SILICIFIED SILURIAN TRILOBITES FROM MAINE

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CONTENTS

INTRODUCTION AND ACKNOWLEDGMENTS

The trilobite exoskeletons described in this account are silicified, and so can be freed from the enclosing rock with acid. They are not only the best-preserved specimens known from Silurian rocks, but also the only ones which include a variety of growth stages. They provide a wealth of new information, and have enabled us to refine generic and familial definitions, as well as to make new suggestions regarding relationships to trilobites of older and younger systems. It is a fortunate if unexpected circumstance that such a fauna should be discovered in the strongly folded and slightly metamorphosed rocks of northwestern Maine. The very excellence of the preservation, however, militates against comparisons with less well-preserved and incomplete specimens. The study of Silurian trilobites, in North America as in other continents, has been neglected. There are no modern, critical accounts of the morphology and stratigraphical occurrence of trilobites from the type Silurian Series in Britain, nor from the classical regions of North America such as northern New York State and the central states. The fauna from Maine is peculiar in composition, lacking the illaenids, calymenids, cheirurids and lichids that typify earlier-described Silurian

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faunas, and rich in proetids and otarionids that are the least well-known elements in such North American faunas. All these factors combine to make it difficult to assess the age more precisely than Middle to Upper Silurian, and rule out meaningful consideration of faunal affinities.

Terms used in the systematic section are those defined by Harrington, Moore and Stubblefield (*in* Moore, 1959), glabella being used to include the occipital ring. In describing *Proetus*, the anterior subdivision of the axial ring is called the preannulus (Richter and Richter, 1956; cf. Moore, 1959, fig. 292). Other special terms and notations are explained in Figures 1, 7–10.

Blocks from Baker Pond were first collected by Professor Arthur J. Boucot in 1952, and subsequently prepared by Dr. A. R. Palmer, U.S. Geological Survey. Whittington is grateful to Dr. Palmer for inviting him to study this material, and to Professor Boucot for guiding him to the locality and helping to make a large additional collection in 1959. This material was prepared at the Museum of Comparative Zoology, and Campbell's visit in 1965 gave us the opportunity to study it. We express our thanks to the National Science Foundation, Grant GB-3577, for having made Campbell's visit possible, and for paying the costs of printing the plates; Grant GB-1807 provided technical assistance to Whittington. Text-figures have been drawn by Mr. Arnold Clapman. Mrs. Marjorie Korringa has prepared all the photographic prints, lettered the figures, and helped in many other ways. The major part of the collection, including all type and figured specimens, is deposited in the U.S. National Museum (abbreviated below as USNM).

Dr. David L. Bruton kindly gave us unpublished information on certain odontopleurid species, Dr. J. S. Jackson lent type specimens from the National Museum of Ireland, and Dr. A. Martinsson lent the type specimen of *Proetus concinnus* from the Palaeontological Institute, Uppsala, Sweden. We are also indebted to Mr. R. P. Tripp for discussing with us the new encrinurid genus and notation of glabellar tubercles, and to Dr. Robert R. Hessler for comments on certain morphological aspects of these trilobites, but we assume responsibility for interpretations expressed herein.

LOCALITY, CORRELATION, AND AGE OF THE FAUNA

The blocks of grey, silty limestone containing the trilobite fauna were selected from those lying on the central part of the east shore of Baker Pond, centre of Spencer Quadrangle, Somerset County, Maine. These limestones are different in appearance and fossil content from others that are present to the northeast and southwest, all included within the outcrop of the Hardwood Mountain Formation of Boucot (1961, pl. 34). Consideration of the regional geology (James B. Thompson, Jr., personal communication) suggests that the blocks cannot have been derived from the northwest, but that they came from a part of the formation now concealed by glacial deposits.

When dissolved in dilute hydrochloric acid the blocks yielded a residue of silicified trilobite exoskeletons, ostracode valves, rare bryozoans and brachiopods. The replacement of the trilobite exoskeletons preserves in remarkable detail the original surfaces. In large specimens the replacement is in the form of two layers, one at the original outer surface, the other at the original inner surface (e.g. Pl. 1, figs. 1–3; Pl. 10, fig. 11; Pl. 11, fig. 20; Pl. 13, fig. 17). These two layers, separated by a narrow space, are readily apparent in damaged specimens. In the smaller specimens a single layer replaces the entire thickness of the exoskeleton. Silt grains adhering to the surface are difficult or impossible to remove without damaging the specimen, and may be seen in many photographs (e.g. Pl. 1, figs. 5, 23, 24, 30, 31). Table 1 lists the trilobite fauna and gives a measure of its relative abundance. Dr. Jean M. Berdan (*in* Boucot, 1961, p. 181) named four ostracode genera from the formation. However, Dr. Berdan informs us (personal communication) that ostracodes from the silicified blocks are different from those obtained from other outcrops of the formation, and show some resemblance to ostracodes from the Henryhouse Formation, Oklahoma. Professor Boucot (personal communication) notes that the brachiopod fauna from the Baker Pond locality is rather different from that at other localities assigned to the Hardwood Mountain Formation. He concludes that the age is within the span of Wenlock to early Ludlow, and in terms of the North American sequence could be as old as the Waldron Shale. The trilobite fauna is dominated by proetids and otarionids, American Silurian species of which are poorly and incompletely known, and less common is the new encrinurid genus *Fragiscutum*. Encrinurids are not known to be present in rocks of Devonian age, so that the Silurian age of the fauna seems beyond question.

North American mid-continental Silurian trilobite faunas include illaenids, cheirurids, calymenids and lichids (cf. Weller, 1907; Raymond, 1916; Walter, 1927), but these families are not represented in the Baker Pond collection. Difficulties in correlation stem from this lack, and from the lack of recent work on Silurian trilobites. Campbell (in press) has studied trilobites of the Henryhouse Formation, Oklahoma, and while no one species is in common with the Baker Pond fauna, those of *Proetus*, *Fragiscutum* n. gen., and *Dalmanites* are alike. The Henryhouse Formation has not yielded otarionids, and only a poorly preserved free cheek of *Leonaspis*. The Baker Pond species of *Leonaspis* is compared to younger, Lower Devonian species, simply because these are the only well-known American species to which comparisons can be made. Species of *Leonaspis* are known to be long-ranging, and this single comparison cannot be taken to imply that the Baker Pond fauna is early Devonian in age. The balance of the evidence suggests that it is of about the same age as the Henryhouse—that is, near the Wenlock-Ludlow boundary. This age is consistent with comparisons between Baker Pond and Bohemian, British, and Swedish species made in the systematic section, and with age determinations based on brachiopods and ostracodes. Trilobites of Lower Silurian (Llandovery Series) age are not well known, but such comparisons as can be made do not suggest that the Baker Pond fauna is early Silurian.

SUMMARY OF MORPHOLOGICAL AND TAXONOMIC FINDINGS

The new morphological information, combined with data revealed by the growth stages, gives clues to relationships with older and younger groups. Some of the main points, elaborated in the systematic section, are:

1. Ordovician to Devonian proetids, typified here by *Proetus*, appear to be ancestral to Carboniferous genera like *Paladin*. A triangular rostral plate and the apparent absence of a sutural junction between the hypostome and the remainder of the cephalon characterise *Proetus*. In *Paladin*, however, the rostral plate is subquadrangular in outline and the hypostome is joined to the remainder of the cephalon by a suture.

2. *Otarion* (Ordovician to Devonian) also has a triangular rostral plate. Growth stages are remarkably like those of the Ordovician *Dimeropyge*, and suggest derivation from this older group. The supposed brachymetopid genus *Cordania* appears likely to be derived from otarionids.

3. Within the Proetacea, as presently conceived, there are thus two main phyletic lines, one leading through proetids to certain Carboniferous genera, the other being the dimeropygid-otarionid-brachymetopid line.

4. Three species of *Otarion* and one made the type of a new otarionid genus are described, based on cephala. Isolated

TABLE 1. TRILOBITE FAUNA OF THE HARDWOOD MOUNTAIN FORMATION AT BAKER POND, SOMERSET COUNTY, MAINE. INDICATION OF RELATIVE ABUNDANCE GIVEN BY TOTAL NUMBERS OF CRANIDIA OF ALL SIZES (INCLUDING FRAGMENTARY SPECIMENS) IN THE SAMPLE DISSOLVED.

Proetus pluteus n. sp.	150
Rhinotarion sentosum n. gen., n. sp.	8
Otarion instita n. sp.	148
Otarion plautum n. sp.	44
Otarion sp. ind.	38
Scutelluid gen. ind.	2
Fragiscutum rhytium n. gen., n. sp.	18
Dalmanites puticulifrons n. sp.	9
Xanionurus boucoti n. gen., n. sp.	8
Leonaspis cf. *williamsi* Whittington, 1956	10

segments and pygidia can only in a few cases be assigned to these species. Whether these are four distinct species, or whether one form may be a sexual dimorph of another, is an open question.

5. The type material of M'Coy's *Harpidella megalops* is redescribed, and it is concluded that the generic name is a subjective synonym of *Otarion*.

6. A new encrinurid genus is based on superbly-preserved material, including the first described developmental stages. These show that each ring of the pygidial axis represents a segment. Anterior bands of the thoracic pleurae are reduced to articulatory flanges, concealed in dorsal aspect. The pleural ribs of both thorax and pygidium are posterior bands. Canals, diminishing in diameter dorsally, traverse these bands and the axial rings, but appear not to open on either surface.

7. Incomplete developmental stages of *Dalmanites*, beginning with the late protaspis, reveal the remarkable similarity to similar stages of the ancestral Ordovician *Dalmanitina*.

8. Developmental stages of two odontopleurid species show the same major spine pattern as species of various Ordovician genera. One species, type of a new genus, appears to lie on a phyletic line between the Ordovician *Diacanthaspis* and the Devonian *Radiaspis*.

SYSTEMATIC PALEONTOLOGY

Superfamily PROETACEA Salter, 1864

Discussion. The discovery by Dr. W. T. Dean (personal communication) of a species of *Otarion* and a proetid from the Arenig of southern France shows the early separation between these two groups. A third group, the dimeropygids, is also present in the early Ordovician (Whittington, 1963: 45–50). *Phaseolops* from the Llanvirn of Newfoundland (Whittington, 1963: 36–40) is considered to be a proetid, and among other characters it exhibits a triangular rostral plate, though the axial rings of the thorax do not have the pre-annulus. In the later Ordovician and the Silurian, proetids and otarionids are more abundant and widespread. The present material of *Otarion* shows the characteristic triangular rostral plate, the narrow panderian notch situated close to the posterior margin of the segmental doublure, the absence of the pre-annulus, the characteristic long median spine of one thoracic segment, and a development of both cephalon and pygidium which recalls that of *Dimeropyge* (Whittington and Evitt, 1954). The species of *Proetus* described here reveal the triangular rostral plate, the typical pre-annulus of the segments, and the V-shaped panderian notch which is medially situated in the doublure of the segments. The hypostome is characteristic in shape but appears not to be attached at a hypostomal suture to the rostral plate and doublure of the free cheeks. The early developmental stages of *Proetus* differ from those of otarionids, notably in the absence of paired spines. A relationship between otarionids and dimeropygids is suggested not only by the development but also by many aspects of holaspid morphology, including the single median thoracic spine characteristic of many species.

Relationships between Silurian otarionids and proetids and Devonian and younger proetaceans present many problems. For example, the Lower Devonian genus *Cor-*

dania (Whittington, 1960) has an otarionid-like cephalon, a wide (tr.) sub-triangular rostral plate, and the thoracic segments lacking the pre-annulus, but the pygidium is unlike the otarionid pattern in that it is large and has some ten axial rings. In recent publications *Cordania* has been placed in the Brachymetopidae (Whittington, 1960; Amos, Campbell, and Goldring, 1960; Hessler, 1962a; Hahn, 1964), a Devonian-Carboniferous group embracing forms with the above characters, except that two of its Carboniferous members, *Brachymetopus* and *Australosutura* have a rostral plate that is not sub-triangular but extends close to the genal angle. We suggest that *Cordania* was derived from an otarionid rather than a proetid, but more information is needed before lines of descent of the Carboniferous Brachymetopidae can be discerned.

Silicified material of the Carboniferous genus *Paladin* (Whittington, 1954) shows that it is proetid-like in the shape and arrangement of the glabellar furrows, presence of the shallow panderian notch in the cephalic doublure, the form of the segments, nature of articulating arrangements, outline of the panderian notch on the thoracic segments, and the presence of the pre-annulus. On the other hand, however, the hypostome of *Paladin* has a wing process on the large anterior wing which appears to rest in a depression on the surface of the anterior boss, and there is a hypostomal suture linking it to the rostral plate and the doublure of the free cheeks. The rostral plate is transverse, subtrapezoidal in outline. The shape of the plate and mode of attachment of the hypostome distinguish *Paladin* from *Proetus* but the features in common indicate that *Paladin* and its allies may have been derived from the proetids.

Hessler (1962b; 1963; 1965) has described and discussed Lower Carboniferous trilobites which he refers to the Proetidae. His figures suggest that in species of *Griffithides* (1962b, pl. 176, figs. 12, 14) and possibly of *Phillipsia* (1963, pl. 61, figs. 3, 4) a pre-annulus is present on the first axial ring of the pygidium, while in other species he describes this ridge is not developed. Use of this thoracic and pygidial character, as well as ventral cephalic characters, may help to disentangle the relationships of Carboniferous and younger trilobites to each other and to different Devonian groups.

This discussion suggests that from early Ordovician onward there may have been two main phyletic lines within Proetacea—a proetid line leading to various Carboniferous groups, and a dimeropygid-otarionid line from which at least some brachymetopids may be derived.

Family PROETIDAE Salter, 1864
Subfamily PROETINAE Salter, 1864
Genus *PROETUS* Steininger, 1831
***Proetus pluteus* n. sp.**
Plates 1, 2; Plate 3, figs. 6–8, 10, 13–16; Figs. 1–5, 6C.

Holotype. USNM 154457, cranidium and free cheek.

Description. Glabella widening from the posterior edge to a maximum width across midpoint of lateral occipital lobes, narrowing abruptly forward to the anterior margin of this lobe, less abruptly inside the palpebral lobes, to the well rounded frontal lobe. Axial furrow lightly impressed, except posteriorly; preglabellar and anterior border furrows confluent medially, deeper. Occipital furrow with an almost vertical anterior slope and more gentle posterior slope, the course gently convex forward medially, swinging forward and outward and deepening in front of the lateral lobe; latter moderately convex, extending back almost to posterior margin of ring, separated from ring by a furrow which becomes faint distally. Glabellar furrows may be faintly impressed on external surface and are indicated by smooth areas; shape and arrangement shown in Figure 1A (compare Pl. 1, fig. 8). On the inner surface the muscle areas may also appear faintly im-

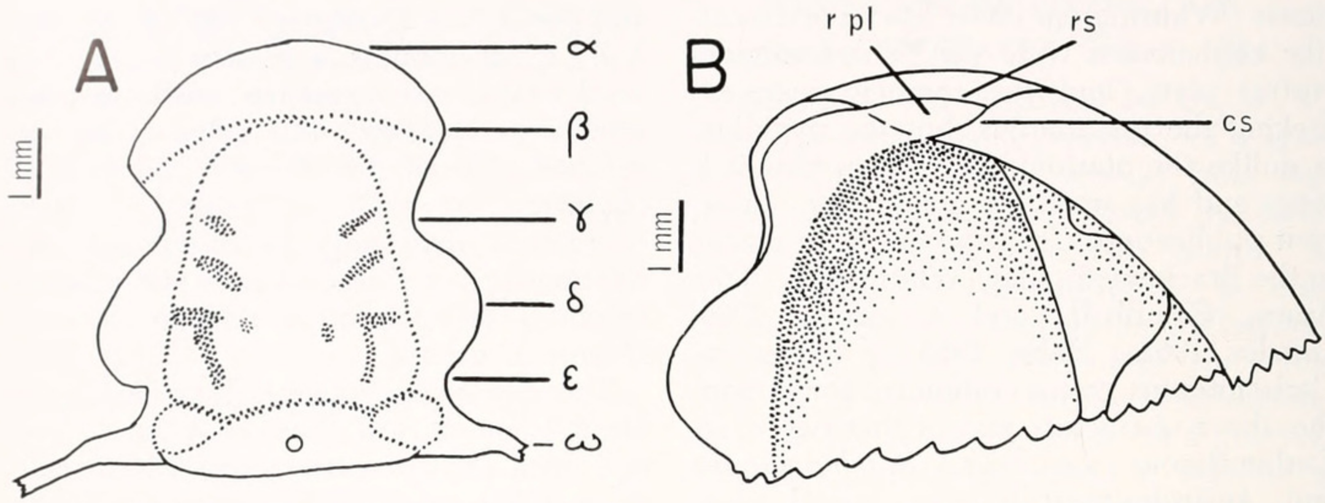

Figure 1. *Proetus pluteus* n. sp. A) Muscle areas of glabella and notation of points on facial suture (after Richter and Richter, 1940) based on original of Plate 1, figure 8. B) Restoration of rostral plate, based on originals of Plate 2, figure 2. Abbreviations: cs, connective suture; r pl, rostral plate; rs, rostral suture.

pressed, or the replacing silicification may be broken over these areas (Pl. 2, fig. 2).

Eye lobe elongate, gently convex eye surface steeply sloping, apparently smooth externally and internally—the preservation does not reveal any facets. Palpebral lobe flattened. Outside eye lobe, cheek curves down to borders; posterior border widening outward and curving posterolaterally into base of short, pointed fixigenal spine. Posterior border furrow moderately deep, curving out on to base of fixigenal spine; lateral and anterior borders broad and gently convex, separated from the cheek by a broad shallow border furrow. Doublure (Pl. 2, figs. 2, 3) of approximately same width as lateral and anterior borders, gently convex ventrally, the inner edge curved up beneath the groove formed by the border furrows. Beneath posterior border, doublure extends in to the fulcrum (Pl. 1, fig. 4); inside here, edge of exoskeleton has well-developed recess for articulating flange of first thoracic segment; occipital doublure very short (exs.) behind the lateral occipital lobes, but lengthening to about three-quarters length of occipital ring in midline. Shallow panderian notch in margin of lateral border in front of genal angle (Pl. 2, fig. 2). Course of sutures shown in Figure 1 (compare Pl. 2, fig. 2). Anterior branch runs inward and forward from β to α over edge of anterior border and continues inward across doublure as the connective suture, the two sutures meeting in the midline at the inner margin of the doublure. The rostral suture runs along the doublure a short distance in from the anterior margin, and thus isolates a triangular rostral plate. Isolated examples of this plate have not been found, but the outline of the doublure of the free cheek leaves no doubt as to its shape.

Hypostome with strongly convex central body partly subdivided by short, deep, backwardly-directed middle furrows into a large anterior and a small, crescentic posterior lobe; in midline at anterior margin of anterior lobe is a triangular, flattened or gently concave area (Pl. 1, fig. 13). Border furrows well defined except beside anterior wing; anterior border narrow, convex, the edge (which presumably faces forward and downward) having a deep slot along the median portion (Pl. 1, figs 13, 18). Crescentic posterior body gently inflated, especially at the tip where the oval macula is faintly defined by its convexity (Pl. 2, figs. 1, 4). Lateral border widening posteriorly, posterior border flattened and bearing a short, blunt spine at the posterolateral angle. Anterior wing consists of an upward and outwardly directed extension of the edge of the doublure, subtrapezoidal in outline, without a wing process; posterior wing small, subtriangular, directed upward and slightly inward; doublure between wings narrow, widest posterolaterally.

External surface of cephalon (Pl. 1, figs. 8, 11, 13, 14, 17, 18; Pl. 2, figs. 1, 4) inside borders bearing fine, evenly and closely spaced granules; these granules absent in the furrows and on the inner part of the palpebral lobe; posterior border apparently smooth along the crest; outer part of anterior and lateral borders and doublure bearing slightly irregular terrace lines running subparallel to the margin, these terrace lines continuing on to the genal spine. On hypostome, terrace lines on anterior lobe of middle body run subparallel to margins, fanning out anteriorly beside the flattened triangular area. Posterior lobe including macula apparently smooth; terrace lines along borders, subparallel to margins, becoming more widely spaced and curving on the outer surface of the wings.

Number of thoracic segments unknown. Ring subdivided by intra-annular furrow which curves forward distally and joins the more deeply-incised articulating furrow some distance in from the axial furrow; inner part of pleura flat, outer part steeply bent down; inner part relatively narrow (tr.) on anterior segments (Pl. 2, figs. 7, 8) and the outer part deflected backward. Pleural furrow runs diagonally out beyond fulcrum and along edge of broad facet. Doublure extends along posterior margin of outer part of pleura and beneath tip, with a broad, deep panderian notch (Pl. 2, fig. 25). The anterior edge of this notch is raised to form a stop during enrollment; in anterior segments this anterior part of the doublure is narrow and not raised (Pl. 2, fig 24). Articulation between anterior segments of the thorax, the cephalon, and the pygidium is facilitated by the ring process situated at the distal posterior margin of the axial ring, which fits into a socket on the anterior margin; in centre of this socket is the small axial process (Pl. 2, fig. 23) which fits into a corresponding axial socket. The inner anterior edge of the pleura is rounded, and fits into a groove on the posterior edge (Pl. 2, figs. 24, 25, 31). Doublure of ring similar in form to that beneath the occipital ring, medially extending forward as far as articulating furrow; anterior edge of articulating halfring with a deep slot along its whole width (Pl. 2, fig. 23).

Pygidium with axis ill-defined at tip; first ring stands markedly higher than succeeding seven or eight rings. Pleural regions with inner part adjacent to axis horizontal, outer part sloping steeply down to margin, no border furrow. Three or four pleural and interpleural furrows visible on pleural regions, dying out distally so that border is smooth, especially posteriorly (Pl. 2, figs. 26, 27). Broad, gently convex doublure extends inward for about one-third the width of the pleural regions.

External surface of rings and inner parts of pleurae of thorax and pygidium with fine granulation; terrace lines on pygidial doublure and around dorsal margin; branches from these lines curve forward and inward across the pleural region subparallel to the pleural and interpleural furrows (Pl. 2, fig. 26).

Variation and development of cranidium. Measurements of a size series of cranidia (Figs. 2, 3) show some aspects of the variability, and that this variability is continuous. A size series of cranidia (Pl. 1, figs. 5–7, 9, 10, 15, 16, 19–21, 23–31; Fig. 6c), ranging from a length (sag.) of 1.3 mm upward, shows the relatively minor changes that take place. Most noticeable is the change in longitudinal convexity—from a steep slope in front of the eye lobe to a lesser slope, combined with an increase in the inflation of the anterior border which gives a deeper border furrow.

Variation and development of pygidium. A series of specimens from transitory pygidia (Pl. 3, figs. 10, 13–16) to the small-

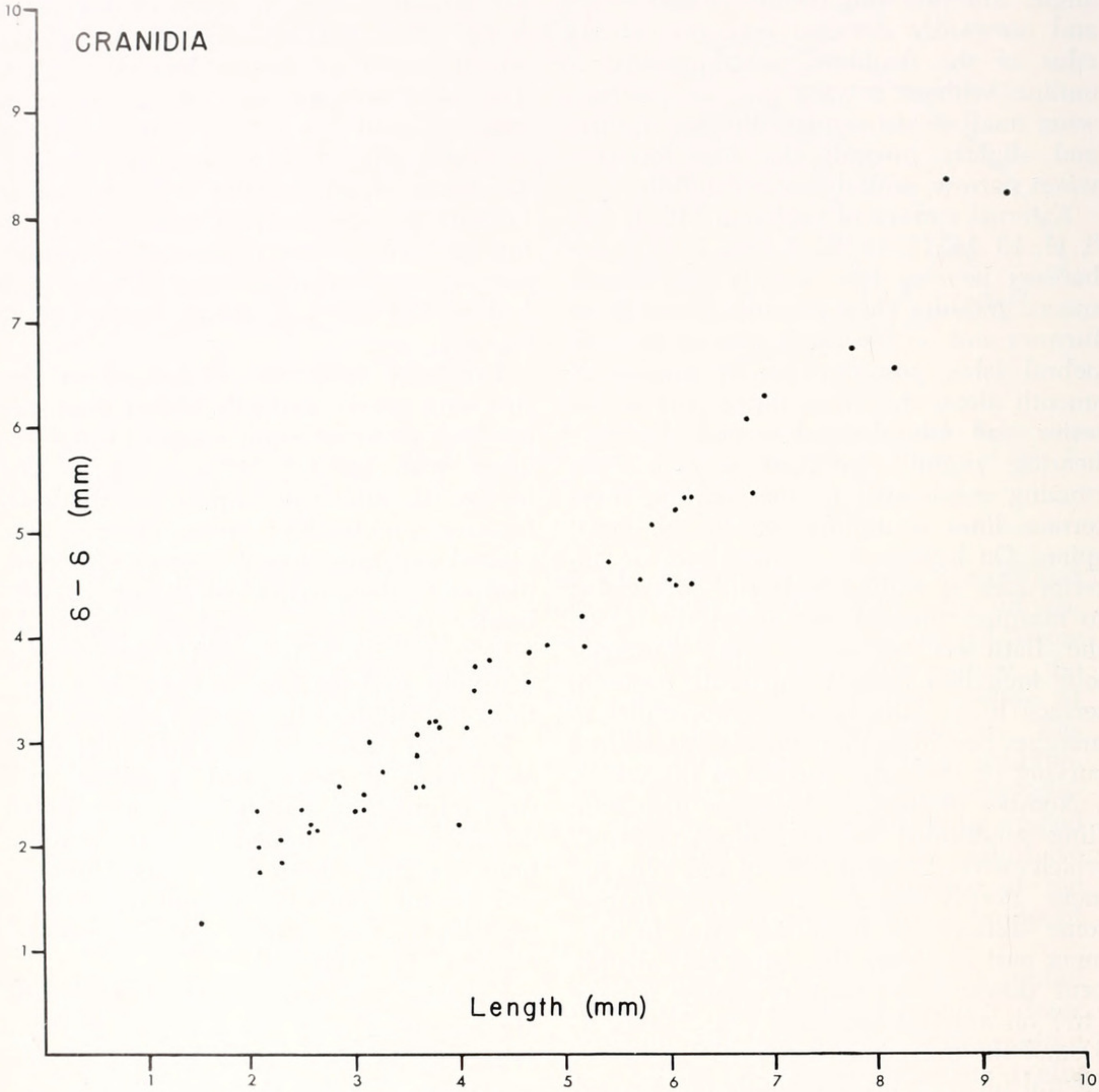

Figure 2. *Proetus pluteus* n. sp. Dimensions of 50 cranidia; length is sagittal; δ–δ is width across palpebral lobes at widest point. Measured cranidia include USNM 154458–60, 154464–6, 154475, 154478, figured specimens, remainder included under 154489.

est true pygidia (Pl. 3, figs. 6–8) to larger ones (Pl. 2, figs. 17, 20, 26–30) shows that there is little change in the series, apart from a tendency to become slightly broader. At a small size, the first ring stands higher than the others. The specimens are variable through a considerable size range, as shown in Figures 4, 5. There is no discontinuity within this variation and the material all appears to belong to one species.

Discussion. The present material, which is of dissociated exoskeletal parts except for one cephalon, is regarded as a single species because of the continuous range of variation. This range is wide, but the material is from a single locality.

Deep, smooth-edged slots run along the edge of the rostral suture of the cranidium

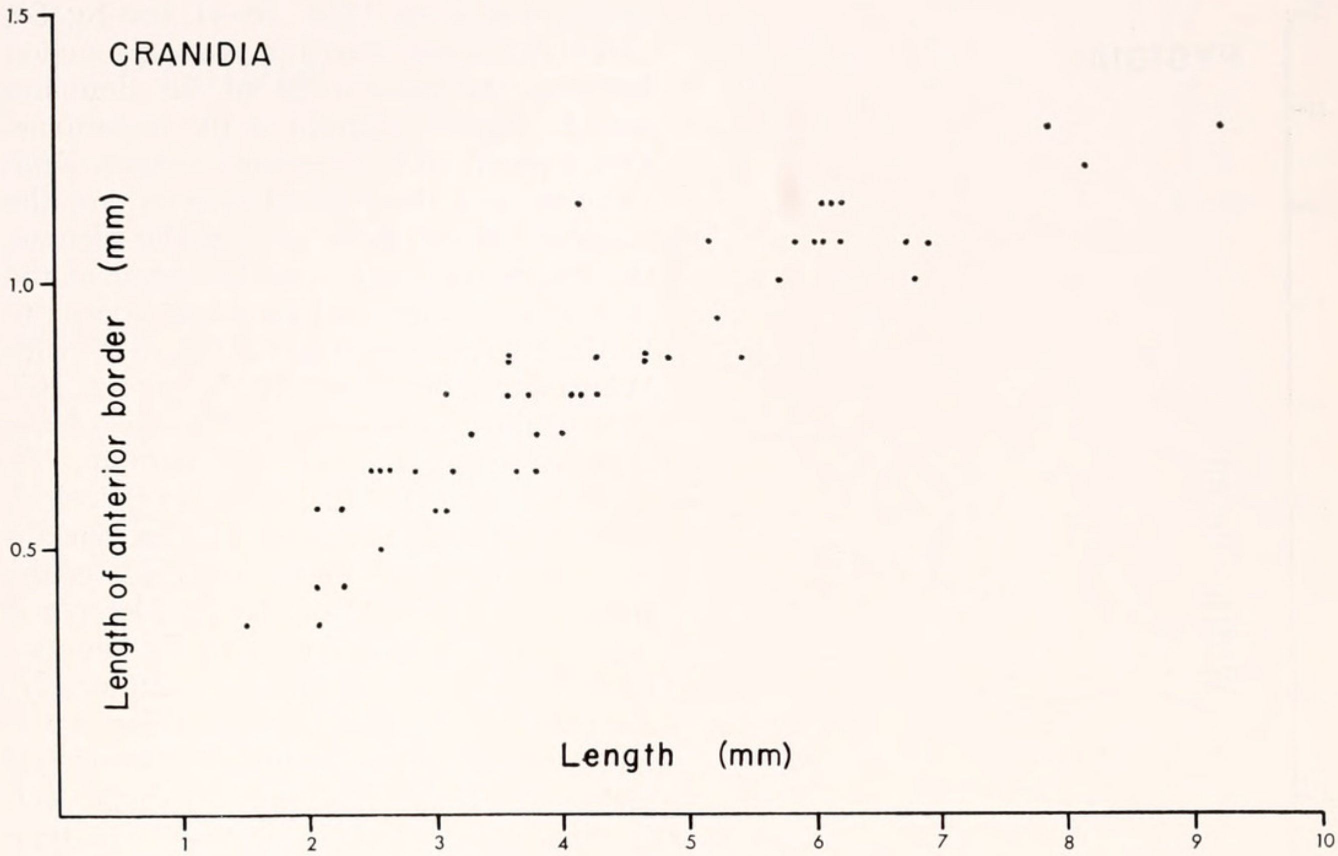

Figure 3. *Proetus pluteus* n. sp. Dimensions of 49 cranidia, both lengths sagittal. Measured specimens the same as Figure 2.

(Pl. 1, fig. 4; Pl. 2, fig. 2), around the edge of the articulating halfring of thoracic segments (Pl. 2, fig. 23) and the pygidium, and along the sutural margin of the hypostome (Pl. 1, fig. 13; Pl. 2, fig. 1). The smooth edges of the slots, and their consistent form in many specimens, argue against these features being the result of silicification, for example as being a gap between a silicified layer on the external and internal surfaces of the exoskeleton. Such double layering is seen (Pl. 1, figs. 1–3, 10), but where it is broken through at the edge of a specimen the margins of the two layers are not straight but ragged and irregular. It appears to us that the slots represent parts of the integument that were uncalcified in life. In the thorax, where such integument extended forward from the margin of the articulating halfring to the doublure of the ring in front, it must have been articulatory in function. Along the rostral suture it is not clear what the function of this uncalcified integument may have been. Between the cephalic doublure and the hypostome its function may have been articulatory, for not only is the sutural margin of the hypostome rounded and slotted (Pl. 2, fig. 1), but also the margin of the doublure of the cheek adjacent to the rostral plate (Pl. 2, fig. 3); these edges did not adjoin along flat surfaces. It is notable also that the margin of the anterior wing of the hypostome is thin and rounded, that the wing bears no wing process, and thus that there is no evidence of a close link between this wing and an anterior pit; indeed, there appears to be no anterior pit in this species. Thus the hypostome of *Proetus* was not rigidly fitted to the remainder of the cephalon, as it appears to be in, for example, *Fragiscutum* n. gen. (see below), and may have been movable.

So far as we are aware, the hypostome of a

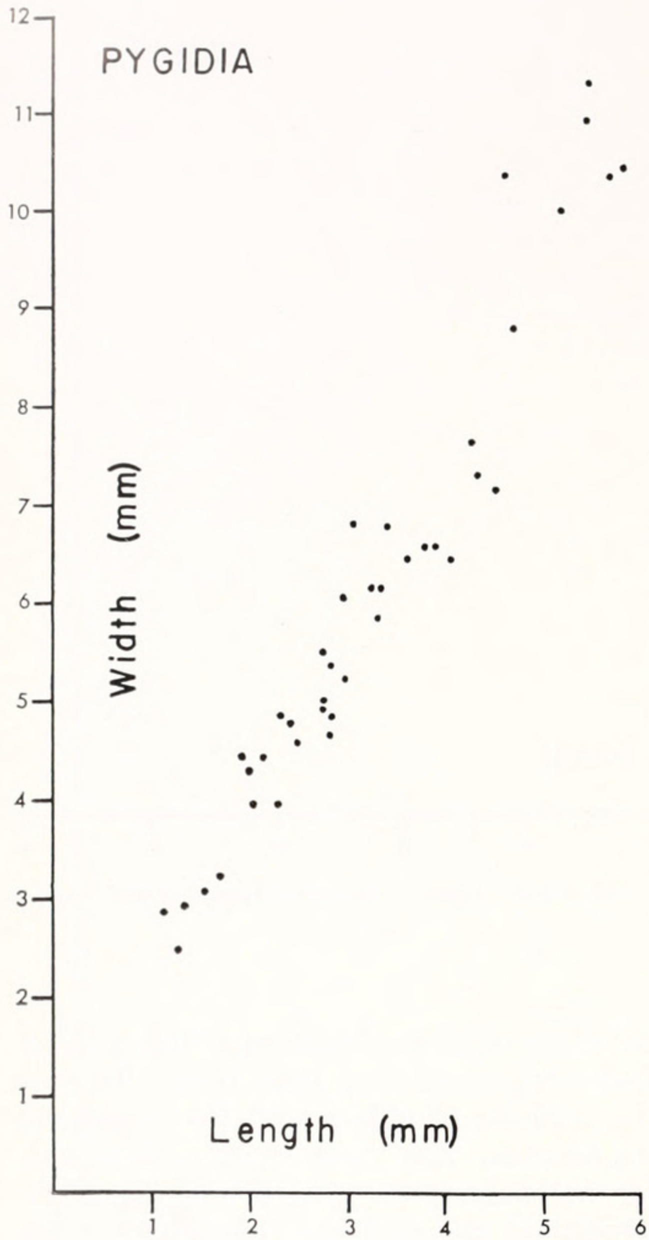

Figure 4. *Proetus pluteus* n. sp. Dimensions of 40 pygidia; length is sagittal (excluding articulating halfring); width is maximum. Measured pygidia include USNM 154482–5, figured specimens, remainder included under 154490.

proetid has not been found in place in any specimen. This evidence supports the view that there was no sutural link between the hypostome and the rest of the cephalon, but rather that the hypostome was kept in position by uncalcified integument and muscles, which decayed after death so that the hypostome was not retained in its original position. The attachment of the hypostome to the remainder of the cephalon has been discussed in *Dimeropyge* (Whittington and Evitt, 1954: 38–41, text-fig. 8), and in that genus there is no sutural junction between the inner edge of the doublure and the anterior margin of the hypostome. Other points of comparison between *Dimeropyge* and the present species are the doublure of the outer part of the pleurae, the panderian notch, and the form of the stop to enrollment, all of which appear to be similar (compare Plate 2, figure 25, with Whittington and Evitt, 1954, text-fig. 10).

New illustrations are given here of the type species of *Proetus, P. concinnus* (Pl. 3, figs. 4, 5, 9, 11, 12), from the Wenlock Series, Gotland, Sweden. The broken anterior border shows on the right side of the specimen the mould of the doublure, and on the left side the course of the anterior branch of the suture, which is continued by the connective suture to the midline at the inner edge of the doublure. The rostral plate was thus triangular in shape (cf. Lovén, 1845: 49, pl. 1, fig. 2b). The type species, *P. pluteus*, and a species from the Henryhouse Formation of Oklahoma being described by Campbell (in press), are exceedingly similar. These similarities include the detailed form of the cephalon (shape of the glabella, form of the muscle areas, position of the eye lobe, shape of the borders, and presence of a triangular rostral plate), and the form of the thoracic segments and pygidium. The latter lacks a clearly defined border and has the pleural furrows of the first one or two segments extending close to the margin. The fine granulation of the external surface of the glabella, the weak pitting on the free cheek inside the border, and the presence of terrace lines on the border (which on the pleural regions of the pygidium curve forward and inward) are characters common to all these species. These close similarities might well be used to limit the subgenus *Proetus* (*Proetus*) to a group of Middle and Upper Silurian species. The latter would probably include *P. fletcheri*, described by Reed (1901:11–14, pl. 1, figs. 5, 6) from the Wenlock Limestone of Britain, and *P. mořinensis*

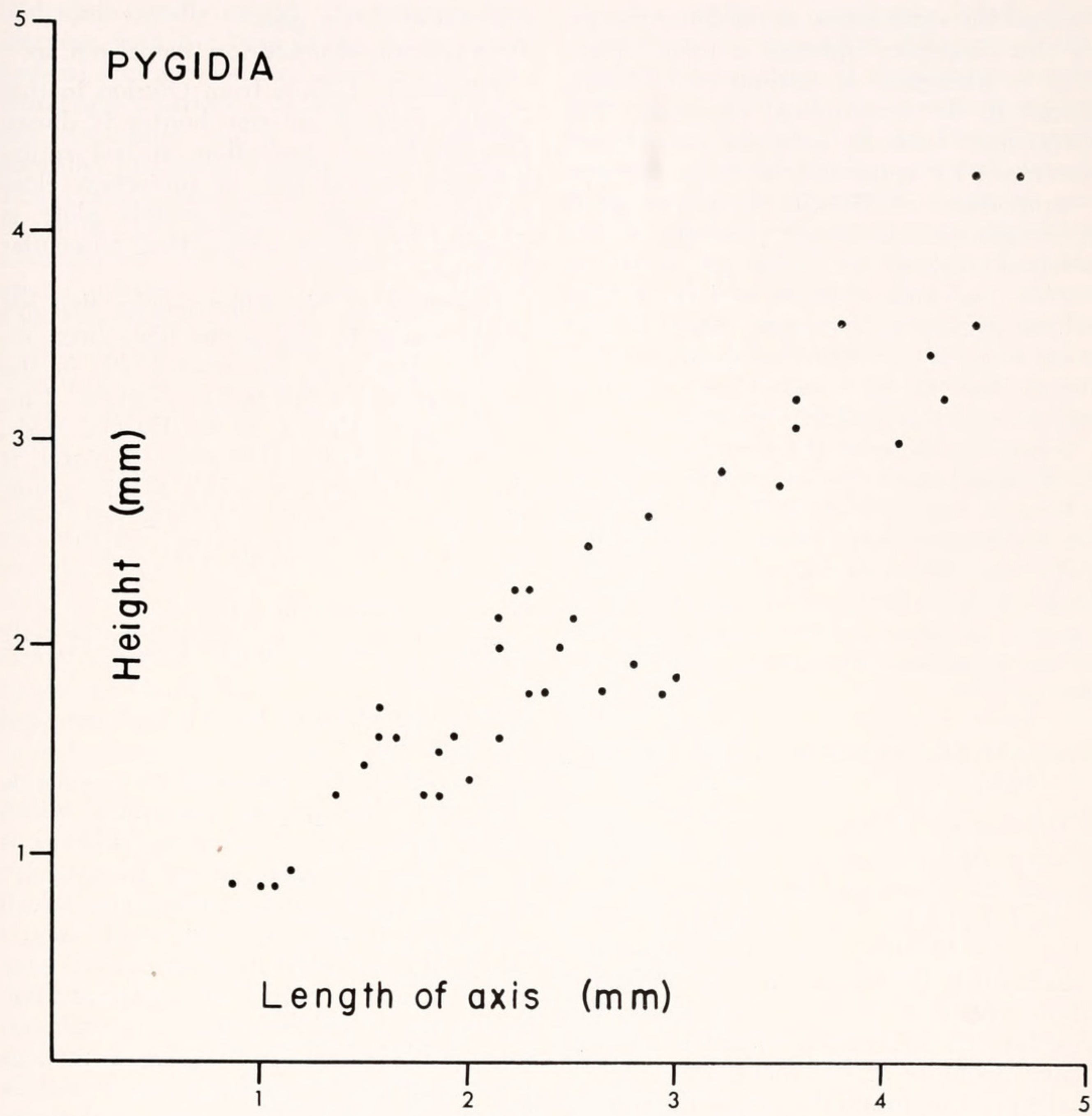

Figure 5. *Proetus pluteus* n. sp. Dimensions of 40 pygidia, length of axis is sagittal, height is maximum. Measured specimens the same as Figure 4.

Přibyl (1960: 204–206, pl. 2, figs. 1–5) from the Kopanina Shale, Lower Ludlow, of Bohemia. However, examination of specimens of *Proetus cuvieri*, from the Middle Devonian of the Eifel district of West Germany (Pl. 3, figs. 1–3; Richter and Richter, 1956), shows that this species is like the type *P. concinnus*. The rostral plate is not the relatively wide (tr.) and short (sag. and exs.) plate figured by Richter and Richter (1956, pl. 5, figs. 33b, c, d), but the doublure of the cephalon (the external mould is preserved in the original of Plate 3, figure 2) curls upward and inward so that the inner edge lies beneath the border furrow. The same specimen has the edge of the left connective suture preserved, and it runs inward and backward to meet the right suture at the inner margin of this doublure, isolating a rostral plate that is triangular in outline and sharply flexed in the longitudinal direction. The differences between holaspid *cuvieri* and *concinnus* are apparently in minor features —proportions of glabella, length of genal spine, presence of strong tubercles on the external surface of some specimens of *cuvieri*, and lack of incurved terrace lines on the pygidium of *cuvieri*. These do not seem to justify a subgeneric distinction between the Middle and Upper Silurian species and this Middle Devonian species.

From *P. concinnus* the new species may be distinguished by its less globose glabella, relatively longer (sag. and exs.) anterior border, shallower axial furrow between the palpebral lobe and the glabella, coarser granulation on the glabella, and shape and number of spines on the posterior border of the hypostome (Lindström, 1901, pl. 6, fig. 21).

Family OTARIONIDAE Richter and Richter, 1926

Discussion. The present material of *Otarion* and *Rhinotarion* n. gen. suggests that to the characters of this family given by Richter, Richter, and Schmidt (*in* Moore, 1959: O 403–404) may be added the convergence backward of the connective sutures to meet at the inner edge of the doublure, the absence of a panderian notch in the doublure of the cheek, the absence of the pre-annulus on the axis of the thorax, the extension of the median pleural furrow out close to the tip of the segment, and the narrow panderian notch situated close to the posterior edge of the segment. The hypostome (Richter, 1914; cf. Prantl and Přibyl, 1951: 443) is unlike that of proetids in having the middle furrow complete and a more prominent, crescentic, posterior lobe of the middle body on which the macula is not distinguishable. In addition, in the present examples, there is a tiny wing process and the anterior wing itself is smaller and differently shaped.

RHINOTARION n. gen.

Type species.—*Rhinotarion sentosum* n. sp.

Diagnosis. Differs from *Otarion* in that median part of anterior border is drawn forward into a projection; rostral suture traverses ventral side of projection close to outer margin, hence rostral plate is inverted "T" shape rather than triangular in outline.

Distribution. No other species that we would assign to this genus have been recorded. However, specimen 17729 in the collection of the Australian National University, from Unit 4 of the Dargile Beds, Locality 47, Parish Heathcote, Victoria, is almost certainly a member of the genus. The only reason for doubt is the poor preservation of the basal glabellar lobes.

Rhinotarion sentosum n. sp.

Plate 4; Plate 5, figures 1–6, 9–11, 13–16, 18.

Holotype. USNM 154211, cephalon and two segments.

Description. Glabella moderately convex, expanding forward to maximum width across basal glabellar lobes, slight but abrupt contraction at lateral furrows 1p, frontal portion rounded; maximum width slightly less than, or equal to, length (sag.). Occipital ring widest in midline, steep posterior slope and more gentle anterior slope to the deep occipital furrow; prominent, slightly backwardly-curved, blunt, median spine. Lateral furrow 1p situated slightly in front of mid-length, narrow and deep, directed inward and backward and reaching the occipital furrow, deepest close to axial furrow; basal lobe lachrymate in outline, moderately convex. Lateral furrow 2p situated opposite anterior margin of eye lobe, a smooth oval area situated a short distance in from the axial furrow. Convex cheek slopes steeply outward, cheeks joined by preglabellar field that is only slightly wider (sag. exs.) than the anterolateral border; borders defined by deep, well marked border furrows. Posterior border narrow (exs.) adjacent to occipital ring, widening rapidly outside the fulcrum and merging with the base of the genal spine. Lateral and anterolateral border with flattened upper surface which is outward sloping, maximum width of border anterolaterally; medially, borders drawn forward into a blunt, rounded projection, which is of width (tr.) similar to the width of the anterolateral border. Preglabellar field gently inflated. Genal spine long, curved and tapering. Eye lobe relatively large (exsagittal length greater than ⅓ sagittal length of glabella) and situated at highest point of inflated inner area of cheek; cheek slopes steeply in all directions downward from margin of eye lobe. Palpebral lobe curves inward and downward, without rim; eye surface convex externally, apparently smooth. Broad, low, eye ridge runs inward and forward to axial furrow opposite frontal glabellar lobe (Pl. 5, figs. 1, 4). Anterior branch of suture runs forward and slightly outward to border furrow, curves over border and runs inward along outer vertical slope to meet rostral suture at a very oblique angle; rostral suture runs along forward and downward facing surface of border close to the margin of the projection. Posterior branch of suture runs directly outward and backward across the cheek and posterior border, down the posterior slope of the latter and curves across the doublure beneath the base of the genal spine. At margins, surface of the border curves evenly around to inner ventral side, where exoskeleton is flexed up almost vertically and extended as the doublure close up to the impression of the border furrows. A shallow impression in the doublure immediately behind the anterior projection; latter is oval in transverse section. Connective sutures run inward and backward to inner margin of the doublure approximately in line (exs.) with the lateral margin of the anterior projection. Rostral plate (Pl. 4, figs. 10–12) is thus an inverted "T" shape, with the posterior edge indented and bent to slope sharply upward and inward. Doublure continues beneath genal angle without either vincular notch or panderian notch, and narrows rapidly inward to disappear at the fulcrum; along edge of exoskeleton inside fulcrum (Pl. 5, fig. 4) is a recess to accept the articulating flange of the first thoracic segment. External surface covered, except in furrows, by large rounded tubercles and smaller thornlike spines; these irregularly scattered but sparse on the upper, inner surface of the cephalic borders, absent distally on the genal spines, and few on the posterior border. On ventral facing surface of border and doublure are prominent terrace lines, these not extending on to the smooth underside of the genal spine. Glabellar furrows not extended ventrally as apodemes. Hypostome unknown.

Number of thoracic segments unknown. Certain isolated segments in the collection, including one with a long median spine (Pl. 5, figs. 9, 10, 13–16, 18), have a median tubercle and three additional pairs on the axial ring, and one to two tubercles scattered along the posterior pleural band, and a group at the posterolateral tip. In these respects they resemble the two segments attached to the holotype cephalon, and differ from isolated segments of type A (Pl. 8, figs. 13–15, 21) or type B (Pl. 9, figs. 1–3, 8), and hence are assigned to this species.

Convex axial ring with distal part curved slightly forward; anterior edge slopes gently to articulating furrow which rises sharply to the articulating halfring. Long median axial spine on one segment. Pleurae flexed down at fulcrum, subdivided by U-shaped pleural furrow which runs straight outward and slightly backward and extends close to the tip; convex posterior band the widest close to the axial furrow, anterior band widest distally. Anterior segment has outer part of pleurae bent slightly back, and facetted so that anterior band is cut off; subsequent segments have the pleurae transverse and parallel-sided, the tip rounded. Articulating ring process on posterior margin, axial socket immediately above it, on anterior margin corresponding ring socket and axial process; on inner part of pleura anterior articulating flange which fits into recess on posterior margin of segment in front; marked fulcral articulating process and socket. Doublure extends along posterior margin of outer part of pleurae and beneath tip, narrow, V-shaped panderian notch (Pl. 5, figs. 13, 18) close to posterior margin, anterior edge raised to form a stop during enrollment. Doublure not extended along anterior margin of outer part. Distal part of articulating furrow broadened and deepened, but not extended ventrally as an apodeme. External surface bearing a fine granulation in addition to the elongate tubercles described above.

Pygidium not known with certainty.

The original of Plate 5, figures 5, 6, appears to be the cranidium of a malformed individual of this species. The part of the glabella in front of the lateral lobes is relatively longer than in other specimens, the preglabellar field is absent medially, and the projection on the anterior border is smaller and upwardly directed. The tip of the projection is either broken (if so the break is remarkably even) or terminated by the rostral suture which runs up the sides and over the top of the tip.

Genus *OTARION* Zenker, 1833

Type species.—*Otarion diffractum* Zenker, 1833.

Synonym (subjective). *Harpidella* M'Coy, 1849.

Discussion. The type species of *Harpidella, H. megalops* (M'Coy, 1846), is redescribed below and reasons are given for regarding *Harpidella* as a synonym of *Otarion.*

Specimens from Maine referred to *Otarion* are distinguished from those of *Rhinotarion* in that the projection from the anterior border is absent. Cephala (excluding the hypostome) are readily divisible into two kinds, and a possible third. Only one example of the latter has a thoracic segment articulated with it, so that the segments, pygidia and their developmental stages, cannot readily be matched with these three types of cephala. The procedure adopted is to describe the two most abundant types of cephala as two distinct species, and the third as a possible but unnamed additional species. Then follow descriptions of a hypostome that probably belongs within this genus, segments, pygidia, and transitory pygidia. Whether or not two or three species are represented is problematical, and there is also the possibility that two of them are sexual dimorphs of one species, or even that one of them is a sexual dimorph of *Rhinotarion sentosum* n. gen., n. sp.

Developmental series of the cranidium and pygidium are described below. There is a remarkable similarity between the small cranidia and pygidia of *Otarion* and those of the Ordovician *Dimeropyge,* a greater similarity than that between small stages of *Otarion* and *Proetus* described here. The paired spines, present in *Otarion* but not in *Proetus* (Fig. 6), are the major feature in which *Otarion* resembles *Dimeropyge.* This resemblance in developmental stages may be taken to suggest a closer relationship between otarionids and dimeropygids than between otarionids and proetids.

Recent descriptions and diagnoses (Prantl and Přibyl, 1951; Richter, Richter, and Schmidt *in* Moore, 1959) do not give information on the rostral plate in this genus. A topotype specimen of the type species is here illustrated (Pl. 10, figs. 12, 14–16) for comparison with the Maine material, and it has been prepared to reveal the rostral plate (Pl. 10, fig. 15). The rostral suture runs parallel to the outer margin of the doublure, and is situated a short distance in from it. The anterior branch of the suture (Pl. 10, fig. 16) runs inward and forward over the edge of the border, and is continued inward across the doublure by the connective suture. The inner edge of the doublure is curled upward beneath the border furrow, but clearly the connective sutures are close together, or meet at the inner margin. The rostral plate is thus triangular in outline, and flexed in the longitudinal direction. The rostral plate in the Maine species (Pl. 5, fig. 26; Pl. 6, figs. 2, 9; Pl. 7, figs. 6, 7) is similar in shape.

Otarion megalops (M'Coy, 1846)

Plate 19, figures 1–14, 16.

Holotype. National Museum of Ireland, internal mould of incomplete cranidium (Pl. 19, figs. 1–4), from Boocaun, near Cong, County Galway, Eire. The strata at this locality are of Upper Llandovery age (Whittard, 1938: 101–102; Harper, 1949: 54).

Other material. Two topotype cranidia, and a cranidium from strata of the same age at Tonlegee, near Cong.

Description. The glabella is widest across the elongate-oval, inflated basal lobes, rounded anteriorly; lateral furrow 1p curving inward and backward, shallowing posteriorly before it merges with the broad occipital furrow; furrow 2p is a short, shallow depression running directly inward from the axial furrow. The cheek is highest posteriorly, the large palpebral lobe curving up from the summit (Pl. 19, figs. 12, 13); the line δ-δ runs across the basal glabellar lobe at about one-third the length. Inside the palpebral lobe the cheek is convex and descends steeply to the axial furrow. In front of the palpebral lobe the cheek descends at first steeply, then there is a break to a gentler slope before it curves steeply down to become vertical adjacent to the border furrow. The break in slope mentioned runs from immediately in front of the palpebral lobe, forward and inward to meet the axial furrow opposite the most anterior part of the glabella; this break in slope has been interpreted by M'Coy and later authors as an eye ridge. The preservation as internal moulds in medium-grained sandstones makes it uncertain that this change in slope is truly an eye ridge—no distinct ridge can be seen. Preglabellar field is convex, descending vertically, anterior border jutting forward. Anterior branches of sutures are straight and diverge forward, on the crest of the anterior border curving to run inward. The posterior branch runs backward and slightly outward, so that the posterior part of the fixed cheek (Pl. 19, figs. 1, 13, 16) is short (exs.) and narrow (tr.). Median occipital tubercle on posterior margin of occipital ring.

Discussion. The cranidium of M'Coy's species differs from that of the type species of *Otarion* (Pl. 10, figs. 12, 14, 16) in the presence of a distinct lateral furrow 2p, in the larger palpebral lobe which is situated farther back, in the relative narrowness (tr.) of the posterior part of the fixed cheek, and the relatively shorter (sag. and exs.) preglabellar field. These differences do not seem to be worthy of generic rank. The two new species and one indeterminate species of *Otarion*, described below, are like *megalops* in the presence of lateral glabellar furrow 2p, the size and position of the eye lobe, and the narrow (tr.) posterior part of the fixed cheek. A Middle Devonian species having a large eye lobe and probably of this type is *O. unguloides ranunculum* Erben, 1953. Přibyl (1960: 218–220, pl. 3, figs. 5, 6) has used *Harpidella* for Barrande's species *novella* and certain North American species. A cranidium of *O. novella* (MCZ 8552) from the Kopanina beds, Lower Ludlow, at Kopanina, shows that while lateral glabellar furrow 2p is present, and there is a distinct eye ridge, the palpebral lobe is small and similarly situated to that of *O. diffractum*, and the posterior part of the cheek is as wide as in the latter species. *O. novella* is thus intermediate between *diffractum* and *megalops*, and we consider *Harpidella* should not be used as Přibyl suggests. Re-investigation of many species is necessary as well as more complete material, before any subdivision of *Otarion* can be placed on a sound footing.

Otarion instita n. sp.

Plate 5, figure 24; Plate 6; Figure 6a.

Holotype. USNM 154220, cranidium with left free cheek.

Description. Glabella is subparallel-sided, bluntly rounded anteriorly, and moderately convex; occipital furrow deep and transverse behind median lobe, curving back behind basal lobe. Latter isolated by straight furrow 1p which runs from opposite midpoint of palpebral lobe diagonally inward and backward to occipital furrow; basal lobe convex, length (exs.) about one-quarter of sagittal length of glabella. Conspicuous smooth muscle area (Pl. 6, fig. 4) runs in from axial furrow along anterior side of furrow 1p for about half its length; similar but shorter (tr.) muscle area 2p runs directly inward from axial furrow in line with anterior end of eye lobe. Cheeks inside border furrows united by broad (sag. and exs.) preglabellar field which slopes gently forward and at its margin drops abruptly vertically to the inner edge of the border. Border broadest anteriorly and anterolaterally, flattened upper surface is horizontal anteriorly but outward sloping laterally. Posterior border narrow (exs.) between axial furrow and fulcrum, beyond here widening rapidly and merging with broad lateral border at genal angle; genal spine long, gently tapering and curved. Large eye lobe of length (exs.) approximately one-third sagittal length of cephalon; convex eye surface apparently smooth externally, but internal surface showing many minute facets (Pl. 5, fig. 24). Median pit in palpebral lobe. Anterior branches of suture moderately divergent, crossing border in line (exs.) with midpoint of palpebral lobe, posterior branch running straight outward and backward across border a short distance inside base of genal spine. Doublure flattened on under surface, extending inward to lateral and anterior border furrows, curved up at the inner edge so that this edge lies close beneath the furrow. Doublure extends inward beneath posterior border as far as fulcrum. Rostral suture runs along vertical face of anterior border; connective sutures converge backward to isolate a triangular rostral plate (Pl. 6, figs. 2, 9), the innermost portion of which is flexed upward and indented. External surface bearing closely-spaced tubercles on glabella except in furrows; large median occipital tubercle; similar tubercles along anterior portion, and steeply sloping edge of preglabellar field and anterior part of cheek; elsewhere, external surface apparently smooth, except for terrace lines on edge of border, genal spine and doublure.

Development. A size series of cranidia (Pl. 6, figs. 8, 9, 13–16, 18–24; Fig. 6a) has been picked out, the smallest example approximately 1 mm in length (sag.). In this specimen the glabella as well as the cranidium as a whole is more convex than in larger examples; the anterior border is relatively narrower (sag. and exs.) and less flattened on the upper surface; the basal glabellar lobe is present and of approximately the same relative size as in larger examples. Most striking are the spines, a median occipital, three pairs on the glabella (of which the posterior is the longest and thickest), a median pair on the preglabellar field and the anterior border, and accessory pairs on the fixed cheeks, palpebral lobe and borders. With increase in size there is a rapid reduction of these spines, and a loss of the symmetrical arrangement, followed by a gradual assumption of the pattern of the large examples. A size series of the free cheek is difficult to pick out, but small examples which probably belong (Pl. 6, fig. 17) bear many short spines which are rapidly reduced and disappear (Pl. 6, figs. 10–12).

The form of the small cranidia, and particularly the arrangement of paired spines, resembles that of small cranidia of the Ordovician *Dimeropyge* (Whittington and Evitt, 1954: 44–46; and compare Pl. 6, figs. 18, 19, 24 with Whittington and Evitt, 1954, pl. 3, figs. 16, 17, 21–26; pl. 22, figs. 1–10). In the Ordovician genus there is an increase in convexity of the cranidium during development, there is no basal glabellar lobe, the palpebral lobe is smaller, but the spines are reduced in size and lose the symmetrical arrangement, as in *Otarion*.

Otarion plautum n. sp.

Plate 7, figures 1–9, 11–15, 17–19, 23–25: Figure 6b.

Holotype. USNM 154231, cephalon lacking hypostome.

Description. Much less abundant than *O. instita* are cephala and cranidia of this type, distinguished by the glabella having a width across the base approximately equal to the length (sag.), the flatter transverse profile of both glabella and cephalon, the more divergent anterior branches of the suture, the narrower border anteriorly and anterolaterally, the stronger backward flexure of the posterior border outside the fulcrum, and the shorter, more rapidly-tapering genal spine. A faint eye ridge (Pl. 7, figs. 6, 8) runs inward and forward to the axial furrow. The doublure is narrow, forming with the border a tube-like structure, the rostral plate triangular (Pl. 7, figs. 6, 7) and relatively short (sag.). The external surface is tuberculate, and there is a slightly larger median occipital tubercle. Tubercles are irregularly but closely spaced on the glabella, fixed cheek inside the eye lobe, and preglabellar field.

A developmental series of cranidia has been picked out (Pl. 7, figs. 8, 11–14, 17–19, 23–25; Fig. 6b), which is distinguished from that of *O. instita* (Pl. 6, figs. 8, 9, 13–24) by the consistently steeper slope of the preglabellar area, as well as the more divergent anterior branches of the suture and the stronger backward flexure of the posterior border. The smallest example (Pl. 7, figs. 19, 24, 25) is extremely like that of *O. instita* (Pl. 6, figs. 18, 19, 24), and bearing spines of similar relative size and paired arrangement. The glabella is subparallel-sided and bluntly rounded anteriorly with a small, convex basal lobe. With increasing size there is a general reduction in convexity, and the glabella gradually assumes the broader, relatively shorter appearance. Spines are rapidly reduced and the irregular arrangement of tubercles assumed. As in the case of *O. instita*, attention is drawn to the similarity between this developmental series and that of *Dimeropyge* (Whittington and Evitt, 1954).

Otarion sp. ind.

Plate 5, figures 7, 8, 12, 17, 19–23, 25, 26.

Description. This type of cephalon is almost as abundant as that of *O. plautum*. It is intermediate between *O. instita* and *O. plautum* in the convexity of the cephalon, the outline of the glabella, and the width of the anterior border. The outline of the anterior margin is bluntly and obliquely angulate, as is the course of the anterior border furrow; these outlines are more angulate than those of *O. instita*, while those of *O. plautum* are rounded. On the other hand, the cephalon resembles that of *O. plautum* in having the short genal spines and stronger backward flexure of the outer part of the posterior border. Doublure is similar to that of the other species, and there is a triangular rostral plate (Pl. 5, fig. 26). No very complete developmental series of cranidia has been recognized, because of the obvious difficulty of picking out this intermediate type. The smallest cranidium that appears to belong to it (Pl. 5, figs. 22, 23) is of length (sag.) 1.5 mm. The external surface bears elongate, irregularly scattered tubercles and paired spines on the glabella, the posterior pair in line with the posterior part of the palpebral lobe being notably longer and thicker.

One specimen (Pl. 5, figs. 19, 25, 26) has the anterior thoracic segment linked to the cephalon. The axial ring bears a number of tubercles; the outer part of the pleural region is facetted so that only the posterior band extends to the tip, and bears on the external surface tubercles, including a small group at the tip.

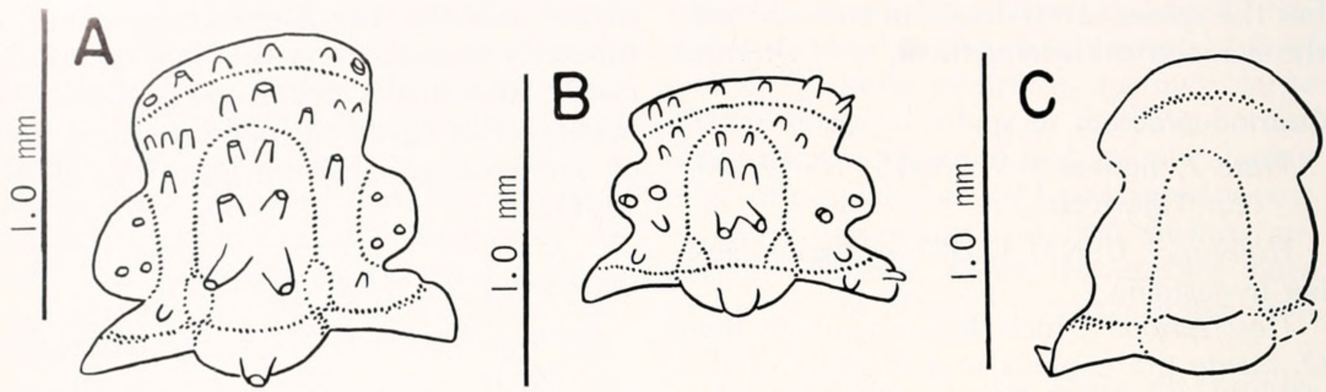

Figure 6. Smallest cranidia in size series showing some paired spines. A) *Otarion instita* n. sp. (original of Pl. 6, figs. 18, 19, 24). B) *Otarion plautum* n. sp. (original of Pl. 7, figs. 19, 24, 25). C) *Proetus pluteus* n. sp., USNM 154491, slightly smaller than original of Plate 1, figs. 23, 24, 30, 31.

Otarionid Hypostome

Plate 7, figures 10, 16, 20–22, 26, 27.

Description. The small number of specimens shows a variety of form—some relatively long (Pl. 7, figs. 10, 16), others relatively broader (Pl. 7, figs. 21, 22). In both types the anterior lobe of the middle body is moderately convex, separated by a complete middle furrow from the inflated, crescentic posterior lobe of the middle body. Macula not discernible. Shallow lateral and posterior border furrows, borders narrow, distinct shoulder at a point beyond the mid-length, short spine at posterolateral angle. Anterior wing triangular, directed upward and outward, tip rounded, on anterior margin near tip a small process directed forward. Doublure commences behind anterior wing and posterolaterally is of similar width to the border; posterior wing a pointed process directed upward and inward from the margin of the doublure beneath the shoulder.

Smaller examples are similar, the smallest (Pl. 7, fig. 20) distinguished by the relatively larger posterior lobe of the middle body, the relatively wider posterolateral border bearing a number of short spines, and the downwardly flexed anterior edge.

Otarionid hypostomes have rarely been found; the present examples are similar to that of the Middle Devonian *Otarion ceratophthalmus* portrayed by Richter (1914, text-fig. 1).

Otarionid Thoracic Segments and Pygidium, Type A

Plate 8, figures 1–6, 9, 10, 13–15, 19, 21–26.

Description. These are the most abundant types as isolated specimens, including segments with a median spine, and in three examples with several posterior segments articulated with a pygidium. The segments are typically otarionid, the narrow, shallow, pleural furrow running out almost to the tip before dying out. Inner part of pleura relatively narrow (tr.), with anterior flange and posterior recess; doublure commences outside this recess and runs along the posterior edge and beneath the tip of the outer part. Narrow panderian notch (Pl. 8, fig. 15) situated beneath posterior margin of pleural furrow, anterior edge raised to form a stop during enrollment. Pygidium transverse, broad axis extends back to inner margin of border and is bluntly rounded. Only first ring indicated by faint ring furrow. Pleural regions subdivided by first interpleural furrow, and one to three pleural furrows, the second and third extremely faint. Narrow border developed as a faint convexity without border furrow. Doublure is widest laterally, behind tip of axis becoming narrow and strongly convex (Pl. 8, fig. 10). External surface of both segments and pygidium finely granulate, the axial ring in larger examples (Pl. 8, figs.

13, 14, 23, 25) bearing numerous tubercles.

The tubercles on the axis and lack of tuberculation on the pleural regions suggest that these segments and pygidia may belong to either *Otarion instita* or *O. plautum*, their abundance indicating that they may belong to the former. The more posterior segments, particularly in the smallest example (Pl. 8, figs. 3, 6, 9) have the posterior tip bluntly pointed and directed backward. This may be a feature associated with small segments, for in the largest example the tips (Pl. 8, figs. 24, 25) are rounded on all segments; on the other hand, this may be a specific difference.

Otarionid Thoracic Segments and Pygidium, Type B

Plate 9, figures 1–14.

Description. These segments are differentiated chiefly by the external surface, which is tuberculate on the axial ring and the posterior bands, with a group of small, short spines projecting backward and outward from the posterolateral margin of the tip. In front of this group of spines the edge of the tip is slightly excavated, giving a characteristic scalloped outline (Pl. 9, figs. 1, 8). The occipital ring and posterior border of the cephalon of *Otarion* sp. ind. (Pl. 5, figs. 19, 25) bear scattered tubercles and short spines, as does the axial ring and posterior pleural band of the attached segment. The latter is strongly facetted, but the posterolateral tip appears to bear a few outwardly directed tiny spines. It appears that these segments may belong with this cephalon, and the axis is notably more convex than in type A.

No pygidium is known articulated with these segments; less abundant than those of type A are those placed here (Pl. 9, figs. 4–7, 9–14). Distinctive of the largest specimen (compare Pl. 9, figs. 4–7, with Pl. 8, figs. 1, 4, 10) is the slightly more prominent axis, the more triangular outline, the lack of any distinct border and the presence of the tubercles or short spines on axial rings and pleural regions. Three axial rings and a faint fourth ring are marked out by the first two ring furrows and bands of tubercles; on the pleural regions the first interpleural furrow and three pleural furrows may be distinguished, posteriorly as smooth bands between rows of tubercles. The doublure is similar to that of type A, narrow and convex behind the axis.

Otarionid Pygidium, Type C

Plate 8, figures 7, 8, 11, 12.

Description. One example of this distinctive pygidium is known, the outer part of the pleural regions steeply sloping and with a marked angle between outer and inner parts along the anterior margin. The doublure is of approximately constant width, and there is no border. The first axial ring is distinct, as is the first pleura, with a shallow pleural furrow. The general form and the external granulation suggest that this pygidium may belong with *Rhinotarion sentosum*, particularly if the angle between the inner and outer parts of the pleural regions is compared with that of the most posterior segment referred to this species (compare Pl. 8, figs. 7, 12, with Pl. 5, figs. 9, 14).

Otarionid Pygidium, Type D

Plate 8, figures 16, 17, 18, 20.

Description. This pygidium is quite like type A, but is distinguished by a more rapidly tapering axis, the less distinct ring and pleural furrows, and the lack of distinct narrowing of the doublure posteriorly.

Otarionid Transitory Pygidia

Plate 9, figures 15–27.

Description. Size series are known of some of the types of pygidia described above, and in addition there are transitory pygidia such as those shown in Plate 9, figures 15–26, which appear to form a series. The relatively narrow axis bears median spines on the rings, one of which is much stouter and longer than the others. This stout spine may be on the third axial ring (Pl. 9, figs. 15, 16, 19, 20, 23–25), or the first (Pl. 9, figs. 17, 21, 26), or be absent (Pl. 9, figs. 18, 22). It thus appears to progress forward, and its absence suggests that the segment bearing it has been released into the thorax. The pleural regions slope gently outward from the axis, more steeply distally. In larger specimens pleural and interpleural furrows are well-marked (Pl. 9, figs. 17, 21). At the distal change in slope there is a spine on the posterior band of each segment, and a second spine further inward (Pl. 9, fig. 17). These same rows of spines are present on the example lacking median axial spines (Pl. 9, figs. 18, 22). The external surface is granulate between the spines. The doublure is flat and of even width.

A different type of transitory pygidium, without prominent axial spines and with less conspicuous spines on the posterior bands of the pleurae, having well marked pleural and interpleural furrows, and with the ends of the segments extended into short backward pointing spines, is shown in Plate 9, figure 27. Possibly it is an earlier stage of type A, in which the posterolateral tip of the segment is also bluntly pointed in small examples (Pl. 8, figs. 3, 5, 6, 9).

Discussion. These transitory pygidia are considered to belong to *Otarion* because paired spines are also conspicuous in the early development of the cranidium of *Otarion*, and because of the presence of the median axial spine. It has not been possible to make any specific separations between them. The outline, the median axial spine and its progress forward, and the spines on the posterior pleural bands (most conspicuous distally) are points of strong resemblance between these transitory pygidia and those of the Ordovician *Dimeropyge* (Whittington and Evitt, 1954, pl. 3, figs. 13–15, 18–20; pl. 23, figs. 18–25).

Comparisons with other Silurian species

Few species have been described from Silurian rocks, and either the descriptions are old and inadequate or the more recently described specimens are fragmentary. Material in the Museum of Comparative Zoology, limited in quantity and vaguely localized, has enabled us to make the following comments:

Otarion sp., presumably *O. elegantula* Lovén, 1845, MCZ 8595, enrolled exoskeletons from Gotland, Sweden. Preglabellar field is short (sag. and exs.), steep, and the anterior border flat, but not as broad (sag. and exs.) as in *O. instita*. Cephalon appears to range in outline between that of *O. plautum* and *O.* sp. ind., but the flat border is distinctive. Thorax of 12 segments, and there is no median axial thoracic spine.

Otarion sp., from Wenlock Limestone, Dudley, England (Salter, 1853; Whittard, 1938: 102–103), MCZ 8597. The narrow preglabellar field and border are of length (sag.) about one-third that of the glabella, and the eye lobe is relatively small and high. The outline of the glabella resembles that of *O.* sp. ind., but the form of the cephalon is not the same. There are 11 thoracic segments, and a prominent median axial spine on the 6th segment.

Otarion christyi (Hall, 1879), MCZ 8596, cephala and complete exoskeletons from the Waldron Shale, Waldron, Indiana. Cephala range in outline and convexity between that of *O. plautum* and *O.* sp. ind., and like these forms, the eye lobe is relatively large. There are 12 thoracic segments, and no median axial spine. Of the three species discussed here, *O. christyi* is most like *O. plautum* and *O.* sp. ind. from Maine. Pending the redescription of adequate Waldron material, the Maine species are regarded as distinct.

Family SCUTELLUIDAE Richter and Richter, 1955

Scutelluid gen. ind.

Plate 10, figures 4, 6–8, 13.

Description. Two incomplete fragmentary cranidia only have been found, and

TABLE 2. ARRANGEMENT OF GLABELLAR TUBERCLES IN 11 SPECIMENS OF *Fragiscutum rhytium*, LISTED IN ORDER OF DECREASING SIZE, THE ARRANGEMENT EXPRESSED IN THE FORMULA OF TRIPP (1957, 1962).

USNM 154272 (Pl. 11, fig. 2):	ii-1; II-1, 2; III-1, 3; iv-1; IV-0_*, 1, 2, 3; v-0, 1, 2; V-0_*, 1, 2, 3; VI-0.
USNM 154273 (Pl. 12, fig. 8):	II-0_*, 1, 2; III-0_*, 1, 2, 3; iv-0, 1; IV-0^*_*, 1, 2, 3; V-0^*_*, 1, 2, 3; VI-1, 2.
USNM 154275 (Pl. 12, fig. 1; Fig. 7b):	ii-1; II-1, 2; III-1, 3; iv-1, 2; IV-0, 1, 2, 3; v-0, 1, 2; V-0, 1, 2, 3; VI-1, 2.
USNM 154290:	ii-0; II-1, 2; III-1, 3; iv-1; IV-0, 1, 2, 3; v-0, 1; V-0, 1, 2, 3; VI-1, 2.
USNM 154291:	ii-0; II-1, 2; III-1, 3; iv-0^*_*, 1, 2; IV-0, 1, 2, 3; V-0, 1, 2, 3; VI-1.
USNM 154277 (Pl. 12, fig. 4):	ii-0_*; II-1, 2; iii-0_*; III-1, 3; IV-0, 1, 2, 3; v-1, 2; V-0, 1, 2, 3; VI-1, 2.
USNM 154278 (Pl. 12, fig. 6):	II-1, 2; III-1, 3; iv-1; IV-0^*_*, 1, 2, 3; v-1, 2; V-1, 2, 3.
USNM 154279 (Pl. 12, fig. 9):	ii-1; II-1, 2; III-1, 3; iv-0^*_*, 1; IV-1, 2, 3; V-1, 2, 3.
USNM 154292:	ii-0; II-1, 2; III-1, 3; iv-0; IV-1, 2; v-0; V-0, 1, 2, 3; VI-0.
USNM 154280 (Pl. 12, fig. 15; Fig. 7a):	II-1, 2; III-1, 3; iv-1; IV-0_*, 1, 2, 3; v-1, 2; V-1, 2, 3; VI-1.
USNM 154281 (Pl. 12, fig. 18):	II-1, 2; III-1, 3; iv-0; IV-1, 2, 3; V-0^*_*, 1, 2, 3.

both have a large, curved, backwardly-directed median occipital spine, and a small spine projecting back from the posterior margin of the palpebral lobe. The glabella expands forward and is moderately convex, reaching to the anterior margin where it merges with the anterior border. The palpebral lobe is placed far back and in line (exs.) with the outermost part of the glabella, the anterior branches of the suture divergent. Glabellar furrows cannot be distinguished. On the external surface there are terrace lines running concentrically on the anterior slope of the glabella.

Discussion. Species of several genera described by Šnajdr (1960) exhibit both the occipital and palpebral spines, and without information on the glabellar furrows it is not possible to be sure to which genus these specimens may belong. Species of *Kosovopeltis*, *Decoroscutellum*, and *Spiniscutellum* are present in the upper Silurian of Bohemia. Species of *Kosovopeltis* exhibit occipital and palpebral spines in the smaller specimens, but they are absent in the larger ones; species of *Decoroscutellum* commonly have two spines on the palpebral lobe, and species of *Spiniscutellum* have a wider anterior border than in the present specimens.

Family ENCRINURIDAE Angelin, 1854
FRAGISCUTUM n. gen.

Type species. *Fragiscutum rhytium* n. sp.

Diagnosis. Basic tubercle pattern (Table 2) includes: II-(1), 2; III-1, 3; iv-1; IV-(0), 1, (2), 3; V-(0), 1, 2, 3; VI-1; lateral glabellar lobe 1p reduced to a small lateral remnant, so that apodeme 1p lies almost in the same transverse line as the median part of the occipital furrow. True and "false" preglabellar furrows weak, "false" anterior border short (sag. and exs.) and with weak tuberculation. Extremely small fixigenal spine. Rostral plate trapezoidal, widest at hypostomal margin; hypostome with median lobe not extending beyond anterior margin, macula inconspicuous. Vincular furrow extends along anterolateral part of ventral surface of border. Granulation on borders, crests of large tubercles, and between the bases of these tubercles. Ten thoracic segments, none with a median axial spine. Axis of pygidium with less than 20 axial rings, weak median smooth band commencing behind second ring. Pleural region rounded posteriorly, where pleural bands curve inward.

Discussion. Various authors have distinguished groups of species within the genus *Encrinurus* (Reed, 1928; Rosenstein, 1941; Tripp, 1957, 1962), but while there is agreement between these authors that the groups center around certain species, the composition of particular groups has been disputed. Tripp used a combination of cephalic and pygidial, but not thoracic, characters in defining particular groups. We have followed his approach, and elected to give generic status to the new group. The "species-group" most closely allied to *Fragiscutum* is that of *Encrinurus variolaris* (Reed, 1928; Temple, 1956). Temple referred to this group as "advanced" and noted the reduction of the preglabellar furrow. Other characters which this group has in common with *Fragiscutum* are the absence of a median axial spine on the thorax, the rounded pygidial termination and the relative fewness of the axial rings of the pygidium. The *E. variolaris* group is distinguished from *Fragiscutum* by the pattern of tubercles on the glabella (Tripp, 1962, pl. 65, figs. 17–20), particularly in the presence of a distinct row I, the 11 thoracic segments and the absence of a median band on the pygidium.

Fragiscutum rhytium n. sp.

Plate 10, figure 11; Plates 11–13; Figures 7, 8.

Holotype. USNM 154272, incomplete exoskeleton.

Description. Occipital ring widest (sag.) medially. Lateral glabellar lobe 1p short (exs.) and limited to the lateral part of the glabella immediately in front of the outermost part of the occipital ring, so that furrow 1p and occipital furrow are united medially. Furrow 2p commences as a deep pit in the axial furrow and extends inward as a shallow depression, the furrows uniting medially to isolate a 2p glabellar ring. Furrow 3p, situated opposite the anterior margin of the eye lobe, is shallow and short. Curved apodemes, expanded distally, present at outer ends of occipital, 1p and 2p furrows (Pl. 11, fig. 3; Pl. 12, figs. 2, 3). Anterior margin of glabella (Pl. 12, fig. 5) faintly defined laterally by shallow preglabellar furrow which dies out medially. Axial furrow deep, wide and steep-sided, with a U-shaped cross-section on cranidium, continued on free cheek (Pl. 11, figs. 16, 18) as a much shallower depression which dies out toward the anterior margin. Anterior pit (Pl. 11, fig. 13) a deep depression immediately inside the margin of the cranidium. Highest point of cheek bearing the large eye lobe, the midpoint of which is situated in line with lateral glabellar lobe 3p. Posterior border furrow proximally as deep as axial furrow, shallowing distally where it curves forward inside the genal angle and continues as the shallow lateral border furrow (Pl. 11, fig. 1). Posterior border narrow and strongly convex in the inner part, outer part broader and less convex; tiny fixigenal spine in largest specimens (Pl. 10, fig. 11). Anterior border furrow shallow and ill-defined (Pl. 11, figs. 16, 18), running parallel to anterior margin and closer to this margin than to suture line. Anterior branch of suture runs forward and inward across cheek and axial furrow, curves around subparallel to preglabellar furrow, and makes an oblique angle with the short (tr.) rostral suture (Pl. 11, fig. 13). Posterior branch of suture runs outward and backward, curves over the border at the genal angle to reach the posterior margin immediately outside the tiny fixigenal spine, and crosses the doublure (Pl. 12, figs. 2, 3). Connective suture runs downward and slightly outward (Pl. 12, fig. 5), so that rostral plate was evidently trapezoidal in outline and widest at the anterior margin. Doublure of cephalon extends from immediately inside genal angle forward beneath the cheek border, and is widest posterolaterally where it extends inward as far as the border furrow. Anterolaterally the rolled margin is indented by a shallow vincular furrow (Pl. 12, fig. 3), which dies out before reaching a point in line with the axial furrow. Anteriorly, doublure is narrower where it is bounded by the hypostomal suture. On the free cheek (Pl. 11, fig. 19) this suture may be seen forming the inner edge of the doublure, running from the anteroventral margin inward to meet the inner margin of the doublure immediately beneath the anterior pit. From this posterior end of the hypostomal suture a flexure (Pl. 12, fig. 3) runs diagonally across the doublure of the free cheek.

Hypostome of width approximately equal to length (sag.), elongate-oval to diamond shaped in outline. Central body strongly inflated and with a pronounced, narrow anterior median lobe which projects forward below the anterior border furrow. Latter shallow, separated from the sutural margin by a narrow band. Shallow furrow at side of steep slope of median lobe runs backward and slightly outward to die out level with the anterior wing. Lateral border narrow and convex, border furrow deep and inflated middle body overhangs this border; posterior border widest medially, flattened, separated from the middle body by a shallow border furrow, and forming a flat posteriorly-directed projection. Macula (Pl. 11, fig. 21) a faint low swelling at posterolateral margin of the middle body. Anterior wing of hypostome (Pl. 11, figs. 6, 7, 12, 13) greater in height than the central body; outer tip of wing twisted and deflected outward and backward; inner, dorsal edge of wing deflected forward and produced into a slender process with a concave inner side which probably lies against the anterior pit of the cephalon; wing process does not extend as high as above mentioned process and lies outside it. Transverse slit-like pit in outer face of wing corresponds with this process; elongate boss on outer face of wing dorsad of pit. Posterior wing an inwardly and upwardly directed subrectangular projection, situated about halfway between the anterior wing and the rear of the central body; doublure wide between wings, behind posterior wing narrow, but widening beneath posterior border though it does not extend inward as far as the lateral or posterior border, except medially where there is a small cusp which extends forward almost to beneath the border furrow.

External surface, except in furrows, bearing large scattered tubercles. The arrangement of these on the glabella is shown in Figure 7, and in Table 2. Arrangement of tubercles on cheek and border is shown in the photographs; notable is the single row on the cranidium between the preglabellar furrow and the sutural margin, the median and faint additional tubercles present on the occipital ring, and low tubercles on the posterior border. A fine granulation is present on and between the tubercles (Pl. 11, fig. 20), on the ventrally facing part of the border, and on the hypostome. This granulation is not present in the deeper parts of the furrows.

Thorax of 10 segments; axis about one-third total width (tr.) at the fifth segment; axial furrows slightly impressed; axial rings with a faint elongate swelling distally. Inner part of pleura horizontal, outer part flexed steeply down; broad, convex pleural band is four times the width (exs.) of the narrow, flattened anterior flange, the two separated by a sharp change in slope rather than a pleural furrow. Lateral to the fulcrum, anterior flange expands to form a broad flattened facet; the pleural band tapers slightly, and is curved in an anteriorly concave arch, the tip extended as a

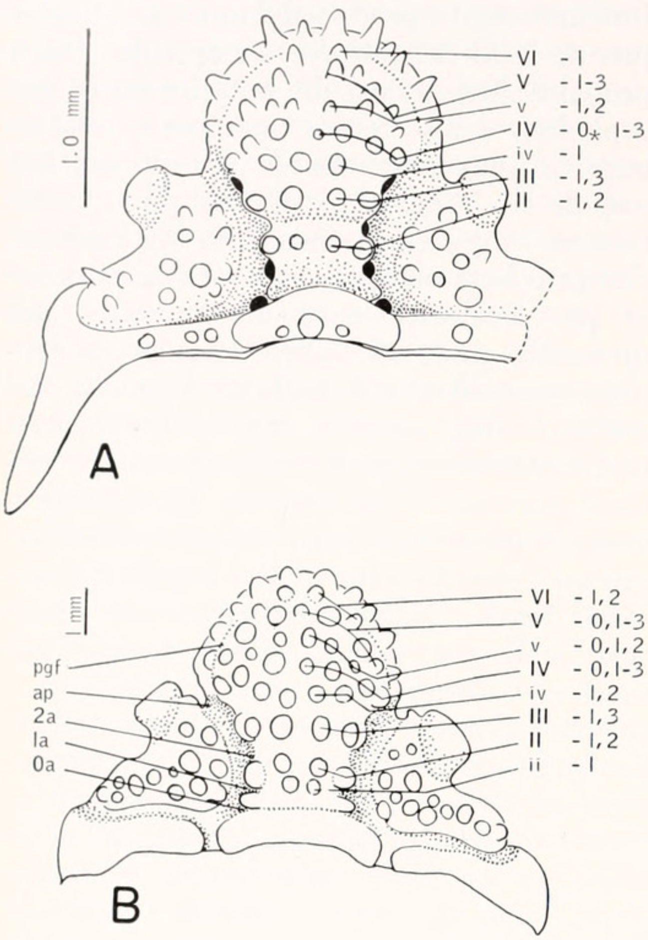

Figure 7. *Fragiscutum rhytium* n. gen., n. sp. Two cranidia showing notation (after Tripp, 1957, 1962) of glabellar tubercles. A) Original of Plate 12, figure 15. B) Original of Plate 12, figure 1. Abbreviatons: 0a, 1a, 2a, positions of occipital, first and second apodemes; ap, anterior pit; pgf, preglabellar furrow.

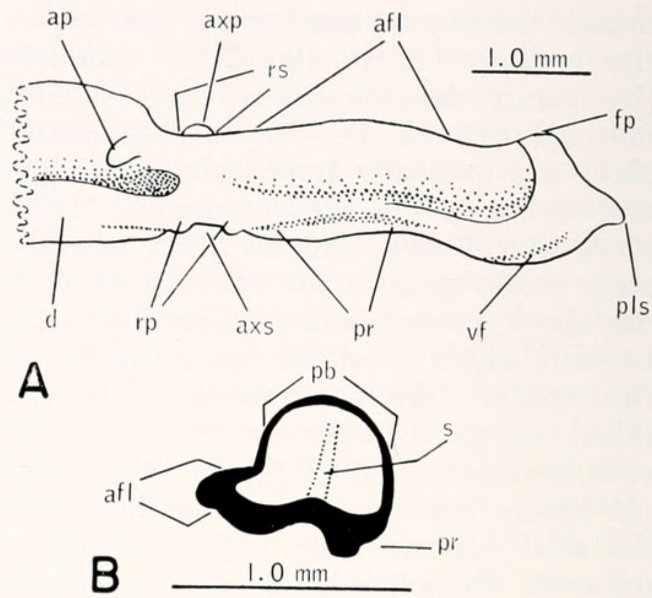

Figure 8. *Fragiscutum rhytium* n. gen., n. sp. A) Ventral view of part of a segment. Compare Plate 12, figures 13, 14, 17, 20. B) Section through inner part of pleura, in exsagittal plane. Solid black is replaced outer portion of exoskeleton. Abbreviations: afl, anterior flange; ap, apodeme; axp, axial articulating process; axs, axial articulating socket; d, doublure of axial ring; fp, projection at anterior margin of facet; pb, pleural band; pls, pleural spine; pr, posterior recess; rp, ring articulating process; rs, ring articulating socket; s, silicified lining of canal, appearing as a hollow cone (compare Pl. 13, fig. 17); vf, vincular furrow.

short, blunt spine. Apodeme (Pl. 11, fig. 3; Pl. 12, figs. 13, 17) is curved inward and downward, and situated a short distance in from the axial furrow. Ventral surface of pleura does not reflect dorsal surface (Fig. 8b); anterior half is convex downward, and there is a deep groove which curves outward just inside the narrow doublure; latter widens and extends across the pleura at the tip. The various structures that facilitate articulation between the segments and limit enrollment are shown in Figure 8a (compare Pl. 11, figs. 1–3; Pl. 12, figs. 13, 14, 17, 20). The downward-projecting ring process fits into a ring socket that surrounds the axial process. The anterior flange on the inner part of the pleura fits beneath the narrow posterior recess so that in dorsal aspect only the pleural bands are visible. Along the posterior edge of the outer part of the doublure is the vincular furrow, which receives the anterior edge of the pleural band of the succeeding segment. A limit to enrollment occurred when the outer parts of the pleural bands moved against each other and the thickened projections of the facets approached each other. Anterior two thoracic segments have outer parts of pleurae slightly shorter (tr.) than succeeding segments; posterior border of cephalon with structures for articulation corresponding to those along posterior margin of segment. Cross section of inner part of pleura of segment (Fig. 8b) shows exceptional thickness of exoskeleton in this region, and the exoskeleton of both the axial ring and outer part of the pleura must have been similarly thickened. As certain specimens show (Pl.

10, fig. 11; Pl. 13, fig. 17), along the transverse midline of the axial ring and pleura, the exoskeleton was partially traversed by canals, preserved in the silicified material as hollow cones extending from the inner toward the outer surface of the exoskeleton. These canals, however, did not open on either the inner or the outer surface of the exoskeleton, so far as the silicified specimens show (Pl. 12, fig. 20; Pl. 13, figs. 11, 14–17). Similar structures have been seen in specimens in which the exoskeleton is preserved as calcium carbonate (Campbell, in press), and when weathered the canals may be seen as perforations, but again they are apparently not visible on unweathered surfaces and it is uncertain whether or not they traversed the outermost layers of the exoskeleton.

Pygidium triangular in outline, width/length/height ratio approximately 5/4/2.5. Axis with flattened profile in cross section (similar to that of axial rings of thorax), larger specimens (Pl. 13, fig. 11) with 18 axial rings, ring furrows deeply incised laterally; behind second ring these furrows weaken so that a smooth median track runs posteriorly along the axis. Four or five large median axial tubercles, the first on ring 3 or 4, the second on ring 6 or 7, the third on ring 10 or 11, the fourth and fifth present close to the tip of the axis. Pleural regions curve steeply down, subdivided by deep furrows into eight pleural bands, the posterior pair curving inward distally and merging behind the tip of the axis; inside this pair there is a ninth pair and a faint median strip visible on larger specimens. The first five furrows extend to the margin, and the tips of the pleural bands project and are slightly expanded (Pl. 13, figs. 14, 15); behind here the pleural furrows die out before reaching the margin. Anterior margin of pygidium like that of anterior margin of segment, with anterior flange and facet, the latter crossed by a shallow (pleural?) furrow (Pl. 12, fig. 23; Pl. 13, fig. 15). Below tips of first five pleurae border of pygidium projects downward; behind here it is flattened on the ventral side; the projecting anterior part is shaped to fit inside the doublure of the cephalon during enrollment. There is a deep notch in the doublure beneath the tip of the axis; this notch received the projecting median lobe of the hypostome during enrollment.

External surface of thorax and pygidium granulated, except in the furrows. The granulation extends over the ventral-facing part of the pygidial border, but not on to the inward facing doublure. The median axial tubercles of the pygidium are present in both small and large specimens, but some specimens show no other tubercles on either axial rings or pleural bands. In some specimens four or five extremely faint tubercles may be recognized amid the granulation on the pleural bands; these are analogous to the very faint tubercles which may sometimes be recognized on the posterior border of the cephalon.

Development. Characteristic of the small exoskeleton is the spininess—the larger tubercles are elongated as blunt spines, and smaller tubercles as thorn-like spines. There is a curving fixigenal spine and the posterior bands of both thorax and pygidium are extended as spines. On the smallest cranidium (Pl. 12, figs. 12, 18; length 1.3 mm) the arrangement of tubercles on the glabella (Table 2) is like that in larger specimens, showing that the main outlines of this pattern are established at an early stage. Tubercles additional to the median are present on the occipital ring, and also on the posterior border and base of the fixigenal spine. The external surface of the free cheek (Pl. 12, fig. 11) also is spinose rather than tuberculate. The small hypostome (Pl. 11, figs. 11, 14, 15, 17) has the forward projection of the middle body less prominently developed, and the posterior border relatively narrower. This border bears a median posterior and three pairs of tiny spines on the margin. With increase in size the main changes in the cephalon are reduction of the spines to tubercles and a rapid relative reduction of the fixigenal spine beyond a length (sag.) of 1.5 mm (Pl. 12, figs. 1, 4, 6, 9, 15, 18).

The smallest transitory pygidium (Pl. 13, figs. 4, 9, 13) includes at least six segments, the axis tapering rapidly backward to the rounded tip, the third ring bearing a long upwardly and backwardly directed median spine and a shorter, more backwardly directed spine behind this, possibly on the fifth segment. The pleural regions curve down steeply and extend in a narrow band behind the tip of the axis; pleural bands are extended as spines, the longest on the first band directed backward, successive spines directed slightly inward. Each pleural band bears a prominent tubercle at about the mid-length, these tubercles forming a line that curves back subparallel to the axial furrow. Doublure narrow, curled under, narrowest medially where the margin is arched upward in posterior view, but lacking the median notch of large specimens (Pl. 13, fig. 14). The lack of a notch corresponds with the lower convexity of the median hypostomal lobe at this stage (Pl. 11, figs. 14, 17).

Larger transitory pygidia (Pl. 13, figs. 1–3, 5–8, 12) contain more segments, but are generally similar in form. Up to three median axial spines may be present, these spines apparently situated on every third ring. The border spines of the posterior pleural bands are relatively shorter but similarly directed. There may be two rows of tubercles on the pleural bands, and there is also a fine granulation on the rings and bands. As a small segment shows (Pl. 12, figs. 21, 22), these segments with a median axial spine and spines on the pleural band are released into the thorax during development. Apparently the median spines, as well as the additional tubercles on axial ring and pleural bands, are reduced and disappear in the larger stages; the same is true in the pygidium, though in rare specimens tubercles on the pleural bands may be distinguished. It seems probable that each of the five tubercles along the median axial band of the pygidium is also a reduced remnant of an axial spine. The median tubercles in the holaspid pygidium are not situated opposite every third ring as they appear to be in the transitory pygidia. This arrangement may result from the crowding of the rings in the axis, which evidently takes place at a developmental stage subsequent to that of these transitory pygidia.

Discussion. A second species of the new genus, from the Henryhouse Formation of Oklahoma, is being described by Campbell (in press). Other American Silurian species (e.g., Raymond, 1916; Best, 1961) are either unlike the present one or known only from such fragmentary material, including internal moulds, that comparisons are not possible.

Several authors (Rosenstein, 1941: 57, pl. 2, fig. 2; Temple, 1954; Tripp, 1962, pl. 67, figs. 2, 9b, 10; Whittard, 1938: 120, pl. 4, fig. 7) have described the hypostome of Silurian species of *Encrinurus* and the way in which it was attached to the remainder of the cephalon. The preservation of the present material shows clearly the form of the anterior wing of the hypostome (Pl. 11, fig. 7) and how it was related to the cranidium (Pl. 11, fig. 13). The anterior and posterior wings are joined in a single structure by a broad portion of the doublure; the anterior wing is the larger and is twisted so that its distal cross section is U-shaped, the open end of the 'U' facing anteriorly. From the inner surface projects the wing process, and there is a pit corresponding to this process on the outer, posterior surface. On the outer surface of the wing, inside this pit, there is an elongate projection from the surface of the wing—this apparently corresponds to the knob described by Temple. Inside this knob, the inner extremity of the wing is extended forward as a long flange, projecting directly anteriorly (Pl. 11, fig. 12). On the inner surface of the cranidium the axial furrow forms a broad prominent ridge, and just inside the sutural margin is the boss reflecting the anterior pit in the external surface. When the hypostome was in position, presumably the tip of the wing process was close to the backward-facing slope of the anterior boss. There does not appear to be a distinct pit in this backward-facing slope that received the tip of the wing process, similar to that seen for example in *Ceraurinella* (Whittington and Evitt, 1954, pl. 12, fig. 30). It is clear that the curved extremity of the wing is so shaped as to fit around close to the slopes of the axial furrow, the flange on the inner tip of the wing extending beside the steep inner slope of this furrow. When the hypostome was in place, with the relatively broad, flat surfaces along the hypostomal suture in contact with the rostral plate and free cheeks, the anterior wing wrapping around the anterior boss, it is difficult to imagine that any relative movement was possible between the hypostome and the cephalon.

In Whittington's (1965: 420–421) recent diagnosis of Encrinuridae, reference is made to anterior and posterior pleural bands of the thorax. In the present species, no pleural furrows and anterior bands are visible in the articulated thorax (Pl. 11, fig. 2; Pl. 13, fig. 17). What appears to be an anterior band in an isolated segment (Pl. 12, fig. 14) is a narrow strip, here termed the articulating flange, which fits beneath the posterior recess (Fig. 8) of the segment in front. The only pleural furrow visible is that on the facet of the pygidium (Pl. 12, fig. 23; Pl. 13, fig. 15). We have thus referred to pleural bands of thorax and pygidium, but the pleural furrow on the first segment of the pygidium makes clear that these bands are posterior bands and that the anterior band has been reduced. The position of the pleural furrow is at the foot of the slope of pleural band down to articulating flange. Tripp's (1962: 466) description of the thorax of *Encrinurus punctatus* suggests that the condition may be the same in that species. Other encrinurid species (Tripp, 1962, pl. 67, fig. 3; 1957, pl. 11, fig. 17; pl. 12, figs. 11, 16, 17) show clearly anterior bands and pleural furrows on both thorax and pygidium; i.e., in some species the anterior band is not so reduced as in *F. rhytium*. The transitory pygidia show an extremely narrow anterior band (or articulating flange) on only the first segment, not succeeding segments.

Family DALMANITIDAE Vogdes, 1890

Genus *DALMANITES* Barrande, 1852

Dalmanites puticulifrons n. sp.

Plates 14, 15; Plate 19, figures 15, 17.

Holotype. USNM 154302, cranidium, anterior border, and part of left free cheek.

Description. Cephalon of width about twice the length (sag.); longitudinal profile of glabella low, highest point at occipital ring, the profile descending gradually forward to the back of the anterior glabella lobe which is gently inflated; occipital ring more markedly convex, particularly transversely. Occipital furrow broad and well rounded medially, but narrowing rapidly into the deep, slot-like apodeme. Glabellar furrow 1p transverse, shallow adjacent to the axial furrow, deepening inward; furrow 2p directed inward and slightly forward, extremely shallow adjacent to the axial furrow but deepening at the apodeme; furrow 3p directed inward and backward, widest at the axial furrow, narrowing and deepening inward but not extended from the ventral surface as an apodeme. Occipital and 1p apodemes (Pl. 19, fig. 15) triangular in cross section proximally, distally becoming blade-like, and twisted so that the flat, blade-like portion is directed diagonally; apodeme 2p slimmer, blade-like, and not twisted. Median glabellar lobe narrower (tr.) than lateral lobes, anterior lobe diamond-shaped with a broad, shallow median pit in the posterior portion. Axial furrow shallow, curving inward at the anterior edge of the occipital ring, then running forward and slightly outward, rising and gradually shallowing to the mid-length of lateral lobe 3p, in front of here dropping into a broad, well-rounded furrow which curves around the extremity of the anterior lobe; preglabellar furrow shallow. Eye lobe situated in the inner corner of the cheek, the anterior margin abutting against the axial furrow, the posterior margin a short distance in front of the posterior border furrow. Palpebral lobe rises moderately steeply from the axial furrow, palpebral furrow much deeper in its anterior than its posterior half, the palpebral rim standing high above the crest of the lobe, flattened on the crest, with a narrow marginal band; the rim asymmetrical, the anterior part being the larger. Eye surface steeply sloping, facets large and arranged in diagonal lines (Pl. 19, fig. 15). Distinct furrow around the anterolateral margin of the eye lobe, on the outside of which is a low ridge, most prominent anteriorly; outside this ridge the cheek slopes gently outward and downward to the broad lateral border furrow. Lateral border with a flattened, outward-sloping upper surface, which is continuous with that of the anterior border; latter widest medially, forming a blunt projection (Pl. 14, fig. 1). Posterior border furrow sabre-like in outline with its anterior slope steeper than the posterior; posterior and lateral furrows do not merge at the genal angle, but the posterior border terminates slightly above and inside the shallow lateral furrow. Posterior border widening (exs.) rapidly outside the fulcrum, and running out into the base of the genal spine. Posterior branch of suture curves around the posterolateral margin of the eye and then runs straight out and slightly backward across the cheek to the margin; the points ϵ-ϵ and ω-ω are thus in the same transverse line. Anterior branch of suture runs forward in a sweeping curve a short distance outside the axial furrow and over the upper surface of the anterior border close to the inner edge, the two branches meeting in a smooth curve. Points β-β in line with the maximum width of the glabella across the anterior lobe.

Doublure of cephalon beneath lateral border of same width as border, wider anteriorly (Pl. 14, fig. 4). Beneath posterior border doublure extends from base of genal spine to fulcrum but not beneath inner part of border. At the inner margin the lateral doublure is bent sharply dorsad; this flexure dies out anteriorly and is absent along the hypostomal suture. Hypostome unknown.

External surface finely granulated (Pl. 19, fig. 17) except in axial, glabellar, and palpebral furrows and at base of median glabellar pit.

Three thoracic segments known, axial rings evenly arched transversely, longitudinally flattened; articulating furrow with slopes equally steep; axial furrow impressed only at the rear of each segment. Pleura having anterior band much higher than posterior band, with a vertical or slightly undercut posterior slope down to the pleural furrow; anterior slope of anterior band gentle, passing out beyond the fulcrum into the broad facet; faint articulating flange along anterior edge of pleura, dying away distally. Pleural furrow running in a slightly sigmoid course from inner anterior corner to the posterior border of the tip, dying out at a point directly above the inner edge of the doublure; furrow shallow and rounded near the axis, broader and with a flat base near the fulcrum, narrowing distally; posterior band of pleura with a gentle anterior slope throughout. Doublure extends along the posterior margin of segment halfway in to the fulcrum, but is not so extended along the anterior side.

Axis of pygidium with 12 complete rings and terminal portion, behind eighth ring axis tapers more gently and the ring furrows become shallower; in this differentiated posterior part of the axis the tip is rounded and prominent, the ring furrows are present only on the outer part, shallow and outwardly and slightly backwardly directed. Articulating halfring three-fifths the length of the remainder of the first segment; excavation in posterior margin of first axial ring of similar length (sag.), much smaller excavations in the posterior margin of the succeeding two rings. In longitudinal profile all except most posterior rings with a much steeper posterior than anterior slope. The outer quarter of the ring furrow is deep, and on the inner surface there is an apodeme on the inner part of this deepened region, the apodemes present on the articulating furrow and the next eight ring furrows (Pl. 14, fig. 14). Proximally the apodemes are triangular in section, the acute edge on the outer side, tapering to a blade-like tip directed downward and slightly forward. Pleural regions curving downward from the axial furrow to the narrow, flattened, and steeply sloping border on which pleurae are not marked. The first seven interpleural furrows sharply incised, the eighth indicated only by a smooth band in the granulation; pleural furrows narrow (exs.) adjacent to the axial furrow then widening rapidly and with a broad, flat floor extending out to the inner edge of the border; on all segments anterior slope steep, posterior slope much more gentle. Anterior band well rounded on all segments, each standing higher than the posterior band immediately in front of it, these posterior bands narrow and flattened. At posterior tip, border extended into a median spine which is flattened on the under surface (Pl. 14, figs. 15, 16). Doublure of about the same width as the border, the inner edge bent up vertically (Pl. 14, fig. 14).

External surface of thorax and pygidium (Pl. 14, fig. 12) bearing granules, which are present on the axial rings, in the articulating furrow and adjacent edge of the articulating halfring of the thorax, and are coarsest along the posterior margin of the ring; the rings of the pygidium are similar, but the ring furrow is smooth. The coarsest granulation on the pleural regions is on the crests of the anterior and posterior bands, with a finer granulation in the pleural furrows, on the facets, pygidial border and spine. An extremely narrow smooth strip on the anterior margin of the anterior pleural band. Doublure granulated along the outer portion, the granulation diminishing and disappearing inward.

Development. One protaspis (Pl. 15, figs. 5, 6, 10, 14, 17), lacking the free cheeks and hypostome, has the cephalic portion of length (sag.) 0.66 mm. The form is extremely like that of the protaspis from the Devonian described by Whittington (1956a: 105–106, pl. 24, figs. 1–5; text-fig. 1). Glabella shows a similar division into an extremely short (sag.) occipital ring with a prominent median tubercle, three glabellar rings of approximately equal length, and a wider anterior lobe which has the lateral portions faintly set off from the median region. On the preglabellar area there are two pairs of spines; the palpebral lobe is situated on the anterolateral margin of the shield, its position and the course of the sutures as in the Devonian example. The narrow posterior border is directed straight outward and turns vertically downward on the flank, where the specimen is broken. The protopygidium is also broken, but shows the convex axis, and apparently two segments, having backwardly directed spines on the outer part of the pleurae. The external surface of the fixed cheek is pitted (as in the Ordovician *Dalmanitina* protaspis of Temple, 1952, pl. 10, fig. 6), and there are paired granules on the cheek, including one halfway across the cheek, situated immediately in front of the posterior border furrow. Six conspicuous granules on the median occipital tubercle.

Cranidia of length 1.0 mm to 1.3 mm are meraspides (Pl. 15, figs. 7, 11, 15). The frontal lobe of the glabella is expanded and bent down more steeply with increasing size—the width becoming three-quarters the length (sag.) of the cranidium rather than less than half as in the protaspis. The palpebral lobe moves relatively backward as well as inward as shown by the position of the line δ-δ. In the protaspis this line runs just behind the anterior margin of the third glabellar ring, one-third the length (sag.) of the glabella from the anterior margin. In progressively larger specimens the line δ-δ moves to about the mid-length (Pl. 15, fig. 7) of the glabella, thence to a position about two-thirds the length (Pl. 15, fig. 1), where it crosses the second glabellar ring. Not only the frontal glabellar lobe but lobes 2p and 3p become relatively wider so that the axial furrows are strongly divergent forward (Pl. 15, figs. 1, 4), and glabellar furrow 3p ceases to be transverse, and becomes inclined to the transverse line. On the inner surface of the small cranidia there are rounded projections adjacent to the outer ends of the occipital furrow and glabellar furrows 1–3p, but strongly projecting apodemes are developed only in large cranidia.

In the original of Plate 15, figure 1 (5.2 mm in length [sag.]), granulation is present, the median occipital tubercle is almost completely reduced, and the pit is present in the frontal glabellar lobe.

The original of Plate 15, figures 9, 12, 13, 16, a transitory pygidium, shows the completely formed articulating halfring of the second segment beneath the first ring. The spines on the ends of the pleurae appear to be the combined tips of the anterior and posterior bands, which bands are more equal in width (exs.) than in larger stages. Scattered short spines are present on the axial rings and pleural bands, as well as granulation; short apodemes are present. A specimen of the same size (Pl. 15, fig. 8) does not have the articulating halfring of the second segment developed, and may be a small holaspid, but in dorsal aspect is very similar to the other example.

Discussion. Numerous American Silurian species of *Dalmanites* have been described (Delo, 1940: 37–52) but only ten of them are known from both cephalon and pygidium. The form of cephalon and pygidium, the depressed profile, the shape of the genal spines, shape of the posterior border and its relation to the lateral border furrow, and the relatively uniform nature of the granulation, ally this species with *D. limulurus* (Green, 1832) from the Rochester Shale. However, *D. puticulifrons* has a relatively larger eye lobe, no nodes at the extremities of the thoracic rings, deeper pleural furrows terminating at the rear edge of each thoracic segment, more numerous segments in the pygidium, a shorter terminal spine, and coarser granulation on the external surface.

A new species of *Dalmanites* being described by Campbell (in press), from the Henryhouse Formation of Oklahoma, has many features in common with *D. puticulifrons* and *D. limulurus*, the cephalon being very like that of *D. puticulifrons.* It may be distinguished by having a pygidium of different shape, with fewer rings and pleurae, and the granulation which varies more markedly in density and size on different parts of the cephalon. The British Silurian species *D. myops* (see Dean, 1960), from the Wenlock Series, belongs to the same species group and examination of specimens in the Museum of Comparative Zoology suggests that it is distinct from *D. puticulifrons* in having, among other characters, a shorter palpebral lobe, the facial suture lying in the preglabellar furrow, larger tubercles on the surface of the glabella, and differently shaped pleural furrows on both the thorax and pygidium.

According to Richter, Richter and Struve (*in* Moore, 1959: O 471–2), *Odontochile* differs from *Dalmanites* in that the anterior branches of the suture line are farther from the frontal glabellar lobe, in the number of spines on the margin of the hypostome and in the greater number of segments in the pygidium. The course of the anterior branches of the suture in *D. puticulifrons* is like that in *Odontochile*, but the hypostome is unknown. Delo (1940: 55) used number of segments in the pygidium as the main criterion in placing various American Devonian species in *Odontochile.* The value of this single character is open to question. Much more needs to be known of Silurian and Devonian dalmanitids before generic criteria can be clarified, and particularly the use of *Dalmanites* and *Odontochile*.

Family ODONTOPLEURIDAE Burmeister, 1843

Genus *LEONASPIS* R. and E. Richter, 1917

Leonaspis cf. *williamsi* Whittington, 1956

Plate 16, figures 1–14, 16–18, 20–22; Plate 17, figures 1–12, 16; Figure 9.

Description. The material is excellently preserved, and while it shows that there is individual variation (compare Pl. 16, figs. 1, 2, with Pl. 16, figs. 5, 6), it is not adequate to show the range of this variation. The exoskeletal parts are like, but apparently not identical with, those of the Lower Devonian species *Leonaspis tuberculatus* from New York and those of the species *L. williamsi* from Oklahoma (Whittington, 1956b: 507–510, pl. 57, pl. 58, figs. 1–4, 6, 7). The uncertainty regarding identity is partly because the New York and Oklahoma specimens are less perfectly preserved, and partly because the material from any one of the localities is limited. In these circumstances we have chosen to compare the Maine form to *williamsi*, as the better-known of previously described species. Some of the differences between the Maine specimens and those from the other localities are:

1) median occipital spine is longer than that of *williamsi*, not as long as that of *tuberculatus*;

2) eye lobe higher than that of *williamsi*; eye lobe of available specimens of *tuberculatus* is broken;

3) number of thoracic segments is unknown; *tuberculatus* has 9, *williamsi* has 8;

4) in such details as the number of tubercles on the anterior border of the cranidium, number of spines on the outer edge of the border of the free cheek and spacing of these spines, curvature and length of the posterior pleural spines of the thorax, and border spines of the pygidium, it is exactly like *williamsi*. The Maine specimens are unlike *tuberculatus* in the shorter genal spines and length of pleural thoracic spines. In *williamsi* (Whittington, 1956b, pl. 58, figs. 1, 2) there are five tubercles along the posterior border of the cephalon, several tubercles at the base of the posterior pleural spine, as well as two prominent tubercles on the pleural ridge of the pygidium. In the Maine specimens there are only two tubercles on the posterior border of the cranidium, large tubercles are lacking at the base of the posterior pleural spines, and only one tubercle is present on the pleural ridge of the pygidium.

These differences are in details, and it is difficult to assess their taxonomic significance.

The specimens from New York, Oklahoma and Maine (Pl. 17, figs. 5, 8–12) exhibit the anterior pleural spines, which are fused at the base and branch distally. The present material shows (Pl. 17, figs. 1, 2, 4) that on the first, and probably second, thoracic segments the anterolateral portion is beveled and facetted, so that on these segments there is only a short, rapidly tapering posterior pleural spine. The anterior pleural spine is not developed. More posterior segments of the thorax show the narrow doublure which lies immediately inside the base of the anterior pleural spine (Pl. 17, fig. 5). The anterior corner of this doublure projects forward as an articulating process; the posterior end shows a notch to receive the articulating process of the following segment, this notch lying beneath the base of the posterior pleural spine.

The two small cranidia (Pl. 16, figs. 7, 9, 10, 12–14) are the only known developmental stages of a species of this genus. In the smallest the palpebral lobe is far back, in line with the anterior edge of the occipital furrow, and the glabella has the specific outline. It also shows typical features of a small odontopleurid in that the rounded tubercles of the larger stages are represented by thorn-like spines, and the median occipital spine is much longer than in larger stages. The major spines (Fig. 9) are typical of the cranidium of

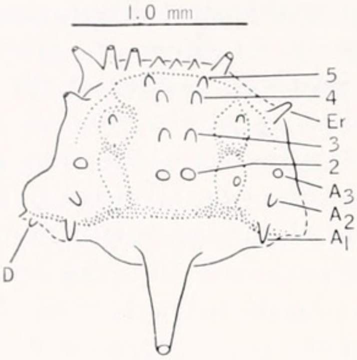

Figure 9. *Leonaspis* cf. *williamsi* Whittington, 1956. Major paired spines of a small cranidium, original of Plate 16, figures 12–14, lettered following Whittington, 1956c, text-fig. 1.

an early odontopleurid developmental stage. These include pairs 2 to 5 on the glabella, A_{1-3} on the fixed cheek, and the spine on the eye ridge (compare Whittington, 1956c, text-figs. 1, 6, 9, 22, for corresponding spines in developmental stages of other genera).

XANIONURUS n. gen.

Type species. *Xanionurus boucoti* n. sp.

Diagnosis. Differs from *Radiaspis* in that:

1) lateral glabellar lobes are not fused, but separated by deep 1p furrow;

2) there is a distinct, shallow occipital furrow and the occipital ring is relatively much shorter (sag.);

3) second axial ring of pygidium low, faintly divided by median longitudinal furrow and bearing pair of spines;

4) border of pygidium with 14 (not 16) spines, the posterior band of the anterior segment running into the base of the 5th (not the 6th) border spine;

5) besides the main paired spines on the glabella there are many additional spines and granules; similarly, on the cheek there are spines on the upper surface of the border, and many scattered spines and granules as on the pygidium. In *Radiaspis* the exoskeleton is smooth between the main spines.

Geological range. Upper Wenlock to Ludlow.

Discussion. Bruton (personal communication) points out that *Radiaspis* is like *Diacanthaspis* in lacking major border spines on the pygidium and in the radiating arrangement of the border spines. We agree with this, and add that the early developmental stages of the cranidium of the two genera appear to be similar, and the thoracic segments are alike. As in *Acidaspis* and *Dudleyaspis* there is a stout posterior sutural ridge in the new genus and a steeply inclined row of spines on the lower edge of the cheek border. However, *Xanionurus* lacks the characteristic inflation of the posterior band of the thoracic segments at the fulcrum, seen in these two genera, and the pygidia are unlike. It is possible that there is a line of descent from *Diacanthaspis* to *Xanionurus* to *Radiaspis*, independent of the possible line leading from *Primaspis* to *Acidaspis* and *Dudleyaspis* and of the line from *Primaspis* to *Leonaspis* and *Odontopleura*. If these views are correct they would suggest some modification of the phylogeny suggested by Whittington (1956c, text-fig. 3).

Xanionurus boucoti n. sp.

Plate 16, figures 15, 19; Plate 17, figures 13–15, 17–26; Plate 18, figures 1–9, 11–15; Figure 10.

Holotype. USNM 154449, incomplete cephalon.

Description. Glabella moderately convex transversely and longitudinally, widest at occipital ring, in front of lateral lobes 1p tapering forward to rounded anterior margin. Occipital ring about three times as wide as long (sag.), bearing a pair of curved posterodorsally directed spines which arise from the rear edge; much shorter median tubercle directed almost vertically, the tip exhibiting four small pits arranged at the corners of a square (Pl. 18, fig. 6). Occipital lobe poorly defined on inner surface, occipital furrow shallow, well rounded medially, distally passing into deep pit-like apodeme. Median glabellar lobe standing higher than lateral lobes, parallel-sided;

frontal lobe of similar width. Lateral lobes 1p and 2p oval in outline, independently convex, 1p one and one-half times longer than 2p, lateral furrow 1p diagonally directed and deepening adaxially into an apodemal pit; lateral furrow 2p similar in form. Third lateral lobes not developed. Axial furrow moderately deep. Cheek quarter-circle in outline, outward-sloping, eye lobe situated at highest point and in line with anterior part of lateral glabellar lobe 1p; prominent eye ridge curves inward and forward to shallow axial furrow opposite extremity of frontal glabellar lobe. Cheek inside eye inflated, shallow furrow runs along inner edge of eye ridge, posterior sutural ridge runs outward from eye lobe to curve back and merge with swollen base of librigenal spine. Anterior branch of suture runs along upper surface of eye ridge and over narrow anterior border in line with axial furrow; posterior branch of suture runs along sutural ridge to cross posterior border between spine B and base of librigenal spine. Posterior border widens rapidly distally, curving forward slightly to base of genal spine. Gently convex anterolateral border wider than anterior border, edge curled under and directed upward and inward as the narrow doublure. Outer margin of border bears 10 closely-spaced, downwardly and outwardly directed spines which diminish progressively in length anteriorly; marked gap between posterior spine and base of curved genal spine; shallow antennal notch immediately inside anterior spine. Rostral plate not known but rostral suture runs transversely along outer edge of anterior border; connective suture runs inward and upward across doublure (Pl. 18, fig. 2), hence rostral plate is short (sag. and exs.) and wide, trapezoidal in outline. Hypostome not known. Inner surface of cephalon shows short, blunt apodemes formed by inner end of deepest part of occipital furrow and lateral glabellar furrows 1p and 2p. Anterior pit not developed on outer surface, nor as apodeme on inner surface. External surface of cephalon bearing spines of various sizes, between which is a fine granulation. Three main pairs of spines (2–4; see Fig. 10) are visible on the frontomedian glabellar lobe, with pair 2a situated close together immediately in front of the occipital furrow. Spines A_{1-3} visible on inner part of cheek; prominent spine B on posterior border distally; row of 6 spines on crest of anterolateral border, the posterior situated above the base of the third-from-the-last downwardly directed border spine, and the anterior above the outer part of the rostral plate. Granulation is absent only from the deepest parts of furrows.

Number of thoracic segments unknown. Convex axial ring with pair of prominent sharp spines, articulating halfring long (sag.), equal in length to the ring; articulating furrow with anterior slope undercutting articulating halfring; apodemes blunt and short. Inner part of pleura extends out horizontally, divided by shallow pleural furrow into anterior band which is one-third the width (exs.) of the posterior band and lies below the convex posterior band. Two prominent spines on the posterior band (Pl. 17, figs. 15, 22, 25), the inner situated at about half the width (tr.), the outer situated at the fulcrum and directed upward and outward. Anterior pleural spine generally stubby, but becoming progressively longer (tr.) toward the rear, and directed outward and downward throughout; posterior pleural spine much more prominent and longer, directed downward and backward—the medial segments having this spine directed more steeply downward and more directly outward than in the more posterior segments, in which the posterior pleural spine is quite strongly curved (compare Pl. 17, figs. 15, 17, 18, 22, with Pl. 17, figs. 23–25). The first one or two segments (Pl. 17, figs. 13, 14) differ in that the pleura curves outward to end in a short, blunt, posterior pleural spine, the anterior pleural spine being merely a small projection; the segment is beveled to fit under the cephalon and as a consequence

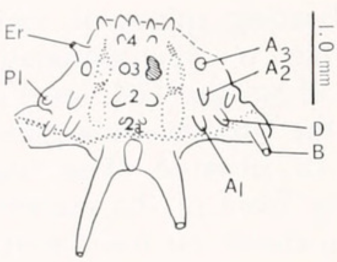

Figure 10. *Xanionurus boucoti* n. gen., n. sp. Major paired spines of small cranidium, original of Plate 18, figures 8, 9, 11, 12. Spines lettered as in Figure 9.

the outer spine on the posterior pleural band is not developed. External surface bearing granules of various sizes on axial rings, single row of granules along rear edge of articulating halfring; flattened strip behind posterior pleural band smooth; smooth areas on crest of posterior band between the spines and between the inner spine and the axial furrow; upper surfaces of both pleural spines smooth, apart from scattered granules on distal half of posterior spine; a band of elongate, sharp granules runs along the leading and trailing edges of both pleural spines, those on the posterior spine being larger; tubercles present along anterior band. The doublure is present only at the extremity of the segment, and there is a deep embayment for articulation between the doublure and upper surface on both anterior and posterior edges.

Pygidium (Pl. 17, figs. 19–21, 26), exclusive of spines, of width 3½ to 4 times length (sag.). Axis consisting of two segments; axial furrow shallow beside first ring but very deep beside second ring except at extreme tip, where it shallows. Articulating halfring like those of the segments; first axial ring prominent with one pair of spines. Second ring depressed below level of anterior ring and having a faint median longitudinal depression, the lateral parts bearing one pair of small, thorn-like spines. Pleural region subdivided by triangular depression of pleural furrow into a transverse anterior band and a diagonally directed pleural ridge; border convex and bearing seven pairs of border spines, none of which is more prominent than any other, directed more steeply downward anteriorly than posteriorly, the arrangement radial. Fifth border spine from anterior is opposite pleural ridge. Border curls under on ventral side to form a narrow doublure in which there is a distinct median embayment. Upper surface of border bearing spines as prominent as those on axial rings, situated at base of fourth to seventh border spines, that at the base of the fifth larger than the others. Elsewhere external surface granulate, except in deepest depressions, one or two larger spines on anterior band of first segment.

Development. Two small cranidia (Pl. 18, figs. 8, 9, 11–15; Fig. 10) show the relatively large paired spines typical of odontopleurid developmental stages. In outline, glabellar lobation, position of the palpebral lobe, as well as spine pattern, these cranidia are like those of the Ordovician *Diacanthaspis* (Whittington, 1956c, pl. 4, figs. 12–14). The long, curved occipital spines, general shape and spine pattern are also like those of the Ordovician *Apianurus* (Whittington, 1956c, pl. 19, figs. 14–16; text-fig. 22f), but the small spines are thick and straight in *Xanionurus* (not slim and curved as in *Apianurus*) and the posterior part of the fixed cheek is wider (tr.).

Discussion. Prantl and Vaněk (in Horný, Prantl, and Vaněk, 1958: 265–266, pl. 3, fig. 5) described an incomplete pygidium from the Upper Wenlock of Czechoslovakia which is like that of the present species in the number of pairs of border spines, relation of the fifth spine to the pleural ridge, and appearance of the second axial ring. They refer this species, *formosa*, with question to *Radiaspis*. Bruton (personal communication) has identified an entire specimen of this species (Pl. 18, fig. 10), flattened in shale. It is quite like the present one, differing in that the genal spine is relatively much longer (reaching back to the pygidium), the posterior pleural thoracic spines are longer, particularly on the anterior segments where they are directed slightly forward, the pygidial border spines are slimmer, the external surface appears to bear fewer and more scattered spines and to be granulated. We regard *formosa* as congeneric with our species and differing from the type species of *Radiaspis* in the characters given above in the generic diagnosis.

Transitory pygidium, undetermined
Plate 10, figures 1–3, 5, 9, 10.

Discussion. The two examples placed here may represent the same species, and are characterized by the axis tapering gently backward, the ring furrows deep distally, the pleural regions horizontal and subdivided by interpleural furrows, the pleural bands bearing prominent border spines which are outwardly and backwardly directed, more strongly backwardly directed posteriorly. The tip is bent down (Pl. 10, fig. 3), and the pleural border spines alternate in size, this latter feature particularly shown by the larger example (Pl. 10, figs. 1, 5). External surface of rings and pleural bands finely granulate, no larger tubercles or spines.

The shape of this pygidium, including the flat pleural regions and bent-down tip, is reminiscent of that of the cheirurid *Ceraurinella* (Whittington and Evitt, 1954, pl. 12, figs. 1–3, 9–11; pl. 28, figs. 1–14). The alternation in size of the pleural border spines distinguishes the present examples, as does the lack of a pleural furrow. No other cheirurid material has been identified among the present collection; the lack of paired axial or pleural spines appears to exclude this pygidium from odontopleurids, and the lack of a pleural furrow from the other groups.

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