).

Stratigraphical and geographical range. Ashgill–Wenlock; North America (Illinois, Indiana, Ohio), Ireland, England, Scotland, Sweden, Morocco, ?Japan.

Diagnosis. Lichine with glabella moderately convex (sag., exsag.) and not overhanging anterior border. Longitudinal furrow normally terminating at base of bullar lobe but may extend weakly to occipital furrow. Bullar lobe fused with L1b; L1a circumscribed, not extending as far abaxially as occipital ring. Pygidium with first two pleurae ending in short spines; remainder of pygidial margin rounded or obtusely pointed medially. Axis one third to one half sagittal length of pygidium; postaxial band initially narrowing behind axis but expanding strongly distally.

Remarks. The name *Lichas* and its various derivatives have generally been regarded as masculine in gender but were considered to be feminine by some early workers, such as Beyrich (1845, 1846), Dames (1877) and Schmidt (1885); however, Schmidt (1907) later regarded them as masculine. This matter was discussed by Tripp (1960, p. 233) in a submission to the International Commission on Zoological Nomenclature (ICZN), who subsequently ruled in Opinion 615 (*Bull. zool. Nom.* **18**, 359 (1961)) that *Lichas* is masculine in gender.

Autolichas was proposed by Reed (1923) as a subgenus of *Lichas* to include *L. affinis* and *L. laciniatus*, with the former as type species (see preceding discussion on history of classification). We agree with Warburg (1939) that *L. affinis* is indistinguishable from *L. laciniatus* at the generic or subgeneric level, and therefore regard *Autolichas* as a junior subjective synonym of *Lichas*.

Kobayashi & Hamada (1974, p. 79) erected *Apolichas* for their species *A. truncatus* from the Silurian of Japan. The type material of *A. truncatus* consists of an incomplete cranidium, a hypostome, and two fragmentary pygidia (Kobayashi & Hamada 1974, pl. 8, figs 9–12) (figure 11 herein). The hypostome is unlike that of any known lichid in the shape of the lateral border and the convexity of the middle body, and we consider that it probably belongs to a species of the cheirurid genus *Sphaerexochus*. We have examined casts of the other specimens and consider them to be so incomplete as to be virtually uninterpretable. Kobayashi & Hamada stated that the cranidium has a longitudinal furrow that extends to the occipital furrow and a bullar lobe that is fused with L1 (expressed in our terminology). These features cannot be determined from the specimen itself, however, because the posterior part of the glabella is not preserved and the occipital ring and occipital furrow are absent (although Kobayashi & Hamada described the occipital ring as 'ill-preserved', and mentioned the presence of a rudimentary 'occipital lobe'). From the pygidium it is impossible to be certain about the shape of the axis (although it certainly does not narrow to a point posteriorly, as shown in Kobayashi & Hamada's reconstruction in their text-fig. 6A), the number of pleural furrows, or the presence of marginal spines. The segment adjacent to the postaxial band, however, does not have a distal spine, the shallow notch in the margin of the pygidium in Kobayashi & Hamada's pl. 8, fig. 10 being due to breakage. In the absence of a posterior pair of marginal spines, and in the strongly expanded postaxial band, the pygidium is similar to pygidia of *Lichas* species, and we therefore tentatively synonymize *Apolichas* with that genus.

Genus *Arctinurus* Castelnau, 1843

[Objective synonyms: *Platynotus* Conrad, 1838 non Fabricius, 1801;
Oncholichas Schmidt, 1885; *Pterolichas* Gürich, 1901]
Figures 12, 16–22, plate 1; and ?23–27 and 29, plate 2.

Type species. Monotypy; *Paradoxus* [*sic*] *boltoni* Bigsby, 1825, p. 365, from the Rochester Shale (Wenlock) of New York. Holotype: exfoliated dorsal exoskeleton with glabella broken away to reveal hypostome, BM It15690; figured Bigsby (1825, pl. 23), Morris & Fortey (1985, pl. 7, fig. 1).

Other species. A. clairensis Thomas, 1929; *A. occidentalis* (Hall, 1863*a*); *A. thompsoni* Miller & Unklesbay, 1944; *A? norvegicus* (Angelin, 1854); *A? obvius* (Hall, 1870).

Stratigraphical and geographical range. Llandovery–Wenlock; Canada (Ontario), U.S.A. (Arkansas, Illinois, Indiana, ?Iowa, New York, Tennessee, Wisconsin), ?England, ?Norway.

Diagnosis. Lichine with glabella rather flattened (sag., exsag.) posteriorly, curving gently downwards anteriorly; anterior border expanded medially to form broadly rounded, subpointed or spatulate process. Longitudinal furrow terminating in a broad curve at base of bullar lobe. Bullar lobe confluent with L1b abaxially, more inflated than median glabellar lobe; L1a very small, circumscribed and slightly depressed. Width (tr.) of occipital ring greater than palpebral width of cranidium. Palpebral lobe large and flattened (tr.), anterior edge lying adjacent to bullar lobe and posterior edge level with median part of occipital furrow. Pygidium subquadrate to subpentagonal in outline, posterior margin with three pairs of spines whose tips all lie behind midlength of postaxial band. Axis one third to two fifths sagittal length of pygidium, and one quarter to one third maximum width; postaxial band expanding distally or subparallel-sided. First two pleural furrows flexed backwards at fulcrum to lie subparallel to sagittal line; third pleural furrows converging slightly distally. Pleural furrows extend virtually to tips of marginal spines; third spine pair also carries extension of furrow outlining postaxial band.

Remarks. Conrad (1838) erected the genus *Platynotus* for *A. boltoni* but the former name had previously been used by Fabricius (1801, p. 138) for a genus of Coleoptera. Schmidt (1885, p. 31) was unaware of the existence of *Arctinurus* and chose *A. boltoni* as the type species of his 'group' *Oncholichas*, in which he also included *Pseudotupolichas ornatus* and several other unrelated species. Gürich (1901, p. 527) noted that *A. boltoni* differs from *P. ornatus* in several features of the cephalon. He proposed to restrict *Oncholichas* to species he considered to be similar to *P. ornatus*, and erected *Pterolichas* for a group of North American species that included *A. boltoni*. Reed (1902) subsequently designated *A. boltoni* as type species of *Pterolichas*. Hence *Oncholichas* and *Pterolichas* are both junior objective synonyms of *Arctinurus*, despite the fact that Reed (1902, 1923) sought to retain *Oncholichas* by nominating *P. ornatus* as type species instead of *A. boltoni*.

In previous diagnoses of *Arctinurus* (Weller 1907, p. 247; Phleger 1937*a*, p. 255; Tripp in Moore 1959, p. O496) it has been stated that the longitudinal furrow extends to the occipital furrow, but in *A. boltoni* and closely related species from the Silurian of North America, the longitudinal furrow terminates in a hook-like curve at the base of the bullar lobe. There is, however, a tendency in these species for the abaxial part of L1b behind the bullar lobe to be slightly concave (tr.). These poorly defined concave areas are not impressed furrows and do not interrupt the exoskeletal tuberculation, but in the line drawings of *A. boltoni* given by Phleger

(1936, fig. 17) and Tripp (in Moore 1959, fig. 392, 4a) they are inaccurately shown as short extensions of the longitudinal furrow parallel to the sagittal line. In addition to the form of the longitudinal furrow, *Arctinurus* is characterized especially by the weak convexity of the glabella, the considerable width (tr.) of the occipital ring, the very small L1a, the large palpebral lobe with its posterior edge level with the occipital furrow, and the pygidium whose first two pleurae are flexed strongly backwards abaxially, so that the tips of their marginal spines lie well behind the axial terminus.

On the basis of this combination of characters, we consider that most of the species listed by Tripp (1958, p. 575) as belonging to *Arctinurus* should be excluded from the genus. Many of the excluded species are known only from cranidia characterized, among other features, by a longitudinal furrow that extends to the occipital furrow. Some of these species can be accommodated in *Pseudotupolichas* but others, such as *Lichas constrictus* Whittard, 1938 and *Amphilichas shallopensis* Twenhofel, 1928, appear to represent unnamed genera. We assign two species to *Arctinurus* with question. *A? norvegicus* (Angelin, 1854) is based on a pygidium originally believed to be from the lower Ordovician of Norway, but Warburg (1937) showed that the specimen came from strata of Llandovery age, and figured a cranidium that she considered possibly to belong to the same species. That this cranidium is correctly assigned to *norvegicus* is proven by an articulated exoskeleton shown to us by Dr G. Helbert, who is redescribing the species. The pygidium of *norvegicus* appears to be indistinguishable from those of *Arctinurus* species, but the cranidium differs in having a longitudinal furrow that extends to the occipital furrow, an anterior border that is not expanded medially, and a slightly larger L1a. Warburg (1937) tentatively included *norvegicus* in *Trimerolichas* but we consider that that genus should for the present be restricted to the type species, which in any case differs somewhat from *norvegicus* in the shape of the lateral glabellar lobe. *A? norvegicus* was also recorded by Whittard (1938) from the Llandovery of England. *A? obvius* (Hall, 1870), from the Llandovery or Wenlock of Iowa, is known only from an incomplete internal mould of a cranidium but resembles *A? norvegicus* in those features that are preserved.

Genus *Dicranopeltis* Hawle & Corda, 1847

[Objective synonym: *Trachylichas* Gürich, 1901. Subjective synonyms:
Dicranopeltoides Phleger, 1936; *Raymondarges* Phleger, 1937*c*;
Tsunyilichas Chang, 1974]
Figures 28, 30–42 and 45, plate 2.

Type species. Subsequent designation Reed (1902, p. 61); *Lichas scabra* Beyrich, 1845, p. 28, from the Liteň Formation (Wenlock), Czechoslovakia. Holotype: pygidium, PMB k159; figured Beyrich (1845, fig. 16) (figure 36 herein).

Other species. D. arkansana (Van Ingen, 1901); *D. bifurcata* (Reed, 1896); *D. canadensis* (Logan, 1846); *D. decipiens* (Winchell & Marcy, 1865), *D. eopolytoma* Kolobova, 1978; *D. fragosa* Phleger, 1937*c*; *D. greeni* Mason, 1934; *D. imperfecta* Šnajdr, 1975; *D. lindstroemi* (Pompecki, 1890); *D. nereus* (Hall, 1863*b*); *D. norrisiensis* Shrock & Twenhofel, 1939; *D. polytoma* (Angelin, 1854); *D. pustulosa* (Chang, 1974); *D. reporyjensis* (Phleger, 1937*c*); *D. salteri* (Fletcher, 1850); *D. scabra propinqua* (Barrande, 1846); *D. triquetra* (Lindström, 1885); *D. woodwardi* (Reed, 1903).

Stratigraphical and geographical range. Ashgill–Ludlow; North America (Arkansas, Illinois, Newfoundland, New York, Ontario, Quebec, Wisconsin), Ireland, England, Scotland, Sweden, Germany, Czechoslovakia, U.S.S.R. (Kazakhstan, Tadzhikistan), China (Guizhou Province).

Diagnosis. Lichine with glabella strongly convex (sag., exsag.), sometimes overhanging anterior border; median lobe rarely extended from its highest point into a long anterodorsally directed spine. Glabella narrowing anteriorly and posteriorly towards S1. Bullar lobe circumscribed; longitudinal furrow may extend behind bullar lobe as a broad, shallow depression not disrupting exoskeletal tuberculation. L1 usually subdivided into L1a and L1b, but these are commonly confluent abaxially. Posterior margin of cephalon with deep subgenal notch; genal spine slender. Hypostome with well-developed sculpture of tubercles and pits on middle body and terrace ridges on lateral border; anterior lobe of middle body subrhombic. Pygidium with three pairs of marginal spines; axis one-third to one-half sagittal length of pygidium; postaxial band narrowing posteriorly.

Remarks. The hypostome of *Dicranopeltis* is distinctive in having the middle furrow meeting the lateral border furrow at the anterolateral extremity of the middle body, opposite the anterior wings (Thomas 1981, pl. 19, figs 9, 13). As a result, the anterior lobe of the middle body is rhombic in outline, as it is also in *Pseudotupolichas* (figure 67). In most other lichines the intersection of the middle furrow and the lateral border furrow lies well behind the level of the anterior wings, so that the anterior lobe of the middle body is subrectangular or trapezoidal. This is the arrangement in *Lichas* (figure 10), *Uralichas* (figure 85), *Arctinurus* (figure 17) and *Oinochoe* (figure 49).

We agree with Tripp (1957; in Moore 1959) that *Dicranopeltoides* and *Raymondarges* are synonyms of *Dicranopeltis*. *Dicranopeltoides* was erected by Phleger (1936, p. 612) for *Lichas decipiens* Winchell & Marcy, 1865, from the Silurian of Illinois (figures 30, 33 and 35). He distinguished his genus from *Dicranopeltis* by S1 ('third lateral glabellar furrow' in his terminology) being continuous across the median lobe in the latter but not in the former. It is true that some cranidia of *D. scabra* (such as that in figure 32) have a shallow depression joining the adaxial ends of S1, but this feature is absent in other specimens (Prantl & Vaněk 1958, pl. 6, figs 1, 4) and we consider its presence to be due to compression. Even if it were a primary structure, we would not attribute much taxonomic importance to such shallow depressions which do not interrupt the exoskeletal granulation. Phleger also considered *Dicranopeltoides* to differ from *Dicranopeltis* in having a pygidium with 'three pairs of discrete ribs', and an 'axial lobe' (actually the postaxial band) that narrows to a point posteriorly. We can see no difference between *D. scabra* and *D. decipiens* in the pygidial pleural ribs, and the degree of taper of the postaxial band is variable even within *D. scabra* itself (see Vaněk 1959, pl. 4, figs 6–10). In erecting *Raymondarges*, Phleger (1937*c*, p. 421) contrasted it with *Trochurus*, as he believed it to be closely related to that genus. However, his description and illustration of the type species, *R. reporyjensis*, from the Wenlock of Czechoslovakia, show that it belongs to *Dicranopeltis*, and in fact we consider that it is probably a synonym of *D. scabra*.

The genus *Tsunyilichas* was based by Chang (1974) on his species *T. pustulosus* from Guizhou Province, China. He gave the age of the species as early Lower Silurian, but Mr Zhou Zhiyi (personal communication) informs us that it is now considered to be Ashgill. Chang's diagnosis and illustrations of *Tsunyilichas* show no features by which this genus may be distinguished from *Dicranopeltis*.

Makromuktis Phleger, 1936 was also listed as a synonym of *Dicranopeltis* by Tripp (1957; in Moore 1959). However, we consider it to be synonymous with *Trochurus* and it is discussed further in the remarks on that genus.

Genus *Nonix* Lane, 1984

Figures 43 and 44, plate 2.

Type species. Original designation; *Nonix sauroter* Lane, 1984, p. 62, from the Wenlock of Hall Land, north Greenland. Holotype: pygidium, MGUH 16.338; figured Lane (1984, pl. 3, fig. 14) (figure 44 herein).

No other species are described.

Stratigraphical and geographical range. As for type species.

Diagnosis. Like *Dicranopeltis* but pygidium has additional pair of furrowed pleurae and nine marginal spines.

Remarks. Nonix sauroter is known only from isolated pygidia and associated cranidia. The latter are not generically distinguishable from *Dicranopeltis* cranidia, whereas the pygidia resemble those of such species as *D. salteri* in their general construction (compare Lane (1984), pl. 3, figs 12, 13 with Thomas (1981), pl. 19, figs 7, 8). *Nonix* pygidia differ from those of *D. salteri* in having an additional axial ring, an extra pair of furrowed pleurae and nine (not six) marginal spines which are slender and elongated rather than being flat and short.

Genus *Oinochoe* gen.nov.

Figures 46–57, 60 and 63, plate 3.

Name. Greek *oinochoe*, a wing jug, referring to the shape of the median glabellar lobe. Gender feminine.

Type species. Lichas pustulosus Hall, 1859, p. 366, from the New Scotland Limestone (Gedinnian) of New York. The syntypes include NYSM 4558 (cranidium), NYSM 4560–4561 (librigenae) and NYSM 4529, 4559, 4562–4564 (pygidia), all figured by Hall (1861, pl. 77, figs 9–11, pl. 78, figs 1–7).

Other species. O. bigsbyi (Hall, 1859); *O. coccymelum* (Campbell, 1977).

Stratigraphical and geographical range. Gedinnian; North America (New York, Oklahoma).

Diagnosis. Lichine with longitudinal furrow extending to occipital furrow; L1a very small, circumscribed, may be weak; L1b fused with bullar lobe or separated from it only by a slight change of slope. Basal part of median glabellar lobe laterally expanded and convex (sag.), separated by change of slope from depressed region just in front; anterior part of median lobe subconically inflated and overhanging anterior border, initially expanding forwards at 50–60° but rate of expansion increasing anteriorly around front of bullar lobe. Pygidium subpentagonal to subelliptical in outline, with four pairs of marginal spines. Axis less than one quarter pygidial width and less than one third its length, not segmented or only very weakly so; postaxial band expanding posteriorly. Pleural furrows extend virtually to tips of first three marginal spines; furrow outling postaxial band meets pygidial margin between third and fourth spines.

Remarks. The types of *O. pustulosa* include five pygidia, three of them having the margins more or less complete. Two of these pygidia have four pairs of marginal spines (figures 60 and 63). The other pygidium was incorrectly depicted by Hall (1861, pl. 78, fig. 7) as having four pairs of marginal spines, but actually has three pairs of spines and a lobate posterior median projection (figure 54); (see also Hall & Clarke 1888, p. 81, pl. 19, fig. 9). We consider this specimen to belong to a teratological individual in which the posterior pair of spines has failed to divide. Hall & Clarke (1888, pp. 80, 81) argued that the pygidia with four pairs of spines had been incorrectly assigned to *pustulosa* because cranidia indistinguishable from that species had been found at a different locality in association with pygidia having only two pairs of spines and a rounded posterior margin (see Hall & Clarke 1888, pl. 19, fig. 8). They therefore tentatively assigned the pygidia with four pairs of spines to *O. bigsbyi.* The only pygidium amongst the types of *bigsbyi* is very incomplete (figure 51), as are also pygidia assigned to *O. coccymelum*, and it is impossible to be certain about the number of marginal spines (although Campbell 1977, text-fig. 36, reconstructed the pygidium of *coccymelum* with three pairs of spines). The types of *bigsbyi*, however, come from Albany and Columbia Counties (not from Schoharie County as stated by Hall & Clarke 1888, p. 81), whereas the pygidia with four pairs of marginal spines are known only from localities in Schoharie County, where they are the most common type (Hall & Clarke 1888, p. 81) and occur in association with cranidia of *pustulosa.* On this evidence we believe that these pygidia are correctly assigned to *pustulosa.*

O. bigsbyi and *O. pustulosa* were assigned to *Echinolichas* by Gürich (1901, p. 530) and Tripp (1958, p. 576); Tripp, however, only included *pustulosa* in the genus with question, not giving any reasons for his uncertainty. Campbell (1977, p. 128) noted that *bigsbyi* and his species *coccymelum* differ from the type species of *Echinolichas* in the presence of 'occipital' lobes (L1a in our terminology), and the inflation of the basal part of the median glabella lobe. He implied that a new genus would eventually be required for *bigsbyi* and *coccymelum*, but preferred in the meantime to assign these species tentatively to *Echinolichas.*

In addition to the features mentioned by Campbell, *Oinochoe* differs from *Echinolichas* in having a glabella that is relatively wider at the occipital ring and strongly constricted in front of it. The lateral glabellar lobes do not rise so steeply from the occipital furrow, and the rate of expansion of the median lobe increases anteriorly instead of decreasing. The pygidium has marginal spines that are broad and flattened rather than being rounded in cross section, and there is no posterior median spine. The pygidial axis is relatively smaller and lacks an upwardly directed spine. The pleural bands on the pygidium are more flattened, especially the posterior ones, and the postaxial band is longer and expands posteriorly instead of contracting. We consider these differences sufficient to assign *Oinochoe* and *Echinolichas* to separate subfamilies.

The cranidium of *Oinochoe* bears some resemblance to that of *Pseudotupolichas* in the shape of the median and lateral glabellar lobes, and indeed Schmidt (1885, p. 31) associated *O. pustulosa* and *O. bigsbyi* with *P. ornatus* in his 'group' *Oncholichas.* The cranidium of *Oinochoe* differs from that of *Pseudotupolichas* in that the median glabellar lobe is more inflated anteriorly, the laterally expanded basal part of the median lobe is longer and more convex (sag.), L1a is present, and L1b is more distinct. The pygidium of *Oinochoe* does not closely resemble that of *Pseudotupolichas*, but is similar to that of *Arctinurus* in overall shape, the proportions of the axis, and the form of the postaxial band. The *Oinochoe* pygidium differs from that of *Arctinurus* in that the pleurae on the first two segments are not flexed as strongly backwards abaxially, there is an additional pair of marginal spines, and the furrow outlining the postaxial band does not extend onto the posteriormost spine, but meets the margin at the notch between the spine and the one in front.

Genus *Pseudotupolichas* Phleger, 1936
[Subjective synonym: *Arctinuroides* Phleger, 1936]
Figures 66–78, plate 4.

Type species. Original designation; *Lichas ornatus* Angelin, 1854, p. 72, from the Wenlock of Gotland, Sweden. The syntypes consist of a cranidium and a pygidium figured by Angelin

(1854, pl. 37, figs 7, 7a); their present location and the horizon from which they were collected are unknown, but we have seen material of this species from both the Högklint Beds and the Slite Beds.

Other species. P. anamosa (Walter, 1925); *P. arenaceus* (Twenhofel, 1928); *P. araneus* (Lindström, 1885); *P. chicagoensis* (Weller, 1907); *P. concinnus* (Angelin, 1854); *P. plicatus* (Lindström, 1885); *P. visbyensis* (Lindström, 1885).

Stratigraphical and geographical range. Llandovery–Wenlock; North America (Illinois, Iowa, Quebec), Sweden, Norway, east Baltic,? Scotland.

Diagnosis. Lichine with glabella moderately convex (sag., exsag.), not overhanging anterior border; longitudinal furrow extending to occipital furrow, curving strongly outwards posteriorly. L1 obsolete or fused with bullar lobe to form compound lateral lobe that is more inflated posteriorly than median lobe, and has its long axis orientated at about 23° to sagittal line; L1a absent. Occipital ring not contracting appreciably abaxially, its width (tr.) almost equal to palpebral width of cranidium. Palpebral lobe small, anterior edge distant from axial furrow but joined to it by well-defined eye ridge that curves inwards around front of lateral glabellar lobe; palpebral furrow strongly curved, continuous anteriorly with deep furrow along inside of eye ridge. Posterior section of facial suture directed laterally from ϵ and subsequently curving sharply backwards through 90°. Pygidium with three pairs of marginal spines, posterior pair with a rather broad, shallow notch between them. Axis approximately one half sagittal length of pygidium, and one-third to one half maximum pygidial width; postaxial band initially decreases in width posteriorly but expands slightly distally. First two pleural furrows commonly extend to tips of marginal spines; third pleural furrow and furrow outlining postaxial band commonly extend to tip of third spine.

Remarks. Phleger (1936) erected *Arctinuroides* for *Arctinurus chicagoensis* Weller, 1907, from the Niagaran of Illinois, and placed the genus together with *Pseudotupolichas* in his subfamily Echinolichadinae. His diagnoses for both genera are brief and inadequate, that given for *Arctinuroides* including only cranidial characters. He did not discuss the differences between *Pseudotupolichas* and *Arctinuroides*, but comparison of his diagnoses suggests that he considered *Arctinuroides* to differ mainly in having a more inflated glabella. It is impossible to be certain of the overall convexity of the glabella in *Arctinuroides*, because the front of the glabella and the anterior border are not preserved in either of the two cranidia amongst the types of *chicagoensis* (figures 73, 74); the remainder of the glabella, however, does not differ greatly in convexity from that of *Pseudotupolichas*. The absence of the anterior border in Phleger's (1936, fig. 11) drawing of *chicagoensis* (based on the illustration given by Weller (1907, pl. 23, fig. 7)) gives the erroneous impression that the glabella overhangs the border and obscures it in dorsal view. *Pseudotupolichas* and *Arctinuroides* are so alike in most other features, including those listed in the generic diagnosis above, that we consider these genera to be synonymous. *Pseudotupolichas* is chosen as senior synonym (in accordance with Article 24a of the ICZN Rules) because its type species is better preserved than that of *Arctinuroides* and there is no doubt about its identity, even though the whereabouts of the type specimens are unknown.

Tripp (1957; in Moore 1959) considered *Pseudotupolichas* and *Arctinuroides* to be synonyms of *Arctinurus*. *Pseudotupolichas* differs from *Arctinurus*, however, in that the glabella is more convex (sag., exsag.), especially posteriorly, the longitudinal furrow extends to the occipital furrow, and L1a is not developed. The palpebral lobe is smaller and not in contact with the axial furrow anteriorly, there is a distinct eye ridge, and the posterior section of the facial suture is deflected more abruptly backwards abaxially. The pygidium has a much larger axis and the first two pleurae are not flexed as strongly backwards abaxially, so that the tips of their spines lie farther forward with respect to the axial terminus.

The hypostome of *Pseudotupolichas* is known in *P. ornatus* (figure 67) and *P. chicagoensis* (Weller 1907, pl. 22, fig. 14). In both species it is distinctive in having the middle furrow meeting the lateral border furrow well forward, almost level with the anterior wings; in the middle body being much wider across the posterior lobe than across the anterior lobe; and in the lack of a distinct notch in the lateral border at the anterior wing.

Howells (1982, pl. 13, figs 22a–c) figured an incomplete cranidium from the Upper Llandovery of Scotland as *Platylichas* cf. *P. scoticus* (Reed, 1906). The generic assignment cannot be determined with certainty because the posterior part of the glabella is not preserved, but the shape of the median lobe and orientation of the lateral lobes suggest that the specimen may belong to *Pseudotupolichas*.

Genus *Trimerolichas* Phleger, 1936

Type species. Original designation; *Lichas marginatus* Lindström, 1885, p. 58, from the Högklint Beds (Wenlock), Gotland, Sweden. Syntypes: two cranidia, RM Ar2366–2367; figured Lindström (1885, pl. 14, figs 8, 9), Tripp (in Moore 1959, fig. 393, 394a, b).

Remarks. The type species is known only from the syntype cranidia. Warburg (1937) mentioned that she had seen a pygidium possibly belonging to the same species but we have been unable to trace this specimen.

Tripp (1957; in Moore 1959) considered *Trimerolichas* to be a synonym of *Arctinurus*, and illustrated the syntypes of *T. marginatus* in the *Treatise* as representative of that genus. These specimens differ from *Arctinurus* cranidia in having a relatively long anterior border that is not extended into a process medially, a longitudinal furrow that extends to the occipital ring, and a somewhat narrower (tr.) occipital ring. We regard these differences as of generic importance, but until information is available on other exoskeletal parts of *T. marginatus* we consider it advisable to restrict *Trimerolichas* to the type species.

Genus *Uralichas* Delgado, 1892

[Subjective synonyms: *Platopolichas* Gürich, 1901;
?*Bohemolichas* Přibyl & Vaněk, 1972]

Figures 61, 64 and 65, plate 3; figures 79, 80 and 83–85, plate 4; ?58, 59 and 62, plate 3.

Type species. Monotypy; *Lichas* (*Uralichas*) *Ribeiroi* Delgado, 1892, p. 5, from the Valongo Formation (Llandeilo) of Portugal. The syntypes include the distorted remains of several very large and almost complete cranidia, librigenae, hypostomes and pygidia figured by Delgado (1892, pls 1–6), and said by him to be in the collections of the Commissão dos trabalhos geologiços de Portugal, Lisbon.

Other species. *U. avus* (Barrande, 1872); *U. heberti* (Rouault, 1849); *U. hispanicus* (Verneuil & Barrande, 1855); *U. frangipana* Šnajdr, 1984*a*; *U. giganteus* Klouček, 1916; *U*? *incola* (Barrande 1872).

Stratigraphical and geographical range. Llanvirn–Llandeilo; Portugal, Spain, France, Czechoslovakia.

Diagnosis. Lichine with glabella moderately convex, frontal lobe descending vertically to anterior border. Bullar lobe circumscribed or confluent abaxially with L1b; L1a large and well defined. Longitudinal furrow may be developed behind bullar lobe as broad, shallow depression not interrupting exoskeletal granulation; axial furrow shallow or indistinguishable alongside L1b. Palpebral lobe small, posterior edge situated level with or in front of base of bullar lobe. Pygidium with two to four pairs of pleural furrows (five in *U. giganteus*) and two to four pairs of flattened marginal spines (possibly more in *U. giganteus*). Pygidial axis merging posteriorly with rounded (tr.) postaxial ridge that is continuous with long posterior spine; three or four axial rings present, last one or two defined by shallow ring furrows that are obsolete medially. Some species of genus attain exceptionally large size.

Remarks. Delgado (1892) considered *U. ribeiroi* to be closest to *Lichas heberti* Rouault, 1849 from Britanny, and *L. hispanicus* Verneuil & Barrande, 1855 from Spain, but these species are so poorly known that worthwhile comparisons cannot be made with them. The other species that have been assigned to *Uralichas* – *L. avus* Barrande, 1872, *L. incola* Barrande, 1872 and *L. giganteus* Klouček, 1916 – are all from the Llanvirn of Czechoslovakia, and include the type species of *Platopolichas* and *Bohemolichas*.These species show similarities with *U. ribeiroi* in their cranidia and hypostomes (although the hypostome of *L. giganteus* is not known) but differ considerably from *U. ribeiroi* and from each other in their pygidia. From the information available it is difficult to make judgments on the amount of morphological variation that should be accommodated in *Uralichas*, and on the usefulness of *Platopolichas* and *Bohemolichas*.

L. avus, the type species of *Platopolichas*, resembles *U. ribeiroi* most notably in the presence of a long posterior spine on the pygidium, a feature that is unusual within the Lichida and one that suggests that these species may be closely related. *L. avus* differs from *U. ribeiroi* in that the bullar lobe is circumscribed instead of being confluent with L1b abaxially, the axial furrow is absent alongside L1b rather than being weakly impressed, and the pygidium has four pairs of furrowed pleurae ending in marginal spines, rather than two. (Note that although some of the cranidia of *U. ribeiroi* figured by Delgado (1897) appear to have circumscribed bullar lobes, we attribute this to the accentuation of S1 by deformation.) The differences in the cranidia do not seem to be of great significance, in view of the variation that exists within other lichid genera. Tripp (1957) suggested that the difference in the number of pygidial pleurae may be due to the posteriormost thoracic segment remaining fused to the pygidium in *avus*, and did not consider this to be of much taxonomic importance. However, the pygidium of *avus* includes two more pairs of pleural furrows and marginal spines than that of *ribeiroi*, the drawing given by Tripp (1957, text-fig. 6) being incorrect in showing only three pairs of marginal spines. The number of segments in the thorax of *avus* is unknown and so it is not possible to determine whether the extra pleurae in the pygidium represent fused thoracic segments, but we consider it to be more likely that they are additional segments generated in the pygidium during ontogeny. The problem is to determine whether the greater number of pygidial segments warrants the placement of *avus* in a separate genus from *ribeiroi*. *L. giganteus* has a cranidium that is very similar to that of *avus*, but its pygidium has five pairs of pleural furrows (Vaněk 1959, pl. 1, figs 1, 2). It is not known, however, how many pairs of marginal spines were present, or whether there was a median posterior spine. We conclude that the number of pygidial segments was very variable among these species, and we therefore assign both *avus* and *giganteus* to *Uralichas*, which we regard as a senior synonym of *Platopolichas*.

L. incola was included in *Uralichas* by Tripp (1957, 1958), but Vaněk (1959) preferred to retain this species in *Lichas*. Přibyl & Vaněk (1972) subsequently made *incola* the type species of their genus *Bohemolichas*, which they considered to be closest morphologically to *Lichas* and

Platylichas. *L. incola* does show some similarities with *Platylichas* species in the shape of the glabella and its constituent lobes, and in the overall form of the pygidium. In cranidial characters, *incola* is even more similar to some species of *Metopolichas*, such as *M. contractus* and *M. patriarchus*. The hypostome figured by Vaněk (1959, pl. 3, fig. 6), however, is closer to that of *Uralichas* than to homolichine hypostomes (but see discussion below). There seems to be no doubt that this hypostome is correctly assigned, because Barrande (1872, pl. 10, fig. 5) figured an almost complete exoskeleton of *incola* showing the external mould of a similar hypostome in life position. Within the Lichinae, *L. incola* is most similar to *U. ribeiroi* but differs mainly in lacking a posterior spine on the pygidium, the unfurrowed part of the pleurae adjacent to the postaxial band ending in a pair of spines similar to those on the first two segments. We accept that this difference may be sufficient to warrant the recognition of *Bohemolichas* as a separate genus or subgenus, but until more is known of the relationships of *incola* we prefer to include the species with question in *Uralichas*. The species *Lichas praecursor* Holub, 1911, based on a single incomplete pygidium from the Arenig of Czechoslovakia, was also included in *Bohemolichas* by Přibyl & Vaněk (1972). We consider this species to be so poorly known as to be unassignable to a genus.

In his diagnosis of *Uralichas*, Tripp (in Moore 1959) described the middle body of the hypostome as 'faintly defined posteriorly'. This is true in *U. avus* (Vaněk 1959, pl. 2, fig. 5), but the hypostomes of *U. ribeiroi* (figure 85) and *U*? *incola* (Vaněk 1959, pl. 3, fig. 6) have deeply impressed posterior border furrows. In this respect, these hypostomes resemble those of the Homolichinae, presumably reflecting the origin of *Uralichas* in a member of that subfamily (see §6). In other features, notably the ratio of length to width, and the width of the lateral border, the hypostomes of *ribeiroi* and *incola* (and that of *avus*) are closer to hypostomes of lichines than homolichines.

(*d*) Subfamily ECHINOLICHINAE Phleger, 1936
[*nom. correct.* Balashova in Chernysheva 1960 ex Echinolichadinae Phleger, 1936]

Diagnosis. Lichidae with glabella subparallel-sided, no wider at occipital ring than across basal part of lateral lobes. Longitudinal furrow extending to occipital furrow or terminating at base of bullar lobe; posterior half of median glabellar lobe constricted and depressed below level of bullar lobes; anterior half of median lobe inflated and subparallel-sided or elliptical. S1 very weak or obsolete; L1a absent. Pygidium (known only in *Echinolichas* and *Terataspis*) with three pairs of pleural furrows and four pairs of slender marginal spines that are rounded in cross section; posterior pleural bands longer (exsag.) and more inflated than anterior bands.

Genera included. *Echinolichas* Gürich, 1901; *Ceratolichas* Hall & Clarke, 1888; *Gaspelichas* Clarke, 1907; *Terataspis* Hall, 1863b.

Stratigraphical range. Siegenian–Eifelian.

Remarks. This subfamily comprises a small group of rather poorly known genera restricted to the Lower and Middle Devonian of North America. These genera were included in the Lichinae by Tripp (1957; in Moore 1959) but they differ from members of that subfamily in having a glabella that is subparallel-sided instead of being greatly expanded in width at the occipital ring and constricted across L1a or L1b. The median glabellar lobe is constricted opposite the posterior edge of the palpebral lobe as it also is in the Lichinae, but is subparallel-sided or elliptical anteriorly instead of expanding strongly around the front of the bullar lobes. In addition the posterior pleural bands on the pygidium are longer (exsag.) and more convex than the anterior bands, instead of being flattened and approximately equal in length to the anterior bands, and the pygidial marginal spines are rounded in cross section rather than flattened. The pygidia of *Echinolichas* and *Terataspis* have one more pair of marginal spines than most lichines, with the exception of *Oinochoe* (*Echinolichas* also has a posterior median spine). This appears to be due to the development of spines on the segment or segments incorporated in the postaxial band, rather than to the fusion of the posteriormost thoracic segment with the pygidium, because the number of pygidial pleural furrows is the same as in the Lichinae.

Echinolichine hypostomes are known in *Echinolichas* (figure 82) and *Terataspis* (Ludvigsen 1979, fig. 50A) but are remarkably dissimilar in these genera. In *Echinolichas* the hypostome is almost as wide as long (excluding posterior notch), with the shoulders situated at mid-length, deep lateral border furrows, and a middle body with a subquadrate anterior lobe and prominent maculae. The hypostome of *Terataspis* is much wider than long, the shoulders are situated well behind the mid-length, the lateral border furrow is reduced to a vague depression opposite the shoulder, so that the lateral border merges with the posterior lobe of the middle body, the anterior lobe of the middle body is subrhombic, and the maculae are indistinct. The hypostomes of both genera, however, show similarities with lichine hypostomes in the oblique middle furrow and poorly defined posterior border furrow.

Phleger (1936) considered the Echinolichinae to be characterized by 'quadricomposite' glabellar lobes and a spinose exoskeleton, and he included in the subfamily not only the genera listed above but also *Pseudotupolichas*, *Arctinuroides* and *Radiolichas*. Although it is true that most echinolichines have 'quadricomposite' glabellar lobes (that is, the longitudinal furrow extends to the occipital furrow, and the bullar lobe is fused with L1a and L1b), in *Ceratolichas* the longitudinal furrow terminates at the base of the bullar lobe, which is in turn indistinctly separated from L1 by a very weak S1. We do not regard the development of exoskeletal spines in lichids as a feature of importance at the subfamily level. We assign *Pseudotupolichas* and *Arctinuroides* (which we consider to be synonymous) to the Lichinae, and we agree with Tripp (1957; in Moore 1959) that *Radiolichas* is a member of the Trochurinae.

Genus *Echinolichas* Gürich, 1901
Figures 81 and 82, plate 4;
figures 118, 119, 122, 123, 127 and 128, plate 6.

Type species. Subsequent designation Reed (1902, p. 61); *Lichas Eriopis* Hall, 1863*b*, p. 226, from the Onondaga Formation (Eifelian) of New York. Syntypes: cranidium, NYSM 4537, figured Hall (1876, pl. 19, figs 4–7), Hall & Clarke (1888, pl. 19A, figs. 2–5) (figures 127 and 128 herein); pygidium NYSM 4539, figured Hall (1876, pl. 19, fig. 10), Hall & Clarke (1888, pl. 19A, fig. 9) (figure 123 herein); pygidium NYSM 4553 (holotype of *E. hispidus* (Hall & Clarke, 1888)), figured Hall (1876, pl. 19, figs 8, 9), Hall & Clarke (1888, pl. 19A, figs 14, 17).

Other species. *E. bellamicus* (Clarke, 1907); *E. hispidus* (Hall & Clarke, 1888).

Stratigraphical and geographical range. Siegenian–Eifelian; North America (New York, Quebec).

Diagnosis. Echinolichine with glabella moderately convex (sag., exsag.), median lobe overhanging anterior cephalic border. Longitudinal furrow extending to occipital furrow; bullar lobe fused with L1, resulting compound lateral lobe inflated posteriorly and rising steeply from occipital ring. Posterior section of facial suture curving backwards behind eye to run parallel to sagittal axis, deflected strongly outwards across posterior border. Pygidium with four pairs of marginal spines and a shorter posterior median spine; first two segments at least with long, upwardly directed spines arising from posterior pleural bands at fulcrum. Axis approximately one half sagittal length of pygidium, inflated behind first ring and bearing a long median spine. Postaxial band gently convex (tr.), subparallel-sided and almost as wide as axis, constricted posteriorly and extending almost to pygidial extremity.

Remarks. See discussion under *Oinochoe* gen.nov., *Ceratolichas* and *Terataspis*.

Genus *Ceratolichas* Hall & Clarke, 1888

Figures 96, 97, 100 and 101, plate 5.

Type species. Subsequent designation Reed (1902, p. 61); *Lichas* (*Ceratolichas*) *gryps* Hall & Clarke, 1888, p. 84, from the Onondaga Formation (Eifelian), New York. Syntypes: cranidium, NYSM 4550, figured Hall & Clarke (1888, pl. 19B, figs 7, 8) (figures 96 and 97 herein); cranidium, NYSM 4551, figured Hall & Clarke (1888, pl. 19B, figs 9–11) (figures 100 and 101 herein); fragment of median glabellar lobe, NYSM 4552, figured Hall & Clarke (1888, pl. 19B, figs 12, 12a, 13).

Other species. *C. dracon* (Hall & Clarke, 1888).

Stratigraphical and geographical range. Eifelian; North America (New York).

Diagnosis. Echinolichine with cranidium strongly convex (sag., exsag.); glabella descending steeply in front of palpebral lobes and overhanging anterior border. Axial and longitudinal furrows shallow; longitudinal furrow not extending to occipital furrow but curving outwards around base of bullar lobe and joining very faint S1. Palpebral lobe short (approximately one eighth sagittal length of cranidium), joined to anterolateral extremity of median lobe by distinct eye ridge. Large, paired spines present on occipital ring, highest part of median lobe, and outer part of bullar lobe adjacent to palpebral lobe.

Remarks. This genus is known only from the cranidium, which differs from that of *Echinolichas* in being more convex (sag., exsag.), in having the longitudinal furrow extending only to the base of the bullar lobe instead of to the occipital furrow, and in having the bullar lobe separated from L1 by a weak S1. The lateral glabellar lobes do not rise as steeply from the occipital furrow as in *Echinolichas*, and there are large spines on the occipital ring, median glabellar lobe and bullar lobes (one pair of spines on the median lobe in *C. gryps*, and two pairs in *C. dracon*). The palpebral lobe is smaller than in *Echinolichas*, and there is a distinct eye ridge. Because of these differences, we do not agree with the suggestion of Tripp (1957, p. 114, that *Ceratolichas* and *Echinolichas* may be synonymous.

The line drawings of *C. gryps* given by Phleger (1936, figs 12, 13) and Tripp (in Moore 1959, fig. 394, 395a–b) were based on the figures in Hall & Clarke (1888, pl. 19B, figs 7, 8). These illustrations are all inaccurate in showing the longitudinal furrow apparently extending to the occipital furrow. The error may have arisen because the cranidium in Hall & Clarke's pl. 19B, fig. 7 is orientated with the anterior margin tilted upwards from the dorsal position, so that the preoccipital part of the glabella is foreshortened.

A number of features of *Ceratolichas* are reminiscent of the Trochurinae. These features include the convexity of the glabella and its steepness anteriorly, the strongly inflated median glabellar lobe, the large cranidial spines, the small palpebral lobe, and the distinct eye ridge. *Ceratolichas* differs from trochurines in that the axial furrow is clearly defined alongside L1, and

L1 is very reduced in length (exsag.), being only as long as the occipital ring. In addition, the large spines situated adaxial to the palpebral lobes in such trochurines as *Terranovia*, *Trochurus* and some *Acanthopyge* (*Jasperia*) are of fixigenal origin (see §4), whereas in *Ceratolichas* they occur on the bullar lobes. Because of these differences, and because of the similarity to *Echinolichas* in the overall shape of the glabella and the form of the occipital ring, we consider *Ceratolichas* to be a member of the Echinolichinae rather than the Trochurinae.

Genus *Gaspelichas* Clarke, 1907

Figures 86–88 and 90, plate 5.

Type species. Monotypy; *Lichas* (*Gaspelichas*) *forillonia* Clarke, 1907, p. 167, from the Grande Grève Formation (Siegenian), Quebec. Syntypes: cranidium, NYSM 9740, figured Clarke (1907, unnumbered fig. on p. 168; 1908, pl. 2, figs 1, 2) (figures 87 and 90 herein); cranidium, NYSM 9741, figured Clarke (1908, pl. 1, figs 1, 2, pl. 2, fig. 3); cranidium, NYSM 9742, figured Clarke (1908, pl. 3, fig. 1) (figure 6 herein); cranidial fragment, NYSM 9743, figured Clarke (1908, pl. 3, fig. 2) (figure 88 herein); cranidial (?) fragment, NYSM 9744, figured Clarke (1908, pl. 3, figs 3, 4).

Diagnosis. Echinolichine with cranidium rather elongate, sagittal length being approximately equal to width across palpebral lobes; axial, longitudinal and occipital furrows broad, shallow and poorly defined. Bullar lobe and anterior part of median glabellar lobe each with two pairs of long, upwardly directed spines; three stout spines present on posterior edge of occipital ring, and another pair of long spines on proximal part of posterior border. Longitudinal furrow extending to occipital furrow; bullar lobe fused with L1, resulting compound lateral lobe gently inflated. Occipital ring long (approximately one sixth sagittal length of cranidium, excluding spines), flattened, and sloping forwards weakly. Anterior half of median glabellar lobe gently inflated, but descending steeply in front of anterior pair of spines.

Remarks. The genus is known only from the type material of the type species, which consists of the poorly preserved remains of five cranidia. Two of the specimens, NYSM 9740 and NYSM 9741, have been extensively reconstructed in plaster and other materials, no attempt at accuracy having been made in the reconstruction of the latter specimen which consists of little more than several of the large cranidial spines. In NYSM 9740 the reconstructed parts include an additional, third pair of spines on the front of the median glabellar lobe (figures 87 and 90), although there is no evidence for the existence of these spines in the other specimens. Another two specimens, NYSM 9743 and NYSM 9744, which are both external moulds, were interpreted by Clarke (1908) as librigenae. We consider the former specimen to represent the right posterolateral part of a cranidium, including the fixigena and parts of the bullar lobe and occipital ring (figure 88). We have seen only a gutta percha cast of NYSM 9744 and this is virtually uninterpretable, but the specimen possibly represents part of the occipital ring and adjacent fixigena.

The large spines on the glabella and posterior border and the weak furrows give the cranidium of *Gaspelichas* a very distinctive appearance. It is, however, very similar to the cranidium of *Terataspis* in overall proportions and in the shape of the glabellar lobes. It differs from *Terataspis*, in addition to the features mentioned above, in that the lateral glabellar lobe and anterior part of the median lobe are more weakly inflated, the anterior and posterior parts of the median lobe are not separated by a transverse furrow, and the occipital ring is more flattened (sag., exsag.).

Genus *Terataspis* Hall, 1863*b*

Figures 89, 91–95, 98, 99, 102 and 103, plate 5.

Type species. Monotypy; *Lichas grandis* Hall, 1861, p. 82, from the Schoharie Formation (Emsian), New York. Holotype: almost completely exfoliated cranidium lacking the anterior part of the median glabellar lobe, NYSM 4543; figured Hall (1876, pl. 17, figs 4, 5), Hall & Clarke (1888, pl. 17, figs 4, 5) (figures 91 and 92 herein). There seems to be little doubt that this is the specimen on which Hall's original description was based, although he did not figure it until later.

No other species are described.

Stratigraphical and geographical range. ?Siegenian–Eifelian; North America (New York, Ontario, ?Oklahoma).

Diagnosis. Echinolichine with glabella that may be weakly constricted opposite posterior edge of palpebral lobe. Longitudinal furrow very broad and well-rounded in cross section, extending to occipital furrow posteriorly; joining anterior border furrow in a uniform curve. Bullar lobe fused with L1; resulting compound lateral lobe flattened (tr.) anteriorly, subconically inflated posteriorly and bearing two stout spines at its summit. Anterior and posterior parts of median glabellar lobe separated by transverse furrow; anterior part ellipsoidally inflated, overhanging longitudinal and anterior border furrows, and projecting in front of lateral lobes by one half its length; posterior part of median lobe merging with longitudinal furrows. Palpebral lobe small; posterior section of facial suture meeting cephalic margin on flank of subgenal notch. Pygidium with four pairs of long, barbed marginal spines; posterior pleural bands with large dorsal spines at fulcrum. Axis approximately one half length of pygidium, composed of two long (sag., exsag.), poorly defined rings and an inflated terminal piece with a stout median spine. Postaxial band expanding posteriorly, outlined by furrows extending towards margin between third and fourth spines. Individuals typically reaching large size.

Remarks. T. grandis is known mainly from very large and rather poorly preserved cranidia and pygidia, but an almost complete exoskeleton was reported by Reimann (1945) from the Onondaga Formation (Eifelian) of New York. This specimen shows that the two thoracic segments illustrated by Hall & Clarke (1888, pl. 19, figs 6, 7) were incorrectly assigned to *T. grandis*. These segments, which are characterized by a massive pair of erect and divergent spines on the axial ring, most probably belong to a species of dalmanitacean.

Terataspis differs from *Echinolichas* in that the anterior part of the median glabellar lobe is more inflated, projects farther in front of the lateral glabellar lobe, and is separated from the posterior part of the median lobe by a transverse furrow. The posterior part of the median lobe is more depressed than in *Echinolichas* and is indistinctly separated from the longitudinal furrow, the lateral lobe is more inflated, and the posterior section of the facial suture is not deflected strongly backwards behind the palpebral lobe. The pygidium lacks a posterior median spine, and the postaxial bands expands distally instead of contracting.

(*e*) Subfamily HOMOLICHINAE Phleger, 1936

[*nom. correct.* Tripp 1957 ex Homolichadinae Phleger, 1936]

Diagnosis. Lichidae with prominent L1a which indents occipital ring; L1b not independently inflated, may be fused with bullar lobe or fixigena. Median glabellar lobe strongly expanding (tr.) anteriorly. Longitudinal furrow typically extends to occipital furrow, bullar lobe (or composite lateral lobe formed by fusion of bullar lobe with L1b) invariably circumscribed. Hypostome wider than long; middle body distinctly circumscribed, with transverse middle furrows; lateral border expanded and flap-like. Pygidium with three pairs of spinose pleurae; anterior and posterior pleural bands usually of similar elevation; postaxial band tapering backwards over most of its length, but widening again distally.

Genera included. Homolichas Schmidt, 1885; *Autoloxolichas* Phleger, 1936; *Conolichas* Dames, 1877; *Hoplolichas* Dames, 1877; *Hoplolichoides* Phleger, 1936; *Leiolichas* Schmidt, 1885; *Metalichas* Reed, 1902; *Otarozoum* gen.nov.; *Platylichas* (*Platylichas*) Gürich, 1901; *Platylichas* (*Rontrippia*) subgen.nov.; ?*Metopolichas* Gürich, 1901.

Stratigraphical range. Tremadoc?, Arenig–Wenlock, Ludlow?

Remarks. The distinctive hypostomal morphology of homolichines (e.g. figures 173 and 187) is approached in some lichines (e.g. *Dicranopeltis* cf. *salteri*, see Thomas 1981, pl. 19, fig. 13). In tentatively assigning *Metopolichas* to the Homolichinae (rather than to the Lichinae) we weight its hypostomal characters above its essentially lichine cranidial morphology (also see remarks on *Metopolichas* below).

Genus *Homolichas* Schmidt, 1885

Type species. Subsequent designation Reed (1902, p. 61); *Lichas depressus* Angelin, 1854, p. 70, from Ordovician (Caradoc?) erratic, Öland, Sweden. Lectotype selected herein: cranidium figured Angelin (1854, pl. 36, fig. 4), untraced (the reasons for this lectotype selection are discussed below); paralectotype pygidium, RM Ar6017a, figured Angelin (1854, pl. 36, fig. 4a), Warburg (1939, pl. 6, fig. 8).

Remarks. Angelin's diagnosis of *L. depressus* was evidently based on the cranidium. Warburg (1939, p. 71) incorrectly described this specimen as the holotype and stated that its whereabouts were unknown. The pygidium which Angelin attributed to *depressus* was described and refigured by Warburg and we agree with her that this specimen most likely belongs to *Conolichas deflexus* (Angelin). Warburg restricted *depressus* to Angelin's missing cranidium and we follow her intentions as first reviser by selecting that specimen as lectotype.

Schmidt (1885, p. 94) and such later authors as Reed (1902, p. 78) essentially used *Homolichas* to include those species here referred to a new genus, *Otarozoum*. Warburg (1939, p. 13) regarded *Homolichas* as a junior synonym of *Conolichas*, arguing that the differences between the two were either too small to be of generic significance or based on the incorrect interpretation of rather fragmentary material. Angelin's illustration (1854, pl. 36, fig. 4) suggests that *depressus* might belong to *Otarozoum* but this cannot be verified without reference to the original specimen: at best, the species is very poorly known. We therefore consider it best to restrict both *depressus* and *Homolichas* to the missing lectotype and to accommodate apparently similar species in our new genus *Otarozoum*. Should Angelin's specimen subsequently be found and prove to be congeneric, then *Otarozoum* would become a subjective junior synonym of *Homolichas*.

Genus *Autoloxolichas* Phleger, 1936

Figures 185, 186 and 188–192, plate 9; figures 212 and 213, plate 10.

Type species. Original designation Phleger (1936, p. 614); *Lichas st. mathiae* Schmidt, 1885, p. 115 from the Caradoc of Estonia. Schmidt's syntypes (pl. 5, figs 11–16) include three cranidia, two pygidia and a hypostome, one specimen quoted as being housed in the Petrovsk Academy (now Timiryazev Academy of Agricultural Sciences: M. N. Chugaeva, personal communication) in Moscow and the others in the Reval (now Tallinn) Museum. Dr R. Männil informs us that this material cannot now be traced at Tallinn but she has provided us with photographs of a topotype cranidium (figure 213) and of the rather poor specimen figured by Öpik (figure 212).

Other species. A. crescenticus (Reed, 1935); *A. glenos* (Whittington, 1962); *A. halli* (Foerste, 1888); *A. laxatus* (McCoy, 1846); *A. micus* (Antcygin in Varganov, 1973); *A. noctua* (Price, 1980); *A. nodulosus* (McCoy, 1851); *A. thraivensis* (Reed, 1935); *A?. gracile* (Kummerow, 1928); *A? inconsuetus* (Raymond, 1925); *A? miseneri* (Foerste, 1920).

Stratigraphical and geographical range. Arenig, Urals; Caradoc–Ashgill, North America (Indiana, Ohio, ?New York), Ireland, England, Scotland, Wales, Norway, Sweden, Estonia, arctic U.S.S.R. (Vaigach Island and Pai-Khoi), north German erratics.

Diagnosis. Homolichine with anterior cephalic border comprising about one eighth sagittal cranidial length. Long axis of bullar lobe usually approximately parallel to sagittal line but may diverge anteriorly at an angle up to 20°. Maximum width of bullar lobe about twice that of median lobe measured across same transverse line. Longitudinal furrow meets axial furrow at adaxial extremity of L1a; L1b apparently obsolete or fused with bullar lobe (see remarks below). Pygidial axis comprising half sagittal pygidial length or more, with three to four axial rings; last ring furrow commonly incomplete medially. Postaxial band narrow, connected to third pleural furrow by distinct border furrow; border most distinct posteriorly but typically interrupts first and second pleural furrows abaxially. Three pairs of rather long and slender marginal spines.

Remarks. Although we have been unable to trace the type material of *A. sanctamathiae* we are confident that the Estonian specimen figured here belongs to that species because it agrees with Schmidt's illustrations in all essential respects, even to the extent of the distinctive scale-like sculpture on the front of the median glabellar lobe. We therefore base our concept of the type species on this specimen. Schmidt's illustrations of the pygidium of *A. sanctamathiae* are inadequate to determine whether or not they are likely to be correctly associated with the cranidia. So far as can be seen they could belong either to *Autoloxolichas* or *Platylichas*.

The species here assigned to *Autoloxolichas* have previously been placed in *Platylichas*. Earlier conceptions of that genus (see, for example, Warburg 1939; Tripp 1957, 1958; in Moore 1959) have been rather broad and we consider it possible to distinguish several species-groups: species of *Autoloxolichas* comprise one such group to which we accord formal taxonomic status. The cephalon of *Autoloxolichas* particularly differs from that of *Platylichas* as diagnosed here in having the long axis of the bullar lobe more exsagittally directed. The central section of the median lobe is thus uniformly narrower and less strongly expanding forwards than in *Platylichas* (compare figures 174 and 188). In *Platylichas* L1b is fused with the fixigena so that the axial furrow is locally effaced (figure 174) whereas in *Autoloxolichas* it seems either that L1b is fused with the bullar lobe or that L1b is suppressed and represented by the small depressed area anterior to L1a: in either event the axial and longitudinal furrows in *Autoloxolichas* converge at the adaxial end of L1a (figure 188). In *Platylichas* these furrows intersect at the base of the bullar lobe (e.g. figures 174 and 184). The pygidium of *Autoloxolichas* has a relatively longer axis, a distinct pygidial border is developed and the marginal spines are more slender and more nearly cylindrical than those of *Platylichas*. Also see remarks under *Otarozoum*.

Three species are assigned to *Autoloxolichas* with question. *A? inconsuetus* is based on a single cranidium and the only available illustration is poor (Raymond 1925, pl. 6, fig. 12). *A? miseneri* is known only from an incomplete thorax and pygidium, the latter having been extensively reconstructed posteriorly (Foerste 1920, pl. 10, fig. 1; 1917, pl. 1, fig. 2). *A*? *gracile* is founded on a pygidium (Kummerow 1928, pl. 1, fig. 24a, b) which probably belongs to this genus, but which is too fragmentary for certain identification.

Genus *Conolichas* Dames, 1877

[Subjective synonym: *Cypholichas* Phleger, 1936]

Figures 129–138, 140–142 and 146, plate 7.

Type species. Subsequent designation Vogdes (1890, p. 122); *Lichas aequiloba* Steinhardt, 1874, p. 30, from Ordovician erratic, north Germany. Holotype: cranidium figured Steinhardt (1874, pl. 3, fig. 6), Dames (1877, pl. 13, fig. 5), from the Mascke Collection, untraced. Dr H. Jaeger (personal communication 14 February 1984) informed us that Mascke's Collection might be at Göttingen. Dr H. Jähnke, however, informs us that they have no record of this collection at the Göttingen Geological–Palaeontological Institute, but that their collections were partly destroyed by bomb damage in World War II.

Other species. *C. angustus* (Beyrich, 1846); *C. branconis* (Pompecki, 1890); *C. deflexus* (Angelin, 1854); *C. monticulosus* (Öpik, 1937); *C. sjoegreni* (Warburg, 1939); *C. triconicus* (Dames, 1877).

Stratigraphical and geographical range. Caradoc; Sweden, Estonia, Urals, and in erratics of this age in the Baltic.

Diagnosis. Homolichine with cranidium strongly convex (sag. & exsag.), glabella overhanging narrow anterior border. Bullar lobe fused with L1b, inflated composite lobe so defined elliptical in outline, exsagittally elongated, about three quarters length of median lobe in palpebral view. Maximum width of lateral lobe about three times that of median lobe measured across same transverse line. Median lobe inflated anteriorly, sometimes greatly so, in which case posterior part of lobe is depressed. Pygidium without border; axis approaching half sagittal pygidial length. First two interpleural furrows extend to margin, pleurae so defined end in short, broad-based spines. A third pair of somewhat broader spines present posteriorly. Third pleural furrow confluent posteriorly with furrow outlining postaxial band.

Remarks. The type species of this genus is poorly known, Steinhardt's holotype cranidium having been refigured only by Dames (1877, pl. 13, fig. 5). Schmidt (1885, pl. 5, figs 4–10) attributed both cranidia and pygidia to the species. The pygidia, however, seem to be rather extensively reconstructed: the extension of the pleural furrows onto the marginal spines, for instance, is not matched in any known homolichine. Thus the diagnosis of the genus given here is based largely on better known species which appear to be congeneric with Steinhardt's species, so far as the imperfect illustrations available allow us to judge.

Phleger (1936, p. 604) based his *Cypholichas* on *L. branconis* (Pompecki, 1890, pl. 48, p. 2, fig. 26, 26a), a species very similar to such forms as *C. deflexus* (figures 129–133 and 135). Phleger restricted *Conolichas* to species in which the median glabellar lobe is greatly inflated anteriorly and depressed posteriorly, a condition well seen in *C. monticulosus* (Öpik 1937, pl. 8, fig. 14) and *C. triconicus* (figures 140, 141 and 146 herein), and apparently to a lesser extent in the type species. All the species here assigned to *Conolichas* have similar glabellar proportions and we do not consider the relative inflation of the median lobe to be a sufficient criterion for generic status. We therefore regard *Cypholichas* as a junior synonym of *Conolichas*.

For comparative remarks see below under *Hoplolichoides* and *Otarozoum*.

Genus *Hoplolichas* Dames, 1877
[Subjective synonym: *Cyranolichas* Phleger, 1936]
Figures 151–159 and 162, plate 8.

Type species. Subsequent designation Vogdes (1890, p. 122); *Lichas tricuspidata* [*sic*] Beyrich, 1846, p. 7, from Ordovician erratic, Sorau, north Germany. Holotype: cranidium, PMB k179; figured Beyrich (1846, pl. 1, fig. 7a, b) (figures 153 and 155 herein). Dames (1877, p. 795) and Warburg (1939, p. 80) stated that *L. tricuspidatus* is a junior synonym of *L. dissidens* Beyrich, 1845, which is based on a pygidium, PMB k161, figured Beyrich (1845, unnumbered plate, fig. 18) (figure 162 herein), some locality and horizon.

Other species. *H. longispinus* Schmidt, 1885; *H. proboscideus proboscideus* Dames, 1877; *H. p. elongatus* Warburg, 1939; *H. medius* Pompecki, 1890; *H? oelanicus* (Angelin, 1854); *H? schmidtii* (Dames, 1877).

Stratigraphical and geographical range. Llanvirn?, Llandeilo–Caradoc; Estonia, and in erratics of this age in Sweden and North Germany.

Diagnosis. Homolichine with median glabellar lobe not depressed posteriorly, but inflated anteriorly to overhang narrow anterior border. Bullar lobe and L1b indistinctly separated by slight change in slope; bullar lobe with long axis subparallel to sagittal line and widest anteriorly where it approaches width of median lobe; L1a rounded and only slightly extended transversely. Median lobe may be produced into a spine anteriorly or bear a group of smaller spines. Occipital spine present. Pygidial axis with one or two prominent rings, tapering evenly back into postaxial band. Anterior two interpleural furrows extend to margin, pleurae so defined ending in long slender spines, second pair longer than first. Anterior two pleural furrows terminate at prominent border; third pleural furrow describes a loop posteriorly and merges with furrow defining postaxial band. Third pair of marginal spines commonly fused proximally.

Remarks. We have taken a somewhat narrower view of *Hoplolichas* than either Warburg or Tripp. In his diagnosis, Tripp (in Moore 1959, p. O498) relied on the presence of an occipital spine as a primary feature of the genus and therefore included a number of species which we refer to *Hoplolichoides* (q.v.). We do not regard occipital spinosity as a feature of substantial importance and distinguish *Hoplolichas* on a combination of glabellar and pygidial characters.

Phleger (1936, p. 605) based his *Cyranolichas* on *H. proboscideus* (Dames 1877, pl. 12, fig. 4, pl. 13, figs 2, 3, non 4) because of the presence of a prominent anterior spine. In other respects this species is very like *H. tricuspidatus* and we therefore follow Warburg (1939, p. 9) and Tripp (in Moore 1959, p. O498) in considering *Cyranolichas* to be a junior synonym of *Hoplolichas*.

Two species are assigned to the genus with question. *H? oelandicus* is founded on the single fragmentary pygidium redescribed by Warburg (1939, p. 73, pl. 3, fig. 11). She discounted an assignment to *Hoplolichas* because of the presence of a third pleural furrow and so, although noting the similarity to species of that genus, assigned the specimen with question to *Conolichas*. The generic assignment of such fragmentary material is inevitably uncertain but the overall morphology of the specimen, particularly the elongated second pleural spines, suggests to us that *oelandicus* is closer to *Hoplolichas*. The species is older than those referred without doubt to the genus so some morphological contrasts might be expected. *H? schmidtii* was originally described from a single cranidium (Dames 1877, pl. 8, fig. 6a–c). The glabellar lobation resembles that of *Hoplolichas* species except that the median lobe is upwardly rather than forwardly inflated, somewhat in the manner of certain *Conolichas* species. The same specimen was refigured by Schmidt who associated with it a second cranidium and a pygidium (1885, pl. 4, figs 36–38). The pygidium as drawn resembles *Otarozoum* species rather than *Hoplolichas*, but it seems to have been extensively reconstructed posteriorly. Until this material has been revised we provisionally assign the species to *Hoplolichas*.

Genus *Hoplolichoides* Phleger, 1936

Figures 139, 143 and 150, plate 7; figures 193–197, plate 10.

Type species. Original designation Phleger (1936, p. 605); *Lichas conico-tuberculata* Nieszkowski, 1859, p. 365, from the Caradoc of Estonia. Syntype cranidium figured Nieszkowski (1859, pl. 1, figs 7, 8), possibly GIE Tr 2099 (figure 195 herein) if the partial exfoliation and preparation of the occipital spine took place subsequently; syntype pygidium figured Nieszkowski (1859, pl. 1, fig. 9), untraced; syntype hypostome figured Nieszkowski (1859, pl. 1, fig. 10), GIE Tr 2109 (figure 196 herein).

Other species. *H. curvifrons* (Warburg, 1939); *H. furcifer* (Schmidt, 1885).

Stratigraphical and geographical range. Llandeilo–Caradoc of Estonia, and in erratics of this age in Sweden and north Germany.

Remarks. The three species included in *Hoplolichoides* closely resemble each other and also share some features with species of *Hoplolichas*, *Otarozoum* and *Conolichas*. This might be taken as grounds for synonymizing the four genera, but the resultant taxon would then include species displaying a great range of morphology and would be almost impossible to diagnose satisfactorily

In cranidial convexity and glabellar proportions *Hoplolichoides* is most like *Otarozoum*, but species of the former have L1b indicated by a weak break in slope and/or a posterior shallowing of the longitudinal furrow (e.g. figure 150). In these respects, and in the possession of occipital spines, *Hoplolichoides* is more similar to *Hoplolichas*. *Hoplolichoides* pygidia are incompletely known, especially the margins, so that a full comparison with other genera is currently impossible. We would not erect a separate genus based only on this combination of characters. Because *Hoplolichoides* is available, however, we think it best to use the taxon, pending the availability of further morphological data, to avoid blurring of generic boundaries.

Genus *Leiolichas* Schmidt, 1885

Figures 144, 145 and 147–149, plate 7; figures 201, 202, 204 and 207–210, plate 10.

Type species. Original designation Schmidt (1885, p. 46); *Platymetopus illaenoides* Nieszkowski, 1857, p. 622, originally described from the Caradoc of Estonia. The species also occurs in erratic boulders of this age in Sweden and North Germany. Lectotype selected Warburg (1939, p. 139): incomplete cranidium, GIE Tr 2108a, figured Nieszkowski (1857, pl. 3, figs 3, 5) (figure 207 herein).

Stratigraphical and geographical range. No other species assigned: distribution as for type species.

Diagnosis. Homolichine with cranidium convex and largely effaced externally where only axial structures visible are the occipital ring, circumscribed L1a and axial furrow. On internal surface a narrow median lobe is visible flanked by much wider lateral lobes. Pygidium highly effaced externally and with entire margin. On internal surface axis is seen to taper gently posteriorly and pleural and interpleural furrows are impressed adaxially.

Remarks. Effacement commonly occurs in many groups of trilobites and such species as *Amphiliches lineatus* (figure 266) display the condition to a mild degree. *Leiolichas*, however, is the only lichid genus in which effacement is well developed. Effacement here has been achieved by external suppression of the dorsal furrows and by an increase in exoskeletal convexity, but without an increase in relative width of the axis (see Lane & Thomas 1983, p. 145). Among the problems caused by effacement is that of determining relationships: *Leiolichas* was assigned to the Lichinae by Tripp (1957, 1958; in Moore 1959) but we follow Phleger (1936, p. 605) in regarding the genus as more likely to be an effaced homolichine. In particular, the narrow median lobe and much wider lateral lobes are most similar to those of some *Conolichas* species. Deeply impressed longitudinal furrows do not extend all the way back to L1a in *Leiolichas* even internally (figure 147) but a faint furrow in this position is visible (Neben & Kreuger 1973, pl. 60, fig. 3; Warburg 1939, pl. 3, fig. 7). The hypostomal morphology of *Leiolichas* might help clarify the taxonomic position of the genus, but no hypostome has so far been described.

Pompecki (1890, p. 44) based his *Lichas gageli* on a single pygidium from the Ashgill of 'the Baltic'. On the basis of shape and convexity Pompecki assigned the species, with some reservations, to *Leiolichas*. Warburg (1939, p. 139) indicated that the affinities of the species could not be determined with certainty in the absence of the cranidium but thought it most likely to belong to *Leiolichas* and Tripp (1958, p. 575) listed *gageli* under that genus. Notwithstanding the gross similarities, *gageli* differs from the type species in being coarsely tuberculate, in having the pleural and interpleural furrows impressed externally and in having the margin not quite entire (Pompecki 1890, pl. 2, fig 33, 33a). These features suggest that *gageli* probably belongs to an undescribed genus.

Genus *Metalichas* Reed, 1902

Type species. Original designation; *Metalichas cicatricosus* Reed, 1902, p. 75, from the Caradoc of Estonia. Lectotype selected herein: cranidium figured Schmidt (1885, pl. 5, fig. 25a–c). See below for discussion concerning the type species and lectotype selection.

Remarks. Considerable nomenclatural confusion surrounds this genus. *Metalichas* was erected by Reed (1902, pp. 73–75, 82) for *Lichas cicatricosa* [*sic*] Schmidt non Lovén, Reed rightly considering two species to be represented. (Lovén's species (also see Warburg 1925, p. 281; 1939, p. 115) belongs to *P*. (*Rontrippia*).) *L. cicatricosus* of Schmidt, however, is a composite species, the pygidium belonging to *Amphilichas* (Warburg 1925, pp. 257, 282) whereas the lectotype cranidium is basically of *Platylichas*-type. Phleger (1936, p. 614) commented on these points and concluded that there was no basis for Reed's genus. Under the ICZN Rules concerning the deliberate use of misidentification, however, *Metalichas* is available and the type species should be known as *M. cicatricosa* Reed (Article 70c(i)).

Öpik (1937, p. 69) based *Trochurus mastocephalus* (figures 211, 215 and 220) partly on a cranidium from the Schmidt collection and included in his species the lectotype of *M. cicatricosus*. Indeed this specimen may be the holotype of *mastocephalus* (Öpik 1937, pl. 23, fig. 4); certainly the figures suggest that the same species is represented. The pygidium which Öpik (1937, pl. 23, fig. 5, pl. 26, fig. 2) (figure 215 herein) associated with these cranidia has narrow, convex posterior pleural bands unlike those of most homolichines (although similar structures are seen in *Autoloxolichas*). It also differs from most members of the subfamily in lacking a distinct third pleural furrow. We consider that this pygidium could be incorrectly associated, and the name *mastocephalus* should therefore be restricted to the holotype and paratype cranidia. On this basis *mastocephalus* is a junior synonym of *M. cicatricosus* Reed, possibly an objective synonym. Öpik assigned *cicatricosus* to *Trochurus*, but his was done largely because of the morphology of the associated pygidium. The cranidia are broadly similar to those of *Platylichas* species though the bullar lobes are highly inflated and almost globular in form. Certainly, there is no close similarity in cranidial structure to any trochurine and we consider *Metalichas* to be more closely related to *Platylichas* species; Tripp (in Moore 1959, p. O498) regarded the two genera as synonymous.

In view of the fragmentary nature of the material, and to avoid further nomenclatural confusion, we suggest that *Metalichas* should be restricted to the type species until better specimens become available.

Genus *Otarozoum* gen. nov.

Figures 160, 161, 163–170, plate 8; figures 198–200, 203–206, plate 10.

Name. Latinized from the Greek *otaros*, 'large eared' and *zoon*, 'animal'; alluding to the appearance of the composite lateral glabellar lobes. Neuter.

Type species. Lichas (*Homolichas*) *melmerbiensis* Reed, 1907, p. 396, from the Caradoc, Cross Fell Inlier, northern England. Lectotype selected Dean (1962, p. 121): internal mould of articulated specimen, SM A29638; figured Reed (1907, pl. 17, fig. 2), Dean (1962, pl. 18, figs 3, 4) (figure 167 herein).

Other species. O. eichwaldi (Nieszkowski, 1857); *O. peri* (Warburg, 1939); *O. pahleni* (Schmidt, 1885); *O. tardum* (Petrunina, 1975); *O? acerbigranum* (Burskij, 1966).

Stratigraphical and geographical range. Caradoc; Wales, England, Sweden, Estonia, the Urals, arctic U.S.S.R. (Vaigach Island and Pai-Khoi), southern Tyan-Shan, and in Baltic erratics of the same age.

Diagnosis. Homolichine having cranidium with very short (sag., exsag.) anterior border; glabellar lobes lacking significant independent convexity. Bullar lobe fused with L1b to form composite lobe; this is five sixths length of median lobe, its long axis approximately parallel to sagittal line. Maximum width of composite lobe slightly greater than that of median lobe measured across same transverse line. L1a transversely oval, in contact with base of composite lobe across its complete width. Pygidium without border. Axis about half sagittal pygidial length, with two prominent axial rings; postaxial band narrowing only slightly posteriorly. Anterior two pairs of interpleural furrows extend to margin, pleurae so defined ending in short, broad spinose tips. Third pleural furrow not confluent posteriorly with furrow defining postaxial band. Short pair of third pleural spines present behind axis.

Remarks. Otarozoum is particularly distinguished from *Conolichas* by the relatively wider median glabellar lobe and correspondingly narrower and more weakly inflated lateral lobes. In addition, the median lobe is never inflated anteriorly and depressed posteriorly, as it is in some species of *Conolichas*. Pygidia of the two genera are broadly similar but the third pleural furrow in *Conolichas* is confluent with that defining the postaxial band so as to describe a loop posteriorly. The cranidium of *Otarozoum* also resembles those of *Autoloxolichas* species. The median glabellar lobe of the latter is more greatly expanded (tr.) anteriorly and the bullar (or composite?) lobe terminates directly in front of the inner end of L1a, whereas the bullar lobe and L1b are clearly fused in *Otarozoum* and this composite lobe abuts L1a along the whole width of the latter. Pygidia of *Otarozoum* and *Autoloxolichas* are unlikely to be confused (compare figure 163 with figure 192).

Also see remarks under *Homolichas*.

The figured material of *O? acerbigranum* (Burskij, 1966, pl. 2, figs 5, 6) suggests that the species is most closely related to *Otarzoum*, differing principally in having L1a extending abaxial of the posterior end of the composite lobe.

Genus *Platylichas* Gürich, 1901

Type species. Original designation; *Lichas margaritifer* Nieszkowski, 1857, p. 568, from the Caradoc of Estonia. The whereabouts of the holotype, a cranidium (Nieszkowski 1857, pl. 1, fig. 15, Schmidt 1885, pl. 15, fig. 17) has been unknown for some time (Öpik 1937, p. 57). Dr R. Männil has provided us with photographs of the topotype specimen figured by Öpik (1937, pl. 22, figs 3, 4) (figures 216 and 221 herein).

Diagnosis. Homolichine with anterior cephalic border commonly short (sag., exsag.) and of approximately constant length around front of glabella, but may be extended sagittally into a blunt spine or spatulate process. Bullar lobe circumscribed, its long axis diverging outwards at between 20° and 50° to sagittal line. Maximum width of bullar lobe equal to, or up to twice width of, median lobe measured across same transverse line. Longitudinal furrow meeting occipital furrow; median lobe expanded (tr.) posteriorly and separating bullar lobe from adaxial extremity of L1a. Axial furrow obsolete between L1a and S1 so that L1b is indistinguishable from fixigena. Pygidium without border, first and second interpleural furrows extending to margin. Three pairs of flat, broad-based marginal spines.

Remarks. See below under *Platylichas* (*Rontrippia*).

Subgenus *Platylichas* (*Platylichas*) Gürich, 1901

[Subjective synonym: *Lingucephalichas* Phleger, 1936]

Figures 171–181 and 183, plate 9.

Type species. As for genus.

Other species. P. (*P.*) *bottniensis* (Wiman, 1908); *P.* (*P.*) *docens* (Schmidt, 1885); *P.* (*P.*) *fossulatus* Öpik, 1937; *P.* (*P.*) *latus* (Törnquist, 1884), *P.* (*P.*) *lingua* Warburg, 1939; *P.* (*P.*) *nasutus* (Wigand, 1888); *P.* (*P.*) *planifrons* (Angelin, 1854); *P.* (*P.*) *robustus* Warburg, 1925; *P.* (*P.*) *scoticus* Reed, 1906; *P.* (*P.*) *validus* (Linnarsson, 1869); *P.* (*P.*) *warburgae* Thorslund, 1930; *P.* (*P.*) *wegelini* Warburg, 1925.

Stratigraphical and geographical range. Caradoc–Llandovery; Scotland, Norway, Sweden, Estonia, arctic U.S.S.R. (Vaigach Island and Pai-Khoi).

Diagnosis. Platylichas with pygidium about one and a third times as wide anteriorly as long (sag.). Pygidial axis about one third sagittal pygidial length; postaxial band gradually narrowing posteriorly. Up to three axial rings present, but posterior two ring furrows may be incomplete. Third pleural furrow not confluent posteriorly with furrow outlining postaxial band.

Remarks. Some *Platylichas* (*Platylichas*) species possess a median anterior extension of the cranidial border. In some (e.g. *P.* (*P. nasutus*, figure 174) this is blunt and short, but in others there is a large spatulate process (e.g. *P.*(*P.*) *lingua*, figures 175, 178, 179 and 183 herein). It was these species that Warburg (1939, p. 125) described as composing her *P. lingua*-group and for which Phleger (1936. p. 614) erected *Lingucephalichas* with *P. planifrons* as type. Apart from the anterior process, itself a variably developed feature, these species are similar to typical *Platylichas* species. We agree with Tripp (1957; in Moore 1959) that the anterior process is not a sufficient feature to be diagnostic at generic level and therefore place *Lingucephalichas* in the synonymy of *Platylichas* (*Platylichas*). The hypostome of members of the *P. lingua*-group is distinctive in being relatively long (figure 173). In these species the rostral suture is curved forwards (figure 178) and the elongation of the hypostome is principally achieved by enlargement of the middle body and curvature of the anterior margin to fit the hypostomal suture. It therefore seems that this hypostomal morphology is intimately related to the presence of the frontal process.

For comparative remarks see below under *P.* (*Rontrippia*).

Subgenus *Platylichas* (*Rontrippia*) subgen. nov.

Figures 182, 184 and 187, plate 9.

Name. After Mr R. P. Tripp in recognition of his work on lichids.

Type species. Lichas grayii Fletcher, 1850, p. 237, from the Wenlock of England and Gotland. Lectotype selected Thomas (1981, p. 79): cranidium, SM A10258; figured Fletcher (1850, pl. 27, fig. 8), Thomas (1981, pl. 21, fig. 11).

Other species. P. (*R.*) *cicatricosus* (Lovén, 1845); *P.* (*R*?) *angulatus* Warburg, 1925; *P.* (*R*?) *dalmani* Warburg, 1939; *P.* (*R*?) *parvulus* Cooper & Kindle, 1936; *P.* (*R*?) *telleri* (Weller, 1907); *P.* (*R*?) *vultuosus* Öpik, 1937.

Stratigraphical and geographical range. Caradoc?, Ashgill–Wenlock, Ludlow?; North America? (Wisconsin?, Quebec?), Wales, England, Sweden, Gotland, Ireland?, Estonia?.

Diagnosis. Platylichas with pygidium up to twice as wide anteriorly as long (sag.). Axis about half sagittal pygidial length, distinctly constricted posteriorly. Two complete ring furrows, third and fourth increasingly discontinuous adaxially. Third pleural furrow describes a loop posteriorly and is confluent with furrow bounding postaxial band.

Remarks. We consider that the division of *Platylichas* into two subgenera best reflects the cephalic similarities found in species of the genus and also takes account of the existence of two rather distinctive types of pygidia. Pygidia of *P.* (*Rontrippia*) principally differ from those of *P.* (*Platylichas*) species in being relatively wider and shorter, with a longer axis which is more distinctly constricted behind, and with the third pleural furrow describing a loop posteriorly. *P.* (*Platylichas*) species mostly have longer and more blade-like marginal spines. Only two species are assigned to the new subgenus with certainty because only these two are known from both pygidia and cranidia. The cranidia (figure 184 herein) (Warburg 1939, pl. 12, fig. 15a–c) differ from most *P.* (*Platylichas*) species in having the bullar lobe of similar maximum width to the median lobe, as measured across the same transverse line, and the bullar lobes diverge less strongly forwards. A short, adaxially directed furrow is commonly present on the median lobe opposite the posterior end of the bullar lobe. Similar cranidial features are seen in those species assigned to the subgenus with question but a firm assignation cannot be made in the absence of pygidia. This is particularly so because *P.* (*P.*) *scoticus* has a similar cranidial morphology but we assign the species to the nominate subgenus because of the characters of the pygidium (Howells 1982, pl. 13, figs 15, 21). Judging from the published drawings *Dicranopeltis telleri* Weller (1907, pl. 22, figs 8, 9) probably belongs to *P.* (*Rontrippia*). We have traced three syntype cranidia (USNM 96658) of which one was the basis of Weller's illustration. His figure is inaccurate in showing the axial furrow impressed abaxial of L1a, although there is a slight change in slope in that area, and in all essential respects the cranidia resemble those of *P.* (*R.*) *grayii* and *P.* (*R.*) *cicatricosus* (Lovén).

Platylichas? *hamatus* (Schmidt, 1885) cannot be accommodated in either subgenus, but appears more similar to *Platylichas* than to other homolichines. The bullar lobes are apparently almost parallel-sided and only weakly diverging, and the associated pygidium is very fragmentary (Schmidt 1885, pl. 6, figs 22, 23). Until the species is revised we assign it to *Platylichas* (*s.l.*) with question.

Also see remarks under *Autoloxolichas*.

?Genus *Metopolichas* Gurich, 1901

[pro *Metopias* Eichwald, 1842, non Gory, 1832
Subjective synonyms: *Macroterolichas* Phleger, 1937b; *Holoubkovia* Přibyl & Vaněk, 1969]
Figures 222–235, 237, 238, ?236, 239 and 240, plate 11.

Type species. Subsequent designation of Reed (1902, p. 61); *Metopias Hüberni* Eichwald, 1842, p. 62, from the Tallinna Limestone (Lasnamägi Stage, upper Llanvirn–lower Llandeilo), Estonia. The holotype, a partly exfoliated cranidium figured by Eichwald (1842, pl. 3, figs 21, 22) and Schmidt (1885, pl. 1, fig. 13a, b), was reported by Schmidt (1885, p. 66) to be in the Petrovsk (now Timiryazev) Academy of Agricultural Sciences in Moscow; Dr M. N. Chugaeva has informed us, however, that she was unable to locate it there.

Other species. *M. anderkensis* Weber, 1948, *M. celorrhin* (Angelin, 1854); *M. coniceps* (Leuchtenberg, 1843); *M. contractus* MacGregor, 1963; *M. erici* (Warburg, 1939); *M. kuckersianus* (Schmidt, 1885); *M. longerostratus* (Schmidt, 1885); *M. pachyrhinus* (Dalman, 1828); *M. pakrianus* (Öpik, 1937); *M. patriarchus* (Wyatt-Edgell, 1866); *M. platyrhinus* (Schmidt, 1907); *M. sinensis* (Sun, 1931); *M. squamulosus* (Öpik, 1937); *M. verrucosus verrucosus* (Eichwald, 1842); *M. verrucosus circumscriptus* (Schmidt, 1907); *M. wimani* (Öpik, 1925); *M. yuanbaensis* Zhou, 1975; *M*? *klouceki* (Růžička, 1926); *M*? *tongziensis* Yin, 1980.

Stratigraphical and geographical range. ?Tremadoc, Arenig–Llandeilo or lowermost Caradoc; England, Wales, Norway, Sweden, north German erratics, east Baltic, U.S.S.R., China (Yunnan, Shaanxi and ?Guizhou provinces), ?Czechoslovakia.

Diagnosis. Homolichine with gently to strongly convex glabella; median lobe sometimes markedly overhanging anterior border, or extended into long anterior process. Longitudinal furrow usually terminating at base of bullar lobe but may extend weakly to occipital furrow; bullar lobe sometimes circumscribed but usually confluent with L1b abaxially. Pygidium with three pairs of pleural furrows and marginal spines; axis approximately one third sagittal length of pygidium, indistinctly separated from postaxial band, and with two axial rings.

Remarks. The type species is very poorly known, the only specimen we have been able to locate being the cranidium figured by Öpik (1937, pl. 7, fig. 2). Schmidt (1885, pl. 1, figs 13a, b, 14a–c) figured the holotype and another, less complete, cranidium that he considered to be conspecific. The second cranidium differs from the holotype, however, in having circumscribed bullar lobes and a sculpture of tubercles rather than pits, suggesting that it may belong to a different species. In 1907, Schmidt (pl. 2, figs 6, 7) figured another fragmentary cranidium of *huebneri* and an incomplete pygidium with a punctate sculpture similar to that of the holotype, but these illustrations are too poor for detailed comparison with other species. Our concept of *Metopolichas* is therefore based largely on better known species such as *M. celorrhin*, *M. pachyrhinus* and *M. verrucosus*. These have cranidia similar to those of Öpik's specimen of *huebneri* except that they have a sculpture of tubercles instead of pits. The pygidia of these species, however, have three pairs of marginal spines, whereas Schmidt (1907, p. 38) described the pygidium attributed by him to *huebneri* as of semicircular outline, without distinct spines. No marginal spines are evident in his photograph of the specimen but the margin appears to be retouched. (The drawing given by Tripp (in Moore 1959, fig. 392, 1d), which is said to be based on Schmidt's illustration, shows two pairs of marginal spines.) If Schmidt's interpretation of the pygidial morphology of *huebneri* should be proved correct by the discovery of additional material, then the concept of *Metopolichas* will have to be revised.

Most species of *Metopolichas* are similar to *Lichas* in cranidial characters, especially in having the longitudinal furrow terminating at the base of the bullar lobe, and the bullar lobe fused or partly fused on L1b. The hypostome of *Metopolichas*, however, is like those of homolichines rather than lichines in being wider than long and having a circumscribed middle body and very wide lateral borders (figure 231). This was pointed out by Tripp (1957, p. 113) who compared the hypostome of *Metopolichas* with that of *Conolichas*; nevertheless, he assigned *Metopolichas* to the Lichinae rather than to the Homolichinae. We consider the form of the hypostome to be of primary importance in assessing relationships at the subfamily level, and therefore include *Metopolichas* in the Homolichinae. It is noteworthy that some species assigned to the genus, such as *M. squamulosus* and *M. wimani* (Öpik 1937, pl. 6, figs 1, 2) more closely resemble other homolichines in having the longitudinal furrow extending to the occipital furrow, or almost so.

Macroterolichas was included in a list of lichid genera and species by Phleger (1937*b*), although the name had not previously been formally proposed. The only species assigned to the genus was *Lichas longerostratus* Schmidt, 1885. This differs from *M. huebneri* and similar species mainly in having the median glabellar lobe extended into a long anterior process, but for reasons advanced elsewhere (§3) we do not consider this feature to warrant recognition at the generic level.

Holoubkovia was erected by Přibyl & Vaněk (1969, p. 372) for *L. klouceki* Růžička, 1926 from the Tremadoc of Czechoslovakia. The material of the type species consists of a fragmentary cranidium, a hypostome, and an incomplete pygidium, all of them very small (figures 236, 239 and 240). Přibyl & Vaněk did not assign their genus to a subfamily, but compared it with *Platylichas*, implying that they considered it to be related to the Homolichinae (Tripp (1957, p. 118), however, suggested affinities with the Lichinae). We agree that the hypostomal morphology suggests that *klouceki* belongs to the Homolichinae, and tentatively assign the species to *Metopolichas* on the basis of the longitudinal furrow that terminates at the base of the bullar lobe, the bullar lobe that is confluent with L1b abaxially, the prominent L1a, and the pygidium with three pairs of marginal spines. The pygidium differs from those of *Metopolichas* species in having the posterior pleural bands slightly raised distally, the relatively long and slender marginal spines, and the well-developed border. In these features there are similarities with *Autoloxolichas*, a resemblance noted by Vaněk (1959, p. 115) who compared *klouceki* with *A. laxatus*.

M? *tongziensis* from the early Middle Ordovician of Guizhou Province, China is known only from a cranidium that is too incomplete for confident assignment to the genus.

(*f*) Subfamily TETRALICHINAE Phleger, 1936
[*nom. correct.* Tripp 1957 ex Tetralichadinae Phleger, 1936]

Diagnosis. Lichidae with fused lateral glabellar lobes, typically defined adaxially and abaxially by distinct longitudinal and axial furrows which extend to occipital furrow.

Hypostome about one and a half times as wide as long, shoulders situated abaxially in transverse line with posterior border furrow. Pygidium with pleurae ending in flat, blade-like spines. Pleural furrows typically short and only 1st and 2nd pairs are commonly developed. Axis only weakly separated from postaxial band; these two forming a conical structure extending sagittal length of pygidium or almost so (except in *Probolichas*); one or two complete axial rings typical.

Genera included. Amphilichas Raymond, 1905; *Apatolichas* Whittington, 1963; *Lyralichas* Weber, 1948; *Probolichas* Phleger, 1936.

Stratigraphical range. Arenig/Llanvirn–Ashgill.

Genus *Amphilichas* Raymond, 1905

[pro *Paralichas* Reed, 1902 non White, 1859; pro *Platymetopus* Angelin, 1854
non Dejean, 1829. Subjective synonyms: *Acrolichas* Foerste, 1919;
Kerakephalichas Phleger, 1936; *Tetralichas* Phleger, 1936]
Figures 244 and 245, plate 11; figures 246–258, 261, 262 and 266, plate 12;
?figure 217, plate 10; ?figures 241–243, plate 11.

Type species. Monotypy; *Platymetopus lineatus* Angelin, 1854, from the Ashgill of Dalarne, Sweden. Lectotype selected herein: cranidium, RM Ar 6040; figured Angelin (1854, pl. 38, fig. 12, 12a) (figures 262 and 266 herein). Paralectotype pygidium figured Angelin (1854, pl. 38, fig. 13), untraced: this pygidium belongs to *Sphaerexochus*.

Other species. A. antiquarius (Bradley, 1930); *A. ardmillanensis* (Reed, 1914); *A. aspratilis* (Bradley, 1930); *A. atavus* Warburg, 1925; *A. batchaticus* Weber, 1928; *A. bicornis* (Ulrich, 1892); *A. borealis* Twenhofel, 1928; *A. clermontensis* Slocum, 1913; *A. conifrons* Ruedemann, 1916; *A. conradi* Chatterton & Ludvigsen, 1976; *A. cornutus* (Clarke, 1894); *A. cucullus cucullus* Meek & Worthen, 1868; *A. c. ottowaensis* (Foerste, 1919); *A. dalecarlicus* (Angelin, 1854); *A. declivis* Tripp, 1954; *A. encyrtos* Webby, 1974; *A. fryi* Whittard, 1961; *A. harrisi* (Miller, 1878); *A. hibernicus* (Portlock, 1843); *A. holmi* (Schmidt, 1885); *A. karakensis* Weber, 1948; *A. laevis* (Eichwald, 1857); *A. latifrons* Warburg, 1925; *A. marchica* Kummerow, 1928; *A. minganensis* (Billings, 1865); *A. nasutus* Webby, 1974; *A. obliteratus* Petrunina, 1975; *A. odakensis* Lisogor, 1965; *A. panoplos* Tripp, 1980; *A. parvulus* Warburg, 1925; *A. planus* Tripp, 1954; *A. priscus* Tripp, 1965; *A. prominulus* (Raymond, 1925); *A. punctatus* (Weber, 1948); *A. rhinoceros* Slocum, 1913; *A. rubrus* Cooper & Kindle, 1936; *A. schidertensis* Lisogor, 1965; *A. shideleri* (Foerste, 1919); *A. sniatkovi sniatkovi* (Weber, 1923); *A. s. kolymensis* Chugaeva, 1975; *A. stableri* Hussey, 1941; *A. subdisjunctus* (Bradley, 1930); *A. subpunctatus* Esker, 1964; *A. tibetanus* (Salter, 1865); *A. transversus* (Reed, 1926); *A. trentonensis* (Conrad, 1842); *A. wahlenbergi* Warburg, 1925; *A? browni* (Sun, 1931); *A? hexadactylus* (Nieszkowski, 1857); *A? narrawayi* (Foerste, 1919); *A? periformis* Warburg, 1925; *A? pulcher* Teichert, 1937; *A? welleri* (Foerste, 1920).

Stratigraphical and geographical range. Llanvirn–Ashgill: U.S.A. (Illinois, Iowa, Michigan, Minnesota, Missouri, Nevada, New Jersey, New York, Oklahoma, Pennsylvania, Virginia, Wisconsin), Canada (District of Mackenzie, Newfoundland, Ontario, Quebec), Ireland, Wales, England, Scotland, Norway, Sweden, north German erratics, Czechoslovakia, U.S.S.R. (Estonia, Kazakhstan, Kirghiz Steppe, Kuznetsk Basin, Pai-Khoi, eastern Siberia, Turkestan, Urals, Vaigach), central Himalayas, China, New South Wales, Tasmania, ?north Greenland.

Diagnosis. Tetralichine with complete axial furrow in cranidium. Longitudinal furrow commonly complete and adaxially defining parallel-sided lateral lobe, but may be effaced posteriorly. Pygidium with three pairs of spinose pleurae; furrows defining postaxial band meeting at posterior margin or only a very short distance in front of it. Pygidial axis typically with only one complete ring furrow, up to five such furrows occur exceptionally.

Remarks. Amphilichas was specifically proposed as a replacement name for *Paralichas* Reed and *Platymetopus* Angelin, which are junior homonyms of coleopteran genera. Because *Platymetopus lineatus* was the only species that Angelin (1854, p. 68) unquestionably assigned to his genus, that species is type by monotypy (Warburg 1939, p. 139), despite sporadic statements to the contrary (see, for example, Reed 1902, p. 62).

The type species of *Amphilichas* is distinctive in having the glabella expanded in width and the longitudinal furrows effaced externally so that on the first impression the species seems quite distinct from many of those assigned to this genus (compare figures 254 and 258). Only the cranidium of *A. lineatus* is described from Sweden but conspecific cranidia are known from Norway, and these are associated with other exoskeletal parts (Owen 1981, p. 67, pl. 16, figs 7–15) not generically distinguishable from those of more 'typical' *Amphilichas* species (referred to below as of *A. wahlenbergi*-type). Moreover, such species as *A. conradi* Chatterton & Ludvigsen (1976, p. 80, pl. 18, figs 36–61) and *A. planus* Tripp (1954, p. 657, pl. 1, figs 5, 6) show degrees of longitudinal furrow effacement intermediate between that developed in *lineatus* and that found in the majority of *Amphilichas* species such as *A. wahlenbergi* (figure 246).

Phleger (1936, p. 606) restricted *Amphilichas* to those species in which the longitudinal furrows are effaced posteriorly, erecting *Tetralichas* for species in which these furrows are complete (*A. wahlenbergi*-type). Because of the points noted above, however, we follow Warburg (1939, p. 14) and Tripp in regarding these genera as synonymous. We also follow those authors in regarding *Acrolichas* Foerste and *Kerakephalichas* Phleger as subjective junior synonyms of *Amphilichas*. Foerste (1919) erected *Acrolichas* for several American species that he believed to differ in pygidial characters from Baltic species of *Amphilichas*. The apparent contrasts, however, arose only because of Schmidt's (1885) incorrect association of generically distinct cranidia and pygidia (Warburg 1925, p. 256). *Kerakephalichas* (type species *A. rhinoceros*, figure 255) was distinguished from *Amphilichas* only on the presence of horn-like spines on the cranidium. We do not consider this to be a character of generic importance.

A? browni was redescribed by Zhou *et al.* (1984, p. 32, fig. 8b, c, k). Cephala of this species resemble the type species of *Amphilichas* in general morphology (including that of the hypostome: R. P. Tripp, personal communication), but differ from all species assigned with certainty to the genus in having L1a circumscribed. *Amphilichas? hexadactylus*, from the Caradoc of Estonia, is known only from the holotype pygidium (Nieszkowski 1857, pl. 1, fig. 14; Opik 1937, pl. 6, fig. 4) (figure 217 herein). This pygidium differs from species placed without question in *Amphilichas* in having two complete axial rings, a narrow and ridge-like postaxial piece, and three pairs of pleural furrows of which the first two pairs are long. The marginal spines are elongated and lobate. Some of these characters seem to be shared by the Canadian species *A? narrawayi* (see Foerste 1920, pl. 1, fig. 2), which is likewise only known from the pygidium. It is possible that a distinct genus is represented by *A? hexadactylus* and *A? narrawayi* but knowledge of the other exoskeletal parts is needed before this possibility can be further evaluated. *A? periformis* is known only from the small syntype cranidia, one of which is figured here (figures 241–243). The pyriform median glabella lobe flanked by bean-shaped lateral lobes give the species a highly distinctive appearance. More material, particularly larger specimens and examples of other exoskeletal parts, are required to confirm the lichid affinites of this species. *A? pulcher*, from the Ordovician of Washington Land north Greenland, is known only from an incomplete hypostome and a fragment of genal spine possibly belonging to a second individual (Teichert 1937, pl. 4, figs 5–8). This material is too fragmentary to allow positive generic determination.

Koroleva (1959) described '*Acrolichas*' *clavus*, *Amphilichas kolmakensis*, *A. koksorchsis* and *A. satpaevi* from Kazakhstan. We have been unable to obtain a copy of this publication.

Genus *Apatolichas* Whittington, 1963

Figures 259, 263, 267 and 271, plate 12.

Type species. Original designation; *Lichas jukesi* Billings, 1865, p. 282, from allochthonous boulder in Cow Head Breccia, Lower Head, western Newfoundland (Arenig–lower Llanvirn; see Fortey 1980, p. 15). Holotype: incomplete cephalon, GSC (Geological Survey of Canada) 671a; figured Billings (1865, fig. 269a, b), Whittington (1963, pl. 32, figs 4, 5).

No other species assigned.

Stratigraphical and geographical range. Arenig–Lower Llanvirn; Newfoundland, Nevada.

Diagnosis. (Modified from Whittington 1963, p. 104.) Tetralichine differing from *Amphilichas* in effacement of axial furrow between midpoint of palpebral lobe and a point just in front of L1a. Latter weakly inflated, may be defined adaxially as well as abaxially. Pygidial axis not extending to posterior margin; postaxial piece short and blunt.

Remarks. Variation in the cephalic characters of *A. jukesi*, especially furrow depth, was discussed by both Billings (1865, p. 335) and Whittington (1963, p. 105). The contrasting appearance of internal and external surfaces is particularly notable (see, for example, Whittington 1963, pl. 34, figs 10, 11: there the bullar lobe is defined posteriorly and L1a is circumscribed on the internal surface, but both are largely effaced externally).

Genus *Lyralichas* Weber, 1948

Figures 260, 264, 268, 269 and 272, plate 12.

Type species. Original designation; *Lichas* (*Amphilichas*) *bronnikovi* Weber, 1932, p. 60, from Ordovician, Karatan Range, Tamdy River, Turkestan. Syntypes listed Weber (1932, pp. 60, 137) and some figured Weber (1932, pl. 4, figs 46–49). Dr I. M. Kolobova has supplied us with plaster casts of a syntype cranidium, pygidium and hypostome (all numbered 349) from the collections of the Central Museum (VSEGEI), Leningrad.

Remarks. The genus is known only from the type specimens of the type species and is best restricted to that material until it is revised.

The cranidium of *Lyralichas* is essentially of *Amphilichas*-type except that the longitudinal furrow curves adaxially and terminates about two thirds the way back along the cranidium, and the axial furrow turns strongly outwards just before meeting the occipital furrow (figure 260). Tripp (1957, p. 117) suggested that this deflection of the axial furrow might represent the residual expression of L1a. The *Lyralichas* pygidium (figure 264) differs from those of typical *Amphilichas* species in having two complete axial ring furrows, and there are three pairs of interpleural furrows and four pairs of pleural furrows and marginal spines.

Genus *Probolichas* Phleger, 1936

Figures 265, 270 and 273, plate 12.

Type species. Original designation; *Lichas* (*Hoplolichas*) *robbinsi* Ulrich, 1892, p. 271, from the Caradoc of Minnesota. Holotype: untraced cranidium; figured Ulrich (1892, fig. 1a, b, p. 271).

Other species. P. pandus (Evitt, 1951).

Stratigraphical and geographical range. Llandeilo–Caradoc; U.S.A. (Minnesota, Oklahoma, Virginia).

Diagnosis. Cranidium of *Amphilichas wahlenbergi*-type, but with frontal lobe extended into long, proboscis-like spine. Pygidial axis about half sagittal pygidial length; with three pairs of long, isolated marginal spines.

Remarks. Both Phleger (1936, p. 606) and Evitt (1951, p. 614) considered the anterior prolongation found in *Probolichas* to be generically diagnostic. We agree with Warburg (1939, p. 14) that this character is not particularly important, especially since similar structures occur sporadically within other genera such as *Dicranopeltis* and *Platylichas* (q.v.). In other cranidial characters *Probolichas* species closely resemble *Amphilichas* species of *wahlenbergi*-type.

Shaw (1974, p. 46, pl. 12, figs 17, 19, 20) described two *Probolichas* cranidia and a fragmentary pygidium from a locality in the Bromide Formation of Oklahoma. Mr J. Page has shown us additional specimens from this locality, including an almost complete pygidium (figure 273). Because of sculptural similarities it seems likely that these cranidia and pygidia are correctly associated, especially because the only other lichid recorded from this locality (Shaw 1974, p. 49) is easily distinguished on sculptural grounds. The Oklahoma cranidia closely resemble those of *robbinsi* and *pandus* but the pygidium is unusual among tetralichines in the relatively short axis, long and wide postaxial band, long pleural and interpleural furrows and greatly elongated marginal spines. Given these highly distinctive pygidia alone, we would not assign then to a subfamily with any certainty. We tentatively accept the association of cranidia and pygidia, however, and because *Probolichas* is available, we think it best to use the name to separate this group of species. Further morphological information, and particularly confirmation that the association of exoskeletal parts in correct, is required before the usefulness of this genus can be assessed further.

(*g*) Subfamily TROCHURINAE Phleger, 1936
[= Argetinae Gürich, 1901; Euarginae Phleger, 1936; Acanthopyginae Erben, 1952; Ceratarginae Tripp, 1957]

Diagnosis. Lichidae with longitudinal furrow terminating at base of bullar lobe or extending more or less distinctly to occipital furrow; axial furrow usually effaced alongside L1 but present in some species of *Hemiarges* and *Uripes*. S1 deep behind bullar lobe, except in *Hemiarges* and *Uripes*, shallow or not impressed behind median lobe; L1a may be defined. Palpebral lobe relatively small; posterior margin of cephalon commonly with subgenal notch. Hypostome wider than long, with circumscribed middle body that narrows posteriorly; middle furrow narrow (tr.), more or less transverse, and commonly weak; medial embayment in posterior margin broad and shallow. Pygidium with 2–8 pairs of pleural furrows (usually 2) and 6–16 slender marginal spines that are rounded in cross section. Posterior pleural bands more inflated than anterior bands; postaxial band narrow and convex (tr.).

Genera and subgenera included. Trochurus Beyrich, 1845; *Acanthopyge* (*Acanthopyge*) Hawle & Corda, 1847; *Acanthopyge* (*Jasperia*) subgen.nov.; *Acanthopyge* (*Lobopyge*) Přibyl & Erben, 1952; *Acanthopyge* (*Perunaspis*) Přibyl, 1949; *Akantharges* Phleger, 1936; *Ceratarges* Gürich, 1901; *Craspedarges* Gürich, 1901; *Dicranogmus* Hawle & Corda, 1847; *Eifliarges* Richter & Richter, 1917; *Hemiarges* Gürich, 1901; *Mephiarges* Richter & Richter, 1930; *Radiolichas* Reed, 1923; *Richterarges* Phleger, 1936; *Terranovia* Maksimova, 1977; *Uripes* gen.nov.

Stratigraphical range. Llanvirn–Givetian.

Remarks. The name Argetinae Gürich, 1901 is invalid under Article 39 of the ICZN Rules because it is based on a generic name that is a junior homonym. Tripp (1957, p. 117) proposed Ceratarginae as a replacement name but the genera included in that subfamily by him had previously been placed by Phleger (1936) in the two subfamilies Trochurinae and Euarginae of his family Trochuridae. We consider his Trochurinae and Euarginae to be synonymous, and choose the name Trochurinae as having precedence (in accordance with ICZN Article 24a) because the type genus of Euarginae is a junior synomyn of *Acanthopyge*. Erben (1952, p. 316) used the name Acanthopyginae (attributing authorship to Phleger) in place of Euarginae, presumably because of the synonymy of the type genus of the latter, but this does not constitute grounds for the rejection of a family-group name (ICZN Article 40).

Trochurine hypostomes resemble those of homolichines and tetralichines in overall proportions, the narrow, more or less transverse middle furrow, and the sharply impressed posterior border furrow. Two points of difference are that the posterior hypostomal border in trochurines is not as deeply indented medially as in the other subfamilies, and the middle furrow is commonly weaker.

Genus *Trochurus* Beyrich, 1845

[Subjective synonyms: *Corydocephalus* Hawle & Corda, 1847;
Plusiarges Gürich, 1901; *Makromuktis* Phleger, 1936]
Figures 104–117, 120, 121 and 124–126, plate 6; ?figures 280 and 285, plate 13.

Type species. Monotypy; *Trochurus speciosus* Beyrich, 1845, p. 31 from the high Liteň Formation (Wenlock), Czechoslovakia. Lectotype: pygidium, HUB k162; figured Přibyl & Vaněk (1975, pl. 1, fig. 7), figure 105 herein; this is possibly the pygidium figured by Beyrich (1845, pl. 1, fig. 14; 1846, pl. 1, fig. 1c), although Dr H. Jaeger informs us that Beyrich did not specifically indicate this on the specimen label. Přibyl & Vaněk (1975, p. 51) referred to this specimen as the holotype but it is the lectotype because Beyrich (1845) also assigned a cranidium (actually belonging to *Staurocephalus murchisoni*) to his species. As a result of the rediscovery of the lectotype, the designation of a neotype by Vaněk (1959, p. 146) is unfortunate.

Other species. T. bartonensis (Fletcher, 1950); *T. bulbosus* Phleger, 1937*c*; *T. byrnesanus* (Miller & Gurley, 1893); *T. depauperatus* (Van Ingen, 1901); *T. halli* Foerste, 1917; *T. hanoverensis* (Miller & Gurley, 1893); *T. nasutus* (Weller, 1907); *T. phlyctainodes* (Green, 1837); *T. sarfi* Snajdr, 1980; *T. toernquisti* Gürich, 1901; *T*? *welleri* Foerste, 1917.

Stratigraphical and geographical range. Ashgill–Wenlock, ?Ludlow; North America (Arkansas, Illinois, Indiana, New York, Ohio, Wisconsin), Ireland, England, Wales, Sweden, Czechoslovakia, New South Wales.

Diagnosis. Trochurine with highly convex (sag., exsag.) glabella strongly overhanging anterior border; median glabellar lobe more inflated than bullar lobe. Longitudinal furrow not curving strongly outwards towards front of bullar lobe, terminating posteriorly at base of bullar lobe or extending weakly to occipital furrow. L1a circumscribed; L1b merging with adaxial part of fixigena to form inflated lobe bounded laterally by shallow furrow which is continuous anteriorly and posteriorly with axial furrow. Medial portion of L1 short (sagittal length similar to that of occipital ring), commonly depressed and bearing transverse row of two or three large tubercles. Pygidium with three pairs of marginal spines, posterior pair placed close together; convex border present behind anterior pair of spines.

Remarks. Trochurus differs from other members of the subfamily in that the part of the cranidium between the bullar lobe and L1a forms an inflated lobe bounded laterally by a shallow furrow or change in slope. This furrow has previously been interpreted as the axial furrow, but we consider the latter to be effaced and the inflated posterolateral lobe to be composed of L1b together with part of the fixigena (see §4).

Corydocephalus (type species *C. flabellatus* Hawle & Corda, 1847, by subsequent designation of Reed (1902, p. 61)) and *Plusiarges* (type species *Lichas palmata* Barrande, 1846) are both based on species now considered to be junior synonyms of *T. speciosus* (see Tripp 1958, p. 579). Phleger (1936, p. 612) based *Makromuktis* on *Dicranopeltis nasuta* Weller, 1907 from the Niagaran of Wisconsin, and distinguished his genus from *Dicranopeltis* by its more inflated glabella that is extended into a process anterodorsally. Tripp (1957, p. 114; in Moore 1959, p. O496) listed *Makromuktis* as a synonym of *Dicranopeltis*, but Tripp 1958 (footnote on p. 575) stated that after seeing photographs of *nasuta* he believed the species may actually belong to *Trochurus*. We have examined casts of the types (figures 121 and 125–126) and agree with Tripp, both that the characters on which *Makromuktis* are based are not worthy of recognition at the generic level, and that *nasuta* should be referred to *Trochurus*. Features characteristic of the latter genus rather than *Dicranopeltis* include the greater convexity (sag., exsag.) of the glabella, the longitudinal furrows that are subparallel instead of diverging anteriorly, the inflated posterolateral cranidial lobe that is indistinctly separated from the remainder of the fixigena, and the smaller palpebral lobe.

T. bartonensis from the late Llandovery or Wenlock of New South Wales is known only from the cranidium (figure 114) and was included in *Dicranogmus* by Fletcher (1950, p. 226) and Tripp (1958, p. 577). Fletcher, however, stated that the assignment was made with some hesitation and that there were similarities with *Trochurus*, though none were listed. *T. bartonensis* differs from species of *Dicranogmus* in that the longitudinal furrow is deeply impressed anteriorly, the glabella is not as wide in relation to its length, and the bullar lobes are much narrower than the median lobe. We consider the species to be best assigned to *Trochurus*, even though the posterolateral cranidial lobes are not so inflated as they are in most species of that genus.

T? *welleri* (figures 280 and 285) from the late Wenlock–Ludlow of Illinois is based on specimens figured by Weller (1907, pl. 22, figs 1–4) as *Corydocephalus phlyctainodes* Green. The species differs from undoubted members of *Trochurus* in the presence of long, upwardly directed spines on the median glabellar lobe, the posterolateral cranidial lobes, and the posterior edge of the occipital ring (although the last spines are not shown in Weller's illustration). In addition, the marginal spines on the first two pygidial segments are very long and curved, the spine on the first segment being directed laterally at its base. It is not possible to determine whether a third pair of spines was present in the pygidium illustrated by Weller because the specimen is incomplete, but the pygidium of a closely related, undescribed species from the Wenlock of Arkansas has a posterior pair of tiny, bifid spines. The presence or absence of cranidial spines in lichids is in our view usually worthy of recognition only at the species level, but taken in conjunction with the other differences, may warrant the placing of *T*? *welleri* and the Arkansas species in a separate genus or subgenus.

Genus *Acanthopyge* Hawle & Corda, 1847

Type species. Subsequent designation of Reed (1902, p. 60); *A. Leuchtenbergii* Hawle & Corda, 1847, p. 144, from the Acanthopyge Limestone (Eifelian), Czechoslovakia. Lectotype:

cranidium, NMP L15148, selected Šnajdr (1984*b*, p. 169); figured Barrande (1852, pl. 28, figs 40, 41), Šnajdr (1984*b*, pl. 5, fig. 13). Horný & Bastl (1970, p. 192) considered this specimen to be the holotype by monotypy, but Hawle & Corda (1847, pl. 1, figs 5–7) figured a hypostome and a pygidium in addition to a cranidium. The designation of a pygidium as lectotype by Vaněk (1959, explanation to pl. 5, fig. 3) is not valid as the specimen concerned is not a definite syntype (Horný & Bastl 1970, p. 153; Šnajdr 1984*b*, p. 169). *A. leuchtenbergii* has been shown to be junior synonym of *Lichas haueri* Barrande, 1846 (see Tripp 1958, p. 579; Šnajdr 1984*b*, p. 169).

Diagnosis. Trochurine with strongly convex (sag., exsag.) glabella usually not overhanging anterior border; in dorsal view glabella approximately as wide across bullar lobes as long, median lobe typically projecting strongly in front of bullar lobe. Longitudinal furrow extending to occipital furrow but shallower behind S1 than in front, diverging strongly around front of bullar lobe. Medial portion of L1 very short (sagittal length less than that of occipital ring), depressed, and bearing a prominent tubercle; L1a not defined. S1 well impressed behind median glabellar lobe, commonly merging with occipital furrow on sagittal line. Posterior margin of cephalon with deep subgenal notch. Pygidium with two or three pairs of pleural furrows and three or four major pairs of marginal spines; major spines sometimes with secondary spines between them; convex border may be weakly developed behind anterior pair of spines.

Remarks. We recognize four subgenera of *Acanthopyge* that differ in pygidial morphology but are similar in most features of the cranidium. Several species of *Acanthopyge* that are known only from cranidia cannot be assigned to any one of these subgenera with certainty, and until their affinities are clarified we refer them to *Acanthopyge* (s. l.). These species include *A.* (s. l.) *convexa* (Chernysheva, 1951), *A.* (s. l.) *latilobe* Nan, 1976; *A.* (s. l.) *meridionalis* (Frech, 1887), *A.* (s. l.) *peneaui* Pillet, 1973; *A.* (s. l.) *permarginata* (Přibyl & Erben, 1952), and *A.* (s. l.) *pulex* (Haas, 1968).

Subgenus *Acanthopyge* (*Acanthopyge*) Hawle & Corda, 1847

[Subjective synonyms: *Euarges* Gürich, 1901; *Nipponarges* Kaneko, 1984]
Figures 274–279 and 281, plate 13.

Type species. As for genus.

Other species. A. (*A.*) *mediosulcatus* (Kaneko, 1984).

Stratigraphical and geographical range. Eifelian; Czechoslovakia, Germany, U.S.S.R., Japan.

Diagnosis. Acanthopyge with cranidium having maximum width across posterior part of fixigena. Pygidium with three pairs of marginal spines that are long, slender and rounded in cross section, first two pairs diverging strongly; distance between first and second pairs of spines almost equal to that between second and third pairs. Two pairs of pleural furrows, meeting lateral margin in front of marginal spines, pleural and interpleural furrows almost straight. Width to length ratio of pygidium (excluding marginal spines) varying from 1.0 to 1.3; axis comprising one third to two fifths anterior width of pygidium and approximately half sagittal length.

Remarks. As type species of his taxon *Euarges*, Gürich (1901, p. 527) named *Lichas haueri* Barrande, 1846, which as noted above is a senior synonym of *A.* (*A.*) *leuchtenbergii*; *Euarges* is thus a junior subjective synonym of *A.* (*Acanthopyge*). Reed (1923, p. 455) used the name *Euarges* instead of *Acanthopyge* because he considered the latter to be preoccupied by *Acanthopyga*

Gray, 1838 (Reptilia), and Phleger (1936, p. 610) presumably followed his example. Richter (1924, p. 134) pointed out, however, that *Acanthopyga* and *Acanthopyge* are not homonyms.

Kaneko (1984, p. 478) considered the most important diagnostic feature of his genus *Nipponarges* to be the presence on the median glabellar lobe of two transverse furrows which he interpreted as S2 and S3. The material of the type species, *N. mediosulcatus* from the Eifelian of Japan, is strongly deformed and fragmentary, and includes only a single cranidium. The transverse furrows referred to by Kaneko are shallow, and we believe that they may be artefacts caused by deformation. The deformation would also account for most of the other supposed differences from *Acanthopyge* listed by Kaneko, especially those involving the convexity and proportions of the cranidial lobes and the length of the anterior border. The pygidium of *N. mediosulcatus* is very similar to that of *A.* (*A.*) *haueri* in overall proportions, the relative size of the axis, the straightness of the posterior pleural bands on the first two segments, and apparently also the form of the marginal spines. We therefore regard *Nipponarges* as a junior synonym of *A.* (*Acanthopyge*).

Also see remarks under *A.* (*Jasperia*) and *A.* (*Lobopyge*).

Subgenus *Acanthopyge* (*Jasperia*) subgen.nov.

Name. After Wee Jasper, the locality of the type species.

Type species. Acanthopyge (*Mephiarges*) *bifida* Edgell, 1955, p. 138, from the Taemas Limestone Formation (Emsian–?Eifelian) of New South Wales. The syntypes, which are numbered 8305 in the palaeontological type collections of Stanford University, U.S.A., include a cranidium, two librigenae, a hypostome, two thoracic segments and a pygidium. Edgell (1955, p. 141) referred to these specimens collectively as the holotype, but they were etched from limestones as disarticulated silicified exoskeletal parts, and their size indicates that they could not have belonged to a single individual.

Other species. A. (*J.*) *duplicispinata* Kaneko, 1984.

Stratigraphical and geographical range. Emsian–Eifelian; New South Wales, Japan.

Diagnosis. Acanthopyge with cranidium having maximum width across palpebral lobes. Large paired spines present on median glabellar and posterolateral cranidial lobe; posterior edge of occipital ring with median spine and a pair of lateral spines. Pygidium with three major pairs of marginal spines and several secondary spines between second and third major ones; distance between first and second spines less than half that between second and third major spines; third pair of major spines fused proximally and flexed upwards. First two pygidial pleurae with upwardly directed spines arising from posterior bands, and with pleural furrow meeting lateral margin in front of marginal spines. Excluding marginal spines, pygidium almost as long as wide, with axis comprising approximately two thirds anterior width and three quarters sagittal length or more.

Remarks. Compared with *A.* (*Acanthopyge*), the pygidium of *A.* (*Jasperia*) is characterized by the marked reduction in width and length (sag.) of the pleurae, and the reduction in length (exsag.) of the anterior pleural bands on the first two segments. As a result, the axis is relatively larger in *A.* (*Jasperia*), and the first two marginal spines are placed much closer together. Other differences from *A.* (*Acanthopyge*) include the upwardly directed spines on the posterior pleural bands of the first two segments, the presence of numerous secondary spines between the second and third pairs of major spines, and the proximal fusion of the third pair of spines which are flexed upwards instead of lying horizontally. Cranidia of *A.* (*Jasperia*) differ from those of

A. (*Acanthopyge*) in being wider across the palpebral lobes than across the posterior part of the fixigena, and in having a distinctive pattern of spines on the cranidial lobes and occipital ring.

A. (*J.*) *bifida* was assigned to *Acanthopyge* (*Mephiarges*) by Edgell (1955) and Chatterton (1971) because of the presence of glabellar spines, pedunculate eyes, and barbed genal spines. We consider that *Mephiarges* should be restricted at present to the type species *M. mephisto*, which is very poorly known (see discussion on *Mephiarges*). Nevertheless, the cephalon of *M. mephisto* differs from that of *A.* (*J.*) *bifida* in having a more convex (sag., tr.) glabella, the maximum width of the pygidium lies across the posterior part of the fixigena, the fixigena is wider (tr.) below the eye, the posterolateral cranidial lobe lacks a large, upwardly directed spine, and the spine on the palpebral lobe is much larger. These differences, some of which were pointed out by Whittington (1956, p. 1204), suggest that *M. mephisto* and *A.* (*J*) *bifida* are probably not closely related.

In the arrangement of upwardly-directed spines on the cranidium and pygidial pleurae, *A.* (*J.*) *bifida* resembles *A. consanguinea* (Clarke, 1894) from the Lower Devonian of New York. This led Whittington (1956, p. 1204) and Chatterton (1971, p. 41) to suggest a relationship between these species, although Chatterton *et al.* (1979, p. 820) stated that the relationship may not be as close as previously suggested. We consider *A. consanguinea* to belong to *A.* (*Lobopyge*), and another member of that subgenus, *A.* (*L.*) *sinuata* (Ratte, 1886) also has a similar pattern of large tubercles on the cranidium (Chatterton *et al.* 1979, pl. 109, figs 1–3). We would therefore place little weight on this feature alone in assessing relationships among species of *Acanthopyge* (s. l.).

The only species apart from *A.* (*J.*) *bifida* that we assign to the subgenus is *A.* (*J.*) *duplicispinata* Kaneko, 1984 from the Eifelian of Japan. Kaneko (1984, p. 485) noted that his species possesses several features in common with both *A.* (*J.*) *bifida* and *A.* (*L.*) *consanguinea* but concluded that it is not closely related to either of them. Of the differences between *duplicispinata* and *bifida* mentioned by Kaneko, we consider the proportions of the glabellar lobes, the smaller palpebral tubercle and the sculpture on the middle body of the hypostome to be of importance only at the species level. Some of these differences may also be attributable to preservational factors, as the material of *duplicispinata* is deformed. The dorsally directed spines on the posterior pleural bands of the first two pygidial segments were stated by Kaneko to be absent in *duplicispinata*, but in the pygidium illustrated in his pl. 89, fig. 3a, b the first of these spines is present and the second one appears to have been broken off. Other similarities with pygidia of *bifida* not mentioned by Kaneko include the closeness of the first two pairs of marginal spines, and the presence of secondary spines between the second and third pairs of major spines.

Subgenus *Acanthopyge* (*Lobopyge*) Přibyl & Erben, 1952

Figures 282 and 283, plate 13; figures 301 and 302, plate 14.

Type species. Original designation; *Lichas Branikensis* Barrande, 1872, p. 43, from the Dvorce–Prokop Limestone (Pragian), Czechoslovakia. Lectotype: pygidium, NMP IT1378, selected Přibyl & Erben (1952, p. 147); figured Barrande (1872, pl. 16, fig. 31), Přibyl & Erben (1952, pl. 11, fig. 6), Vaněk (1959, pl. 7, fig. 10) (figure 283 herein).

Other species. A. (*L.*) *altirhachis* (Chernysheva, 1951); *A.* (*L.*) *australiformis* Chatterton, Johnson & Campbell, 1979; *A.* (*L.*) *australis* (McCoy, 1876); *A.* (*L.*) *balliviani* (Kozłowski, 1923); *A.* (*L.*) *brevis* (Maksimova, 1968); *A.* (*L.*) *campbelli* Chatterton & Wright, 1986; *A.* (*L.*)

consanguinea (Clarke, 1894); *A.* (*L.*) *contusa* (Hall & Clarke, 1888); *A.* (*L.*) *decheni* (Holzapfel, 1895); *A.* (*L.*) *docekali* (Vaněk, 1959); *A.* (*L.*) *erinacea* (Haas, 1968); *A.* (*L.*) *hexapteryx* (Přibyl & Erben, 1952); *A.* (*L.*) *hirsuta* (Fletcher, 1850); *A.* (*L.*) *limbata* (Maksimova, 1968); *A.* (*L.*) *longiaxis* (Maksimova, 1968); *A.* (*L.*) *orientalis* Wu, 1977; *A.* (*L.*) *parva* (Barrande, 1846); *A.* (*L.*) *pervasta* Přibyl *et al.* 1986; *A.* (*L.*) *pragensis* (Bouček, 1933); *A.* (*L.*) *pusilla* (Angelin, 1854); *A.* (*L.*) *pustulosa* Morzadec, 1983; *A.* (*L.*) *richteri* (Vaněk, 1959); *A.* (*L.*) *rohri* (Perry & Chatterton, 1977); *A.* (*L.*) *sibirica* (Chernysheva, 1951); *A.* (*L.*) *sinuata* (Ratte, 1886); *A.* (*L.*) *uralensis* Maksimova, 1979.

Stratigraphical and geographical range. Wenlock–Eifelian, ?Givetian; North America (Baillie-Hamilton Island, New York, Ontario), Bolivia, England, Wales, Sweden (Gotland), Germany, Czechoslovakia, Turkey, U.S.S.R. (central Kazakhstan, Kuznetsk Basin), China (Guizhou Province), New South Wales, Victoria.

Diagnosis. *Acanthopyge* with cranidium having maximum width across posterior part of fixigena. Pygidium with three major pairs of marginal spines that are relatively short, slightly flattened in cross section, and directed strongly backwards; a pair of secondary spines may be present between successive pairs of major ones. Two pairs of pleural furrows, not meeting pygidial margin but running onto bases of marginal spines; pleural and interpleural furrows curving backwards abaxially. Excluding marginal spines pygidium approximately one and a half times as wide as long; axis comprising two fifths to one half anterior width and two-thirds to three-quarters sagittal length.

Remarks. Tripp (1957; in Moore 1959) regarded *Acanthopyge* (s. s.) and *Lobopyge* as synonyms. Chatterton *et al.* (1979) stated that there is gradation between these taxa in some features but that on a balance of characters it is possible to assign species to one form or the other. We agree with Chatterton *et al.* and follow them in regarding *Lobopyge* as a subgenus of *Acanthopyge*.

Pygidia of *A.* (*Lobopyge*) typically differ from those of *A.* (*Acanthopyge*) in being relatively wider, with a much shorter postaxial region. The pleural and interpleural furrows are flexed backwards abaxially instead of being almost straight, and the marginal spines are shorter, more flattened, and directed more strongly backwards. Přibyl & Erben (1952, p. 145) pointed out that the first two marginal spines in *A.* (*Acanthopyge*) are formed only from the posterior pleural bands, but that in *A.* (*Lobopyge*) both anterior and posterior bands are incorporated into the spines. As a result, in *A.* (*Acanthopyge*) the pleural furrows meet the pygidial margin in front of each of the spines (figure 277), whereas in *A.* (*Lobopyge*) the pleural furrows do not reach the margin but tend to run onto the bases of the spines (Chatterton *et al.* 1979, pl. 108, figs 14, 19, 25). This distinction is not always clear-cut, however, and in species such as *A.* (*L.*) *orientalis* (Wu 1977, pl. 3, fig. 6), *A.* (*L.*) *parva* (Vaněk 1959, pl. 6, fig. 2) and *A.* (*L.*) *decheni* (Holzapfel 1895, pl. 2, fig. 18) the extent to which the anterior pleural bands contribute to the formation of the spines is not clear (in the case of *decheni* this may be due to inaccuracy in Holzapfel's drawing). This uncertainty in the form of the marginal spines led to *parva* and its junior synonym *Lichas parvula* Novák, 1890 being included in *A.* (*Acanthopyge*) by Vaněk (1959) and Přibyl & Erben (1952). In other features such as the overall proportions of the pygidium, the length of the postaxial region, the curvature of the pleural and interpleural furrows and the posteriorly directed marginal spines, *orientalis*, *parva* and *decheni* are all closer to *A.* (*Lobopyge*) than to *A.* (*Acanthopyge*).

Přibyl & Erben (1952) suggested that pygidia of *A.* (*Lobopyge*) also differ from those of *A.* (*Acanthopyge*) in the length (exsag.) of the anterior pleural bands and the convexity of the posterior bands. We can see little difference in the convexity of the posterior bands. It is true that the anterior bands in most species of *A.* (*Lobopyge*) are shorter than they are in *A.* (*A.*) *haueri*, but this feature cannot be used to distinguish the pygidium of *A.* (*Lobopyge*) sp. figured by Chatterton *et al.* (1979, pl. 109, fig. 23) from that described by Přibyl & Erben (1952, pl. 9, fig. 1) as *Acanthopyge* n. sp. (ex aff. *haueri*), which clearly belongs to *A.* (*Acanthopyge*). Chatterton *et al.* (1979, p. 819) distinguished *A.* (*Lobopyge*) from *A.* (*Acanthopyge*) by a combination of cephalic and pygidial characters but some of these also seem to be of little value in this regard. For example, we can see no significant differences from *A.* (*Acanthopyge*) in the inflation of the glabella or the size of the cheeks, and the proportions of the hypostome are variable within *A.* (*Lobopyge*), as was stated by Chatterton *et al.* and can be seen from comparison of their pl. 108, fig. 15, and pl. 109, fig. 13. A well-developed pygidial border is present in some species of *A.* (*Lobopyge*), such as *A.* (*L.*) *pusilla* (G. Helbert, personal communication) and *A.* (*L.*) *hirsuta* (Thomas 1981, pl. 20, figs 4, 17), as well as in smaller pygidia of *A.* (*A.*) *haueri* (figure 281); in larger pygidia of *A.* (*A.*) *haueri* (which are relatively longer than those of *A.* (*Lobopyge*) species, not shorter as stated by Chatterton *et al.*) the border is faint or absent (figure 276).

Perry & Chatterton (1977) included several disarticulated exoskeletal parts in their species *Hemiarges rohri* from the Wenlock of Baillie-Hamilton Island in the Canadian arctic. The pygidia, which include the holotype of the species, have the same number and arrangement of marginal spines as species of *A.* (*Lobopyge*), but the cranidia resemble those of *Richterarges*. Until it can be demonstrated otherwise, we consider the cranidia and pygidia to belong to different genera and assign *rohri* to *A.* (*Lobopyge*).

Subgenus *Acanthopyge* (*Perunaspis*) Přibyl, 1949

[Subjective synonym: *Lobopyge* (*Nitidulopyge*) Přibyl & Erben, 1952]

Figure 289, plate 13.

Type species. Original designation; *Perunaspis longispinus* [*sic*] Přibyl, 1949, p. 316, from the Trebotov Limestone (Eifelian), Czechoslovakia. Holotype: meraspide transitory pygidium, NMP L6345; figured Přibyl (1949, pl. 1, figs 5, 6), Horný & Bastl (1970, pl. 18, fig. 6) (figure 289 herein).

Other species. A. (*P.*) *helga* Přibyl *et al.* 1986; *A.* (*P.*) *minuta* (Barrande, 1846); *A.* (*P.*) *sexlobata* Roemer, 1855.

Stratigraphical and geographical range. Pragian–Eifelian of Czechoslovakia, Emsian of Germany.

Remarks. A. (*Perunaspis*) resembles *A.* (*Lobopyge*) in the cranidium and in such pygidial features as overall proportions, size of the axis, curvature of the pleural and interpleural furrows, and form of the marginal spines. *A.* (*Perunaspis*) differs from *A.* (*Lobopyge*) in having a pygidium with an extra pair of pleural furrows and marginal spines, and an additional axial ring in some specimens. These differences could be due to the posteriormost thoracic segment remaining fused to the pygidium into the holaspid period, and may not be of great taxonomic importance. For this reason we have chosen to regard *Perunaspis* as a subgenus of *Acanthopyge*.

Přibyl & Erben (1952) based *Lobopyge* (*Nitidulopyge*) on *Lichas nitidulus* Barrande, 1872, and also included in the subgenus *Lichas sexlobatus* Roemer, 1855 and their new species *L.* (*Nitidulopyge*) *devonica*. According to Prantl & Vaněk (1958) and Vaněk (1959), *L. nitidulus* is identical with the species that Barrande (1846) named *Cheirurus minutus* but which actually belongs to *A.* (*Perunaspis*), whereas *L.* (*N.*) *devonica* is a synonym of *A.* (*P.*) *longispina*. On this basis, *L.* (*Nitidulopyge*) is a junior subjective synomyn of *A.* (*Perunaspis*).

Přibyl (1949) erected *A.* (*P.*) *longispina* for a pygidium that he considered to be most closely related to the proetid *Prionopeltis*. This pygidium is tiny (1.8 mm in length; Horný & Bastl (1970, explanation to pl. 18)), and has six pairs of marginal spines and six or seven axial rings. The somewhat larger pygidia of *longispina* figured (as *L.* (*Nitidulopyge*) *devonica*) by Přibyl & Erben (1952, pl. 12, figs 7, 8) have four pairs of marginal spines and two or three axial rings, the same numbers as pygidia of other species assigned to *A.* (*Perunaspis*). This evidence suggests that the holotype of *longispina* is a meraspid transitory pygidium. Two different types of cranidia have also been assigned to *longispina*. That figured by Vaněk (1959, pl. 7, figs 4, 7) appear to be similar to those of *A.* (*Acanthopyge*) and *A.* (*Lobopyge*), but the specimen in Vaněk's pl. 7, fig. 6 differs in having the median glabellar lobe narrowing more strongly towards the base of the bullar lobe. The last specimen is slightly smaller in size that the other two and so it is possible that the differences may be due to ontogenetic changes, although this appears unlikely.

Genus *Akantharges* Phleger, 1936

Figures 299, 300, 303–305 and 307–309, plate 14.

Type species. Original designation; *Lichas Gourdoni* Barrois, 1886, p. 126, from the 'schistes à trilobites de Cathervielle' (Eifelian), central Pyrenees, France. The syntypes, which are housed in the Museum d'Histoire Naturelle in Nantes, include two incomplete exoskeletons, CB 154 (Barrois 1886, pl. 2, fig. 1f) (figure 309 herein), and CB 155 (Barrois 1886, pl. 2, fig. 1g) (figure 308 herein); an incomplete cephalon, CB 160 (Barrois 1886, pl. 2, fig. 1d) (figure 304 herein); a cranidium, CB 158 (Barrois 1886, pl. 2, fig. 1a) (figure 305 herein); and an incomplete thorax and pygidium, CB 156 (Barrois 1886, pl. 2, fig. 1c) (figure 307 herein); Barrois also illustrated another cranidium and an almost complete exoskeleton in his pl. 2, fig. 1b, e. The types are at present under study by Dr R. Feist who has provided us with photogrphs of them. For discussion on the age of the type species see Destombes (1960).

Other species. None named, but see remarks below.

Stratigraphical and geographical range. Eifelian; central Pyrenees, Morocco.

Diagnosis. Trochurine with strongly convex (sag., exsag.) glabella not overhanging anterior border; longitudinal furrow weakly impressed anteriorly and behind bullar lobe, containing subcircular pit at junction with S1. L1 as long sagittally as occipital ring, depressed, and separated from median lobe by poorly defined furrow; L1a not defined. Palpebral lobe small, situated low on cheek and far from posterolateral cranidial lobe; anterior and posterior sections of facial suture colinear. Inflated ridge bearing a transverse row of three large tubercles or spines curves anteromedially from fixigena behind palpebral lobe and extends onto posterolateral cranidial lobe; this ridge bounded posteriorly by a sharply impressed furrow that dies out proximally and meets posterior border furrow distally. Subgenal notch very shallow or absent; genal spine long and blade-like.

Remarks. The material of the type species is poorly preserved and very deformed, but in the collections of the British Museum (Natural History) there is a well-preserved cranidium of an undescribed species from Morocco clearly belonging to the same genus (figures 299, 300 and 303). This specimen, with the types of *A. gourdoni*, show that the reconstructions of *Akantharges* given by Barrois (1886, pl. 2, fig. 1h), Phleger (1936, fig. 56) and Tripp (in Moore 1959, figs 396, 397) are incorrect in having the cranidium too elongated, the longitudinal furrow incomplete anteriorly, the axial furrow apparently reaching the occipital furrow, the genal spine probably too long and flexed too strongly backwards, and in showing posterior and lateral border furrows meeting at the base of the genal spine.

What appears in the reconstructions to be the axial furrow abaxial to L1 is in fact a sharply impressed furrow running behind an inflated, transverse ridge on the fixigena. This furrow is shown in the reconstructions as meeting the axial furrow at the outer end of S1, but it actually meets the posterior border furrow distally and curves backwards adaxially towards the outer end of the occipital ring, before dying out (figures 300 and 303). A similar but much weaker furrow is present in *Ceratarges*, running behind the posterior sutural ridge abaxially (figures 315 and 317). In *Akantharges*, however, the inflated ridge in front of the furrow does not carry the facial suture, and the palpebral lobe is situated low on the cheek in front of the distal end of the ridge. *Akantharges* is unique among trochurines (and indeed among lichids in general) in having the palpebral lobe situated so far from the glabella, instead of lying with its anterior edge adjacent to the bullar lobe.

The structure of the pygidium is not clear in the photographs of *A. gourdoni*, and we have therefore not included pygidial characters in the diagnosis. The axis is at least two thirds the total pygidial length and contains at least nine axial rings, of which only the first two are defined by complete ring furrows. Dr R. Feist informs us that there are three pairs of marginal spines, the same number shown in the reconstructions given by Barrois (1886), Phleger (1936) and Tripp (in Moore 1959). Anterior and posterior pleural bands on each segment appear to be inflated, and apparently terminate abaxially well inside the pygidial margin, at the bases of dorsally directed spines or tubercles (figure 307). The posterior pair of these spines or tubercles is situated close to the postaxial ridge.

Genus *Ceratarges* Gürich, 1901
[pro *Arges* Goldfuss, 1839 non De Haan, 1833]
Figures 312–317, plate 14.

Type species. Monotypy; *Arges armatus* Goldfuss, 1839, p. 355, from the Eifelian (Lauch to Ahrdorf beds) of the Eifel district, western Germany. Goldfuss (1839, pl. 33, fig. 1a–e) figured two specimens that he assigned to his species, one a complete exoskeleton with articulated hypostome and the other an incomplete thorax and pygidium actually belonging to a species of *Leonaspis*. Dr H. Jaeger informed us that these specimens are in Bonn, and Barrande (1852, p. 593) stated that he had seen them there, but Dr W. Hass has advised that they are not in the University's Palaeontological Institute and that they may be lost.

Other species. C. faouensis Morzadec, 1970.

Stratigraphical and geographical range. Lower Couvinian of France (Britanny) and Eifelian of western Germany (Eifel, Sauerland).

Diagnosis. Trochurine with subconically inflated glabella overhanging anterior border; a pair of long, backwardly curved divergent spines arising from highest point of median lobe. Longitudinal furrow gently diverging in both directions towards glabellar spines, indistinct behind S1. S1 shallow behind median glabellar lobe, meeting occipital furrow on sagittal line; L1a not defined. Eye borne on long stalk that at its base merges anteriorly and posterolaterally with strong sutural ridges; shallow furrow behind posterior sutural ridge curves posteromedially across fixigena towards outer end of occipital ring. Pygidium (excluding marginal spines) approximately one and a quarter times as wide as long. Axis comprising almost half maximum width of pygidium and approximately three-quarters sagittal length, having one prominent axial ring and several additional rings faintly indicated abaxially. Convex (exsag.) posterior pleural bands on first two segments extended abaxially into spines, of which second is longer than first, is directed more dorsally, and curves backwards distally. Third pleural rib running almost exsagittally from about two thirds length of axis, merging abaxially with bifid postaxial ridge and extended into long, diverging spine. Gently convex border present between bases of second and third spines. Numerous fine secondary marginal spines present between major spines, and lying directly beneath second and third major spines; posteromedian spine slightly larger than other secondary spines.

Remarks. See comments on *Terranovia.*

Genus *Craspedarges* Gürich, 1901

Type species. Original designation; *Craspedarges Wilcanniae* Gürich, 1901, p. 532, from erratic boulders derived from the Amphitheatre Group (Pragian), New South Wales. The whereabouts of the syntypes, stated by Gürich (1901, p. 519) to consist of two incomplete cranidia and four fragmentary pygidia, are unknown. The specimens are not in the Autralian Museum (Dr A. Ritchie, personal communication), nor in the University Museum in Wrocław (formerly Breslau), Poland (Dr J. Gorczyca-Skala, personal communication), where Gürich was Professor at the time his paper was published. Gürich subsequently became Director of the Mineralogisch–Geologisches Staatsinstitut in Hamburg, but Dr W. Weitschat has advised us that the institute's collections were destroyed in World War II.

Remarks. The type species is known only from the illustrations given by Gürich (1901, pl. 18, figs 1, 1a, 6–8). These show that the cranidium is characterized by a relatively long (sag., exsag.) anterior border, a longitudinal furrow extending to the occipital furrow, a narrow, subparallel-sided median glabellar lobe approximately equal in width to the bullar lobe, L1 approximately as long sagittally as the occipital ring and separated from the median lobe by a deeply impressed S1, and apparently no L1a. There are similarities with species of *Richterarges* in most of these features. The pygidial fragments figured by Gürich indicate the presence of numerous subequal marginal spines but the number of spines is indeterminate. Kobayashi & Hamada (1977, p. 94) argued from the symmetrical appearance of the doublure margin (but not the spines) in the pygidium in Gürich's pl. 18, fig. 7 that there were five paired spines and a median unpaired spine, the same number as in their species *C. superbus*. If this were true the pygidium of *wilcanniae* has been illustrated in an oblique orientation, and would have a transverse shape unlike the pygidium of *superbus* or any other known lichid. In the absence of so much morphological information on the pygidium and other exoskeletal parts of *C. wilcanniae* we consider that *Craspedarges* is best restricted to the missing types, and we prefer to assign *superbus* with question to *Richterarges*.

Genus *Dicranogmus* Hawle & Corda, 1847

[Objective synonym: *Liparges* Gürich, 1901]
Figures 290, 291 and 295, plate 13.

Type species. Monotypy; *Dicranogmus pustulatus* Hawle & Corda, 1847, p. 146, from the Kopanina Formation (Ludlow), Czechoslovakia. Holotype: cranidium, NMP L11413; figured Hawle & Corda (1847, pl. 7, fig. 77a, b), Šnajdr (1984*b*, pl. 7, fig. 10) (figures 290, 291 and 295 herein). Šnajdr (1984*b*, p. 184) identified this cranidium as belonging to Hawle's collection and designated it as lectotype, but it must be the holotype because Barrande (1852,

p. 609) stated that the species was based on a single specimen. The designation of a different cranidium as lectotype by Vaněk (1959, pl. 1, fig. 4) is thus invalid (see also Horný & Bastl 1970, p.283).

Other species. D. aequalis (Törnquist, 1884); *D. guizhouensis* Wu, 1977; *D. scabrosus* Zhou & Zhou, 1982; *D. skinneri* Perry & Chatterton, 1977.

Stratigraphical and geographical range. Ashgill–Ludlow; Canadian arctic (Baillie-Hamilton Island), Greenland, Sweden, Czechoslovakia, China (Guizhou Province and Inner Mongolia).

Diagnosis. Trochurine with strongly convex (sag., exsag.) glabella overhanging anterior border; in dorsal view, glabella wider across bullar lobes than long (sag.) and smoothly curved in outline anteriorly, median and bullar lobes there lacking independent convexity. Longitudinal furrows subparallel in front of S1, usually dying out approximately half way to front of bullar lobe, may extend behind S1 as poorly defined depressions not interrupting exoskeletal granulation. Maximum width of bullar lobe almost equal to width of median lobe. L1a usually clearly circumscribed; S1 may be present behind median lobe as weak, concave–forward depression not interrupting exoskeletal granulation and meeting occipital furrow on sagittal line.

Remarks. Barrande (1852, p. 608) considered *D. pustulatus* to be a junior synonym of *Lichas simplex* Barrande, 1846, and this has been accepted by later workers (see, for example, Reed 1902, 1923; Warburg 1925, 1939; Phleger 1936; Tripp 1958; in Moore 1959; Vaněk 1959; Horný & Bastl 1970; Dean 1974; Šnajdr 1984*b*). The holotype cranidium of *simplex* was refigured by Horný & Bastl (1970, pl. 18, fig. 3) and differs from the cranidium of *pustulatus* in having a less convex (sag.) glabella that does not markedly overhang the anterior border, and is narrower across the bullar lobes than long (sag.). The median glabellar lobe is relatively narrower than in *pustulatus*, the longitudinal furrow does not die out anteriorly but is weakly impressed around the front of the bullar lobe, and the poorly defined median portion of S1 lies much farther from the occipital furrow. The differences in glabellar proportions and convexity cannot be attributed to the way in which the type of *simplex* is orientated in Horný & Bastl's photograph because the specimen is orientated so that the posterior edge of the occipital ring is transverse, as are the cranidia of *Dicranogmus* figured by Perry & Chatterton (1977, pl. 6, fig. 13) and Wu (1977, pl. 3, fig. 16). We therefore regard *pustulatus* and *simplex* as separate species, and in fact consider *simplex* to belong to *Richterarges* rather than to *Dicranogmus*. The cranidia attributed to *simplex* by Vaněk (1959, pl. 1, figs 4–7) belong in our view to *pustulatus*.

The presence of L1a in the illustrations of *simplex* given by Barrande (1852, pl. 28, figs 14, 15) is anomalous as this structure is absent in *Richterarges*, although it is normally well developed in *Dicranogmus*. The posterolateral part of the cranidium is not shown in Horný & Bastl's photograph of the holotype and we have not examined the specimen, so that we are unable to confirm the presence or absence of L1a. However, in the lateral view of the cranidium given by Barrande the occipital ring is shown to be broken off and L1a is significantly larger than it is in the dorsal view, in which the occipital ring is intact. It is possible that the lateral view of the cranidium was based not on the holotype of *simplex* but on Hawle & Corda's specimen of *pustulatus*, to which Barrande (1852, p. 609) stated that he had access. L1a may have been added to the dorsal view of the holotype so that it agreed in this feature with the lateral view.

Gürich (1901, p. 529) included *simplex* in his subgenus *Liparges*, and Reed (1902, p. 61) subsequently designated it as type species. If this designation were accepted then *Liparges* would be a senior subjective synonym of *Richterarges*, rather than a junior subjective synonym of *Dicranogmus* as believed by Reed and later authors. (Tripp in Moore (1959) stated that *Liparges* is an objective synonym of *Dicranogmus*, despite the fact that he considered it to have a different nominal type species.) In erecting *Liparges*, Gürich (1901, p. 528) made the following statement regarding species he assigned to the taxon: 'Hall has revived Corda's old name *Dicranogmus* for these forms. For the reasons already stated I let this fall and propose *Liparges* instead of it' (our translation). Gürich's reasons for this action, stated earlier in the same paper (1901, p. 525) when he proposed *Trachylichas* in place of *Dicranopeltis*, lay in what he regarded as uncertainty in Hawle & Corda's diagnoses and concepts of their own genera. It is clear, therefore, that Gürich was not proposing *Liparges* as a new taxon but as a replacement name for *Dicranogmus*, and under Article 67 (h) of the ICZN Rules it must have the same type species, namely *D. pustulatus*. Gürich presumably did not list *pustulatus* as belonging to *Liparges* because he followed Barrande in considering *pustulatus* to be a junior synonym of *simplex*, although he did not explicitly state this.

Most species of *Dicranogmus* including *D. pustulatus* are known only from the cranidium, but Perry & Chatterton (1977, pl. 6, figs 16–21) figured hypostomes and pygidia that they considered to belong to their species *D. skinneri*, and stated that the morphology of these specimens supported the inclusion of the genus in the Trochurinae. The hypostomes certainly belong to a trochurine, as shown by their overall proportions, the deeply impressed posterior border furrow, and especially the poorly defined, almost transverse middle furrow and shallow median notch in the posterior margin. The pygidia differ from those of trochurines, however, in having pleurae with flattened anterior and posterior pleural bands, marginal spines that are broad and flattened, and a postaxial band that is broad and poorly differentiated from the axis anteriorly, and posteriorly is flattened and narrows to a point. Perry & Chatterton (1977, p. 309) noted a resemblance to pygidia of *Amphilichas*, and there are similarities also with *Dicranopeltis* (see Thomas 1981, pl. 19, figs 7, 8); we therefore consider these pygidia to belong either to a lichine or a tetralichine (though the latter subfamily is not recorded from post-Ordovician rocks). Cranidia of *Dicranogmus* are assigned to the Trochurinae mainly on the basis of the glabellar convexity and the absence of the axial furrow alongside L1b, but neither of these features would exclude the genus from the Lichinae or the Tetralichinae. The affinities of *Dicranogmus* will therefore need to be reassessed if the pygidia figured by Perry & Chatterton should be correctly assigned to *D. skinneri*. We note, however, that the pygidia come from a different stratigraphical horizon from the holotype cranidium and one of the hypostomes.

Warburg (1925, p. 262; 1939, p. 148) noted that *D. aequalis* differs from *D. pustulatus* in having the longitudinal furrows extending to the front of the glabella, although they are very narrow and weak anteriorly where the bullar and median lobes lack independent convexity. We agree with her that this difference is not of generic importance. The cranidium from the Ashgill of Ireland figured by Dean (1974, pl. 41, figs 2, 3, 9) as *D.* aff. *aequalis* has the longitudinal furrows deeply impressed anteriorly and the bullar and median lobes are independently convex, although not markedly so. We consider that this cranidium should be assigned with question to *Trochurus*. The three cranidia from the Wenlock of Greenland figured by Lane (1972, pl. 61, fig. 1a, b, pl. 64, figs 5a–c, 8a–d) as *Dicranopeltis*? sp. belong in our view to *Dicranogmus*, the specimen in Lane's pl. 64, fig. 8a–d differing from other known species of the genus in having L1a very indistinctly defined anteriorly.

Genus *Eifliarges* Richter & Richter, 1917

Figure 311, plate 14.

Type species. Monotypy; *Lichas* (*Eifliarges*) *caudimirus* Richter & Richter, 1917, p. 55, from the Upper Calceola Beds (Eifelian), western Germany. Richter & Richter (1917, p. 66) indicated that the syntypes include two more or less complete dorsal exoskeletons and two pygidia, in the collections of the Senckenberg Museum and the University of Frankfurt am Main. We have been able to examine only a plaster cast of the pygidium figured by Richter & Richter (1917, pl. 5, fig. 2).

Other species. None known.

Stratigraphical and geographical range. As for type species.

Diagnosis. Trochurine having cephalon similar to that of *Acanthopyge* but with smaller bullar lobe, a broader median lobe, and larger, more globose eye. Pygidium subtriangular, approximately 1.7 times as wide as long, excluding marginal spines. Axis about one third maximum width of pygidium and two thirds sagittal length, with three distinct rings, the last ring incomplete medially. Pleurae with eight pairs of slender, subequal marginal spines, all but the last two pairs forming extensions of short (exsag.) pleural ribs. Postaxial band narrow, merging posteriorly with poorly defined border formed by abrupt shallowing of furrows between pleural ribs.

Remarks. The type species has not been revised since its original description and the syntypes remain the only specimens known. The most unusual features of the genus are the relatively large number of pygidial pleural ribs and marginal spines (at least twice the number in any other lichid). Richter & Richter (1917, p. 65) considered the ribs to be formed only by the posterior pleural bands, the anterior bands being reduced to weak swellings in the furrows between the ribs. A very short (exsag.) anterior pleural band is present, however, on the first segment. An alternative explanation for the pygidial morphology is that the anterior and posterior pleural bands have become equal in height and length (exsag.) and have both developed marginal spines. We consider this hypothesis to be less likely than the previous one because of the weak swellings in the inter-rib furrows. The pygidium of *Eifliarges* shows striking similarities to meraspide transitory pygidia of *Acanthopyge* (*s. l.*) (see Chatterton 1971, pl. 6, figs 1A, B, 2, 8A, B), and this could be used to argue that *Eifliarges* arose by paedomorphosis. If this were true, *Eifliarges* would be expected to have fewer thoracic segments than adults of its presumed ancestor, but Richter & Richter (1917, p. 63) reported 11 thoracic segments in *E. caudimirus*, the same number as in virtually all other lichids. Hence the pygidial morphology of *Eifliarges* was probably derived by the generation of additional segments, rather than by the failure to release segments into the thorax.

Eifliarges was recorded from the Middle Devonian of Yugoslavia by Stevanovic (1975, pl. 1, fig. 3, 3a) but the solitary pygidium on which the record is based is too poorly preserved for us to confirm the generic assignment.

Genus *Hemiarges* Gürich, 1901

[Subjective synonym: *Choneilobarges* Phleger, 1936]

Figures 214, 218 and 219, plate 10; figures 322, 323 and 327, plate 15.

Type species. Subsequent designation Reed (1902, p. 61); *Lichas* (*Arges*) *Wesenbergensis* Schmidt, 1885, p. 44, from the Rakvere Limestone (Caradoc), Estonia. The types include a cranidium and pygidium figured by Schmidt (1885, pl. 6, figs 1a, b, 2); Dr R. Männil has informed us that these specimens are housed in the Geological Institute of the Soviet Academy of Sciences (GIN) in Moscow.

Other species. H. angustifrons Tripp, 1954; *H. antelucanus* Tripp, 1954; *H. extremus* Owen, 1986; *H. inghami* Tripp, 1979; *H. insolitus* Tripp, 1967; *H. maccullochi* (Reed, 1914); *H. memorans* Öpik, 1937; *H. paulianus* (Clarke, 1894); *H. turneri turneri* Chatterton & Ludvigsen, 1976; *H. turneri rasettii* Tripp & Evitt, 1981; *H*? *aeolus* Sinclair, 1944; *H*? *bartoni* Raymond, 1925; *H*? *illaeniformis* (Wigand, 1888); *H*? *leviculus* Bradley, 1930.

Stratigraphical and geographical range. Llanvirn–Ashgill; North America (District of Mackenzie, Minnesota, Ontario, Virginia, Missouri?), Scotland, Norway, Estonia, northern Germany? (erratics).

Diagnosis. Trochurine with longitudinal furrow converging gently backwards towards midlength of glabella, dying out at base of bullar lobe, or extending weakly to occipital furrow. S1 commonly obsolete, or impressed only behind adaxial part of bullar lobe, rarely continuous across entire width of glabella. L1 approximately as long sagittally as occipital ring; L1a indistinctly separated from L1b. Palpebral lobe with δ–δ level with or just in front of base of bullar lobe. Posterior margin of cephalon lacking subgenal notch. Pygidium transverse, with four pairs of marginal spines, of which second is largest. Axis one third or more maximum width of pygidium, and more than one half sagittal length.

Remarks. Whittington (1961, p. 434) and Thomas (in Thomas & Narbonne 1979, p. 12) noted that species included in *Hemiarges* by Tripp (1957, 1958) may be divided into two groups based mainly on the type of glabellar lobation. We consider these species to include three groups that are distinguished by both cranidial and pygidial characters. We restrict *Hemiarges* to one of these species groups and refer the other two groups to *Richterarges* Phleger, 1936 and *Uripes* gen. nov. respectively. The remarks on those genera include discussion of their differences from *Hemiarges*.

Phleger (1936, p. 610) based *Choneilobarges* on *Lichas* (*Corydocephalus*) *maccullochi* Reed, 1914, from the Ashgill of Scotland, and stated that his genus differs from *Hemiarges* in that S1 is continuous across the median part of the glabella, and L1 confluent with the fixigena. The second feature is, however, characteristic of most trochurines. In the medial continuation of S1, and also in its extension abaxially to meet the axial furrow, there are similarities with *Richterarges*, and Tripp (1957), Whittington (1961) and Thomas (in Thomas & Narbonne 1979) associated *maccullochi* with the type species of that genus, *R. ptyonurus*. However, *maccullochi* most closely resembles species of *Hemiarges* in the curvature of the longitudinal furrow and its depth anteriorly, the indistinctly defined L1a, and the overall form of the pygidium, including the arrangement of marginal spines. We therefore include *maccullochi* in *Hemiarges*, which we consider to be a senior synonym of *Choneilobarges*.

We include four species in *Hemiarges* with question. All of these species are known only from crandida that are too incomplete or too poorly illustrated for definite assignment.

Genus *Mephiarges* Richter & Richter, 1930

Type species. Original designation; *Lichas* (*Euarges*) *Mephisto* Richter & Richter, 1918, p. 146, from the Middle Devonian of Germany. Holotype: cephalon, SMF X721a; figured Richter & Richter (1918, fig. 2; 1930, fig. 7a–c).

Remarks. The genus is known only from the holotype cephalon of the type species. This resembles cephala of *Acanthopyge* in convexity and the development of lobes and furrows, but is characterized by the presence of stout, upwardly directed spines on the palpebral lobe, the highest part of the median glabellar lobe, and the posterior edge of the occipital ring. There is a pair of smaller spines on the bullar lobes, and the eyes are borne on short stalks. The reconstruction given by Richter & Richter (1930, fig. 7c) also shows the genal spine to be strongly barbed but this cannot be confirmed from their photograph. The closest similarity seems to be with *Terranovia*, which differs, however, in having a large, upwardly directed spine on the fixigena just adaxial to the palpebral furrow, rather than on the palpebral lobe. It is impossible to assess the affinities of *Mephiarges* further without knowledge of other exoskeletal parts and, in the meantime, we consider that the genus is best restricted to the type species.

Genus *Radiolichas* Reed, 1923
[Subjective synonyms: *Diplolichas* Phleger, 1936;
?*Septidenta* Maksimova in Mennera, 1975]
Figures 284, 286–288, 292–294 and 296–298, plate 13.

Type species. Original designation; *Lichas aranea* Holzapfel, 1895, p. 32, from the Massenkalk Limestone (Givetian), West Germany. Syntypes, unnumbered specimens housed in the geological and palaeontological department of the Rheinisch–Westfälische Technische Hochschule, Aachen (RTHA) two cephala (figures 284 and 286–288 herein), one figured Holzapfel (1895, pl. 13, fig. 1, 1a); a hypostome (figure 294 herein), figured Holzapfel (1895, pl. 13, fig. 16); three pygidia (figures 293, 297 and 298 herein), two figured Holzapfel (1895, pl. 13, figs 2, 3); the cephalon figured Holzapfel (1895, pl. 3, fig. 11, 11a) is apparently missing.

Other species. *R. devonianus* (Whidborne, 1889); *R. maureri* (Novák, 1890); *R? asiaticus* Maksimova, 1974; *R? bogdanovi* (Maksimova in Mennera, 1975).

Stratigraphical and geographical range. Givetian of West Germany and England; Lower to lower Middle Devonian of U.S.S.R.? (Kazakhstan and Mongolian Altai).

Diagnosis. Trochurine with moderately convex (sag., exsag.) glabella not overhanging anterior border: median glabellar lobe not elevated above bullar lobe. Longitudinal furrows subparallel adaxial to bullar lobe but diverging anteriorly and posteriorly, meeting occipital furrow; maximum width of bullar lobe greater than width of median lobe measured across same transverse line. L1 obsolete or very short (exsagittal length less than or equal to that of occipital ring) behind posterior extremity of bullar lobe, and obsolete behind median lobe; L1a not defined. Prominent tubercle situated in subtriangular depressed region at intersection of S1 and occipital and longitudinal furrows. Posterior margin of cephalon with deep subgenal notch, within which is a laterally directed spine; librigena reduced to slender spine with median longitudinal furrow. Pygidium with seven long, slender, abaxially expanding marginal spines radiating from narrow pleural region; paired spines divided longitudinally by pleural furrows which die out near bases of spines; median posterior spine with longitudinal ridge distally. Axis subrectangular, rather weakly inflated, with one distinct ring. Postaxial ridge broad (approximately half axial width) and gently convex (tr.).

Remarks. Tripp (1957; in Moore 1959) proposed the name *araneiformis* as a replacement for Holzapfel's name *aranea*, which he regarded as a possible junior homonym of *Lichas araneus* Lindström, 1885, and sought approval for this action from the ICZN (Tripp 1960). The commission subsequently ruled that no homonymy is involved and rejected *araneiformis* as an invalid name (Opinion 615, *Bull. zool. Nom.* **18**, 359 (1961)).

Reed (1923, p. 459) considered *aranea* to be closely related to *Lichas* (*Arges*) *contusus* Hall & Clarke, 1888 and *L. maureri* Novák, 1890, and Přibyl & Erben (1952, p. 168) also suggested a relationship with *L. devonianus* Whidborne, 1889; Tripp (1958), however, included the last three species in *Acanthopyge*. We consider *contusus* to belong to *A.* (*Lobopyge*); *maureri* and *devonianus* are both known only from cranidia and we assign them to *Radiolichas* rather than to *Acanthopyge* because of the moderate glabellar convexity, the median lobe that is narrower than the buller lobes and not elevated above them, and L1 that is very short or obsolete behind the bullar lobe. Phleger (1936, p. 608) named *maureri* (incorrectly spelled by him as *maueri*) as type species of his genus *Diplolichas*, which we therefore regard as a junior subjective synonym of *Radiolichas*.

Phleger (1936) considered the lobes flanking the median glabellar lobe in *Radiolichas* to be quadricomposite, and on this basis included the genus in his subfamily 'Echinolichadinae'. Přibyl & Erben (1952, p. 167) pointed out that these lobes are enlarged bullar lobes, and that the cranidial lobation is otherwise similar to that of *A.* (*Acanthopyge*) and *A.* (*Lobopyge*). Enlargement of the bullar lobes in *Radiolichas* has apparently been achieved mainly by the reduction in length (exsag.) of L1, rather than by its lateral displacement as suggested by Přibyl & Erben. Evidence against Přibyl & Erben's view lies in the fact that in *R. devonianus* the axial furrow is weakly defined posteriorly (figure 296) and indicates that the glabella is no wider here than it is in those species of *A.* (*Acanthopyge*) and *A.* (*Lobopyge*) also having the axial furrow weakly impressed adjacent to L1 (see Vaněk 1959, pl. 5, fig. 1. pl. 8, fig. 2). Furthermore, the width of the cranidium across the posterior part of the fixigena in comparison with the width across the bullar lobes is less in *R. aranea* than it is in species of *A.* (*Acanthopyge*) and *A.* (*Lobopyge*), but would be expected to be greater in *R. aranea* if lateral displacement of L1 had occurred. Přibyl & Erben were in some doubt about the form of the cheek in *R. aranea*, pointing out that the illustration given by Holzapfel (1895, pl. 13, fig. 1) shows two spinose projections on the posterior margin adaxial to the genal spine, but that these projections are not shown in the cephalon in Holzapfel's pl. 3, fig. 11 a. The specimen on which Holzapfel's pl. 13, fig. 1 was based confirms the presence of a posterolaterally directed spine within the subgenal notch, located just adaxial to the posterior end of the facial suture (figure 286). The narrow (tr.) portion of the fixigenal margin adaxial to the subgenal notch is not well preserved in either of the syntype cephala available to us. It presumably articulated with the anteriormost thoracic segment, and does not appear to be as spinose as shown in Holzapfel's illustration.

Maksimova (in Mennera 1975), p. 128) erected the subgenus *Acanthopyge* (*Septidenta*) for her species *A.* (*S.*) *bogdanovi* from the Lower Devonian of Kazakhstan. The published illustrations are poor but show a similarity to *Radiolichas* in the convexity of the glabella, the narrow (tr.) median lobe that is not elevated above the bullar lobes, the enlarged bullar lobes, and the presence of seven marginal spines on the pygidium. The pygidium differs from that of *R. aranea* in that the marginal spines are much shorter, more curved, and do not expand distally, and the pleural region adaxial to the spines is wider and seems to be crossed by at least the first pleural furrow. Until *bogdanovi* becomes better known and the taxonomic significance of these differences can be evaluated, we include the species tentatively in *Radiolichas*. *R*? *asiaticus* from the lower Middle Devonian of the Mongolian Altai is also assigned to *Radiolichas* with question because the single poorly preserved pygidium on which it is based lacks a posterior median spine, although it resembles *R. aranea* in all other features discernible in the photograph (Maksimova 1974, pl. 1, fig. 11).

Genus *Richterarges* Phleger, 1936

Figures 318–321, 324–326, 330–333, 336–337, plate 15.

Type species. Original designation; *Lichas* (*Dicranogmus*) *ptyonurus* Hall & Clarke, 1888, p. 86, from the Cobleskill Limestone (upper Přídolí), New York. Lectotype: cranidium, NYSM 4555, selected Whittington (1961, p. 435); figured Hall & Clarke (1888, pl. 19B, fig. 19), Whittington (1961, pl. 55, figs 1–4) (figure 20 herein).

Other species. *R. aquilonius* (Whittington, 1961); *R. bigener* (Bolton, 1965); *R. bucklandii* (Milne Edwards, 1840); *R. echinatus* (Thomas in Thomas & Narbonne, 1979); *R. ethnikos* (Lane, Dawes & Peel, 1980); *R. gibbus* (Angelin 1854); *R. mikulici* (Perry & Chatterton, 1977); *R. ormistoni* (Whittington, 1961); *R. rolfei* (Lamont, 1965); *R. simplex* (Barrande, 1846); *R? superbus* (Kobayashi & Hamada, 1977).

Stratigraphical and geographical range. Late Llandovery–Přídolí; North America (Canadian Arctic Archipelago, New York), North Greenland, England, Scotland, Sweden (Gotland), Czechoslovakia; ?Coblencian or Eifelian of Japan.

Diagnosis. Trochurine with anterior cephalic border commonly very long (up to one eighth sagittal length of cranidium). Longitudinal furrow subparallel to sagittal line over much of its length, commonly very weak in front of bullar lobe but extending behind bullar lobe more or less distinctly to occipital furrow. S1 well impressed behind bullar lobe, shallower and more diffuse medially; L1 as long or longer than occipital ring medially, L1a not defined. Palpebral lobe with δ–δ level with or behind base of bullar lobe. Subgenal notch very shallow or non-existent. Pygidium as wide or wider than long; axis comprising one quarter to one third maximum pygidial width, and one half to two thirds sagittal length (excluding marginal spines); 7–11 axial rings, first two prominent and remainder much weaker. First two pygidial pleurae usually ending distally in short spines; remainder of pygidial margin with 4–13 spines (most commonly 5), or rarely lacking spines.

Remarks. *Richterarges* was considered by Tripp (1957; in Moore 1959) to be a synonym of *Hemiarges*. It differs from *Hemiarges* in that the longitudinal furrows are almost straight and subparallel adaxial of the bullar lobes instead of being gently curved and converging posteriorly, the bullar lobes are circumscribed instead of being confluent with L1 abaxially, L1a is not defined, and the palpebral lobes are more posteriorly placed. The pygidium is typically longer than in *Hemiarges*, with a longer, narrower axis that has a greater number of axial rings and does not extend as close to the posterior margin. The first two pygidial pleurae are not flexed as strongly backwards abaxially, the marginal spines (when present) are shorter, and there is usually a posterior median spine.

Whittington (1961, p. 434) noted the differences in cranidial characters between *Hemiarges* and species that we assign to *Richterarges* but considered there to be so much variation in the pygidium and other features that it was impossible to recognize *Richterarges* as a separate genus. Thomas (in Thomas & Narbonne 1979, p. 12) expressed agreement with this view. Whittington and Thomas overestimated the degree of variation, however, because some of the species they included in *Hemiarges* actually belong to *Uripes* gen. nov., which they did not recognize as a separate genus. Nevertheless, there is a great deal of variation among *Richterarges* species in the proportions of the pygidium and the arrangement of the marginal spines. For example, the pygidium of *R. ptyonurus* lacks a posterior median spine (figure 336), *R. echinatus* has numerous small spines between the fourth pair of marginal spines (Thomas & Narbonne 1979, pl. 5, fig. b, c, e, h, g), and in *R. ormistoni* the pygidial marginal spines are vestigial or absent (Whittington 1961, pl. 55, figs 17, 19). Pygidia of *R. bucklandii* (figure 321) and *R. mikulici* (Perry & Chatterton 1977, pl. 5, fig. 5, pl. 6, figs 3, 4) are relatively wider than those of more typical members of the genus and have a much shorter postaxial region; in these respects they resemble pygidia of *Hemiarges* species, but they differ from the later in the relative length of the axis, the curvature of the pleural and interpleural furrows, and the presence of a posterior median spine. Despite this variation in the pygidia, we consider that the similarities in the cranidia and some pygidial features indicate that the species here included in *Richterarges* are more closely related to each other than they are to species of either *Hemiarges* or *Uripes*.

R? *superbus* from the Coblencian or Eifelian of Japan resembles *Richterarges* species in most cranidial features and in the proportions of the pygidium and size of the pygidial axis. It differs in that S1 merges with the occipital furrow medially, the pygidium has an additional marginal spine apparently emanating from the anterior pleural band on the second segment, and there are one or two extra segments defined in the pygidial pleurae. *R*? *superbus* was included in *Craspedarges* by Kobayashi & Hamada (1977) but we consider that that genus should be restricted to the type species.

Genus *Terranovia* Maksimova, 1977
Figures 306 and 310, plate 14.

Type species. Original designation; *T. nalivkini* Maksimova, 1977, p. 173, from the Valnev Horizon (Pragian) of Novaya Zemlya, arctic U.S.S.R. Holotype: pygidium and counterpart mould, TSNIGR (Central Museum Leningrad) 10466; figured Maksimova (1977, pl. 5, figs 1, 2) Yolkin & Ormiston (1985, fig. 5.11) (figure 306 herein).

Other species. *T. gratsianovae* Yolkin & Ormiston, 1985; *T. radugini* (Weber, 1949).

Stratigraphical and geographical range. Lochkovian–Dalejan of U.S.S.R. (Salair, Gorny Altai, Novaya Zemlya, Omulev Mountains) and arctic Canada (Ellesmere and Prince of Wales Islands, District of Mackenzie, Yukon); ?late Zlichovian – early Dalejan of New South Wales.

Diagnosis. Trochurine with moderately to strongly convex (sag., exsag.) glabella, sometimes overhanging anterior border; median lobe descending steeply in front of large paired, backwardly curved spines. Longitudinal furrows diverging gently at front of bullar lobe and around base of glabellar spines, indistinct behind S1. S1 shallow and poorly defined behind median glabellar lobe; sagittal length of L1 less than or equal to that of occipital ring; L1a not defined. Large, upwardly directed spine present on cranidium adaxial to palpebral lobe. Occipital ring with prominent median tubercle or spine, and one or two pairs of large spines on its posterior margin. Pygidium (excluding marginal spines) almost as long as wide: seven major marginal spines present, and two or three pairs of long, upwardly directed spines situated abaxially on posterior pleural bands of first two segments and on pleural region behind second segment. Axis one third to two fifths maximum pygidial width, and one half to three fifths sagittal length, excluding marginal spines; first axial ring distinct and second poorly defined medially. Numerous secondary spines present on marginal spines, and on pygidial margin between spines; poorly defined border may be present posteriorly.

Remarks. Three pairs of upwardly directed pleural spines are present on pygidia of *T. gratsianovae* and *T. radugini* (Yolkin & Ormiston 1985) but the pygidium of *T. nalivkini* has only two such pairs, those on the second segment being absent.

Maksimova's (1977) description of *T. nalivkini* was based only on the holotype pygidium and a hypostome, but she had seen the material of *T. gratsianovae* which includes cranidia and on this basis compared *Terranovia* with *Acanthopyge* (*Acanthopyge*), *A.* (*Lobopyge*) and *Radiolichas*. Ormiston (1982) described more complete material of *T. nalivkini*, including cranidia, from arctic Canada. He considered *Terranovia* to be most closely related to *Ceratarges* because of the similarities in glabellar lobation and the presence of large spines on the median glabellar lobe and pygidial pleurae. The differences from *Ceratarges*, some of which are mentioned by Ormiston (1982, pp. 1260, 1264), include the non-pedunculate eyes, the presence of an upwardly directed cranidial spine adaxial of the palpebral lobe, and the presence of occipital spines. The pygidium is longer than that of *Ceratarges* and has a relatively smaller axis, longer (exsag.) and more weakly inflated posterior pleural bands on the first two segments, an upwardly directed pleural spine on the first segment, no border immediately behind the second segment, a non-bifid postaxial ridge, and fewer marginal spines, which are also longer and bear numerous secondary spines. In addition, the posteriormost pygidial pleural spine in *Terranovia* is surrounded by a subcircular inflated area, whereas in *Ceratarges* the spine is situated at the junction of an exsagittal ridge and one branch of the bifid postaxial ridge. The differences between *Terranovia* and *Ceratarges* suggest to us that these genera are not closely related, and we consider the development in both of long glabellar and pygidial pleural spines to be due to homoeomorphy. In such features of the pygidium as the overall proportions, the relative size of the axis, the structure of the pleurae (except for the upwardly directed spines) and the form of the marginal spines (but not the number) *Terranovia* is most similar to *A.* (*Acanthopyge*), and we consider that its affinities probably lie with that taxon (see §6*b*).

Terranovia is known mainly from the Lower Devonian of the U.S.S.R. and arctic Canada, but several cranidia and a hypostome from the Lower Devonian of New South Wales were questionably assigned to the genus by Chatterton & Wright (1986).

Genus *Uripes* gen. nov.

Figures 328, 329, 334, 335, 338 and 339, plate 15.

Name. Latin *Uria*, a water-bird, and *pes*, meaning foot, referring to the appearance of the pygidium in the type species. Gender masculine.

Type species. Lichas scutalis Salter, 1873, p. 130, from the Much Wenlock Limestone Formation (late Wenlock), England. Lectotype, selected Thomas (1981, p. 76): almost complete dorsal exoskeleton, SM A3483; figured Reed (1901, pl. 1, figs 1, 4 (pars)), Thomas (1981, pl. 21, fig. 1a, b).

Other species. U. ambiguus (Barrande, 1846); *U. geikiei* (Etheridge & Nicholson in Nicholson & Etheridge, 1879); *U. heteroclytus* (Barrande, 1846); *U. maia* (Reed, 1920); *U. obtusicaudatus* (Troedsson, 1928); *U. serus* (Reed, 1935).

Stratigraphical and geographical range. Late Ordovician (Ashgill?)–Ludlow; Greenland, England, Scotland, Wales, Czechoslovakia.

Diagnosis. Trochurine having cranidium with relatively long anterior border (approximately one tenth sagittal length of cranidium). Longitudinal furrows converging markedly towards midlength of glabella, dying out at base of bullar lobe or extending with only slight decrease in depth to occipital furrow. Maximum width of bullar lobe much greater than width of median lobe across same transverse line. Axial part of L1 gently inflated but not separated from remainder of median lobe by distinct furrow; L1a commonly bounded in front by oblique furrow continuous anteriorly with axial furrow; L1b poorly defined, confluent with bullar lobe. Pygidium wider than long, commonly with three pairs of marginal spines, first two pairs very short and third pair broad, subtriangular and flattened; spines vestigal or absent in some species. Axis approximately one third maximum width of pygidium and one-half sagittal length.

Remarks. Species of *Uripes* have previously been included in *Hemiarges* but differ from members of that genus in having a longer (sag.) anterior cephalic border, wider bullar lobes, and a correspondingly narrower median lobe. The pygidium has three instead of four pairs of marginal spines, or else lacks spines altogether, and the pleural and interpleural furrows are not flexed as strongly backwards abaxially. In species of *Uripes* with pygidial spines the first two pairs are smaller than in *Hemiarges* and the third pair are broad, subtriangular and flattened.

In most species of *Uripes* the longitudinal furrow extends to the occipital furrow where it is joined by an oblique furrow that bounds L1a anteromedially and is continuous with the axial furrow. This oblique furrow is well-developed in *U. geikei* (Tripp 1958, pl. 85, fig. 17), *U. serus* (Tripp 1958, pl. 85, fig. 15; Howells 1982, pl. 14, figs 1a, b, 4, 7a) and *U. heteroclytus* (Vaněk 1959, text-fig. 41). In these species the part of the glabella immediately in front of this furrow is not clearly separated from the bullar lobe but apparently represents L1b because it lies posterior to the point at which the longitudinal furrow abruptly shallows (we interpret this shallowing as marking the position of S1, which is not impressed). *U. scutalis* differs from the other species listed above in that the longitudinal furrow does not extend behind the bullar lobes, the oblique furrow in front of L1a is not present, and L1b is less reduced in size, so that it is more clearly distinguishable from the bullar lobe (figures 338 and 339).

(*h*) Family LICHAKEPHALIDAE Tripp, 1957
[= Eoacidaspididae Poletaeva, 1957]

Diagnosis. Lichida with subtrapezoidal glabella; this as wide or almost as wide at L2 as at base of L1, but constricted at S1. L1 partly or completely subdivided into subsidiary lobes L1a and L1b by oblique or transverse furrow. Up to five pairs of glabellar furrows present; S1 confluent adaxially with posteromedially curved S2, enclosing elliptical L2; S3 subparallel to outer part of S2; S4 and S5 shallow or absent, narrower (tr.) than S3 and directed slightly forwards from axial furrow. Fixigena inflated adjacent to glabella, sloping steeply posterolaterally behind palpebral lobe. Eye ridge typically present. Anterior sections of facial sutures diverging forwards or subparallel.

Genera included. Lichakephalus Sdzuy, 1955; *Acidaspidella* Rozova, 1963; *Eoacidaspis* Poletaeva, 1956; *Lichakephalina* Antcygin in Varganov, 1973; ?*Acidaspidina* Lazarenko, 1960; ?*Brutonia* gen.nov.

Stratigraphical range. Middle Cambrian–Arenig.

Remarks. Tripp erected the Lichakephalidae to include only *Lichakephalus*. Because of its glabellar morphology, we have no doubt that this genus is closely related to the Lichidae in spite of the contrasts in pygidial structure (see § 3 and discussion of *Lichakephalus*). Some of the features currently used to separate *Lichakephalus* at the family level – the presence of S3 and forwardly diverging anterior sections of the facial sutures, for instance – are probably merely primitive characters that do not provide the sound basis for an independent family. Among lichids, the gross glabellar morphology of *Lichakephalus* is most similar to that of certain homolichines, especially *Platylichas* (see figures 174 and 344), and some species of *Metopolichas*, such as *M. erici* Warburg, 1939. If a close relationship between these taxa is confirmed, than a revised family and subfamily structure may ultimately be required within the Lichida. Until the relationships between the taxa concerned are clarified, however, we retain the Lichakephalidae as a separate family.

The only other genus previously assigned to the family was *Lichakephalina* (see Antcygin in Varganov *et al.* 1973, p. 109, pl. 19, figs 11, 12, 15, 16), from the Arenig of the Urals. *Lichakephalina* is based on very fragmentary material and the association of different exoskeletal parts is doubtful (see generic discussion). The glabellar lobation, however, is very similar to that of *Lichakephalus* and we assign *Lichakephalina* to the same family on that basis.

Sduzy (1979, p. 68) noted that *Lichakephalus* is similar in cranidial morphology to the Eoacidaspididae, and may have been derived from a member of that family (a possibility previously raised by Temple 1972, p. 374). Genera assigned to the Eoacidaspididae are poorly known, all material being fragmentary and consisting mainly of cranidia. These cranidia exhibit a wide range of morphologies and we consider the family as previously constituted to be polyphyletic. The type species of *Eoacidaspis*, however, is so similar to *Lichakephalus* in the cranidium that we consider both genera to belong to the same family. *Acidaspidella* is also assigned there on the basis of its cranidial morphology. The name Lichakephalidae has priority for the family because it was published five months earlier than Eoacidaspididae. Of the other genera previously included in the Eoacidaspididae, we follow Bruton (1983) in assigning *Acidaspides* to the Odontopleuridae (see discussion on *Brutonia* gen.nov.). We assign *Acidaspidina* and *Brutonia* to the Lichakephalidae with question because their glabellae are not constricted laterally, L2 is not circumscribed by conjoined S1 and S2, and there is a deep pit in the glabella lying posteromedially to the inner end of S2.

Based on cranidial morphology alone it is possible that the lichakephalids as defined here constitute a genuine monophyletic group, with such genera as *Acidaspidina* and *Eoacidaspis* being derived from an *Acidaspidella*-like form by various degrees of effacement. Several other trilobites, however, particularly the damesellacean *Bergeronites* (see Feist & Courtessole 1984), have rather similar cranidial features (*Bergeronites* cranidia particularly differ from those of *Lichakephalus* in being less strongly constricted at S1, in lacking S3 and in not having the fixigena inflated adjacent to the axial furrow), and so the possibility of polyphyly or paraphyly arises. The problem is especially difficult because no articulated lichakephalid material is known and so our circumscription of the family is necessarily tentative.

Pygidia of lichakephalid genera are poorly known, and Bruton (1983, p. 876) doubted that those attributed to *Eoacidaspis*, *Acidaspidella* and *Acidaspidina* were correctly assigned. These pygidia are all characterized by narrow axes, broad, rather flattened pleurae with distinct pleural furrows and interpleural furrows that are faint or absent, and non-spinose margins (see Lazarenko 1960, pl. 4, figs 11, 12; 1968*a*, pl. 17, figs 12, 13, 16; 1968*b*, pl. 12, fig. 15; Rozova in Zuravleva & Rozova 1977, pl. 3, fig. 11). They have a granular or scale-like sculpture similar to that found on the associated lichakephalid cranidia. In other respects, however, they are similar to pygidia of dikelocephalids and anomocaridids, and some of the latter occur in the same horizons as lichakephalid cranidia in the late Middle Cambrian of Siberia. Because of the uncertainty surrounding assignment of the pygidia, the generic diagnoses given below are based on cranidial characters alone.

Genus *Lichakephalus* Sdzuy, 1955

Figures 340–345, plate 16.

Type species. Original designation; *Lichakephalus erbeni* Sdzuy, 1955, p. 28, from the Leimitz Shales (Tremadoc) of Germany. Holotype: cranidium, SMF X1812a; figured Sdzuy (1955, pl. 5, fig. 29, text-fig. 26a) (figure 341 herein).

Other species. None known.

Stratigraphical and geographical range. As for type species.

Diagnosis. Lichakephalid with glabella strongly constricted at L1b, where axial furrow is very shallow. L1a large (maximum width about one third glabellar width measured across same transverse line), strongly indenting front of occipital ring and bounded anteriorly by deep furrow. L2 circumscribed by deep conjoined S1 and S2; S3 as deep as outer part of S2 and parallel to it; S4 and S5 not impressed. Posterior edge of palpebral lobe lying well behind glabellar mid-length; eye ridge absent, but deep furrow runs forwards from palpebral furrow to join axial furrow at outer end of S2. Anterior sections of facial suture strongly divergent; anterior border flattened and raised anteriorly, shorter (sag., exsag.) in front of glabella. Exoskeleton with tubercles or coarse granules.

Remarks. There is little doubt that the pygidia attributed to the type species are correctly assigned, because they occur together with the cranidia and have similar sculpture. The pygidia are fragmentary but show the presence of a conical axis with four complete ring furrows (posterior two of these shallow), flattened pleurae with five pairs of deep furrows, and a wide doublure (figures 343 and 345). Tripp (in Moore 1959, p. O504) described the pygidium of lichakephalids as having 'approximately 3 pairs of furrowed pleurae', thus believing that both pleural and interpleural furrows are present. However, we interpret all of the deep furrows on the pygidial pleurae of *L. erbeni* as pleural furrows, and consider the interpleural furrows to be very weak or effaced. Evidence for this interpretation lies in the fact that successive furrows are approximately equally spaced proximally, and the second furrow meets the axial furrow slightly behind the second ring furrow (figure 345 herein) (see also Sdzuy 1955, p. 29). Moreover, in the pygidium figured by Sdzuy (1955, pl. 5, fig. 33b) it appears that there may be a very weak interpleural furrow present between the first and second pleural furrows. Sdzuy himself stated (1955, p. 28) that possibly only pleural furrows are developed, and that the anterior and posterior pleural bands are fused, in contrast to the situation in members of the Lichidae. In the construction of the pleurae, therefore, the pygidium of *Lichakephalus* is similar to the pygidia attributed to *Eoacidaspis*, *Acidaspidella* and *Acidaspidina*. It is not known whether the pygidium of *Lichakephalus* also resembles those attributed to the other genera in the absence of marginal spines. The line drawings given by Tripp (1957, text-fig. 2B; in Moore 1959, fig. 397B), appear to show at least one marginal spine, but comparison with the specimen on which the drawings were based (Sdzuy 1955, pl. 5, fig. 33a) (figure 345 herein) suggests that this 'spine' is an artefact caused by breakage. Tripp's own interpretation of the pleural structure of *L. erbeni* (which we do not accept) also makes the existence of this 'spine' unlikely, because the furrow running onto the 'spine' would correspond with an interpleural furrow.

Genus *Acidaspidella* Rozova, 1963
Figure 346, plate 16.

Type species. Original designation; *Acidaspidella limita* Rozova, 1963, p. 9, from the Upper Cambrian of the northwestern Siberian Platform. Type material untraced.

Other species. None known.

Stratigraphical and geographical range. Upper Cambrian – basal Ordovician, Siberia.

Diagnosis. Lichakephalid with glabella narrower posteriorly than long, slightly constricted across L1b and in front of L3. L1a large (approximately one third glabellar width), elliptical and inflated, separated from depressed L1b by shallow furrow. L2 only slightly larger than L1a, inflated, with long axis parallel to sagittal line. L2 surrounded by conjoined S1 and S2 that is very deep along adaxial side of lobe but shallower anteriorly and posteriorly. S3 and S4 very narrow (tr.). Posterior edge of palpebral lobe level with glabellar mid-length; eye ridge closer to cranidial border than to glabella, deflected forwards anteriorly to merge with lateral extremities of frontal lobe. Anterior sections of facial suture subparallel; anterior border upturned at margin, narrowing (sag., exsag.) in front of glabella. Inflated portion of fixigena adjacent to glabella bounded posterolaterally by shallow depression running in abaxially convex curve from posterior border furrow to palpebral lobe. Posterior border with small spine at fulcrum. Exoskeleton granular.

Remarks. Acidaspidella cranidia (see *A.* cf. *limita* in Bruton 1983, pl. 88, figs 5, 6, 10, 19) differ from those of *Lichakephalus* in having the glabella much less strongly waisted at L1b, a larger L1a and smaller L2, the frontal lobe less strongly expanded (tr.), anterior sections of the facial suture that are subparallel instead of strongly divergent, and in possessing a narrow S4 and an eye ridge (compare figures 346 and 344).

Genus *Eoacidaspis* Poletaeva, 1956
[Subjective synonym: ?*Belovia* Poletaeva, 1956]
Figures 347, 348 and ?349–351, plate 16.

Type species. Original designation; *E. salairica* Poletaeva, 1956, p. 175, from the Upper Cambrian of western Siberia. Cast of paratype cranidium, PMO 108.538; figured Bruton (1983, pl. 88, figs 8, 9).

Other species. E. amplicauda Lazarenko, 1968*a*; *E*? *aliquantula* (Rozova, 1964); *E*? *calva* (Chernysheva in Poletaeva, 1956; *E*? *cyclica* (Rozova, 1964); *E*? *laeta* (Rozova, 1964; *E*? *media* (Poletaeva, 1977); *E*? *raduginae* (Poletaeva, 1977); '*E*? *salairica* (Poletaeva 1960)'.

Stratigraphical and geographical range. ?Middle Cambrian, Upper Cambrian–Tremadoc; Siberia, Kazakhstan.

Diagnosis. Lichakephalid with glabella as wide posteriorly as long, strongly constricted at base of L2; axial furrow very shallow in front of L2. L1a confluent with L1b distally but separated adaxially by weak furrow; L2 with long axis strongly oblique to sagittal line, circumscribed by conjoined S1 and S2 that is deepest posteromedially. S3 more or less transverse, very close to S2 and deeper than it; S4 and S5 narrow (tr.), weak, directed slightly forwards from axial furrow. Glabellar furrows weak or effaced in some species. Posterior edge of palpebral lobe situated behind glabellar midlength; eye ridge much closer to glabella than to cranidial border. Anterior sections of facial suture strongly divergent; anterior border flattened and raised. Exoskeleton smooth or finely granular.

Remarks. The type species (see Bruton 1983, pl. 88, figs 8, 9) is very similar to *Lichakephalus* in cranidial morphology, the main differences being that in *Lichakephalus* the axial furrow is weaker alongside L1b, L1a is larger and is separated from L1b by a deep furrow, S4 and S5 are not defined, and there is no eye ridge (compare also figures 344 and 347).

Bruton (1983, p. 879) noted the close resemblance between *Eoacidaspis* and *Belovia* (see Bruton 1983, pl. 88, figs 1–4, 8, 9), with the existence of morphologically intermediate species, the two genera mainly being distinguished by various degrees of furrow effacement. On cranidial morphology alone we see no need to recognize two genera (compare figures 347 and 350) and choose *Eoacidaspis* to have priority (ICZN Article 24). If the synonymy of these genera is confirmed when more exoskeletal parts are described, then *Belovia salairica* Poletaeva, 1960 will be a junior homonym of *E. salairica* Poletaeva, 1956 and a replacement name will be necessary for the former.

Genus *Lichakephalina* Antcygin in Varganov, 1973
Figures 355 and 358, plate 16.

Type species. Original designation; *Lichakephalina schilikta* Antcygin in Varganov 1973, p. 109, from the lower Arenig of the Middle Urals. Holotype: cranidium, UGS 1078/25; figured Antcygin in Varganov *et al.* (1973, pl. 19, fig. 11).

Other species. None known.

Stratigraphical and geographical range. As for type species.

Remarks. This genus is described from very fragmentary material. The holotype cranidium is poorly preserved but a circumscribed L2 is present, with S3 a short distance in front of it. A fragmentary but better preserved cranidium is figured here (figure 355, plate 16). The associated hypostome is of lichine construction. The pygidium is styginid-like with an entire margin, greatly expanded pleural areas and effaced interpleural furrows (Antcygin in Varganov *et al.* 1973, pl. 19, figs 15, 16) (figure 358 herein).

Lichakephalina is similar to *Lichakephalus* in overall cranidial morphology, but is easily distinguished by the smaller and shorter L2 and smaller L1b. The pygidium of *Lichakephalina* is distinctive, though it could have been derived from that of an *Eoacidaspis*-like form by inflation of the pleural areas and modification of the axis.

?Genus *Acidaspidina* Lazarenko, 1960
Figures 353, 354, 356 and 357, plate 16.

Type species. Original designation; *Acidaspidina plana* Lazarenko, 1960, p. 39, from the Upper Cambrian of the northern Siberian Platform. Types in the Central Museum, Leningrad.

Other species. None known.

Stratigraphical and geographical range. As for type species.

Diagnosis. ?Lichakephalid with glabella as wide posteriorly as long, narrowing anteriorly; axial furrow gently deflected outwards around L2. Occipital ring almost as long exsagittally as sagittally; L1a and L1b defined anteriorly only by shallow, diffuse depressions. L2 small (less than one quarter glabellar width across same transverse line), slightly inflated; S2 shallow, curving backwards adaxially and indistinctly connected to deeper, oblique depression lying posteromedially to L2. S3 not directed so strongly backwards as S2; S4 and S5 running slightly forwards from axial furrow. Posterior edge of palpebral lobe level with glabellar midlength;

anterior sections of facial suture diverging forwards; anterior border gently curved between β–β. Exoskeleton with tiny granules.

Remarks. Acidaspidina is most similar to *Brutonia* gen.nov. in the absence of marked constriction of the glabella behind L2; the small, weakly inflated L2 and substantially effaced S2, and the depression in the glabella situated posteromedially to L2 (compare Rozova 1968, pl. 3, figs 16–18; Zuravleva & Rozova 1977, pl. 3, figs 7–10 with Bruton 1983, pl. 88, figs 11, 14, 16–18). *Acidaspidina* is distinguished from *Brutonia* by the occipital ring that is not contracted abaxially, the more pronounced outward deflection of the axial furrow around L2, the more weakly defined L1a, more anteriorly placed palpebral lobe, the forwardly divergent anterior sections of the facial suture, and the more weakly curved anterior cranidial margin.

?Genus *Brutonia* gen.nov.

Name. After Dr D. L. Bruton in recognition of his work on lichakephalids.

Type species. Acidaspides borealis Chernysheva, 1960*b*, p. 254, from the Upper Cambrian, northern Siberia. Types in Central Museum, Leningrad.

Other species. B? entis (Khramova, 1977).

Stratigraphical and geographical range. As for type species.

Diagnosis. ?Lichakephalid with glabella slightly narrower posteriorly than long, subparallel-sided or expanding slightly just in front of occipital furrow and thereafter narrowing gradually. L1a small, about one quarter glabellar width, confluent with L1b except adaxially where it is separated by a very shallow furrow. L1b not distinguishable from L2. S2 directed obliquely backwards from axial furrow, separated by raised area from deep, subcircular pit at inner end. Posterior edge of palpebral lobe lying behind glabellar midlength, crossed by shallow exsagittal furrow directly in front of outer end of S3. Anterior sections of facial suture subparallel, or converging forwards; anterior border short (sag., exsag.) and upturned at margin. Posterior border with small spine at fulcrum.

Remarks: Bruton (1983, p. 882) noted the strong similarities between the type species of *Acidaspides*, *A. precurrens* Lermontova, 1951, and odontopleurids, especially members of the Miraspidinae. We agree with his observations and follow him in assigning the genus to the Odontopleuridae. Typically odontopleurid features of *A. precurrens* not mentioned by Bruton include the shallow longitudinal furrow separating nodular lateral glabellar lobes from a subparallel-sided median lobe, and the occipital furrow that is shallow medially and very deeply impressed behind L1. The pygidium doubtfully assigned to *A. precurrens* by Lermontova (1951, pl. 6, fig. 9; figure 352, plate 16) also resembles pygidia of odontopleurids rather than lichakephalids in its transverse shape and numerous posteriorly directed marginal spines, although the pleural ribs are not typically odontopleurid in form. Bruton (1983) also included in *Acidaspides* the species *A. borealis* and *A. lermontovae* Chernysheva, 1953, but we consider the former to more closely resemble lichakephalids, whereas the latter appears to have much in common with some members of the Damesellidae, especially *Palaeodotes* Öpik, 1967 (compare Bruton 1983, pl. 88, fig. 7, and Öpik 1967, pl. 50, figs 4–6). We therefore restrict *Acidaspides* to the type species and erect *Brutonia* for *A. borealis*.

B? entis is described from an incomplete internal mould of a cranidium (Khramova, 1977, pl. 15, figs 3a–c), which may be congeneric with *B. borealis*.

6. PHYLOGENY AND AFFINITIES

(*a*) *Relationship with other groups of trilobites*

Although lichid genera are morphologically diverse they are easily distinguishable from those belonging to other trilobite higher taxa. Particularly because of their distinctive glabellar structure, we have no doubt that the Lichidae constitutes a monophyletic group. The glabellar morphology of *Lichakephalus* (q.v.) is essentially identical with that of certain lichids and so we include the Lichakephalidae and Lichidae in the same order. The former family is only provisionally circumscribed here, however, and may in any case comprise a collection of genera united more by the possession of common primitive characters than by particularly close relationship (see §5*h*). The distinctive appearance of lichides compounds the general difficulties which arise when considering the relationships between groups of trilobites at a high taxonomic level (Eldredge 1977, p. 320). It could be asserted that the Lichida occupies a rather isolated position within the class, an assertion that could be correct but which is certainly unproven.

Lichids and odontopleurids were considered to be probably closely related by a number of earlier authors (e.g. Warburg 1925, p. 71; Poulsen 1927, p. 327; Richter 1933, fig. 33; Henningsmoen 1951, p. 201) and Swinnerton (1915, table on p. 542) assigned the two groups, together with the 'Bronteidae', to his suborder Odontopleurida. Sdzuy (1979, p. 542) argued that *Lichakephalus* and the Eoacidaspididae are closely related, and that both the Lichidae and Odontopleuridae were derived from this group, perhaps from a common ancestor similar to *Acidaspidella*. Tripp & Evitt (1981, p. 674) supported the idea that *Lichakephalus* and the eoacidaspidids may have had a common ancestor. Because of certain contrasts in protaspide morphology (Whittington 1956, p. 1200) and thoracic structure (Bergström 1973, pp. 27, 39), however, other authors have regarded a close relationship between lichids and odontopleurids as unlikely. In principle, three lines of reasoning may be used to evaluate a hypothetical relationship between these two groups: comparative ontogeny, comparative morphology of holaspides and the interpretation of lichakephalid morphology.

In reviewing the implications of protaspide morphology for suprageneric classifications, Chatterton (1980, p. 8) inferred that the shift from a pelagic to a benthic mode of life may have occurred within the protaspid stage. Because these two modes of life are associated with contrasting morphologies, protaspides with similar life habits, but belonging to different groups, may be remarkably alike. Hence care must be taken not to interpret the ontogenetic data in too naïve a way. Whittington (1956, p. 1200) noted that lichid and odontopleurid protaspides resemble each other in outline, convexity and spinosity. On the basis of the material available to him, however, he argued that a close relationship between these groups is unlikely because the lichid protaspis is twice the size of those of the odontopleurids, and also differs in having deeper axial furrows, broader anterior and anterolateral borders, no fixigenal spines and a shorter protopygidial axis. A wider range of juvenile lichids has been described in recent years and some of the contrasts noted by Whittington have been shown subsequently to be incorrect (see, for example, Tripp & Evitt 1981, p. 674) or less significant than he thought.

Based on these new data Chatterton (1980, p. 12) noted the similarities between protaspides of the Lichida, Odontopleurida, Proetida and Scutelluina (sensu Lane & Thomas 1983). In particular, lichid and odontopleurid protaspides possess distinctive paired spine or tubercle patterns on the cephalon and protopygidium, have an anterior border, a distinct axis and marginal spines on the protopygidium and are generally opisthoparian. The paired tubercle or spine patterns constitute an especially distinctive common character. Odontopleurid protaspides are distinguished by their smaller size and absence of the slit-like invaginations of the lateral hypostomal border found on lichid (and styginid) protaspides. Because of the similarity of their early ontogenetic stages Chatterton suggested that the Lichida and Odontopleurida are sister groups and we agree that this is a likely possibility.

Comparative morphology of holaspides sheds little light on the problem. Certain similarities between the two groups (e.g. spinosity, sculpture) are clearly of no value at a high taxonomic level, while others (e.g. opisthoparian facial sutures) are primitive for trilobites as a whole. There are some important morphological contrasts between the two orders: odontopleurids show no sign of the subdivision of L1, lack ventral terrace ridges and have an unusual thoracic segment structure. The two groups do share a wide and short rostral plate, a feature they have in common with most Scutelluina but which separates them from many other trilobite groups. We consider that this rostral structure may be an important unifying character, but its significance cannot be fully evaluated in the absence of data on the ventral morphologies of many Cambrian taxa.

The contrasts between lichide and odontopleuride holaspides are perhaps no more than one might expect between groups that diverged in the Middle Cambrian: even earlier if *Eodontopleura* Qian & Lin in Zhang *et al.*, 1980 is correctly assigned to the Odontopleuridae. *Eodontopleura* bears some similarity to members of that family but Dr P. Jell has suggested to us that its affinities may lie with the oryctocephalids.

Especially because of their age, comparative morphology of lichakephalid genera is potentially very informative in evaluating lichide: odontopleuride relationships. For the reasons discussed above (§5*h*) we have no doubt that *Lichakephalus* and *Acidaspidella* are closely related and Bruton (1983, p. 882) noted the similarities between certain lichakephalids? and odontopleurids (but see discussion of *Brutonia*). If these various similarities are confirmed when lichakephalids become better known, and if the group proves to be monophyletic, then they would add powerful weight to the inferences drawn from ontogenetic comparisons.

The limited amount of data available suggest that the Lichida and Odontopleurida may be sister groups and these two share some common features with the Scutelluina. However, only the comparative morphology of protaspides provides evidence of relationship which is at all compelling. Improved understanding of the Lichakephalidae is necessary to test this possible relationship. If new data from this source confirm a close affinity between the Lichida and Odontopleurida, then the two would be best regarded as suborders within the Odontopleurida Swinnerton, 1915.

(*b*) *Relationships within the Lichida*

Certain morphological characters appear to have evolved independently in what we consider to be only distantly related lichid genera. In some cases, such as the development of anterior cephalic prolongations, no major problems arise in adducing relationships, but in other instances more serious difficulties are encountered. The lichine *Dicranopeltis* and the trochurine *Trochurus*, for example, have similar cranidial morphologies and our inferences concerning the relationships of these genera are largely based on other exoskeletal parts, particularly hypostomes and pygidia. Relationships are more difficult to determine in cases where genera are incompletely known, and even reference to a subfamily may be rather tentative (e.g. see discussion of *Dicranogmus*). To try to overcome these problems we have based our inferences concerning relationships on as broad a range of characters as possible (also see §3).

In the account that follows we discuss the relationships between the genera included in each lichide family and subfamily as well as between the various family-group taxa. Our inferences are summarized in cladograms (figures 359–364). Figure 365 presents our interpretation of lichide phylogeny and includes data on stratigraphical ranges.

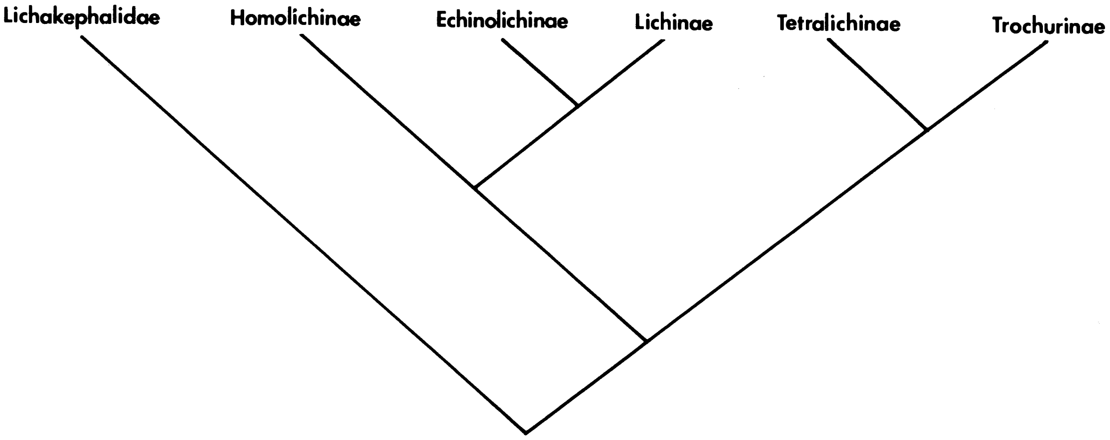

FIGURE 359. Cladogram illustrating inferred relationships among lichide family-group taxa.

Lichakephalidae. Because of the very incomplete data available for members of this family we find it impossible properly to assess relationships between its constituent genera. The similarities between *Lichakephalus*, *Platylichas* and some species of *Metopolichas*, however, we take to suggest that the homolichines were directly derived from the Lichakephalidae. We also consider that the similarities between *Eoacidaspis* and *Lichakephalus* suggest a direct relationship between the two.

Lichinae (figure 360). This subfamily probably has its origins in *Metopolichas*, which was included in the Lichinae by Tripp (in Moore 1959) but which we assign provisionally to the Homolichinae (q.v.). The oldest known lichine genus is *Uralichas* which occurs in the Llanvirn and Llandeilo and has a cranidial morphology very similar to that of some *Metopolichas* species, especially *M. erici* from the Arenig and lower Llanvirn of the Baltic region (Warburg 1939, pl. 5, figs 1, 2). *Uralichas* may have been derived from *Metopolichas* by shallowing of the axial furrow adjacent to L1b, elongation of the hypostome, and development of a posterior median spine on the pygidium. *U*? *incola* from the Llanvirn of Czechoslovakia has a cranidium and hypostome similar to those of *Uralichas* but a pygidium with three pairs of marginal spines and no posterior spine; the species is thus morphologically intermediate between *Metopolichas* and *Uralichas*.

Tripp (1957, p. 119, text-fig. 7) suggested that *Uralichas* gave rise to *Lichas* and possibly *Dicranopeltis*, both of which appeared in the Ashgill. We consider the most likely ancestor of *Lichas* and *Dicranopeltis* to be a form such as *U*? *incola* because of the absence of a posterior spine on the pygidium. *Lichas* may have been derived from such a form by a decrease in the size of L1a, a slight increase in width of the occipital ring, and the loss of the third pair of marginal spines on the pygidium. *Trimerolichas* resembles *Lichas* in the width of the occipital ring and shape of the glabellar lobes, and may have arisen from a species of that genus by the extension

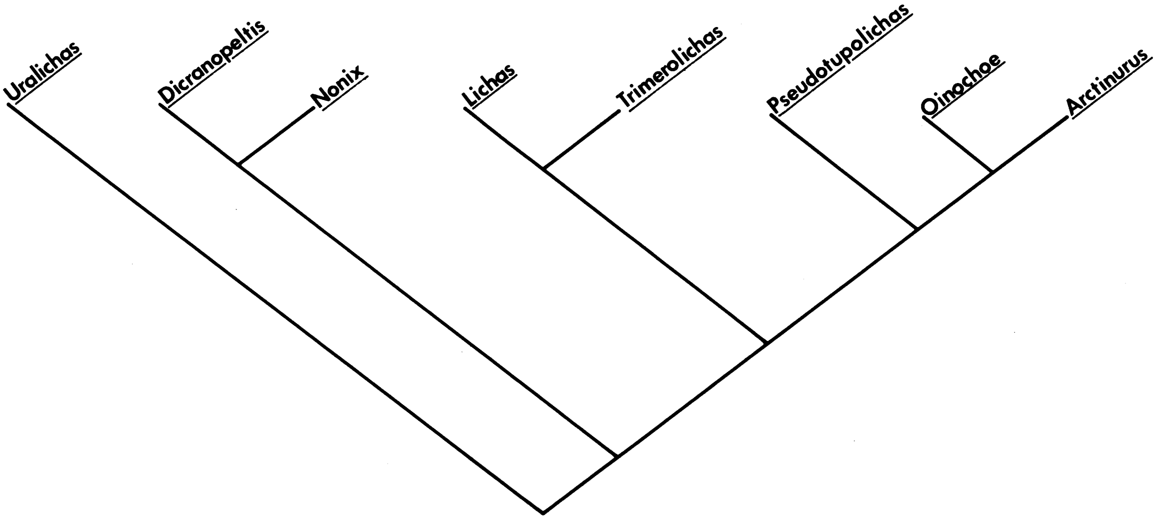

FIGURE 360. Cladogram illustrating inferred relationships within the Lichinae.

of the longitudinal furrows to the occipital furrow and the increase in length (sag., exsag.) of the anterior border. Knowledge of the pygidial morphology of *Trimerolichas* is required to test this suggestion. The cephalon of *Dicranopeltis* is distinctive among lichines in having circumscribed bullar lobes, a glabella that is constricted at S1 instead of at the occipital furrow, and a deep subgenal notch. Cranidia of similar morphology were included by Lane (1984) in the type species of *Nonix*, and if these cranidia are correctly assigned *Nonix* was probably derived from *Dicranopeltis* by the incorporation of the most posterior thoracic segment into the pygidium or by the generation of an additional pygidial segment during ontogeny.

A greatly expanded (tr.) occipital ring is characteristic of *Arctinurus* and *Pseudotupolichas* from the Llandovery and Wenlock, and *Oinochoe* from the Gedinnian. Tripp (1957, p. 119) suggested that *Arctinurus* developed from *Lichas* but we regard this as unlikely because of the absence of a third pair of pygidial spines in the latter. We consider that *Arctinurus* and *Pseudotupolichas* are probably descendants of an unknown form sharing a common ancestry with *Lichas*. *Pseudotupolichas* resembles *Oinochoe* in having the longitudinal furrows extending to the occipital furrow, and in the shape of the median and lateral glabellar lobes. The absence of L1a in *Pseudotupolichas*, however, suggests that *Oinochoe* is unlikely to have arisen from that genus. In pygidial morphology *Oinochoe* most closely resembles *Arctinurus* but differs from it in having an additional pair of spines; *Oinochoe* was therefore probably derived from *Arctinurus* by an increase in convexity of the cranidium, extension of the longitudinal furrows to the occipital furrow, and the generation of an additional pair of marginal spines in the postaxial part of the pygidium.

Echinolichinae (figure 361). The ancestry of the Echinolichinae probably lies in a species of the lichine *Oinochoe*, which has similarities with *Terataspis* in the form of the longitudinal furrow and glabellar lobes, the hypostome, and the structure of the pygidial pleurae, including the number of marginal spines and the shape of the postaxial band. Relationships within the subfamily are poorly understood because of the shortage of morphological information for most of the genera, especially *Ceratolichas* and *Gaspelichas* which are known only from cranidia. *Ceratolichas* is most similar to *Echinolichas* in the proportions and inflation of the glabellar lobes,

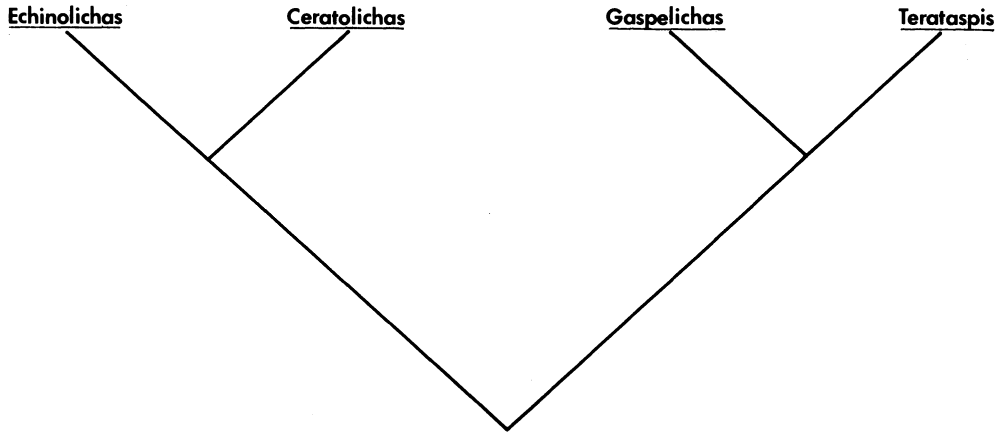

Figure 361. Cladogram illustrating inferred relationships within the Echinolichinae.

and may have been derived from that genus by an increase in overall convexity of the cranidium, effacement of the posterior part of the longitudinal furrows, and the development of large paired spines on the median and bullar lobes and on the occipital ring. *Gaspelichas* is possibly most closely related to *Terataspis*, which it resembles in cranidial proportions and the shape of the glabellar lobes.

Homolichinae (figure 362). This subfamily seems to be most closely related to the Lichinae. This is suggested both by the hypostomal similarities between the two groups and by *Metopolichas*, which has an essentially lichine cranidial morphology but a hypostome of homolichine construction (see also Tripp 1957, p. 119, text-fig. 7). Most homolichines are known from the Caradoc and Ashgill of Europe, particularly the Baltic states. Our limited knowledge of homolichine stratigraphical and geographical distribution, together with imperfect understanding of the constituent genera, make it difficult to draw conclusions concerning relationships within the subfamily.

Apart from Arenig species of *Metopolichas*, the oldest described homolichine is a species of

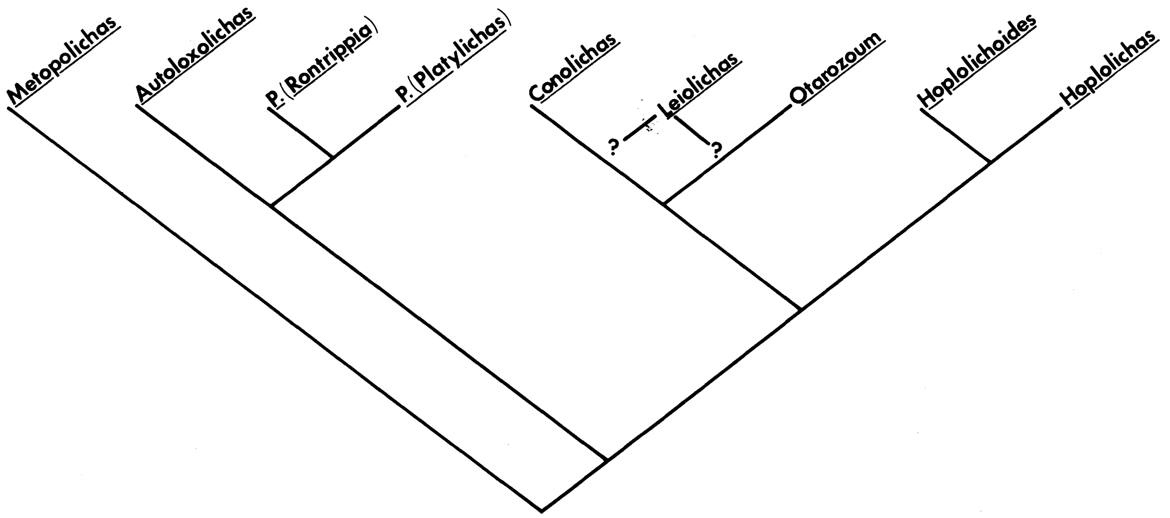

Figure 362. Cladogram illustrating inferred relationships within the Homolichinae.

Autoloxolichas from the Arenig (or possibly lower Llanvirn; see faunal list in Varganov *et al.* (1973), p. 20) of the U.S.S.R. The glabellar morphology of *Autoloxolichas* is not fully understood but, if our interpretation is correct, the apparent suppression of L1b is a unique character. Alternatively if L1b is simply very short (exsag.) and fused with the fixigena, then this is a character shared with *Platylichas* subgenera, which are the only homolichine taxa demonstrably to display this condition. The pygidial morphology of *Autoloxolichas* is also distinctive among homolichines, particularly in the rather well-developed border and slender marginal spines. In view of these morphological characters and the early stratigraphical appearance of the genus, we consider *Autoloxolichas* to occupy a rather isolated position within the subfamily, possibly being most closely related to *Platylichas*.

Hoplolichas first appears certainly in the Llandeilo and is one of a group of homolichine genera (also including *Conolichas*, *Otarozoum*, *Leiolichas* and *Hoplolichoides*) in which L1b is more or less distinctly fused with the bullar lobe. The internal morphology of the cranidium of *Leiolichas* most closely resembles that of *Conolichas* in the proportions of the glabellar lobes, but is more similar to *Otarozoum* in lacking differential inflation of these lobes. We therefore regard *Leiolichas* as a highly effaced derivative of one of these genera. In *Conolichas* and *Otarozoum* the bullar lobe is completely fused with L1b and this provides a contrast with *Hoplolichas* and *Hoplolichoides* species where bullar and L1b sections of the composite lateral lobe are distinguishable. The latter condition is most reasonably interpreted as the more primitive. The *Hoplolichas* pygidium is rather highly derived, particularly as regards the differential development of the second pair of pleural ribs and their associated spines.

Tetralichinae (figure 363). The tetralichines are probably most closely related to the Trochurinae, hypostomes of the two groups being remarkably similar. Tripp (1957, text-fig. 7) proposed a common origin for the two subfamilies, and Whittington (1963, p. 105) noted that *Apatolichas* shares some similarities with both *Amphilichas* and early trochurines, suggesting that *Apatolichas* might be the ancestor of both; we agree with this view. *Lyralichas* is not well known but closely resembles *Amphilichas* in cranidial morphology, the pygidium being distinguished by its additional axial ring and pair of pleurae. *Lyralichas* was therefore probably derived from an *Amphilichas* species either by the incorporation of the most posterior thoracic

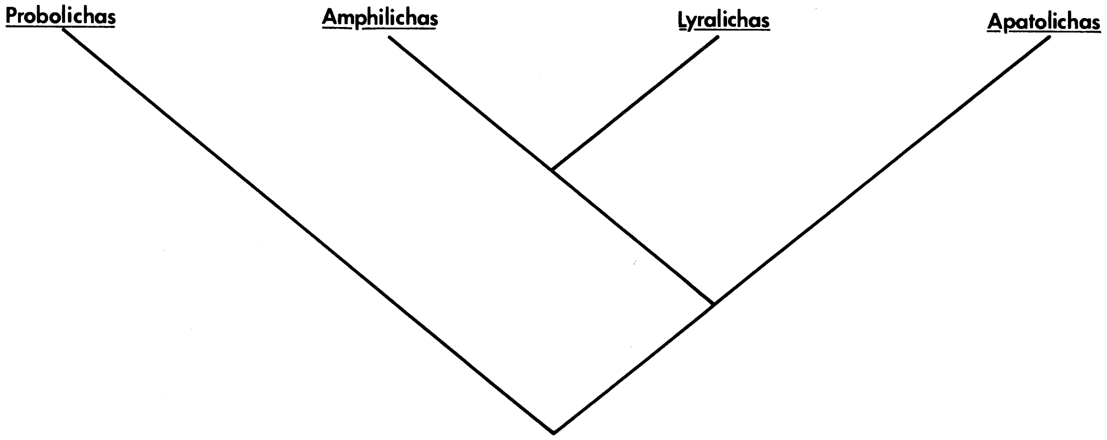

FIGURE 363. Cladogram illustrating inferred relationships within the Tetralichinae.

segment into the pygidium, or by the generation of an additional pygidial segment during ontogeny. *Probolichas* is also similar to *Amphilichas* in cranidial morphology but its pygidium is highly modified and quite distinct from pygidia of *Amphilichas*, *Lyralichas* and *Apatolichas*. For this reason we show *Probolichas* as occupying a rather isolated position within the subfamily.

Trochurinae (figure 364). The oldest known member of the subfamily is *Hemiarges* which appeared in the Llanvirn, possibly having developed from *Apatolichas* by effacement of the longitudinal furrow posterior to the bullar lobe, constriction of the glabella across L1b (see discussion in §4), and modification of the pygidium. *Hemiarges* seems to have been the main root stock from which other trochurines arose later in the Ordovician and in the early Silurian.

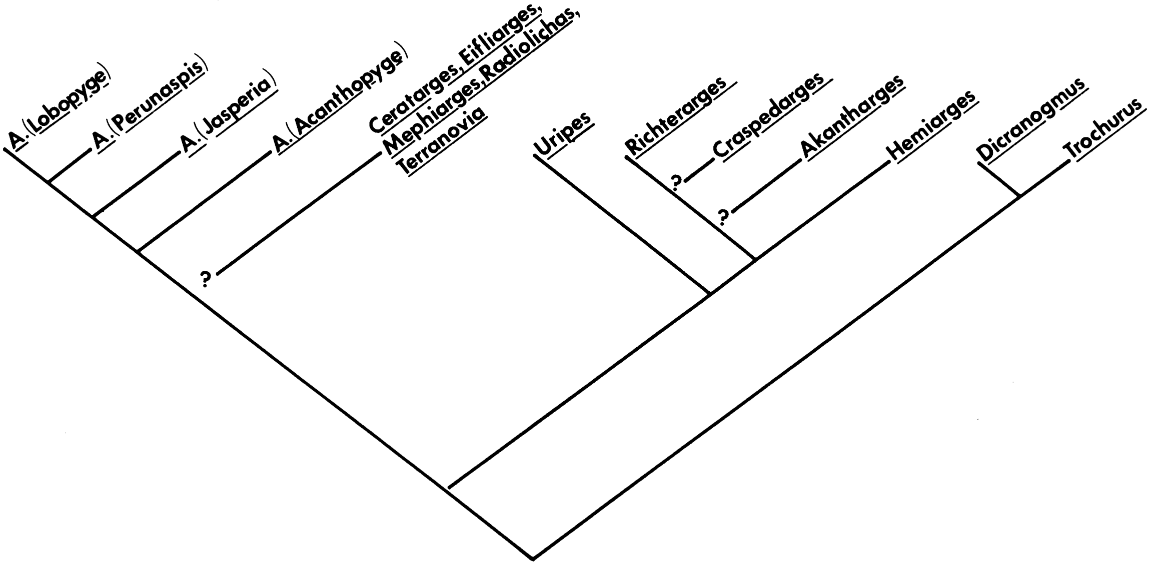

FIGURE 364. Cladogram illustrating inferred relationships within the Trochurinae.

Uripes appeared in the Ashgill, possibly being derived from *Hemiarges* by expansion (sag., exsag.) of the anterior cephalic border, enlargement of the bullar lobes and a corresponding decrease in width of the median glabellar lobe, and modification of the marginal spines on the pygidium. The broad, subtriangular third pair of pygidial spines in *Uripes* may have developed by enlargement of either the third or fourth pairs of spines in *Hemiarges*, or by fusion of those spines. The last possibility may be the most likely because in some species of *Hemiarges*, such as *H. maccullochi*, the third and fourth pairs of pygidial spines appear to be partly fused (figure 322). Also appearing in the Ashgill are *Trochurus* and *Dicranogmus* which closely resemble each other in the marked convexity of the cranidium, the shape and proportions of the median glabellar and bullar lobes, the medially reduced (sag.) L1, and the well-defined L1a. If *Dicranogmus* is correctly assigned to the Trochurinae (see generic discussion), this genus and *Trochurus* may be descended from a common ancestor derived from *Hemiarges*.

Acanthopyge commences its long history in the Wenlock with the appearance of *A.* (*Lobopyge*). Whittington (1961, p. 435) and Perry & Chatterton (1977, p. 307) noted similarities in glabellar lobation between *Acanthopyge* and species that we include in *Richterarges*, and suggested that *Acanthopyge* may have been derived from such forms. The oldest-known species of *Richterarges* is of late Llandovery age, and species such as *R. bucklandii* and *R. mikulici* from the

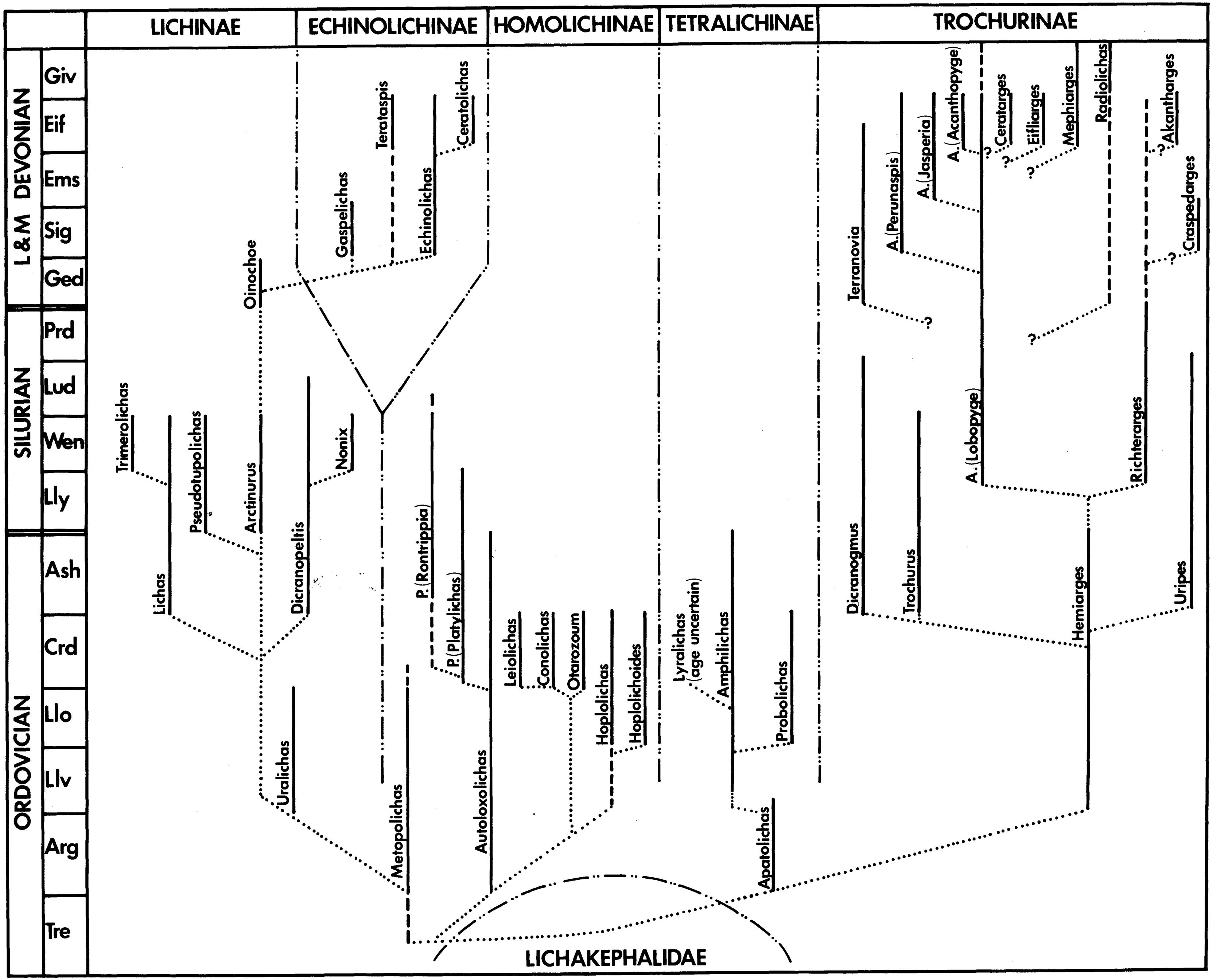

FIGURE 365. Inferred phylogeny of the Lichida. The boundaries recognized between family-group taxa are indicated. Solid and dashed lines respectively represent known and uncertain ranges of genera; dotted lines indicate suggested relationships. The lichine/homolichine/echinolichine group diverged from the tetralichine/trochurine group in the Early Ordovician, but the diagram should not be taken to imply that the Lichidae is diphyletic.

Wenlock are very similar to *A.* (*Lobopyge*) in pygidial proportions and the form of the pygidial axis, lending support to this suggestion. In the curvature of the longitudinal furrow and proportions of the glabellar lobes, however, *A.* (*Lobopyge*) is closer to *Hemiarges* than to *Richterarges*. Hence *A.* (*Lobopyge*) and *Richterarges* may have both evolved from *Hemiarges*, possibly via an intermediate form, and this is the relationship that we have shown in figure 365.

The Trochurinae underwent an evolutionary radiation during the Early and Middle Devonian, many of the forms appearing at this time being characterized by their extreme spinosity. *A.* (*Acanthopyge*), *A.* (*Jasperia*) and *A.* (*Perunaspis*) were probably derived from *A.* (*Lobopyge*), mainly by modification of the pygidium; *A.* (*Perunaspis*) almost certainly arose by the incorporation of the posteriormost thoracic segment into the pygidium. Few conclusions can be drawn on the origins of the remaining late trochurines, because they are either too poorly known or too distinctive morphologically. Those genera with deep subgenal notches and a medially reduced (sag.) L1 (*Ceratarges*, *Eifliarges*, *Mephiarges*, *Radiolichas* and *Terranovia*) may have been derived from *Acanthopyge*, as suggested by Tripp (1957, p. 121). *Craspedarges* resembles *Richterarges* in some cranidial characters, and may have arisen from that genus. *Akantharges* may have also been derived from *Richterarges*, which it resembles in the sagittal length of L1, the absence of a subgenal notch, the proportions of the pygidium, and the length of the pygidial axis.

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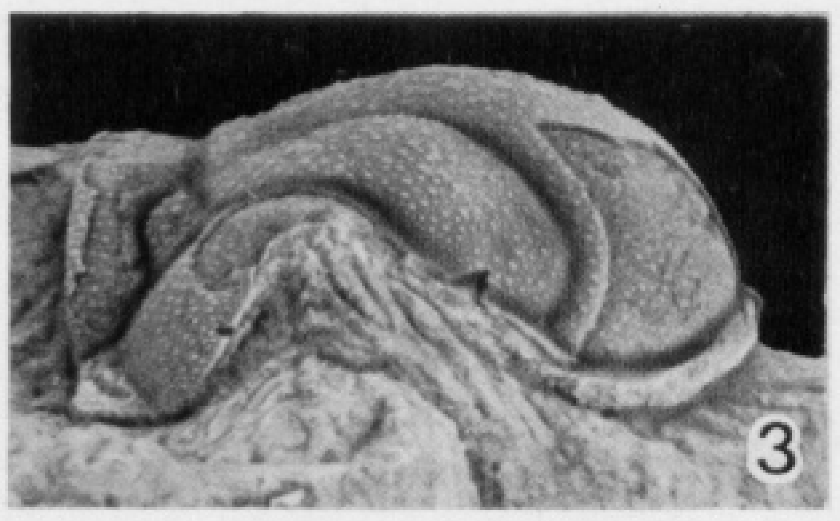
Note added in proof (*8 June* 1988). Since submission of the typescript we have seen the paper by Kobayashi & Hamada (1987) in which the new lichid genera *Metaleiolichas* and *Paraleiolichas* are erected. These genera are each based on a single incomplete cranidium from the Silurian of Shikoku, Japan, and through the courtesy of Dr P. D. Lane we have been able to examine casts of the type specimens.

In *Metaleiolichas* (type species *M. tuberculatus*) the longitudinal furrow meets the occipital furrow at the adaxial extremity of L1a, the bullar lobe is separated from the occipital furrow by a laterally expanded median lobe, and the axial furrow is effaced alongside L1b (Kobayashi & Hamada 1987, fig. 3.4a–c). In these characters, and in the convexity of the cranidium and the shape of the lobes, *Metaleiolichas* closely resembles our subgenus *Platylichas* (*Rontrippia*). *Paraleiolichas* (type species *P. globulus*), has a relatively long (sag., exsag.) cranidial border, circumscribed bullar lobes that are wider than the median lobe measured across the same transverse line, an axial furrow that is impressed behind the bullar lobe, and a poorly defined, depressed area (L1b?) immediately behind the bullar lobes (Kobayashi & Hamada 1987, figs. 2.4, 3.1a, b). These features are all characteristic of our genus *Uripes*.

It appears, therefore, that *Metaleiolichas* and *Paraleiolichas* may be senior synomyms of *Platylichas* (*Rontrippia*) and *Uripes*, respectively, but more complete material of the Japanese type species, including pygidia, is required for a reliable comparision. In the meantime we consider it preferable to continue to use our names. We do not consider *Metaleiolichas* and *Paraleiolichas* to be allied with *Leiolichas*, as suggested by Kobayashi & Hamada (1987).

Reference

Kobayashi, T. & Hamada, T. 1987 The third addition to the Silurian trilobite fauna of Yokokura-yama, Shikoku, Japan. *Trans. Proc. palaeont. Soc. Japan* (n.s.) **147**, 109–116.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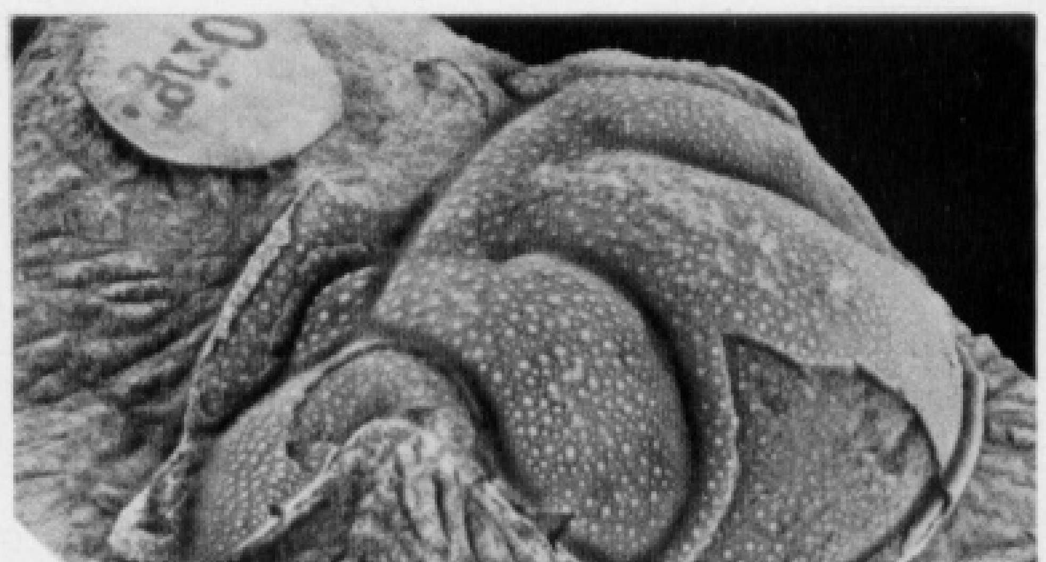
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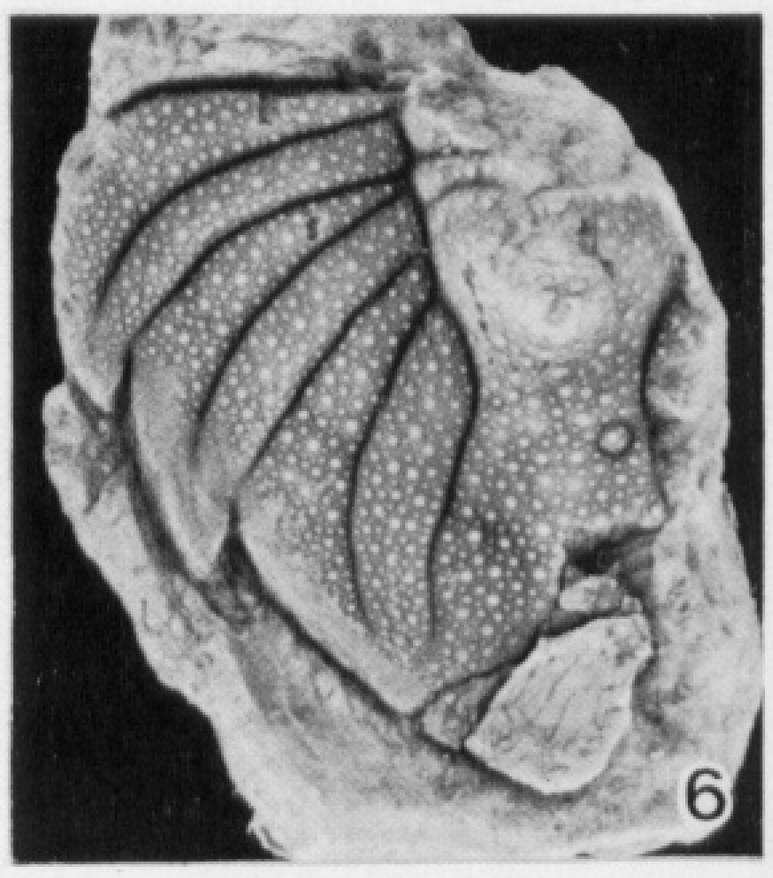
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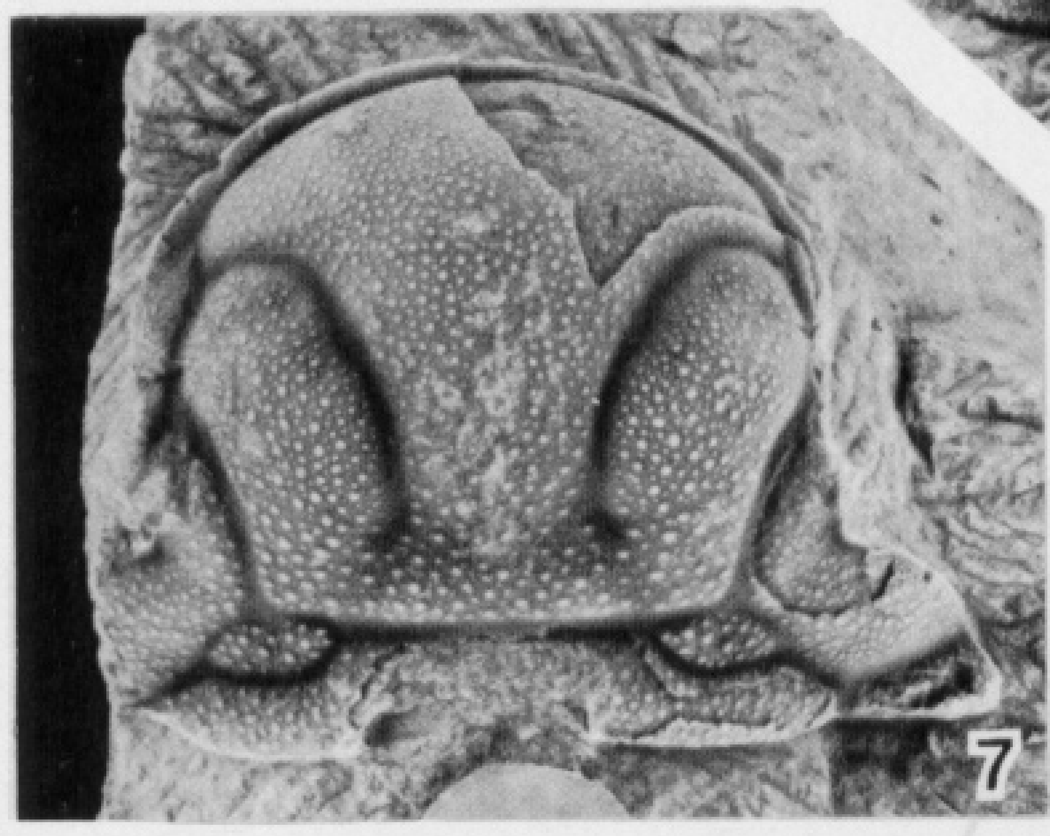
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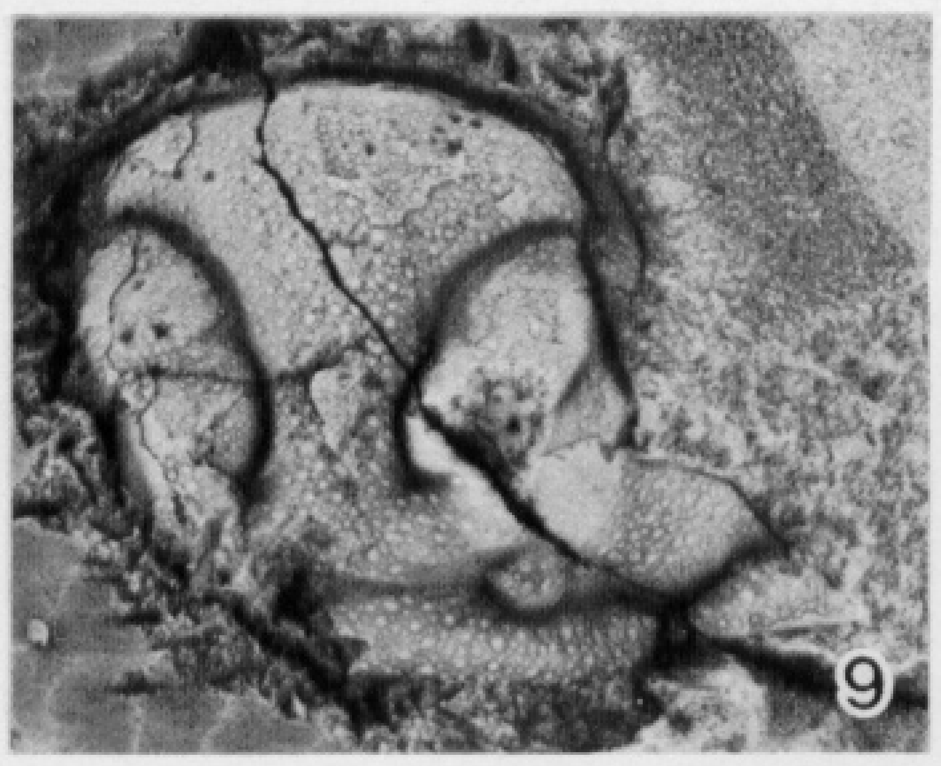
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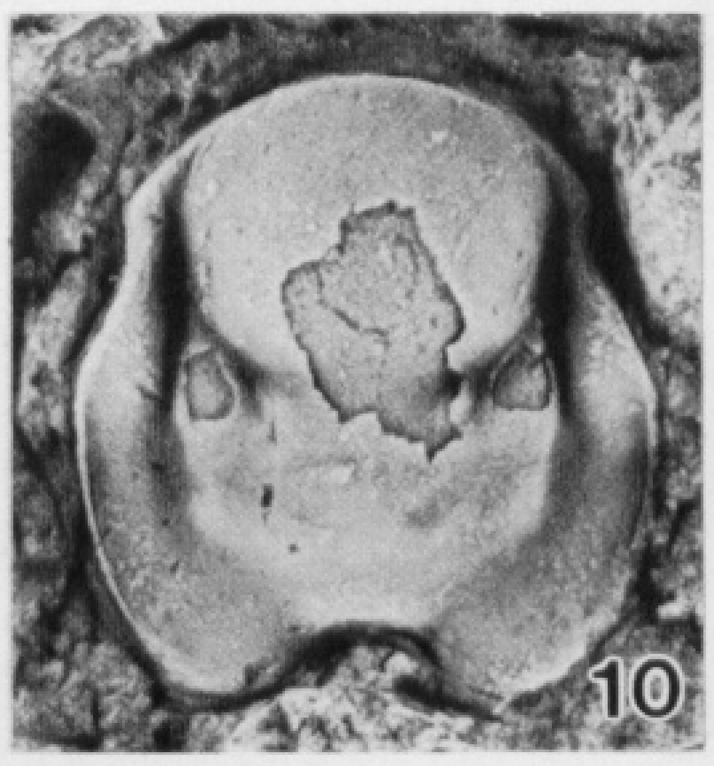
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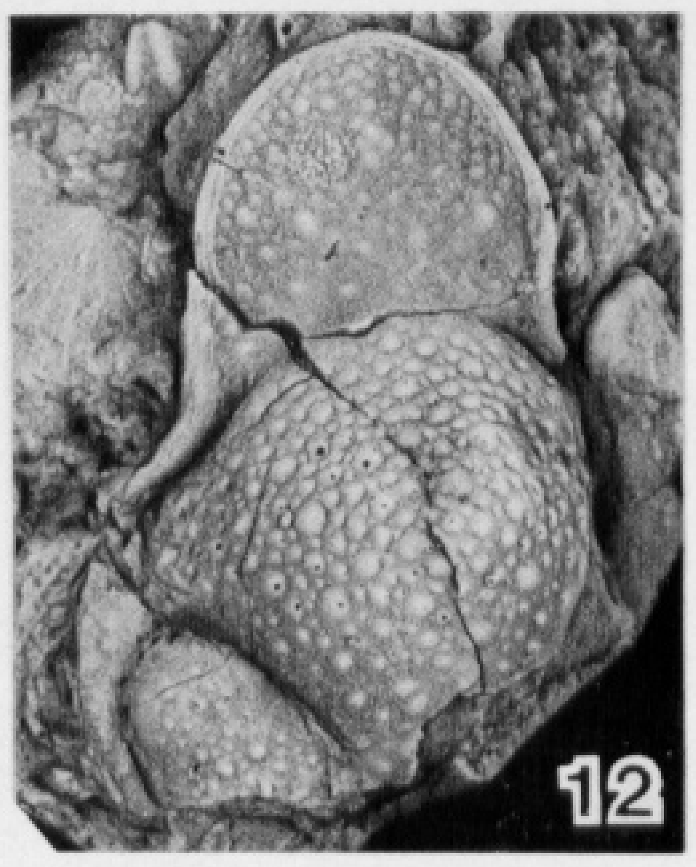
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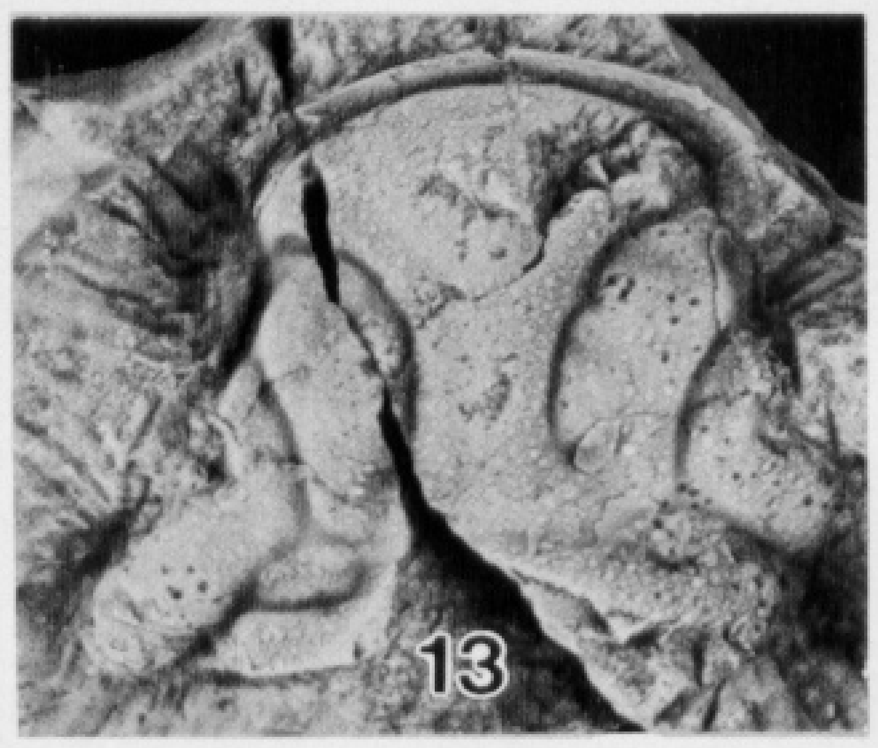
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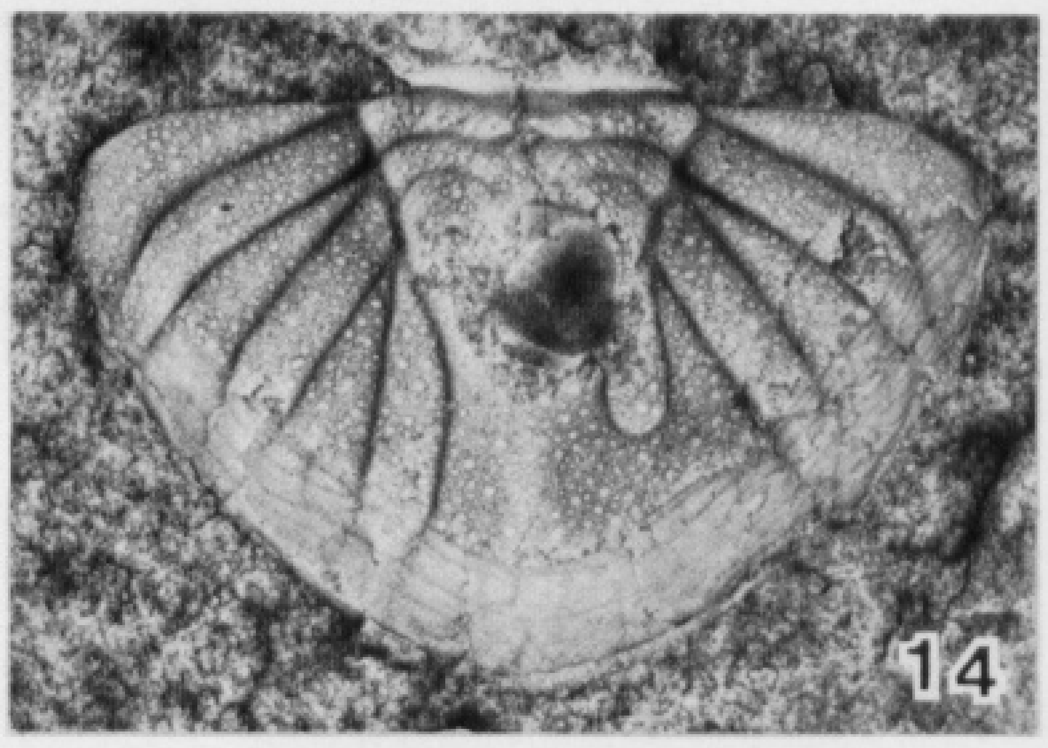
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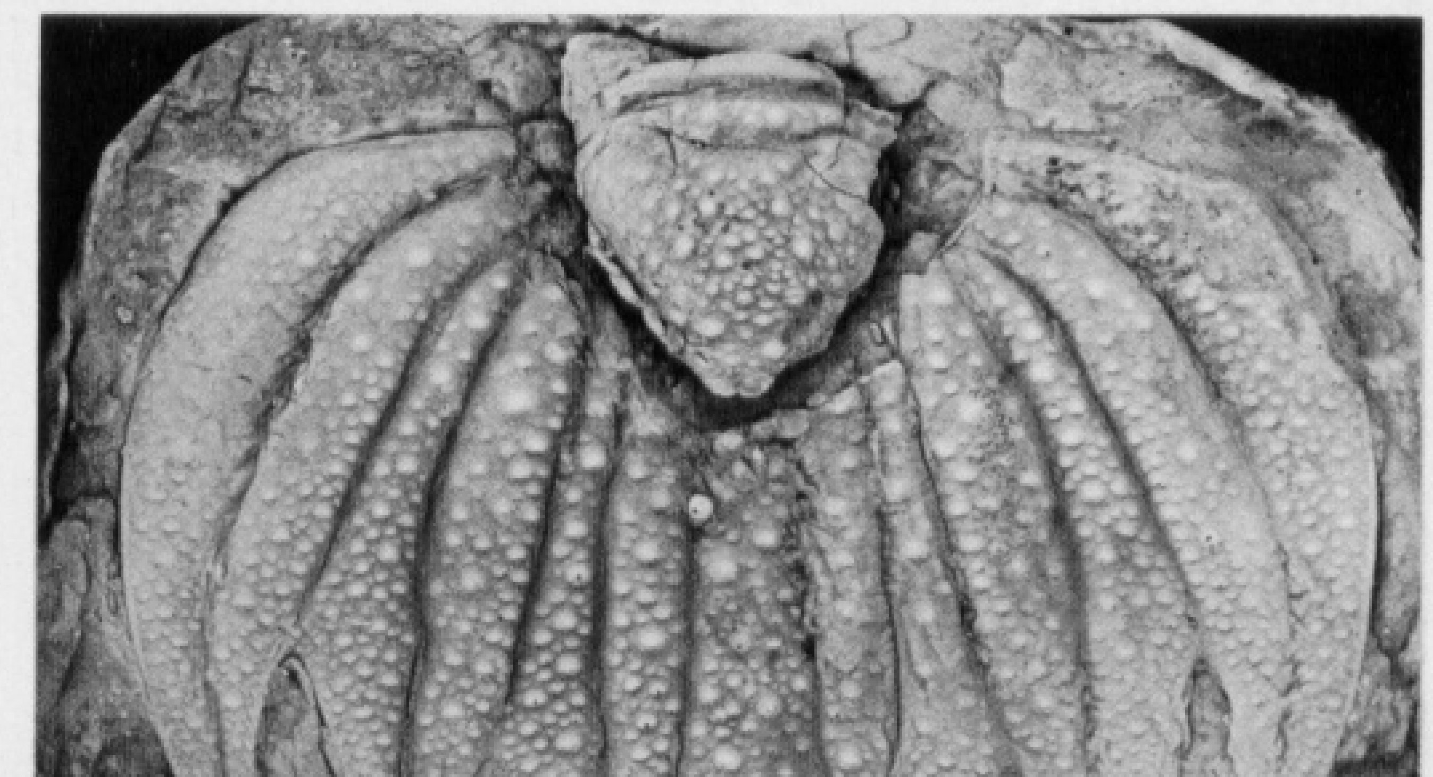
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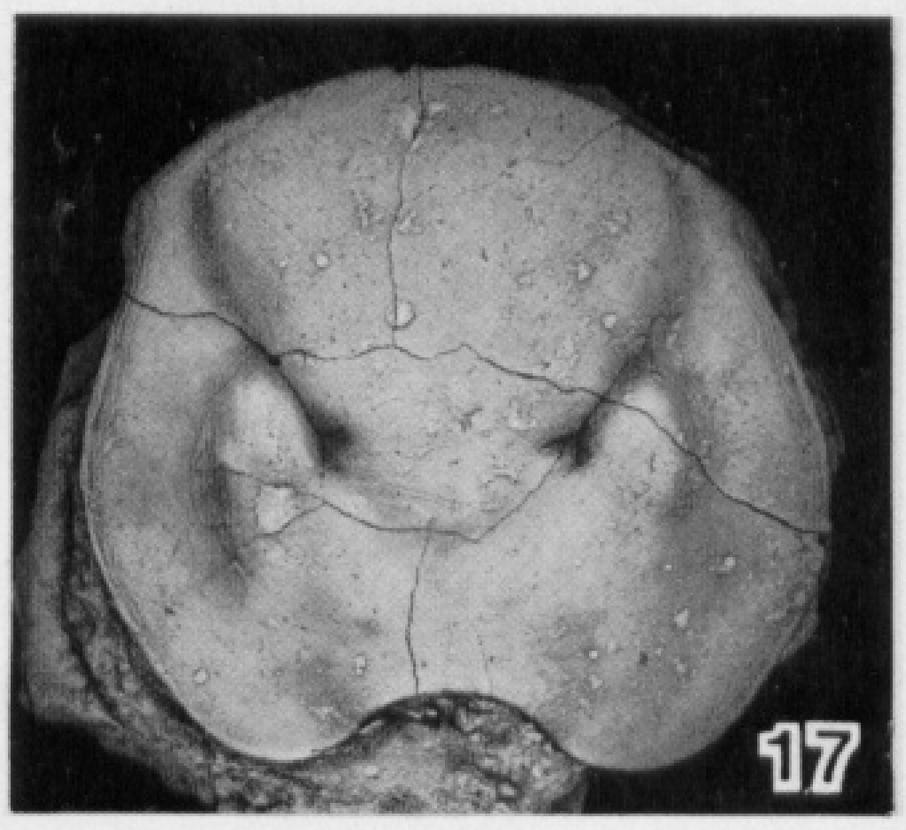
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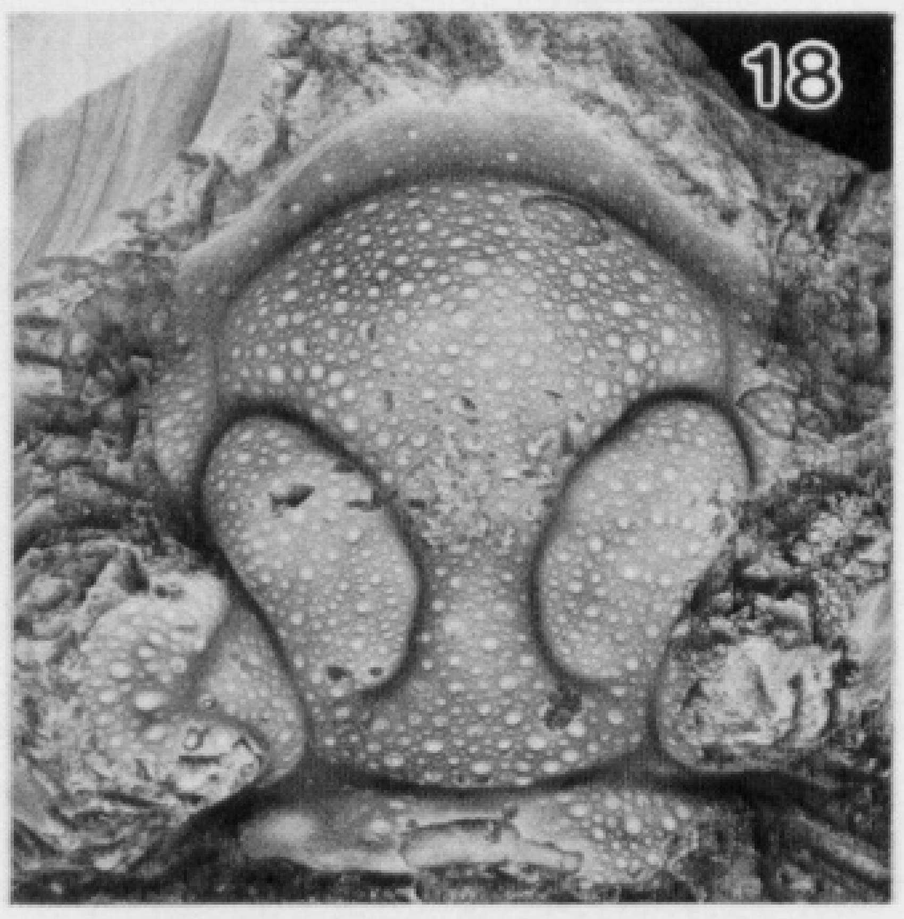
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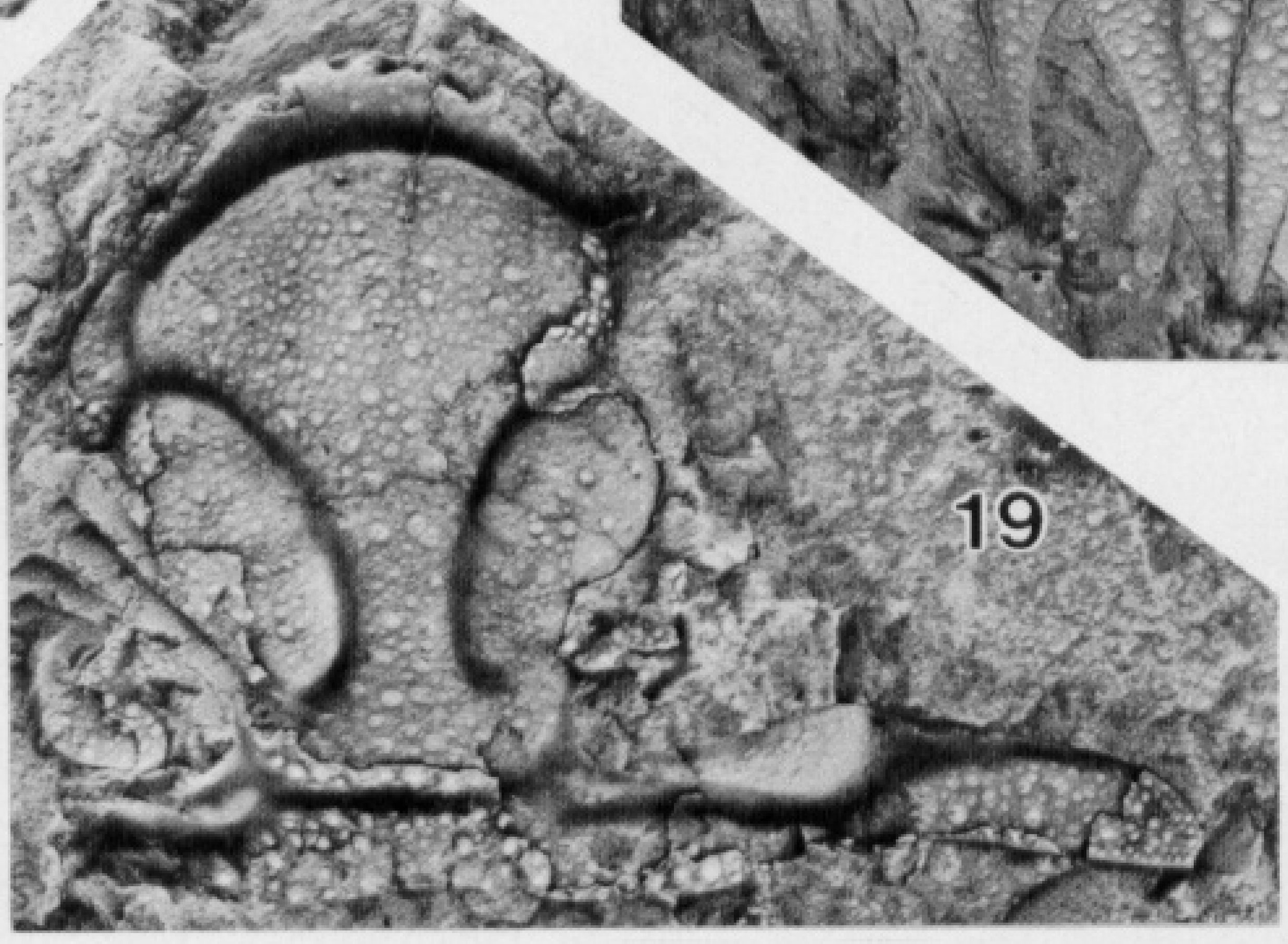
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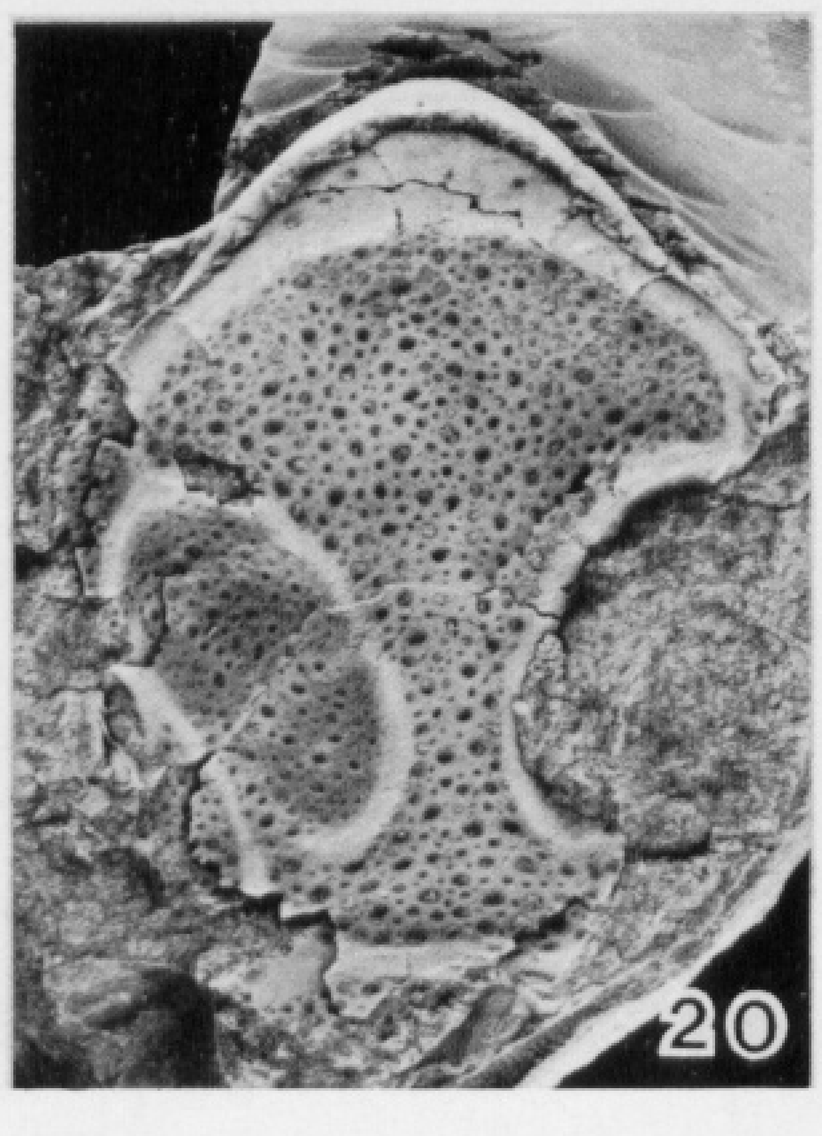
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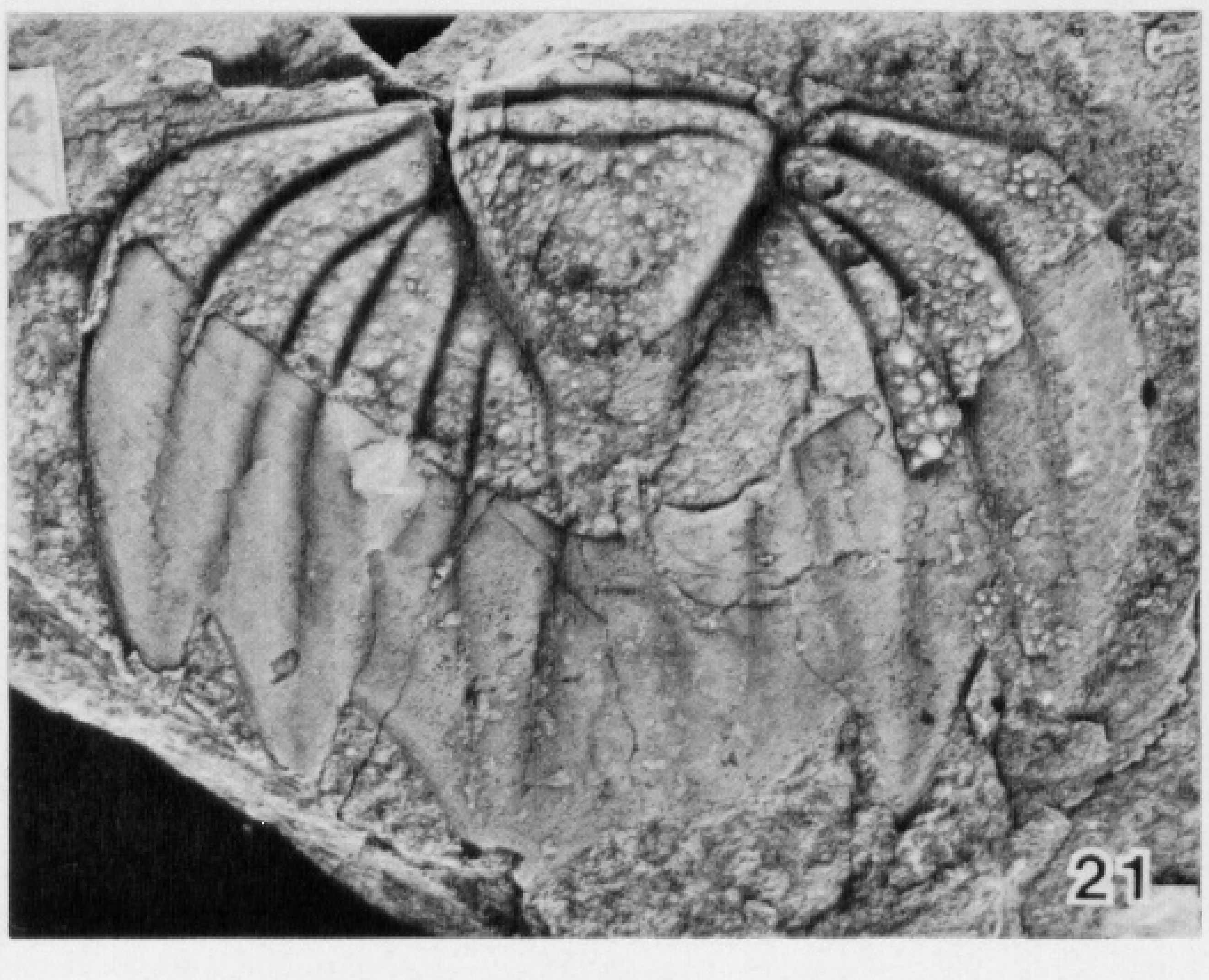
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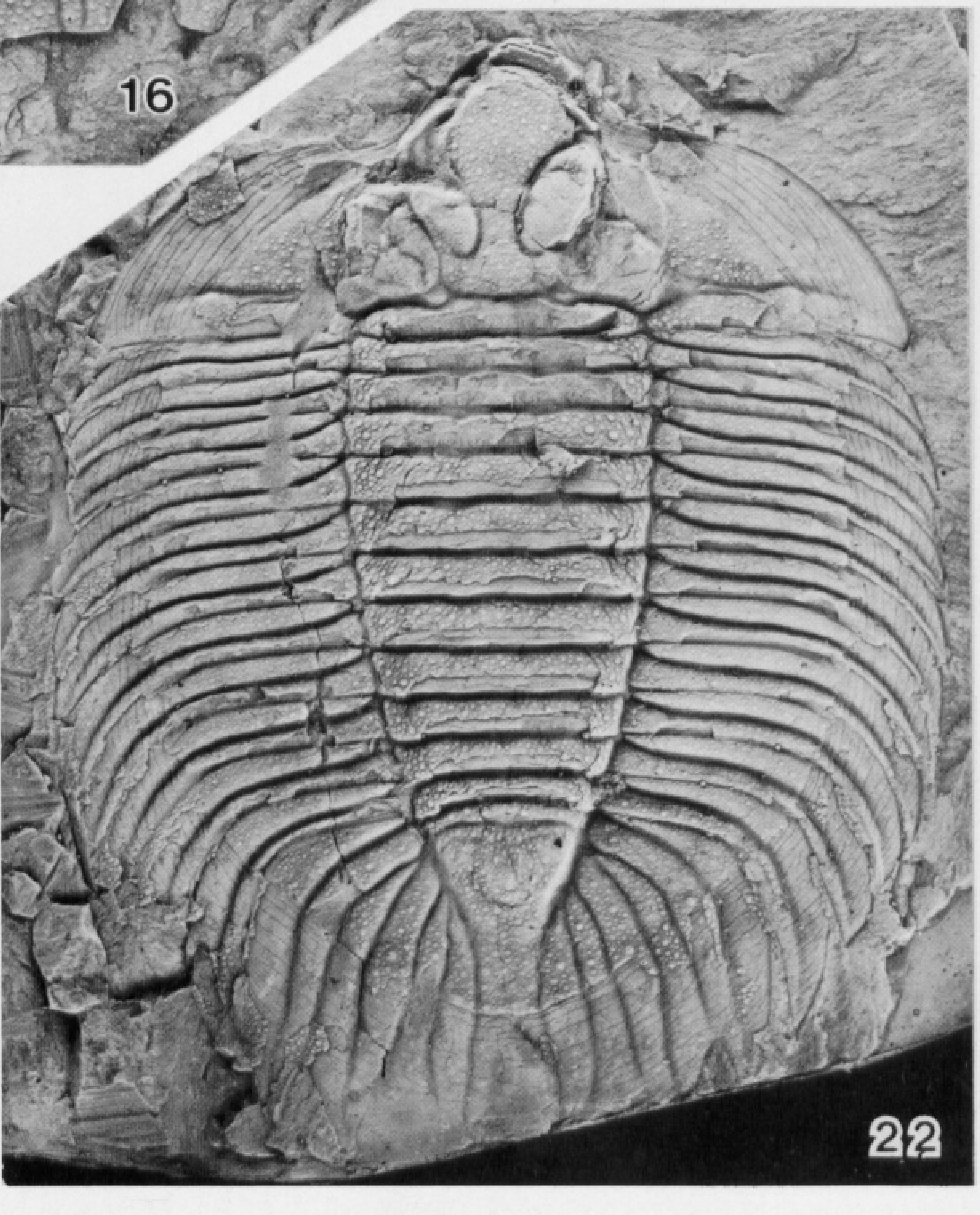
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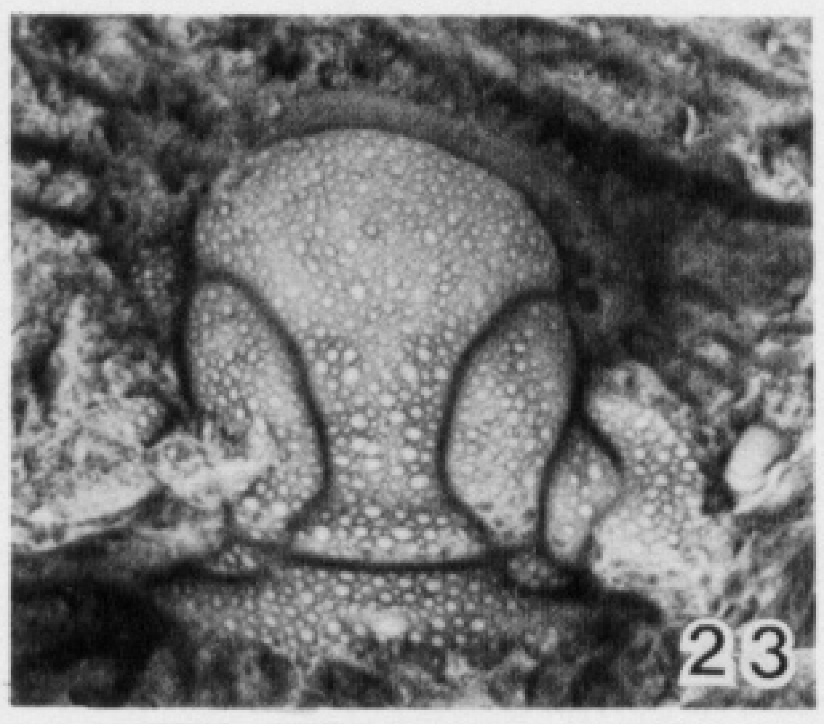
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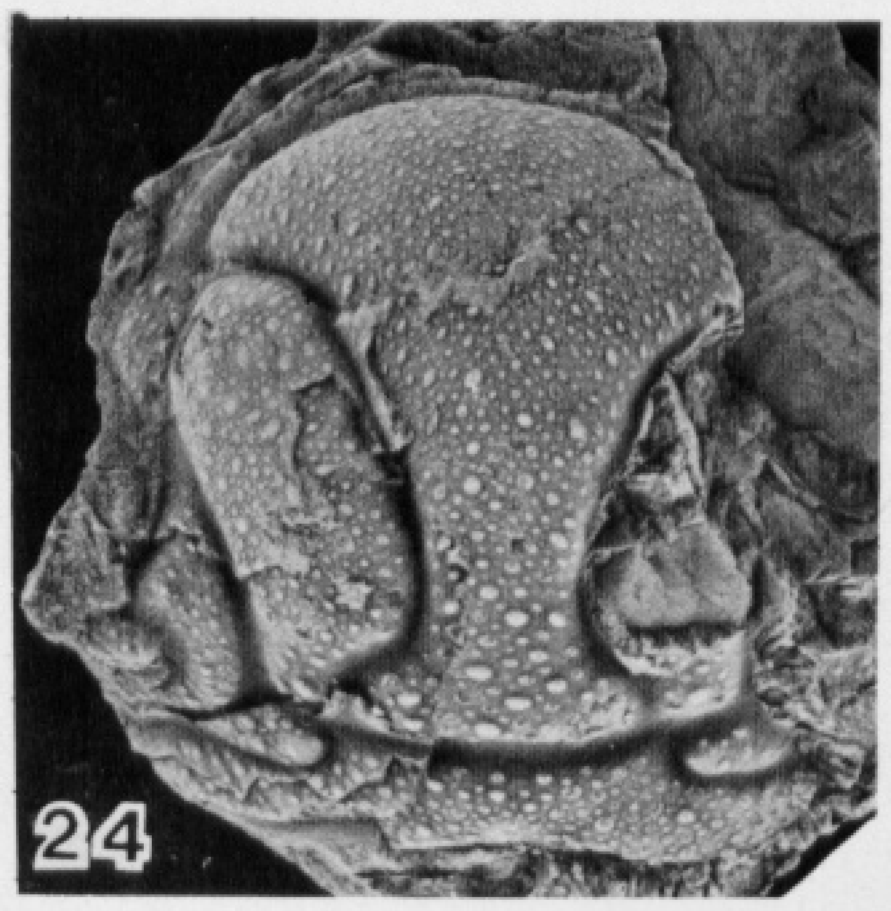
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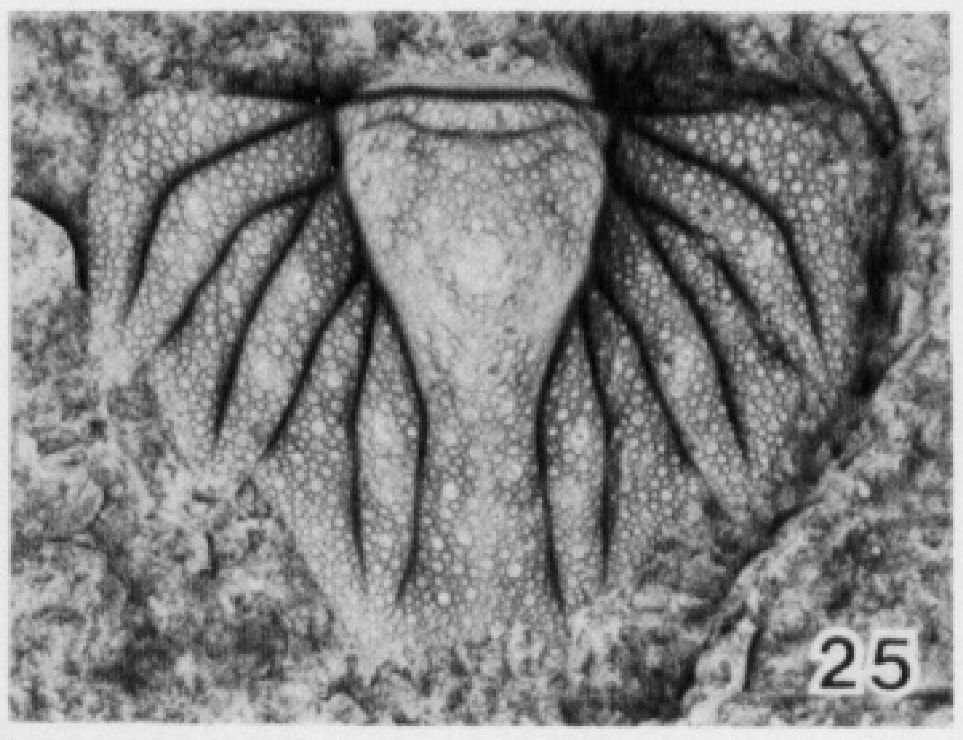
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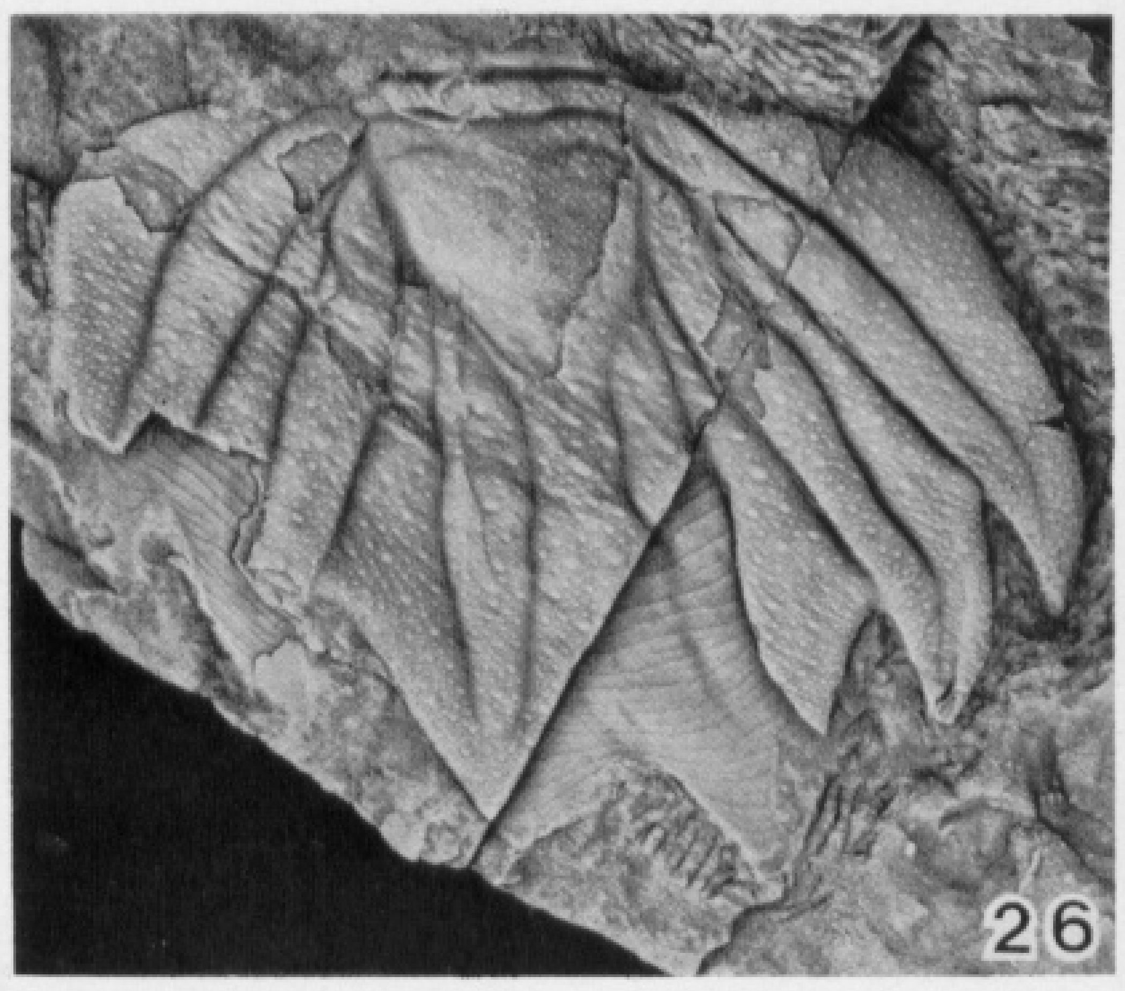
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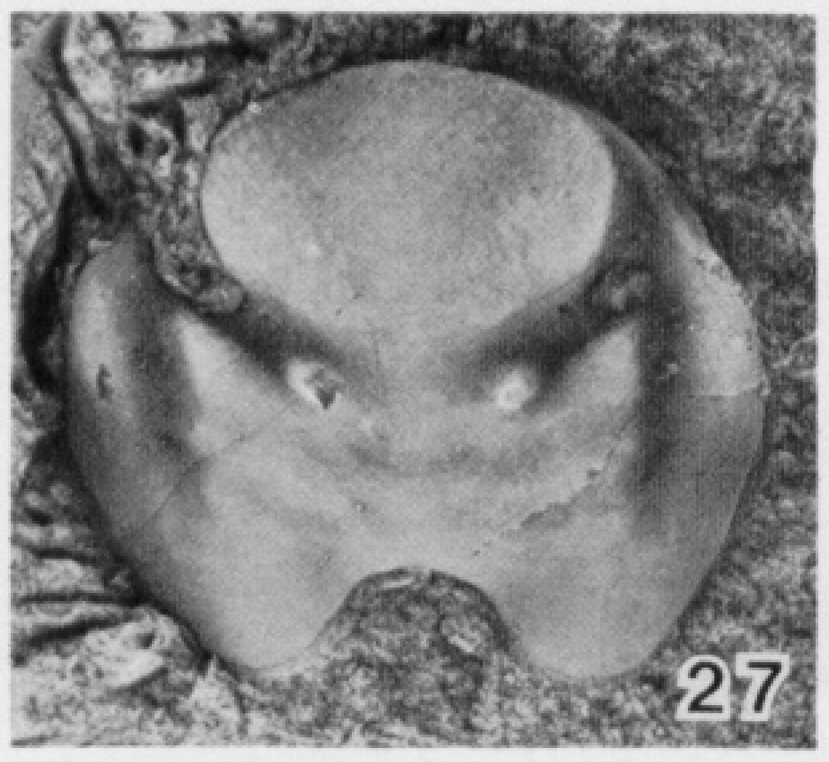
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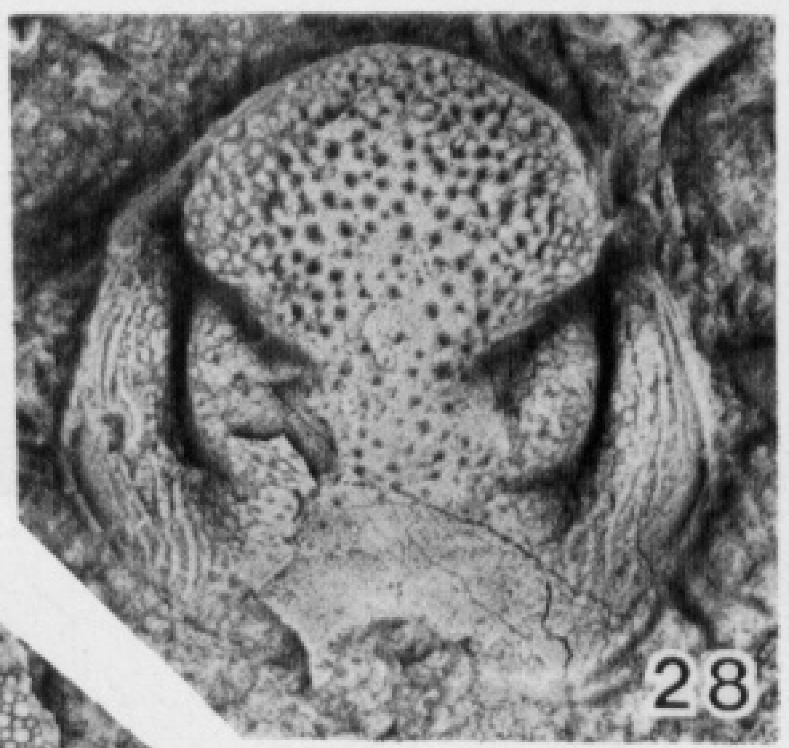
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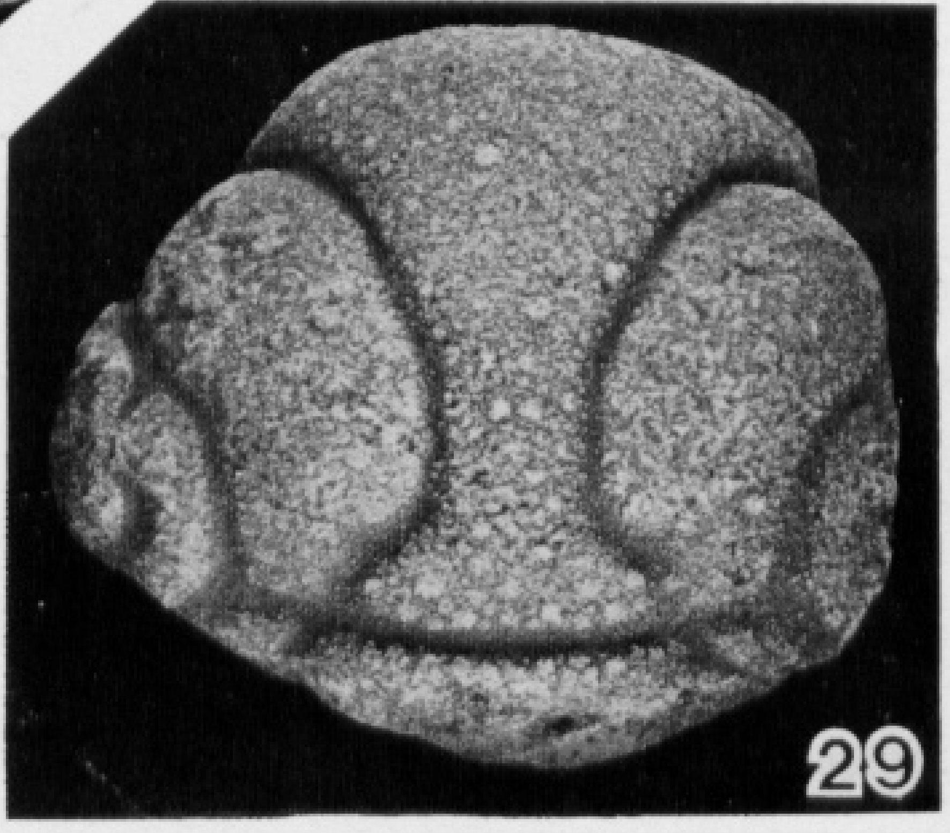
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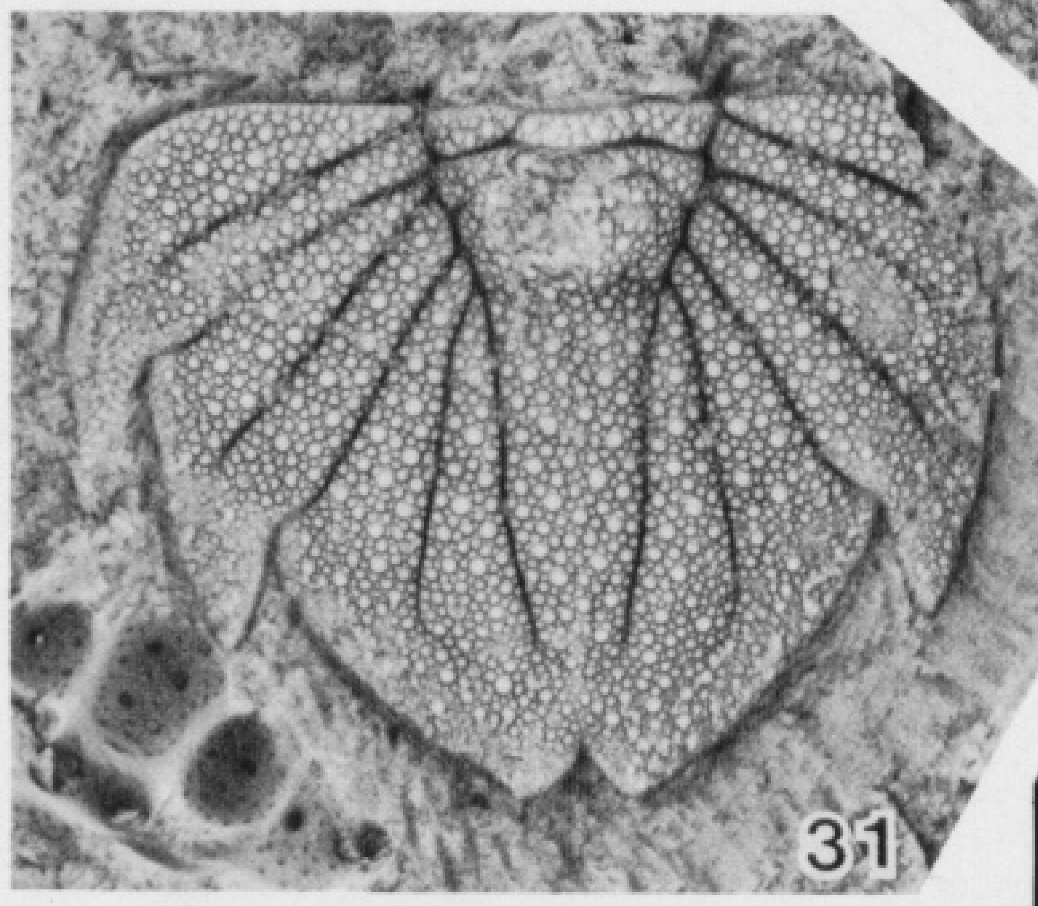
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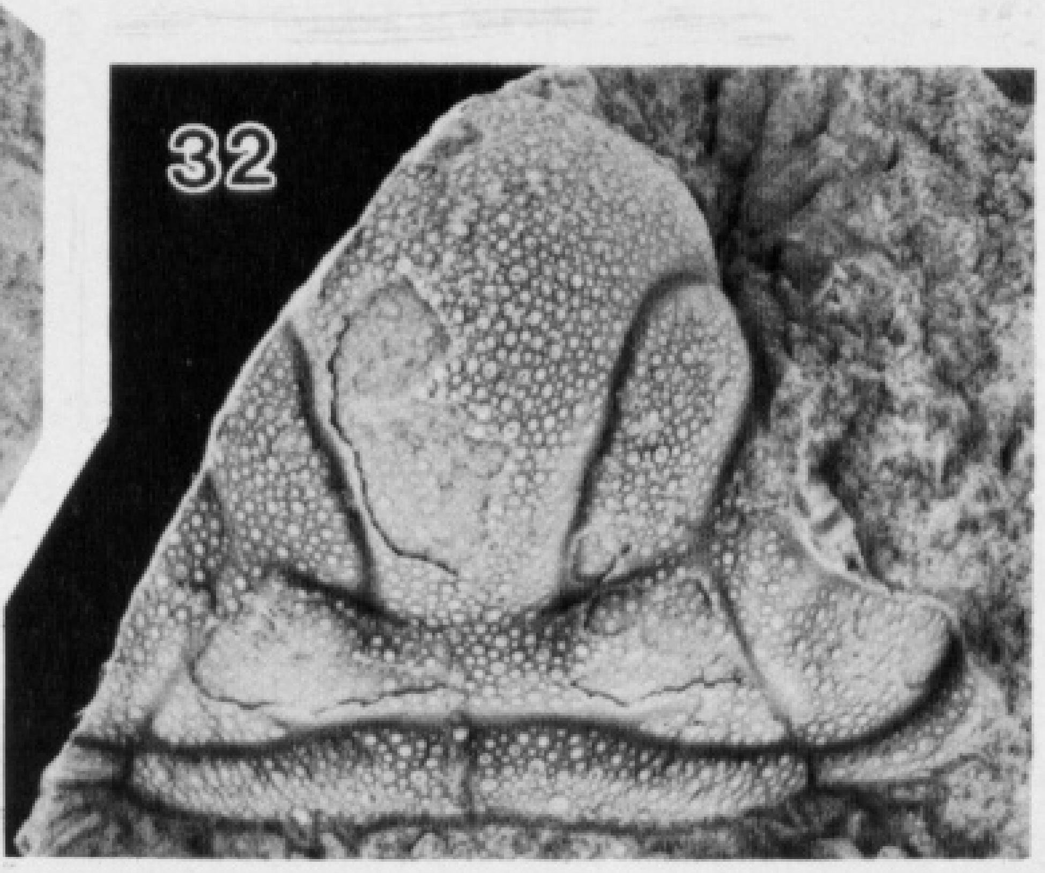
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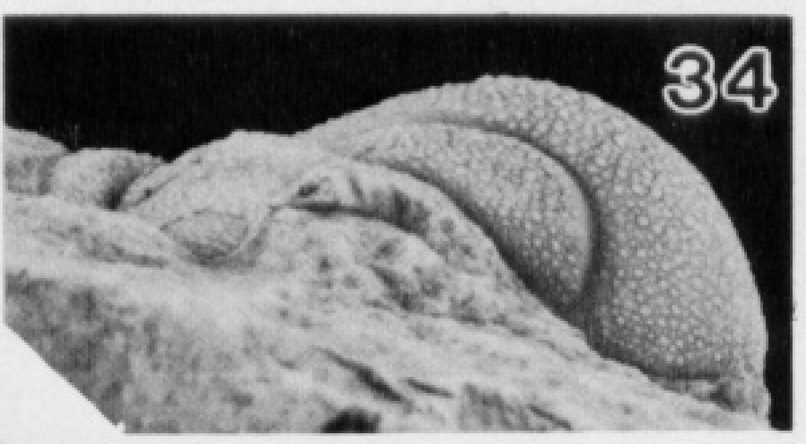
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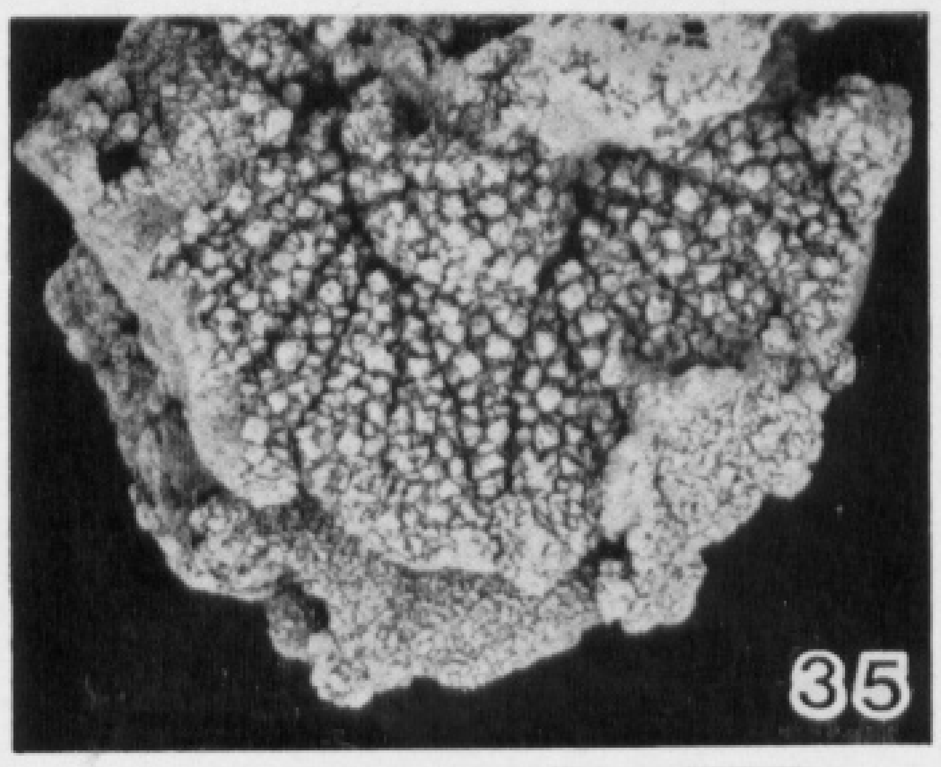
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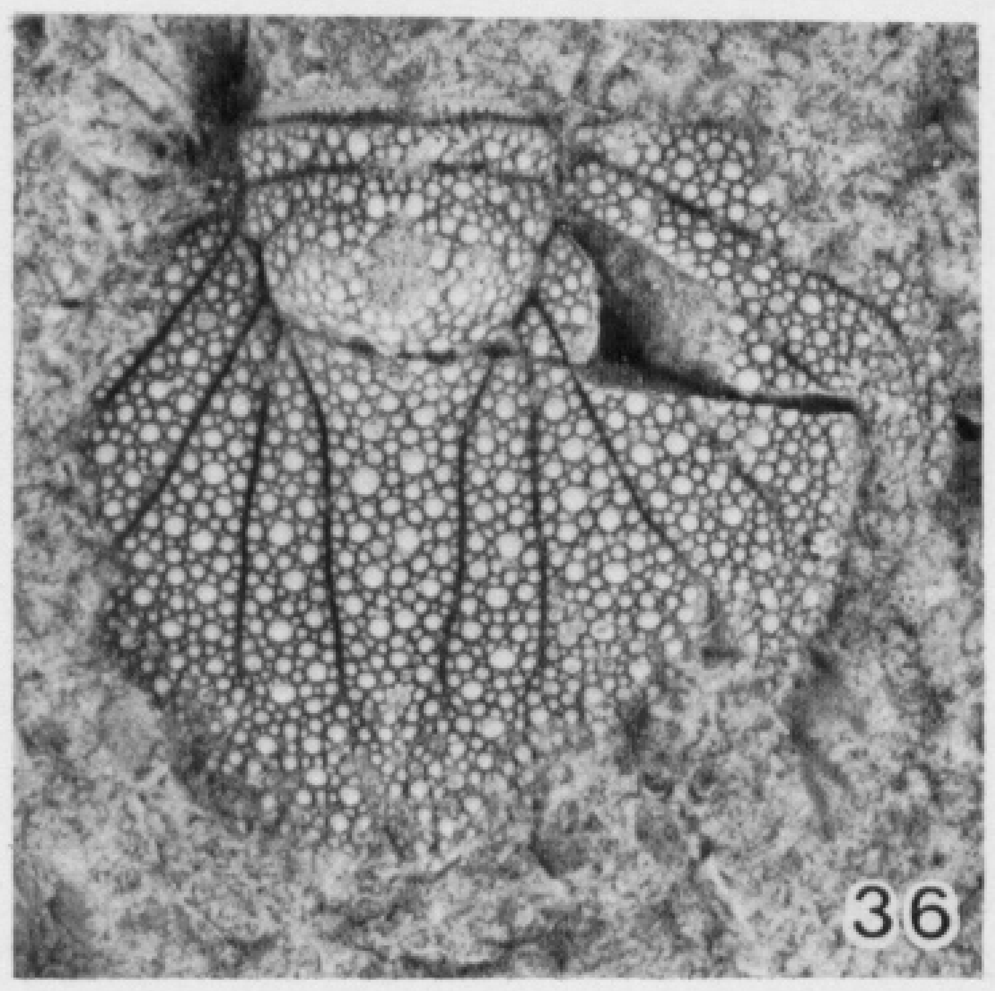
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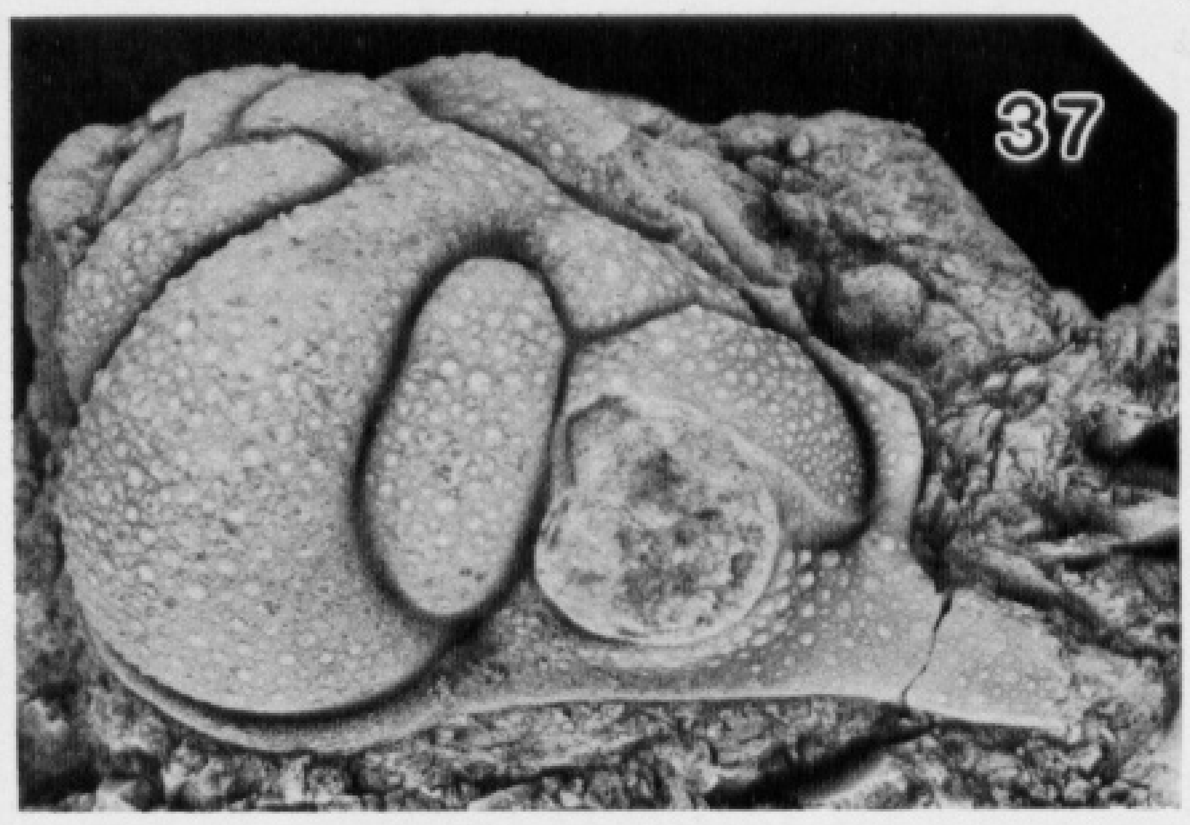
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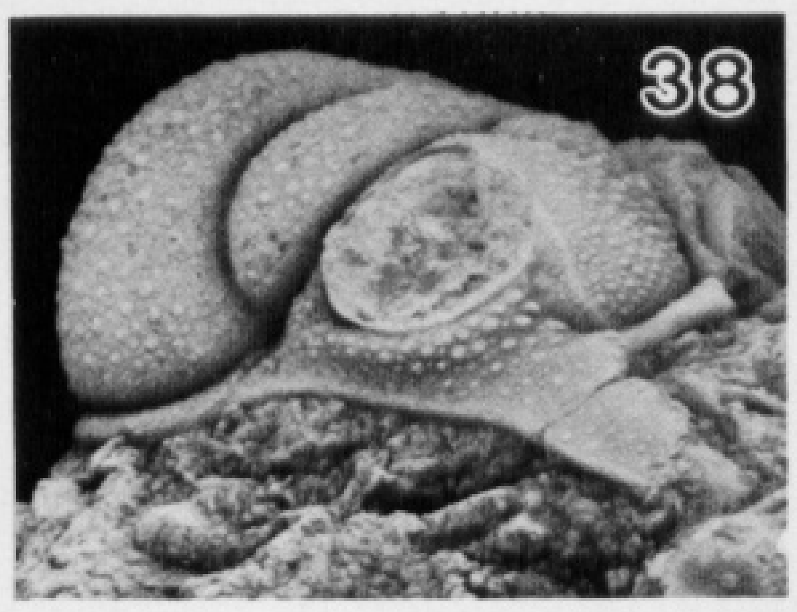
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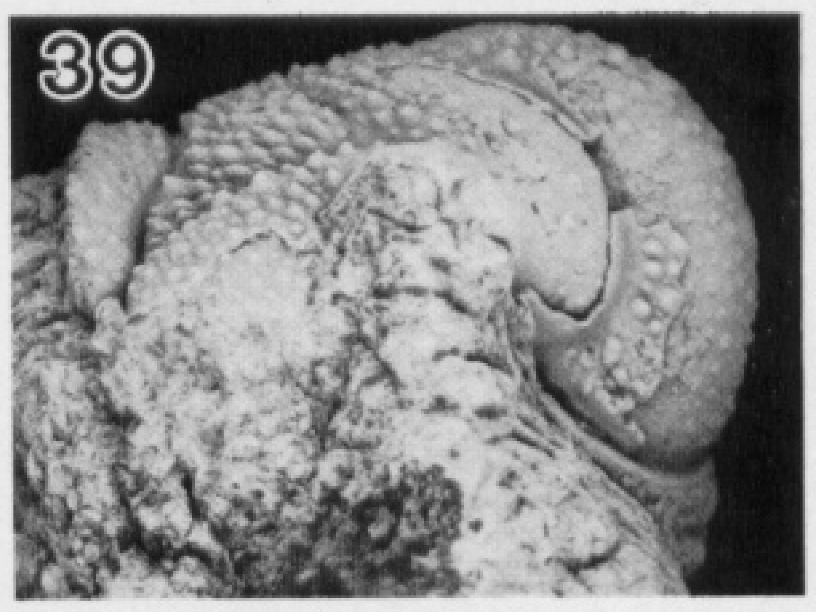
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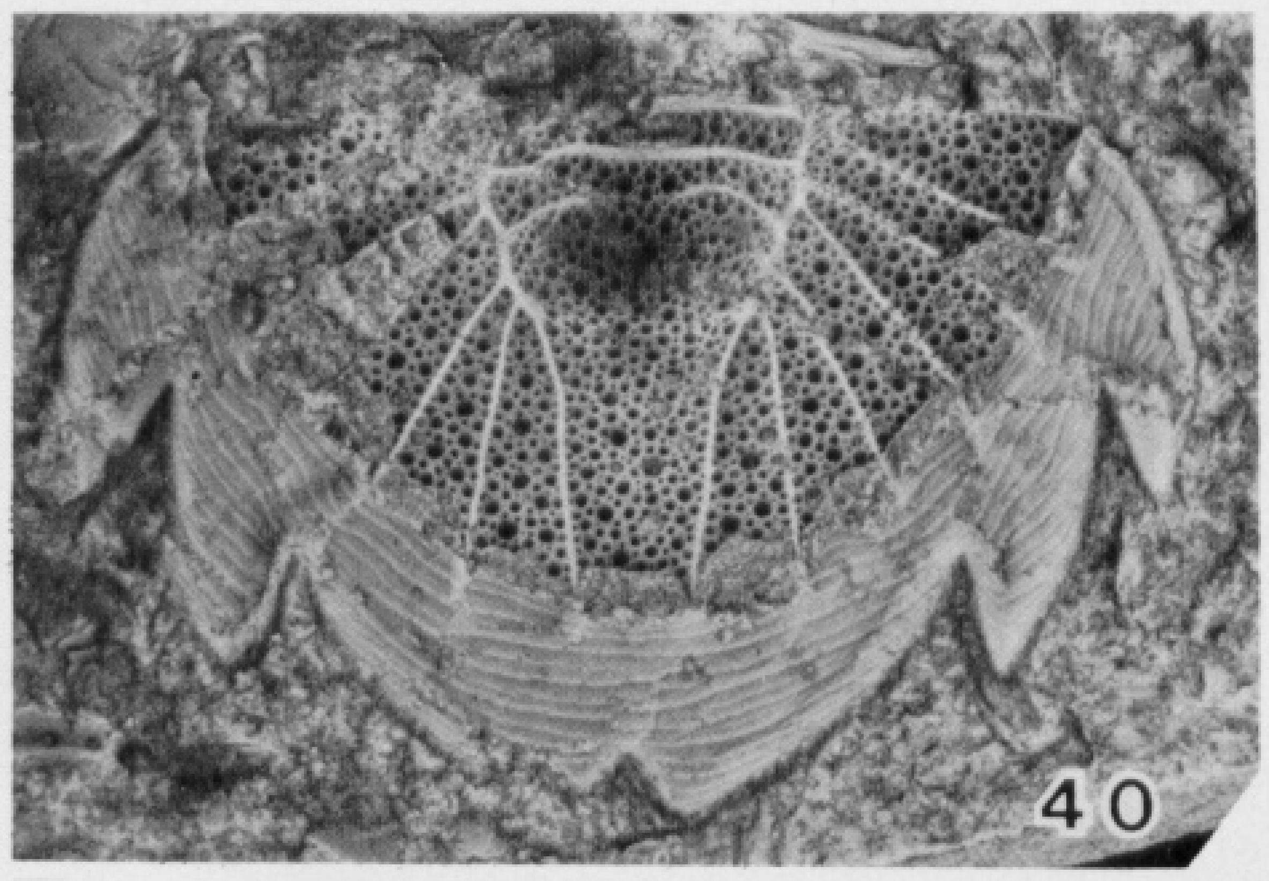
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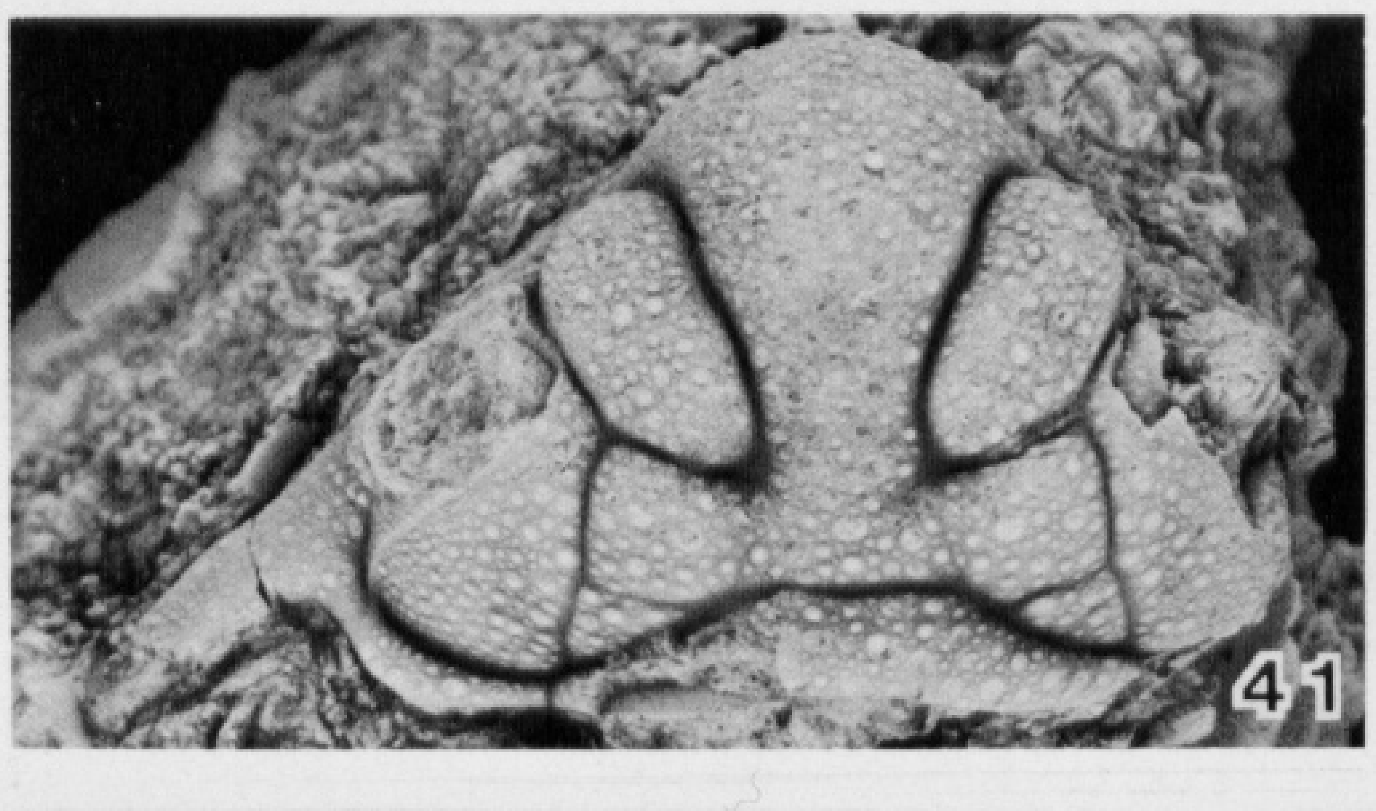
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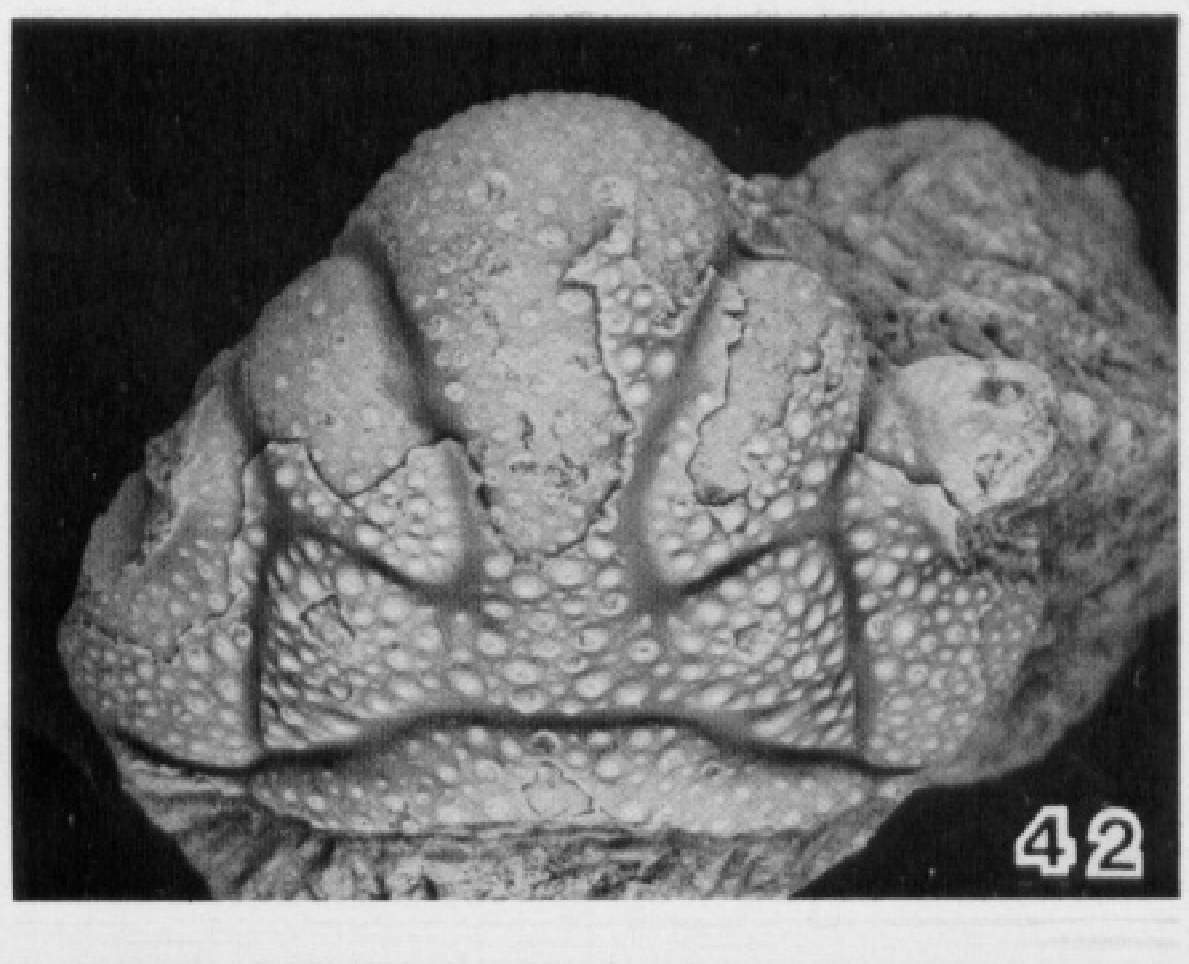
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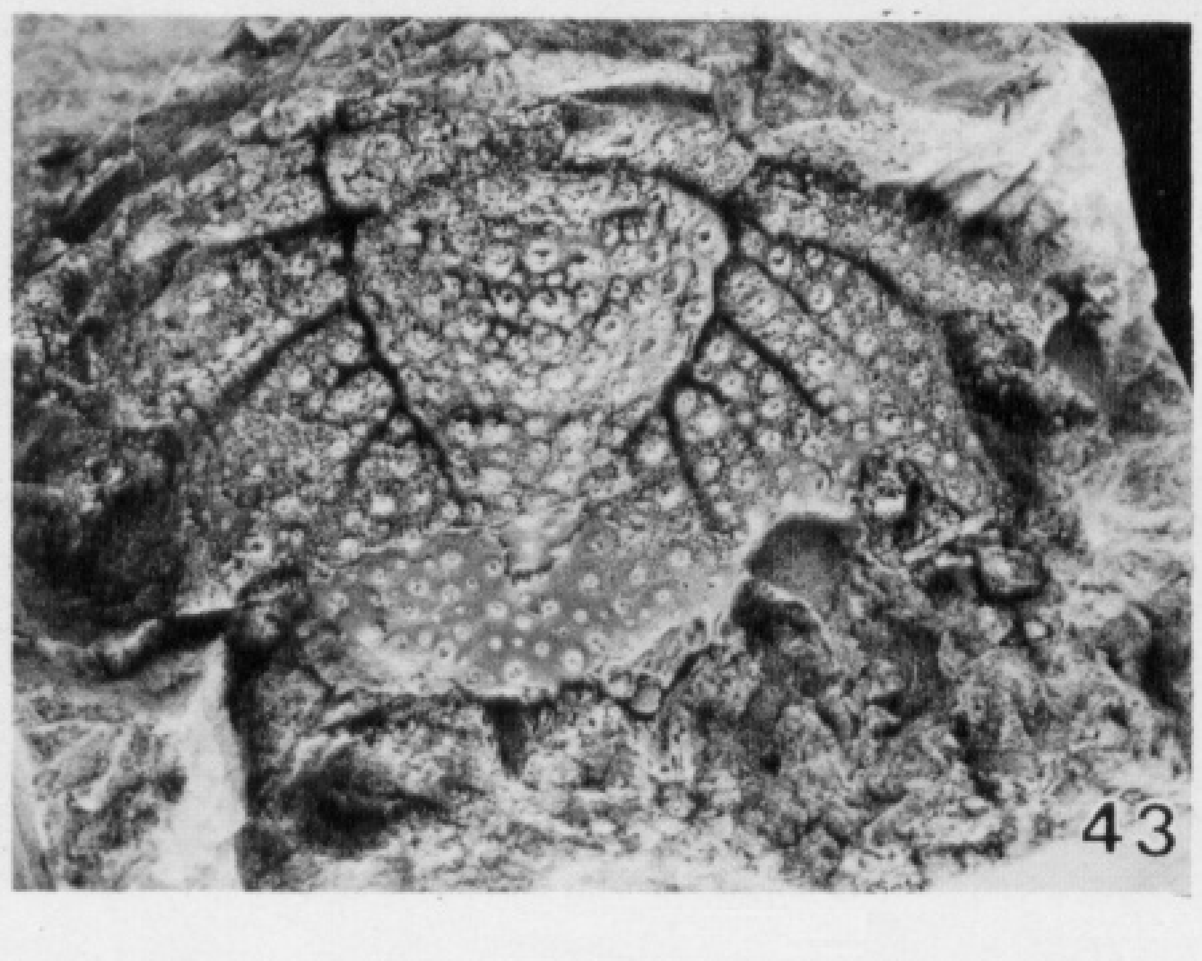
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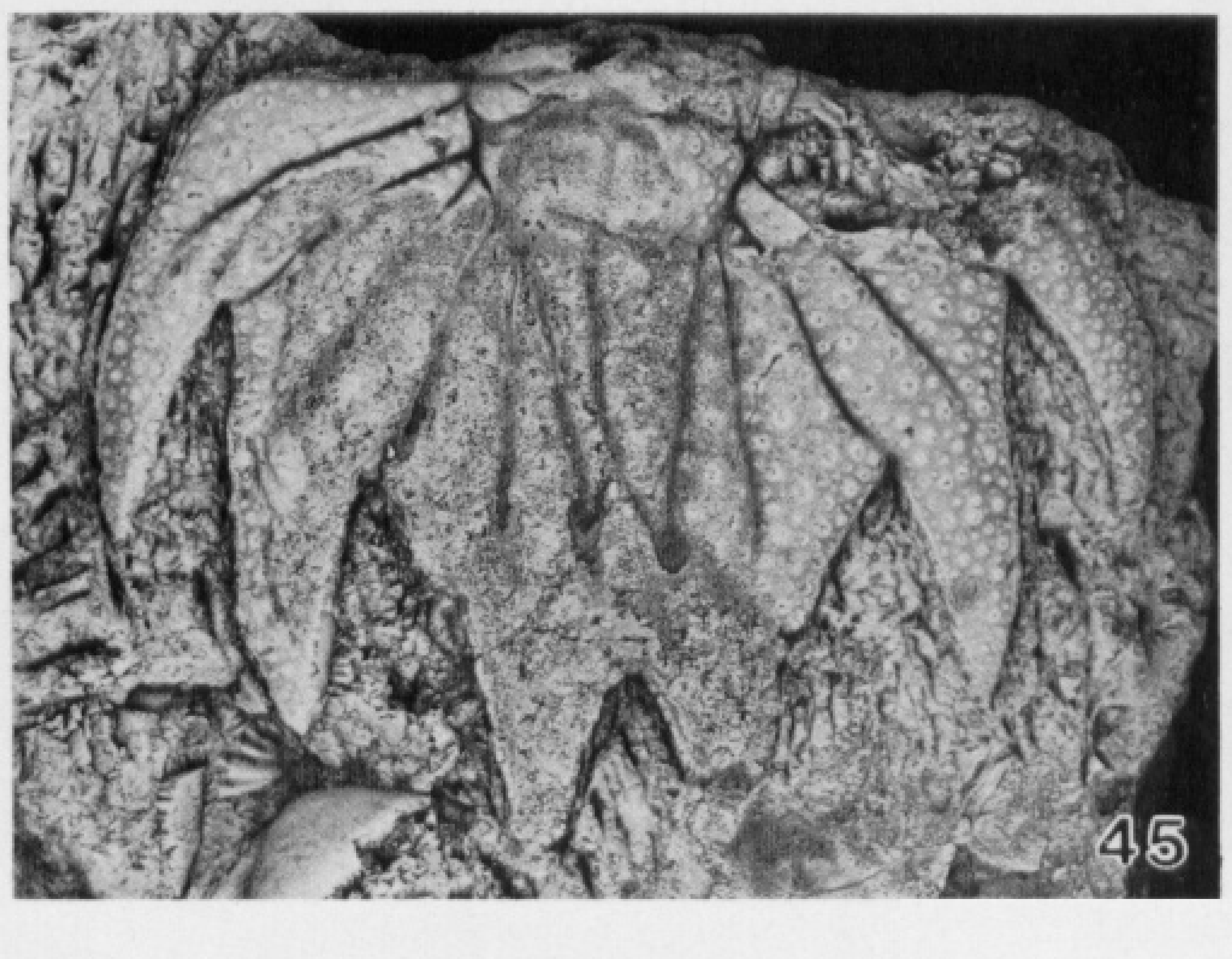
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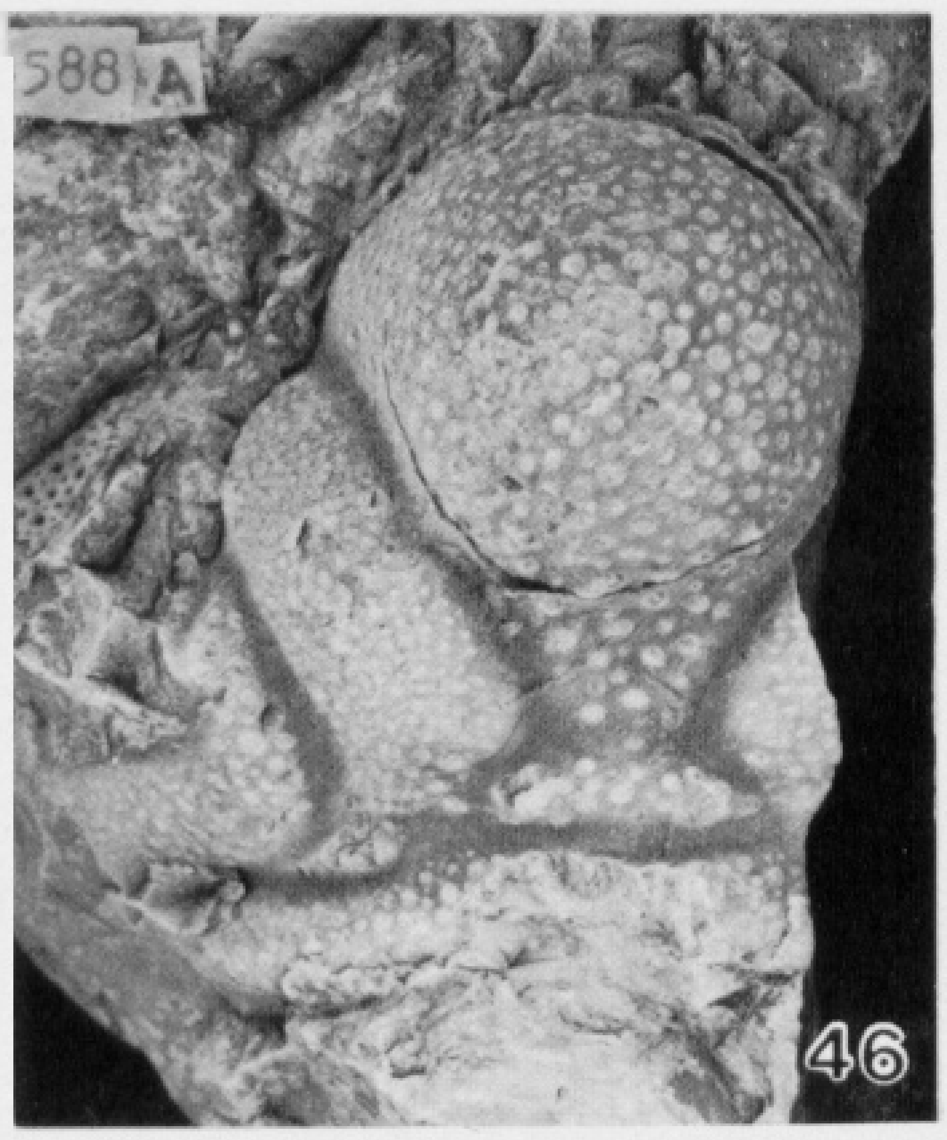

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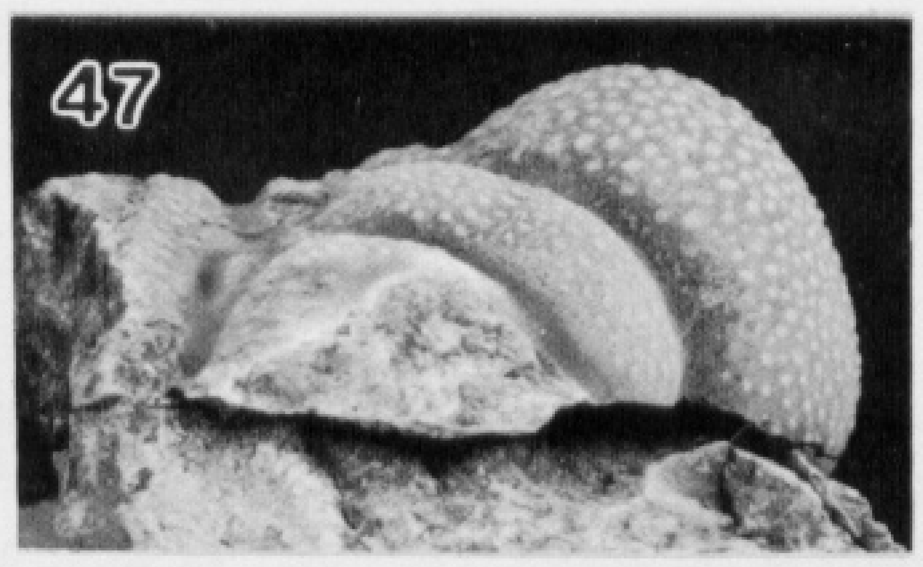
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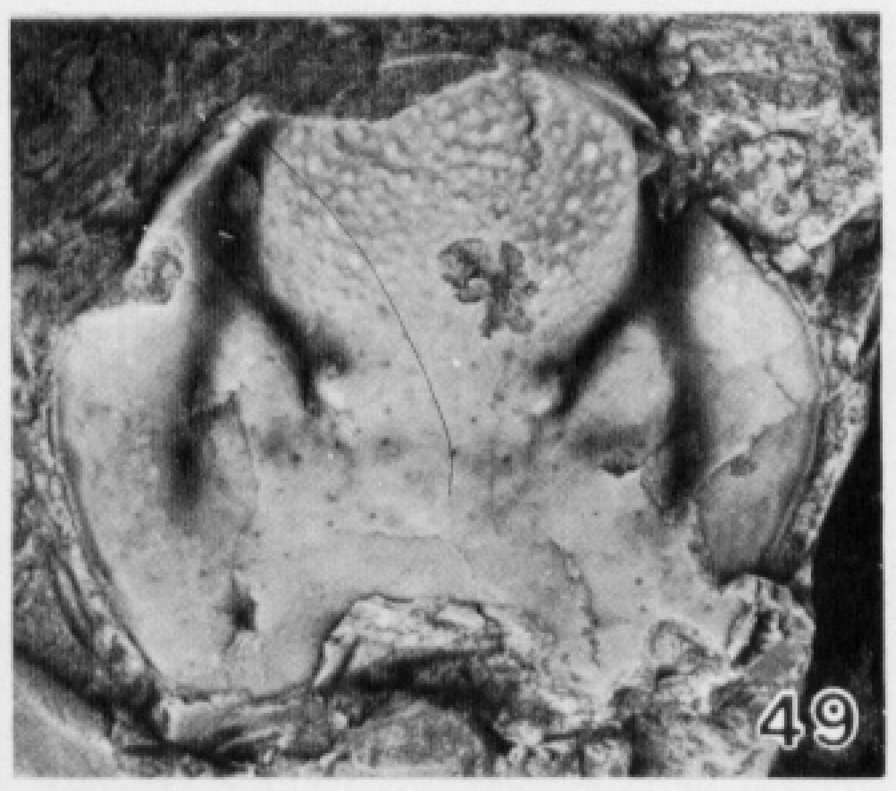
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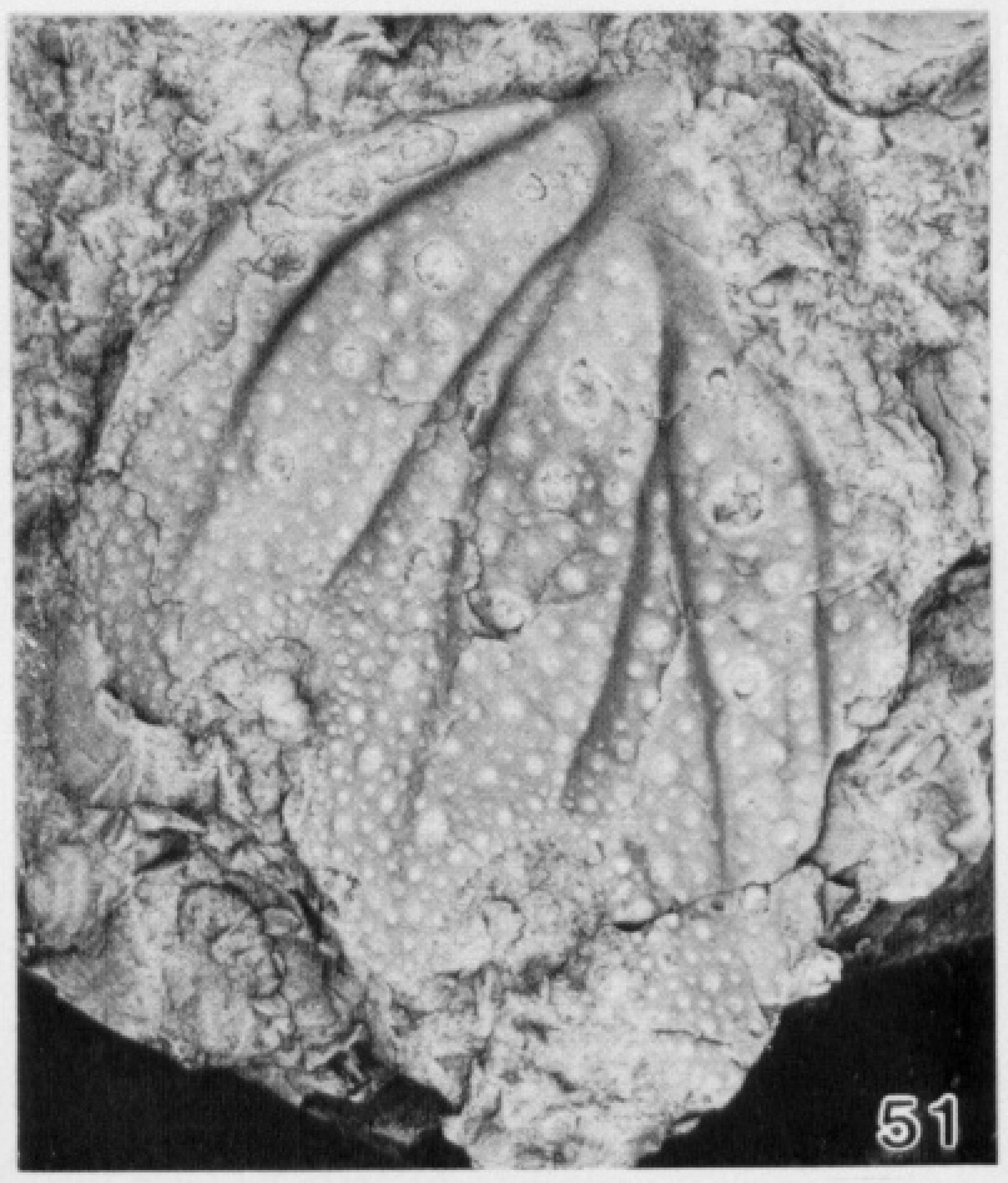
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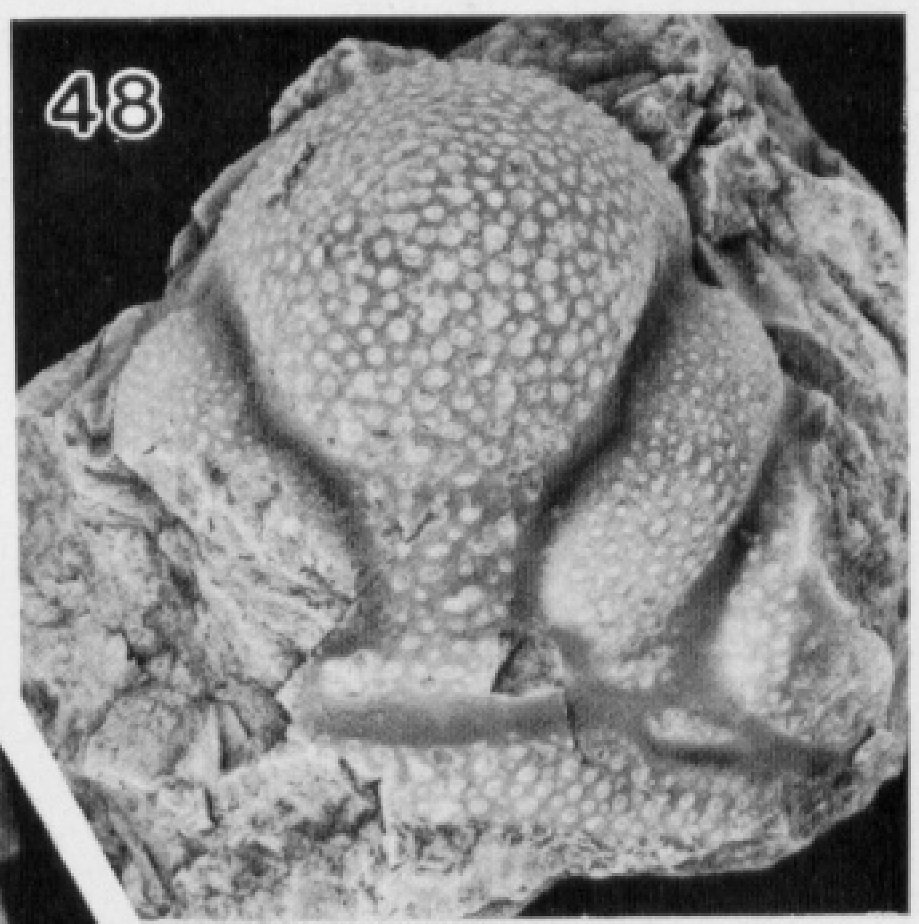
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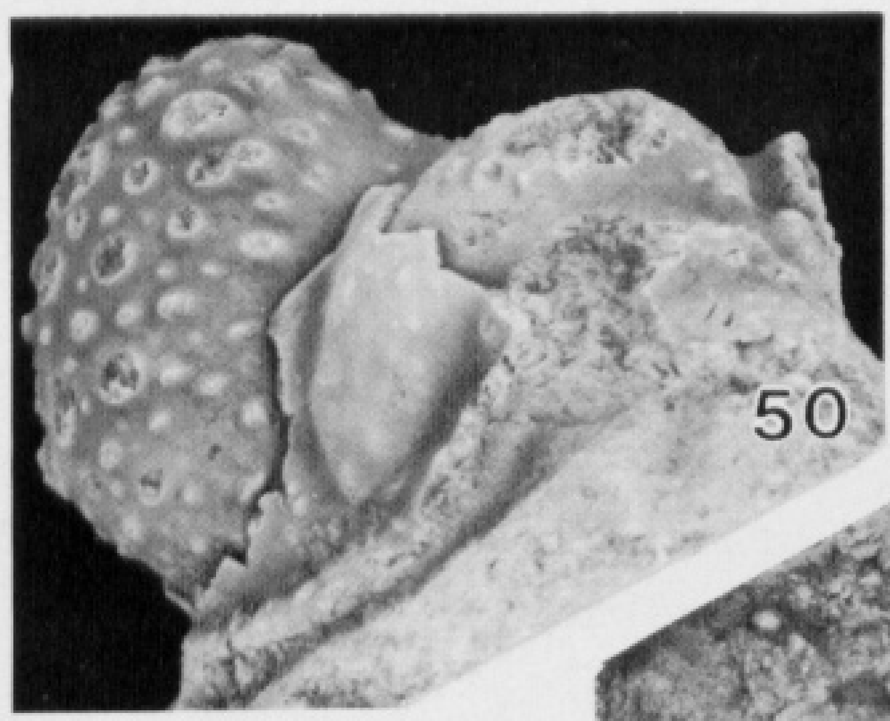
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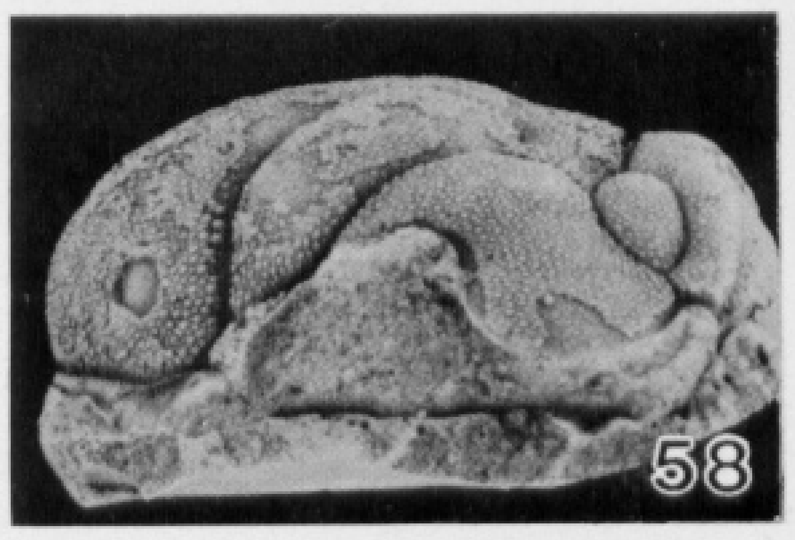
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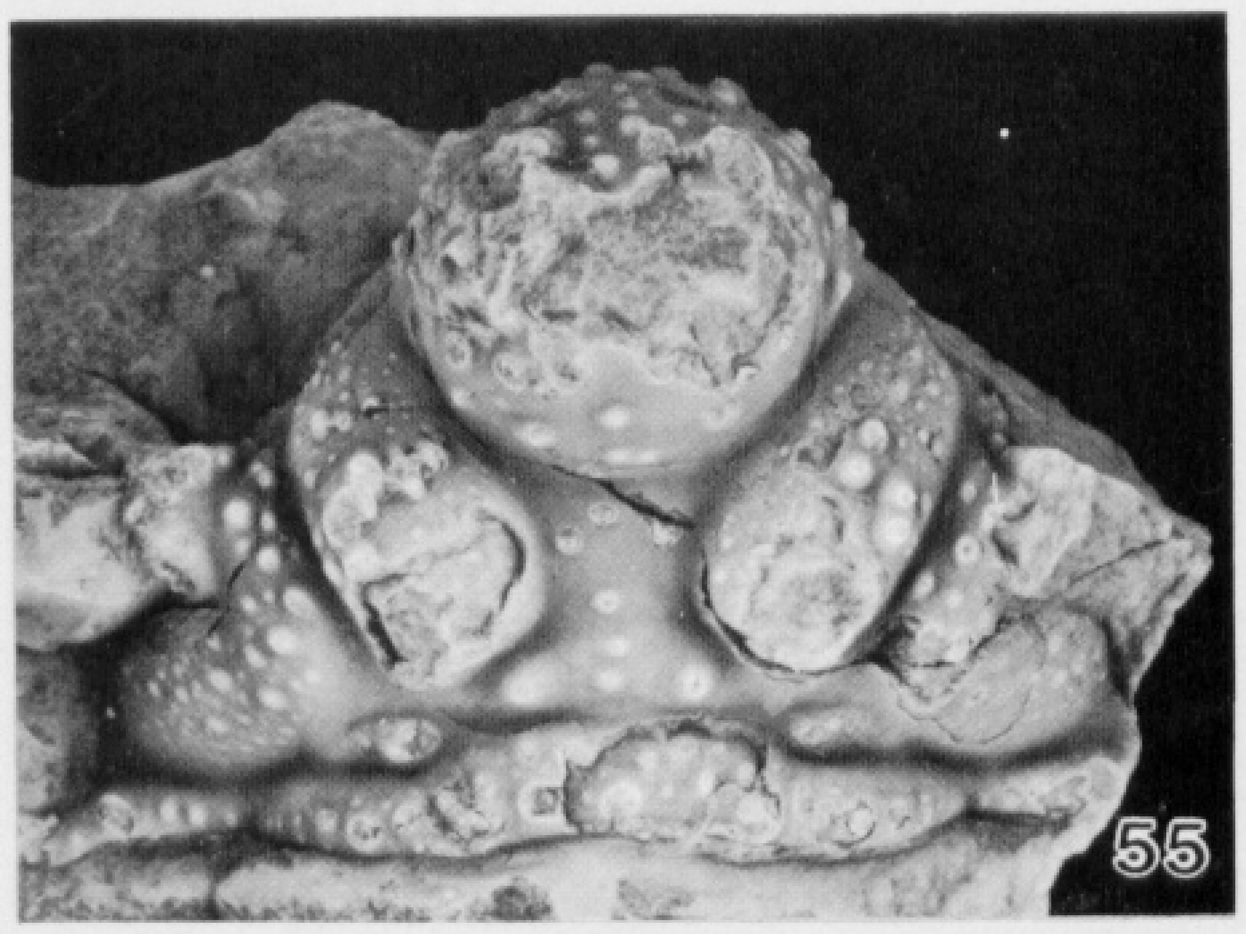
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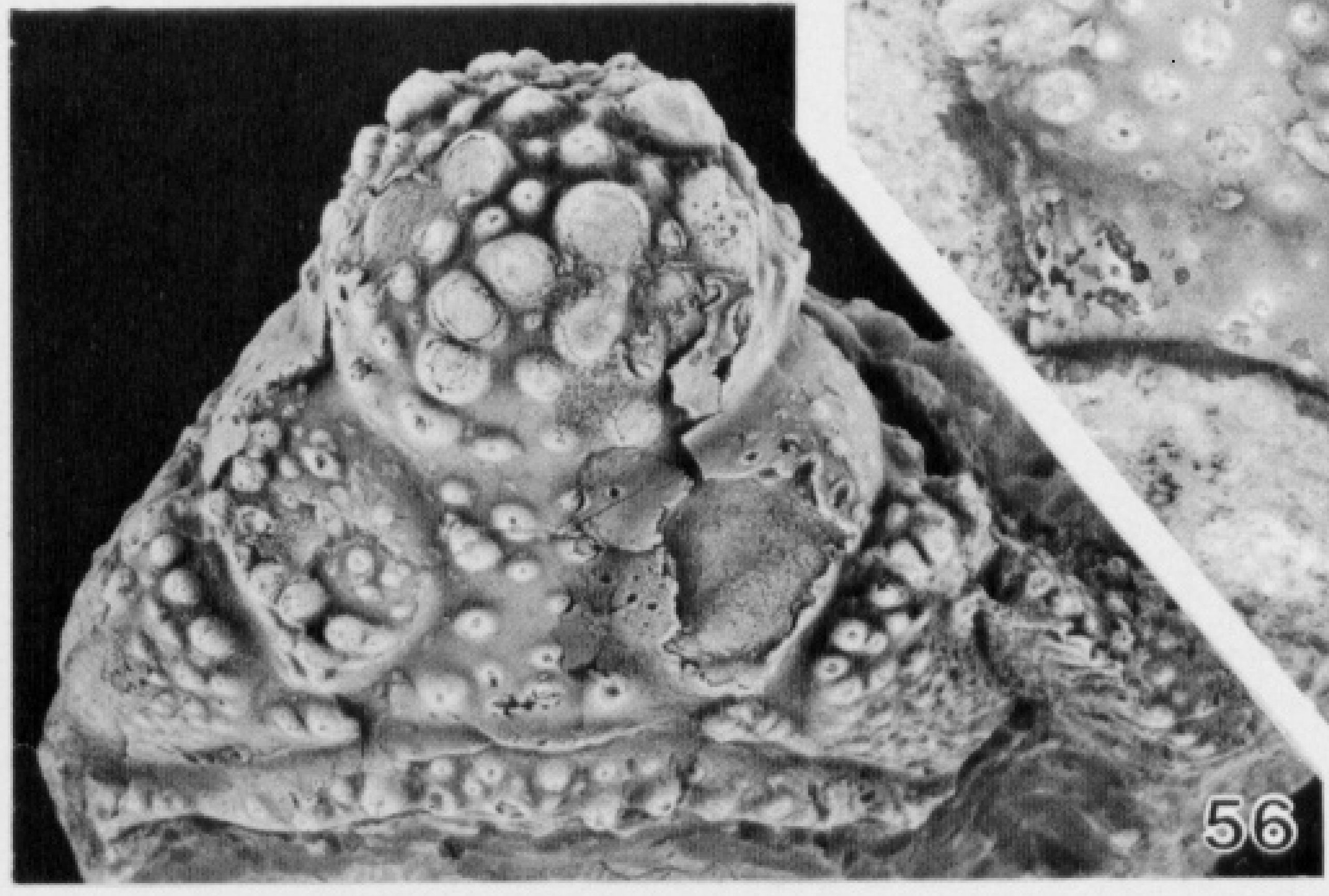
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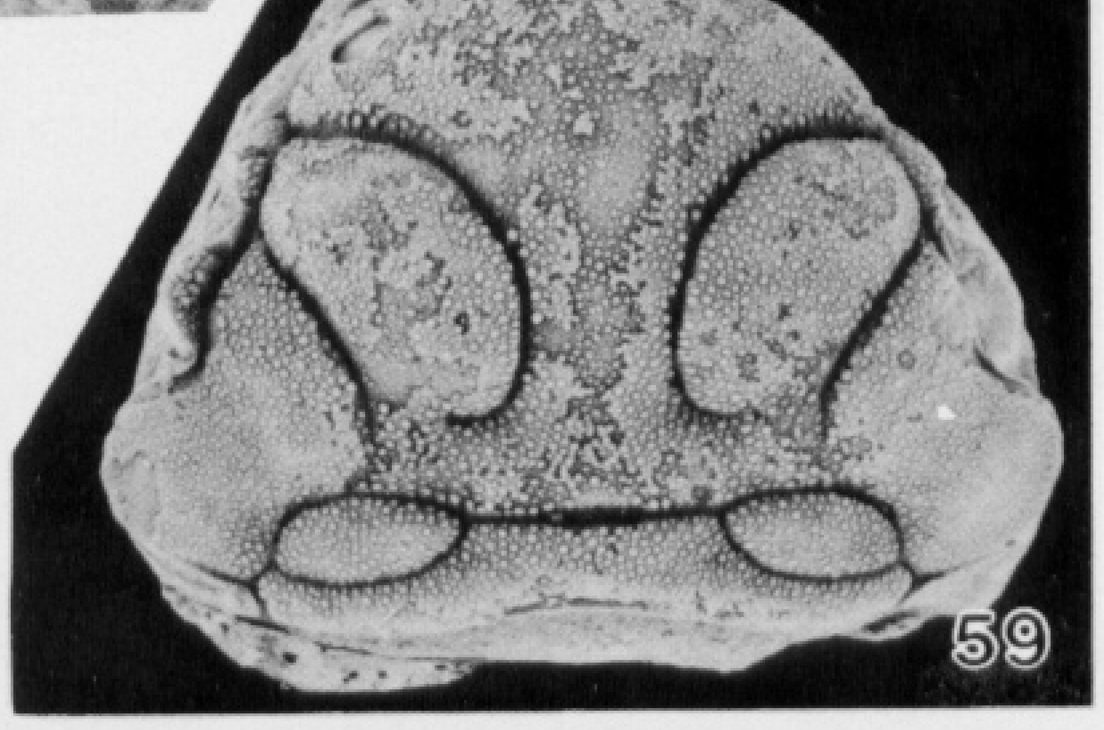
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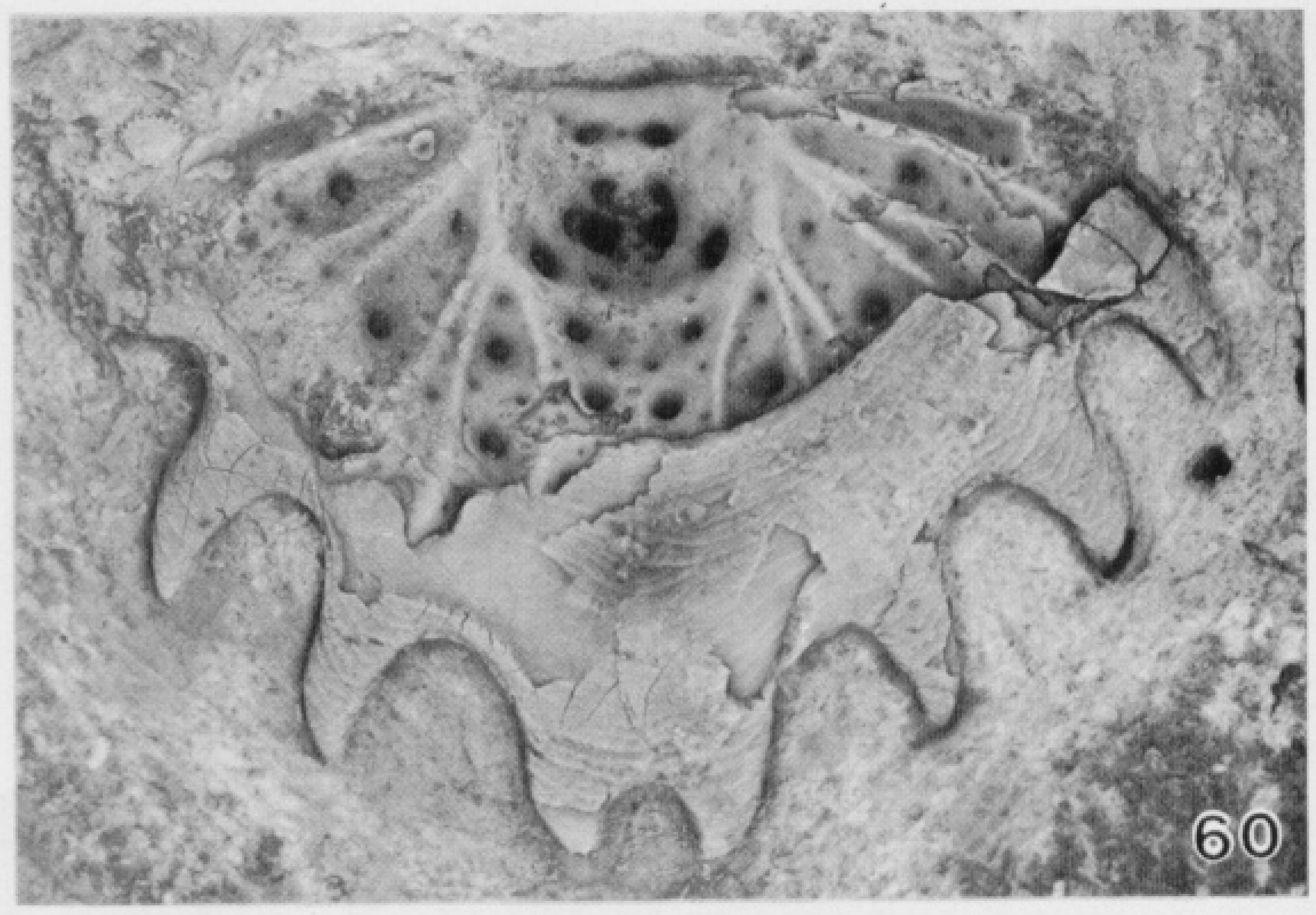
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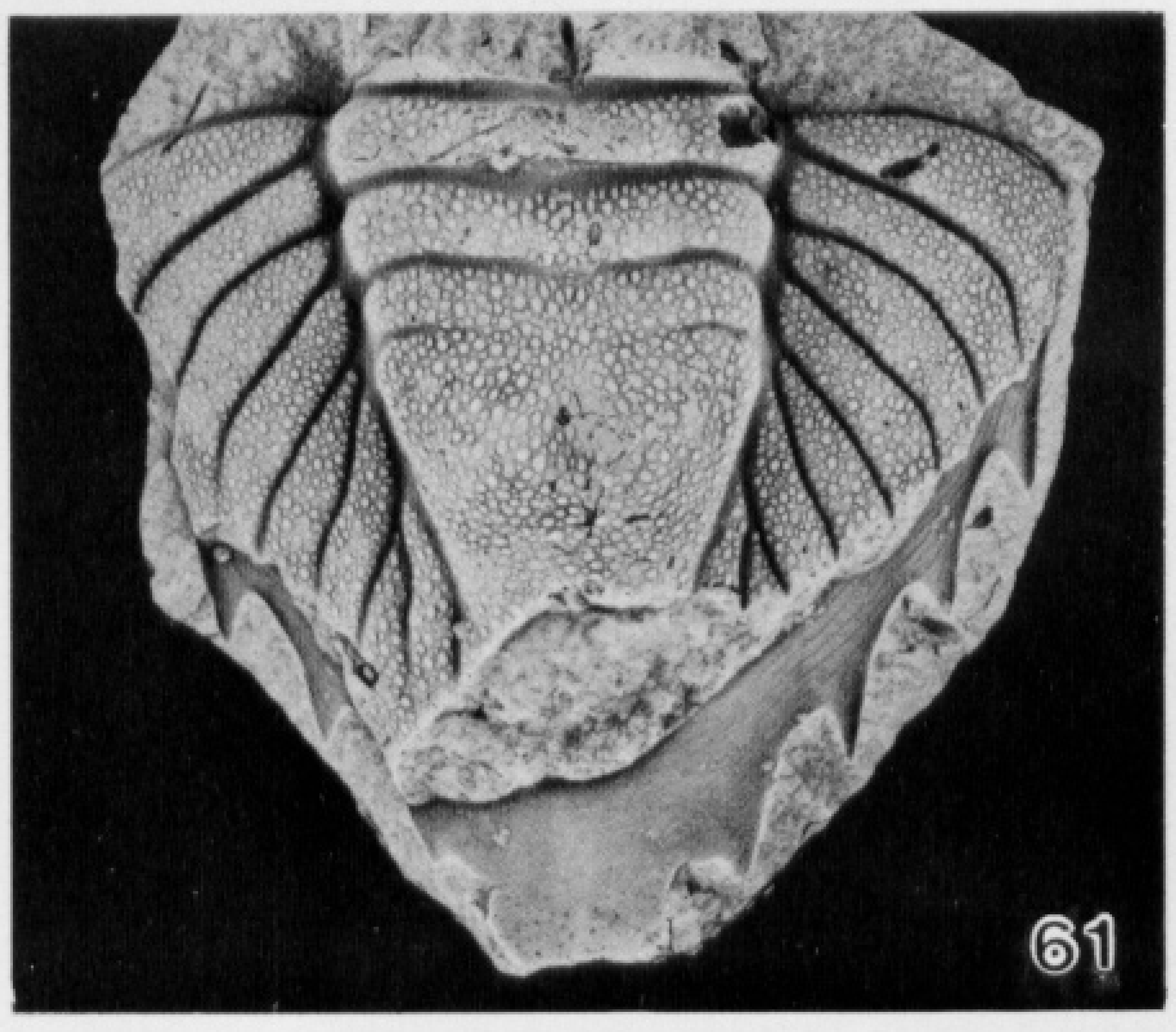
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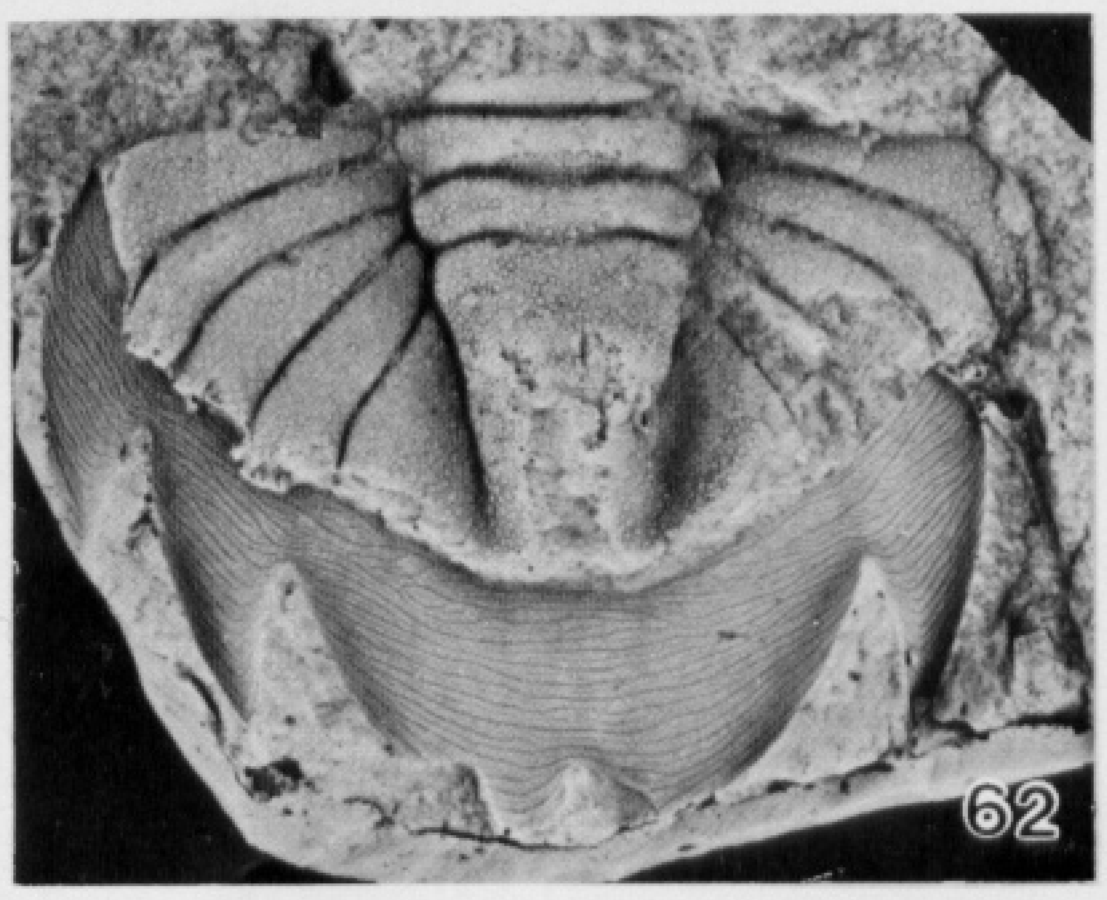
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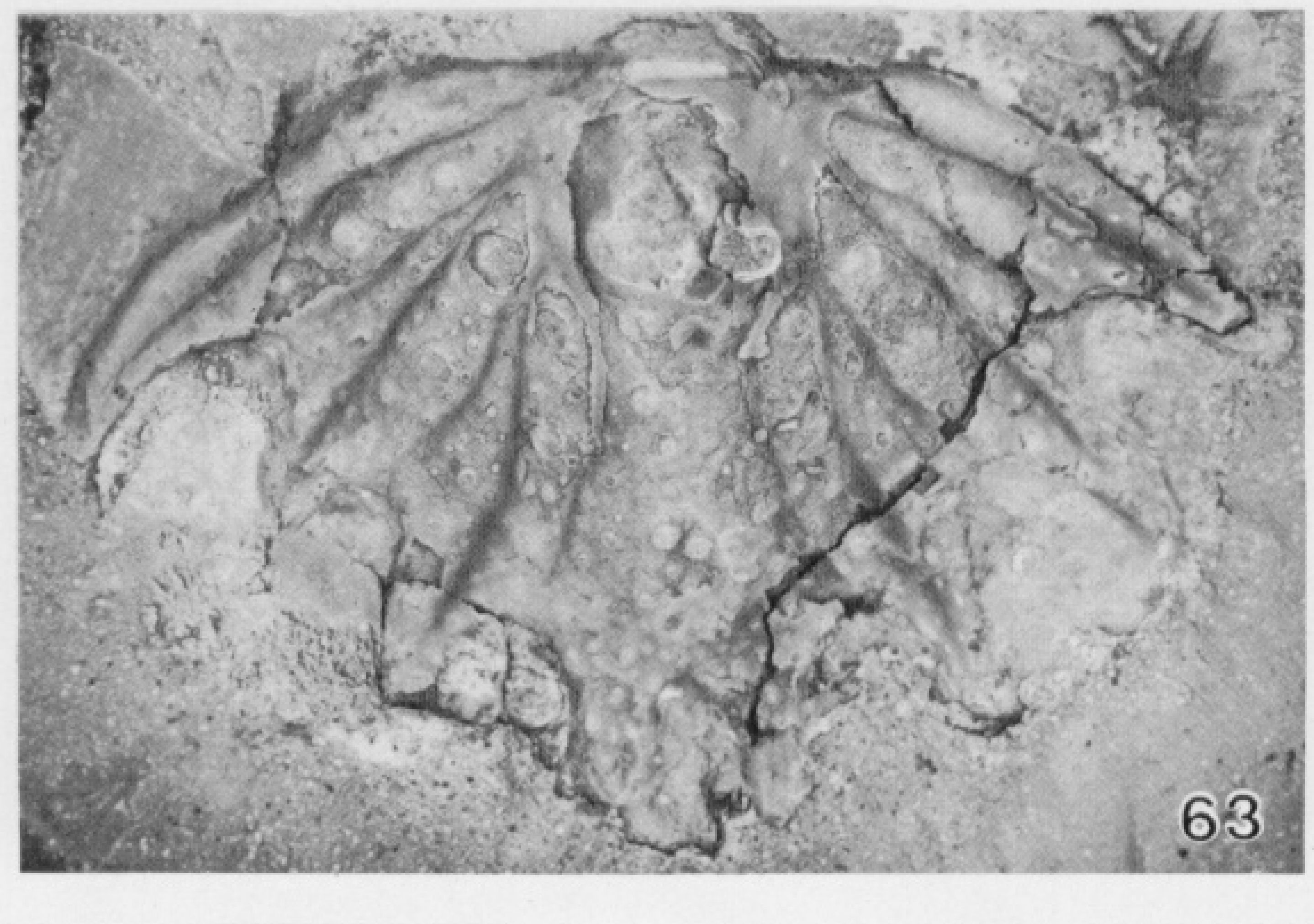
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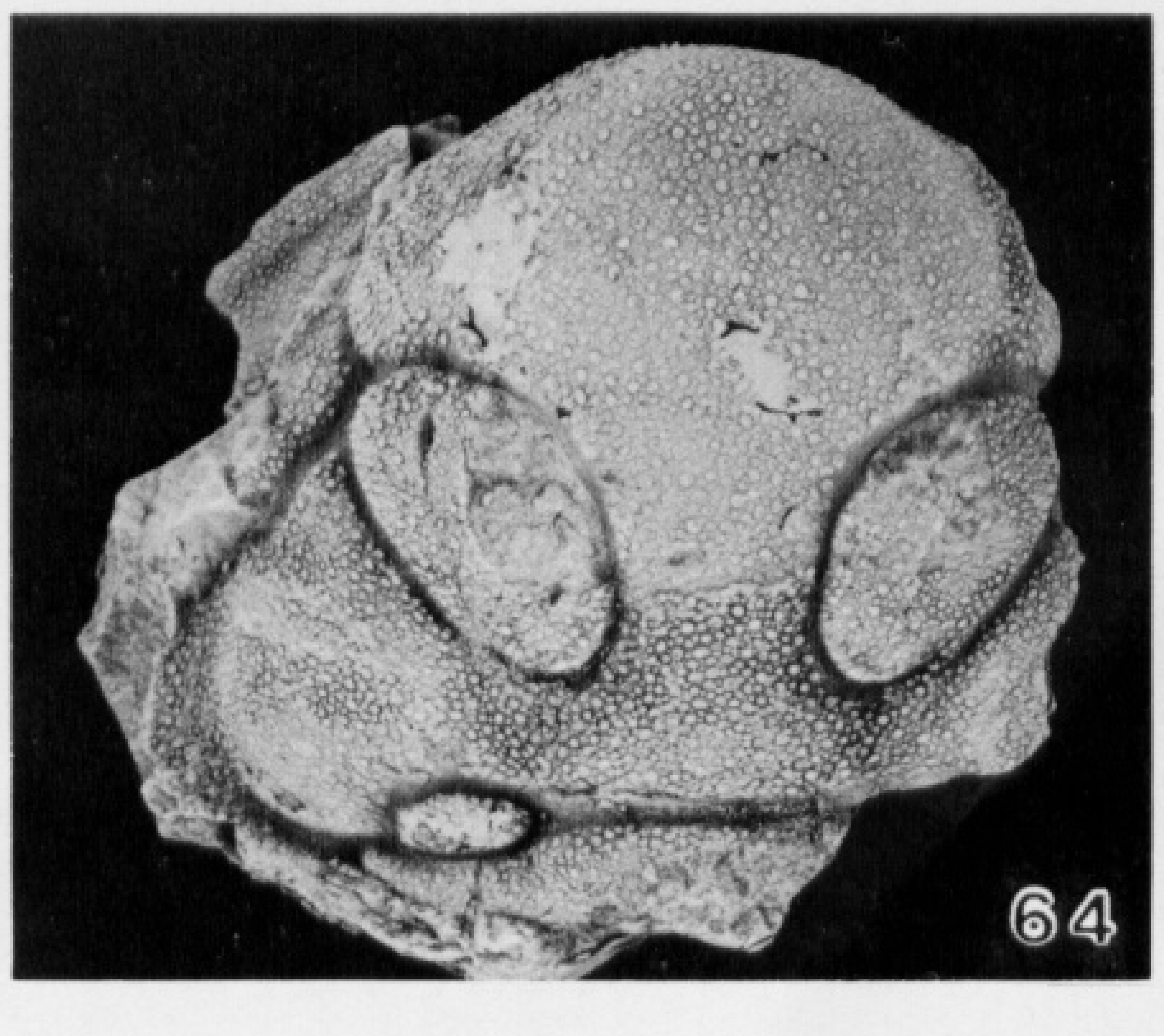
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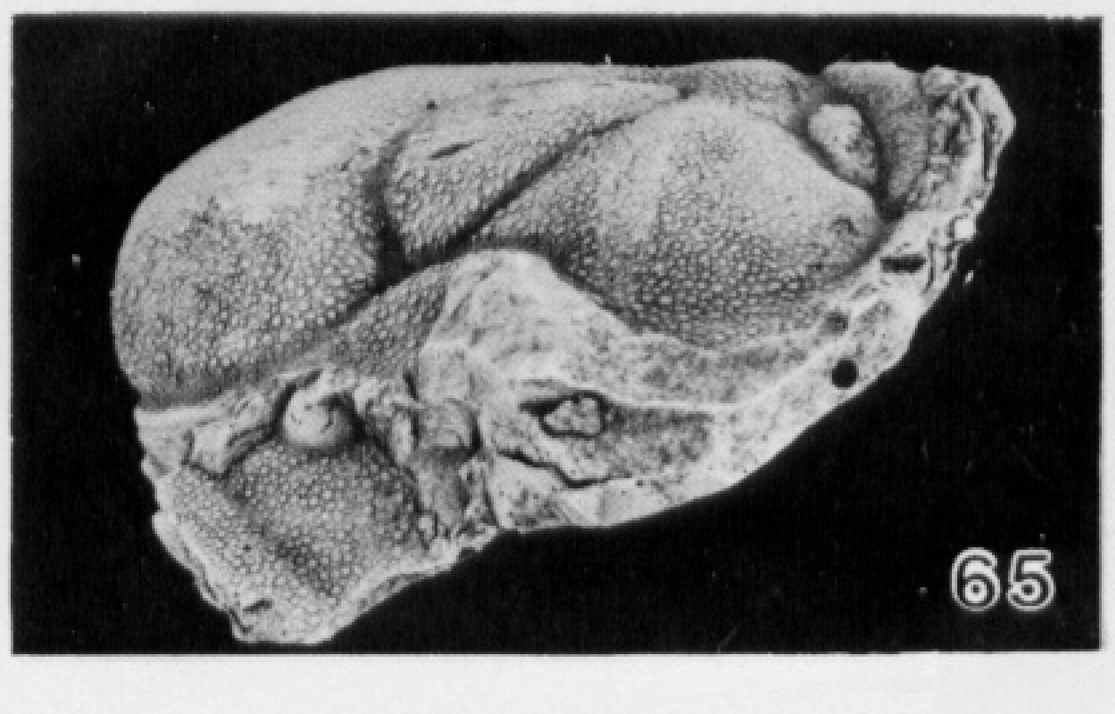
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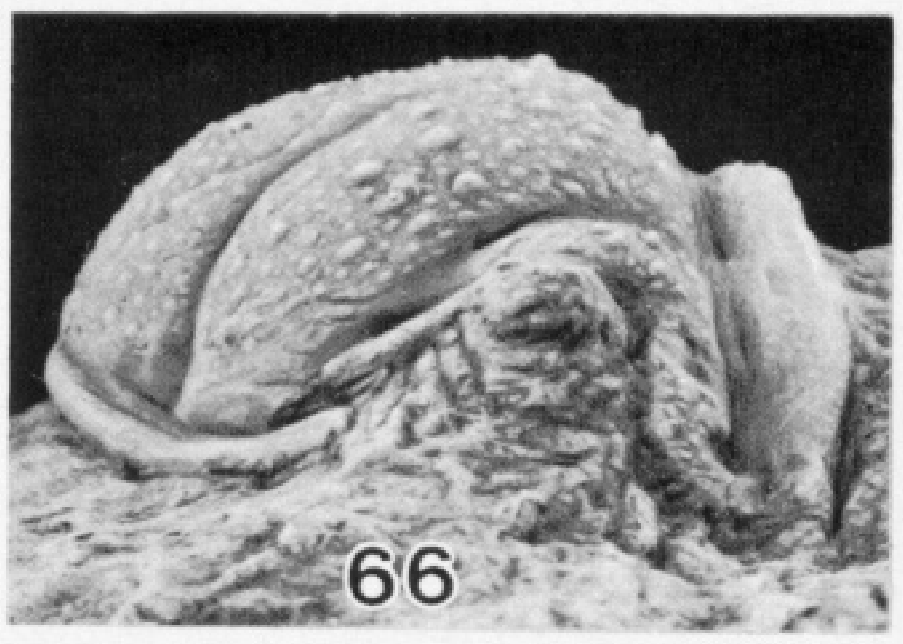
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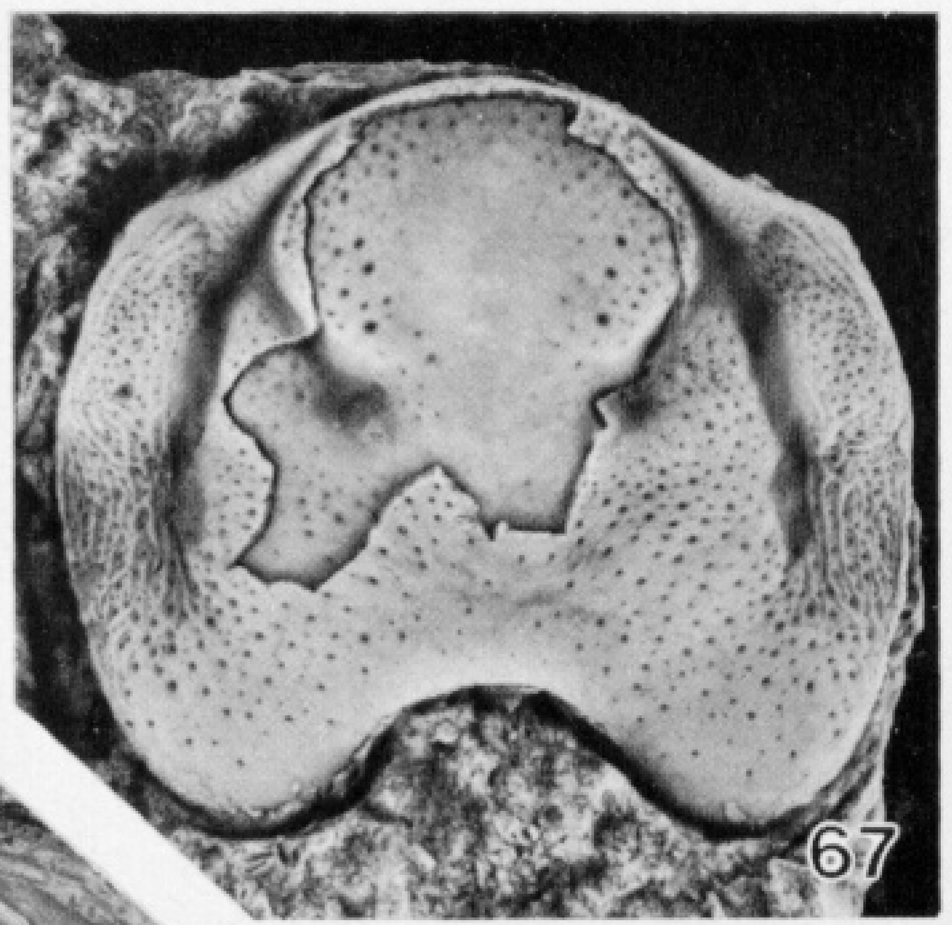
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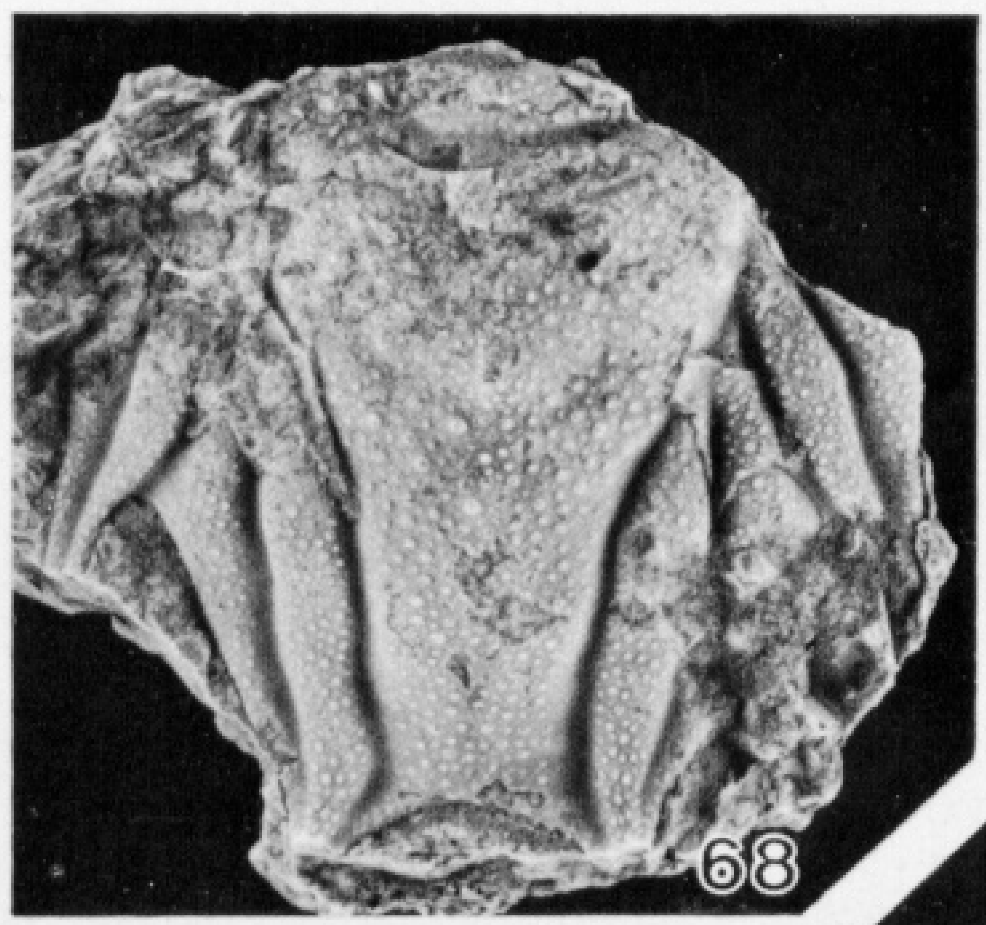
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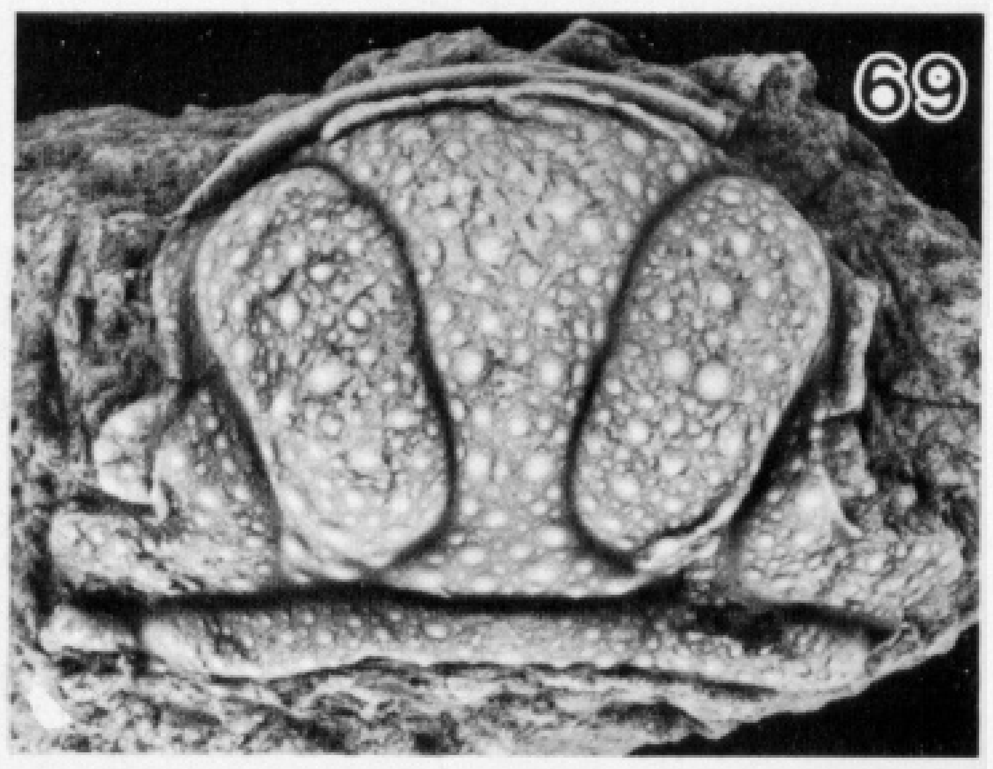
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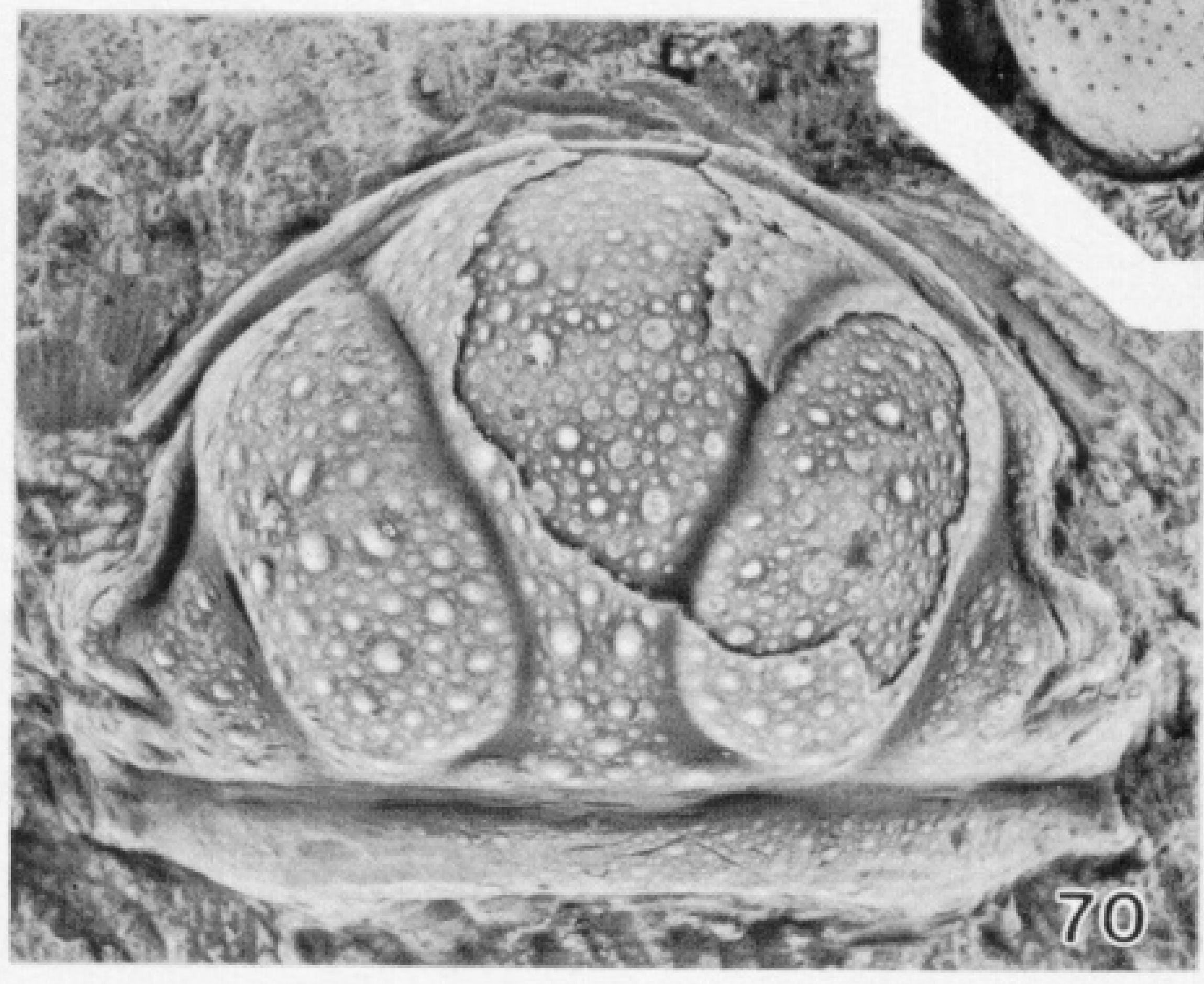
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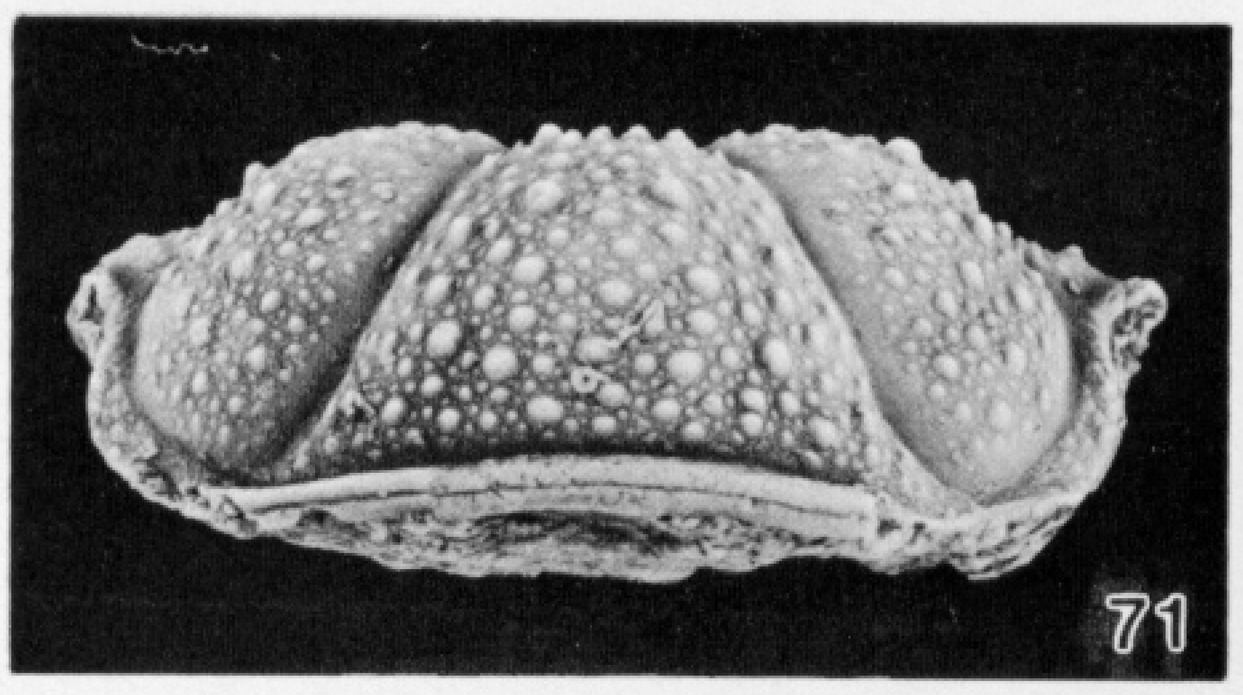
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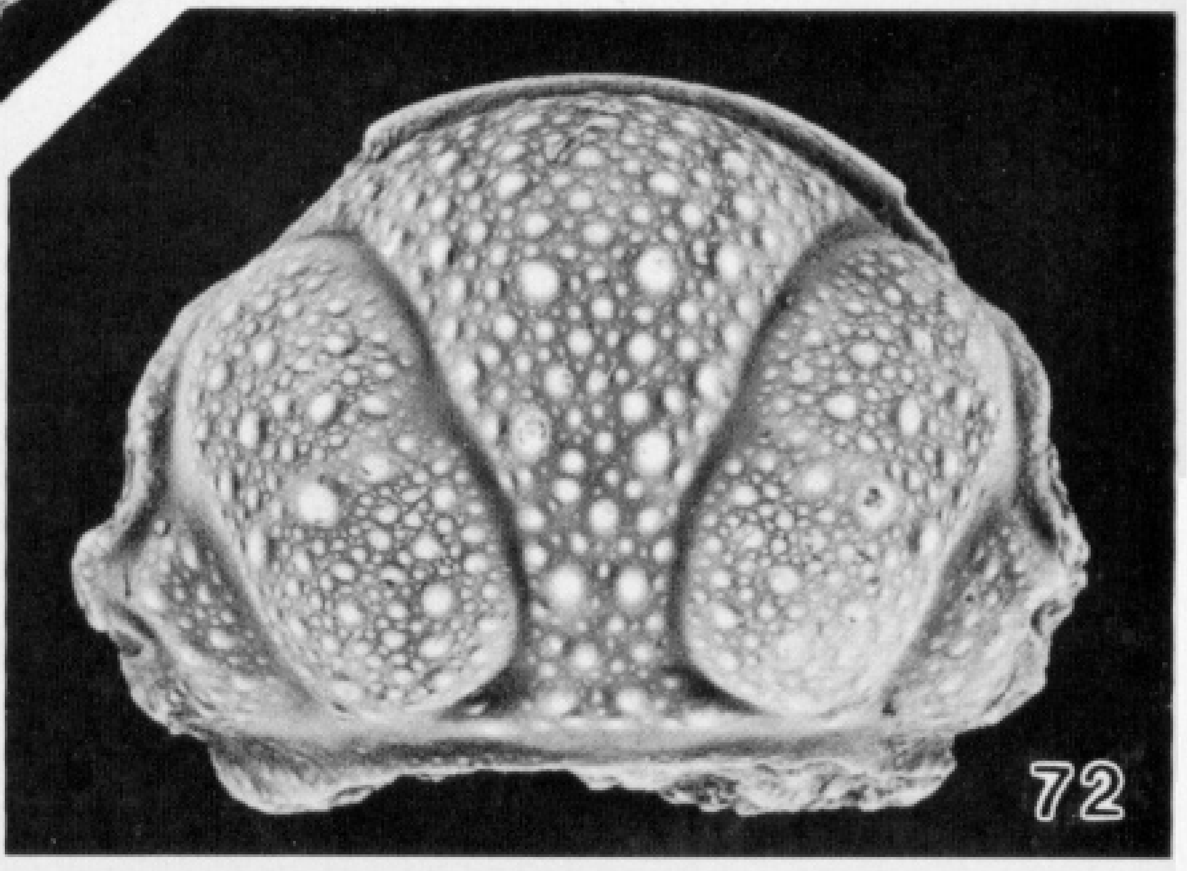
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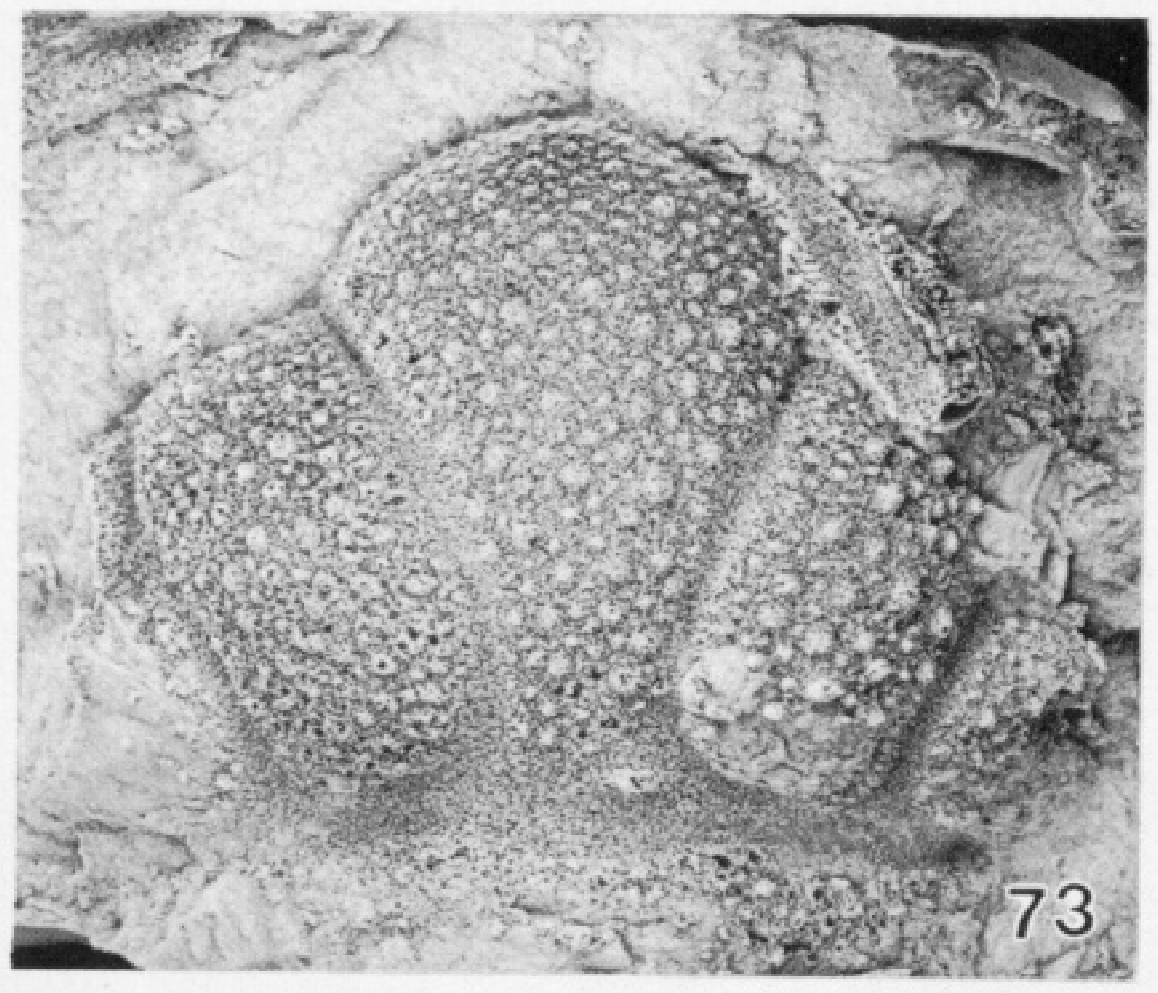
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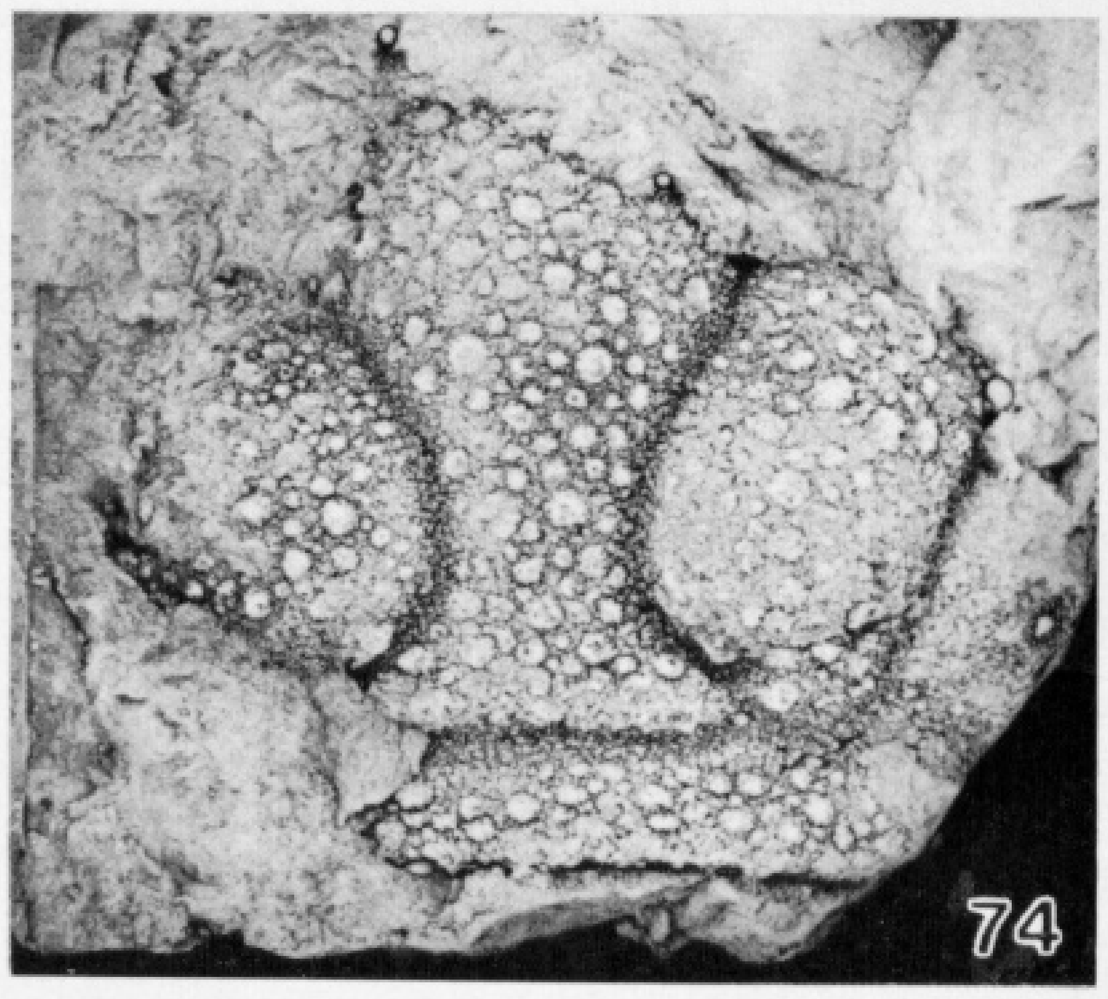
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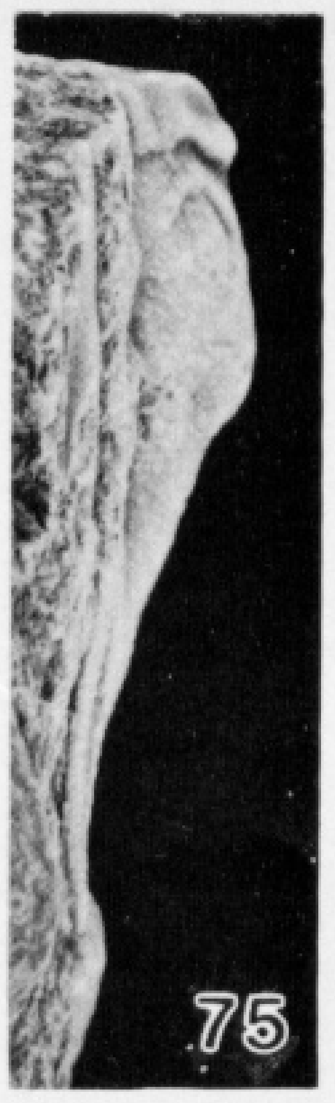
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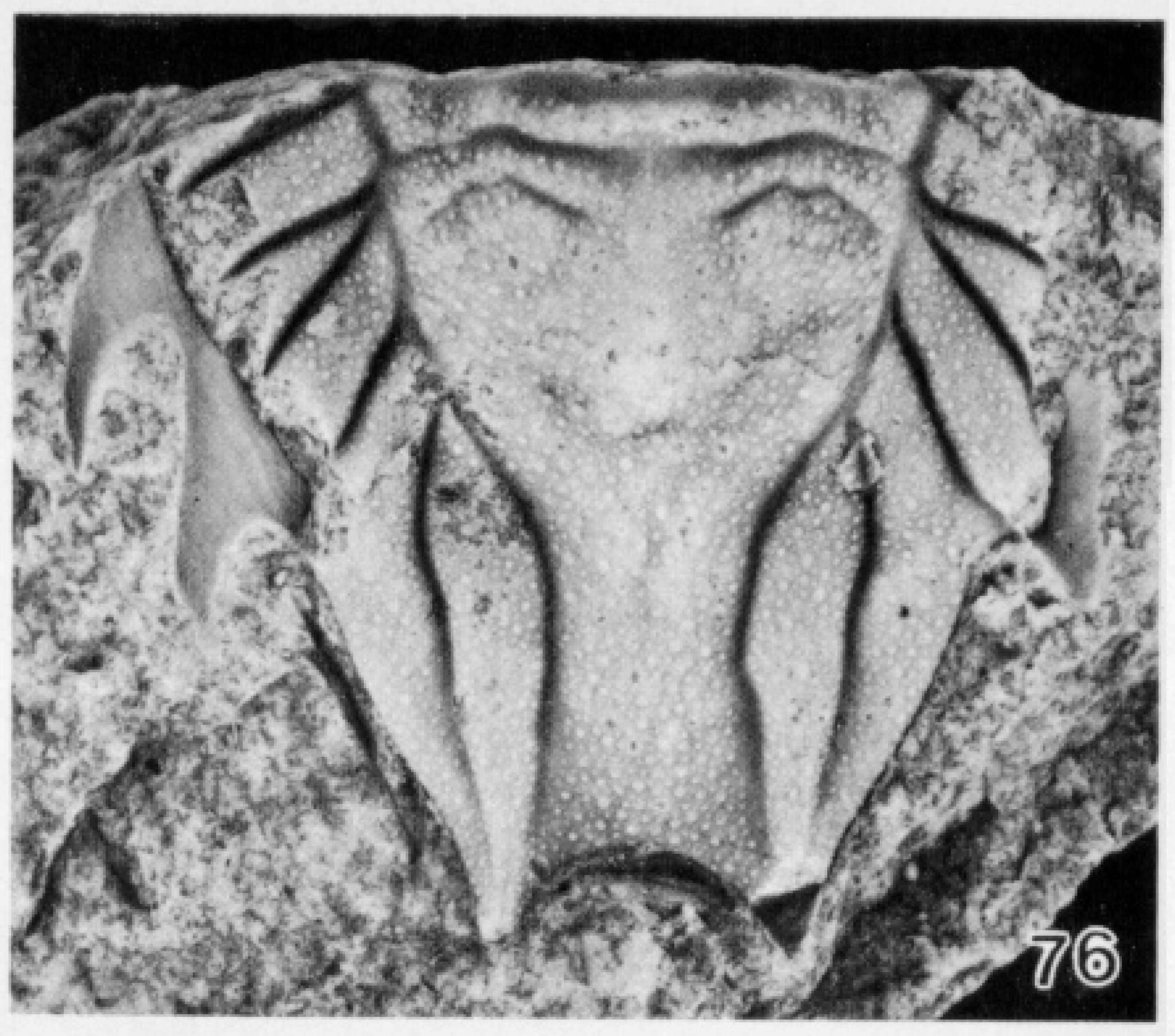
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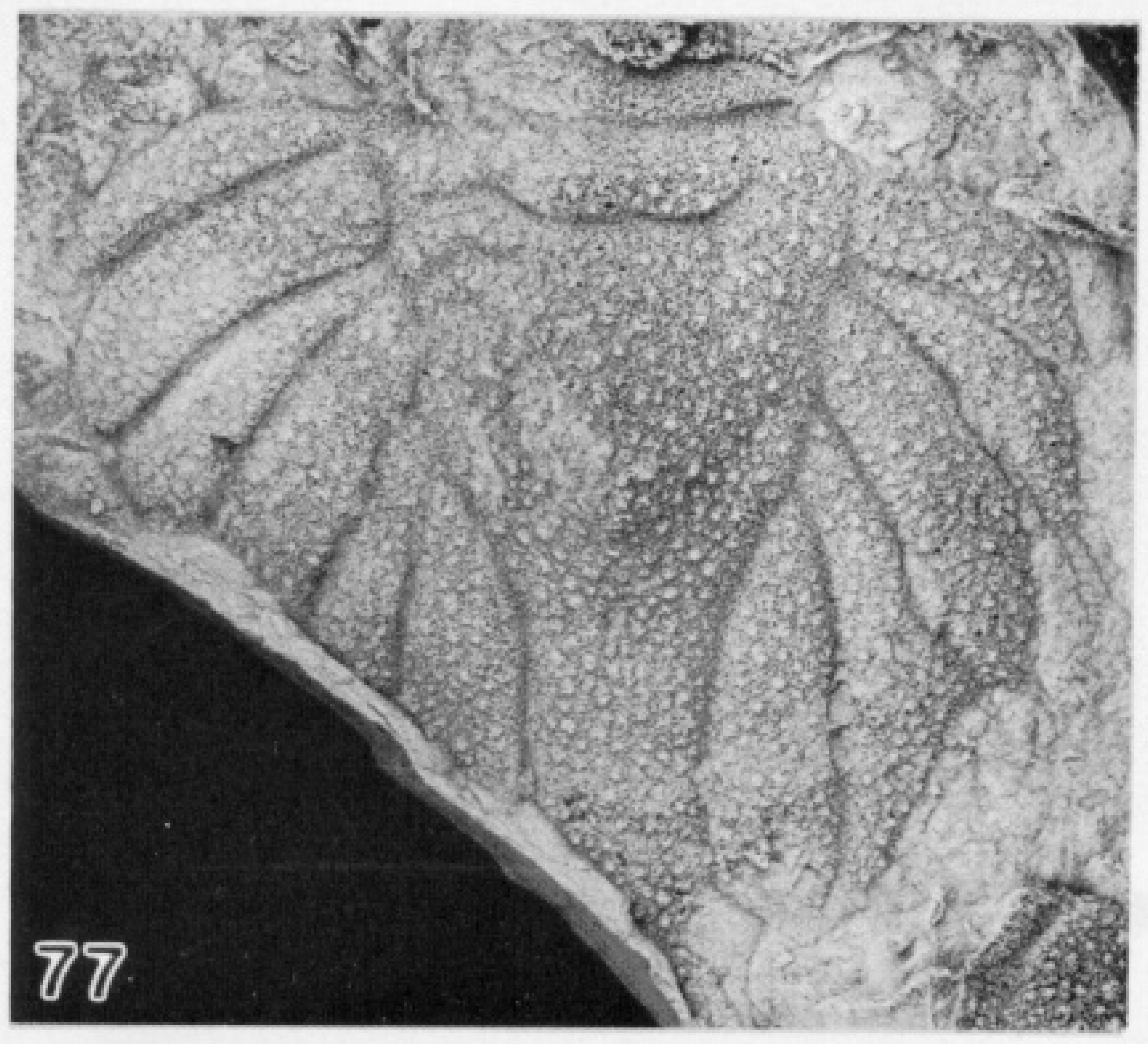
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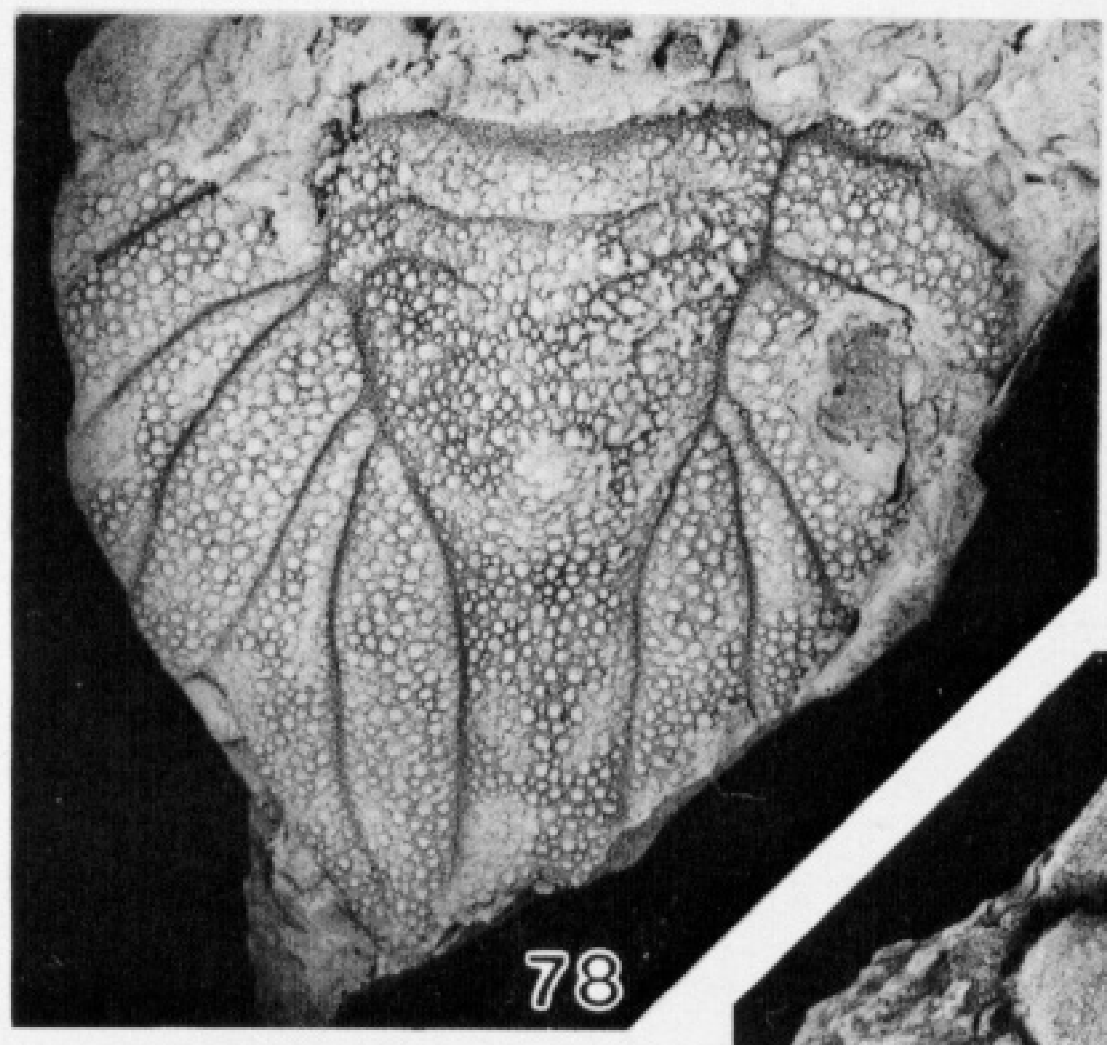
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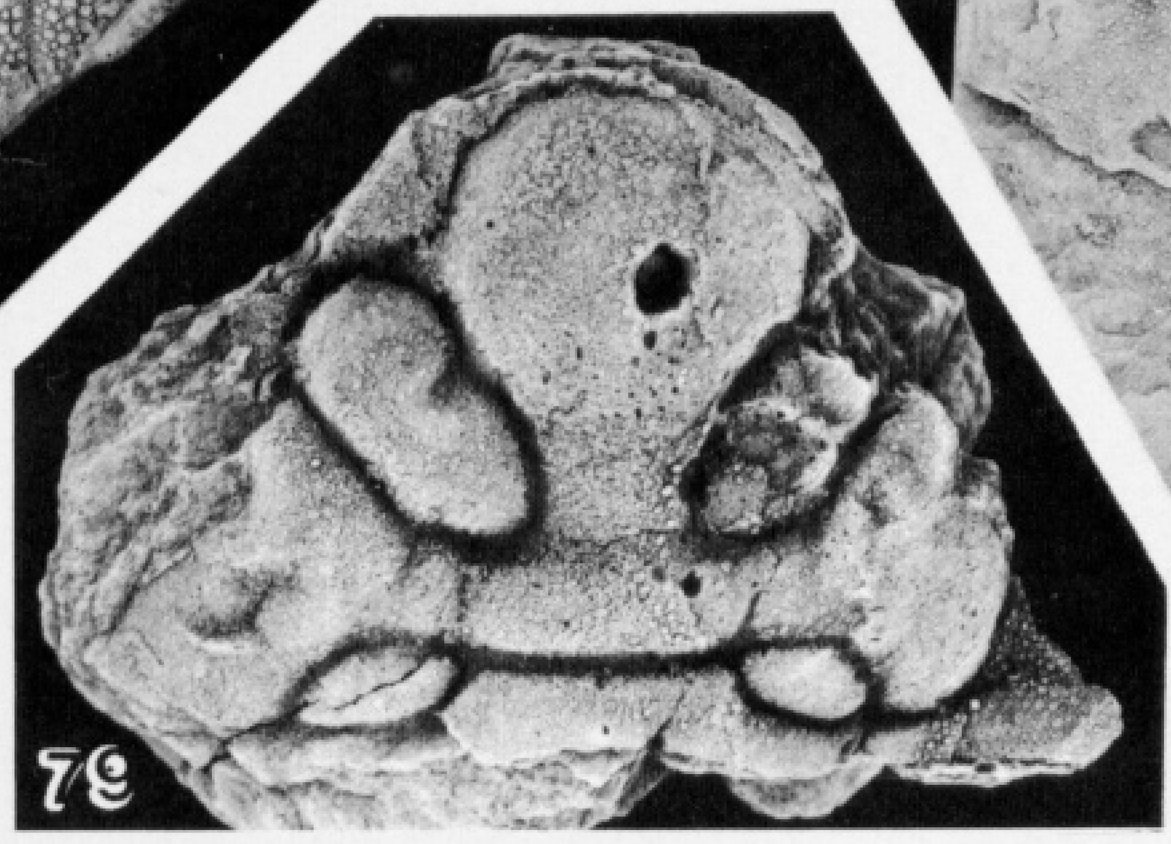
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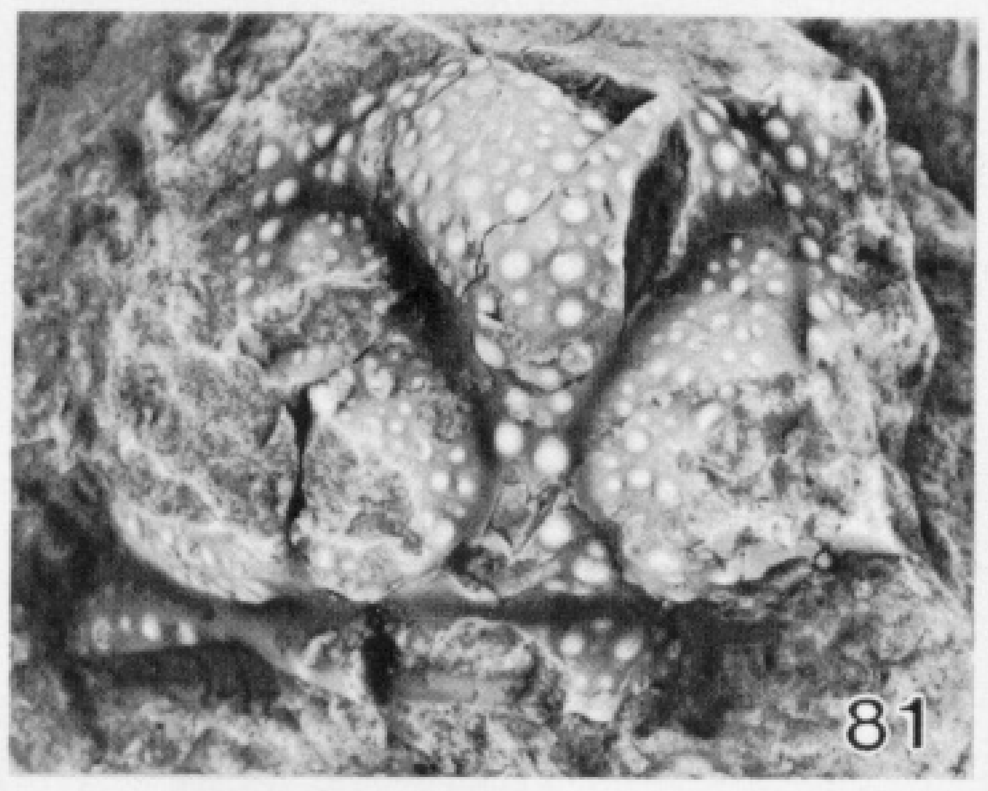
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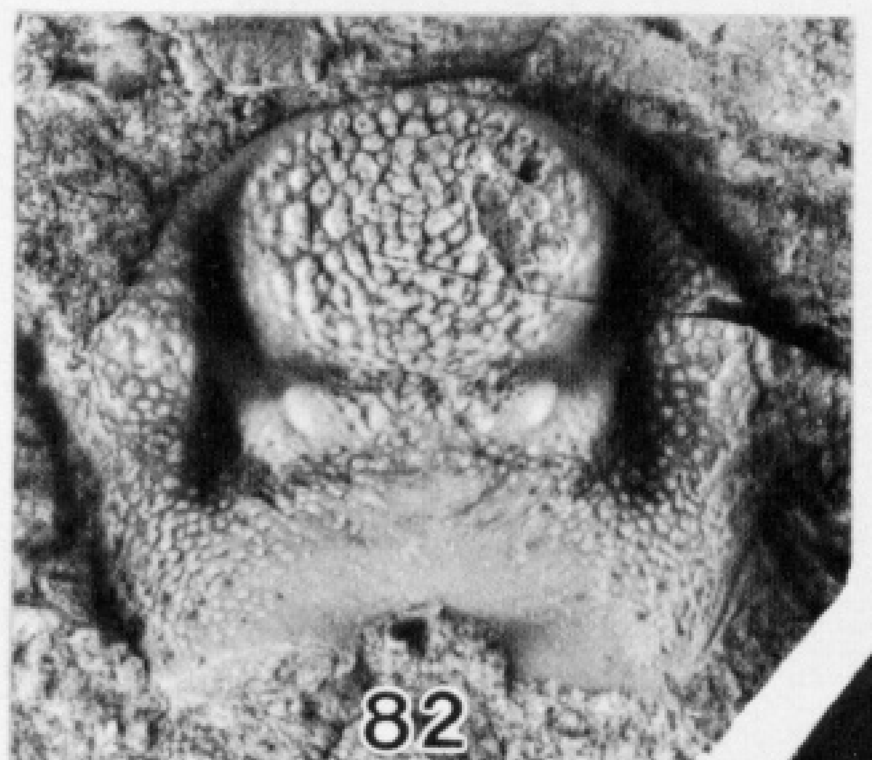
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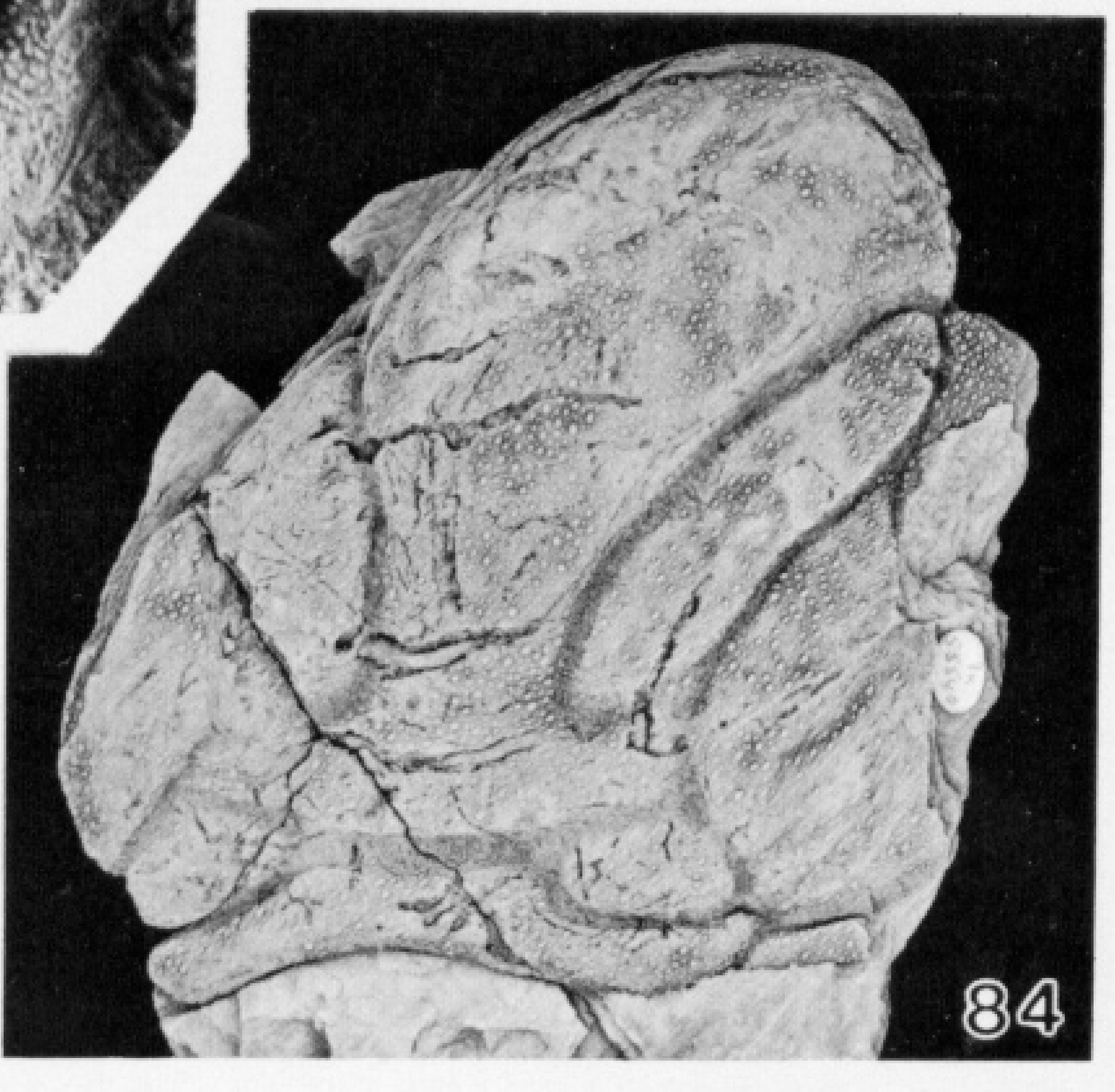
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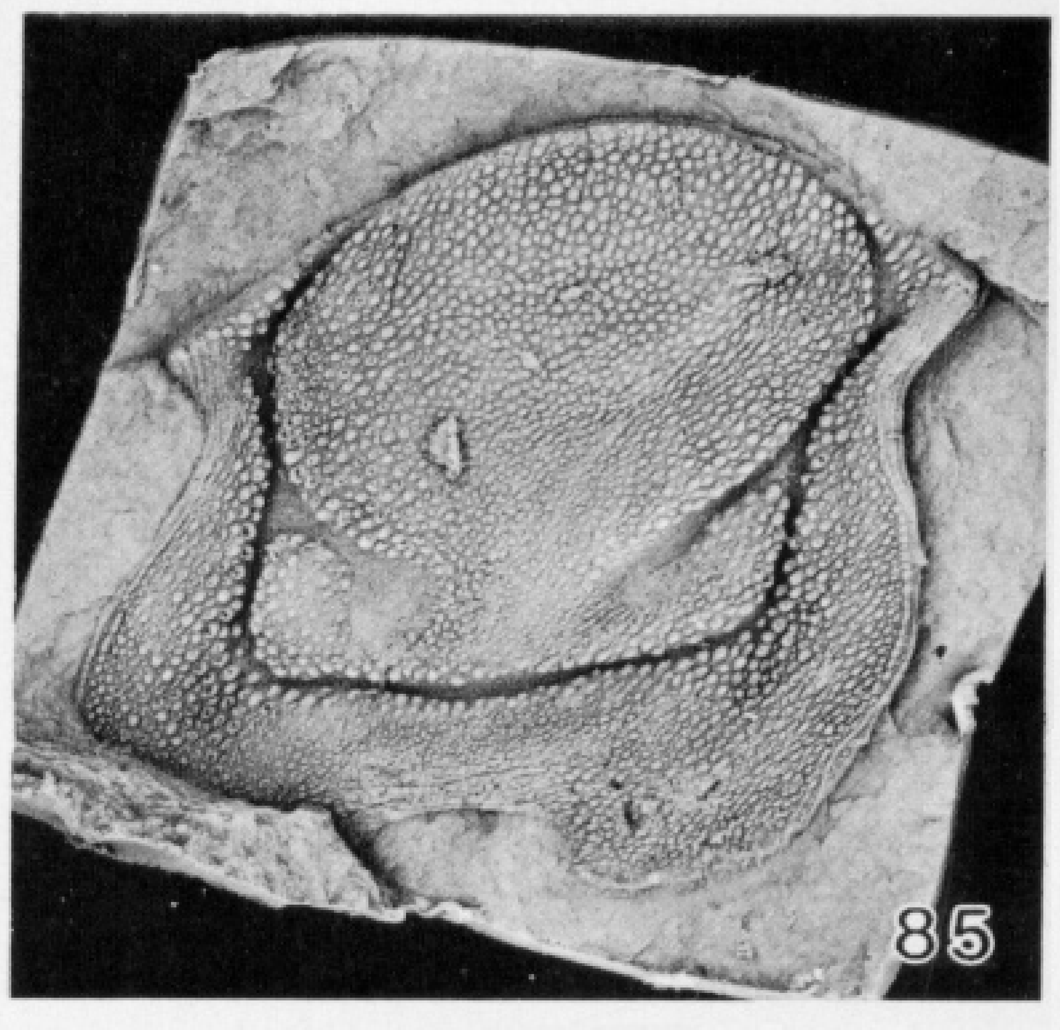
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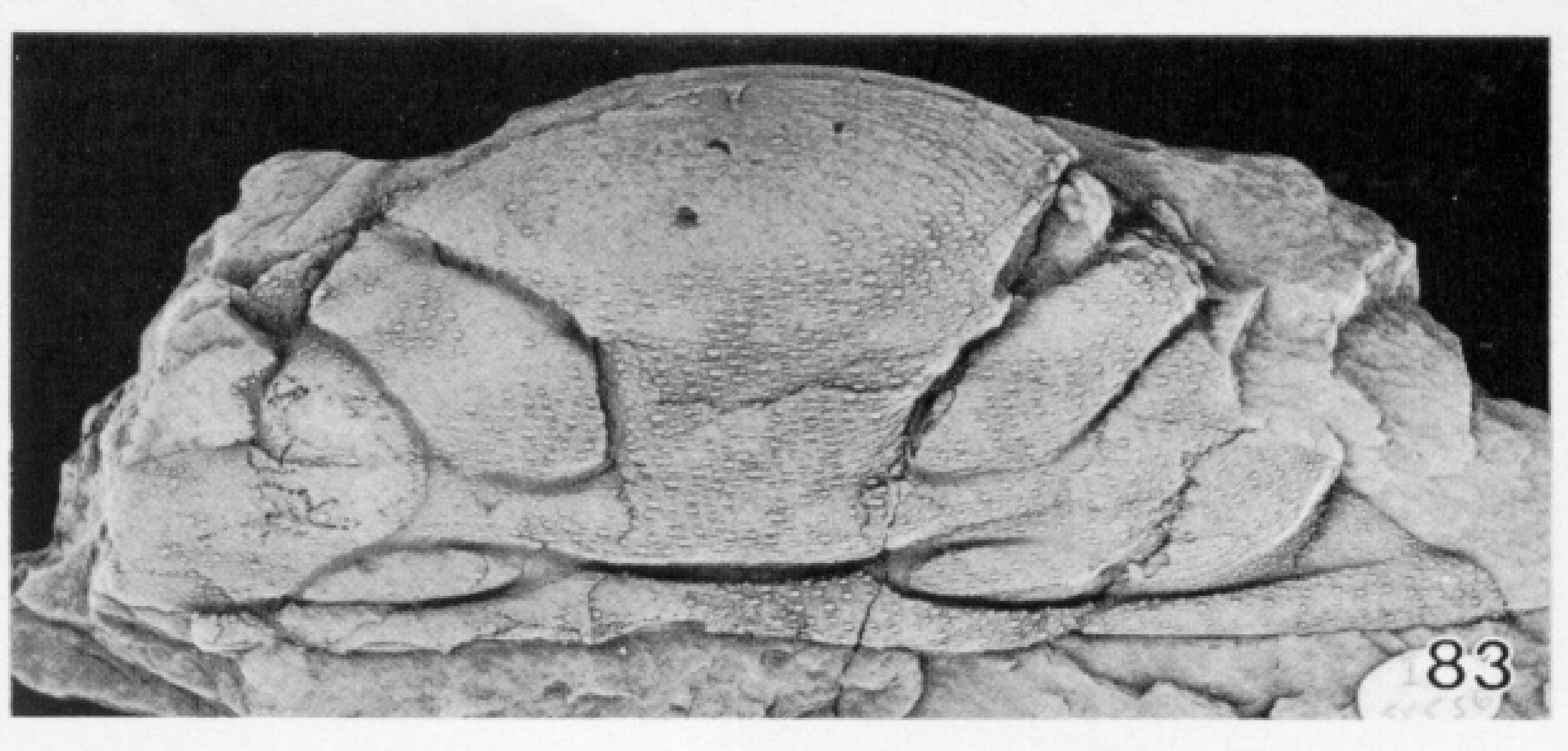
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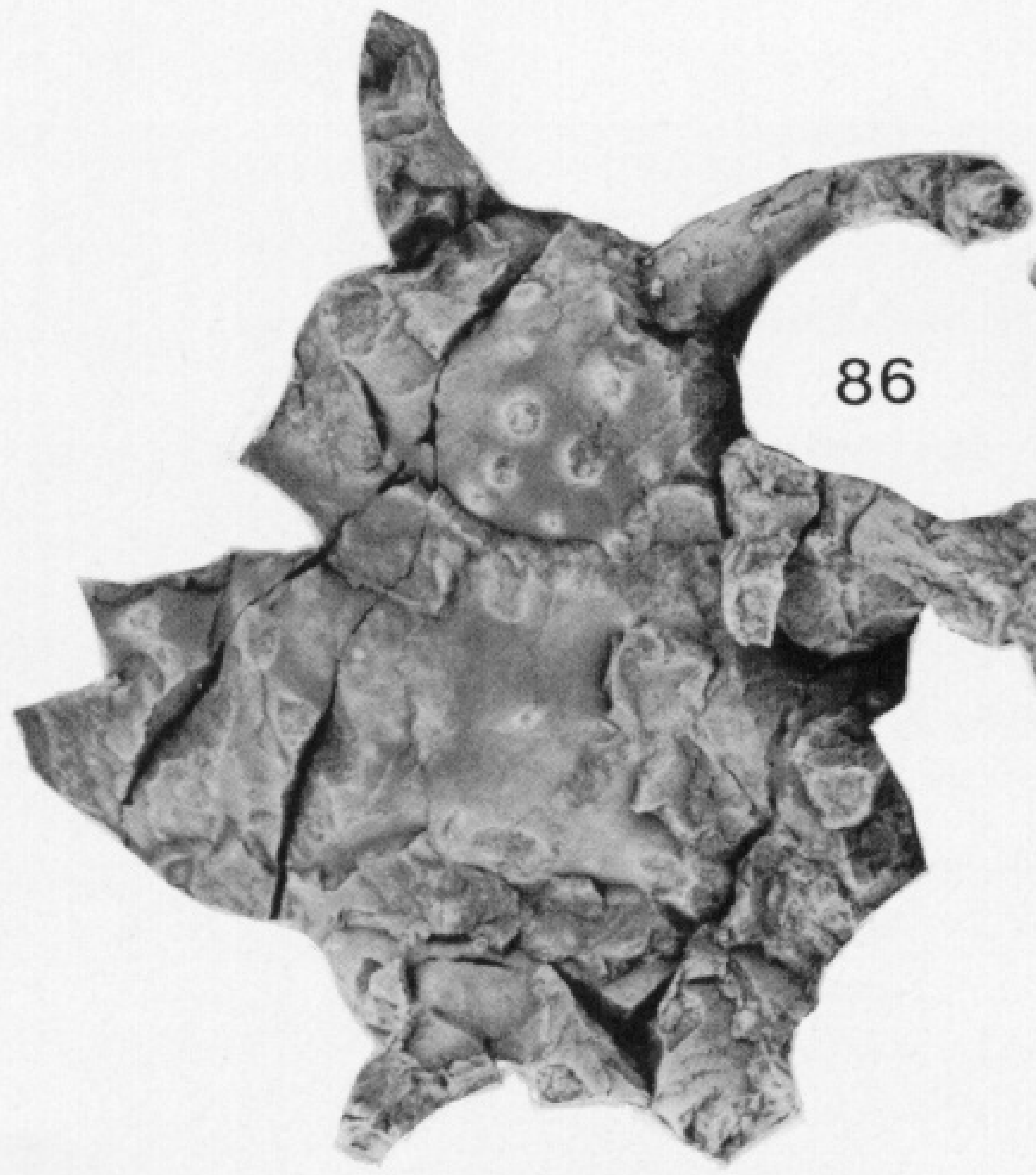
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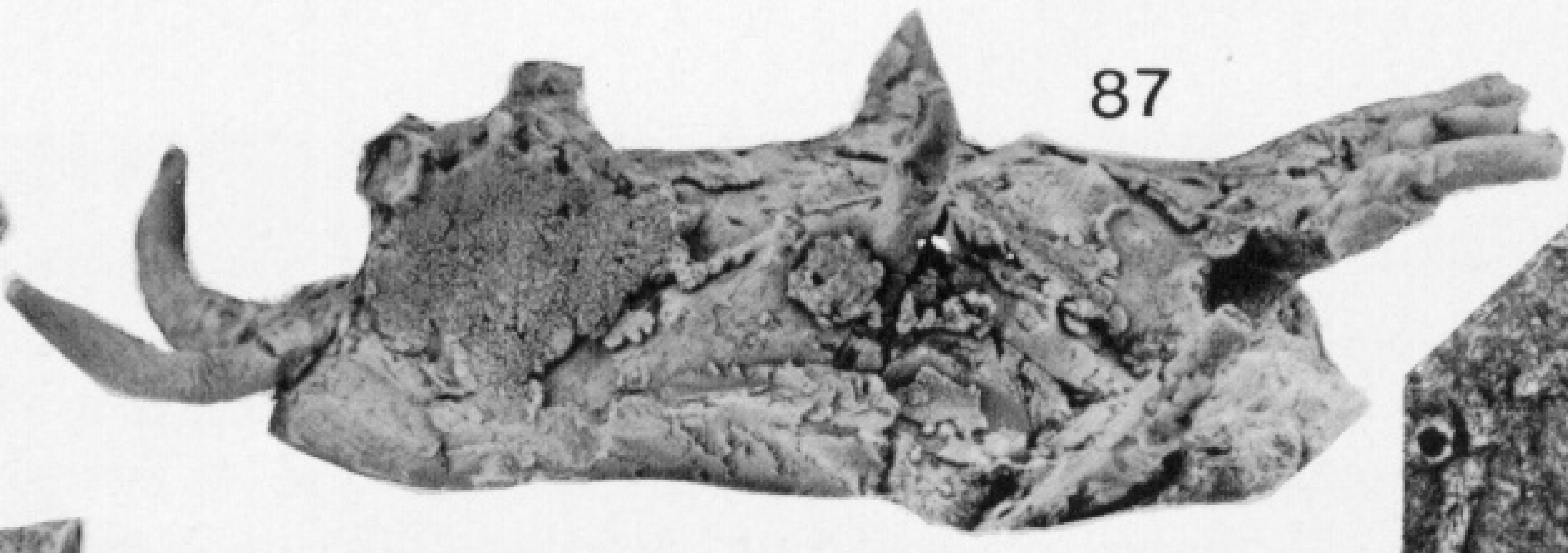
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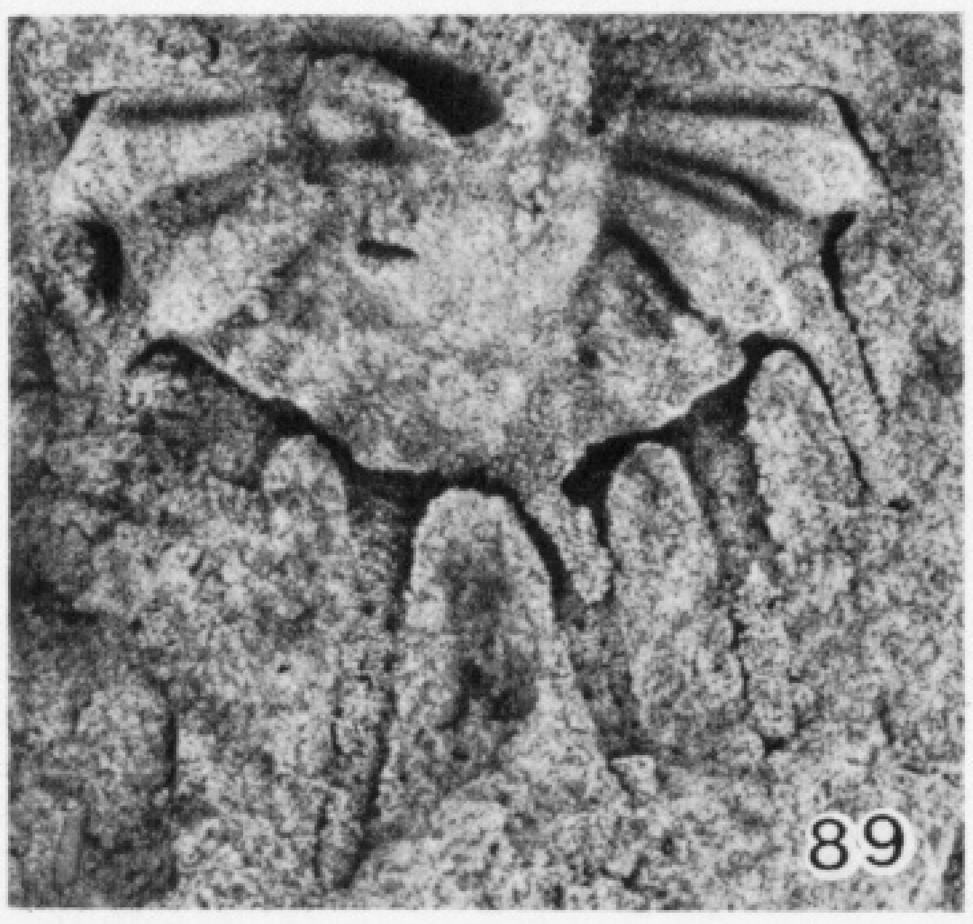
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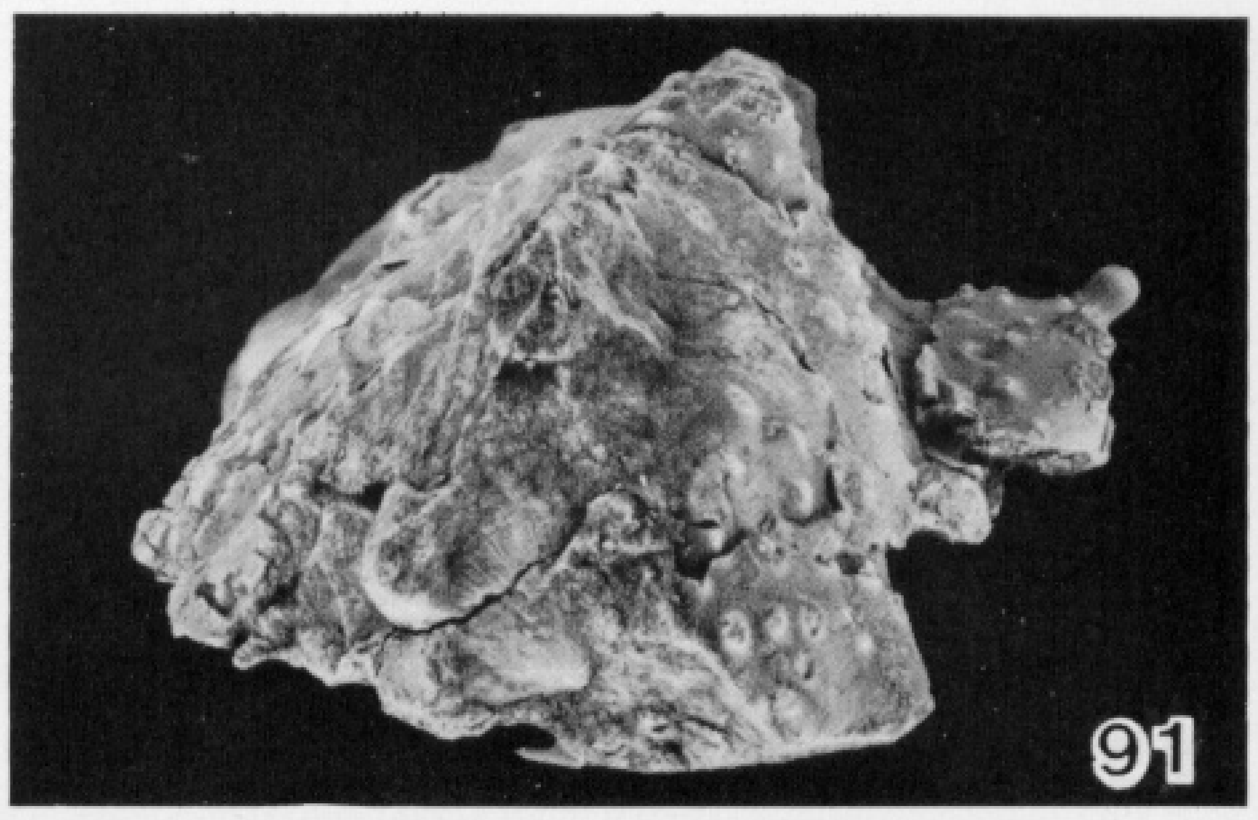
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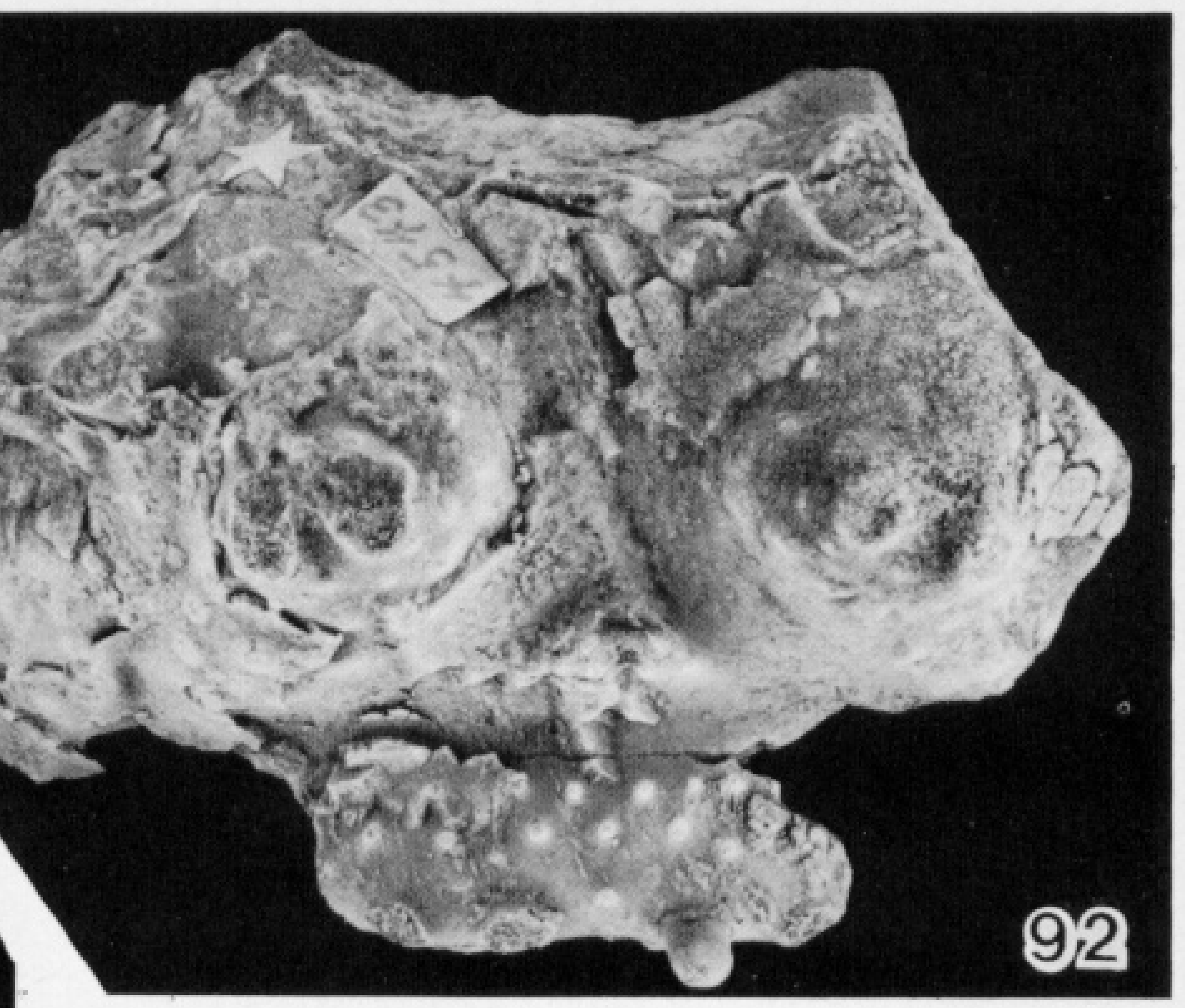
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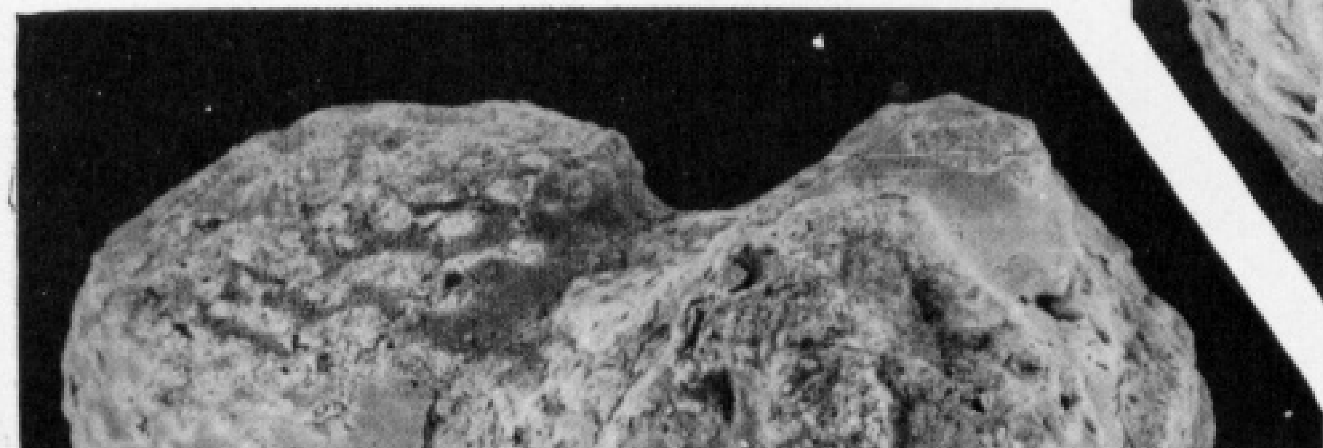
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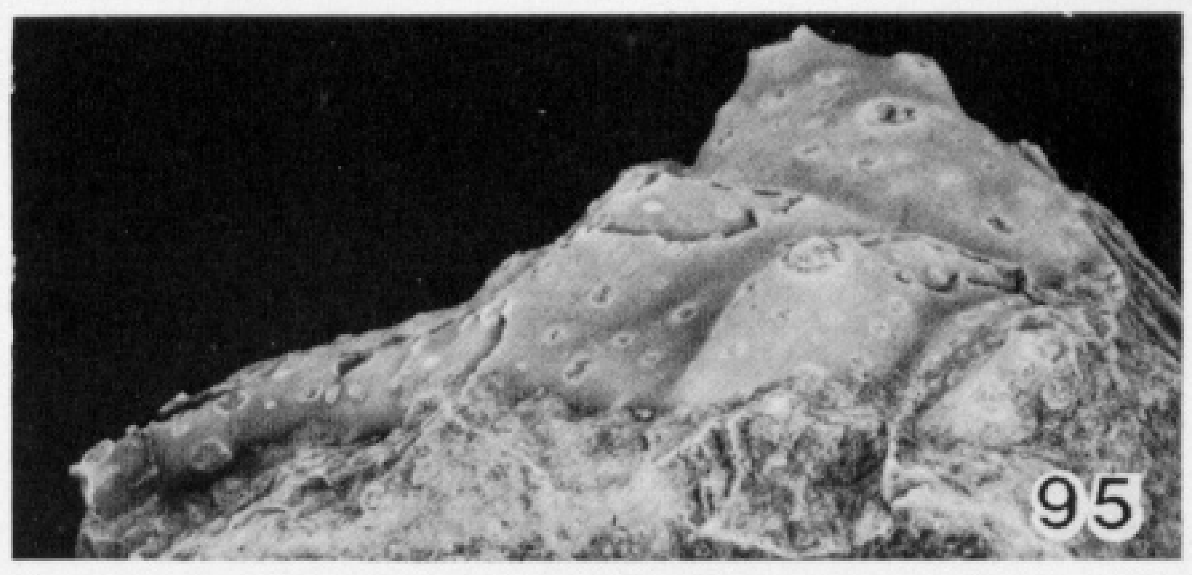
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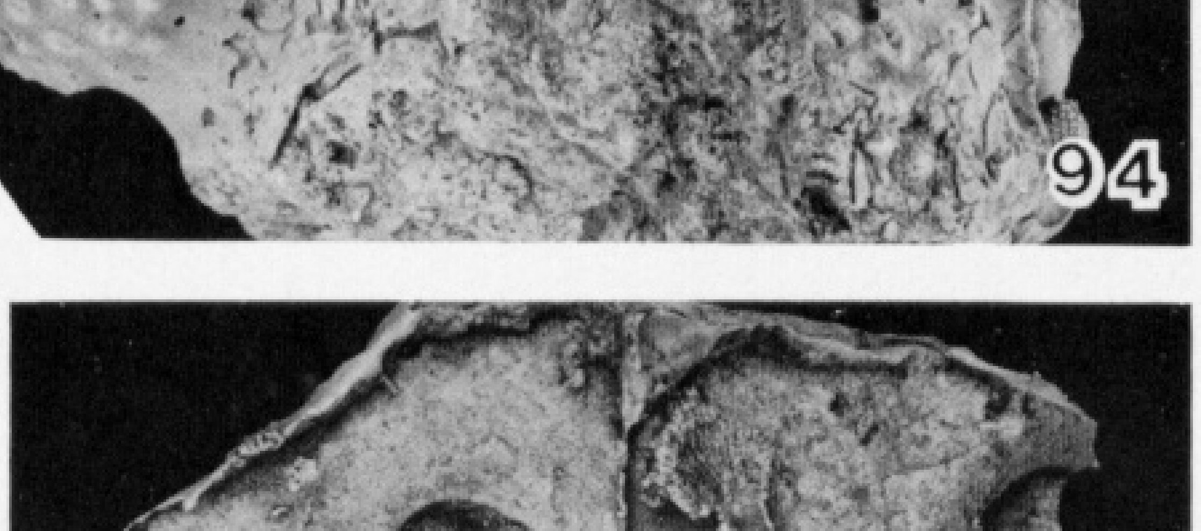
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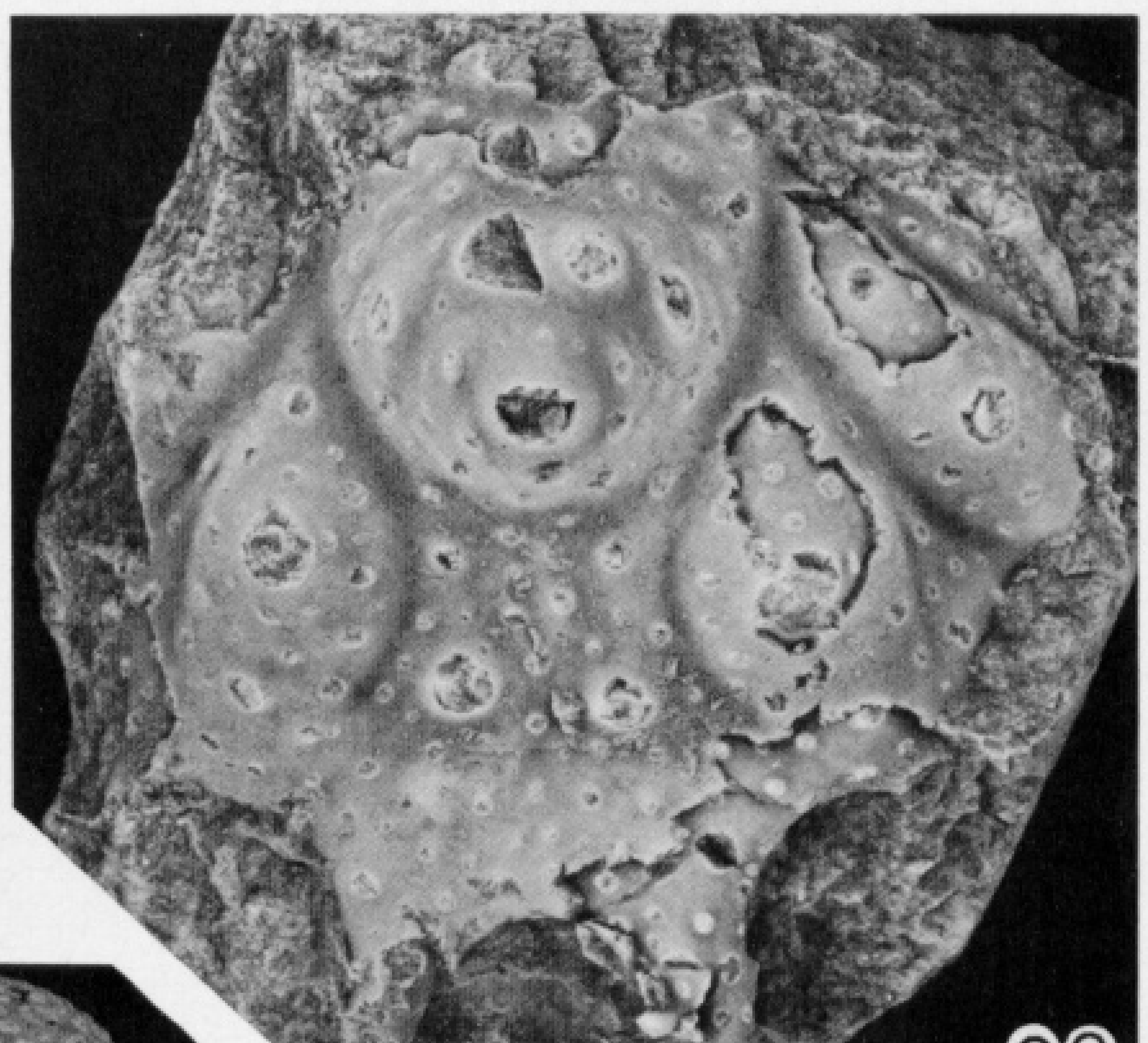
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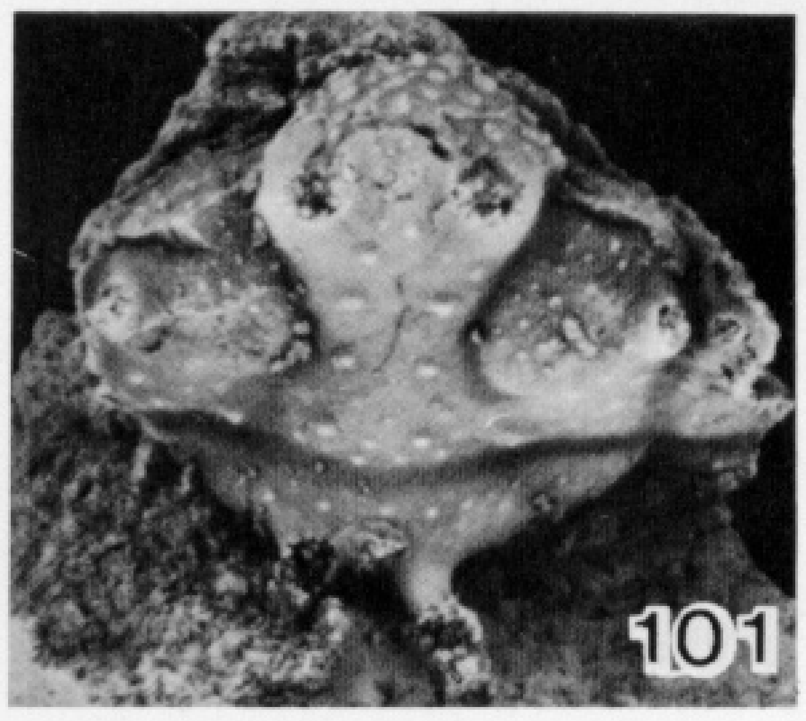
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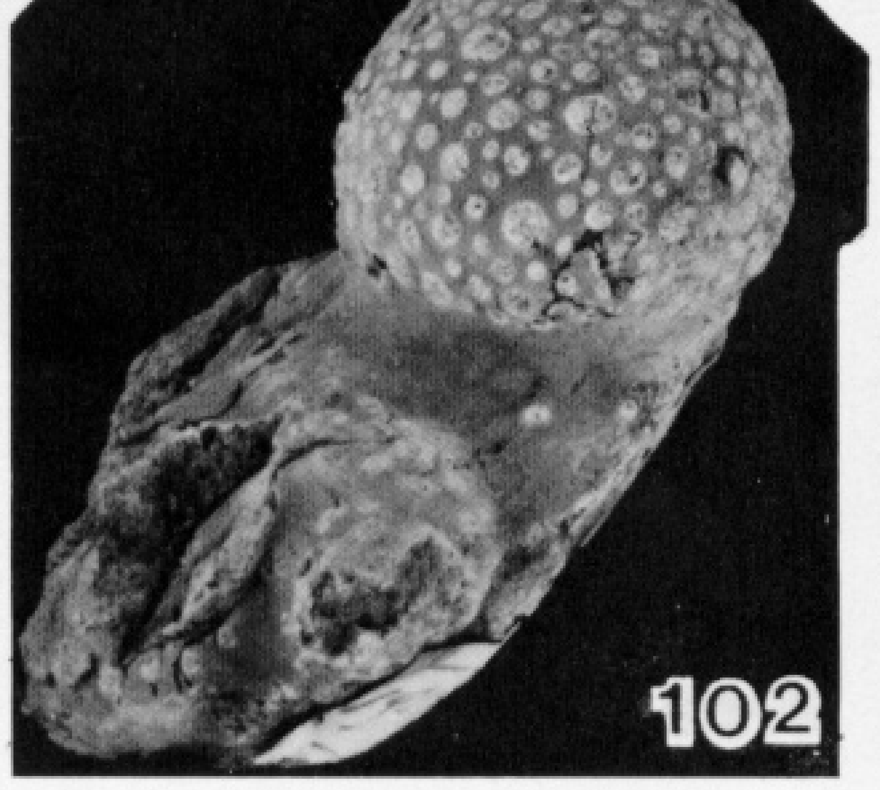
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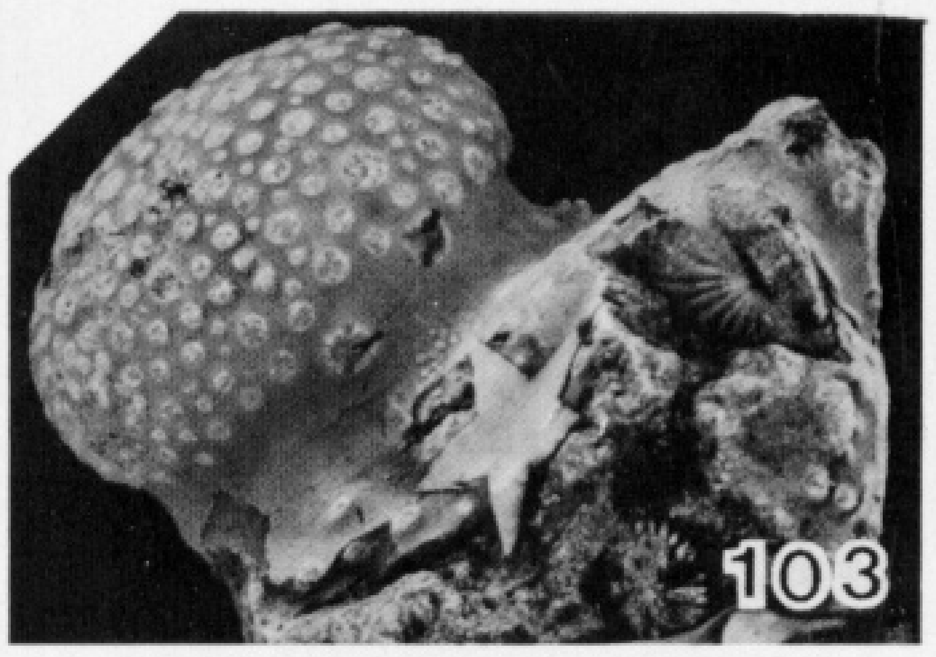
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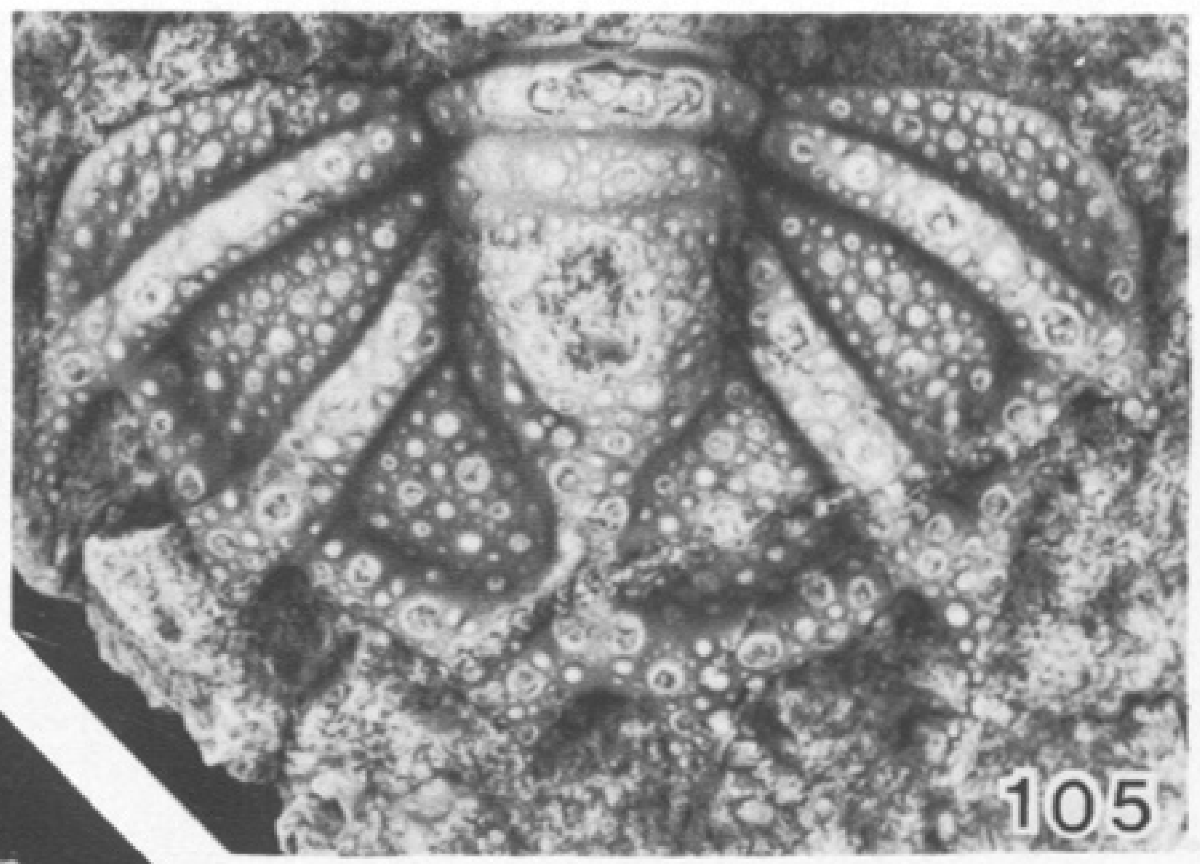
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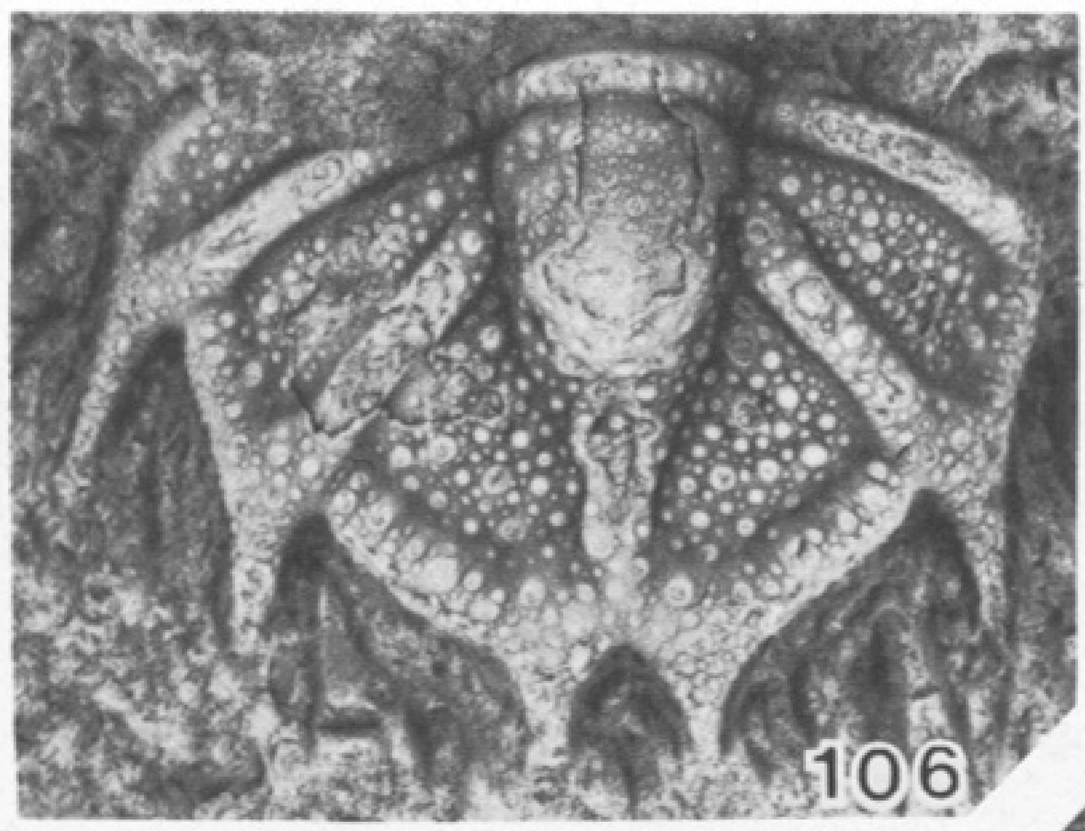
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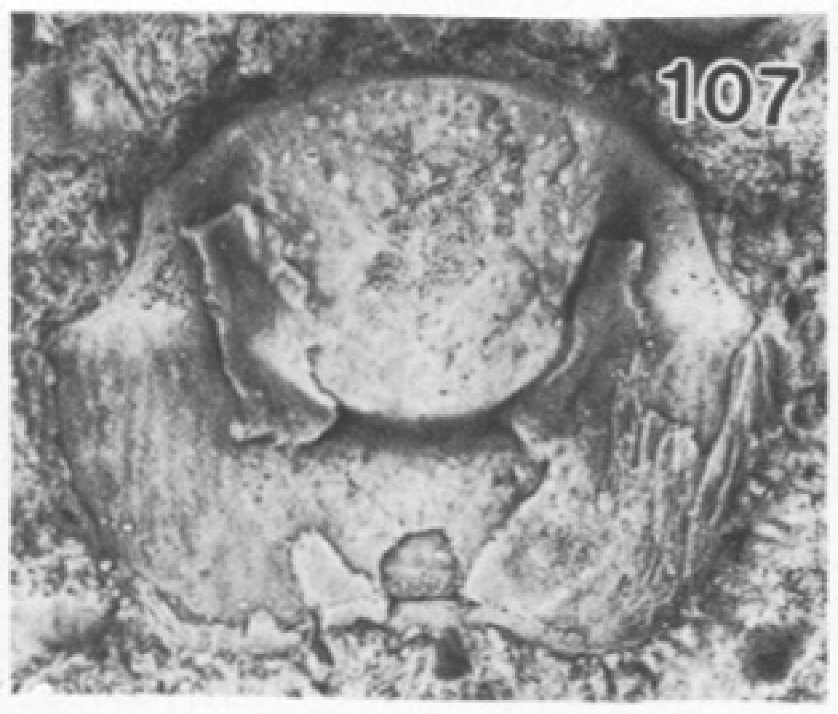
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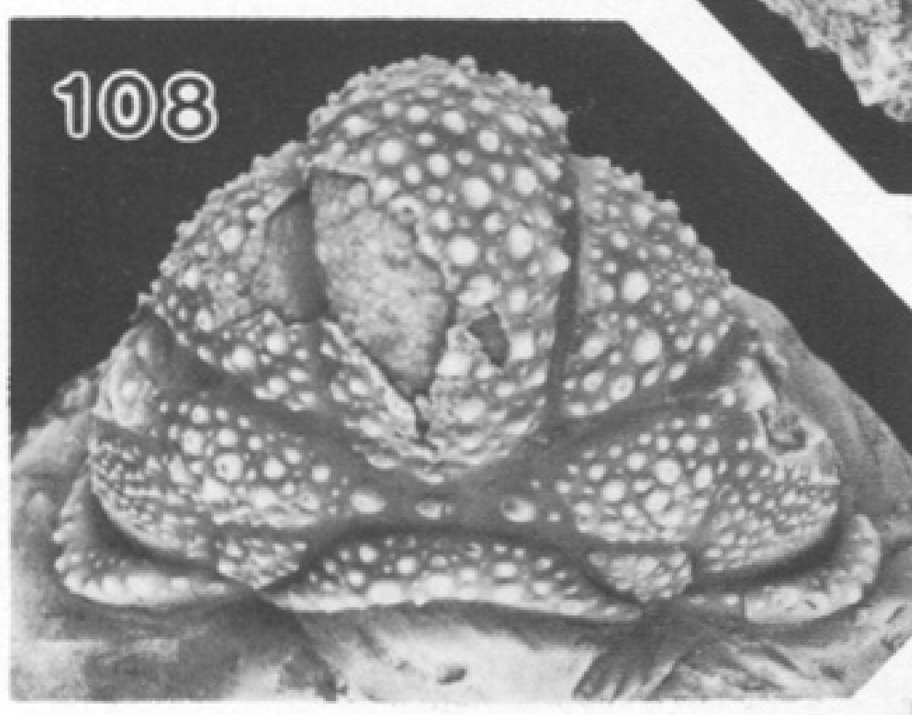
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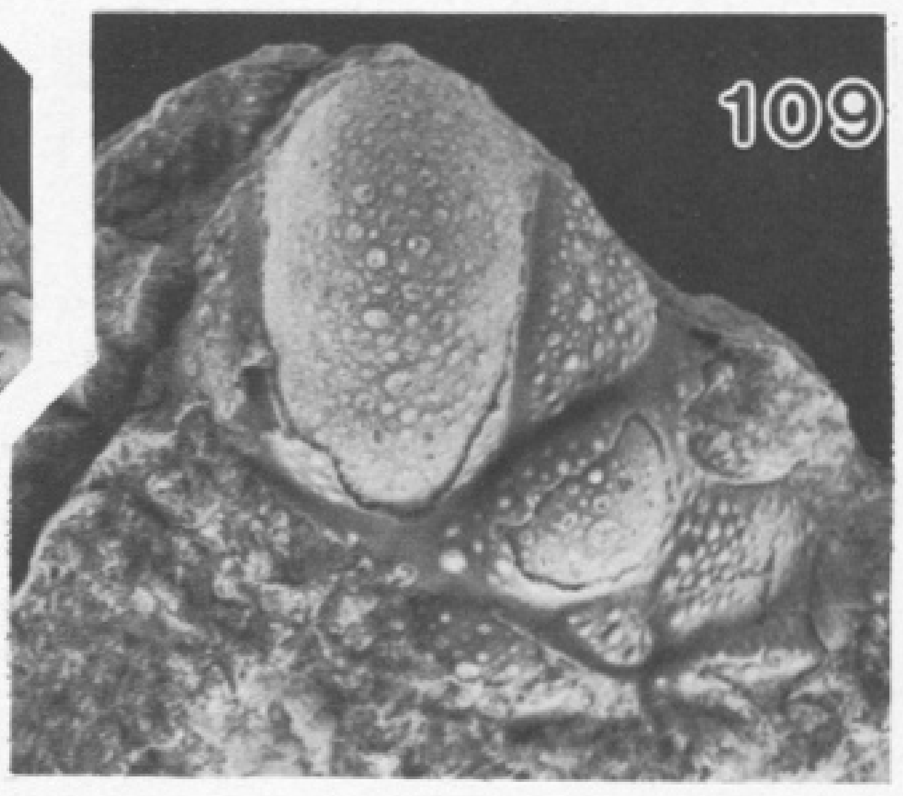
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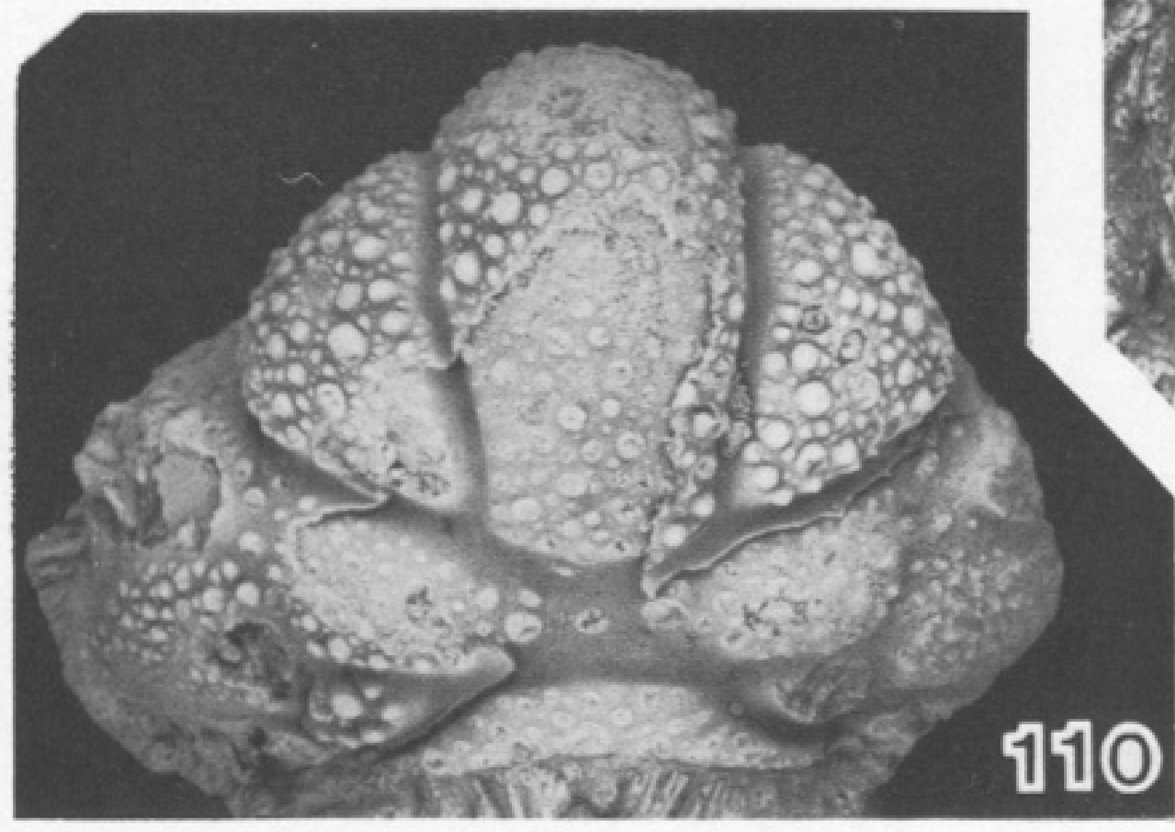
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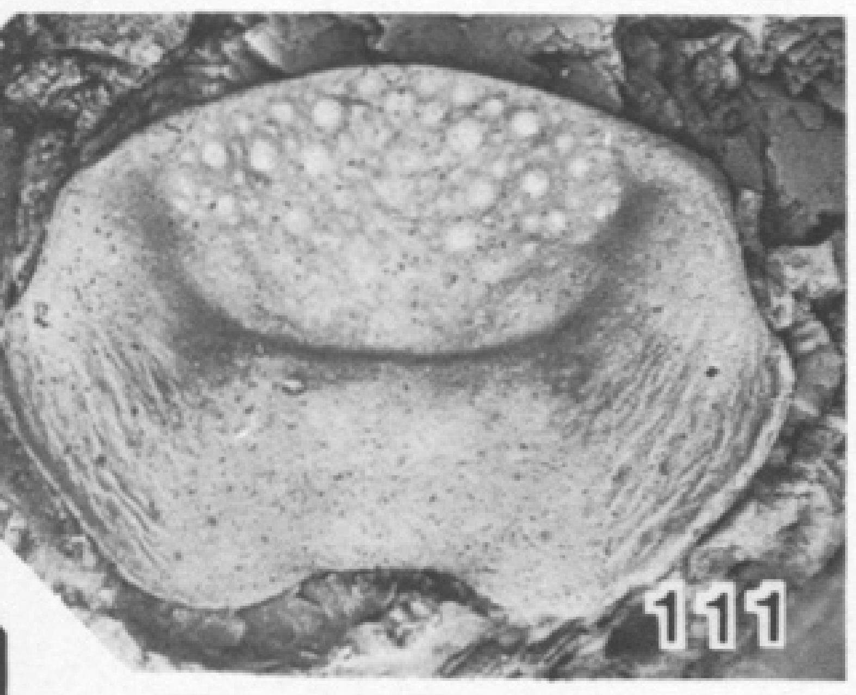
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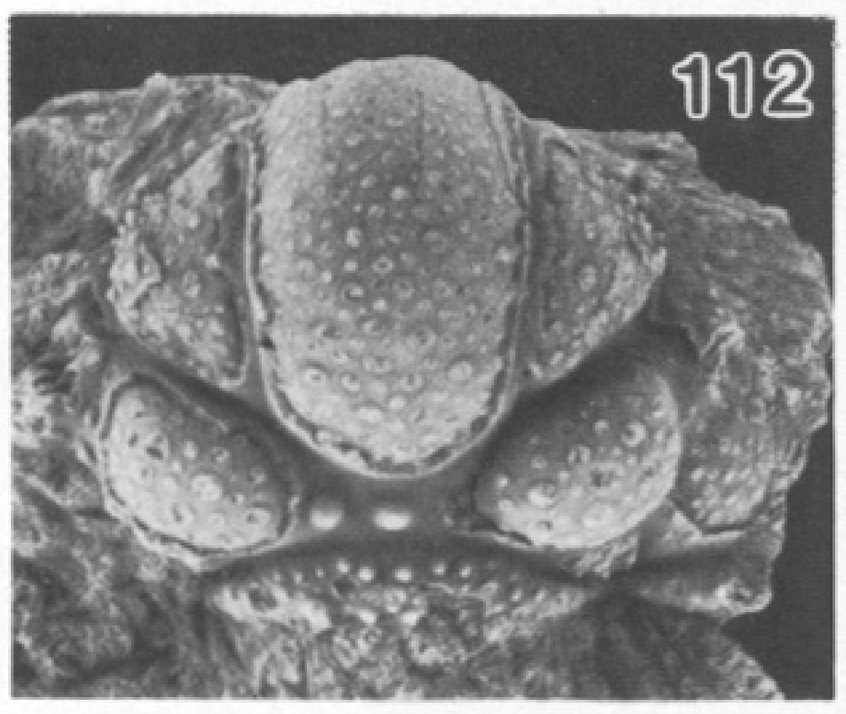
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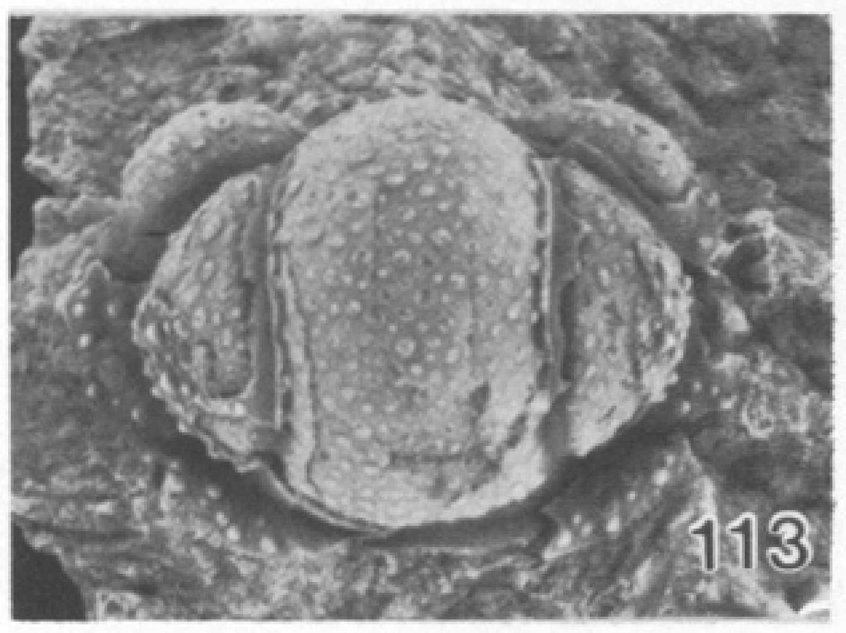
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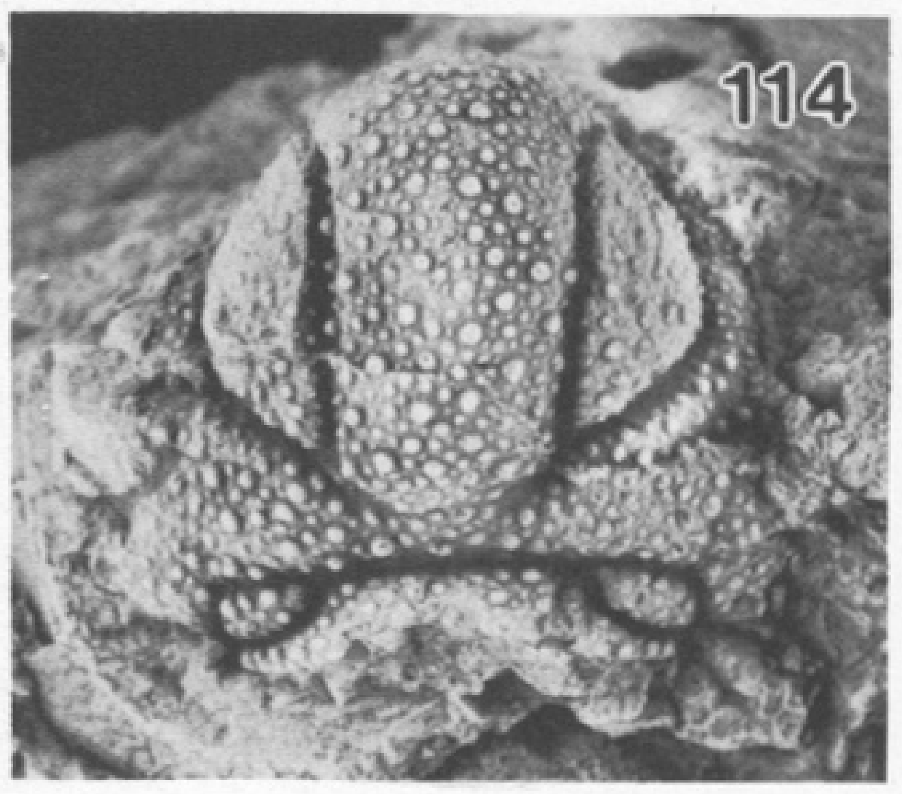
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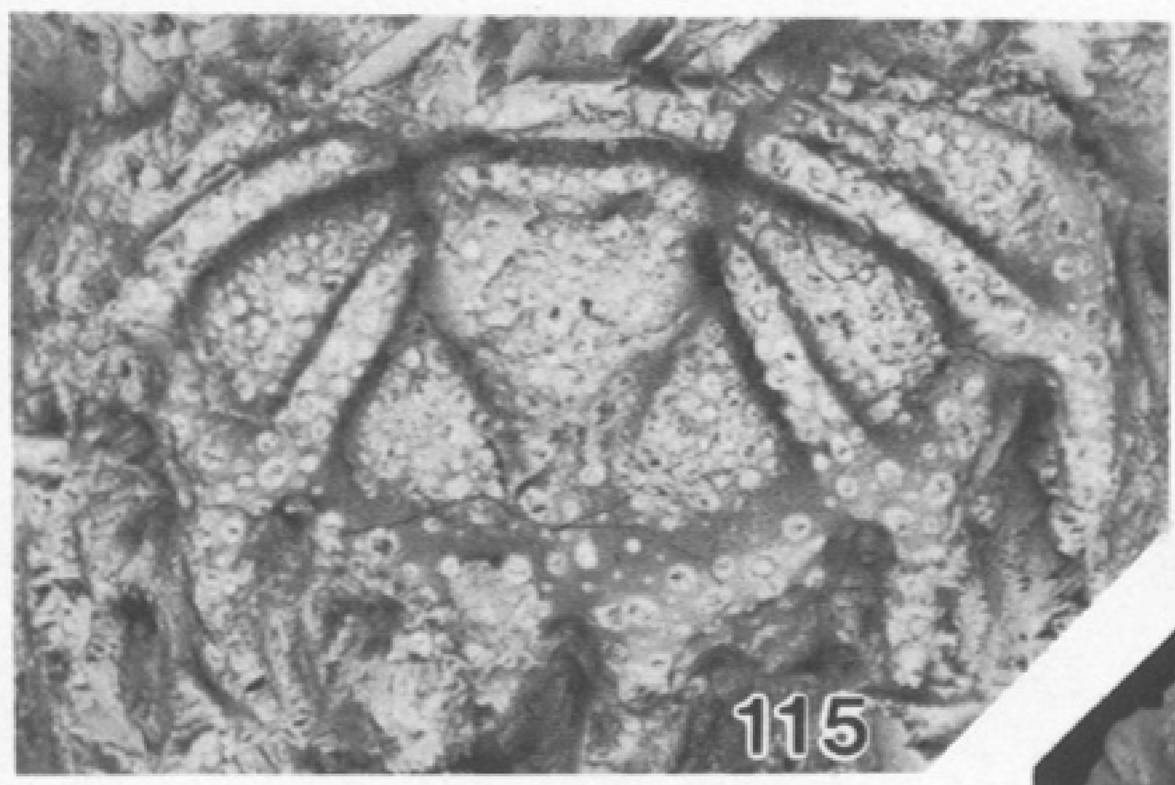
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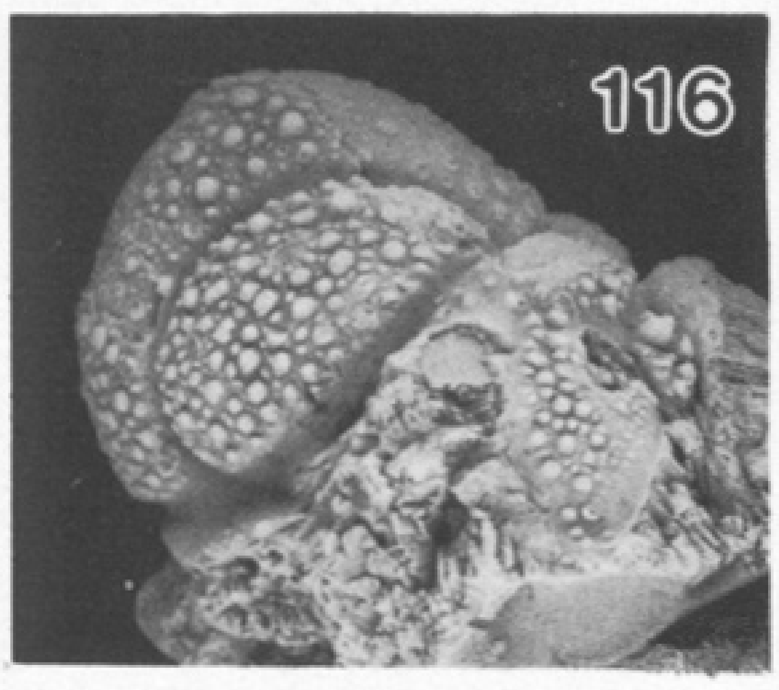
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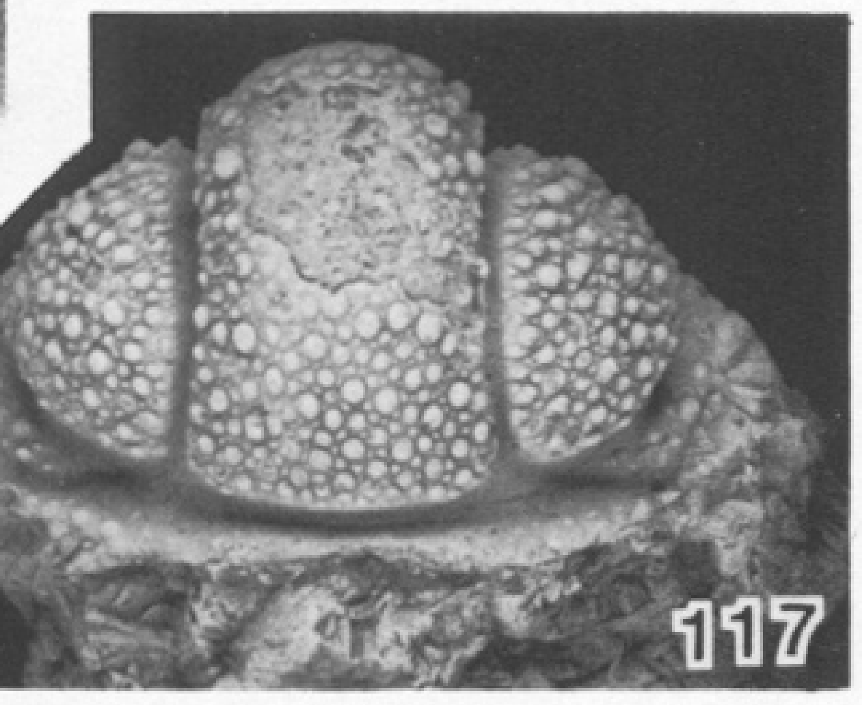
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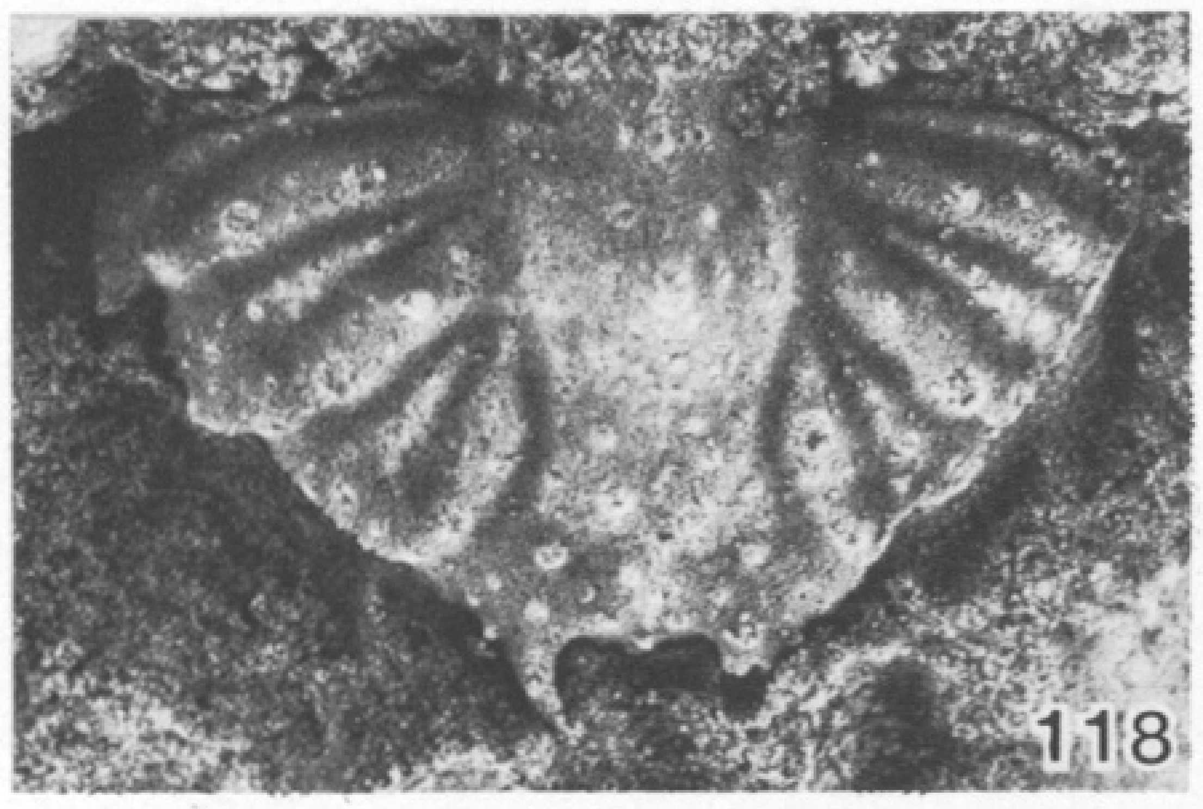
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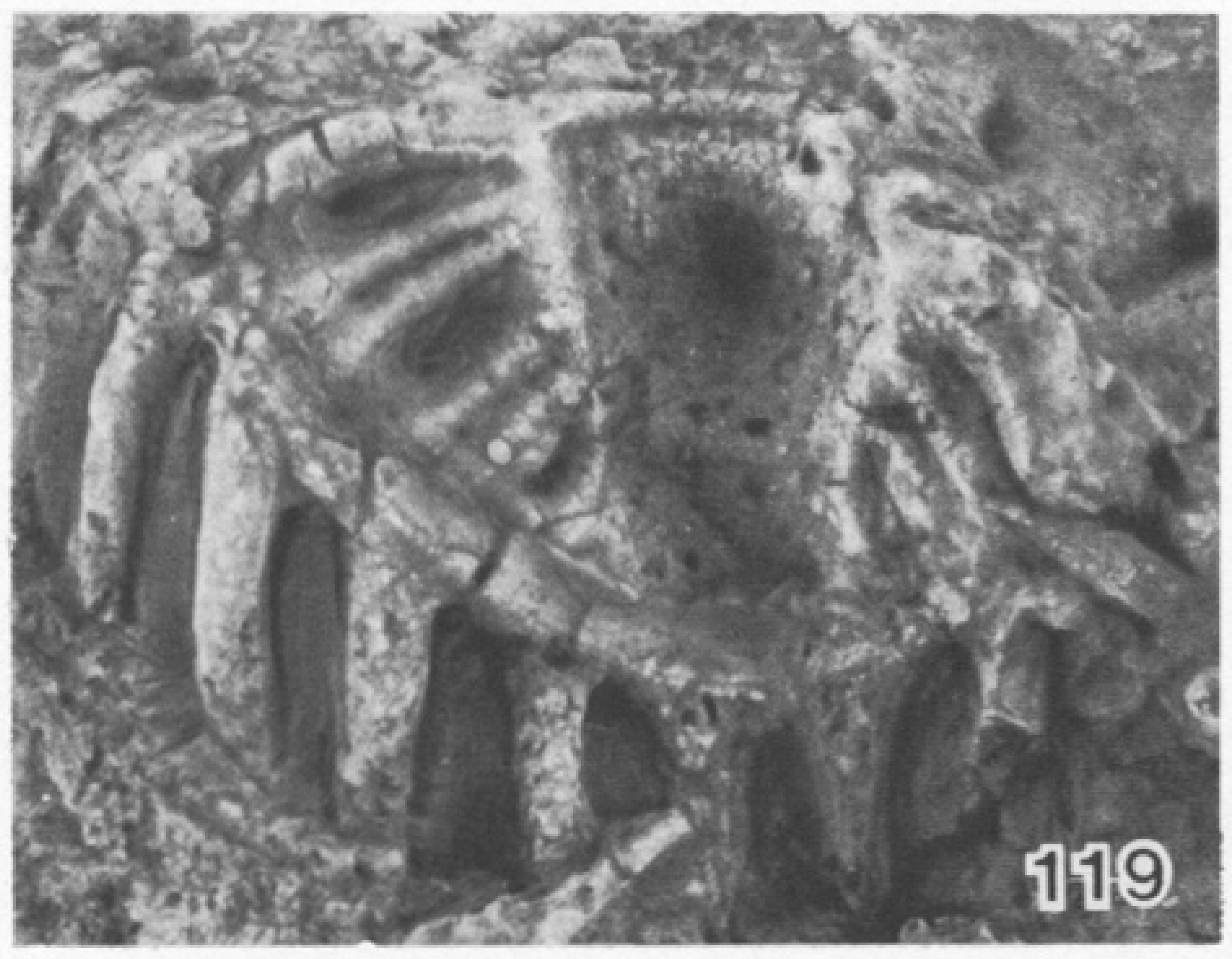
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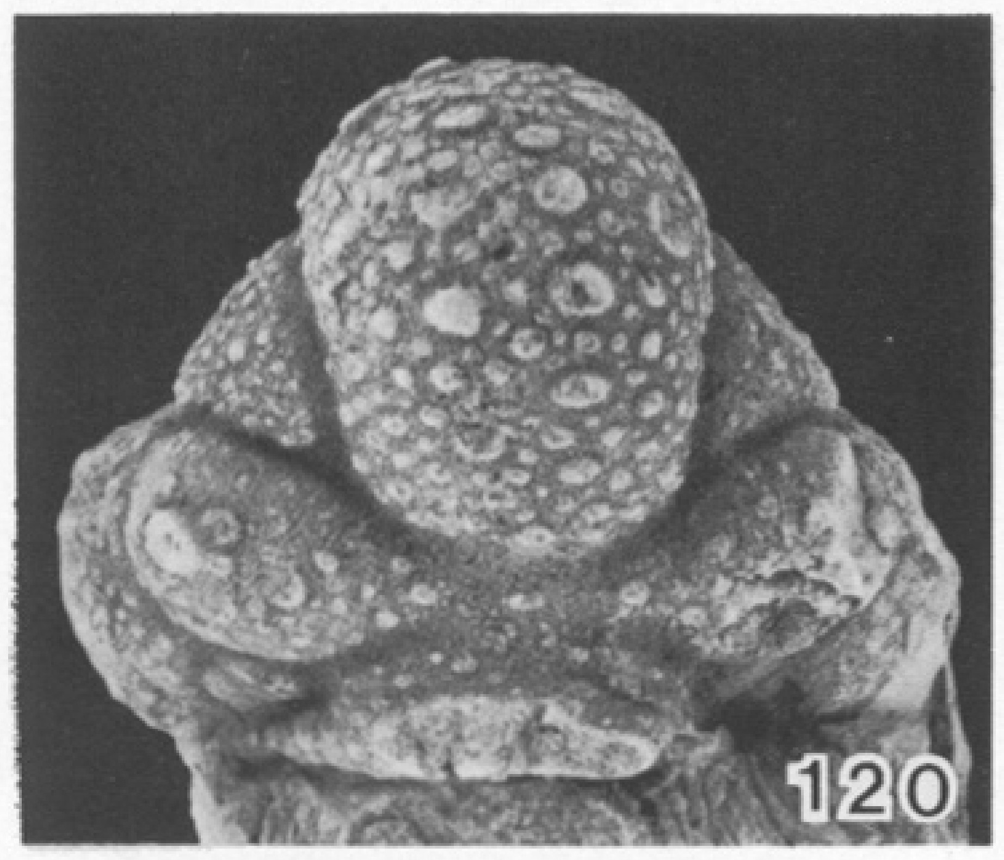
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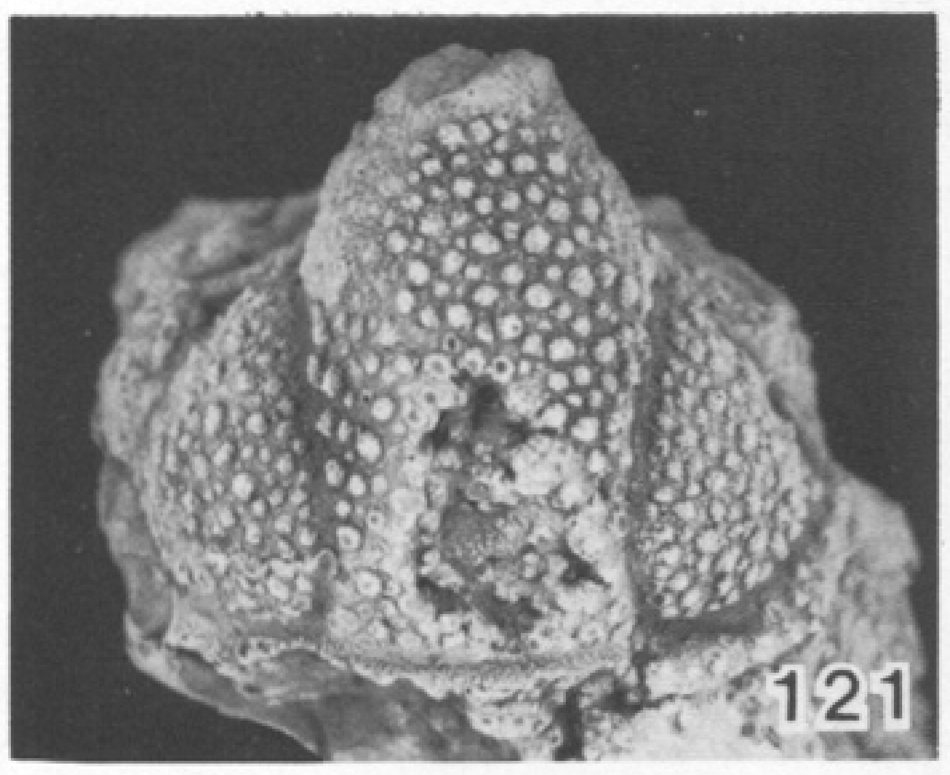
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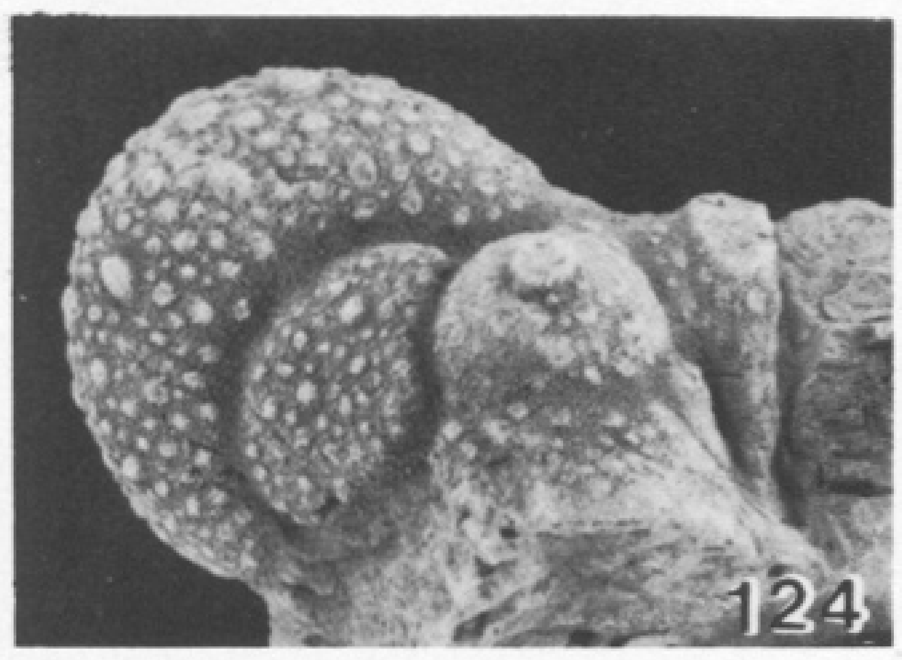
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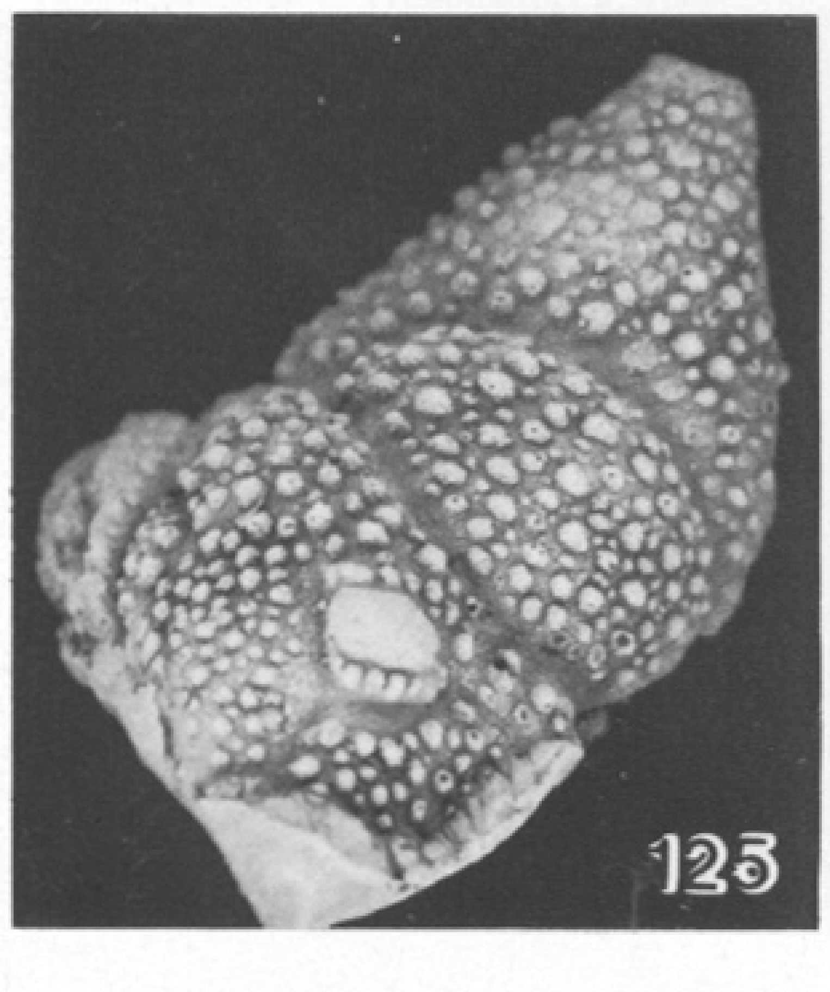
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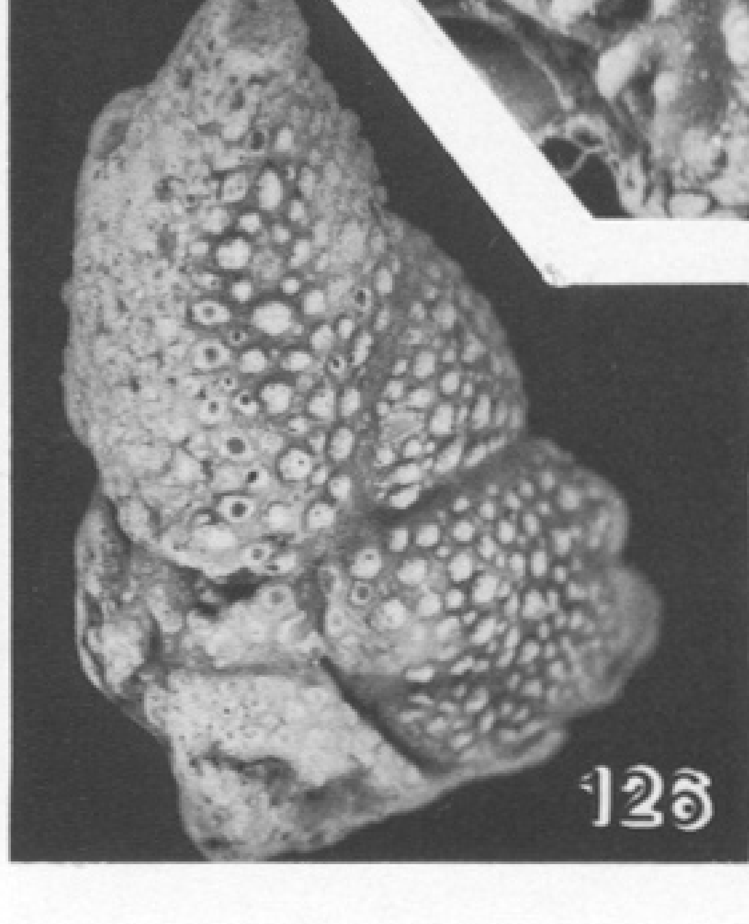
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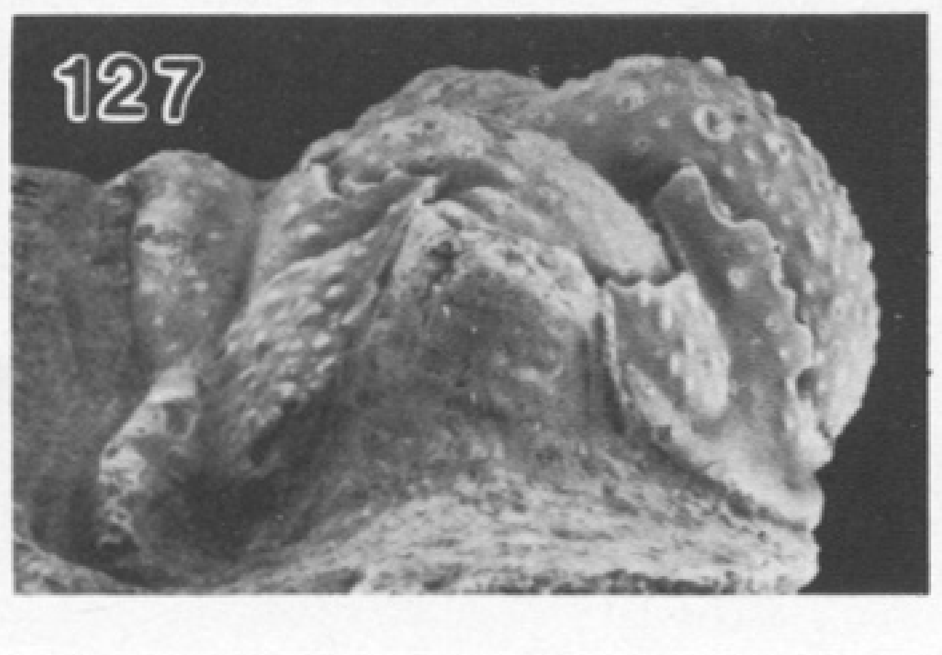
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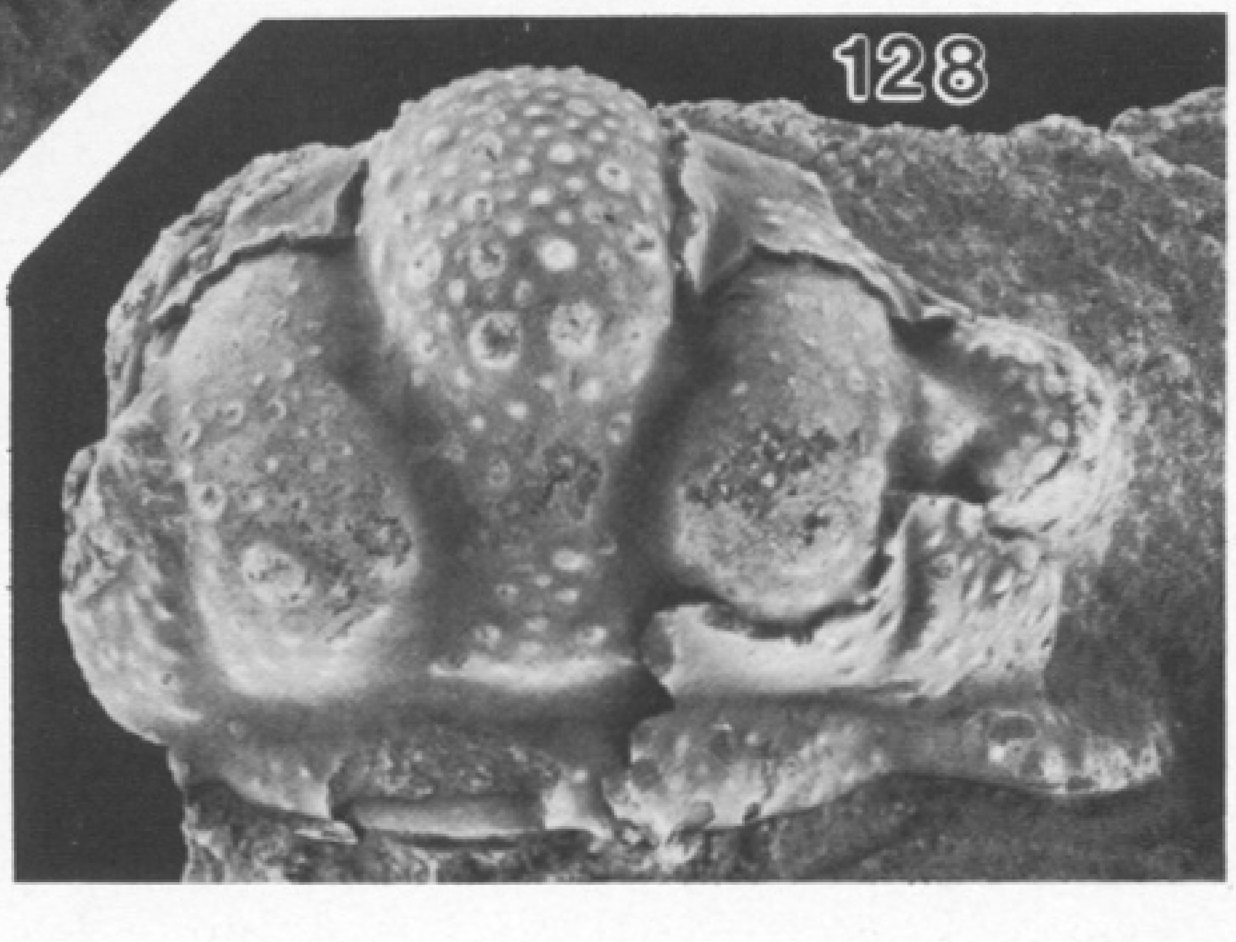
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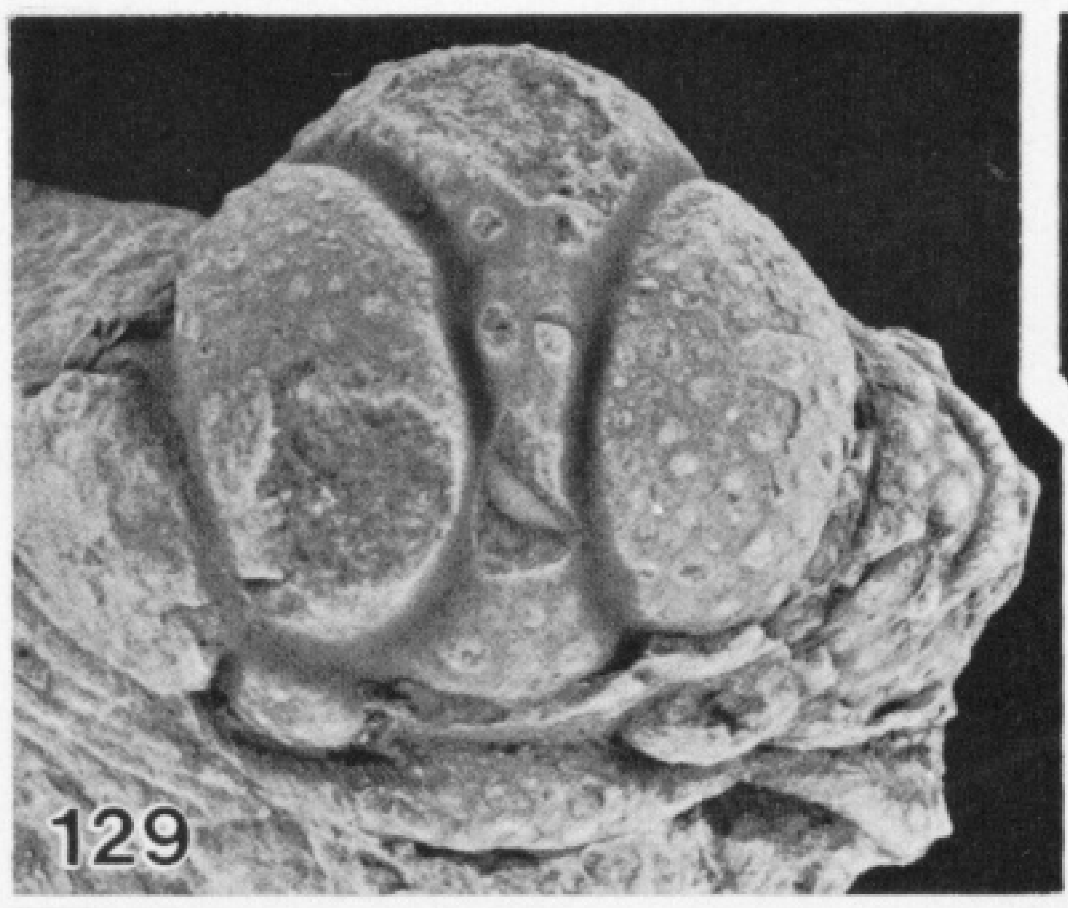
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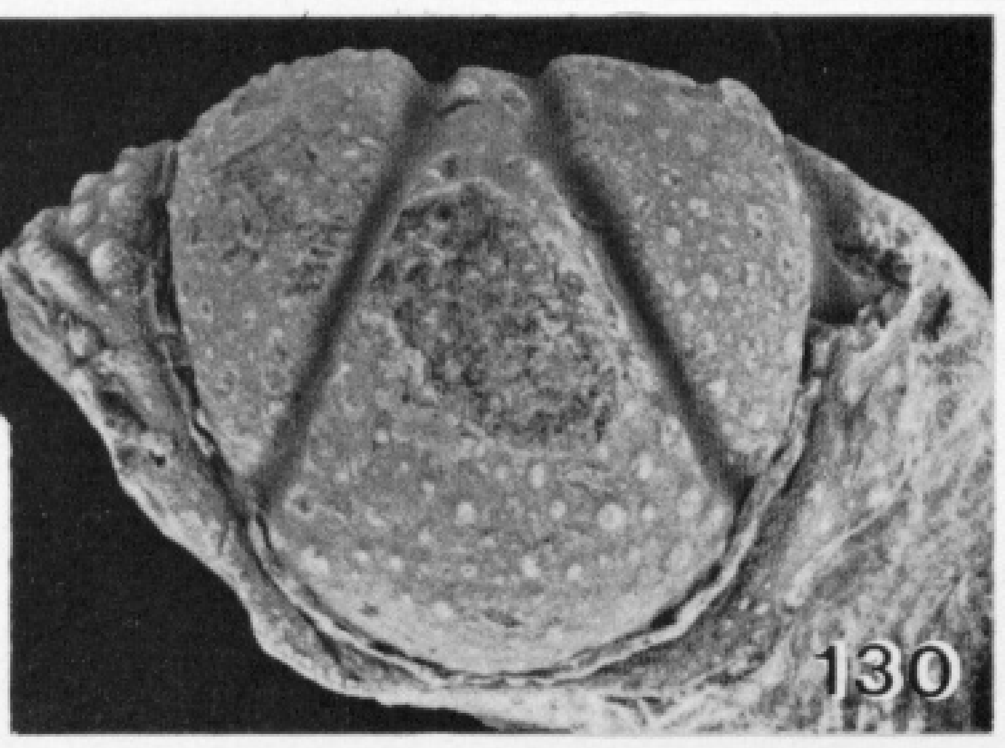
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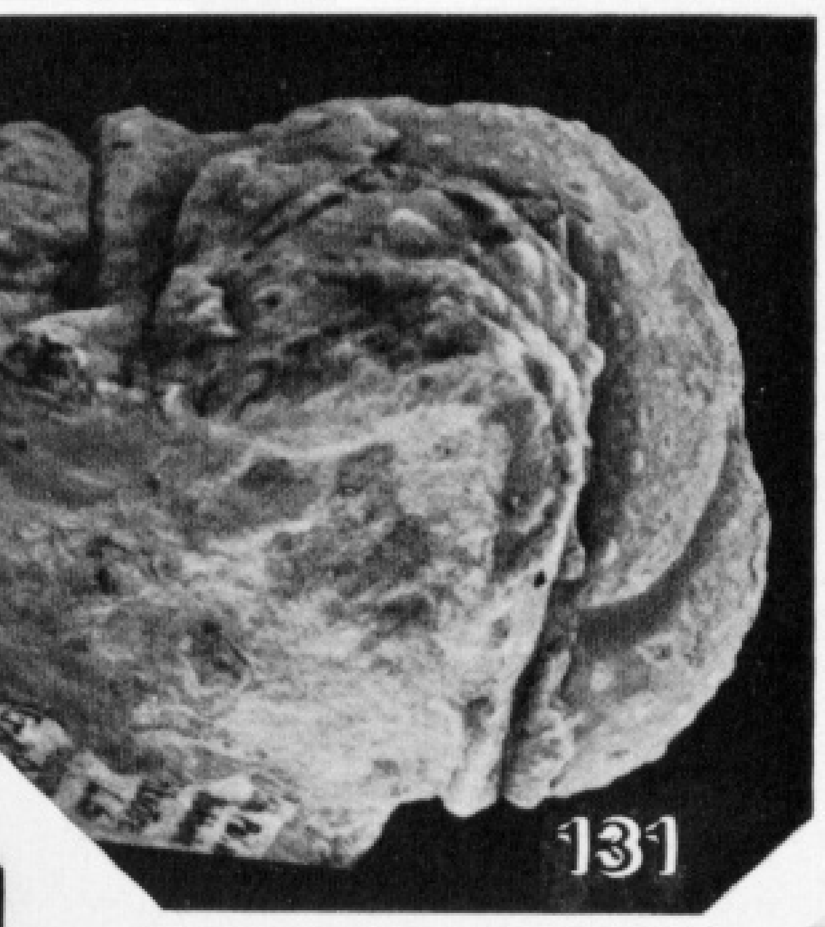
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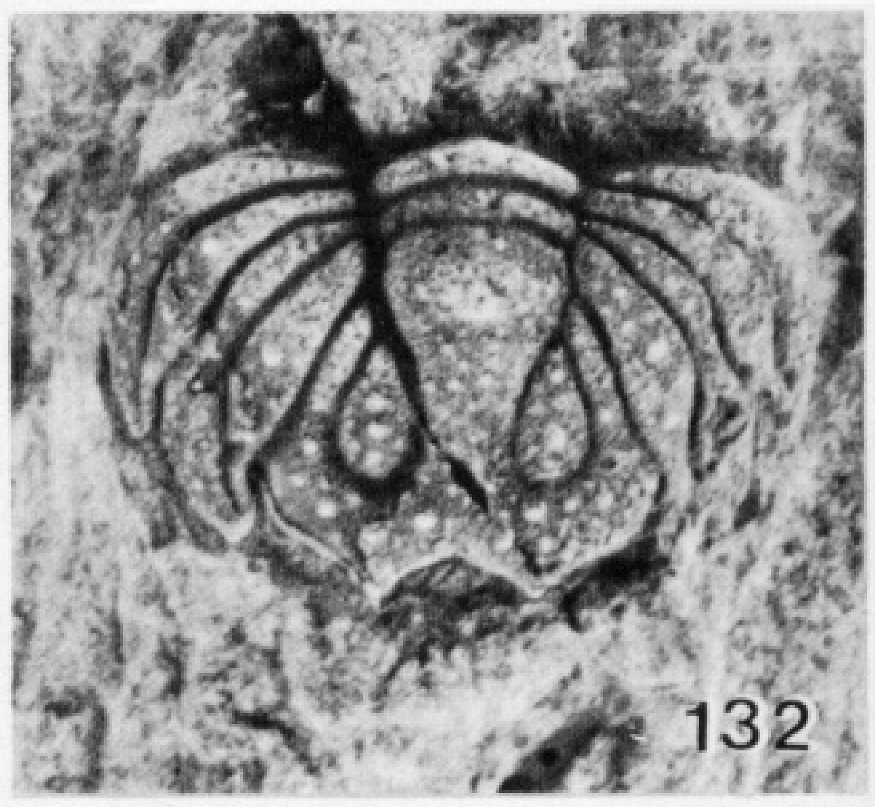
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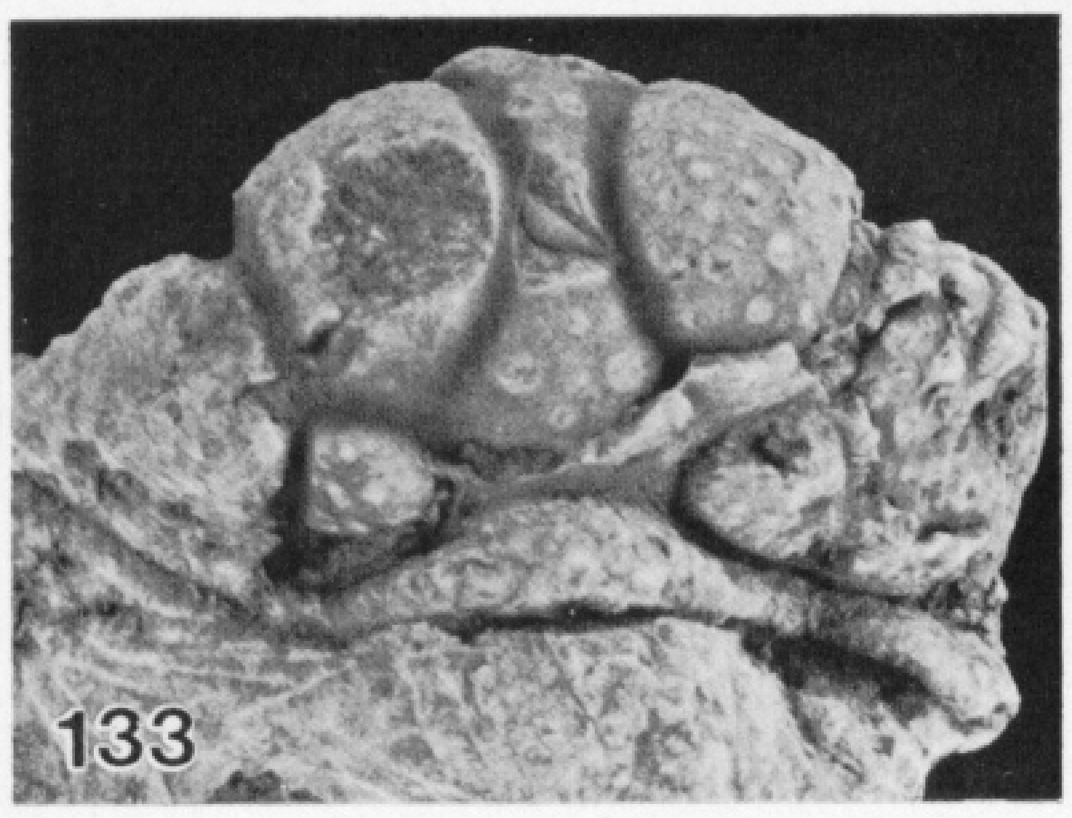
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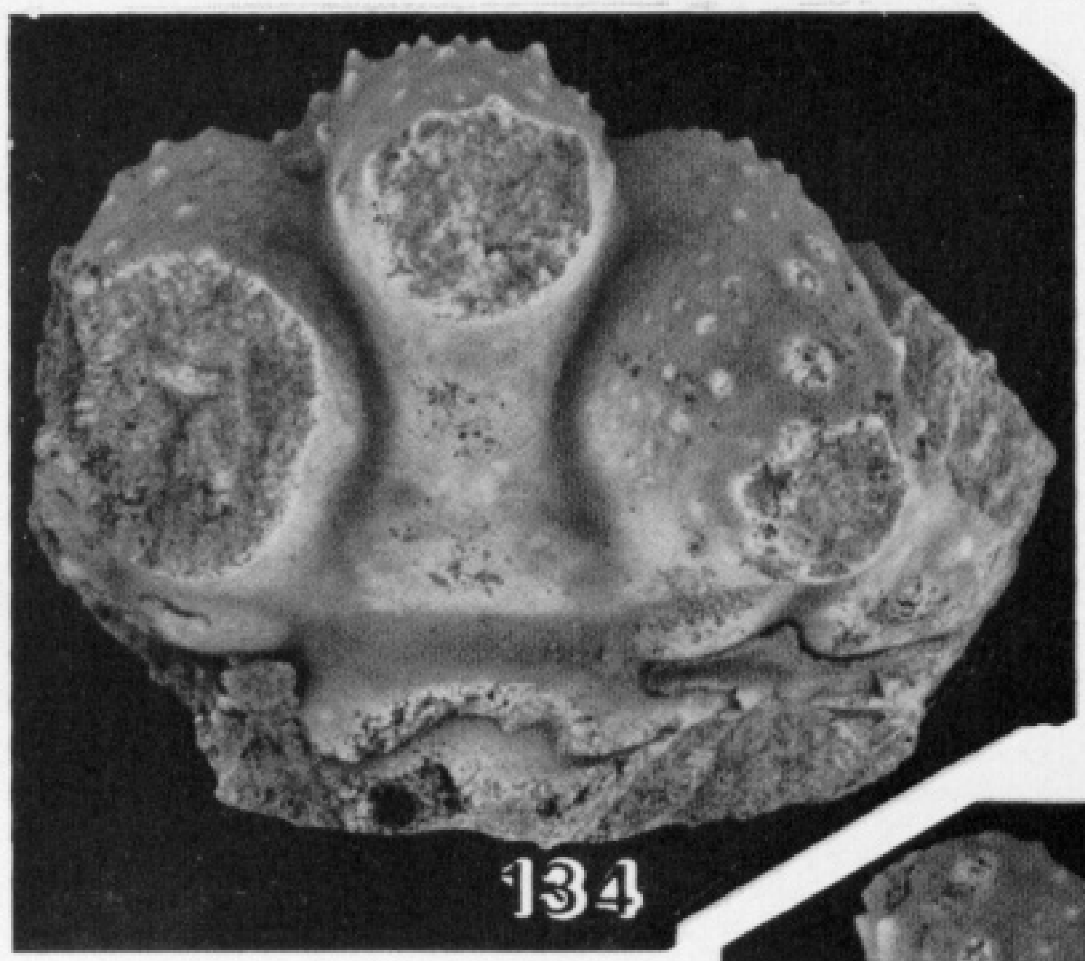
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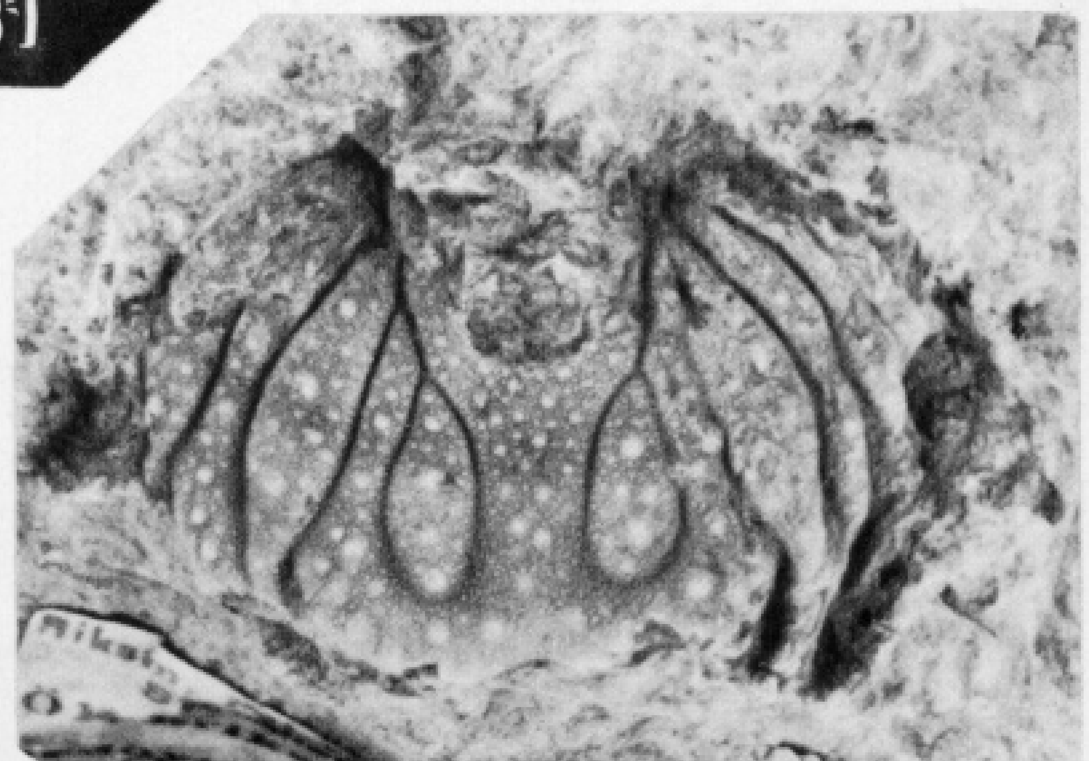
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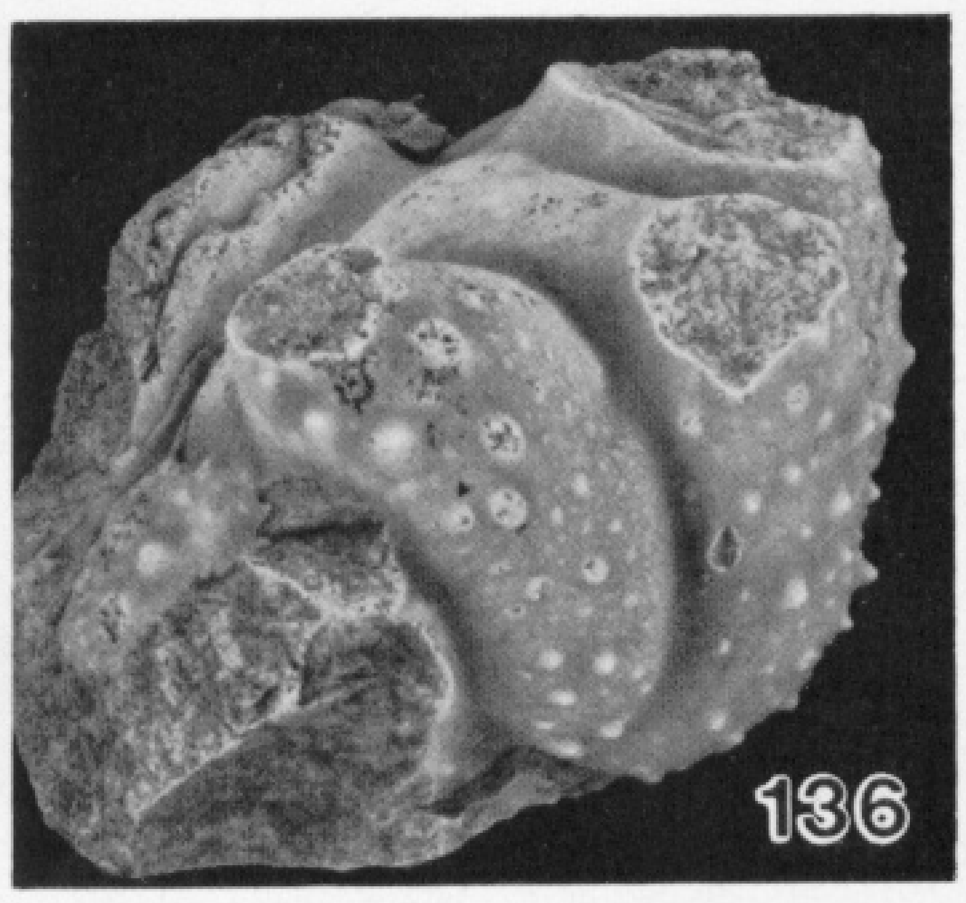
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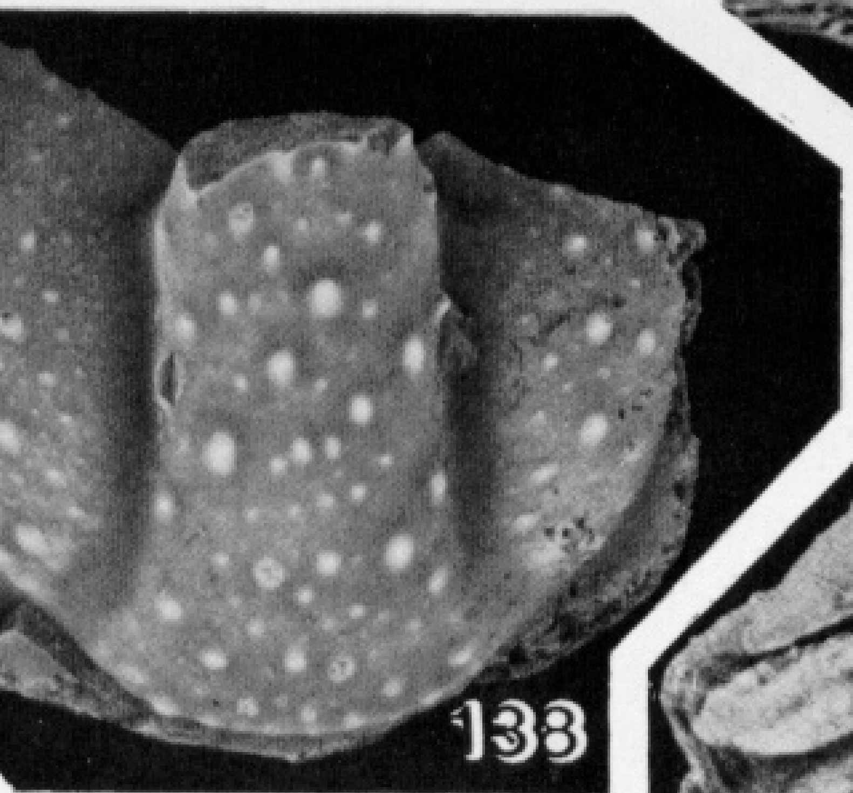
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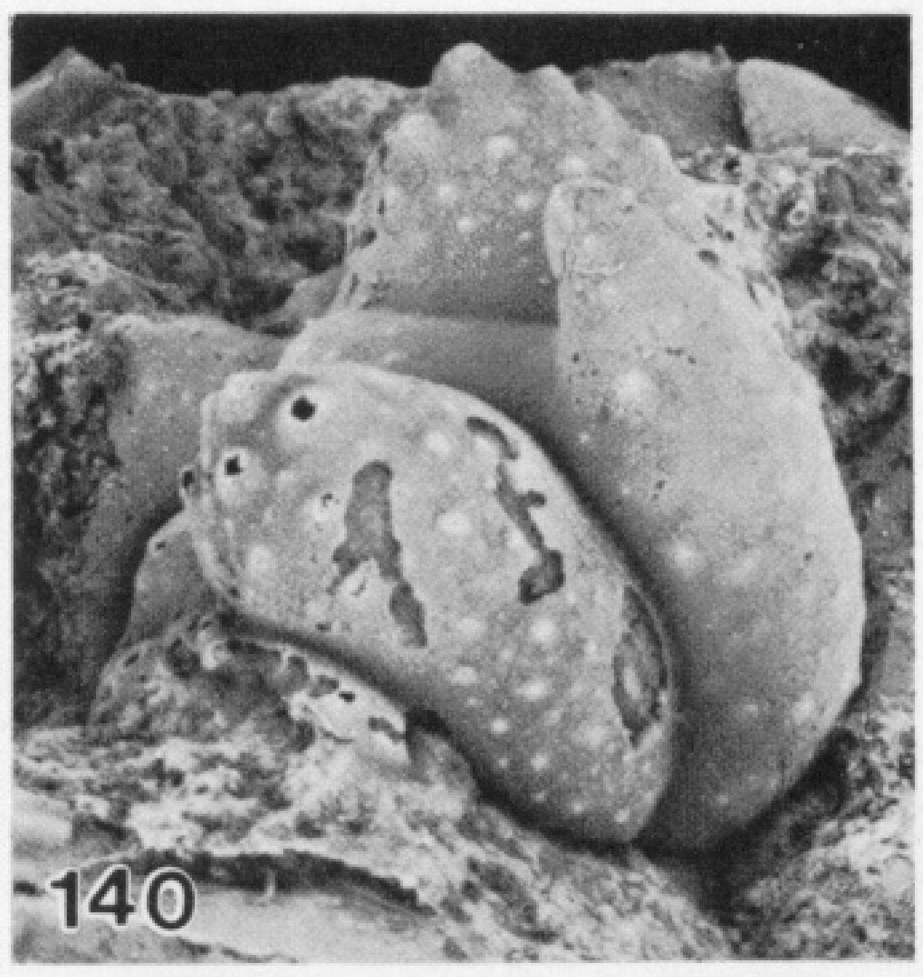
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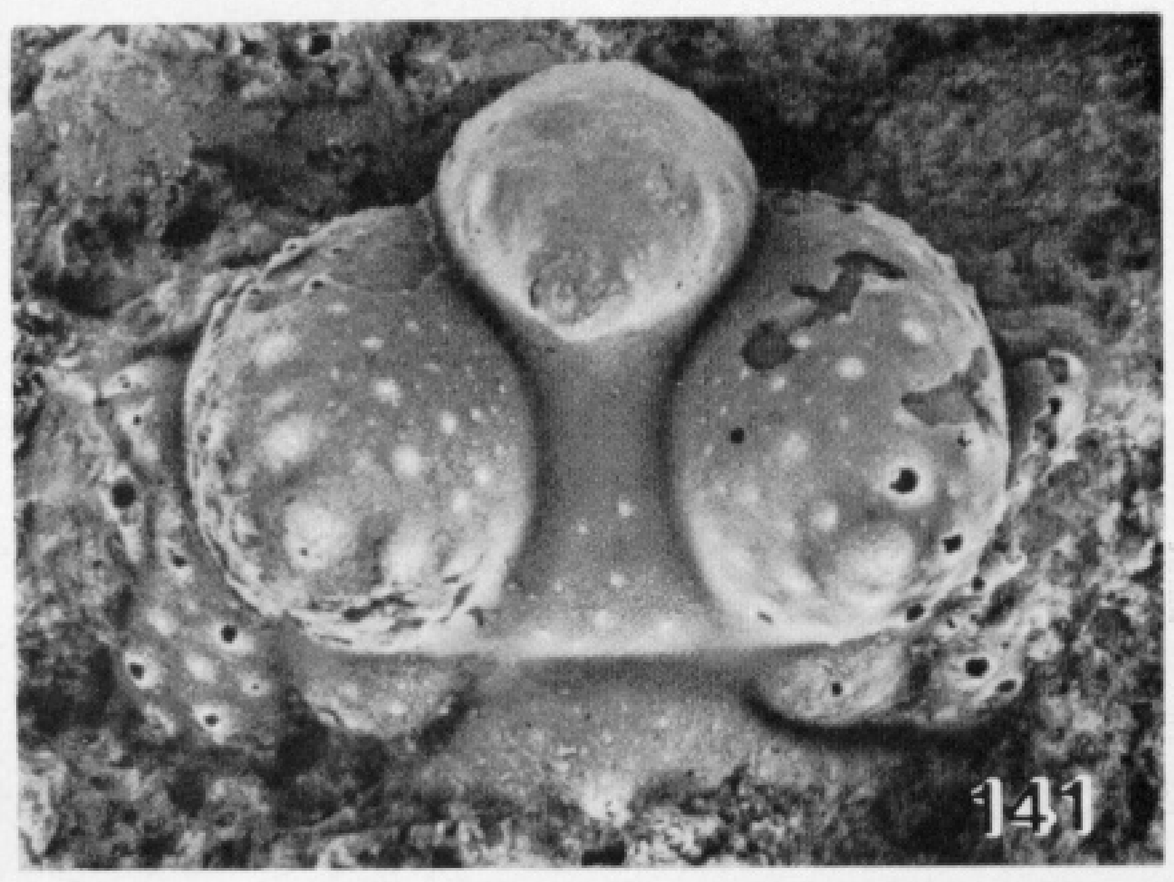
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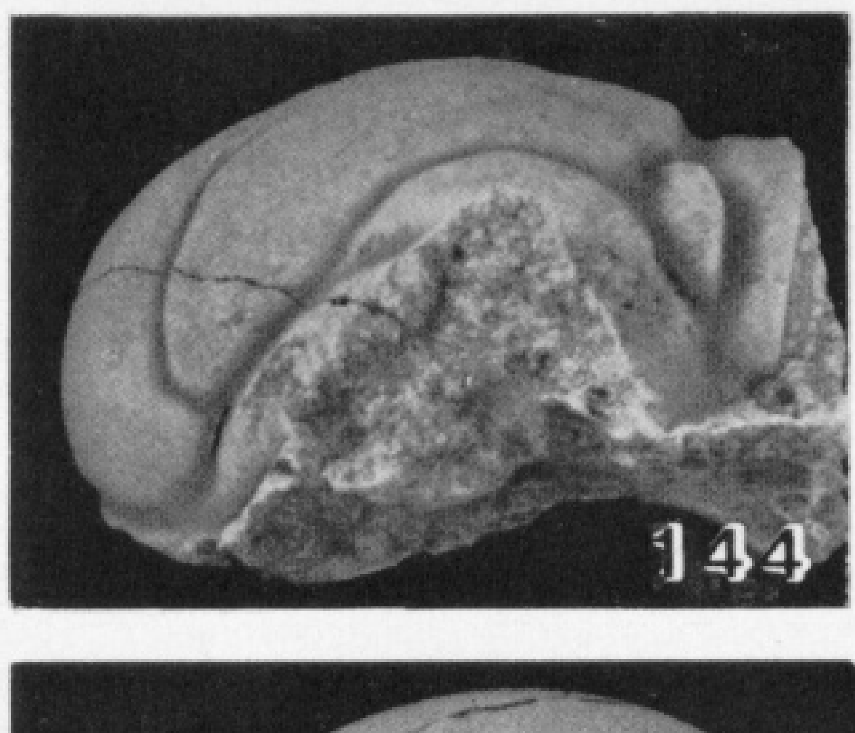
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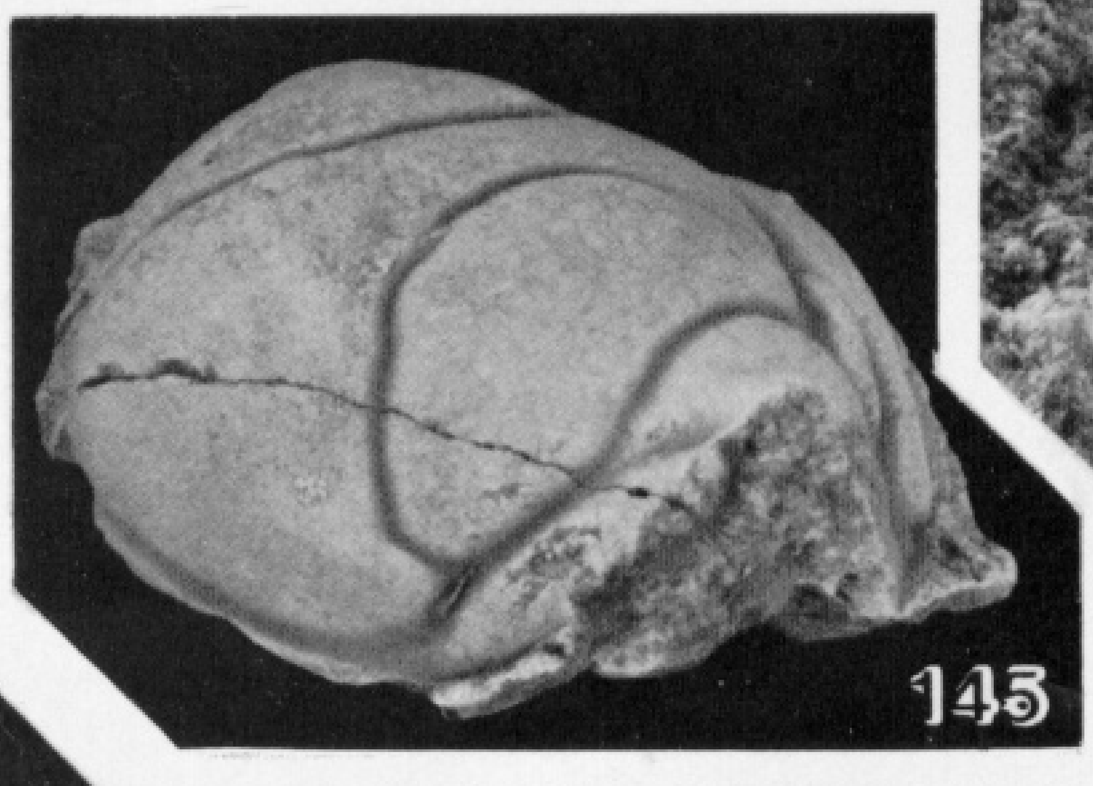
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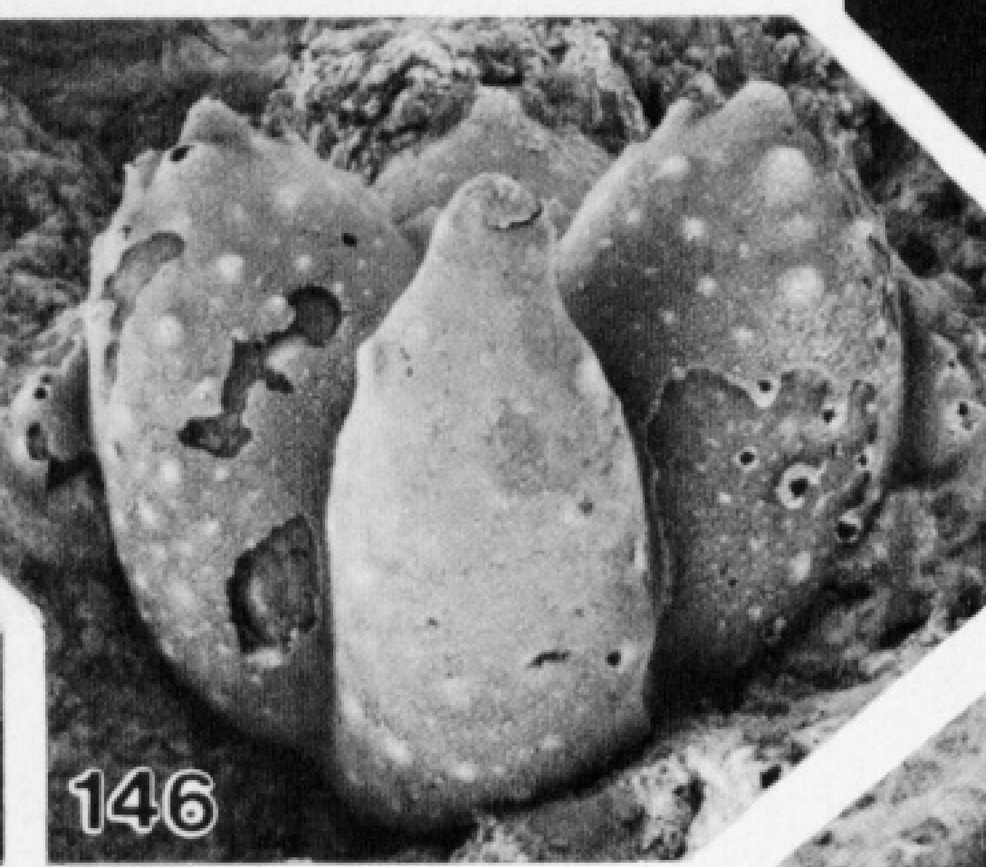
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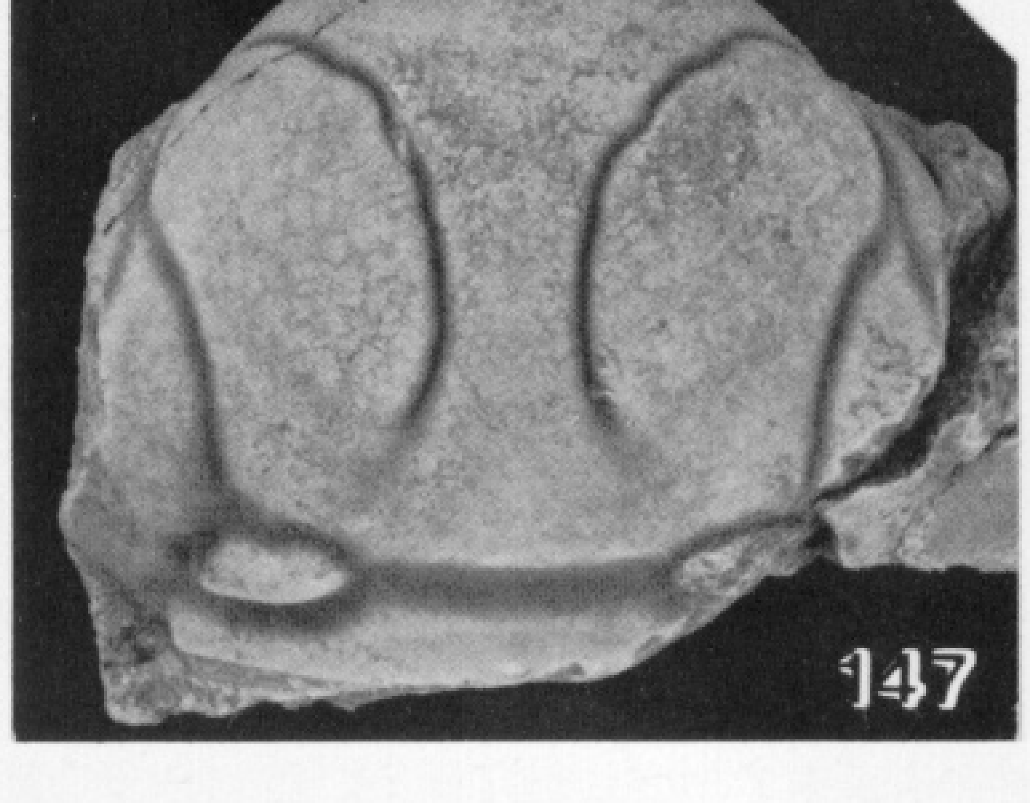
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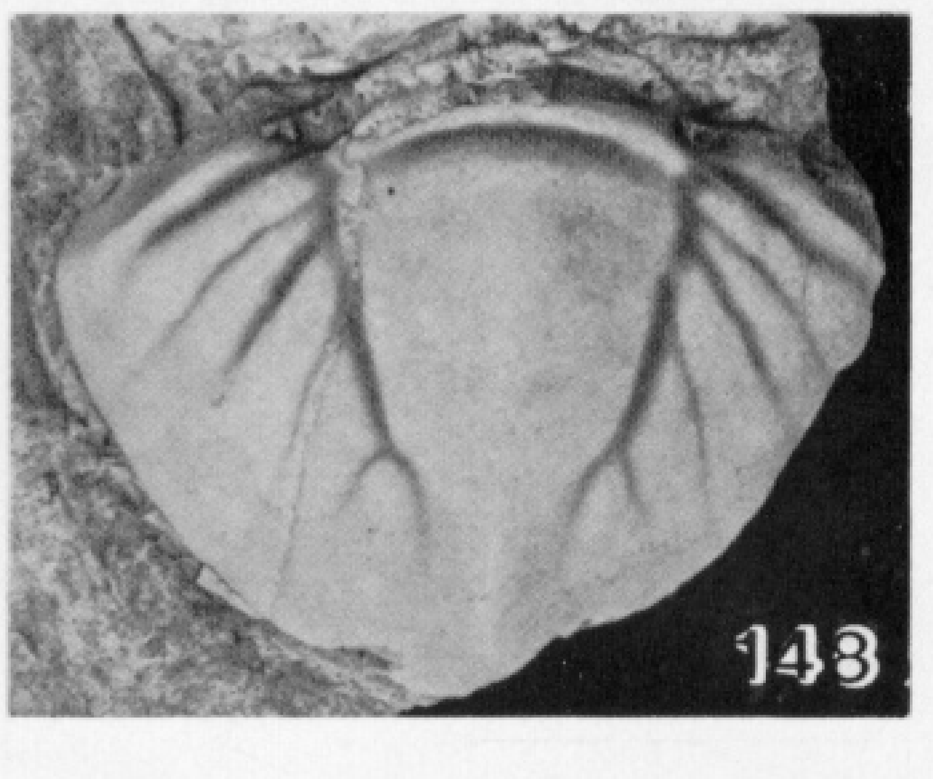
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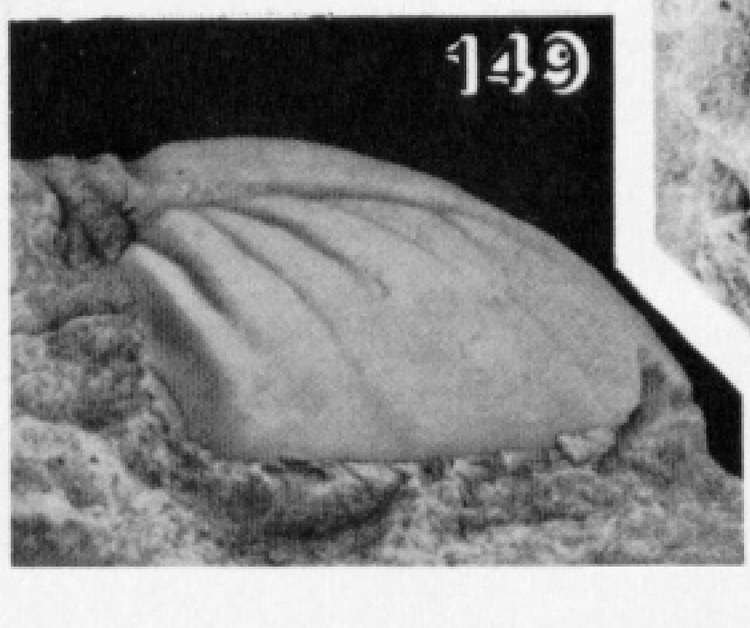
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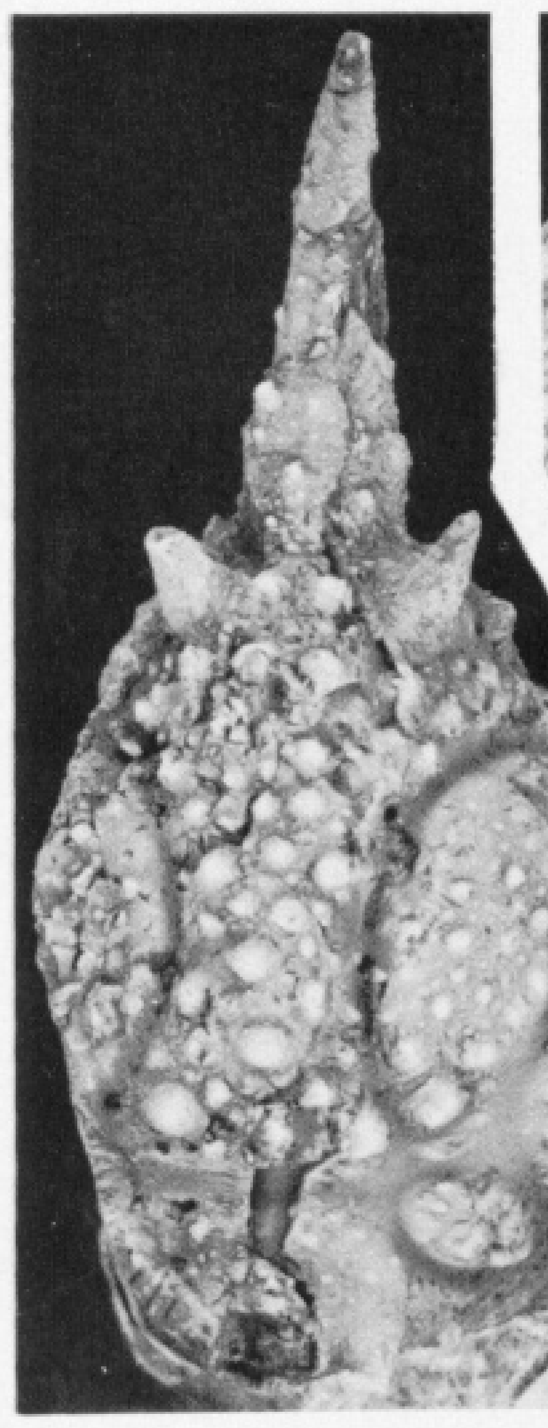
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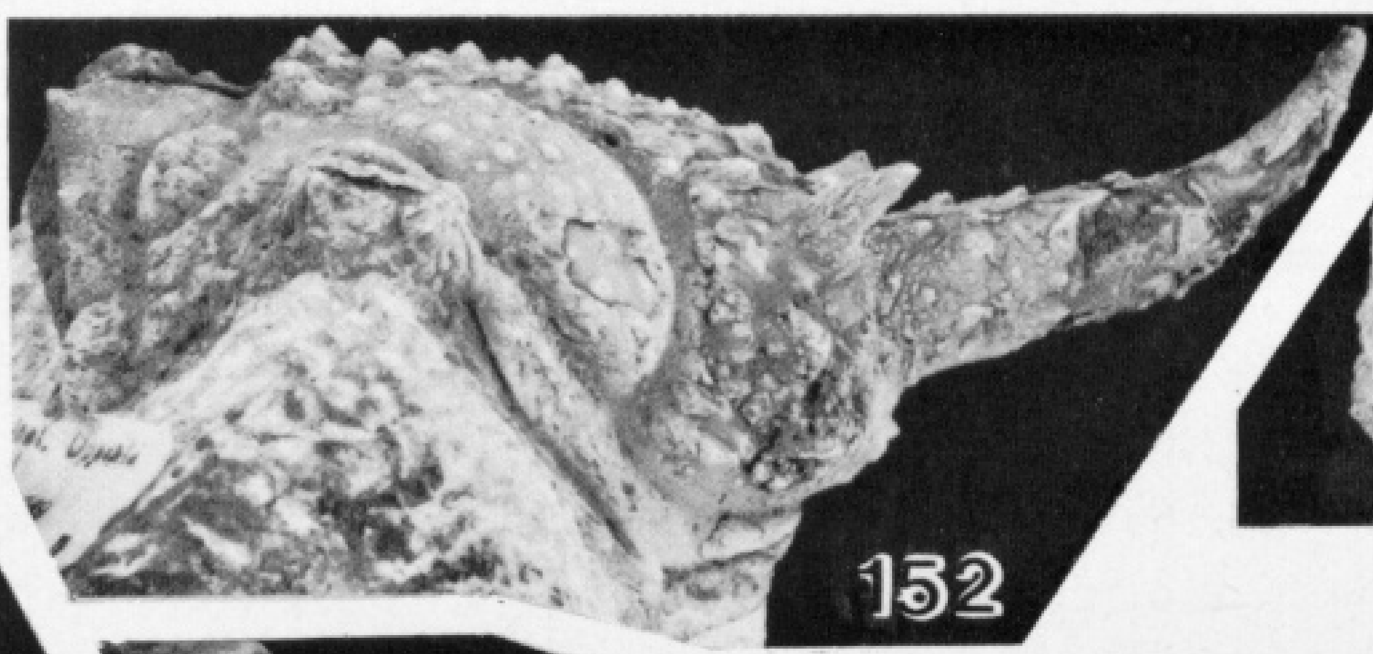
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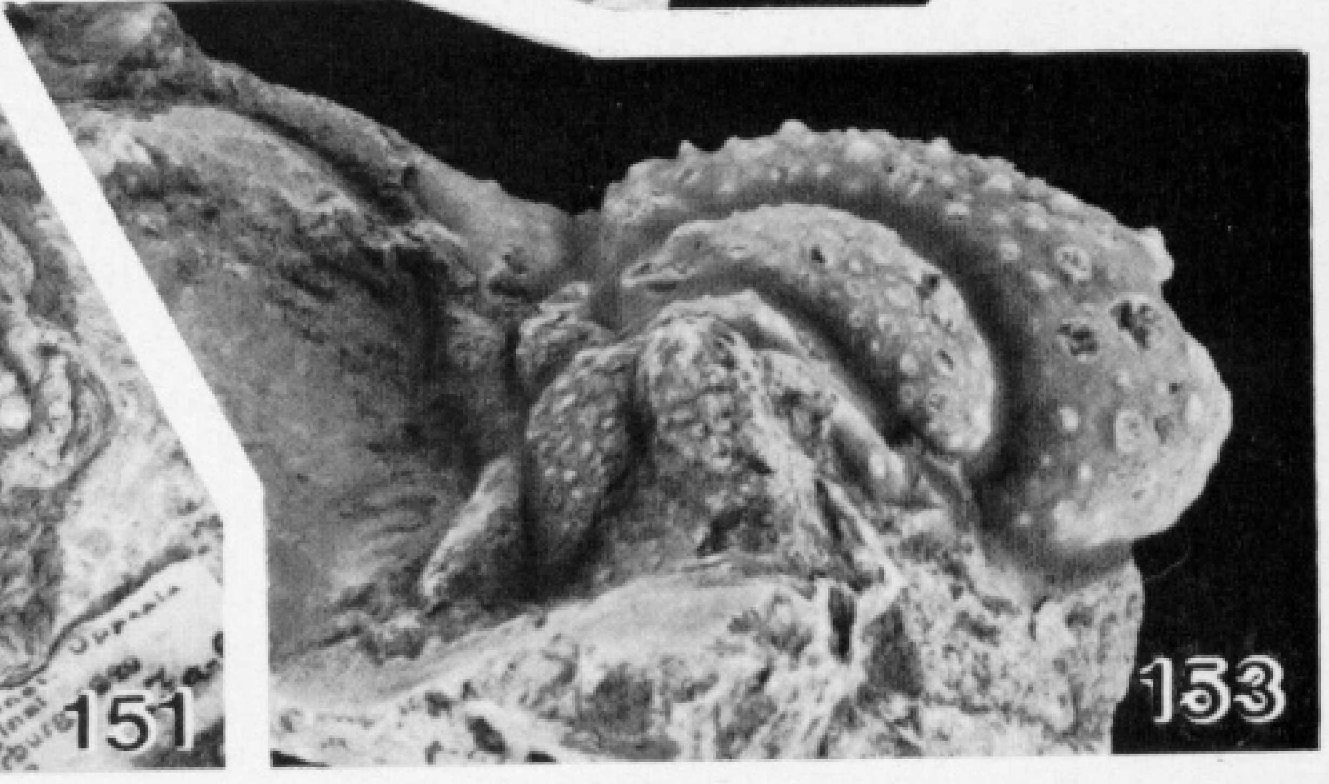
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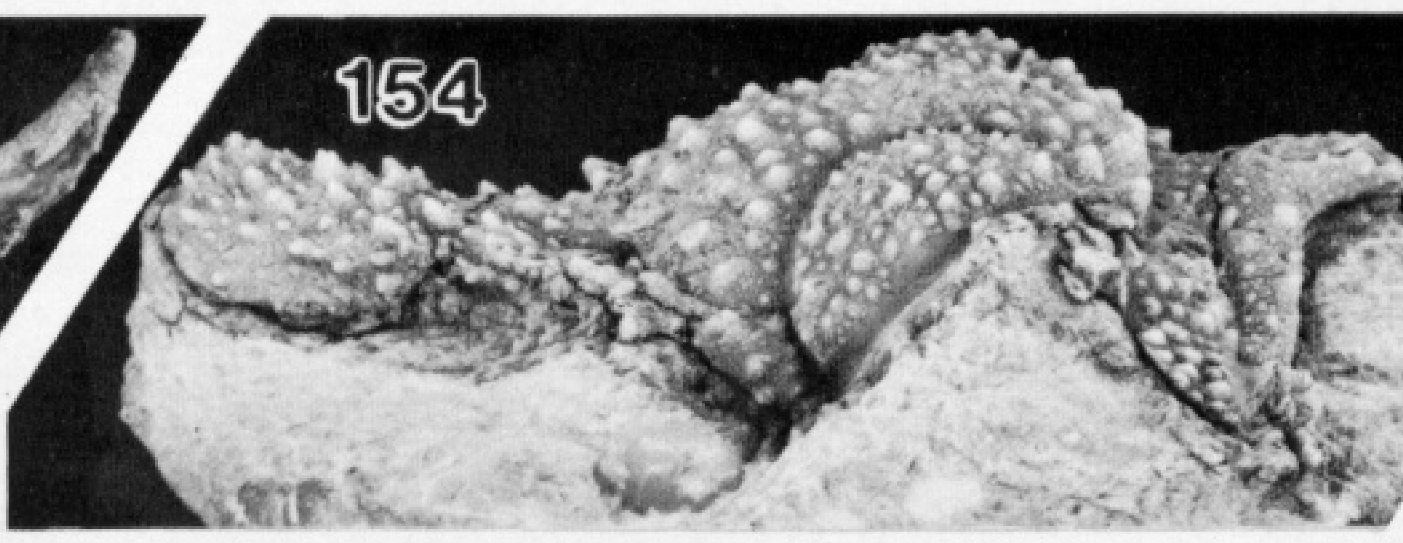
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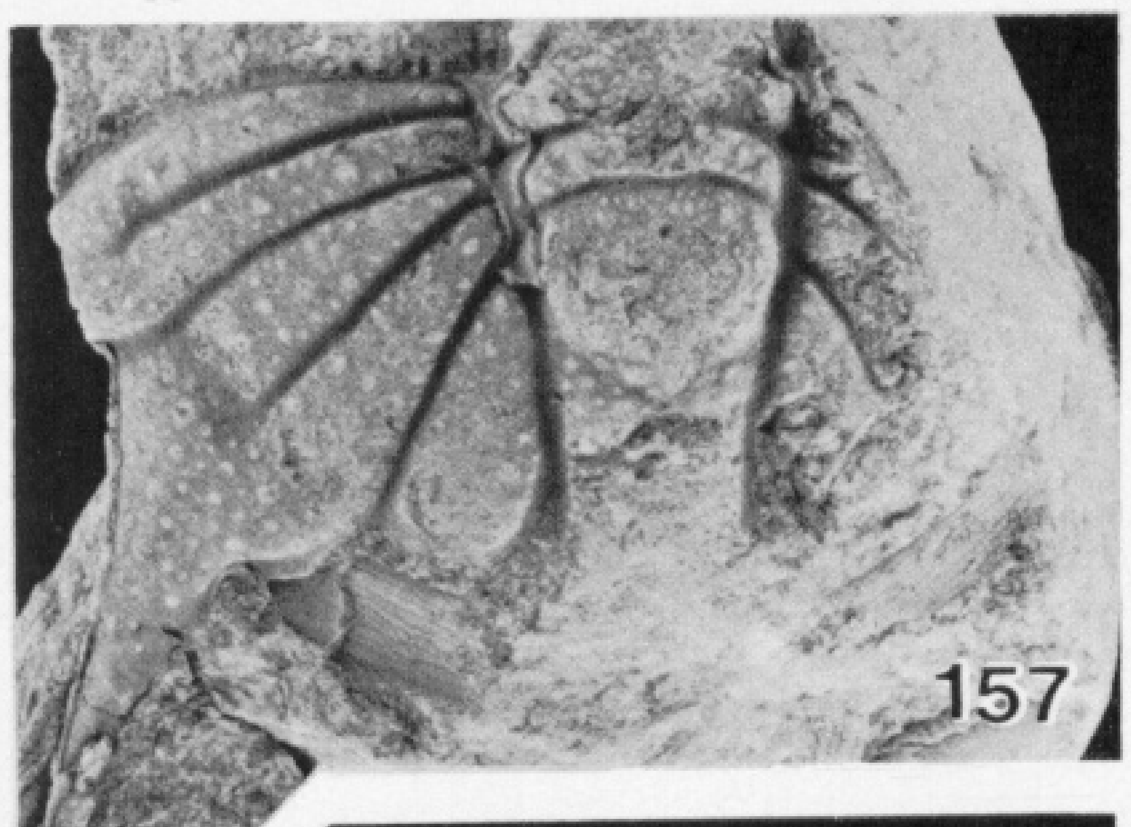
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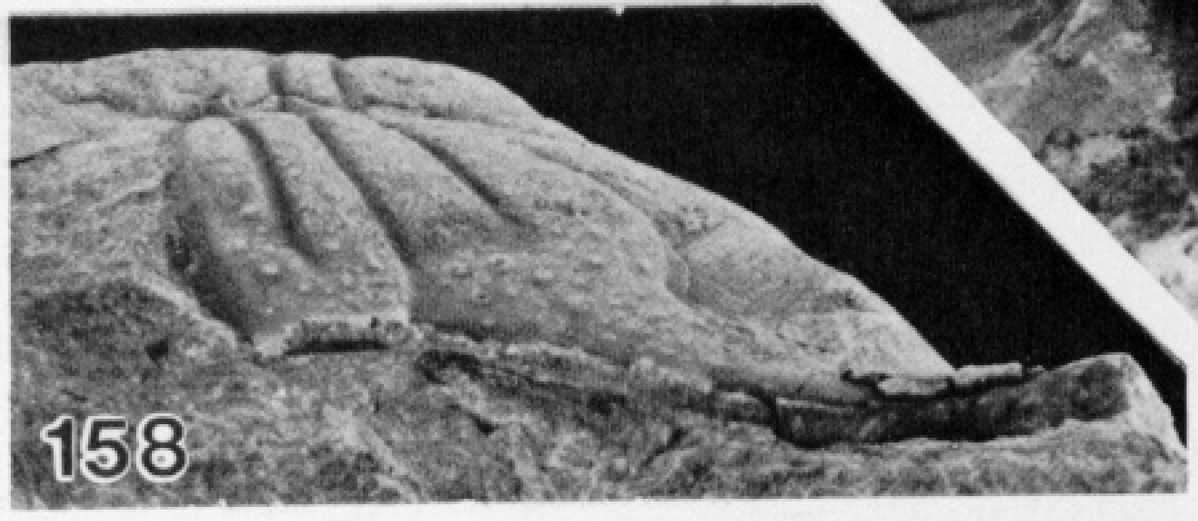
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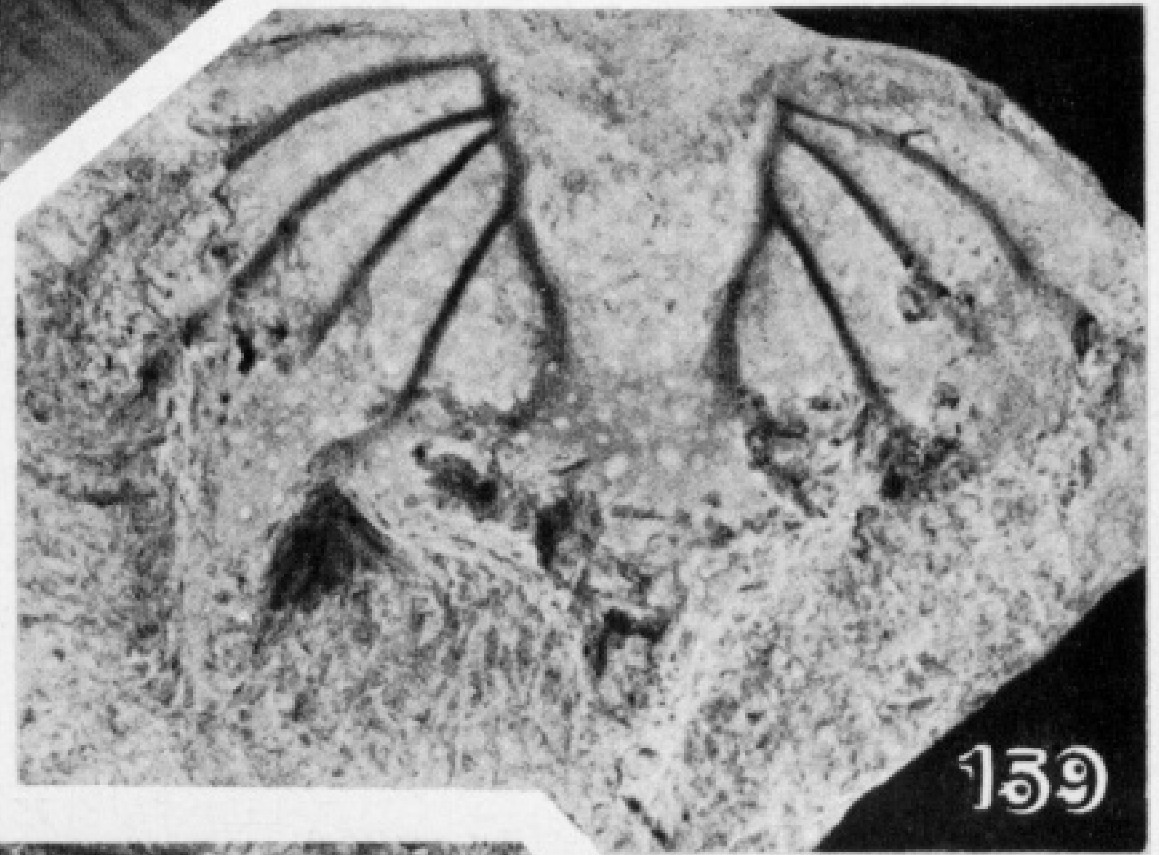
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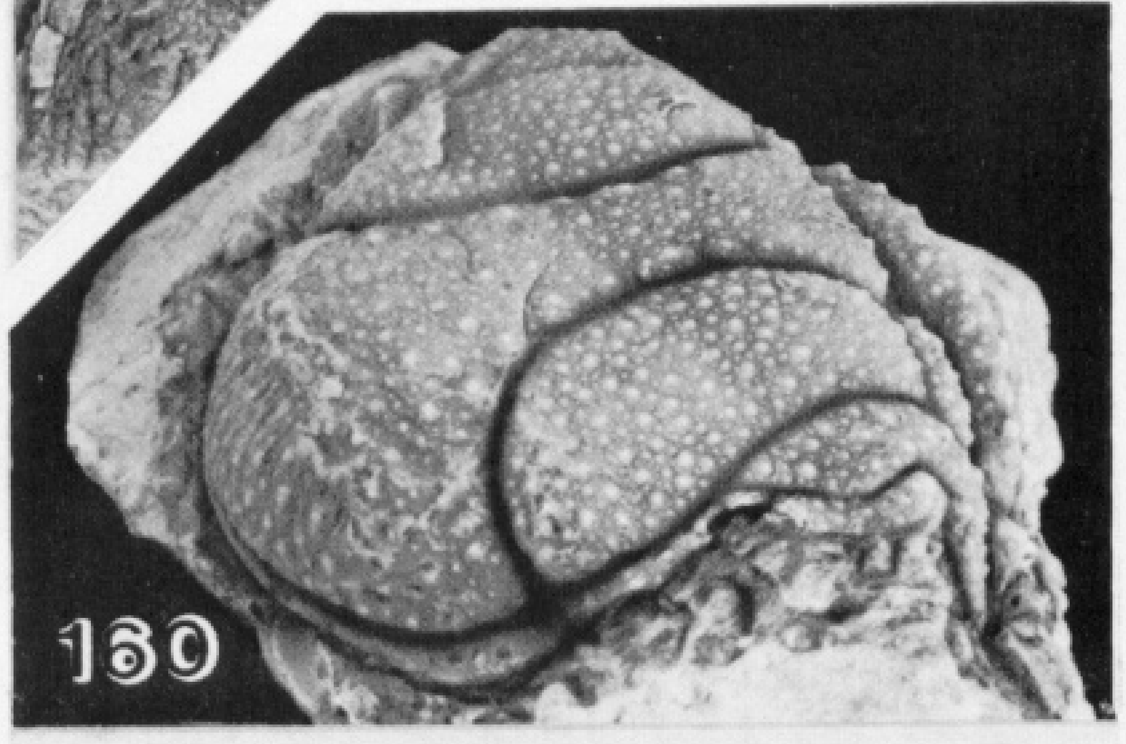
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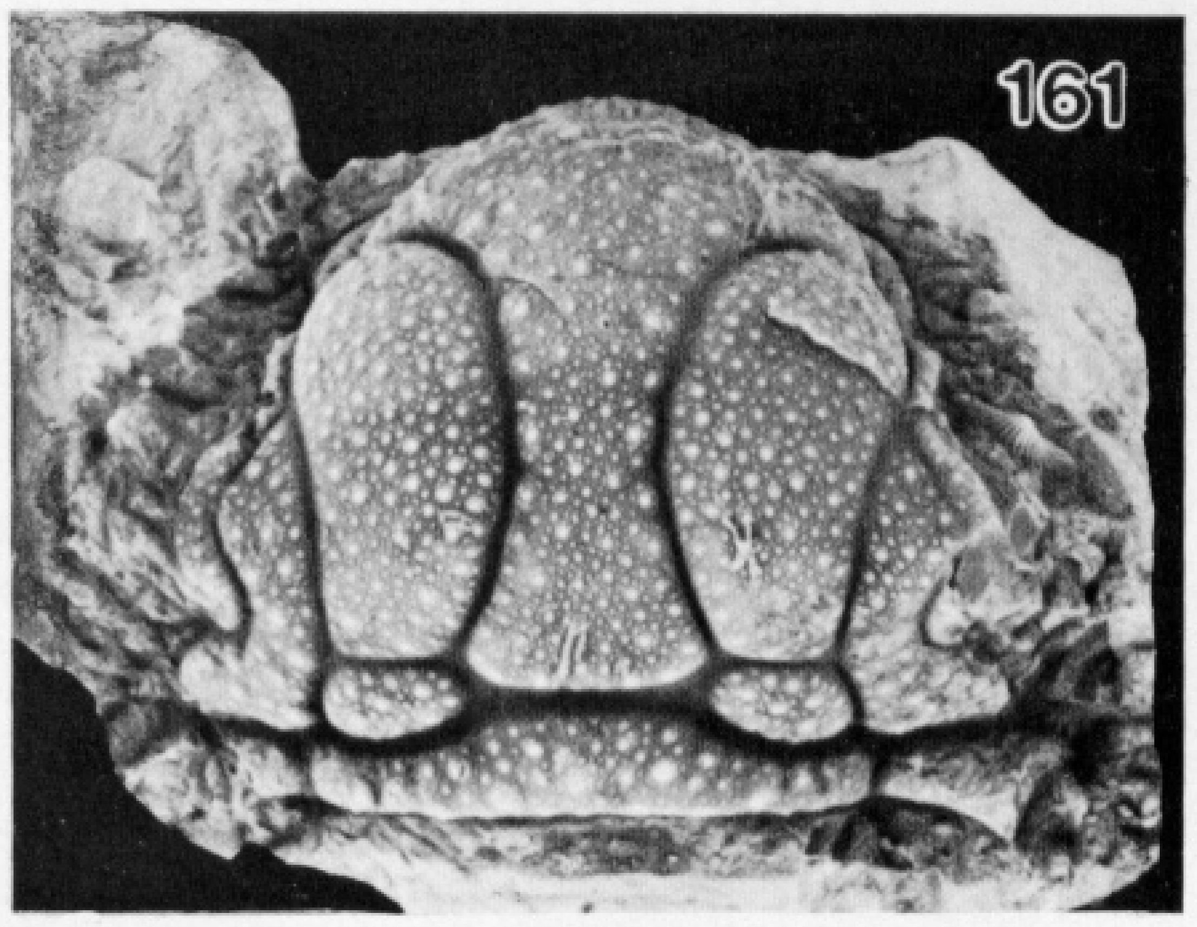
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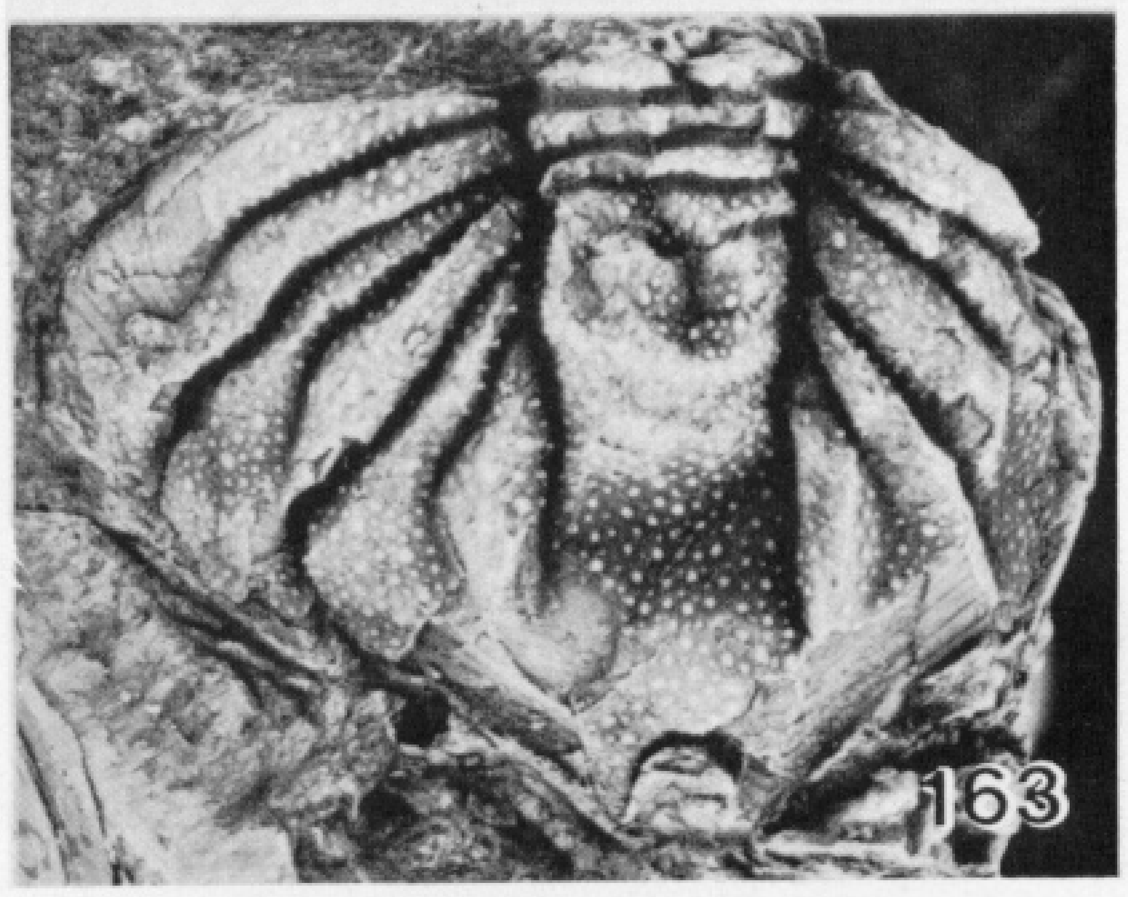
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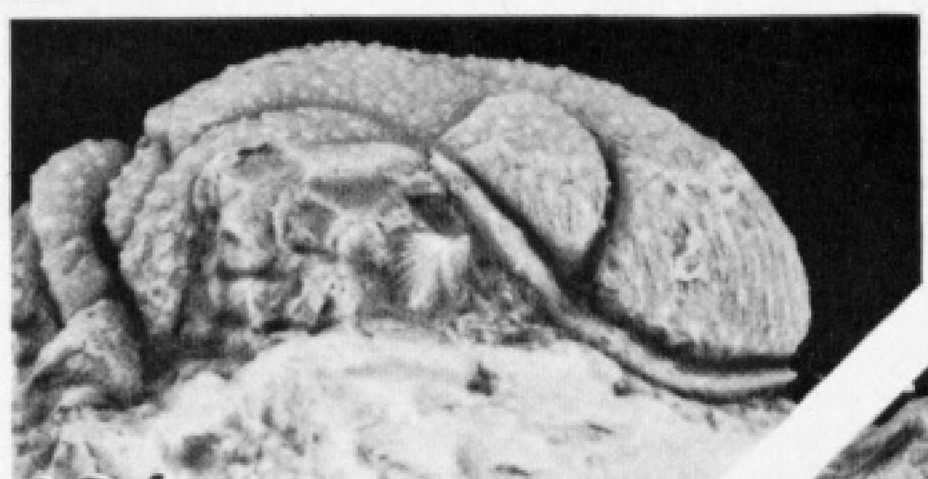
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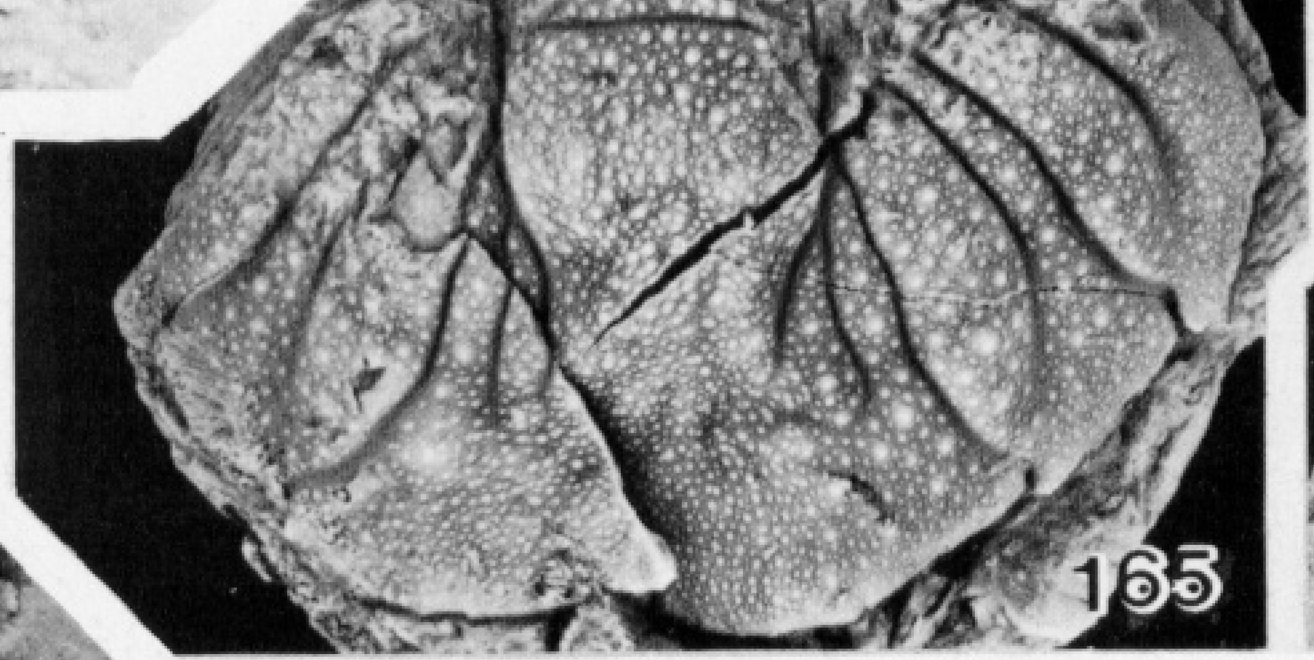
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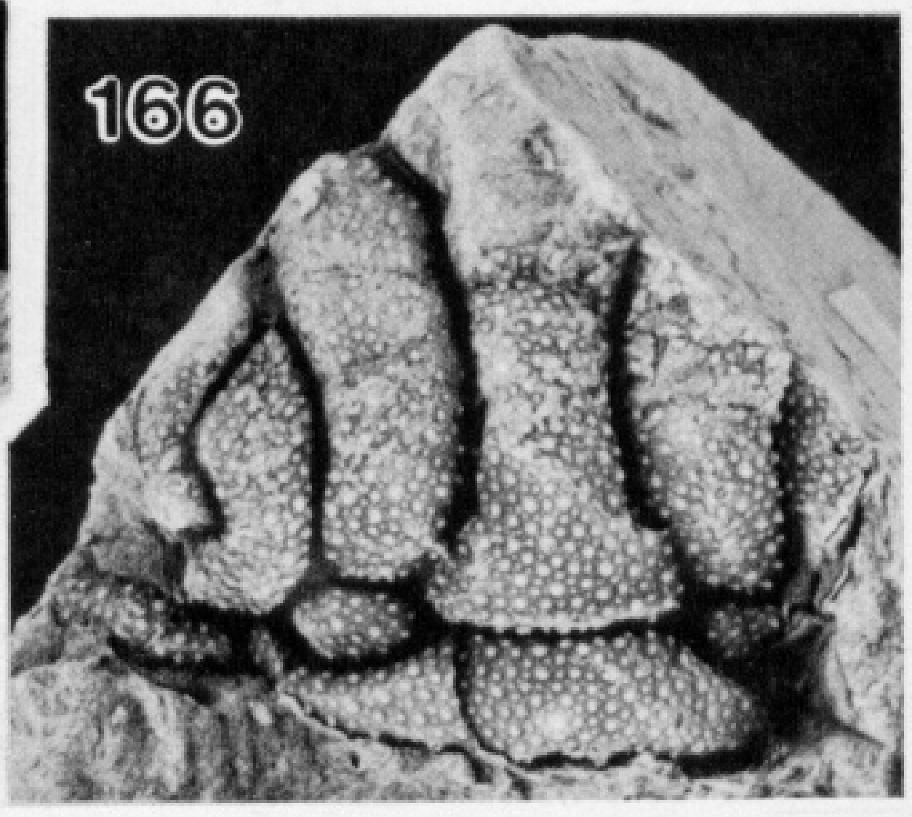
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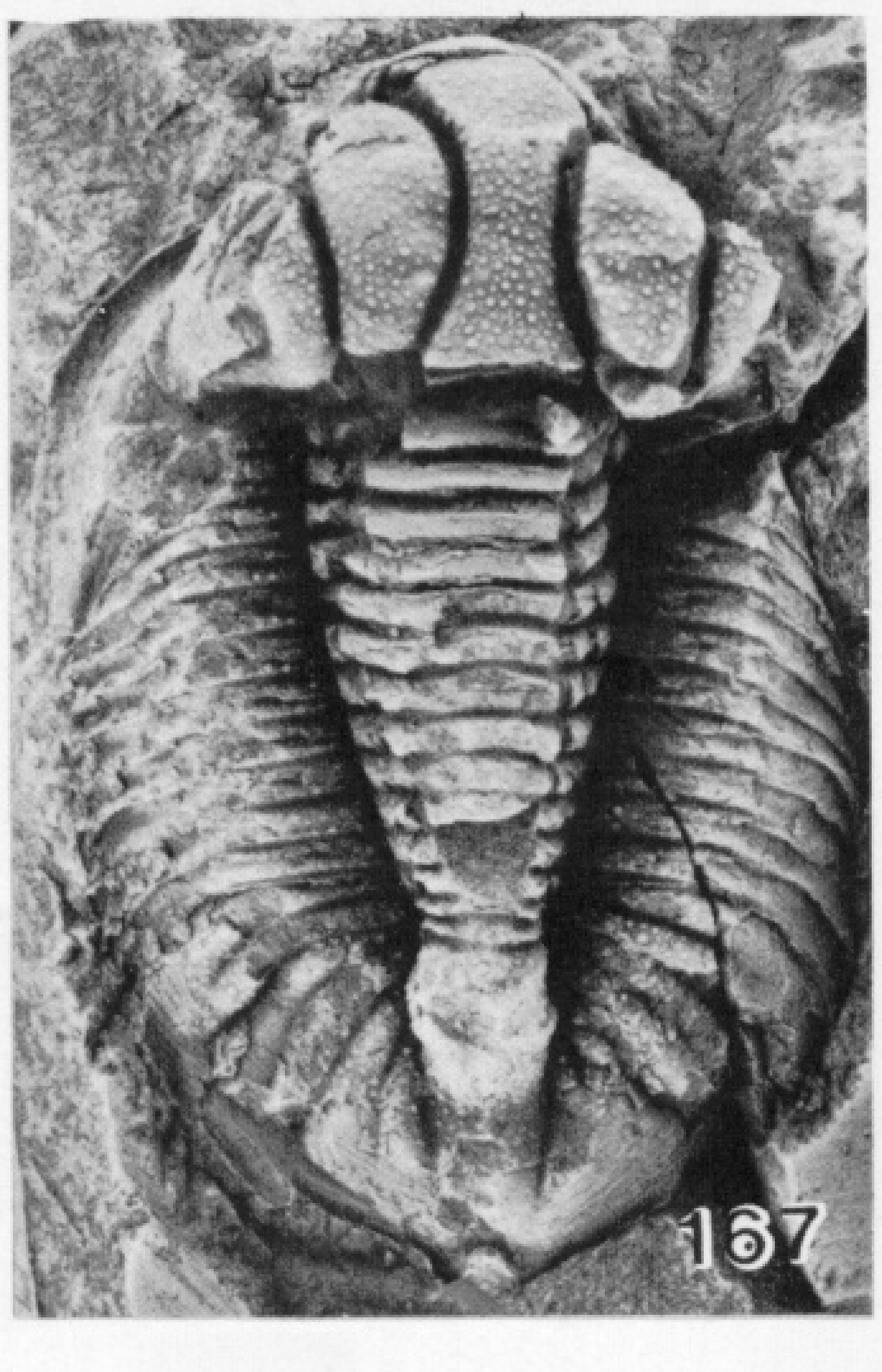
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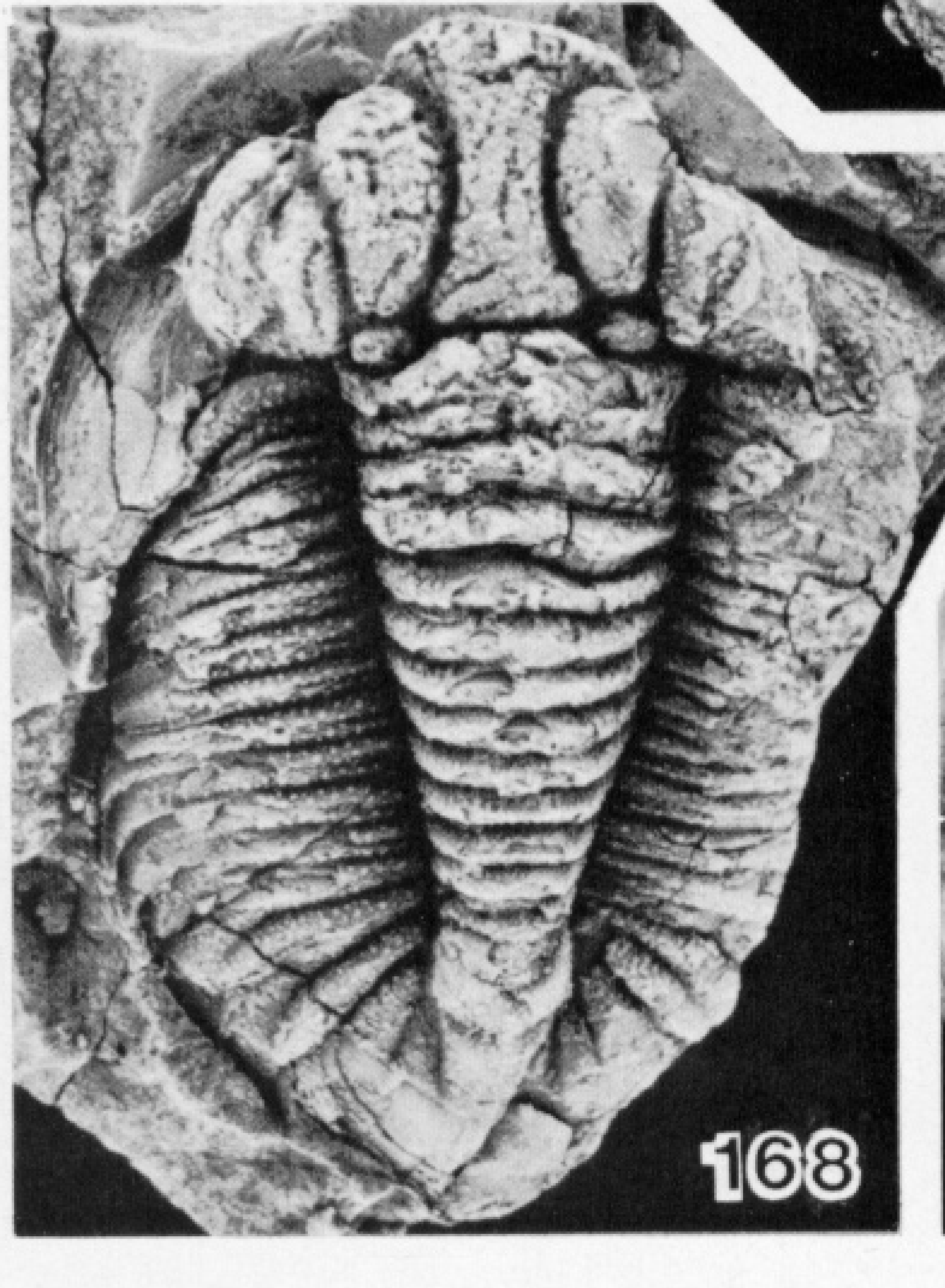
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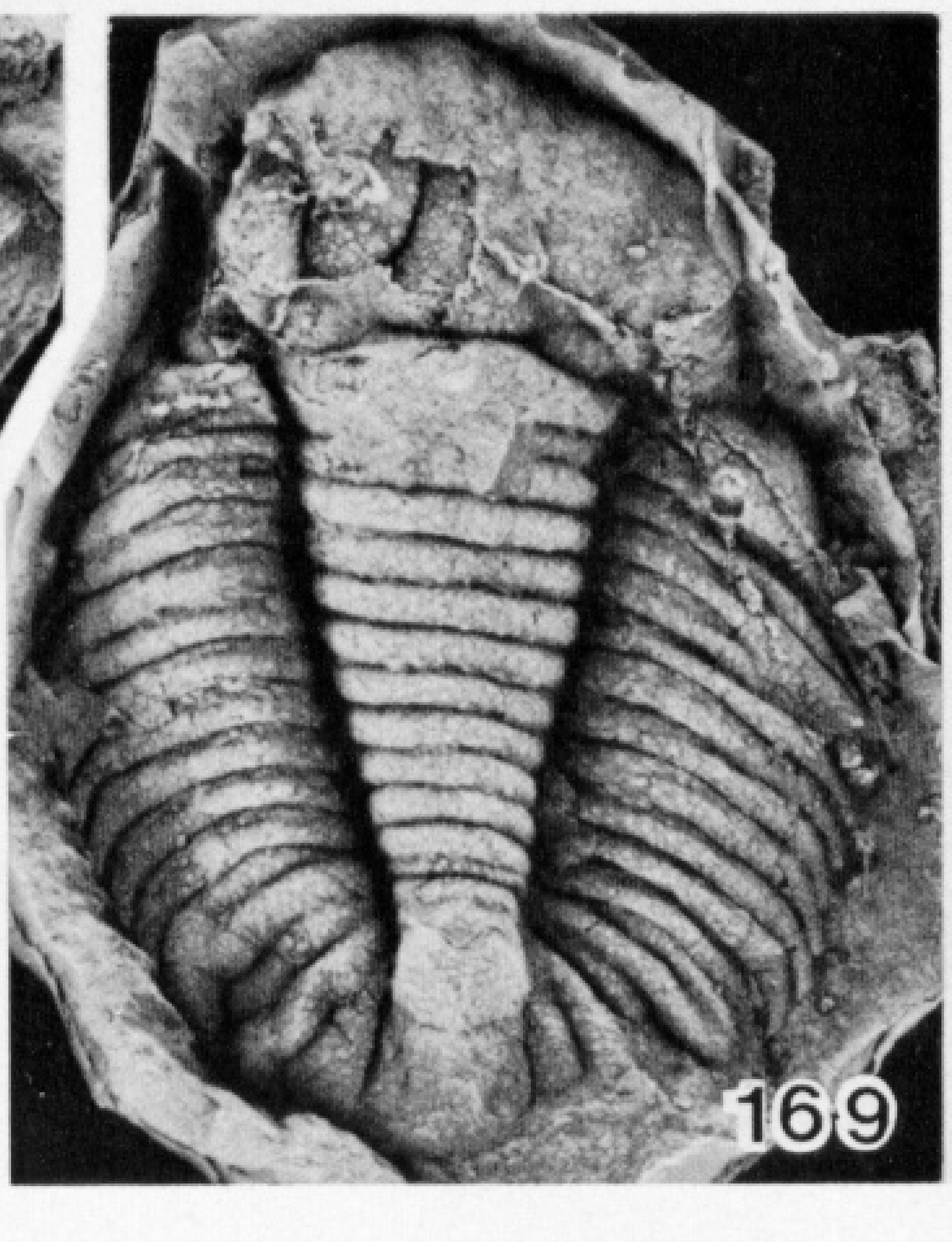
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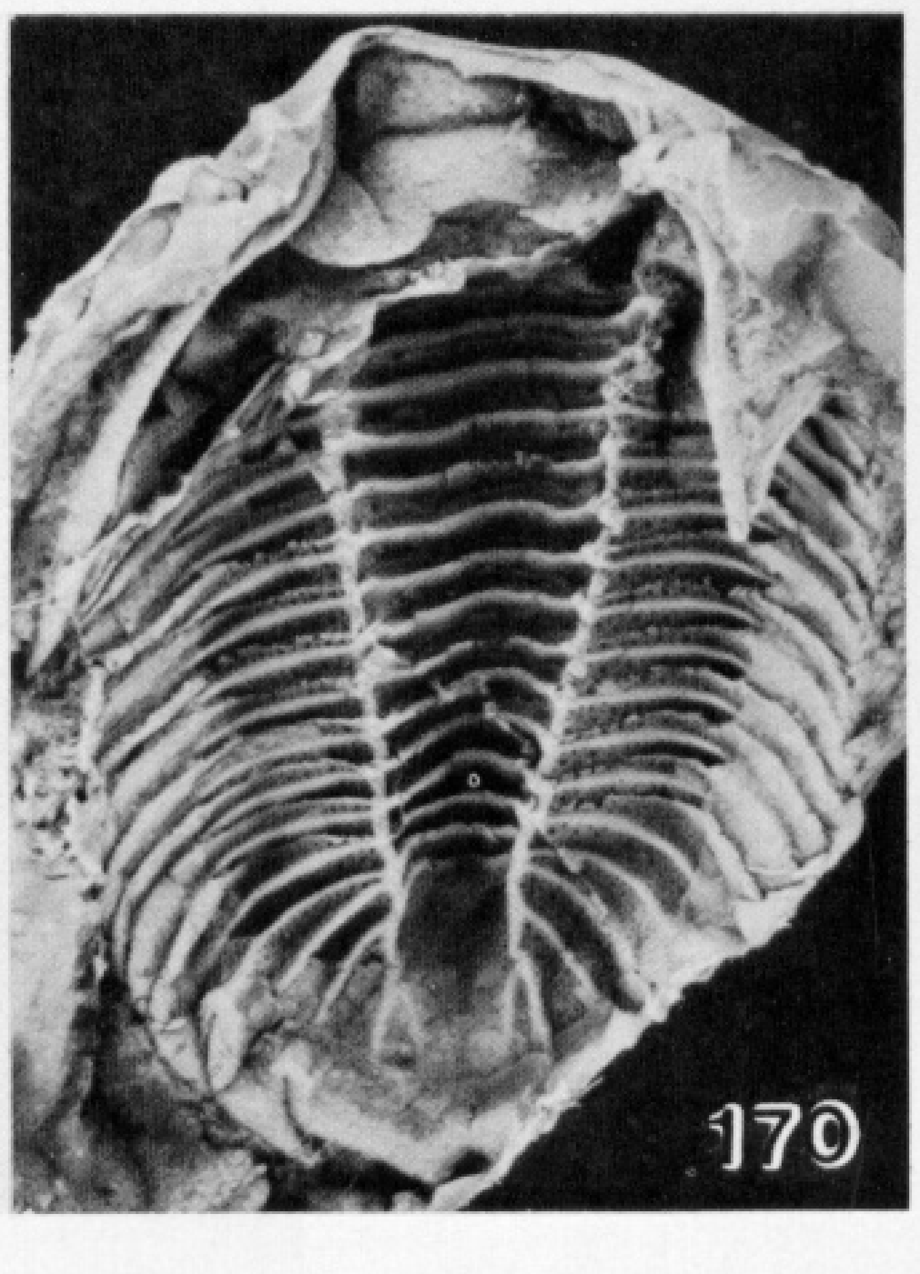
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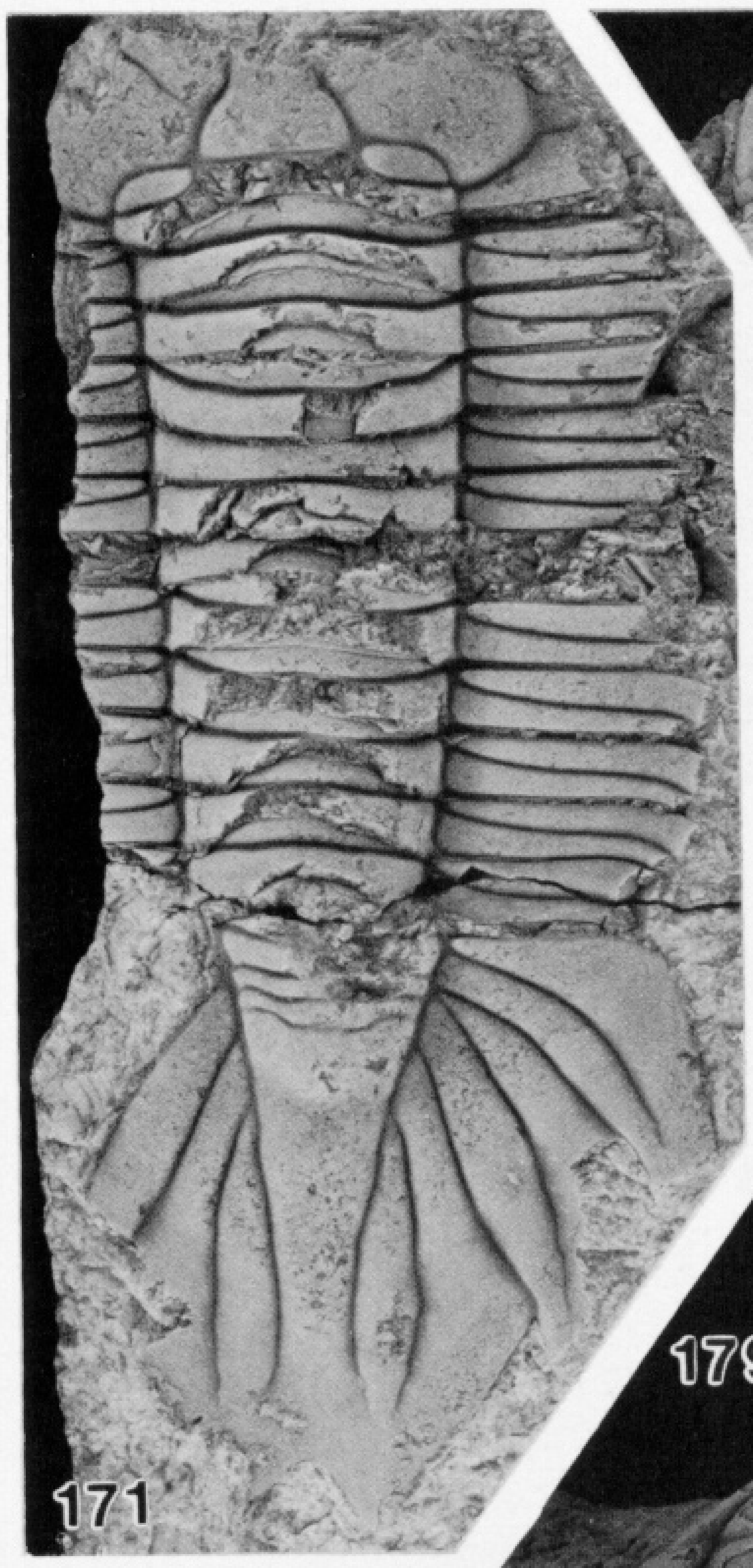
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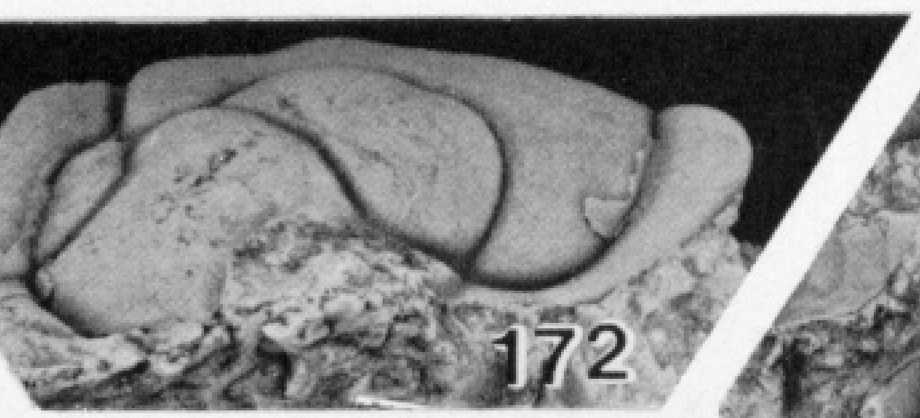
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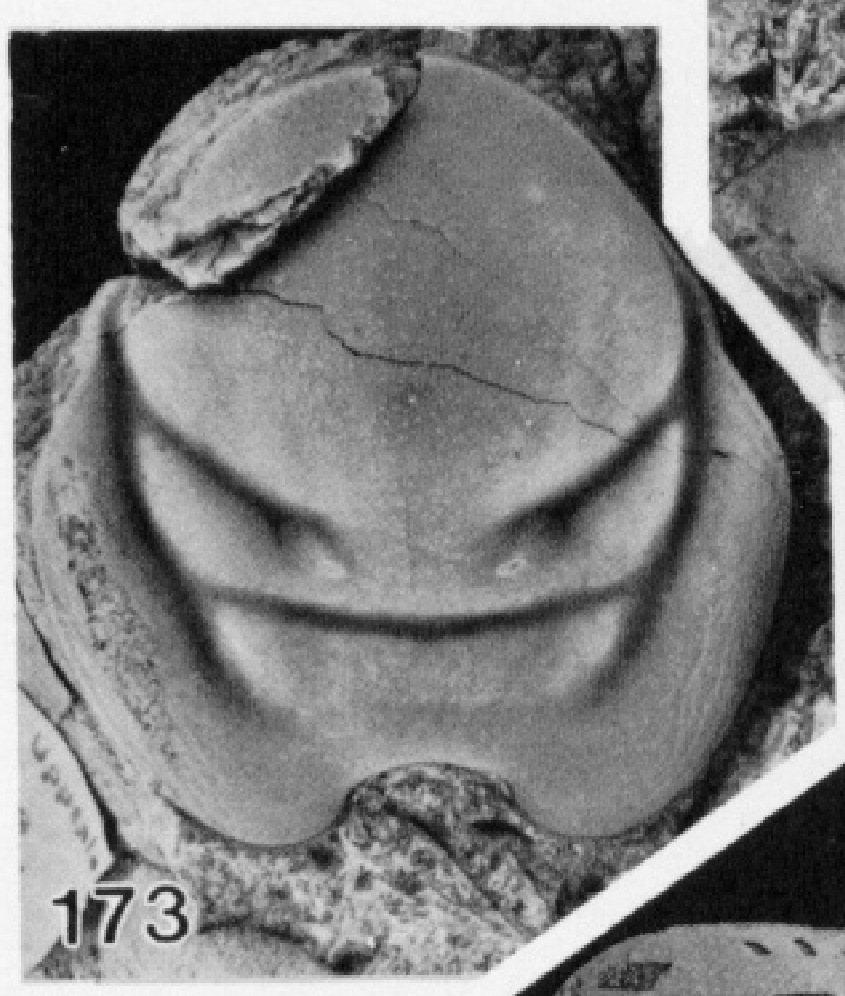
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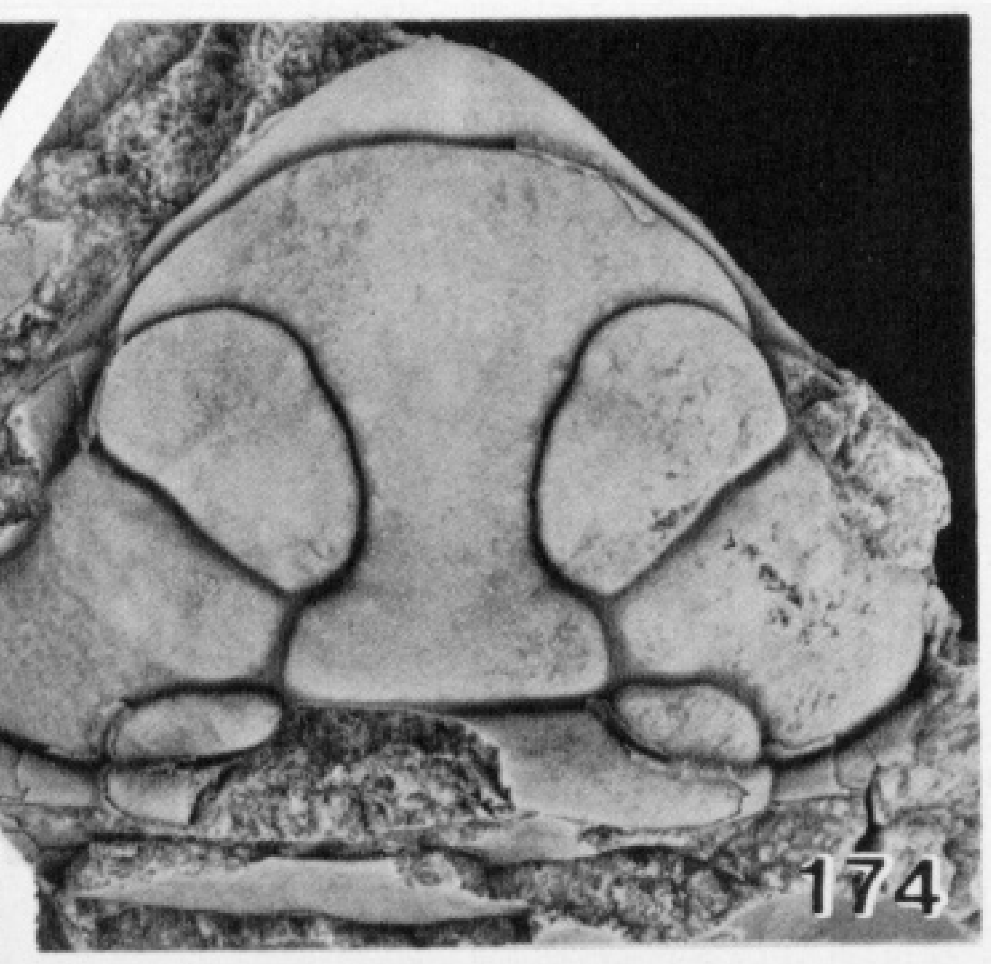
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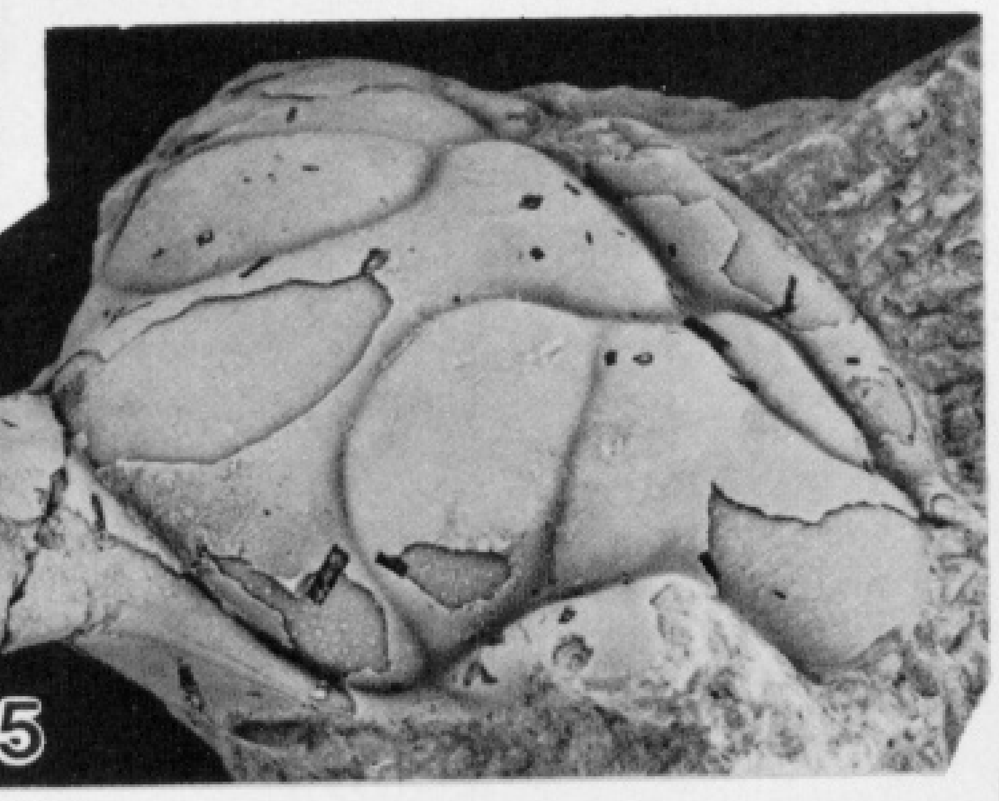
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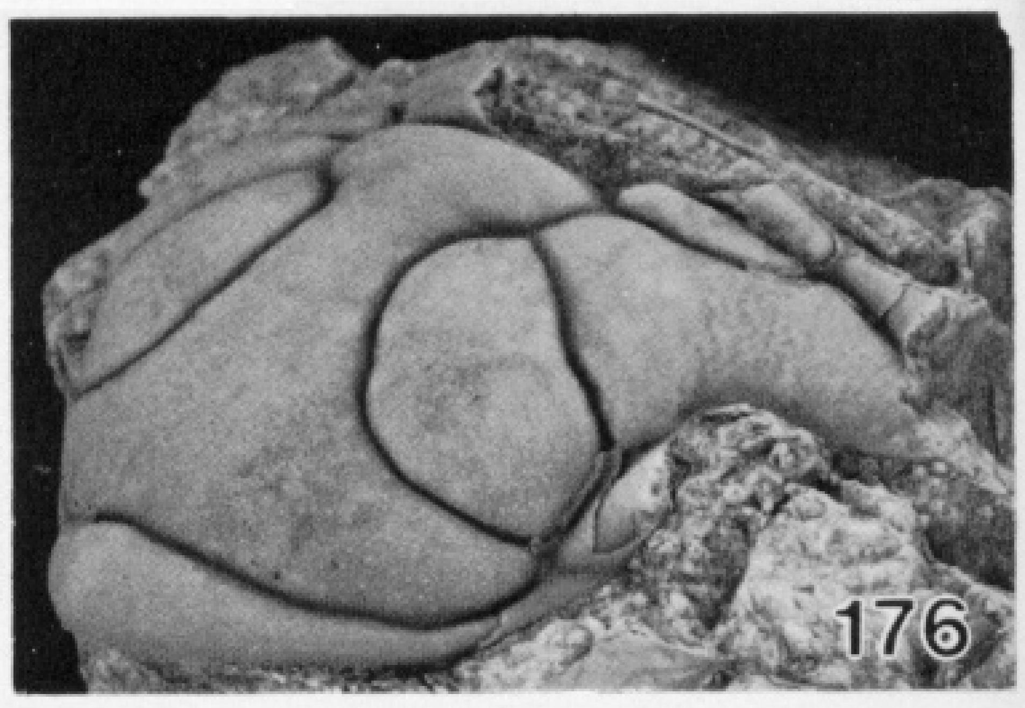
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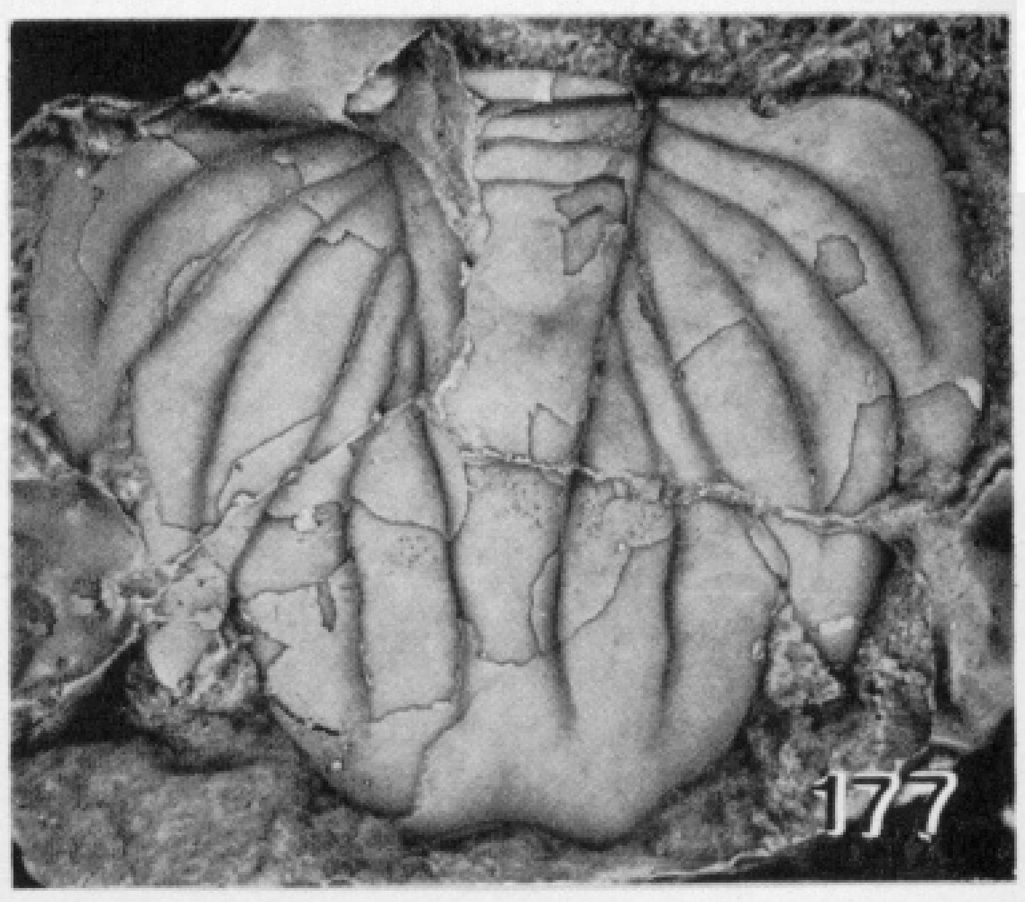
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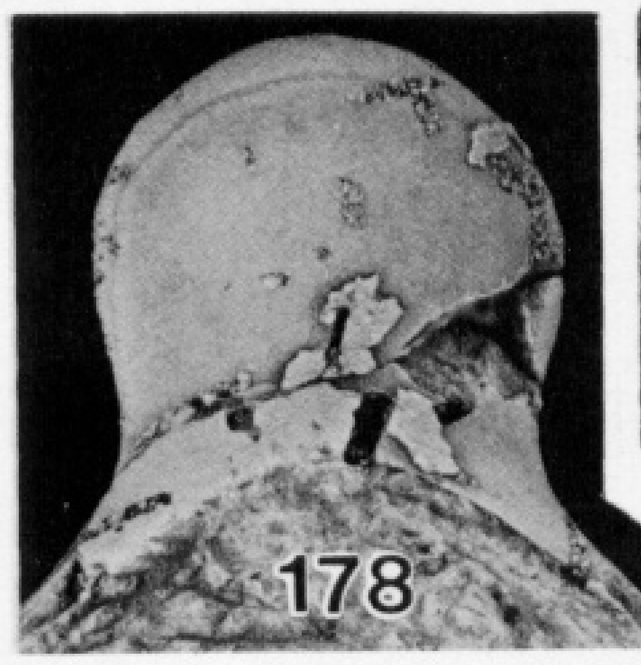
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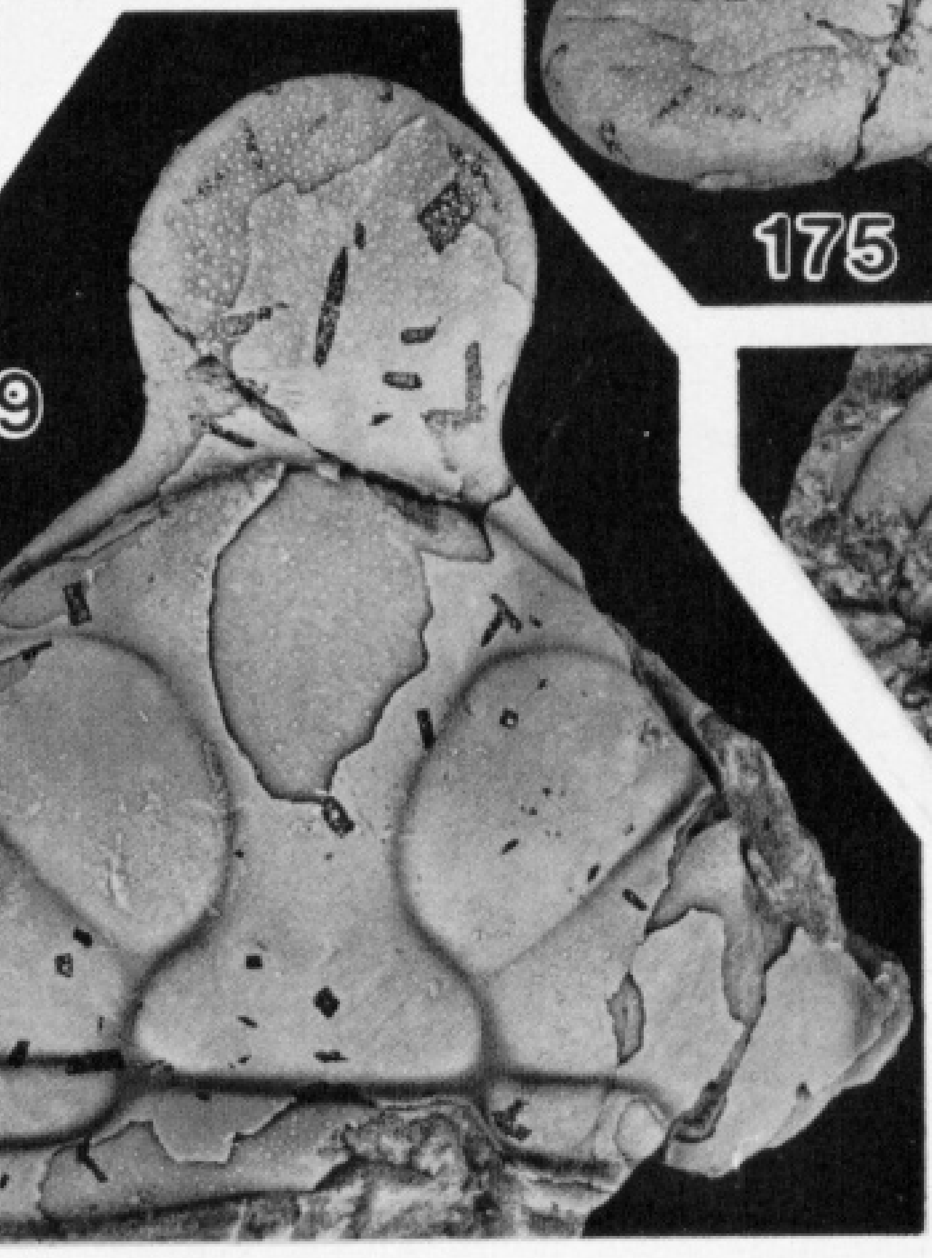
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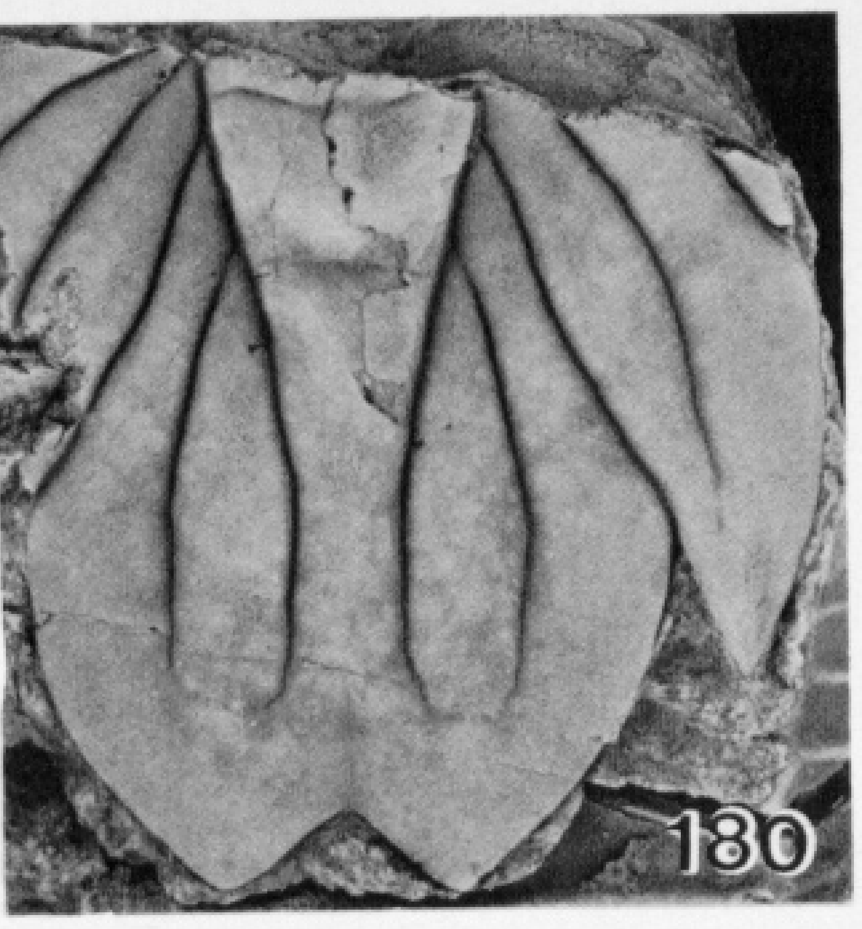
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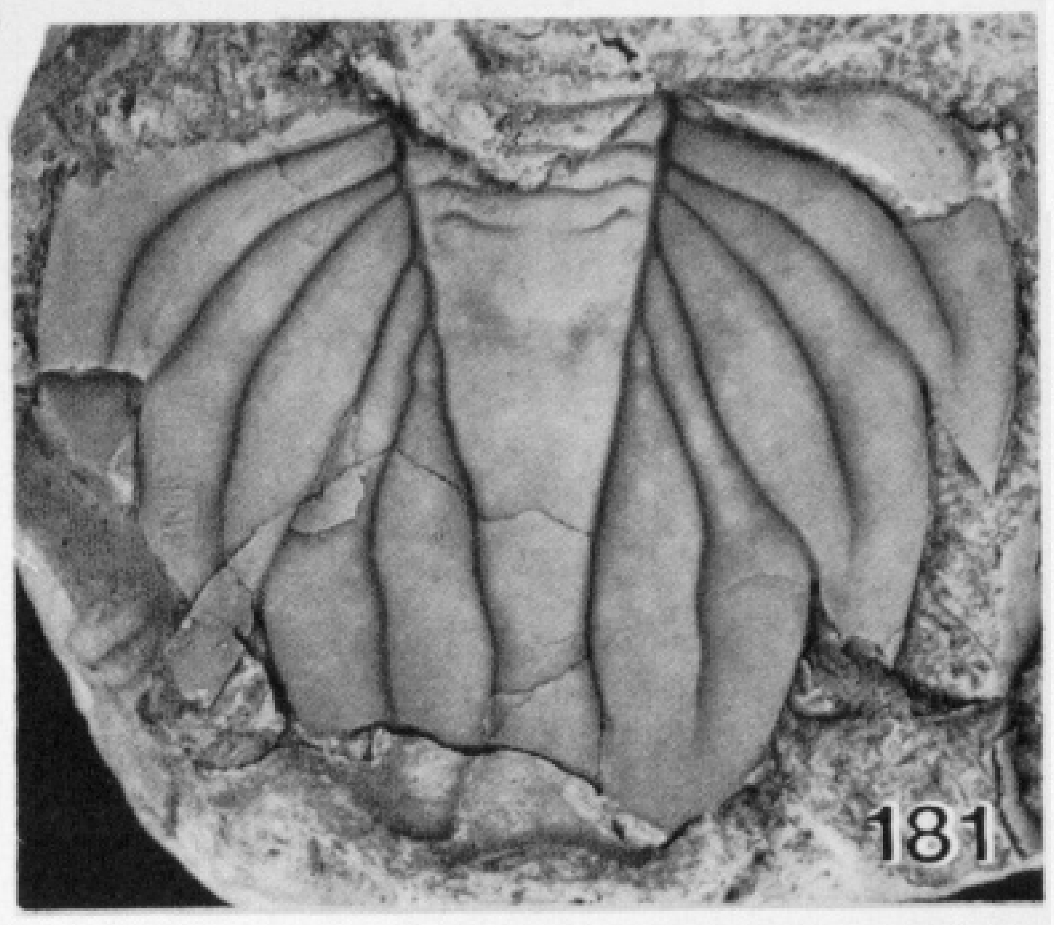
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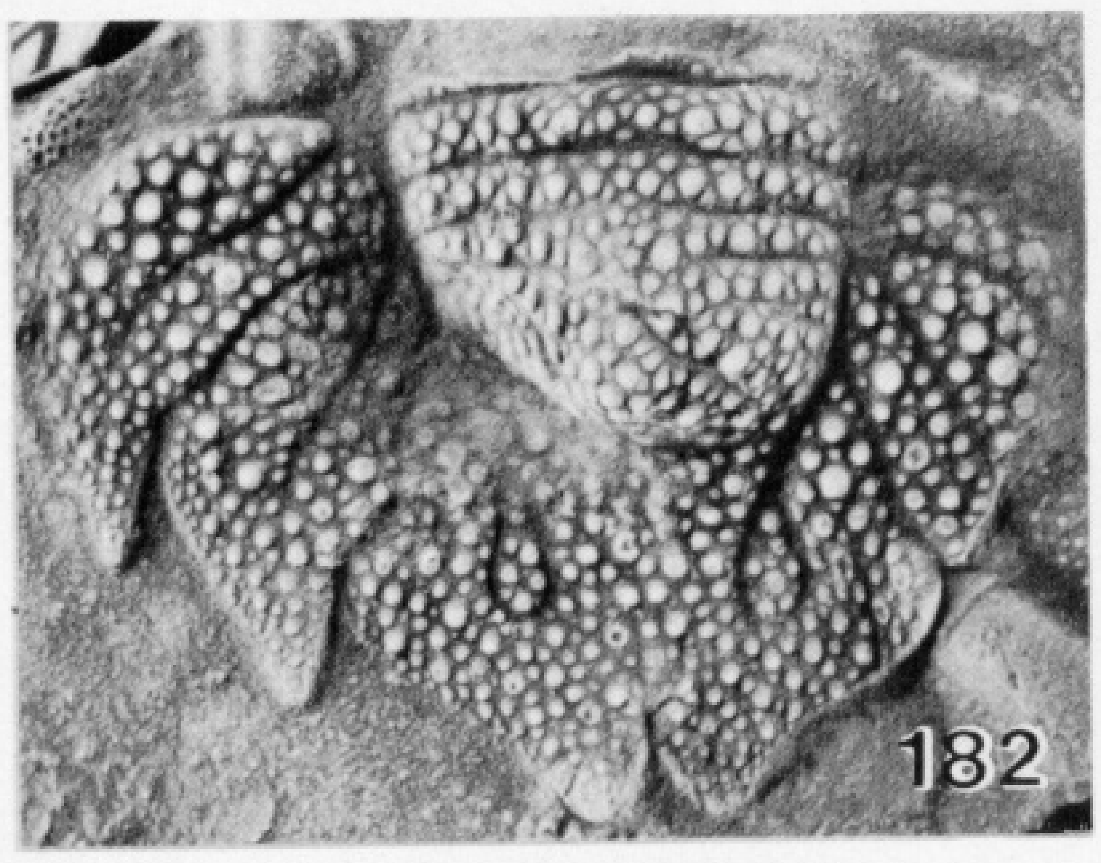
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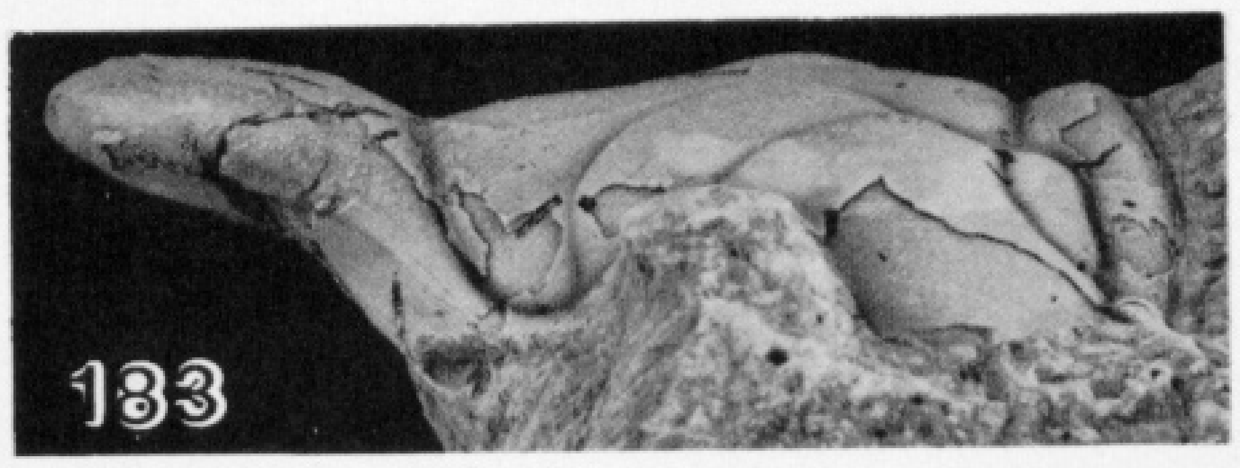
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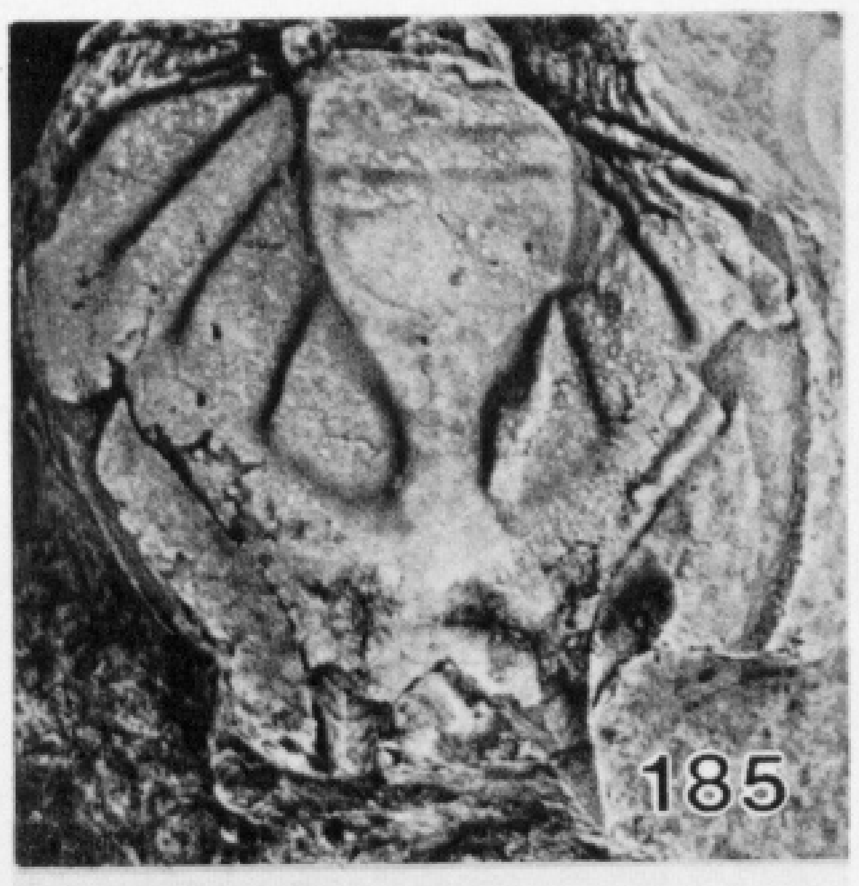
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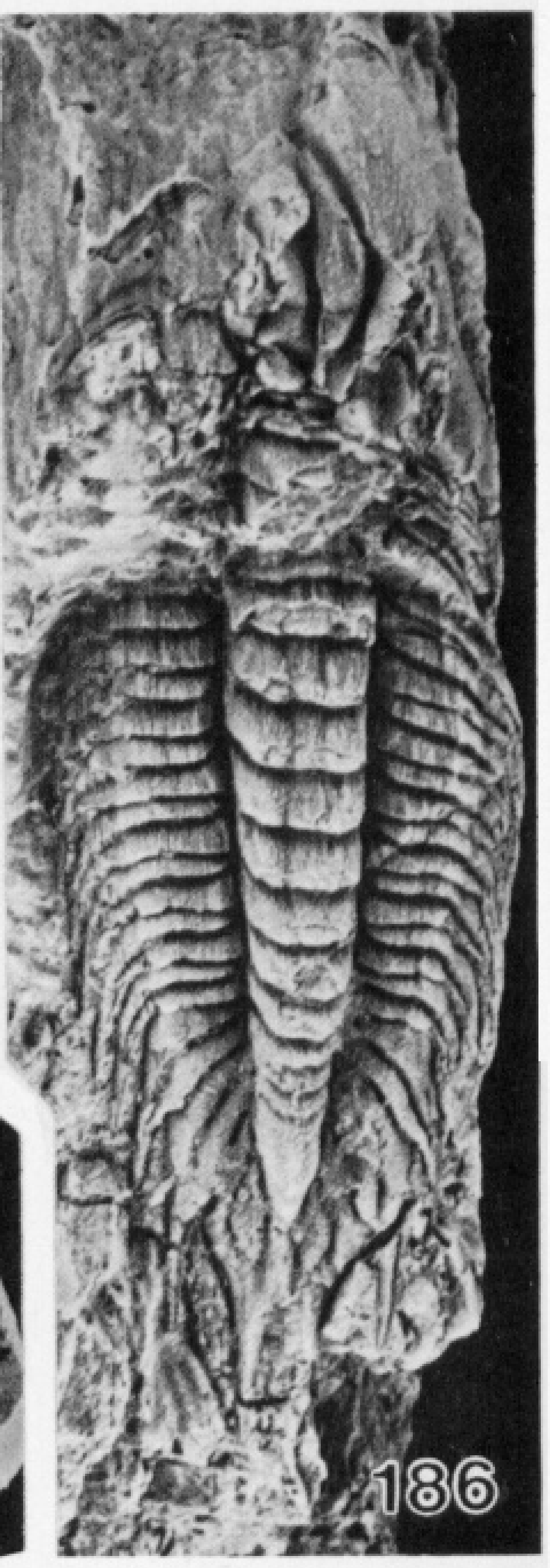
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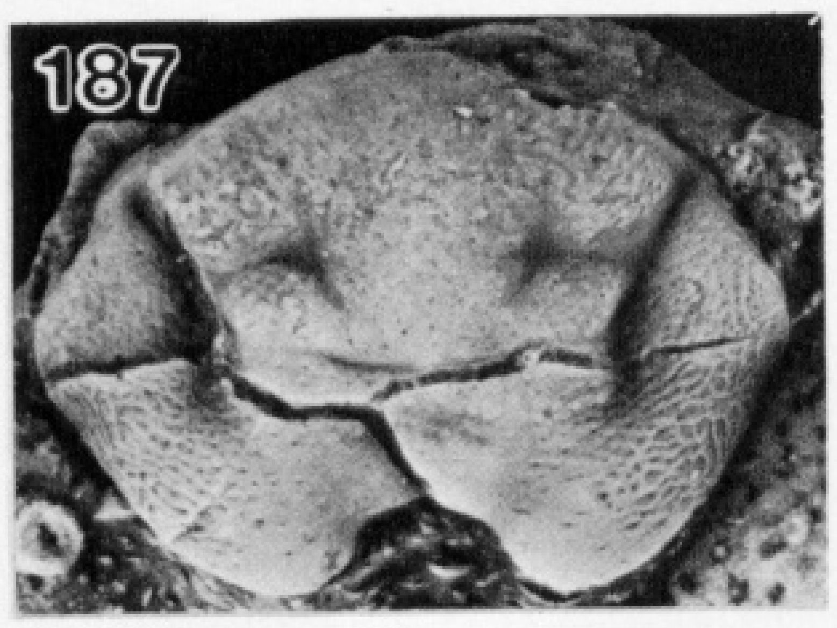
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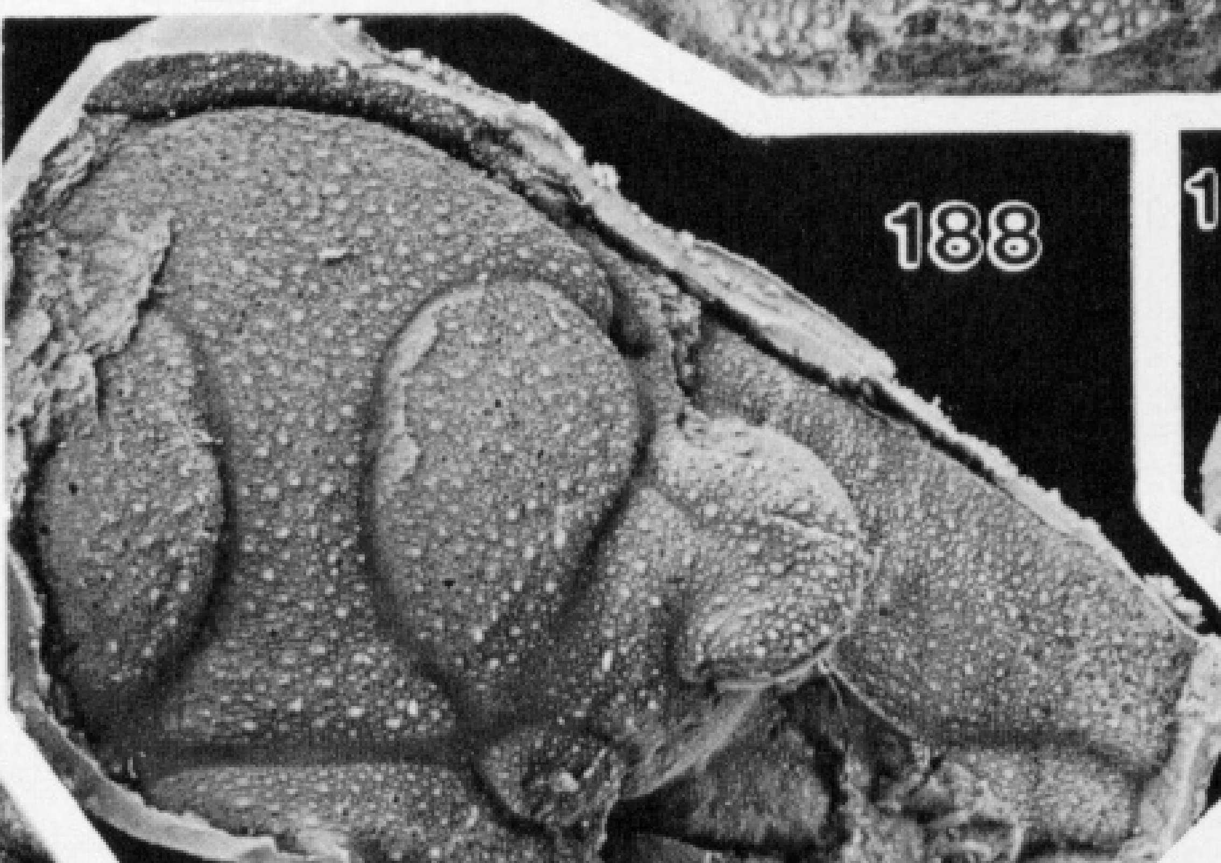
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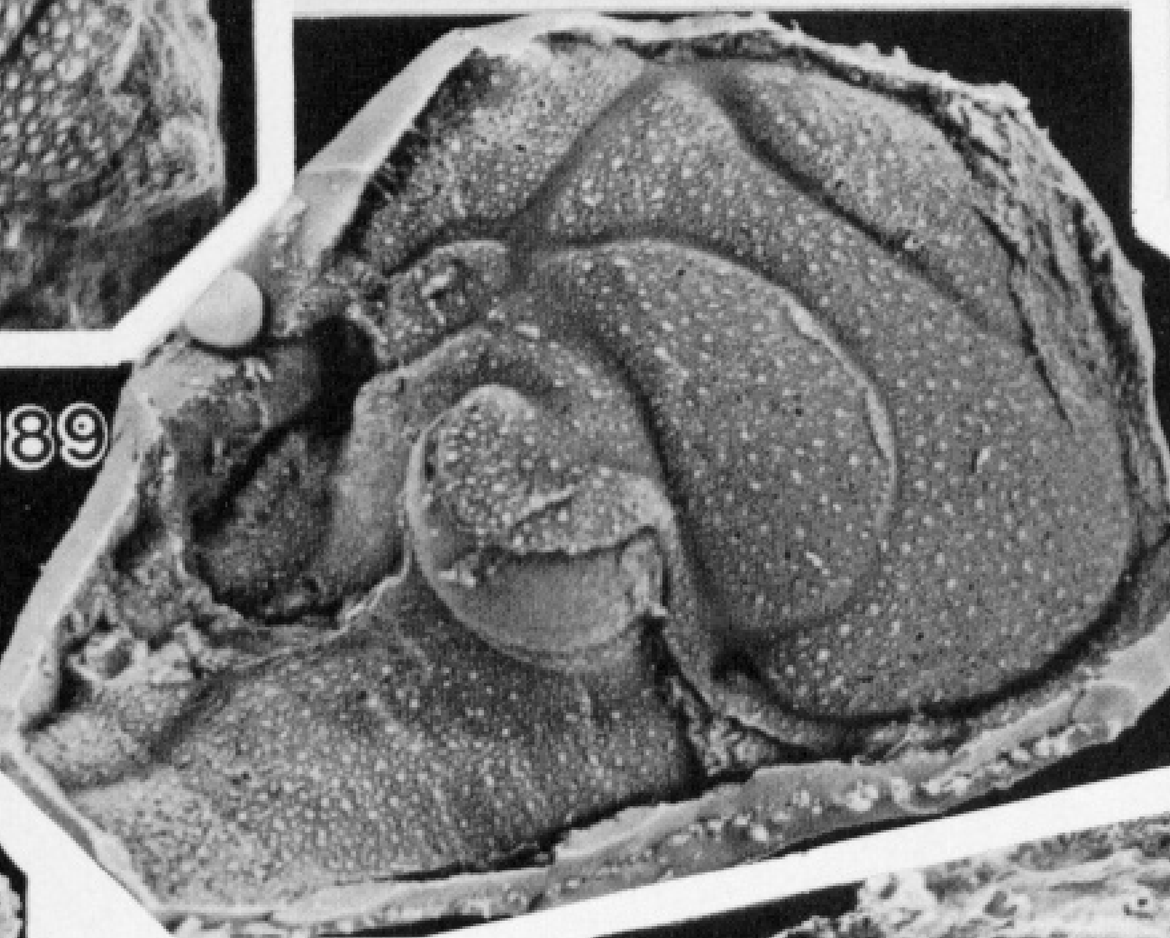
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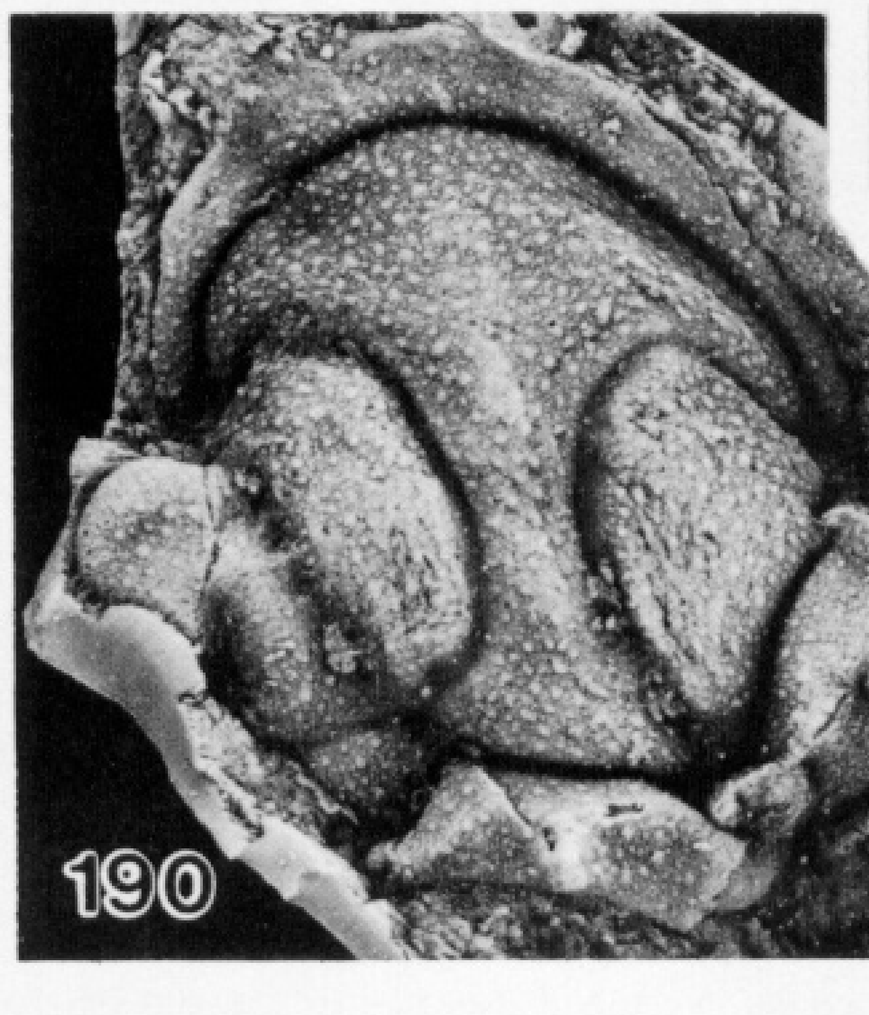
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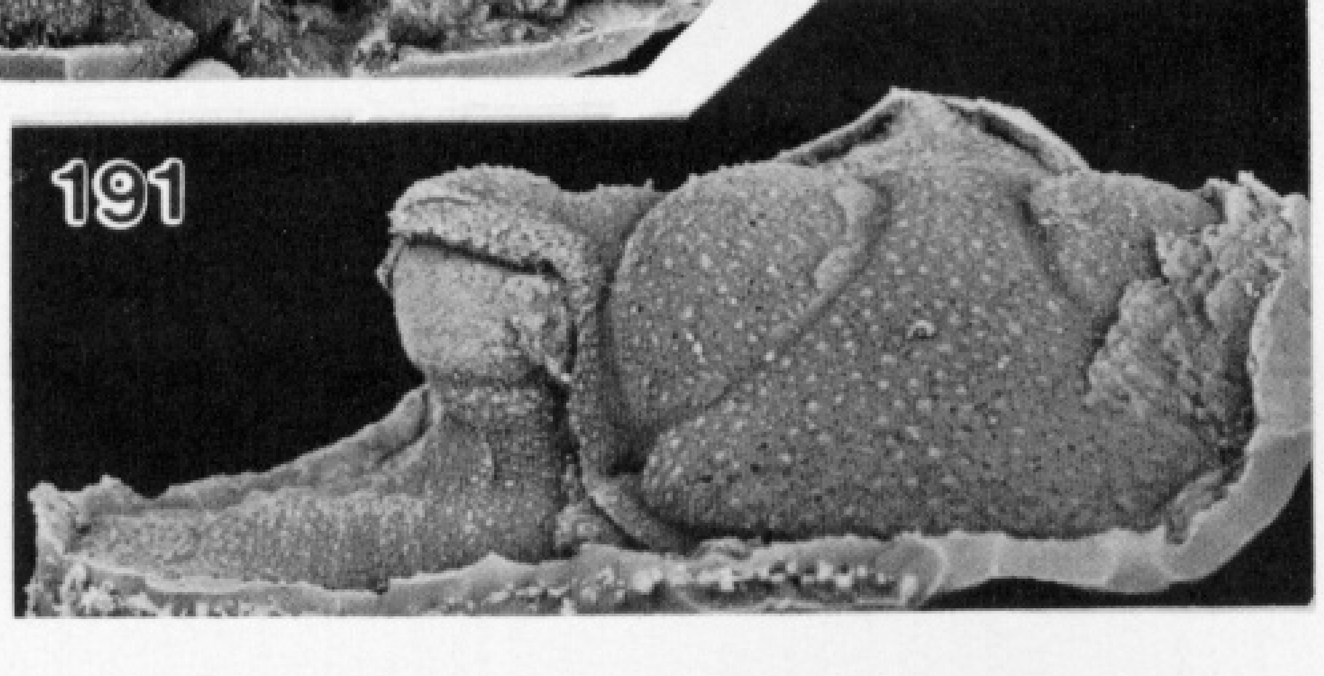
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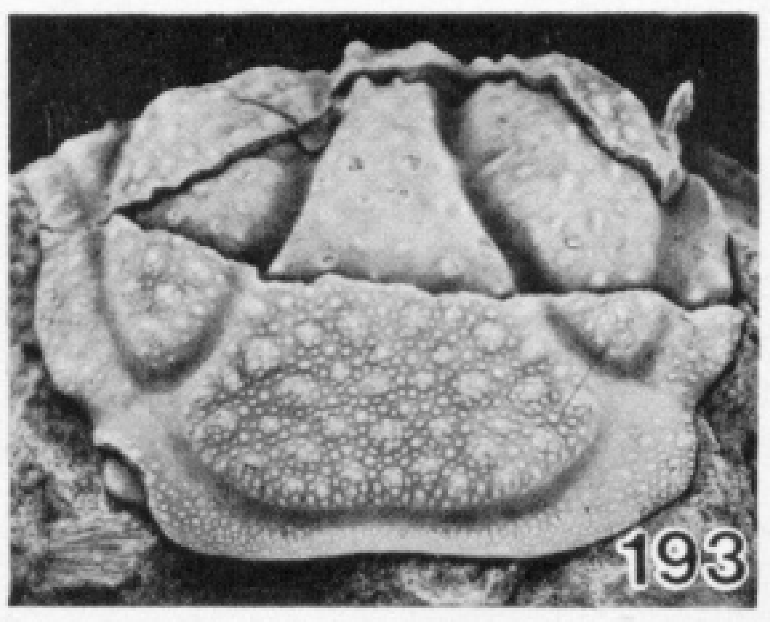
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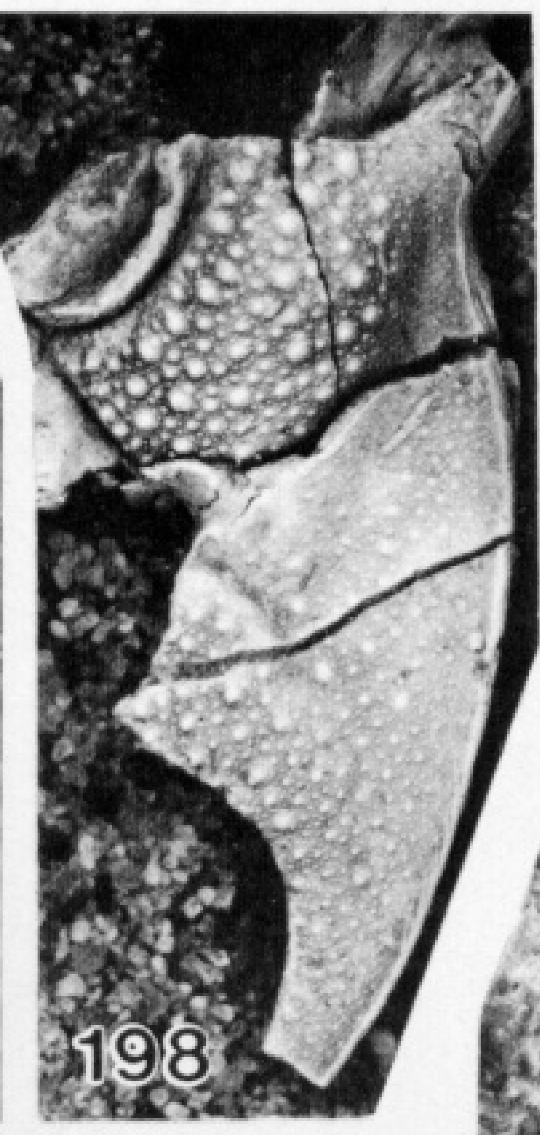
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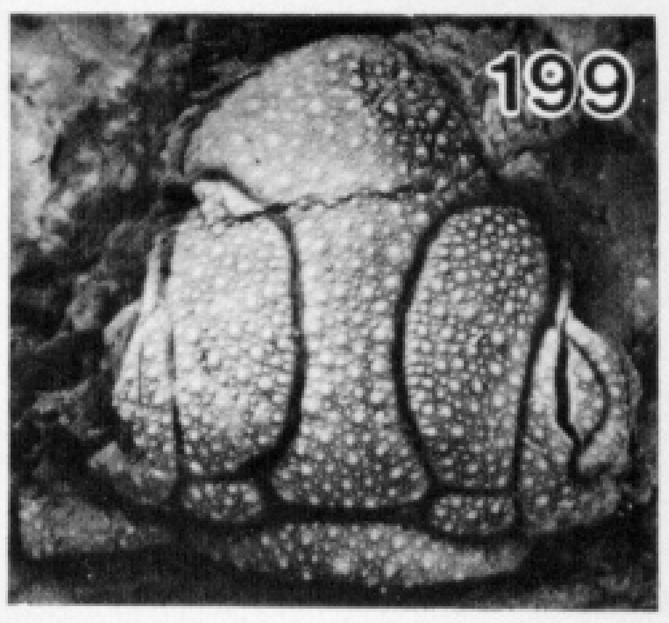
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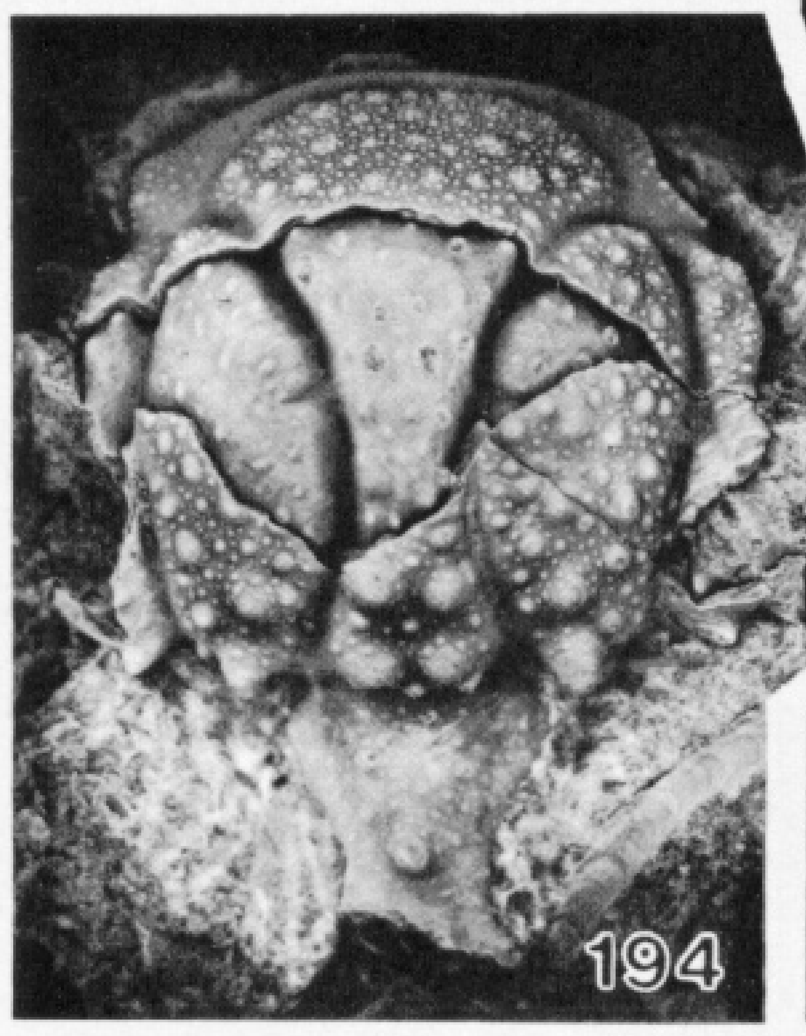
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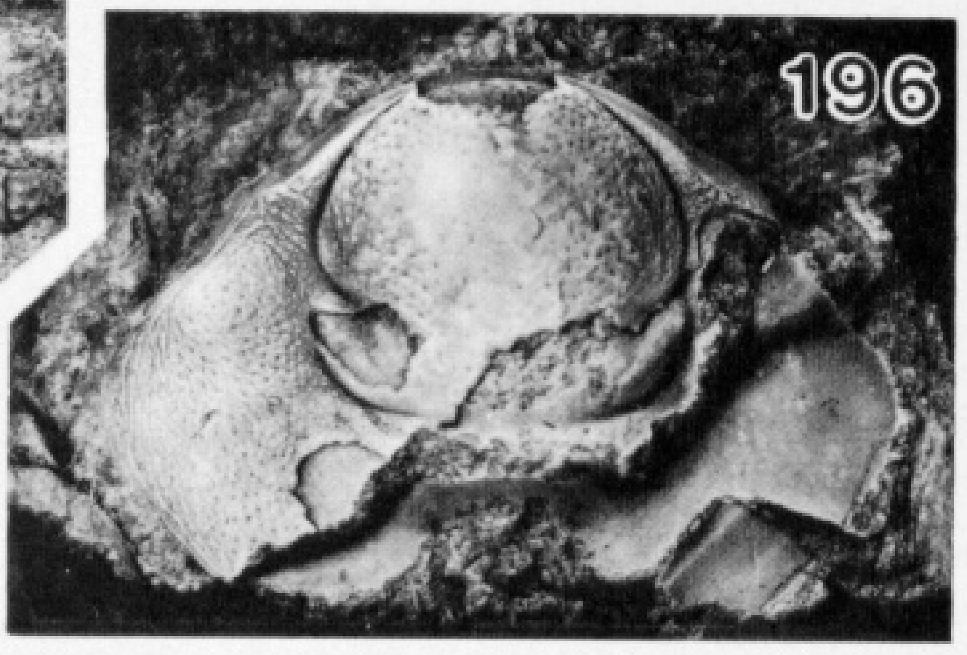
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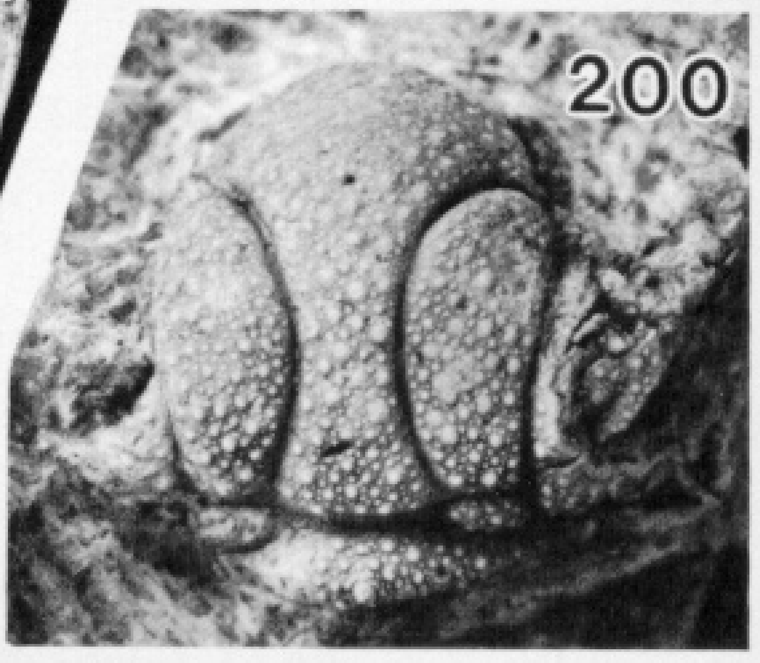
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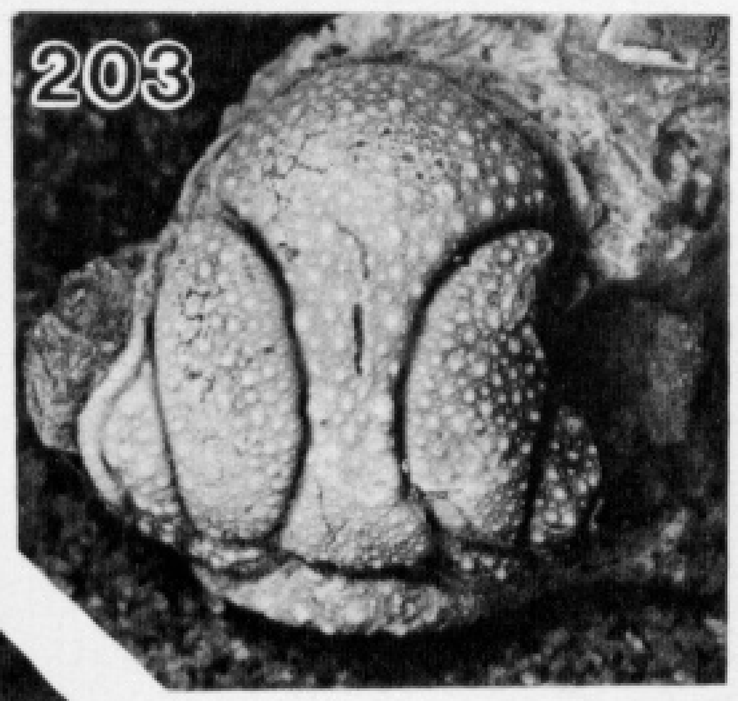
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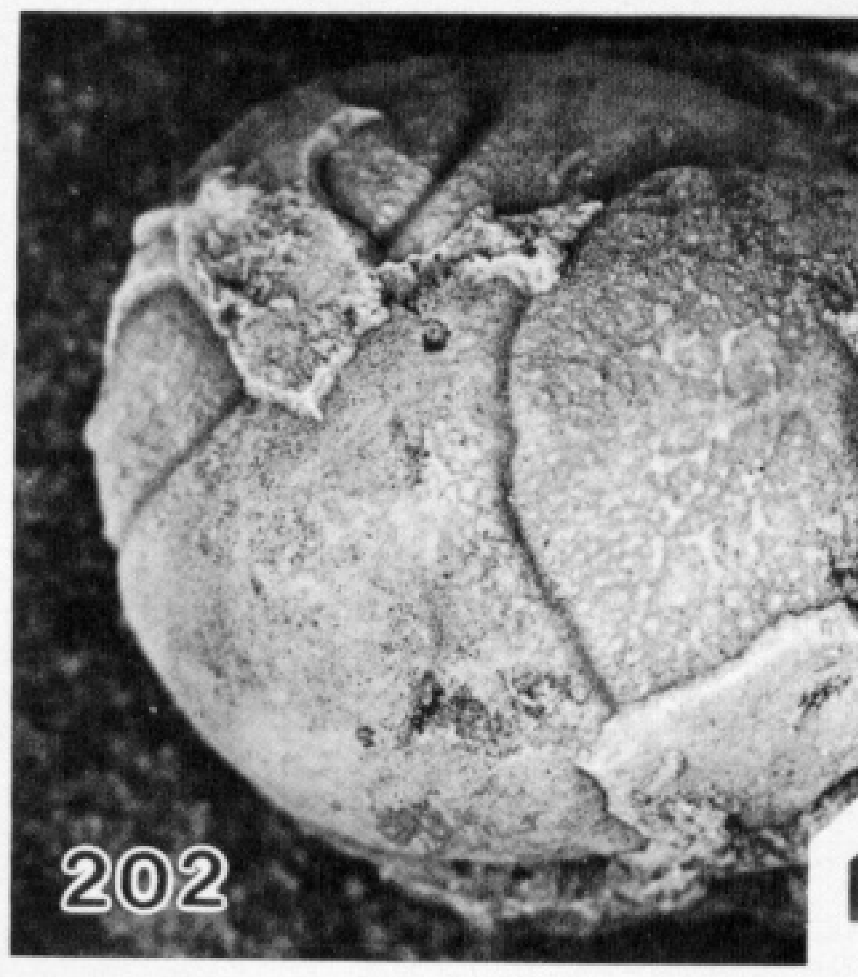
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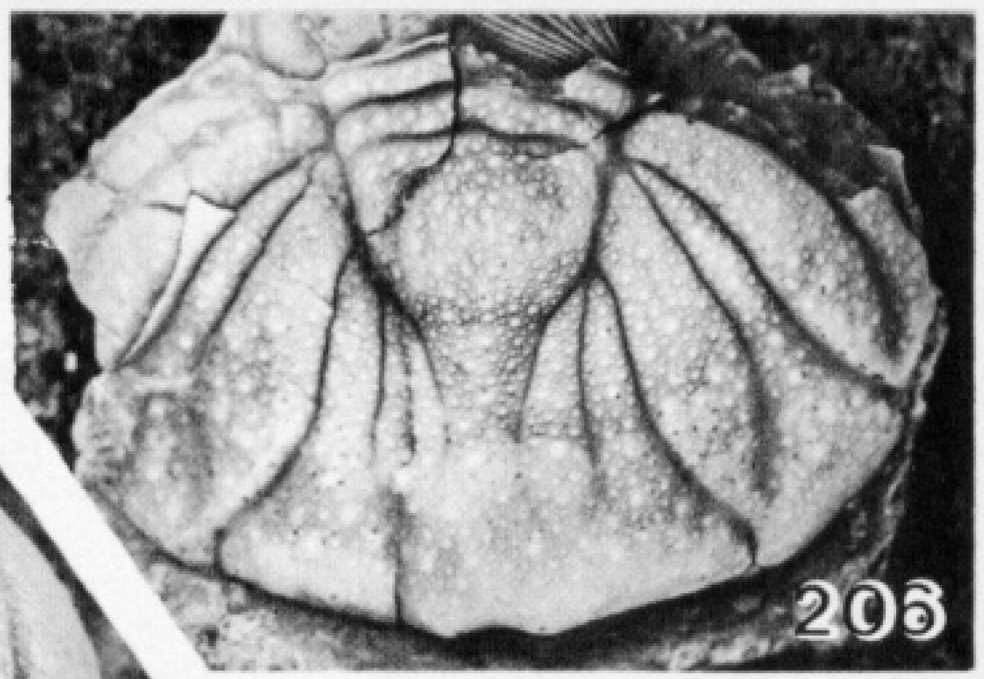
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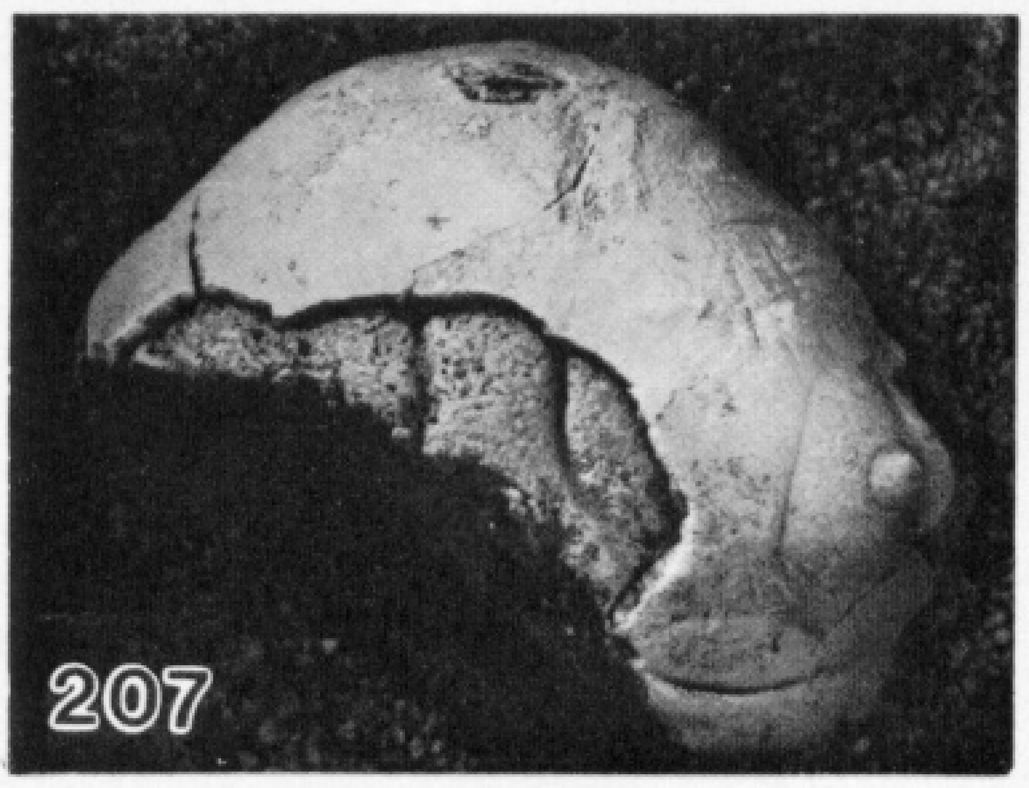
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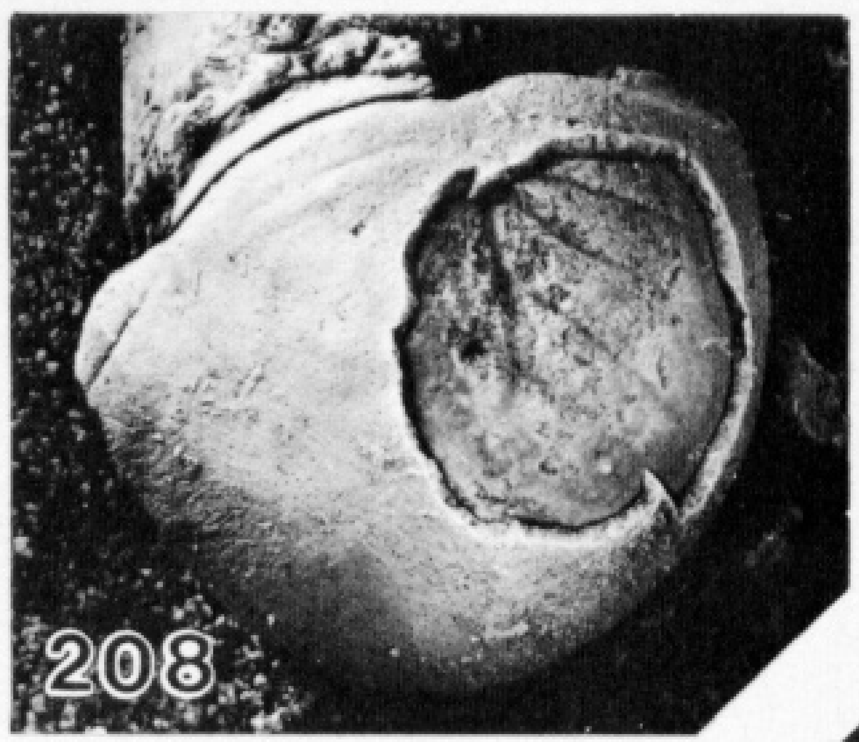
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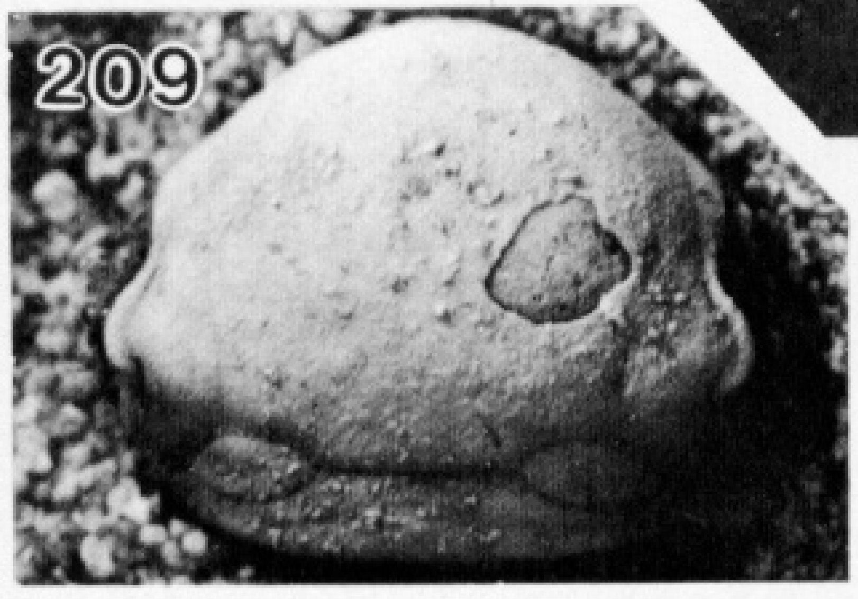
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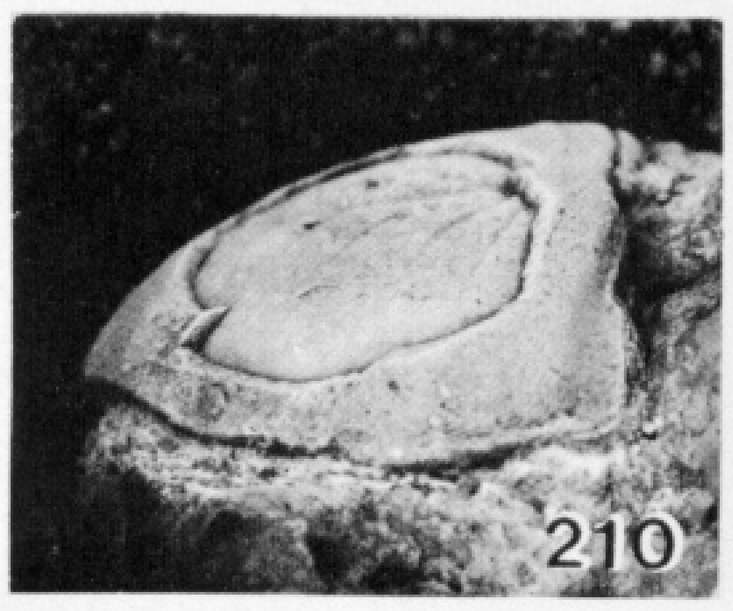
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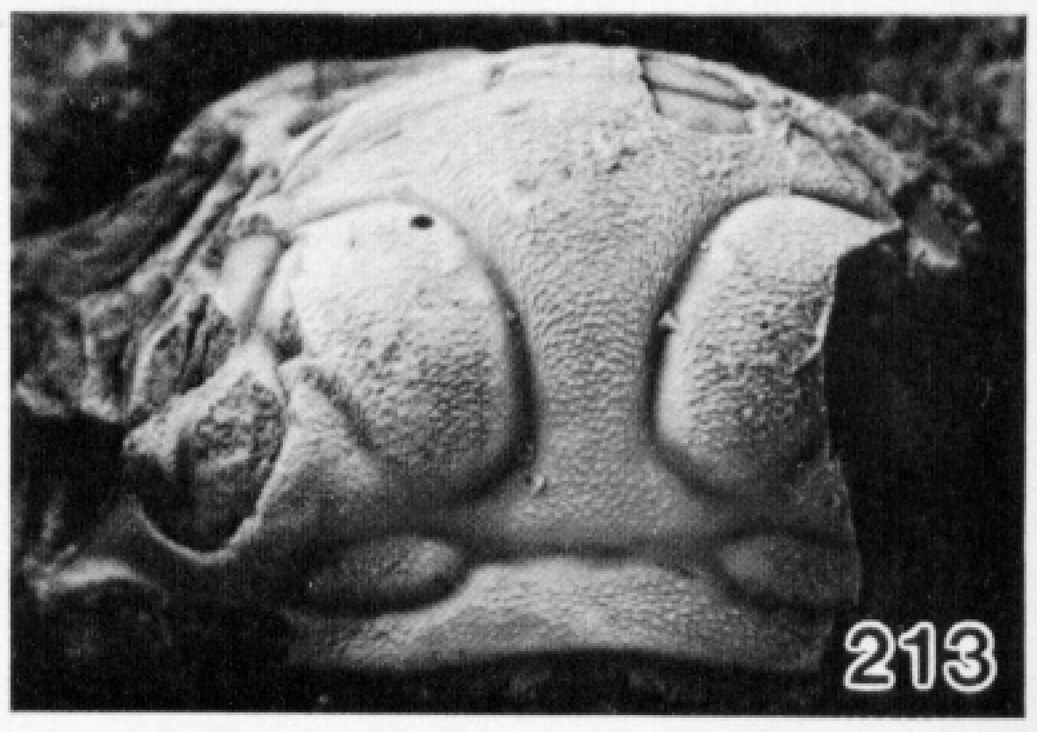
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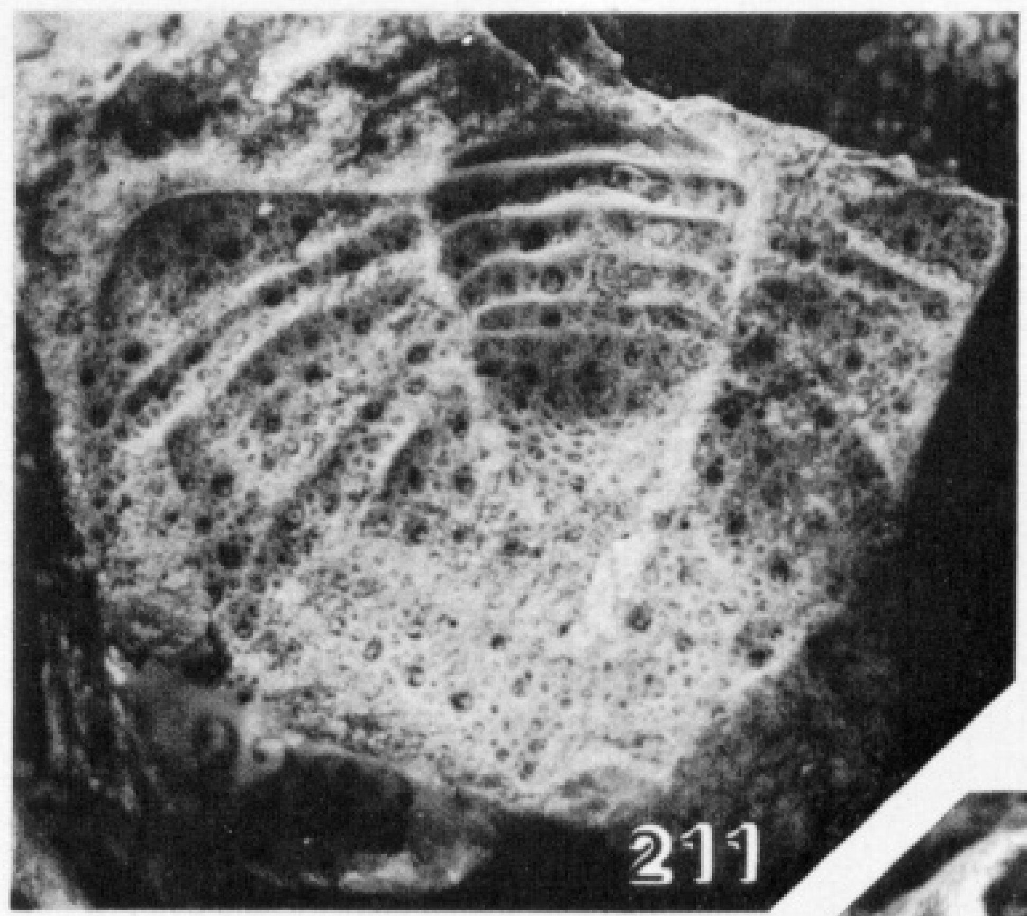
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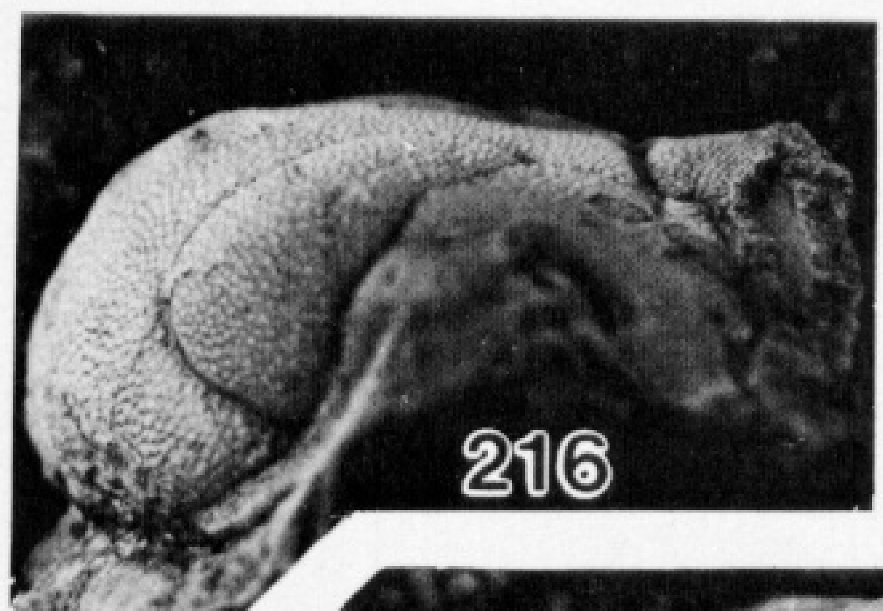
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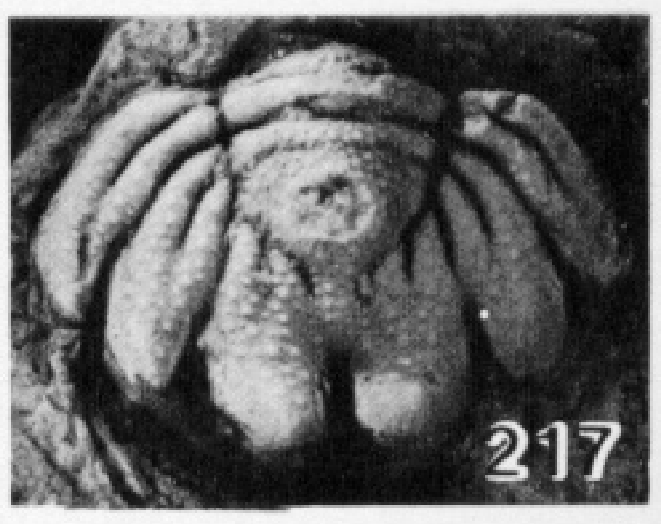
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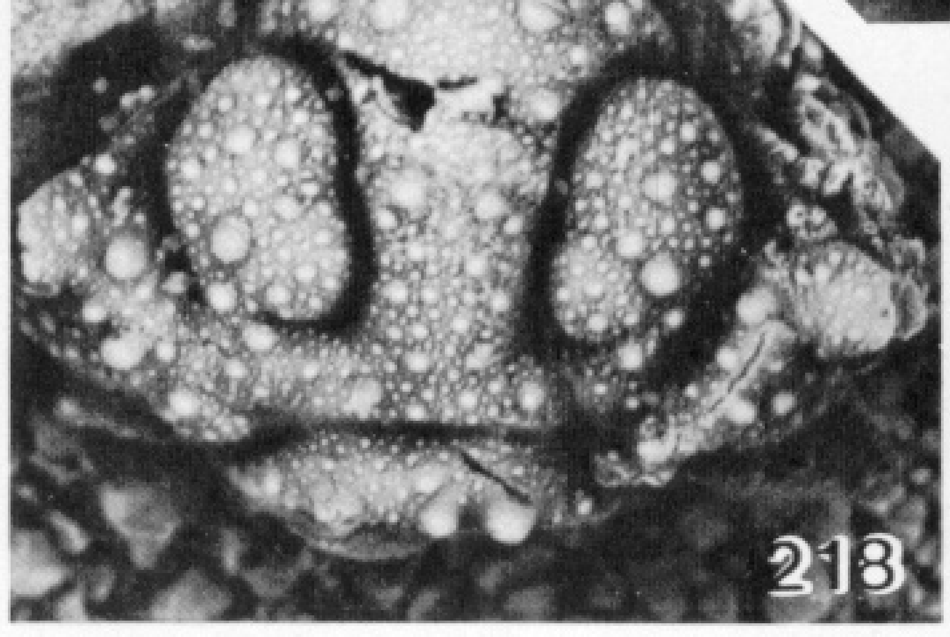
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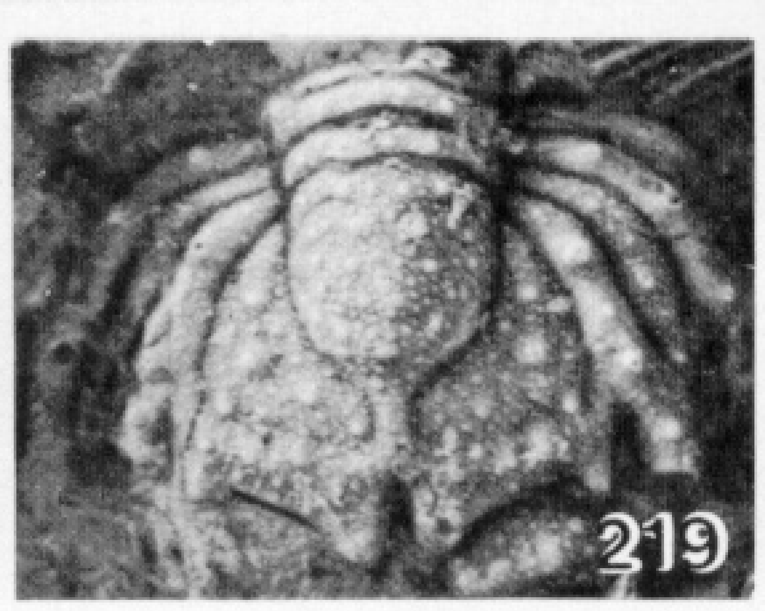
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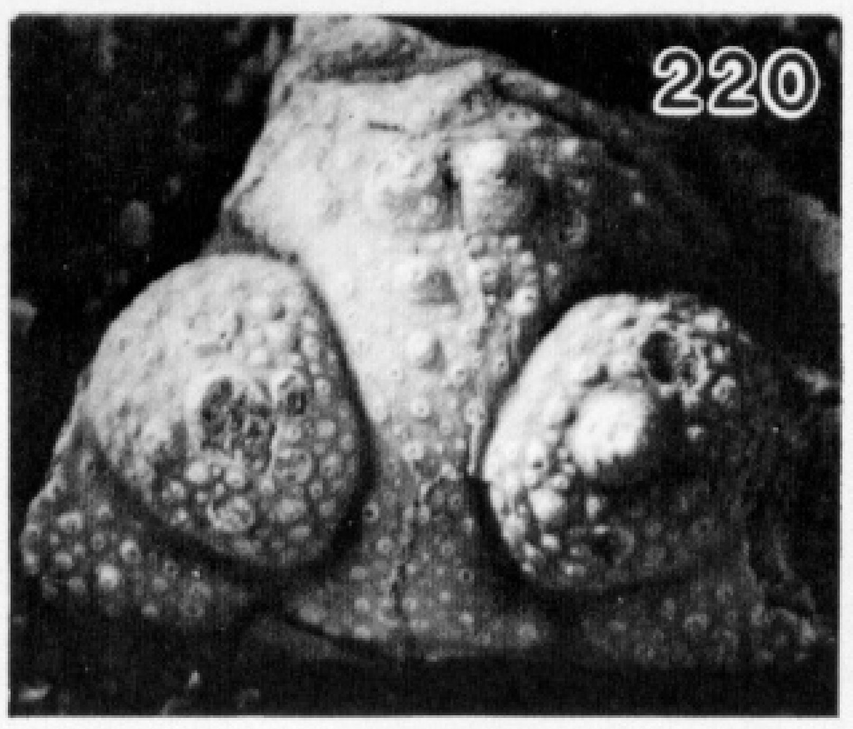
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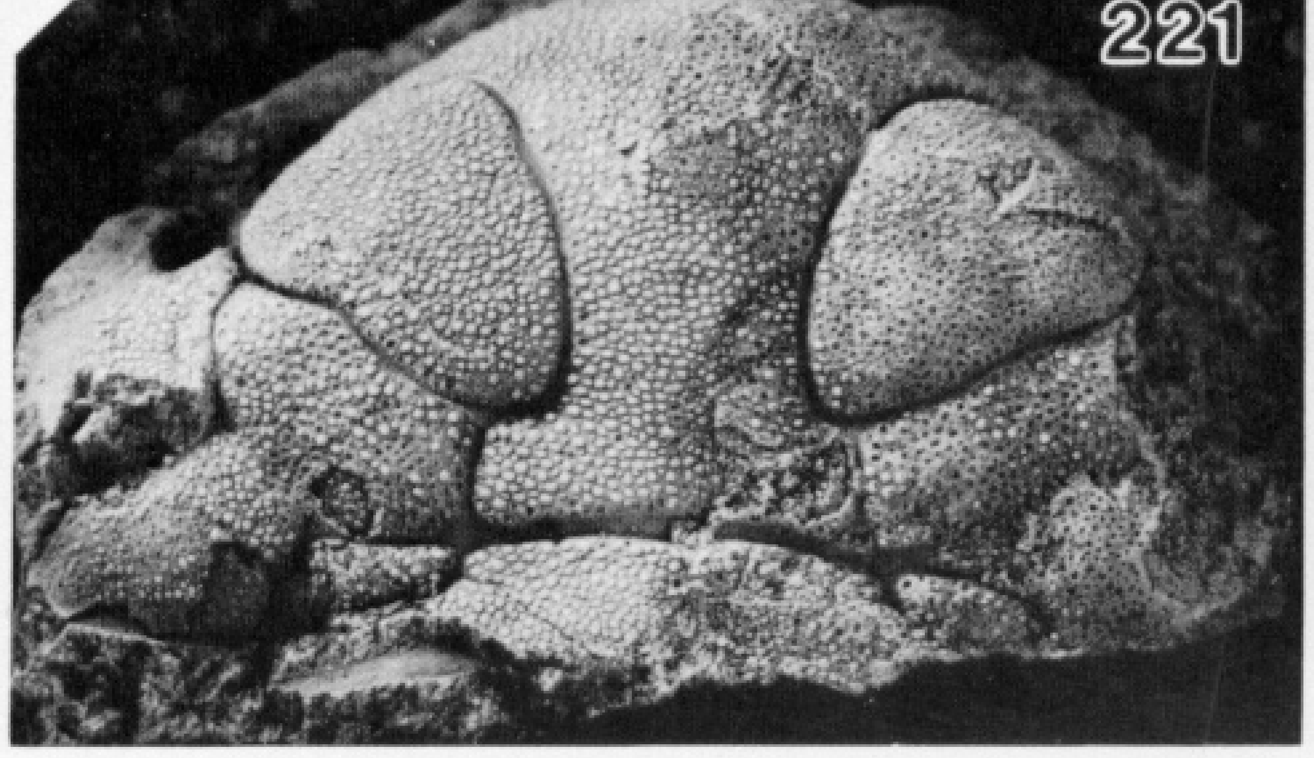
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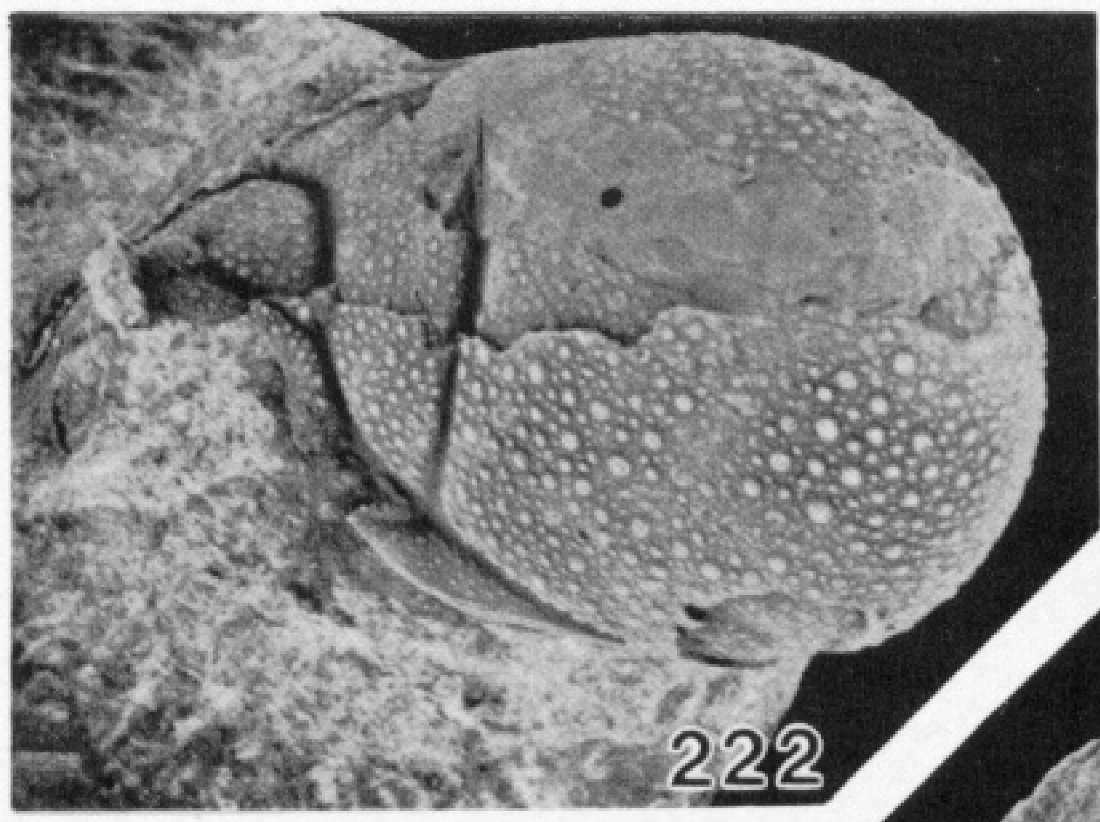
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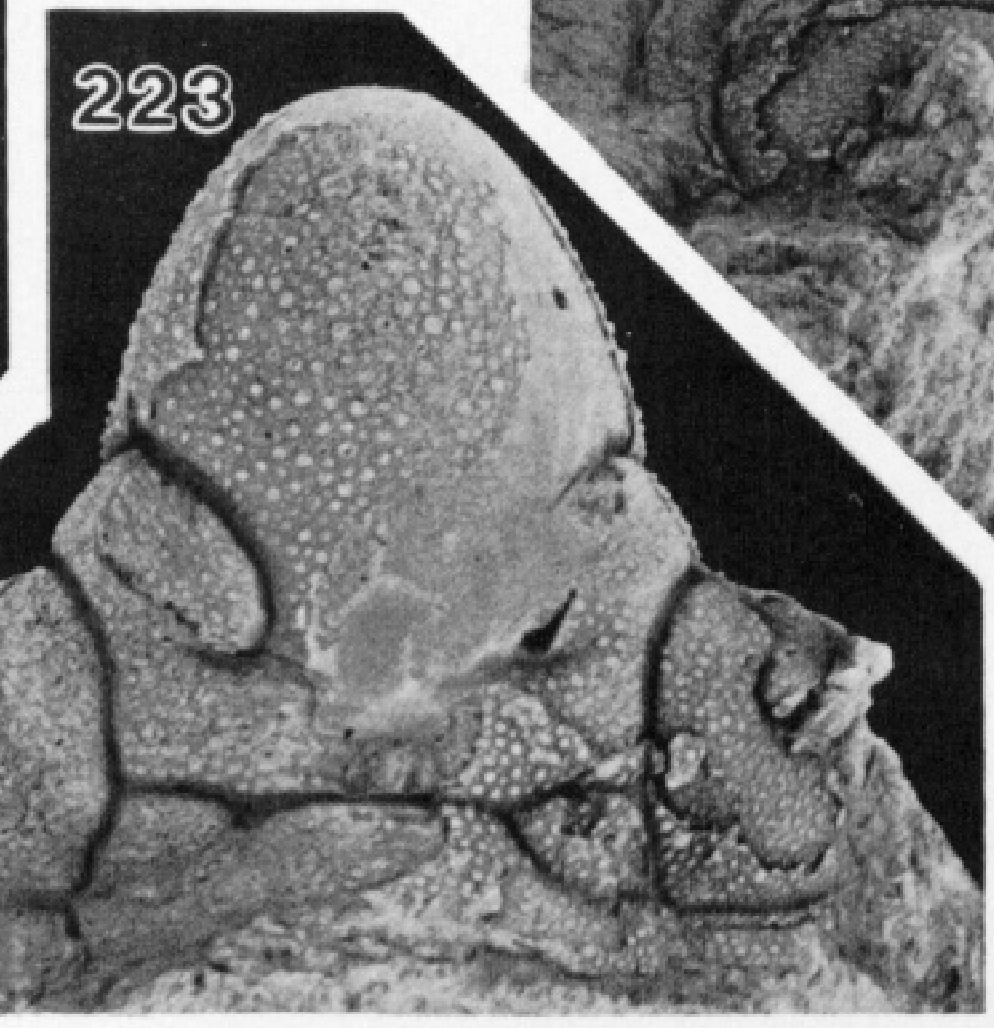
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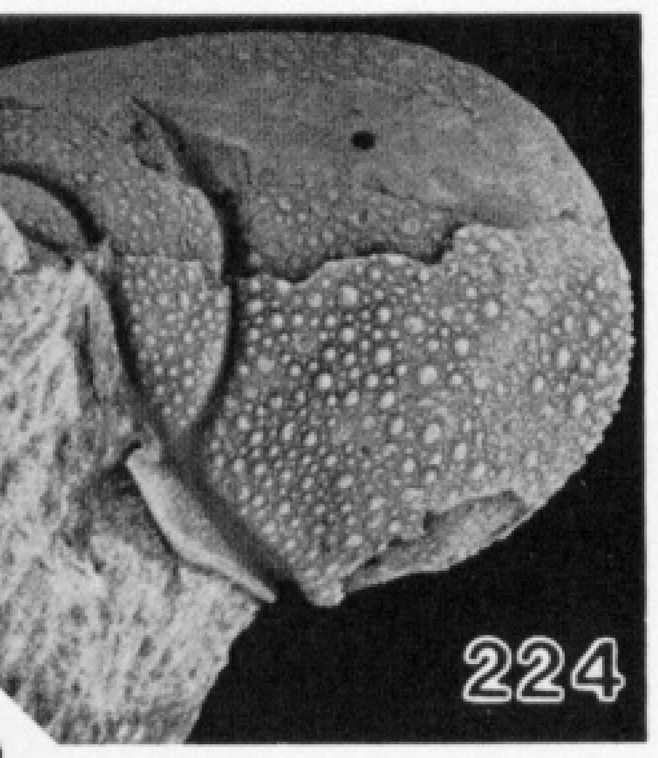
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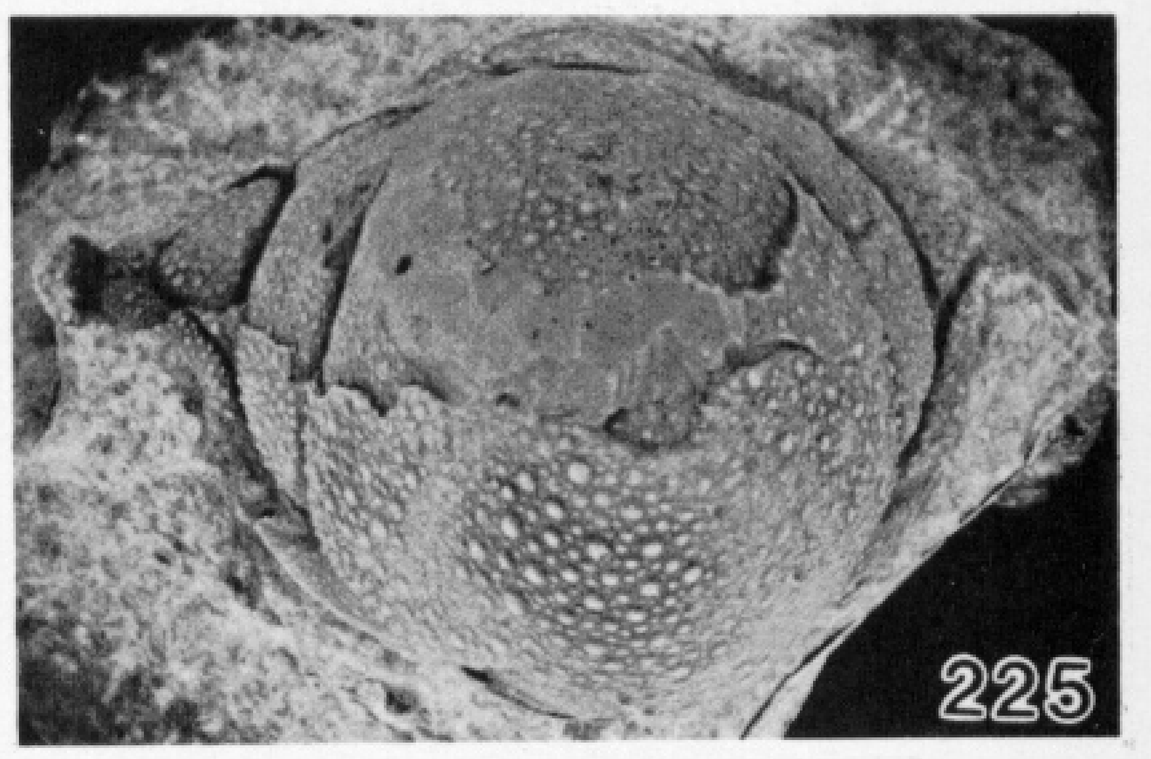
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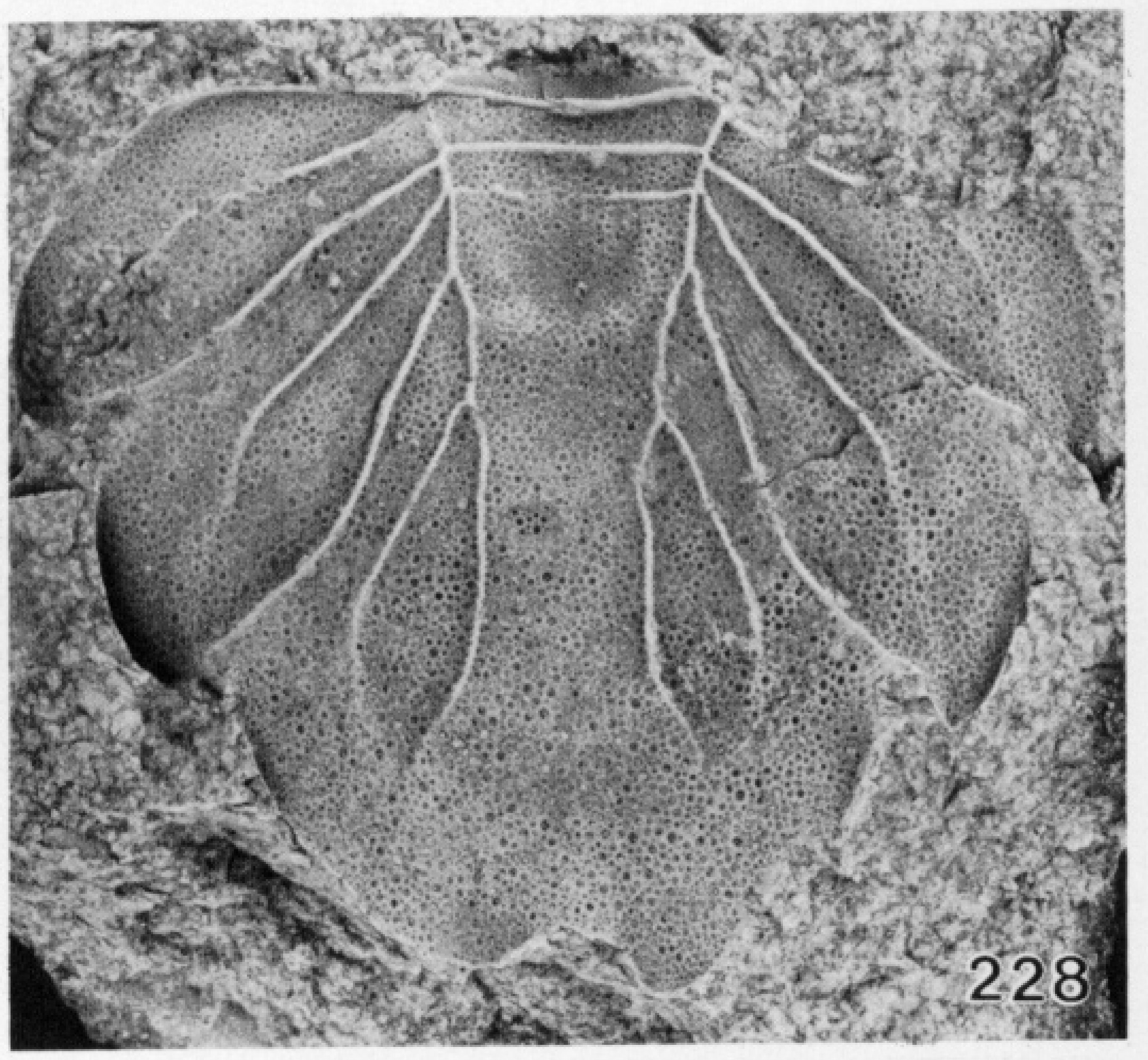
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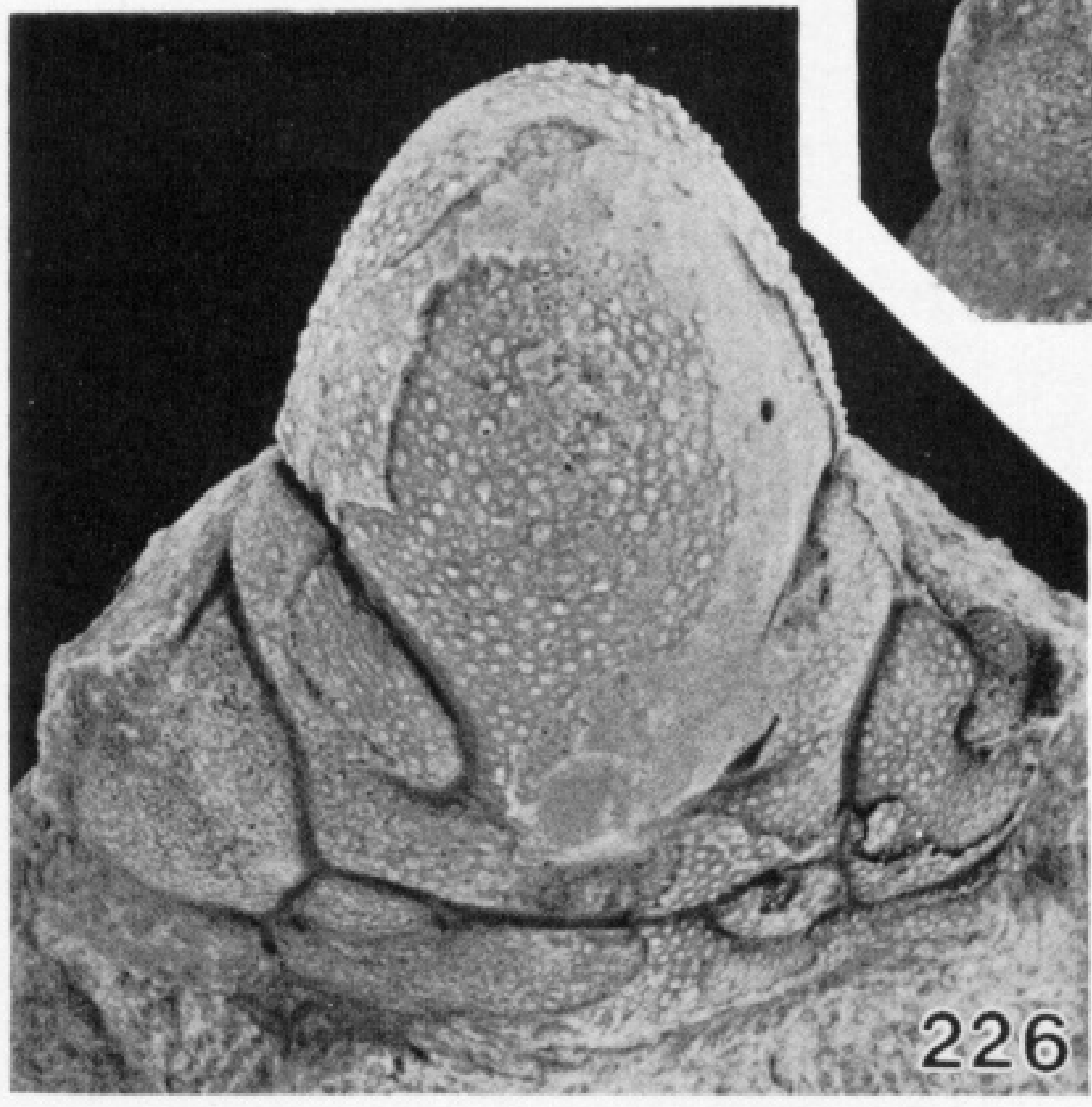
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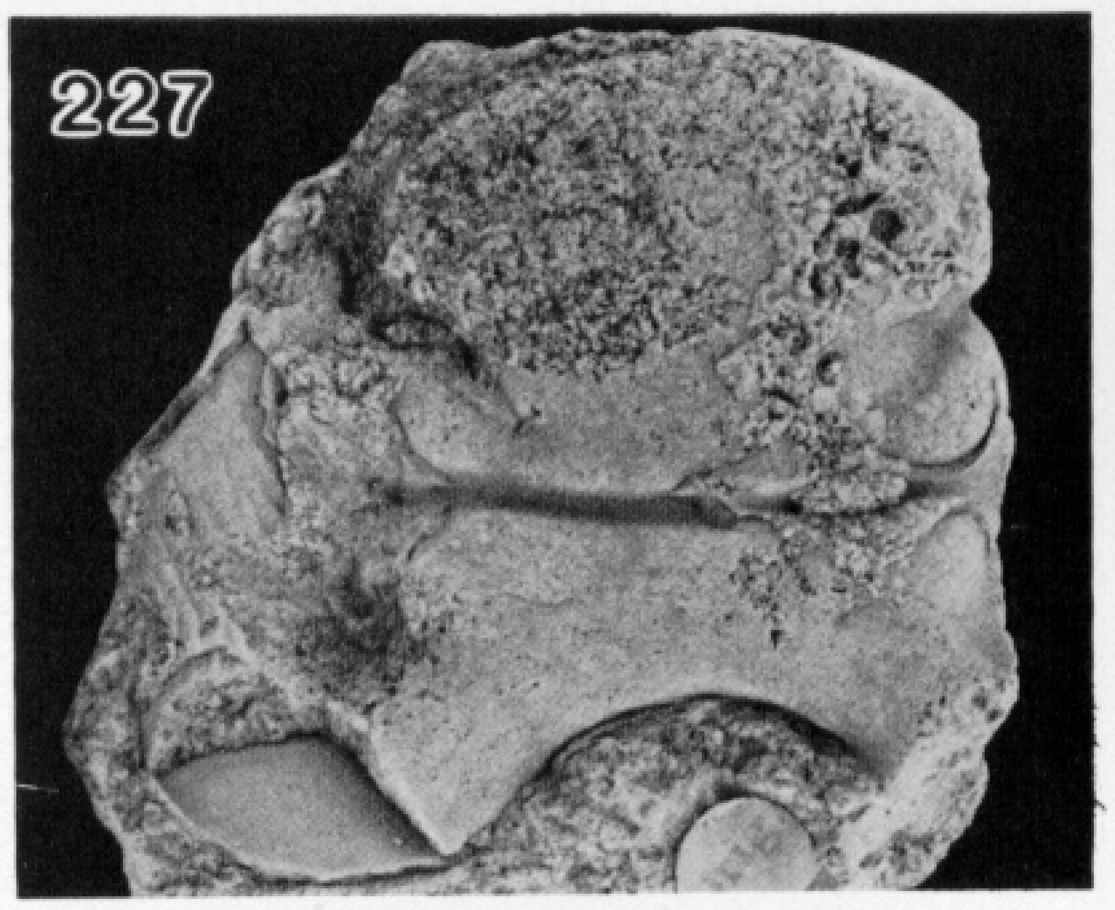
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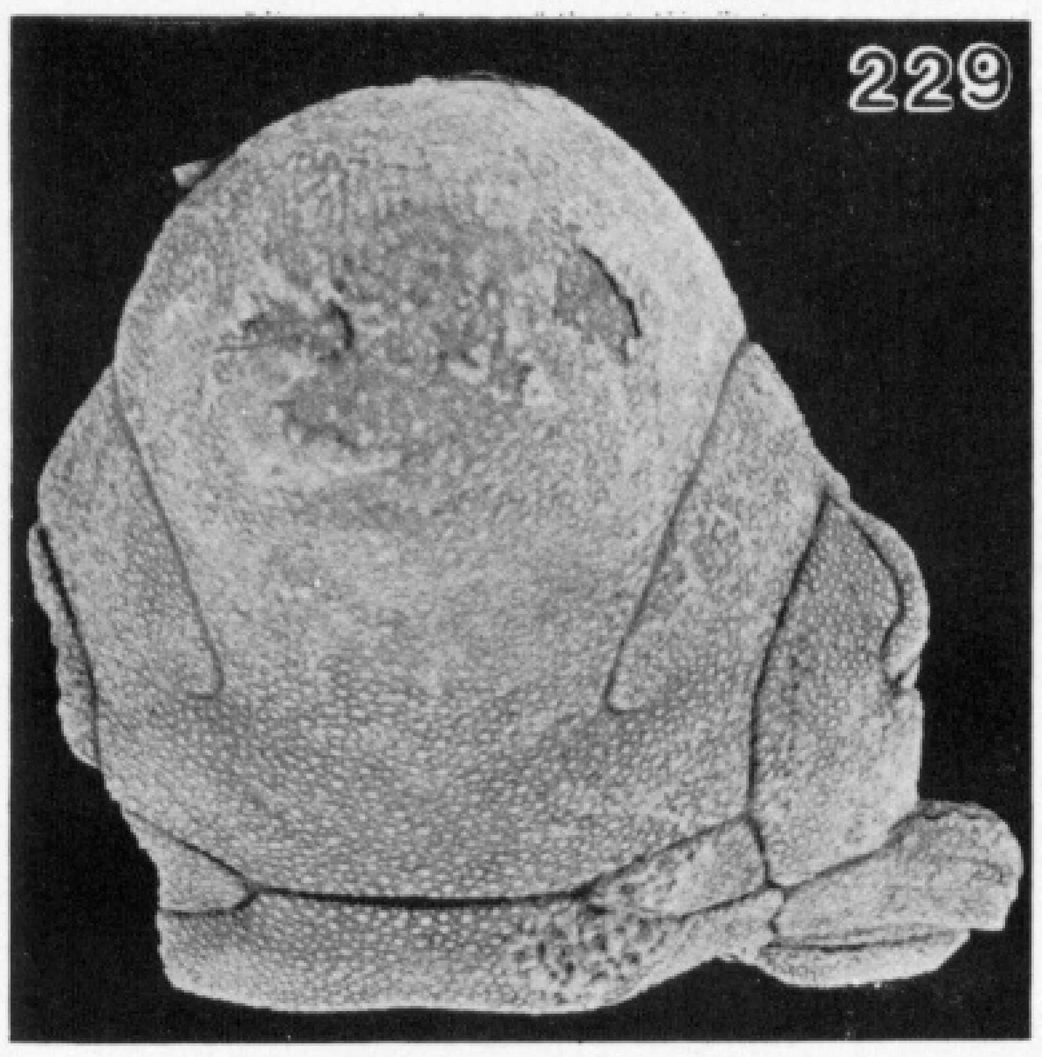
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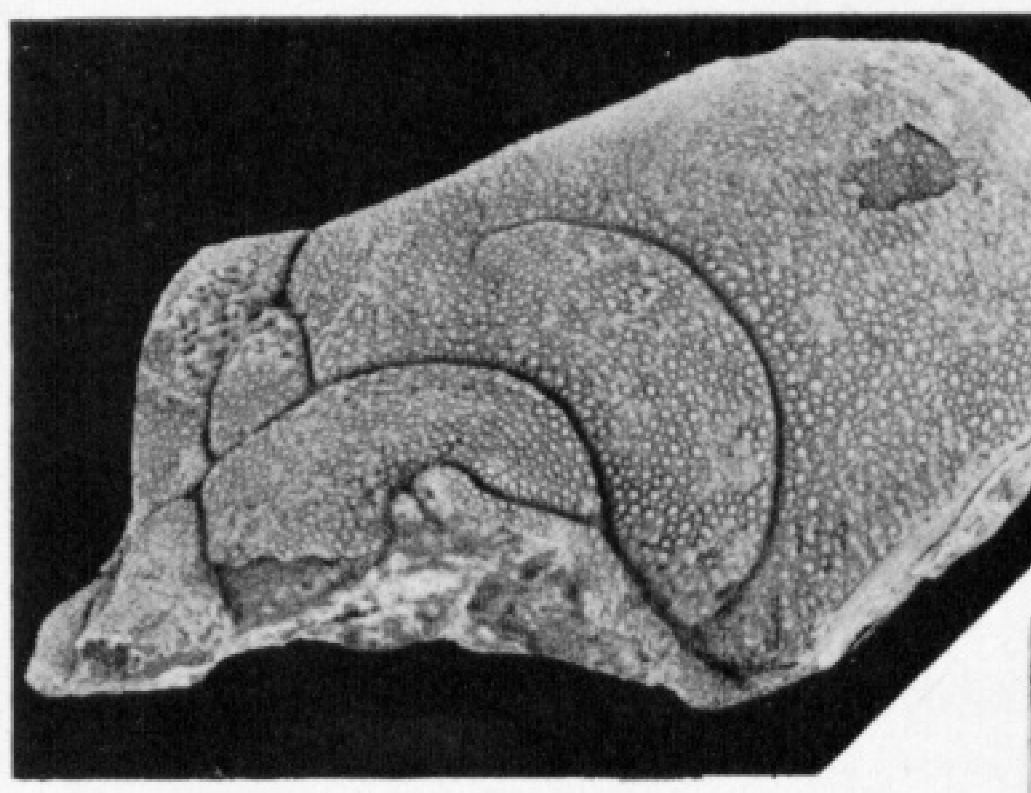
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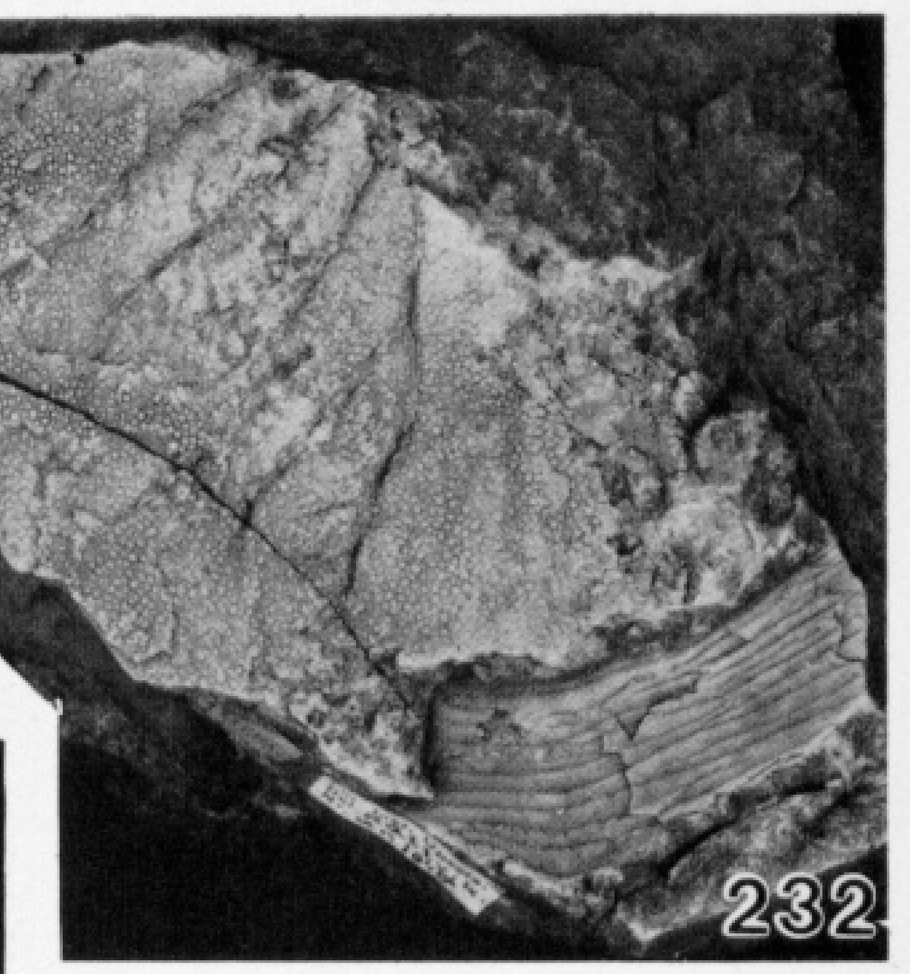
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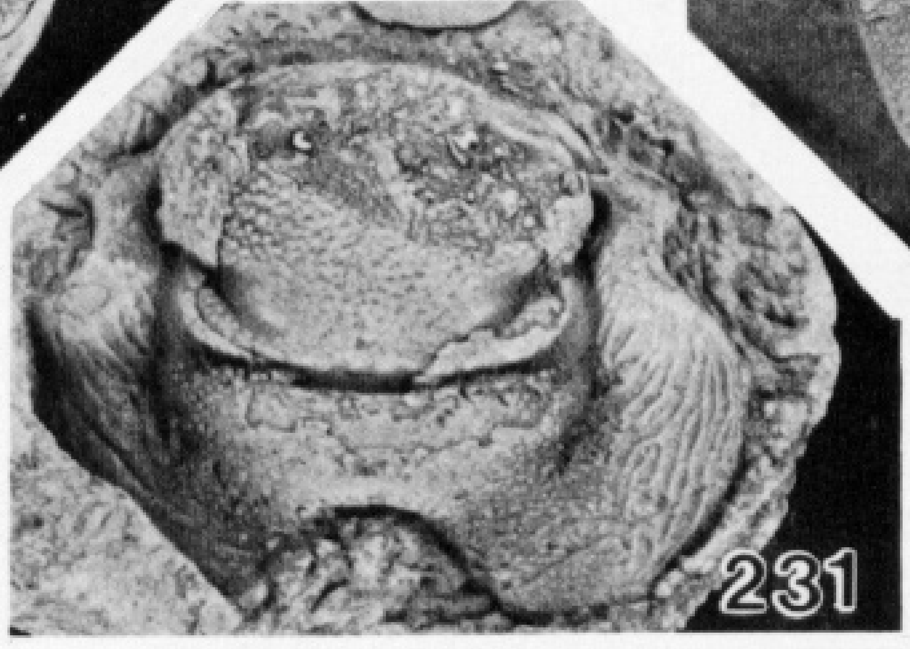
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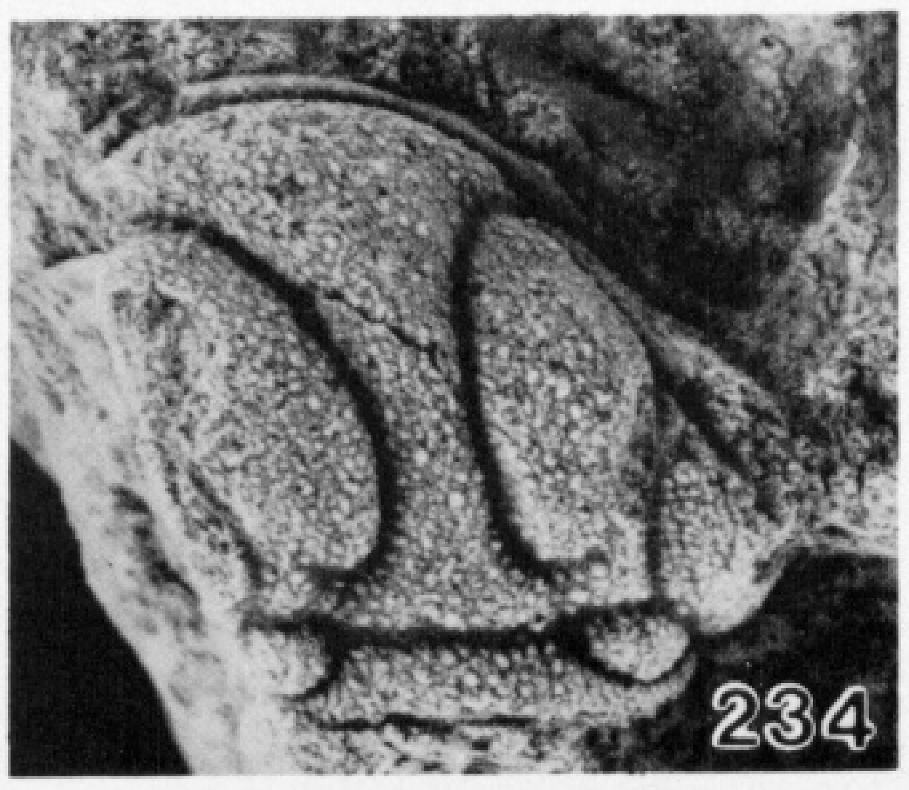
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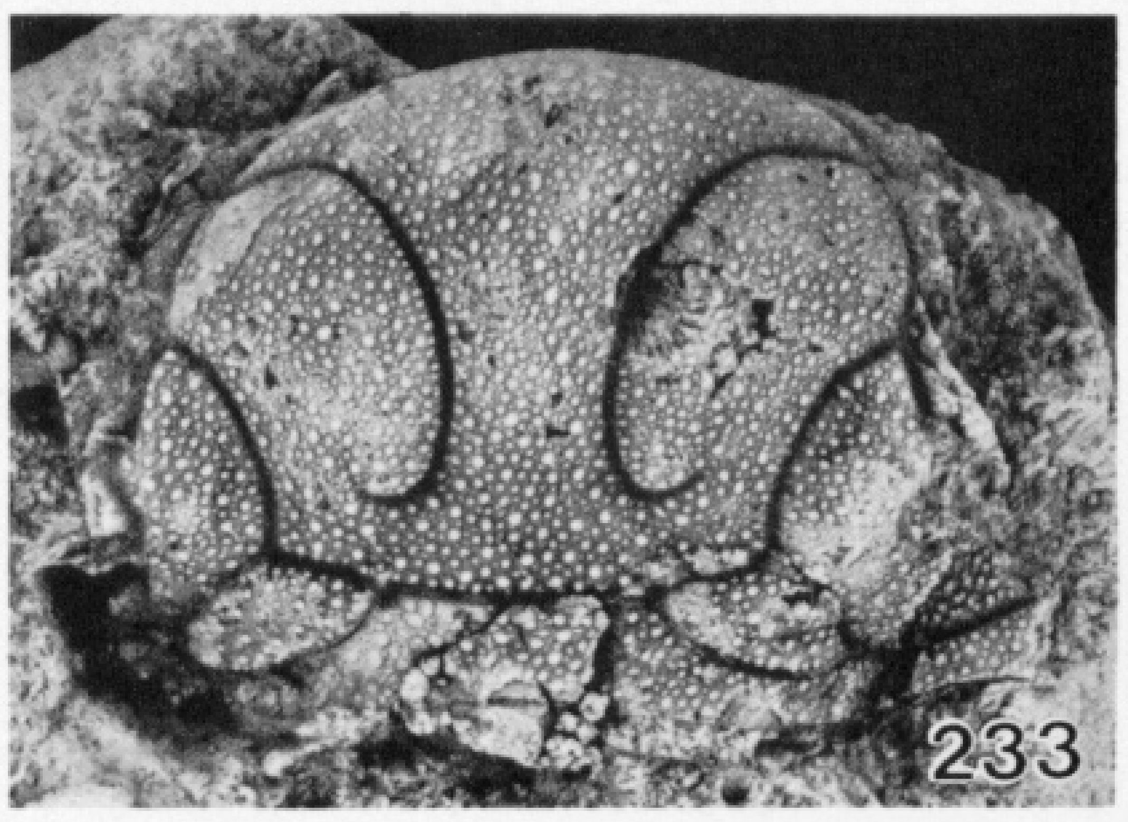
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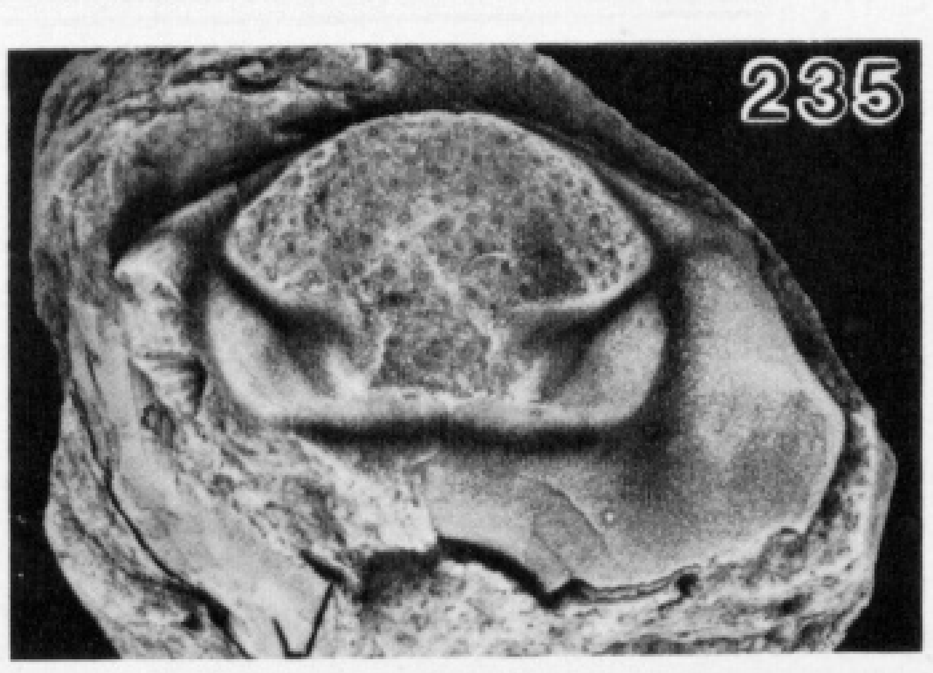
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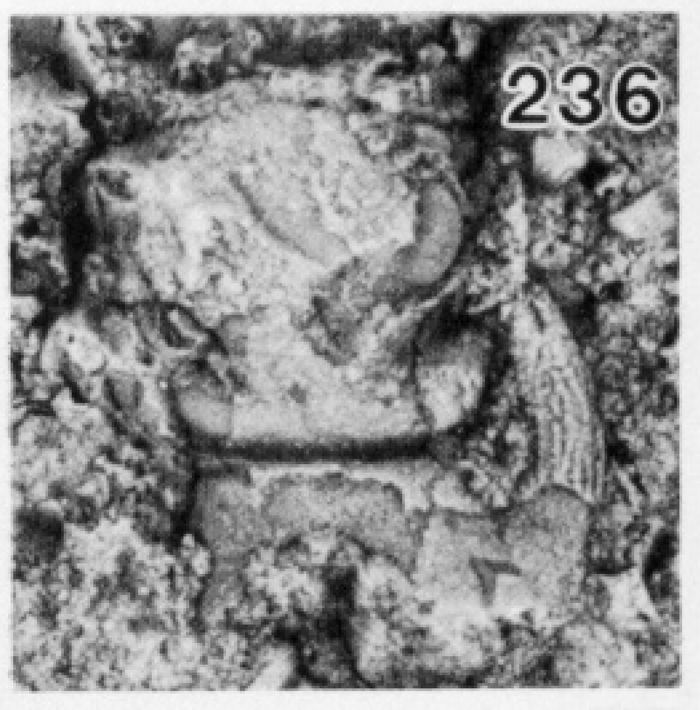
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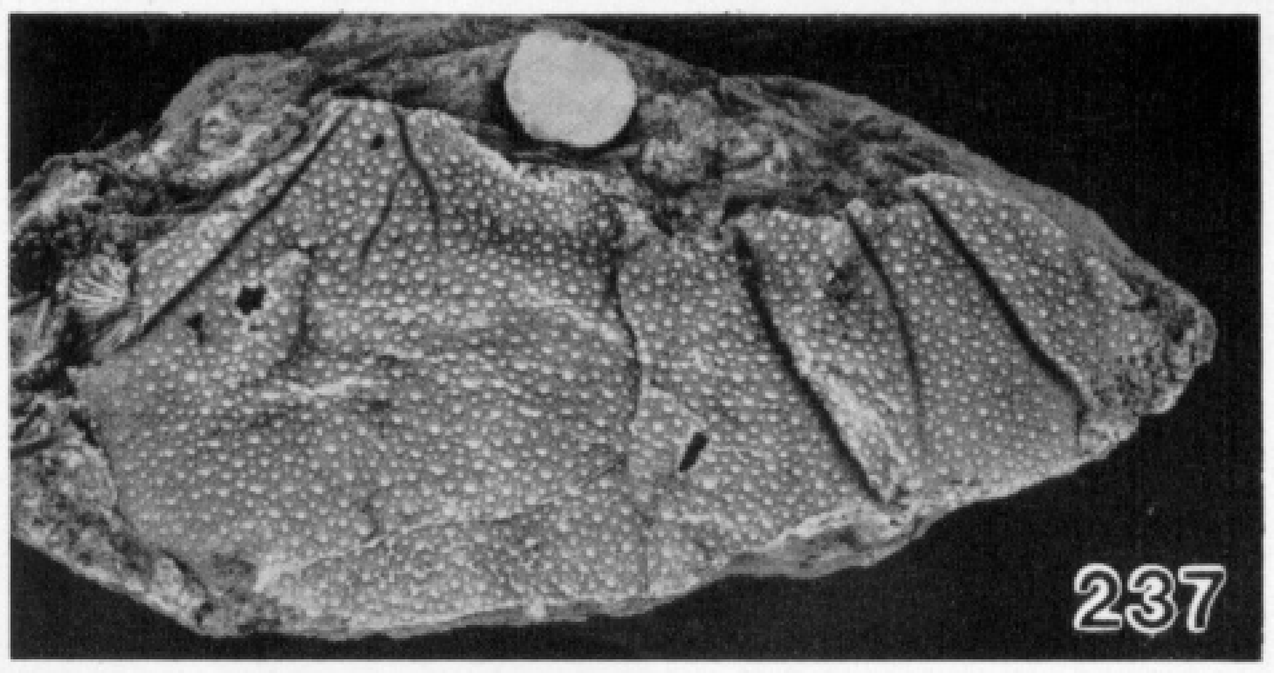
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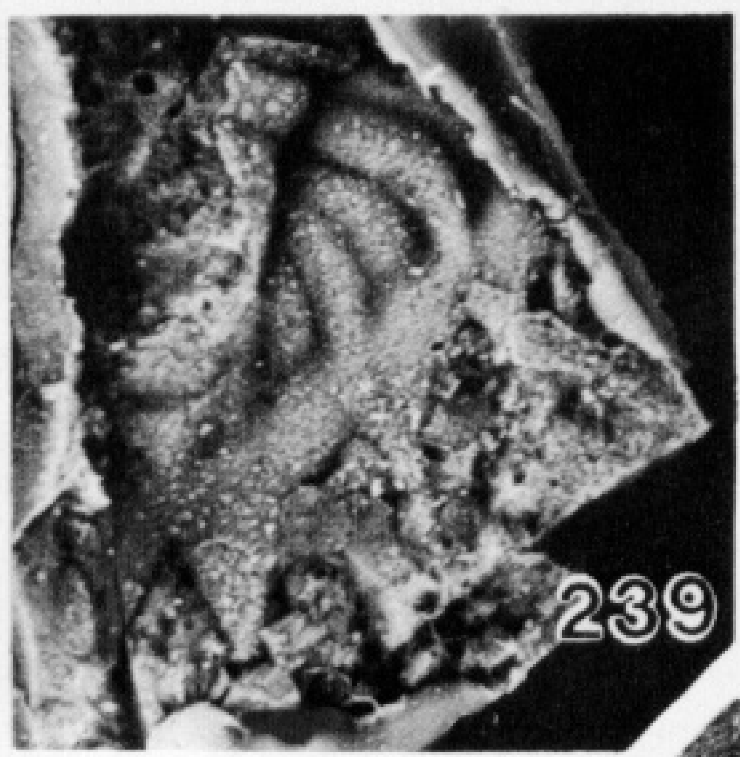
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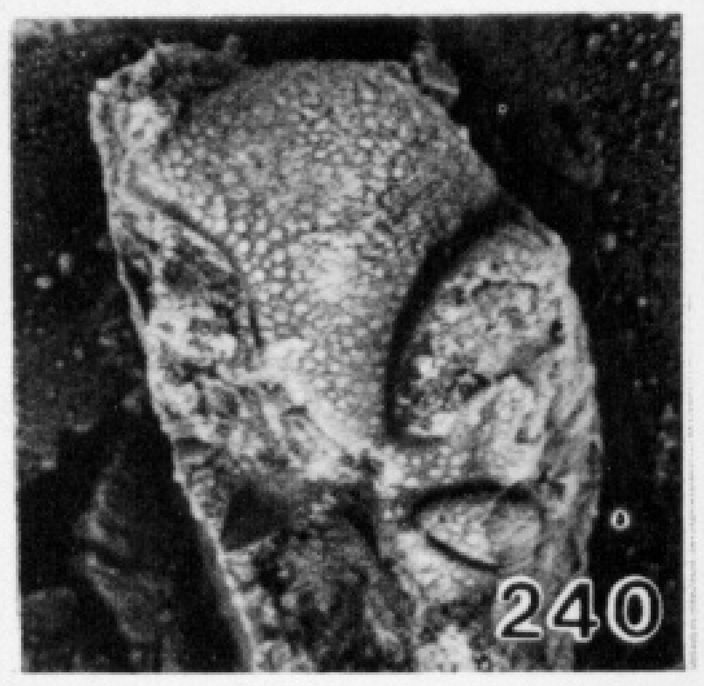
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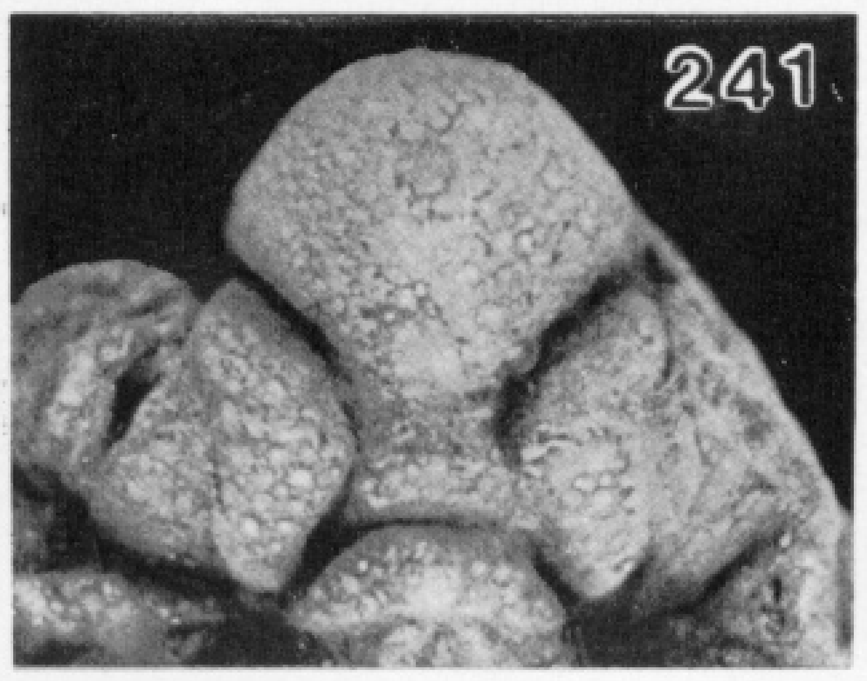
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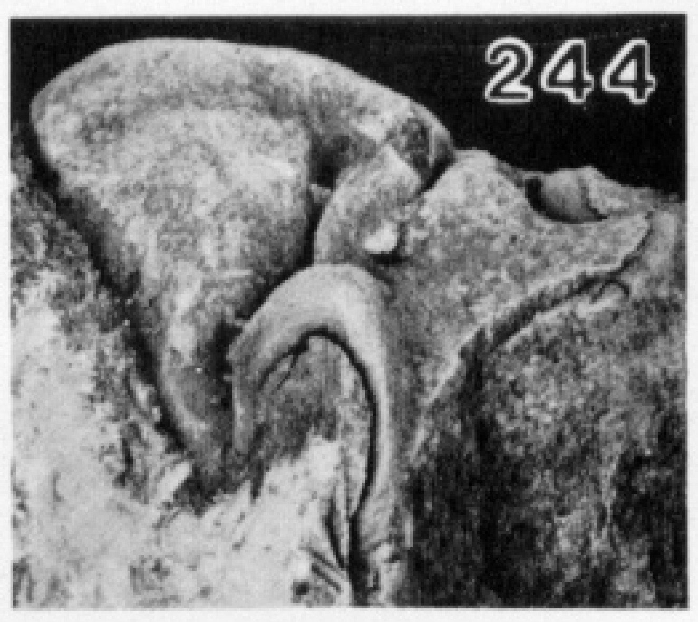
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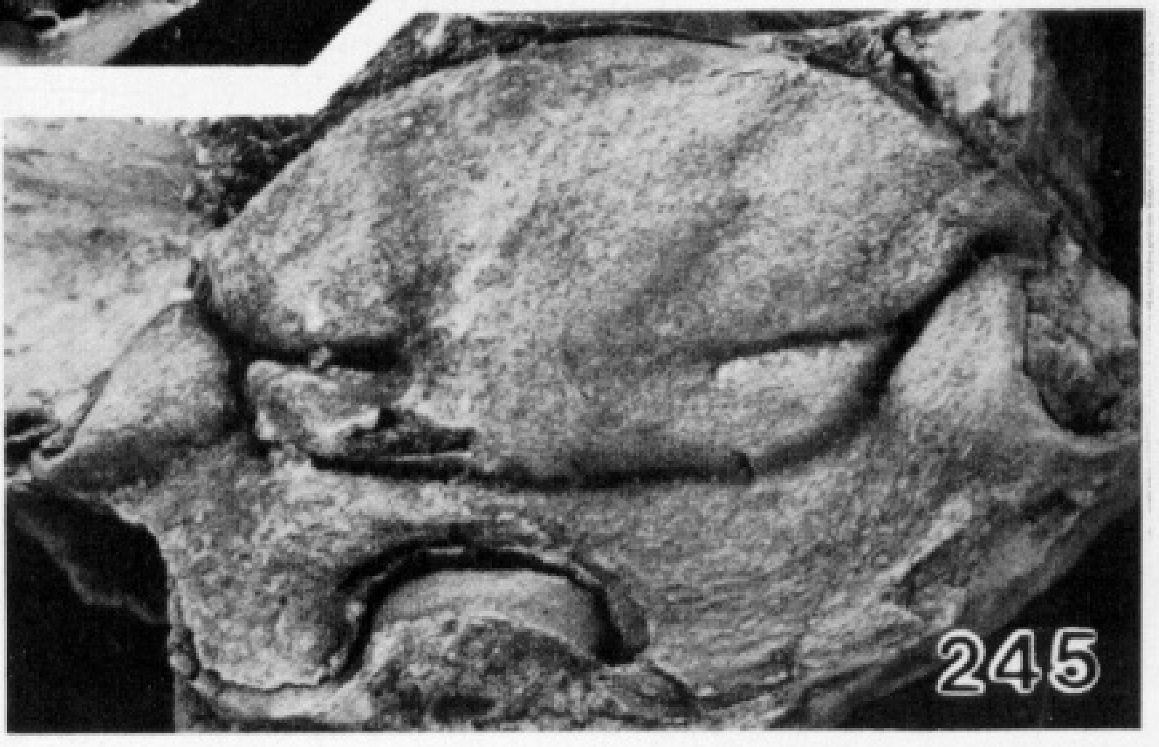
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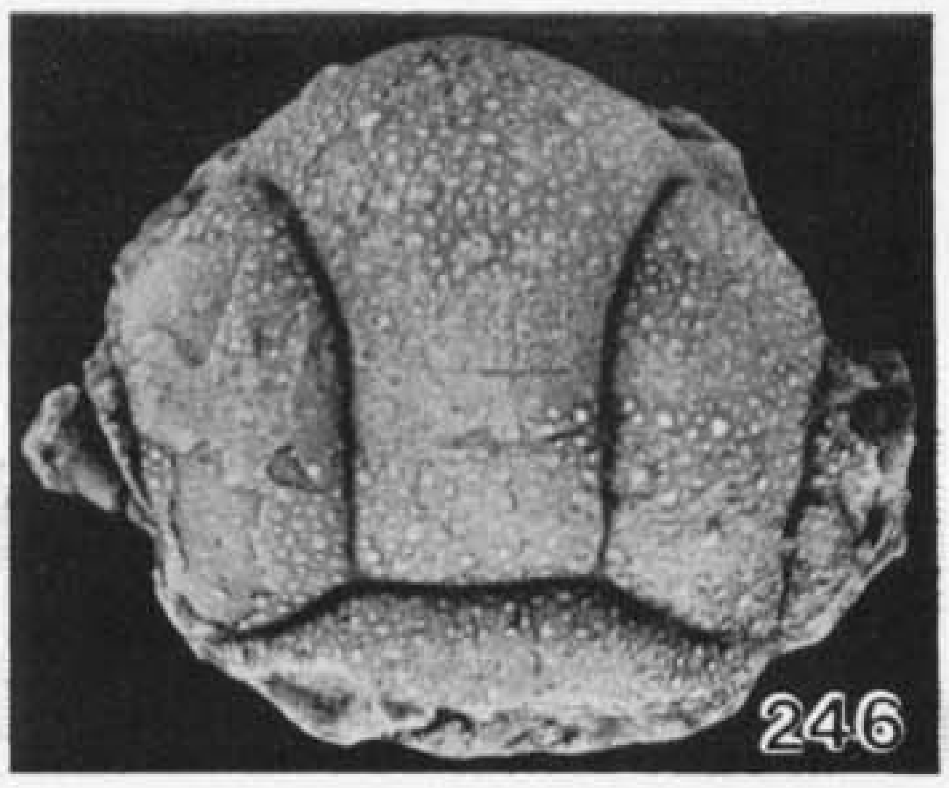
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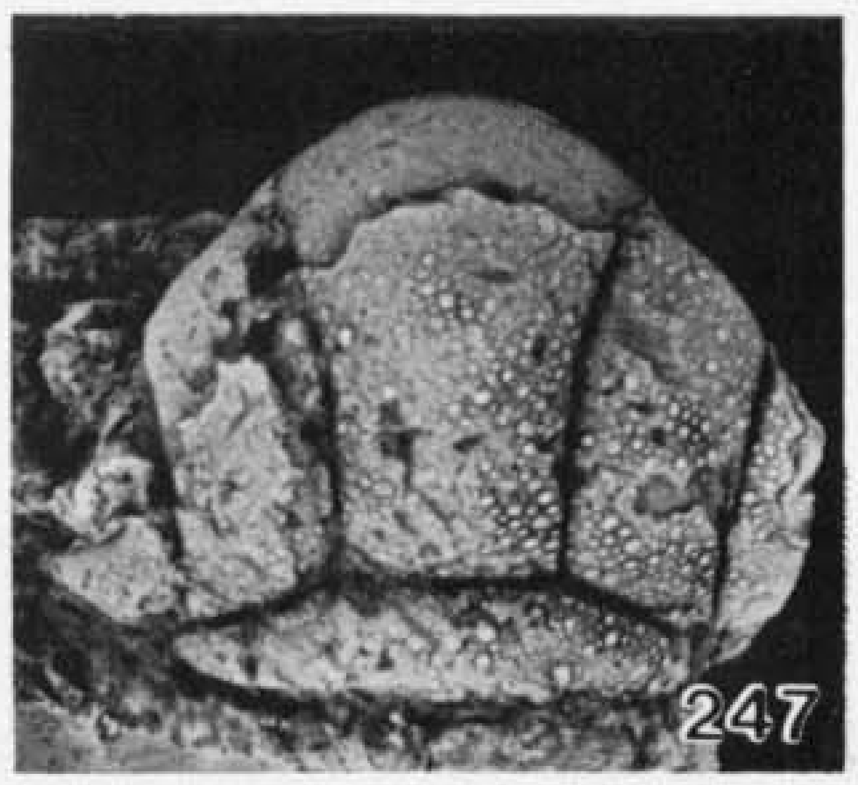
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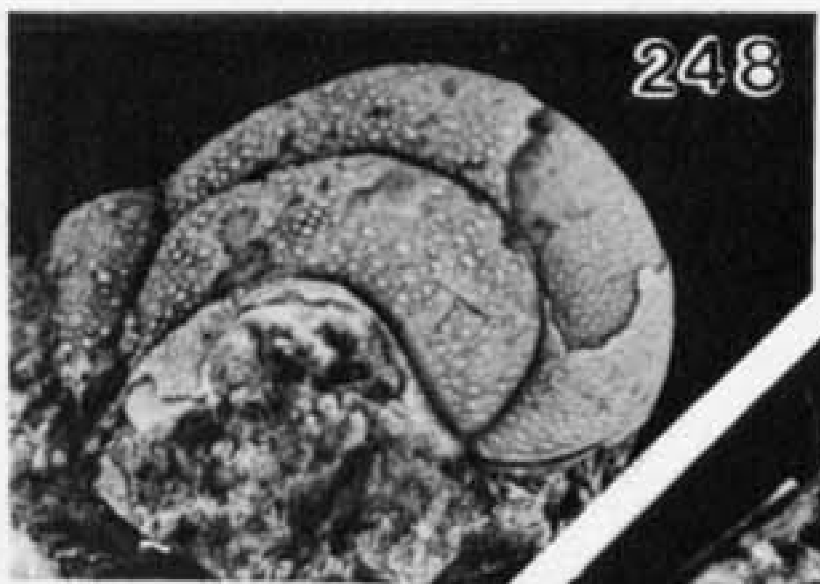
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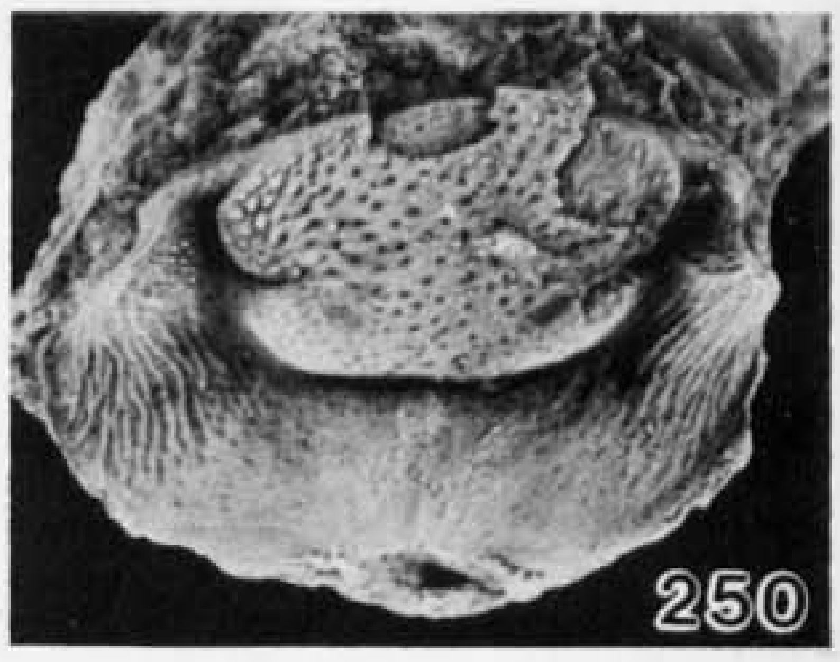
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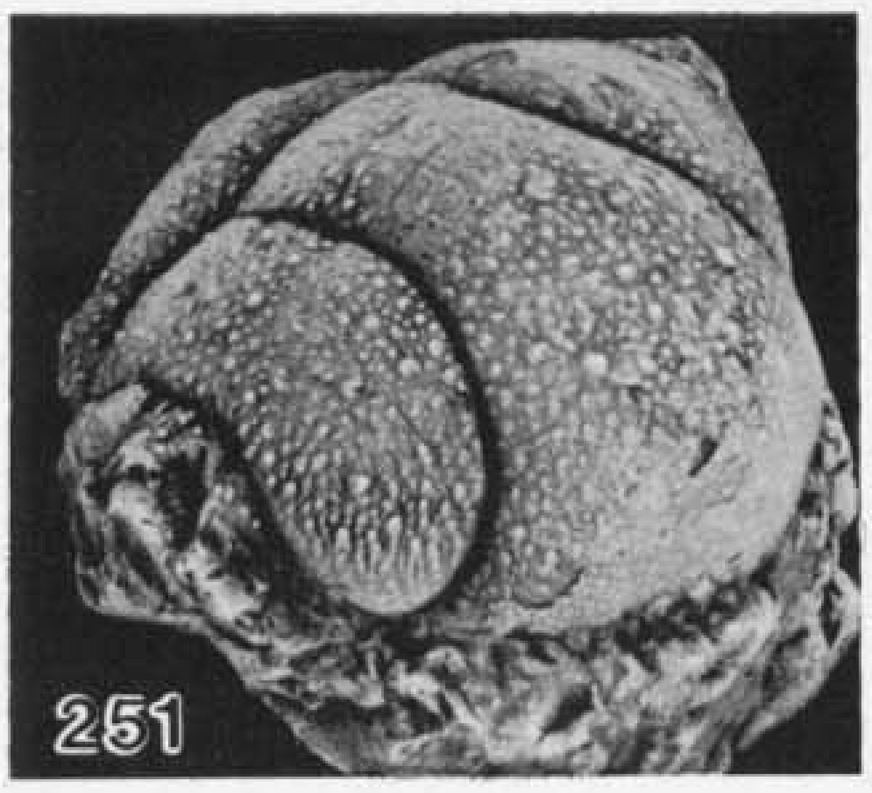
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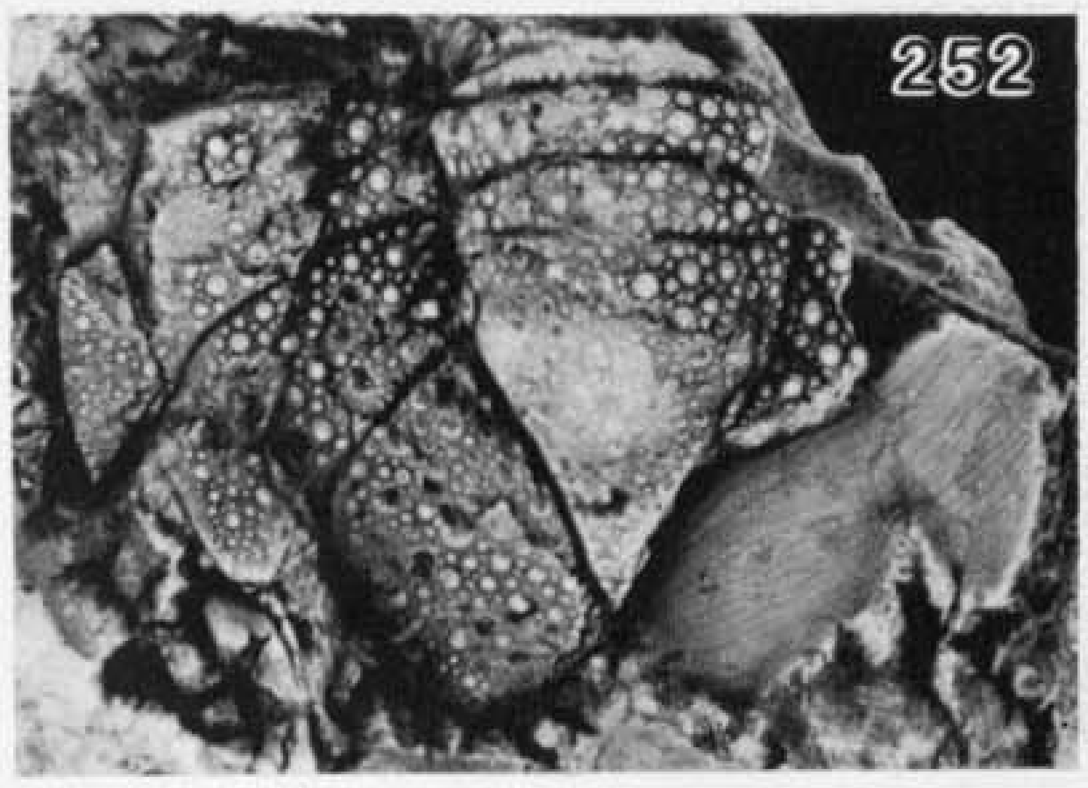
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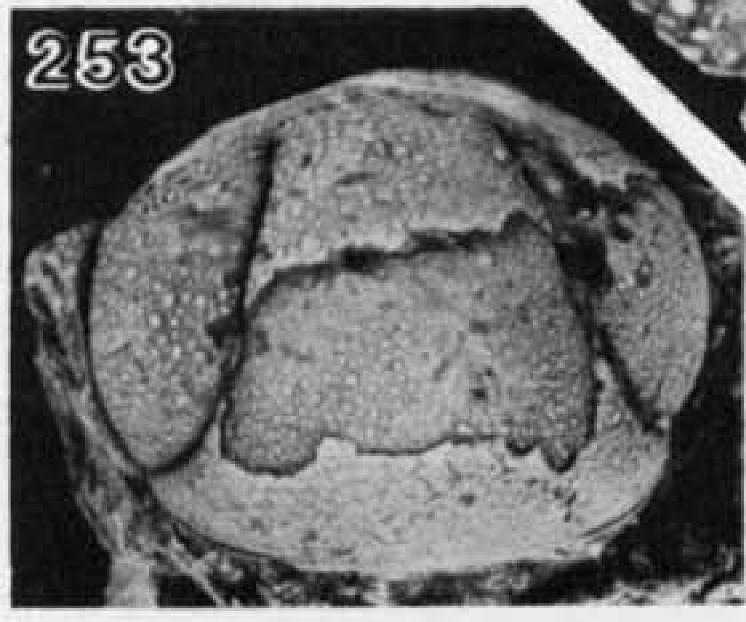
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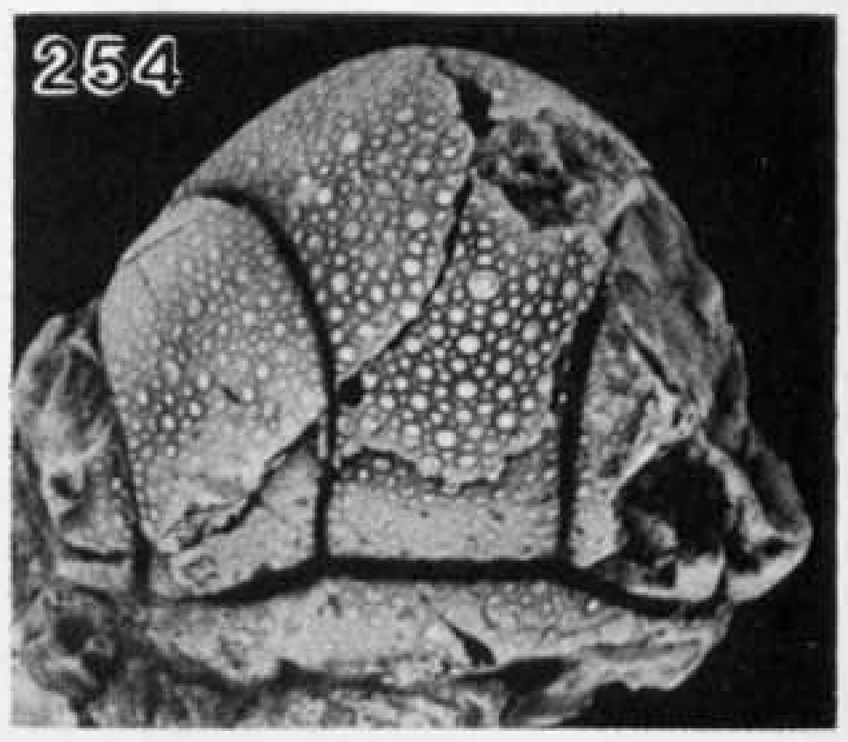
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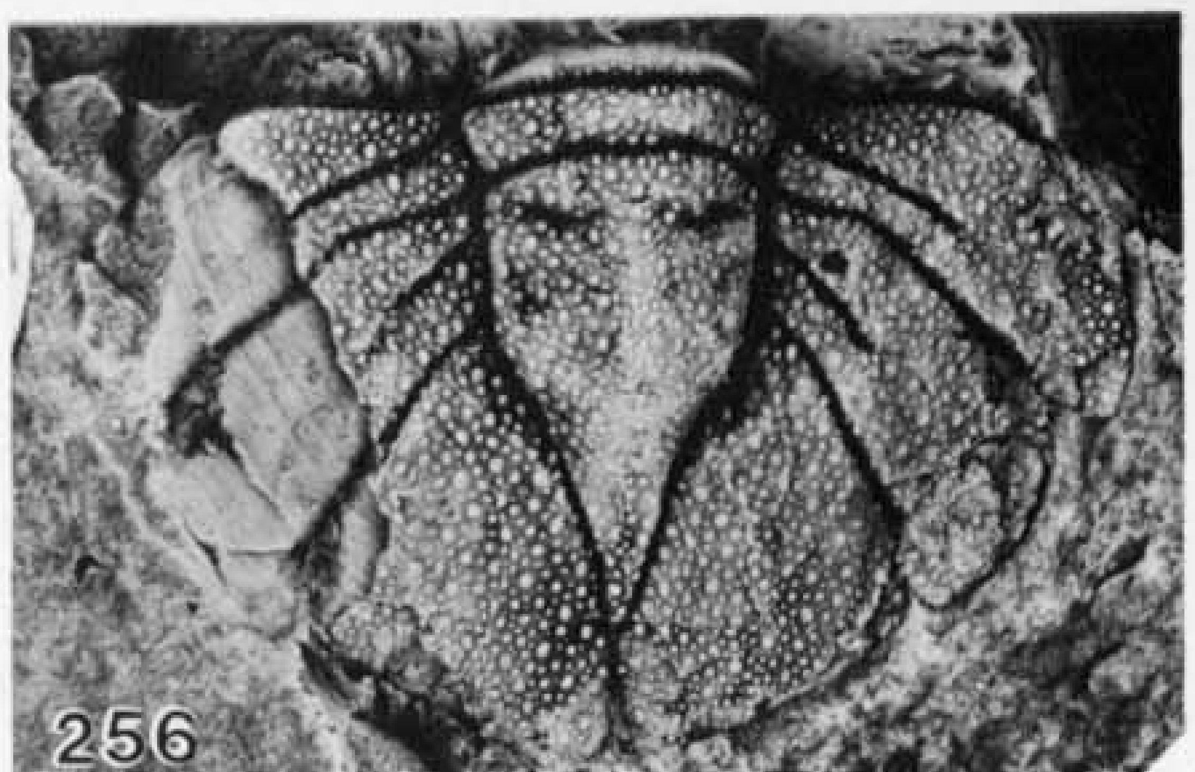
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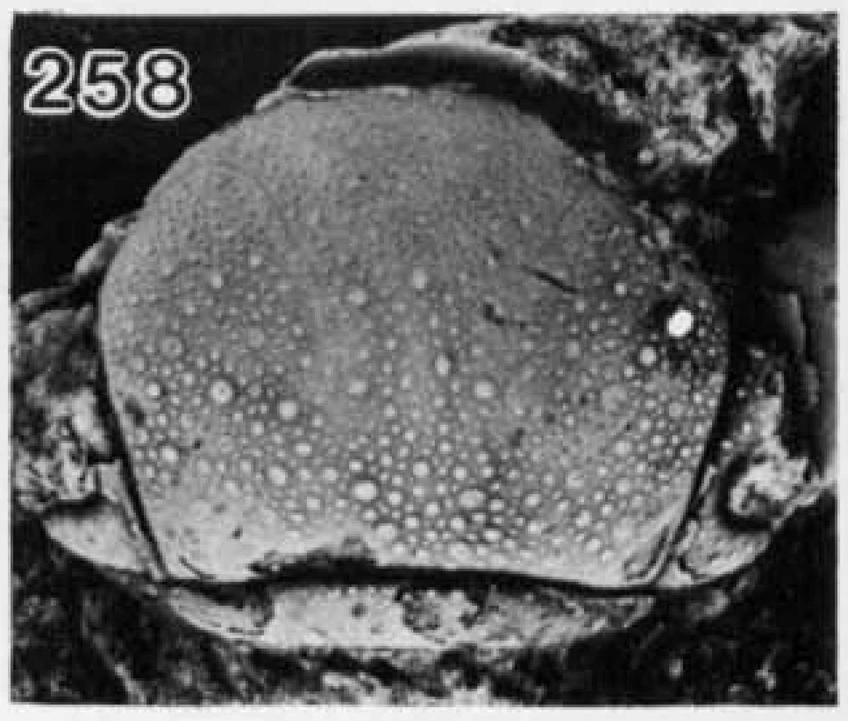
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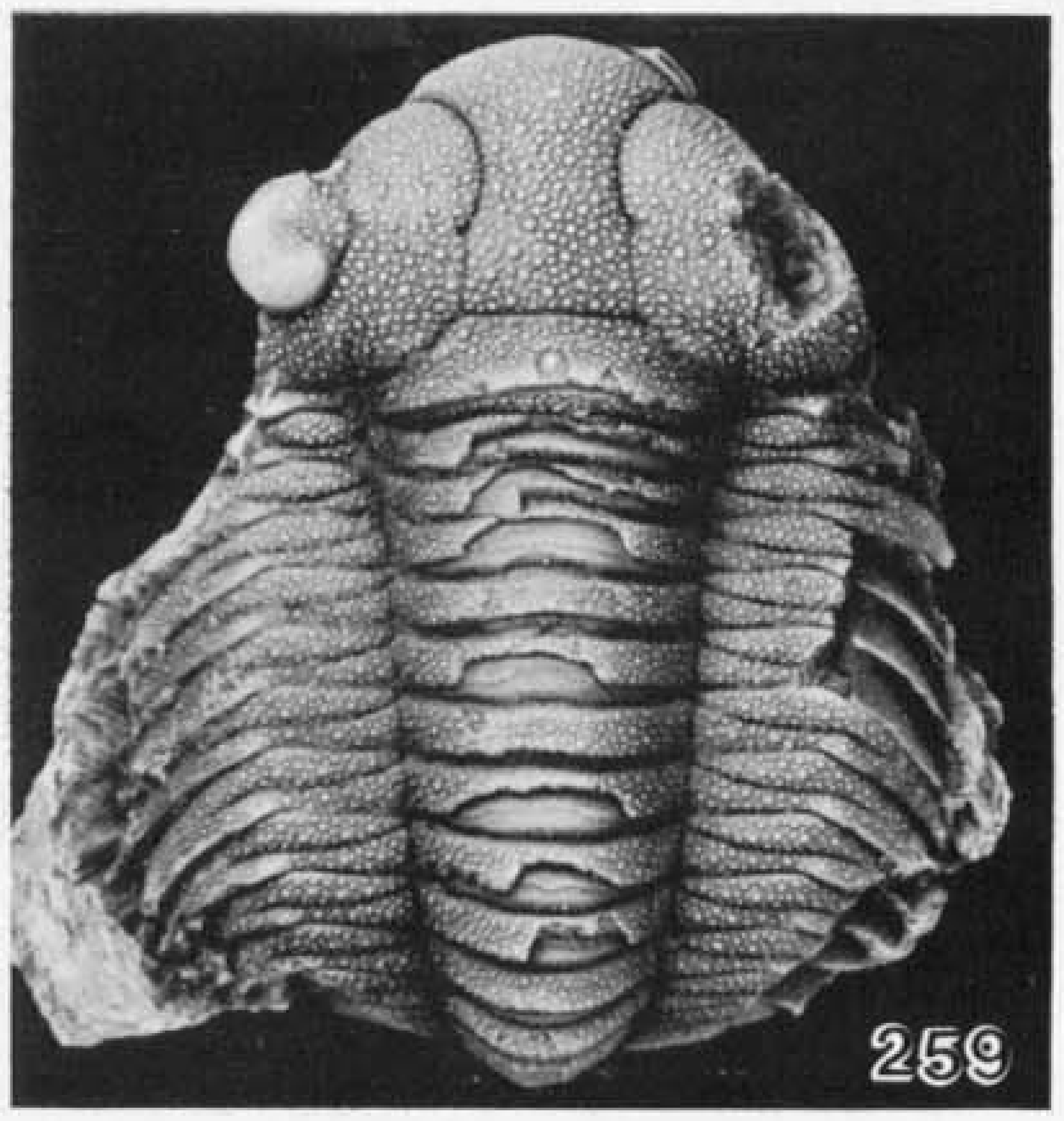
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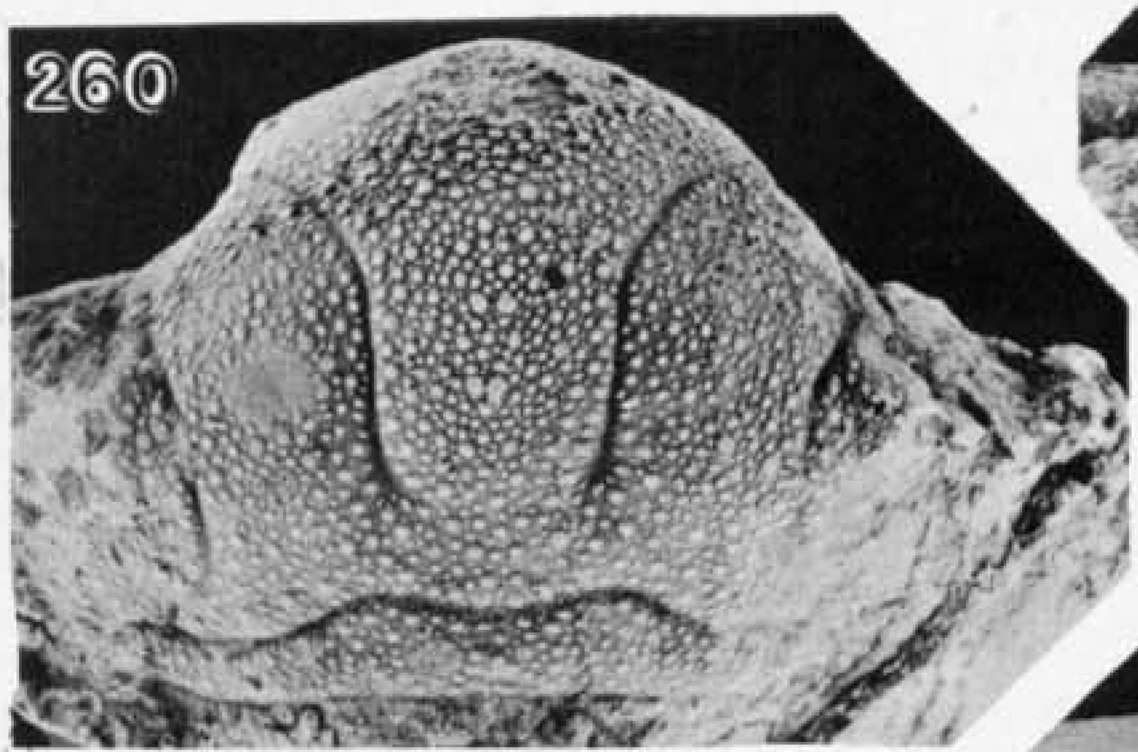
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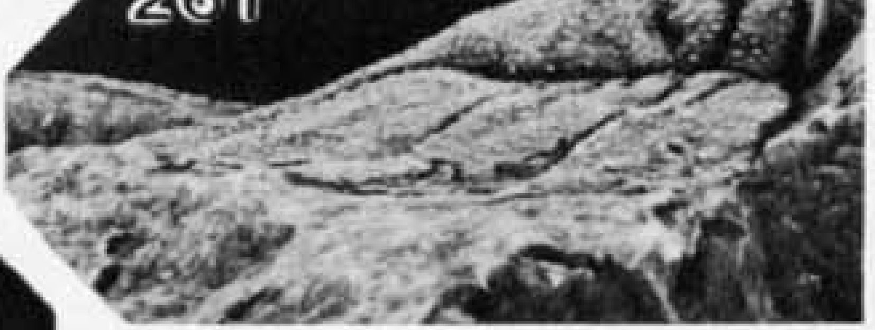
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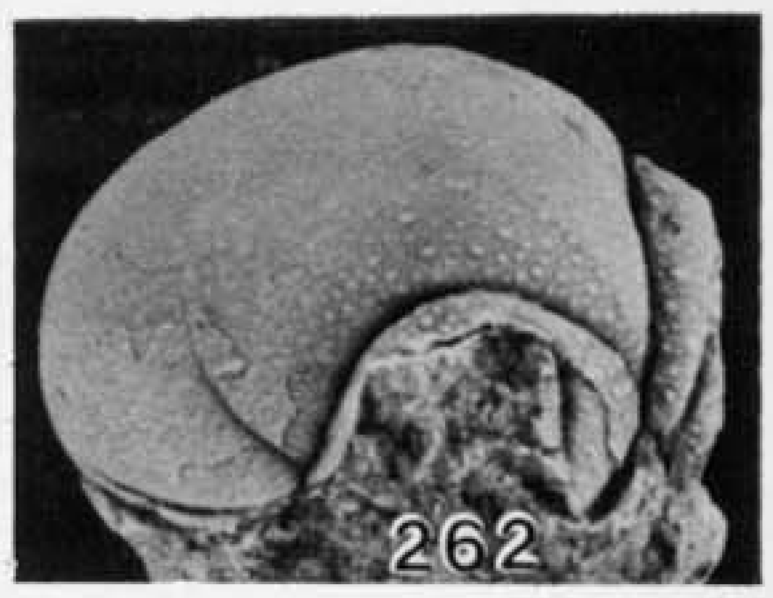
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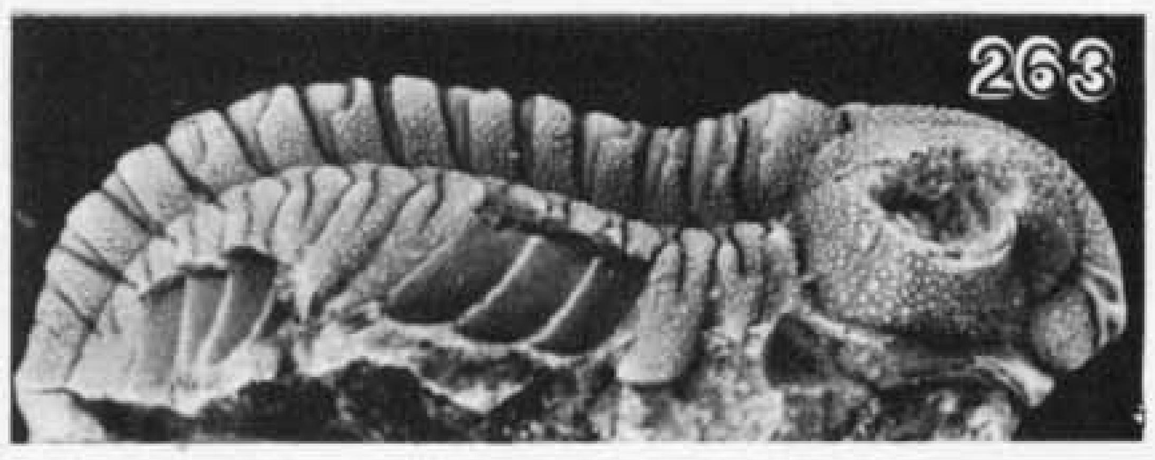
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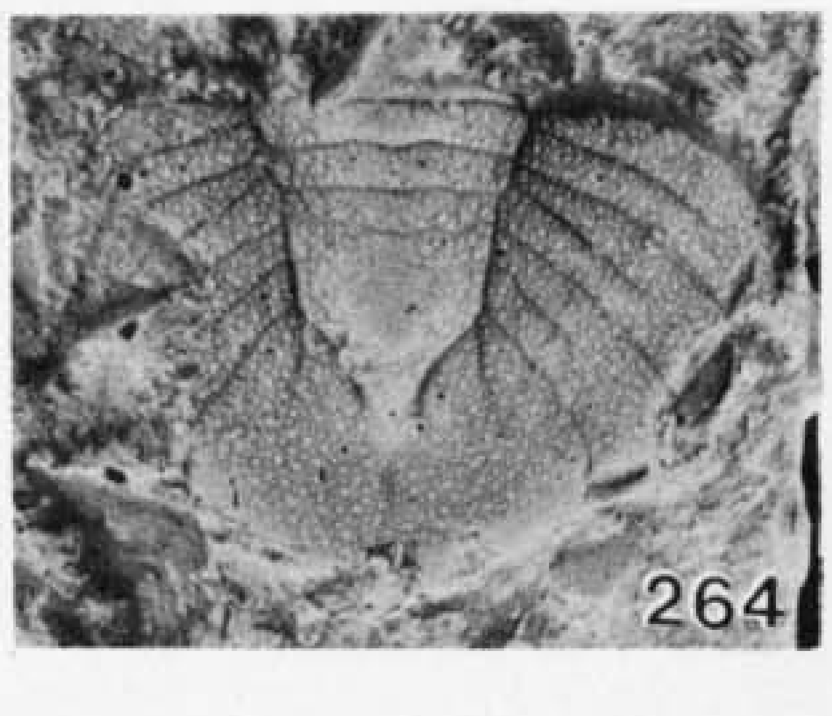
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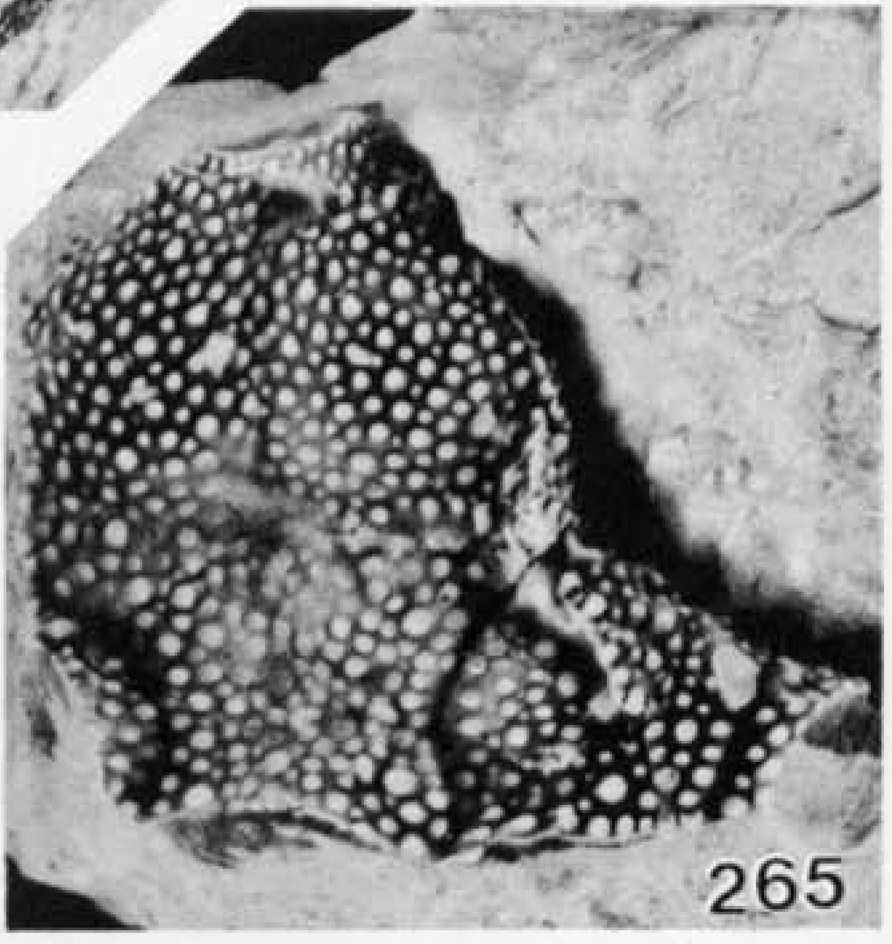
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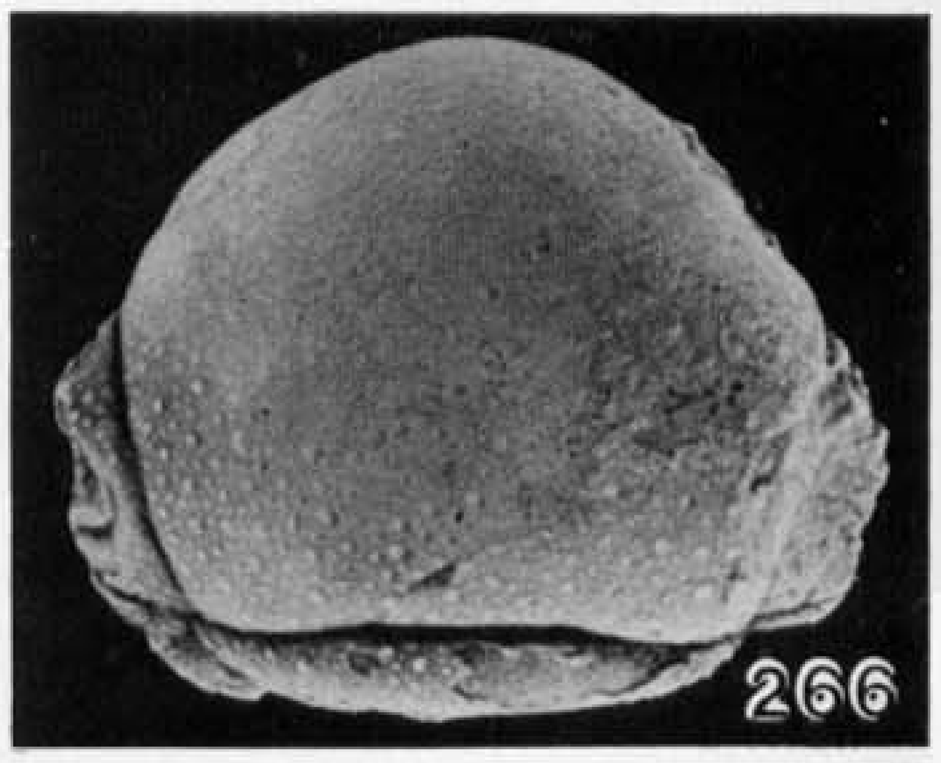
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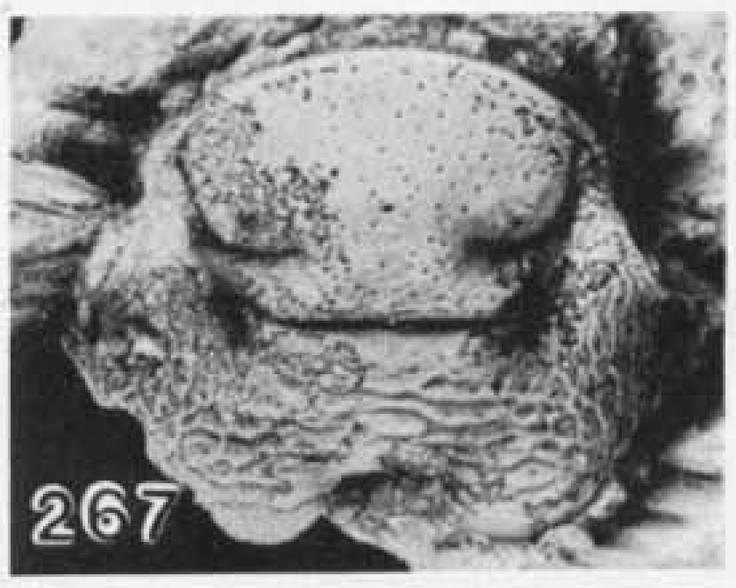
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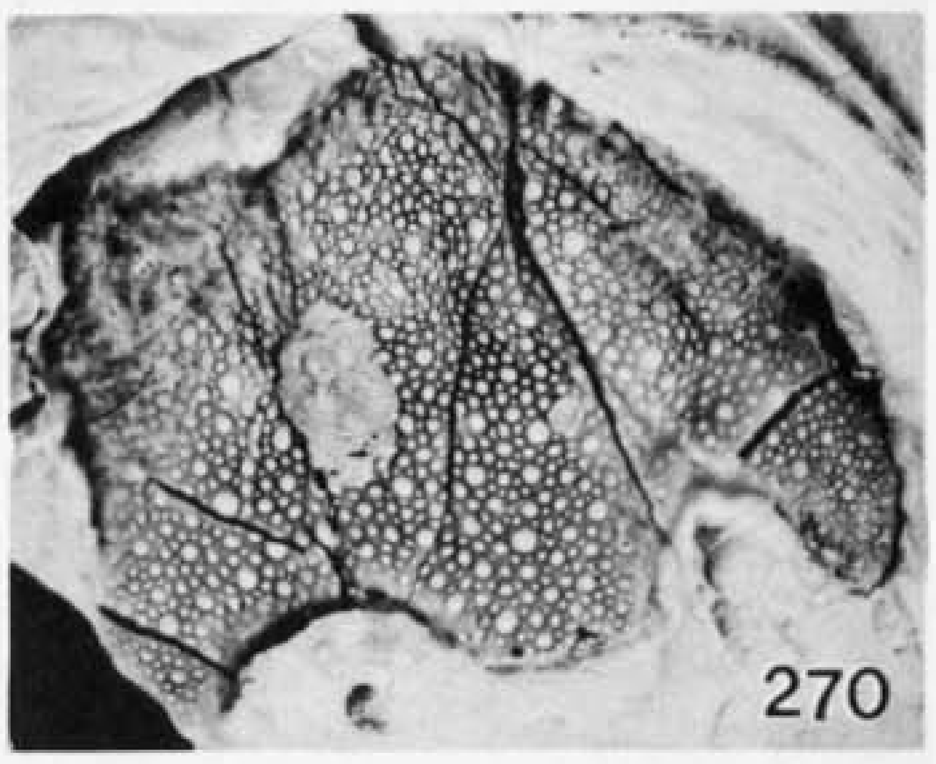
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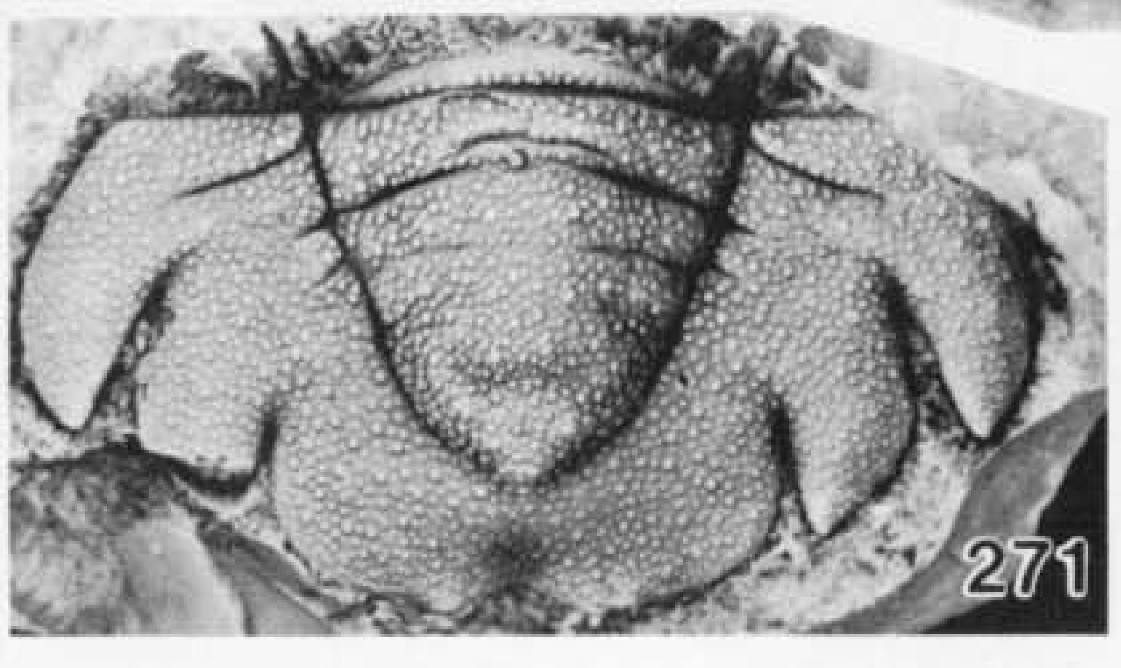
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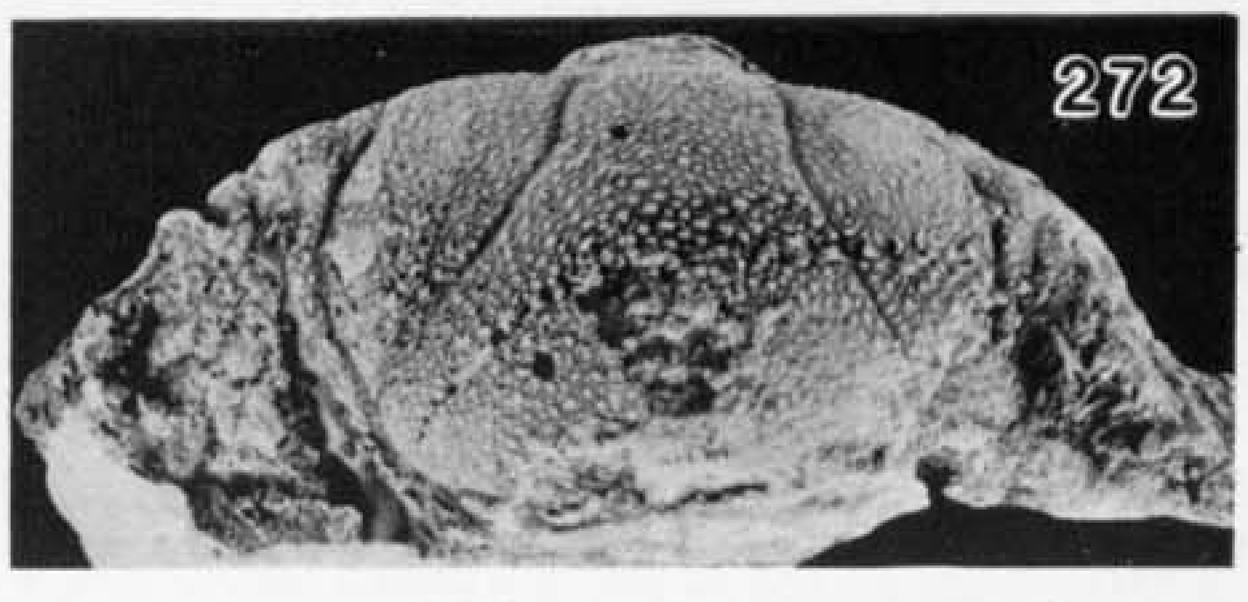
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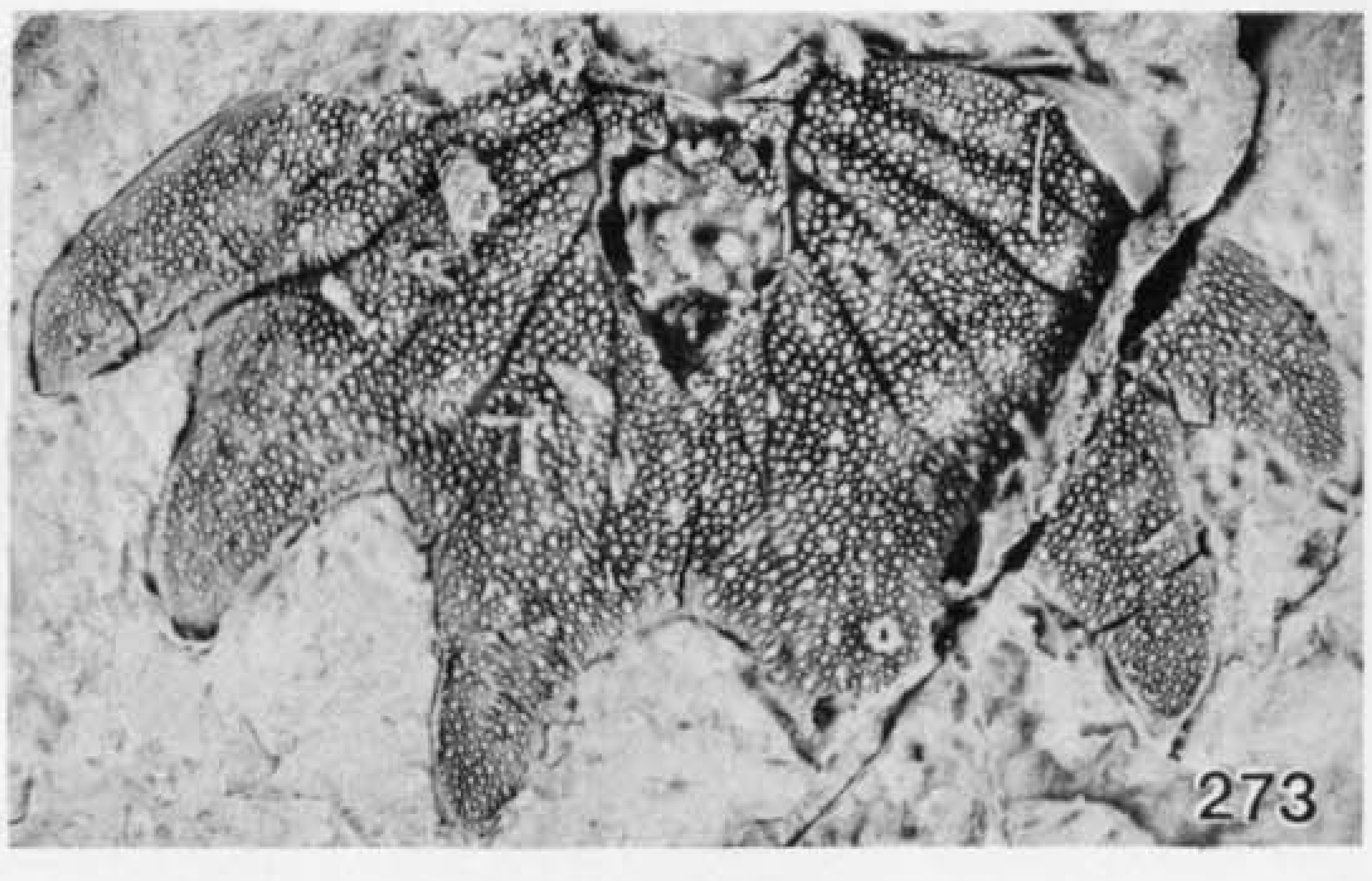
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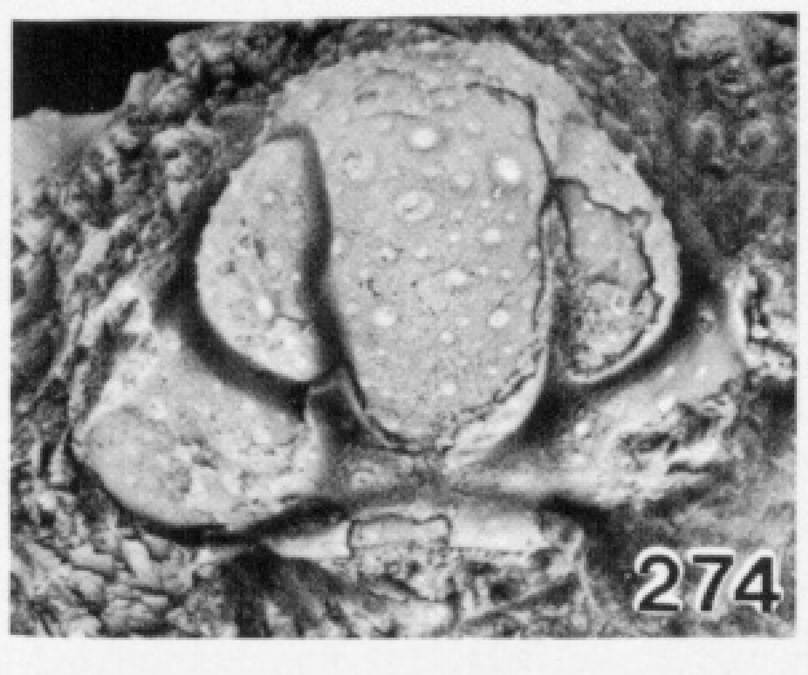
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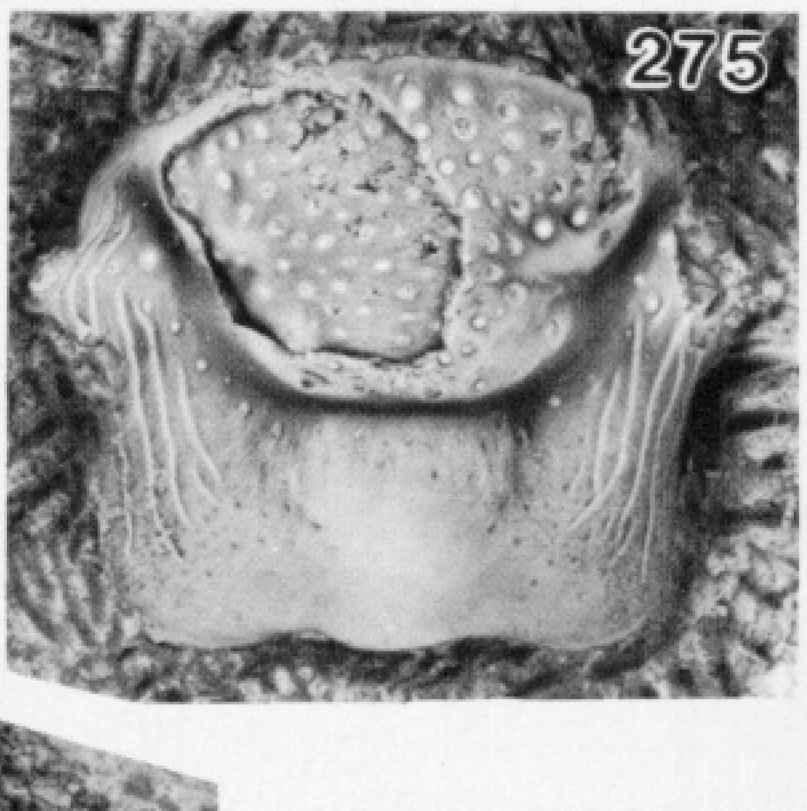
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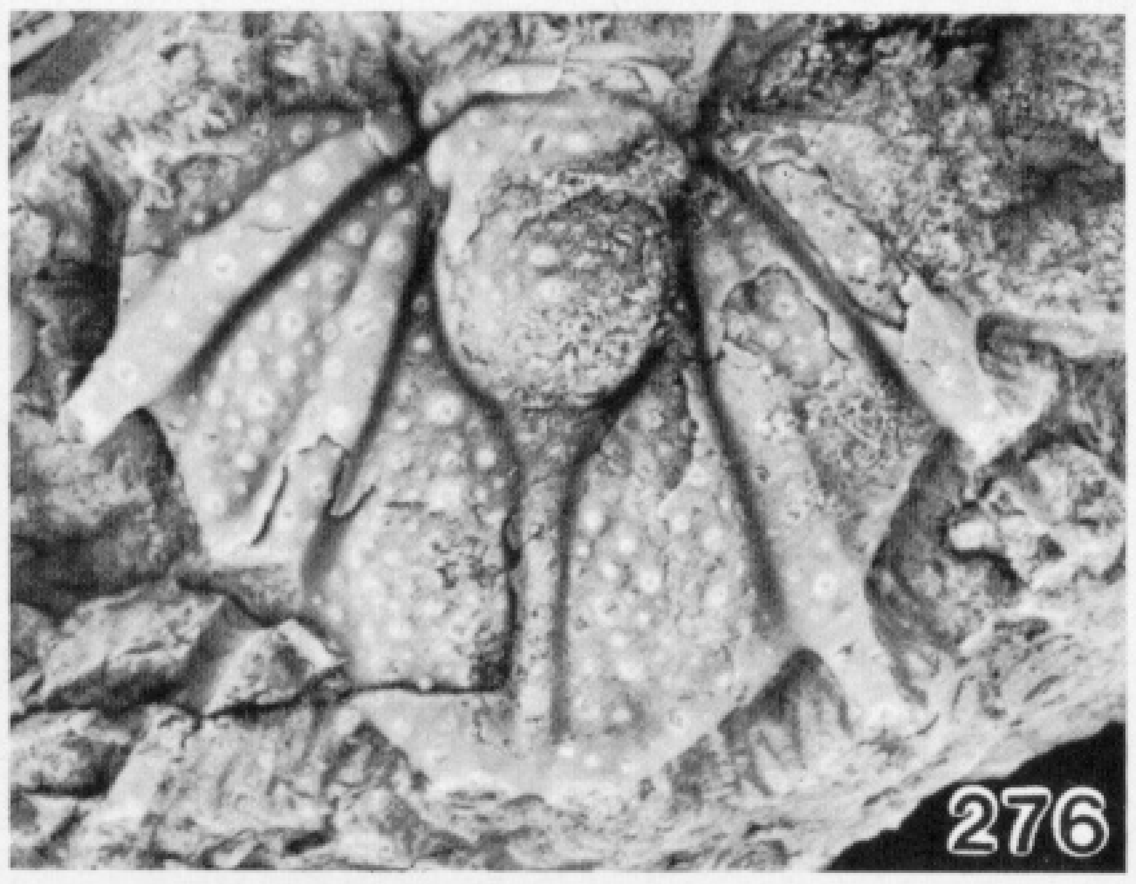
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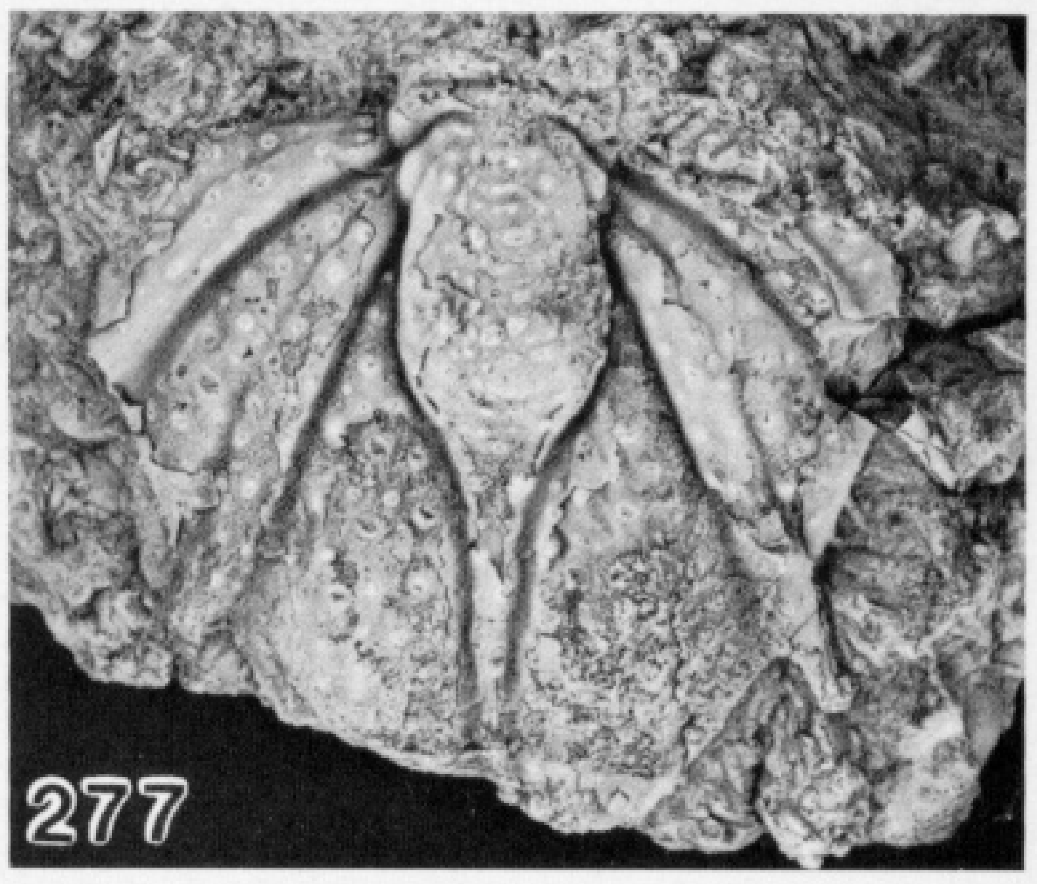
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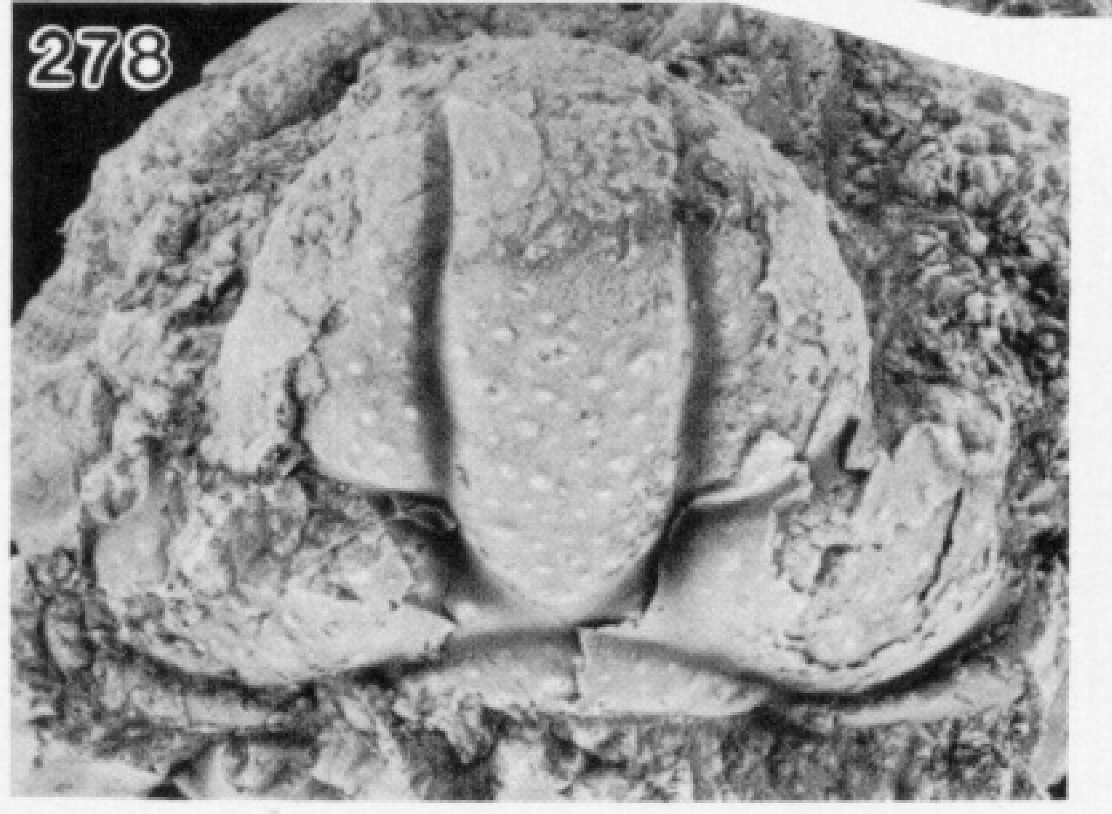
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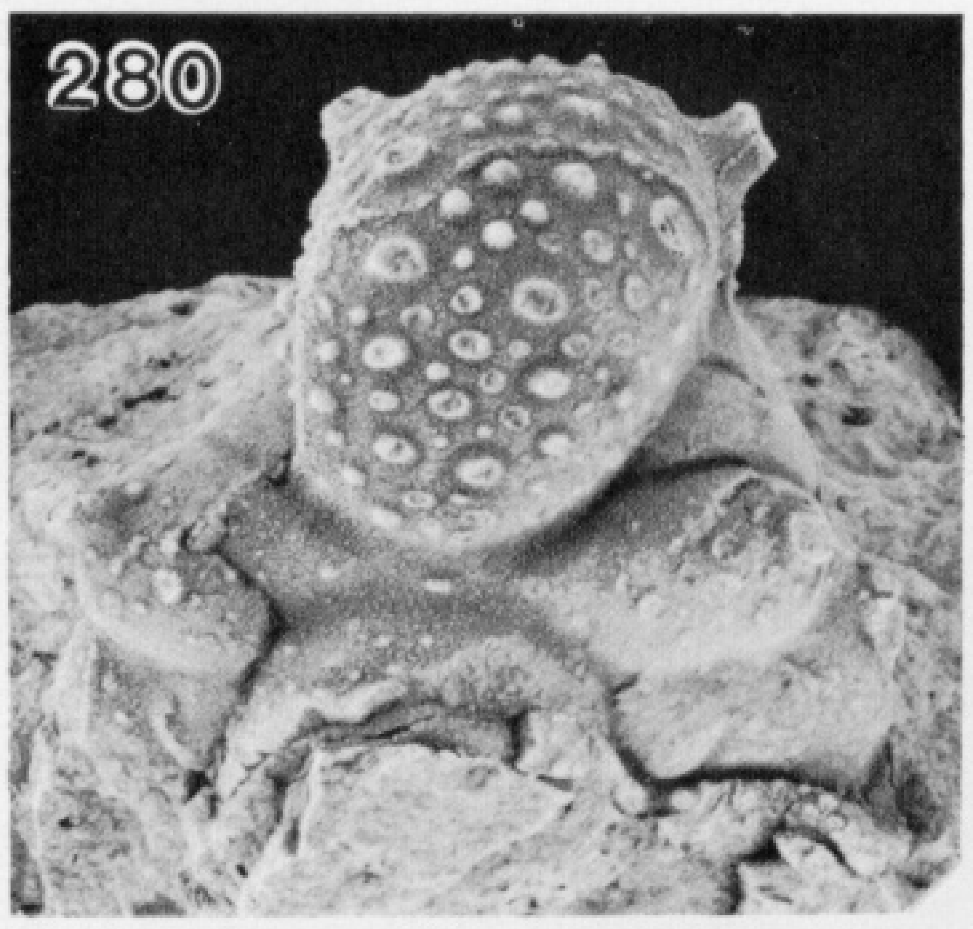
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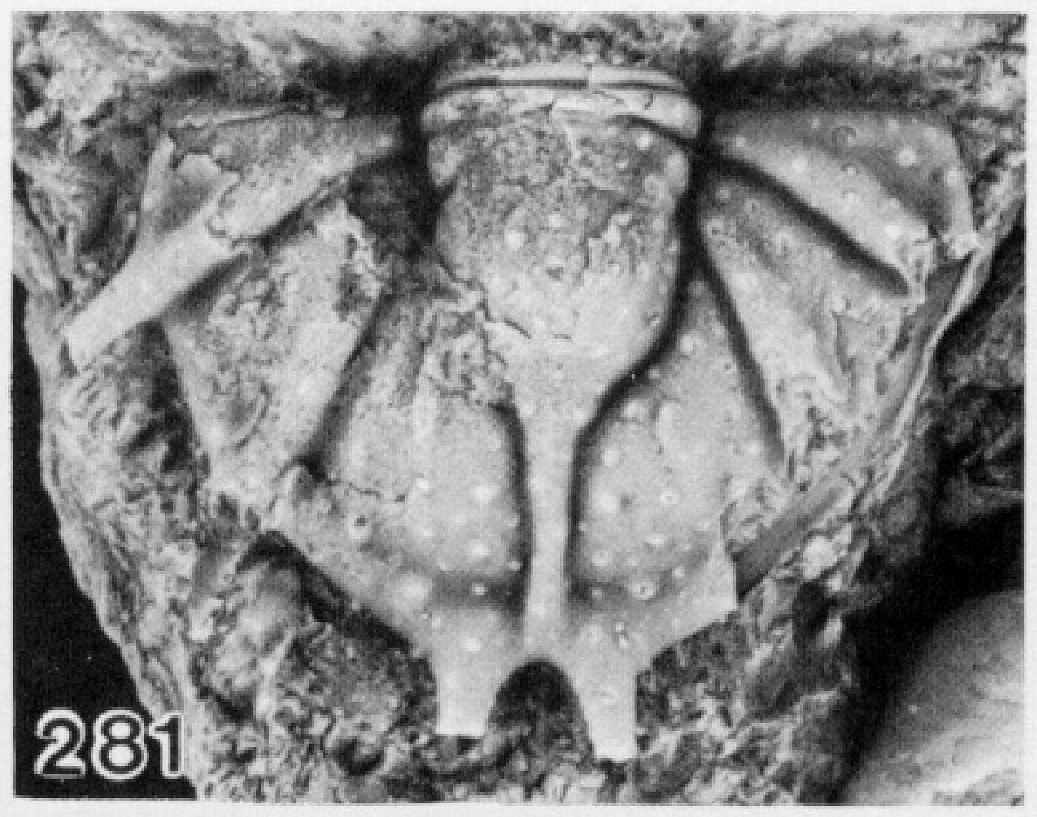
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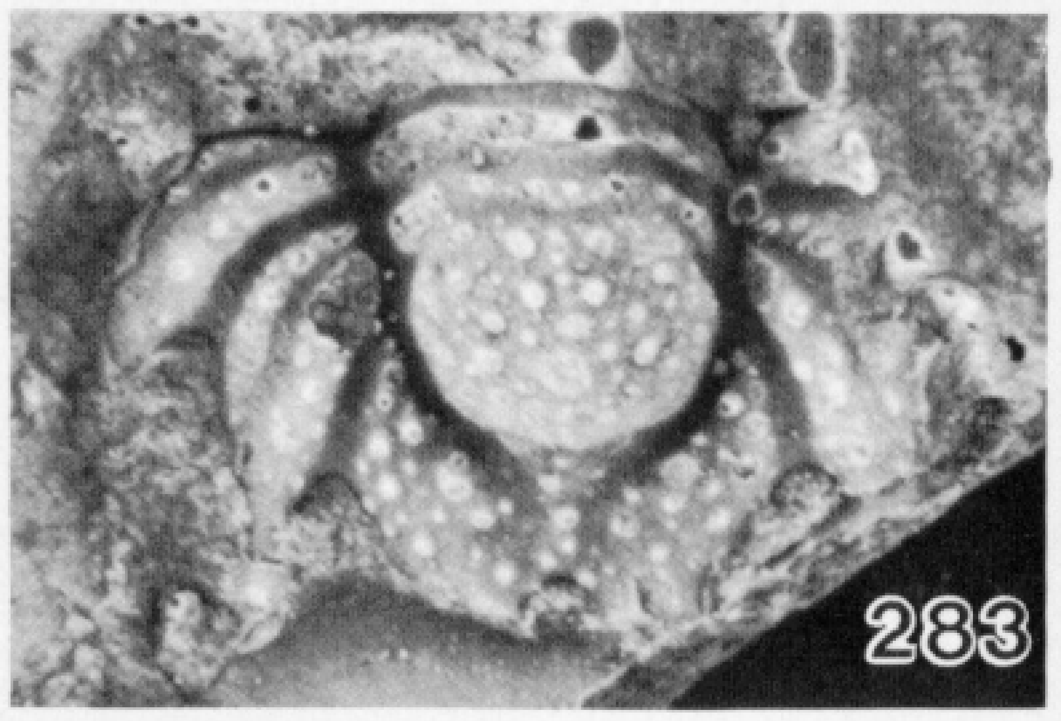
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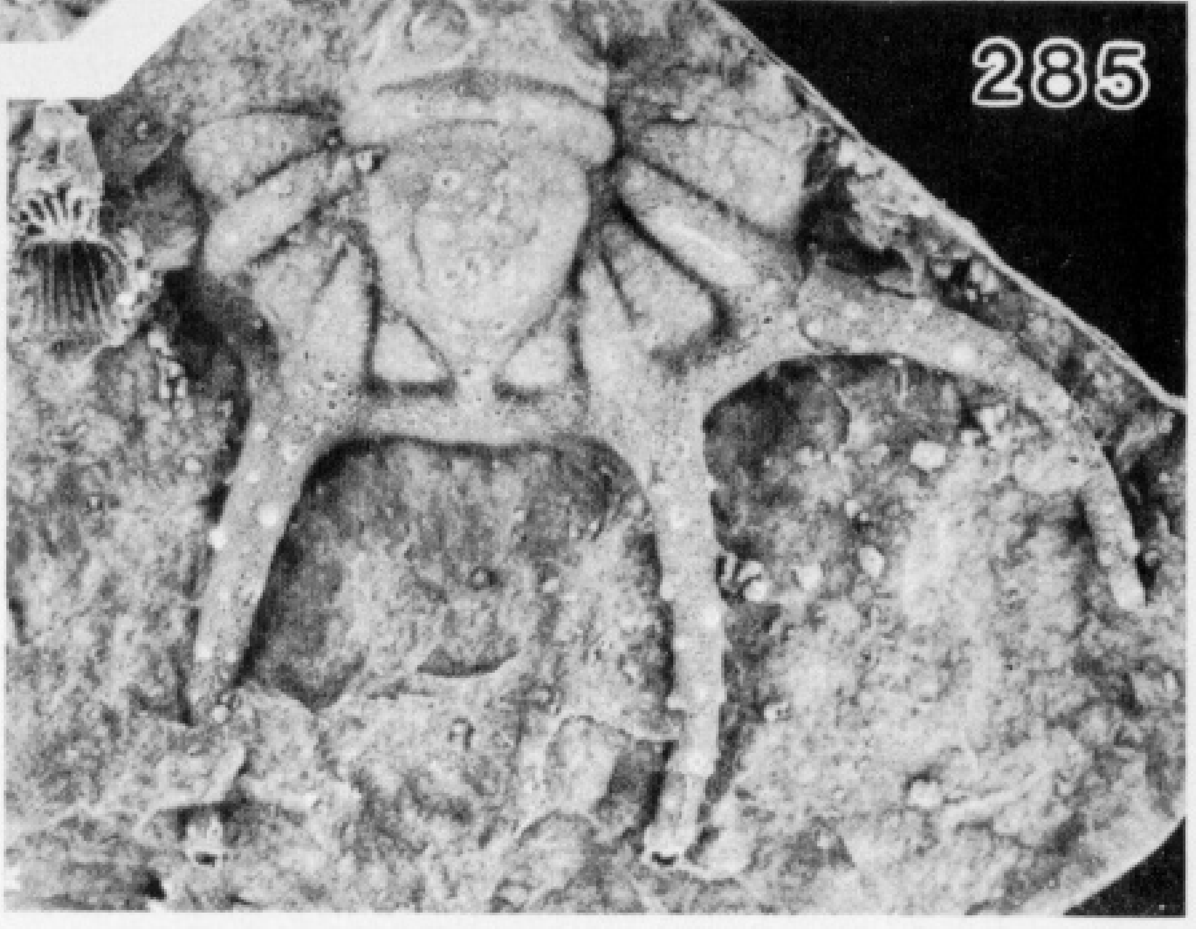
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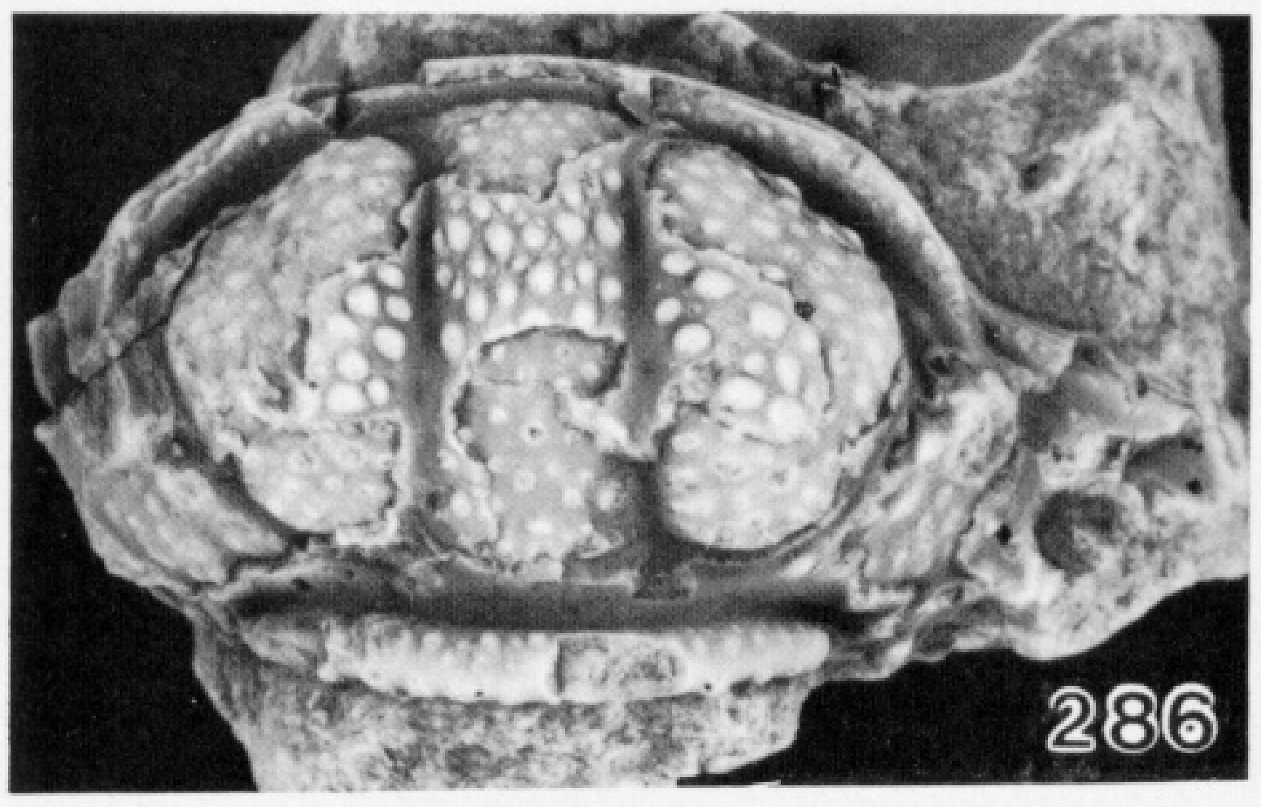
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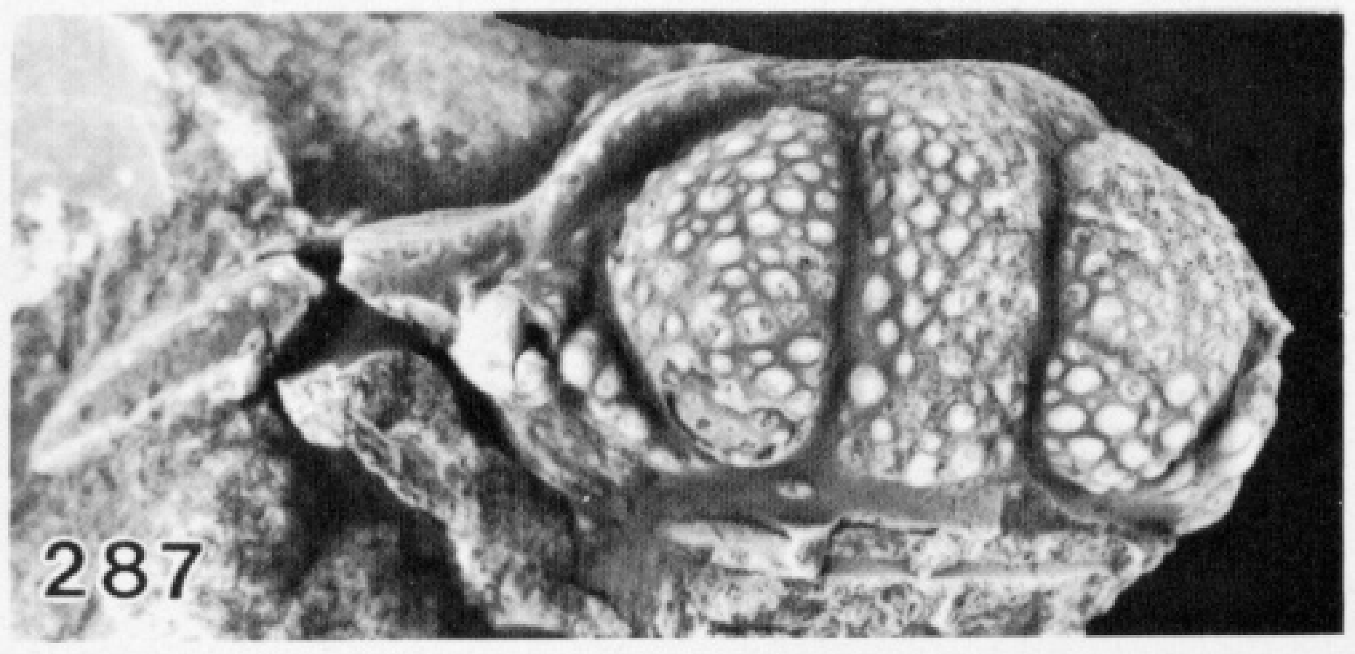
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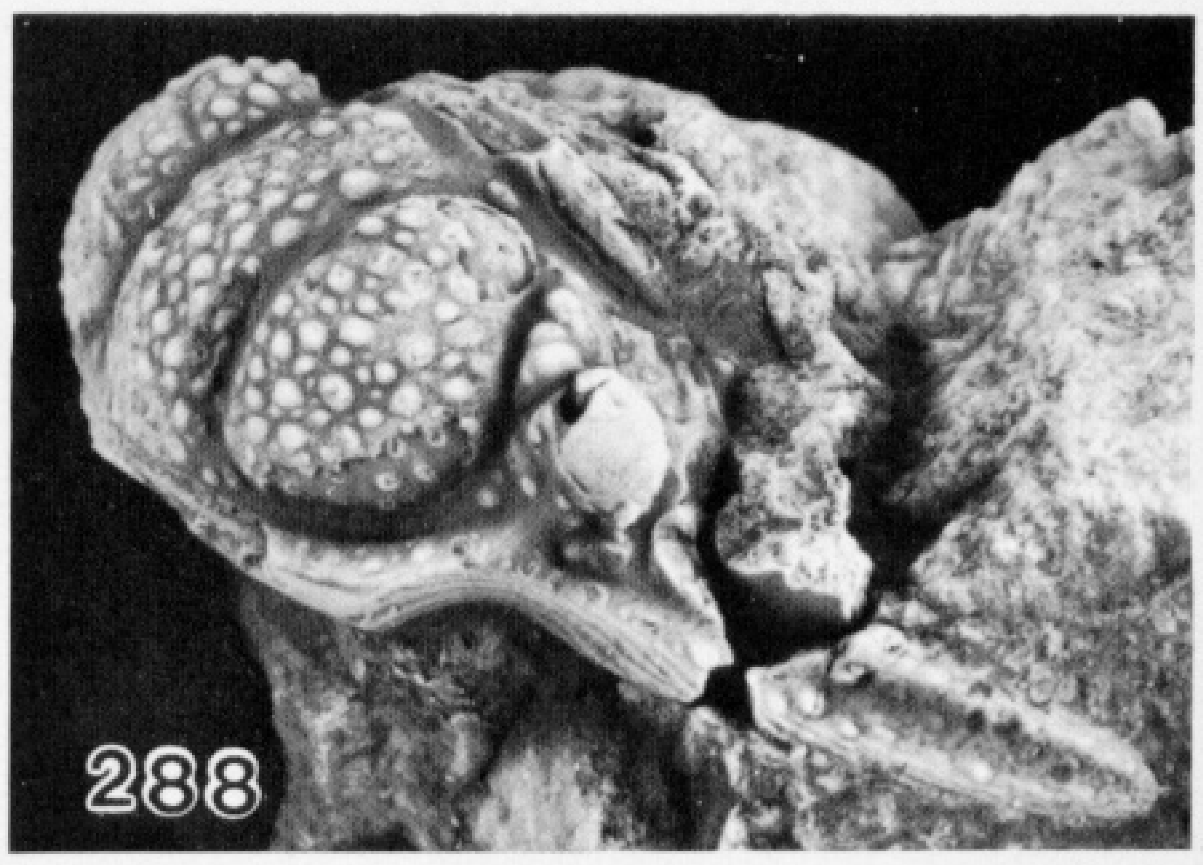
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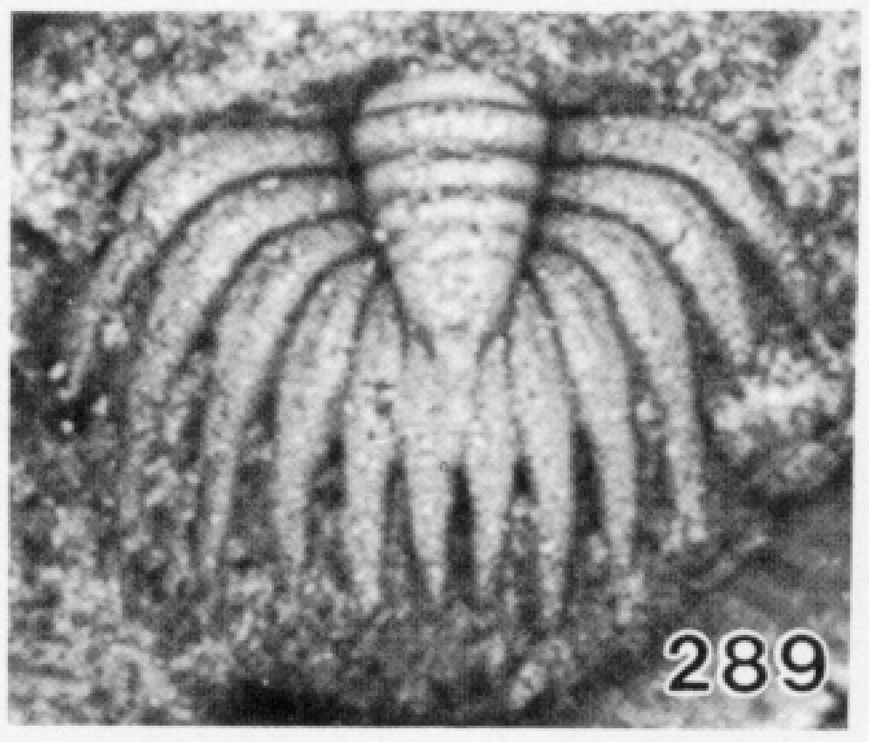
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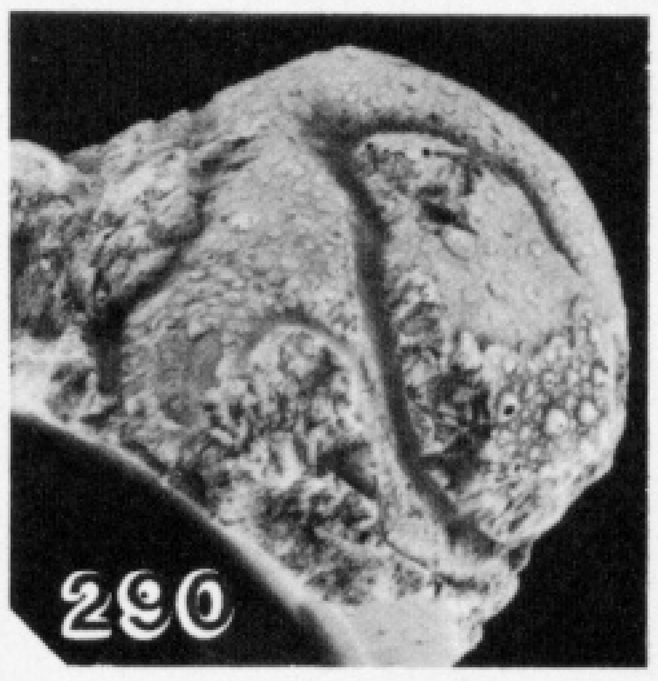
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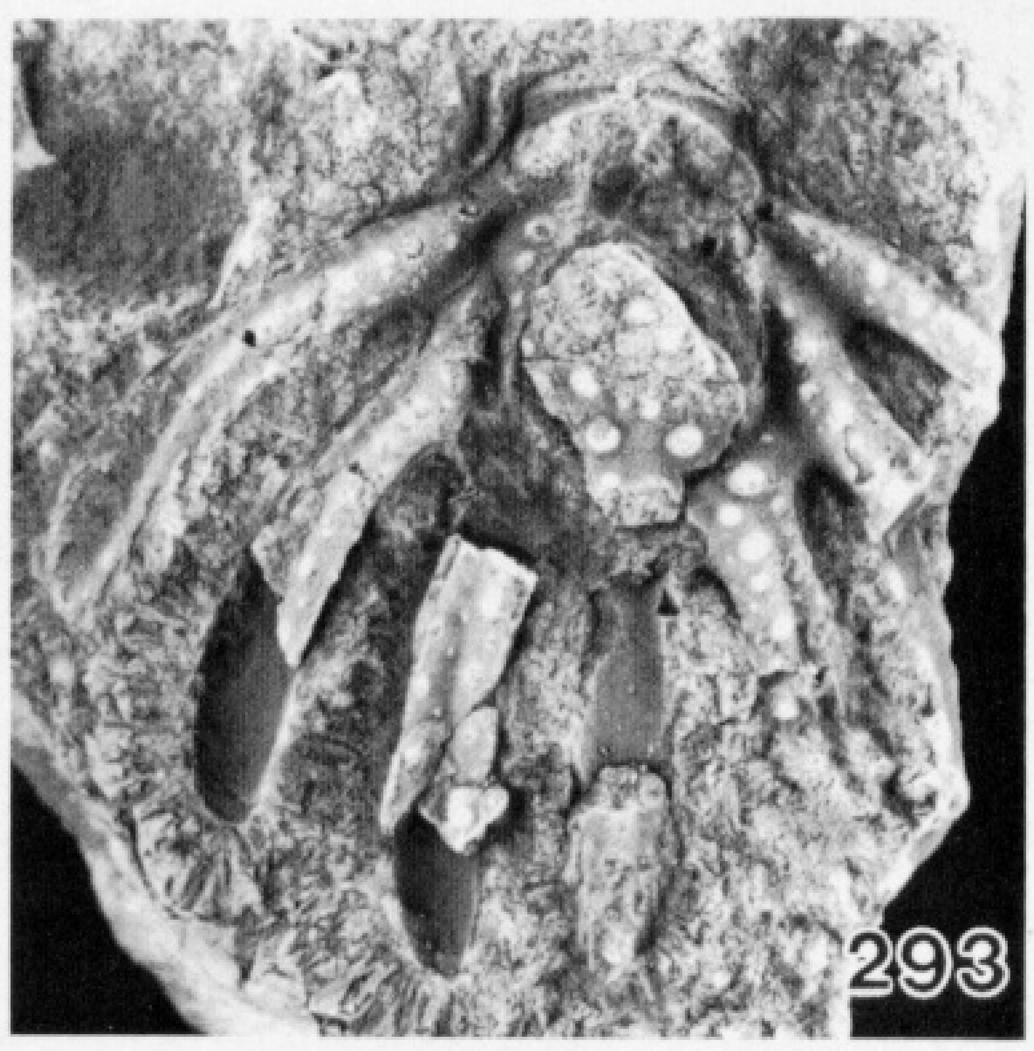
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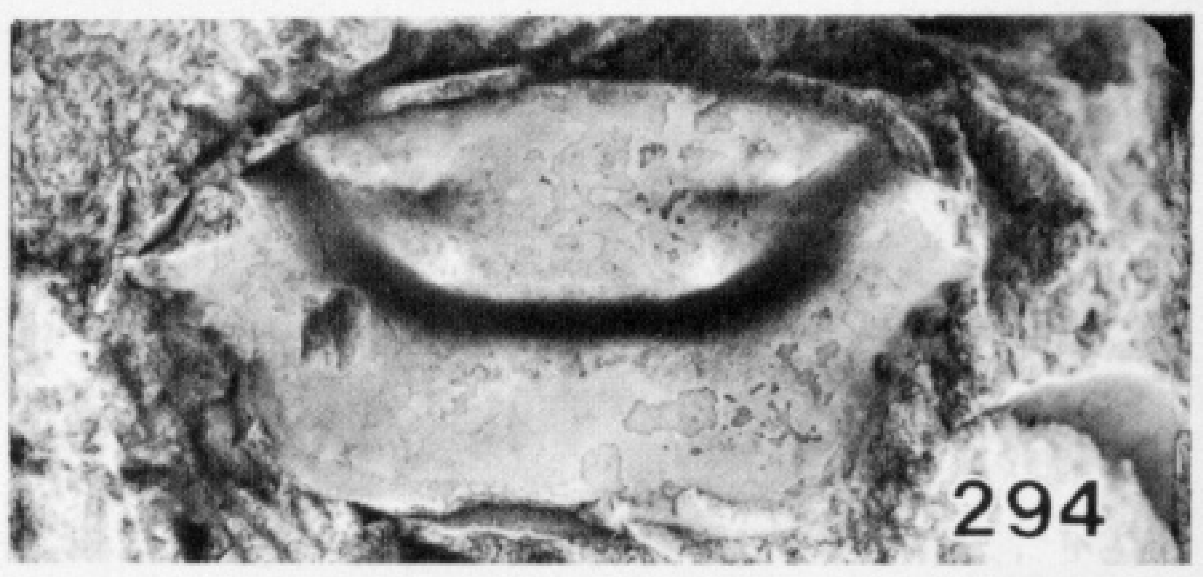
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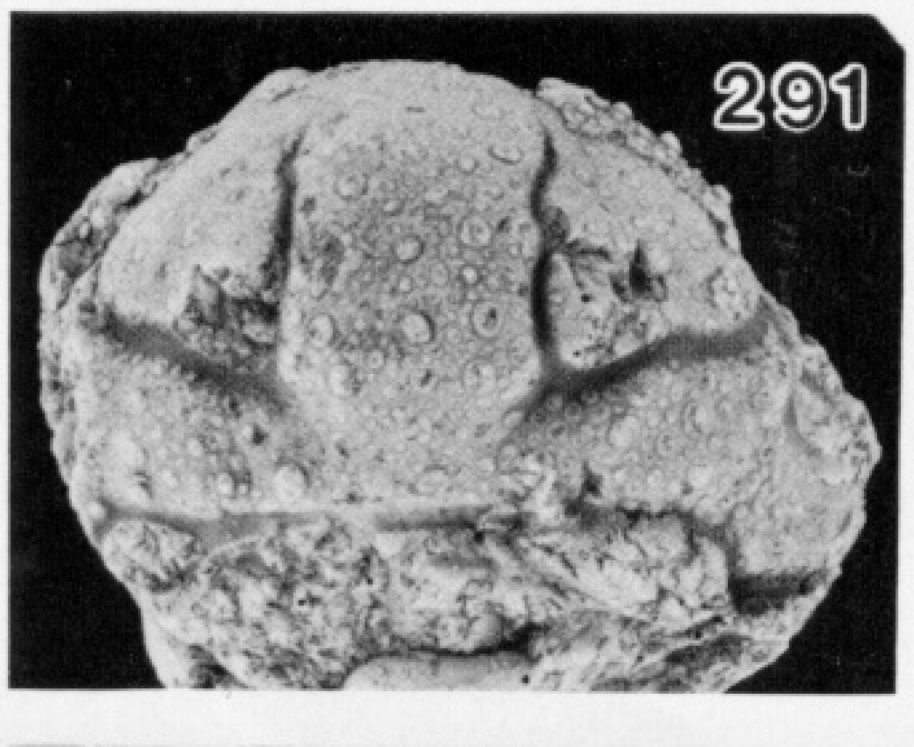
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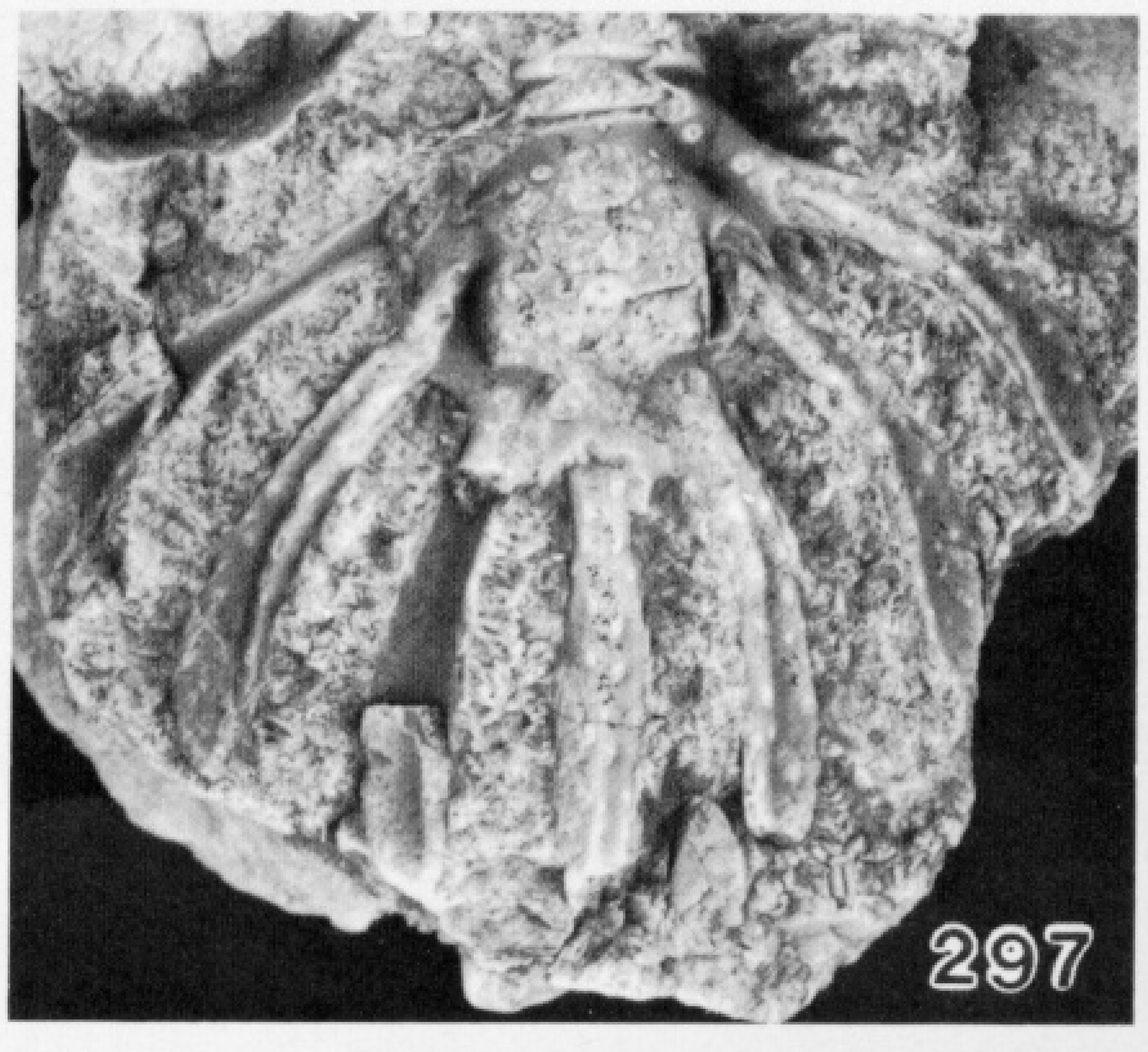
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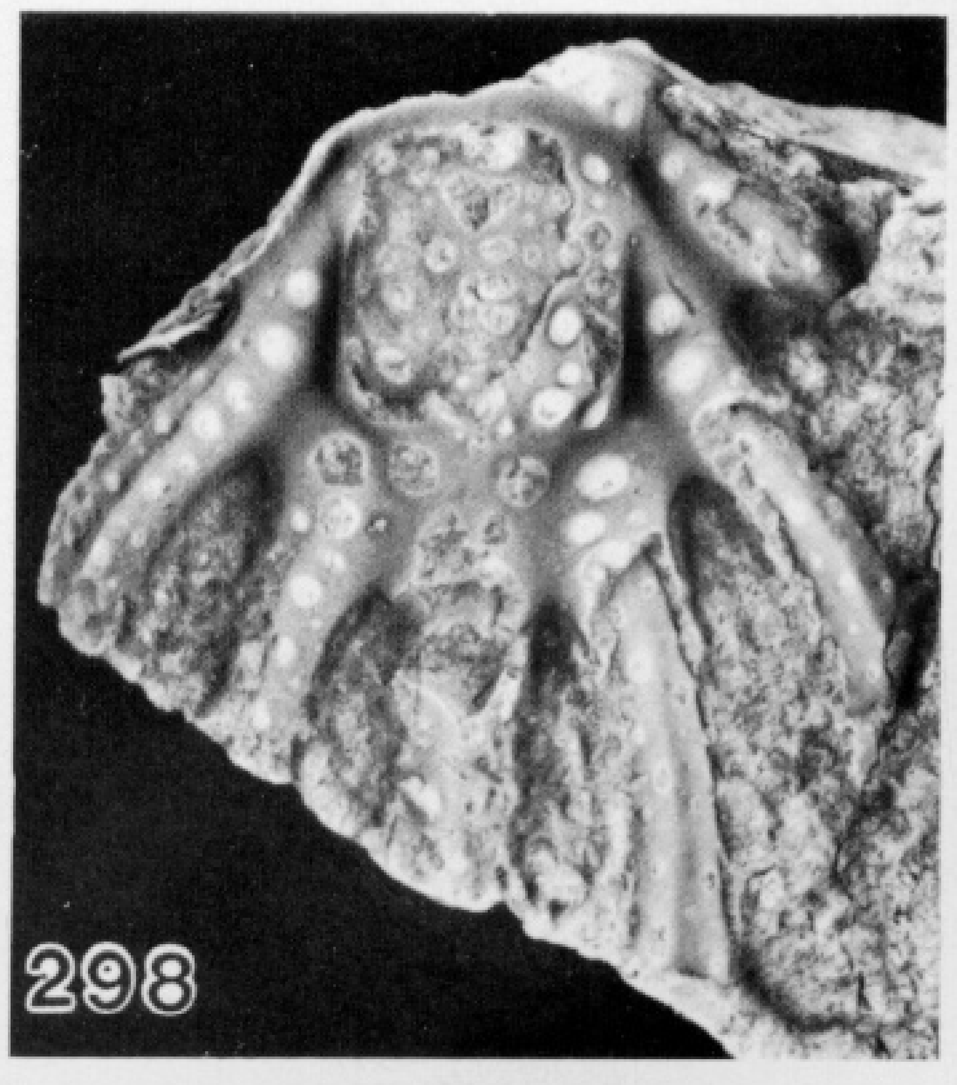
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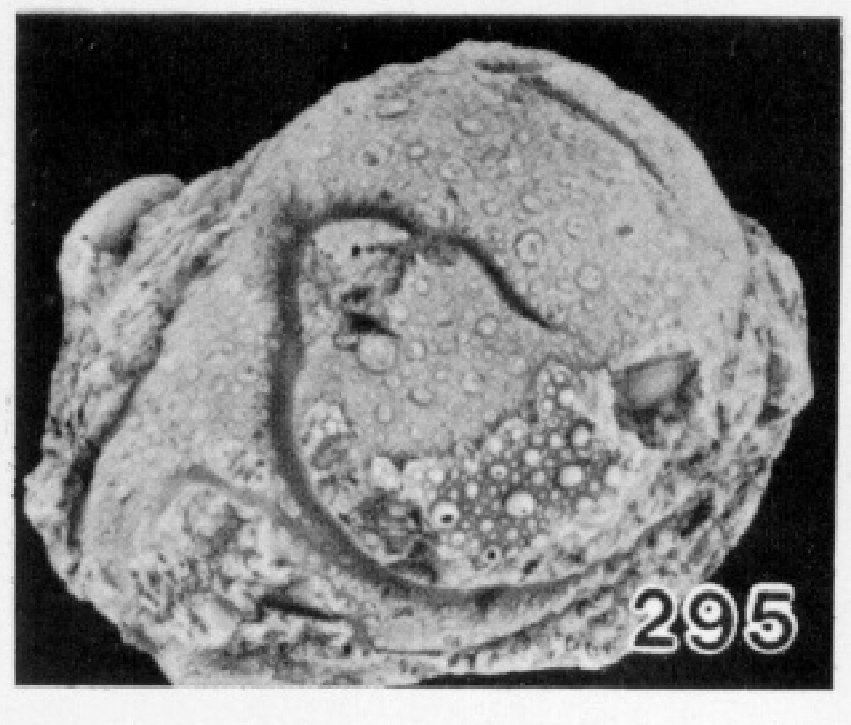
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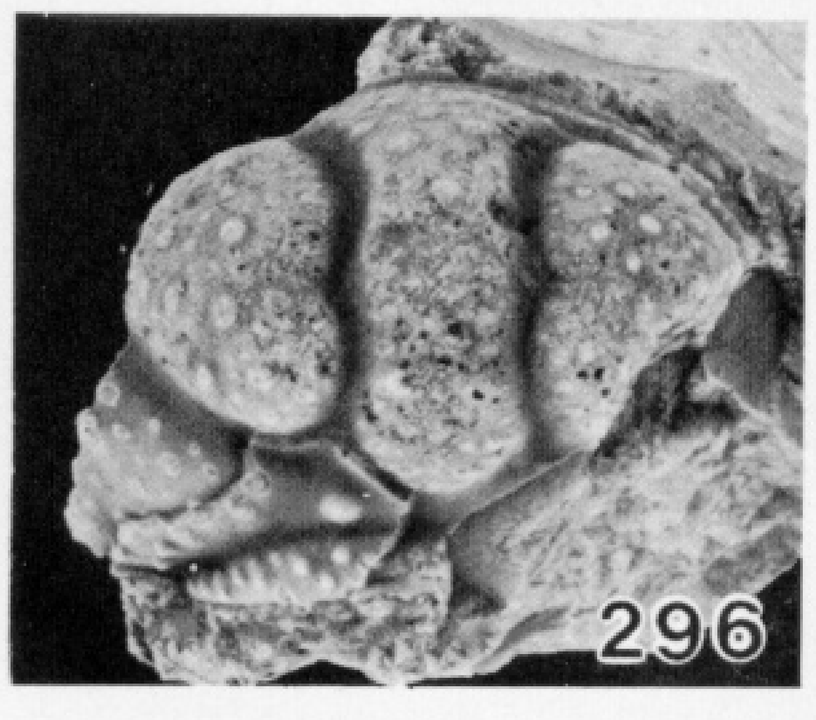
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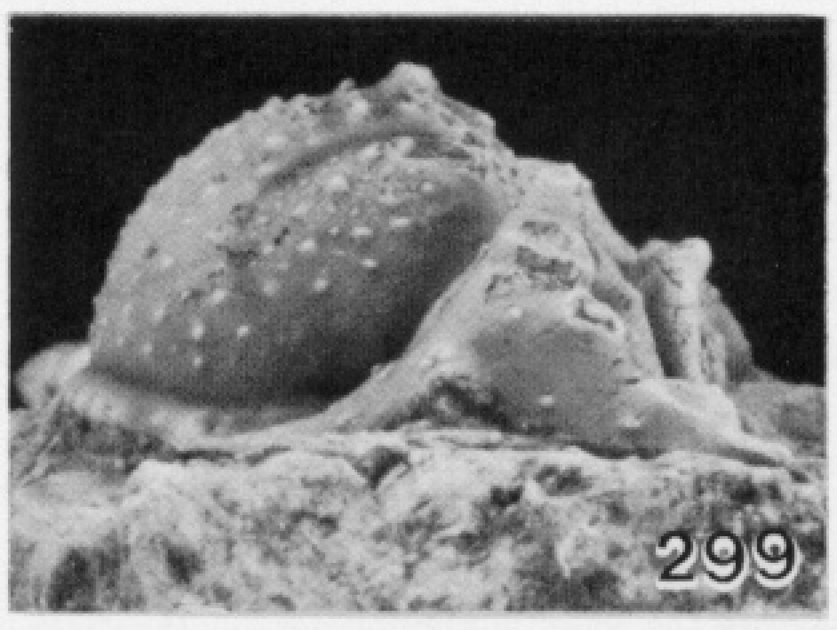
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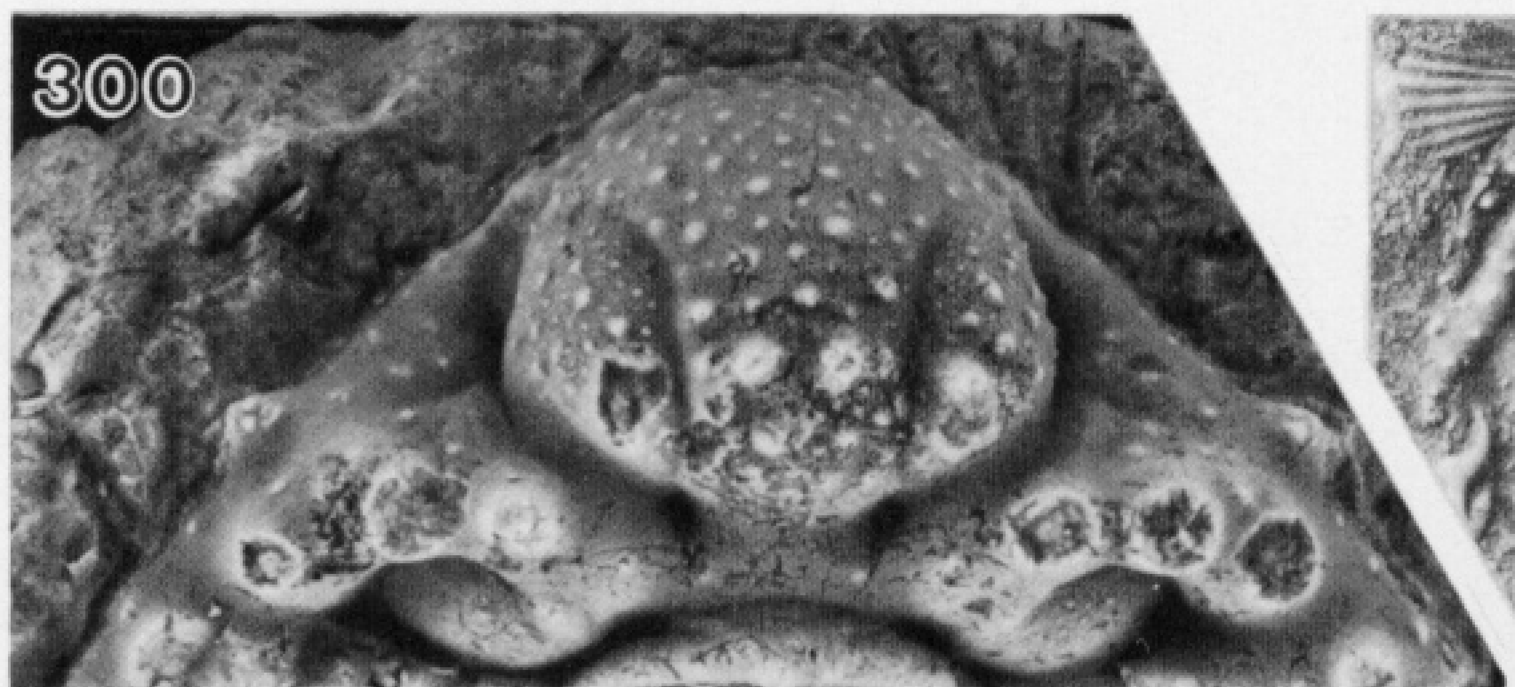
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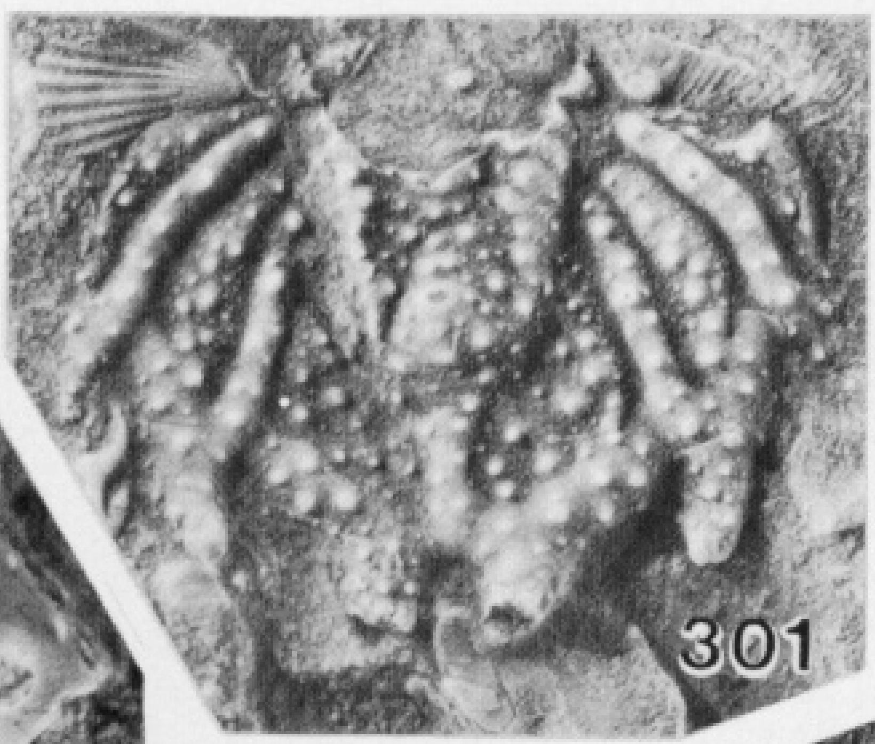
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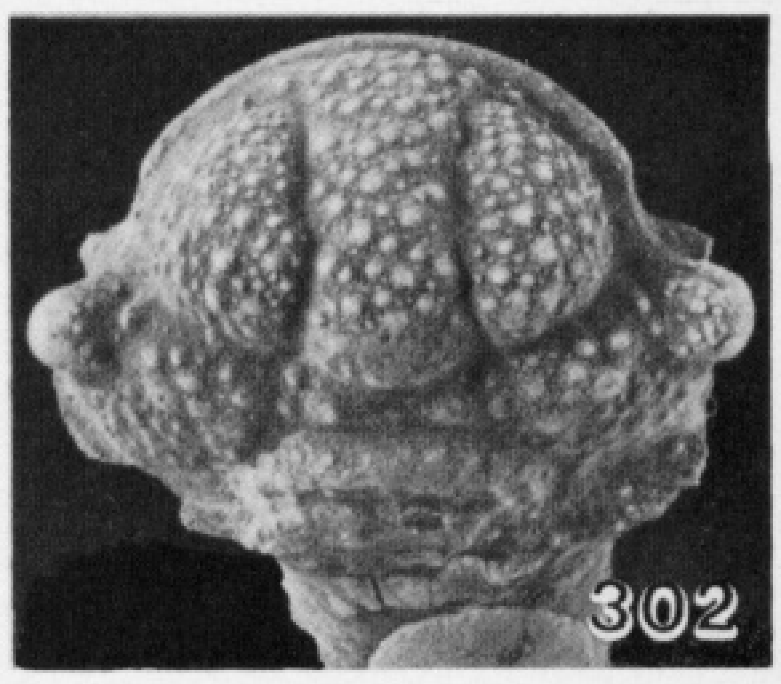
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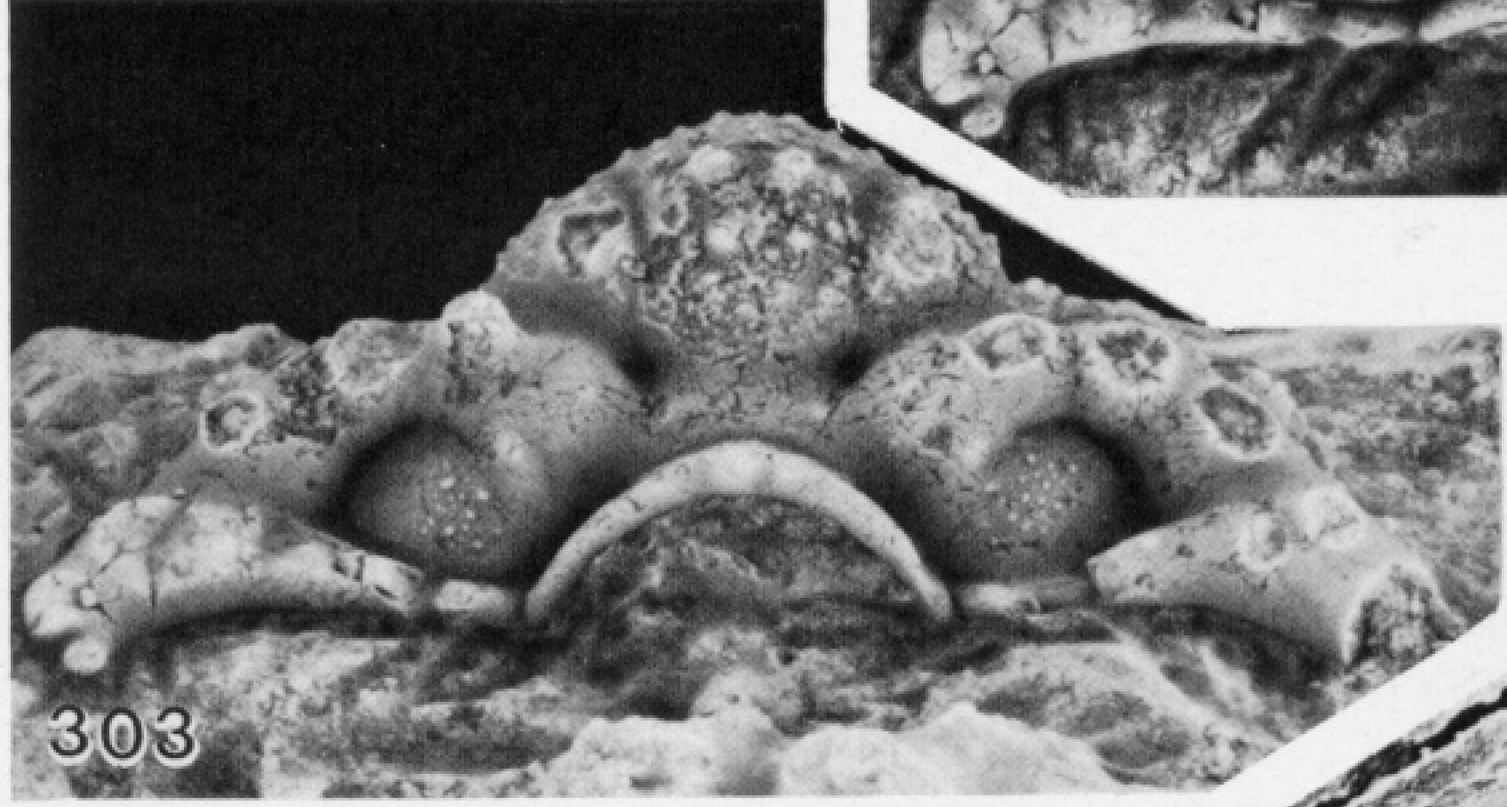
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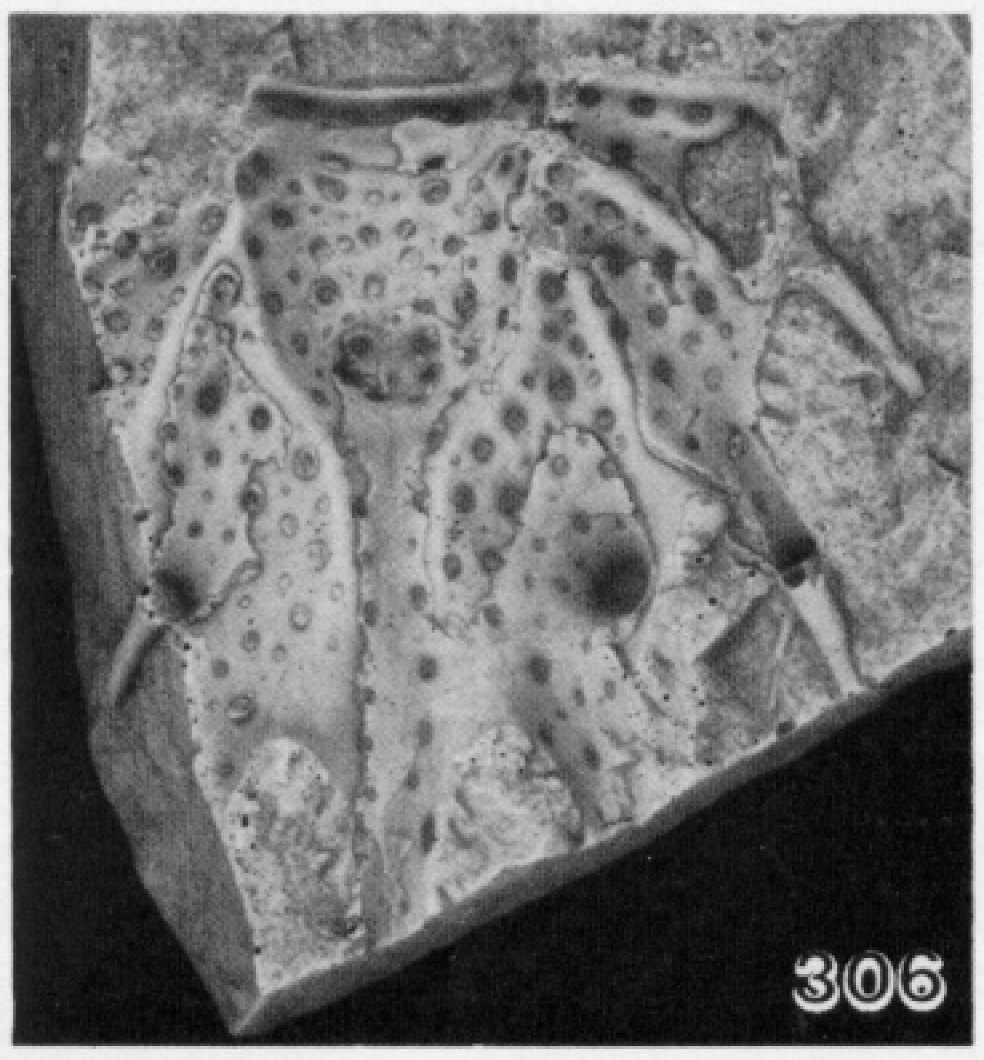
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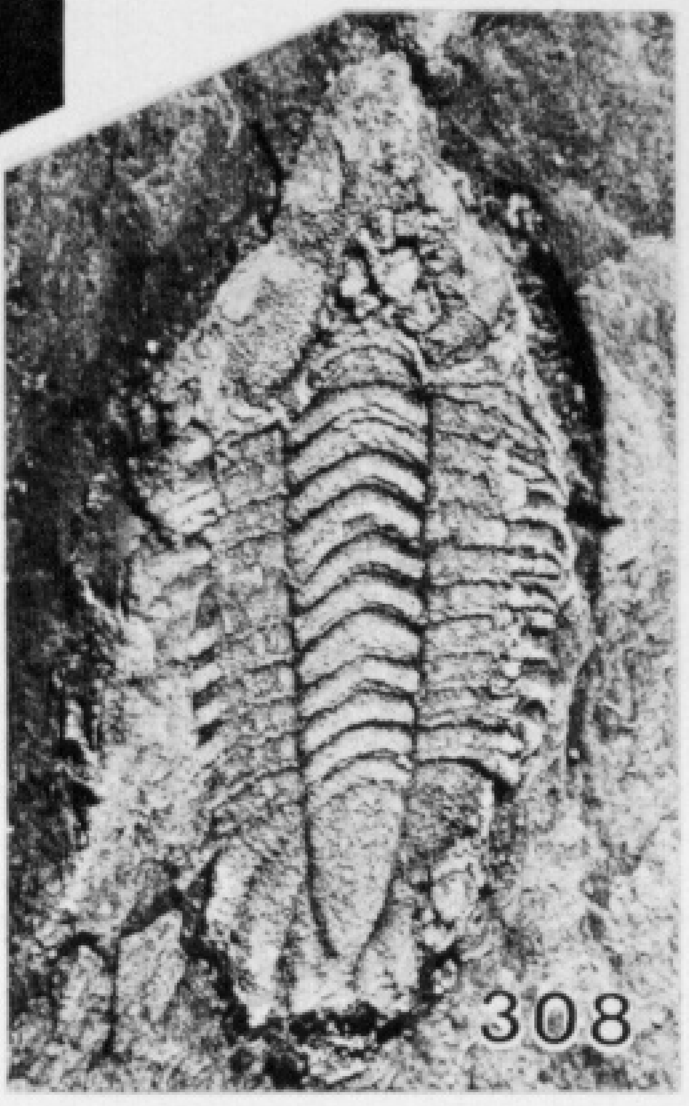
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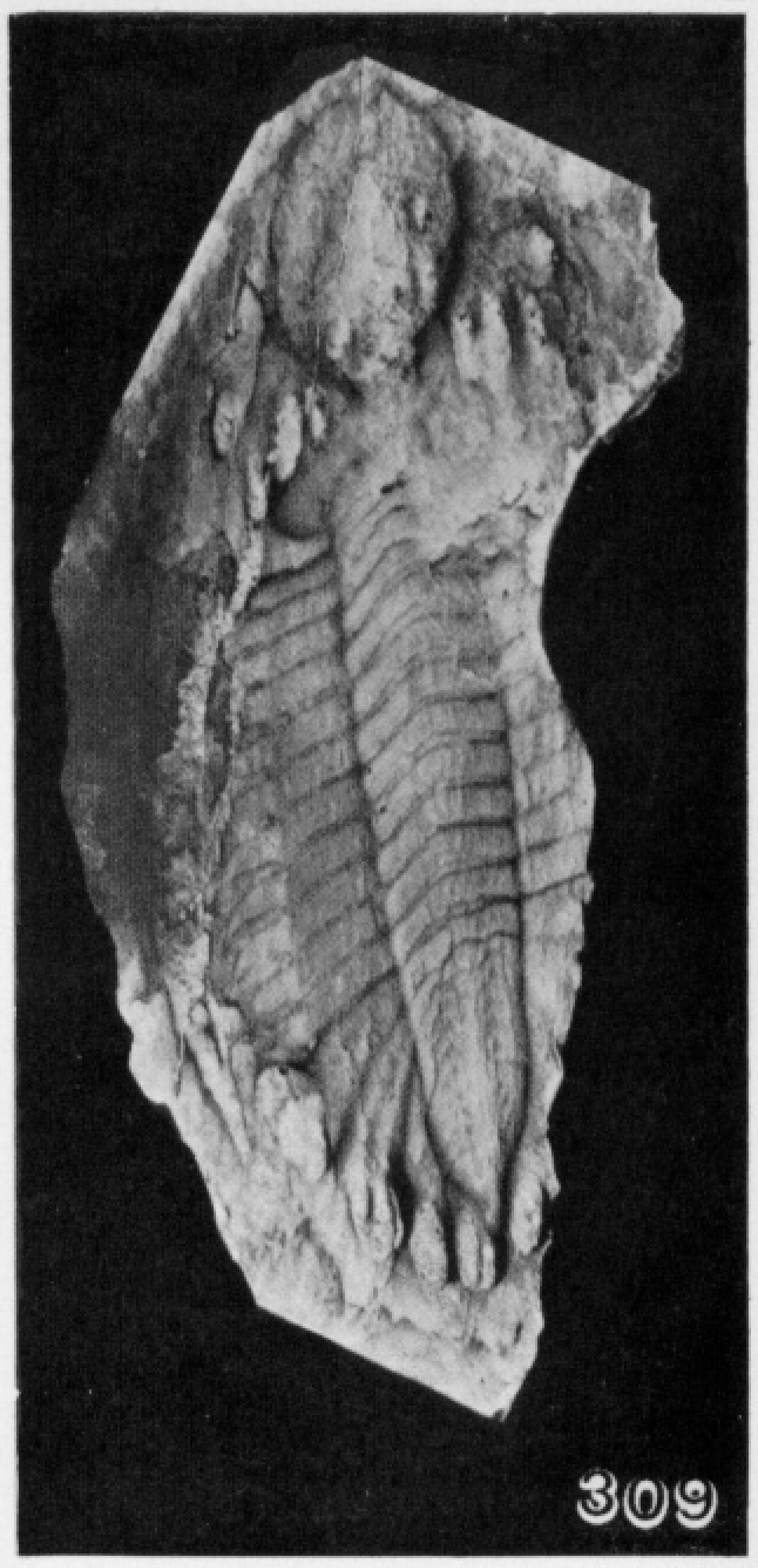
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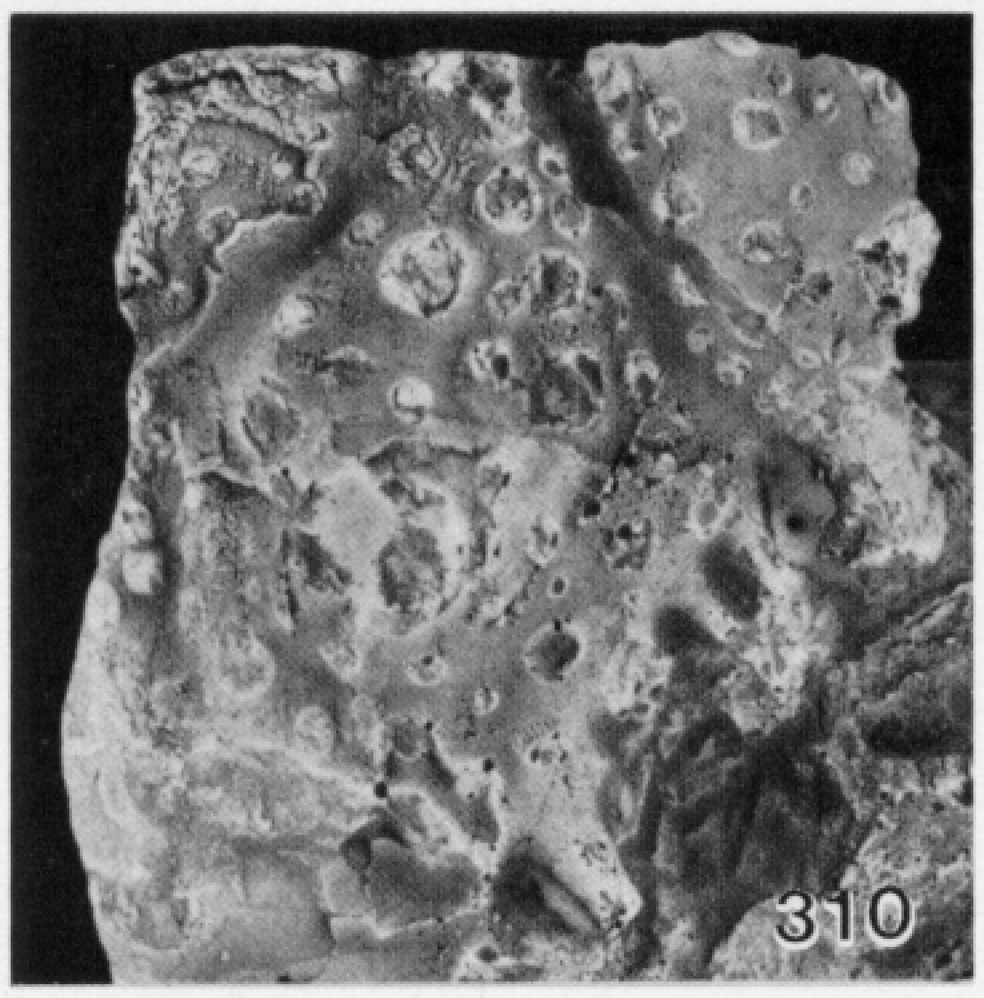
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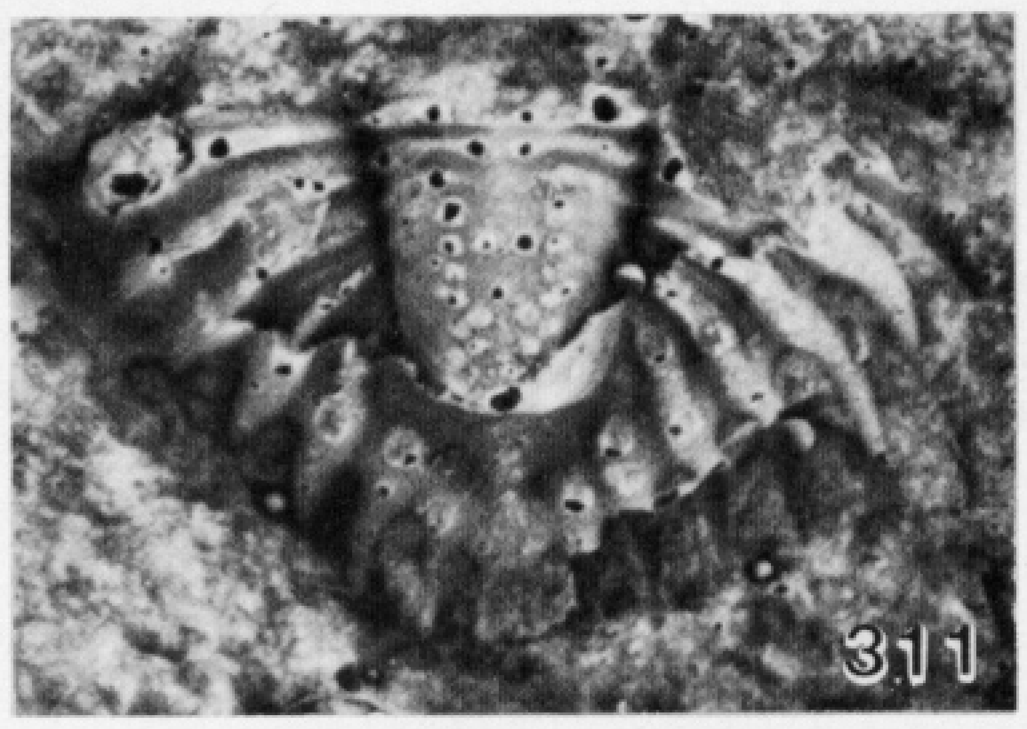
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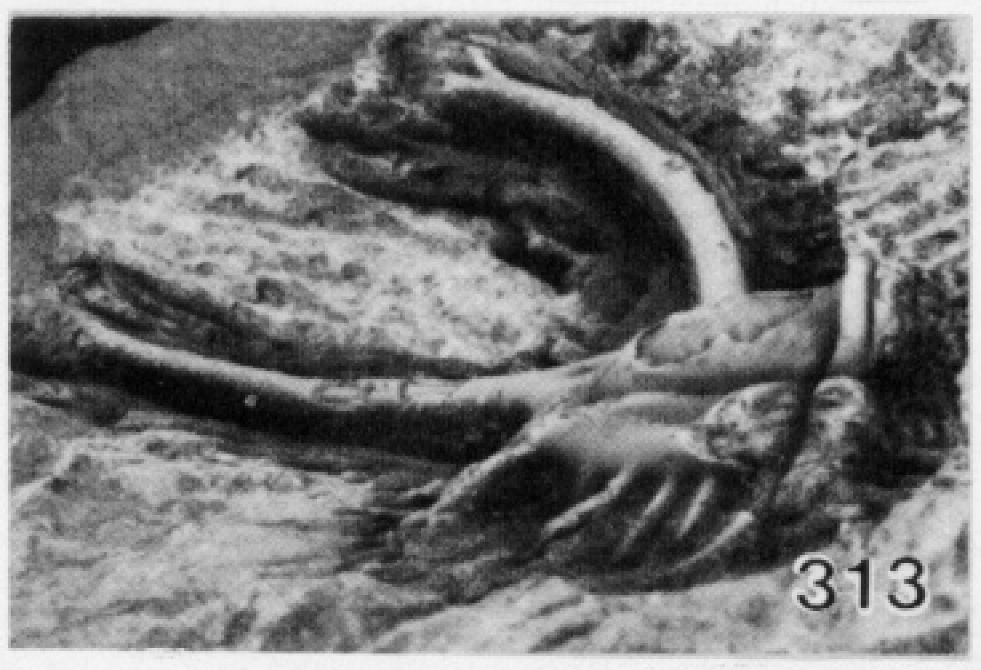
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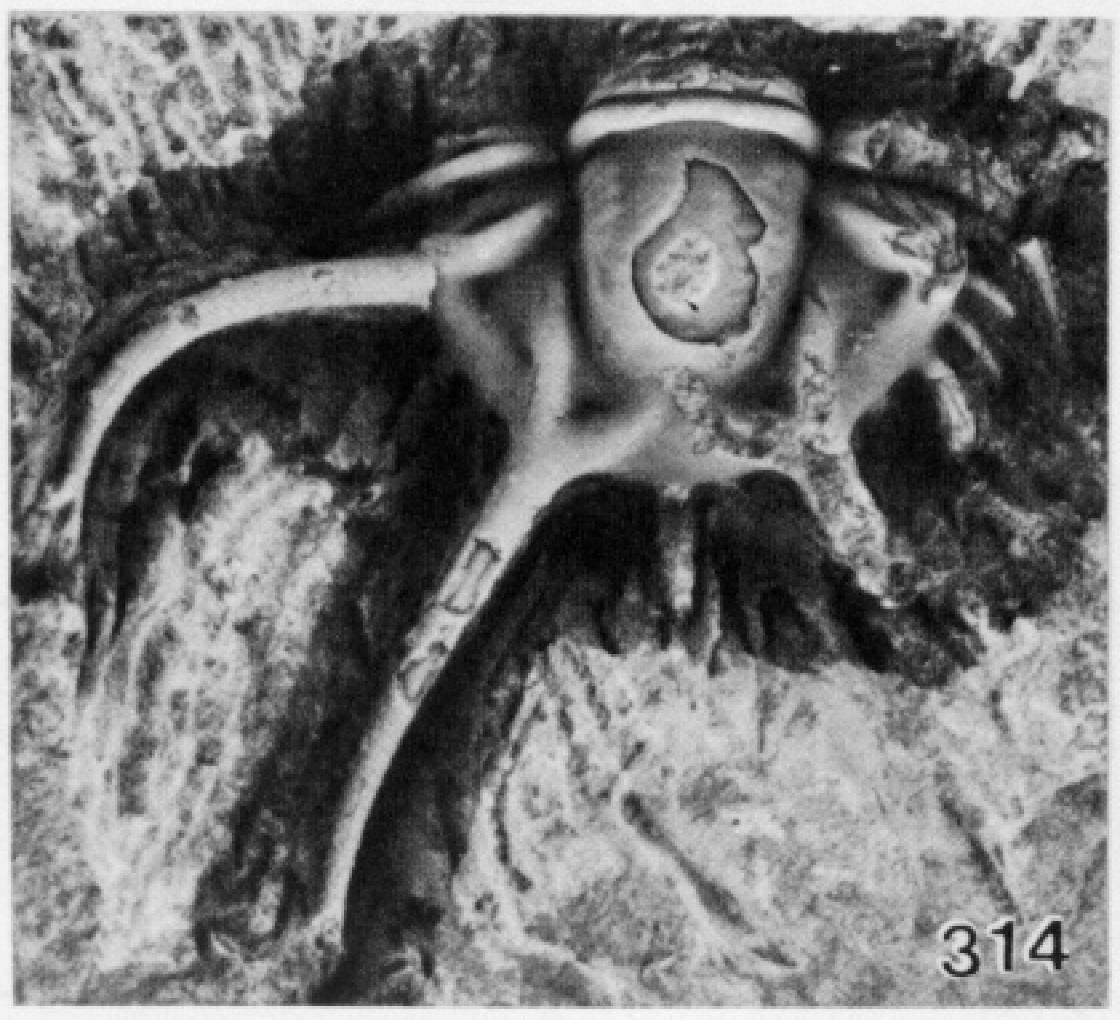
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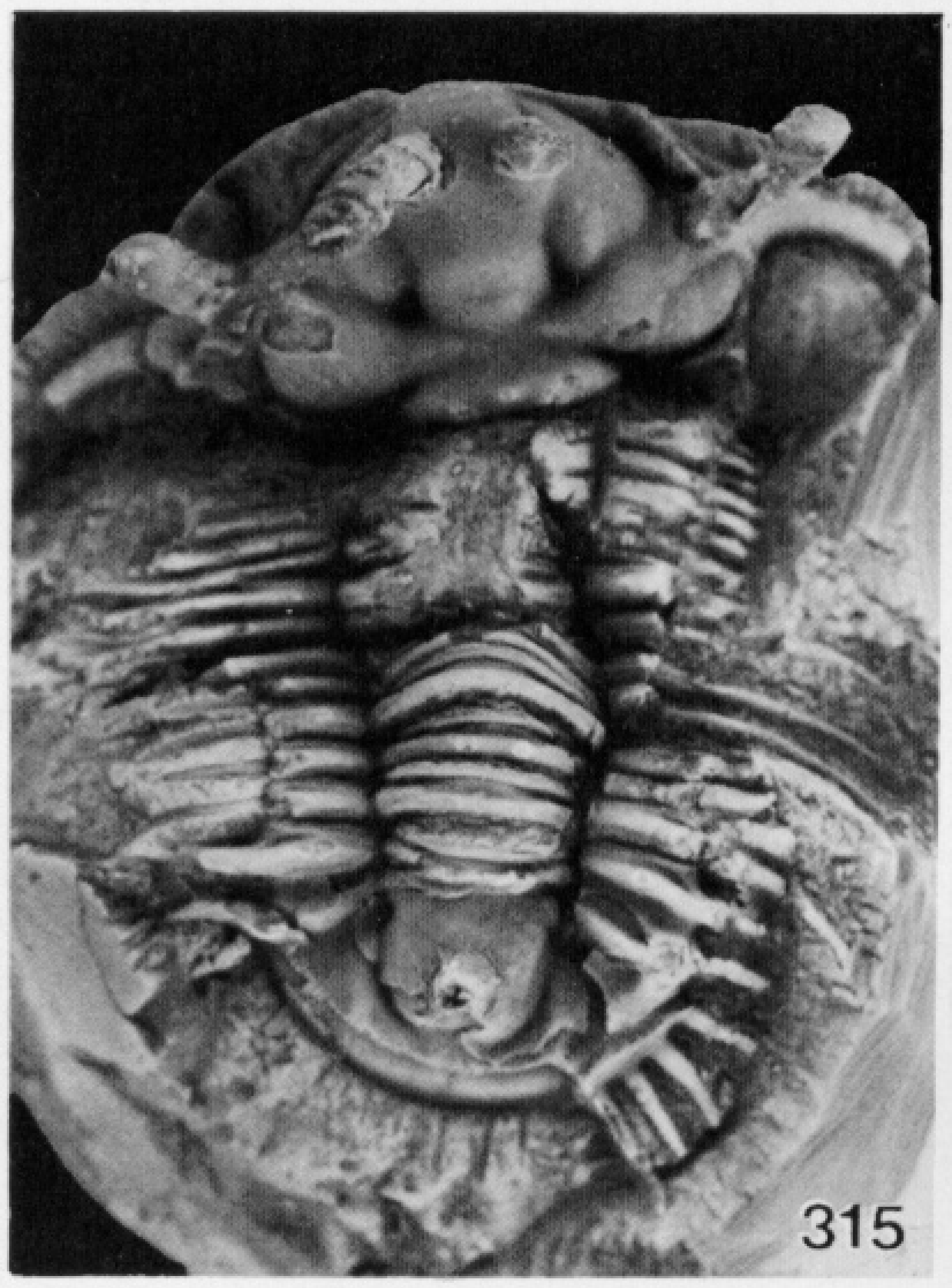
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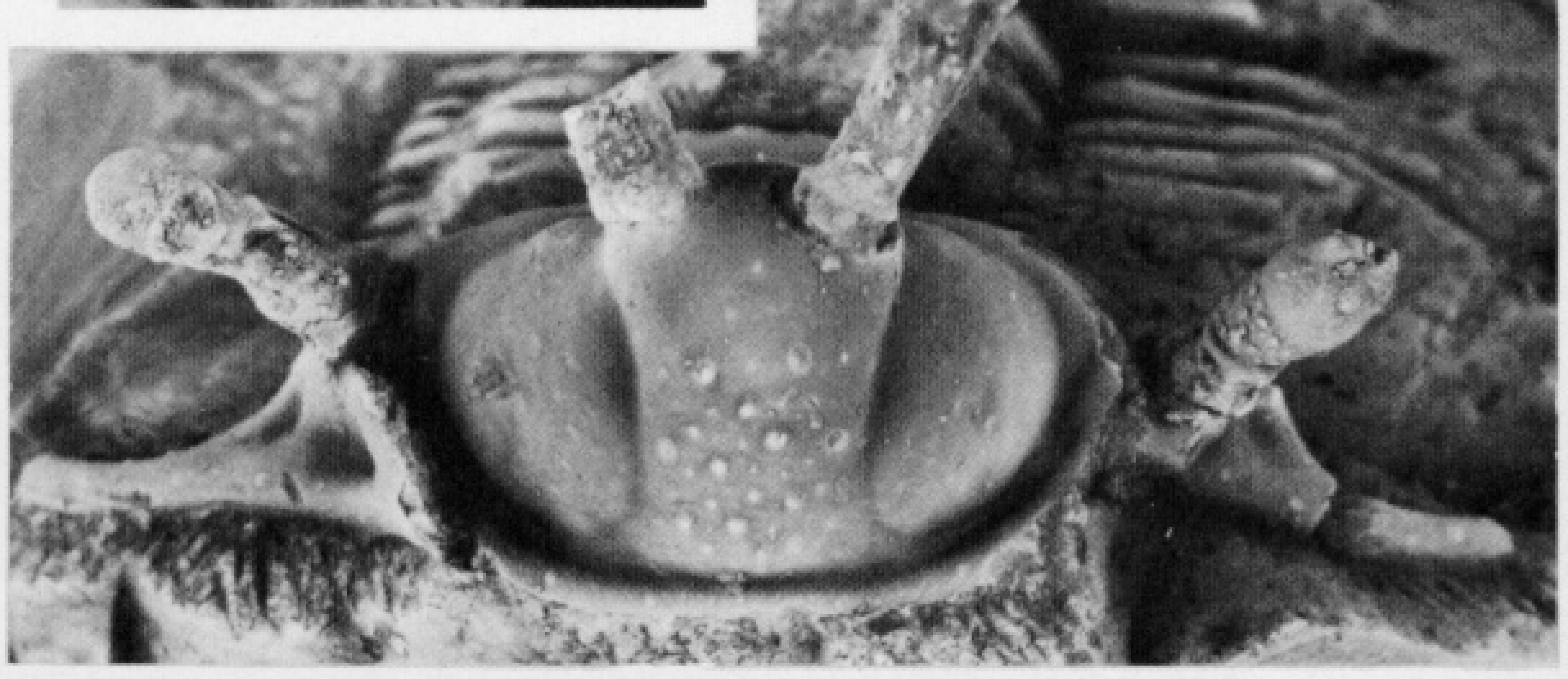
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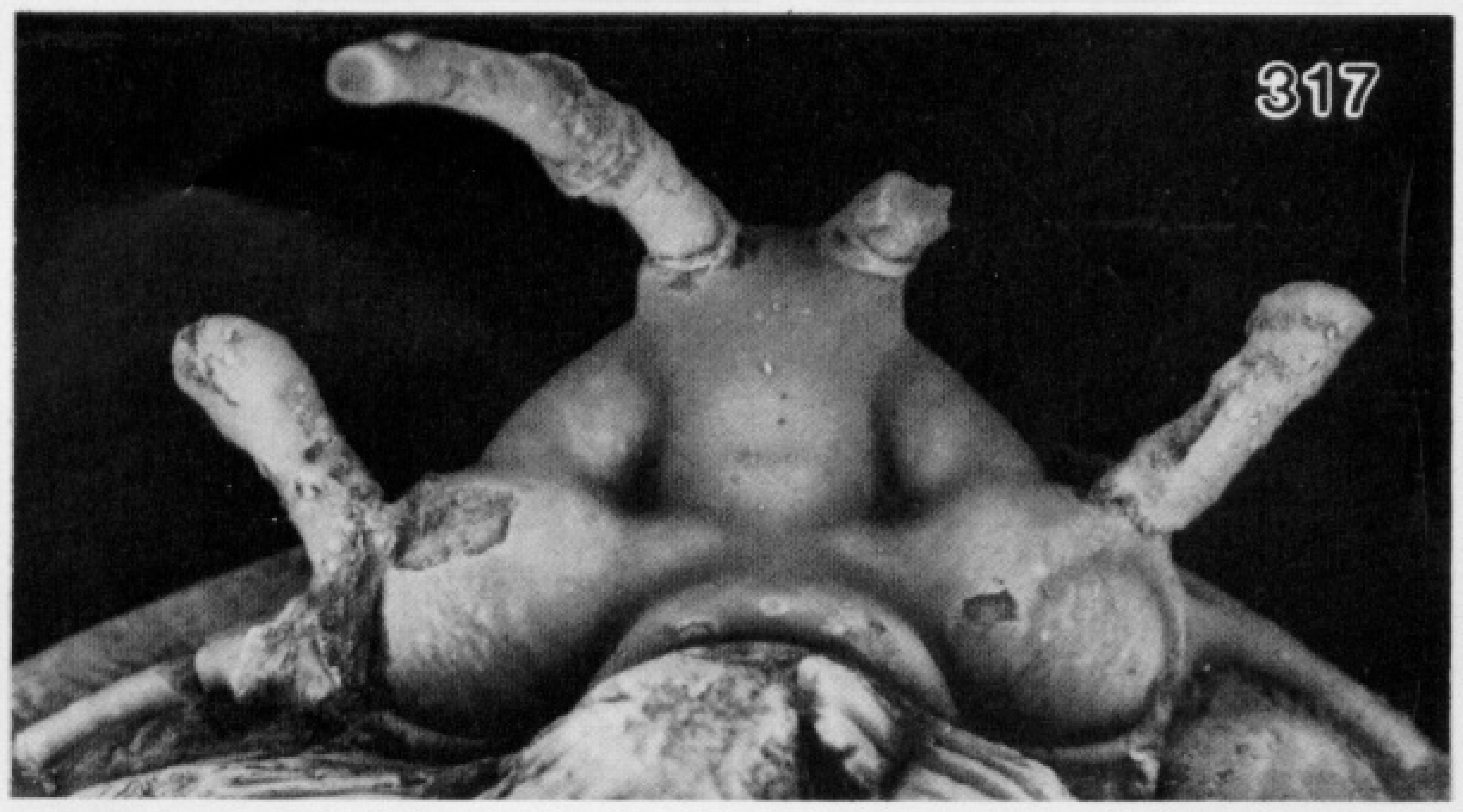
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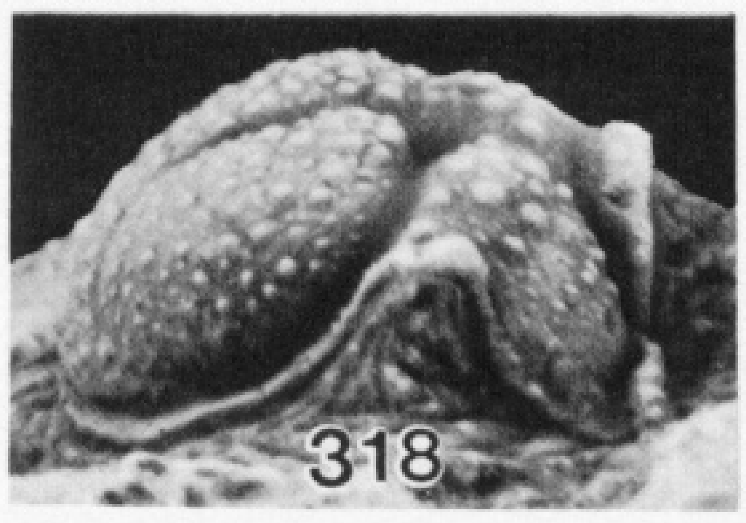
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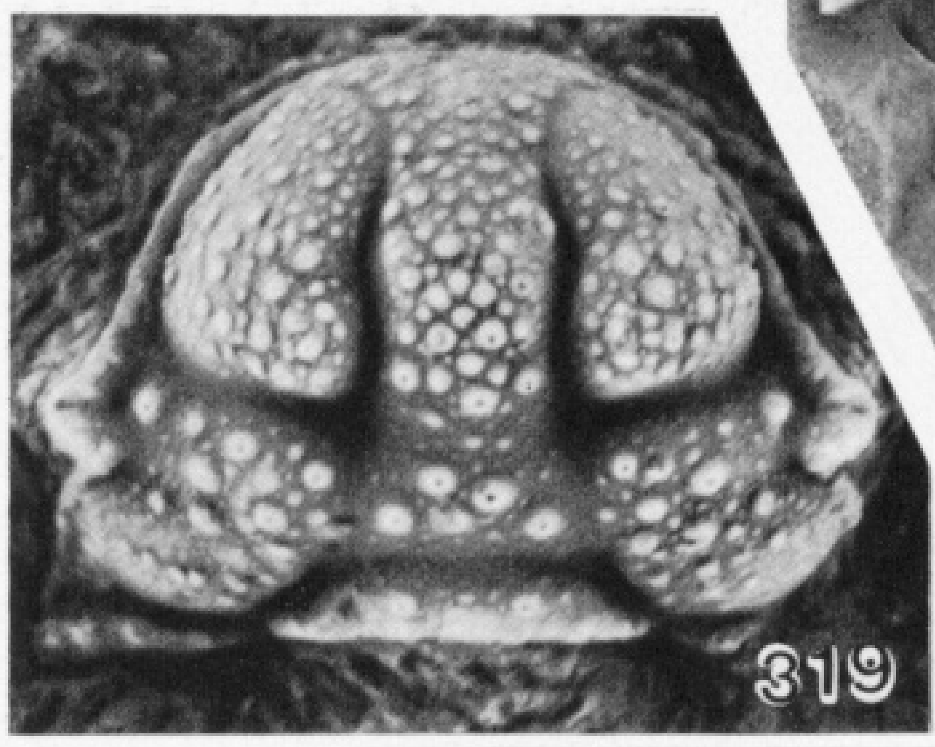
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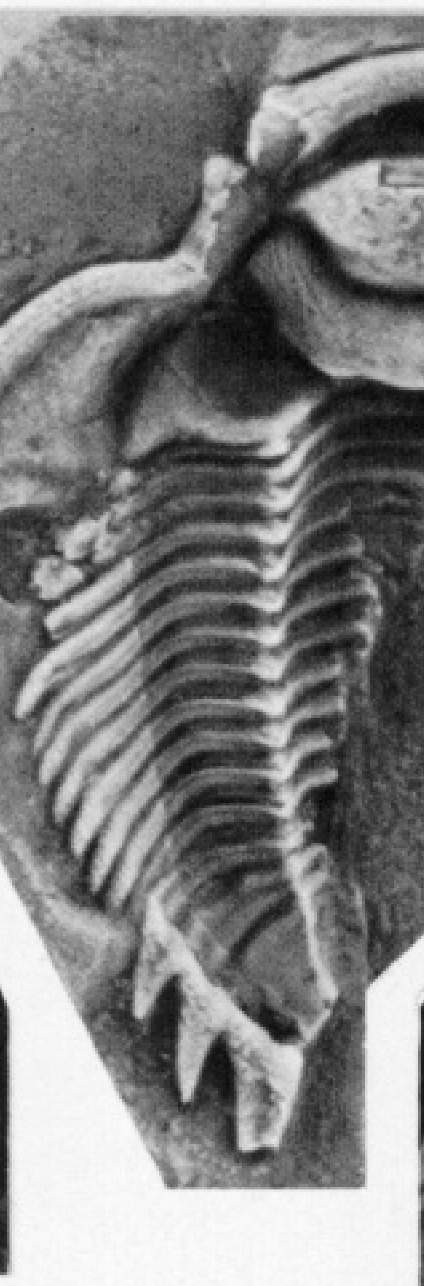
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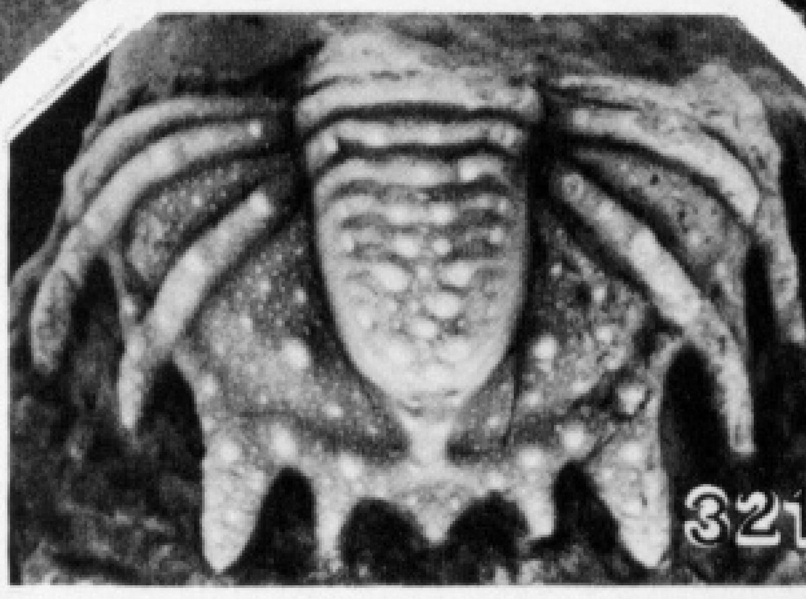
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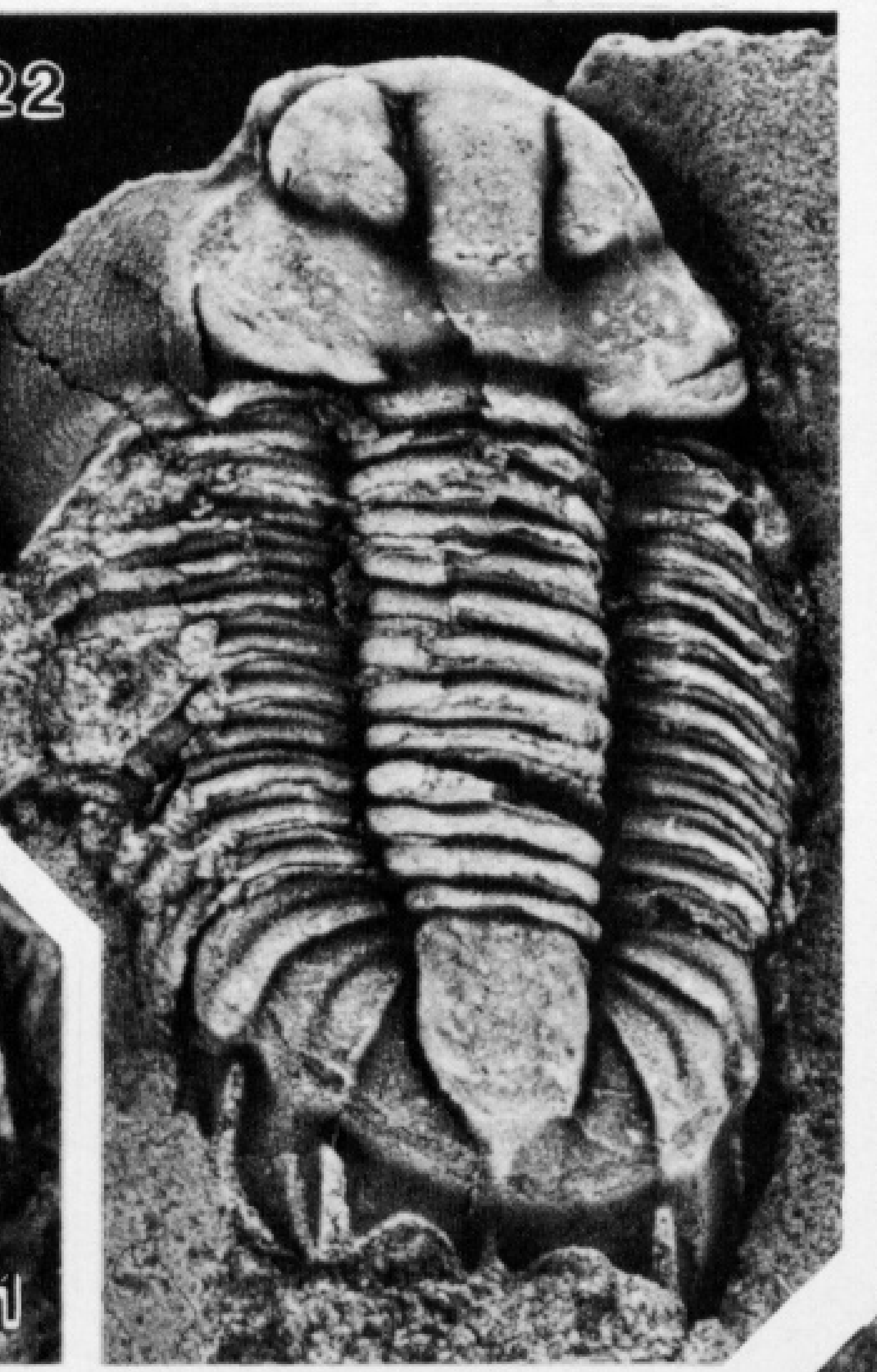
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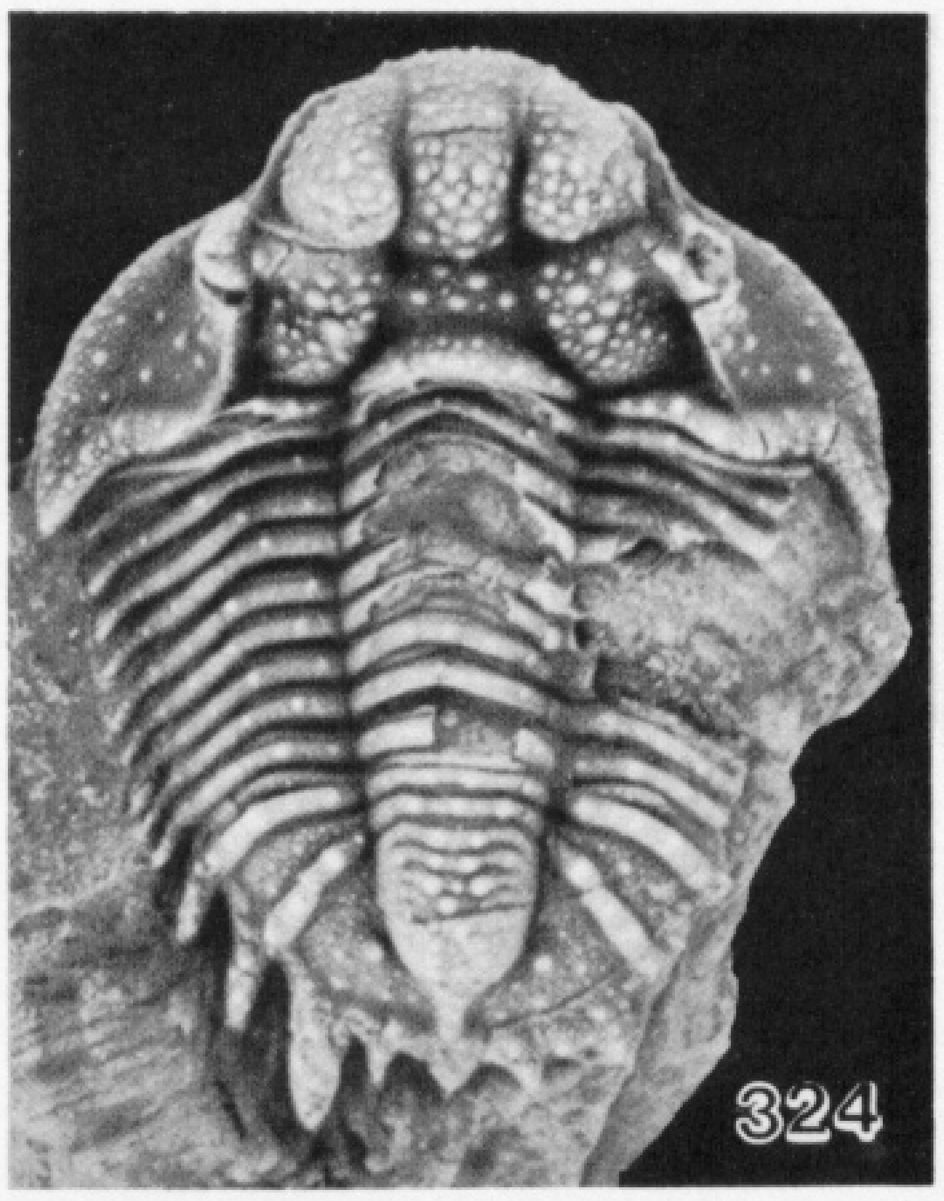
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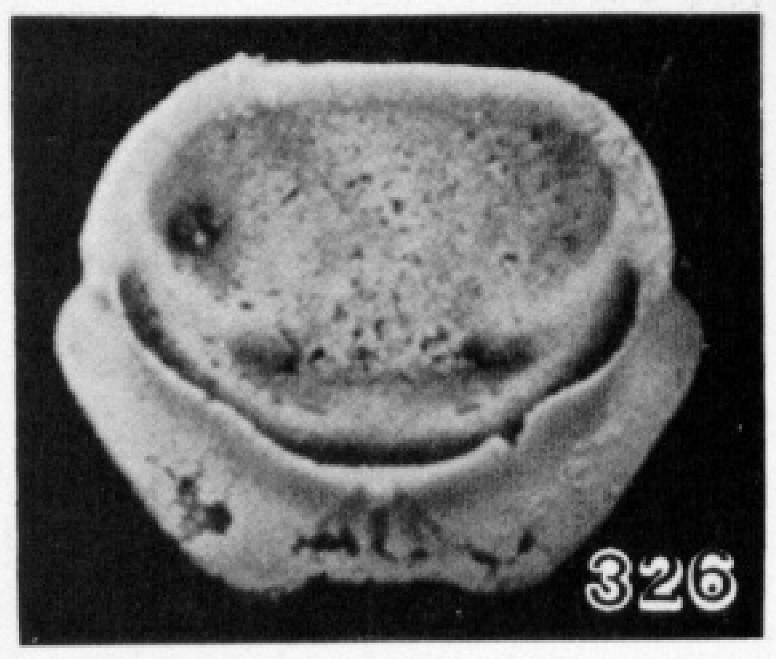
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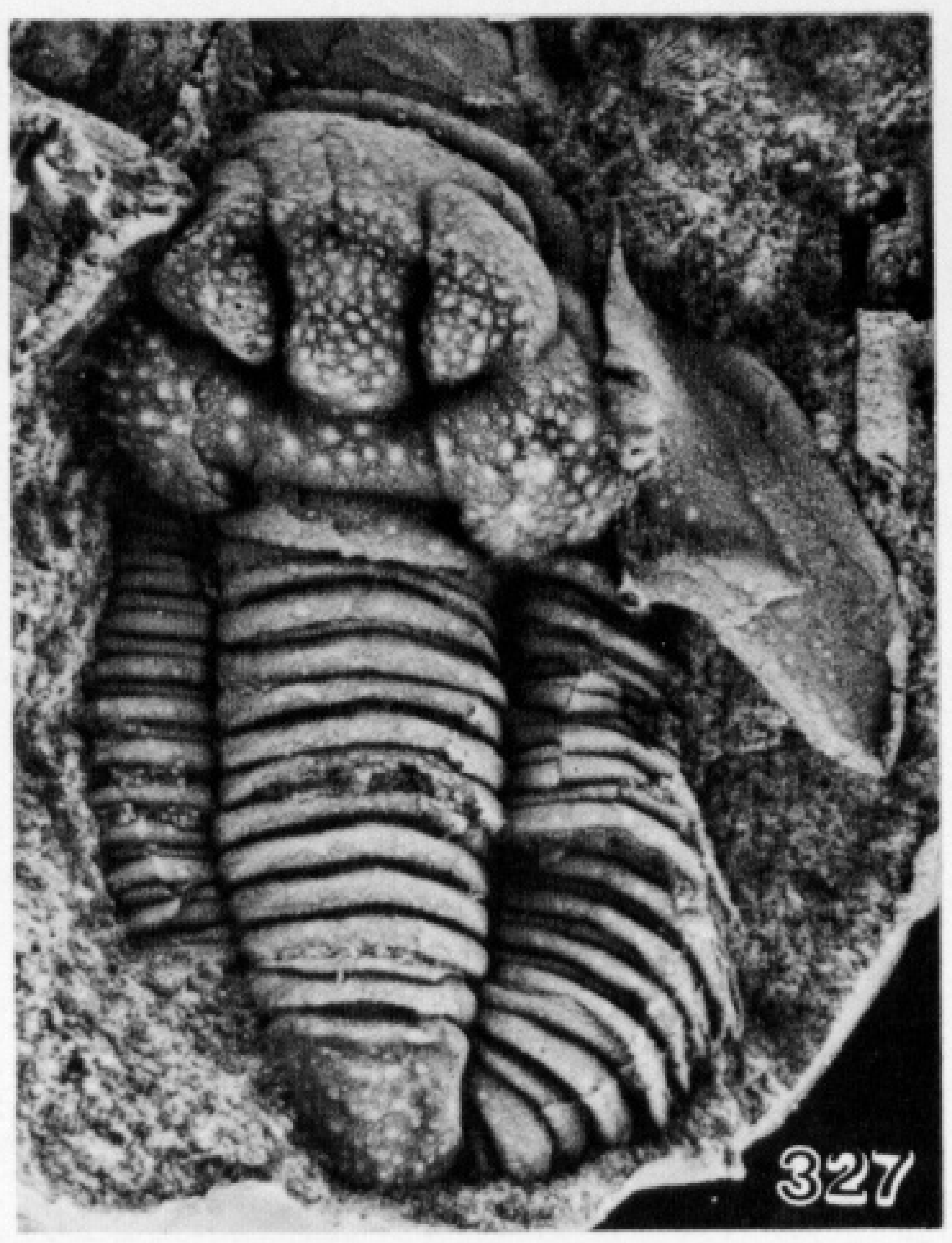
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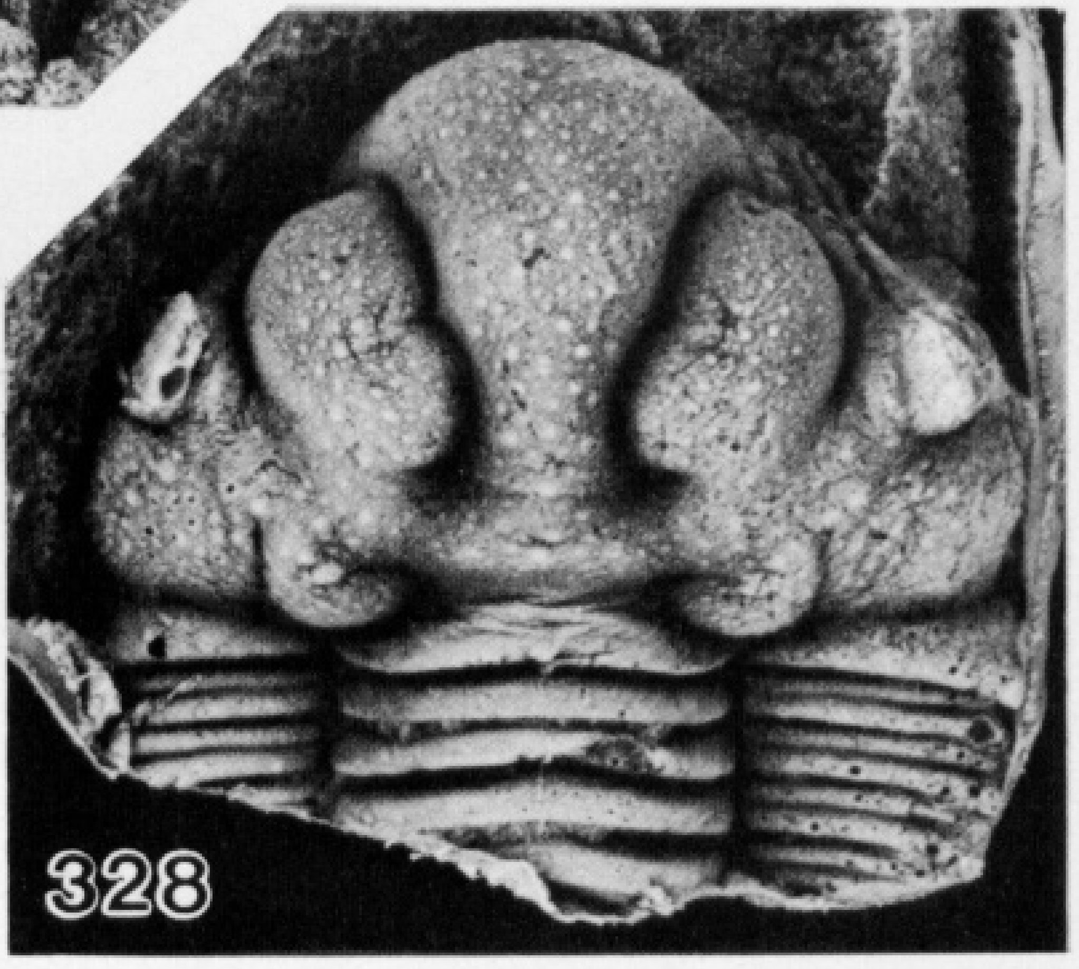
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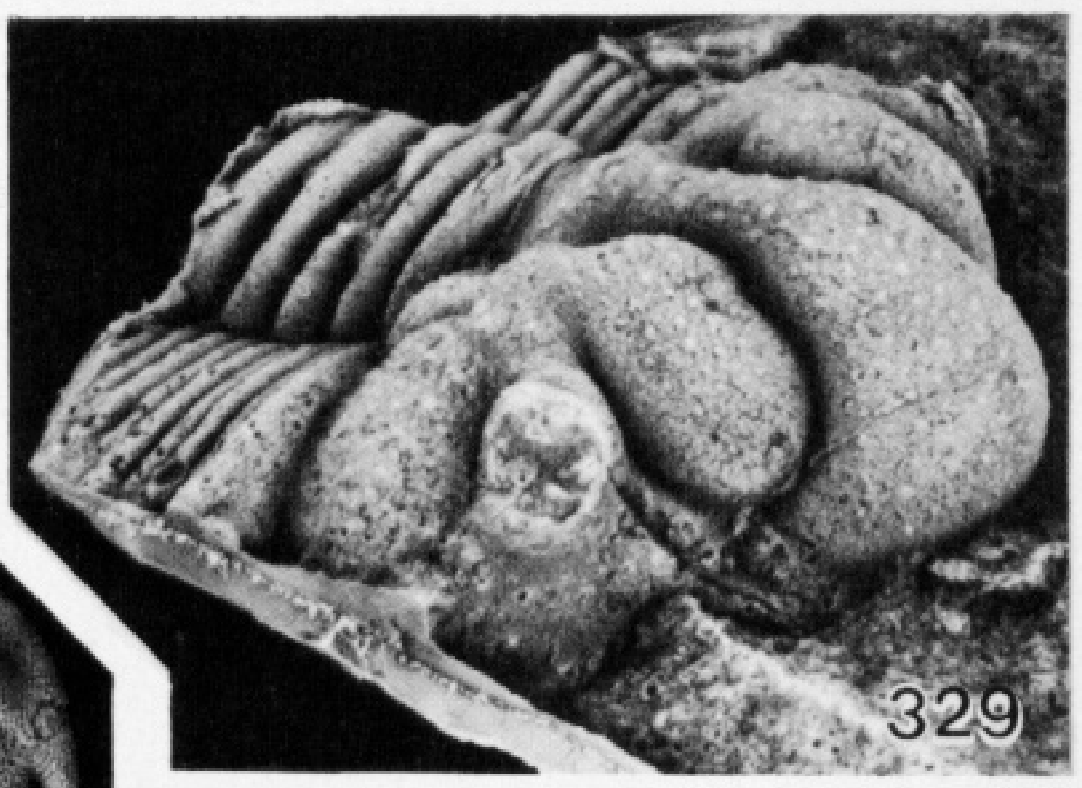
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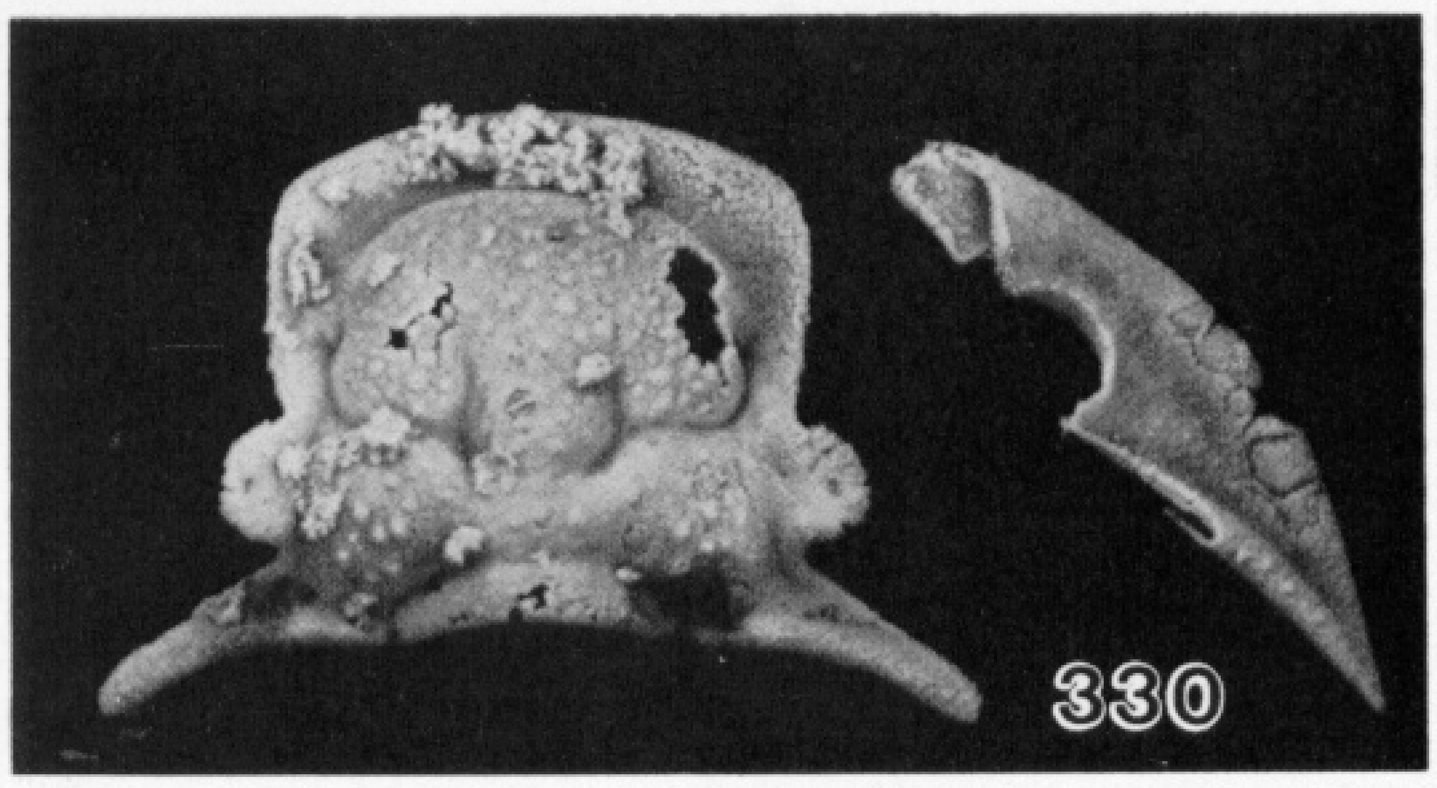
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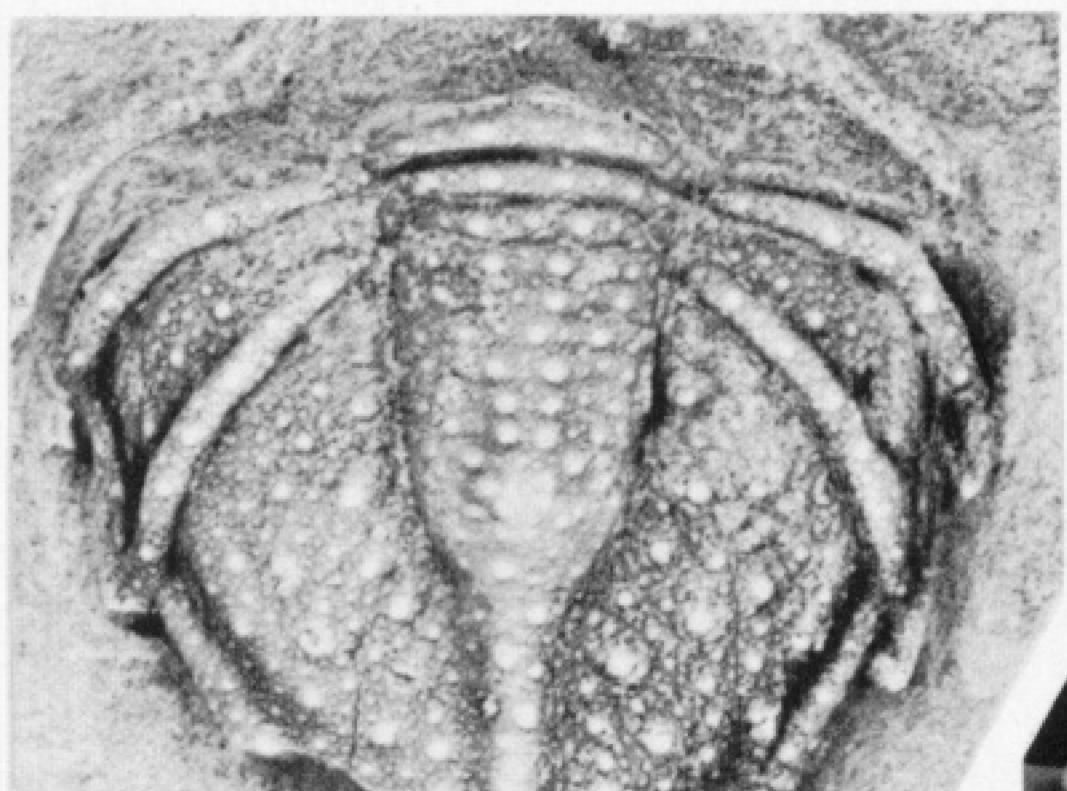
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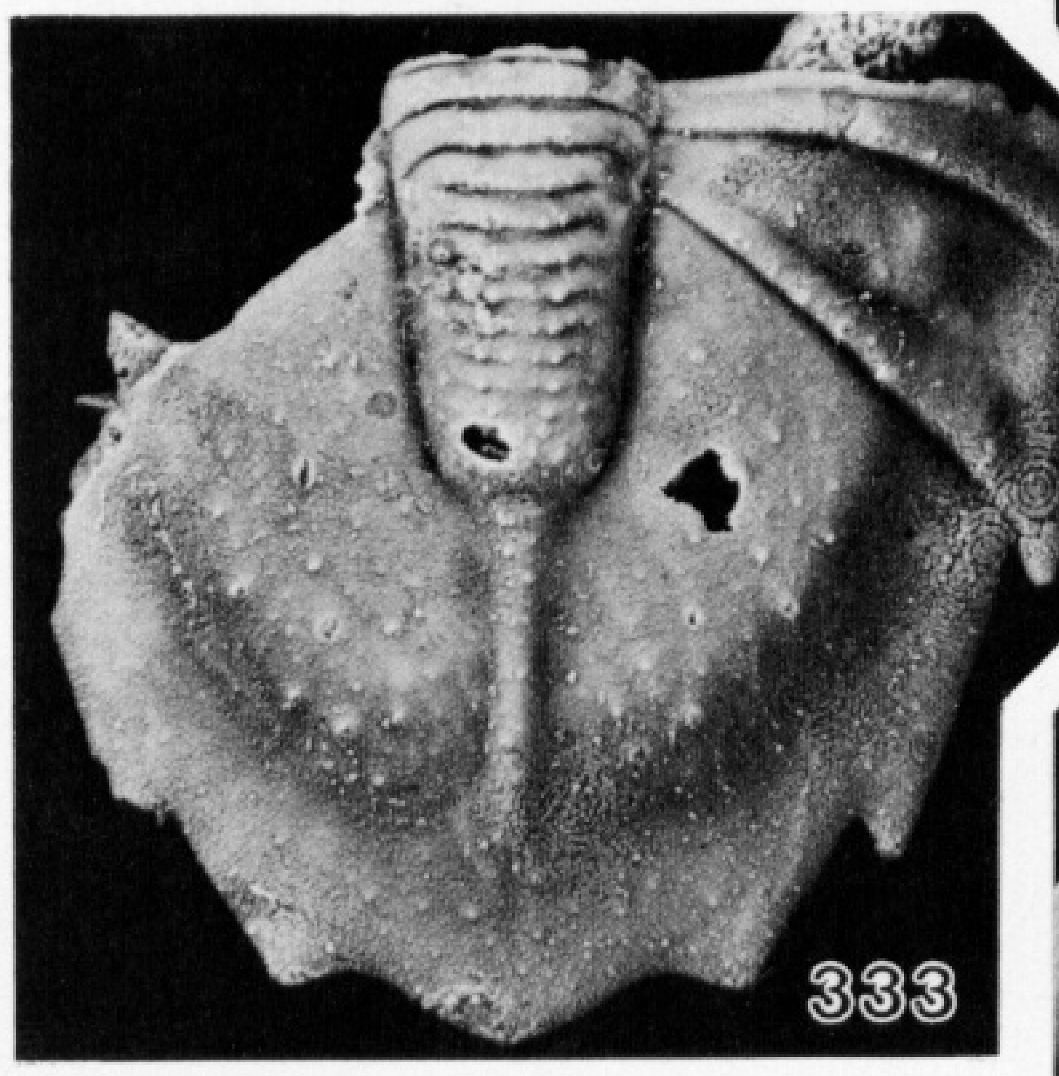
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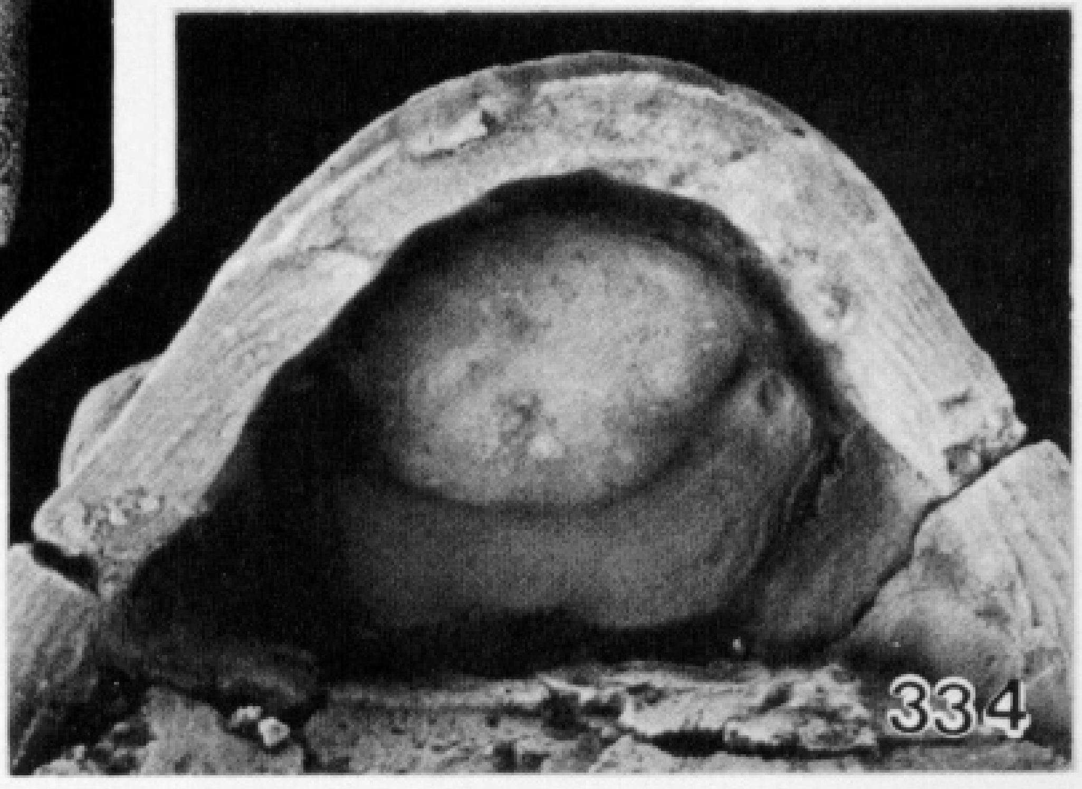
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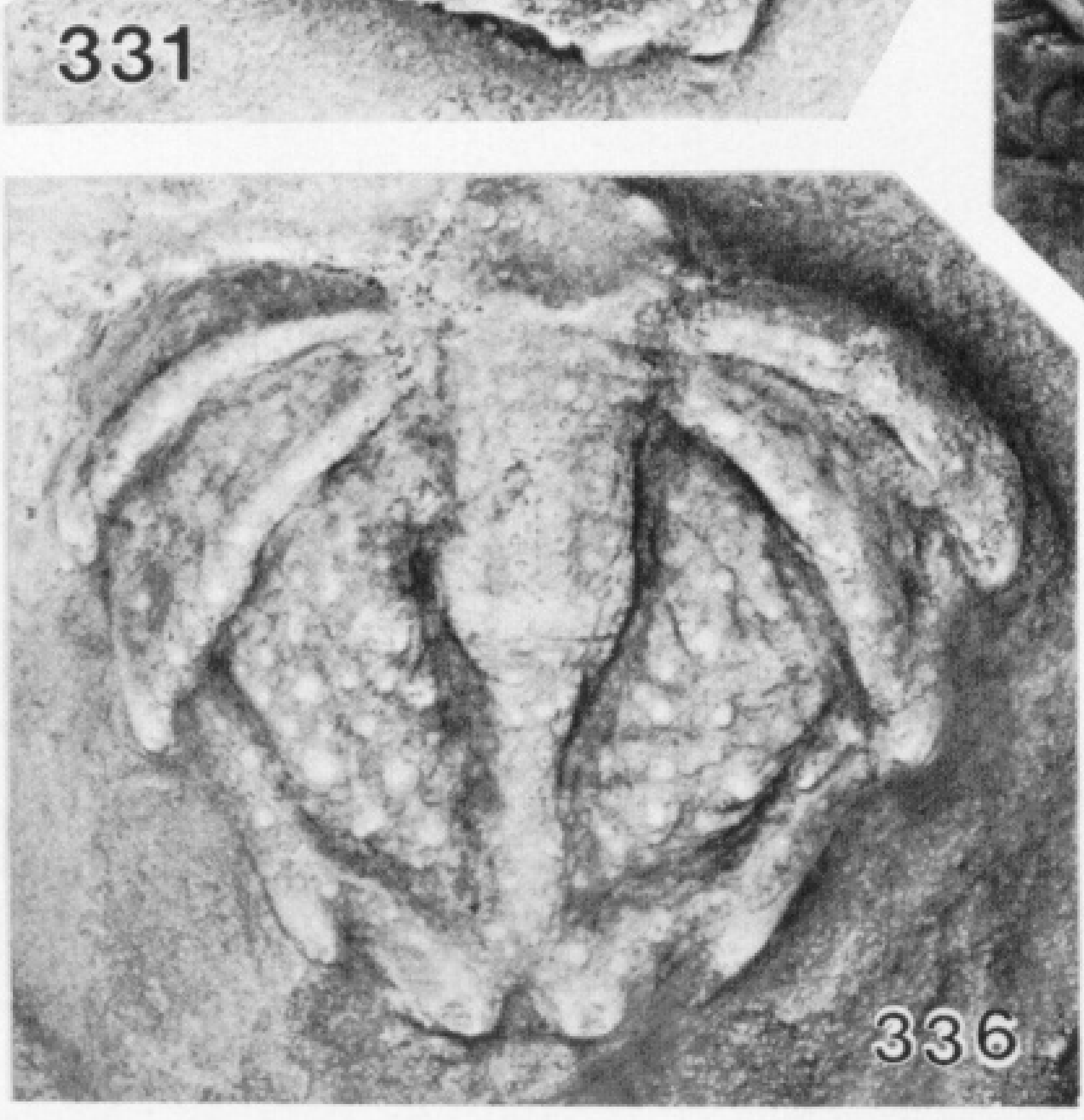
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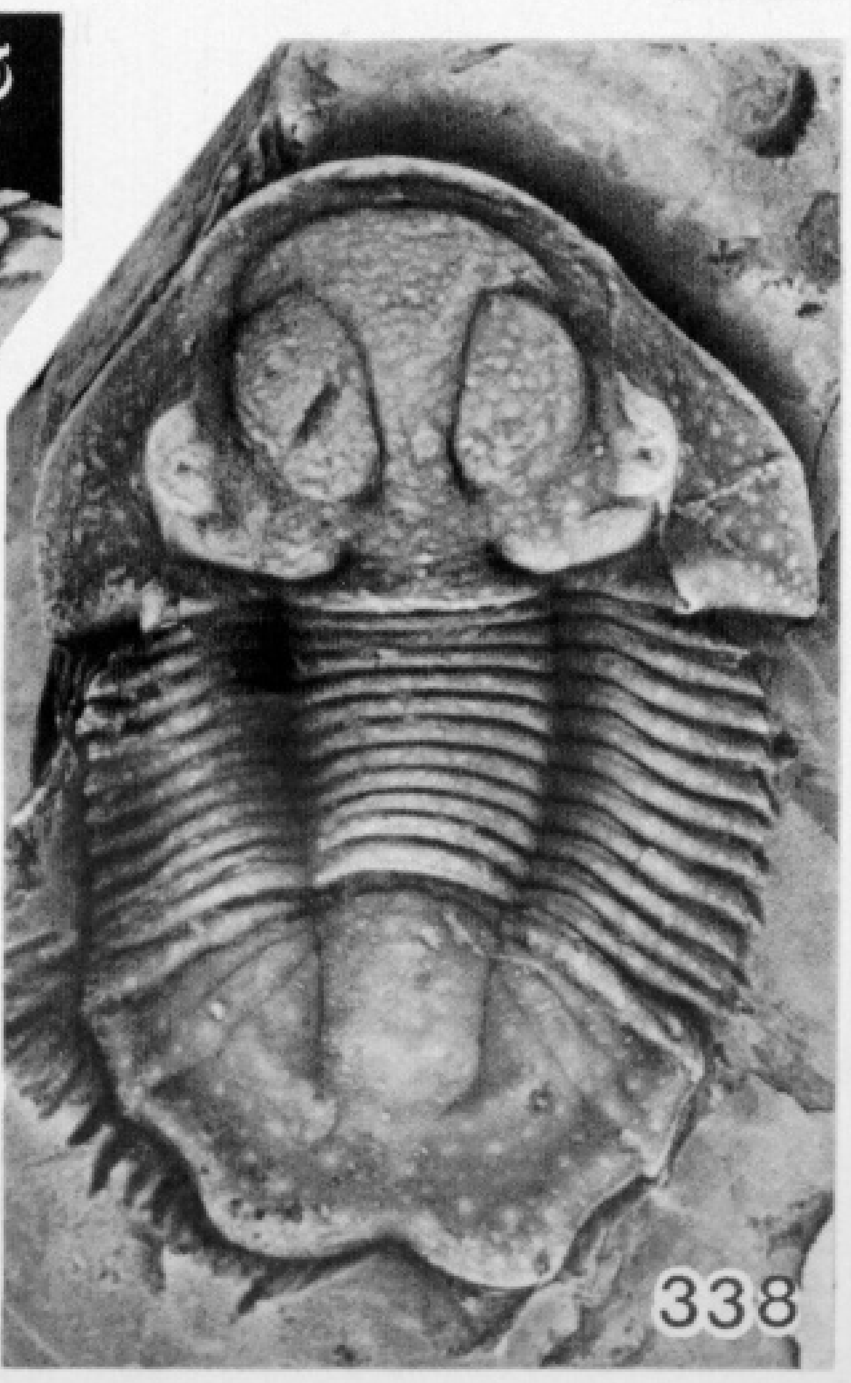
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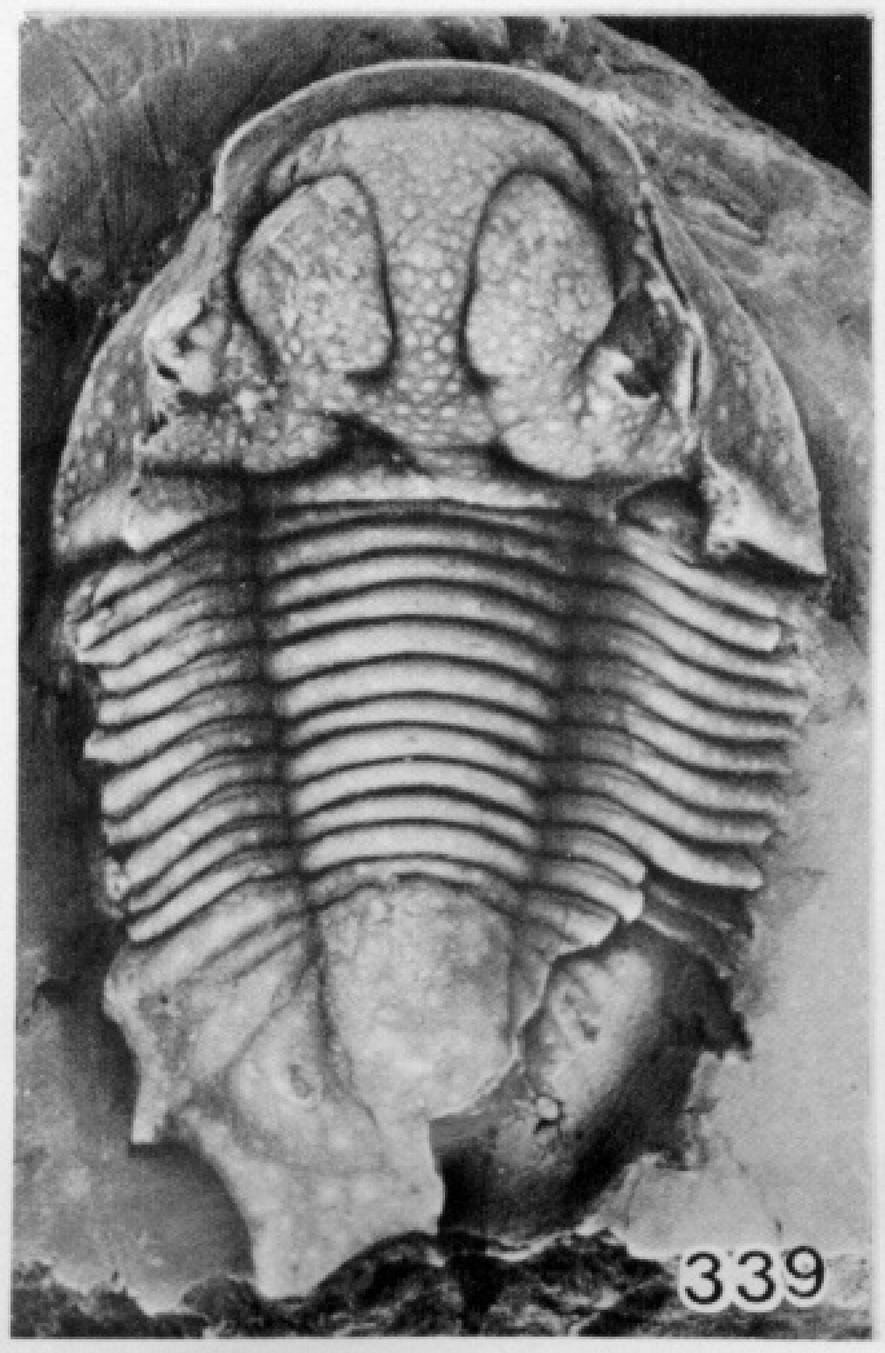
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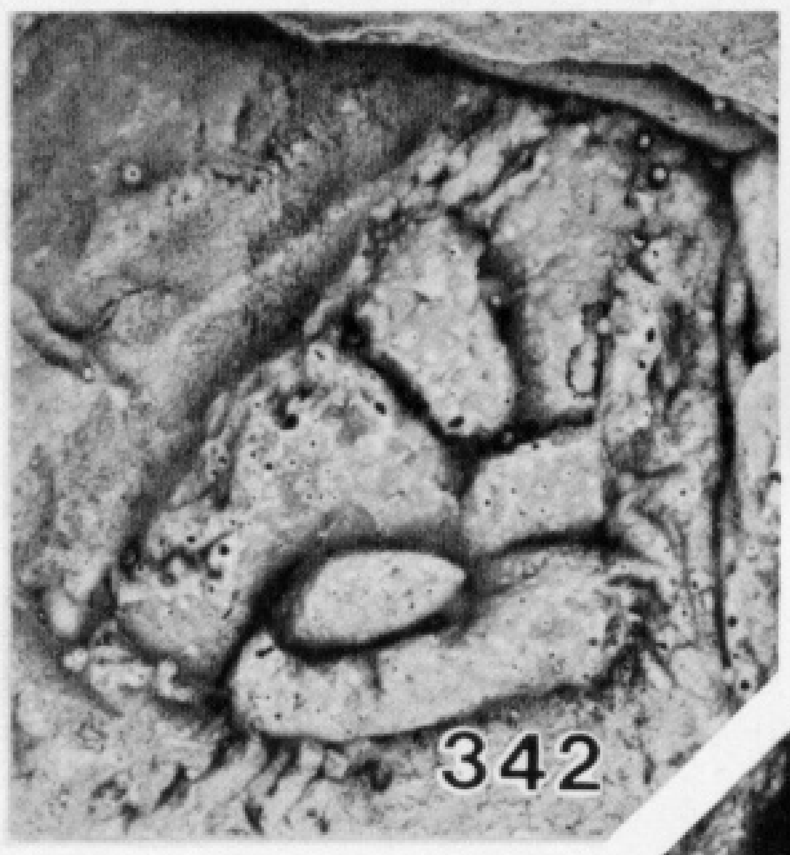
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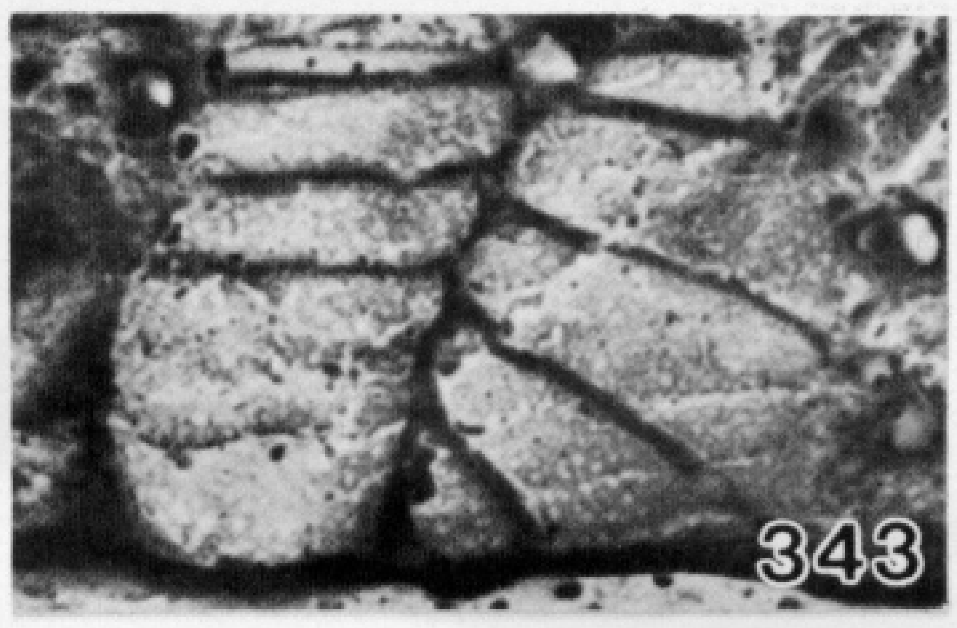
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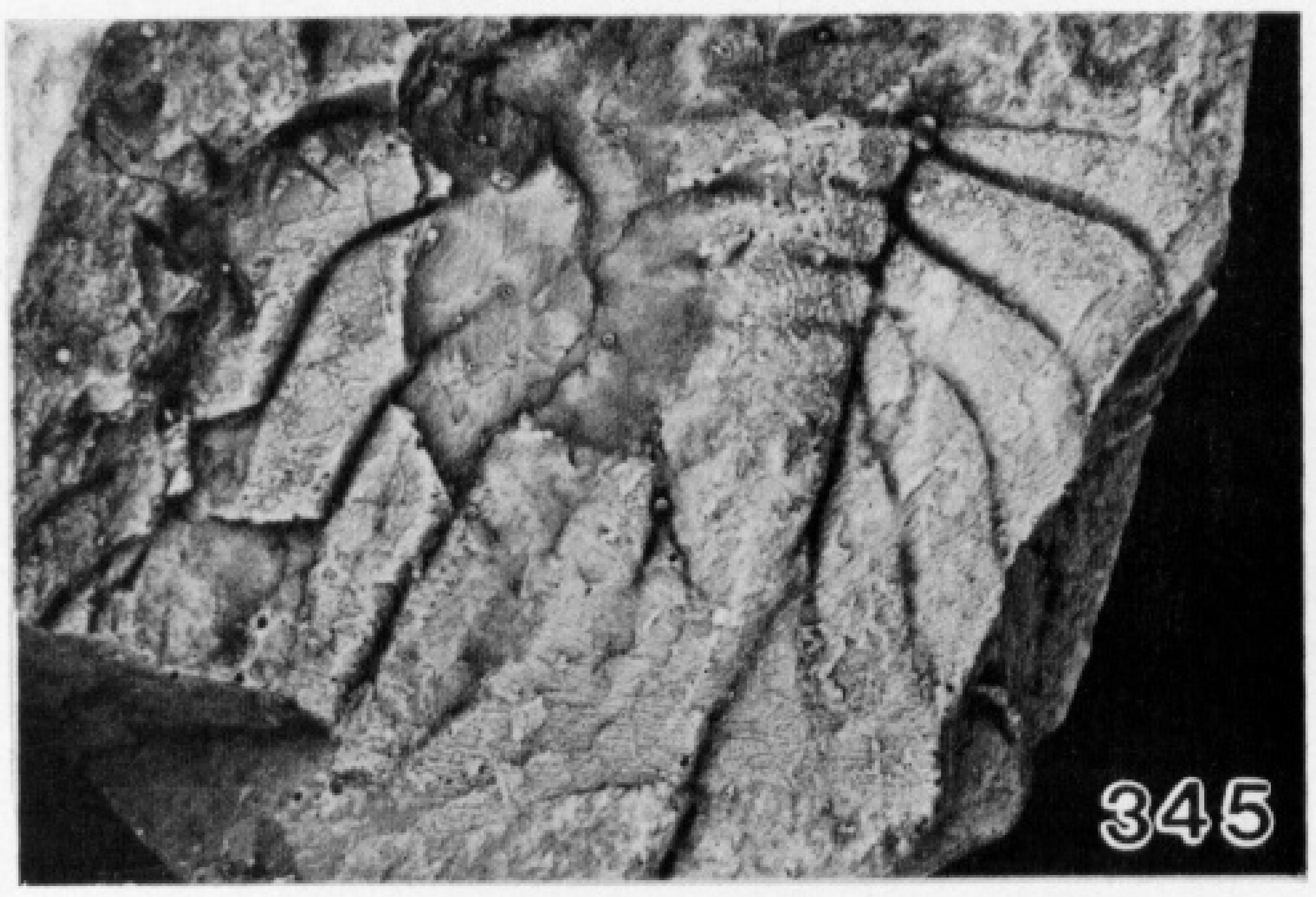
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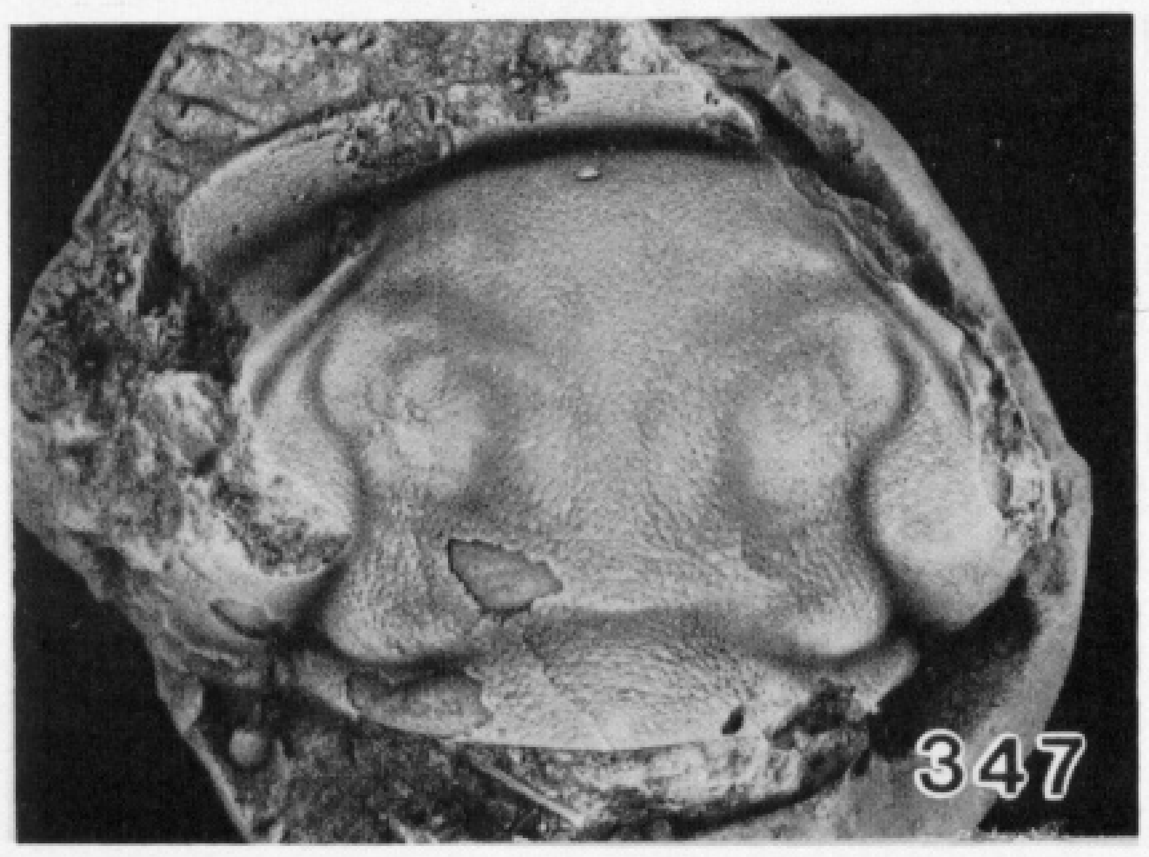
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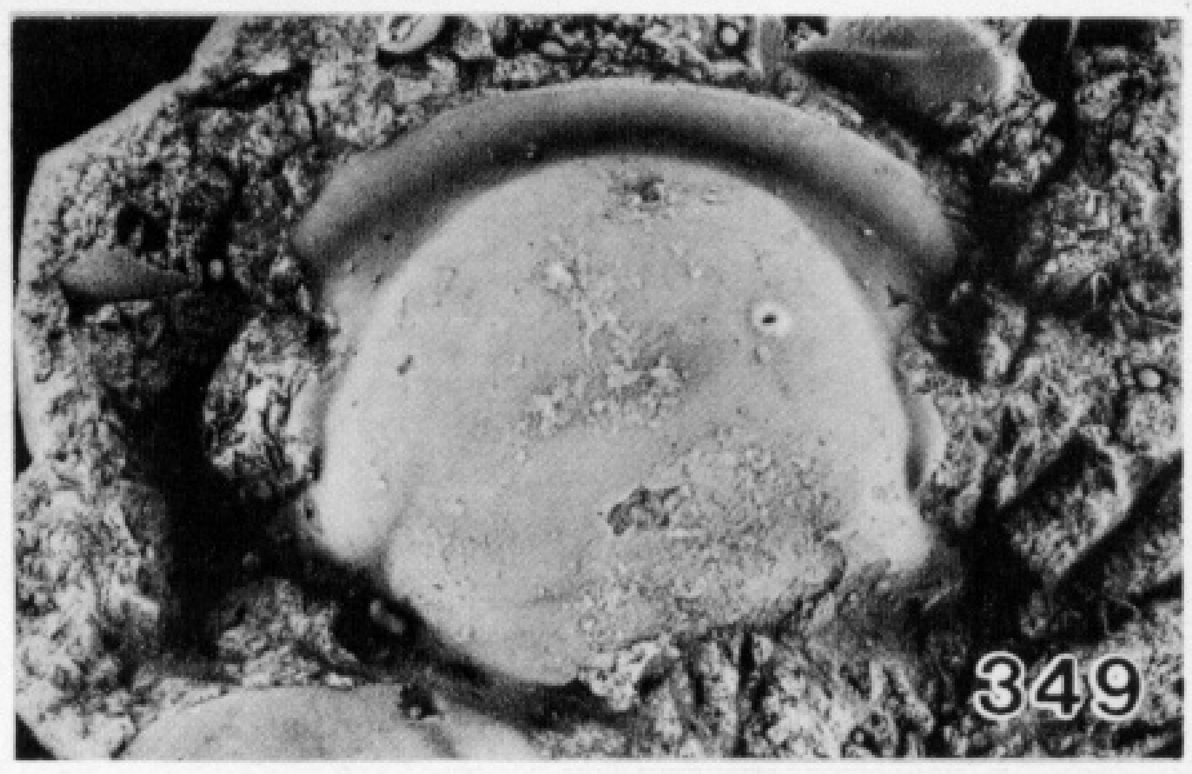
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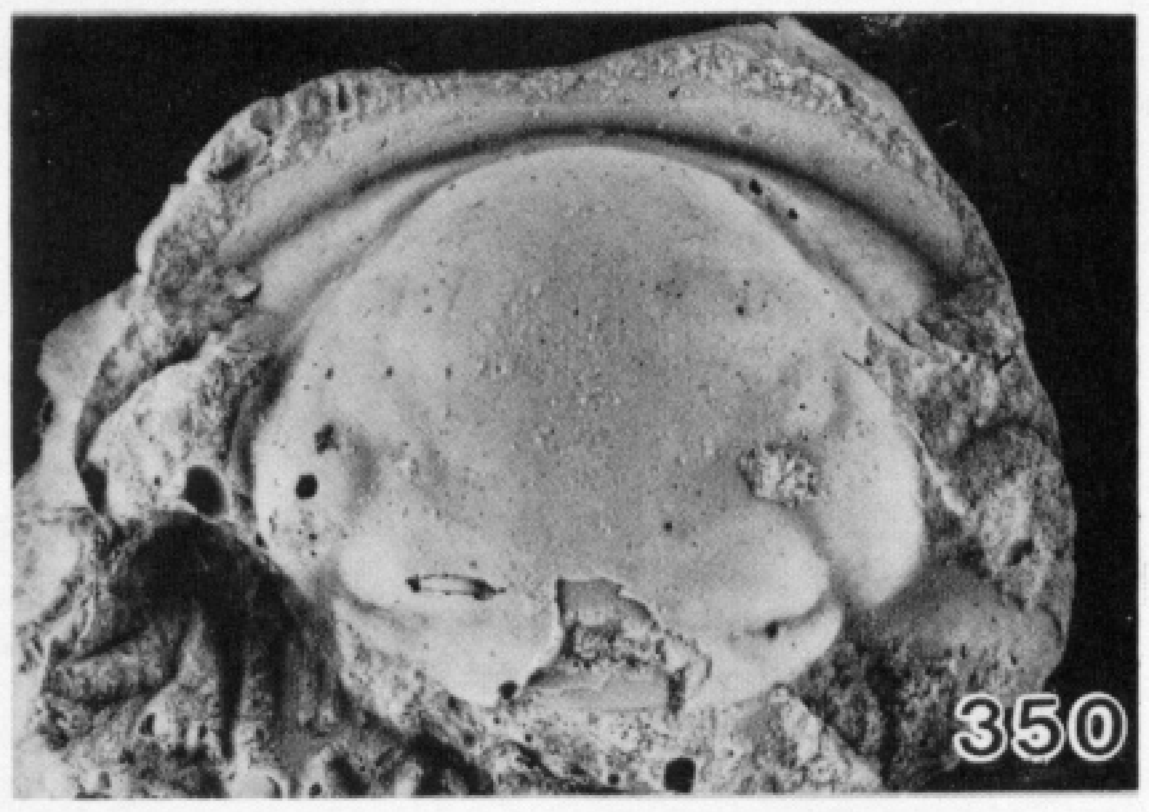
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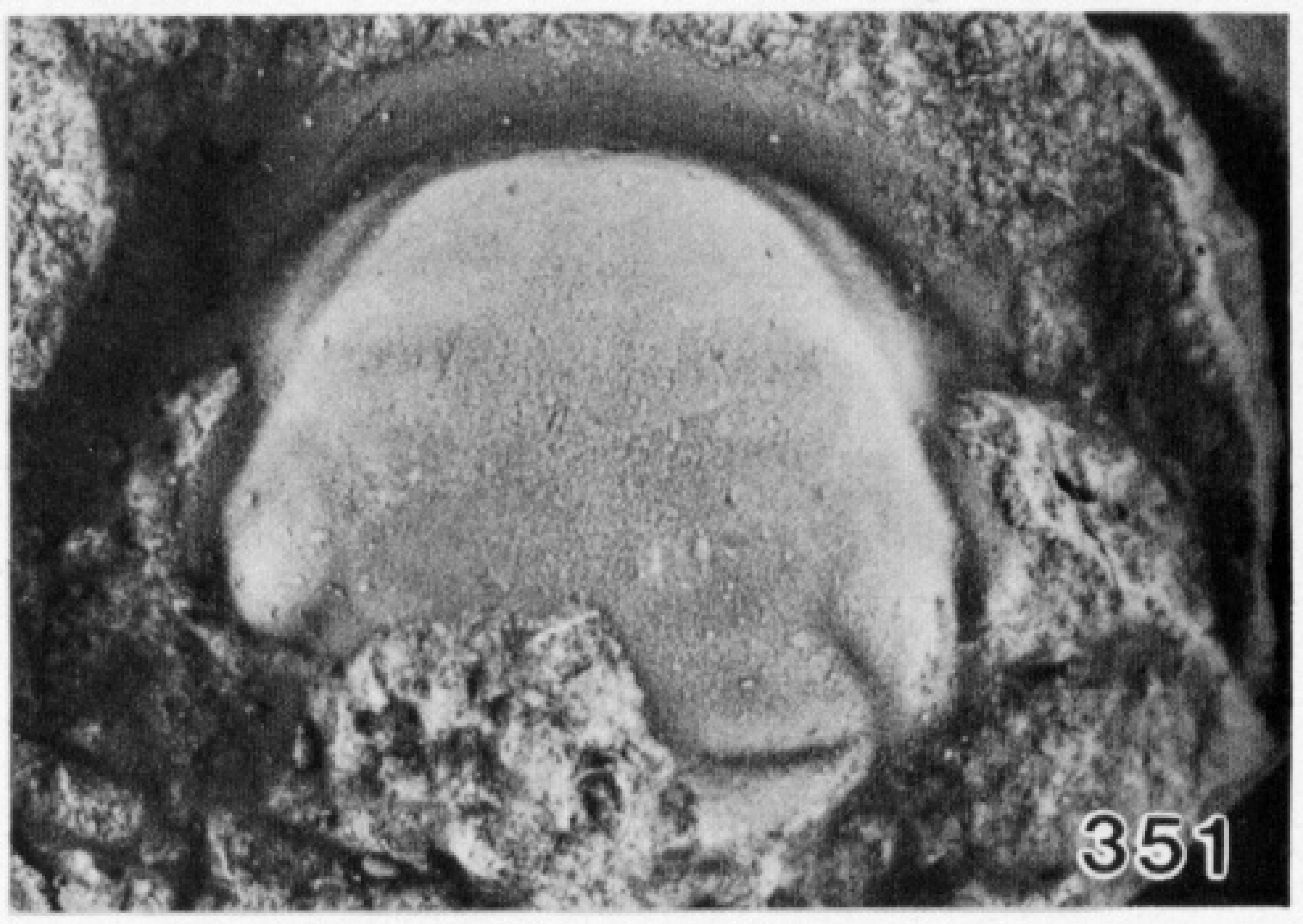
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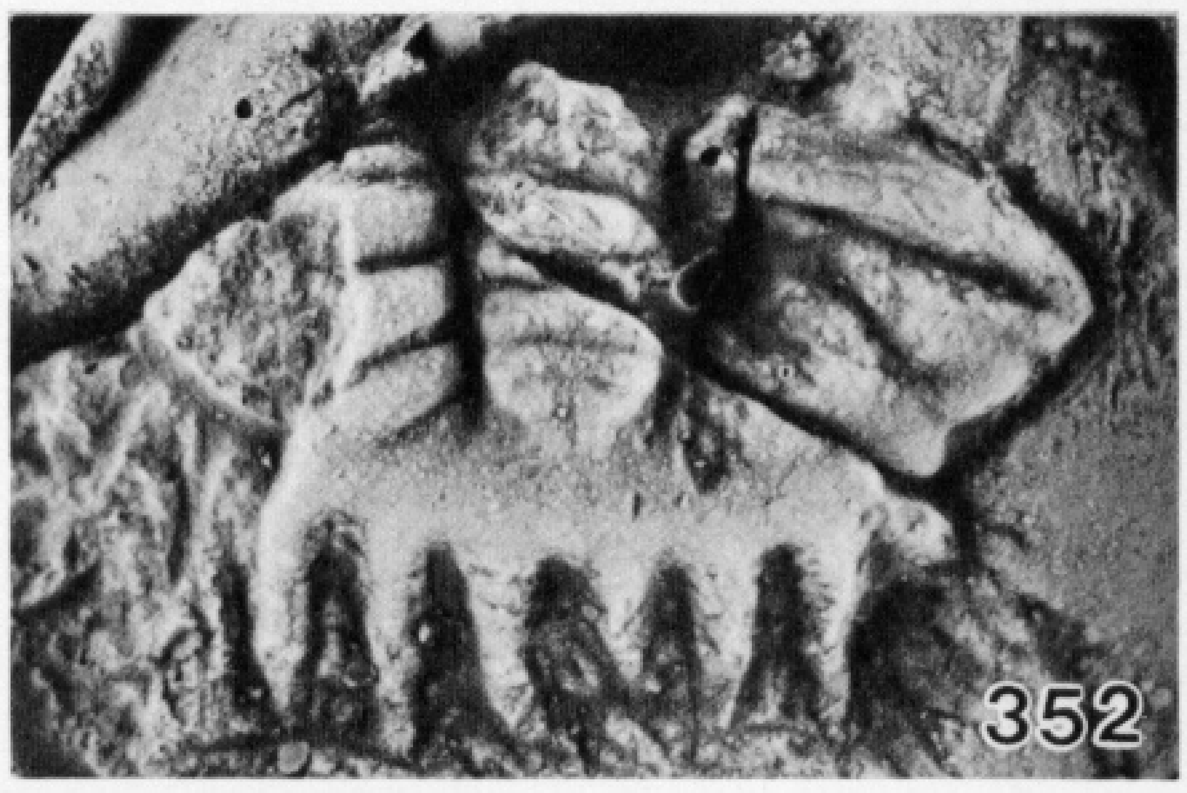
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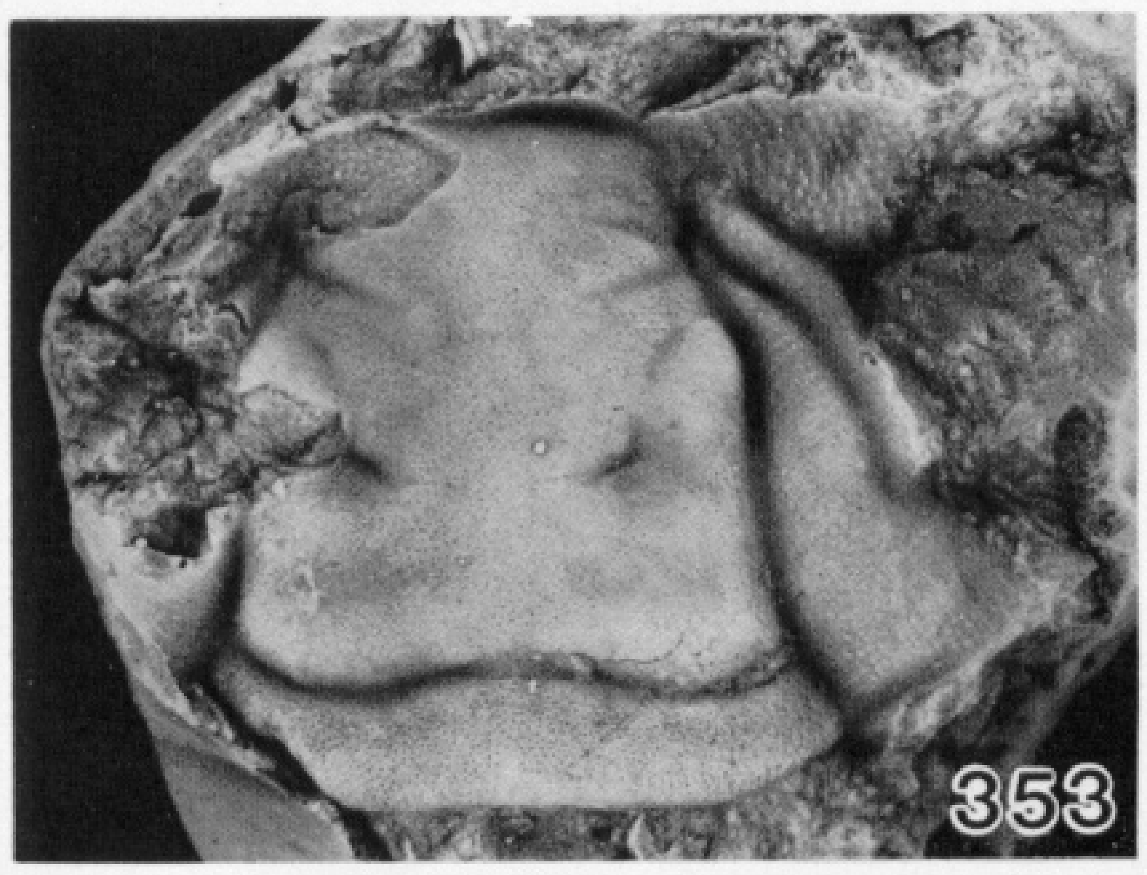
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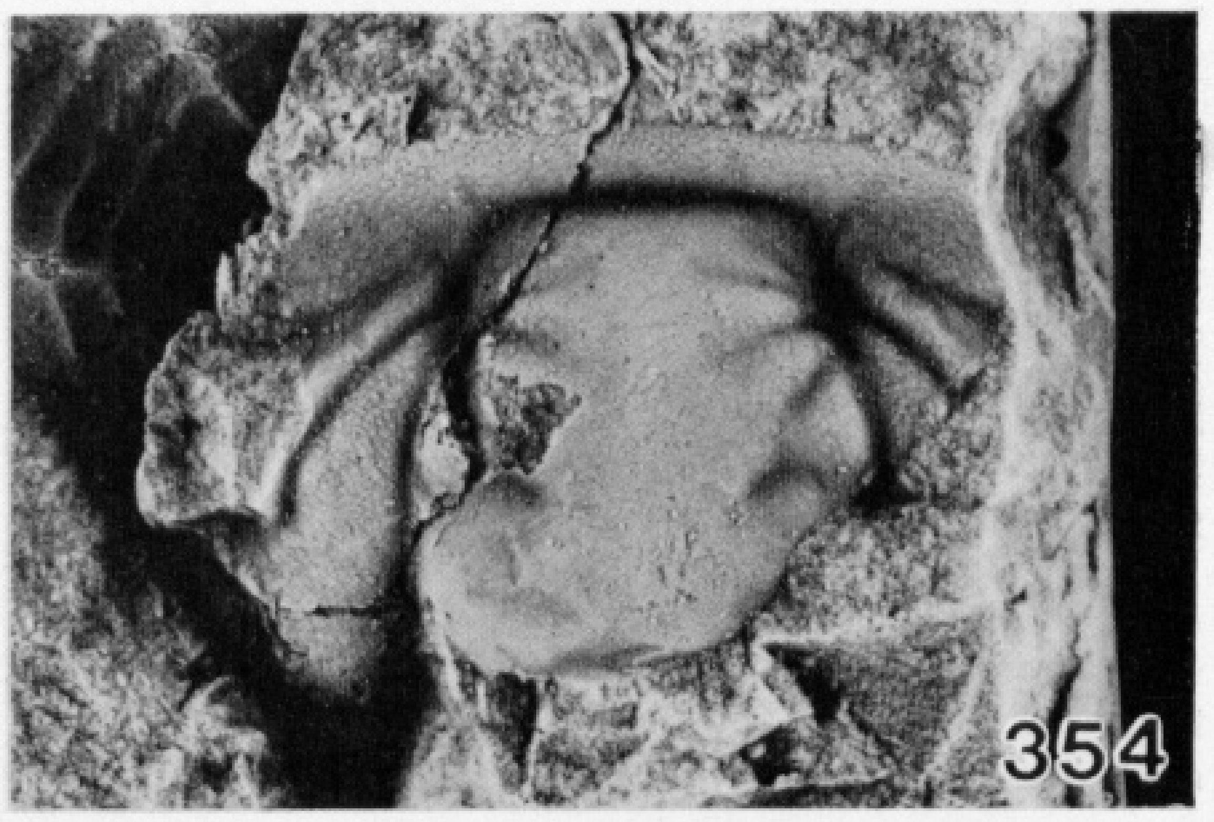
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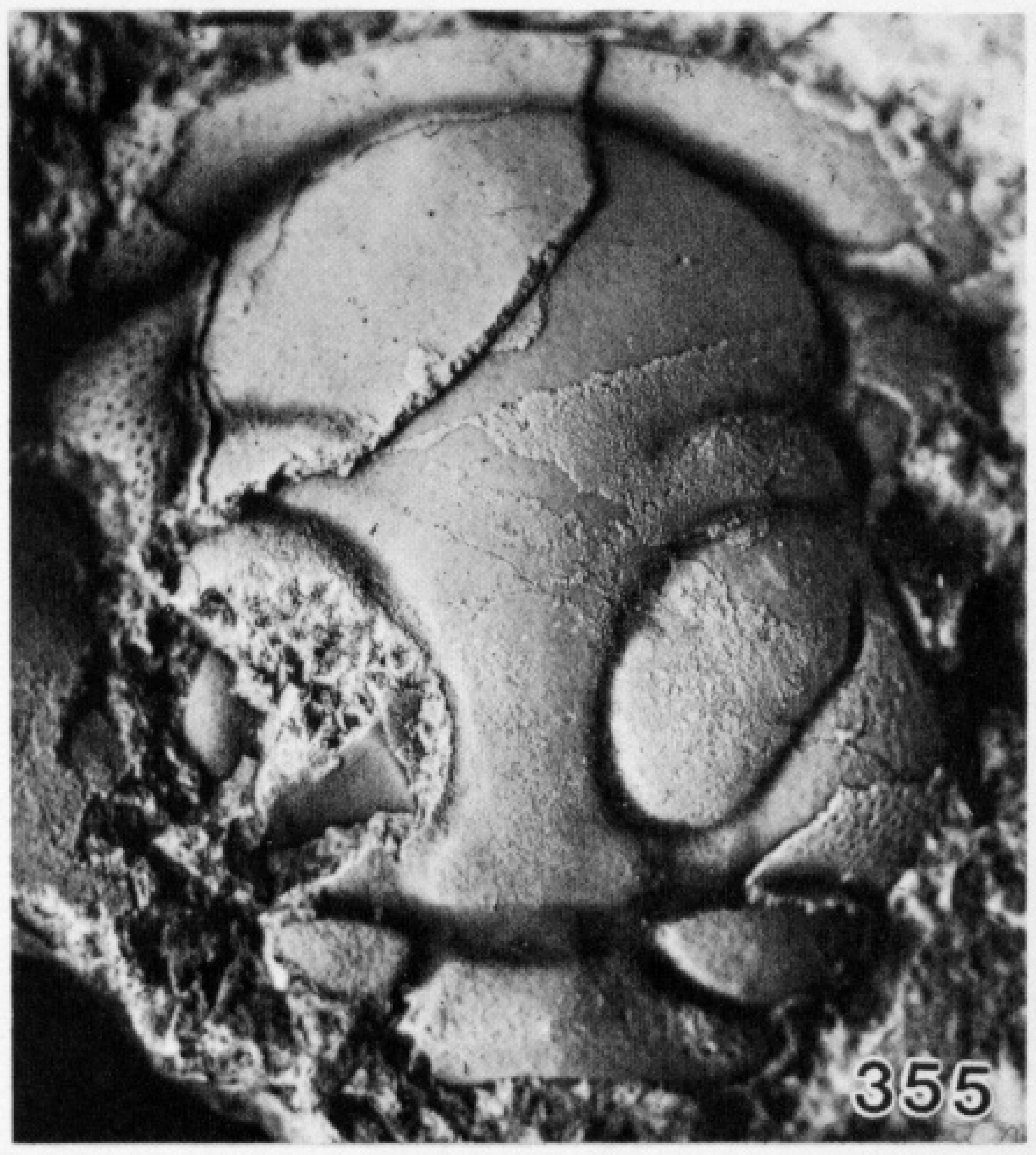
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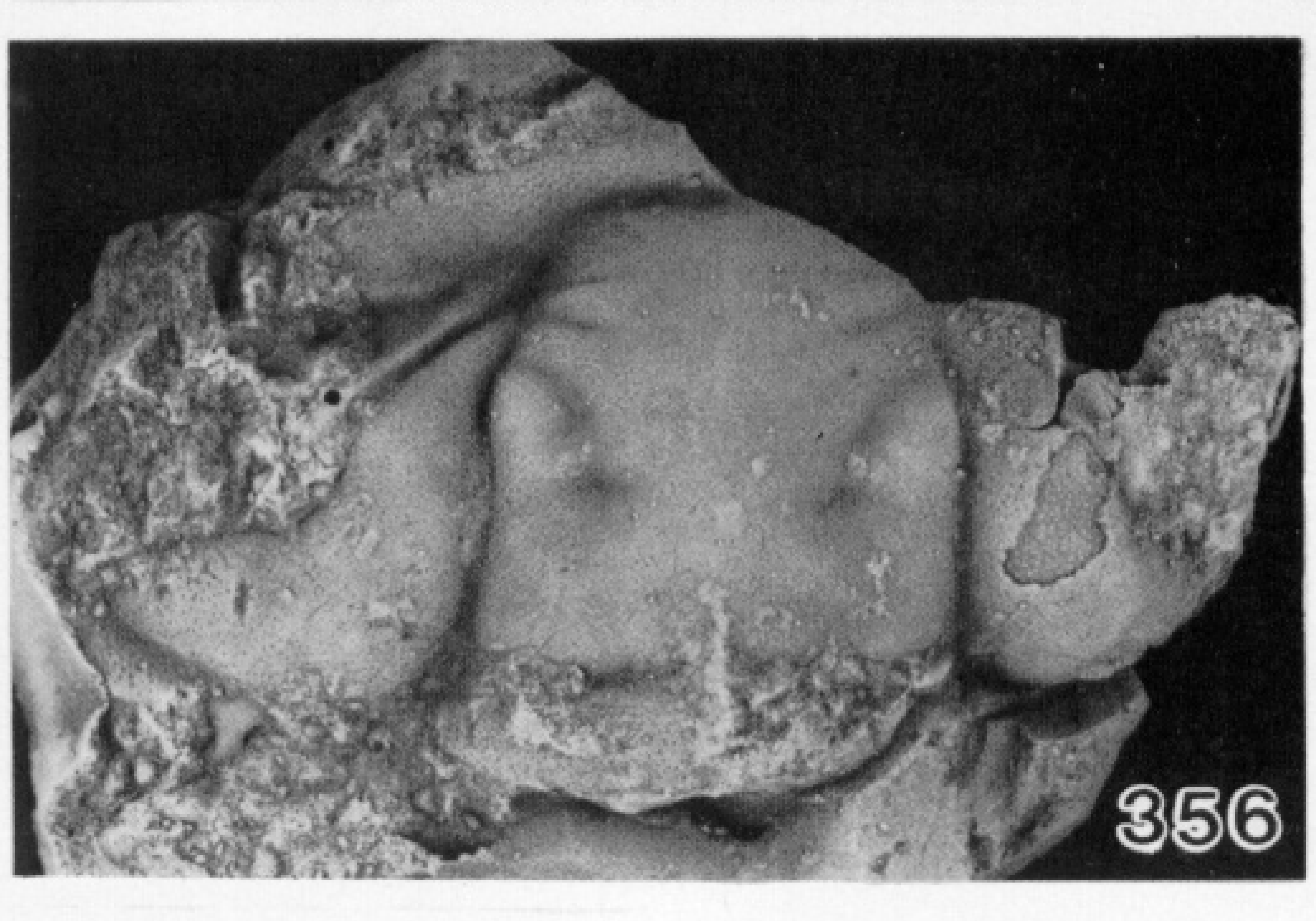
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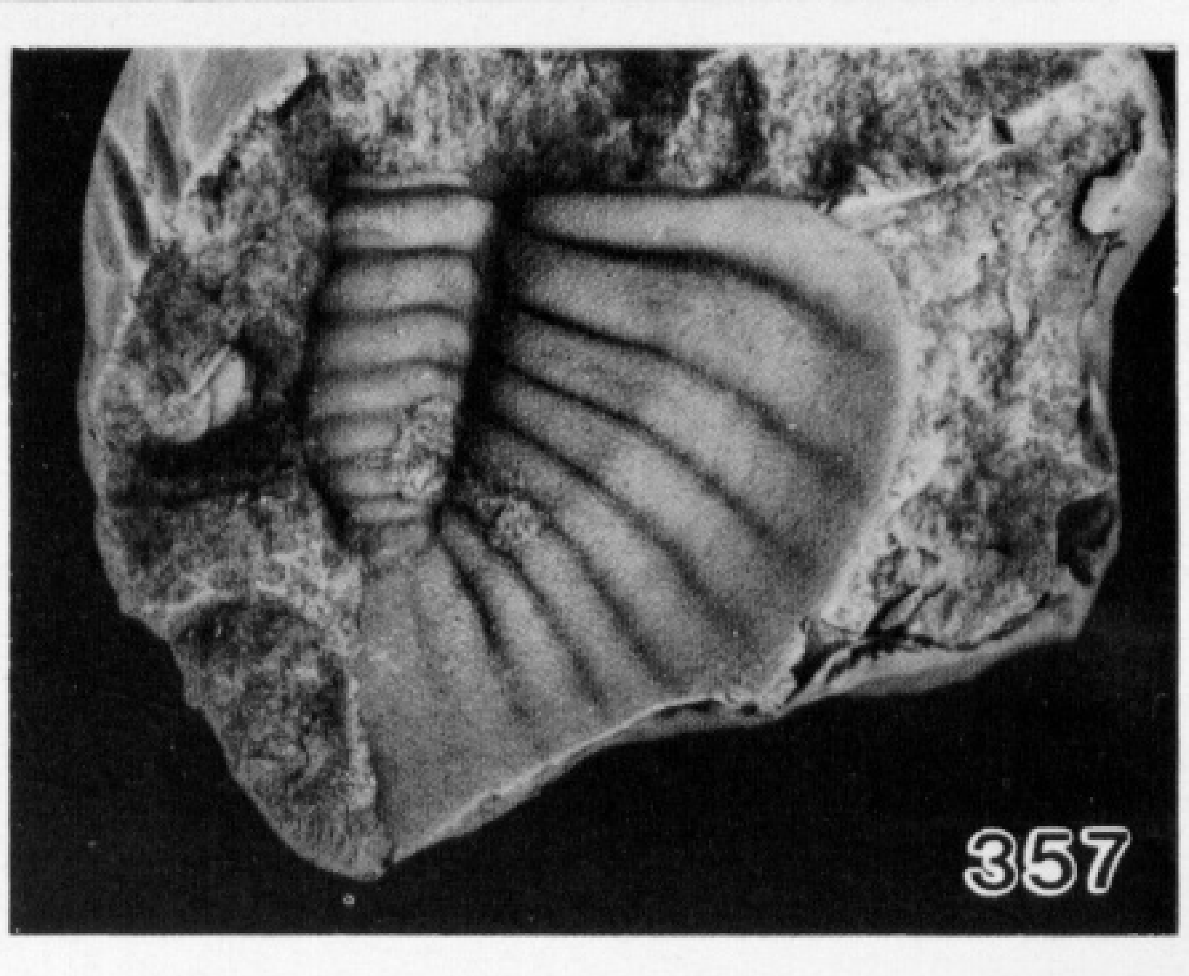
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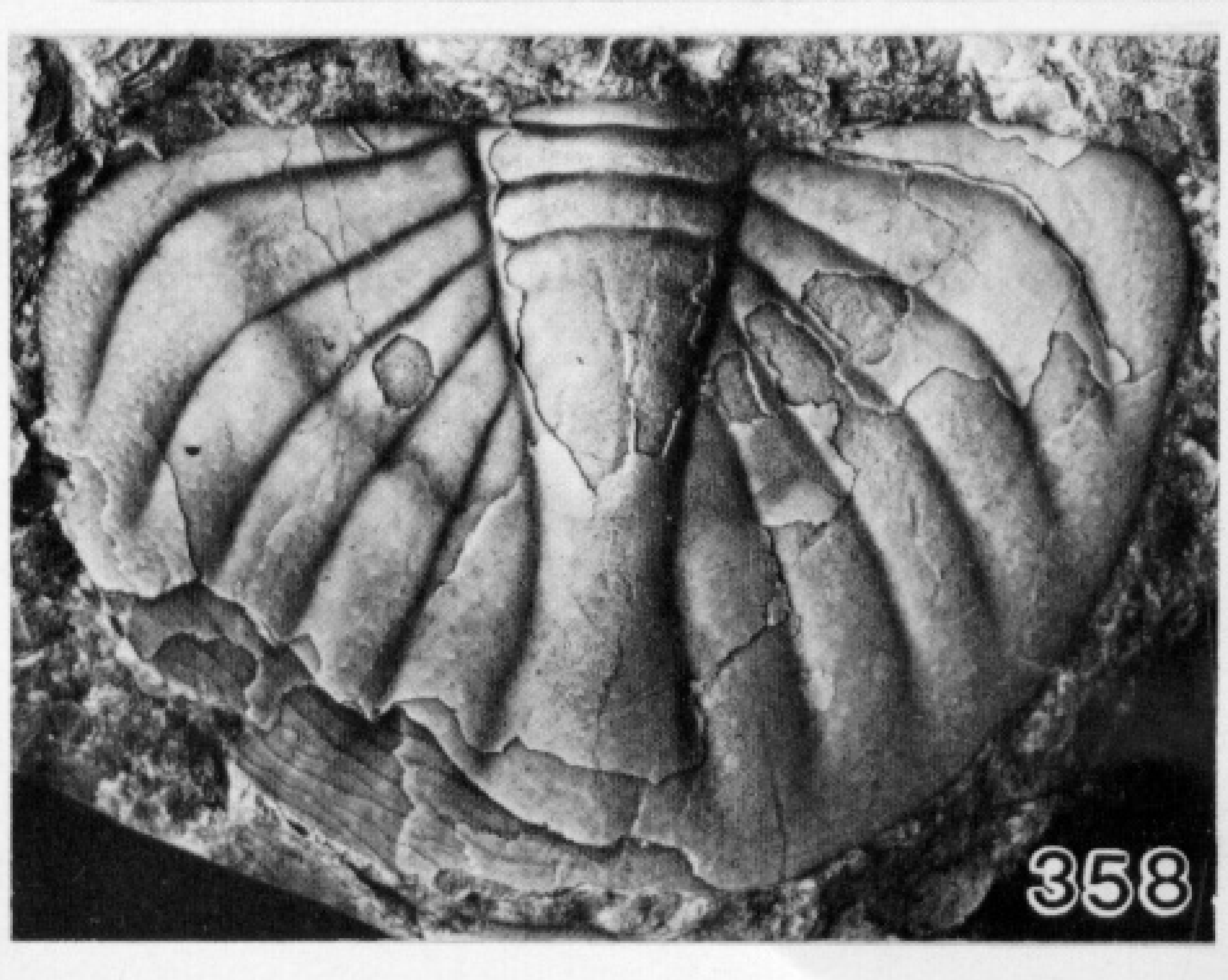
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