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UNIVERSITY OF ALBERTA

SYSTEMATICS OF SILURIAN TRILOBITES FROM NORTHERN LAURENTIA

BY

JONATHAN MARK ADRAIN ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

DEPARTMENT OF GEOLOGY

Edmonton, Alberta

FALL 1993

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UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled SYSTEMATICS OF SILURIAN TRILOBITES FROM NORTHERN LAURENTIA submitted by JONATHAN MARK ADRAIN in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

Brian D.E. Chatterton

Douglas A. Craig

Richard C. Fox

Richard C. Fox

Brian Jones

Rolf Ludvigsen

Mark Wilson

Mark V.H. Wilson

ABSTRACT

Diverse Silurian trilobite faunas occur in northwestern Canada and the central Canadian arctic. Elements of these faunas are treated herein, together with a small fauna from southwestern Alaska. Five new genera or subgenera are proposed and 21 new species described.

Odontopleura and *Sinespinaspis* n. subgen. are monophyletic odontopleurid sister-groups. *Odontopleura* (*Odontopleura*) *arctica* n. sp. is described from Llandovery (since revised to Ludlow) rocks of Cornwallis Island, central Canadian arctic. A method of unordered parsimony analysis is advocated.

The genus *Otarion* is revised to include a restricted Wenlock-Middle Devonian group of aulacopleurid trilobites. New species from northwestern Canada include *O. huddyi* and *O. beukeboomi*. *Otarion coppinsensis* is a new species from New South Wales, Australia. The genera *Otarion*, *Cyphaspis*, *Namuropyge*, and possibly *Dixiphopyge*, constitute the Tribe Otarionini.

Borealarges is a new trochurine genus with exceptional diversity in the Wenlock and Ludlow of northern Canada. New species from the Cape Phillips Formation of the central Canadian arctic include *B. reedi* (type species), *B. morrisoni*, *B. tuckerae*, and *B.* s.l. *calei*.

Goodsiraspis packardi n. gen. n. sp. is a derived rorringtoniid that occurs in Ludlow (Ludfordian) rocks of the lower member of the Barlow Inlet Formation at Goodsir Creek, Cornwallis Island.

Llandovery representatives of the Subfamily Aulacopleurinae in northwestern Canada include *Aulacopleura andersoni* n. sp., *A*.? *ranfordi* n. sp., and *Songkania smithi* n. sp.

Llandovery trilobites from southwestern Alaska include *Paracybantyx occidentalis* n. sp., *Ligiscus smithi* n. sp., *Calymene* s.l. *hoholitnensis* n. sp., unnamed species of *Scotoharpes*, *Scharyia*, possibly *Protocerauroides*, and an undetermined warburgelline.

New genera of encrinurids from the Douro Formation of the central Canadian arctic include the encrinurine *Aegrotocatellus* (type species *A*. *jaggeri* n. sp.) and the coronocephaline *Perirehaedulus* (type species *Kailia*? *capra* Thomas). *Perirehaedulus richardsi* n. gen. n. sp. is a second species of the latter.

Harpidella and *Maurotarion* are distinct otarionine clades. New species from northwestern Canada include *H*. *kurrii*, *H*. *tikkaneni*, *H*. *greggi*, and *M*. *messieri*.

ACKNOWLEDGEMENT

I thank Brian Chatterton for extremely generous technical support throughout.

Greg Edgecombe contributed informed reviews of all of the papers collated in this thesis. We have discussed trilobites almost daily for over two years, often boring friends and acquaintances to distraction.

Mike Caldwell and Allan Lindoe assisted during the arctic field seasons of 1991 and 1992, respectively.

J.J. Packard made the material described in Chapter 5 available for study, and Bob Blodgett both arranged study of the material described in Chapter 7 and contributed a short section on locality to it.

Formal journal reviews have been provided by A.T. Thomas and C. Patterson (Chapter 2), Thomas and R.M. Owens (Chapter 3), Thomas and D.J. Holloway (Chapter 4), Owens and R.A. Fortey (Chapter 5), R. Ludvigsen and G.D. Edgecombe (Chapter 6), and E.N.K. Clarkson and L. Ramsköld (Chapter 7).

My participation in fieldwork in the Mackenzie Mountains in 1990 was funded by a grant from the Boreal Institute for Northern Studies (now the Canadian Circumpolar Institute). My arctic field program in 1991 and 1992 was funded by further grants from the CCI, grants under the research agreements program of the Federal Department of

Energy, Mines, and Resources, and the Natural Sciences and Engineering Research Council, and logistic support from the EMR's Polar Continental Shelf Project. Further support has been received via a grant-in-aid from the American Assocation of Petroleum Geologists (1990) and a Wray Trust grant-in-aid from the Paleontological Society.

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CHAPTER I

INTRODUCTION

SILURIAN TRILOBITES are found in three major geographic areas of northern Laurentia (i.e. that portion of the paleocontinent lying to the north of the Transcontinental Arch; see Figure I-1): North Greenland, Arctic Canada, and an area encompassing the southwest part of the Northwest Territories and the east-central Yukon Territory. Other minor occurrences include, for example, the Llandovery Tegart Formation of southeastern British Columbia (Norford, 1962, 1969), and the Llandovery fauna from southwest Alaska described in Chapter VII.

The chapters contained within deal mainly with elements of Silurian faunas from the northern Canadian areas. The overall diversity and sheer numbers of faunas from these regions is immense. Most remain to be described, and many have only been discovered during the course of work for this thesis. Hence, the concerns of this study are almost purely systematic. Descriptive study of the trilobites is necessary before they can provide data for works on more general themes. Diversity of the faunas is so extreme (over 250 new species, for example, have thus far been identified in new Arctic collections) that the present work will ultimately represent only a fraction of the overall effort. Nevertheless, both the taxa described herein and others, either previously described or upon which work is in progress, have begun to suggest several interesting implications for biostratigraphy, paleobiogeography, and biotic events. These are explored briefly in Chapter X, while Chapters II through IX are taken up with detailed systematic study of particular trilobite clades and faunas.

RESPONSIBILITY

Of the studies grouped in this thesis, all except Chapter IV have or will ultimately appear in print as jointly authored works, with the writer the senior author. This situation is not unusual, and the arrangement is in accordance with Faculty regulations. Nevertheless, it is as well to be clear about the contribution of others to what is, after all, the writer's thesis. R. B. Blodgett facilitated study of the trilobites described in Chapter VII, wrote the short section on locality information, and provided the locality map. G. D. Edgecombe contributed to the preparation and interpretation of the trilobites described in Chapter VIII; part of this chapter reflects truly joint scientific content. Finally, six of the chapters have or will appear in joint authorship with B. D. E. Chatterton, who supervised this thesis. Chatterton's contribution includes initiating some of the projects through the years, including collecting and preparing samples and undertaking intitial scientific assessment of their implications, considerable photographic assistance (particularly Chapters II and V), technical and financial support of all of this work, and subsequent discussion and editorial input. Responsibility for the technical presentation of this work (most of the photography, all of the plate and line drawing preparation, except as noted), and particularly for the scientific content (except as noted) rests almost wholly with the writer.

SURVEY OF DIVERSITY AND PREVIOUS WORK

The number of works predating the modern era that describe or refer to northern Laurentian Silurian trilobites is low (e.g. Salter, 1852; Holtedahl, 1914; Poulsen, 1934), due probably to the remoteness of the area. It was not until the 1950s that geological exploration of Arctic Canada was begun in earnest by the Geological Survey of Canada, not until the 1960s that much work in North Greenland was done, and not until the 1970s that diverse Silurian trilobite faunas were discovered in the Northwest Territories. The first significant modern Silurian trilobite study from any of the major northern Laurentian regions was by Lane (1972; but see Raasch et al., 1961; Whittington, 1961; Bolton, 1965). Perry and Chatterton (1977) were first to describe diverse Canadian arctic collections, while Perry and Chatterton (1979) began description of the rich Mackenzie Mountains faunas. There follows a brief sketch of occurrences of Silurian trilobites, and prior study, in each region.

North Greenland.--Lane (1972, 1979, 1984, 1988; Lane and Owens, 1982; Lane and Siveter, 1992) has described faunas primarily from platform carbonates of the Llandovery and early Wenlock of North Greenland. Most of these faunas have few direct correlates across northern Laurentia, but this seems certainly to be related to biofacies, and due simply to the rarity of trilobite-bearing platform carbonates in the region. Where similar rocks are exposed (e.g. Ludvigsen and Tripp, 1990; Chapter VII), comparisons with contemporaneous faunas from North Greenland are often possible. Geological mapping and exploration is still underway in North Greenland, but thus far trilobites have not been described from the platform-margin and basinal occurrences that are typical of northern and arctic Canada.

Northwest Territories and Yukon Territory.--Raasch et al. (1961) first reported Silurian trilobites from this region. Diverse silicified faunas were first dealt with by Perry (1974; Perry and Chatterton, 1979), but the most numerous and best preserved of the Mackenzie Mountains faunas were not discovered until the late 1970s (Lenz, 1977; Chatterton and Perry, 1983). Description of these faunas is ongoing, and includes Chapters III, VI, and IX.

Arctic Canada.--Trilobites are known (but not completely described) from diverse Wenlock and Ludlow occurrences (Perry and Chatterton, 1977; Thomas and Narbonne, 1979; Chapters IV and VIII), a single Llandovery occurrence (undescribed), and sporadic, low-diversity Přídolí occurrences (Whittington, 1961) in the central Canadian Arctic. They occur in several rock units with several general types of preservation, discussed below.

GEOLOGIC SETTING

As trilobites are described herein from several localities almost spanning the breadth of northern Laurentia, it is not surprising that their field occurrences include several very distinct rock types. A correlation chart for the Silurian rock units of all areas dealt with is given in Figure I-2. There follows a discussion of the major rock units from which trilobites are described herein.

Douro Formation.--In the central Canadian Arctic (Figure I-3), abundant trilobites, brachiopods, sponges, tabulate corals, ostracods, echinoderms, and bryozoans occur in rubbly weathering argillaceous and dolomitic limestones of the Douro Formation. The rather unique sedimentological character of these rocks has been dealt with by Jones et al. (1979), who concluded that they were a result of incipient hardground formation through subtidal lithification soon after deposition. Fossils are found largely in situ, with brachiopods and sponges often found in life position and articulated corpses of trilobites at least relatively common. While the Douro Formation is likely diachronous (Jones and Dixon, 1977), it represents a comparatively narrow stratigraphic interval (upper Ludlow to possibly lowest Prídolí).

Trilobites are moderately diverse in the Douro Formation. The species *Frammia arctica* is large, often found articulated, and easily detected in the field. It is often the only trilobite listed in more general studies (usually as *Encrinurus*; Morrow and Kerr, 1977; Jones and Dixon, 1977). Field investigation by the writer, however, at both Prince Alfred Bay on northern Devon Island, and Garnier Bay on northern Somerset Island, has shown that much greater diversity exists. As an example, Garnier Bay section C of Jones and Dixon (1977) contains the following fauna: *Frammia arctica* (Salter), *Frammia* cf. *hyperborea* (Thomas), *Frammia* n. sp., *Aegrotocatellus* n. sp. B of Chapter VIII herein, *Perirehaedulus richardsi* Adrain and Edgecombe, *Borealarges* n. sp. 1, *Borealarges* n. sp. 2, *Paracybantyx*? n. sp., *Cyphaspis* sp., *Waigatchella* n. sp., *Prantlia* n. sp., *Parayoungia* sp., cheirurine sp.

Cape Phillips Formation.--The Cape Phillips Formation conformably overlies the Caradoc Irene Bay Formation throughout its substantial distribution in the central Arctic (the Cape Phillips Basin of Melchin, 1989). Its stratigraphic range is Ashgill to Prídolí or Lochkovian, and its typical lithology is calcareous, graptolitic, shale, interbedded with argillaceous limestones or dolomites, and with resedimented carbonates becoming more common higher in the column. The formation is divided into three members.

Relatively little detailed sedimentological analysis has been carried out, but Melchin (1989) interpreted the lowermost Member A to represent a distal carbonate ramp deposit, ranging from the base of the formation to the Telychian. Member B is composed mainly of chert and nodular limestone, with minor shale partings, and is developed over a limited portion of the area of outcrop. Member C ranges from the Telychian to the top of the formation, and is characterized by shales interrupted only by minor carbonate gravity flow deposits. A distinct basin/platform topography was established at the onset of deposition of this member, and the unit is a lateral equivalent of the Read Bay Group over most of the study area. Exceptions occur in the Prídolí, during which the Devon Island Formation was deposited in the Prince Alfred Bay region, and the Somerset Island Formation on Somerset Island.

A few trilobites occur in situ in the Cape Phillips Formation (asaphids in the basal Ashgill carbonate beds, an undescribed <u>Aulacopleura</u> near the base of Member C on Bathurst Island, and the trilobite described in Chapter II), but the majority occur as disarticulated elements of carbonate turbidites and debris flows in a zone near to the facies change to platform carbonates along the basin margin. Fossils in these debris flows are often silicified, and the lower Wenlock to lower Ludlow part of the formation has yielded the most complete and most diverse record of trilobites known from this interval from anywhere in the world (see Chapter IV; also Perry and Chatterton, 1977).

Sections in the Upper Silurian part of the Cape Phillips Formation have been measured and collected on the south shore of Baillie-Hamilton Island and near Abbott River, on northwestern Cornwallis Island (Figures I-4 and I-5).

Whittaker Formation and Delorme Group.--Trilobites collected from these units in the vicinity of Avalanche Lake in the central Mackenzie Mountains (Figure I-6) are described in Chapters III, VI, and IX. The measured sections are near to the facies change between carbonates of the Mackenzie Platform and shales (Road River Formation) of the Selwyn Basin, and indeed the lithologies typically interfinger through the section (Figure I-2). The Whittaker Formation and the lower part of the Delorme group in the sections are represented mainly by black, fine-grained, argillaceous limestones, often with an abundant and well-silicified benthic shelly fauna, and interpreted as the distal part of the Mackenzie Platform. The units thin and become dolomitic farther onto the platform to the northwest. Morrow (1984) applied formational nomenclature to the Delorme Group in the Root Basin, but Over and Chatterton (1987) could not apply the scheme in the Selwyn Basin.

Almost all of the Silurian trilobites from this area are found in situ (the only exception are a few very rare gravity flows in the Wenlock). Trilobites occur in lowermost Llandovery through highest Wenlock rocks. Faunas that may potentially be Ludlow are known, but not confidently dated.

FIELDWORK AND MATERIAL STUDIED

Mackenzie Mountains.--Extensive collections from Silurian sections in the central Mackenzie Mountains (Figure I-6) have been made by B.D.E. Chatterton and various colleagues and students. Locality data cited herein follows Chatterton and Perry (1983), Over and Chatterton, (1987), and Chatterton et al. (1990). The writer participated in fieldwork in the area during 1990, and has been given primary responsibility for description of trilobites of the Family Aulacopleuridae (Chapters III, VI, and IX). Almost all of the material studied is from collections built up over the years, but during the course of this thesis approximately 100 kg of limestone was dissolved by the writer, from most of the significant horizons.

Arctic Canada.--B.D.E. Chatterton made several collections from this region in the late 1970s. These collections served as important guides for further fieldwork, but arctic material described in Chapters IV and VIII was derived entirely from collections made by the writer during 1991 and 1992 (see Figures I-3, I-4 and I-5). Some 2500 kg of rock were recovered during these field seasons. Approximately 2100 kg of limestone from the Cape Phillips Formation has been dissolved during the course of this thesis. The trilobites described in Chapter II were collected by R. Thorsteinsson, and number only a few specimens. Those of Chapter V were collected by J.J. Packard, and are represented by about 20 specimens.

Alaska.--Trilobites described in Chapter VII were collected by T.N. Smith, and forwarded for study by R.B. Blodgett. The collection is small, consisting initially of about 20 small (ca. 1-10 cm in diameter) pieces of bioclastic limestone. These were broken up into many smaller pieces during preparation, and the final number of identifiable specimens was approximately 200, most of which were of a single species.

Other.--In the course of dealing with the taxonomy of various clades (which generally required worldwide revision), it was sometimes possible to include new illustrations of established taxa (Chapters III, IX). Almost all of this material had either been collected by or purchased by B.D.E. Chatterton over the years. The exceptions are type material of _Harpidella_ _spinafrons_ (Williams), which was borrowed from the United States National Museum of Natural History, and of _Harpidella megalops_, which was borrowed from the National Museum of Ireland.

METHODS

Chapters II and V are based on specimens preserved as natural internal and external molds in shales. This material was studied mainly through preparation and light photography of latex casts.

Chapters VII and VIII are based mainly on calcareous specimens preserved in limestones. These specimens were isolated using a rock saw, then mechanically prepared with vibrotools and needles prior to light photography.

Chapters III, IV, VI, and IX are based on silicified specimens. Trilobites were isolated by dissolving limestones in 10-15 percent hydrochloric acid in standard fashion, followed by sieving and microscope-assisted picking of undigested residues. Material from the Mackenzie Mountains (Chapters III, VI, IX) often includes small growth stages, for which scanning electron micrographs have been prepared. Larger specimens, including all of the more coarsely preserved material from the Cape Phillips Formation (Chapter IV and part of Chapter VIII) were mounted on toothpicks and photographed under normal light.

All light photography involved blackening specimens with graphite paint and covering with a very light coating of ammonium chloride sublimate prior to photography.

FORMAT

This thesis is arranged in paper format, and Chapters II through IX include versions of works that have either been published, are in press, or have been submitted for publication. The papers are presented in chronological order of completion. No attempt has been made to "update" the contents of the chapters relative to one another; they are presented as much as possible in published form. Thus, assuming the chronologic order, internal cross-references are consistent. Papers are presented in the editorial style of the Journal of Paleontology. Locality and repository data are given or referred to in each individual chapter.

FIGURE _I-1_--Map showing major Paleozoic basins and uplifts in northern Laurentia (from Petersen et al., 1980), with Silurian trilobite localities. _1_, Offley Island Formation; _2_, Cape Phillips Formation, Douro Formation, Barlow Inlet Formation (see Figure I-3 for more detailed geographic position of Arctic localities); _3_, Road River Formation; _4_, Delorme Group; _5_, Gazelle Formation; _6_, Scotch Grove Formation; _7_, Racine Dolomite; _8_, Eramosa Formation; _9_, Henryhouse Formation; _10_, St. Clair Limestone; _11_, Brownsport Formation; _12_, Waldron Shale; _13_, Lilley Dolomite, Springfield Dolomite, Cedarville Dolomite; _14_, Rochester Shale; _15_, McKenzie Limestone; _16_, Hardwood Mountain Formation; _17_, Edmunds Formation; _18_, Wabash Formation; _19_, Ellis Bay Formation, Becsie Formation, Gun River Formation, Jupiter Formation, Chicotte Formation; _20_, Beaverfoot Formation, Tegart Formation; _21_, Attawapiskat Formation; _22_, White Head Formation.

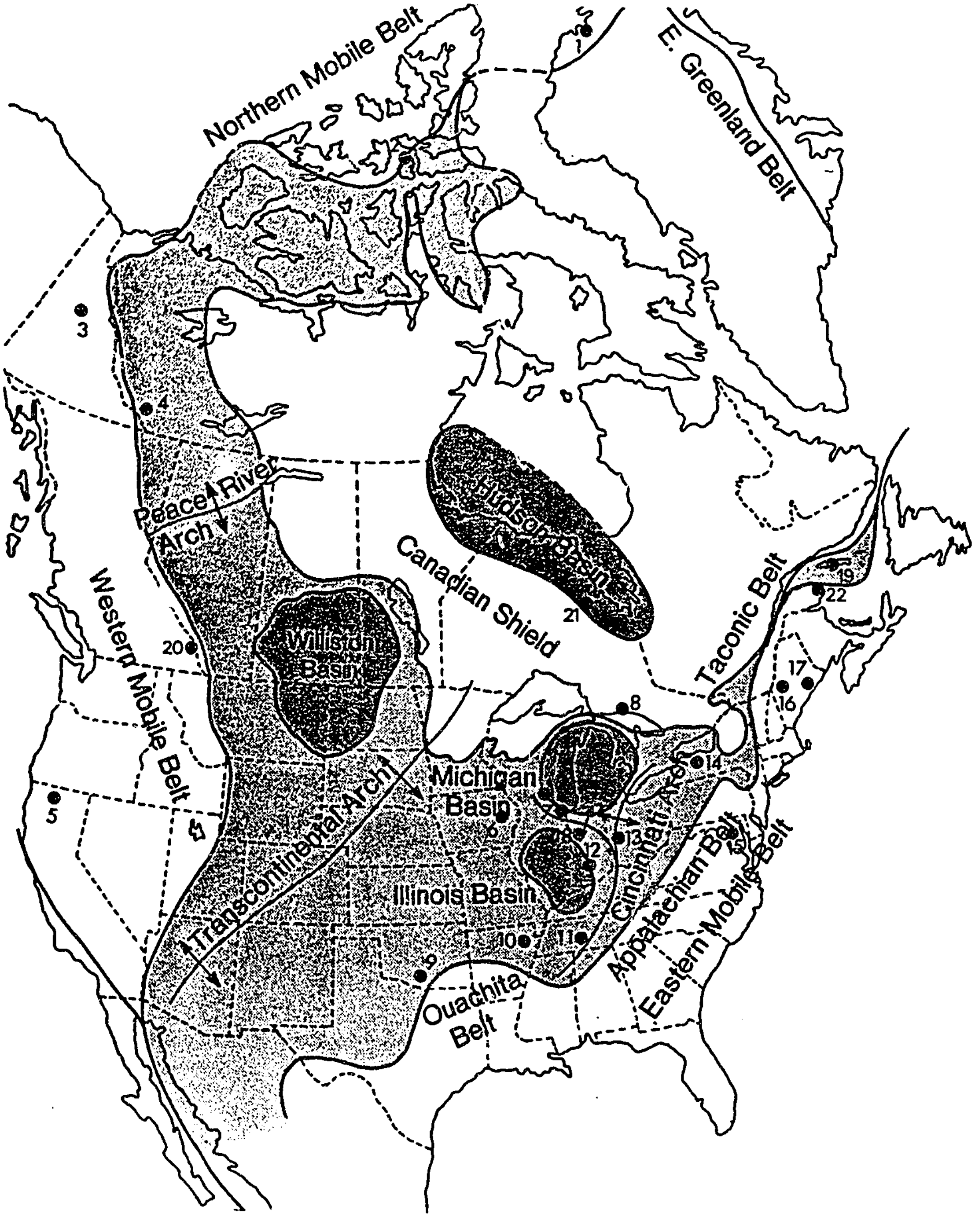

Northern Mobile Belt
E. Greenland Belt
1
3
4
Peace River Arch
Western Mobile Belt
20
5
Williston Basin
Hudson Basin
Canadian Shield
21
Taconic Belt
19
22
17
16
8
14
Michigan Basin
Transcontinental Arch
6
7
18
12
13
Cincinnati Arch
15
Illinois Basin
10
11
9
Appalachian Belt
Eastern Mobile Belt
Ouachita Belt

FIGURE I-2--Correlation of the major Silurian formations of the northen Laurentian region, from which material is described herein.

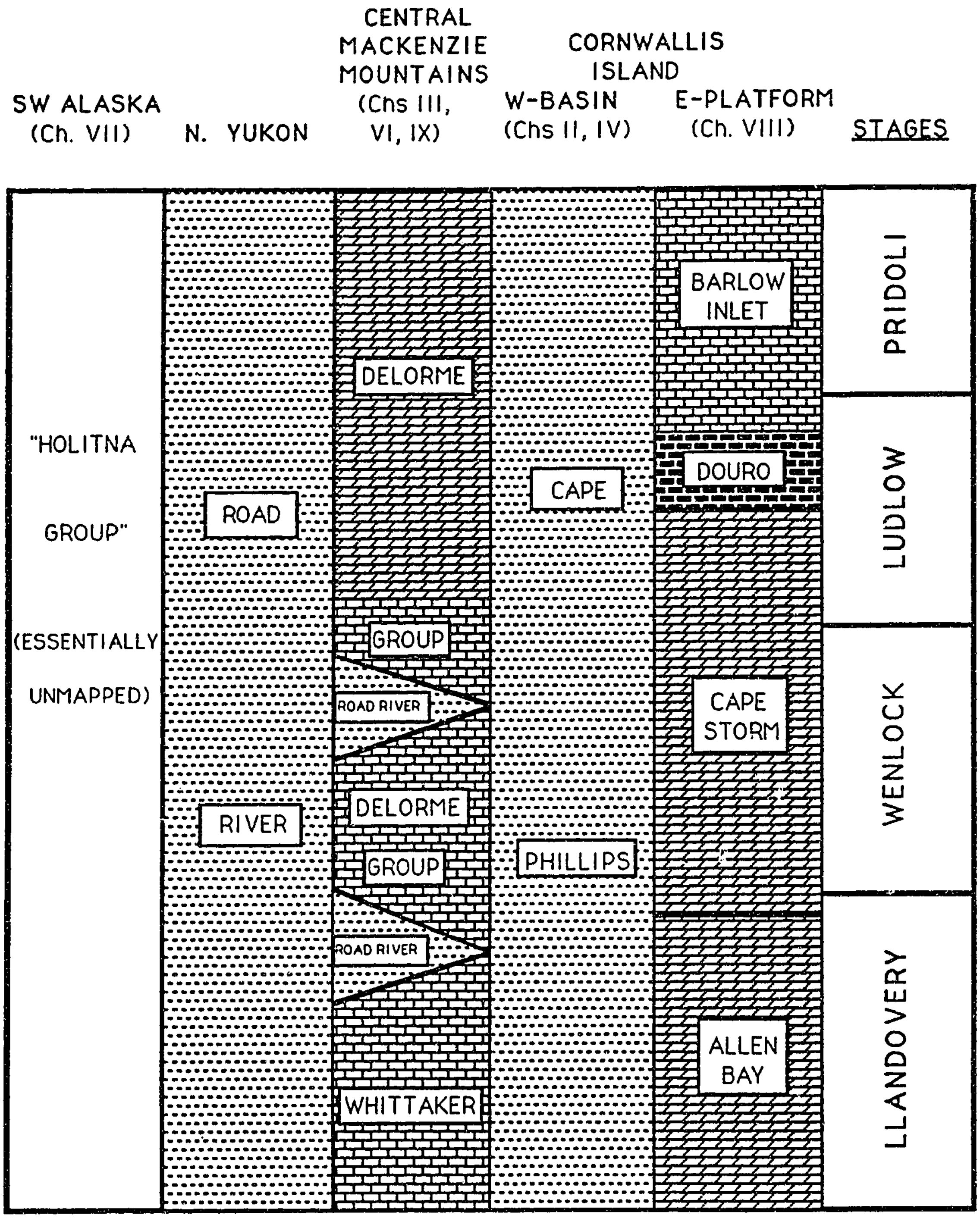

SW ALASKA (Ch. VII)
N. YUKON
CENTRAL MACKENZIE MOUNTAINS (Chs III, VI, IX)
CORNWALLIS ISLAND
W-BASIN (Chs II, IV)
E-PLATFORM (Ch. VIII)
STAGES
"HOLITNA GROUP" (ESSENTIALLY UNMAPPED)
ROAD
RIVER
DELORME
GROUP
ROAD RIVER
DELORME
GROUP
ROAD RIVER
WHITTAKER
CAPE
PHILLIPS
BARLOW INLET
DOURO
CAPE STORM
ALLEN BAY
PRIDOLI
LUDLOW
WENLOCK
LLANDOVERY

FIGURE I-3--Map showing geographic position of localities in the central Canadian arctic from which material described in Chapters IV, V, and VII was collected.

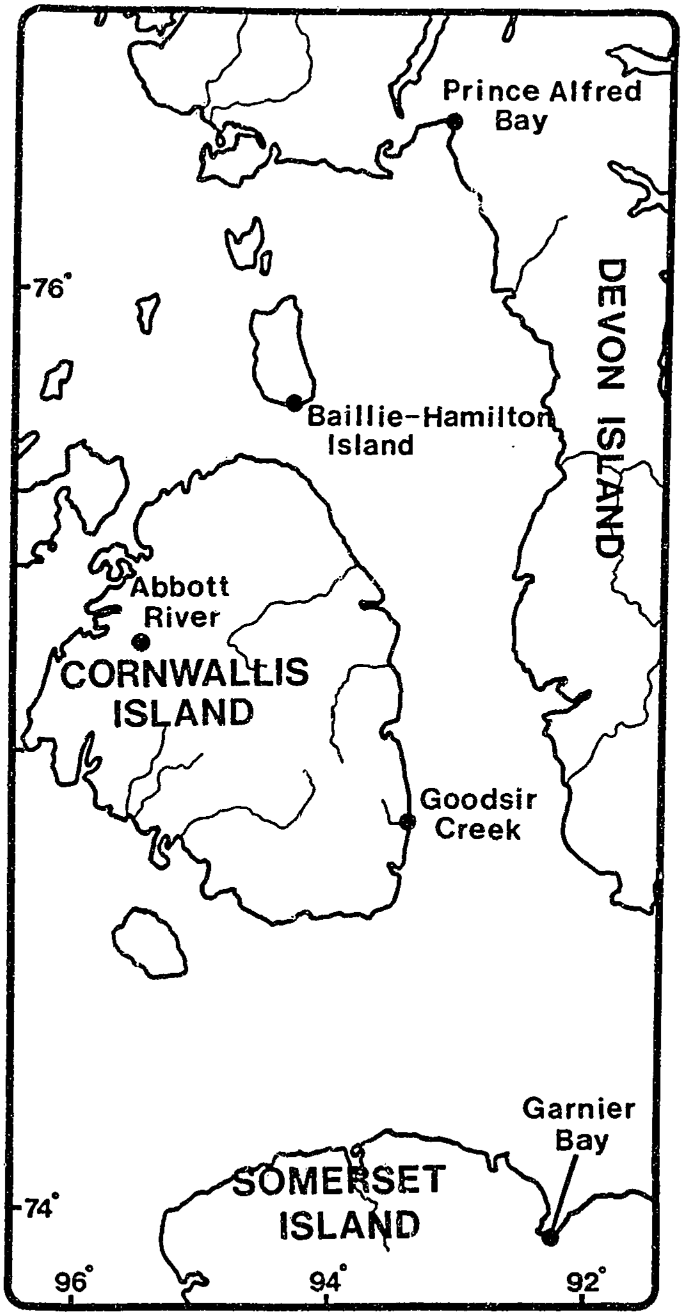

Prince Alfred Bay
76°
Baillie-Hamilton Island
DEVON ISLAND
Abbott River
CORNWALLIS ISLAND
Goodsir Creek
Garnier Bay
SOMERSET ISLAND
74°
96°
94°
92°

FIGURE I-4--Stratigraphic columns and graptolite zonation of Sheinwoodian sections in the Cape Phillips Formation on southern Baillie-Hamilton Island. Sections BHJ 1 and BHL 1 are alternate lines of section no more than 50 m along strike from BH 1 and the lithologic information is not repeated. Horizons indicated by number have yielded silicified faunas.

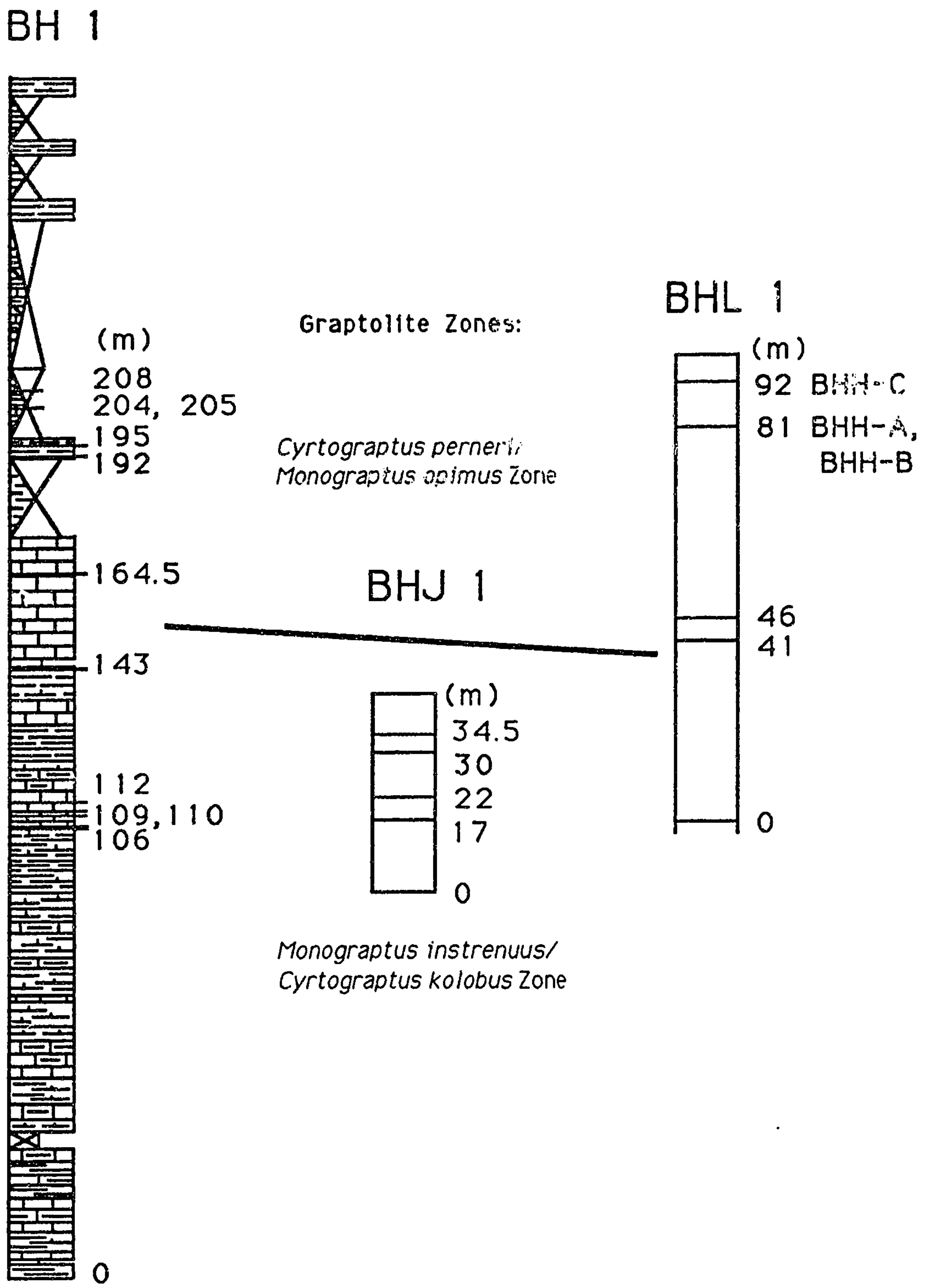

BH 1
(m)
208
204, 205
195
192
164.5
143
112
109,110
106
0
Graptolite Zones:
Cyrtograptus perneri/
Monograptus opimus Zone
BHJ 1
(m)
34.5
30
22
17
0
Monograptus instrenuus/
Cyrtograptus kolobus Zone
BHL 1
(m)
92 BHH-C
81 BHH-A,
BHH-B
46
41
0

FIGURE I-5--Homerian and Gorstian sections of the Cape Phillips Formation on southern Baillie-Hamilton Island (BH 2) and near Abbott River, northwestern Cornwallis Island (ABR 1 and 3). Format as in Figure I-4.

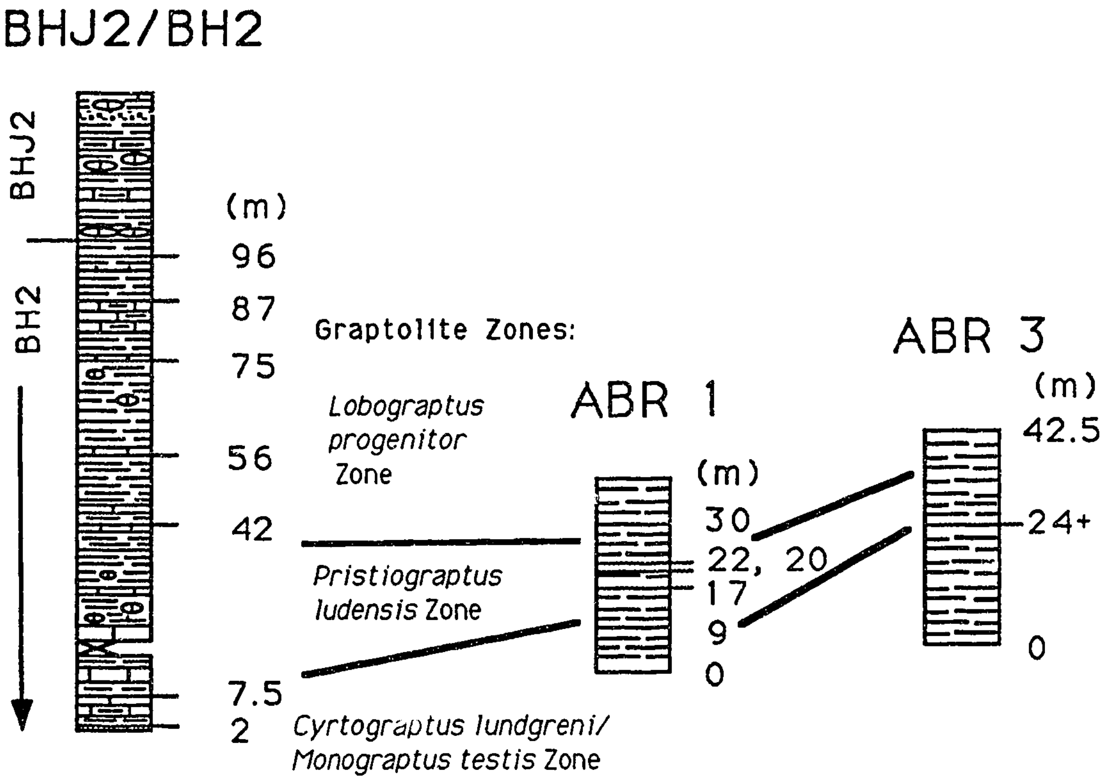
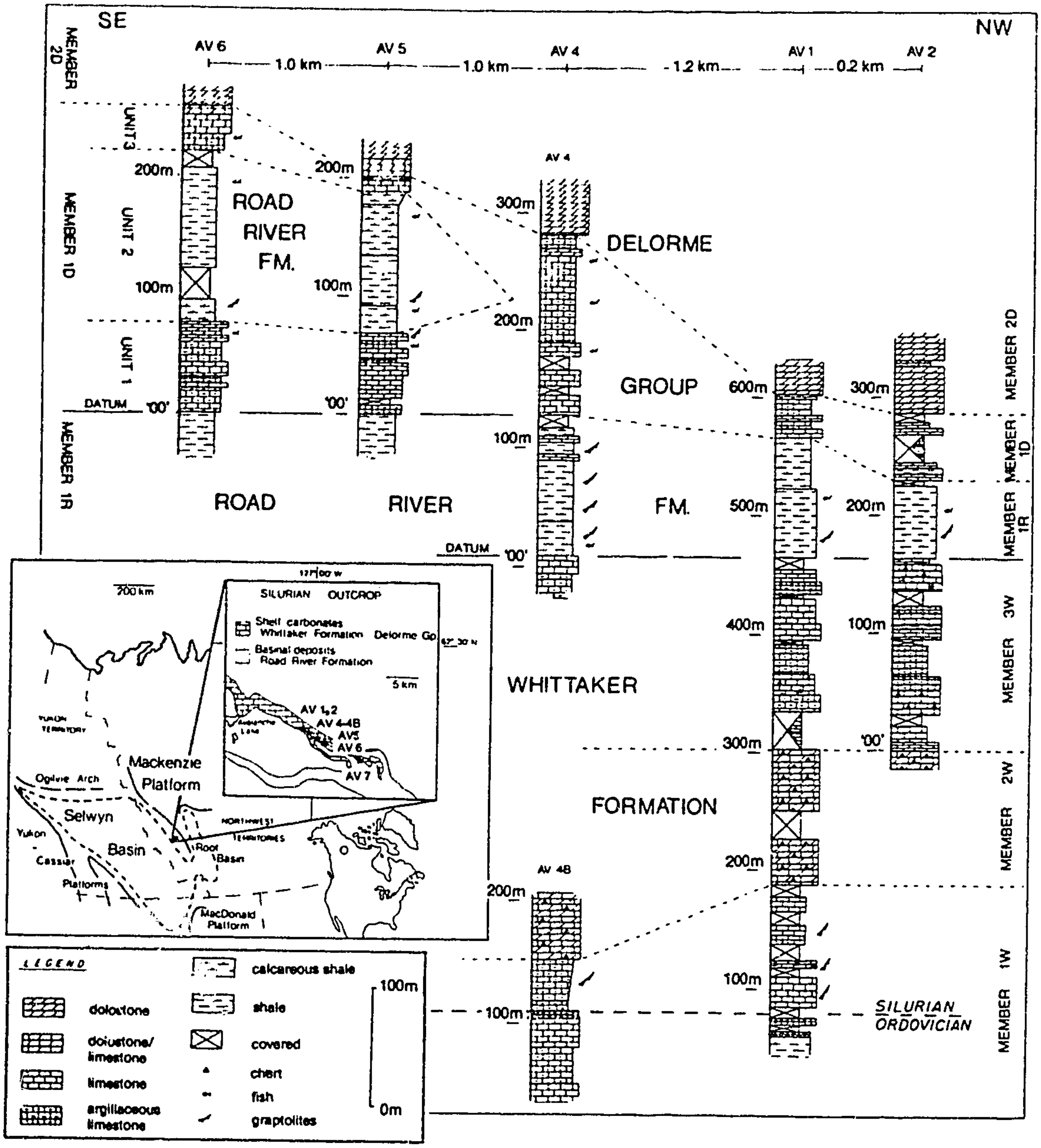

BHJ2/BH2
BHJ2
BH2
(m)
96
87
75
56
42
7.5
2
Graptolite Zones:
Lobograptus progenitor Zone
Pristiograptus ludensis Zone
Cyrtograptus lundgreni/ Monograptus testis Zone
ABR 1
(m)
30
22, 20
17
9
0
ABR 3
(m)
42.5
24+
0

FIGURE _I-6_--Locality map and stratigraphic columns for sections in the central Mackenzie Mountains, Northwest Territories, Canada, from which material described in Chapters III, VI, and IX was collected.


SE
NW
AV 6
1.0 km
AV 5
1.0 km
AV 4
1.2 km
AV 1
0.2 km
AV 2
MEMBER 2D
UNIT 3
MEMBER 1D
UNIT 2
UNIT 1
MEMBER 1R
DATUM
'00'
200m
100m
300m
600m
500m
400m
ROAD RIVER FM.
DELORME
GROUP
FM.
ROAD
RIVER
WHITTAKER
FORMATION
AV 4B
SILURIAN
ORDOVICIAN
MEMBER 1D
MEMBER 1R
MEMBER 3W
MEMBER 2W
MEMBER 1W
200 km
127°00' W
67°30' N
SILURIAN OUTCROP
Shelf carbonates Whittaker Formation Delorme Gp
Basinal deposits Road River Formation
5 km
AV 1, 2
AV 4-4B
AV5
AV 6
AV 7
Yukon Territory
Mackenzie Platform
Ogilvie Arch
Selwyn Basin
Yukon
Cassiar
Platforms
Root Basin
Northwest Territories
MacDonald Platform
LEGEND
dolostone
dolostone/limestone
limestone
argillaceous limestone
calcareous shale
shale
covered
chert
fish
graptolites
100m
0m

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CHAPTER II[1]

ODONTOPLEURA (TRILOBITA, SILURIAN), AND A METHOD OF CONSTRAINED CONGRUENCY ANALYSIS

INTRODUCTION

THIS WORK describes a new odontopleurine trilobite, Odontopleura (Odontopleura) arctica n. sp., from the Canadian Arctic Archipelago. The six available specimens were collected in 1953 by R. Thorsteinsson from the Marshall Peninsula (96 degrees, 05 minutes west, 75 degrees, 26 minutes north) on the northwest coast of Cornwallis Island (see Figure II-1). The specimens occur on a single slab of argillaceous limestone, most often as external or internal moulds, but in one case with the exoskeleton preserved. The sample is a glacial erratic. According to Thorsteinsson's field notes (T.E. Bolton, personal commun.), the lithology and matrix of the sample, together with its position in the glacial drift, suggests that it was derived from the Cape Phillips Formation and that its horizon was above the highest undoubted Ordovician graptolites and below the lowest undoubted Silurian graptolites. Very poorly preserved monograptid fragments do, however, occur on the sample, indicating a Silurian age. Hence the block can reasonably be assigned to the lowermost Llandovery. The

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specimens are housed in the type collections of the Geological Survey of Canada (abbreviated GSC).

Previous work on Silurian trilobites from the Canadian Arctic includes Whittington (1961), Bolton (1965), Perry and Chatterton (1977), Chatterton and Perry (1979), and Thomas and Narbonne (1979). This paper represents the first Arctic record of the genus Odontopleura Emmrich. This taxon also occurs in the Canadian Northwest Territories (Chatterton and Perry, 1983), the Baltic region (Bruton, 1967; Schrank, 1969), Great Britain (Thomas, 1981), southwest Ireland (Siveter, 1989), the Carnic Alps (Gaertner, 1930), the Polish Holy Cross Mountains (Tomczykowa, 1957; see Bruton, 1968, p. 9), the southern Urals (Bruton, 1968, p. 9), Bohemia (Bruton, 1968; Snajdr, 1984b), and Kazakhstan (Apollonov, 1980). An attempt has been made to clarify the phylogenetic relationships of the species included in Odontopleura by means of unordered cladistic analysis. The resulting phylogeny clearly supports a distinction between two major species groups, recognized as the nominate subgenus and Sinespinaspis n. subgen.

METHODOLOGY

The aim of this study is not to summarize the general procedures of and justifications for cladistic methodology (many such review articles exist; an excellent review and introduction to the literature from a paleontological viewpoint is provided by Schoch, 1986). However, the method of cladistic analysis adopted herein differs radically from the outgroup-based procedures familiar to most paleontologists. In addition, a particular ontology of the term 'character' is advocated. Both of these areas require explication.

Characters.--When one has assembled and delimited the group of taxa to be analyzed, the procedure begins by the development of taxonomic characters. A character is not a discrete entity, but rather a basis for comparison between taxa (see Ghiselin, 1984; Colless, 1985a; Duarte Rodrigues, 1986 for discussion). Those aspects of taxa being compared are themselves not discrete objects ('parts': Colless, 1985a, p. 230), but rather descriptive statements about objects ('attributes': Colless, 1985a, p. 230). Therefore, with respect to a single (i.e. homologous) organismic 'part' or 'feature,' one can group the study taxa into mutually exclusive classes according to their possession of an attribute of this part. An example from the present study will clarify the issue. Most odontopleurine trilobites have interior pygidial border spines, defined herein as those border spines lying between the major border spines. 'Interior pygidial border spine' is the part. 'Number of interior pygidial border spines' is the basis for comparison, or character. '2' and '4' (i.e. 'has 2,' 'has 4,' Colless, 1985a, p. 230) are the attributes, or character-states. Some of the implications of this ontology are discussed by Ghiselin (1984) and Duarte Rodrigues (1986).

It is emphasized here that characters are not inherent to the organisms we study. Characters are something we create by specifying a basis of comparison between attributes of homologous parts of those organisms. They are subjective, not objective, in nature. As Meacham (1984, p. 27) has put it: "The creation of a qualitative character [=character, in this discussion] is a complex operation that requires a great deal of biological interpretation and intuition. Because synthesis and interpretation are so predominant in character construction, this process resembles an act of invention more than discovery."

Compatibility and parsimony.--Once each study taxon has been assigned to a particular character state for each character, the task is to assess the best possible grouping of taxa, given that different groupings will likely be indicated by different characters. Many methods are currently advocated. One technique is character compatibility analysis, or clique methods (see Meacham, 1980, 1981, 1983 and references therein). These procedures generally seek to identify the largest possible set of congruent characters (i.e. those whose character-state groupings of the study taxa are in agreement). The non-congruent characters are then discarded, and relationships are resolved through application of parsimony to the remainder. As Farris (1983) has pointed out, use of such a technique involves assuming that if a character exhibits any homoplasy (incongruency) whatever, it must be homoplasious in all cases. As homoplasy increases in the data set, more and more characters are excluded, and compatibility methods will explain an ever smaller subset of the original observations (Farris and Kluge, 1979; Farris, 1983). An alternative, favored here, is the use of a cladistic, or methodological, parsimony criterion according to the Wagner methods formalized by Kluge and Farris (1969), Farris (1970), and Farris et al. (1970). Cladistic parsimony holds simply that homoplasy should be minimized in tree construction. For a succinct demonstration that this methodological criterion is independent of evolutionary assumptions, see Farris (1983). For an attempt to provide a formal justification for the criterion and discussion of the philosophical problems involved, see Sober (1983, 1985) and Felsenstein and Sober (1986).

Outgroups.--Cladistic parsimony analysis conventionally seeks a directed result. Direction is often derived through use of an outgroup criterion. In most basic terms, this involves some type of comparison between the ingroup and what is assumed to be a related monophyletic group, by means of which the primitive character-state for each character is specified. Ideally, one derives these ancestral character-states by reference to the sister-group of the ingroup.

Maddison et al. (1984) have provided a rigorous treatment of this type of analysis. What bears emphasis here is that much of their discussion is concerned with cases in which relationships among the outgroups used are resolved. It has long been argued (eg. Colless, 1967, 1969, 1985b) that analysis under these circumstances involves circular reasoning. One analyzes the ingroup by recourse to an already known higher level phylogeny. This phylogeny, however, can only have been derived by reference to some other prior knowledge (of a still higher level phylogeny), and so on in an infinite regress.

A second type of outgroup procedure escapes this charge of circularity by dispensing with the insistence that relationships among outgroups be known. In its most general invocation, this criterion holds that <u>any</u> group can be used as an outgroup for analysis, with those character-states that occur in both the outgroup and ingroup taken as primitive. Hence, the method will work equally well regardless of the choice of outgroup, with the obvious restriction that as the phylogenetic distance between outgroup and ingroup increases, homologues may become fewer in number, and the potential for homoplasy will increase. In effect, however, this type of analysis yields an assessment of ingroup relationships based upon the supposition that the chosen outgroup is in fact the monophyletic sister group of the ingroup. The opinion is often expressed (e.g. Michaux, 1989, p. 22) that the use of multiple outgroups will improve the analysis. If we (somehow) have knowledge of the pattern of relationship between them, this may be true, according to the reasoning outlined by Maddison et al. (1984). However, if we accept that such knowledge cannot be acquired by analysis but must rather be asserted a priori, and choose instead this second, more general, outgroup criterion, multiple outgroups do not help at all. When the outgroup is changed, a new, different, hypothesis of sister-group relationship is in effect formulated. The central parameter of the analysis, that determining polarity, has been altered. No concensus can be derived among the resulting phylogenies. They have fundamentally different parametric bases and are not comparable. Support for each reduces to reexamination of the criteria by which the outgroup in question was selected. Hence, under this more general invocation of the outgroup criterion, additional outgroups simply compound uncertainty.

From an operational viewpoint, the outgroup criterion is sometimes difficult to invoke. Often, for a variety of reasons, no prospective outgroup may be apparent. Indeed, in the case of many extinct groups, higher-level relationships are completely obscure, and the outgroup criterion cannot be applied.

All of this is not to say that outgroups have no utility. In some cases, there may be a mass of corroborative circumstantial evidence supporting a sister-group relationship, just as in some cases there may be a body of physical evidence supporting claims by stratigraphic paleontologists of direct ancestry in their fossil sequences. As long as the assumptions involved are made explicit, outgroup analysis may provide useful insights about ingroup relationships. The point we wish to stress is that outgroup analysis involves making a large and restrictive a priori assumption of ancestry, and does not have universal applicability.

Unordered analysis.--Meacham (1984, p. 27, Figures 1-3) has identified three types of cladistic characters. The character-states of unordered characters are not arranged in a transformation series. There are two types of ordered characters. The character-states of undirected characters are arranged in a transformation series, but the polarity of the series is not specified. The character-states of directed characters are arranged in a polarized transformation series.

Analysis using unordered characters is advocated here. Such analysis will determine the most parsimonious arrangement of taxa, given that any character-state may transform into any other (of the same character), and that reversals are possible. No ordering or direction restrictions are placed upon the data. Such restrictions amount to a priori assumptions about relationship. Rather, to use Meacham's (1984) phrase, the characters should be allowed to speak for themselves.

However, in and of themselves, characters have nothing to say about direction. Undirected analysis results in an undirected tree, a minimum length Wagner Network. In order to generate a directed hierarchy, one must decide upon the position of a root. To accomplish this, some methodological assumption is necessary. One alternative is to apply the outgroup criterion. With a hypothetical ancestor in hand, one can either include it in the unordered analysis and place the root at the terminal node occupied by it, or use the procedure advocated by Lundberg (1972), in which the ancestor is excluded from the analysis, but used to root the Network by determining the position at which it achieves the most parsimonious fit. If outgroups are to be used, the second is clearly the less restrictive, most assumption-free, and most parsimonious (Farris, 1982) option. If not, what then are the options for ingroup analysis?

Ontogeny.--Ontogenetic generality criteria may provide important and useful ways of producing ordered characters. Obviously, they require knowledge of development. To the extent that detailed knowledge of ontogenetic development is generally unavailable in paleontology, ontogenetic criteria are of limited application. Of course, to the extent that such information is available, for example in many trilobite groups, these criteria are relevant and useful, and the reader is referred to Weston (1988) for a recent review.

Patterson's method.--Patterson (1988) has suggested that what he terms 'general congruence' is the best method of ingroup analysis. This is described (Patterson, 1988, p. 74) as "...demanding that the information within the character set dictates the polarity of characters." This is the central theme of the present paper: The best initial idea of relationship, and the most assumption-free cladogram, is that derived solely from analysis of ingroup morphology.

Patterson (1988, p. 74) noted that for *n* study taxa, there are $2^n - (n + 2)$ possible 'cladistically informative characters' (hereafter abbreviated CIC). A CIC is one which defines a subset of the study taxa. Here, any character-state in which two or more study taxa have membership corresponds to a CIC. For *n* >= 2 study taxa, there are (2k-3) fully resolved cladograms (Cavalli-Sforza and Edwards, 1967; Felsenstein, 1978). Patterson's (1988) method is to examine all possible rooted cladograms for the study taxa, and to score them for the number of CIC that they accommodate. His favored cladogram is the highest scoring.

This method, however, may yield an unparsimonious result. If a CIC does not fit the highest scoring cladogram at some point as a unique and unreversed synapomorphy - i.e. if it demonstrates some homoplasy - it is entirely ignored, and therefore assumed to be homoplasious in all occurences. This is a form of compatibility analysis, as Patterson (1988, p. 77) readily admits. Compatibility analysis, as stated above, explains less data than cladistic parsimony analysis as homoplasy in the data set increases.

Method employed.--Patterson's (1988) goal, that the cladogram be derived solely from ingroup data, is endorsed. Rather than accommodating the most congruent arrangement of character-states possible, however, it is argued that the primary consideration should be that the preferred cladogram is as parsimonious as possible. Unordered analysis will result in one or a number of maximally parsimonious Wagner Networks. Congruency can then be used to select a preferred cladogram from the family of trees implied by these networks.

An important point here is that the tree chosen by congruency scoring all possible rootings of a given network (a network with *n* terminal nodes has 2*n* - 3 possible root positions) is equivalent to that derived by placing the root on the longest branch of that network (i.e. the branch across which the greatest number of character transformations are required), assuming branch lengths are unambiguous for the topology being considered. Hence, if analysis yields a single most parsimonious network, the preferred cladogram is immediately obvious, as it is that derived from a root positioned on the longest branch of that network. If there are multiple equally parsimonious networks, the competing candidates for the final cladogram are the longest-branch rooting of each. These competing cladograms can then be congruency scored, and the highest scoring taken as the final cladogram. In the case of a tie, a consensus tree may be derived according to a variety of available techniques (see Kluge, 1989 for a summary).

Patterson (1988) used congruency to determine final tree topology. Here, tree topology is constrained by the criterion of parsimony. The preferred cladogram is that which accommodates the maximally congruent arrangement of character-states, given that its topology requires also the fewest possible number of character transformations. We therefore propose to refer to this method as constrained congruency.

Unordered analysis is inherently more likely to produce multiple equally parsimonious networks than ordered or directed techniques, since it imposes no restrictions upon the types of character transformations possible. Constrained congruency is a methodological criterion for deriving a limited number of directed trees from a larger number of undirected networks, by maximizing the number of unambiguous synapomorphies uniting taxa.

Finally, we note that although we prefer herein to treat all characters as unordered, and to select final cladograms by the criterion of constrained congruency, we do not deny that assumptions about ancestral states may often contribute important elements to a phylogenetic analysis. In our opinion, however, such assumptions should be made only when there is a strong and explicit reason to do so. Blanket hypotheses of primitiveness of the sort required by directed outgroup analysis are undesirable.

The constrained congruency method can be outlined as follows.

Step 1. Create a character matrix, assigning membership in character-states as described above.

Step 2. Run the data as an unordered analysis to obtain a rootless Wagner Network (or a number of equally parsimonious Wagner Networks) for the study taxa.

Step 3. If a single network is obtained, choose the tree obtained by rooting the network on its longest branch. If multiple networks are encountered, examine the longest-branch rootings of each, and score for the number of unique synapomorphies accommodated. This is accomplished by examining each node, and scoring for the number of character-states which include all of the taxa encompassed by that node, and exclude all of the taxa not encompassed by that node (see Patterson, 1988).

Step 4. Choose the highest scoring cladogram. If multiple cladograms have an equally high score, the final cladogram can be derived by a variety of available consensus techniques (see Kluge, 1989).

ANALYSIS OF ODONTOPLEURA

Data.--The characters and character-states used to code for unordered analysis of Odontopleura are shown in Table II-1. The sources consulted for coding are listed in Table II-2. Table II-3 gives the character matrix used in the analysis. Note that while O. (Sinespinaspis) bombini is placed in tentative synonymy with O. (S.) nehedensis below, the taxa are treated separately for purposes of analysis. Some of the characters and character-states are illustrated and contrasted in Figures II-2 to II-4. The data were run on Swofford's (1985) PAUP program, treating all multistate (i.e. non-binary) characters as unordered. Midpoint rooting was used, an option that roots the calculated Wagner Network at the midpoint of its longest branch, thereby determining the candidate trees for the choice of preferred cladogram.

Results.--Analysis yielded 7 equally parsimonious Wagner Networks, each with a consistency index of 67.4%. This statistic was developed by Kluge and Farris (1969) and is a measure of the range of the data (the sum of the minimum number of character transformations implied by the data) divided by the length of the Network (the number of transformations required for the maximally parsimonious topology). When the 7 candidate cladograms were congruency scored, 2 were found to be highest-scoring, each accommodating 15 of the CICs. These alternatives are shown in Figure II-5. Note that they differ only in the relative positions of _O_. (_Odontopleura_) _ovata_ and _O_. (_Odontopleura_) _brevigena_. The possible character-state assignments for the non-terminal nodes of each of the alternative cladograms are given in Tables II-4 and II-5. The consensus cladogram derived from the two maximally congruent rootings is shown in Figure II-6, and should be taken as the most favoured hypothesis of relationship as determined by the parameters of this study.

Discussion.--The analysis reveals two major species groups, each characterized by a suite of diagnostic features, and separated in the analysis by a branch length of 10. Each would appear to represent a natural phyletic group, and a distinction is thus made at the subgeneric level between the nominate subgenus and _Sinespinaspis_ n. subgen. A major question, which this analysis has not attempted to resolve, is whether or not the subgenera do in fact constitute sister taxa. If the study group is monophyletic, they do. In order to test this, it would be necessary to include in the analysis various species from what are assumed to be closely related genera.

SYSTEMATIC PALEONTOLOGY

Terminology.--One new term is introduced. Whittington (1956) and subsequent authors have used the term O_p to refer to a spine pair on the occipital ring. Whittington's example (1956, Figure 1) was a Degree 0 meraspid cranidium of _Apianurus_ _barbatus_ Whittington. The intention, presumably, was that the holaspid occipital spine pair that develops from this juvenile pair should be called O_p. However, a distinction is required in many odontopleurine genera, including *Odontopleura* and *Diacanthaspis*, between the large exaxial occipital spines and a pair of smaller adaxially placed occipital spines. This latter pair would appear to represent the serial homologues of the major spine pairs found on the thoracic axes, at least in *Odontopleura* (*Odontopleura*) *arctica* (see Figure II-7.1, II-7.2, II-7.4). Hence, this pair likely developed from the pair present in early ontogeny on the occipital ring, and strictly speaking should be called O_p. However, we do not wish to create confusion by altering the traditional descriptive function of the term O_p by insisting on a strict interpretation of homology, since in some cases whether or not the prominent occipital spines are serial homologues of the thoracic axial pairs is not immediately obvious. Therefore, whenever there occurs a prominent occipital spine pair, we suggest it should be referred to as O_p. Whenever it encloses a less prominent pair as in *Odontopleura* (*Odontopleura*), or whenever a non-prominent pair occurs in isolation as in some species of *O*. (*Sinespinaspis*), the less prominent pair should be referred to as O_{ap}, designating paired axial-occipital spines (see Figure II-2).

The following terms are used to distinguish between pygidial border spines. The *major border spines* are those which run from the pleural ribs derived from the first axial ring, regardless of their length. The exterior pygidial border spines are those which occur laterally to the major border spines. The interior pygidial border spines are those which occur between the major border spines.

Family ODONTOPLEURIDAE Burmeister, 1843

Subfamily ODONTOPLEURINAE Burmeister, 1843

Genus ODONTOPLEURA Emmrich, 1839

Type species.--*Odontopleura ovata* Emmrich, 1839, p. 53; from a Graptolithengestein glacial erratic of late Wenlock to early Ludlow age, Nieder Kunzendorf, Silesia.

Diagnosis.--Odontopleurine trilobites with large 1L and 2L lobes; eyes small, nonpedunculate, set opposite middle or rear of 1L lobe, usually separated from glabella by at least width of 1L; 3L lobe rudimentary to absent; occipital lobes moderately developed to absent; large paired occipital spines may be present; numerous cephalic border spines (at least 15 on each free cheek), increasing in length posteriorly, at least posteriormost border spine occurring on lateral aspect of genal spine; genal spine slender, curved, length measured as straight line from tip to base slightly shorter to longer than length of free cheek measured as straight line from base of genal spine to anterior end of facial suture; thoracic segments with long to short tubular anterior spines and long, slender posterior spines; usually three dominant spine pairs on thoracic pleurae and a single dominant pair on rachis; second ring furrow of pygidium usually absent; 2-4 (rarely more) subequal interior pygidial border spines; 3-5 (rarely 2) pairs of exterior pygidial border spines; major pygidial border spines long and slender.

Discussion.--Whittington (1956) compared Odontopleura to Leonaspis, and later (1959, p.O504) provided a diagnosis for Odontopleura. Chatterton and Perry (1983) emended this diagnosis to accommodate the Llandovery species they assigned to the genus. Their diagnosis is itself emended above to reflect the concept of Odontopleura adopted in this paper.

Prantl and Pribyl (1949), in a major revision of odontopleurid trilobites, recognized only two species of Odontopleura, O. ovata Emmrich, 1839 from the Bohemian and Baltic Wenlock and Ludlow, and O. dufrenoyi Barrande, 1846 from the Bohemian Wenlock. Snajdr (1979) rehabilitated O. prevosti Barrande, 1846 in a short note which referred to a single pathological specimen. O. prevosti had previously been considered a synonym of O. ovata by Prantl and Pribyl (1949) and Bruton (1968). Chatterton and Perry (1983) described a new Wenlock species from the Canadian Northwest Territories, O. brevigena, together with four Llandovery species which they considered best fit in an expanded concept of Odontopleura. These workers also proposed that Taemasaspis llandoveryana Snajdr, 1975, from the late

Llandovery of Bohemia, be assigned to *Odontopleura*. Snajdr (1984a) removed *O. dufrenoyi* from the genus and grouped it with the Llandoverian *Miraspis rarissima* Snajdr, 1975 in the new genus *Ivanopleura*. Snajdr (1984b) undertook a revision of the Bohemian representatives of *Odontopleura*, and where Bruton (1968) had recognized two species, *O. ovata* and *O. dufrenoyi*, Snajdr (1984b) now proposed or rehabilitated no fewer than thirteen species and subspecies names, but did not recognize with certainty the occurrence of *O. ovata*. The specimen that Snajdr (1979) had originally used to rehabilitate *O. prevosti* he now referred to a new species, *O. salma*, while at the same time proposing four subspecies for *O. prevosti*. Pribyl et al. (1986) considered the material assigned by Snajdr (1975, 1978) to *Taemasaspis llandoveryana* to belong to both *Primaspis* (*Meadowtownella*) Pribyl and Vanek, 1965 and *Odontopleura*. Siveter (1989) placed most of the taxa introduced or rehabilitated by Snajdr (1984b) in synonymy with *Odontopleura ovata*, and considered *Ivanopleura* to be a subgenus of *Odontopleura*.

Almost all of the Bohemian material is compacted, resulting in the loss of some surface detail and making taxonomy problematic. Snajdr's (1984b) proposals are difficult to accept. We believe, in agreement with Siveter (1989), that most of the names proposed or rehabilitated by Snajdr (1984b) should be considered synonyms of *O. ovata*. Almost all are based upon little more than subjective assessments of spinosity, often between specimens from the same or equivalent horizons. We further question the validity of the lower Ludlow *O. palava* Snajdr, 1984b. Siveter (1989, p. 142) accepted this species because of "The general lack of glabellar granules except for the larger paired granules..." However, Snajdr (1984b) erected this taxon on the basis of five incomplete cranidia, and of the two figured, this lack of glabellar ornament is only distinct on the holotype (Snajdr 1984b, Plate 1, Figure 8). The major paired spines dominate, but other spines and tubercles are clearly present, and the specimen shows some evidence of abrasion. The other figured specimen seems to have plenty of accessory granules on its glabella. With nothing known of the rest of the trilobite, these late representatives of the genus are not demonstrably distinct from *O. ovata*, and should probably be referred to that taxon. In any case, the very brief descriptions and paucity of illustrations of taxa given by Snajdr (1984a, 1984b) make his proposals difficult to incorporate into detailed comparative studies.

Subgenus IVANOPLEURA Snajdr, 1984a

Type species.--*Odontopleura dufrenoyi* Barrande, 1846 from the Liten Formation (upper Wenlock, *Monograptus flexilis* to *M. testis* zones), Svatý Jan pod Skalou, Lodenice, and Sedlec, Czechoslovakia.

ODONTOPLEURA (IVANOPLEURA) DUFRENOYI Barrande, 1846

Odontopleura Dufrenoyi BARRANDE, 1846, p. 56.

Odontopleura dufrenoyi Barrande. BRUTON, 1968, p. 9, Pl. 1, figs. 5,10 (with synonymy).

Miraspis rarissima Snajdr. SNAJDR, 1975, p. 315, Pl. 2, fig. 4; SNAJDR, 1978, p. 32, Plate 10, figs. 4-8, Pl. 12, fig. 10; PRIBYL, VANEK, AND HÖRBINGER, 1986, p. 267.

Leonaspis pokornyi Snajdr. SNAJDR, 1975, p. 315, Pl. 2, fig. 8; SNAJDR, 1978, p. 35, Pl. 9, figs. 15-18.

Ivanopleura dufrenoyi (Barrande). SNAJDR, 1984a, p. 50, Pl. 1, figs. 1-4 (with synonymy).

Ivanopleura rarissima (Snajdr). SNAJDR, 1984a, p. 50, Pl. 1, figs. 5,6, Pl. 2, figs. 1,2.

Discussion.--Snajdr (1984a) erected *Ivanopleura* to accommodate *Odontopleura dufrenoyi* Barrande and *Miraspis rarissima* Snajdr. Siveter (1989, p. 137) expressed the opinion that in overall morphology, these species so resembled *Odontopleura* that *Ivanopleura* was best considered a subgenus of that genus. We are of the opinion that similarities between the taxa have long been overestimated. With no new information to add, however, we follow Siveter (1989) and place *Ivanopleura* within *Odontopleura* (but see section on paleoecology and paleogeography below). As is evident from the above synonymy, there appear to be no objective differences between *O.* (*I.*) *dufrenoyi* and the marginally older (latest Llandovery versus earliest Wenlock)

Miraspis rarissima Snajdr. Snajdr (1984a) separated the species only by relative spinosities of the cephalon and dimensions of the pygidium. _M_. _rarissima_ is regarded here as a subjective junior synonym of _O_. (_I_.) _dufrenoyi_.

Despite the lengthy taxonomic history of this species, it remains unsatisfactorily known. The specimens referred to it are generally incomplete cranidia and pygidia or severely abraded articulated individuals. That at least most of the cranidia belong together and represent a single distinct species seems certain. The following characters serve to distinguish _O_. (_I_.) _dufrenoyi_ from other species included in _Odontopleura_: The fixed cheeks are very narrow, and the eye is positioned less than the width of the 1L glabellar lobe from the glabella. The cephalic ornament consists of large, sparsely distributed tubercles, with the paired glabellar spines identifiable and occasionally prominent, whereas in mature holaspids of other _Odontopleura_ species, the paired glabellar spines are indistinguishable from accessory glabellar spines and tubercles. There are strongly divergent O_p spines. The O_{ap} spines occur lateral to the median occipital spine, on the axes of the O_p spines. This contrasts with the condition in _O_. (_Odontopleura_), where the O_{ap} spines are invariably placed posteriorly to the median occipital spine, and between the O_p spines.

Subgenus ODONTOPLEURA Emmrich, 1839

Type species.--As for genus.

Species included.--*O. ovata* Emmrich, 1839, from the upper Llandovery to lower Ludlow of Europe; *O. brevigena* Chatterton and Perry, 1983, from the Wenlock of the Mackenzie Mountains, Northwest Territories, Canada; *O.* (*O.*) *arctica* n. sp., from the lowermost Llandovery of the Canadian Arctic Archipelago; *Diacanthaspis serotina* Apollonov, 1980, from the lowermost Llandovery of Kazakhstan.

Diagnosis.--Species of *Odontopleura* with O_p developed laterally to O_{ap}; O_{ap} positioned distinctly posterior to median occipital spine; 3P glabellar furrow visible at least ventrally; median occipital spine placed distinctly forward from posterior border of cranidium, separated from posterior border by distance greater than 1 width of median occipital spine; posteroventral (doublural) part of posterior facial suture not directly opposite posterodorsal part; sutural ridge along posterior facial suture on free cheek faint to absent; cephalic border spines on free cheek reduced to small denticles posterior to contact with anterior facial suture; anterior pleural spines elongate and tapering, especially on posterior thoracic segments; pygidium distinctly rounded and subsemicircular in ventral outline.

Discussion.--Members of this subgenus can be readily distinguished from those of *O.* (*Sinespinaspis*) n. subgen. by their possession of O_p spines, anteriorly positioned median occipital spine, non-aligned posterior facial suture, denticulate as compared with fully developed anterior free cheek border spines, faint to absent as opposed to strongly developed sutural ridge along posterior facial suture on free cheek, long as opposed to short and barb-like anterior pleural spines, and subsemicircular as opposed to subtriangular pygidium (see Figures II-2 to II-4).

Diacanthaspis laokuangshanensis Lu and Chang, 1974, from uppermost Ashgill strata of Sichuan Province, China, may well belong to this subgenus. If so, it would represent the earliest known *Odontopleura*, and the only known Ordovician species. A thorough reinvestigation and additional material would be required to arrive at any firm taxonomic conclusions, however, and no attempt has been made to include the species in the present analysis.

ODONTOPLEURA (ODONTOPLEURA) OVATA Emmrich, 1839

Odontopleura ovata EMMRICH, 1839, p. 53, Pl. 1, fig. 3.

Odontopleura (*Odontopleura*) *ovata* Emmrich; SIVETER, 1989, p. 138, Pl. 20, figs. 1-7, 11-21, Pl. 21, figs. 1, 3, 4, 8 (with full synonymy).

Discussion.--The taxonomic history of this species was discussed under the genus *Odontopleura*. Siveter (1989) has provided a comprehensive review.

O. (*O*.) *ovata* can be distinguished from the other three species included in the subgenus by the presence of dorsally expressed 3L glabellar lobes, relatively strongly developed occipital lobes, eyes placed a transverse distance from the

1L lobe about subequal to the width of the 1L lobe, as opposed to a distance greater than the width, and the presence of a weakly impressed second ring furrow on the pygidium (see Siveter, 1989, Pl. 20, figs. 12, 16, Pl. 21, fig. 4).

Chatterton and Perry (1983, p. 18) reported the possible occurrence of this species from upper Wenlock to lower Ludlow strata of the Delorme Range of the Mackenzie Mountains. The available material is still insufficient to allow proper specific assignment. It has become evident, however, that it does not represent a Laurentian occurence of O. (O.) ovata, as it clearly lacks the distinctive glabellar morphology (well-defined 3L and occipital lobes) of that species. The material may represent a distinct new species, or possibly a variant of O. (O.) brevigena, with longer O_p spines. Proper description will await the accumulation of adequate material.

Occurrence.--Upper Llandovery to lower Ludlow of Bohemia (Bruton, 1968; Snajdr, 1984b); Wenlock to Ludlow of the Baltic Region (Bruton, 1967; Schrank, 1969; Alberti, 1970), Poland (Tomczykowa, 1957), Great Britain (Thomas, 1981); possibly the Silurian of the Carnic Alps (Gaertner, 1930); possibly the upper Wenlock of the Southern Urals (Bruton, 1968, p.9); mid-upper Wenlock to lowermost Ludlow of the Annascaul Inlier, County Kerry, Ireland (Siveter, 1989); non Wenlock to lower Ludlow of the Mackenzie Mountains, Northwest Territories, Canada (Chatterton and Perry, 1983, p. 18; Siveter, 1989, p. 142).

ODONTOPLEURA (ODONTOPLEURA) BREVIGENA Chatterton and Perry, 1983

Odontopleura brevigena CHATTERTON AND PERRY, 1983, p. 18, Pl. 1, figs. 1-34.

?Odontopleura perpeta SNAJDR, 1984b, p. 103, Pl. 2, figs. 1, 2.

Odontopleura (Odontopleura) brevigena Chatterton and Perry; SIVETER, 1989, p. 142.

Discussion.--It should be noted that Chatterton and Perry's (1983, Pl. 1, figs. 6-9) holotype has a teratological pygidium, with 5 interior pygidial border spines. Further specimens collected from the type locality have yielded two more teratological pygidia, each with 6 fully developed interior pygidial border spines. Such examples are rare, however, as these specimens compare with dozens of normal pygidia collected from the same locality.

O. (O.) brevigena differs from the other species assigned to the subgenus in the presence of a hypostome with a distinctly crennate posterior margin (see Chatterton and Perry, 1983, Pl. 1, figs. 16, 25), relatively short O_p spines, and having genal spines distinctly shorter than the remainder of the free cheek.

As noted by Siveter (1989, p.142), O. perpeta Snajdr, 1984b, seems very similar to O. (O.) brevigena, and may be a junior synonym. The Bohemian material, however, is as yet too poorly known to permit a proper comparison.

Occurrence.--Wenlock of the Mackenzie Mountains, Northwest Territories, Canada.

ODONTOPLEURA (ODONTOPLEURA) SERŌTINA (Apollonov, 1980)

Diacanthaspis serotina APOLLONOV, 1980, p. 111, Pl. 31, figs. 1-5.

Discussion.--Although not especially well known, the form of the cranidium and free cheek leaves no doubt that this species belongs in the subgenus. It appears to be closely related to the contemporaneous Odontopleura (Odontopleura) arctica n. sp., united in particular by the distinctive anterior facial sutures, which are initially divergent, and do not begin to converge until opposite the middle of the 2L glabellar lobe. The pygidium, if correctly associated, is unusual for Odontopleura, as the major border spines do not appear to be exceedingly long, and the dorsal surface is much less spinose than normal.

Odontopleura (Odontopleura) serotina can be distinguished from all other species assigned to the subgenus particularly by its deep axial furrows, which serve to separate the anterolateral portion of the 1L glabellar lobes from the fixed cheeks, and by the presence of much shorter major pygidial border spines. O. (O.) serotina and O. (O.) arctica n. sp. differ collectively from the other two species assigned to the subgenus by the presence of initially divergent anterior facial sutures, and the presence of three, as opposed to four, exterior pygidial border spines. O. (O.) serotina differs further from O. (O.) arctica n. sp. in having a much narrower, slightly longer, and much less spinose pygidium.

It is acknowledged that some of these differences could be due to the quality and mode of preservation. That O. (O.) serotina represents a distinct species, phylogenetically close to O. (O.) arctica, does not seem at issue. More and better illustrated material would be required, however, for a truly satisfactory differential diagnosis.

Occurrence.--Lowermost Llandovery of Kazakhstan.

ODONTOPLEURA (ODONTOPLEURA) ARCTICA n. sp.

Figure II-7.1 to II-7.6

Diagnosis.--A species of Odontopleura (Odontopleura) with 3L glabellar lobes defined ventrally only; axial furrows very shallow at anterior of 1L glabellar lobes; occipital lobes weakly defined; eyes placed a transverse distance from 1L glabellar lobe greater than width of 1L lobe; O_p spines long, reaching as far as 6th thoracic segment; anterior facial sutures long and divergent opposite 2L glabellar lobe; posterolateralmost cranidial marginal spine long, extending to midlength of 2nd thoracic segment; genal spine subequal in length to slightly longer than remainder of free cheek; pygidium with three pairs of exterior border spines;

major pygidial border spines at least three times as long as exsagittal length of pygidium measured directly anterior to them; pygidium approximately four times as wide as sagittal length; second ring furrow of pygidium wholly absent.

Discussion.--A comparison with *Odontopleura* (*Odontopleura*) *serotina* may be found under the discussion of that species.

Odontopleura (*Odontopleura*) *arctica* differs from *O.* (*O.*) *brevigena* in having longer O_p spines; anterior facial sutures which are divergent, as opposed to convergent opposite the 2L glabellar lobes; longer posterolateralmost cranidial marginal spines; longer genal spines; three as opposed to four exterior pygidial border spines; and longer major pygidial border spines.

Odontopleura (*Odontopleura*) *arctica* differs from *O.* (*O.*) *ovata* in lacking dorsally expressed 3L glabellar lobes; having weak as opposed to strongly defined occipital lobes; eyes placed a greater transverse distance from the 1L glabellar lobes; anterior facial sutures divergent as opposed to convergent opposite 2L glabellar lobes; longer posterolateralmost cranidial marginal spines; three as opposed to four pairs of exterior pygidial border spines; longer major pygidial border spines; pygidium about four, as opposed to three, times as wide as sagittally long; and lacking any impression of the 2nd ring furrow of the pygidium.

GSC 95878 (Figure II-7.5) appears to represent a moult ensemble. The configuration of the associated elements indicate that this species behaved during ecdysis in a manner similar to that of O. (O.) brevigena (Chatterton and Perry, 1983, p. 19, Pl. 1, figs. 1-4), the only other species of Odontopleura for which evidence for such behaviour has been presented. Moulting in both of these species involved a separation and rotation of the free cheeks and displacement of the hypostome. According to Chatterton and Perry (1983, p. 19), the trilobite then crawled out from beneath the remaining articulated elements, and over the separated hypostome and free cheeks. This analysis is supported here, as the cranidium (Figure II-7.5) has clearly remained in close articulation with the 1st thoracic segment.

Material.--Holotype GSC 95875, an external mould of a complete individual. Paratypes GSC 95876, an external mould of a complete individual; GSC 95877, an internal mould of a complete individual; GSC 95878, an associated cranidium, two free cheeks, and thoracic segment; GSC 95879, a pygidium with original shell material preserved; GSC 95880, an isolated thoracic segment (not figured). All from a single block of shale, a glacial erratic collected from the Marshall Peninsula, northwest coast of Cornwallis Island, Canadian Arctic, and assigned to the lowermost Llandovery, Cape Phillips Formation.

Subgenus SINESPINASPIS n. subgen.

Type species.--Odontopleura greenwoodi Chatterton and Perry, 1983.

Species included.--Odontopleura greenwoodi Chatterton and Perry, 1983; Odontopleura maccallai Chatterton and Perry, 1983; Odontopleura nehedensis Chatterton and Perry, 1983; ?Odontopleura bombini Chatterton and Perry, 1983; all from the Llandovery of the Mackenzie Mountains, Northwest Territories, Canada; Taemasaspis llandoveryana Snajdr, 1975, from the Llandovery of Bohemia.

Diagnosis.--Odontopleurine trilobites with 3L glabellar lobes usually completely absent; occipital lobes usually weak or absent; occipital furrow usually shallow and indistinct; occipital ring with O_{ap} spines only, or entirely lacking paired occipital spines; O_p never developed; anterior facial suture generally short, subparallel to convergent opposite 2L glabellar lobe; spine usually absent from posterolateralmost aspect of cranidial margin; median occipital spine either at posterior cranidial margin or within one median spine width from margin; genal spine usually shorter than remainder of free cheek; posteroventral (doublural) part of posterior facial suture aligned with posterodorsal part; strong sutural ridge along posterior facial suture on free cheek; cephalic border spines at anterior of free cheek persist as fully developed spines to contact with anterior facial suture; anterior pleural spines very short and barb-like; number of interior pygidial border spines may be reduced in number to two; pygidium subtriangular in ventral outline, usually with an anterior inflection of the median ventral doublure.

Discussion.--This subgenus was contrasted with Odontopleura (Odontopleura) under the discussion of that subgenus.

Etymology.--From the Latin preposition sine, without, the Latin noun spina, spine, and the Greek noun aspis, a shield. Gender is feminine.

ODONTOPLEURA (SINESPINASPIS) GREENWOODI Chatterton and Perry, 1983

Odontopleura greenwoodi CHATTERTON AND PERRY, 1983, p. 19, Pl. 2, figs. 1-20, Pl. 3, figs. 28-43.

Discussion.--An autapomorphy of Odontopleura (Sinespinaspis) greenwoodi among all species of Odontopleura is the presence of two, as opposed to one, free cheek border spines occurring on the lateral aspect of the genal spine.

As Odontopleura (Sinespinaspis) greenwoodi is both the best known and stratigraphically longest ranging species assigned to the subgenus, it was chosen as the type species. It has, however, many morphological features which would tend to ally it with those species included in O. (Odontopleura), including long and convergent anterior facial sutures, small spines present on the posterolateral cranidial margins, and long genal spines. It does, however, have in common with the other species assigned to O. (Sinespinaspis) a suite of uniquely shared characters, just as *O*. (*Odontopleura*) is defined by a similar suite (as shown by the cladograms of Figure II-5).

An argument could be put forward for the presence of O_p spines in *Odontopleura* (*Sinespinaspis*) *greenwoodi*. The occipital ring (Chatterton and Perry, 1983, Pl. 2, figs. 1, 7, Pl. 3, figs. 29, 30, 32) typically has two pairs of occipital spines. The median pair corresponds to the dominant pairs on the thoracic axes, and represents O_{ap}. The lateral pair could therefore be construed as O_p, and taken as homologues of the large O_p spines of *O*. (*Odontopleura*). The O_p spines of that subgenus, however, have no obvious serial homologues on the thoracic axes. The lateral spine pair of *O*. (*S*.) *greenwoodi* has very clear serial homologues (contrast Chatterton and Perry, 1983, Pl. 2, figs. 1 and 3). Hence, while topologically similar structures, the evidence suggests that the lateral spine pair of *O*. (*S*.) *greenwoodi* and the O_p spines of members of *O*. (*Odontopleura*) are non-homologous.

Occurrence.--Middle Llandovery (*Pterospathodus celloni* zone) of the Mackenzie Mountains, Northwest Territories, Canada.

ODONTOPLEURA (SINESPINASPIS) MACCALLAI Chatterton and Perry, 1983

Odontopleura maccallai CHATTERTON AND PERRY, 1983, p. 21, Pl. 4, figs. 17-37.

Discussion.--*Odontopleura* (*Sinespinaspis*) *maccallai* can be distinguished from O. (S.) greenwoodi by the presence of shallower longitudinal furrows at the posterior of the 1L glabellar lobes, a slightly deeper and better defined occipital furrow, the absence of O_{ap} spines, short and subparallel anterior facial sutures, lack of posterolateral cranidial marginal spines, a much shorter genal spine, and a variable (2-4) number of interior pygidial border spines, as opposed to a constant four.

Odontopleura (Sinespinaspis) maccallai differs from O. (S.) nehedensis in the following features: axial furrows at anterior of 1L glabellar lobes shallow as opposed to deep; occipital lobes weakly defined as opposed to wholly absent; occipital furrow shallow but evident as opposed to indistinct; eyes placed transversely farther from the 1L glabellar lobes; O_{ap} spines absent; four as opposed to three pairs of exterior pygidial border spines.

Occurrence.--Llandovery (Pterospathodus celloni zone) of the Mackenzie Mountains, Northwest Territories, Canada.

ODONTOPLEURA (SINESPINASPIS) LLANDOVERYANA (Snajdr, 1975)

Taemasaspis llandoveryana SNAJDR, 1975, p. 314, Pl. 1, fig. 6, Pl. 2, Fig. 7; SNAJDR, 1978, p. 28, Pl. 7, figs. 1-12, Pl. 8, figs. 9-14, Pl. 12, fig. 3; RAMSKÖLD, 1984, p. 249; PRIBYL, VANEK, AND HÖRBINGER, 1986, p. 267.

Odontopleura llandoveryana (Snajdr); CHATTERTON AND PERRY, 1983, p. 18.

Taemasaspis llandoveryiana Snajdr; SIVETER, 1989, p. 137.

Discussion.--The association of the sclerites figured by Snajdr (1975, 1978) as Taemasaspis llandoveryana has been questioned by Pribyl et al. (1986), who considered most of the material to belong to Primaspis (Meadowtownella), with some of the pygidia (they did not specify which) referred to Miraspis rarissima Snajdr, 1975, a species they included in Odontopleura. Following Chatterton and Perry (1983) and Siveter (1989), the figured cranidia seem more similar to the Mackenzie Mountains Llandovery species here grouped in Odontopleura (Sinespinaspis) than to Primaspis (Meadowtownella). That most of the pygidia figured by Snajdr (1978) belong with the cranidia seems reasonable, since his Pl. 7, fig. 7 illustrates the dorsal surface of a relatively well preserved articulated exoskeleton, confirming the association. Snajdr's (1978) Pl. 8, fig. 12 would appear to be the only questionable assignment, and was not used in the cladistic analysis herein (see Table II-2).

The relationships of this species are somewhat problematic. By parsimony, there are two equal length networks differing in their placement of Odontopleura (Sinespinaspis) llandoveryana (one of which was discarded by congruency). This is partly a problem of the material available, and the standards of preservation and illustration of that material. Of more consequence, however, is the simple fact that, with regard to the subgenus, O. (S.) llandoveryana is highly autapomorphic. It has no fewer than five character-states (in characters 1, 4, 5, 20, and 21) not shared with any other member of the subgenus. Following from this, *O.* (*S.*) *llandoveryana* may be distinguished from all other species included in *Sinespinaspis* by the following features: 3L glabellar lobes expressed dorsally; occipital lobes strongly defined; occipital furrow deep; pygidium about 4, as opposed to 3, times as wide as long; strongly impressed 2nd ring furrow of pygidium present.

An undescribed odontopleurine species from the Llandovery of the Forbes district, New South Wales, closely resembles *Odontopleura* (*Sinespinaspis*) *llandoveryana* (L. Sherwin, personal commun.). This material consists of well preserved external moulds of articulated individuals, and its description should provide a sound basis for comparison and evaluation of the Bohemian material.

Occurrence.--Upper Llandovery, Hýskov area, near Beroun, Czechoslovakia.

ODONTOPLEURA (SINESPINASPIS) NEHEDENSIS Chatterton and Perry, 1983

Odontopleura *nehedensis* CHATTERTON AND PERRY, 1983, p. 20, Pl. 3, figs. 1-27.

?*Odontopleura* *bombini* CHATTERTON AND PERRY, 1983, p. 22, Pl. 4, figs. 1-16.

Discussion.--Chatterton and Perry (1983) recognized *Odontopleura* (*Sinespinaspis*) *nehedensis* and *O.* (*S.*) *bombini* as separate species. They speculated (p. 13) that the slightly older *O.* (*S.*) *nehedensis* might be a direct ancestor of *O.* (*S.*) *bombini*, the latter occurring 37 m higher in the same section (each occurs by itself in other sections, but only in section AV 1 are they found in stratigraphic succession). They did not provide a differential diagnosis for the species. From a purely morphological standpoint, the species differ only in the relative depth of the longitudinal furrows at the posterior of the 1L glabellar lobes, the position of the median occipital spine, and in the number of interior pygidial border spines. Of these, the first could be a function of preservation and of comparison of differently sized specimens, as all available *O.* (*S.*) *bombini* material is very small (Chatterton and Perry, 1983, p. 23). The second seems genuine, with the median spine set very slightly forward from the posterior cranidial margin in *O.* (*S.*) *nehedensis* but directly at the margin in *O.* (*S.*) *bombini*. As for the condition of the pygidial border spines, the number of interior spines ranges from 2 to 4 in *O.* (*S.*) *nehedensis*, but is restricted to 2 in *O.* (*S.*) *bombini*. The entire sample of pygidia of *O.* (*S.*) *bombini* is quite small, however, and this character exhibits some variability even in species for which the number is all but constant (see *O.* (*O.*) *brevigena* above). In all other aspects of morphology, *O.* (*S.*) *nehedensis* and *O.* (*S.*) *bombini* are identical, and given the discussion above, distinction between them is of very limited biostratigraphical utility. The possibility must therefore be acknowledged that the two taxonomic species represent temporally separated populations of the same phyletic lineage. Therefore, pending further information, they are placed in questionable synonymy.

Odontopleura (*Sinespinaspis*) *nehedensis* was contrasted with *O*. (*S*.) *maccallai* under the discussion of that species. It may be distinguished from *O*. (*S*.) *llandoveryana* by the absence of the latter species' many autapomorphies. *O*. (*S*.) *nehedensis* differs from *O*. (*S*.) *greenwoodi* in the following features: axial furrows at anterior of 1L glabellar lobes deep as opposed to shallow; occipital lobes entirely absent; eyes placed transversely nearer to the 1L glabellar lobes; anterior facial sutures shorter; no spines at posterolateral part of cranidial margin; genal spines shorter than remainder of free cheeks; 1 as opposed to 2 border spines occurring on lateral aspect of genal spines; 3 as opposed to 4 pairs of exterior pygidial border spines; usually less than 4 as opposed to 4 (or more) interior pygidial border spines.

Occurrence.--Middle to upper Llandovery (*Pterospathodus celloni* to *P*. *amorphognathoides* zones) of the Mackenzie Mountains, Northwest Territories, Canada.

PALEOECOLOGY AND PALEOGEOGRAPHY

Studies of Silurian trilobite paleoecology are few, but include Thomas (1980), Mikulic (1980), Mikulic and Watkins (1981), Männil (1982), and Chlupac (1987). Both subgenera of Odontopleura were widely distributed. Hence no particular paleobiogeographic pattern can be recognized among the ten known species. This broad distribution seems likely to have been directly related to the trilobites' choice of habitat. All of the species included in Odontopleura had, on present evidence, a relatively narrow ecological valence, preferring the deeper waters of the outer shelf or of the shelf-slope transition zone. An exception is Odontopleura (Ivanopleura) dufrenoyi. This Bohemian species occurs in shallow water deposits, included by Chlupac (1987) in his Bumastus-Sphaerexochus-Cheirurus assemblage, which he assigned to Boucot's (1975) Benthic Assemblage 3 or 2. Thus, the doubt expressed above about the systematic position of this species is borne out by an ecological division between it and all other species included in Odontopleura.

Odontopleura (Sinespinaspis) llandoveryana is included by Chlupac (1987) in his Stenopareia-Aulacopleura assemblage, assigned to Boucot's (1975) Benthic Assemblage 4. Odontopleura (Odontopleura) ovata is included by Chlupac (as O. prevosti) in his Aulacopleura konincki assemblage, assigned to Boucot's (1975) Benthic Assemblage 4 or 5. The Irish O. (O.) ovata material was regarded by Siveter (1989, p. 156) as occurring in a distal shelf environment. All of the Mackenzie Mountains species are known from relatively deep water, distal shelf-slope environments (Chatterton and Perry, 1983). The drift block upon which the known specimens of _O_. (_O_.) _arctica_ n. sp. occur is composed of dark, fine-grained, argillaceous, micritic limestone. The only other fossils present are the above-mentioned graptolite fragments, and a single pedicle valve of a smooth atrypid, or possibly athyridid, brachiopod. The lithology of the sample, the presence of graptolites, and the undisturbed nature of the articulated trilobites suggest a low energy, probably low oxygen, deep water environment. As deeper water forms, therefore, members of _Odontopleura_ were not subject to the endemism of more onshore species, having wider opportunities for dispersal and being less affected by eustatic sea level fluctuations. This accounts for their almost global distribution through Lower and Middle Silurian times.

TABLE II-1--Characters used in undirected analysis of Odontopleura. Note that the states 0, 1, and 2 carry no connotations of polarity.

Cranidium

1. 3L glabellar lobe: 0, absent; 1, defined ventrally only; 2, defined both ventrally and dorsally.
2. longitudinal furrow at posterior of 1L glabellar lobe: 0, very shallow, 1L lobe confluent with median glabellar lobe; 1, deep, separating 1L from median glabellar lobe.
3. axial furrow at anterior of 1L glabellar lobe: 0, very shallow, 1L lobe confluent with fixed cheek; 1, deep, separating 1L lobe from fixed cheek.
4. occipital lobe: 0, absent, sometimes with ventral trace of furrow; 1, weakly defined; 2, strongly defined.
5. occipital furrow: 0, deep; 1, shallow and broad; 2, indistinct.
6. transverse distance of eye from 1L glabellar lobe: 0, subequal to width of 1L lobe; 1, greater than width of 1L lobe.
7. length of O_p spines/sagittal length of cranidium: 0, O_p absent; 1, less than 0.35; 2, greater than 0.80.
8. position of O_{ap} spines: 0, O_{ap} absent; 1, distinctly posterior to median occipital spine; 2, approximately lateral to median occipital spine.
9. anterior facial suture: 0, short, subparallel to

TABLE II-1 (Continued)

convergent opposite 2L glabellar lobe; 1, long, convergent opposite 2L glabellar lobe; 2, long, distinctly divergent opposite 2L glabellar lobe.

10. length of posterolateralmost cranidial marginal spine: 0, absent; 1, short; 2, long, extending opposite middle of 2nd thoracic segment.

11. sagittal length from anterior margin to median occipital spine base/sagittal length of cranidium: 0, 0.97-1.0; 1, 0.89-0.95; 2, 0.86-0.87.

Free Cheek

12. length of genal spine (measured as straight line from tip to base)/length of remainder of free cheek (measured as straight line from base of genal spine to anterior end of facial suture): 0, 0.61-0.63; 1, greater than 0.88.

13. number of border spines on lateral aspect of genal spine: 0, 1; 1, 2.

14. course of posterior facial suture: 0, reentrant (doublural) part not aligned with posterodorsal part; 1, posteroventral and posterodorsal parts aligned.

15. cephalic border spines at anterior of free cheek: 0, reduced to small denticles posterior to contact with anterior facial suture; 1, persist as well defined spines to contact with anterior facial suture.

TABLE II-1 (Continued)

Thorax

16. length and shape of anterior pleural spine on 9th thoracic segment: 0,long and tapering; 1, very short, barb-like.

Pygidium

17. number of pairs of exterior pygidial border spines (dominant number in boldface): 0, **3**-4; 1, **4**-5.
18. number of interior pygidial border spines: 0, 2-3; 1, 4.
19. length of major border spines/exsagittal length of pygidium measured directly anterior to them: 0, less than 2.2; 1, 2.4-2.5; 2, greater than 2.8.
20. sagittal length pygidium/maximum width pygidium: 0, 0.3[illegible]-0.36; 1, 0.23-0.27.
21. 2nd ring furrow: 0, absent; 1, present.
22. shape of pygidial outline: 0, subsemicircular; 1, subtriangular.

TABLE II-2--Species and sources used in unordered analysis of _Odontopleura_.

Odontopleura _ovata_ Emmrich, 1839

Bruton (1967, Pl. 30, fig. 1; 1968, Pl. 1, figs. 1-4,6,7)

Schrank (1969, Pl. 1, figs. 1-7, Pl. 2, figs. 1-5)

Siveter (1989, Pl. 20, figs. 1-7,11-21, Pl. 21, figs. 1,3,4,8)

Odontopleura _brevigena_ Chatterton and Perry, 1983

Chatterton and Perry (1983, Pl. 1, figs. 1-34)

Odontopleura _(Odontopleura)_ _arctica_ n. sp.

Figure II-7.1 to II-7.6

Diacanthaspis _serotina_ Apollonov, 1980

Apollonov (1980, Pl. 30, figs. 1-5)

Odontopleura _greenwoodi_ Chatterton and Perry, 1983

Chatterton and Perry (1983, Pl. 2, figs. 1-20, Pl. 3, figs. 28-43)

Odontopleura _maccallai_ Chatterton and Perry, 1983

Chatterton and Perry (1983, Pl. 4, figs. 17-37)

Taemasaspis _llandoveryana_ Snajdr, 1975

Snajdr (1975, Pl. 1, fig. 6, Pl. 2, fig. 7; 1978, Pl. 7, figs. 1-12, Pl. 8, figs. 9-11, 13, 14, Pl. 12, fig. 3)

Odontopleura _bombini_ Chatterton and Perry, 1983

Chatterton and Perry (1983, Pl. 4, figs. 1-16)

Odontopleura _nehedensis_ Chatterton and Perry, 1983

TABLE II-2 (Continued)

Chatterton and Perry (1983, Plate 3, Figures 1-27)

TABLE II-3--Character matrix for unordered analysis of *Odontopleura*. ? = missing data.

	Character																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
ovata	2	0	0	2	1	0	2	1	1	1	2	1	0	0	0	0	1	1	1	0	1	0
brevigena	1	0	0	1	1	1	1	1	1	1	2	0	0	0	0	0	1	1	1	1	0	0
arctica	1	0	0	1	1	1	2	1	2	2	2	1	0	0	0	0	0	1	2	1	0	0
serotina	1	0	1	1	1	1	2	1	2	?	2	1	0	0	0	?	0	1	0	0	0	0
greenwoodi	0	1	0	1	2	1	0	2	1	1	1	1	1	1	1	1	1	1	1	0	0	1
maccallai	0	0	0	1	1	1	0	0	0	0	1	0	0	1	1	1	1	0	?	0	0	1
llandoveryana	2	1	1	2	0	0	0	0	0	0	0	?	0	?	1	1	0	1	0	1	1	1
bombini	0	1	1	0	2	0	0	2	0	0	0	0	0	1	1	1	0	0	0	0	0	1
nehedensis	0	0	1	0	2	0	0	2	0	0	1	0	0	1	1	1	0	0	?	0	0	1

TABLE II-4--Possible character-state assignment for non-terminal nodes of cladogram of Figure II-5.1. Nodes are numbered from left to right, as shown in Figure II-6.1. When more than one character-state is possible, the choices are shown vertically.

	Characters																					
Node	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	1	1	2	1	1	0	2	0	1	1 2	2	0	1	0	1	0 1	0 1 2	0	0	0	0	0
2	1	1	2	1	1	0	1	0	1	1	2	0	1	1	1	0 1	1	0	0	0	0	0
3	0 1 2	1	2	1	1	0	1	0	1	1	2	0	1	1	1	0	1	0	0	0	0	0
4	0	1	0	1 2	1	0 1	1	0	0 1 2	1	1	0	1	1	1	0	1	0	1	1	1	1
5	0	1	0	1 2	1	0 1	0	0	0 2	0	1	0	0	1	0 1	0	0 1	0	1	1	1	1
6	0	0 1 2	0	0 1 2	0	0 1	0	1	0 2	0	1	0	0	0	0 1	0	0	0	1	1	1	1
7	0	0	0	2	0	0 1	0	1	2	0	0	0	0	0	0	0	0	0	1	1	1	1

TABLE II-5--Possible character-state assignments for the non-terminal nodes of the cladogram of Figure II-5.2. Format as in Table II-4.

Characters

Node	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	1	1	2	1	1	0	2	0	1	1 2	2	0	1	0	1	0	0 1 2	0	0	0	0	0
2	1	1	2	1	1	0	1	0	1	1	2	0	1	1	1	0	1	0	0	0	0	0
3	1	1	0 1 2	1	1	0	1	0	1	1	2	0	0 1	1	1	0	1	0	0	0	0	0
4	0	1	0	1 2	1	0 1	1	0	0 1 2	1	1	0	0 1	1	1	0	1	0	1	1	1	1
5	0	1	0	1 2	1	0 1	0	0	0 2	0	1	0	0	1	0 1	0	0 1	0	1	1	1	1
6	0	0 1	0	0 1	0	0 1	0	1	0 2	0	1	0	0	0	0 1	0	0	0	1	1	1	1
7	0	0	0	2	0	0 1	0	1	2	0	0	0	0	0	0	0	0	0	1	1	1	1

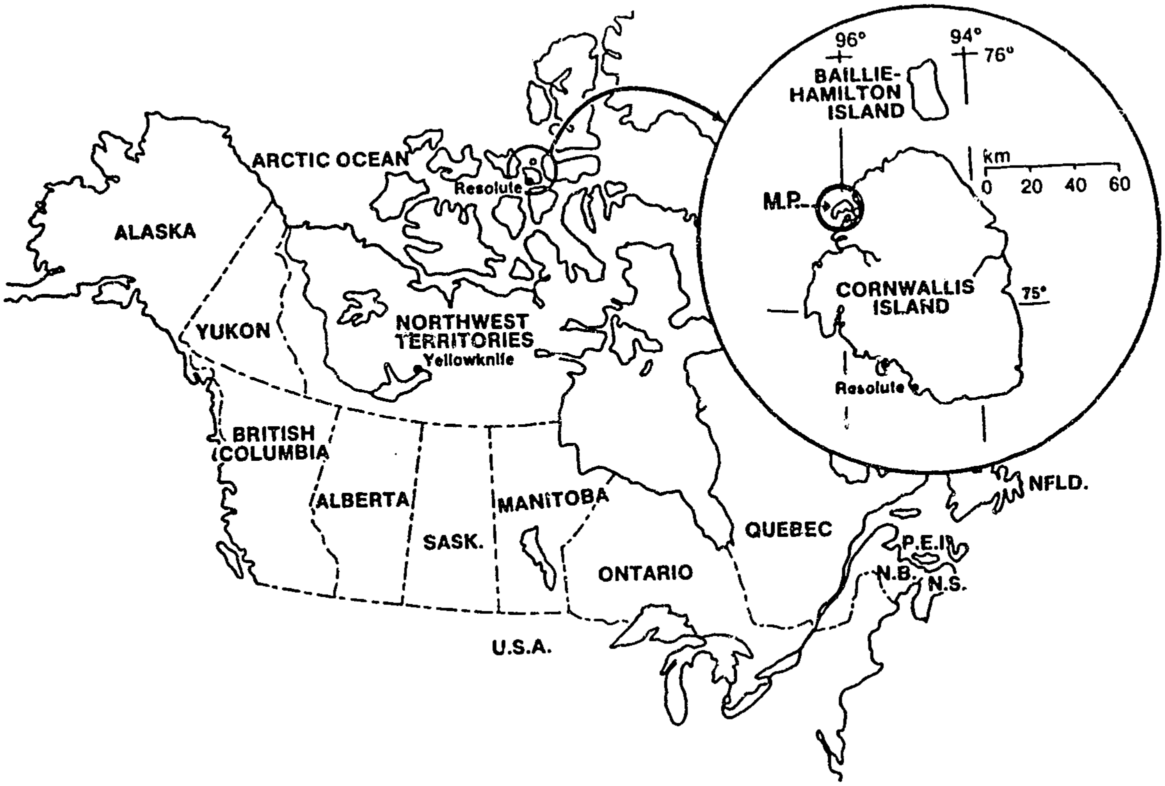


FIGURE II-1--Map showing location of the Marshall Peninsula (M. P.), from which the drift block containing the specimens described herein was collected.

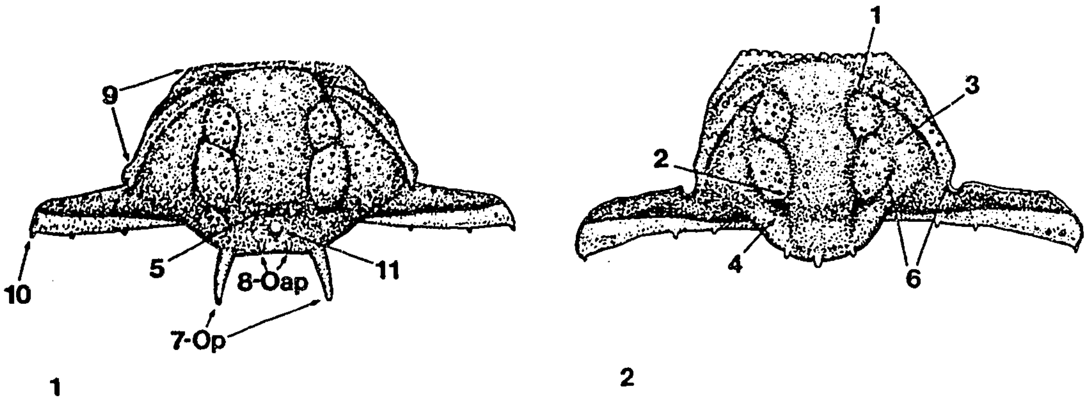


FIGURE II-2--1, dorsal view of cranidium of *Odontopleura* (*Odontopleura*) *brevigena* Chatterton and Perry, x9. 2, dorsal view of cranidium of *Odontopleura* (*Sinespinaspis*) *greenwoodi* Chatterton and Perry, x11. Numbers refer to characters listed in Table II-1. The character-states illustrated above, given as character (*brevigena* state/*greenwoodi* state), are: 1 (1/0), 2 (0/1), 3 (0/0), 4 (1/1), 5 (1/2), 6 (1/1), 7 (1/0), 8 (1/2), 9 (1/1), 10 (1/1), 11 (2/1).

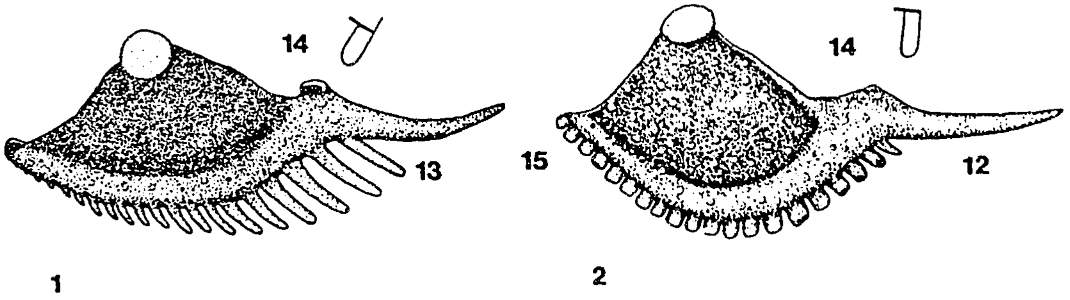


FIGURE *II-3*--*1*, external view of free cheek of *Odontopleura* (*Odontopleura*) *brevigena* Chatterton and Perry, x9. *2*, external view of free cheek of *O*. (*Sinespinaspis*) *maccallai* Chatterton and Perry, x13. Character-states, given as in Figure II-2, are: 12 (0/0), 13 (0/0), 14 (0/1), 15 (0/1). Inset, schematic cross-sections taken just forward from the genal spine base, to illustrate character 14, demonstrating the nonaligned (II-3.1) and aligned (II-3.2) states of the opposing aspects of the posterior facial suture.

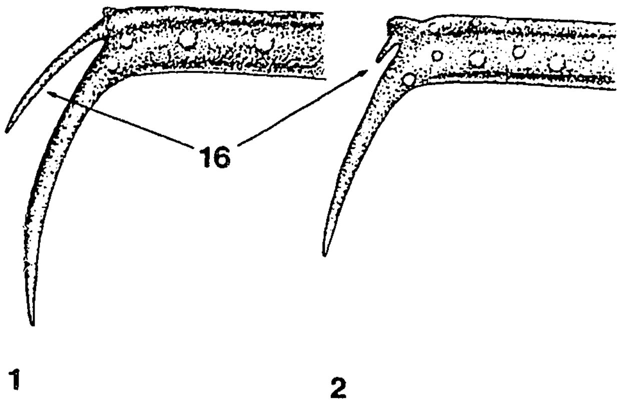


FIGURE II-4--1, Dorsal view of posterior thoracic segment of Odontopleura (Odontopleura) brevigena, x2. 2, dorsal view of posterior thoracic segment of O. (Sinespinaspis) nehedensis, x2. States of character 16, given as in Figure II-2, are (0/1).

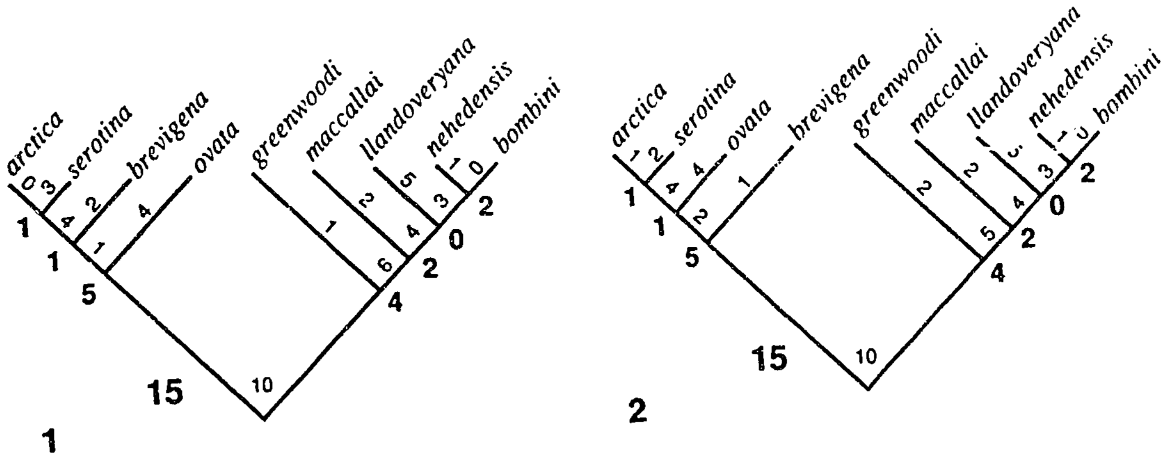
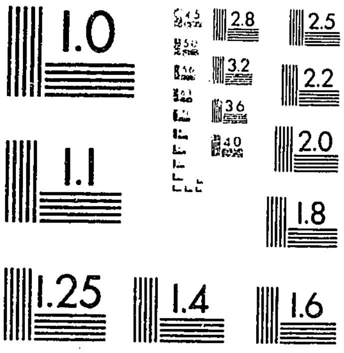


FIGURE II-5-- 1,2, Two preferred trees of the 105 possible cladograms for the 7 most parsimonious networks. Numbers on branches indicate branch lengths. Numbers beside each node indicate number of CIC (see text) accommodated at that node. Large numbers beside cladograms indicate total number of CICs accommodated. Consistency index for each cladogram is 67.4 %. Note that cladograms differ only in their relative placement of Odontopleura (Odontopleura) brevigena and O. (O.) ovata.

2



MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS
STANDARD REFERENCE MATERIAL 1010a
(ANSI and ISO TEST CHART No. 2)

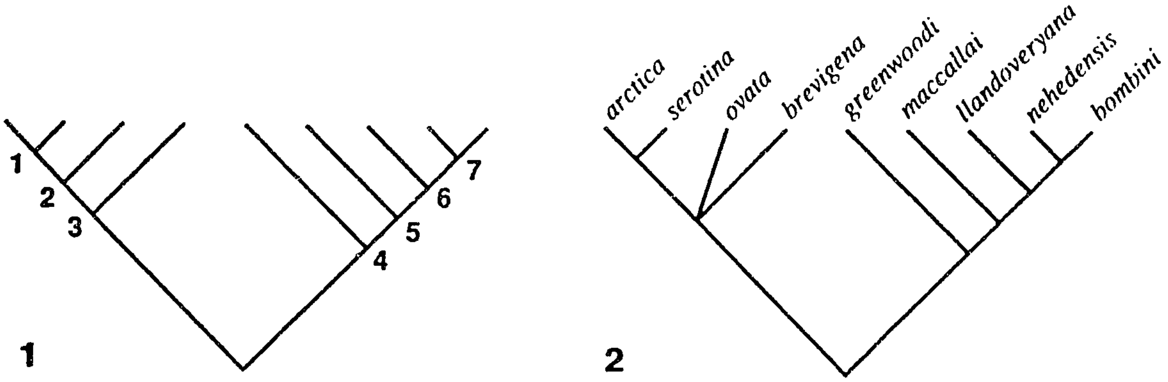
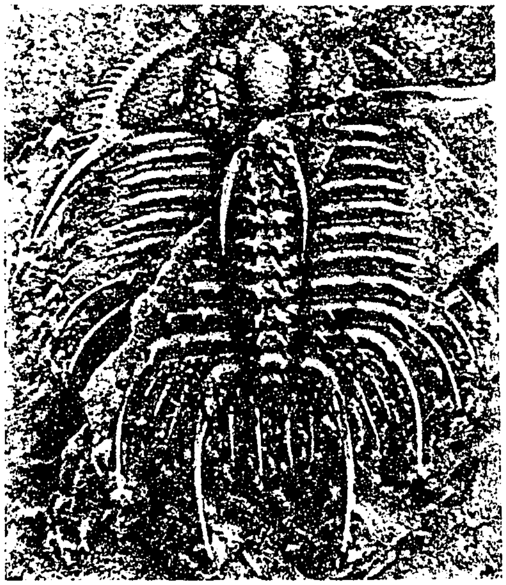
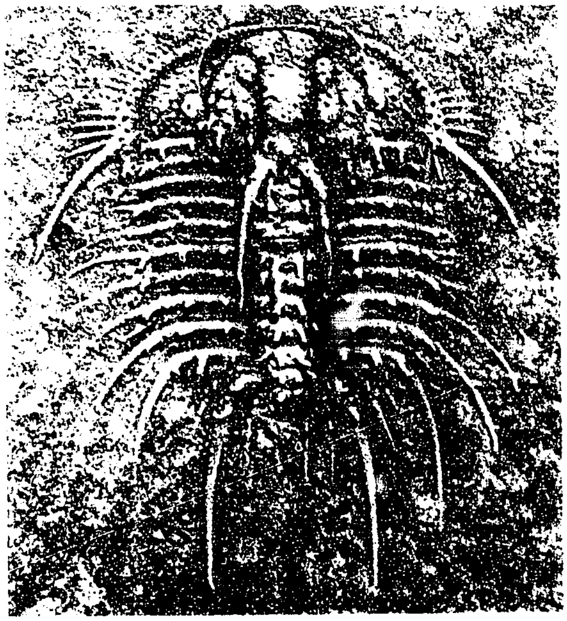


FIGURE II-6-- 1, Numbering of internal nodes of cladograms in Figure II-5.1 and II-5.2, for listing of possible character-state assignments, given in Tables II-4 and II-5. 2, Consensus cladogram derived from cladograms of Figure II-5.1 and II-5.2.

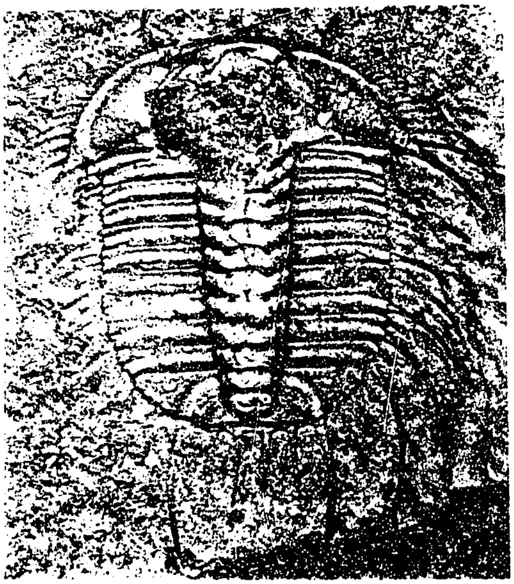
FIGURE _II-7_-- _1_-_6_, _Odontopleura_ (_Odontopleura_) _arctica_ n. sp. _1_, dorsal view, latex cast of holotype, GSC 95875, external mould of complete individual, x3. _2_, _4_, dorsal and dorsolateral views, 2 separate latex casts of paratype GSC 95876, external mould of complete individual, both x4. _3_, dorsal view, paratype GSC 95877, internal mould of complete individual, x2.5. _5_, ventral view, latex cast of paratype GSC 95878, internal and external mould of moult ensemble, x5. _6_, dorsal view, latex cast of counterpart external mould of paratype GSC 95879, pygidium with exoskeleton preserved, x5.



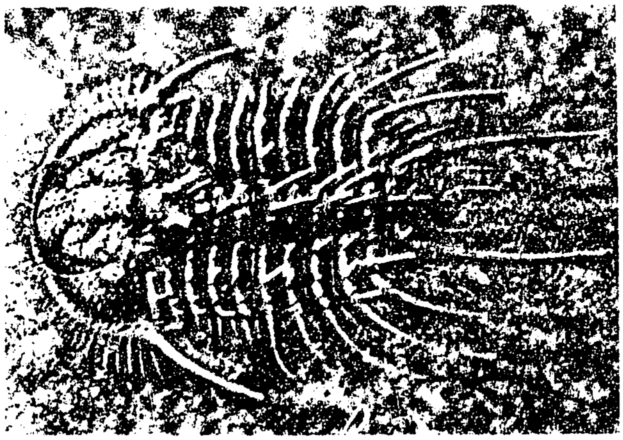
1



2



3



4

5

6

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CHAPTER III[1]

THE AULACOPLEURID TRILOBITE OTARION, WITH NEW SPECIES FROM THE SILURIAN OF NORTHWESTERN CANADA

INTRODUCTION

SILICIFIED TRILOBITES from the Whittaker Formation and Delorme Group in the southern Mackenzie Mountains, Northwest Territories, Canada, have been studied systematically by Perry and Chatterton (1979, general survey of Delorme Range faunas), Chatterton and Perry (1983, odontopleurids; 1984, cheirurids), Edgecombe and Chatterton (1990a, 1990b, 1992, encrinurids), and Edgecombe and Ramsköld (1992, encrinurids). Material from this region has also been used to illustrate works with more general themes (Edgecombe and Chatterton, 1987; Edgecombe et al., 1988; Chatterton et al., 1990a, 1990b). The current paper is the first in a series describing the aulacopleurid trilobites of these strata. Locality data follow Chatterton and Perry (1983, 1984) and Over and Chatterton (1987). The graptolite zonal scheme referred to in discussions of age is that developed by Lenz and Melchin (1990) and Lenz (1990).

OTARIONINE ONTOGENY

Otarionine trilobites share a basic pattern of juvenile paired cephalic spines that is universal throughout the

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[1] A version of this paper has been accepted for publication. Adrain, J. M., and Chatterton, B. D. E. Journal of Paleontology.

group. While these spines may be visible on well preserved protaspides, they are most fully developed in the meraspid period, usually retained but progressively reduced in the young holaspid, and often almost entirely effaced in mature individuals. Variation in development and distribution of these spines provides much information for analysis of otarionine phylogeny. Three major patterns may be recognized, the youngest of which characterizes the monophyletic tribe Otarionini.

The first pattern is developed in the oldest well known otarionine, <u>Beggaspis</u> <u>spinicaudatum</u> (Shaw, 1968), from the late Llandeilo (Chazy) of New York State (Figure III-1.1). Two major palpebral spines are developed (P1-2, numbered anteriorly), although others may be present in early ontogeny. Four major pairs of fixigenal spines (Fx1-4) are present. Fx1 is positioned just in front of the posterior border furrow, slightly adaxially to the position of the fulcrum on the thorax. Fx4 is positioned atop the universally developed eye ridge, with Fx2 and Fx3 spaced evenly between Fx4 and Fx1. A further two or more spine pairs may be developed anterior to the eye ridge in some otarionines, with opposing spines more closely spaced around the front of the glabella, and the series curving in to meet on the preglabellar field. Where necessary, numbering can be continued anteriorly. A single row of cephalic border spines is developed. <u>Beggaspis</u> <u>spinicaudatum</u> does not bear any paired glabellar spines. Whether this represents the plesiomorphic condition for Otarioninae is uncertain. It is tentatively interpreted as so, for all younger and more morphologically advanced species of the subfamily bear such spines (where ontogenies are known). Nevertheless, many potential outgroup taxa, including dimeropygids, possess paired glabellar spines, and the possibility exists that the condition seen in B. spinicaudatum was derived through secondary loss of spines.

The second major pattern is shared by all remaining otarionines with the exception of members of the Otarionini. The former assemblage is considered paraphyletic, but the pattern is characteristic of such genera as Harpidella M'Coy, 1849, Maurotarion Alberti, 1969, and various as yet unnamed forms. The major innovation over the condition seen in Beggaspis spinicaudatum is the development of three glabellar spine pairs, numbered G1-G3 anteriorly (Figure III-1.2). Two palpebral spines are retained, all fixigenal spines are retained and usually robust, and the glabellar spines are of similar size and spaced evenly along the median lobe. A single row of cephalic border spines is maintained.

The third pattern is diagnostic of the tribe Otarionini, and represents the last major innovation in aulacopleurid evolution, aside from the paedomorphic events that gave rise to the post-Devonian genera (see below).

This pattern, and the group it characterizes, is first known from the Wenlock. At the time of first appearance, the genera Cyphaspis and Otarion are distinct, as the oldest known species of each occur together at section Avalanche Lake Four, 126 m above its base. Ontogenies of these species are available. Although meraspid cranidia of the genera can be separated on several morphological grounds, the cephalic spine pattern is virtually identical. The tribe Otarionini is characterized (Figure III-1.3; see also Figures III-7 and III-9) by reduction of the palpebral spines to a single pair, partial suppression of Fx2 and Fx3 so that they are considerably smaller than Fx1 and Fx4, and shunting forward of the glabellar spines. G3 is small and anteriorly placed, crowded just in front of G2. G1 is placed nearly half the distance anteriorly along the median glabellar lobe. Furthermore, a second row of cephalic border spines is developed ventral to the major row.

Other groups in the order Proetida Fortey and Owens, 1975 also feature the development of juvenile paired spines (dimeropygids, glaphurids, cyphoproetines, "hystricurines," etc.). Analysis of spine development and topology in these groups is certainly of relevance to interpretation of patterns within Aulacopleuridae. However, many of these groups are in taxonomic disrepair, are not demonstrably monophyletic, and are somewhat haphazardly represented by well documented ontogenies. Much more work will be required before a synthesis of the spine-bearing proetides is possible.

MORPHOCLINES, PERAMORPHOSIS, AND "LINEAGES"

Chatterton and Perry (1983, 1984) have established a case for the existence of phyletic (i.e. ancestor-descendant) lineages in odontopleurid and cheirurid trilobites from the study region. Thomas et al. (1989, p. 248) have gone so far as to opine that "evolutionary lineages of closely related species potentially provide the most reliable stratigraphic control", citing Chatterton and Perry's (1983) work on odontopleurids as exemplar. It is important to note that Chatterton and Perry (1983, p. 10) expressly contested the use of morphological information alone in determining phylogenetic relationships. Their lineages were constructed and interpreted in light of an elaborate "evolutionary model," essentially an application and modification of Palmer's (1965, 1979) biomere concept.

These issues are of relevance to the present work, as three of the species of Otarion dealt with below occur in stratigraphic sequence in section Delorme Range, and could easily be envisaged as members of an ascending lineage. Otarion huddyi n. sp. occurs in the interval DR 35-52.4 m, followed by O. brauni Perry and Chatterton, 1979, at DR 114.3-147 m, and O. beukeboomi n. sp. at DR 182.9 m. Many aspects of their morphology fulfill Chatterton and Perry's (1983, p. 10) criterion of "directional morphological changes with time." Taken together, in fact, the species illustrate a pattern of peramorphic evolution which can be extended to species from elsewhere, and which appears to have governed the Silurian radiation of the genus.

Trends in which morphology shows unreversed modification upsection include: an increase in number of pygidial axial rings (from three in the oldest *O. huddyi*, to four in *O. brauni*, to five in *O. beukeboomi*, and further in Devonian species such as *O. couvinianum* Strnad, 1960, seven, and *O. arcticum* Spassky, 1989, eleven); a steady increase in degree of glabellar elongation; an increase in the depth and prominence of glabellar furrow S2; an increase in the relative length of the genal spine; an expansion of the area of the librigenal field; a steady decrease in the expression of cephalic tuberculation; a progressive effacement of the eye socle; and many more.

Of these trends, many (genal spine decrease; suppression of ornament; suppression of eye socle; etc.) are not only represented by comparison of holaspid morphology upsection, but are also incorporated into the developmental morphology of younger species. That is, the adult state of older species becomes a juvenile state in younger species. Evolution has evidently proceeded through peramorphosis, or terminal addition of states to ontogenetic sequences. Essentially, the juvenile morphologies of younger species resemble the adult morphologies of older, in a general sense "ancestral," species (compare, for example, the young holaspid cranidium of *Otarion brauni* illustrated in Figure III-8.12 with the mature *O. huddyi* cranidia of Figure III-5; also the late meraspid or young holaspid cranidium of *O. beukeboomi* of Figure III-10.16 with the mature *O. brauni* cranidia of Figure III-8).

All of these unidirectional trends, whether observably peramorphic or not, might serve to support a hypothesis of ancestor-descendant relationships in the Delorme Range *Otarion* succession. In fact, given the strong gross similarities between the species, and the sheer number of trends observable (it is scarcely possible to find morphological bases of comparison that are *not* stratigraphically correlated), the case might seem quite compelling.

If the Delorme Range *Otarion* species do form an ancestral-descendant lineage (Figure III-2.1), this tree can be represented by the cladogram shown in Figure III-2.2. A means of testing the lineage hypothesis is to see if these relationships obtain when the Delorme Range species are compared with other species from elsewhere. In order to pass the test, two requirements must be fulfilled: 1) the topology shown in Figure III-2.2 must be maintained; and 2) the species must form a clade to the exclusion of other species. If they do, the lineage finds support but is not proven (as it may yet be contradicted by new discoveries of

Otarion species). If they do not, assuming the hypothesis of relationship represented by the cladogram is accurate, the lineage is clearly incorrect. Such a test, a cladistic analysis of all well known Silurian species of Otarion, is attempted next.

ANALYSIS OF OTARION

Character list.--Description of each character is given, followed by information used to determine polarity and a list of character-states (the terms "character" and "character-state" are used as defined by Adrain and Chatterton (1990)). The case for a sister group relationship between Otarion and Cyphaspis has been outlined above and below (see section on tribe Otarionini). The oldest known species of each genus occur at the same stratigraphic horizon in the southern Mackenzie Mountains (Avalanche Lake Four, 126 m above base). Each clearly demonstrates the apomorphies of its respective genus, but the degree of overall similarity between the species is striking (the Cyphaspis species is presently unnamed). The species, and hence genera, are united by a virtually identical juvenile spine array, of the derived and highly distinctive type shown in Figure III-1.3. Taken together, these facts strongly suggest that the AV 4 126 m species represent Cyphaspis and Otarion relatively near in time to their common ancestry. As a result, this seems an ideal situation to make use of the outgroup criterion for assessing character polarity. Hence, all but two of the characters used in the following analysis are polarized, with the plesiomorphic state determined by reference to the oldest _Cyphaspis_ species. In most cases, mention is made of the distribution of the character within _Cyphaspis_. Morphoclines are hypothesized for all multistate characters. Characters in which peramorphic evolution is hypothesized can be ordered by ontogeny, and this is indicated where applicable. Finally, where the character morphocline and polarity are supported by stratigraphic first occurrences, this is mentioned. Note that this does not constitute a strict endorsement of the use of stratigraphic sequence to determine morphoclines; rather, stratigraphy is invoked in cases where it lends additional credence to morphoclines determined on outgroup or ontogenetic evidence.

Character _1_.--Degree of glabellar elongation.

States. 0-not elongate, 1-elongate.

Polarity. Outgroup, stratigraphy. _Cyphaspis_ features a short, inflated glabella. Note that state 1 "lumps" a number of progressively elongate morphologies; this character discriminates between the ancestral condition and a series of progressively derived conditions, discrete states of which are not apparent.

Character _2_.--Degree of glabellar inflation.

States. 0, strongly inflated, 1-low, only moderately inflated.

Polarity. Outgroup, stratigraphy. *Cyphaspis* always features a highly inflated glabella which overhangs the preglabellar field in dorsal orientation.

Character 3.--Depth of S2.

States. 0-shallow, not prominent dorsally, 1-deep, strong notch dorsally.

Polarity. Outgroup, stratigraphy. S2 is never prominent, and often not discernable, in *Cyphaspis*.

Character 4.--Length of preglabellar field.

States. 0-short, 1-long.

Polarity. Outgroup, stratigraphy. *Cyphaspis* typically displays a very short preglabellar field. Again, state 1 includes a variety of derived lengths; see comment under character 1.

Character 5.--Median node on preglabellar field.

States. 0-not evident on dorsal surface, 1-prominent.

Polarity. Outgroup. This feature is never developed in *Cyphaspis*.

Character 6.--Width of interocular fixigena. Point of comparison is directly adaxial to midlength of palpebral lobe.

States. 0-narrow, 1-wide.

Polarity. Outgroup. *Cyphaspis* typically shows the palpebral lobe almost abutting the glabella, with the interocular fixigena greatly narrowed.

Character 7.--Area of librigenal field.

States. 0-small, 1-moderate, 2-large.

Polarity. Outgroup, stratigraphy. The librigenal field is small in all Cyphaspis.

Character 8.--Length of genal spine.

States. 0-longer than remainder of free cheek, excluding anterior projection, 1-about two thirds length of remainder of cheek, 2-about one half length of remainder of cheek.

Polarity. Outgroup, stratigraphy, ontogeny. The genal spine is universally longer than the remainder of the free cheek in Cyphaspis. Otarion brauni shows reduction in genal spine length in ontogeny.

Character 9.--Tuberculate ornament on librigenal field.

States. 0-easily discernible on mature holaspides, 1-almost wholly effaced in mature holaspides.

Polarity. Outgroup, stratigraphy, ontogeny. Cyphaspis is always highly tuberculate. All known Otarion ontogenies show reduction in tubercle expression between late meraspides or early holaspides and mature holaspides.

Character 10.--Degree of effacement of eye socle.

States. 0-all lobes prominent, not effaced, 1-partially effaced, anterior lobe always discernable, 2-nearly completely effaced.

Polarity. Outgroup, stratigraphy, ontogeny. The eye socle is never effaced in Cyphaspis. The eye socle loses definition in the ontogenies of both Otarion huddyi and O.

brauni.

Character 11.--Height of eye. Comparisons should be in exact lateral view.

States. 0-high, about one half height of glabella, 1-low, only reaching base of glabella.

Polarity. Outgroup, stratigraphy. The eye of *Cyphaspis* is very high, and has often been characterized as "stalked."

Character 12.--Number of pygidial axial rings. This character is subject to intraspecific variation, as some individuals may display a single tiny, incipient ring in addition to the number coded. The number coded, however, is the minimum number developed within the species and is always by far the most common. Coding is therefore not considered equivocal in any cases.

States. 0-3, 1-4, 2-5.

Polarity. Outgroup, stratigraphy. Three pygidial axial rings are a universal feature of Silurian (and most Devonian) *Cyphaspis* species.

Character 13.--Definition of pygidial axis posteromedially.

States. 0-poorly defined, axial furrows effaced posteriorly and not meeting posteromedially, 1-axial furrows meeting posteromedially to fully define axis.

Polarity. Unordered. While *Cyphaspis* holaspides generally feature state 0, ontogenies of *Otarion* species with state 0 invariably show progressive effacement of the posteromedial area with maturity (compare, for example, the young holaspid pygidium of *O. huddyi* illustrated in Figure III-7.8 with the mature pygidia of Figure III-6.24 and III-6.28).

Character 14.--Degree of anterior divergence of preocular facial sutures.

States. 0-subparallel, not widely divergent, 1-prominently divergent.

Polarity. Unordered. Silurian *Cyphaspis* species demonstrate a range in variation in this character similar to that observed in *Otarion*.

Character 15.--Prominent smooth area along anterior edge of glabellar furrow S1.

States. 0-absent, 1-present.

Polarity. Outgroup. S1 is much reduced in most *Cyphaspis* species, with little suppression of the glabellar ornament over this muscle attachment site.

Results of analysis.-- All of the satisfactorily known Silurian species of *Otarion* were included, numbering only seven (including an as yet undescribed species from Arctic Canada shown as *Otarion* n. sp. A). The data matrix is shown in Table III-1. The data were run on PAUP, version 3.0g (Swofford, 1989). Given the low number of taxa analyzed, it was possible to make use of PAUP's exhaustive search option, in which all possible trees connecting the taxa are examined. A single minimal length tree was obtained (Figure

III-3).

The Delorme Range species are marked with an asterisk on Figure III-3. The first requirement of the test has been met: the topology of the three-taxon statement of Figure III-2.2 is incorporated in the cladogram. The second requirement, however, has not been met. Each Delorme Range species is more closely related to a species or species from elsewhere in the world than to any of the other Delorme Range species. The Delorme Range *Otarion* species do not form a clade excluding all other species. Clearly, if this pattern of relationship is correct, the possibility of the existence of a phyletic lineage linking the Delorme Range *Otarion* species has been eliminated.

We would therefore like to emphasize that phyletic lineages, no matter how compelling they may seem, should only be hypothesized with a consideration of wider phylogenetic context. Ancestor-descendant lineages in which sister-taxon relationships are not preserved when additional species are considered are demonstrably incorrect.

SYSTEMATIC PALEONTOLOGY

Taxonomic philosophy.--The theoretical requirement that taxa be monophyletic can no longer be seriously contested (Edgecombe and Chatterton, 1990b; Fortey, 1990; Ramsköld and Werdelin, 1991). In trilobite systematics, however, theory and practice, especially at the generic level, remain very far apart. Particular problems are the use of separate generic classifications for different time periods (e.g., Upper Ordovician and Silurian; see Ramsköld, 1991) and the recognition of monotypic genera based on autapomorphies (e.g., Rhinotarion Whittington and Campbell, 1967, which creates paraphyly in Harpidella).

While the recognition of paraphyla should be avoided, it is often desirable to recognize limited monophyletic radiations within genera, particularly when they are diagnosible through a host of distinctive apomorphies. Recognition of these subgroups, however, may leave a series of species which nest as progressive sister groups to the smaller monophyletic unit of interest. As opposed to demanding separate supraspecific names for each of these, and hence a series of monotypic genera or subgenera, the use of non-obligate subgenera is advocated herein. What this means is that subgenera should be used only to recognize monophyletic subunits of a genus. Species which are included in the genus but excluded from these subunits (and which therefore do not form a monophyletic group) should simply be assigned the generic name, with no misleading subgeneric assignment. Essentially, it is argued that the use of subgeneric names within a genus should not of necessity entail the assignment of all species to a subgenus. Only those subsets of a genus that are monophyletic should be recognized as subgenera. The same reasoning is used below to support the recognition of the most highly derived clade of the subfamily Otarioninae as the tribe Otarionini, in the absence of a corresponding tribe for the remainder of the subfamily.

Terminology.--Terms are applied following guidelines for the revised edition of the Treatise on Invertebrate Paleontology, Part O. Jell (1978, fig. 3B) proposed to refer to the ridge-like caecal structure found on the librigenal field of many trilobites as the genal artery. This term is somewhat assumption-laden, as it refers to one hypothesis of function. We prefer the neutral term "genal trunk". A second type of prominent caecal trunk occurs often in aulacopleurids (including Otarion), running from the adaxial end of the eye ridge towards beta.

Order PROETIDA Fortey and Owens, 1975

Superfamily AULACOPLEUROIDEA Angelin, 1854

Family AULACOPLEURIDAE Angelin, 1854

Discussion.--Thomas and Owens (1978) recognized two subfamilies of aulacopleurids, Aulacopleurinae (which included all of the trilobites traditionally assigned to the group) and Scharyiinae Osmólska, 1957. Pribyl and Vanek (1981) recognized four aulacopleurid subfamilies: a monotypic Aulacopleurinae; Otarioninae, which included most conventional aulacopleurids; Brachymetopinae; and Cyphaspidinae. Siveter (1989) discussed the contrasting schemes, but followed the classification of Thomas and Owens (1978). Owens (in Owens and Hammann, 1990) has since revised the concept of Scharyiinae, transferring most of the genera to his new Rorringtoniidae, and assigning Scharyiinae to the Brachymetopidae.

An assessment of higher aulacopleuracean interrelationships is beyond the scope of this paper, but Owens' (in Owens and Hammann, 1990) concept of the scope of the family is essentially that adopted herein, with exceptions discussed below. Pribyl and Vanek's (1981) separation of *Aulacopleura* into a separate subfamily, however, is followed. The subfamily Aulacopleurinae includes also the genus *Songkania* Chang, 1974, and will be the subject of a forthcoming work.

Subfamily OTARIONINAE Richter and Richter, 1926

Diagnosis.--Aulacopleurid trilobites with prominent paired cranidial spines or tubercles and one or two rows of cephalic border spines in meraspid period, sometimes retained in holaspid; thick, dorsally convex cephala; elongate median occipital spine sometimes developed; hypostome subquadrate, with prominent middle furrow and lateral or (usually) posterior pair of border spines; 14 or less thoracic segments, often with axial spine on segment six or seven; usually micropygous.

Genera included.--*Beggaspis* Pribyl and Vanek, 1981; *Cyphaspis* Burmeister, 1843; *Dixiphopyge*? Brezinski, 1988; *Harpidella* M'Coy, 1849; *Maurotarion* Alberti, 1969; *Namuropyge* Richter and Richter, 1939; *Otarion* Zenker, 1833;

Otarionides? Alberti, 1969.

Discussion.--The nature and content of *Harpidella* (with synonym *Rhinotarion* Whittington and Campbell, 1967), and the validity of *Maurotarion* (with synonyms *Tricornotarion* Chatterton, 1971, *Malimanaspis* Baldis and Longobucco, 1977, and *Branisella* Pribyl and Vanek, 1981) will be discussed in a forthcoming work.

Cyphaspides Novák, 1890 (synonym *Protocyphaspides* Pribyl and Vanek, 1976) has long been regarded as an aulacopleurid. No species of *Cyphaspides*, which is a Gondwanan endemic, are at all well known. Few aspects of its morphology, however, convincingly suggest a relationship with aulacopleurids. It does not seem well established that the taxon even belongs in Proetida. In any event, much more information will be required before the genus can be assessed in a meaningful way, and it is at present excluded from further consideration.

Pseudotrinodus Kobayashi and Hamada, 1971 was erected for a single very poorly known species from the Devonian of Malaysia. The original assignment was to the Agnostida, but Thomas and Owens (1978, p. 74) argued that *P*. *aenigma* was in fact an aulacopleurid. The only actual evidence in support of this classification was that the *Pseudotrinodus* cephalon "resembles those of certain aulacopleurids - especially species such as *Cyphaspis* (s.l.) *stigmatophthalmus* Richter, 1914." Again, the assignment to the family is by no means unequivocal, and until more information surfaces it is perhaps best regarded as Proetida *incertae sedis*.

The type species of *Otarionella* Weyer, 1965, *Cyphaspis davidsoni* Barrande, 1852, has been illustrated by Horný and Bastl (1970, Pl. 12, fig. 5), and was assigned to *Otarion* (*Conoparia*) by Pribyl and Vanek (1981). This Early Devonian species is clearly a paedomorph, as it retains its juvenile cephalic spine array in the holaspid. Thomas and Owens (1978, p. 73) have made the point that "...it is probable that spinosity has developed independently in several lineages." Given the demonstration herein that the spinose morphology is paedomorphic, this seems certainly to be true, and the currently accepted concept of *Otarionella*, essentially including any otarionines with prominent cephalic border spines, is undoubtedly polyphyletic. *Otarion davidsoni* falls in a group, discussed below, with gross morphology similar to the type species of *Conoparia*, *C. convexa* Hawle and Corda, 1847. This morphology itself is clearly paedomorphic (see below). Hence, neither *Otarionella* nor *Conoparia* can be supported as monophyletic units of *Otarion*, and the names should therefore be treated as subjective junior synonyms of the latter genus.

Otarionides Alberti, 1969 was erected as a monotypic subgenus of *Otarion*. The type species, *Otarionides franconicum*, is very poorly known, but has a distinctive morphology of very wide fixed cheeks, prominent Fx4, and small or perhaps even absent palpebral lobes. The holotype (Alberti, 1969, Pl. 34, fig. 8) appears to retain G1-G3 with even spacing, and thus the species probably does not belong within the Otarionini (see below). Beyond this assertion, Otarionides is impossible to evaluate, and shall remain so until its type species is better known. Its status is therefore ambiguous, and it is recognized with question herein.

The genus Namuropyge Richter and Richter, 1939, has traditionally been assigned to Brachymetopidae or more commonly Aulacopleuridae. Owens (1986, p. 6) reviewed the history of Namuropyge's classification and followed Thomas and Owens' (1978) assignment to Aulacopleuridae. Little explicit character information, however, has been put forward to support this classification. Problematic features of the genus include the presence of large spines developed over parts of the exoskeleton, a low number of thoracic segments (six or seven), and a pygidium whose morphology is unlike that seen in any older aulacopleurid holaspides.

With a new understanding of otarionine ontogeny, all of these features are easily explained, and Namuropyge can be assigned with confidence to the Otarioninae, and specifically to the Otarionini. Namuropyge (Figure III-4) bears a single palpebral spine, two rows of cephalic border spines, and glabellar spines with the spacing and position only slightly altered from that seen in meraspides of *Otarion* and *Cyphaspis* (Figure III-1.3; see also Figures III-7 and III-9). G3 has been shifted slightly forward, while G2 and G1 have each fused into a single median spine or tubercle. This latter development is paralleled elsewhere in the species *Maurotarion struszi* (Chatterton, 1971), in which all three glabellar spine pairs are fused medially, with the process of fusion observable through early ontogeny. In addition, *Namuropyge* cf. *N. cuyahogae* (Claypole, 1884) of Brezinski (1988, fig. 3.16, 3.17) seems to retain G1 and G2 as unfused spine pairs. The pygidium resembles transitory pygidia of older species, with a row of border spines, and a second more proximal row of fulcral spines (compare Owens, 1986, Pl. 2, figs. 10-13 with Figure III-7.7, III-7.9). Finally, the presence of only six or seven thoracic segments leaves little doubt that *Namuropyge* originated through paedomorphosis from a Degree Six or Seven meraspid of a conventional, probably Devonian, member of the Otarionini.

The task of determining which older group gave rise to the *Namuropyge* clade remains. This is often a problem with paedomorphic taxa, as their morphology is by definition juvenile, generalized, and plesiomorphic. The only firm indication available is *Namuropyge*'s relatively long glabella (see Owens, 1986, Pl. 2, fig. 2b), which might indicate it was derived from a member of *Otarion*. If this hypothesis could be more strongly supported, classification of the Otarionini would need to be revised to reflect monophyly of the clades identified. With only two Siluro-Devonian genera currently assigned to the tribe, and with a considerable stratigraphic interval (Givetian to Chadian) separating them from *Namuropyge*, it seems preferable to retain the latter as a distinct genus, while recognizing the need for further work as more data become available.

Brezinski (1988) has recognized a second potential post-Devonian aulacopleurid, *Dixiphopyge*, from Kinderhookian strata in Missouri. While poorly known, *Dixiphopyge armatus* (Vogdes, 1891) shares several morphological features with *Namuropyge*. Most compelling is the structure of the pygidium, which differs mainly through possession of a greater number of segments. Brezinski (1988, p. 104) pointed out the similarity of the cranidium to that of *Cyphaspis*, with which it shares a strongly inflated glabella that overhangs a very short preglabellar field. The structure of L1 in *Dixiphopyge* is not similar to that of *Cyphaspis*, as S1 is broad and shallow, and L1 is relatively large, with considerable transverse extent (Brezinski, 1988, fig. 1.4). In addition, the paired occipital spines developed in *Dixiphopyge armatus* are without precedent in Aulacopleuridae. Much more information is necessary before an unequivocal assignment of the taxon can be made. Its similarity to *Namuropyge*, and the implication of an analagous origin, are the reasons for assignment of *Dixiphopyge* with question to the Otarionini herein (see below). If this assignment can be confirmed, the same problems of classification created by *Namuropyge* will arise (see above).

Tribe OTARIONINI Richter and Richter, 1926

Genera included.--*Cyphaspis* Burmeister, 1843; *Namuropyge* Richter and Richter, 1939; *Otarion* Zenker, 1833; ?*Dixiphopyge* Brezinski, 1988.

Diagnosis.--Otarionines with juvenile cephalic spine array of single P1; Fx2 and Fx3 suppressed; G3 and G2 crowded toward the anterior of the glabella, with G1 positioned just posterior to the glabellar midlength (sag.); and two rows of cephalic border spines.

Discussion.--The highly distinctive juvenile morphology is reflected in all known ontogenies of taxa assigned to the tribe (most are unpublished, but see Chatterton (1971, Pl. 18, figs. 13, 17) for *Cyphaspis dabrowni*, herein for members of *Otarion*, and Owens (1986) for *Namuropyge*, in which the array is maintained in holaspides). It stands in contrast to the more general and less derived condition shown in Figure III-1.2, characteristic of most other otarionines (e.g., species of *Maurotarion* illustrated by Whittington and Campbell, 1967). Note that the group of genera defined by inclusion in the Otarioninae but exclusion from Otarionini is almost certainly paraphyletic, and is therefore not given an equivalent tribe name. This, however, does not preclude the possibility of the recognition of further monophyletic tribes among them pending additional work.

Genus OTARION Zenker, 1833

Conoparia HAWLE AND CORDA, 1847.

Otarionella WEYER, 1965.

Type species.--Otarion diffractum Zenker, 1833, from the Kopanina Fm. (Ludlow), Bohemia, Czechoslovakia.

Annotated species list.--The format of this list follows that of Ramsköld and Werdelin (1991, p. 70-74). Information is given in the following order: name; author; date; original generic designation; age; formation; area; remarks. The list includes all valid species of Otarion, together with several questionable assignments and nomina dubia.

?akkae Alberti, 1969; Otarion (Otarion); Pragian, northwest Africa; single cranidium; nomen dubium.

arcticum Spassky, 1989; Otarion; Lower Devonian, Arctic Russia; two cranidia, two pygidia.

beukeboomi n. sp.; Otarion; latest Wenlock or earliest Ludlow, Delorme Group, southern Mackenzie Mountains, Northwest Territories, Canada; cranidia, free cheeks, hypostome, pygidia.

brauni Perry and Chatterton, 1979; Otarion; Wenlock, Delorme Group, southern Mackenzie Mountains, Northwest Territories, Canada; cranidia, free cheeks, hypostomes, thoracic segment, pygidia.

convexa Hawle and Corda, 1847; type species of Conoparia; Pragian, Dvorce-Prokop Limestone, Bohemia, Czechoslovakia; Šnajdr (1983, p. 147, Pl. 6, fig. 3) has discussed the species and refigured the holotype; Erben (1952) listed the species from the Harz Mountains, Osmólska (1957) from Poland; single cranidium.

conveximarginatum Kuo, 1962; subspecies of Otarion diffractum; Wenlock or Ludlow, Er-tao-gou Group, Jilin, China; cephala, pygidium; known from molds, latex casts of which have never been figured; probably Otarion, and certainly specifically distinct from Otarion diffractum.

coppinsensis n. sp.; Otarion; Wenlock, limestones interbedded with Walker Volcanics, near Coppins Crossing, New South Wales, Australia; cephala, pygidium; see Chatterton and Campbell (1980).

coriolan Šnajdr, 1984; Otarion; Prídolí, Prídolí Formation, Beroun, Bohemia, Czechoslovakia; single cranidium.

couvinianum Strnad, 1960; Otarion (Otarion); upper Eifelian, Stínava-Chabicov Formation, Horní Benešov, Moravia, Czechoslovakia; revised by Chlupác (1969); cranidia, thorax, pygidia.

davidsoni Barrande, 1852; Cyphaspis; Eifel, Suchomasty Limestone, Koneprusy, Bohemia, Czechoslovakia; type species of Otarionella Weyer, 1965; lectotype cephalon figured by Horný and Bastl (1970, Pl. 12, fig. 5) and Pribyl and Vanek (1981, Pl. 3, fig. 17).

hollandi Siveter, 1989; *Conoparia*; Wenlock or Ludlow, Annascaul Formation, Dingle Peninsula, County Kerry, Ireland; cranidia, free cheeks, pygidium; herein a questionable subjective junior synonym of *Otarion brauni*.

huddyi n. sp.; *Otarion*; Wenlock, Delorme Group, southern Mackenzie Mountains, Northwest Territories, Canada; cranidia, free cheeks, hypostomes, thorax, pygidia.

hystrix Haas, 1968; *Otarion* (*Otarion*); Pragian, several units, northwest Turkey; cranidia, free cheek, hypostome, pygidia.

inculpatum Pribyl and Vanek 1981; *Otarion* (*Conoparia*); Wenlock, Liten Formation, Bohemia, Czechoslovakia; the holotype of this species, a poorly preserved internal mold of an articulated exoskeleton, has eleven thoracic segments, a small pygidium with three axial rings, and a highly inflated glabella with a short preglabellar field, all of which indicate a member of *Cyphaspis*; two other cranidia were assigned, but they seem unlikely to be conspecific with the holotype, or even with each other; Šnajdr (1984) reported that one of them (Pribyl and Vanek, 1981, Pl. 8, fig. 7) was of Pragian age; *nomen dubium*.

lacrimarum Pribyl and Vanek 1981; *Otarion* (*Otarion*);

Dalejan, Acanthopyge Limestone, Bohemia, Czechoslovakia; two internal molds of cranidia.

latum Alberti, 1967; *Otarion* (*Otarion*); Pragian, northwest Morocco; two cranidia.

ofelia Šnajdr, 1984; *Conoparia*; Prídolí, Prídolí Formation, Bubovice, Bohemia, Czechoslovakia; impossible to meaningfully assess, although the single specimen evidently should be assigned to *Otarion*; single incomplete cranidium; *nomen dubium*.

regificum Pribyl and Vanek, 1981; *Otarion* (*Conoparia*); Pragian, Dvorce-Prokop Limestone, Bohemia, Czechoslovakia; three cranidia, one free cheek, one pygidium.

rigunthis Pribyl and Vanek, 1981; *Otarion* (*Conoparia*); Dalejan, Trebotov Limestone, Bohemia, Czechoslovakia; four cranidia, one free cheek.

rusticor Pribyl, Vanek, and Hörbinger, 1985; *Otarion* (*Otarion*); Ludlow, Kopanina Formation, Kosov Quarry, near Králuv Dvur, Bohemia, Czechoslovakia; the holotype cranidium (Pribyl et al., 1985, Pl. 2, fig. 1) probably belongs to *Cyphaspis*; the pygidia assigned to this species seem to belong to *Otarion diffractum*; *nomen dubium*.

seligra Šnajdr, 1984; *Conoparia*; Ludlow, Kopanina Formation, Dlouhá hora, near Beroun, Bohemia, Czechoslovakia; regarded herein as a junior subjective synonym of

Otarion diffractum.

tafilaltense Alberti, 1967; *Otarion* (*Otarionella*); Emsian, southeast of Erfoud, northwest Sahara; two cranidia.

testificatum Pribyl, Vanek, and Hörbinger, 1985; *Otarion* (*Conoparia*); Ludlow, Kopanina Formation, Kozolupy, near Beroun, Bohemia, Czechoslovakia; single incomplete cranidium, single pygidium; *nomen dubium*.

?*validum* Alberti, 1969; *Otarion* (*Otarion*); Pragian, northwest Africa; single cranidium; *nomen dubium*.

verrucosum Hawle and Corda, 1847; *Conoparia*; Ludlow, Kopanina Formation, Kolednik, Bohemia, Czechoslovakia; lectotype selected and figured by Šnajdr (1983, p. 201, Pl. 15, fig. 10); herein considered a junior subjective synonym of *Otarion diffractum*.

Diagnosis.--Glabella only moderately inflated, usually elongate, never overhanging preglabellar field and anterior border; preglabellar field moderately long; cephalic tuberculation generally subdued; librigenal field broad, caeca prominent, and cephalic ornament commonly reduced or absent; genal spine short, posteroventrally directed; thorax of twelve or thirteen segments, axial spine invariably present on sixth; pygidia with three to eleven axial rings, usually with transverse rows of tubercles restricted to anterior segments; pygidium large (for subfamily) relative to cephalon; pygidium wide relative to length (sag.); pygidial doublure narrow.

Discussion.--Diagnosis of *Otarion* is complicated by its long stratigraphic range and the variety of morphologies developed within it. Characters of the monophyletic tribe including *Otarion* and *Cyphaspis* are given above; the generic diagnosis is directed towards separating *Otarion* from *Cyphaspis*. In the following comparison, it is important to bear in mind that the type species of *Cyphaspis*, *C. ceratophthalma*, is a derived Devonian member of the clade. In several respects it is not representative of the common, less derived, morphology of the group (e.g., it possesses a non-tuberculate pygidum with four or five axial rings versus the much more common three). The following differential diagnosis accounts primarily for contrasts among the bulk of species, nearer in time to the divergence of the genera. It does not necessarily account for possible convergences in the Devonian.

Otarion is distinguished from *Cyphaspis* by the possession of twelve or thirteen versus eleven thoracic segments; a less inflated glabella; a generally longer preglabellar field; generally broader fixed cheeks; free cheeks with broader, longer genal fields; shorter, less robust genal spines; the absence of the prominent development of the genal trunk seen in many members of *Cyphaspis*; pygidium larger relative to cephalon, generally with more than three versus commonly three axial rings; pygidium wider relative to length, with tuberculation usually restricted to anterior part as opposed to usually robustly developed on axial rings and pleural bands of all three segments; pygidial doublure distinctly narrower.

Conoparia Hawle and Corda, 1847 was long considered a synonym of *Otarion*, but was reestablished as a valid subgenus by Pribyl and Vanek (1981). Pribyl and Vanek included a tremendous number of poorly known, morphologically disparate species in their concept of the taxon. More recently, Siveter (1989) has considered *Conoparia* to be a separate genus. Although he did not specify any morphological criteria for recognition of the group, Siveter (1989, p. 120) implied that it included the species *elachopos* Thomas, 19[illegible], *horani* Etheridge and Mitchell, 1893 (not Chatterton, 1971, as given by Siveter), and *tridens* Ingham, 1970. The first two belong in *Cyphaspis*, and will both be dealt with by us in a forthcoming work on that genus. "*Otarion*" *tridens* is poorly known, but likely belongs in *Beggaspis* Pribyl and Vanek, 1981, as Ingham (1970) outlined resemblances to the contemporaneous type of that genus, *B*. *tenuis* (Kielan, 1960). It certainly bears none of the apomorphies of any genus of the Otarionini as understood herein.

Although not recognized by the above workers, there is a group of Silurian and Devonian species with cranidial morphologies very similar to the type of *Conoparia*, *C*. *convexa*. This group includes *Otarion* *huddyi* n. sp., *O*.

hystrix Haas, 1968, *O. davidsoni* (Barrande, 1852), and several of the poorly known species described as *Otarion* (*Conoparia*) by Pribyl and Vanek (1981; see species list above). All are species with non-elongate glabellas, prominent palpebral lobes, short preglabellar fields, small librigenal fields, and relatively long genal spines. A case could therefore be made for recognition of *Conoparia* at either the subgeneric or generic level. The shared morphology forming the basis for the taxon, however, is considered herein to be plesiomorphic. This is supported by reference to the ontogenies of Silurian species, in which the "*Conoparia* morphology" seen in *O. huddyi* transforms with maturity to the "*Otarion* morphology" seen in younger species including the type. In addition, the Devonian species demonstrating the "*Conoparia* morphology" typically retain their juvenile cephalic spine array in holaspid stages (and as a result many have been artificially grouped in *Otarionella*). This retention strongly supports the notion that these species had a paedomorphic origin, in which trilobites with an advanced "*Otarion* morphology" were arrested at a "*Conoparia*" stage of development. Hence, while the *Conoparia* group would be morphologically coherent, it would almost certainly be polyphyletic, and would create paraphyly in *Otarion*. *Conoparia* is therefore regarded as a subjective junior synonym of *Otarion*.

OTARION HUDDYI n. sp.

Figures III-5 to III-7

Otarion sp. PERRY AND CHATTERTON, 1977, p. 292, Pl. 6, fig. 26.

Diagnosis.--Otarion with preglabellar field short; fixed cheeks adaxial to middle of palpebral lobe subequal in width (trans.) to L1; eyes relatively high, raised to about half maximum height of glabella in lateral view; palpebral lobes relatively large; free cheek with genal field about as tall as long (exsag.); genal spine longer than remainder of cheek, excluding anterior projection; eye socle prominent; thorax of twelve segments; pygidium with width three times length; three axial rings, often with incipient fourth; prominent tubercles on first posterior pleural band, on proximal part of second, and rarely on third; tubercles on first and second axial rings, rarely on third; only first pleural furrow deeply impressed; pleural and interpleural furrows becoming increasingly effaced posteriorly.

Description. Cranidium. Cranidium subquadrate in palpebral view, length (sag.) subequal to width across palpebral lobes; anterior branches of facial suture anteriorly convergent immediately in front of palpebral lobes, moderately anteriorly divergent from half distance to anterior border furrow; anterior margin and anterior border furrow both with inverted "V" shape; anterior border with gentle dorsal convexity, long (sag., exsag.), and of similar length medially and laterally; preglabellar field with dorsal convexity independant of that of glabella, ornament of closely set, fine, caecal pits and few to many small, scattered tubercles; preglabellar field approx. 1.5 times length of anterior border in sagittal profile; palpebral lobes of small to moderate size, surface smooth except for very small pit at midlength near lateral margin and single slightly adaxially placed tubercle set near center of lobe; fixigena opposite palpebral lobe narrow, with prominent transverse convexity, ornament of scattered tubercles of larger size than those on preglabellar field; caecal pits not developed on fixigenae; glabella in palpebral view with maximum width across L1 approx. 90 percent of sagittal length (excluding occipital ring); axial furrows displaced laterally around L1, subparallel in front of L1; preglabellar furrow describing strong anteriorly directed arc; row of small fixigenal tubercles lining abaxial side of axial furrows; glabella ornament of evenly distributed tubercles, of largest size developed on cranidium; tubercles sparse in stratigraphically low individuals, dense to very dense in most specimens; L1 elongate, usually with ornament of many small tubercles, much smaller than those on median lobe; S1 deep, shallowing posteriorly before contact with occipital furrow; S2 visible dorsally as very subdued notch opposite anterior half of palpebral lobe; S3 not apparent; posterior branches of facial suture slightly posteriorly divergent behind palpebral lobe, then strongly divergent across posterior border furrow and posterior border; occipital furrow deep, depth similar to axial furrow and anterior part of S1; posterior border furrow curving posteriorly initially, then describing broad anteriorly directed arc, distal part running alongside small sutural ridge; occipital ring slightly shorter (sag., exsag.) than anterior border, ornament varying from almost smooth to densely tuberculate; when present, tubercles concentrated near posterior margin; subdued median tubercle present on all specimens; posterior border usually smooth, sometimes with a few very low tubercles in a transverse row.

Librigena. Field with height 55-60 percent length in external view; eye small; eye socle of two swollen lobes, anterior lobe larger and more prominent; field with ornament of dense caecal pits, tubercles subdued to absent in mature individuals; prominent genal trunk running from rear of anterior lobe of eye socle to genal angle; posterior border furrow deeper than shallow lateral border furrow; posterior border, base of genal spine, and lateral border subequal in width; very faint furrow running dorsally on genal spine, strongest near genal angle; genal spine slightly longer than remainder of librigena, tapering gently to sharp point; genal spine with strong basal curvature in ventrolateral view; borders and genal spine smooth dorsally; lateral border with fine, close-set, parallel ridges developed laterally and ventrally; doubure broader anteriorly than posteriorly.

Rostral plate. Rostral plate triangular; anterior margin with small median anterior inflection; connective sutures long, transversely set, meeting posteromedially; fine ridges of librigenal doublure continuous across connective sutures.

Hypostome. Hypostome with length (sag.) approx. 90 percent maximum width across anterior wings; anterior margin with strong anterior convexity, turned ventrally to form ventral "lip"; anterior wings not strongly laterally displaced, subquadrate but tapering laterally, and with prominent centrally placed pit; lateral margins subparallel behind anterior wings, displaced laterally around prominent shoulder; posterior margin transversely straight; small spines developed at posterolateral corners; middle body smooth, with gentle ventral inflation; middle furrow placed about two thirds distance posteriorly, with strong posterior convexity; lateral border with ornament of fine ridges, subparallel to lateral margin; lateral and posterior border furrows of similar depth as middle furrow; doublure not developed anterior to shoulder, narrow posteriorly; very small posterior wings running dorsomedially from shoulder.

Thorax. Thorax of twelve segments, widest at segment four, tapering rapidly posteriorly; thoracic axial spine on sixth segment, probably extending posteriorly slightly past pygidium; spine leaving thorax at approx. 45 degree angle in sagittal profile, with even posteroventral curvature; axial lobe slightly narrower than pleural lobe; axial furrow shallow; ring furrow deep; articulating half-ring lacking preannulus, longest medially; pleural furrow deep, not extending to pleural tip distally, and not communicating with axial furrow proximally; anterior and posterior pleural bands of similar length; anterior margin of pleura proximal to fulcrum forming very short tongue-like facet that articulates with groove-like facet developed ventrally on posterior margin of next segment; articulating facets on distal part of pleura weakly developed; pleural tip subquadrate, with several very short, laterally directed spines.

Pygidium. Pygidium with maximum width approx. three times sagittal length, excluding articulating half-ring; three prominent axial rings developed, sometimes with faint fourth; first and second rings with pseudoarticulating half-rings; usually only first two rings with ornament of small tubercles in transverse row; first pleural and interpleural furrow well incised, posterior furrows becoming increasingly effaced; posterior pleural band of first segment with transverse row of tubercles, anterior band with much fainter row; posterior band of second segment with tubercles distally, anterior band usually lacking tubercles; tubercles usually not developed posterior to second segment; subtle but distinct border matching narrow ventral extent of doublure; axial furrows effaced posteromedially; posterior margin transverse laterally in posterior view, but with prominent dorsal inflection medially; doublure slightly broader laterally.

Discussion.--Some stratigraphic variation in morphology is observable in this species. The type horizon, Avalanche Lake Four, 126 m, correlates with the interval 274-279 m in nearby section Avalanche Lake Two. Lower in the latter section, samples of Otarion huddyi from Avalanche Lake Two, 249 m (Figure III-5.1, III-5.2, III-5.5, III-5.6) attain slightly larger maximum size, show variation in the width of their palpebral lobes, and generally have many fewer cranidial tubercles. In other proportions and disposition of features, however, the specimens are identical with those from the higher samples, and are hence regarded as a stratigraphically early morphotype.

Among named species, Otarion huddyi compares most closely with the Australian species O. coppinsensis n. sp., from which it differs primarily through possession of a less elongate glabella, less divergent preocular facial sutures, and less effaced eye socle.

Otarion huddyi differs from the slightly younger O. brauni Perry and Chatterton, 1979 in the possession of a narrower glabella; narrower fixigenae; larger palpebral lobes; less elongate glabella; longer genal spine; librigenal field not as long (exsag.) relative to height;

eye socle less effaced; pygidium with three as opposed to four well developed axial rings; posterior pygidial axial rings and pleural bands usually lacking prominent rows of tubercles; pygidium with more pronounced median flexure in posterior view; and apparently smaller maximum size.

Otarion huddyi is the oldest known member of the genus. Its morphology is also the most plesiomorphic, as indicated by the ontogenies of younger species (see above) and comparisons with the oldest known Cyphaspis species. Reasons for considering O. huddyi phylogenetically removed from Devonian species with a similar general morphology have been given above, under discussion of the synonymy of Conoparia.

Etymology.--After Charlie Huddy.

Material.--Holotype cranidium UA 8510; paratypes UA 8508, 8509, 8511-8559.

Occurrence.--Wenlock (probably Cyrtograptus aff. rigidus-Monograptus aff. riccartonensis Zone) Avalanche Lake Four, 115-128 m; Avalanche Lake One, 580-599 m; Avalanche Lake Two, 242-279 m; Avalanche Lake Five, 0-7 m; Avalanche Lake Six, 0 m; Avalanche Lake Seven, 0-27 m; Delorme Range, 35-52.4 m; known also from correlative horizons in the Cape Phillips Formation, Baillie-Hamilton Island, Canadian Arctic (Perry and Chatterton, 1977; J. M. A., unpublished data).

OTARION BRAUNI Perry and Chatterton, 1979

Figures III-8, III-9

Otarion brauni PERRY AND CHATTERTON, 1979, p. 578-580, Pl. 70, figs. 1-17, 19-21 (non fig. 18, a proetid; non fig. 22, =Harpidella n. sp.).

?Conoparia hollandi Siveter, 1989, p. 120-124, Pl. 17, figs. 1-15.

Diagnosis.--Otarion with glabella moderately long; fixigenae adaxial to midlength of palpebral lobe slightly wider than maximum width of L1; palpebral lobe relatively low, reaching about one third distance up glabella in lateral profile; palpebral lobe relatively small; librigenal field usually longer than maximum height, with very faint tuberculate ornament retained in large holaspides; anterior lobe of eye socle visible, remainder generally effaced; genal spine slighly shorter than length (exsag.) of librigenal field, directed strongly inward and ventrally; four well developed pygidial axial rings, sometimes with an incipient fifth.

Discussion.--When proposed, Otarion hollandi (Siveter, 1989) was distinguished from O. brauni in possession of (Siveter, 1989, p. 124) "...a straighter genal spine, only three to four pygidial axial rings, three pairs of pygidial pleural ribs, and a much weaker pygidial border furrow." With the better material of O. brauni figured herein, all of these supposed differences disappear. The free cheeks assigned to Otarion brauni are virtually identical to one of Siveter's (1989, Pl. 17, fig. 14) two illustrated cheeks.

Given the small available sample of *O. hollandi*, and the differences in proportions of the librigenal field of the second assigned cheek (upon which the comment regarding the curvature of the genal spine was based), the question of conspecificity of the two sclerites arises. With the greater sample of *Otarion brauni* pygidia now available, it becomes apparent that the sole pygidium assigned to *O. hollandi* falls within the range of variation of *O. brauni*. Comparison of Siveter's illustration (1989, Pl. 17, fig. 13) with Figure III-8.34 reveals pygidia with four well defined axial rings, an incipient fifth, four pairs of pleural ribs, and relatively strongly defined borders. In fact, the only compelling difference between the species appears to be a glabella that is generally longer in sagittal profile in *O. brauni*. This is not altogether convincing, and the possibility exists that *O. hollandi* may fall in synonymy of *O. brauni*. More material of *O. hollandi* would be required to resolve the issue unequivocally, but it is placed in questionable synonymy of *O. brauni* herein.

A comparison with *Otarion huddyi* was given above under the discussion of that species. *Otarion brauni* is distinguished from the younger *O. beukeboomi* by the possession of a less elongate glabella; coarser ornament on medial glabellar lobe; cranidium wider relative to length; librigenal field not as long relative to height, with tuberculate ornament retained versus nearly completely effaced in mature individuals; genal spine slightly longer; anterior lobe of eye socle quite prominent versus almost wholly effaced; pygidium narrower relative to length, subsemicircular in plan view, and with generally four as opposed to universally five axial rings.

Material. Figured specimens UA 8560-8590. Perry and Chatterton (1979) list type material.

Occurrence.--Avalanche Lake Four, 165-167 m and 232-248 m; Delorme Range, 114.3-147 mlate Wenlock (probably Pristiograptus ludensis Zone).

OTARION BEUKEBOOMI n. sp.

Figure III-10

Diagnosis.--Otarion with elongate glabella lacking tuberculate ornament on anterior part; strongly impressed S2; broad librigenal field with tuberculate ornament wholly suppressed in large holaspides; short, barblike genal spine; pygidium approaching subquadrate in plan view, with five prominent axial rings.

Discussion.--Otarion beukeboomi was compared with O. huddyi and O. brauni under discussions of those species.

Otarion beukeboomi is most similar to the type species, O. diffractum, from the Ludlow of Bohemia. The age of O. beukeboomi in the Mackenzie Mountains is not well established. The species is restricted to a narrow stratigraphic interval in section Delorme Range, and is not known to occur at Avalanche Lake or elsewhere. Tentative age assignments are made possible by correlation of the trilobites with those of the Cape Phillips Formation in Arctic Canada (J. M. A., unpublished data), which occur in debris flows interbedded with graptolitic shales. *Otarion brauni*, which occurs stratigraphically below *O. beukeboomi* in section Delorme Range, occurs in strata probably belonging to the latest Wenlock *Pristiograptus ludensis* Zone in the Arctic. Material likely conspecific with *O. beukeboomi* occurs in the Arctic in strata securely dated as earliest Ludlow *Lobograptus progenitor* Zone. Hence, *O. beukeboomi* is likely of early Ludlow age, but further work will be necessary to establish this without question.

Otarion beukeboomi is distinguished from *O. diffractum* by possession of a shorter preglabellar field; less tuberculate cephalic ornament; slightly shorter glabella; absence of prominent median node on preglabellar field; librigenal field with relatively smaller area; lateral border furrow of similar depth anteriorly and posteriorly versus effaced posteriorly; pygidium wider relative to length, with less prominent border. The species are otherwise similar, and are united particularly in the possession of five pygidial axial rings. Some of the differences noted, particularly regarding ornamentation, could be a result of comparing differently sized specimens, as the largest available *O. beukeboomi* specimens are only slightly over half the size of typical large *O. diffractum*.

Large trilobites (particularly encrinurids) occur with O. beukeboomi, however, and it seems unlikely that the illustrated sample is not representative of the species' typical size. Hence, a preferred hypothesis is that O. diffractum represents a more advanced morphotype, in a fashion similar to the way in which O. beukeboomi represents advances over the morphologies seen in the older O. brauni and O. huddyi.

Etymology.--After Jeff Beukeboom.

Material.--Holotype cranidium UA 8592; paratypes UA 8591, 8593-8602.

Occurrence.--Delorme Range, 182.9 m; probably early Ludlow (Lobograptus progenitor Zone).

OTARION COPPINSENSIS n. sp.

Figure III-11

Otarion aff. O. horani (Etheridge and Mitchell, 1893).
CHATTERTON AND CAMPBELL, 1980, p. 87, Pl. 9, figs. 11-20.

Diagnosis.--Otarion with moderately elongate glabella; entire cephalon with even and moderately coarse tuberculate ornament; eye socle effaced; preocular facial sutures strongly anteriorly divergent; genal spines relatively long; pygidium with three axial rings.

Discussion.--Chatterton and Campbell (1980) discussed what they perceived to be the close similarity between their Wenlock species and the Ludlow Cyphaspis horani Etheridge and Mitchell, 1893 (see Chatterton, 1971, Pl. 24, figs. 1-6; Chatterton and Campbell, 1980, Pl. 11, figs, 13, 14). The only difference between the species then apparent was the more tuberculose cephalon of the Coppins Crossing species. *Cyphaspis horani*, however, has 11 thoracic segments, a strongly inflated, but not elongate, glabella, and a pygidium which is narrow relative to its length, bears three axial rings, and has both rings and posterior pleural bands ornamented with single rows of relatively coarse tubercles. All of these make its assignment to *Cyphaspis* unambiguous, and serve to differentiate it from the older Coppins Crossing species. Hence, we recognize the latter as a new species. *Otarion coppinsensis* is most similar to (although probably more derived than) *O. huddyi*, with which it was compared above.

Etymology.--After Coppins Crossing, near which the type locality is located.

Material.--Holotype ANU 35315; see Chatterton and Campbell (1980) for remainder of available material.

Occurrence.--Calcareous shales interbedded with the Walker Volcanics, Wenlock, near Coppins Crossing, New South Wales, Australia.

OTARION DIFFRACTUM Zenker, 1833

Figure III-12

Otarion diffractum ZENKER, 1833, p. 44, Pl. 4, figs. O-R; WHITTINGTON AND CAMPBELL, 1967, p. 460, Pl. 10, figs.

12, 14-16; HORNÝ AND BASTL, 1970, Pl. 12, fig. 1 (with extensive synonymy in species lists); THOMAS AND OWENS, 1978, p. 66, Pl. 7, figs. 1-3, 5, 6; PRIBYL AND VANEK, 1981, p. 192, Pl. 2, figs. 1-6.

Conoparia verrucosa HAWLE AND CORDA, 1847, p. 83.

Conoparia seligra ŠNAJDR, 1984, p. 288, Pl. 1, figs. 6, 7.

Diagnosis.--Otarion with very broad genal and frontal areas; glabella elongate and low; prominent median node on preglabellar field; tuberculate cephalic ornament restricted to fixed cheeks and rear of glabella; caecal trunks prominently developed on lateral aspects of frontal area and posteriorly on librigenal field; lateral border furrow strongly shallowing just anterior to genal angle; thorax of thirteen segments; pygidium large relative to cephalon (for genus), with five axial rings and strongly developed border.

Discussion.--Otarion diffractum is most similar to O. beukeboomi, with which it was compared above.

Thomas and Owens (1978, p. 67) gave the number of thoracic segments in Otarion diffractum as 13-15. All complete specimens that have thus far been illustrated, however, including their own (Thomas and Owens, 1978, Pl. 7, figs. 1, 6; see also Whittington and Campbell, 1967, Pl. 10, figs. 12, 14-16; Horny and Bastl, 1970, Pl. 12, fig. 1; and Figure 12.1-12.4 herein) appear to show 13.

Thomas and Owens (1978) united Otarion and Aulacopleura as subgenera of Otarion. This action was taken with reference only to the type species of Otarion (at that time, the only species at all well known). Otarion diffractum's broad, non-tuberculate genae and long, low glabella converge on aspects of the morphology of Aulacopleura, particularly that of A. roquemailerensis Chaubet, 1937 (see Thomas and Owens, 1978, Pl. 7, fig. 9). With the range of Silurian Otarion species now adequately described, however, it becomes apparent that these resemblances are secondarily derived. The most primitive species of Otarion known, O. huddyi, shows little detailed similarity to Aulacopleura. Aulacopleura and Otarion are assigned to separate subfamilies herein.

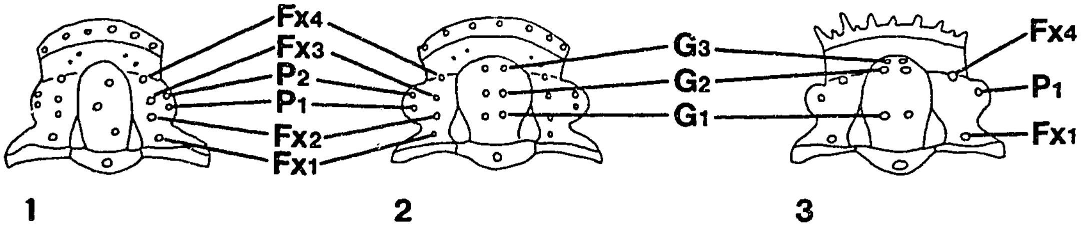
Material.--Figured specimens UA 8603, 8604.

Occurrence.--Kopanina Formation, Ludlow, Bohemia, Czechoslovakia.

TABLE III-1--Data matrix for cladistic analysis of adequately known Silurian species of the genus *Otarion*. All characters except 13 and 14 are ordered. Data were run on Swofford's PAUP, version 3.0g, using exhaustive search. See Figure III-3 for result.

Species	Character														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
O. huddyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
O. n. sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
O. brauni	1	1	0	0	0	1	1	1	0	1	1	1	0	0	1
O. coppinsensis	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0
O. beukeboomi	1	1	1	1	0	1	2	2	1	2	1	2	1	0	0
O. hollandi	1	0	0	0	0	1	1	1	0	1	1	1	0	0	1
O. diffractum	1	1	1	1	1	1	2	2	1	2	1	2	1	1	0

FIGURE III-1--Patterns of juvenile cranidial spine distribution in otarionine meraspides. Three major patterns are recognized. 1, *Beggaspis* pattern. Note two pairs of palpebral spines (P1-2), four major pairs of fixigenal spines (Fx1-4), and single row of spines on anterior border. Note particularly the absence of paired glabellar spines. *Beggaspis spinicaudatum* (Shaw, 1968), Llandeilo, Crown Point Formation, New York State, based on unpublished micrographs. 2, *Maurotarion*-*Harpidella* pattern. This pattern is very similar to the *Beggaspis* pattern, but features the development of three evenly spaced pairs of glabellar spines (G1-3). *Maurotarion* n. sp., Llandovery, Whittaker Formation, southern Mackenzie Mountains, Northwest Territories, Canada, based on unpublished micrographs. 3, Otarionini pattern. Palpebral spines are reduced to a single pair (P1), Fx2 and Fx3 are suppressed, G3 is reduced in size and positioned at the very front of the glabella, with G2 crowded immediately behind it, and not one but two rows of spines are developed on the cephalic border. *Otarion huddyi* n. sp., Wenlock, southern Mackenzie Mountains, Northwest Territories, Canada. Based on specimens illustrated in Figure III-7. The pattern is also well displayed in meraspides of *Otarion brauni*, illustrated in Figure III-9.


Fx4
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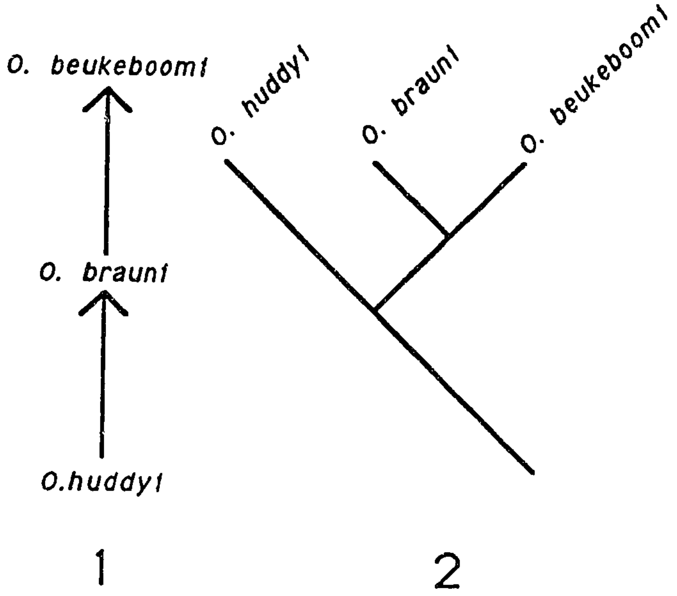
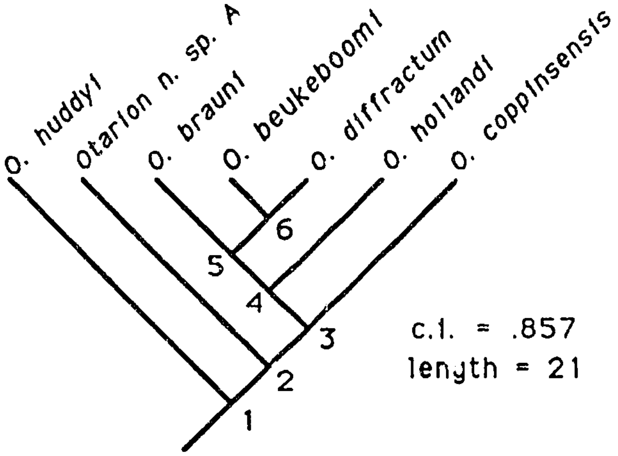


FIGURE III-2--1, potential phyletic lineage for species of Otarion from section Delorme Range, based on multiple morphological trends, many demonstrably peramorphic, which are observable and unreversed upsection (see text for details). 2, the hypothesized lineage may be represented cladistically as a tree with this topology. The hypothesis may then be tested, and finds support only if the depicted cladistic relationships remain intact and the species form an exclusive clade when relationships with other species of Otarion are considered. See Figure III-3 for the results of such a test.

FIGURE III-3--Cladogram depicting relationships among adequately known Silurian species of the genus Otarion. Otarion n. sp. A is an undescribed species that occurs stratigraphically just above Otarion huddyi in the Cape Phillips Formation on the south shore of Baillie-Hamilton Island, Arctic Canada (J.M.A., unpublished data). The data shown in Table III-1 were run on PAUP, version 3.0g (Swofford, 1989), on a MacIntosh LC, using the exhaustive search option. Apomorphies at numbered nodes are given as node:character(state). 3: 1(1), 10(1). 4: 6(1), 7(1), 8(1), 11(1), 12(1). 5: 15(1). 6: 3(1), 4(1), 7(2), 8(2), 9(1), 10(2), 12(2), 13(1). The species involved in the potential phyletic lineage in section Delorme Range depicted in Figure III-2 are marked with asterices. Note that while the topology shown in Figure III-2.2 is maintained when other species of Otarion are considered, the Delorme Range species do not form an exclusive clade. The hypothesized lineage is shown to be incorrect; each of its member species is more closely related to other species from elsewhere in the world than to either of the other Delorme Range species. Thus, phyletic lineages, no matter how compelling they may seem, should never be hypothesized without reference to wider phylogenetic context.


O. huddyi
Otarion n. sp. A
O. brauni
O. beukeboomi
O. diffractum
O. hollandi
O. coppinsensis
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c.i. = .857
length = 21

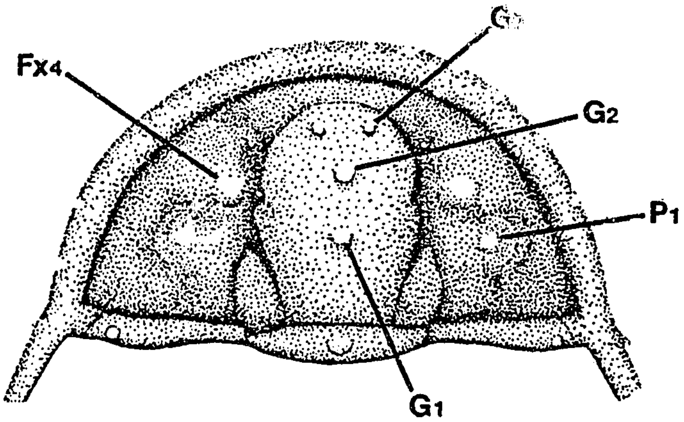

FIGURE III-4--Namuropyge decora (Miller, 1973), illustrating homologies of the cephalic spines. The bases of the hyperdeveloped spines have been left white. Note that the pattern compares closely with that of the Otarionini illustrated in Figure III-1.3, to which Namuropyge is now assigned. See text for discussion. Drawing based on Owens (1986, Pl. 2, fig. 1a).

FIGURE *III-5*--*Otarion* *huddyi* n. sp. From the Delorme Formation, section Avalanche Lake Four, 126 m, except where otherwise indicated; x10 except where otherwise indicated. *1*, *5*, UA 8508, cranidium, dorsal and lateral views, Avalanche Lake Two, 249 m; *2*, *6*, UA 8509, cranidium, dorsal and lateral views, Avalanche Lake Two, 249 m; *3*, *7*, UA 8510, holotype cranidium, dorsal and lateral views; *4*, *8*, UA 8511, cranidium, dorsal and lateral views; *9*, *13*, UA 8512, cranidium, dorsal and lateral views; *10*, *14*, UA 8513, cranidium, dorsal and lateral views; *11*, *15*, UA 8514, cranidium, dorsal and lateral views; *12*, UA 8515, cranidium, anterior view; *16*, *17*, *21*, UA 8516, cephalon, lateral oblique, anterodorsal, and dorsal views, Avalanche Lake One, 590 m; *18*, UA 8517, cranidium, x15; *19*, *20*, UA 8518, cranidium, dorsal and lateral views; *22*, UA 8519, cranidium and left librigena, ventral view; *23*, *24*, UA 8520, cranidium, dorsal and lateral views, x15; *25*, *26*, UA 8521, cranidium, dorsal and lateral views, x20; *27*, UA 8522, cranidium and thorax, Avalanche Lake Two, 255-260 m; *28*, UA 8523, cephalon, ventral view; *29*, *30*, UA 8524, cranidium, dorsal and lateral views, x20; *31*-*33*, UA 8525, cranidium with left free cheek, dorsal, anterior, and lateral views, Avalanche Lake Two, 255-260 m.

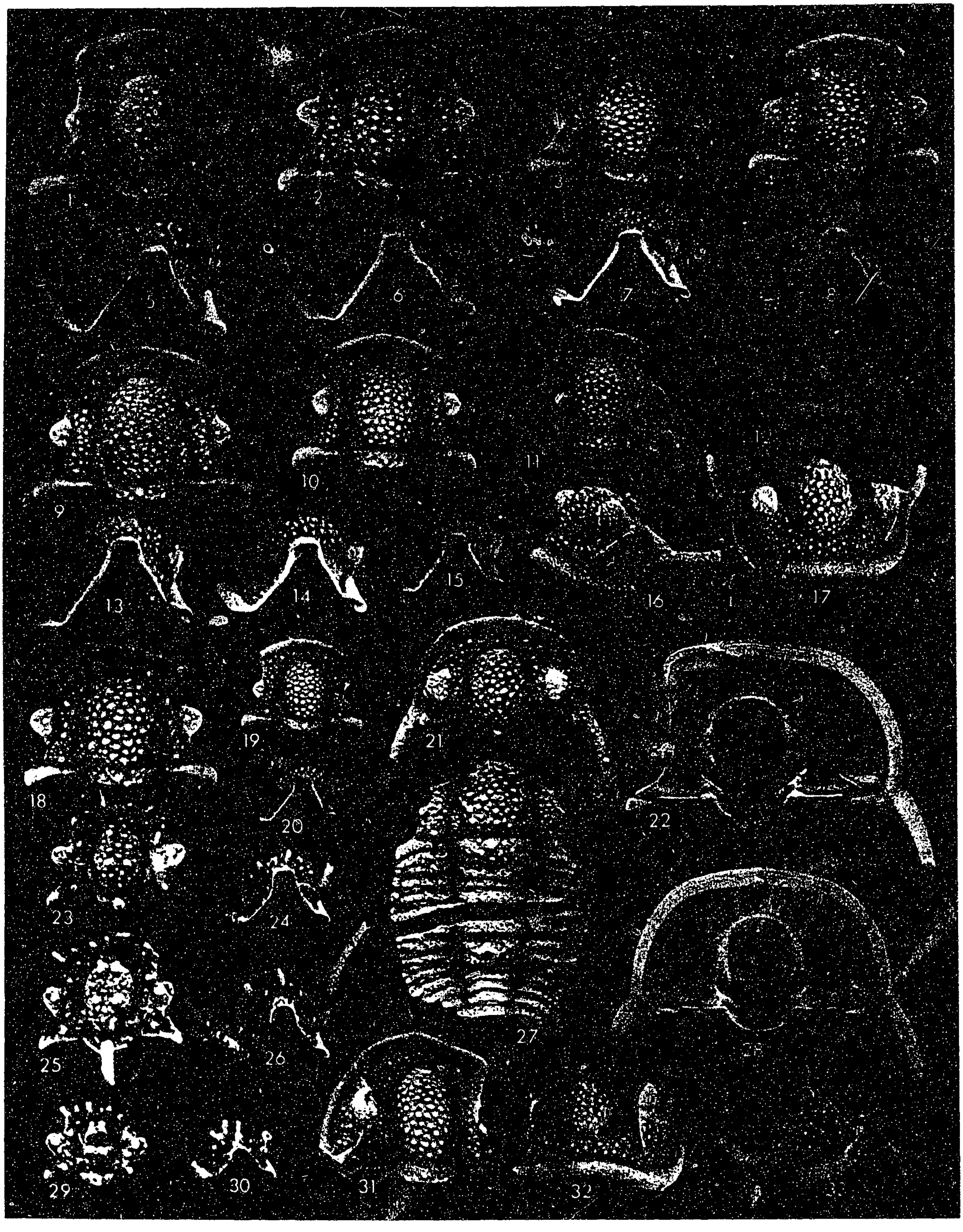
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FIGURE III-6--Otarion huddyi n. sp., from the Delorme Formation,section Avalanche Lake Four, 126 m, except where otherwise noted; x10, except where otherwise noted. 1, 4, UA 8526, left free cheek, external and ventrolateral view; 2, UA 8527, right free cheek, external view, Avalanche Lake Four, 126-127 m; 3, UA 8528, right free cheek, external view; 5, UA 8529, right free cheek, external view, Avalanche Lake Four, 126-127 m; 6, UA 8530, left free cheek, internal view; 7, UA 8531, left free cheek, external view; 8, UA 8532, left free cheek, external view; 9, 13, 17, UA 8533, right free cheek, external, ventrolateral, and dorsal views; 10, UA 8534, left free cheek, internal view; 11, UA 8535, right free cheek, external view, x15; 12, UA 8536, left free cheek, external view; 14, UA 8537, right free cheek, external view, x15; 15, UA 8538, left free cheek, external view, x15; 16, UA 8539, left free cheek, lateral view; 18, UA 8540, hypostome, ventral view, x15, Avalanche Lake Four, 126-127 m; 19, UA 8541, hypostome, ventral view, x15; 20, UA 8542, hypostome, dorsal view, x15; 21, UA 8543, left free cheek, external view, x15; 22, thoracic segment, dorsal view, Avalanche Lake Four, 128 m; 23, 26, UA 8544, thoracic segment, dorsal and lateral views; 24, UA 8545, pygidium, dorsal view, x15; 25, 31, UA 8546, pygidium, dorsal and posterior views, x15; 27, UA 8547, hypostome, ventral view, x15; 28, UA 8548, pygidium, dorsal view, x15; 29, 30, UA 8549, pygidium, posterior and dorsal views, x15; 32, UA 8550, pygidium, dorsal view, x15; 33, UA 8551, pygidium and thoracic segment, ventral view, x15.

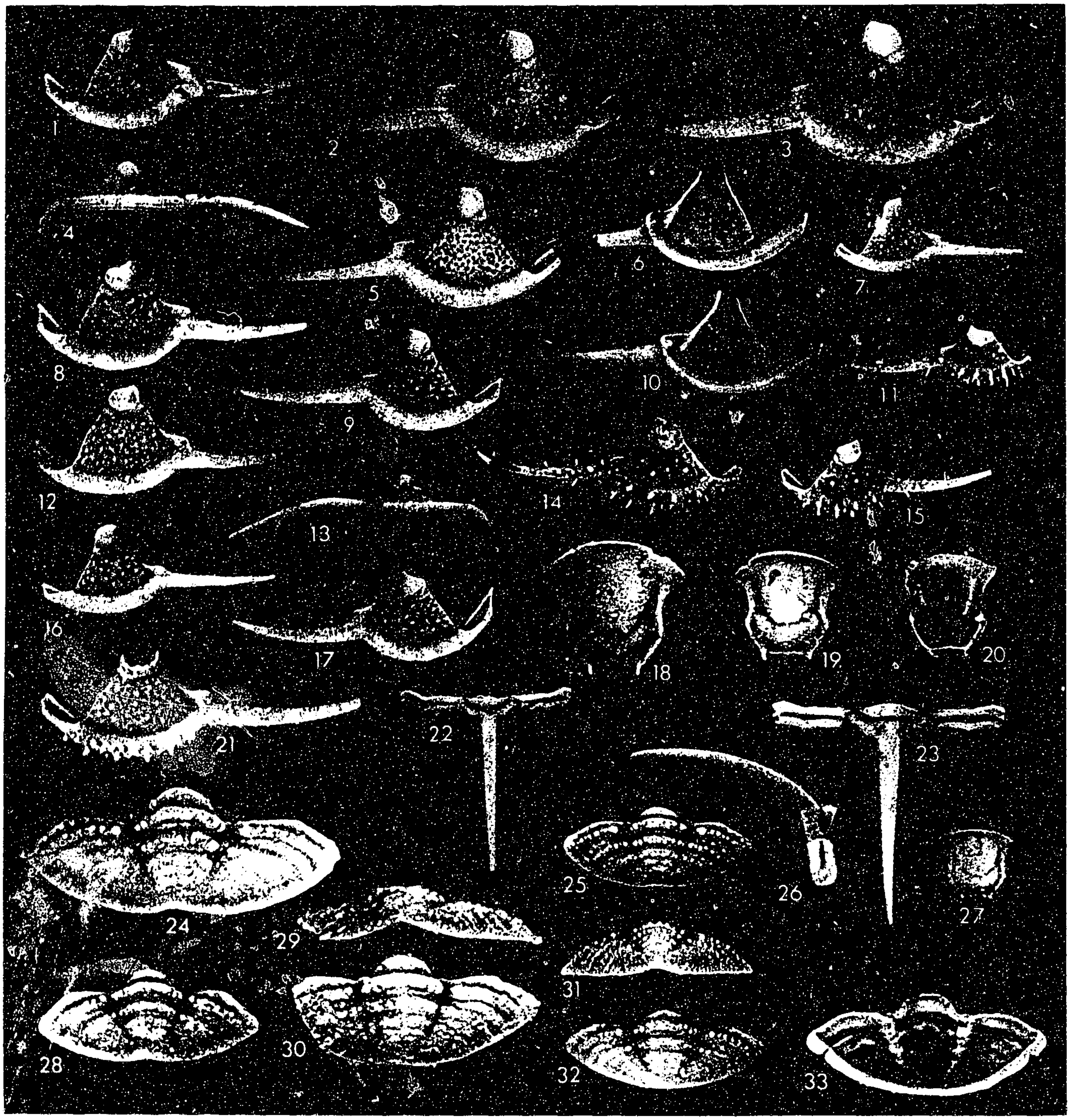
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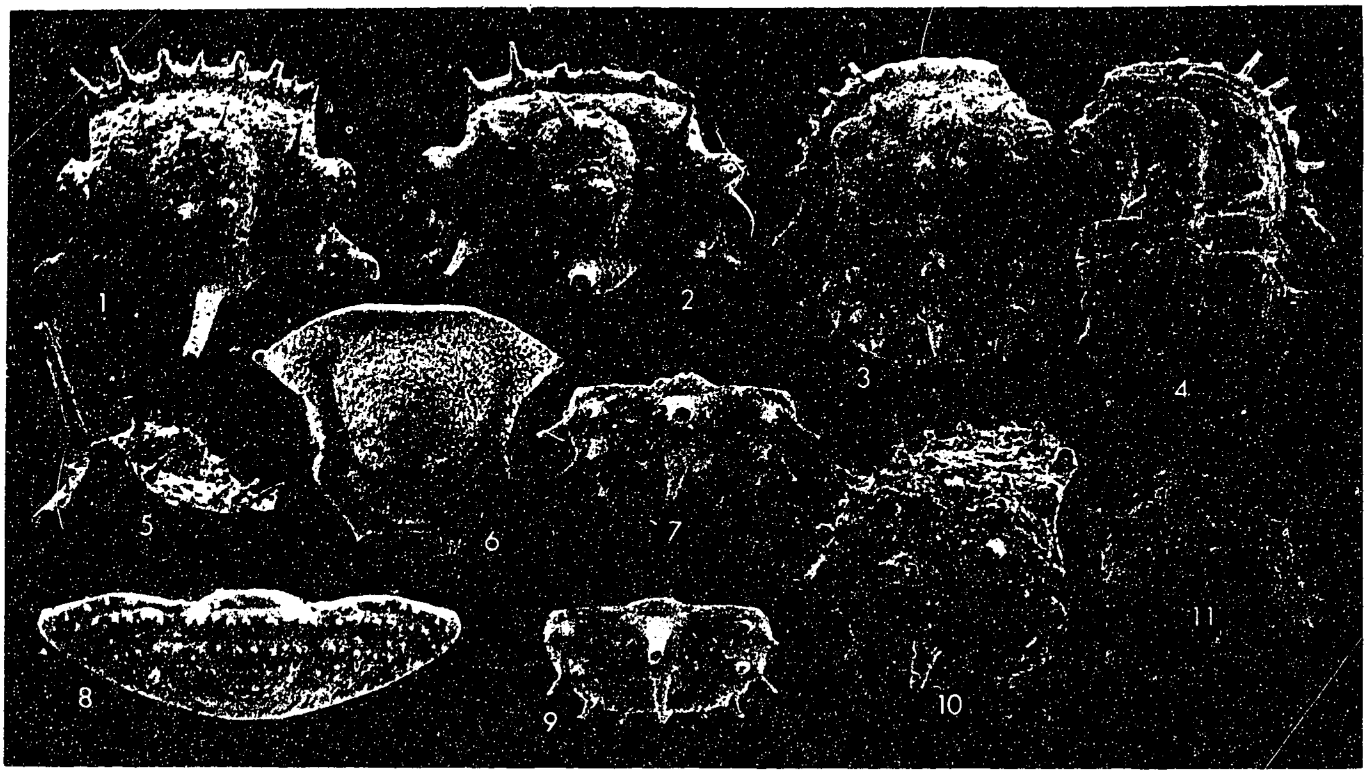
FIGURE III-7--Otarion huddyi n. sp., from the Delorme Formation, section Avalanche Lake Four, 126 m; all figures are scanning electron micrographs. 1, 5, UA 8552, cranidium, dorsal and lateral views, x32.5; 2, UA 8553, cranidium, dorsal view, x50; 3, 4, UA 8554, Degree One meraspid, dorsal and ventral views, x62; 6, UA 8555, hypostome, ventral view, x24; 7, UA 8556, transitory pygidium, dorsal view, x65; 8, UA 8557, pygidium, dorsal view, x31; 9, UA 8558, transitory pygidium, dorsal view, x65; 10, 11, UA 8559, Degree Zero meraspid, right dorsolateral and right lateral views, x90.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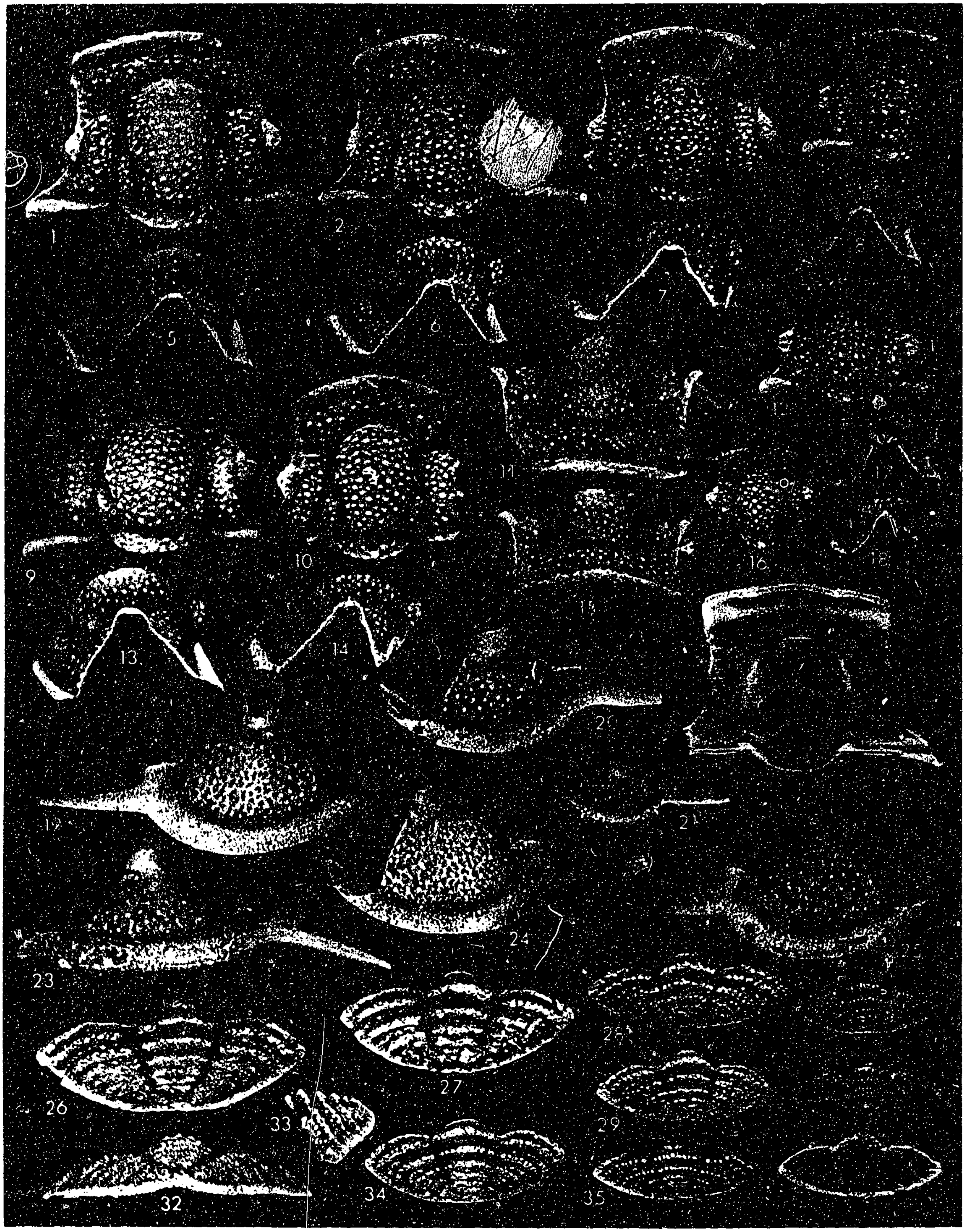
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FIGURE III-9--*Otarion brauni* Perry and Chatterton, 1979, from section Avalanche Lake Four, 248 m; all figures are scanning electron micrographs. 1, 5, UA 8583, cranidium, dorsal and anterodorsal oblique views, x30; 2, UA 8584, cranidium, dorsal view, x32; 3, UA 8585, cranidium, dorsal view, x33; 4, UA 8586, cranidium, dorsal view, x50; 6, UA 8587, right free cheek, external view, x30; 7, UA 8588, left free cheek, external view, x20; 8, UA 8589, hypostome, ventral view, x31; 9, UA 8590, hypostome, ventral view, x25.


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FIGURE III-10--*Otarion beukeboomi* n. sp., from the Delorme Formation, section Delorme Range, 182.9 m; figures x10 except where otherwise noted. 1, 5, 12, UA 8591, cranidium, dorsal, lateral, and anterior views; 2, 7, UA 8592, holotype cranidium, dorsal and lateral views; 3, 8, 9, 19, cranidium, dorsal, lateral, anterior, and ventral views; 4, UA 8593, hypostome overgrown by pyrite crystals, ventral view; 6, 11, UA 8594, left free cheek, external and internal views; 10, 13, UA 8595, left free cheek, external and ventrolateral views; 14, UA 8596, right free cheek, external view; 15, 16, 20, UA 8597, cranidium, lateral, dorsal, and anterior views, x20; 17, UA 8598, right free cheek, external view; 18, 23, 26, UA 8599, pygidium, lateral, posterior, and dorsal views; 21, UA 8600, pygidium, dorsal view; 22, 25, 27, UA 8601, pygidium, posterodorsal, dorsal, and ventral views; 24, UA 8602, pygidium, dorsal view.

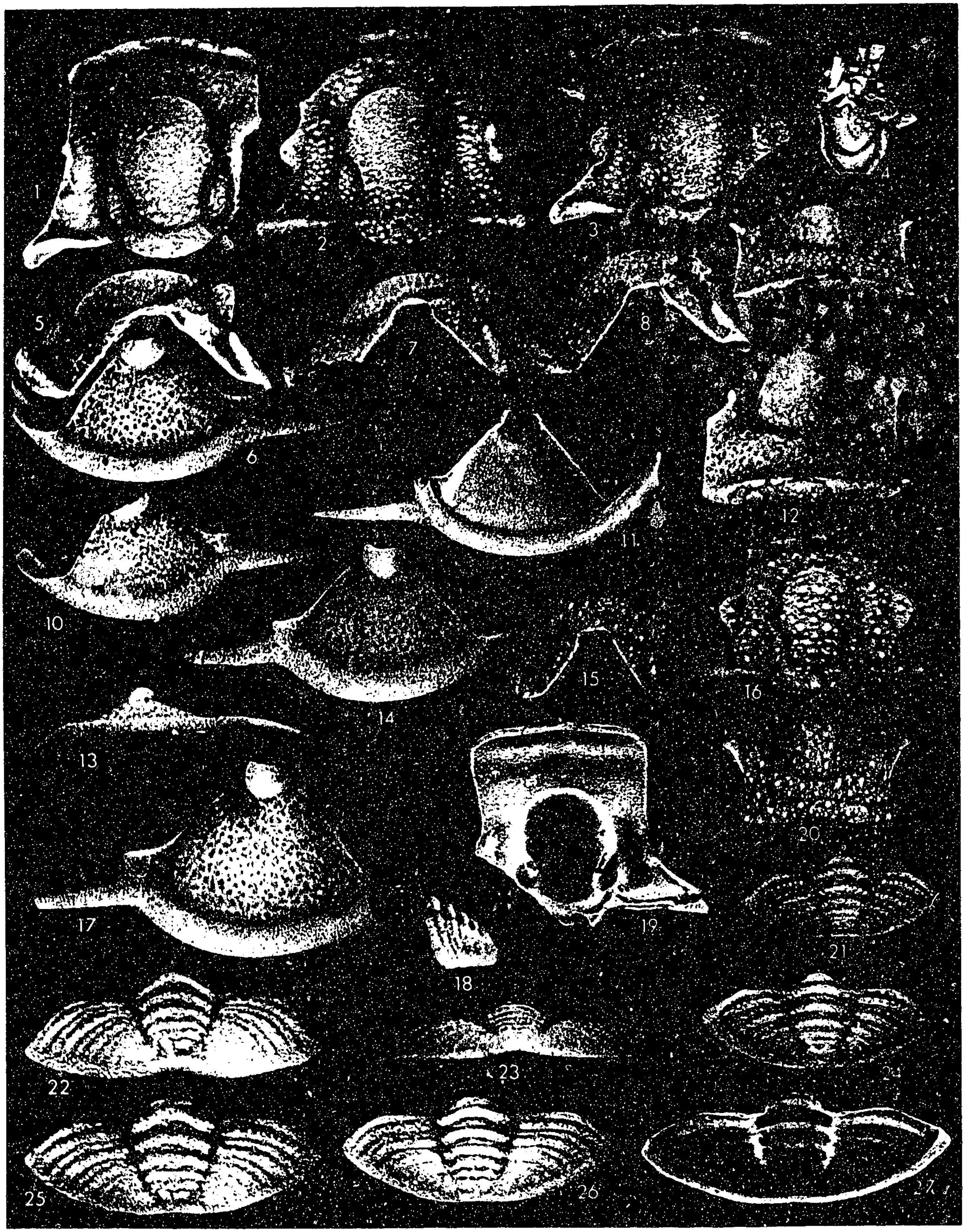
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FIGURE III-11--Otarion coppinsensis n. sp., from calcareous shales interbedded with the Walker Volcanics, Wenlock, near Coppins Crossing, New South Wales, Australia (see Chatterton and Campbell, 1980); x10 except where otherwise noted. 1, CPC 18024, cephalon, lateral view; 2, CPC 18027, right free cheek, external view; 3, ANU 35315, holotype cephalon, dorsal view, x7.5; 4, ANU 35322, pygidium, dorsal view.

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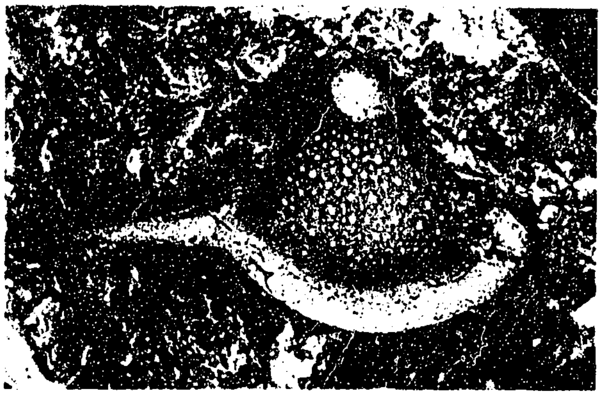

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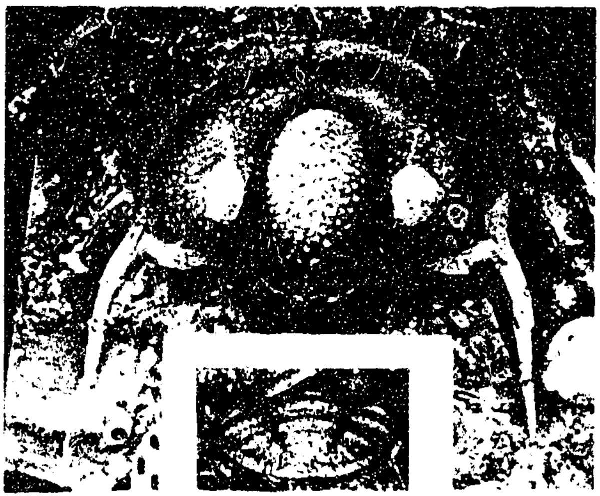

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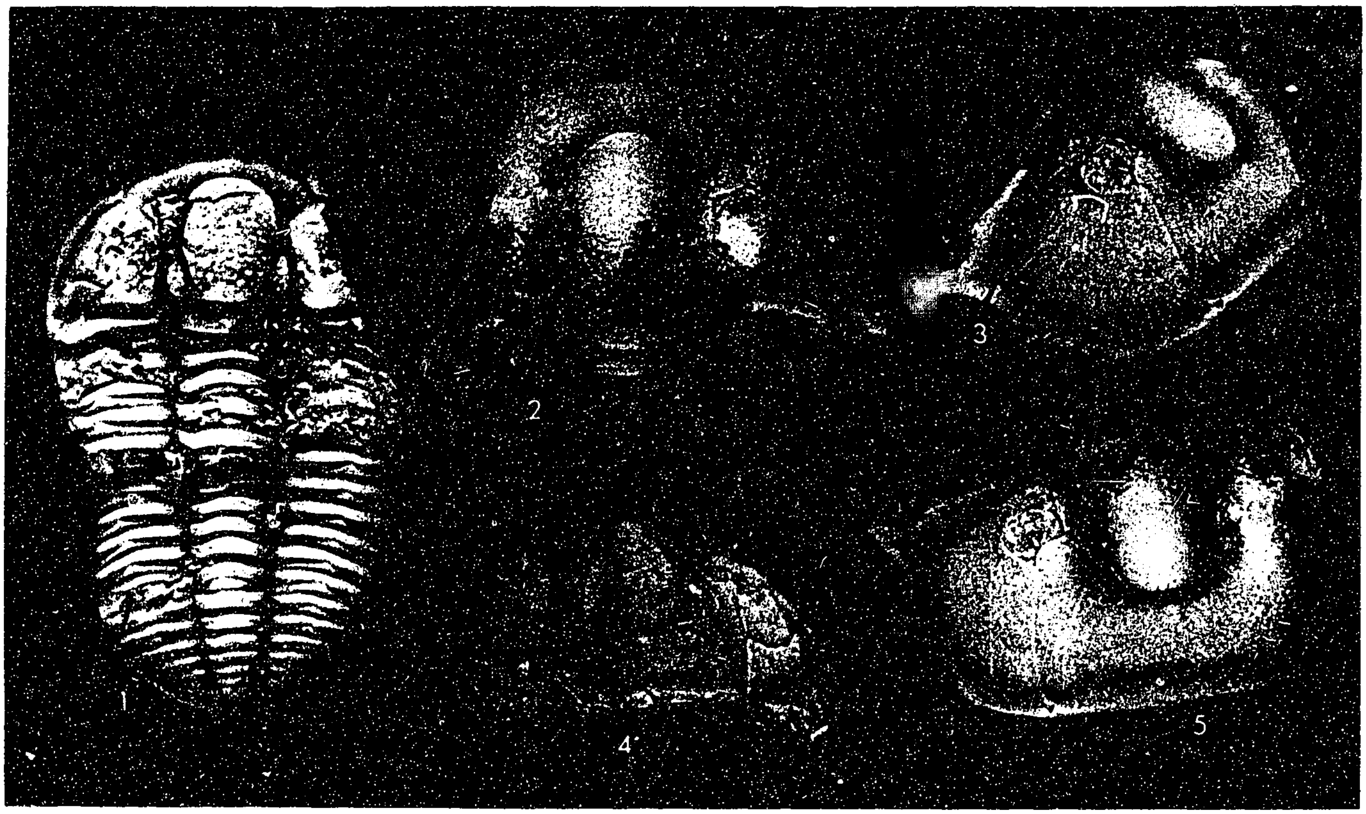
FIGURE _III-12_--_Otarion_ _diffractum_ Zenker, 1833. From the Kopanina Formation, Ludlow, exact locality unknown, Bohemia, Czechoslovakia. All figures x4. _1_, _4_, UA 8603, articulated exoskeleton, dorsal, and anterior views. _2_, _3_, _5_, UA 8604, cephalon and partial thorax, dorsal, dorsal, lateral oblique, and anterodorsal views.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CHAPTER IV[1]

THE LICHID TRILOBITE BOREALARGES N. GEN., WITH SPECIES FROM THE SILURIAN OF ARCTIC CANADA

INTRODUCTION

DIVERSE TRILOBITE faunas occur in debris flows of Wenlock and Ludlow age in the Cape Phillips Formation at various localities in the Canadian Arctic Archipelago. Perry and Chatterton (1977) were first to survey some of these faunas. The present study describes some species of the new lichid genus Borealarges, a taxon that is of ubiquitous occurrence in the faunas under study. The localities mentioned herein (Figure IV-1) are equivalent to those described by Perry and Chatterton (1977) and Chatterton and Perry (1979), except that new stratigraphic sections have been measured and new age data collected. Precise information is given under treatment of individual species. The graptolite zonation used is that of Lenz and Melchin (1990).

The species treated in this work are similar enough that only Borealarges reedi n. gen. n. sp. is given a full description. The remaining species are treated with shorter differential diagnoses. With the exception of a single thoracic segment possibly belonging to B. s.l. calei n. gen.

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n. sp., thoraces of the species under study have not been illustrated, as intact examples are unknown among the sampled material and specific assignments are presently impossible when more than one species is present. The thorax of *B*. s.l. *bucklandii* (Milne Edwards, 1840) is well known, however, and indicates that the nature of at least the posterior thoracic segments can be inferred from that of the anterior pygidial segment.

Illustrated material is housed in the paleontological collections of the Department of Geology, University of Alberta, with specimen numbers prefixed UA, and in the Natural History Museum, London, with specimen number prefixed BM.

CLASSIFICATION OF THE *BOREALARGES* GENUS GROUP

Ordovician ancestry.--Two major clades can be recognized among Silurian trochurines, each having its origin in the paraphyletic late Ordovician "*Hemiarges*" group. The relationships of other trochurine genera, including *Trochurus* Beyrich, 1845, *Uripes* Thomas and Holloway, 1988, and *Dicranogmus* Hawle and Corda, 1847 are unresolved, but taken together these genera may form a third clade. The clade of interest here includes *Borealarges* n. gen., *Richterarges* Phleger, 1936, *Terranovia* Maximova, 1977, and possibly *Ceratarges* Gürich, 1901 (see Ormiston, 1982). It is referred to as the "*Borealarges* genus group". Most of its known diversity is Silurian, with *Terranovia*, a probable relict distribution of *Borealarges* (see below), and *Ceratarges* (if it belongs to the group) persisting into the Devonian. A second clade includes trilobites of the *Acanthopyge* type which, while fairly common in the Silurian, underwent a significant radiation during the Early Devonian. Thomas and Holloway (1988, fig. 365) classified Silurian members of this clade in an expressly paraphyletic *Acanthopyge* (*Lobopyge*) Pribyl and Erben, 1952.

Ordovician "*Hemiarges*" species all share several features that are primitive for Trochurinae. These include four pairs of pygidial border spines, confluence of the bullar lobe with L1, and at least partial definition of L1a (Thomas and Holloway, 1988, p. 236, used these character-states to distinguish between their concepts of *Richterarges* and *Hemiarges*). The Silurian *Acanthopyge* clade features reduction of the pygidial border spines to three pairs, while the *Borealarges* genus group retains four but adds a median spine. Circumscription of the bullar lobe posterolaterally and loss of definition of L1a was apparently achieved independently within each clade.

Among the Ordovician "*Hemiarges*" species, there are some that show morphological development toward one or the other of the Silurian clades. The type species, *H. wesenbergensis* Schmidt, 1885, for example, has a pygidium (see Thomas and Holloway, 1988, Pl. 10, fig. 219) very similar to that of Silurian species such as *Acanthopyge*

(Lobopyge) hirsuta (Fletcher, 1850) (cf. Thomas, 1981, Pl. 20, figs. 3, 4, 17). The single substantive difference is the presence in the older species of an extra pair of border spines just adaxial to the second pleural spine pair. It seems likely that the Acanthopyge clade evolved from the H. wesenbergensis group through loss of these spines.

Some Devonian species (e.g., Acanthopyge (Lobopyge) sinuata (Ratte, 1886); see Chatterton et al., 1979) do in fact have these spines developed in the holaspid period. There are several possible explanations for this. First, the spines in this position could be secondarily acquired evolutionary novelties, and hence not homologous with those of Hemiarges. Second, the spines might be homologous with those in Hemiarges, and their occurrence in mature holaspides could be due to paedomorphosis, assuming the presence of the extra spine pair could be demonstrated to occur early in the ontogeny of three-spined Silurian species. Finally, the spines might be homologous with those of Hemiarges due to the survival of a distinct four-spined clade through the Silurian. At present, there is not enough information to assess these options.

The earliest and most plesiomorphic members of the Borealarges genus group are "Hemiarges" turneri Chatterton and Ludvigsen, 1976 and related species. "Hemiarges" turneri has a pygidium that is very broad relative to its length, with an outline in plan view that approaches subrectangular. While it retains four pairs of pygidial spines, the spines are rather inflated and cylindrical, very similar to those of the *Borealarges* pygidia illustrated herein. The only significant innovation necessary to evolve from the pygidium of "*H*." *turneri* (Chatterton and Ludvigsen, 1976, Pl. 19, figs. 23, 24, 26) to that of *Borealarges* is the development of a posteromedian pygidial border spine.

Silurian radiation.--Llandovery trochurine diversity is not well known. The earliest known Silurian member of the *Borealarges* genus group is *B*.? *rolfei* (Lamont, 1965) from the upper Llandovery of Scotland (see Clarkson and Howells, 1981, p. 532, Pl. 79, figs. 13-15; Howells, 1982, p. 51, Pl. 14, figs. 5, 6, 11, 12, 14, 15). The nature of the initial radiation of the genera recognized, together with their exact interrelationships, is not yet clear. Detailed assessments of phylogenetic structure must await treatment of the great number of undescribed northern Laurentian species of relevance. Nevertheless, the following ideas can now be put forward.

1. The primitive pygidial morphology for the Siluro-Devonian *Borealarges* genus group features nine border spines, including two anterior pairs running from the pleural bands of the anterior pygidial segments, a third pair (often largest) at the posterolateral "corner" of the pygidium, and three spines set medially along the posterior margin. All Wenlock members of the clade show this

morphology in the holaspid period, and it is either retained or incorporated into the ontogeny of more derived post-Wenlock species (e.g., members of Richterarges; see below). Other subsequent variations on the theme include reduction or effacement of the spines and insertion of additional ones.

2. The genus Richterarges Phleger, 1936, can be restricted to a monophyletic Upper Silurian group endemic to Laurentia.

3. Wenlock diversity of the Borealarges genus group is very high in northern Laurentia. All currently known species (most of which are as yet undescribed) are very similar, and show the generalized nine-spined pygidial morphology. As this morphology is presumed to be plesiomorphic, and since this assemblage possibly gave rise to both Richterarges and Terranovia (see below), the Wenlock group is not clearly monophyletic. Nevertheless, the bulk of the species may eventually be found to form a clade. Additionally, the group includes a great number of Wenlock and early Ludlow species that closely resemble each other, but which cannot be accommodated in any currently recognized genus without treating such a unit as an unnatural taxon of convenience. The problem of generic assignment of such species, until such time as a detailed phylogeny can be worked out, must now be addressed.

One solution is to assign the species, for the present, to the already available non-natural taxon *Hemiarges*. A major difficulty with this is that the type species of *Hemiarges* (see above) has apparent affinity not to the *Borealarges* genus group, but to the *Acanthopyge* clade, and hence any possible resolution of *Hemiarges* as a natural taxon cannot include members of the *Borealarges* group. A second way of dealing with the situation is discussed next.

4. A major subunit of the Wenlock-early Ludlow members of the *Borealarges* group can be supported as a monophyletic taxon, recognized herein as *Borealarges* n. gen. Other Wenlock-early Ludlow species which lack the diagnostic features of *Borealarges* s.s. are nevertheless more similar (although this resemblance may be primitive) to species of *Borealarges* s.s. than they are to any other members of the genus group. Their inclusion in *Borealarges* may render the taxon paraphyletic, or it may not; there is not enough information available at present to be certain. The best course of action seems to be to refer them to *Borealarges* s.l., recognizing the fact that their generic assignment may be revised as more data become available.

5. In summary, the *Borealarges* genus group includes three or four well supported monophyletic taxa (*Borealarges* s.s., *Richterarges*, *Terranovia*, and possibly *Ceratarges*). It includes also a number of Wenlock-Ludlow species whose phylogenetic position with respect to these clades is ambiguous. They are most similar to members of *Borealarges*

s.s., and are herein referred to *Borealarges* s.l.

Terranovia.--Thomas and Holloway (1988, p. 237-238) discussed the problem of the origin of *Terranovia* Maximova, 1977. Ormiston (1982) considered the genus to be most closely related to *Ceratarges* Gürich, 1901. Thomas and Holloway, however, supported a close relationship with *A*. (*Acanthopyge*), based primarily upon what they considered to be similarities among pygidial features.

Both *A*. (*Acanthopyge*) and *Terranovia* have elongate pygidia with long border spines. *Terranovia*, however, has a complement of spines identical in number and general position to that of *Borealarges* (Figure IV-2), and it is possible to specify one-to-one homologies. Furthermore, at least *T*. *nalivkini* Maximova, 1977, possesses anterolateral cranidial projections identical to those of *Borealarges* s.s. (see Ormiston, 1982, Pl. 1, fig. 1). It is at least possible that *Terranovia* represents the sister group of *Borealarges* s.s., evolving from the general *Borealarges* genus group condition through elongation of all spines, migration of the third pair dorsally, and extensive broadening and lengthening of the postaxial region, with hypertrophy of the three median spines. The third pair of border spines are of radically different position (i.e., positioned dorsally with their base almost vertical) in *Terranovia*, but it seems that they are positioned on the dorsal aspect of a greatly lengthened pygidial border, and not on the pleural field. Hence, their homology with the horizontally held border spines in earlier members of the genus group is supported.

The issue is far from settled, but the alternative hypothesis, that *Terranovia* is closely related to *Acanthopyge* (*Acanthopyge*) (Thomas and Holloway, 1988, p. 238), requires many more ad hoc assumptions. Most importantly, for it to be true, three of *Terranovia*'s nine pygidial spines must have been independently acquired evolutionary novelties, and nearly identical anterolateral cranidial projections must have been developed independently in two separate clades (see below for a discussion of similar, but non-homologous, structures developed in some species of *Acanthopyge* (*Lobopyge*)).

Intriguingly, *Borealarges* *tuckerae* n. gen. n. sp. has an inflated median glabellar lobe bearing short spines and a pygidium with the three lateral spine pairs considerably longer than in any other member of the genus. It is conceivable that *B*. *tuckerae* is a highly plesiomorphic *Terranovia*, seen relatively near in time to its common ancestry with *Borealarges*. This suggestion would help to account for the lengthy ghost lineage (Norell, 1992) separating the Devonian *Terranovia* from its Silurian sister taxon. Assignment of *B*. *tuckerae* to *Terranovia* seems premature, however, in the absence of further information or of any knowledge of potential Upper Silurian members of the

Terranovia clade.

The question of the origin and affinities of the stratigraphically late and highly derived taxon *Ceratarges* remains. Ormiston (1982, p. 1257) listed similarities with *Terranovia*, but beyond the occurrence in both taxa of long median glabellar spine pairs, there are few convincing points of similarity. Unlike *Terranovia*, no clear comparison of either cranidial or pygidial morphology of *Ceratarges* can be made, despite its obvious assignment to Trochurinae. Its phylogenetic position is perhaps best considered in light of a thorough reconsideration of all Siluro-Devonian members of the subfamily, a task beyond the scope of the present work.

Devonian relicts.--While *Richterarges* apparently became extinct at the end of the Silurian, two species from the Early Devonian of east Asia seem to represent a relict distribution of *Borealarges*. *Craspedarges superbus* Kobayashi and Hamada, 1977 and the closely related *C. bicornis* Zhou, 1987, both differ from most Silurian members of the genus in the following features (some of which were listed by Thomas and Holloway, 1988, p. 237): the presence of an additional pygidial border spine pair located behind the anteriormost; the apparent definition of the pleural bands of at least the third pygidial segment; the longer post-axial ridge; the inflation of the anterior part of the glabella in front of the bullar lobe; the great expansion of the anterior border; and the strong anterior divergence of the anterior branches of the facial suture (seen more prominently in B. superbus). Of these, only the extra pair of pygidial border spines has been observed in Silurian species, in undescribed material from the Wenlock-Ludlow of Arctic Canada. Nevertheless, in other features (length of pygidial axis, width of axis relative to that of pygidium, shape and expression of cranidial lobes, shape of hypostome, etc.) the species agree well with earlier members of the genus, and their assignment to Borealarges s.l. is well supported. Borealarges is not known from either China or Japan in the Silurian.

SYSTEMATIC PALEONTOLOGY

Terminology.--Morphological terms are applied following Thomas and Holloway (1988). The furrow circumscribing the rear of the bullar lobe (running between the longitudinal and axial furrows) is considered S1. Borealarges generally has two (and sometimes three) prominent pairs of tubercles positioned on the anterior part of the median glabellar lobe. These undoubtedly represent retentions of some particular pairs present throughout ontogeny. Silurian Borealarges genus group ontogenies are not well known, however. While Chatterton (1971, Fig. 9) has suggested a scheme for a member of the Acanthopyge clade (Acanthopyge (Jasperia) bifida (Edgell, 1955)), its application to holaspid specimens of Borealarges is difficult. The prominent tubercle pairs may correspond to Chatterton's pairs 5 and 6, but until a taxonomically comprehensive terminology for paired cephalic spines or tubercles is worked out, those present in adult *Borealarges* are referred to simply as the first and second median glabellar tubercle pairs, numbered from the back.

Family LICHIDAE Hawle and Corda, 1847

Subfamily TROCHURINAE Phleger, 1936

Genus RICHTERARGES Phleger, 1936

Type species.--*Lichas* (*Dicranogmus*) *ptyonurus* Hall and Clarke, 1888, p. 86, from the Cobleskill Limestone (Prídolí), New York State; by original designation.

Other species.--*Hemiarges aquilonius* Whittington, 1961, Ludlow, Arctic Canada; *H*. *bigener* Bolton, 1965, Upper Silurian, Arctic Canada; *H*. *echinatus* Thomas in Thomas and Narbonne, 1979, Ludlow, Arctic Canada; *H*. *ethnikos* Lane, Dawes, and Peel, 1980, Upper Silurian, Greenland; *H*. *ormistoni* Whittington, 1961, Upper Silurian, Arctic Canada.

Diagnosis.--Trochurines with long anterior border; longitudinal furrow usually effaced anteriorly, convergent anteriorly beside anterior half of bullar lobe; longitudinal furrow shallow posteriorly beside posterolateral glabellar lobe; anterior sections of facial sutures subparallel or only slightly anteriorly convergent, giving cranidium a subquadrate outline; cranidial sculpture of low subdued tubercles; S1 nearly straight and not markedly oblique;

hypostomal suture straight adaxially but abruptly deflected posteriorly abaxially; hypostome with generally effaced sculpture; mature pygidia with sagittal length (excluding articulating half ring and posteromedian spine, if present) at least 70 percent to commonly 80 percent of anterior width; maximum axial width commonly 23-27 percent of maximum pygidial width; pygidial axis with 10-12 discernible axial rings; second anterior pleural band long (exsag.); postaxial ridge long; pygidium with varying complements of marginal spines.

Discussion.--Thomas and Holloway (1988, p. 237) recognized a distinction between most of the species they assigned to *Richterarges* and both *R. bucklandii* and *R. mikulicorum*. With the description of a further four species of this separate morphological type, it becomes apparent that a relatively large, morphologically coherent group is involved. Herein, at least part of this assemblage is hypothesized to form a monophyletic group, which possibly forms a clade with *Terranovia* and which therefore may not even represent the sister taxon of *Richterarges* (although *Borealarges*, *Terranovia*, and *Richterarges* taken together likely form a monophyletic group). Accordingly, a new genus is erected for it. A comparison between *Richterarges* and *Borealarges* n. gen. is given under discussion of the latter genus below.

Richterarges ethnikos (Lane, Dawes, and Peel, 1980) has a plesiomorphic pattern of nine border spines similar to that of *Borealarges*, although other aspects of its morphology, particularly cranidial features, make assignment to *Richterarges* unambiguous. *Richterarges aquilonius* (Whittington, 1961) also has nine border spines, and late meraspid transitory pygidia that are very similar to mature *Borealarges* pygidia, if one ignores the fused protothoracic segments (compare Whittington, 1961, Pl. 56, fig. 5 with the large pygidia of *Borealarges* illustrated herein). As discussed above, this indicates derivation from the general nine-spined morphology that is primitive for the entire genus group (excluding potential Ordovician members), despite the variety of pygidial spine arrays developed in members of *Richterarges*.

The group to which *Richterarges* can now be restricted is almost entirely northern Laurentian, and appears to have become extinct at the end of the Silurian. The only geographic exception is the late Prídolí type species, *R. ptyonurus*, from New York State. A very similar distribution can be observed in the proetid trilobite *Hedstroemia* Pribyl and Vanek, 1978. This genus has a confirmed distribution for most of the Silurian almost identical to that of *Borealarges* (widespread in northern Laurentia; also in England and Baltica), but enters the eastern United States in the Prídolí in the form of *H. pachydermata* (Barrett, 1878) from New Jersey (see Lütke, 1990).

Genus BOREALARGES n. gen.

Type species.--*Borealarges reedi* n. gen. n. sp., from the Cape Phillips Formation, Wenlock (Homerian; *Pristiograptus ludensis* Zone), section Abbott River One, 22 m above base, northwestern Cornwallis Island, central Canadian Arctic.

Species assigned to Borealarges *s.s.*--*Hemiarges mikulicorum* Perry and Chatterton, 1977, Wenlock, Arctic Canada; *B. morrisoni* n. gen. n. sp., Wenlock, Arctic Canada; *B. tuckerae* n. gen. n. sp., Wenlock, Arctic Canada; *Hemiarges* sp. of Perry and Chatterton (1979, p. 595, Pl. 76, figs. 25, 27-30, but not fig. 26, which appears to belong to *Dicranogmus*), Wenlock, Northwest Territories, Canada.

Species assigned to Borealarges *s.l.*--*Craspedarges bicornis* Zhou, 1987, Gedinnian, China; *Peltura bucklandii* Milne Edwards, 1840, Wenlock, England; *Borealarges* s.l. *calei* n. gen. n. sp., late Wenlock, Arctic Canada; *Craspedarges superbus* Kobayashi and Hamada, 1977, Eifelian, Japan; ?*Hemiarges rolfei* (Lamont, 1965), late Llandovery, Scotland; *Trochurus* sp. indet. of Churkin (1961, p. 172, Pl. 35, fig. 7), Wenlock?, California; *Hemiarges* aff. *aquilonius* of Thomas (in Thomas and Narbonne, 1979, Pl. 5, figs. j, m, n, p), Ludlow, Arctic Canada.

Diagnosis.--Trochurines with short anterior border; bullar lobe fully circumscribed anteriorly; anterolateral corners of cranidium often with small projections formed by sharp anteriormost divergence of anterior section of facial suture; cranidial sculpture of relatively coarse tubercles with paired median glabellar tubercles retained and often prominent in large holaspides; S1 strongly anteriorly directed and with considerable posterior convexity; hypostomal suture usually describing a gentle, continuous arc with no abrupt posterior deflection; hypostomal middle body with ornament of fine to moderately coarse pits and tubercles anteriorly; pygidia with basic pattern of two pairs of pleural spines, two pairs of marginal spines, and single posteromedian spine (sometimes secondarily lost); pygidium with length (sag., excluding articulating half ring, and measured to base of posteromedian spine) 58-64 percent of maximum width (rarely 50 percent); axis with maximum width 38-41 percent of maximum pygidial width and usually with 7 to 8 discernible axial rings; postaxial ridge prominent but short.

Discussion.--Borealarges n. gen. differs from Richterarges Phleger, 1936 in its generally shorter anterior border; development in some species of a projection on the anterolateral corner of the cranidium; longitudinal furrow impressed anteriorly to fully circumscribe bullar lobe versus at least partly effaced anteriorly; pygidium much shorter relative to width; pygidial axis correspondingly shorter and with fewer discernable axial rings (7-8 versus 10-12); pygidial axis broader relative to maximum pygidial width (usually about 40 percent versus about 25 percent);

pygidial border spines relatively long, cylindrical, and of fixed pattern, versus shorter, dorsoventrally flattened, and of widely varying pattern that may show intraspecific variation.

Two species groups can be identified within *Borealarges*. The first, (including the type species, *B. morrisoni*, *B. mikulicorum*, and probably *B. tuckerae*), is characterized by possession of anterolateral cranidial projections, relatively long genal spines, and widely spaced median pygidial spines. This species group, at least, seems very likely to be monophyletic, an assertion supported most compellingly by the distinctive anterolateral cranidial projections and their consistent correlation with the character-states given above. Some Devonian species currently assigned to *Acanthopyge* (*Lobopyge*) (i.e. *A.* (*L.*) *australiformis* Chatterton, Johnson, and Campbell, 1979; *A.* (*L.*) *sinuata* (Ratte, 1886)) have somewhat similar structures, but these species have six small tubercles arranged along the anterior margin of the cranidium. The projection is small in *A.* (*L.*) *sinuata* and minute in *A.* (*L.*) *australiformis*, and is obviously produced through placement of the most adaxial tubercle directly against the anterior section of the facial suture. *Borealarges*, on the other hand, lacks these anterior border tubercles, and the anterolateral projections are much larger, triangular, and formed as evaginations of the border itself, not tubercles atop it. Hence, the structures are analagous, but topologically dissimilar and almost certainly not homologous.

A second group, *Borealarges* s.l. as discussed above, includes *B*. s.l. *calei* and *B*. s.l. *bucklandii*. It differs from the *B*. *reedi* group in lacking the anterolateral cranidial projections, possession of smaller palpebral lobes, shorter genal spines, and more closely spaced median pygidal border spines (compare, for example, Figures 4.1 and 7.1). Among undescribed Arctic diversity of the *B*. s.l. *calei* group are species which reduce the median pygidial spine through ontogeny to secondarily lose it altogether in the holaspid, and this fact has been reflected in the generic diagnosis. The monophyly of the *B*. s.l. *calei* group is ambiguous.

Currently known post-Wenlock diversity of *Borealarges* is almost entirely northern Laurentian. However, this is possibly a function of lack of published data from other areas, as the Ludlow lichid faunas of both Britain and the Baltic region remain poorly known. The east Asian Devonian species *B*. s.l. *superba* and *B*. s.l. *bicornis* were discussed above.

Etymology.--Latin *boreas*, north, and the name *Arges* Goldfuss, 1839 (=*Ceratarges* Gürich, 1901), in reference to the taxon's mainly northern and Arctic present-day distribution.

BOREALARGES MIKULICORUM (Perry and Chatterton, 1977)

Figures IV-3.1 to IV-3.25, IV-4.5, IV-4.8 to IV-4.17

Hemiarges mikulici PERRY AND CHATTERTON, 1977, p. 304-307, Pl. 5, figs. 5?, 6?, 21-25, Pl. 6, figs. 1-11.

Richterarges mikulici (Perry and Chatterton). THOMAS AND HOLLOWAY, 1988, p. 236-237.

Nomenclatural note.--When Perry and Chatterton (1977, p. 304-307) erected this species, they clearly stated that it was named after the Donald Mikulic family. The species name should therefore be mikulicorum, not mikulici. This corresponds exactly to an example of a permissible name change given under Article 32c(ii) of the ICZN (1985), and the species is henceforth referred to as mikulicorum.

Diagnosis.--Borealarges with first glabellar tubercle pair very prominent in large holaspides; anterior sections of facial suture nearly subparallel and short; cranidium of only moderate sagittal convexity; glabellar sculpture of very densely distributed tubercles of medium to small size in addition to paired tubercles; hypostome with only a few very fine tubercles located anteriorly on middle body; pygidia nearly semicircular in outline, with narrow posterior pleural area.

Discussion.--The collections studied by Perry and Chatterton (1977) were made with only very approximate stratigraphic control, and the sclerite associations were often based upon stratigraphically mixed samples. As systematic work progresses based upon subsequent well-controlled collections, approximate correlations between the localities given by Perry and Chatterton and those used in the present study can be given. Perry and Chatterton's (1977) localities GSC C-22184 and C-22185 correspond well with horizon BH 1 110 m/BHL 1 0 m. It is very likely that most of the material from the former localities in Perry and Chatterton's paper is from this bed (or from BH 1 106 m, 109 m, or 112 m, all of which contain an identical fauna). A few sclerites reported by Perry and Chatterton to be from these localities, however, are clearly from strata higher in the succession, and caution must still be exercised. The remaining localities (GSC C-22186, C-22187, 402 Y, and 402**) are mixed collections likely derived from horizons BH 1 143-209 m and BHL 1 27-92 m. Three quite distinct faunas are now known in stratigraphic succession in this interval.

Fortunately, the problems of association in the latter interval do not affect the holotypes of the four species erected by Perry and Chatterton (1977); all are from either locality GSC C-22184 or C-22185, agree in all respects with material from horizon BH 1 110 m/BHL 1 0 m (or in the case of Hemiarges rohri, a slightly higher horizon), and can safely be assumed to have been derived from this bed (or nearby ones; see above). Hence there is little chance of confusion surrounding formal taxonomic names. Borealarges sclerites illustrated by Perry and Chatterton (1977) from the interval of mixed samples are given specific assignment below, where possible.

Thomas and Holloway (1988, p. 225-226) have restricted *Hemiarges rohri* to the pygidia assigned to it by Perry and Chatterton (1977, Pl. 5, figs. 4, 17, 20), and have reassigned the species to *Acanthopyge* (*Lobopyge*). Work in progress has shown that the species should be restricted to its holotype pygidium. The remaining pygidia are older than the holotype, and belong to an undescribed species of "*Lobopyge*".

Borealarges mikulicorum is most closely comparable to *B. morrisoni* and *B. reedi*. *B. mikulicorum* shares with *B. morrisoni* generally similar cranidial proportions, only moderately anteriorly divergent longitudinal furrows, glabellar sculpture of very densely distributed tubercles, and a hypostome with few middle body tubercles and with the middle lobe of the posterior margin not prominent. Differences include the more prominent anterolateral cranidial projections of *B. morrisoni*, that species' lack of prominent paired glabellar tubercles in mature holaspides, slightly narrower median glabellar lobe, slightly more tuberculate anterior part of anterior lobe of hypostomal middle body, librigenae with narrower lateral borders, particularly anteriorly (compare Figure IV-3.11 to IV-3.14 with Figure IV-8.15 and IV-8.18), and third pair of pygidial border spines subparallel to convergent posteriorly (versus conspicuously divergent), flatter in cross section, and shorter.

Borealarges mikulicorum is comparable to *B. reedi* mainly in general proportions of the pygidia (compare specimens illustrated in Figure IV-4). These differ in that the posterior part of the axial furrows of *B. reedi* are subparallel, with the anterior part starting at the pleural ribs always markedly anteriorly divergent, while those of *B. mikulicorum* do not have as strong a deflection in course, with the entirety of the furrows gently anteriorly divergent (compare Figure IV-4.1 with Figure IV-4.9, IV-4.11). Cranidial differences are profound, including *B. reedi*'s less prominent anterolateral projections, less dense glabellar sculpture, more anteriorly divergent longitudinal furrows, much more anteriorly convergent anterior sections of the facial sutures, palpebral lobes that extend further laterally, and more convex cranidial sagittal profile (compare Figure IV-5.4, IV-5.7 with Figure IV-3.5, IV-3.9).

Material.--Topotype material UA 9196-9210, 9215-9220, from sections BH 1 109-110 m and BHL 1 0 m, Cape Phillips Formation, Wenlock (Sheinwoodian; *Cyrtograptus* aff. *rigidus*-*Monograptus* aff. *riccartonensis* Zone), south shore of Baillie-Hamilton Island, central Canadian Arctic.

BOREALARGES REEDI n. gen. and n. sp.

Figures IV-4.1 to IV-4.4, IV-4.7, IV-5.1 to IV-5.27

Diagnosis.--*Borealarges* with weak anterolateral cranidial projections; strongly anteriorly convergent anterior sections of facial sutures; longitudinal furrows diverging markedly anteriorly; shallow furrow developed across median lobe at rear of bullar lobes; only moderately dense glabellar tuberculation; broad hypostome, posterior border with prominent ventral convexity (in sagittal profile), middle body with sparse, moderately fine pits and a few very fine scattered tubercles anteriorly.

Description.--Cranidium. Anterior border very short medially, overhung by glabella in dorsal view; rostral suture deflected laterally and very slightly anteriorly at lateral extremity to form relatively subdued anterolateral projection of cranidium; anterior branch of facial suture moderately anteriorly convergent, not deflected strongly anteriorly at anterolateral projection; palpebral lobe large, subsemicircular in outline but tapering to blunt lateral point; 7-8 distinct tubercles around rim of palpebral lobe, tubercle row continued posteriorly along sutural ridge as far as posterior border furrow, continued adaxial to anterior section of facial suture only slightly past anterior end of palpebral lobe; distinct but small pit positioned at midlength of palpebral lobe, but displaced laterally from center; posterior section of facial suture slightly more posteriorly divergent than anterior section; longitudinal furrow very weakly impressed in front of occipital furrow, distinctly impressed from rear of bullar lobe, with sharp lateral deflection at half length of bullar lobe; longitudinal furrows markedly anteriorly divergent, fully impressed to contact with axial furrow just behind anterolateral cranidial projections; axial furrow strongly impressed in front of palpebral lobe, with deep, more or less prominent, anterior pit at contact with longitudinal furrow; axial furrow effaced behind anterior extent of palpebral lobe; glabella with moderately dense sculpture of small to medium sized tubercles; first glabellar tubercle pair sometimes prominent; second pair usually discernible, but much reduced; single more prominent tubercle sometimes retained on rear half of bullar lobe, but often not distinguishable from other tubercles; occipital ring of moderate length (sag.), shortened laterally behind abaxial part of L1; occipital furrow well impressed, medially transverse, deflected strongly posterolaterally at swelling of L1a; eyes nearly as high as glabella.

Librigena elongate; lateral and posterior border furrows very broad and shallow; librigenal field with sculpture of very fine, evenly scattered tubercles together with large, coarse tubercles on all parts but concentrated closer to eye; lateral border broad, with moderately fine tubercles interspersed with moderately coarse ones medially and with fine subparallel lines formed of small tubercles in tight rows laterally; lateral margin with even, gentle lateral convexity; posterior border not as broad or well defined as lateral border, of similar sculpture but lacking fine lines; genal spine relatively long, broad; subgenal notch very wide, gently arcuate; prominent eye socle with row of small tubercles developed at mid-height; doublure broad, underlying most of genal field, ornamented with continuation of subparallel lines of lateral border; lines running parallel with lateral margin anteriorly, then curving posteriorly to run transversely across midline of genal spine, then adaxially to oblique contact with subgenal notch; lines more broadly spaced on posteromedial part of doublure; lateral margin with slight notch anteriorly, just behind anterior librigenal projection.

Hypostome broad (sagittal length approximately 75 percent of maximum width); hypostomal suture with more or less even anterior convexity; anterior wing small, subquadrate, directed dorsolaterally; lateral notch pronounced; lateral margin deflected strongly around robust shoulder, with lateral concavity behind shoulder, running smoothly into lateral lobe of posterior margin; posterior margin divided into three lobes of varying relative prominence; posterior border 50 percent of sagittal length; lateral border furrows posteriorly convergent; posterior border furrow transverse and nearly straight; middle furrow completely effaced medially; anterior lobe approximately 70 percent of sagittal length of middle body; middle body with sculpture of relatively sparse, moderately coarse pits and fine scattered tubercles on anterior region of anterior lobe; maculae present as subtle circular depressions with raised, gentle tubercle in center; posterior border smooth medially, with prominent ventral convexity in sagittal profile; lateral border with 5-6 coarse ridges running subparallel to lateral margin, sometimes with scattering of small tubercles on shoulder and abaxial to posterior lobe of middle body; doublure underlying posterior border with two gently concave lateral areas, deep medial area, and ventrally turned lip along anterior edge; three small posteriorly directed spines, median one more prominent, developed at thickened median portion of lip.

Pygidium with sagittal length (excluding articulating half ring and border spine) approximately 60-64 percent of maximum width; first anterior pleural band short (exsag.); second anterior band approximately twice exsagittal length of first; axial ring and posterior pleural band of first and second segments with single transverse row of medium sized tubercles; axis with maximum width approximately 75 percent sagittal length (excluding articulating half ring); only first two axial rings defined medially; 7-8 axial rings usually discernible, with those posterior to three very poorly defined, and visible only at their extreme abaxial extent; anterior pleural band of second segment and remainder of pleural field behind second segment with mixture of medium sized tubercles similar to those on posterior pleural bands and finer, evenly scattered tubercles; postaxial ridge prominent, slightly narrower than pygidial border, with only one or two small tubercles in random pattern; pygidial border relatively narrow, with more or less evenly spaced, medium sized tubercles along dorsal aspect; first pleural spine short, sharply outturned; second pleural spine longer, following inclination of posterior pleural band to run more posteriorly; third border spine pair longest, only slightly posteriorly divergent; fourth border spine pair set near to third, widely spaced, subequal in size to slightly longer than small, subtriangular median spine; posteromedian part of doublure extending anteriorly to rear of axis, doublure narrowing anterolaterally; outer part of doublure with fine, subparallel lines formed of small, closely spaced tubercles in tight rows, matching curvature of pygidial margin; pattern of lines extended disconinuously onto ventral aspect of border spines; lines becoming progressively finer on inner part of doublure, extremely fine and closely spaced at inner margin.

<u>Discussion</u>.--<u>Borealarges</u> <u>reedi</u> occurs together with <u>B</u>. s.l. <u>calei</u> n. gen. n. sp., but the taxa are morphologically distinct and <u>B</u>. <u>reedi</u> is much less common, allowing confident association of sclerites. The species furthermore belong to two different species groups, each of which has certain characteristic features, based firmly upon comparison of species which are known from articulated

individuals or which occur in the absence of congenerics with which they could be confused (e.g., _B_. _mikulicorum_, see above). Nevertheless, there is some slight overlap in the morphology of librigenae. The librigena illustrated in Figure IV-6.20 is assigned to _B_. s.l. _calei_, but its genal spine is sufficiently long that it is possible it could belong to _B_. _reedi_; others like it are known, but the majority of recovered librigenae are easily assigned to one or the other of the species.

Borealarges _reedi_ was compared above with _B_. _mikulicorum_, which it most closely resembles among described species.

Etymology.--After Lou Reed.

Material.--Holotype cranidium UA 9221, paratypes UA 9211-9214, 9222-9232, from section ABR 1 22 m, Wenlock (Homerian; _Pristiograptus_ _ludensis_ Zone), Cape Phillips Formation, northwestern Cornwallis Island, central Canadian Arctic.

BOREALARGES s.l. CALEI n. gen. and n. sp.

Figures IV-6.1 to IV-6.22, IV-7.1 to IV-7.23

Diagnosis.--_Borealarges_ lacking anterolateral cranidial projections; glabellar sculpture of relatively coarse but sparse tubercles together with many very fine, subdued, granular tubercles; palpebral lobe small; genal field with low number of coarse tubercles; genal spine usually short; hypostome with coarse tubercles on anterior part of anterior lobe of middle body, coarse pits on entirety of middle body, pits on anterior and lateral aspects of posterior border, dense smattering of fine tubercles adaxial and posterior to shoulder on lateral border, and posterior border essentially flat in sagittal profile; pygidia with third pair of border spines very long through most of ontogeny, median three spines closely spaced.

Discussion.--Borealarges s.l. calei is most similar to B. s.l. bucklandii. Together the species differ from all of the remaining congenerics in the lack of anterolateral cranidial projections, possession of small palpebral lobes, relatively short genal spines, and pygidial border spines with the median three spines closely spaced, so that the five spines along the posterior aspect of the border are evenly spaced. Borealarges s.l. calei differs from B. s.l. bucklandii most obviously in that pygidia of the former species have only the first and second axial rings defined medially, whereas pygidia of B. s.l. bucklandii (see Thomas and Holloway, 1988, Pl. 15, figs. 321, 324) have at least the first four, and arguably the fifth, continuous and fully defined medially. Other differences include the much wider median glabellar lobe of B. s.l. calei (compare Figure IV-6.1 to IV-6.3 with Thomas and Holloway, 1988, Pl. 15, figs. 319, 324), its relatively sparser glabellar tuberculation, and shorter bullar lobe. It could be argued that some of these differences are ontogenetic, and due to comparison of specimens of different sizes. Cranidia of B. s.l.

bucklandii illustrated by Thomas and Holloway (1988) are over twice as large as the largest known specimens of *B*. s.l. *calei*. Several facts are in conflict with this suggestion, however. First, no larger specimens, even fragmentary, of *B*. s.l. *calei* have been recovered. Second, there is evidence that the sample from ABR 1 22 is not biased towards immature individuals. The encrinurine trilobite *Struszia harrisoni* Edgecombe and Chatterton, in press, known from abundant material at the type horizon of *B*. s.l. *calei*, is represented by very large holaspide specimens. In fact, *S*. *harrisoni* reaches larger maximum size at ABR 1 22 m than a congeneric known from calcareous material from the Ludlow of Gotland, Sweden (*S*. *obtusa* (Angelin, 1851); see Ramsköld, 1986). This comparison holds also for undescribed species of *Dudleyaspis* and *Hedstroemia* from ABR 1 22. Therefore, there is little reason to suspect either that the silicified sample is inherently biased toward small juvenile specimens, or that size sorting has occurred prior to deposition. Taken together, the evidence seems to indicate that the sampled population of *B*. s.l. *calei* simply reached a smaller maximum size than that of *B*. s.l. *bucklandii*.

Etymology.--After John Cale.

Material.--Holotype cranidium UA 9233, paratypes UA 9234-9260, from section ABR 1 22 m, Wenlock (Homerian; *Pristiograptus ludensis* Zone), Cape Phillips Formation, northwestern Cornwallis Island, central Canadian Arctic.

BOREALARGES cf. B. s.l. CALEI n. sp.

Figure IV-9.17, IV-9.19 to IV-9.21

Discussion.--Several sclerites resemble *Borealarges* s.l. *calei* in overall proportions, but seem distinct in the presence of many small tubercles between the larger ones on all parts of the dorsal surface. Other differences include: an apparently longer bullar lobe on the single known cranidium; the single cheek has a border with higher lateral convexity than those assigned to *B*. s.l. *calei*; and the single known pygidium has a median spine which, while imperfectly preserved, seems to be much reduced and ventrally displaced. It is entirely possible that the sclerites belong together and represent a separate, new, species, distinct from *B*. s.l. *calei*. However, it is also conceivable that they fall within the range of intraspecific variation of the latter species, although no obvious intermediates have been found. With only three sclerites presently known, the material is reported in open nomenclature.

Material.--Cranidium UA 9284, librigena UA 9283, and pygidium UA 9285, from section ABR 1 22 m, Wenlock (*Pristiograptus ludensis* Zone), Cape Phillips Formation, northwestern Cornwallis Island, central Canadian Arctic.

BOREALARGES MORRISONI n. gen. and n. sp.

Figures IV-8.1 to IV-8.23, IV-9.1 to IV-9.3,

IV-9.5, IV-9.6, IV-9.8, IV-9.10

Hemiarges mikulici PERRY AND CHATTERTON, 1977, p. 304-307, Pl. 5, 18?, 19?, Pl. 6, fig. 12?

Hemiarges rohri PERRY AND CHATTERTON, 1977, p. 307-308, Pl. 5, figs. 1-3, 6?, 9?, 10?, 11, 12, 15, 16, 18?, 19?

Diagnosis.--Borealarges with very pronounced anterolateral cranidial projections; median glabellar lobe narrow, and lacking prominent paired tubercles in large holaspides; posterolateral cranidial lobe broad and long (exsag.); librigena with lateral border narrow anteriorly; pygidium with relatively short border spines; third pygidial spine pair subparallel to posteriorly convergent; pleural area posterior to second pleural rib broad.

Discussion.--Borealarges morrisoni was compared with B. mikulicorum above. It differs from B. reedi in cranidial features in most of the ways listed for B. mikulicorum (less anteriorly convergent anterior section of facial sutures, more prominent anterolateral projections, denser glabellar sculpture, etc.). The pygidium of B. morrisoni is poorly known, but an obvious difference from that of B. reedi is the possession of shorter, more posteriorly directed border spines, particularly the third pair (compare Figure IV-9.1 with Figure IV-4.1, IV-4.3).

Etymology.--After Sterling Morrison.

Material.--Holotype cranidium UA 9261, paratypes UA 9262-9276, from locality BHH, and sections BH 1 164.5-204 m and

BHL 1 92 m, Wenlock (Sheinwoodian; Cyrtograptus perneri-Monograptus aff. munchi Zone), Cape Phillips Formation, south shore of Baillie-Hamilton Island, central Canadian Arctic.

BOREALARGES TUCKERAE n. gen. and n. sp.

Figures IV-9.4, IV-9.7, IV-9.9, IV-9.11 to IV-9.16,
IV-9.18, IV-10.1 to IV-10.25

Hemiarges mikulici PERRY AND CHATTERTON, 1977, p. 304-307, Pl. 5, figs. 7?, 8?, 13, 14.

Diagnosis.--Borealarges with median lobe of high dorsal convexity and substantial lateral expansion beside bullar lobe; three glabellar tubercle pairs present; glabellar tubercle pairs retained and developed into short spines in large holaspides; hypostome lacking any tubercles on middle body; librigena short, with broad field and high lateral convexity; genal spine long and nearly cylindrical distally; pygidium with very long, slender border spines; pygidial length (sag.) approximately 50 percent of maximum width.

Discussion.--Borealarges tuckerae differs from all described congenerics in its possession of median glabellar spines on an inflated median lobe, three instead of two prominent glabellar tubercle pairs in mature holaspides, long, narrow genal spine, raised eye, and very short pygidium (50 percent of width versus just over 60 percent in all other species) with long, cylindrical border spines. The possibility of an affinity between this species and the genus _Terranovia_ has been discussed above.

Etymology.--After Maureen Tucker.

Material.--Holotype pygidium UA 9281, paratypes UA 9277-9280, 9282-9299, from locality BHH and sections BH 1 164.5-204 m and BHL 1 92 m, Wenlock (Sheinwoodian; _Cyrtograptus perneri_-_Monograptus_ aff. _munchi_ Zone), Cape Phillips Formation, south shore of Baillie-Hamilton Island, central Canadian Arctic.

BOREALARGES n. sp.?

Figure IV-4.6

Discussion.--A single fragmentary pygidium from ABR 1 22 m is unique in the absence of the posterior two pairs of border spines, with only the pleural and median spines retained. In general proportions the specimen seemingly belongs to _Borealarges_. It may represent a teratological specimen of either of the cooccurring species, _B_. _reedi_ or _B_. s.l. _calei_, or possibly a new species.

BOREALARGES s.l. BUCKLANDII (Milne Edwards, 1840)

Figure IV-11

Peltura _Bucklandii_ MILNE EDWARDS, 1840, p. 345, Pl. 34, fig. 12.

Hemiarges _bucklandii_ (Milne Edwards). THOMAS, 1981, p. 74, Pl. 20, figs. 18-20, 22-28 (with full synonymy).

Discussion.--Thomas (1981, p. 74) pointed out that the holotype of this species was lost, but did not select a neotype. As argued herein, _Borealarges_ includes two species groups. Most of the figured material of *B. bucklandii* seems to belong to the *B.* s.l. *calei* group. Some specimens, however, strongly suggest a member of the *B. reedi* group (i.e. *Borealarges* s.s.). For example, a pygidium illustrated by Thomas (1981, Pl. 20, fig. 28) has border spines that are strongly posteriorly divergent, with the median spines widely spaced, a condition diagnostic of *Borealarges* s.s. (cf. *B. mikulicorum*, Figure IV-4.9 to IV-4.11 and *B. reedi*, Figure IV-4.1) and at odds with the typical morphology of specimens assigned to *B. bucklandii* (e.g. Thomas and Holloway, 1988, Pl. 15, figs. 321, 324). Furthermore, specimen BM In52610 (Figure IV-11) has distinct anterolateral cranidial projections and relatively large palpebral lobes. It resembles *B. reedi* (cf. Figure IV-11 and Figure IV-5.1, IV-5.2). Specimen SM A3470 (Thomas and Holloway, 1988, Pl. 15, figs. 318, 319), on the other hand, lacks anterolateral cranidial projections, has relatively small palpebral lobes, and is very similar to cranidia of *B.* s.l. *calei* (cf. Figure IV-6.1). Both horizon ABR 1 22 and the Much Wenlock Limestone Formation at Dudley belong to the latest Wenlock *Pristiograptus ludensis* Zone. Two and possibly three *Borealarges* species occur at ABR 1 22. Given the preceding discussion, it seems very likely that at least two species occur in the Much Wenlock Limestone, one of which is the closest described relative of *B.* s.l. *calei*.

In light of this situation, it becomes desirable to fix the specific concept of B. bucklandii through the selection of an appropriate neotype. As this action ideally involves a thorough search for the missing type specimen and a consideration of the entirety of available material, it is beyond the scope of the present work. It has been assumed for purposes of comparison that either the missing type or a future neotype will conform to the morphology most common among illustrated examples, and reflected by the specimens illustrated by Thomas and Holloway (1988, Pl. 15, figs. 318-321, 324).

FIGURE IV-1--Position of trilobite localities from which material is described herein. Locality BHH and sections BH 1 and BHL 1 are located on the south shore of Baillie-Hamilton Island (1). Section ABR 1 is located on a small northerly flowing tributary of the Abbott River (2).

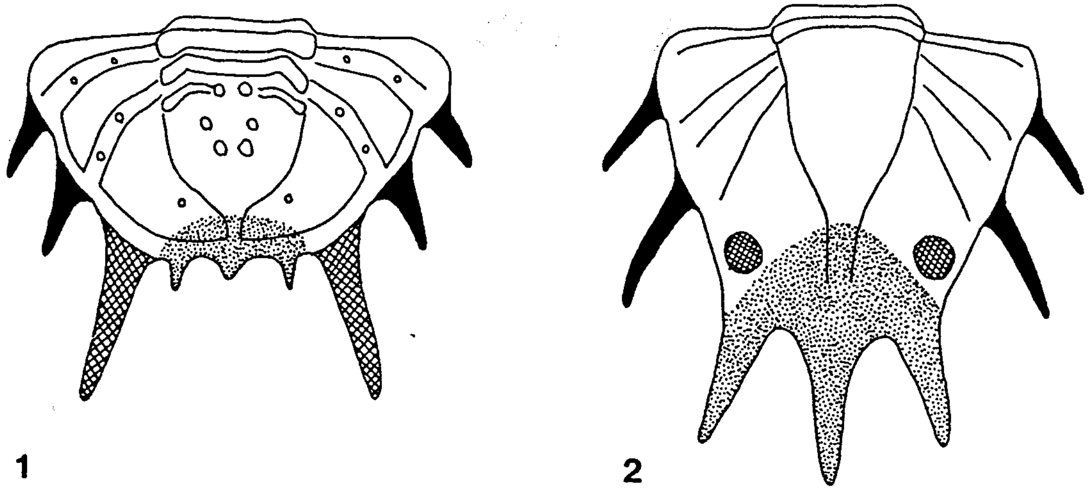

FIGURE *IV-2*--Probable homologies of pygidial border spines of *Borealarges* n. gen. and *Terranovia* Maximova, 1977. Homologies indicated by solid black, stippling, and cross-hatching. *1*, *Borealarges tuckerae* n. gen. n. sp., Wenlock, Cape Phillips Formation, Baillie-Hamilton Island, central Canadian Arctic, schematic reconstruction based on specimens illustrated in Figure 9.11, 9.14, approximately x12; *2*, *Terranovia nalivkini* Maximova, 1977, Emsian, Novaya Zemlya, schematic reconstruction based on holotype (Yolkin and Ormiston, 1985, Fig. 5.11), approximately x1.2; only bases of large, dorsally directed, third spine pair shown (cross-hatching).

FIGURE IV-3--1-25, Borealarges mikulicorum (Perry and Chatterton, 1977), from section BH 1 109-110 m and section BHL 1 0 m, Cape Phillips Formation, Wenlock (Sheinwoodian; Cyrtograptus aff. rigidus-Monograptus aff. riccartonensis Zone), south shore of Baillie-Hamilton Island, central Canadian Arctic. Magnifications are x10 except where otherwise stated. 1, 5, dorsal and left lateral views of cranidium UA 9196 (BH 1 110 m); 2, dorsal view of cranidium UA 9197 (BHL 1 0 m); 3, 4, dorsal and left lateral views of cranidium UA 9198 (BHL 1 0 m); 6, 7, 9, 25, dorsal, anterior, right lateral, and ventral views of cranidium UA 9199, x10 except 25, x7.5 (BHL 1 0 m); 8, ventral view of hypostome UA 9200 (BH 1 110 m); 10, ventral view of hypostome and rostral plate UA 9201 (BH 1 110 m); 11, 20, 22, external, internal, and lateral views of right librigena UA 9202 (BHL 1 0 m); 12, external view of right librigena UA 9203 (BH 1 110 m); 13, external view of right librigena UA 9204 (BHL 1 0 m); 14, external view of right librigena UA 9205 (BH 1 110 m); 15, ventral view of rostral plate UA 9206 (BH 1 109 m); 16, 21, 23, 24, ventral, dorsal, posterior, and anterior view of hypostome UA 9207 (BH 1 110 m); 17, external view of left librigena UA 9208 (BH 1 110 m); 18, external view of left librigena UA 9209 (BH 1 110 m); 19, external view of left librigena UA 9210 (BH 1 110 m).

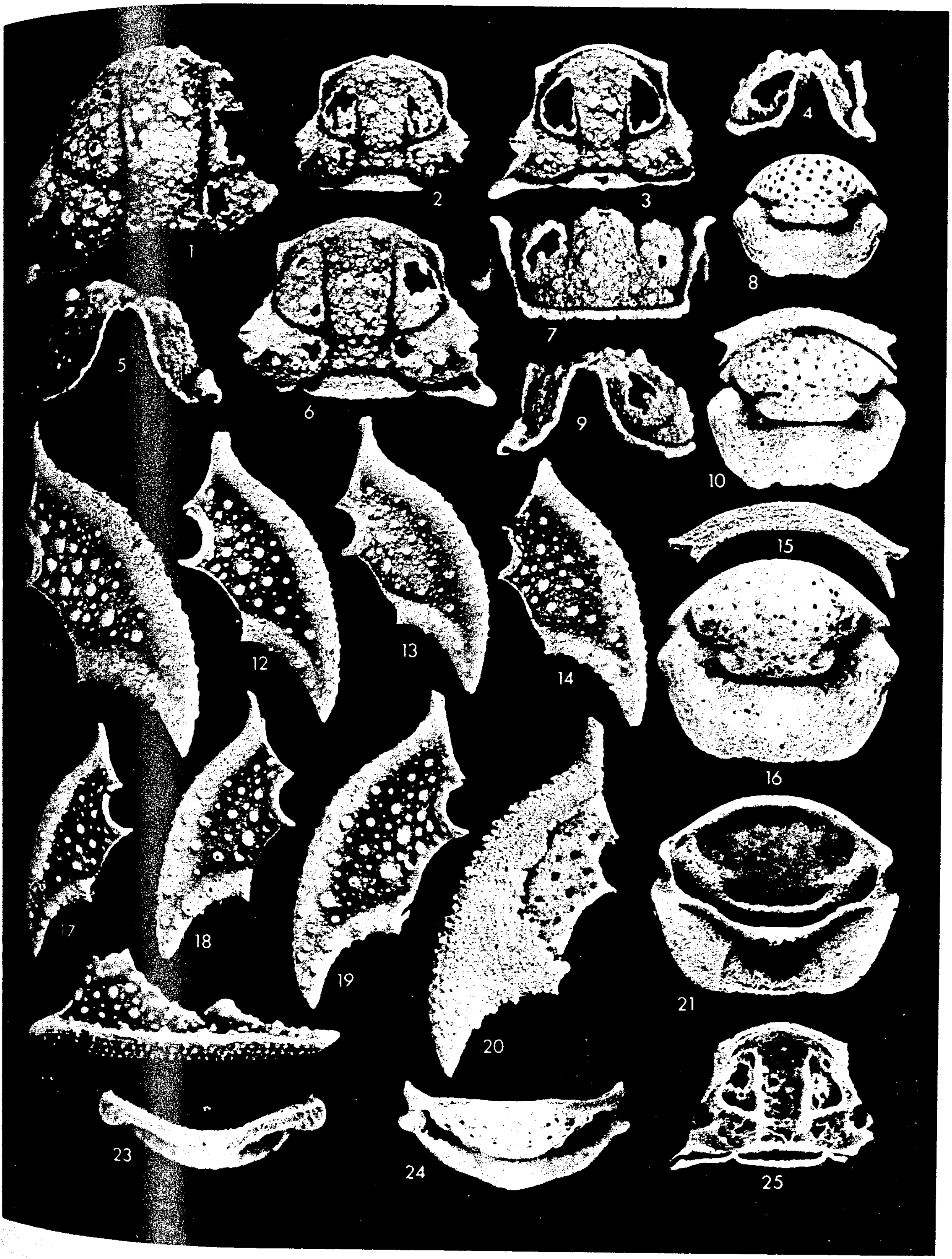
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FIGURE *IV-4*--*1*-*4*, *7*, *Borealarges* *reedi* n. gen. n. sp., from section ABR 1 22 m, Cape Phillips Formation, Wenlock (Homerian; *Pristiograptus* *ludensis* Zone), near Abbott River, northwestern Cornwallis Island, central Canadian Arctic. *1*, *7*, dorsal and ventral views of pygidium UA 9211, x7.5; *2*, dorsal view of pygidium UA 9212, x7.5; *3*, dorsal view of pygidium UA 9213, x7.5; *4*, dorsal view of pygidium UA 9214, x7.5. *5*, *8*-*17*, *Borealarges* *mikulicorum* (Perry and Chatterton, 1977), from sections BH 1 110 m and BHL 1 0 m, Cape Phillips Formation, Wenlock (Sheinwoodian; *Cyrtograptus* aff. *rigidus*-*Monograptus* aff. *riccartonensis* Zone), south shore of Baillie-Hamilton Island, central Canadian Arctic. *5*, *9*, *12*, *17*, left lateral, dorsal, posterodorsal, and ventral views of pygidium with fragment of attached thoracic segment UA 9215, x7.5 (BH 1 110 m); *8*, *10*, *13*, left lateral, dorsal, and posterior views of pygidium UA 9216, x10 (BHL 1 0 m); *11*, *14*, dorsal and posterodorsal views of pygidium UA 9217, x10 (BH 1 110 m); *15*, dorsal view of pygidium UA 9218, x10 (BH 1 110 m); *16*, dorsal view of pygidium UA 9219, x10 (BHL 1 0 m). *6*, *Borealarges* n. sp.?, from section ABR 1 22 m, Cape Phillips Formation, Wenlock (Homerian; *Pristiograptus* *ludensis* Zone), near Abbott River, northwestern Cornwallis Island, central Canadian Arctic, dorsal view of pygidium UA 9220, x10.


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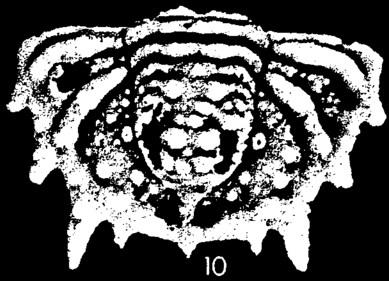
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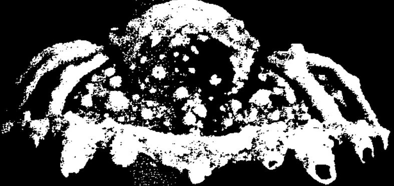
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FIGURE IV-5--1-27, Borealarges reedi n. gen. n. sp., from section ABR 1 22 m, Cape Phillips Formation, Wenlock (Homerian; Pristiograptus ludensis Zone), near Abbott River, northwestern Cornwallis Island, central Canadian Arctic. Magnifications are x10 except where otherwise stated. 1, 4, 18, dorsal, right lateral, and ventral views of holotype cranidium UA 9221; 2, 5, 7, dorsal, anterodorsal, and left lateral views of cranidium UA 9222; 3, 6, 8, dorsal, anterior, and right lateral views of cranidium UA 9223; 9, 12, 13, dorsal, anterior, and left lateral views of cranidium UA 9224; 10, dorsal view of crandium UA 9225; 11, 16, 20, internal, external, and ventrolateral views of left librigena UA 9226, x10 except 11, x7.5; 14, external view of right librigena UA 9227; 15, external view of right librigena UA 9228; 17, external view of left librigena UA 9229; 19, external view of right librigena UA 9230; 21, 22, 23, 25, dorsal, left lateral, ventral, and anterior views of hypostome UA 9231, x5; 24, 26, 27, dorsal, posterodorsal, and ventral views of hypostome UA 9232, x7.5.

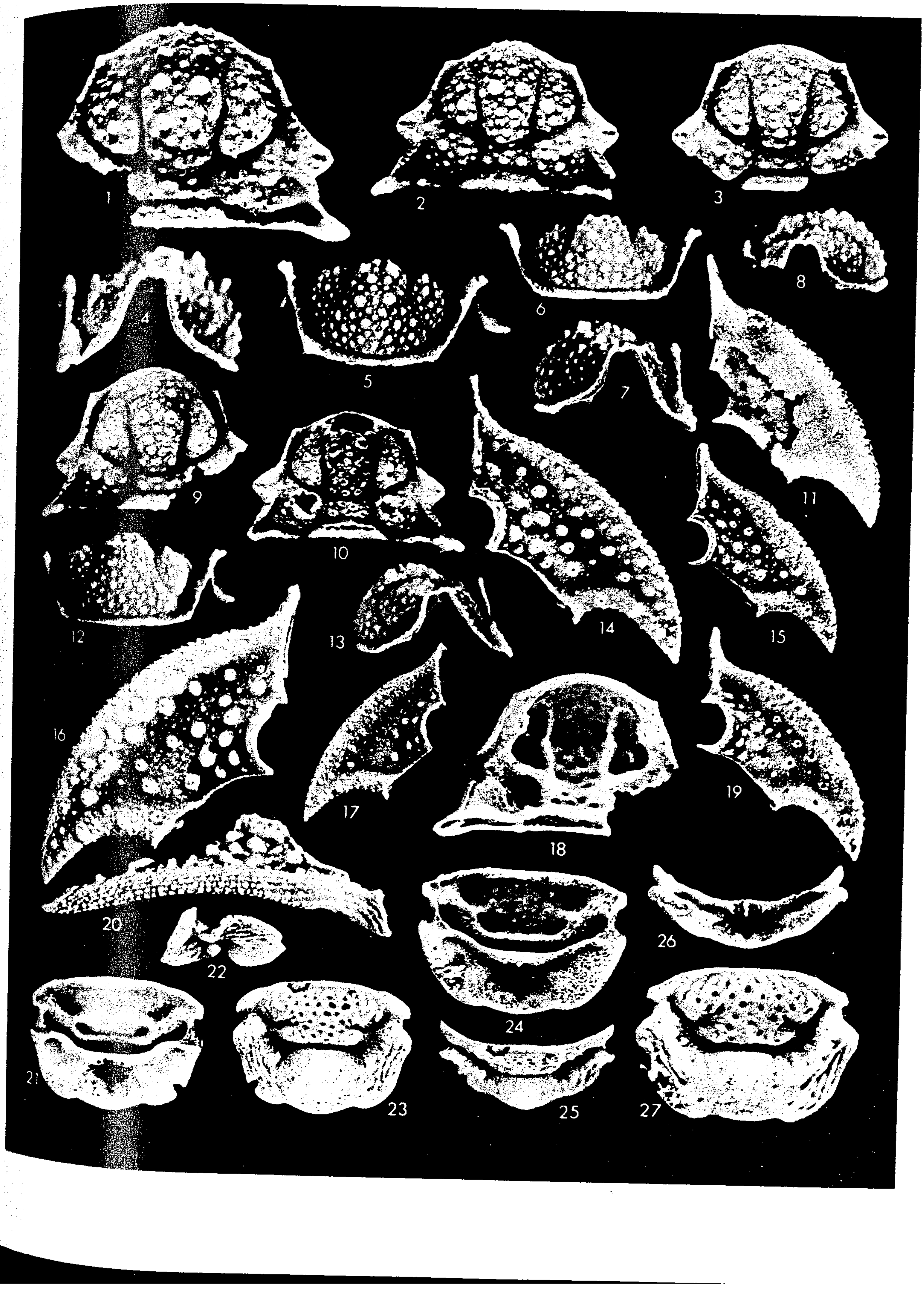
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FIGURE *IV-6*--*Borealarges* s.l. *calei* n. gen. n. sp., from section ABR 1 22 m, Cape Phillips Formation, Wenlock (Homerian; *Pristiograptus* *ludensis* Zone), near Abbot River, northwestern Cornwallis Island, central Canad Arctic. Magnifications are x10 except where stated otherwise. *1*, *4*, *7*, *22*, dorsal, anterior, left later and ventral views of holotype cranidium UA 9233, x10 except 22, x7.5; *2*, *5*, *8*, dorsal, anterior, and righ lateral views of cranidium UA 9234; *3*, dorsal view c cranidium UA 9235; *6*, *9*, *10*, dorsal, anterior, and right lateral views of cranidium UA 9236; *11*, dorsal view of cranidium UA 9237, x15; *12*, *13*, *14*, dorsal, left lateral, and anterior views of cranidium UA 92 x15; *15*, external view of right librigena UA 9239; 1 *19*, external and internal views of right librigena 9240; *17*, external view of right librigena UA 9241; external view of left librigena UA 9242; *20*, dorsolateral view of right librigena UA 9243; *21*, external view of right librigena UA 9244.

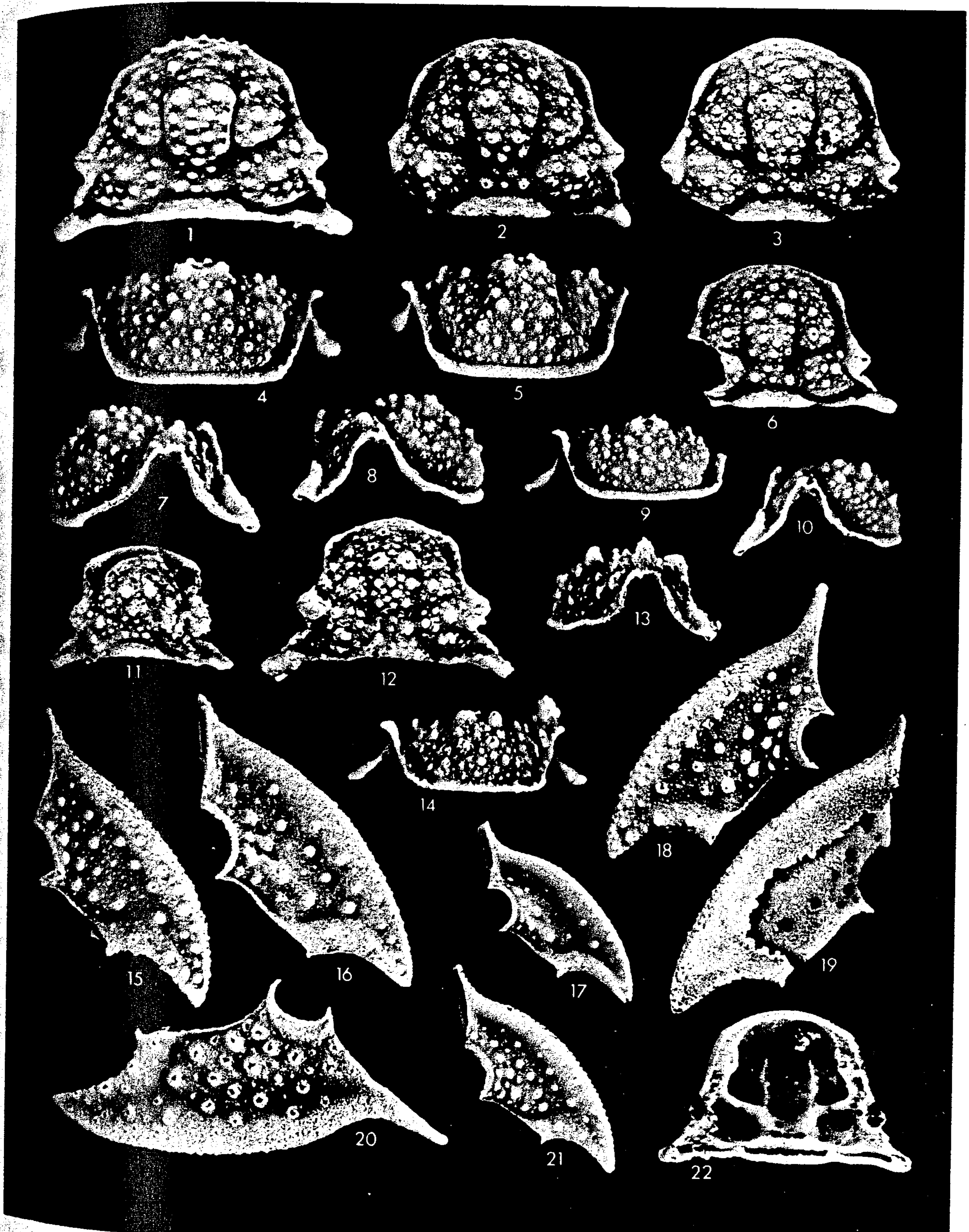
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FIGURE *IV-7*--1-23, *Borealarges* s.l. *calei* n. gen. n. sp., from section ABR 1 22 m, Cape Phillips Formation, Wenlock (Homerian; *Pristiograptus* *ludensis* Zone), near Abbott River, northwestern Cornwallis Island, central Canadian Arctic. Magnifications are x10 except where stated otherwise. *1*, *4*, *7*, *13*, dorsal, posterior, left lateral, and ventral views of pygidium UA 9245, x10 except *13*, x7.5; *2*, dorsal view of pygidium UA 9246, x7.5; *3*, dorsal view of pygidium UA 9247; *5*, *8*, *9*, dorsal, left lateral, and posterior views of pygidium UA 9248; *6*, dorsal view of pygidium UA 9249; *10*, dorsal view of pygidium UA 9250; *11*, dorsal view of pygidium UA 9251; *12*, ventral view of hypostome UA 9252; *14*, dorsal view of Degree 10 transitory pygidium UA 9253, x15; *15*, dorsal view of pygidium UA 9254; *16*, *17*, ventral and left lateral views of hypostome UA 9255; *18*, dorsal view of Degree 9 transitory pygidium UA 9256, x15; *19*, dorsal view of thoracic segment that could also belong to *B*. *reedi* n. gen. n. sp., UA 9257, x7.5; *20*, *21*, dorsal and right lateral views of Degree 8 transitory pygidium UA 9258, x15; *22*, ventral view of hypostome UA 9259, x7.5; *23*, ventral view of hypostome UA 9260.

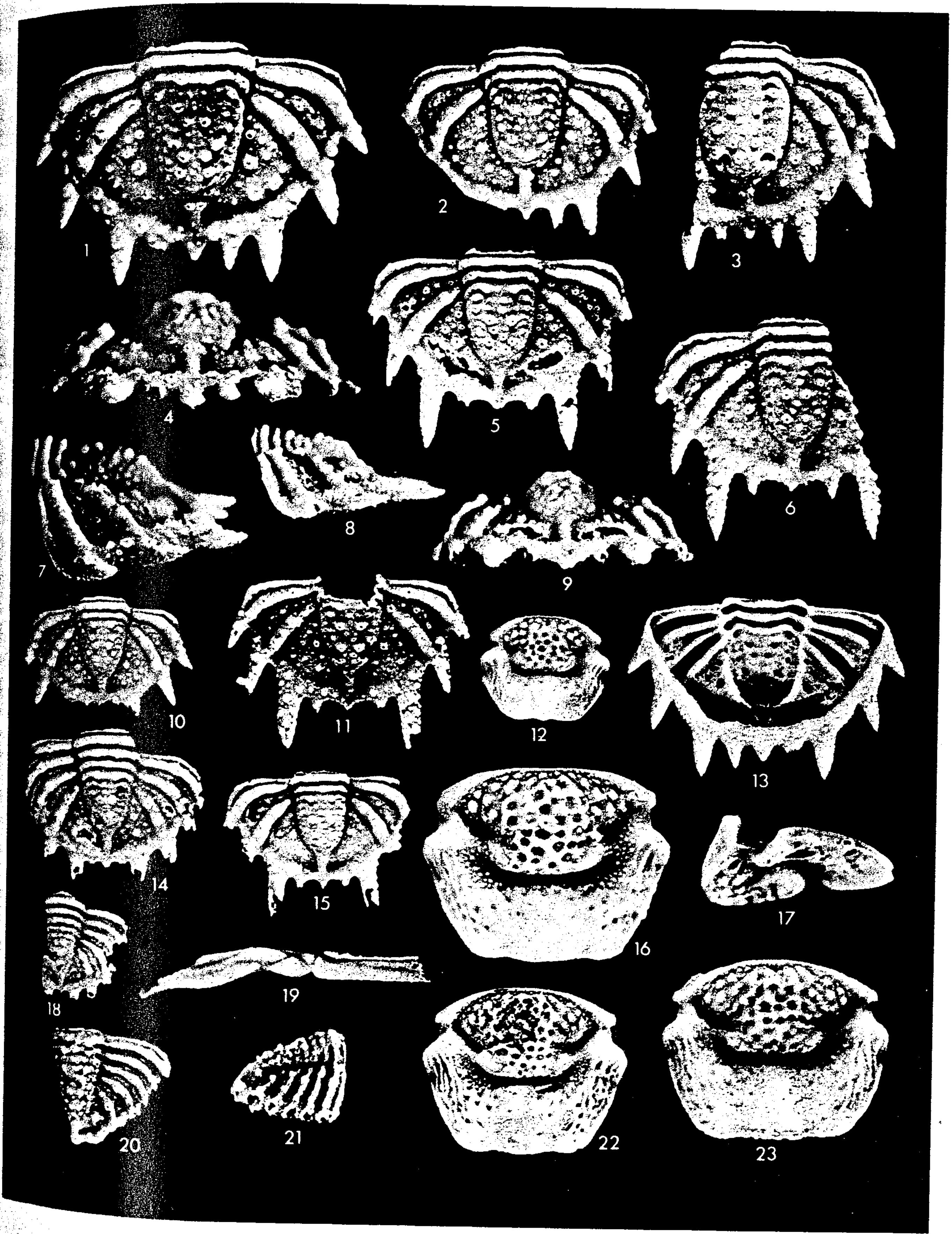
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FIGURE *IV-8*--*1*-*23*, *Borealarges* *morrisoni* n. gen. n. sp., from sections BH 1 164.5-204 m and BHL 1 92 m, Cape Phillips Formation, Wenlock (Sheinwoodian; *Cyrtograptus perneri*-*Monograptus* aff. *munchi* Zone), southern Baillie-Hamilton Island, central Canadian Arctic. Magnifications are x10 except where otherwise stated. *1*, *5*, dorsal and left lateral views of holotype cranidium UA 9261, x7.5 (BH 1 204 m); *2*, dorsal view of cranidium UA 9262 (BH 1 204 m); *3*, ventral view of rostral plate UA 9263 (BHH-C); *4*, *10*, ventral and dorsal views of hypostome UA 9264 (BHH-C); *6*, *7*, *12*, right lateral, dorsal, and anterior views of cranidium UA 9265 (BHH-A), see also Figure IV-9.9; *8*, *11*, *14*, left lateral, dorsal, and anterior views of cranidium UA 9266 (BHL 1 92 m); *9*, *13*, right lateral and dorsal views of cranidium UA 9267 (BHH-A); *15*, *19*, *21*, external, internal, and ventrolateral views of right librigena UA 9268 (BH 1 164.5 m); *16*, external view of right librigena UA 9269 (BHH-C); *17*, ventral view of hypostome UA 9270 (BH 1 204 m); *18*, external view of right librigena UA 9271 (BHH-C); *20*, *22*, external and ventrolateral views of left librigena UA 9272 (BHH-A); *23*, external view of right librigena UA 9273 (BHH-B).

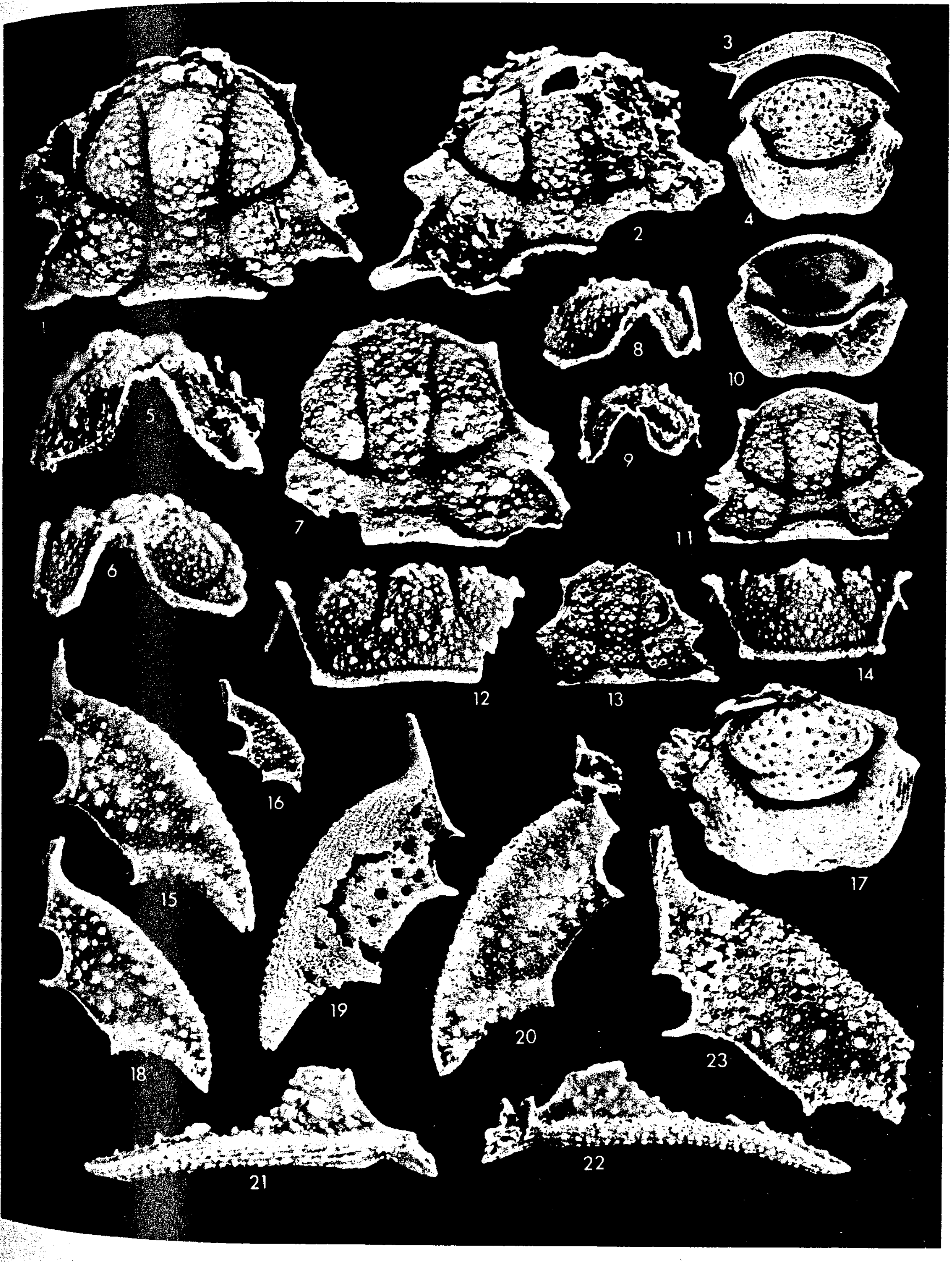
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FIGURE *IV-9*--*1*-*3*, *5*, *6*, *8*, *10*, *Borealarges morrisoni* n. gen. n. sp. from section BH 1 204 m and locality BHH, Cape Phillips Formation, Wenlock (Sheinwoodian; *Cyrtograptus perneri*-*Monograptus* aff. *munchi* Zone), south coast of Baillie-Hamilton Island, central Canadian Arctic. Magnifications are x7.5. *1*, *5*, *6*, *8*, dorsal, ventral, right lateral, and posterior views of broken pygidium UA 9274 (BHH-A); *2*, dorsal view of pygidium UA 9275 (BH 1 204 m); *3*, ventral view of cranidium UA 9265 (BHH-A), see also Figure IV-8.6, IV-8.7, IV-8.12 ; *10*, dorsal view of pygidium UA 9276 (BH 1 204 m). *4*, *7*, *9*, *11*-*16*, *18*, *Borealarges tuckerae* n. gen. n. sp. from sections BH 1 164.5 m and BHL 1 92 m, and locality BHH, Cape Phillips Formation, Wenlock (Sheinwoodian; *Cyrtograptus perneri*-*Monograptus* aff. *munchi* Zone), south coast of Baillie-Hamilton Island, central Canadian Arctic. Magnifications are x10 except where stated otherwise. *4*, external view of right librigena UA 9277 (BHH-A); *7*, dorsal view of pygidium UA 9278 (BH 1 164.5 m); *9*, ventral view of cranidium UA 9286, x7.5 (BH 1 164.5 m), see also Figure IV-10.1, IV-10.4; *11*, *12*, dorsal and ventral views of pygidium UA 9279, x7.5 (BH 1 164.5 m); *13*, dorsal view of pygidium UA 9280 (BH 1 164.5 m); *14*, *16*, dorsal and left lateral views of holotype pygidium UA 9281, x7.5 (BH 1 164.5 m); *15*, dorsal view of pygidium UA 9282 (BH 1 164.5 m); *18*, ventral view of hypostome UA 9291 (BHL 1 92 m), see also Figure IV-10.11, IV-10.15. *17*, *19*-*21*, *Borealarges* cf. *B*. s.l. *calei* n. gen. n. sp., from section ABR 1 22 m, Cape Phillips Formation, Wenlock (Homerian; *Pristiograptus ludensis* Zone), near Abbott River, northwestern Cornwallis Island, central Canadian Arctic. Magnifications are x10. *17*, external view of right librigena UA 9283; *19*, dorsal view of cranidium UA 9284; *20*, *21*, dorsal and ventral views of pygidium UA 9285.

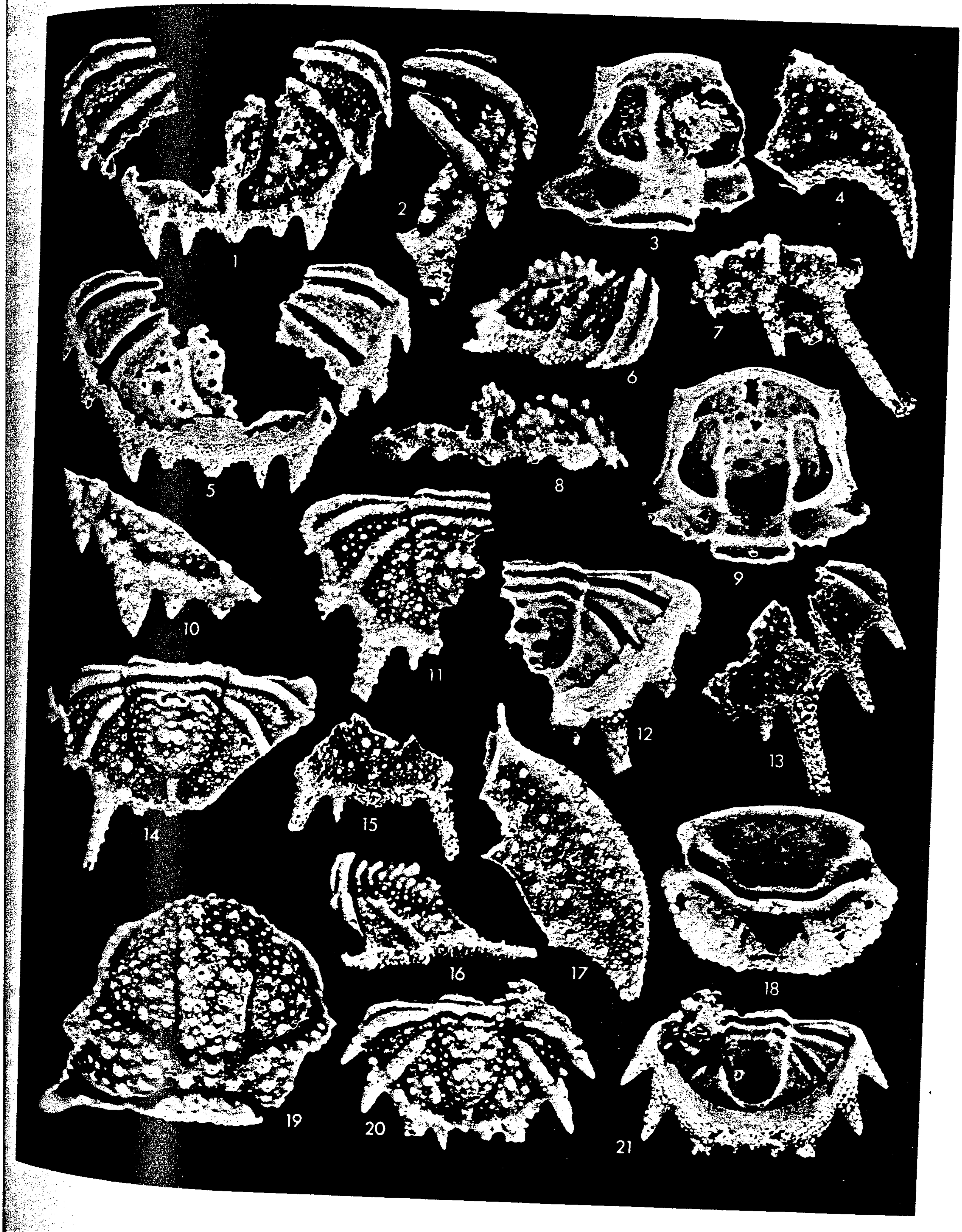
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FIGURE *IV-10*--*1*-*25*, *Borealarges* *tuckerae* n. gen. n. sp., from sections BH 1 164.5 m and BHL 1 92 m, and locality BHH, Cape Phillips Formation, Wenlock (Sheinwoodian; *Cyrtograptus* *perneri*-*Monograptus* aff. *munchi* Zone), south coast of Baillie-Hamilton Island, central Canadian Arctic. Magnifications are x10 except where otherwise stated. *1*, *4*, dorsal and right lateral views of cranidium UA 9286 (BH 1 164.5 m), see also Figure IV-9.9; *2*, *5*, *6*, dorsal, right lateral, and anterior views of broken cranidium UA 9287 (BHH-A); *3*, *7*, dorsal and right lateral views of cranidium UA 9288 (BH 1 164.5 m); *8*, *12*, dorsal and left lateral views of cranidium UA 9289 (BHH-A); *9*, *10*, dorsal and left lateral views of cranidium UA 9290 (BHH-A); *11*, *15*, ventral and left lateral views of hypostome UA 9291 (BHL 1 92 m), see also Figure IV-9.18; *13*, external view of left librigena UA 9292 (BHH-C); *14*, external view of left librigena UA 9293 (BH 1 164.5 m); *16*, *17*, external and internal views of left librigena UA 9294 (BHL 1 92 m); *18*, *23*, external and lateral views of left librigena UA 9295, x7.5 (BHH-A); *19*, external view of left librigena UA 9296 (BHH-A); *20*, external view of left librigena UA 9297 (BHH-A); *21*, *22*, *25*, internal, external, and ventrolateral views of right librigena UA 9298 (BHH-C); *24*, external view of right librigena UA 9299 (BH 1 164.5 m).

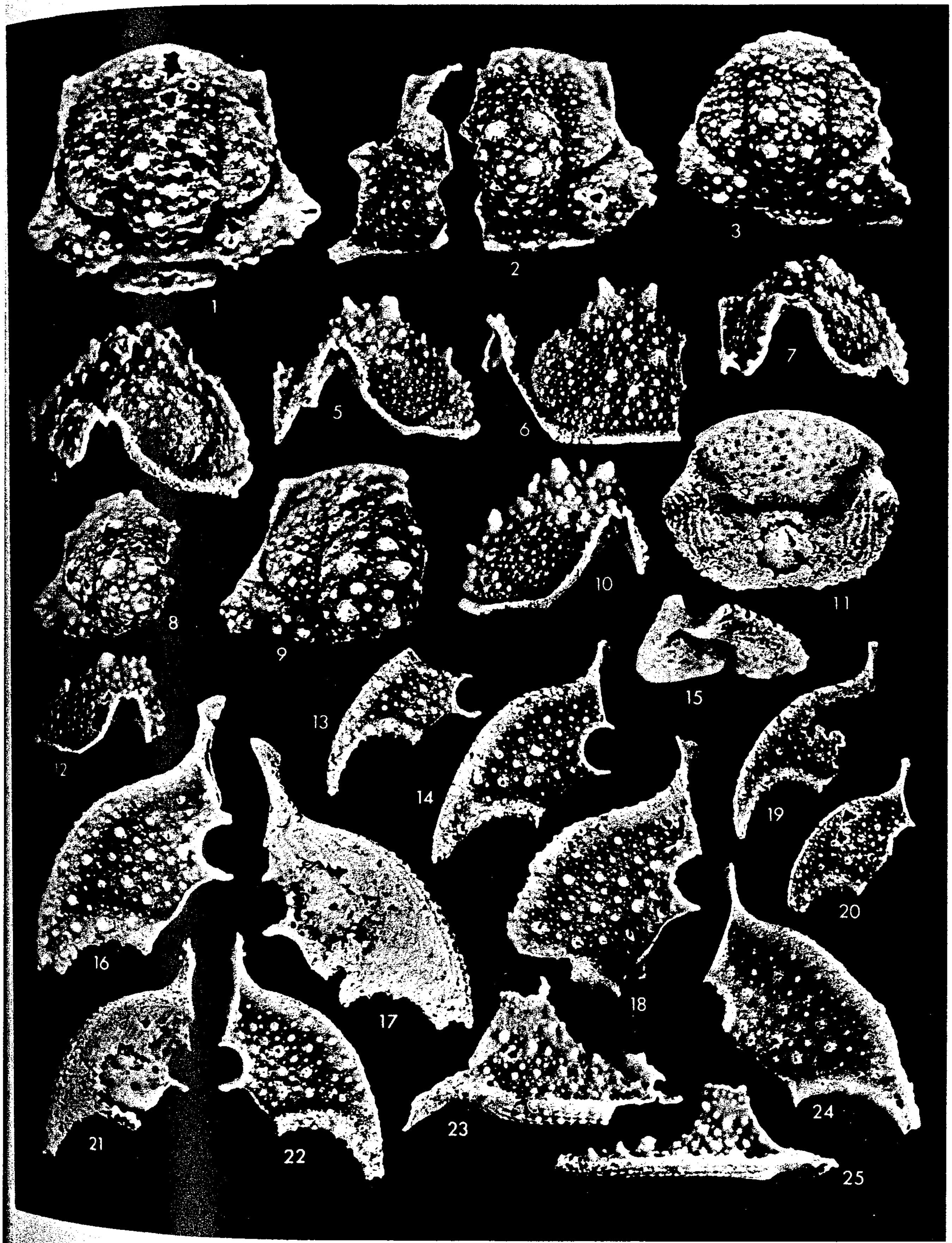
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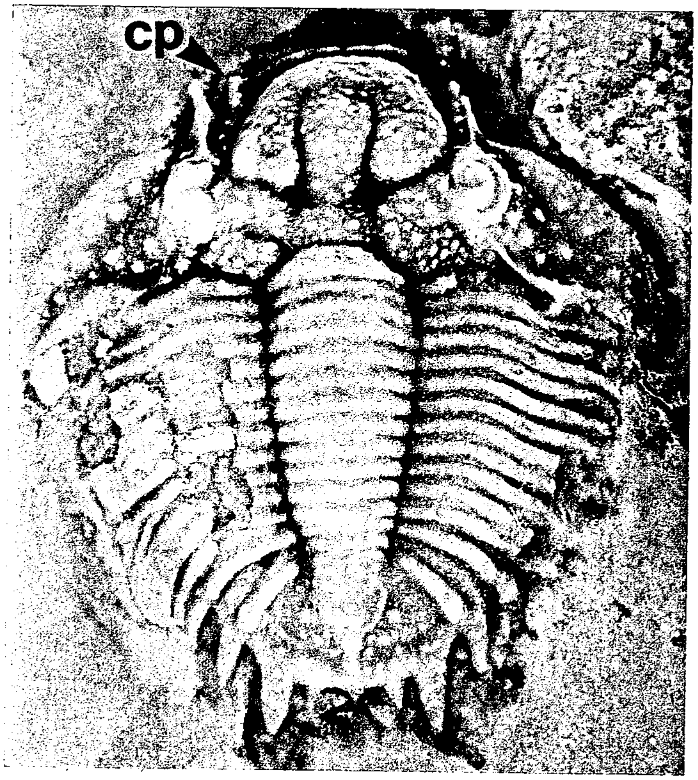
FIGURE IV-11--*Borealarges bucklandii* (Milne Edwards, 1840), BM In52610, from the Much Wenlock Limestone Formation, Wenlock (Homerian; *Pristiograptus ludensis* Zone), Dudley, West Midlands, England, x7.5. Note the relatively large palpebral lobes and prominent anterolateral cranidial projection (*cp*), features not shared with most other material currently assigned to this species (see text).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CHAPTER V[1]

A NEW RORRINGTONIID TRILOBITE FROM THE LUDLOW OF ARCTIC CANADA

INTRODUCTION

SILURIAN TRILOBITES are well enough known that the discovery of a new species whose familial affinities are difficult to determine is of considerable interest. Goodsiraspis packardi n. gen. n. sp. bears strong similarities to members of the Aulacopleuridae, but also has several features unknown in true aulacopleurids. As outlined below, the balance of evidence supports assignment to the family Rorringtoniidae Owens in Owens and Hammann, 1990. The bulk of rorringtoniid diversity is Ordovician, and only a few of its members are at all well known. For these reasons, the discovery of a superbly preserved late Silurian species is of importance. This work is intended to document fully the morphology of this species, and to discuss its systematics and implications for rorringtoniid classification.

The Silurian trilobite faunas of Arctic Canada are not well known. Adrain and Chatterton (1990) have reviewed the existing literature. The only diverse Ludlow fauna described to date is that of the Douro Formation at Goodsir

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[1] A version of this chapter has been accepted for publication. Adrain, J. M., and Chatterton, B. D. E. Canadian Journal of Earth Sciences.

Creek, Cornwallis Island (Thomas in Thomas and Narbonne, 1979). Whittington (1961) and Bolton (1965) have dealt with low diversity occurrences of Upper Silurian species whose precise ages remain uncertain. Adrain and Chatterton (1990) described a new odontopleurid from an erratic block collected on northwestern Cornwallis Island. The block was then considered to be of Llandovery age, but subsequent collecting (A. C. Lenz, personal commun., 1991) indicates that this species, Odontopleura arctica, is of early Ludlow age (Gorstian; Lobograptus progenitor Zone).

The material described herein was collected by J. J. Packard from the Barlow Inlet Formation at Goodsir Creek, eastern Cornwallis Island, Canadian Arctic Archipelago (Figure V-1). Goodsiraspis packardi is the only trilobite represented, and is associated with very few other macrofossils (mainly rare atrypid brachiopods). The available material is mostly articulated, but this has possibly been influenced in part by collecting bias. The trilobites occur as moulds in a green-gray shale. Preservation of detail is excellent, and it has been possible to fully describe all exoskeletal parts, with the exception of the poorly known hypostome.

STRATIGRAPHY

The stratigraphic sequence at Goodsir Creek, on the eastern shore of Cornwallis Island was first studied by Thorsteinsson (1958), who assigned trilobite-bearing rocks to members A through C of the Read Bay Formation (Thorsteinsson and Fortier, 1954). The basal part of the sequence at Goodsir Creek (i.e. the lower part of member A) was assigned by Kerr (1975) to his new Cape Storm Formation. Thorsteinsson (1980) subsequently elevated the Read Bay to group status. That portion of member A overlying the Cape Storm Formation was recognized as the Douro Formation. Members B and C were assigned to Thorsteinsson's (1980) new Barlow Inlet Formation.

The trilobites described herein were collected from the lower member of the Barlow Inlet Formation (formerly member B of the Read Bay Formation). This member consists (Thorsteinsson, 1958, p. 64; 1980, p. 5-6) mainly of medium dark green-gray shale, with minor sandstone and nodular limestone. It reaches its maximum measured thickness (65 m) in a section on the south side of Goodsir Creek, and it is from this locality that the trilobites were collected.

The age of the strata bearing Goodsiraspis packardi has been discussed by Thorsteinsson and Uyeno (in Thorsteinsson, 1980, p. 24, table 1, fig. 17). The underlying Douro Formation belongs to the penultimate Ludlow siluricus Zone. The upper member of the Barlow Inlet Formation belongs to the latialata Zone. According to Thorsteinsson and Uyeno, the balance of evidence indicates that the lower member falls also within this zone, and is hence of latest Ludlow (Ludfordian) age.

SYSTEMATIC PALEONTOLOGY

Order PROETIDA Fortey and Owens, 1975

Superfamily AULACOPLEUROIDEA Angelin, 1854

Family RORRINGTONIIDAE Owens in Owens and Hammann, 1990

Discussion.--Owens (in Owens and Hammann, 1990) has recently established the family Rorringtoniidae for a group of aulacopleuroidean trilobites whose classification has long been difficult. The genus *Rorringtonia* Whittard, 1966 (=*Analocaspis* Owens, 1970) has generally been treated as Proetoidea *incertae sedis*. Owens (1973) assigned the taxon to Proetidae, and later (Owens 1981) to a subfamily Scharyiinae Osmólska, 1957 of the family Aulacopleuridae (see Thomas and Owens, 1978 and Owens, 1979). With the establishment of Rorringtoniidae, most of the remaining genera previously assigned to Scharyiinae (*Isbergia*, Warburg, 1925, *Cyamella*, Owens, 1990) were also transferred to the new taxon. Scharyiinae was restricted to the genus *Scharyia* Pribyl, 1946 by Owens (in Owens and Hammann, 1990), and assigned to the family Brachymetopidae.

Owens (in Owens and Hammann, 1990, Figs. 19 and 20) has presented a classificatory scheme for the superfamily Aulacopleuroidea. This represents the first explicit hypothesis of relationship for this difficult taxon, and is an important advance. It is generally followed herein, but several alternative interpretations are favoured, and some reservations are noted, as reflected in the cladogram given in Figure V-2 and classification given in Table V-1. These differences of opinion are briefly outlined below.

Rorringtoniidae.--Owens (in Owens and Hammann, 1990, p. 241) assigned the subfamily Eodrevermanniinae Hupé, 1953 to Rorringtoniidae on the basis of "...the subtriangulate glabella with incised S1-S3 and subquadrate L1, and the lozenge-shaped occipital ring and long preglabellar field..." It is difficult to see that any of these rather general features are uniquely shared by the two groups. A sub-triangulate glabella is developed in the genera Scharyia and Brachymetopus, M`Coy, 1847. Incised glabellar furrows, "lozenge-shaped" occipital ring, and long preglabellar field would seem to be features developed several times in many proetide groups. Additionally, the only Upper Silurian rorringtoniine, Goodsiraspis n. gen., is not very similar to the eodrevermanniines. If the latter group, which is of early and middle Devonian age, does in fact belong to Rorringtoniidae, it is necessary to account for a ghost lineage (Norell, 1992) of considerable length (i.e. bridging the stratigraphic gap between the eodrevermanniines and their presumptive Ordovician common ancestry with rorringtoniines). This is not to say that Owens's classification should be rejected. The morphology of eodrevermanniines, however, can alternatively be interpreted in terms of the ontogeny of earlier proetides. All of the features of the group, including those listed by Owens and the small size of most species, are characteristic also of the meraspid anatomy of some members of the family Proetidae. The eodrevermanniines possibly represent a radiation with a paedomorphic origin somewhere within the proetids. Much work will be required to determine the group's true close relatives, but its rorringtoniid affinity does not seem clearly established.

Owens (1973, p. 80) placed the genus Phaseolops Whittington, 1963, firmly within the Tropidocoryphinae. He later (in Owens and Hammann, 1990) removed it to Rorringtoniidae. The evidence for this assignment was that the pygidial pleural ribs (Owens in Owens and Hammann, 1990, p. 240) "...are of rather simple construction..." and not of the type described by Owens (1973) as "imbricate," which is characteristic of Tropidocoryphinae. Phaseolops, however, is remarkably similar to some younger tropidocoryphines with incised glabellar furrows (cf. Centriproetus Šnajdr, 1977, Denemarkia Pribyl, 1946). It also has a triangular rostral plate (Whittington, 1963, Pl. 4, fig. 11), a shape developed in tropidocoryphines but dissimilar to the transverse form seen in Goodsiraspis packardi, the only rorringtoniid rostral plate yet described. Again, it is conceivable that Phaseolops does represent a rorringtoniid, but we consider that further information is necessary to assess its affinities with confidence.

Scharyiidae

Owens (in Owens and Hammann, 1990) restricted the subfamily Scharyiinae to the genus Scharyia and assigned the taxon to the family Brachymetopidae. Panarchaeogonus Öpik, 1937, which had been assigned to Scharyiinae by Thomas and Owens (1978) and Owens (1979), was reassigned to Aulacopleuridae. Owens (1974, p. 687, text-fig. 2) had earlier emphasized the considerable similarities between Scharyia and Panarchaeogonus. Evidence given by Owens (in Owens and Hammann, 1990, p. 236, fig. 20) for uniting Panarchaeogonus with aulacopleurids included possession of an isolated L1, more than ten thoracic segments, and a "comparatively short, transverse pygidium." The first is genuine, at least among most currently known species of Panarchaeogonus, but P. acris (Hu, 1976), from the Ordovician of Virginia has S1 considerably effaced. In any case, an isolated L1 seems to be a general aulacopleuroidean condition, as it is developed also in Rorringtonia and many brachymetopines (e.g. Radnoria, Cordania). The second point is seemingly incorrect, as the only species of Panarchaeogonus for which the number of thoracic segments is known (P. trigodus (Warburg, 1925)) has nine (Owens, 1974, p. 207). Lastly, the Panarchaeogonus pygidium is poorly known, but the available illustrations indicate that it is actually quite long relative to its width, unlike that of aulacopleurids, but very similar to that of Scharyia. This is confirmed by work in progress which has shown that pygidia illustrated by Hu (1975, Pl. 1, figs. 21-26) and assigned by him to his *Otarion trilobus* belong to *Panarchaeogonus acris*. We consider that the points of similarity between *Scharyia* and *Panarchaeogonus* given by Owens (1974) are genuine, and that the genera are closely related.

Owens (in Owens and Hammann, 1990) assigned the genus *Niuchangella* Chang, 1974, to Rorringtoniidae. In its elongate glabella, large, laterally displaced L1, and widely anteriorly divergent preocular facial sutures, *N. meitanensis* bears clear resemblances to the species *Cyphaspis holmi* Warburg, 1925, and *Panarchaeogonus phlyzacius* Owens, 1979, both of which were included in *Panarchaeogonus* by Owens (1979). These species are accordingly reassigned to *Niuchangella* herein, a classification supported further by the similarity of the pygidia of *N. meitanensis* and *N. phlyzacius* (cf. Chang, 1974, Pl. 80, fig. 11 and Owens, 1979, fig. 4N). The affinities of *Niuchangella* seem to lie with *Panarchaeogonus*, and the former genus is accordingly assigned to Scharyiidae herein.

Finally, there seems to be little compelling evidence that scharyiids represent the sister group of brachymetopids. The taxa most closely resembling each other are some Siluro-Devonian species of *Scharyia* and species of the Carboniferous genus *Brachymetopus*. Some members of

Brachymetopus show a subtriangular glabella with large palpebral lobes and a strongly isopygous form similar to that of Scharyia. Brachymetopus, however, lacks any indication of Scharyia's cedariform facial suture and has many features indicating derivation from Cordania-like trilobites (e.g. Mystrocephala Whittington, 1960). Similarities with Scharyia are very likely homeomorphic. The earliest brachymetopids, Ordovician species of Radnoria, are not closely similar to Scharyia. Hence, it seems more appropriate to recognize Scharyiidae as a separate aulacopleuroid family, whose immediate affinity has yet to be determined.

Genus GOODSIRASPIS n. gen.

Type species.--Goodsiraspis packardi n. gen. n. sp., Ludlow (Ludfordian), Barlow Inlet Formation, Goodsir Creek, Cornwallis Island, Canadian Arctic Archipelago.

Other species.--Goodsiraspis? beyrichi (Novák, 1890), Eifelian; G.? butorus Holloway, 1980, Wenlock, Clarita Formation, Oklahoma, U.S.A.; G.? novella (Barrande, 1852), Ludlow, Kopanina Formation, Bohemia, Czechoslovakia; Panarchaegonus? sp. 4 of Owens (1979).

Diagnosis.--Rorringtoniids with small median node on preglabellar field; very large L1; prominent bicomposite eye ridge; librigena lacking lobate eye socle and with broad, nontuberculate field; genal spine with broad, flattened base; transverse, subtrapezoidal rostral plate with connective sutures widely separate posteriorly; thorax of fourteen segments, lacking axial spine; pygidium with width twice length, five or six axial rings, and only first one or two ring, pleural, and interpleural furrows well impressed.

Discussion.--In its general proportions and prominent, fully isolated L1, Goodsiraspis packardi shows similarity to aulacopleurids, particularly species of Aulacopleura, which have similar olenimorph (Fortey and Owens, 1990) morphologies, and are also found in deeper water environments. The new species, however, does not agree in detail with any well understood aulacopleurid taxon. Particular points of difference are as follows. First, all aulacopleurids for which information is available (including species assigned to all of the currently recognized genera) have a small, triangular rostral plate, with the connective sutures meeting or nearly meeting posteriorly. Goodsiraspis packardi has a transverse rostral plate (Figure V-4.1, V-4.2) with the connective sutures widely separate posteriorly. Second, G. packardi has a deep, slot-like S2 that is not contiguous with (i.e. shallows abruptly immediately adjacent to) the axial furrow, and has considerable transverse extent (Figure V-3.3 to V-3.6). The most prominent development of this feature in aulacopleurids is as a relatively deep notch, always contiguous with the axial furrow and with very limited transverse extent; frequently, S2 is almost effaced. Third, the librigena of

Goodsiraspis packardi (Figure V-4.7) features a genal spine with a broad, flattened base, along which separate posterior and lateral borders are retained, with the posterior border furrow running unobstructed down its dorsal aspect. While some vestige of the border furrows is often retained on the dorsal aspect of aulacopleurid genal spines, the spines themselves are invariably simple and tube-like, with bases that are usually round and at most broadly ovate, never flattened. Other differences include the occurrence of lobate eye socles in aulacopleurids, but their absence in *G. packardi*, and the presence of posterior spines on the aulacopleurid hypostome, with their apparent absence in *G. packardi* (Figure V-4.8).

The hypothesis that *Goodsiraspis packardi* is an aulacopleurid requires that all of the above features be uniquely derived autapomorphies, leaving only general similarities supporting the relationship. On the other hand, some of the unusual morphological states of the species can be explained by reference to members of the Rorringtoniidae. *Rorringtonia kennedyi* Owens, 1981 has librigenae with the same shape as those of *G. packardi*, lacking a prominent eye socle, with low, elongate eyes, and with broad, flattened genal spine bases. *Rorringtonia kennedyi*, *R. ursina* (Owens, 1970) (see Owens, 1981, Pl. 1, figs. e-h), and *G. packardi* also share glabellae with large, isolated L1, very deep S2 with considerable transverse extent, and small but persistent S3. The nature of the rostral plate is unknown in Rorringtonia, but the available information (see particularly the articulated holotype of R. kennedyi, Owens 1981, Pl. 1, fig. a) does not preclude it having a similar transverse shape to that of G. packardi.

The principal problems with an interpretation of Goodsiraspis as a rorringtoniid are the shape of its pygidium, which is extremely aulacopleurid-like, and its high number of thoracic segments, 14 versus the 8 or 9 typical of Ordovician rorringtoniids. Rorringtonia kennedyi has a broad, low pygidium with at least the first six pairs of pleural ribs strongly defined, a situation unlike that of G. packardi, in which only the first pair is well defined, with the second pair effaced abaxially and posterior pairs progressively less distinct. Rorringtonia ursina and Rorringtonia lenis Owens and Hammann 1990, however, are much closer. In fact, the pygidium of R. lenis has a similar number of axial rings (five), a similar situation with respect to the pleural ribs, and a shape in outline approaching that of the pygidium of G. packardi.

The specimen showing the strongest similarity to G. packardi is the cranidium figured by Owens (1979, Fig. 50) as Panarchaeogonus? sp. 4 from the late Llandeilo or early Caradoc of Estonia. Owens (in Owens and Hammann, 1990, p. 233) reassigned this species to Rorringtonia, and it is here assigned to Goodsiraspis. Of course, much more information would be required to be confident of this relationship, but the only prominent differences between the single cranidium and that of G. packardi are the somewhat longer preglabellar field and less well defined anterior border furrow of the latter.

Several Silurian and Devonian species that have been assigned to the Aulacopleuridae are possibly related to Goodsiraspis packardi. All are either incompletely known or based on relatively poor material, however, and all have morphological features which preclude confident assignment. Nevertheless, there are also problems with assigning any of these species to the Aulacopleuridae. Their certain classification will require more and sometimes better material, but they are assigned with question to Goodsiraspis herein. A brief discussion of each follows.

Goodsiraspis? butorus (Holloway, 1980).--This species is known with certainty only from cranidia (Holloway 1980, Pl. 6, figs. 1-7), which compare closely with those assigned to "Otarion (Maurotarion) cf. novellum" by Alberti (1969, p. 386, Pl. 36, figs. 7, 8). Two pygidia illustrated in open nomenclature (Holloway 1980, Pl. 6, figs. 15, 16) very likely belong. These agree almost exactly with those of G. packardi. The cranidia are similar in their very large L1, presence of a median node on the preglabellar field, and general disposition of features. The substantive difference is the much-effaced S2 and S3 of G.? butorus. A single cranidium belonging to G.? packardi (Figure V-3.9), however, has these furrows somewhat less impressed.

Goodsiraspis? beyrichi (Novák, 1890).--Alberti (1969, Pl. 36, fig. 12) has figured the lectotype of this species. As outlined by Thomas and Owens (1978, p. 68-70), a reconstruction of G.? beyrichi given in the Treatise (Moore, 1959, fig. 309.6) contributed to confusion over the nature of the taxon Paraaulacopleura Chaubet, 1937. In fact, that reconstruction compares more closely with Goodsiraspis packardi than does the specimen upon which it is based. Nevertheless, the structure of the genal spine, with the posterior border furrow deep and continuous along the dorsal aspect together with the presence of a median node on the preglabellar field are similarities with G. packardi. Goodsiraspis? beyrichi may yet prove to be a member of Aulacopleura.

Goodsiraspis? novella (Barrande, 1852).--The best illustration of this species is the single cranidium figured by Thomas and Owens (1978, Pl. 7, fig. 7). The only substantive difference between this specimen and cranidia of G. packardi is its less impressed S2 and S3. As with G.? butorus (see above), the closest resemblance is to a specimen of G. packardi which itself has these features subdued (Figure V-3.9), and from which the cranidium of G.? novella is nearly indistinguishable.

Etymology.--After Goodsir Creek, the type locality of the type species, and aspis, a shield.

GOODSIRASPIS PACKARDI n. sp.

Figures V-3, V-4

Diagnosis.--Goodsiraspis usually with deeply impressed S2 and S3; median node posteriorly placed on preglabellar field; genal spine two fifths length of remainder of librigena; librigena with posterior border furrow extended without interuption along dorsal aspect of flatted genal spine and lateral border furrow shallowing posteriorly but meeting posterior furrow in front of genal angle; pseudo-articulating half ring between first and second pygidial axial rings prominent.

Description.--Cephalon reaching maximum width across tips of genal spines; maximum width approximately two and one quarter times length (sag.). Cranidium subquadrate in plan view, with anterior branches of facial suture moderately anteriorly divergent and posterior branches strongly posteriorly divergent. Glabella subparabolic in outline, L1 protruding laterally only slightly; L1 large, teardrop shaped, with greater medial than lateral convexity; S1 deeply impressed, confluent with axial furrow anteriorly and occipital furrow posteriorly; two very faint furrows running anteromedially from middle part of S1; S2 short, deep, and slot-like, terminating or abruptly shallowing laterally near edge of glabella, not confluent with axial furrow; S3 faint, running very slightly anteromedially, contacting axial furrow at anterior of eye ridge; axial furrows broad, of similar width anteriorly and posteriorly, except for slight widening opposite anterior two thirds of L1; preglabellar furrow describing a gentle, evenly convex arc; glabella low, uninflated, with ornament of a few sparsely distributed and faint tubercles on posterior one quarter to one third of median lobe and on rear of L1; occipital ring two thirds length of L1; posterior half horizontal and flat, anterior half sloping toward relatively deep occipital furrow; occipital ring constricted behind L1, S0 deep and slot-like; occipital ring with low median tubercle set at about one half length (sag.) and small scattered tubercles on posterior half, sometimes arranged in a transverse row at posterior edge; preglabellar field about one and one half times length of occipital ring, sloping steeply from preglabellar furrow, then shallowing abruptly behind anterior border furrow, to form flat band anteriorly, simulating epiborder furrow, and with low median swelling just anterior to preglabellar furrow; anterior border furrow shallow, not evenly convex but describing a broad inverted "v" shape in plan view; anterior border with anterior half dorsally convex and rim-like, posterior half sloping posteroventrally to anterior border furrow; preglabellar field and frontal area with dense caecal pits, but lacking tubercles; prominent bicomposite eye ridge running anteromedially from anterior of palpebral lobe to contact axial furrow opposite S3; caecal pits dense directly in front of eye ridge, but poorly developed on fixigena posterior to eye ridge; fixigena slightly swollen adaxial to palpebral lobe, narrowing slightly posteriorly; fixigena changing slope (exsag.) along transverse band immediately in front of posterior border furrow to run posteroventrally into border; palpebral lobe large, with faint and minute pit set nearer to lateral margin; anterior edge of lobe opposite anteriormost part of L2; posterior edge opposite anterior one third of L1.

Librigena. Genal spine approximately two fifths length of remainder of librigena (excluding anterior doublural projection); base of spine broad, ellipsoid in transverse section; spine tapering rapidly distally; librigenal field two and one half times as long as wide (exsag. vs trans.; measured at midpoint of eye); field ornamented with moderately dense but shallow caecal pits; tubercles absent; eye socle subdued, sometimes weakly inflated, and defined by shallow, somewhat irregular, furrow; lateral border furrow shallow, continuous posteriorly along genal spine; extent of doublure matched posteriorly by a second, shallow epiborder furrow; posterior border furrow deep, curving at genal angle to run posteriorly along median dorsal aspect of genal spine, contacting lateral border furrow near tip of spine; posterior border broad, narrowing slightly above genal angle; second shallow furrow developed at approximately one half length of posterior border, also curving to run posteriorly along genal spine, but petering out before reaching tip; very fine terrace lines developed along adaxial aspect of genal spine; lateral border relatively narrow, with ornament of fine terrace lines, broken and discontinuous on dorsolateral aspect, more linear in form and continuous ventrally; eye low and long; doublure relatively narrow and tube-like in section anteriorly, broadening markedly posteriorly to form flat shelf under genal angle, where it is extended forward to underlie posterolateral part of librigenal field; doublural extension broadening slightly anteriorly to connective sutures; ornament of fine, closely spaced, continuous terrace lines anteriorly; lines becoming more robust and widely spaced posteriorly, then petering out at genal angle or along abaxial edge of genal spine; ventral aspect of librigenal field and anterior part of posterior border ornamented with very fine, closely spaced, granulose tubercles; very fine librigenal trunk visible on ventral surface, running from just behind midlength of eye, converging distally with posterior border furrow.

Rostral plate. Rostral plate slightly curved and subtrapezoidal; posterior width approximately four times sagittal length; fine terrace lines of librigenal doublure continuous across ventral aspect; connective sutures converging posteriorly at an angle of approximately 45 degrees to the axis.

Hypostome. Poorly known. Anterior wings broad and flaring; middle body approximately twice as long as wide; middle furrow positioned at three quarters of length; middle body moderately convex; maculae not apparent; lateral border apparently curving gently into posterior border; no border spines apparent; border narrow and rim-like, with ornament of fine, parallel terrace lines visible posteriorly.

Thorax. Thorax of fourteen segments; thorax one and one half times length (sag.) of cranidium; maximum width across segment five or six, at which axial lobe accounts for approximately thirty percent of total width; axial ring describing shallow "W" shape in plan view; axial ring divided into anterior and posterior bands by faint transverse furrow at one half of sagittal length, transverse row of approximately ten subdued tubercles on posterior band; ring furrow short (sag., exsag.) and well impressed, deepest laterally; very short preannulus present anteriorly; axial furrow in contact with proximal end of pleural furrow; anterior pleural band about three quarters length (exsag.) of posterior band; prominent articulatory boss positioned at anterior edge of fulcrum, at one half width of pleural lobe; pleural furrow shallowing at distal extreme, but continuous to tip of pleura; pleural doublure extending proximally to underlie shallow distal part of pleural furrow; slit-like panderian notch placed approximately under pleural furrow.

Pygidium. Pygidium with width twice sagittal length (excluding articulating half ring); axis with maximum width equal to sagittal length; axial furrows deepest anteriorly, but continuous posteromedially to fully define axis; five and sometimes six discernable axial rings, only first fully defined; prominent pseudoarticulating half ring between first and second ring, very weak one between second and third; first and second ring furrows continuous, posterior ones effaced medially; ring furrows shallow medially, deepest near axial furrow; very weak transverse row of subdued tubercles on first axial ring only; first interpleural furrow nearly reaching lateral margin, posterior ones progressively effaced; anterior pleural band only slightly shorter (exsag.) than posterior band; pleural furrow of first segment reaching lateral margin, posterior ones progressively effaced, fifth furrow often completely effaced; pleurae with fine granulate ornament, tubercles absent; very faint border furrow originating behind first interpleural furrow, continuous posteromedially, narrowing slightly posteriorly; degree of medial flexure of pygidium, if any, uncertain; pygidial doublure underlying border, widest anteriorly, with fine, continuous terrace lines running subparallel to pygidial margin.

Discussion.--Comparison of Goodsiraspis packardi with the remainder of species possibly belonging to the genus was given above under discussion of the genus.

Material.--Holotype dorsal exoskeleton UA 9360 (Figure V-3.1), and paratypes UA 9361-9373, all from the lower member of the Barlow Inlet Formation, Ludlow (Ludfordian), south side of Goodsir Creek, eastern Cornwallis Island, Canadian arctic.

Etymology.--After J. J. Packard, who collected and made available for study the type material.

TABLE <u>V-1</u>.--Classification of the Aulacopleuroidea. Contrast with that of Owens (in Owens and Hammann, 1990).

Family Aulacopleuridae Angelin, 1854

Subfamily Aulacopleurinae Angelin, 1854: <u>Aulacopleura</u> Hawle and Corda, 1847; <u>Songkania</u> Chang, 1974.

Subfamily Otarioninae Richter and Richter, 1926: <u>Beggaspis</u> Pribyl and Vanek, 1981; <u>Cyphaspis</u> Burmeister, 1843; <u>Harpidella</u> M`Coy, 1849 (=<u>Rhinotarion</u> Whittington and Campbell, 1967); <u>Maurotarion</u> Alberti, 1969; <u>Namuropyge</u> Richter and Richter, 1939 (=<u>Coignouina</u> Reed, 1943); <u>Otarion</u> Zenker, 1833 (=<u>Conoparia</u> Hawle and Corda, 1847; =<u>Otarionella</u> Weyer, 1965); ?<u>Dixiphopyge</u> Brezinski, 1988; ?<u>Otarionides</u> Alberti, 1969.

Family Brachymetopidae Prantl and Pribyl, 1950

<u>Australosutura</u> Campbell and Goldring in Amos et al., 1960; <u>Brachymetopus</u> M`Coy, 1847; <u>Cheiropyge</u> Diener, 1897; <u>Cordania</u> Clarke, 1892; <u>Loeipyge</u> Kobayashi and Hamada, 1979; <u>Mystrocephala</u> Whittington, 1960; <u>Proetides</u> Walter, 1924; <u>Radnoria</u> Owens and Thomas, 1975; <u>Tschernyshewiella</u> Toll, 1899.

Family Rorringtoniidae Owens in Owens and Hammann, 1990

<u>Cyamella</u> Owens in Owens and Hammann, 1990; <u>Goodsiraspis</u> n. gen.; <u>Isbergia</u> Warburg, 1925; <u>Protarchaegonus</u> Sdzuy, 1955; <u>Rorringtonia</u>

TABLE V-1 (Continued)

Whittard, 1966.

Family Scharyiidae Osmólska, 1957

Niuchangella Chang, 1974; *Panarchaeogonus* Öpik, 1937; *Scharyia* Pribyl, 1946.

Aulacopleuroidea *incertae sedis*

Madygenia Petrunina, 1975; *Proscharyia* Peng, 1990.

Proetida *incertae sedis*

Cyphaspides Novák, 1890 (=*Protocyphaspides* Pribyl and Vanek, 1976); *Phaseolops* Whittington, 1963.

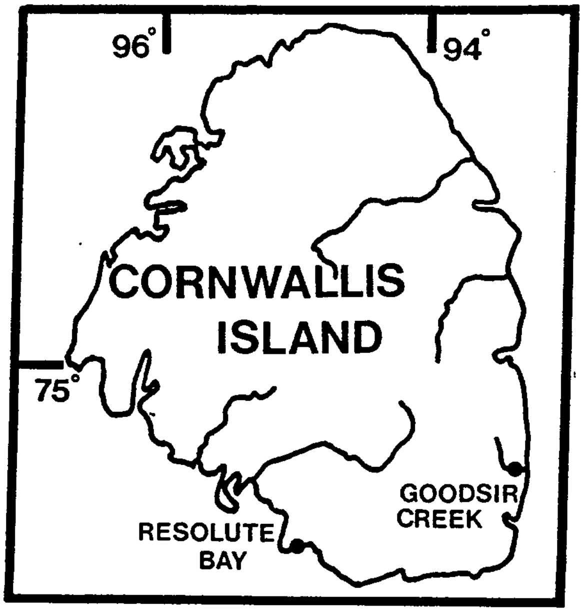

FIGURE V-1.--Map showing position of trilobite locality on Cornwallis Island.

FIGURE V-2.--Cladogram of selected aulacopleuroidean taxa, showing hypotheses of relationship, where possible, favoured herein. See Table V-1 for authorship of taxa. Character-states considered to support selected numbered nodes are as follows (several are based on work in progress by the writers): 1, subtriangulate glabella, large palpebral lobes, large, subsemicircular pygidia; 2, median glabellar spines in early ontogeny, widely divergent anterior branches of facial sutures; 3, transverse rostral plate?, large L1, incised S2 and S3, librigena with broad, flattened base; 4, subquadrate or subrectangular hypostome, usually with posterior spines, moderate to strong micropygosity; 5, subquadrate hypostome with paired posterior spines, bilobate eye socle, tendency for thoracic axial spine, micropygosity, with pygidia much wider than long; 6, cephalic spine array very subdued in early ontogeny, elongate hypostome with narrow middle body, great expansion of cephalic pleural areas and emphasis of genal caeca; 7, otarionine protaspis, single row of cephalic border spines in early ontogeny, usually three pairs of glabellar spines in early ontogeny; 8, suppression of fixigenal spines Fx3 and Fx4, crowding of glabellar spines G2 and G3 at front of glabella, two rows of cephalic border spines (see Adrain and Chatterton, in press).

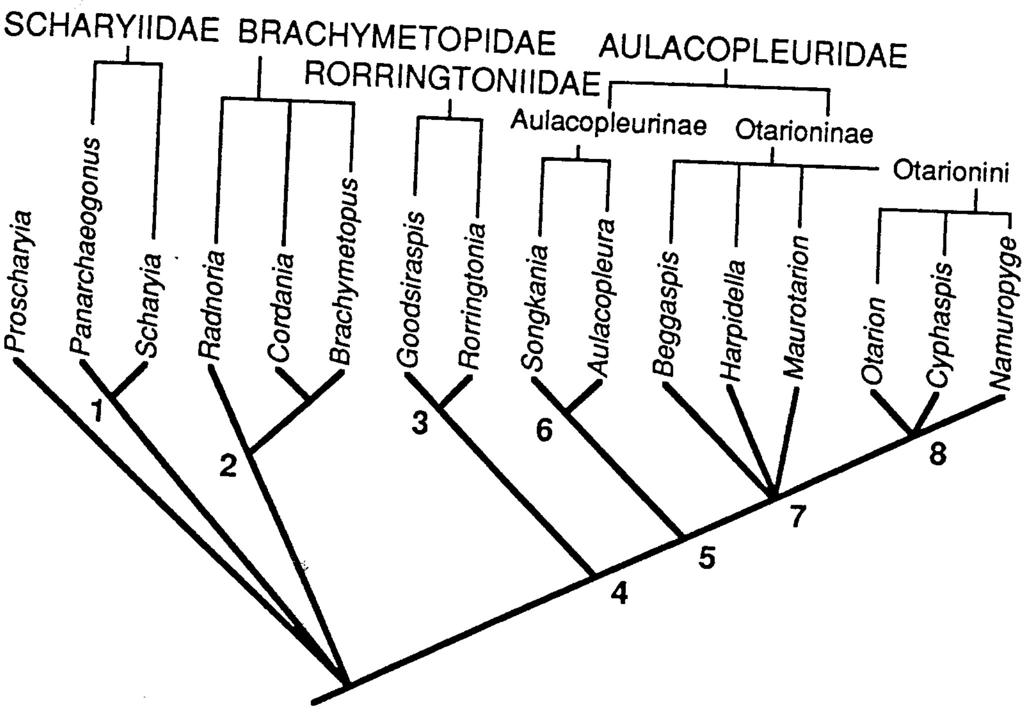
SCHARYIIDAE
BRACHYMETOPIDAE
RORRINGTONIIDAE
AULACOPLEURIDAE
Aulacopleurinae
Otarioninae
Otarionini
Proscharyia
Panarchaeogonus
Scharyia
Radnoria
Cordania
Brachymetopus
Goodsiraspis
Rorringtonia
Songkania
Aulacopleura
Beggaspis
Harpidella
Maurotarion
Otarion
Cyphaspis
Namuropyge
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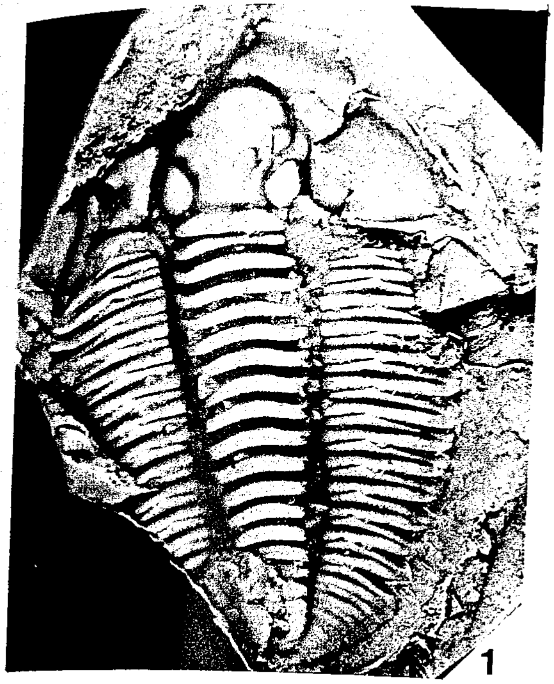
FIGURE V-3.--*Goodsiraspis packardi* n. gen. n. sp., from the Barlow Inlet Formation, Ludlow (Ludfordian), Goodsir Creek, eastern Cornwallis Island, Canadian Arctic Archipelago. All illustrations are of latex casts from moulds. Magnifications are x4 except as noted. 1, holotype dorsal exoskeleton, dorsal view, UA 9360; 2, Dorsal exoskeleton, dorsal view, UA 9361; 3, 12, dorsal exoskeleton lacking librigenae, dorsal and left lateral views, UA 9362; 4, dorsal exoskeleton, dorsal view, UA 9363, see also Figure V-4.7; 5, dorsal exoskeleton lacking librigenae, dorsal view, UA 9364; 6, dorsal exoskeleton lacking librigenae, dorsal view, UA 9365; 7, dorsal exoskeleton, dorsal view, UA 9366, see also Figure V-4.4; 8, 10, 11, thoracopygidium, dorsal, detail of pygidium, and right lateral views, UA 9367, x4 except fig. 10, which is x10; 9, cranidium, dorsal view, UA 9368.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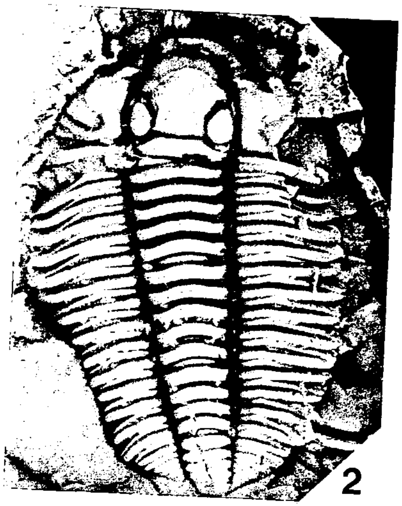
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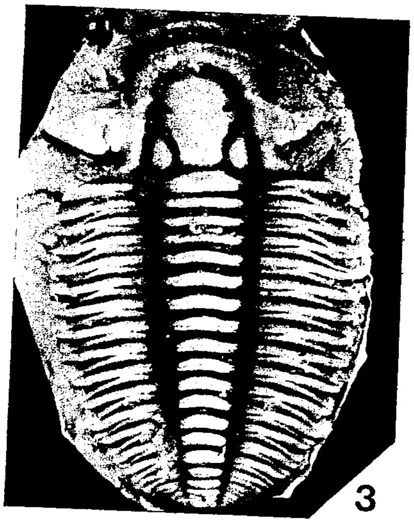
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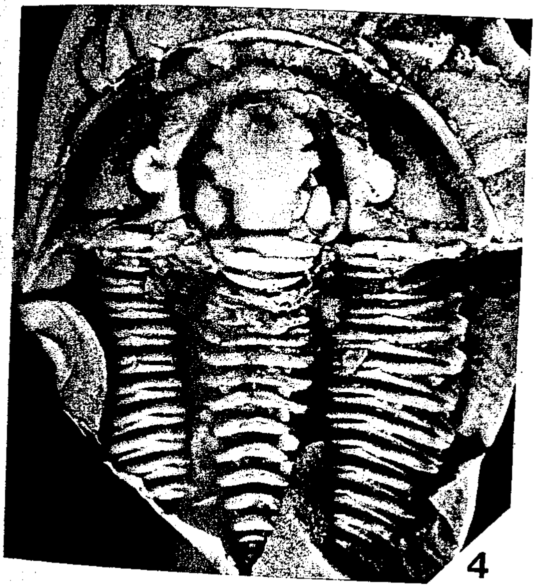
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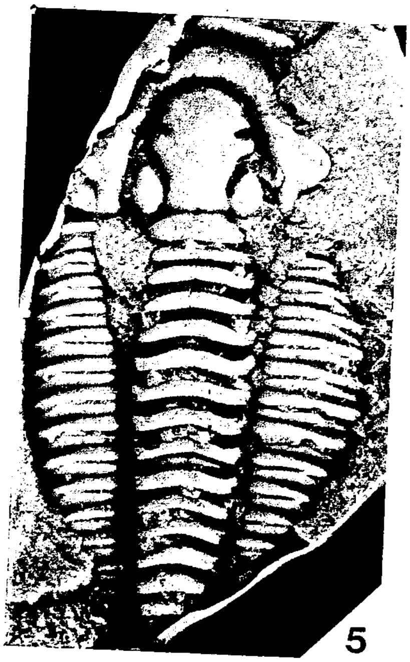
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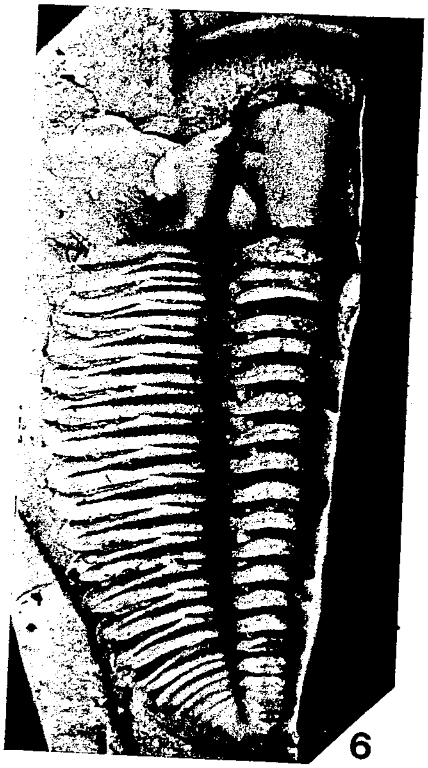
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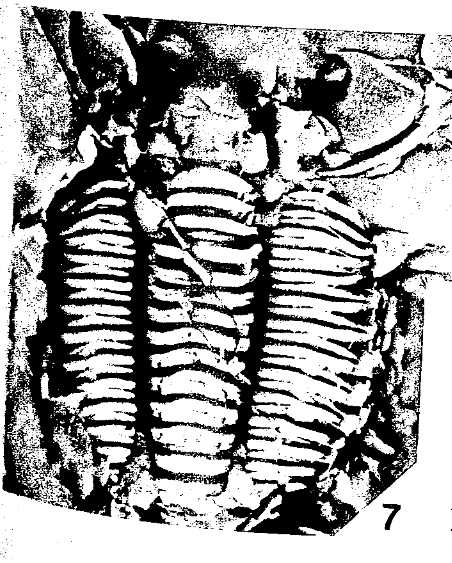
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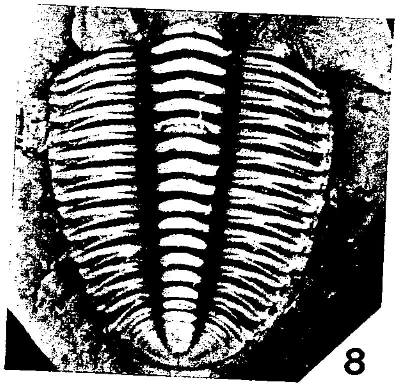
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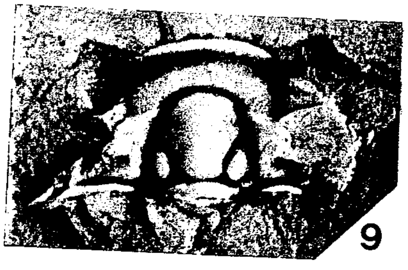
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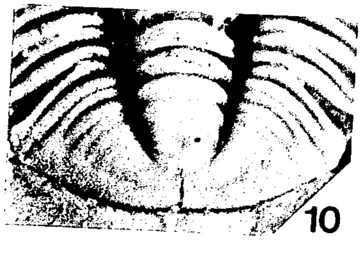
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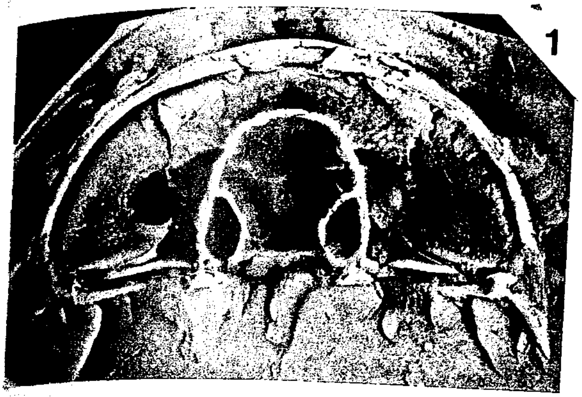
FIGURE V-4.--Goodsiraspis packardi n. gen. n. sp., from the Barlow Inlet Formation, Ludlow (Ludfordian), Goodsir Creek, eastern Cornwallis Island, Canadian Arctic Archipelago. All illustrations are of latex casts from moulds. Magnifications are x4 except as noted. 1, cephalon, ventral view, note transverse, subrectangular rostral plate, UA 9369; 2, cephalon, ventral view, UA 9370; 3, dorsal exoskeleton lacking librigenae, ventral view, UA 9371; 4, dorsal exoskeleton, detail of right librigena, internal view, UA 9366, x10, see also Figure V-3.7; 5, 6, dorsal exoskeleton, ventral view and detail of hypostome, UA 9372, x4 and x10; 7, dorsal exoskeleton, detail of left librigena, external view, x10, see also Figure V-3.4; 8, 9, dorsal exoskeleton, detail of hypostome and ventral view, UA 9373, x10 and x4.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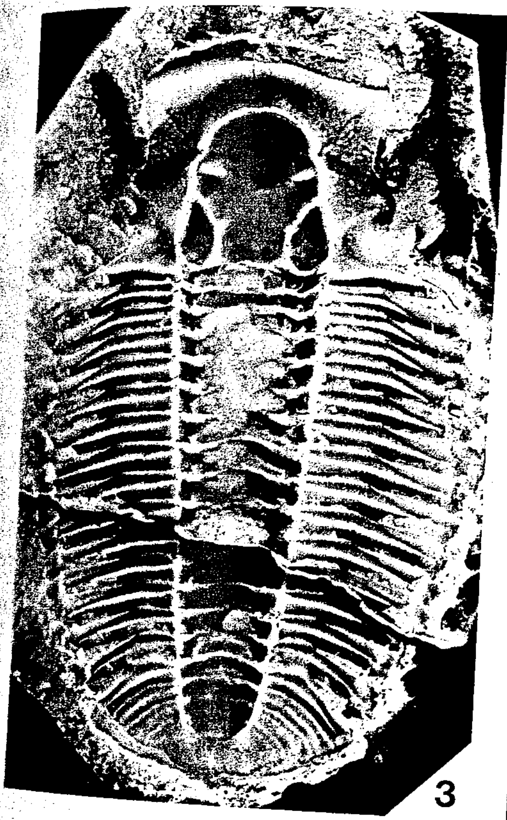
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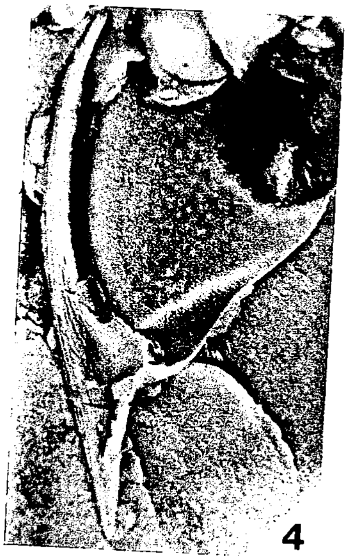
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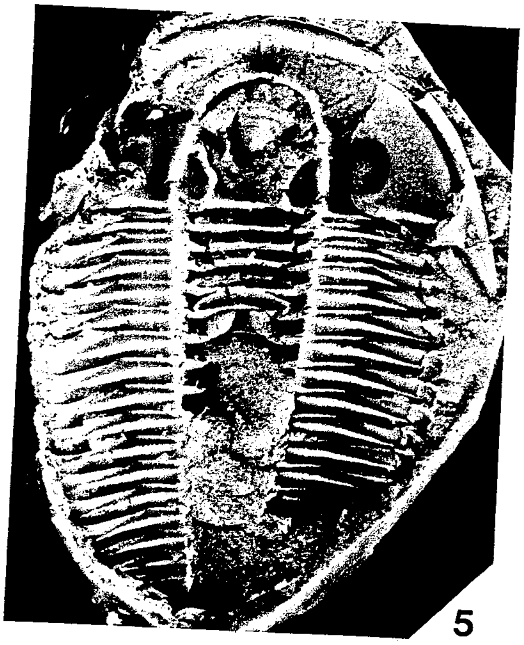
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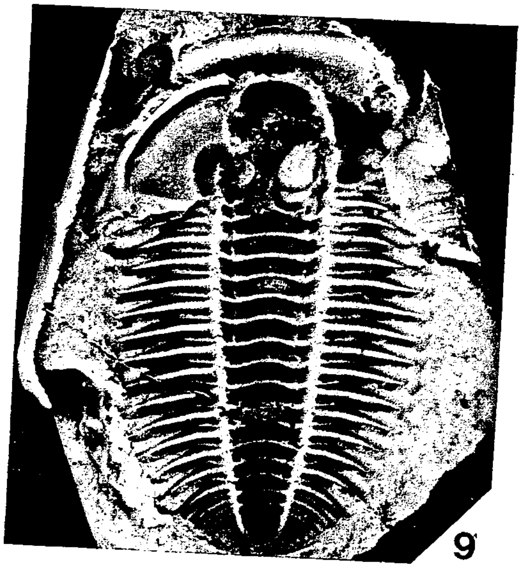
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CHAPTER VI[1]

AULACOPLEURINE TRILOBITES FROM THE LLANDOVERY OF NORTHWESTERN CANADA

INTRODUCTION

THIS PAPER is second in a series describing the aulacopleurid trilobites of the Whittaker Formation and Delorme Group of the central Mackenzie Mountains, Northwest Territories, Canada. Species from these units belonging to the genus Otarion were described by Adrain and Chatterton (in press). A review of prior study and a general introduction were also given in that work. Locality data follow Chatterton and Perry (1983, 1984) and Over and Chatterton (1987).

SYSTEMATIC PALEONTOLOGY

Order PROETIDA Fortey and Owens, 1975

Superfamily AULACOPLEUROIDEA Angelin, 1854

Family AULACOPLEURIDAE Angelin, 1854

Subfamily AULACOPLEURINAE Angelin, 1854

Genera included.--Aulacopleura Hawle and Corda, 1847; Songkania Chang, 1974.

Diagnosis--Frontal and genal areas expanded, with very low, subdued tubercles or lacking tubercles, and with prominent caecal pitting; median glabellar lobe weakly inflated; eye

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[1] A version of this paper has been accepted for

publication. Adrain, J. M., and Chatterton, B. D. E. Journal of Paleontology.

ridge usually prominent in holaspides; paired glabellar spines absent in early ontogeny; single row of very low tubercles developed on dorsal aspect of anterior border in early ontogeny; eye socle subdued, sometimes with anterior lobe weakly inflated; hypostome elongate, with posterior spines greatly reduced or absent; transitory pygidia broad, flattened, and lacking prominent fulcral and distal pleural spines; pygidial doublure very narrow and of similar length medially and laterally.

Discussion.--*Aulacopleura* and *Otarion* have been variously regarded as separate at either the familial (Richter et al. in Moore, 1959) or subfamilial (Pribyl, 1947; Prantl and Pribyl, 1951; Bergström, 1973; Fortey and Owens, 1975; Pribyl and Vanek, 1981) level. The basis for such a distinction has never been made particularly explicit. Thomas and Owens (1978) approached a separate extreme by regarding the taxa as congeneric, a practice that has since been followed by most other workers. Adrain and Chatterton (in press) demonstrated that the similarity of the type species of *Otarion*, *O. diffractum* Zenker, 1833, to the type of *Aulacopleura*, *A. konincki* Barrande, 1846, is a matter of convergence, and gave reasons for classifying *Otarion* with several other genera in a monophyletic subfamily Otarioninae Richter and Richter, 1926, for which a diagnosis was provided. There are obvious differences between holaspides of Aulacopleura and members of the Otarioninae (broad genae, subdued sculpture, elongate hypostomes with small or absent posterior spines, number of thoracic segments, etc.), but Ludvigsen and Tripp (1990) followed Thomas and Owens (1978) in treating the taxon as a subgenus of Otarion, along with the subgenus Songkania Chang, 1974. Songkania is even more superficially similar to O. diffractum than is Aulacopleura, but detailed analysis of its morphology, together with new information on its ontogeny, supports a relationship with Aulacopleura, not Otarion. What is now known of the genera Aulacopleura and Songkania indicates that they fall outside the cladistic structure of the subfamily Otarioninae. The options are to abandon a subfamilial scheme, hence omitting relevant knowledge of phylogeny from the classification, or else to recognize a subfamily Aulacopleurinae, with limited diversity but with robust apomorphies, especially in early ontogeny. The latter course is followed here.

The early ontogeny of members of the Aulacopleurinae is incompletely known, and growth stages of Songkania smithi n. sp. (see below) represent the only relatively complete developmental sequence yet described. Nevertheless, what information there is contrasts sharply with the ontogeny of otarionines. Members of the latter subfamily have convex protaspides with relatively thick cuticles. Almost all have three pairs of prominent glabellar tubercles, four pairs of fixigenal spines, and one or two pairs of cephalic border spines (see Adrain and Chatterton, in press, Figure 1). While both Aulacopleura (e.g. Figure VI-1.10) and Songkania (e.g. Ludvigsen and Tripp, 1990, Pl. 8, fig. 1) have fixigenal spines, glabellar spines are absent and cephalic border spines can be observed only as very small tubercles in the early ontogeny of S. smithi (Figure VI-7.6, VI-7.7, VI-7.21). In addition, the last protaspid stage of S. smithi (Figure VI-7.4, VI-7.11, VI-7.12, VI-7.19) has low convexity and a very thin cuticle. All known otarionine transitory pygidia (most unpublished, but see Chatterton, 1971, for Cyphaspis, and Adrain and Chatterton, in press, for Otarion) are wide relative to their length, relatively convex, and have prominent fulcral and distal pleural spines on each segment. Those of S. smithi (Figure VI-7.8, VI-7.10, VI-7.15, VI-7.18, VI-7.22) are more subquadrate or subrectangular, much lower, and lack spines except for the protothoracic axial spine and possibly very faint tubercles on the fulcrum.

Genus AULACOPLEURA Hawle and Corda, 1847

Type species.--Arethusa koninckii Barrande, 1846a, Wenlock, Liten Formation, Bohemia, Czechoslovakia; by monotypy.

Other species.--Aulacopleura andersoni n. sp., Llandovery, northwest Canada; Aulacopleura bohemica Pribyl, 1947, Pragian, Czechoslovakia; Aulacopleura hercynica Kegel, 1927, Upper Silurian, Germany; Aulacopleura (Paraaulacopleura) ignorata Alberti, 1969, Eifelian, Morocco; Arethusina *inexpectata* Barrande, 1872, Lochkovian, Czechoslovakia; *Aulacopleura krizi* Šnajdr, 1975, upper Llandovery, Czechoslovakia; *Conocephalus* ? *longecornutus* Roemer, 1850, Eifelian, Germany; *Arethusa nitida* Barrande, 1846b, Wenlock, Czechoslovakia; *Aulacopleura*? *ranfordi* n. sp., lower Llandovery, northwestern Canada; *Aulacopleura*? *reedi* Pribyl, 1947, Caradoc, Scotland; *Aulacopleura* (*Paraaulacopleura*) *roquemaillerensis* Chaubet, 1937, Wenlock, France; *Arethusina sandbergi* Barrande, 1868, Upper Devonian, Germany; *Aulacopleura soror* Pribyl, Vanek, and Hörbinger, 1985, Wenlock, Czechoslovakia; *Aulacopleura* (*Paraaulacopleura*) *szechuanica* Lu, 1975, Tremadoc?, China (see discussion below).

Diagnosis.--Cephalon with very subdued tuberculate sculpture; anterior border furrow deflected anteriorly medially; glabella subrectangular, with only slight to moderate forward taper; median glabellar lobe lacking tubercles; occipital ring and thoracic axial rings lacking transverse rows of tubercles; long genal spine lacking tubercles or furrows; thorax of 18-22 segments, lacking thoracic axial spine; pygidium with 5-9 axial rings.

Discussion.--*Aulacopleura* can be distinguished from *Songkania* in its lower overall convexity, "notched" anterior border furrow, lack of glabellar tubercles or occipital ring tubercles except for median node, inflation of the anterior lobe of the eye socle, and greater number of thoracic segments.

Thomas and Owens (1978) considered *Aulacopleura* to range from the Lower Ordovician (Tremadoc) to the Middle Devonian, but did not attempt a comprehensive listing of species. When Thomas (1978) provided such a list, he included only three Ordovician species. One of these, *A.*? *reedi*, is most similar to *A.*? *ranfordi* n. sp. Neither of these species is very similar to the type species, and their generic placement is questionable (see discussion below). The others are two Chinese species described by Lu (1975). *Aulacopleura* (*Paraaulacopleura*) *dawanensis* Lu, 1975, is from the Arenig of China. It shares none of the apomorphies of *Aulacopleura* as understood herein, and should not be included in the genus. While its affinities are difficult to assess based upon the available material, the closest resemblance is with the Upper Ordovician genus *Madygenia* Petrunina, 1975, whose familial placement is uncertain (but see Owens' (in Owens and Hammann, 1990) placement of the genus in the Aulacopleuridae). Features in common include the elongate, apparently convex glabella, seemingly narrow fixed cheeks, and small palpebral lobes.

Aulacopleura (*Paraaulacopleura*) *szechuanica* Lu, 1975, reportedly from the Tremadoc of Szechuan, differs mainly in proportions of the cephalon from Silurian species closely comparable to the type, *A. koninckii*. With the reassignment and questionable placements discussed above and below, no other members of this species group are known from Ordovician rocks. A correct age assignment of A. szechuanica to the Tremadoc would therefore require its close similarity to Silurian species to be convergent, which seems unlikely, or else the survival of the Aulacopleura clade in virtual morphological stasis for the entirety of the Ordovician. Hence, we suggest that the single known specimen of A. szechuanica may have been derived from younger, most probably Silurian, rocks. Its provenance seems best regarded as unknown until further information can be gathered.

There appear to be two major species groups within Aulacopleura (in addition to A.? reedi and A.? ranfordi). The first consists of Silurian species (and A. szechuanica) similar in general morphology to the type species. This group includes almost all of the adequately known species assigned to the genus, and, if monophyletic, constitutes Aulacopleura s.s. A second group includes species with reduced genal areas, a greater number of pygidial axial rings, and a pygidium that is as a consequence much longer relative to its width. This group includes the Wenlock A. roquemaillerensis (see Thomas and Owens, 1978, Pl. 7, fig. 9) and all of the Devonian species assigned to the genus (see for example material of A. bohemica illustrated by Chlupac, 1983).

Aulacopleura roquemaillerensis was designated the type species of the subgenus _Paraaulacopleura_ by Chaubet (1937). As outlined by Thomas and Owens (1978, p. 68-69), confusion over the nature of this taxon was created by the fact that in the _Treatise_ (Richter and Schmidt in Moore, 1959, p. 0405, fig. 309.6) an illustration was given of _Paraaulacopleura_ _beyrichi_, not _roquemaillerensis_. The former species is poorly known (see Alberti, 1969, Pl. 36, fig. 12 for an illustration of the lectotype), and may in fact belong to the rorringtoniid genus _Goodsiraspis_ (see Adrain and Chatterton, submitted). Thomas and Owens (1978) considered _A_. _roquemaillerensis_ to so closely resemble _A_. _koninckii_ that there were no grounds for a subgeneric distinction between them, and hence placed _Paraaulacopleura_ in synonymy of _Aulacopleura_. The differences between the respective groups noted above, however, are quite real. Once the Devonian members of the _roquemaillerensis_ group become better known, the possibility that it forms a monophyletic sister group to _Aulacopleura_ s.s. can be assessed. If this is indicated, it may prove profitable to rehabilitate _Paraaulacopleura_.

AULACOPLEURA ANDERSONI n. sp.

Figures VI-1, VI-2

Diagnosis.--_Aulacopleura_ with narrow cephalic axis; narrow interocular fixigena; pronounced medial "notch" in anterior border furrow; and pygidium with five axial rings, with prominent pseudoarticulating half ring behind first.

Description.--Cranidium long, narrow; cranidial length (sag.) 200-220 percent width of occipital ring; preglabellar field long; glabella and occipital ring with length (sag.) 56-58 percent that of entire cranidium; anterior sections of facial suture strongly anteriorly divergent in front of palpebral lobe, reaching maximum divergence about two thirds distance anteriorly on frontal area, then converging across anterior border; posterior sections of facial suture with very strong posterior divergence; anterior border smooth and unornamented, with only weak dorsal convexity in sagittal profile (strongest anteriorly); anterior border of similar length laterally and medially (although appearing shorter laterally due to course of facial suture), but with anteriorly directed sagittal indentation on posterior edge; anterior border furrow with broad, shallow, inverted "V" shape in plan view, with pronounced anterior flexure sagittally; frontal area with moderately to strongly developed caecal pitting, pits densely but evenly distributed; frontal area with less dense sculpture of small, low tubercles; glabella with trapezoidal outline, low and with little dorsal inflation; axial furrows with slight to moderate anterior convergence; preglabellar furrow nearly transversely straight, with only slight anterior convexity; junction of preglabellar and axial furrow with small fossular pit; glabella smooth and lacking sculpture, except for occasional occurrence of small scattered tubercles on

L1; glabella widest across L1; maximum glabellar width 94-105 percent of sagittal length (excluding occipital ring); axial furrow broad and usually shallow; L1 teardrop-shaped, with slight lateral displacement of glabellar outline; S1 deepest anteriorly, shallowing near contact with occipital furrow; S2 short but usually prominent, posteromedially directed; L2 defined abaxially, but with little independent inflation; S3 visible ventrally as faint furrow near junction of preglabellar and axial furrows, partly obscured by fossula; fixigena narrow opposite midlength of palpebral lobe (approximately equal to width of palpebral lobe); bicomposite eye ridge visible dorsally, running nearly transversely from opposite S3 to anterior part of palpebral lobe; prominent transverse furrow developed immediately in front of eye ridge; eye ridge with single small tubercle set at midlength on adaxial part; fixigena with ornament of caecal pits similar to that of preglabellar field; several faint tubercles sometimes visible, spaced evenly in a longitudinal row along fixigena behind eye ridge; palpebral lobe large, separated from fixigena by very faint palpebral furrow, and with shallow but relatively broad pit set at midlength (exsag.), nearly adjoining palpebral furrow; posterior border furrow long (exsag.) and moderately deep, lengthening abaxially; posterior border short adaxially, lengthening and deflected posteriorly abaxially, distal to fulcrum; occipital furrow shallower medially than posterior border furrow, deepest behind L1; occipital ring with length (sag.) 25 percent of width, and with broad but very faint median node set at sagittal midlength.

Rostral plate triangular; broad, length (sag.) 25 percent of maximum width; connective sutures meeting posteriorly, no posterior margin developed; anterior part of ventral surface flat, posterior part with pronounced posteroventral convexity.

Hypostome unknown.

Librigena. Breadth of field (external view) at midlength (exsag.) of eye 50 percent length; field broad, smooth, with sculpture of evenly distributed caecal pits; pits varying in size, from small to nearly obscure; eye socle of faint, narrow, inflated band around base of eye, with inflated anterior lobe protruding ventrally onto field; posterior and lateral borders of similar width, both with even dorsal convexity; borders lacking sculpture; posterior border furrow and anterior part of lateral border furrow similarly broad and shallow; posterior third of lateral border furrow very shallow; genal spine usually slightly shorter than remainder of librigena, slightly broader than lateral border at base, then tapering evenly to tip; posterior and lateral borders unite at genal angle and continue onto dorsal aspect of genal spine as very faint, laterally set, furrow; doublure slightly less convex than border, so as to form a ventrally flattened tube; doublure broadest posteriorly, where it underlies union of posterior and lateral border furrows; doublure with sculpture of very fine, closely spaced, parallel terrace lines; terrace lines becoming obscure posteriorly, ventral aspect of genal spine with simple granular sculpture; doublural part of posterior section of facial suture running initially abaxially, then curving sharply adaxially.

Thorax unknown.

Pygidium. Pygidium with length (sag., excluding articulating half ring) 33-35 percent maximum width; axis with length (excluding articulating half ring) subequal to maximum width across first axial ring, low dorsal convexity in transverse profile; four distinct axial rings, fifth sometimes distinct from small terminal piece; pseudoarticulating half ring prominent between first and second rings, very faintly developed between second and third, not discernible posteriorly; axial rings bowed anteriorly, longest exsagittally, shortening slightly sagittally; axial furrows deepest between axial rings, shallowing opposite axial rings, converging posteriorly with little or no decrease in depth to fully define axis; pleural furrows deepest anteriorly, shallowing but well defined on posterior segments; interpleural furrows deeper than pleural furrows, both running transversely straight, with posterior deflection just past fulcrum and before terminating at border; border narrow but fully, although weakly, defined;

pleurae proximal to fulcrum nearly flat, pleurae distal to fulcrum with sharp ventral downturn; ventral margin running horizontally, with gentle dorsal inflection posteromedially; doublure very narrow, with faint sculpture of fine terrace lines set parallel with posterior margin.

Ontogeny.--Very little juvenile material of this species has been recovered, and even the smallest cranidia (Figure VI-1.21, VI-1.22) are likely holaspides. Changes in holaspid ontogeny of the cranidia include: a migration backwards of the eye position; a corresponding change in the course of the eye ridge, from running anterolaterally in the smallest cranidia (Figure VI-1.20, VI-1.22) to running transversely straight in cranidia of intermediate size (Figure VI-1.13, VI-1.17), to running posterolaterally in some large cranidia (Figure VI-1.5); an increase in the relative size of the frontal area; the development of the anteriorly directed "notch" in the anterior border furrow; a decrease in the anterior convexity of the preglabellar furrow; an incrase in the relative size of L1; an increase in the size of the palpebral lobes; and a decrease in the degree of dorsal cranidial convexity. No pronounced changes are observable in the available material of remaining sclerites.

Discussion.--Few species of Aulacopleura are well known, and most of these are preserved flattened in shales. Hence, detailed comparison of A. andersoni with other species is difficult, although obvious species differentia exist. Aulacopleura andersoni is most similar to A. krizi Šnajdr, 1975 (see Šnajdr, 1978) and A. koninckii. It shares with A. krizi similarly narrow fixigenae, but differs in its more pronounced "notch" in the anterior border furrow and less rapidly forwardly tapering glabella (cf. Šnajdr, 1978, Pl. 12, fig. 1). Its interocular fixigenae are much narrower than those of A. koninckii. Aulacopleura szechuanica Lu, 1975, is distinct in its much shorter preglabellar field. Aulacopleura roquemaillerensis Chaubet, 1937, and all of the Devonian species assigned differ in their narrower glabellae, and pygidia with a greater number of axial rings toether with a greater length relative to their width.

Etymology.--After Glenn Anderson.

Material.--Holotype cranidium with left librigena UA 9376; paratypes UA 9377-9408.

Occurrence.--Section AV 1 320-346 m; section AV 2 9-47 m; section AV 3 20-62 m; Llandovery (Pterospathodus celloni Zone - Pterospathodus amorphognathoides Zone), Whittaker Formation, central Mackenzie Mountains, Northwest Territories, Canada.

AULACOPLEURA? RANFORDI n. sp.

Figures VI-3, VI-4.1 to VI-4.14

Diagnosis.--Glabella elongate and subrectangular; anterior sections of facial suture strongly anteriorly divergent; interocular fixigena very narrow; eye set far forward; genal spine long and adaxially recurved; pygidium with five axial rings.

Description.--Cranidium moderately convex; anterior sections of facial suture strongly divergent in front of eye, reaching maximum divergence just behind anterior border furrow, then strongly anteriorly convergent, running obliquely across anterior border; posterior sections of facial sutures extremely posteriorly divergent, initially running transversely, then deflected obliquely; cranidium with maximum width posteriorly across fixigenae, width 140 percent of length (sag.); anterior border with even convexity, tube-like, lacking prominent sculpture, and slightly shorter (sag.; exsag.) than occipital ring; anterior border furrow moderately deep, describing an evenly convex, uninterrupted arc; preglabellar field about 40 percent length of median glabellar lobe (sag; excluding occipital ring), with very faint median furrow connecting preglabellar and anterior border furrows; preglabellar field with sculpture of fine, densely but evenly spaced, caecal pits; interocular fixigena narrow, set off from palpebral lobe by faint palpebral furrow, lacking obvious sculpture; palpebral lobe inclined obliquely at about 30 degrees, raised above fixigena at base, length (exsag.) similar to L1, protruded laterally nearly as far as maximum divergence of anterior sections of facial suture; glabella elongate, subcylindrical, weakly inflated, lacking obvious sculpture;

L1 elongate, narrow, broadest posteriorly and tapering strongly forward; S1 deeply impressed, deepest anteriorly; L2 defined as small, slightly laterally protruded swelling; S2 a small, rounded notch; L3 and S3 obscure; preglabellar furrow evenly convex, convexity stronger than that of anterior border furrow; axial furrows subparallel, with very slight forward convergence, deep; occipital furrow not as deep as S1 or axial furrow, relatively long (sag.; exsag.); occipital ring long, shortening abaxially, sculpture not known with certainty; posterior border furrow deep and long (exsag.); posterior border evenly convex (exsag.), shorter than anterior border, lacking obvious sculpture.

Rostral plate triangular, broad anteriorly with long connective sutures running posteromedially and meeting medially; ventral convexity similar to that of librigenal doublure.

Hypostome known only from single small and probably immature specimen; subrectangular in shape; width across shoulders 70 percent length (sag.); middle furrow set at 70 percent distance posteriorly from anterior margin; anterior wings lacking strong lateral protrusion; middle furrow and lateral border furrow of similar shallow depth; posterior margin transversely straight; pair of very small spines at posterolateral corners.

Librigena with eye socle of very faint posterior lobe (visible mainly ventrally) and weakly inflated, abaxially protruded anterior lobe; field lacking tuberculate sculpture, with many fine, evenly spaced caecal pits, and discernible, narrow, genal trunk; eye set forward, with midlength about two thirds distance anteriorly on field; lateral border furrow shallower than moderately impressed posterior border furrow; posterior border furrow deepest near genal spine, shallowing abaxially and continued along posterior section of facial suture to form strong sutural ridge; lateral and posterior border furrows meeting at genal angle to form weak furrow extended distally along dorsal aspect of genal spine; genal spine slightly shorter than remainder of librigena, tapering rapidly from base to sharp point, with even adaxial curvature; lateral and posterior borders of similar narrow width, lacking any obvious sculpture; doublure flattened slightly parallel to plane of field, inner third inclined obliquely to plane of field; doublural part of posterior section of facial suture running abaxially.

Thorax of unknown number of segments; axis of anterior segments one quarter total width of segment, lacking obvious sculpture; axial furrow shallower than, but communicating with, pleural furrow; anterior and posterior pleural bands of similar length (exsag.); pleural furrow shortened (exsag.) distal to fulcrum behind articulating facet; very small articulatory boss present on leading edge of fulcrum; pleural furrow shallowing immediately adaxial to tip of segment; very small nearly posteriorly directed spine at tip of posterior pleural band; doublure very narrow, with small, slit-like Panderian notch on posterior third, underlying position of constricted pleural furrow and behind dorsal articulating facet.

Pygidium with length (excluding articulating half ring) one third width; five axial rings with transverse terminal piece; pseudoarticulating half rings visible behind at least first and second rings; axial furrow deeper anteriorly, converging slightly posteriorly, meeting posteromedially to fully define axis; ring furrows deep and slot-like near axial furrows, shallowing medially, but well defined even on posterior segments; pleural furrows of segments one to four defined, strong anteriorly and become progressively weaker posteriorly; interpleural furrows shallower than pleural furrows, only first three distinctly impressed; pleural and interpleural furrows terminated abaxially by narrow border; pleural area around rear of axis with weak abaxial inflation; doublure narrow and rim-like, of same length medially and laterally.

Discussion.--Aulacopleura? ranfordi compares closely with A.? reedi Pribyl, 1947, from the Caradoc of Scotland (see Morris and Tripp, 1986, for an illustration of the lectotype). With the exception of A. szechuanica (see remarks above), the species together predate all other members of Aulacopleura, and differ from them in many details of morphology. The frontal and genal areas are less expanded, the pleural lobes are narrower, and the pygidia are narrower relative to their length. It is certainly conceivable that these species are the forerunners of more typical, younger, Aulacopleura species. It is also possible, however, that they represent a separate, closely related clade. Until more diversity is discovered it will be difficult to assess these options and the species are both referred with question to Aulacopleura herein.

Ontogeny.--Only a few relatively coarsely preserved early stages of this species have been found, and little can be said about progressive development of features. Of note, however, is that the transitory pygidia agree well with those of Songkania smithi (cf. Figure VI-4.11 to VI-4.14 with Figure VI-7.18, VI-7.22, VI-7.26, VI-7.27) in their overall shape and absence of pleural spines.

Etymology.--After Bill Ranford.

Material.--Holotype cephalon with thoracic segments UA 9409; paratypes UA 9410-9435, 9490-9492.

Occurrence.--Section AV 1 95.5-97.5 m; AV 4B 131.3 m; earliest Llandovery, Distomodus kentuckyensis/Icriodella discreta/Oulodus? nathani Zone, Whittaker Formation, central Mackenzie Mountains, Northwest Territories, Canada.

Genus SONGKANIA Chang, 1974

Type species.--Songkania hanjiadianensis Chang, 1974, from the Llandovery of southwest China; by original designation.

Other species.--Songkania pijiazhaiensis Chang, 1974, Llandovery, southwest China; S. socialis (Poulsen, 1934), Llandovery, north Greenland and northern Yukon Territory, Canada; S. smithi n. sp., Llandovery, Mackenzie Mountains, Canada.

Diagnosis.--Anterior sections of facial suture with very strong anterior divergence; very fine caecal pits densely distributed over very broad frontal and genal areas; eye socle obscure; genal spine usually of moderate length, not prominently curved, tapering evenly from base to sharp point; thorax of 11 or 12 segments; thoracic axial spine present on sixth segment of some species; prominent transverse row of tubercles present on occipital ring, thoracic axial rings, and anterior pygidial axial rings; pygidium long relative to width, with 6 or 7 axial rings and prominent, narrow, border.

Discussion.--Since its erection, Songkania had not been widely commented upon until Ludvigsen and Tripp (1990) referred material from Greenland and northern Canada to it. The Chinese material (Chang, 1974, Pl. 80, figs. 3, 4, Pl. 81, fig. 9) is hardly an adequate basis for comparison. Nevertheless, it agrees in as much morphological detail as is available with the northern Laurentian species recognized here, and there seems little doubt that Songkania is the correct name for this distinctive group of Llandovery aulacopleurines.

SONGKANIA SMITHI n. sp.

Figures VI-4.15, VI-4.16, VI-5 to VI-7

Diagnosis.--*Songkania* with very reduced cephalic tuberculation; eye ridges only faintly expressed in holaspid; fixigenal tubercles only visible in smallest meraspides, completely suppressed in holaspid; eye socle almost completely effaced; mature pygidia very long, broad, and of low convexity; large pygidia semicircular in plan view, with 7 or 8 discernible axial rings; axial furrows effaced posteriorly, terminal piece grades smoothly into postaxial area; border distinct laterally, effaced medially.

Description.--Cranidium strongly convex; anterior sections of facial sutures running in smooth arc from palpebral lobes, without prominent break in course, very strongly anteriorly divergent in front of palpebral lobe, reaching maximum divergence on posterior third of anterior border, then curving to run transversly across anterior aspect of anterior border to small rostral suture; posterior sections of facial suture diverging posteriorly at about 100 degrees to each other, deflected slightly posteriorly distal to fulcrum; anterior border relatively long, subequal in length to slightly longer than occipital ring, dorsally convex, lacking obvious sculpture; anterior border furrow deeply incised, usually evenly arcuate, but sometimes with very faint anterior inflection medially; preglabellar field long, about 80 percent length of glabella (sag.; excluding occipital ring), with subdued sculpture of very fine, densely distributed caecal pits; small, low median swelling set just in front of preglabellar furrow; interocular fixigena broad and lacking sculpture; distinct but very shallow palpebral furrow extended anteriorly along facial suture, and posteriorly to form small sutural ridge; eye ridge low and subdued, but usually discernible in large holaspides; palpebral lobe narrow (tr.), inclined somewhat obliquely, and with very small pit set slightly more than half distance transversely from palpebral furrow to rim; posterior part of fixigena with gentle swelling behind eye and opposite L1; preglabellar furrow describing shallow, approximate inverted "V" shape, deepest medially where a small pit is set, forming relative sharp angular contact with axial furrows; glabella uninflated, with maximum width across L1 subequal to length (sag; excluding occipital ring); sculpture of very subdued scattered tubercles restricted to posterior third of median lobe and adaxial two thirds of L1; L1 elliptical, with only moderate anterior taper; S1 very deep anteriorly, shallower near contact with occipital furrow; L2 about one third size of L1, not protruded laterally; S2 directed posteromedially, running about two thirds distance medially as S1; L3 a small, round structure when defined, often obscure; S3 when impressed very small and shallow, running short distance posteromedially from junction of axial and preglabellar furrows; occipital furrow deepest behind L1, shallow and long medially; posterior border furrow relatively shallow; posterior border short adaxially, becoming progressively longer abaxially, lacking sculpture; very small fossula set ventrally on abaxial aspect of axial furrow immediately opposite distal end of S3.

Rostral plate unknown.

Hypostome with width across shoulder 65 percent of length (sag.); middle furrow set at 70 percent distance posteriorly from anterior margin; anterior border flared slightly ventrally; anterior wing small, protruding laterally past shoulder; lateral margins moderately posteriorly convergent behind anterior wings, strongly outturned to form angular shoulder, then strongly posteriorly convergent behind shoulder; pair of small spines set at posterolateral corners in small specimens, suppressed to form rounded corners in larger specimens; posterior margin with very gentle posterior convexity; lateral border with one or two terrace lines running subparallel to margin; doublure narrow, developed beneath shoulder and posteriorly, absent from anterior portion.

Librigena with wide (tr.) field, sculpture of dense but subdued caecal pits similar to that of frontal area; eye socle obscure; posterior border furrow deeper than lateral border furrow; lateral border furrow shallowing posteriorly immediately in front of genal angle, but uniting with posterior border furrow to form faint furrow running along dorsal aspect of genal spine for most of its length; posterior border and lateral borders of similar width, posterior border lacking sculpture, but lateral border with several fine, closely spaced terrace lines running parallel to margin and occupying distal two thirds of border in external view; terrace lines extended posteriorly onto at least anterior part of genal spine; genal spine slightly more than half length of doublure, only slightly curved, and tapering evenly to sharp point; doublure broader anteriorly than posteriorly, with many fine, closely spaced terrace lines running parallel to margins.

Thorax of at least ten segments, likely more; slender axial spine present on either fifth or more likely sixth segment, running posteriorly to half length of pygidium; individual segments with axis bearing transverse row of six prominent tubercles, along with several scattered smaller tubercles; axis occupying 27 percent of width of thorax, both anteriorly and posteriorly; entire thorax broadening posteriorly from first segment, reaching maximum width at about sixth segment, then tapering to pygidium; anterior width of pygidium about 70 percent maximum width of thorax; axial furrow deep; pleural furrow running from axial furrow almost to tip of segment, deepest at fulcrum; posterior band longer (exsag.) than anterior band; prominent articulatory boss on leading edge of fulcrum; posterior band with several small tubercles on distal extremity; ventrally, posterior edge of posterior pleural band proximal to fulcrum forming grooved posterior recess bounded anteriorly by a transverse ridge, for tongue-and-groove-like articulation with leading edge of anterior pleural band; doublure developed distal to fulcrum to form narrow, flat articulatory facet; doublure beneath pleural tip forming moderately wide Panderian notch.

Pygidium of large holaspides with length (sag.; excluding articulating half ring) half maximum width; axis narrow, 25 percent width of pygidium anteriorly, with 7 axial rings, sometimes very faint eighth; pseudoarticulating half ring prominent behind first two rings, variably defined but usually becoming obscure posteriorly; transverse tubercle row on axial ring well defined on first four rings, obscure on fifth and entirely effaced posteriorly; ring furrows deep and slot like abaxially, near axial furrows, very shallow medially; axial furrows shallow, converging posteriorly, almost totally effaced posteromedially so that axis grades into posteromedian area; first pleural furrow slightly deeper than interpleural furrow, pleural and interpleural furrows of remainder of segments of similar, shallow depth; anterior and posterior pleural bands of similar length; pleural and interpleural furrows becoming progressively effaced posteriorly, but sometimes defined as far as seventh segment; pleural field forming plane proximally and slightly distal to fulcrum, then curved to almost vertical inclination around margin; pleural and interpleural furrows terminated at narrow but strongly defined border; doublure extremely narrow, of same width adaxially and abaxially.

Ontogeny.--Specimens of the first calcified instar are represented (Figure VI-7.20, VI-7.23, VI-7.24), and a nearly complete ontogenetic sequence has been reconstructed. Preservation, however, is not perfect, with the ventral surface often better preserved than the dorsal. What is presumably the last protaspid stage has been identified (Figure VI-7.4, VI-7.11, VI-7.12, VI-7.19), but intermediate stages have not been found and the number of stages is not known. Changes through ontogeny of the cranidium include migration laterally of the anterior and posterior extremeties of the facial suture; suppression of very low border spines; progressive inflation of L1, which is indistinguishable in early meraspid degrees; lateral inflation of the median glabellar lobe, which is nearly cylindrical in early ontogeny; expansion laterally of the palpebral lobes; deepening of the posterior and anterior border furrows; and relative lengthening of the preglabellar field. Changes in the librigena include a relative lengthening of the genal spine; suppression of small lateral border tubercles; increase in the relative width of the field; and multiplication of the number of terrace ridges on the doublure together with their development dorsolaterally on the lateral border. Transitory pygidia grow progressively wider relative to their length; the lateral parts become ventrally inclined as the fulcrum develops; pleural and interpleural furrows become progressively more distinct; the posteromedian margin of early degrees is indented anteriorly, and this is gradually lost; and the doublure becomes relatively narrower.

Discussion.--*Songkania smithi* is most similar to *S. socialis* (Poulsen, 1934), type and additional material of which was illustrated by Ludvigsen and Tripp (1990). A corresponding sister species relationship exists between other trilobites occurring with *S. smithi* in the Mackenzie Mountains and *S. socialis* at Prongs Creek, northern Yukon Territory. The encrinurines *Cromus canorus* Edgecombe and Chatterton, 1992, and *C. princeps* (Poulsen, 1934), are each other's nearest relative, as are the odontopleurines *Sinespinaspis maccallai* (Chatterton and Perry, 1983) and *S. semiglabra* (Poulsen, 1934).

Ludvigsen and Tripp (1990) considered material of *Songkania socialis* from Prongs Creek to be dimorphic. The only express difference noted between the morphs was the presence of a thoracic axial spine in one and its absence in the other. Based on the published illustrations, however, the spineless "morph" (Ludvigsen and Tripp, 1990, Pl. 8, fig. 5) would appear to differ from the spined "morph" in the following additional features: a relatively longer, less convex anterior cephalic border; a slightly shorter preglabellar field and reduced frontal and genal area; a narrower cephalon; a much narrower thorax; the presence of only 11 as opposed to 12 thoracic segments (compare Ludvigsen and Tripp, 1990, Pl. 8, figs. 1 and 5; and a pygidium that is much longer relative to its width. Ludvigsen and Tripp's reconstruction (1990, Text-fig. 5B) conflates elements of both "morphs", as it depicts a 12-spined individual lacking a thoracic axial spine. It seems possible that the spineless "morph" in fact represents a second species living in sympatry with S. socialis, as sclerites belonging unequivocally to the spined "morph" agree in morphological detail with the mainly exfoliated Greenland type material (Ludvigsen and Tripp, 1990, Pl. 13, figs. 3-6).

The number of thoracic segments present in Songkania smithi is difficult to determine, as the only articulated specimen found is a molt ensemble (Figure VI-3.1). The trilobite apparently freed itself from the cephalon, then crawled forward from beneath it, freeing itself from the thoracopyidium by bracing the anterior thoracic segments against the rear of the now loosened cranidium. This resulted in the stacking of the anterior thoracic segments behind and beneath the cephalon. As a result, the number of thoracic segments anterior to that bearing the axial spine is not known with certainty. Four are visible, including that which articulated with the cranidium and that directly anterior to the spine-bearing segment. A fifth could easily be obscured in the insoluble matrix beneath the cranidium. If so, the spine-bearing segment would be the sixth, as in *S. socialis*, and as is the norm in most other spine-bearing aulacopleurids. Only five segments are visible posterior to the spine-bearing segment, and these have remained in articulation. The pygidium is not articulated with the last of these segments, having slipped beneath it, and there is the possibility that the posteriormost segment is also obscured in this fashion. If that were the case, *S. smithi* would likely share a thoracic segment count of 12 with both *S. socialis* and *S. hanjiadianensis*. The last segment visible, however, does seem to match closely the anterior width of the pygidium, and it is difficult to see, given the taper of the thorax, how another could be accommodated. In summation, *S. smithi* had at least 10, but most likely 11 or 12 thoracic segments.

Songkania smithi differs from *S. socialis* (spined "morph") in the following respects: glabellar tuberculation much less prominent; paired fixigenal tubercles entirely suppressed, versus robust in large holaspides of *S. socialis* (Ludvigsen and Tripp, 1990, Pl. 8, figs. 1-3); eye ridge faint in holaspides, versus prominent; posterior branch of facial sutures more widely divergent, with concomitantly greater area of posterior aspect of fixed cheeks, and reduced extent of posterior cephalic border on free cheeks (compare Figure VI-6.1, VI-6.4, VI-6.7, VI-6.8 with Ludvigsen and Tripp, 1990, Pl. 8, figs. 2, 9, 12); thoracic pleurae lateral to fulcrum about same width as, or even wider than, pleurae medial to fulcrum, versus consistently narrower in *S. socialis*; pygidium much longer relative to width in specimens of comparable large size (compare Figure VI-6.12, VI-6.17 with Ludvigsen and Tripp, 1990, Pl. 8, fig. 1). Large pygidia of *S. socialis* resemble much smaller pygidia of *S. smithi* (e.g. Figure VI-6.16).

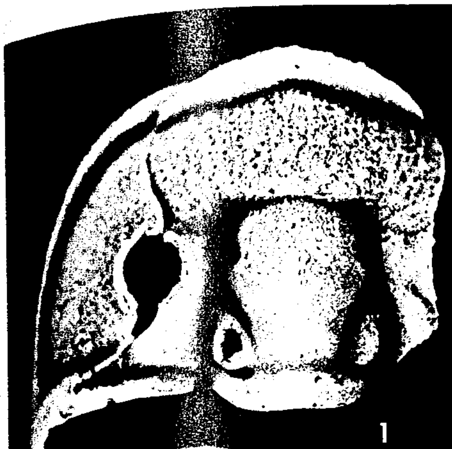
It is not possible to conduct a detailed comparison with either of the Chinese species, based on the published illustrations.

Material.--Holotype dorsal exoskeleton UA 9436, from section Avalanche Lake Two, 6.5 m above base; paratypes UA 9437-9489, 9493, 9494.

Occurrence.--Section AV 1, 320-369 m; AV 2 6-47 m; AV 3 5-20 m; Llandovery (*Pterospathodus celloni* Zone - *Pterospathodus amorphognathoides* Zone), Whittaker Formation, central Mackenzie Mountains, Northwest Territories, Canada.

Etymology.--After Geoff Smith.

FIGURE *VI-1*--*Aulacopleura andersoni* n. sp., from the Whittaker Formation, Llandovery, central Mackenzie Mountains, Northwest Territories, Canada; exact horizons given in parentheses; figures are x10, except where otherwise noted. *1*-*3*, dorsal, anterior, and left lateral views of holotype cranidium and left librigena UA 9376, x7.5 (AV 1 346 m); *4*, ventral view of cranidium and rostral plate UA 9377 (AV 1 336 m); *5*, dorsal view of cranidium UA 9378 (AV 1 336 m); *6*, dorsal view of cranidium UA 9379 (AV 1 336 m); *7*, oblique anterodorsal view of partial cranidium and left librigena UA 9380 (AV 1 336); *8*, dorsal view of cranidium UA 9381 (AV 1 336 m); *9*, dorsal view of cranidium UA 9382 (AV 1 346 m); *10*, dorsal view of cranidium UA 9383 (AV 1 336 m); *11*, *12*, *16*, dorsal, anterior, and left dorsolateral views of cranidium UA 9384 (AV 2 47 m); *13*, dorsal view of cranidium UA 9385 (AV 1 336 m); *14*, left lateral view of cranidium UA 9386 (AV 1 336 m); *15*, left lateral view of cranidium UA 9387 (AV 1 336 m); *17*, dorsal view of cranidium UA 9388 (AV 1 336 m); *18*, dorsal view of cranidium UA 938 (AV 1 336 m); *19*, *20*, left lateral and dorsal views of cranidium UA 9390 (AV 2 47 m); *21*, dorsal view of cranidium UA 9391, x15 (AV 3 62 m); *22*, dorsal view of cranidium UA 9392, x15 (AV 3 62 m).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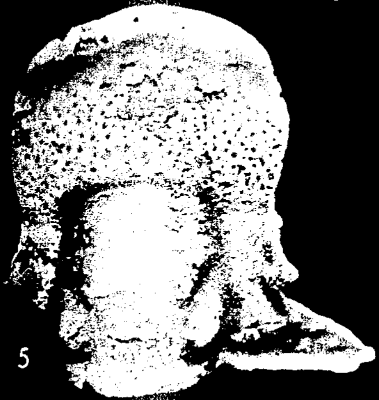
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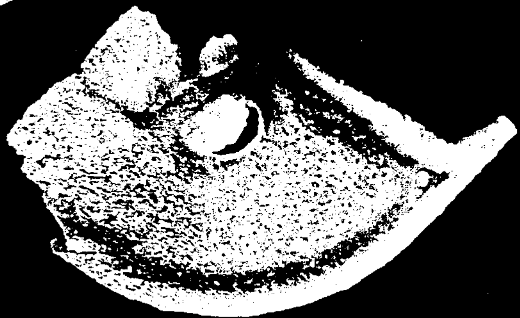
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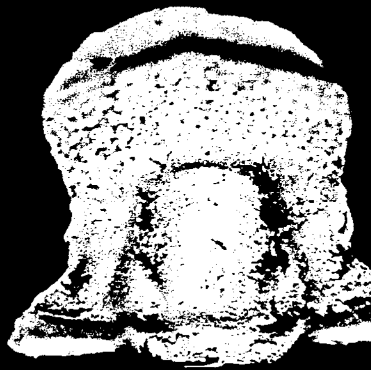
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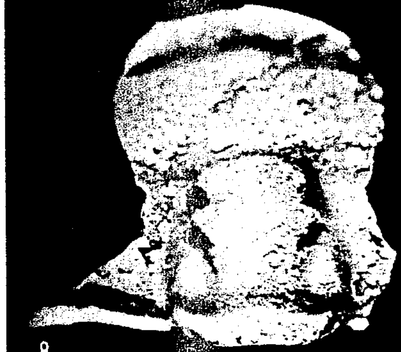
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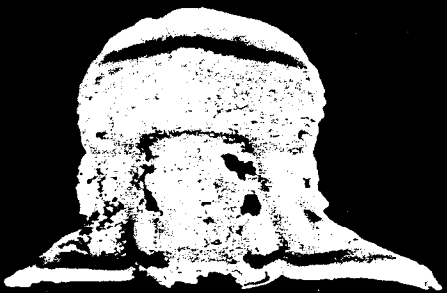
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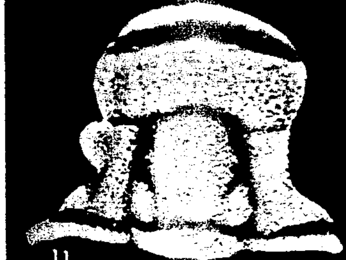
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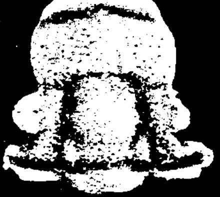
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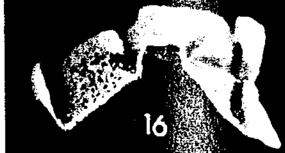
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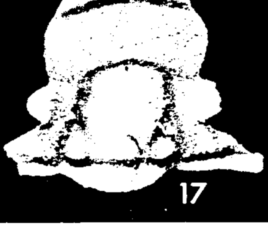
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FIGURE VI-2--Aulacopleura andersoni n. sp., from the Whittaker Formation, central Mackenzie Mountains, Northwest Territories, Canada; exact horizons given in parentheses; figures are x10 except where otherwise noted. 1, external view of left librigena UA 9393 (AV 2 47 m); 2, external view of right librigena UA 9394 (AV 1 336 m); 3, external view of right librigena UA 9395 (AV 1 336 m); 4, internal view of right librigena UA 9396 (AV 1 336 m); 5, internal view of right librigena UA 9397 (AV 1 336 m); 6, external view of right librigena UA 9398 (AV 1 346 m); 7, 8, 10, ventrolateral, internal and external views of left librigena UA 9399, x10 except 8, x7.5 (AV 2 47 m); 9, external view of right librigena UA 9400 (AV 1 336 m); 11, external view of right librigena UA 9401 (AV 3 62 m); 12, dorsal view of pygidium UA 9402 (AV 1 336 m); 13, 17, 18, ventral, posterior, and dorsal views of pygidium UA 9403 (AV 2 47 m); 14, 24, external and dorsal views of right librigena UA 9404 (AV 2 47 m); 15, 21, external and dorsal views of left librigena UA 9405 (AV 2 47 m); 16, 19, 20, dorsal, ventral, and left lateral views of pygidium UA 9406 (AV 2 47 m); 22, dorsal view of cranidium UA 9407 (AV 1 336 m); 23, dorsal view of pygidium UA 9408 (AV 2 47 m).

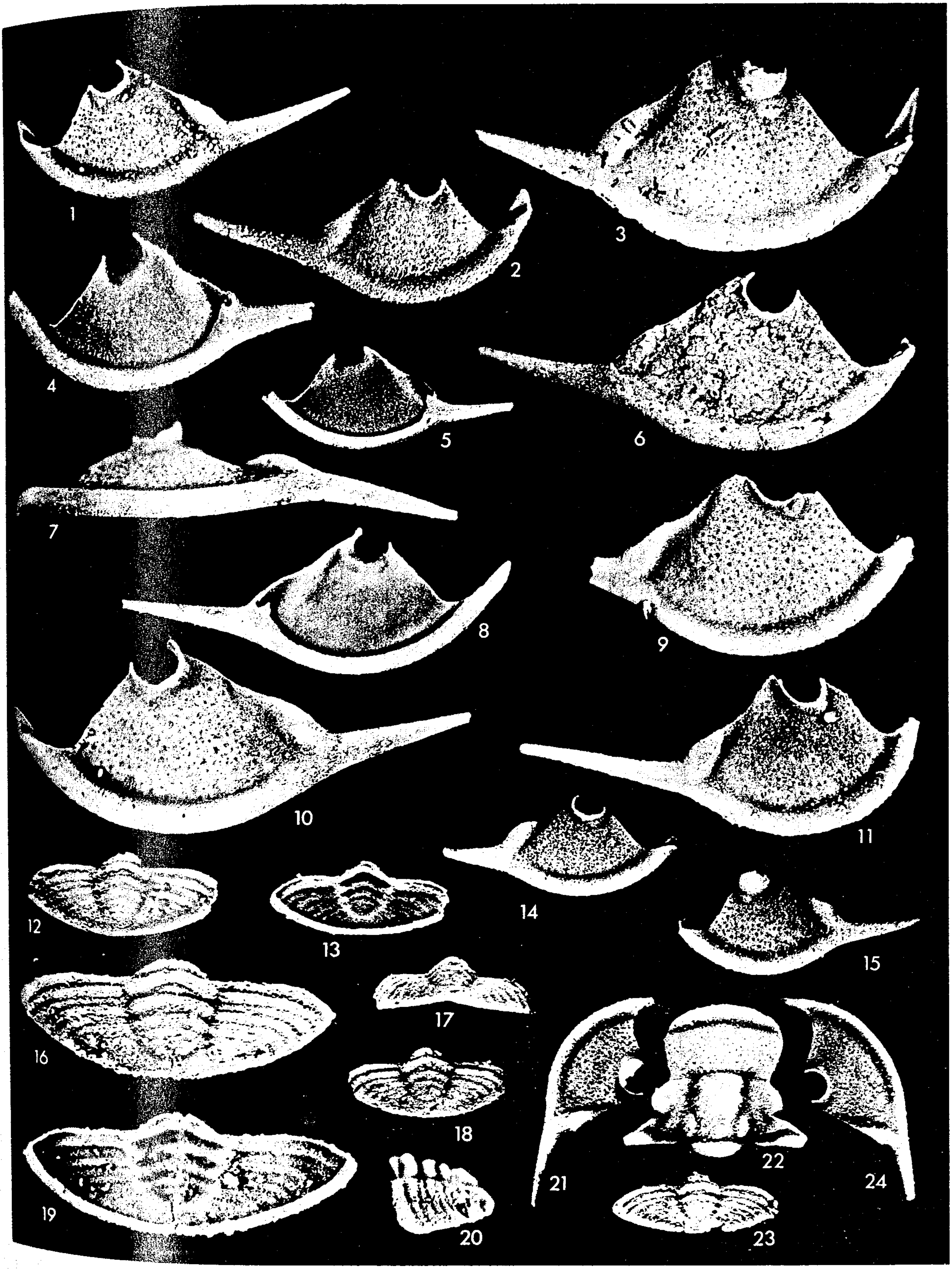
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FIGURE VI-3--Aulacopleura? ranfordi n. sp., from the Whittaker Formation, Llandovery, central Mackenzie Mountains, Northwest Territories, Canada; all figures are x10; specimens are from section Avalanche Lake 4B, 131.3 m above base, except where otherwise noted. 1-4, 6, dorsal, anterior, left lateral, ventral, and posterior views of holotype cephalon with attached thoracic segments UA 9409; 5, 7, 9, 11, dorsal, ventral, left lateral, and posterior views of thoracic segments UA 9410, probably from same individual as UA 9409; 8, 10, 15, dorsal, ventral, and right lateral views of cranidium UA 9411; 12, internal view of right librigena UA 9412; 13, internal view of right librigena UA 9413; 14, external view of left librigena UA 9414; 16, 18, external and ventrolateral views of left librigena UA 9415; 17, 22, dorsal and posterior views of pygidium UA 9416; 19, external view of right librigena UA 9417; 20, 21, internal and external views of left librigena UA 9418 (AV 1 95.5 m); 23, 28, 29, left lateral, dorsal, and posterior views of pygidium UA 9419 (AV 1 95.5 m); 24, dorsal view of pygidium UA 9420; 25, dorsal view of pygidium UA 9421; 26, dorsal view of pygidium UA 9422; 27, dorsal view of pygidium UA 9423; 30, 31, dorsal and ventral views of pygidium UA 9424; 32, dorsal view of pygidium UA 9425.

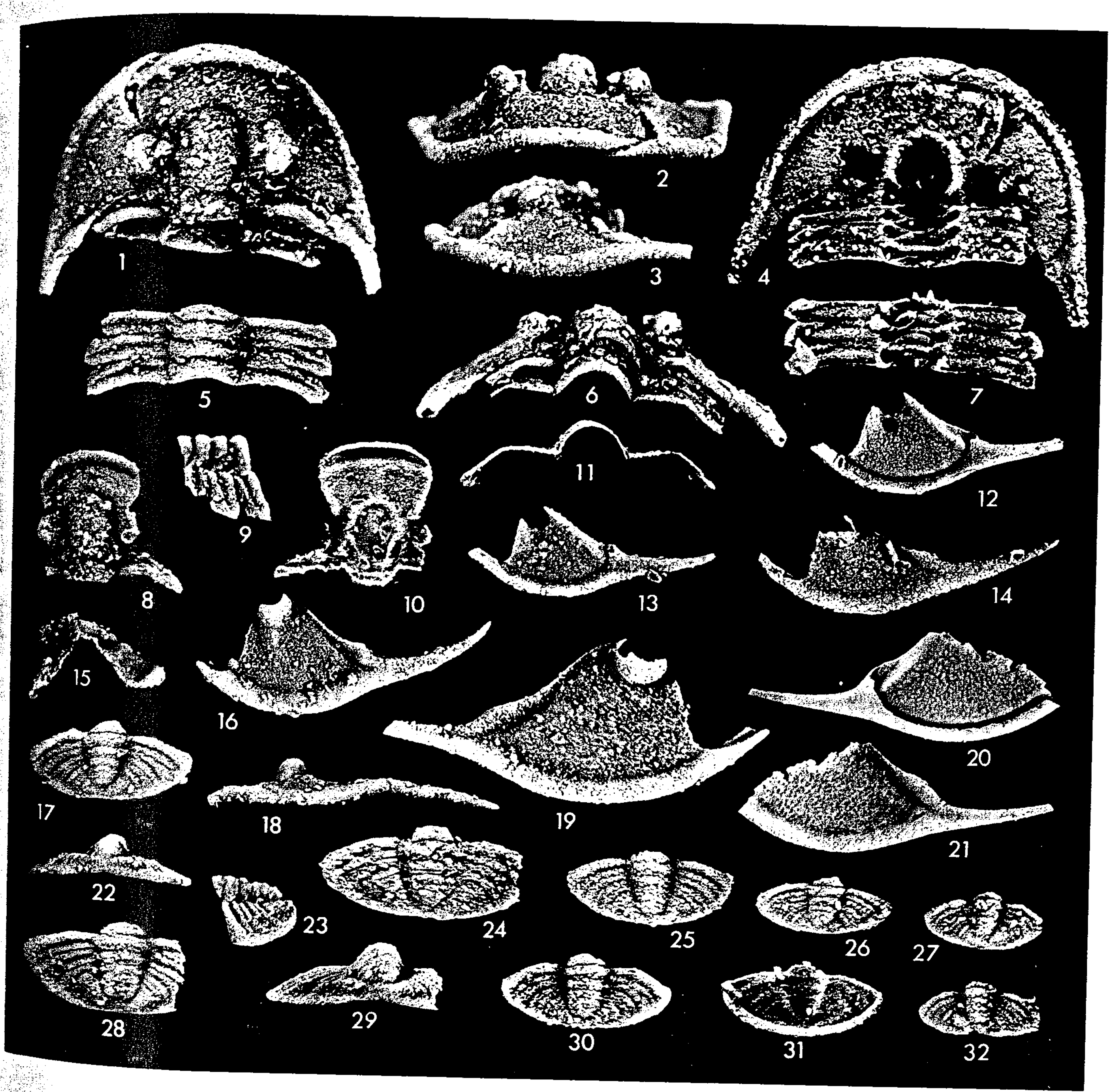
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FIGURE VI-4--1-14, Aulacopleura? ranfordi n. sp., from the Whittaker Formation, Llandovery, central Mackenzie Mountains, Northwest Territories, Canada; from Section Avalanche Lake 4B, 131.3 m above base, except where otherwise noted. All illustrations are scanning electron micrographs. 1, 5, dorsal and left lateral view of cranidium UA 9426, x28; 2, dorsal view of cranidium UA 9427, x28; 3, dorsal view of cranidium UA 9428, x40; 4, anterolateral oblique view of cranidium UA 9429, x28 (AV 1 95.5); 6, anterolateral oblique view of cranidium UA 9430,x55; 7, external view of right librigena UA 9431, x28 (AV 1 98.5); 8, ventral view of hypostome UA 9432, x55; 9, dorsal view of pygidium UA 9433, x28; 10, dorsal view of pygidium UA 9434, x55; 11, dorsal view of transitory pygidium UA 9435, x55; 12, dorsal view of transitory pygidium UA 9490, x55; 13, dorsal view of transitory pygidium UA 9491, x55; 14, dorsal view of transitory pygidium UA 9492, x40 (AV 1 95.5). 15, 16, Songkania smithi n. sp., from the Whittaker Formation, Llandovery, central Mackenzie Mountains, Northwest Territories, Canada; from Section Avalanche Lake Three, 5 m above base. 15, dorsal view of hypostome UA 9493, x28; 16, ventral view of hypostome UA 9494, x28.

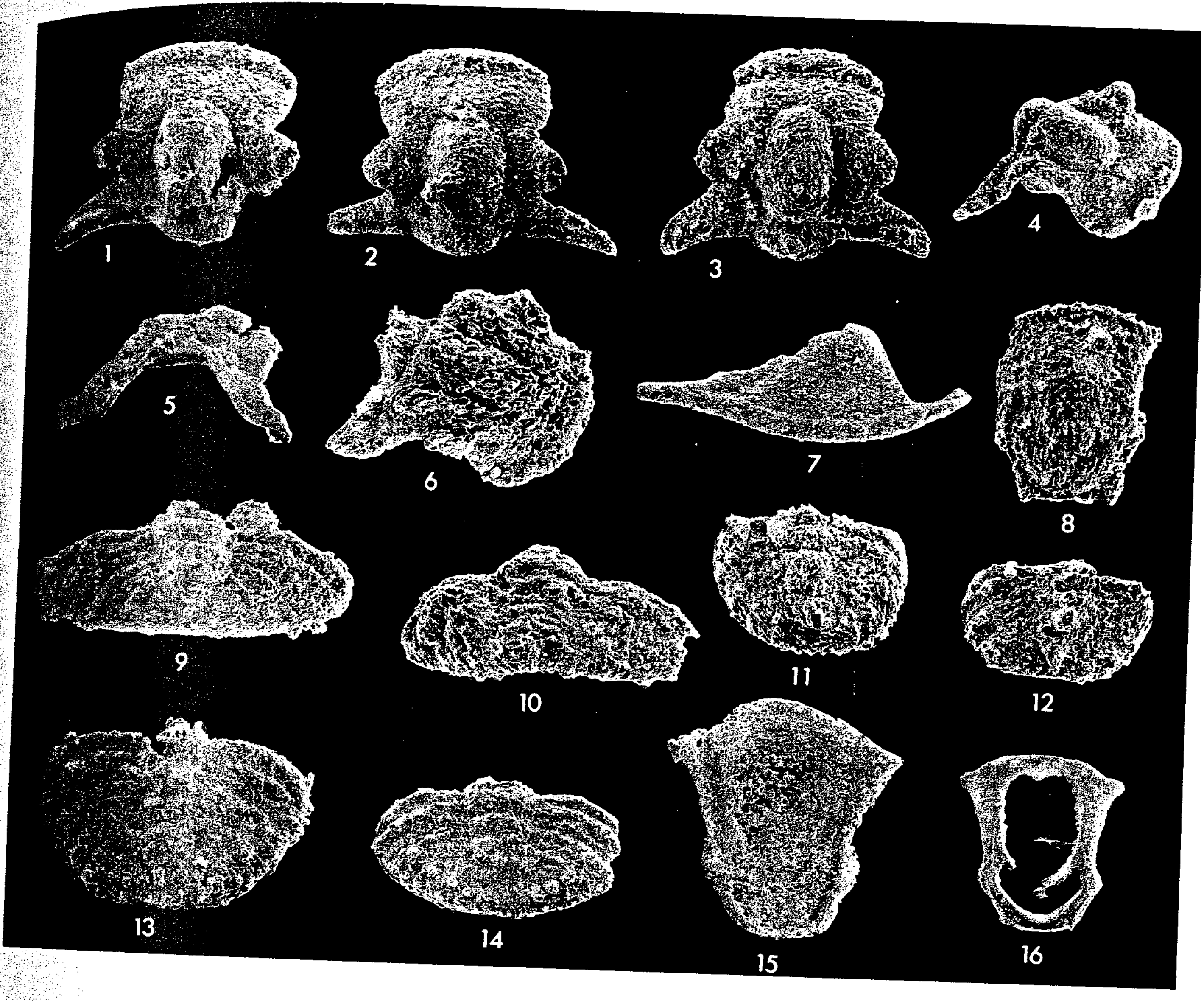
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FIGURE *VI-5*--*1*-*17*, *Songkania smithi* n. sp., from the Whittaker Formation, Llandovery, central Mackenzie Mountains, Northwest Territories, Canada; all figures are x10; exact horizons are given in parentheses. *1*, dorsal view of holotype articulated dorsal exoskeleton UA 9436 (AV 2 6.5 m); *2*, dorsal view of cranidium UA 9437 (AV 3 20 m); *3*, dorsal view of cranidium UA 9438 (AV 3 20 m); *4*, *7*, dorsal and left lateral views of cranidium UA 9439 (AV 1 320 m); *5*, *8*, *11*, *13*, dorsal, left lateral, anterior, and ventral views of cranidium UA 9440 (AV 2 42 m); *6*, *9*, dorsal and left lateral views of cranidium UA 9441 (AV 2 42 m); *10*, dorsal view of cranidium UA 9442 (AV 3 20 m); *12*, ventral view of cranidium UA 9443 (AV 2 42 m); *14*, dorsal view of cranidium UA 9444 (AV 3 5 m); *15*, dorsal view of cranidium UA 9445 (AV 3 5 m); *16*, dorsal view of cranidium UA 9446 (AV 3 5 m); *17*, dorsal view of cranidium UA 9447 (AV 3 5 m).


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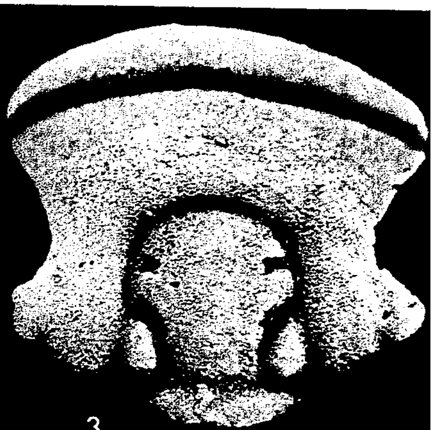
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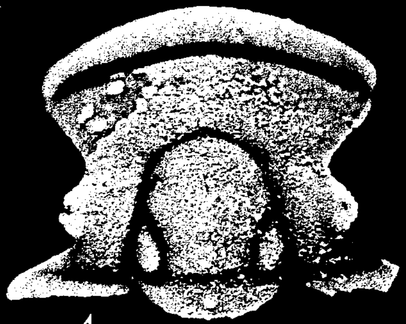
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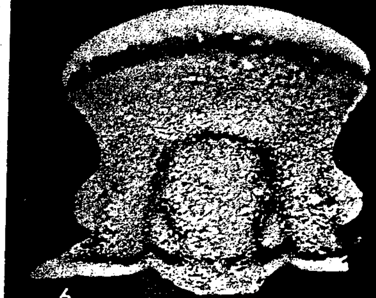
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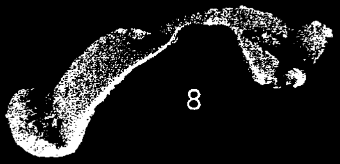
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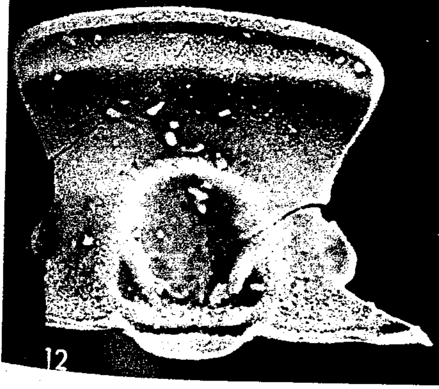
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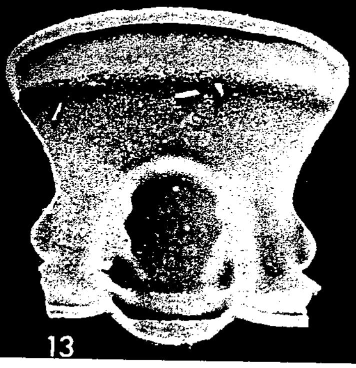
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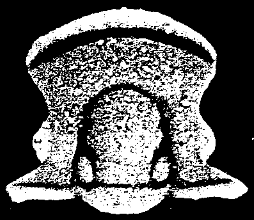
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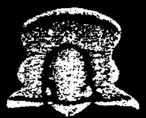
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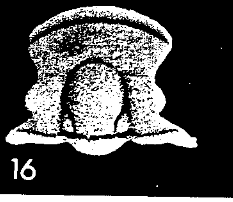
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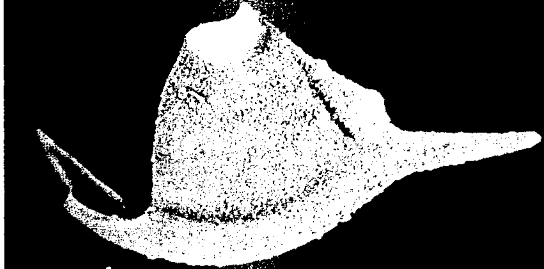
FIGURE VI-6--1-18, Songkania smithi n. sp., Whittaker Formation, Llandovery, central Mackenzie Mountains, Northwest Territories, Canada; exact horizons given in parentheses; all figures are x10. 1, 3, external and internal views of left librigena UA 9448 (AV 1 320 m); 2, external view of left librigena UA 9449 (AV 2 42 m); 4, external view of left librigena UA 9450 (AV 2 42 m); 5, internal view of left librigena UA 9451 (AV 2 42 m); 6, external view of right librigena UA 9452 (AV 1 346 m); 7, external view of right librigena UA 9453 (AV 3 5 m); 8, external view of right librigena UA 9454 (AV 3 20 m); 9, dorsal view of pygidium UA 9455 (AV 3 20 m); 10, internal view of right librigena UA 9456 (AV 3 20 m); 11, ventral view of thoracic segment UA 9457 (AV 1 320 m); 12, 13, dorsal and ventral views of pygidium UA 9458 (AV 3 20 m); 14, dorsal view of pygidium UA 9459 (AV 3 20 m); 15, 17, 18, left lateral, dorsal and posterior views of pygidium UA 9460 (AV 3 20 m); 16, dorsal view of pygidium UA 9461 (AV 3 5 m).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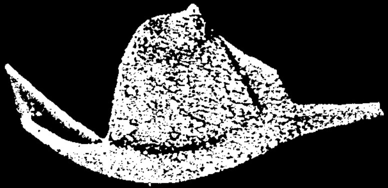
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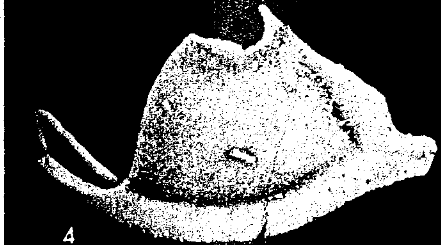
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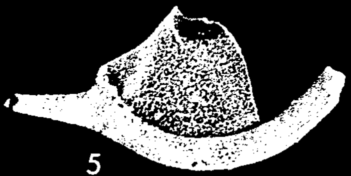
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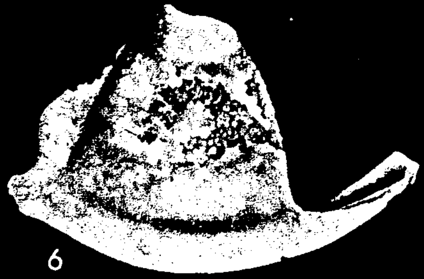
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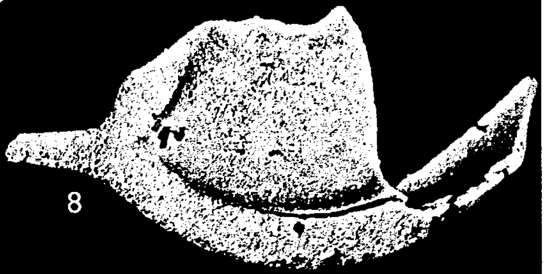
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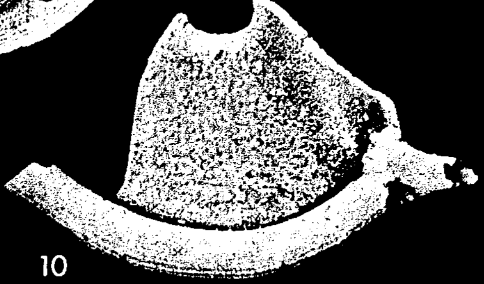
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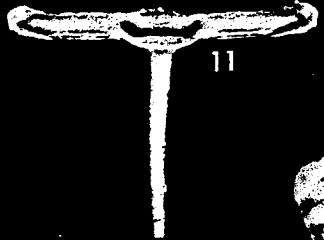
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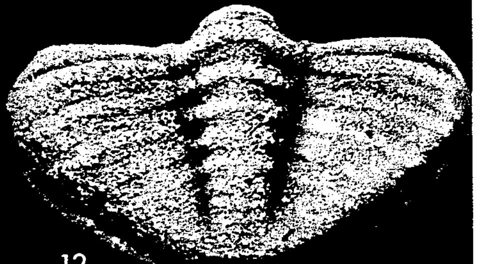
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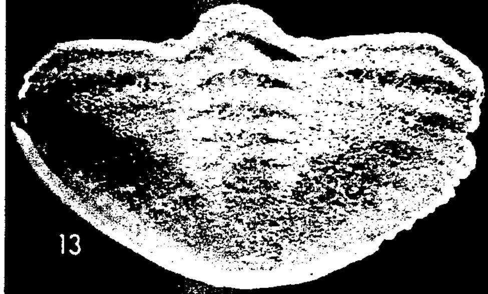
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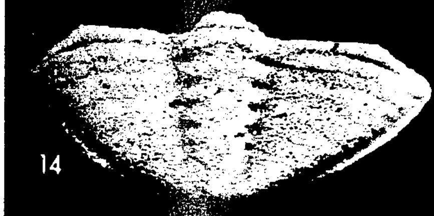
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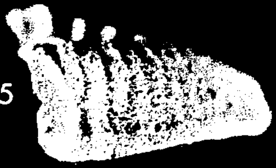
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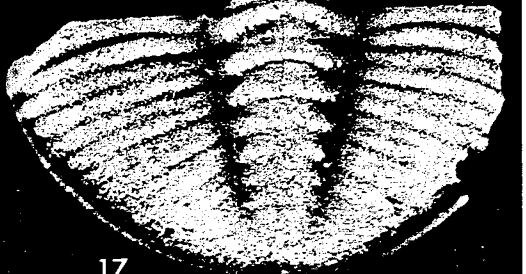
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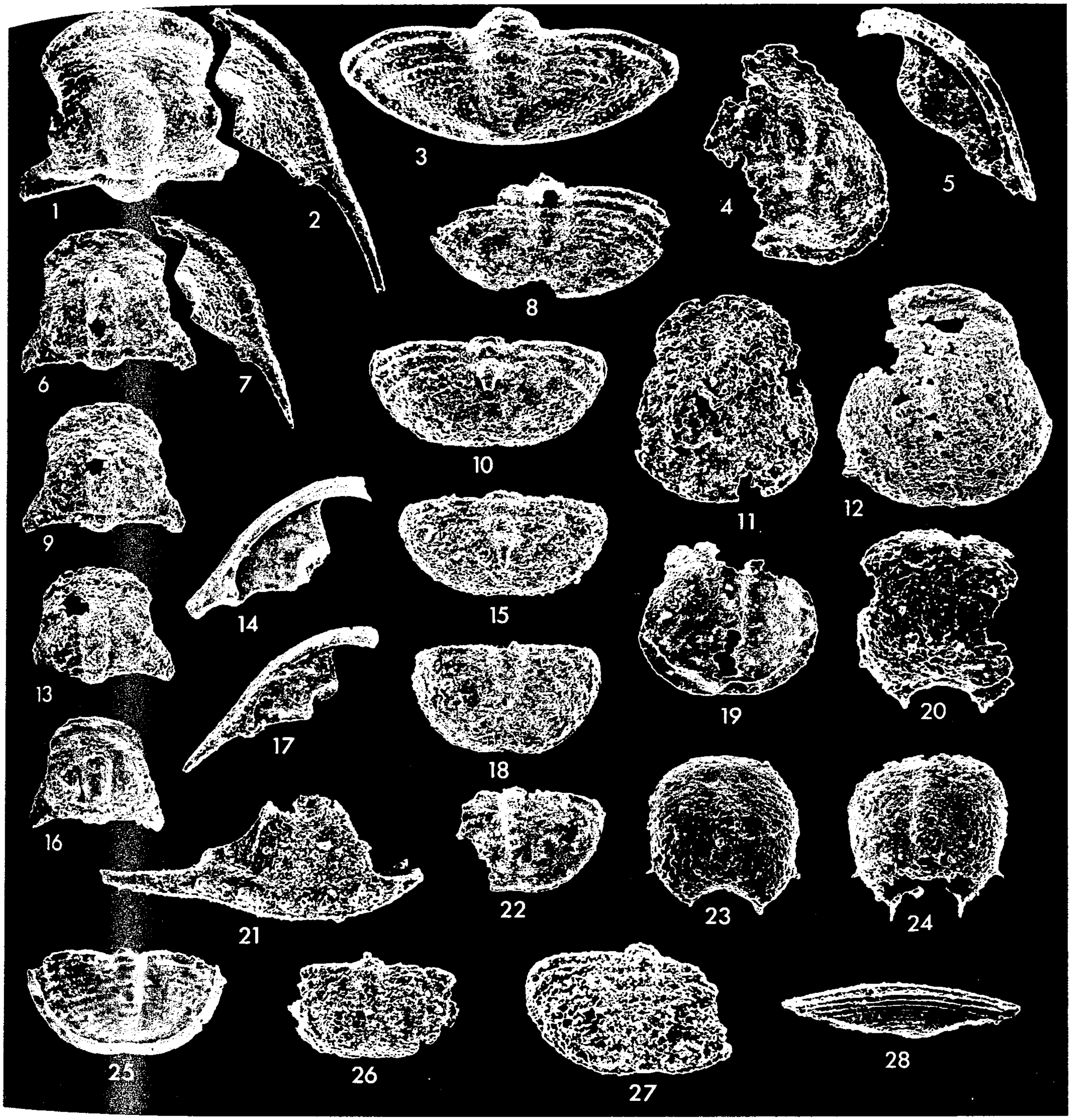
FIGURE VI-7--Songkania smithi n. sp., Whittaker Formation, Llandovery, central Mackenzie Mountains, Northwest Territories, Canada; from section Avalanche Lake Three, 5 m above base, except where otherwise noted; all illustrations are scanning electron micrographs. 1, dorsal view of cranidium UA 9462, x38; 2, dorsal view of right librigena UA 9463, x38; 3, dorsal view of pygidium UA 9464, x38; 4, ventral view of protaspis UA 9465, x56; 5, internal view of left librigenae UA 9466, x56; 6, dorsal view of cranidium UA 9467, x38; 7, dorsal view of right librigena UA 9468, x38; 8, dorsal view of transitory pygidium UA 9469, x38; 9, dorsal view of cranidium UA 9470, x38; 10, dorsal view of transitory pygidium UA 9471, x38; 11, dorsal view of protaspis UA 9472, x56; 12, dorsal view of protaspis UA 9473, x52 (AV 1 320 m); 13, dorsal view of cranidium UA 9474, x38; 14, internal view of right librigena UA 9475, x38; 15, dorsal view of transitory pygidium UA 9476, x38; 16, ventral view of cranidium UA 9477, x38; 17, internal view of right librigena UA 9478, x38; 18, dorsal view of transitory pygidium UA 9479, x38; 19, ventral view of protaspis UA 9480, x56; 20, ventral view of protaspis UA 9481, x80; 21, external view of right librigena UA 9482, x38; 22, dorsal view of transitory pygidium UA 9483, x38; 23, dorsal view of protaspis UA 9484, x80 (AV 1 320 m); 24, dorsal view of protaspis UA 9485, x80 (AV 1 320 m); 25, ventral view of transitory pygidium UA 9486, x38; 26, dorsal view of transitory pygidium UA 9487, x56; 27, dorsal view of transitory pygidium UA 9488, x56; 28, ventral view of rostral plate UA 9489, x38, specific assignment questionable.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CHAPTER VII[1]

SILURIAN TRILOBITES FROM SOUTHWESTERN ALASKA

INTRODUCTION

THIS WORK describes the first Silurian trilobites known from the state of Alaska, along with several machaeridian sclerites found in association. The fauna includes seven trilobite species and three machaeridian species. Although there is as yet no independant corroboration, the affinities of the trilobites indicate firmly a late Llandovery (Telychian) age. Trilobites are by far the most common fossils in the assemblage. Aside from machaeridians, the only other macrofossils occurring are rare gastropods and brachiopods.

LOCALITY AND STRATIGRAPHY

The Silurian trilobites described here were collected during the course of a two-year field study (1983-1984) by the Alaska Division of Geological and Geophysical Surveys. This work involved the participation of one of us (R.B.B.) in a stratigraphic study and analysis for petroleum potential of strata in the Sleetmute, Lime Hills, and Taylor Mountains quadrangles of southwest Alaska. The trilobites were collected by Thomas N. Smith (formerly of the Alaska Division of Geological and Geophysical Surveys; now with

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[1] A version of this chapter has been submitted for publication. Adrain, J. M., Chatterton, B. D. E., and Blodgett, R. B. Journal of Paleontology.

Alaska Division of Oil and Gas) during the summer of 1984from a white bioclastic limestone exposed in the SW1/4, SW1/4, NE1/4, SW1/4, sec. 4, T10N, R24W, Taylor Mountains D-2 quadrangle, and has the following geographic coordinates: latitude 60 degrees, 58 minutes, 59 seconds N, longitude 156 degrees, 44 minutes, 31 seconds W. This locality is designated USGS 11948-SD (=field station 84-TNS-45F), and its location is shown in Figure VII-1.

No formation-rank startigraphic name can be applied to beds from which these specimens were collected. The region from which these fossils are derived (Holitna Lowlands) still remains to be geologically mapped in detail. The stratigraphic term Holitna Group was named and applied by Cady et al. (1955) to the Paleozoic carbonates exposed in this area. No smaller-rank stratigraphic units were designated for inclusion in this group. Fossils of Silurian and Devonian age were reported by Cady et al. (1955), but these authors inferred that Ordovician strata may also be present due to their occurrence in correlative rocks in the Medfra quadrangle to the northeast, as well as the fact that the Silurian and Devonian faunas were recovered only from the upper part of the Holitna Group. These authors estimated the thickness of the group "to be at least 5,000 and probably closer to 10,000 feet thick" (Cady et al., 1955, p. 24). The work conducted by the Alaska Division of Geological and Geophysical Surveys in the summers of 1983 and 1984 indicate that rocks assigned to this group are actually much greater in total thickness and include strata as old as Cambrian and as young as Triassic. It seems reasonable that further mapping will indicate that the term Holitna Group is too broadly defined, and should ultimately be abandoned in favor of more finely subdivided stratigraphic units.

In terms of tectonostratigraphic terrane nomenclature, strata mapped by Cady et al. (1955) as belonging to the Holitna Group in the central Kuskowkim region comprise the southwestern terminus of the Nixon Fork terrane of Patton (1978), which is characterized primarily by lower and middle Paleozoic platform carbonate rocks. To the north and east this assemblage of rocks grades into equivalent, deeper water basinal strata which have been assigned to the Dillinger terrane (Blodgett and Clough, 1985). Decker et al. (in press) have recognized that these "terranes" are genetically related to one another, and proposed the term "Farewell Terrane" to unite them and other genetically related "terranes" as a single tectonic entity. On the basis of regional lithofacies trends and the paleobiogeographic affinities of its contained faunas, the Nixon Fork "terrane" and its related "terranes" were considered by Blodgett and Clough (1985) to form a continental margin sequence which was connected to the northeast with the Paleozoic North America continent.

AGE, PALEOECOLOGY, AND PALEOBIOGEOGRAPHY

Age.--There is little independant biostratigraphic control of the collection, but the age indicated by the trilobites is unequivocally late Llandovery (Telychian). A cheirurine cranidium in the sample belongs either to Radiurus Ramsöld, 1983, or Protocerauroides Chatterton and Perry, 1984. Both genera are restricted to the Telychian in all confirmed occurrences worldwide. Ramsköld (1983, p. 190-191, Pl. 23, fig. 1) discussed an illustrated an exfoliated, fragmentary, pygidium that he assigned to Radiurus. The specimen was from museum collections and "stated to be from Klinteberg, Klinteberg Beds", which are upper Wenlock. If the identification and provenance are correct, this single specimen would be the only non-Telychian Radiurus. Lane (1972, Pl. 63, fig. 7) illustrated a cranidium assigned by Chatterton and Perry (1984) to Protocerauroides. Lane (1972) described his collection as Wenlock, but Scrutton (1975) and Perry and Chatterton (1977) gave reasons for considering some, if not all, of it to be Telychian.

Calymene s.l. hoholitnensis n.sp. belongs to a species group (centered on C. s.l. frontosa Lindström, 1885) that, although ranging into the Sheinwoodian, is largely Telychian. Furthermore, it is very similar to, and interpreted as the sister species of, Calymene s.l. iladon Lane and Siveter, 1991, a form occurring in the Telychian of North Greenland. Bumastine material occurring in Greenland with C. s.l. iladon cannot be distinguished from Paracybantyx occidentalis n. sp., and is assigned to our new species below. Finally, a species of Scotoharpes occurring in the Alaskan fauna has its closest comparison with material from the Telychian of the Yukon Territory.

Paleoecology.--The trilobites occur in a pure white limestone of the type discussed by Lane (1972). As is typical of such assemblages, the collection is numerically dominated by remains of a single species, in this case the bumastine Paracybantyx occidentalis n. sp. which is represented by dozens of sclerites. Precise numerical abundance counts have not been made, due to both the paucity of material available and the fact that the rock is most likely to split and fragment along paths determined by the smooth bumastine cranidia and pygidia, thus obscuring the true relative abundances. Nevertheless, an approximate estimate of the makeup of the fauna is: more than 80 percent P. occidentalis; 10 percent Calymene s.l. hoholitnensis n. sp.; 5 percent Ligiscus smithi n. sp.; and less than five percent the remainder (Scotoharpes aff. raaschi Norford, 1973, is known from less than ten specimens, the remaining species from one specimen each). The fact that three separate species are known from single sclerites indicates that the total trilobite diversity of the fauna has probably yet to be sampled.

Paleobiogeography.--With the exception of a single small

Scharyia pygidium, all of the taxa described below are either conspecific with, or have their closest comparison with, species occurring in platform carbonates of the upper Llandovery of the Yukon Territory or the upper Llandovery or possibly lower Wenlock of North Greenland. Hence, the affinity of the fauna is firmly northern Laurentian. Telychian trilobites are known from northwestern Canada (e.g. Chatterton and Perry, 1983, 1984; Ludvigsen and Tripp, 1990), but faunas described thus far are for the most part deep water, shelf margin associations, representing markedly different biofacies, and with little in common with the Alaskan fauna. An exception is a small fauna from the Illtyd Range, Yukon Territory (Norford, 1973; Ludvigsen and Tripp, 1990), which occurs in unnamed white crystalline limestones of a carbonate bank to the south of the Richardson Trough, and shows generic affinity with both the Alaskan fauna and contemporaneous associations from North Greenland (e.g. Lane, 1979). Wenlock trilobite faunas of unparalleled number and diversity occur in the central Canadian arctic (Adrain, in press). Llandovery trilobites, however, are all but unknown in that region.

SYSTEMATIC PALEONTOLOGY

Family STYGINIDAE Vogdes, 1890

Discussion.--Lane and Thomas (1983, p. 157) dismissed various previous attempts to subdivide the styginid group, considered that there were "as yet no demonstrable phyletic lines of development", and classified all genera in an undivided family Styginidae. Ludvigsen and Tripp (1990, p. 8) returned to the traditional subfamilial groupings of Stygininae, Scutelluinae, and Bumastinae "as an aid to grouping the large number of genera in the family." The family is clearly in need of comprehensive phylogenetic analysis. We do not follow Ludvigsen and Tripp's concept of styginid subfamilies as taxa of convenience. In our opinion, however, the derived scutelluine and bumastine groups may very likely prove to be monophyletic. On this basis, and recognizing the need for much further work, we employ the subfamilial taxa as phylogenetic entities.

Subfamily SCUTELLUINAE Richter and Richter, 1955

Genus LIGISCUS Lane and Owens, 1982

Type species.--Ligiscus arcanus Lane and Owens, 1982, probably late Llandovery, Washington Land, western North Greenland.

Discussion.--Lane and Thomas (1983) regarded "effaced scutelluids" as a polyphyletic group encompassing taxa derived through iterative evolution in the Ordovician and Silurian. Very little actual morphological evidence has been marshalled in support of this view, with the exception of the observation (Lane and Thomas, 1978, p. 356) that the genus Rhax Lane and Thomas, 1978, represented a "morphological intermediate" between Bumastus and "typical scutelluids". As noted above, we consider both bumastines and scutelluines likely to prove monophyletic. Ligiscus would appear to belong to a distinct effaced group within the scutelluines, characterized particularly by the possession of a highly convex, only moderately effaced, pygidium with a distinct axis and eight radiating pairs of ribs. Ordovician members include Alceste Hawle and Corda, 1847, Cekovia Šnajdr, 1956, and Lamproscutellum Yin, 1980 (see Hammann, 1992, for good examples of all). Once the phylogenetic structure of the family is better understood, this group may warrant subfamilial status.

LIGISCUS SMITHI n. sp.

Figures VII-2.1, VII-2.2, VII-2.4 to VII-2.15,
VII-3.13, VII-3.15, VII-3.16

Diagnosis.--Ligiscus with very subdued cranidial median keel; anterior cranidial margin with moderate anterior convexity; cranidial axial furrows very widely divergent anteriorly; cranidial sculpture nearly smooth dorsally, with fine, subparallel terrace lines restricted to anterior part of glabella; median occipital node of cranidium very small and subdued; pygidial furrows deeply impressed (for genus).

Description.--Cranidium with length (sag.) 87 percent of width across midlength of palpebral lobes; axial furrows subparallel opposite palpebral lobes, but diverging slightly backwards and prominently forwards; minimum width of glabella opposite palpebral lobes 45 percent maximum width at anterior margin and 81 percent width at posterior margin;

furrows curve anteriorly to run transversely, and nearly posteriorly at contact with anterior section of facial suture; cranidium with strong dorsal convexity; palpebral lobe large and long, grading into interocular fixigena with no change in slope or sculpture; dorsal part of cranidium with sculpture of very fine pits and very subdued scrobiculate lines, grading anteriorly into fine terrace lines set subparallel to anterior margin and growing more robust nearer to margin; occipital furrow faint in small specimen, almost wholly effaced in holotype; very small and subdued occipital node set at about one half length (sag.) of occipital ring; lunette poorly defined as medial and lateral expansion of axial furrow directly opposite posterior two thirds of palpebral lobes.

Librigena with large eye, inclined forward at about 30 degrees; lateral border furrow shallow but distinct, more well-impressed posteriorly; lateral border rounded and rim-like; genal spine short, broad (tr.), and subtriangular; several subdued terrace lines extending from posterior part of field between posterior margin and lateral border furrow onto dorsal flattened aspect of genal spine.

Hypostome poorly known; anterior margin flaring ventrally from large, moderately inflated middle body; lateral border furrow narrow (tr.) and shallow; macula prominent; middle body with sculpture of robust, subparallel, posteriorly convex terrace lines.

Thorax with dorsal convexity similar to that of cranidium; axial lobe about 40 percent of width (tr.); axial ring of a given segment smooth, bowed faintly forward medially, with length (sag.) even across width and less than 20 percent of width; axial furrow shallow and pleural furrow effaced; fulcrum set at slightly more than half width (tr.) of pleura; anterior part of pleura distal to fulcrum forming articulating facet; posterior pleural band behind facet with fine, posteriorly convex, terrace lines.

Pygidium with length (sag.) 67 percent maximum width; axis with short (sag.; exsag.) articulating half-ring, one effaced segment, and triangular terminal piece; terminal piece with faint median node set posteriorly; axis about 25 percent width of pygidium anteriorly; axial furrow shallow but fully defined posteriorly in small specimens, completely effaced in larger specimens; pygidium with eight segments; first pleural furrow deep, remaining ones shallower but not diminishing in depth posteriorly; pleural furrows more deeply impressed distally, shallowing near axis; border narrow but complete; dorsal sculpture smooth, except for sparse, very fine terrace lines near to and subparallel with margin; doublure broad, scalloped to reflect segmentation, and with many well impressed, subparallel terrace lines generally parallelling course of posterior margin, but anteriorly convex across a single given segment.

Discussion.--Ligiscus smithi n. sp. differs from the type species, L. arcanus, in its less prominent cranidial median keel, more transverse and gently arced anterior cranidial margin, more widely anteriorly divergent axial furrows, more subtly impressed prosopon of transverse terrace lines on the upper part of the glabella, and much more deeply impressed pygidial pleural furrows. The median glabellar tubercle is also apparently less prominent, although most of the Greenland material is exfoliated in this area, so that the size of the tubercle is exaggerated on the internal mold. However, a cuticular specimen illustrated by Lane and Owens (1982, Pl. 3, fig. 7) is only slightly smaller than the holotype of L. occidentalis, and does appear to show a much more prominent tubercle.

Material.--Holotype cranidium and thoracic segment USNM 476680; paratypes USNM 476682-476687, 476700-476702, 476727.

Etymology.--For Thomas N. Smith, State of Alaska, Department of Natural Resources, Division of Oil and Gas, Anchorage, Alaska, who collected the trilobites described herein.

Subfamily BUMASTINAE Raymond, 1916

Genus PARACYBANTYX Ludvigsen and Tripp, 1990

Type species.--Paracybantyx asulcatus Ludvigsen and Tripp, 1990, Ludlow, Road River Formation, Prongs Creek, northern Yukon Territory.

Discussion.--Generic concepts in the Bumastinae are for the most part poorly defined and difficult to apply. As noted above, no attempt is made herein to propose phylogenetic structure, but the rationale for the generic placement of the Alaskan species must be outlined.

Lane and Thomas (in Thomas, 1978, p. 18) diagnosed their new genus <u>Cybantyx</u> on the basis of, among other things, a distinct anterior border and border furrow on the cranidium and a large anterior pit with a median granule. Their diagnosis was directed toward separating the taxon from <u>Bumastus</u> Murchison, 1839. <u>Bumastus</u> does appear to entirely lack an anterior border furrow, but among other bumastines the feature seems often to be present, its prominence in <u>Cybantyx</u> a matter of degree. Similarly, a median granule in the anterior border is apparently a general bumastine feature. The anterior pit is minute in <u>Bumastus</u>, and this could account for the apparent or genuine absence of the granule in the type species, <u>B</u>. <u>barriensis</u> Murchison, 1839. The species <u>B</u>.? <u>phrix</u> Lane and Thomas in Thomas, 1978 does appear to show a very small granule (Thomas, 1978, Pl. 3, fig. 1d).

Most of the criteria listed in the diagnosis of the monotypic <u>Paracybantyx</u> (Ludvigsen and Tripp, 1990, p. 8) are applicable to virtually all bumastines (e.g. axial furrow bowed inward, pygidium effaced, surface finely pitted). The only character that is not general for Bumastinae is the absence of an anterior border and furrow, by which the genus was said to differ from <u>Cybantyx</u>. <u>Paracybantyx</u> <u>asulcatus</u>, however, has a very short but distinct border and furrow visible on all illustrated cranidia (e.g. Ludvigsen and Tripp, 1990, Pl. 1, figs. 3, 8, 9). Hence, on these grounds alone, Paracybantyx should probably be considered a junior subjective synonym of Cybantyx. There is a further morphological feature, however, that appears to define an exclusively northern Laurentian monophyletic group of bumastines, for which the name Paracybantyx should probably be retained.

Virtually all bumastines for which information is available (including, e.g. Bumastus barriensis, B.? phrix Lane and Thomas in Thomas, 1978, B.? xestos Lane and Thomas in Thomas, 1978, and Cybantyx anaglyptos Lane and Thomas in Thomas, 1978) have a rostral plate with a posteromedially convex lobe which is produced into a dorsally reentrant flange, along the posterior edge of which the hypostomal suture runs (see especially Lane and Thomas in Thomas, 1978, Pl. 2, figs. 1b and 1c). We are aware of many undescribed bumastines from the Wenlock and Ludlow of northern and arctic Canada. All of them, together with the species described herein, have a rostral plate lacking this posterior lobe and dorsal flange. Rather, at the posteromedian part of the posterior margin, they have a forwardly convex embayment (VII-Figure 3.4). The hypostomal suture runs along the posterior margin of the main body of the rostral plate and the forward parts of the librigenal doublure, as opposed to along a dorsally recurved flange as in other bumastines. In undescribed silicified material from northern Canada, the hypostome has often developed a tab-like anteromedian projection which presumably articulated with the posteromedian embayment of the rostral plate.

It seems very likely that this hypstome attachment condition is derived within bumastines, defining a northern Laurentian clade to which the new Alaskan species belongs. A major problem with applying the name *Paracybantyx* to this group is that the rostral plate of *P. asulcatus* Ludvigsen and Tripp, 1990, is unknown. However, as noted above, every single Wenlock-Ludlow northern Laurentian bumastine of which we have knowledge has this derived condition. *Paracybantyx asculcatus* occurs in an assemblage whose generic composition is typical of contemporaneous faunas we have collected from arctic Canada. Bumastines in these faunas resemble *P. asulcatus* in virtually all respects. Hence, while the rostral plate of *P. asulcatus* will have to be found to settle the issue decisively, it seems very likely that it will prove to be of the derived condition. On this basis, and pending eventual confirmation, we refer our new species to *Paracybantyx*.

PARACYBANTYX OCCIDENTALIS n. sp.

Figures VII-3.1 to VII-3.12, VII-3.14, VII-4.1 to VII-4.12

Bumastus sp. LANE AND SIVETER, 1991, p. 5, fig. 2e.

Meitanillaenus sp. LANE AND SIVETER, 1991, p. 7, figs. 2f, g.

Diagnosis.--Weak sagittal carina visible mainly on internal molds; anterior pit with small central tubercle; rostral plate lacking posteromedian flange, with narrow (tr.) posteriorly concave area at posteromedial margin; pygidium with sagittal length about 80 percent of maximum width.

Discussion.--Paracybantyx occidentalis is similar enough to the type species that description can be accomplished through a differential diagnosis, in lieu of extended written description.

Paracybantyx occidentalis n. sp. differs from P. asulcatus Ludvigsen and Tripp, 1990, in the following ways: cranidium with length (sag.) 84 percent of width across palpebral lobes as opposed to 94 percent (measured from Ludvigsen and Tripp, 1990, Pl. 1); anterior margin more strongly anteriorly convex; axial furrows less strongly impressed anteriorly; anterior pit less prominent and with smaller median tubercle; anterior node of similar size but set slightly closer to margin; anterior border and border furrow much stronger; occipital node of similar size but set further forward; librigena with larger eye, no depressed area around eye, stronger lateral border and border furrow, field that is narrower (trans.) relative to length, and genal angle that is smoothly curved as opposed to protruded into short genal spine; hypostome with smaller middle body bearing fewer terrace lines, and more prominent lateral and posterior borders bearing two irregular terrace lines; pygidium shorter (sag.) relative to maximum width (about 80 percent versus about 90 percent), lacking median keel, even on effaced specimens, and with more subtly impressed, less rim-like border.

Lane and Siveter (1991, p. 7) placed the genera *Failleana* Chatterton and Ludvigsen, 1976, and *Opsypharus* Howells, 1982, in junior subjective synonymy of *Meitanillaenus* Chang, 1974. This action was taken without comment, and its basis is therefore unclear. Howells (1982, p. 11) gave a differential diagnosis between *Opsypharus* and *Failleana*. The type species *Meitanillaenus binodosus* Chang, 1974, is known from a small number of poorly preserved internal molds. The type species of *Opsypharus*, *O. maccallumi* (Salter, 1867), is also known almost exclusively from internal molds, although somewhat better preserved and more thoroughly illustrated. The type species of *Failleana*, *F. calva* Chatterton and Ludvigsen, 1976, is represented by well preserved silicified material. While it is not inconceivable that Lane and Siveter's synonymy could prove correct, meaningful comparison among the type species is at present scarcely possible, and *M. binodosus*, upon which the synonymy depends, is so poorly known that it is all but impossible to evaluate. Until such time as that species becomes better understood, the most profitable course of action seems to be to restrict Meitanillaenus to its type.

In any case, Lane and Siveter (1991, p. 5, fig. 2e) referred a fragmentary bumastine cranidium in their collection to Bumastus, and thoracic segments and pygidia (Lane and Siveter, 1991, figs. 2f, 2g) to Meitanillaenus. Assignment of the cranidium was based upon "the characteristic broadly oval, exsagittally elongate 1g glabellar muscle impression placed at about 150 % of its own length from the posterior cranidial border shown by species of the genus (Lane and Thomas, 1978, pl. 1, fig. 5)". In fact, 1G (numbered following Bruton, 1968; see Lane and Thomas, 1983, text-figs. 1, 2) is not preserved on the specimen figured, and the feature referred to is apparently the lunette. The morphology and placement of neither 1G nor the lunette were mentioned in Lane and Thomas's (in Thomas, 1978, p. 11) diagnosis of Bumastus. In B. barriensis, to which Lane and Siveter made reference, 1G is broad and subquadrate, and is confluent with an even larger occipital muscle impression (Lane and Thomas, 1983, text-fig. 2a). All three bumastine specimens illustrated by Lane and Siveter are indistinguishable from similar, comparably sized Alaskan specimens of Paracybantyx. We consider that the material represents a single species that is conspecific with the Alaskan material. Hence, it is assigned to Paracybantyx occidentalis herein.

Material.--Holotype cranidium USNM 476706; paratypes USNM

476688-476699, 476703-476705.

Etymology.--Latin *occidentalis*, western.

indeterminate bumastine

Figure VII-2.3

Discussion.--A single bumastine librigena in our collections differs from those of *Paracybantyx occidentalis* in its smaller, more inclined, eye, and field with considerably greater width (tr.) relative to length (exsag.). The morphology of the librigenae assigned to *P. occidentalis* is very stable (Figure VII-3.10 to VII-3.12) over a large sample size. Hence, the specimen illustrated in Figure VII-2.3 likely represents a second, very rare, bumastine. No other sclerites that could be associated with it were found.

Material.--Illustrated specimen USNM 476681.

Family CALYMENIDAE Milne Edwards, 1840

Subfamily CALYMENINAE Milne Edwards, 1840

Genus CALYMENE Brongniart in Brongniart and Desmarest, 1822

Type species.--*Calymene blumenbachii* Brongniart in Desmarest, 1817.

CALYMENE s.l. HOHOLITNENSIS n. sp.

Figure VII-5.1 to VII-5.14

Diagnosis.--*Calymene* s.l. with eyes set forward, anteriormost part of palpebral lobe opposite middle of L3; glabella nearly parallel sided, belling only slightly across L1; cephalic sculpture of relatively dense coarse tubercles with minor finer tubercles everywhere except palpebral lobes, posterior border, and librigenal border roll, where sculpture is of very fine, close-set, granular tubercles; hypostome with maculae very subdued and rhynchos set approximately half way (sag.) between anterior margin and shallow middle furrow.

Discussion.--Calymene s.l. hoholitnensis n. sp. is so similar to C. s.l. iladon Lane and Siveter, 1991, that the need for a extensive written description is obviated by the comparative discussion below.

Similarities include the anteriorly set eyes, transversely arched anterior border, only slightly bell shaped glabella, relatively coarse prosopon, steeply sloping (tr.) posterolateral fixigena, posterior border furrow evenly short (exsag.), librigena with laterally convex margin, and hypostome with extremely reduced maculae. Nevertheless, there do appear to be substantive differences. Although Calymene s.l. hoholitnensis is represented by only a single relatively intact cranidium (and a second fragmentary one), the style of preservation is closely similar to that of C. iladon. Material of neither species has suffered any significant distortion, and specific differentia can be recognized with confidence. Calymene hohlitnensis n. sp. differs from C. iladon in the following: eyes set less anteriorly, with the anterior extent of the palpebral lobe opposite the midlength of L3 as opposed to opposite S3; glabella narrower, and L1 relatively smaller, so that glabella is even less bell shaped; anterior border less inflated, and with a less regular dorsal convexity in anterior profile; librigenal field sculpture slightly more robust; and hypostome with rhynchos set considerably more posteriorly (cf. Figure VII-5.9 with Lane and Siveter, Pl. 1, fig. 3).

Both species form a morphologically close-knit group with species such as _Calymene_ s.l. _frontosa_ Lindström, 1885. These species differ in substantive ways from the group centered around the type species. The _frontosa_ group's relationship to _Calymene_ s.s. is ambiguous, as is its monophyly. We refer these species at present to _Calymene_ s.l.

Material.--Holotype cranidium USNM 476707; paratypes USNM 476708-476713.

Etymology.--After the Hoholitna River, near which the type locality is situated.

Family CHEIRURIDAE Hawle and Corda, 1847

Subfamily CHEIRURINAE Hawle and Corda, 1847

indeterminate cheirurine

Figure VII-5.16

Discussion.--There are two possibilities for generic assignment of this small, fragmentary specimen. Ramsköld (1983) diagnosed his new _Radiurus_ on the basis of both a medially complete anterior border and preglabellar furrow and a distinctive pygidial spine arrangement. The former of these features is not preserved on the small cranidium recovered from the Alaskan fauna, but the specimen closely resembles R. avalanchensis Chatterton and Perry, 1984, in its narrow, elongate glabella and small, subtriangular L1. On the other hand, although not fully preserved, S3 seems complete medially in the Alaskan specimen. If this is the case, the specimen should likely be assigned to Protocerauroides Chatterton and Perry, 1984.

Material.--Illustrated specimen USNM 476715.

Family SCHARYIIDAE Osmólska, 1957

Genus SCHARYIA Pribyl, 1946

Type species.--Proetus micropygus Hawle and Corda, 1847,

SCHARYIA sp.

Figure VII-5.15

Discussion.--A single small Scharyia pygidium is seemingly unique among known species in the manner in which the posterior pleural bands are swollen distally into lobate marginal spines. In most Silurian species, the pleural and interpleural furrows terminate at a well defined border. Many species, however, have prominent tubercles on the border in the position of the spines in the Alaskan species (e.g. S. nympha Chlupac, 1971, S. coronoa Šnajdr, 1980). Scharyia brevispinosa Pribyl, 1967, from the Emsian of Bohemia (see Šnajdr, 1980, Pl. 31, figs. 20-22) combines these features, as it possesses both a prominent tubercle and a small, pointed marginal spine at the distal extremity of each segment. A Scharyia pygidium from the Telychian of northeastern Greenland (Lane, 1972, Pl. 61, fig. 11) has a complete border and is not very similar to the Alaskan specimen, but does have very low swellings at the distal parts of the posterior pleural bands.

Material.--Illustrated specimen USNM 476714.

Family PROETIDAE Salter, 1864

Subfamily WARBURGELLINAE Owens, 1973

indeterminate warburgelline

FIGURE VII-6.10 to VII-6.13

Discussion.--A single warburgelline cranidium is most similar to material from the Telychian of northeastern Greenland described as Warburgella sp. by Lane (1972, Pl. 61, figs. 5, 8, 9, 10). The species share a broad depression behind the anterior and (presumably, since the librigena of the Alaskan species is unknown) lateral border furrows, bounded adaxially by a well expressed tropidial ridge or ridges, a median furrow extending the length of the preglabellar field and connecting with the anterior border furrow, anteriorly divergent anterior sections of the facial suture, glabella with a forwardly convex aligned scrobiculate sculptue, and S1 which is very shallow anteriorly, so that it does not connect with the axial furrow. This combination of features serves to distinguish the two species from other warburgellines, and eventually they should probably be assigned to a new genus. At present, however, neither species is well enough known to name. The Alaskan species differs from the Greenland species in its narrower depression behind the anterior border furrow, possession of intercalating and discontinuous tropidial ridges as opposed to a single, continuous tropidium, more widely divergent anterior sections of facial suture, and longer glabella with more subdued scrobiculate sculpture.

Material.--Illustrated specimen USNM 476720.

Family HARPIDAE Hawle and Corda, 1847

Genus SCOTOHARPES Lamont, 1948

Type species.--*Scotoharpes domina* Lamont, 1948, upper Llandovery, Whether Law Linn Formation, North Esk Inlier, Scotland.

SCOTOHARPES aff. S. RAASCHI Norford, 1973

Figure VII-6.1 to VII-6.9

Discussion.--The Alaskan species resembles material from northwestern Greenland described by Norford (1973) as *Scotoharpes loma* (Lane, 1972), and also *S. raaschi* Norford, 1973, both of which are of a similar Telychian age.

The material assigned to *Scotoharpes loma* by Norford (1973) seems doubtfully conspecific with Lane's (1972, Pl. 62) northeastern Greenland type material, differing particularly in the possession of a longer preglabellar field lacking the distinctive elongate sagittal swelling, a cephalic brim that is only slightly, as opposed to considerably, broader anteriorly than laterally, and a glabella with axial furrows subparallel as opposed to slightly anteriorly convergent. It is likely that Norford's material should be referred to a separate, new, species.

The Alaskan material differs from both of the North Greenland species in its shorter, more convex, glabella with axial furrows moderately anteriorly convergent. In these features it is very similar to _S_. _raaschi_ Norford, 1973, from unnamed carbonates of the Illtyd Range, Yukon Territory. _Scotoharpes_ _raaschi_ is known from only two specimens, the holotype cephalon and a cephalon illustrated by Ludvigsen and Tripp (1990; Ludvigsen and Tripp listed two cephala, but their Pl. 9, fig. 2 is obviously a latex cast from the counterpart external mold of the exfoliated specimen illustrated in their Pl. 9, figs. 1 and 3). The Alaskan species differs from _S_. _raaschi_ in its apparently shorter preglabellar field and relatively narrower (sag., trans.) brim.

Formal naming of the Alaskan species must await more complete material, as the only relatively complete cephalon known (Fig. VII-6.1, VII-6.2, VII-6.4, VII-6.6) is quite small.

Material.--Illustrated specimens USNM 476716-476719.

Class MACHAERIDIA Withers, 1926

Terminology.--Morphological terms are employed as defined by Adrain et al. (1991) and Adrain (1992).

Family TURRILEPADIDAE Clarke, 1896

Genus TURRILEPAS Woodward, 1865

Type species.--Chiton wrightiana de Koninck, 1857, from the Much Wenlock Limestone Formation of Dudley, England.

TURRILEPAS n. sp. A

Figure VII-7.1, VII-7.2, VII-7.4 to VII-7.6

Discussion.--Adrain et al. (1991) restricted Turrilepas to its type species and their new T. modzalevskae. The Alaskan species is hence the oldest known and only Llandovery member of the genus, but so little is known of machaeridians that this may simply reflect lack of study. With only a few sclerites on hand, full comparisons with other species are impossible, but Turrilepas n. sp. A differs from both T. wrightiana and T. modzalevskae in the following ways: rugae slightly less robust and much more closely spaced; I_1L shallower and more obtuse; I_2L set nearly on longitudinal angle and much weaker.

Material.--Illustrated specimens USNM 476721, 476722.

Family PLUMULITIDAE Jell, 1979

Genus COMPACOLEUS Schallreuter, 1985

Type species.--Plumulites compar Barrande, 1872, from the Llanvirn of Bohemia.

COMPACOLEUS sp.

Figure VII-7.7, VII-7.8?

Discussion.----The genus Compacoleus is presently under revision by one of us (J.M.A.) and will be dealt with in detail elsewhere. Schallreuter (1985, p. 166) diagnosed the taxon on the basis of a single feature, the asymmetrical rugae of the outer sclerites. Work in progress has shown that not all species which should be assigned to the genus possess this feature, but it is well displayed by the Alaskan specimen, in which the rugae on the posterior portion of the sclerite are nearly twice as closely spaced as those on the anterior portion (Figure VII-7.7). The inner sclerites of the type species are unknown. A single inner left plumulitid sclerite in our collection (Figure VII-7.8) may or may not be conspecific with the outer sclerite. If it is, it shows that the asymmetry is restricted to the outer sclerites, as the rugae of the inner sclerite are complete and continuous across the entire sclerite width.

Material.--Illustrated specimens USNM 476725, 476726.

Family LEPIDOCOLEIDAE Clarke, 1896

Genus LEPIDOCOLEUS Faber, 1886

Type species.--Plumulites jamesi Hall and Whitfield, 1875, from the Upper Ordovician of Cincinatti, Ohio.

LEPIDOCOLEUS cf. L. BRITANNICUS Withers, 1926

Figure VII-7.3

Discussion.--Among the many species in the very broadly defined Lepidocoleus, a single right series sclerite from Alaska most closely resembles the slightly younger L.

britannicus in its considerable height vs. width and large number of closely set rugae.

Material.--Illustrated specimen USNM 476724.

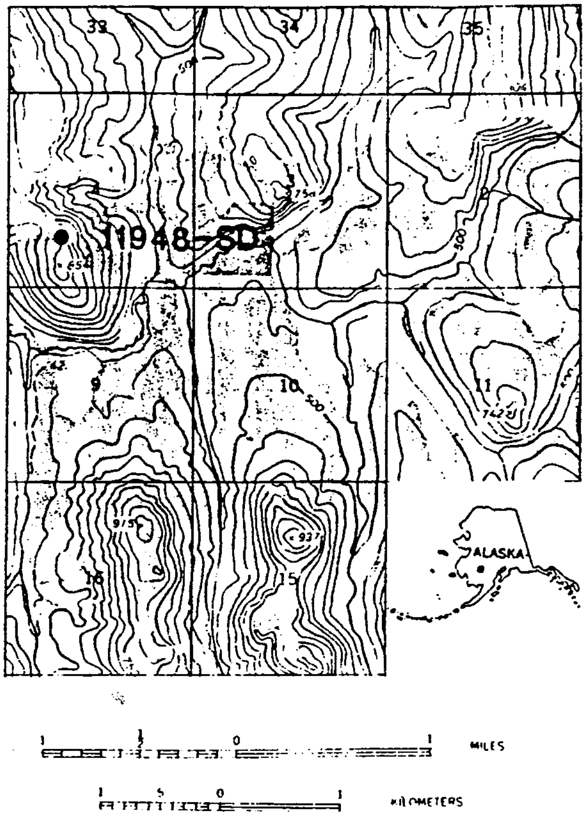
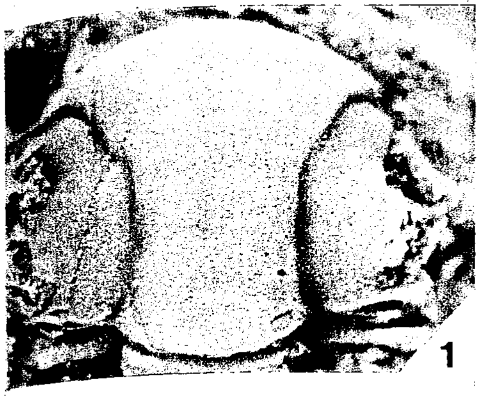


FIGURE VII-1--Index map showing location of USGS locality 11948-SD in the Taylor Mountains D-2 quadrangle, southwestern Alaska.

FIGURE VII-2--1, 2, 4-15, *Ligiscus smithi* n. sp.; 1, 4, 7, holotype cranidium and thoracic segment USNM 476680, dorsal, right lateral, and anterior views, x10; 2, cranidium USNM 476727, oblique dorsolateral view, x10; 5, thoracic segments USNM 476682, dorsal view, x5; 6, left librigena USNM 476683, external view, x10; 8, 9, thoracic segments USNM 476684, dorsal and right lateral views, x5; 10, 13, pygidium USNM 476685, dorsal and posterodorsal views, x5; 11, 14, 15, pygidium USNM 476686, posterior, dorsal, and oblique dorsolateral views, x10; 12, hypostome USNM 476687, ventral view, x10. 3, indeterminate bumastine, right librigena USNM 476681, external view, latex cast, x7.5.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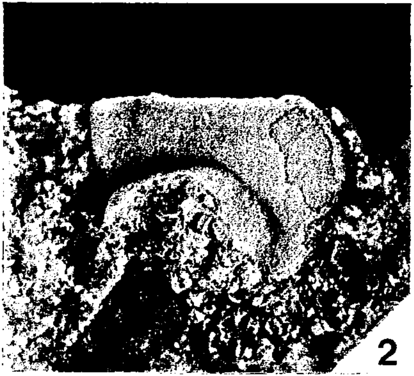
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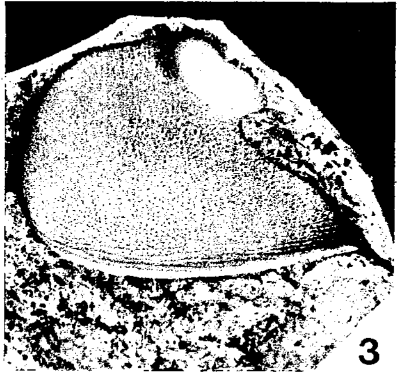
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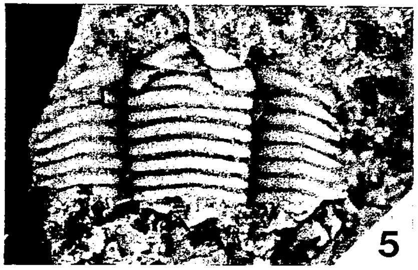
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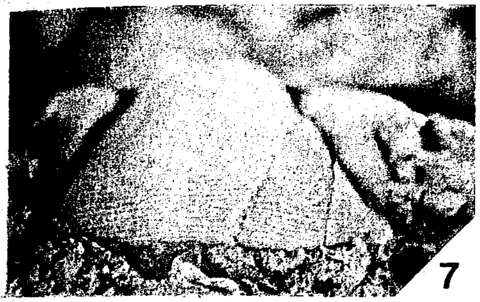
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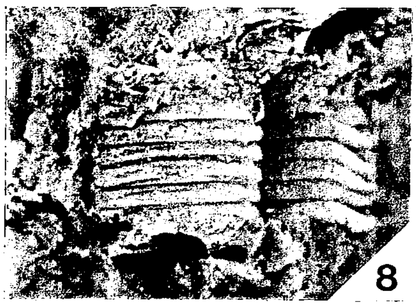
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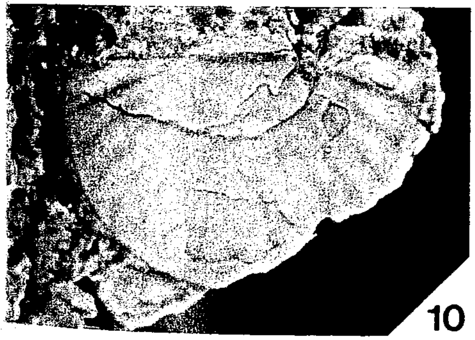
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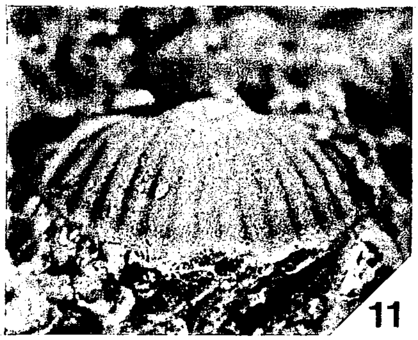
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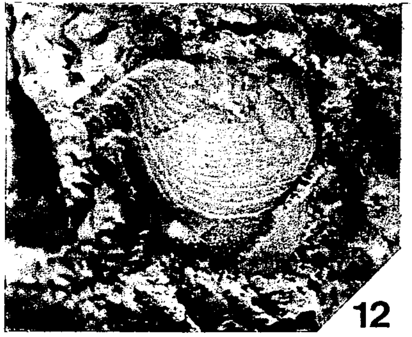
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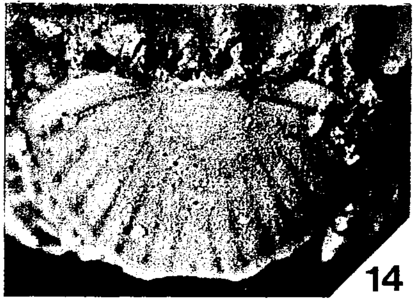
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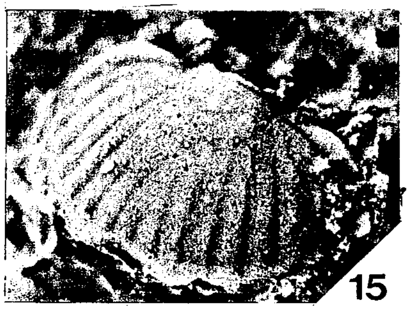
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FIGURE *VII-3*--*1*-*12*, *14*, *Paracybantyx occidentalis* n. sp.; *1*, hypostome USNM 476688, ventral view, x10; *2*, hypostome USNM 476689, ventral view, x10; *3*, hypostome USNM 476690, ventral view, x15; *4*, rostral plate USNM 476691, ventral view, x10; *5*, *6*, pygidium with attached thoracic segments USNM 476692, dorsal and left dorsolateral views, x4; *7*, pygidium USNM 476693, dorsal view, x5; *8*, pygidium USNM 476694, dorsal view, x5; *9*, pygidium USNM 476695, ventral view, latex cast (anterolateral parts missing), x5; *10*, right librigena USNM 476696, external view, latex cast, x7.5; *11*, left librigena USNM 476697, external view, x7.5; *12*, right librigena USNM 476698, external view, x10; *14*, left librigena USNM 476699, internal view, latex cast, x7.5; *13*, *15*, *16*, *Ligiscus smithi* n. sp.; *13*, pyidium USNM 476700, ventral view, x7.5; *15*, small pygidium with attached thoracic segments USNM 476701, dorsal view, latex cast, x10; *16*, pygidium USNM 476702, dorsal view, x5.


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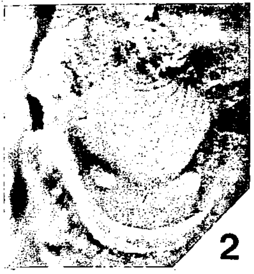
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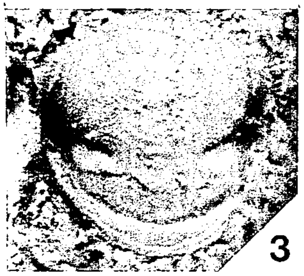
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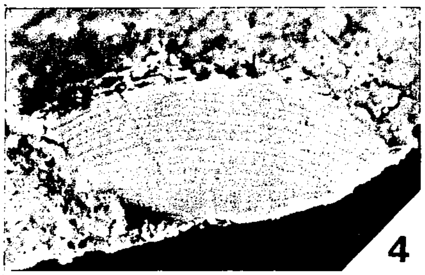
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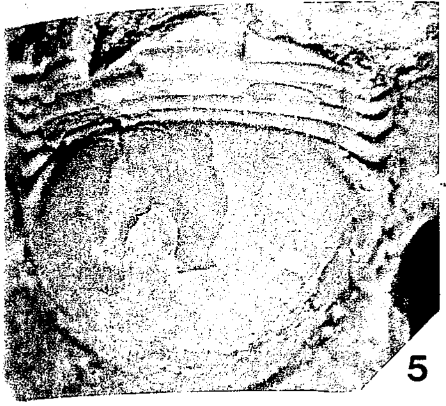
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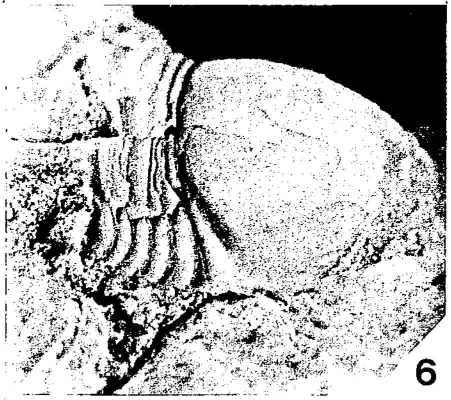
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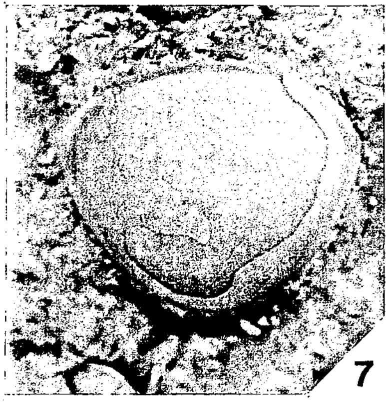
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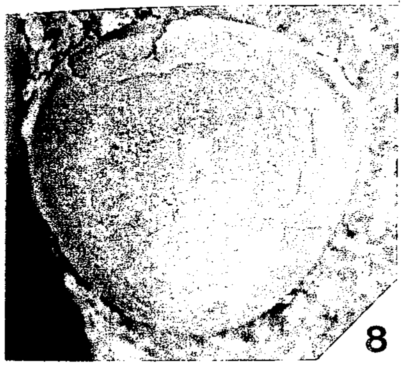
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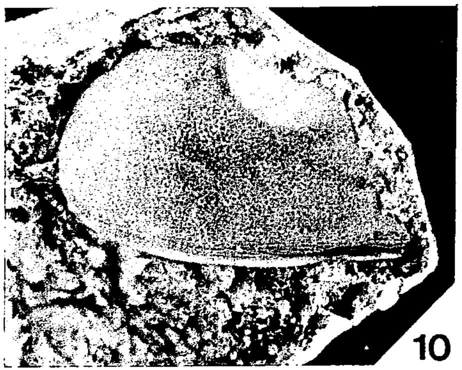
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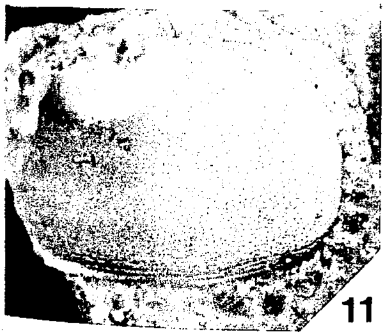
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FIGURE VII-4--Paracybantyx occidentalis n. sp.; 1-3, cephalon USNM 476703, dorsal, anterior, and left lateral views, x4; 4-6, mostly exfoliated cranidium USNM 476704, dorsal, oblique anterolateral, and left lateral views, x5; 7-9, 12, exfoliated cranidium USNM 476705, dorsal, anterodorsal, right lateral, and oblique dorsolateral views, x5; 10, 11, holotype cranidium and thoracic segment USNM 476706, dorsal and right lateral views, x7.5.

FIGURE *VII-5*--*1*-*14*, *Calymene* s.l. *hoholitnensis* n. sp.; *1*-*4*, holotype cranidium USNM 476707, dorsal, left lateral, anterior, and oblique dorsolateral views, x4; *5*, *6*, cranidium USNM 476708, dorsal and oblique dorsolateral views, x3; *7*, right librigena USNM 476709, latex cast, external view, x7.5; *8*, left librigena USNM 476710, external view, x5; *9*, hypostome USNM 476711, ventral view, x10; *10*, pygidium USNM 476712, dorsal view, x10; *11*, *13*, *14*, pygidium, specimen lay atop holotype specimen USNM 476707, and was destroyed during preparation, no specimen number assigned, posterior, dorsal, and right lateral views, x5; *12*, hypostome USNM 476713, left lateral view, x10. *15*, *Scharyia* sp., pygidium USNM 476714, dorsal view, x20. *16*, *Radiurus* sp., cranidium USNM 476715, dorsal view, latex cast, x10.


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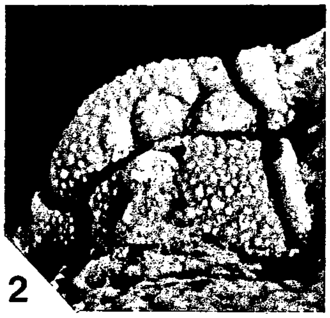
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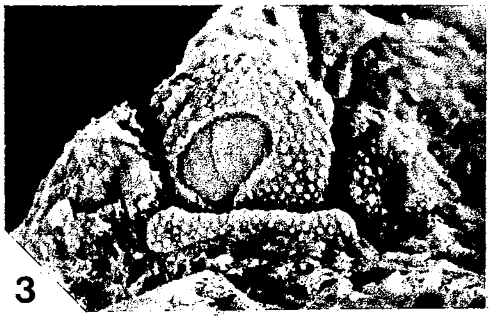
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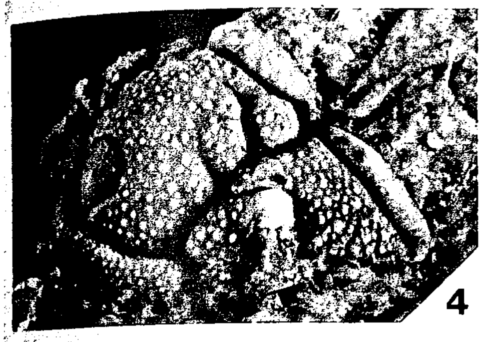
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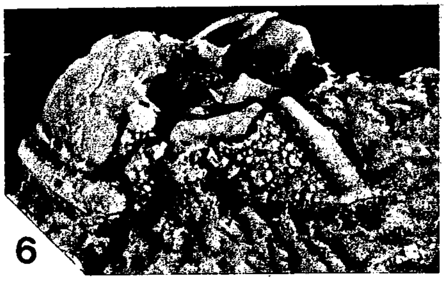
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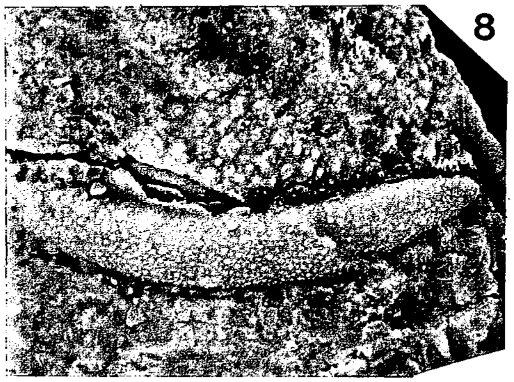
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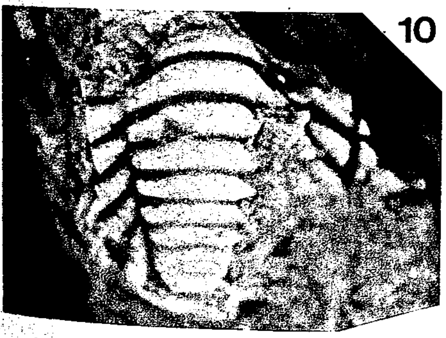
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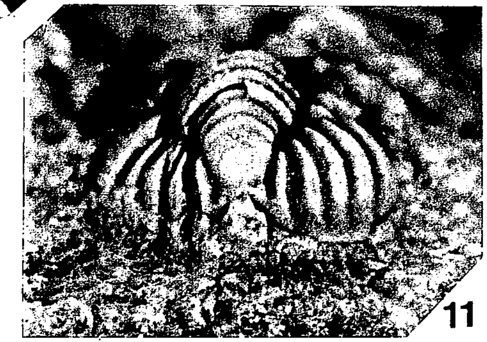
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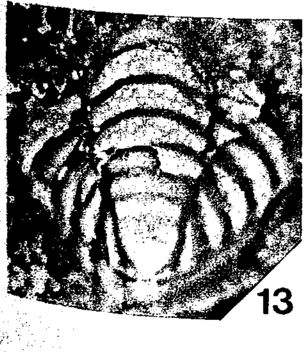
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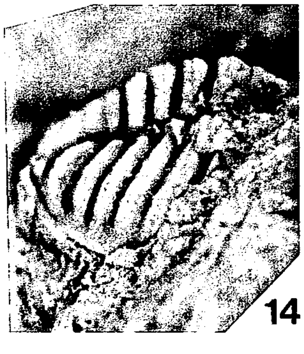
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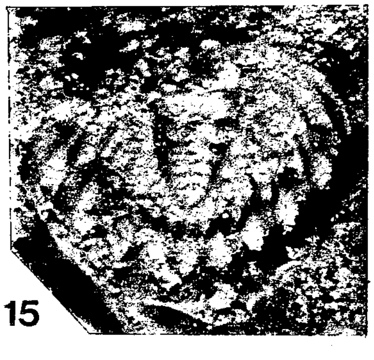
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FIGURE *VII-6*--*1*-*9*, *Scotoharpes* aff. *S*. *raaschi* (Norford, 1973); *1*, *2*, *4*, *6*, cephalon USNM 476716, dorsal, anterodorsal, oblique dorsolateral, and right lateral views, x7.5; *3*, *5*, exfoliated cephalon USNM 476717, dorsal and oblique dorsolateral views, x5; *7*, cephalon USNM 476718, dorsal view, latex cast, x5; *8*, *9*, thorax USNM 476719, dorsal and right lateral views, x7.5. *10*-*13*, warburgelline sp., cranidium USNM 476720, anterodorsal, dorsal, left lateral, and oblique dorsolateral views, x10.


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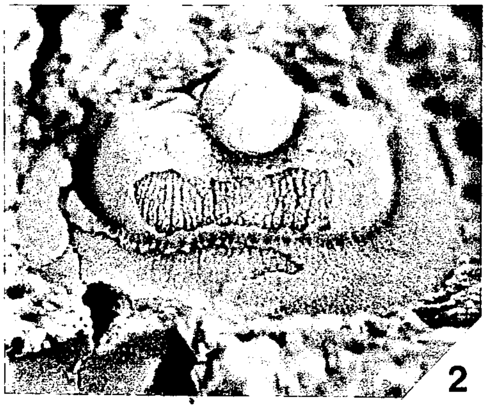
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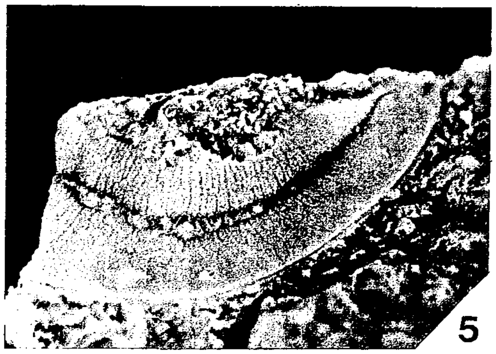
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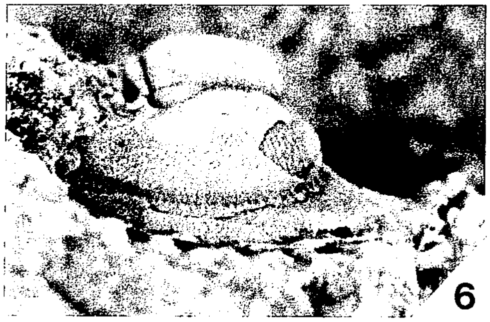
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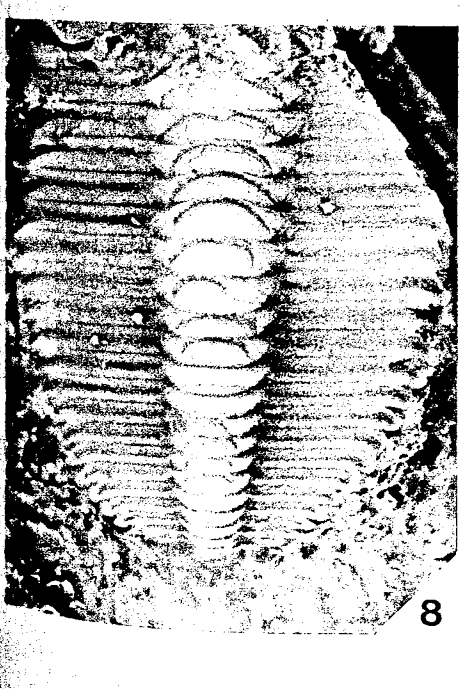
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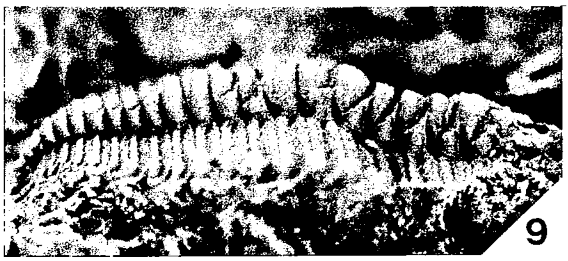
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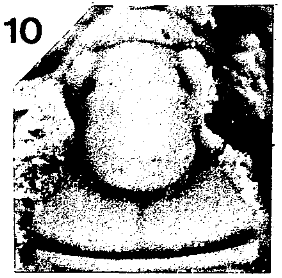
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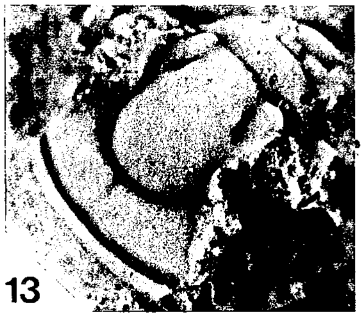
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FIGURE VII-7--1, 2, 4-6, *Turrilepas* sp.; 1, inner left sclerite USNM 476721, external view, latex cast, x10; 2, 5, 6, inner left sclerite USNM 476722, external, lateral, and dorsal views, x5; 4, outer right sclerite USNM 476723, external view, latex cast, x10. 3, *Lepidocoleus* cf. *L. britannicus* Withers, 1926, right sclerite USNM 476724, lateral view, x20. 7, 8, *Compacoleus* sp.; 7, outer right sclerite USNM 476725, ventral view, latex cast, x15; 8, inner left sclerite USNM 476726, dorsal view (anterior to right), latex cast, x10.


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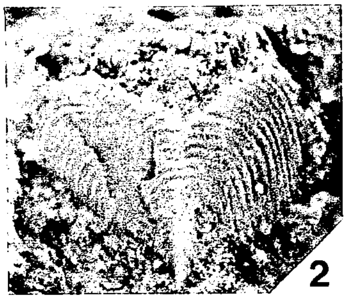
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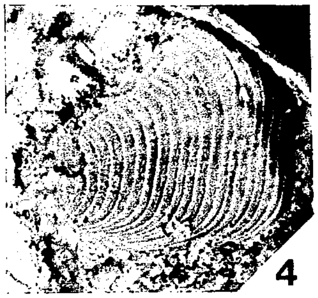
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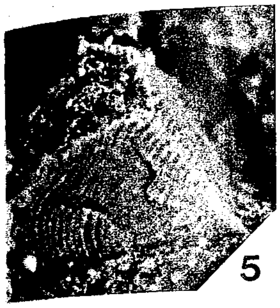
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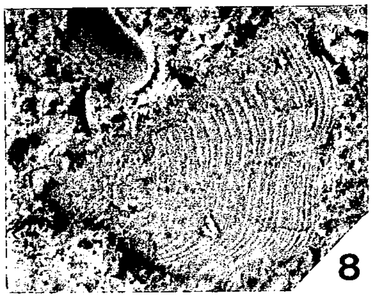
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CHAPTER VIII[1]

AEGROTOCATELLUS AND PERIREHAEDULUS: NEW GENERA OF ENCRINURID TRILOBITES FROM THE DOURO FORMATION (SILURIAN, LUDLOW) OF THE CENTRAL CANADIAN ARCTIC

INTRODUCTION

MODERATELY DIVERSE Ludlow trilobite faunas occur in platform carbonates of the Douro Formation through most of its outcrop in the central Canadian arctic. The present work initiates description (and redescription) of these faunas, based on material collected by J.M.A. from Goodsir Creek (eastern Cornwallis Island) and Garnier Bay (northern Somerset Island) in 1991, and from Prince Alfred Bay (northern Devon Island) in 1992. Species assigned to two new encrinurid genera are described. A new species of the encrinurid Mackenziurus Edgecombe and Chatterton, 1990a, occurs at Goodsir Creek, and will be described elsewhere.

HISTORY OF STUDY

The Silurian sequence at Goodsir Creek on Cornwallis Island was first studied by Thorsteinsson (1958), who reported the presence of the trilobites Encrinurus and Calymene in beds assigned to member A of the Read Bay Formation (Calymene, however, has not subsequently been found). The lower part of this member was assigned to the

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Cape Storm Formation by Kerr (1975). Thorsteinsson (1980) raised the Read Bay to group status, and assigned the remainder of member A to the Douro Formation. The species Frammia arctica (Salter, 1852), was reported from the Douro Formation at an undetermined locality somewhere on the eastern coast of Cornwallis Island. Bolton (1965, Pl. 3, fig. 10) figured associated lichid and encrinurid cranidia from Goodsir Creek as Hemiarges aquilonius Whittington, 1961 (a species which occurs in the upper member of the overlying Barlow Inlet Formation), and "Encrinurus approaching E. (Frammia)". Until the work of Thomas (in Thomas and Narbonne, 1979), these were the sole trilobites either from or possibly from Goodsir Creek to have been figured (see also Tripp et al., 1977). Thomas (in Thomas and Narbonne, 1979) described four new trilobite species, together with several left in open nomenclature. One of these species, Frammia hyperborea (Thomas in Thomas and Narbonne, 1979), has since been illustrated and discussed by Edgecombe and Chatterton (in press).

The specimens assigned to Encrinurus (Frammia) arcticus by Bolton (1965, Pl. 1, figs. 13, 14, Pl. 2, figs. 1, 2, 4) are the only trilobites previously figured from the region of Garnier Bay, northern Somerset Island. No trilobites have previously been figured from Ludlow rocks in the Prince Alfred Bay region, northern Devon Island.

LOCALITIES AND STRATIGRAPHY

The geographic position of the collecting localities is shown in Figure VIII-1. Despite the presence of distinct faunas in each area, with no species yet proven to be shared between them, all are apparently of late Ludlow (Ludfordian) age. Their precise correlation with each other is unknown.

Goodsir Creek.--Exact collecting localities in the area surrounding Goodsir Creek are shown in Figure VIII-2A. A stratigraphic column of the Douro Formation at Goodsir Creek has been given by Thomas and Narbonne (1979, Fig. 2). Two stratigraphically separate trilobite faunas are present, with no species shared. Thomas (in Thomas and Narbonne, 1979, p. 1, Fig. 1) recognized the stratigraphic grouping, but argued that the differences were due mainly to the presence of rare taxa. Nevertheless, only Helokybe spio Thomas in Thomas and Narbonne, 1979 was considered to occur in both assemblages, although most of the material (including the holotype) was from the upper assemblage. New collections have shown that the warburgelline trilobite from the lower assemblage belongs to a different, new, species. The two faunas are herein designated Faunas A and B, in ascending order.

Almost all collections were made from talus some distance down-slope from the outcrop. This is because slightly weathered rocks were found to contain far more obvious and abundant trilobites. Additionally, given the difficulty in preparation of Douro Formation trilobites, it was desirable to recover specimens as nearly weathered free of matrix as possible. This has the disadvantage of making the absolutely exact stratigraphic position of any given specimen impossible to ascertain. Nevertheless, a degree of stratigraphic control similar to that of Thomas and Narbonne has been maintained (their locality GSC 95231, for example, spans nearly 20 m of section), and the relation of the collecting localities described below to those of Thomas and Narbonne, and hence their stratigraphic position, is not at issue.

Locality 1 is equivalent to GSC localities 95230 and 95231 (Thomas and Narbonne, 1979, Fig. 1). Localities 2 and 9 are approximate along-strike equivalents, with identical faunas. Localities 5 and 6 are positioned approximately 20 m above Locality 1, contain fewer elements of the same fauna (but with the addition of <u>Frammia</u> <u>arctica</u> (Salter, 1852)), and presumably correspond to GSC locality 95232. Localities 1, 2, 5, 6, and 9 together contain elements of Fauna A.

Locality 3 is equivalent to localities GSC 95234 and 95235. Locality 4 is entirely frost-heaved talus collections, as the outcrop from which the rocks were derived lies beneath talus of the upper member of the overlying Barlow Inlet Formation. Localities 4, 7, and 8 are along-strike equivalents of Locality 3, and contain identical faunas (the only exception being two fragments of an acanthoparyphine recovered from Locality 8). Localities

3, 4, 7, and 8 together contain elements of Fauna B.

The age of the Douro Formation at Goodsir Creek has been discussed by Thorsteinsson and Uyeno (in Thorsteinsson, 1980, p. 24). They concluded that the unit falls entirely within the long-ranging siluricus Zone, and that the overlying lower member of the Barlow Inlet Formation belongs to the latialata Zone. Hence, based upon conodonts, the trilobite faunas are certainly of Ludlow, and likely late Ludlow (Ludfordian), age. Further resolution is provided by graptolites. A 40 m shale unit (a lateral tongue of the basinal Cape Phillips Formation) occurs between trilobite Faunas A and B at Goodsir Creek. This unit has yielded Bohemograptus bohemicus tenuis (Thorsteinsson, 1980, p. 5), name-bearer of the uppermost Ludow graptolite zone of Lenz (1990), hence confirming a Ludfordian age.

Garnier Bay.--The Upper Silurian stratigraphic sequence in the region of Garnier Bay, northern Somerset Island, has been studied and discussed by Jones and Dixon (1977). Exact collecting localities are shown in Figure VIII-2B. The Douro Formation occurs in cliff-forming outcrop to the west and east of the floodplain of the Garnier River, near its mouth. Jones and Dixon (1977, Table 4) reported a "probably early late Ludlow" age for rocks of the Cape Storm Formation exposed along the river, and inferred a late Ludlow to Prídolí age for the Douro Formation in this area. Trilobites described herein were collected from Douro

Formation rocks above this horizon to the west of the river (Localities GAB 1 and GAB 2, approximately equivalent to section C of Jones and Dixon, 1977) and from presumably correlative rocks (with an identical trilobite fauna) to the east of the river (Locality GAB 5). Thorsteinsson (1980) reported the age of the Douro Formation in all areas of outcrop as Ludlow, and reiterated a late Ludlow to Přídolí age for the Somerset Island Formation (Miall et al., 1978), which overlies the Douro Formation in western Somerset Island. Jones and Dixon (1977), however, showed that the Douro Formation (then regarded as Read Bay Formation) and its contact with the Somerset Island Formation (then unnamed) is diachronous, becoming younger in an easterly direction across northern Somerset Island. Hence, the age of the trilobite faunas seems likely to be either late Ludfordian or Přídolí, and is reported as Upper Silurian below.

Prince Alfred Bay.--The regional stratigraphy of Paleozoic rocks of the Douro Range near Prince Alfred Bay, northern Devon Island, was outlined by Morrow and Kerr (1977). The age of the Douro Formation in this area is not well constrained (Morrow and Kerr, 1977, Appendix 5), as it is based entirely on reference to shelly fossils, and not conodonts, but was considered Ludlow. Thorsteinsson (1980, p. 28) reported a late Ludlow (_Pedavis latialata_ Zone) age for a thin limestone bed separating the Douro Formation from the overlying Devon Island Formation on a section along the Sutherland River (Section 4 of Morrow and Kerr, 1977). At 4.5 m above the base of the Devon Island Formation at this locality, the Přídolí graptolite Monograptus formosus occurs. Trilobites described herein were collected from the Douro formation at Morrow and Kerr's Section 6 (Locality PAB 4) and Section 7 (Locality PAB 3), and are again likely of Ludfordian age.

SYSTEMATIC PALEONTOLOGY

Repository.--All type and illustrated material is housed in the paleontological collections of the Department of Geology, University of Alberta, with specimen numbers prefixed UA.

Family ENCRINURIDAE Angelin, 1854

Subfamily ENCRINURINAE Angelin, 1854

Genus BALIZOMA Holloway, 1980

Type species.--Calymene variolaris Brongniart, 1822, from the Much Wenlock Limestone Formation (Homerian), Dudley, West Midlands, U. K. By original designation.

Other species.--Balizoma aff. B. variolaris, Homerian, Canadian arctic; Balizoma sp., Ludfordian, Canadian arctic (see below for both).

Diagnosis.--Rostral plate extremely narrow, wedge shaped; glabella strongly convex (tr.); interocular fixigena wide, "domed", with significant dorsal convexity; eye stalked; anterior furrow of librigena deep; librigenal field much wider (tr.) than lateral border, with approximately three rows of coarse tubercles; lateral border with adaxial row of 7 or 8 large tubercles and strongly subdued abaxial row of smaller, more numerous tubercles; pygidium with 7^2 to 8^2 ribs and 8-10 axial rings; lateral margins of pygidium in dorsal view tapering rapidly posteriorly, slightly laterally concave.

Discussion.--Given the many refinements in encrinurine taxonomy in recent years (Strusz, 1980; Ramsköld, 1986; Edgecombe and Chatterton, 1990a, 1990b, 1992, in press; Edgecombe and Ramsköld, 1992; Edgecombe, in press; Ramsköld and Edgecombe, in press), it is important to outline the sense in which we use the name *Balizoma*. There follows a brief sketch of the taxonomic history of the genus.

Holloway (1980) introduced the name *Balizoma* for part of what had long been regarded as a "*variolaris* group" within *Encrinurus* (Reed, 1928; Tripp, 1962; Tripp et al., 1977). He distinguished his new genus from his revised concept of *Fragiscutum* Whittington and Campbell, 1967 (in which he included some species that had traditionally been assigned to the *variolaris* group), and from his concept of *Encrinurus* s.s. (i.e., a group centered on the type species, *E. punctatus*), mainly by reference to pygidial morphology. An analysis by Strusz (1980, Text-figs. 9, 14) established a "*variolaris* plexus" which included species assigned to both *Fragiscutum* and *Balizoma* by Holloway (1980), but with a more precise interpretation of phylogenetic structure. Strusz's (1980) scheme has essentially served as a foundation for further refinement of taxonomy within the clade. Ramsköld (1986) used *Balizoma* in a much restricted sense, as a component of Strusz's (1980) *variolaris* plexus. Edgecombe, Ramsköld, and Chatterton (in Edgecombe and Chatterton, in press; see also Edgecombe, in press, Fig. 1) restricted *Balizoma* to its type species, erecting *Struszia* for the remainder of *Balizoma* sensu Ramsköld (1986). The basis for this was the hypothesis that *B. variolaris* possesses many plesiomorphic features indicating that it lies outside the phylogenetic structure of a diverse clade including *Avalanchurus* Edgecombe and Chatterton, in press, *Fragiscutum* Whittington and Campbell, 1967, *Frammia* Holtedahl, 1914, *Mackenziurus* Edgecombe and Chatterton, 1990a, and *Struszia* Edgecombe, Ramsköld, and Chatterton in Edgecombe and Chatterton, in press. Hence, *Balizoma* has been interpreted (Edgecombe and Chatterton, in press; Edgecombe in press) as a monotypic sister group to what is considered a monophyletic post-Llandovery encrinurine radiation.

New collections in the Wenlock and Ludlow of the Canadian arctic have revealed additional occurrences of *Balizoma*, as interpreted above, together with several species of a new taxon, *Aegrotocatellus* n. gen. (see below). *Aegrotocatellus* is diagnosibly distinct, but uniquely shares several features with *Balizoma* and is interpreted as its sister-group. Together, the genera form a clade with at least moderate diversity and a known stratigraphic range from upper Wenlock to upper Ludlow.

Synapomorphies uniting Balizoma and Aegrotocatellus include the following: a tall eye stalk (see Tripp et al., 1977, pl. 113, fig. 3; Figure 3.5; cf. Figures VIII-5.10, VIII-5.11, VIII-5.19, VIII-6.14); prominent row of palpebral tubercles; an eye position that is strongly distal to the axial furrow; possession of prominent tubercles on the posterolateral part of the cephalic border; strongly inflated maculae; a tendency to form median tubercles on thoracic axial rings 7, 9, and 11 (see Tripp et al., pl. 113, fig. 9; median tubercles are present in immature holaspides of Balizoma variolaris on those rings that bear strong median tubercles in adults of Aegrotocatellus jaggeri, see Figure VIII-4); and a pygidium with a low R/P ratio. Both genera further possess a relative abundance of pygidial tubercles, with several well defined tubercles aligned across the axial rings and pleural ribs.

BALIZOMA aff. B. VARIOLARIS (Brongniart, 1822)

Figure VIII-3.1 to VIII-3.15

Discussion.--Adrain (in press) has reported the occurrence of exceedingly diverse and numerous Wenlock and lower Ludlow trilobite faunas in the Cape Phillips Formation of the Canadian arctic. A species of Balizoma occurs as an extremely rare element at a single stratigraphic horizon

(ABR 1 17 m). This horizon falls within the upper Homerian Pristiograptus ludensis Zone, and is hence correlative with the Much Wenlock Limestone Formation.

As is the case with many species described from the latter unit, Balizoma variolaris (see Tripp et al., 1977, Pl. 113) is an extremely variable species. Collections from the Cape Phillips Formation are from event beds (carbonate grain flows) and likely represent single population samples. Significantly, over a wide range of trilobite taxa recovered, there is very little intraspecific variation, certainly nothing like that claimed for some species from the Much Wenlock Limestone (examples in Thomas, 1978, 1981). It is probable that this can at least partly be explained by considering that Much Wenlock Limestone species must frequently be analysed on the basis of poorly localized museum collections (Thomas et al., 1984, p. 54). Some combination of time, biofacies, and geographic mixing seems surely to have played a role in the observed variation of species such as B. variolaris, and it is difficult to accept, without precise geographic and stratigraphic data, that all of the assigned material is actually conspecific.

Nevertheless, the Canadian material corresponds closely to English specimens similar to the neotype of Balizoma variolaris (Tripp et al., 1977, Pl. 133, Figs. 1, 2; see Tripp, 1962, Pl. 65, figs. 17-20; Schrank, 1972, Pl. 13, fig. 8; Thomas, 1981, Pl. 18, fig. 2a-d; Whittington, 1992, Pl. 109, figs. A-C). Particular similarities include the domed interocular fixigenae, similarly stalked eye, almost identical librigenae (a standard external view of a _B. variolaris_ librigena has evidently never been figured, but compare Figure VIII-3.5 with Clarkson and Henry, 1973, fig. 14D, 16E and Thomas, 1981, Pl. 18, fig. 2a-d), and hypostomes with distinctive, bullet-shaped rhynchos and anterior wings positioned relatively far back. Minor differences include the more strongly defined palpebral tubercle row in the Canadian material, and the fact that the hypostomal suture in two of the three Canadian hypostomes (Figure VIII-3.3, VIII-3.7) runs transversely straight, as opposed to in an anteriorly directed "V" shape in _B. variolaris_ (Tripp et al., 1977, Pl. 113, fig. 5). It is possible that the Canadian material and most of the Dudley material is conspecific, but much more would have to known about either occurrence before a confident taxonomic decision could be made.

Material.--Figured specimens UA 8968-8975.

Occurrence.--Section Abbott River One (Adrain, in press), 17 m above base, Cape Phillips Formation, Wenlock, Homerian (_Pristiograptus ludensis_ Zone), southerly-flowing tributary of Abbott River, northwestern Cornwallis Island, central Canadian Arctic. Also occurring in several talus boulders collected across the stream from ABR 1, containing an identical (and unique) fauna, and almost certainly derived from the same stratigraphic horizon. These talus boulders were designated in the field ABR-TTC(1) and ABR-TT*.

BALIZOMA sp.

Figure VIII-3.16 to VIII-3.20

Discussion.--Two sclerites from Locality GSC 8 are obviously distinct from cooccurring encrinurines (Aegrotocatellus n. sp. A, Frammia sp., Mackenziurus sp.). Assignment to Balizoma is indicated by the distinctive domed interocular fixigena, prominent tuberculation on the cranidial posterolateral border, the pygidial rib count of 7^2 combined with the presence of approximately 8 axial rings, and the nearly concave taper of the lateral margins of the pygidium in dorsal view (cf. Figure VIII-3.20 with VIII-3.10, VIII-3.15, and Tripp et al., 1977, Pl. 113, fig. 14). The specimens are significant in extending the range of the taxon into the Ludfordian, but are too few and too poorly preserved for meaningful comparison with the Homerian material.

Material.--Figured specimens UA 8976, 8977, Locality GSC 8, Douro Formation (Ludlow, Ludfordian), near Goodsir Creek, eastern Cornwallis Island, central Canadian Arctic.

Genus AEGROTOCATELLUS n. gen.

Type species.--Aegrotocatellus jaggeri n. gen. n. sp., from Fauna A of the Ludlow (Ludfordian) Douro Formation at Goodsir Creek, Cornwallis Island, Arctic Canada.

Other species.--Aegrotocatellus n. sp. A, from Fauna B of the Ludlow (Ludfordian) Douro Formation at Goodsir Creek, Cornwallis Island, Arctic Canada; *Aegrotocatellus* n. sp. B, from the Upper Silurian Douro Formation at Garnier Bay, northern Somerset Island, Arctic Canada; *Aegrotocatellus* n. sp. C, from the Ludlow (Ludfordian) Douro Formation at Prince Alfred Bay, northwestern Devon Island, Arctic Canada.

Diagnosis.--Cranidial anterior border bearing two pairs of elongate spines, one or three pairs of tubercles; S1 approximately transverse, with shallow impression across glabella; glabellar tuberculation dominated by position-1 pairs; pair of prominent spines on cranidial posterolateral border in front of elongate genal spine; L0 raised above glabella, with pair of posterodorsally directed spines toward posterior edge; eye stalked, strongly distal to axial furrow; librigenal field tubercles at least two deep; rostral plate moderately wide (tr.) at rostral suture; hypostomal rhynchos gently tapering forward, not projecting to anterior margin; sagittal tubercles on axial rings of thoracic segments 3, 5, 7, 9; long, slender fulcral spines on thoracic pleurae (3,) 5, 7, 9, 11; pygidium non-mucronate, with 9^2 or 10^2 pleural ribs; R/P ratio 1.1; sagittal tubercles weakly inflected posteriorly.

Discussion.--Similarities between *Aegrotocatellus* and *Balizoma* were listed under discussion of the latter genus above. Despite their inferred sister group relationships, the taxa are easily distinguished by the presence in

Aegrotocatellus of long cranidial anterior border spines, paired occipital spines, thoracic fulcral spines, stronger thoracic axial tubercles, wider rostral suture, L1 developed as a strong, transverse ridge (versus shortened medially and depressed abaxially in Balizoma), shallower anterior librigenal furrow, and less bullet shaped hypostomal rhynchos.

Some of the peculiar morphological states of Aegrocatellus are extreme modifications of forms present in the early ontogeny of most Silurian encrinurines (e.g., thoracic fulcral spines; cranidial anterior and posterolateral border spines). The anterior border tubercles that are modified into spines in Aegrocatellus jaggeri n. gen. n. sp. are usually spines 2 and 4 (pairs numbered abaxially following Edgecombe and Chatterton, 1987, fig. 5). The homologous pairs 2 and 4 in species of Struszia are the primary spines in early ontogeny (see Edgecombe and Chatterton, 1987), and strongly elongated relative to other border tubercles/spines in meraspides. The relative enlargement of these spines in large holaspides of Aegrotocatellus is thus a paedomorphic retention. The cranidial posterolateral border spines of Aegrotocatellus jaggeri are developed similarly to their homologues in meraspides of Struszia (Edgecombe and Chatterton, 1987, fig. 6G, 7A-B), and are even more strongly elongate in Aegrotocatellus n. sp. A. Other typically juvenile (paedomorphic) states in Aegrotocatellus are pronounced position-1 glabellar tubercle pairs, a strong genal spine, well defined S3 apodeme, and transverse, well-impressed S1.

The stalked eye, coarse palpebral tubercles, pronounced S3 apodeme, and strong genal spine might suggest relationship between Aegrotocatellus and Encrinurus Emmrich, 1844. This hypothesis, however, is not supported by pygidial morphology. The pygidium of Aegrotocatellus jaggeri lacks the mucro that diagnoses Encrinurus, and has a much lower R/P ratio than any species of that genus. The arrangement of thoracic axial spines is also very different. The lengthy spine of Encrinurus is on the tenth segment, while tubercles or very short spines occur on rings 3, 5, 7, and 9 in Aegrotocatellus.

Etymology.--From the Latin aegrotus, ill, and catellus, young dog.

AEGROTOCATELLUS JAGGERI n. gen. n. sp.

Figures VIII-4, VIII-5

encrinurine gen. et sp. indet. THOMAS in THOMAS & NARBONNE,
1979, p. 12, Pl. 4, figs. g, h, j, m, n.

Diagnosis.--Cranidial anterior border bearing two pairs of short to moderately long spines, usually in positions 2 and 4, tubercles in positions (1), 3, and 6 (=PL); adaxial fixigenal tubercles strong, transversely widened; fixigenal field with ring of about five tubercles around eye, middle (exsag.) tubercles transversely widened; several strong tubercles along cranidial posterior border; cranidial posterolateral border with at least two conical tubercles anterior to genal spine.

Description.-- Cephalic axial furrow narrow to moderately wide; glabella moderately convex (sag., tr.); fixigenal field raised above posterior part of glabella; S2-S3 with shallow but distinct impression across glabella; prominent teardrop shaped S1, S2, and fossular apodemes; S3 apodeme smallest, moderately deep; L2-L4 lateral lobes varying from weakly subovate to strongly elliptical, either subdued swellings or discrete/tuberculiform; small tubercles on adaxial part of L2-L4 lateral lobes and PL; PL subrounded tubercle, smaller than L3-L4 lateral lobes; S1 weakly curved forward medially; L1 low transverse ridge, usually with weakly swollen abaxial edge, sometimes bearing coarse, transversely ovate tubercle; I-1 ubiquitous, usually very small, subdued; II-1, III-1 increasing in size; ii-0 absent; small iii-0 rarely present; V-1 occasionally developed as short spines; S0 very short (sag., exsag.), shallow to moderately deep, gently curved forward medially; pair of small, subdued tubercles abaxial to pair of short coarse spines on L0, and anterolateral node may be weakly defined; L0 raised above glabella, flattened (sag.) and moderately steeply sloping downward in front of paired spines, strongly convex (tr.); doublure lengthening medially beneath L0, not extending to S0; preglabellar furrow shallow medially;

anterior border gently lengthening abaxially, with shallow anteromedian impression; anterior border spines in positions 2 and 4 ranging from elongate, conical tubercles to moderately long spines; few small scattered fixigenal tubercles between five tubercles of adaxial fixigenal row and circumocular ring; midlength (exsag.) of palpebral lobe opposite anterior part of L2; palpebral lobe bearing several tubercles aligned in an arcuate row; posterior border furrow short (sag., exsag.), moderately deep, gently directed backward to fulcrum, then slightly more strongly curved back; posterior border short (exsag.) proximally, gently lengthening distal to fulcrum; several strong tubercles on crandial posterior border and along proximal part of genal spine; genal spine long, slender, directed posterolaterally.

Librigenal field much wider (tr.) than lateral border; field tuberculation moderately dense, larger tubercles arranged two or three deep, without definition of rows, numerous small, irregularly scattered tubercles; all field tubercles much smaller than lateral border tubercles; eye socle tall, cylindrical, set off from visual surface by very faint depression; height of eye socle and visual surface subequal to slightly greater than width (tr.) of librigenal field; lateral border furrow narrow, moderately deep; three coarse, elliptical inner row tubercles on lateral border, with equal-sized tubercles of middle row set between and slightly abaxial to these; ventrolateral margin aligned with moderately coarse outer row tubercles; anterior furrow shallow, very weak towards connective suture; precranidial lobe about 75 percent length (exsag.) of field, densely covered with numerous moderately large and small tubercles; shallow vincular furrow beneath lateral border.

Rostral suture moderately wide (tr.); rostral plate poorly known, but bearing three tubercles across dorsal edge.

Hypostome subrhomboid, slightly longer than wide; maximum width across anterior wing at 36 percent leng (sag.) of hypostome; middle body gently convex (sag., tr.), length (including rhynchos) 125 percent of width (tr.), coarsely granulate; rhynchos rounded anteromedially, terminating at anterior border furrow, lateral margins approximately parallel to almost midlength (exsag.), then gently diverging posteriorly; middle body with short (sag.), crescentic posteromedian bulge; anterior border short (sag.); maculae large, ovate, prominently swollen; border furrow moderately wide, shallow posteromedially; posterior border lengthening medially, 17 percent length (sag.) of hypostome; posterior margin with blunt median angulation.

Thorax of 11 segments; axial furrow narrow, moderately deep; axial ring weakly bowed forward medially, with distal edge gently flexed forward, moderately arched (tr.), with break in slope distally; strong sagittal tubercle on rings 3 and 5; very short spines on rings 7 and 9 posteriorly deflected; few additional small, very subdued tubercles aligned across ring; pleural ribs gently turned back and moderately turned down at fulcrum in anterior segments, more strongly turned down and back in posterior segments; each rib aligned with several small tubercles; fulcral spines on segments 5, 7, 9, and 11 directed posterolaterally, gently declined from horizontal, faintly curved inward; third segment with fulcral tubercle or long fulcral spine; distal tip of anterior ribs with blunt point behind articulating facet, posterior ribs with straighter terminae; narrow pleural furrow sharply impressed across most of width (tr.) of articulating facet.

Pygidial length 65 percent of width; axial furrow narrow, moderately deep; axis about 35 percent of pygidial width anteriorly, weakly convex (sag.), moderately arched (tr.) in anterior rings, with weakly convex median region in posterior rings; 9 or 10 distinct inter-ring furrows; axial rings gently lengthening medially, expanded anteriorly and posteriorly as inter-ring furrow shortens and shallows; ring weakly expanded behind distal end of transversely lenticular pseudo-apodeme; three or four strong sagittal tubercles, spaced two or three rings apart, additional subdued tubercle pair on anterior six rings; few small tubercles along inner part of each pleura, relatively prominent tubercle toward adaxial edge, set closer to axial furrow on successively posterior ribs; anterior ribs gently curved down and back to fulcrum, then steeply turned ventrally; posterior ribs steeply sloping down and sharply curved back across width; anterior three or four ribs weakly turned out distally; inter-rib furrows narrow, moderately deep; doublure moderately wide, with approximately straight inner edge back to moderately deep, apparently rounded posteromedian embayment.

Discussion.--*Aegrotocatellus jaggeri* n. gen. n. sp. is known from sufficient material to indicate a range of intraspecific variation. Features that display variability include the following: the cranidial border spines range from conical tubercles (Figs. VIII-4.8, VIII-5.9) to moderately long spines (Fig. VIII-5.1, VIII-5.2), and are consistently elongate in small specimens (Fig. VIII-5.18); V-1 is usually a tubercle pair, but is occasionally developed as spines (Fig. VIII-5.17); L2-L4 and the adaxial fixigenal region may bear subrounded or transversely elliptical tubercles; the abaxial tubercle on L1 varies from a subdued swelling (Fig. VIII-5.9) to a small, rounded tubercle to a strong, transversely ovate tubercle (Fig. VIII-5.8); the fulcral spine on the third thoracic segment is of variable length, ranging from a tubercle (Fig. VIII-4.1, VIII-4.2) to a lengthy spine (Fig. VIII-4.14, VIII-4.16).

Types.--Holotype exoskeleton UA 8978 (Figure VIII-4.1 to VIII-4.3, VIII-4.7 to VIII-4.13), from the Douro Formation, Goodsir Creek, Locality 9; paratypes UA 8979-8993.

Occurrence.--Localities GSC 1, GSC 2, and GSC 9, Douro Formation (Ludlow, Ludfordian), near Goodsir Creek, eastern Cornwallis Island, central Canadian Arctic.

Etymology.--After Mick Jagger.

AEGROTOCATELLUS n. sp. A

Figure VIII-6.1 to VIII-6.5, VIII-6.8, VIII-6.9

Diagnosis.--Cranidial anterior border bearing two pairs of spines and only one pair of tubercles (at PL); tubercles lacking on L1-L3; L0 bearing single pair of long, slender spines; eye stalk tall; single fulcral tubercle on cranidial posterior border; cranidial posterolateral border with two long, slender spines projecting outward anterior to genal spine; fixigenal field sparsely tuberculate; adaxial fixigenal tubercles weakly defined swellings except for stronger anterior tubercle.

Discussion.--*Aegrotocatellus* specimens from Fauna B at Goodsir Creek are readily distinguished from *A. jaggeri* of Fauna A by the paucity of tubercles on the cranidial anterior border and fixigenal field, absence of tuberculation on the posterior part of the glabella, taller eye stalk, longer spine pairs on the posterolateral border and occipital ring, and much more subdued adaxial fixigenal tubercles. A new species is not formalized because of the limited amount of available material, all of which is cranidial.

Material.--Figured specimens UA 8994-8997.

Occurrence.--Localities GSC 3, GSC 4, and GSC 8, Douro Formation (Ludlow, Ludfordian), near Goodsir Creek, eastern Cornwallis Island, central Canadian Arctic.

AEGROTOCATELLUS n. sp. B

Figure VIII-6.6, VIII-6.7, VIII-6.10, VIII-6.14

Diagnosis.--Two pairs of cranidial anterior border spines greatly elongated; L3 and frontal glabellar lobe bearing abundant small tubercles; eye strongly distal to axial furrow, set on very tall stalk; single fulcral spine on cranidial posterior border; very long dorsolaterally directed spine set above genal spine; librigenal field short (exsag.); lateral border tubercles subdued.

Discussion.--Aegrotocatellus from Garnier Bay is most obviously distinguished from A. jaggeri n. gen. n. sp. by greater elongation of the cranidial anterior border spines, the very long spine on the cephalic posterolateral border, and the short (exsag.) librigenal field. It resembles that species rather than Aegrotocatellus n. sp. A in the presence of numerous tubercles on the posterior part of the glabella and on the fixigenal field. The eye stalk of Aegrotocatellus n. sp. B is more distally positioned than in either taxon from Goodsir Creek. Its height, however, is most closely approached by Aegrotocatellus n. sp. A, which it further resembles in the elongation of a cephalic posterolateral border spine as well as the anterior border spines. Both taxa (n. spp. A and B) also possess a single fulcral tubercle on the cranidial posterior border, versus tubercles aligned across the border in A. jaggeri.

Material.--Figured specimens UA 8998, 8999.

Occurrence.--Localities GAB 1 and GAB 2, Douro Formation (Upper Silurian), near Garnier Bay, northern Somerset Island, central Canadian Arctic.

AEGROTOCATELLUS n. sp. C

Figure VIII-6.11 to VIII-6.13, VIII-6.15 to VIII-6.18

Diagnosis.--Many glabellar tubercles developed as short, conical spines; eye socle relatively narrow; eye elongate and low; palpebral lobe long; librigenal lateral border bearing four very large, conical spines, with smaller spine set posterolaterally.

Discussion.--Specimens of Aegrotocatellus n. gen. from the Douro Formation at Prince Alfred Bay are unique in the modification of some cephalic tubercles to conical spines. Notably, numerous glabellar "tubercles" are extended as short, sharp spines, and the librigenal lateral border tubercles are expressed as prominent, conical spines. Aegrotocatellus n. sp. C most closely resembles A. jaggeri with respect to the density of tuberculation on the glabella and fixigenal field (e.g. prominent tubercles just adaxial to the eye), the relatively short occipital and cephalic posterolateral border spines, and lesser height of the eye stalk than in Aegrotocatellus n. spp. A and B.

Assuming _Aegrotocatellus_ evolved through a paedomorphic event, its most primitive member might be expected to display the most obviously juvenile morphology. Among known species, _Aegrotocatellus_ n. sp. C conforms most closely to what is known of the general meraspid morphology of encrinurines. In particular, this species features a less stalked eye than other members of the genus together with spinose glabellar tuberlces dominated by position-1 pairs. The four largest spines on the librigenal lateral border (Figure VIII-6.13, VIII-6.15, VIII-6.16) correspond exactly to the inner row spines of Edgecombe and Chatterton (1992, Fig. 11), which are the primary lateral border spines in encrinurine ontogeny.

Material.--Figured specimens UA 9000-9004.

Occurrence.--Localities PAB 3 and PAB 4, Douro Formation (Ludlow, Ludfordian), near Prince Alfred Bay, northern Devon Island, central Canadian Arctic.

Subfamily CORONOCEPHALINAE Zhang, 1983

Genus PERIREHAEDULUS n. gen.

Type species.--_Kailia_? _capra_ Thomas, 1979 (p. 10, Pl. 4, figs. a-f, i), from the Ludlow (Ludfordian) Douro Formation of Goodsir Creek, eastern Cornwallis Island, Arctic Canada.

Other species.--_Perirehaedulus_ _richardsi_ n. gen. n. sp., from the Upper Silurian Douro Formation of Garnier Bay, northern Somerset Island, Arctic Canada.

Diagnosis.--Coronocephaline with very long, slender, curved spines projecting anterolaterally from anterior part of cranidium; eye ridge distinct; librigenal lateral border furrow very shallow; lateral border lacking tubercles or marginal lobes; precranidial lobe very narrow (tr.); librigenal anterior furrow indistinct; eye stalk tall, slender; genal field pitted; genal spine very long, approximately straight for much of length, curved backward distally; fulcral spine on seventh thoracic pleura; pygidium with about 15 pleural ribs, only a few more axial rings; small sagittal tubercles on a few axial rings.

Discussion.--It is obvious that a close relationship exists between Perirehaedulus n. gen. and Kailia Chang, 1974. Coronocephaline affinities of the Canadian Ludlow taxon are supported by the following synapomorphies: obscure definition of the preglabellar furrow sagittally; a very long genal spine; and a large pygidium with a very narrow axis and many (15) pleural ribs. Among coronocephalines, Kailia and Perirehaedulus uniquely share total suppression of cephalic tuberculation, strong definition of S4 abaxially, complete merging of the frontal glabellar lobe with the cranidial anterior border, and S2 and S3 relatively shallow medially. Thomas (in Thomas and Narbonne, 1979, p. 10) described the preglabellar furrow of Perirehaedulus caprus as "reduced to [a] deep lateral apodeme", but comparison with Kailia (e.g. Zhang, 1983, pl. 4, fig. 9) suggests that this pit represents S4 rather than the abaxial edge of the preglabellar furrow.

Zhang (1983, p. 213) considered *Perirehaedulus caprus* "quite different from the other species referred to *Kailia*", and concluded that it probably represents a new genus. By restricting *Kailia* to what he regarded as Wenlock species from central and southwest China, and limiting Coronocephalinae to *Kailia*, *Senticucullus*, *Coronocephalus*, and *Rongxiella*, he considered the subfamily to be endemic to the Chinese Wenlock (Temple and Wu, 1990, however, have since indicated that Chinese coronocephalines are of late Llandovery age). This "area of endemism" is, however, an artifact of Zhang's taxonomy. *Perirehaedulus* possesses synapomorphies of Coronocephalinae and, more precisely, *Kailia* sensu Zhang (1983); its exclusion from Coronocephalinae (as implied by Zhang's "area of endemism") demands that these similarities are regarded as convergences. Conspicuous differences do exist between *Perirehaedulus* and other coronocephalines, including the absence of tubercles on the librigenal lateral margin, the narrow precranidial lobe, and lower pygidial R/P ratio. Nevertheless, given the lack of compelling support for an alternative relationship for *Perirehaedulus*, a convergence hypothesis has severe methodological flaws.

Etymology.--From the Latin *perire*, lost, and *haedulus*, kid.

PERIREHAEDULUS CAPRUS (Thomas, 1979)

Figure VIII-7

Kailia? capra THOMAS in THOMAS & NARBONNE, 1979, p. 10, Pl. 4, figs. a-f, i; WHITTINGTON, 1992, Pl. 12, figs. A, B,

Diagnosis.--Perirehaedulus with short (sag.) longitudinal median glabellar furrow on anterior part of frontal lobe; glabella strongly broadened across frontal lobe; cranidial anterior spines far apart, with weakly posteriorly-convex cranidial anteromedian margin; L1 slightly shorter (exsag.) than L3; palpebral and eye socle tubercles absent.

Description.--See Thomas (in Thomas and Narbonne, 1979, pp. 10-11), supplemented as follows:

Librigenal field much wider (tr.) than lateral border, bearing moderately dense, small pits; transition to slender eye stalk without well-defined eye socle furrow; lateral border furrow narrow, very shallow; anterior furrow undefined; precranidial lobe very narrow (tr.), much shorter (exsag.) than field; librigenal sculpture of fine, dense granules coarsening marginally; doublure narrow, extending slightly more than half width (tr.) to lateral border furrow.

Discussion.--Because a preglabellar furrow is lacking in Perirehaedulus, the homology of the anterior cranidial spines warrants comment. The anterior border is set off from the frontal glabellar lobe only by a break in slope; the cranidial spines and deepest impression of the longitudinal median furrow lie posterior to this break. As such, the spines originate on the anterior part of the frontal lobe and are presumably homologous with V-1 tubercles in other encrinurids.

Material.--Topotypes UA 9005-9015.

Occurrence.--Localities GSC 3, GSC 4, GSC 7, and GSC 8, Douro Formation (Ludlow, Ludfordian), near Goodsir Creek, eastern Cornwallis Island, central Canadian Arctic.

PERIREHAEDULUS RICHARDSI n. sp.

Figure VIII-8

Diagnosis.--*Perirehaedulus* with anterior cranidial spines closely spaced, relatively stout; frontal glabellar lobe relatively narrow; longitudinal median glabellar furrow obscure; L1 much shorter (exsag.) than L3; palpebral lobe and eye socle bearing a few small tubercles; eye strongly stalked.

Discussion.--*Perirehaedulus richardsi* n. gen. n. sp. from Garnier Bay is most obviously distinguished from its sister species at Goodsir Creek (*P. caprus*) by a complex of states related to its narrower (tr.) frontal glabellar lobe. The frontal lobe spines are relatively longer and stouter, and positioned closer together than in *P. caprus*, and the distinct longitudinal median furrow of that species is lacking. The eye of *P. richardsi* is also more prominently stalked than that of *P. caprus* (cf. Figure VIII-7.11, VIII-7.14 and Figure VIII-8.1, VIII-8.13).

Types.--Holotype cephalon and partial thorax UA 9016 (Figure VIII-8.1, VIII-8.4, VIII-8.8), from the Douro

Formation, Garnier Bay, Locality GAB 1; paratypes UA 9017-9024.

Occurrence.--Localities GAB 1, GAB 2, and GAB 5, Douro Formation (Upper Silurian), near Garnier Bay, northern Somerset Island, central Canadian Arctic.

Etymology.--After Keith Richards.

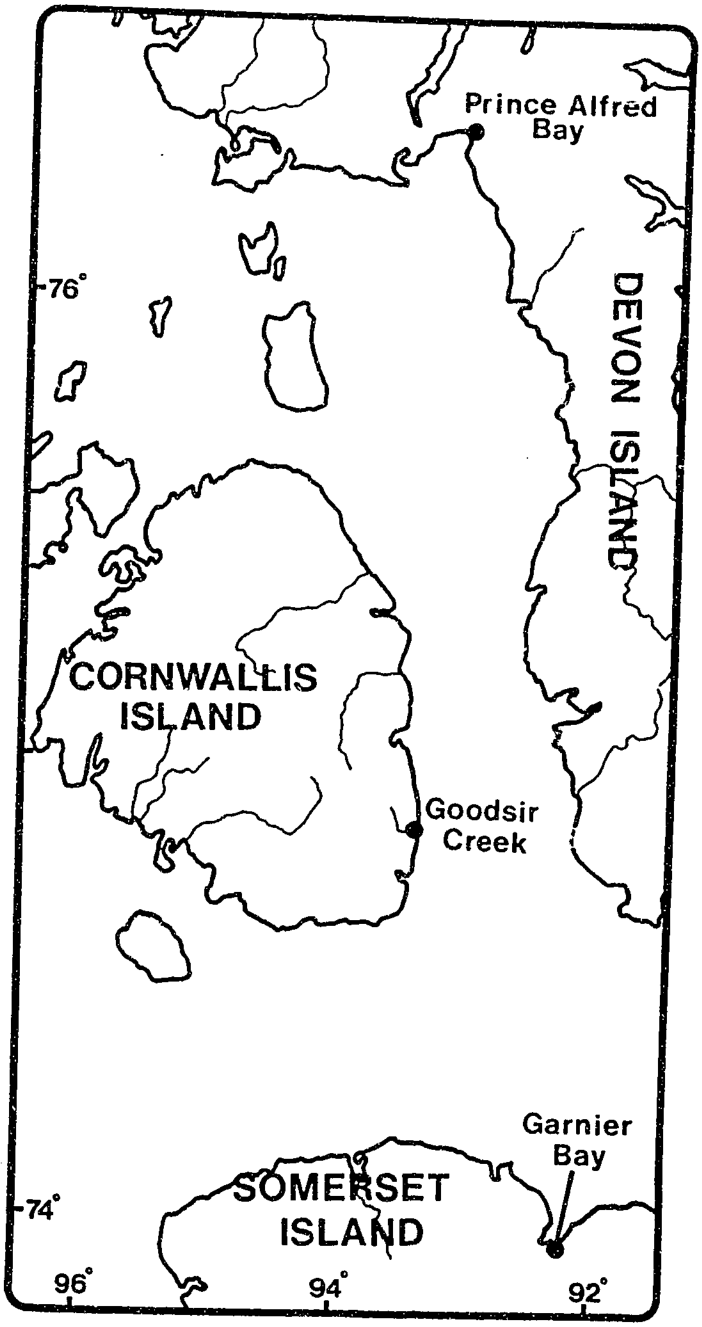
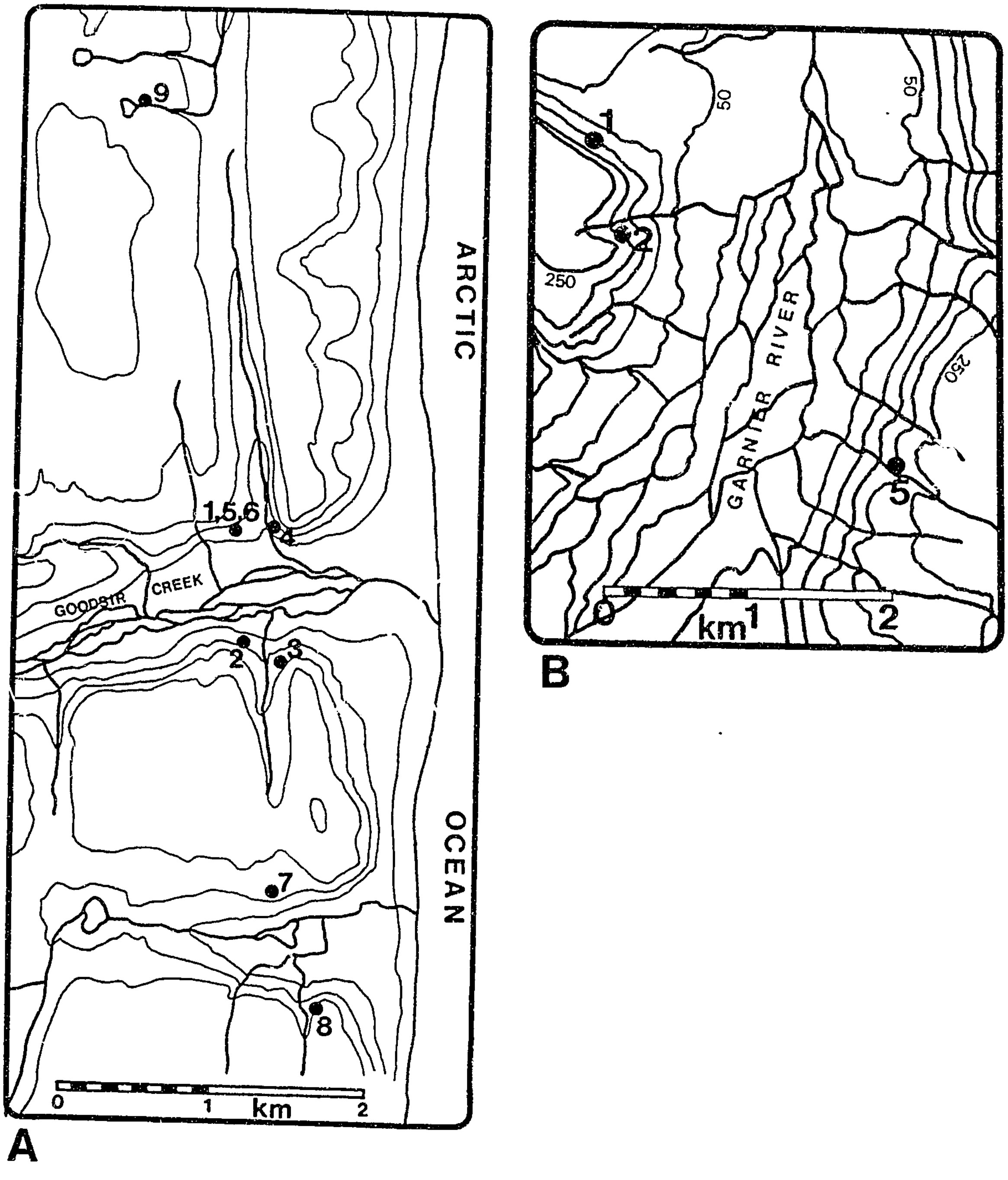


FIGURE VIII-1--Map showing geographic position in the central Canadian Arctic of Douro Formation localities from which material is described herein.

FIGURE VIII-2--Map showing exact position of collecting localities in the Douro Formation in the area of A, Goodsir Creek, eastern Cornwallis Island, and B, Garnier Bay, northern Somerset Island (see Figure VIII-1). Contour interval in both is 50 ft.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GARNIER
RIVER
5
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km
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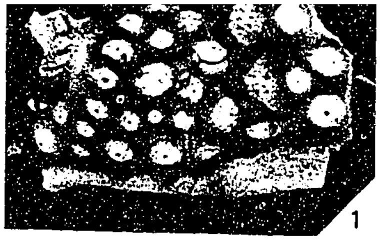
B

(Brongniart, 1822), from section Abbott River One (Adrain, in press), 17 m above base, and talus boulders ABR TTC(1) and ABR TT*, Cape Phillips Formation, Wenlock (Homerian; Pristiograptus ludensis Zone), near Abbott River, northwestern Cornwallis Island, central Canadian Arctic. All specimens are silicified. 1, cranidial fragment UA 8968, dorsal view, x7.5 (ABR TTC(1)); 2, cranidial fragment UA 8969, dorsal view, x7.5 (ABR TTC(1)); 3, hypostome UA 8970, ventral view, x7.5 (ABR TT*); 4, 9, hypostome UA 8971, ventral and dorsal views, x7.5 (ABR 1 17 m); 5, left librigena UA 8972, external view, x7.5 (ABR TT*); 6, 10, 11, 13, pygidium UA 8973, ventral, dorsal, posterior, and left lateral views, x7.5 (ABR 1 17 m); 7, 8, hypostome UA 8974, ventral and right lateral views, x7.5 (ABR TTC (1)); 12, 14, 15, pygidium UA 8975, left lateral, posterior, and dorsal views, x5 (ABR TT*). 16-20, Balizoma sp., from Locality GSC 8, Douro Formation, Ludlow (Ludfordian), near Goodsir Creek, eastern Cornwallis Island, central Canadian Arctic. 16, 17, dorsal and dorsolateral views of cranidium UA 8976, x3; 18-20, left lateral, posterior, and dorsal views of pygidium UA 8977, x5.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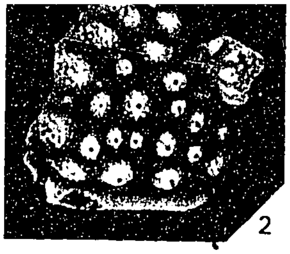
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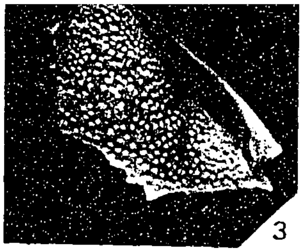
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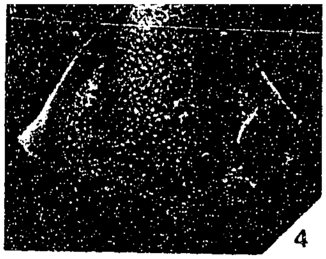
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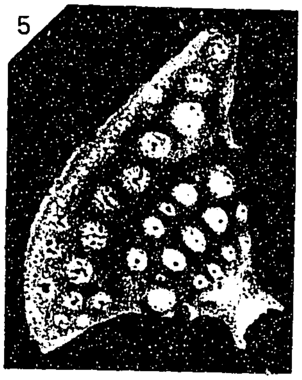
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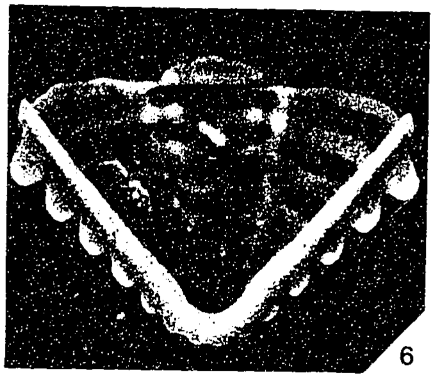
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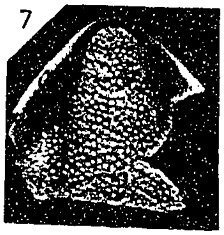
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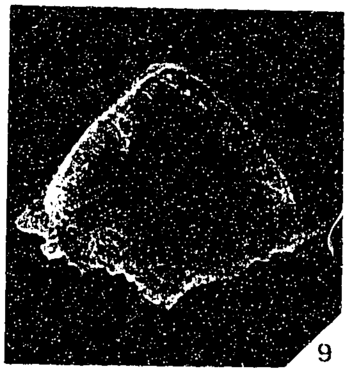
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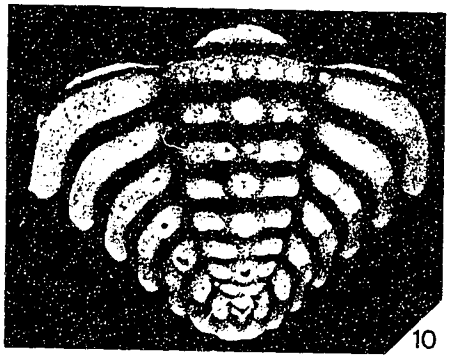
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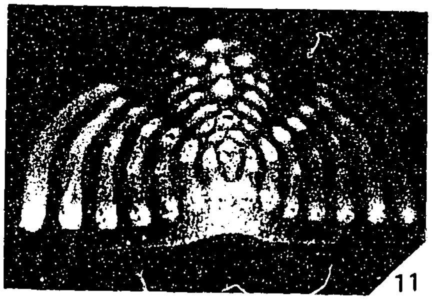
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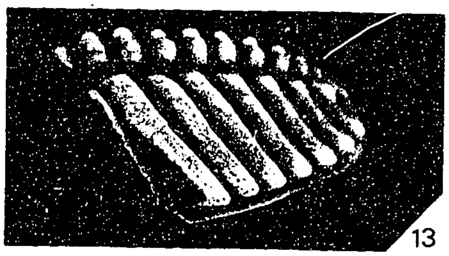
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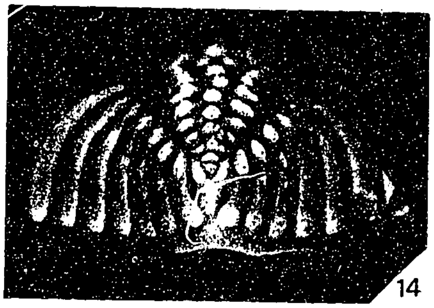
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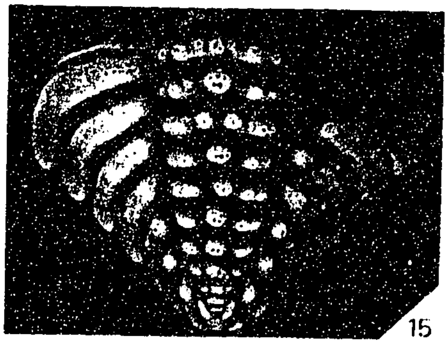
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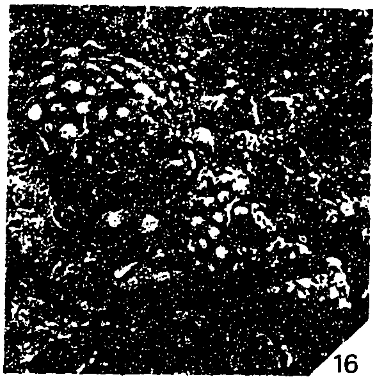
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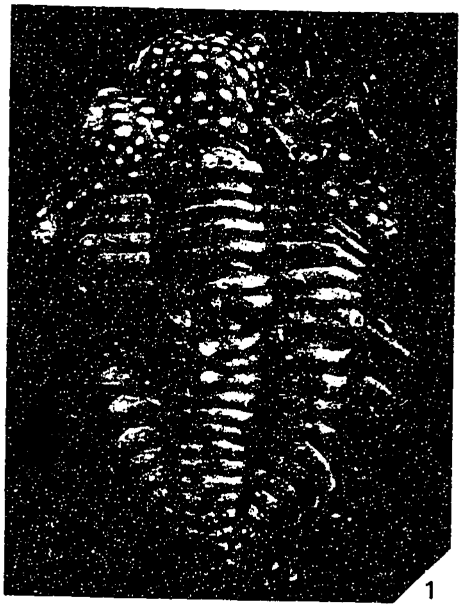
FIGURE VIII-4--*Aegrotocatellus jaggeri* n. gen. n. sp., from Localities GSC 1, and GSC 9, Douro Formation, Ludlow (Ludfordian), near Goodsir Creek, eastern Cornwallis Island, central Canadian Arctic. *1*-*3*, *7*-*13*, holotype exoskeleton UA 8978, dorsal, left lateral, left ventrolateral, posterodorsal, dorsal view of cephalon, oblique ventral, anterior, detail of hypostome, external view of left librigena, and anterodorsal views, all x2 except *11*, x4 (GSC 9); *4*-*6*, pygidium UA 8979, dorsal, left lateral, and posterior views, x5 (GSC 1); *14*-*16*, dorsal exoskeleton UA 8980, posterodorsal, left lateral, and external views, x2.5 (GSC 1).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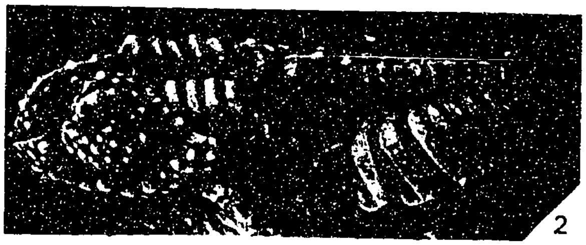
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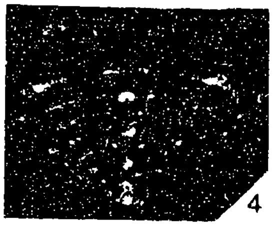
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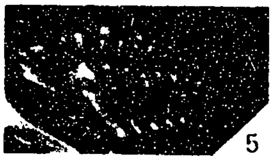
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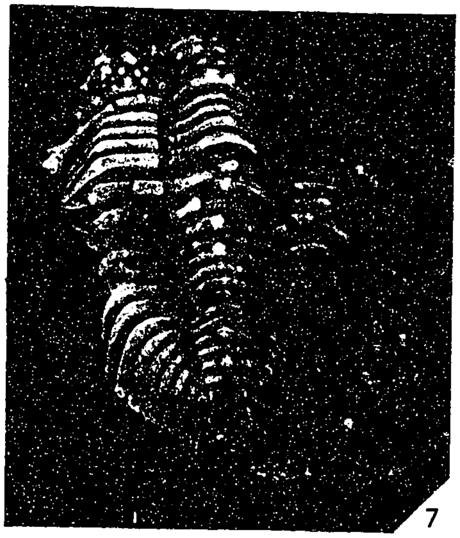
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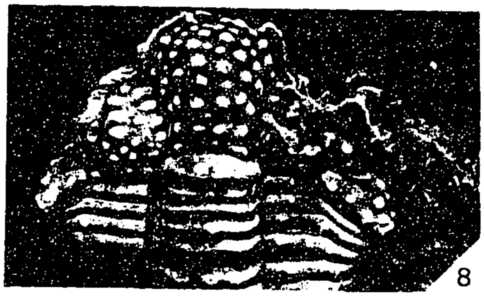
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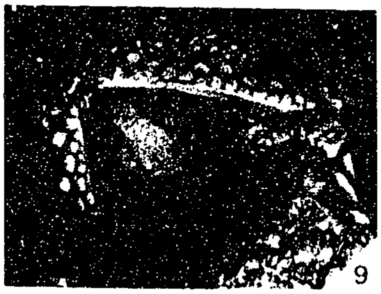
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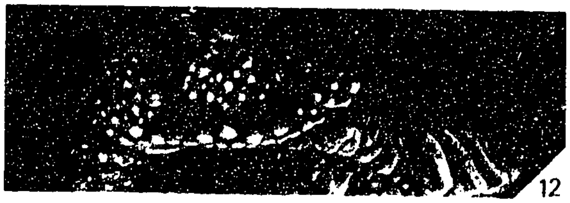
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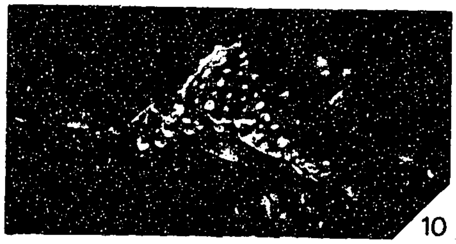
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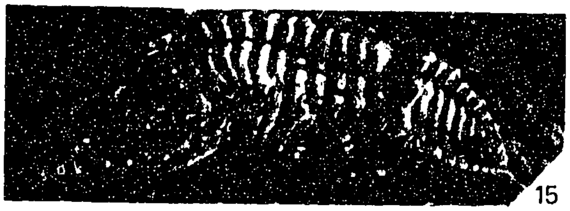
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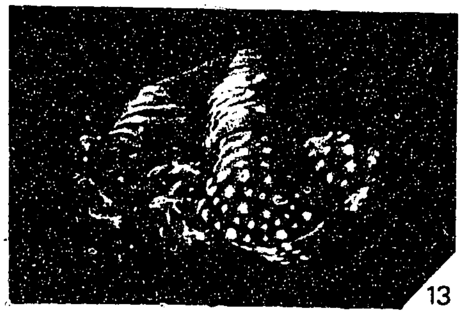
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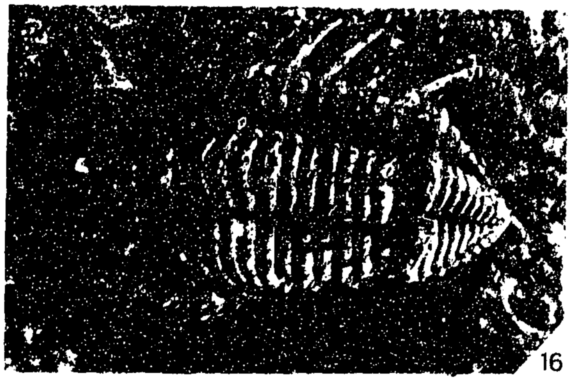
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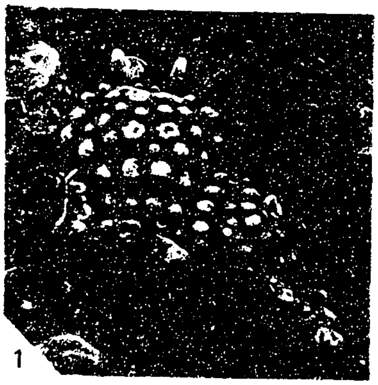
FIGURE VIII-5--*Aegrotocatellus jaggeri* n. gen. n. sp., from Localities GSC 1, GSC 2, and GSC 9, Douro Formation, Ludlow (Ludfordian), near Goodsir Creek, eastern Cornwallis Island, central Canadian Arctic. 1, 4, cranidium UA 8981, dorsal and anterodorsal views, x3 (GSC 1); 2, cranidium and hypostome UA 8982, ventral and dorsal views, respectively, x3 (GSC 9); 3, 6, 7, pygidium UA 8983, dorsal, left lateral, and posterior views, x3 (GSC 9); 5, 9, cranidium UA 8984, anterodorsal and dorsal views, x3 (GSC 1); 8, cranidium UA 8985, dorsal view, x3 (GSC 9); 10, left librigena UA 8986, external view, x3 (GSC 1); 11, left librigena UA 8987, external view, x4 (GSC 1); 12, 16, cranidium UA 8988, dorsal and oblique anterodorsal views, x3 (GSC 9); 13, cranidium UA 8989, dorsal view, x3 (GSC 2); 14, 15, cranidium UA 8990, dorsal and right dorsolateral views, x3 (GSC 1); 17, cranidium UA 8991, dorsal view, x3 (GSC 1); 18, cranidium UA 8992, dorsal view, x5 (GSC 2); 19, left librigena UA 8993, external view, x4 (GSC 2).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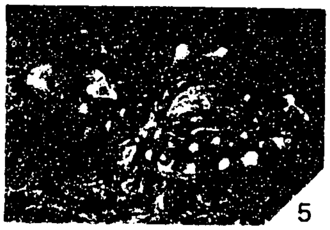
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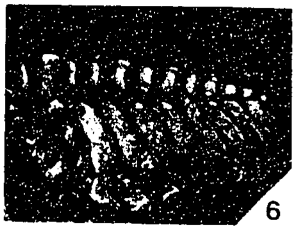
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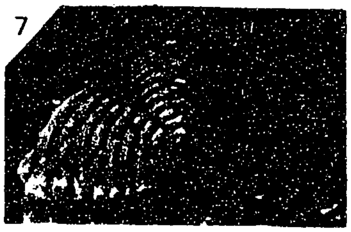
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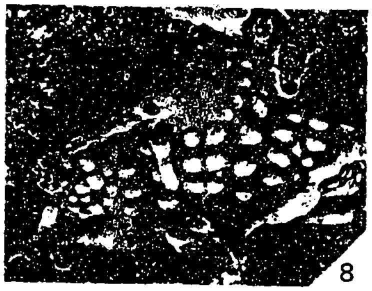
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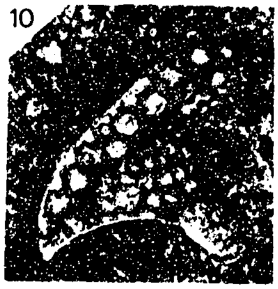
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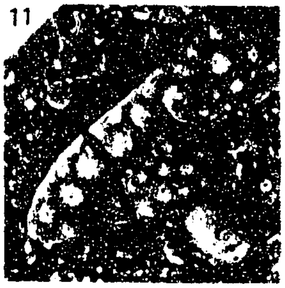
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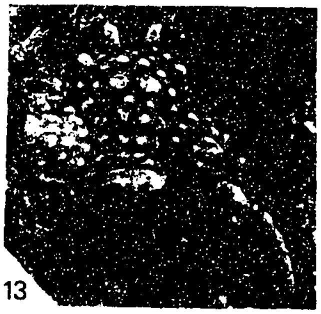
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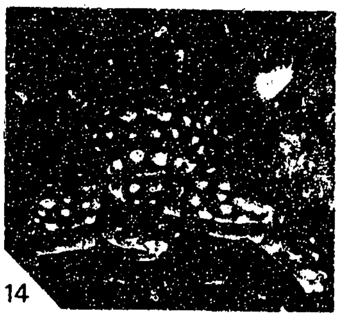
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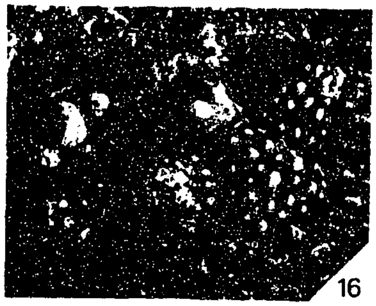
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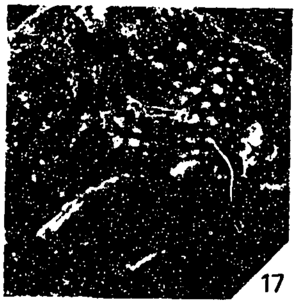
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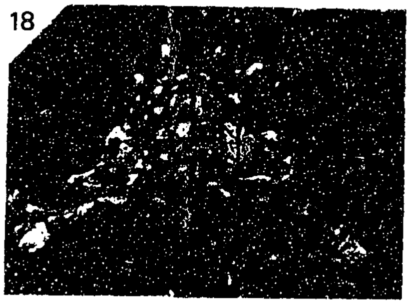
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FIGURE <u>VIII-6</u>--<u>1</u>-<u>5</u>, <u>8</u>, <u>9</u>, <u>Aegrotocatellus</u> n. sp. A, from Localities GSC 3, GSC 4, and GSC 8, Douro Formation, Ludlow (Ludfordian), near Goodsir Creek, eastern Cornwallis Island, central Canadian Arctic. <u>1</u>, <u>4</u>, cranidium UA 8994, dorsal and anterodorsal views, x5 (GSC 8); <u>2</u>, <u>9</u>, cranidium UA 8995, dorsal and right dorsolateral views, x4 (GSC 3); <u>3</u>, cranidium UA 8996, ventral view, x3 (GSC 3); <u>5</u>, <u>8</u>, cranidium UA 8997, anteroventral and ventral views, x4 (GSC 4). <u>6</u>, <u>7</u>, <u>10</u>, <u>14</u>, <u>Aegrotocatellus</u> n. sp. B, from Localities GAB 1 and GAB 2, Douro Formation (Upper Silurian), near Garnier Bay, northern Somerset Island, central Canadian Arctic. <u>6</u>, <u>7</u>, <u>10</u>, cranidium UA 8998, right dorsolateral, dorsal, and anterodorsal views, x3 (GAB 2); <u>14</u>, left librigena UA 8999, external view, x3 (GAB 1). <u>11</u>-<u>13</u>, <u>15</u>-<u>18</u>, <u>Aegrotocatellus</u> n. sp. C, from Localities PAB 3 and PAB 4, Douro Formation (Ludlow), near Prince Alfred Bay, northern Devon Island, central Canadian Arctic. <u>11</u>, <u>12</u>, cranidium UA 9000, dorsal and left dorsolateral views, x4 (PAB 3); <u>13</u>, right librigena UA 9001, external view, x4 (PAB 3); <u>15</u>, <u>16</u>, right librigena UA 9002, dorsal and external views, x3 (PAB 4); <u>17</u>, cranidium UA 9003, dorsal view, x4 (PAB 3); <u>18</u>, cranidium UA 9004, ventral view, x4 (PAB 4).


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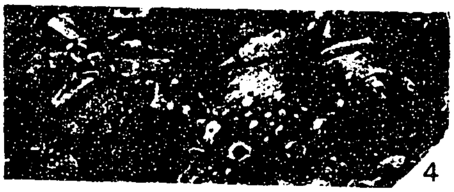
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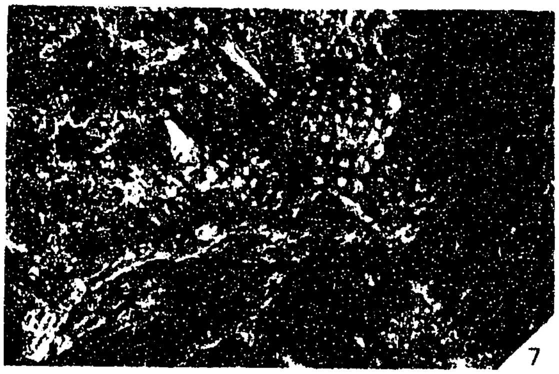
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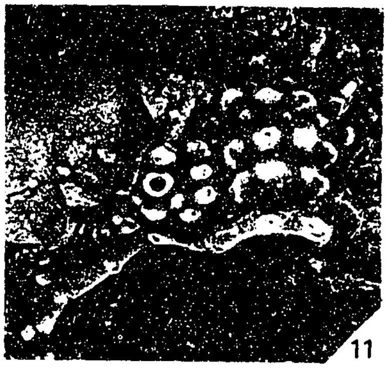
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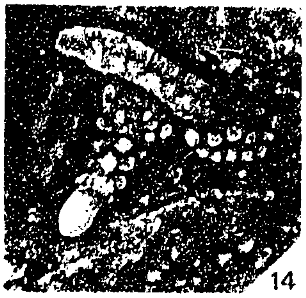
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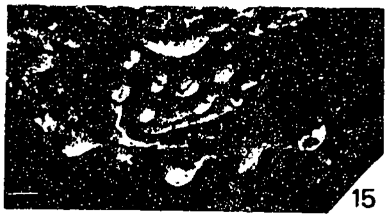
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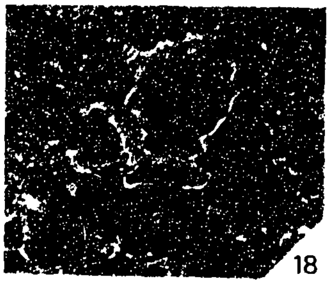
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FIGURE <u>VIII-7</u>--*Perirehaedulus caprus* (Thomas in Thomas and Narbonne, 1979), from Localities GSC 3, GSC 7, and GSC 8, Douro Formation, Ludlow (Ludfordian), near Goodsir Creek, eastern Cornwallis Island, central Canadian Arctic. <u>1</u>, cranidium and thoracic segment UA 9005, dorsal view, x2 (GSC 7); <u>2</u>, cranidium UA 9006, dorsal view, x4 (GSC 8); <u>3</u>, right librigena UA 9007, external view, x4 (GSC 3); <u>4</u>, <u>6</u>, <u>9</u>, cranidium UA 9008, dorsal, left lateral, and anterodorsal views, x3 (GSC 3); <u>5</u>, <u>7</u>, cranidium UA 9009, left lateral and dorsal views, x2 (GSC 7); <u>8</u>, cranidium UA 9010, dorsal view, x3 (GSC 7); <u>10</u>, pygidium UA 9011, dorsal view, x3 (GSC 8); <u>11</u>, right librigena UA 9012, external view, x3 (GSC 3); <u>12</u>, cranidium UA 9013, ventral view, x3 (GSC 3); <u>13</u>, pygidium UA 9014, dorsal view, x3 (GSC 3); <u>14</u>, right librigena UA 9015, internal view, x3 (GSC 8).


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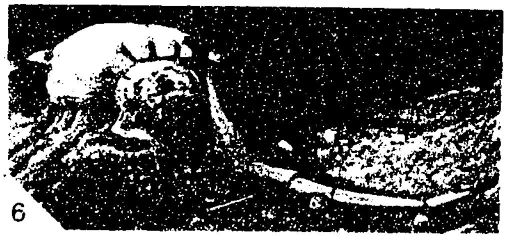
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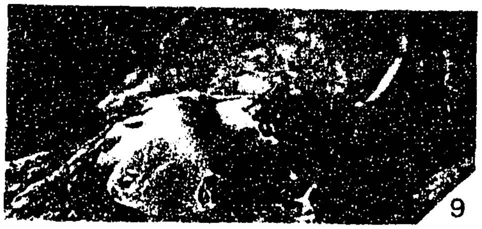
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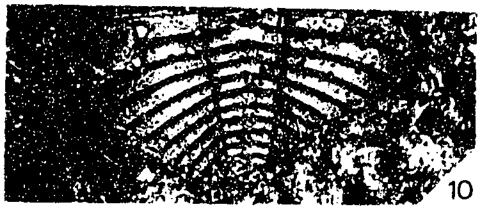
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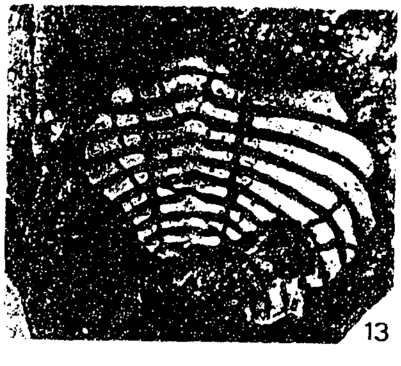
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FIGURE VIII-8--*Perirehaedulus richardsi* n. gen. n. sp., from Localities GAB 1, GAB 2, and GAB 5, Douro Formation (Upper Silurian), near Garnier Bay, northern Somerset Island, central Canadian Arctic. 1, 4, 8, holotype dorsal exoskeleton lacking posterior thoracic segments and pygidium UA 9016, dorsal, left dorsolateral, and anterodorsal views, x3 (GAB 1); 2, 5, 6, cranidium UA 9017, dorsal, anterodorsal, and right dorsolateral views, x3 (GAB 1); 3, cranidium UA 9018, dorsal view, x2 (GAB 2); 7, cranidium UA 9019, dorsal view, x5 (GAB 5); 9, cranidium UA 9020, dorsal view, x3 (GAB 5); 10, pygidium UA 9021, ventral view, x5 (GAB 5); 11, pygidium UA 9022, ventral view, x4 (GAB 5); 12, cranidium UA 9023, dorsal view, x2 (GAB 2); 13, left librigena UA 9024, internal view, x4 (GAB 5).


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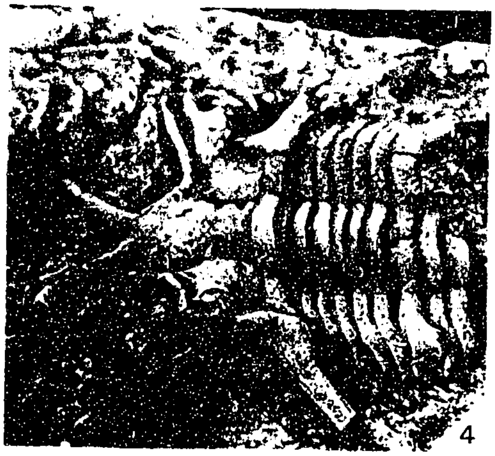
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CHAPTER IX[1]

THE OTARIONINE TRILOBITES HARPIDELLA AND MAUROTARION, WITH SPECIES FROM NORTHWESTERN CANADA, THE UNITED STATES, AND AUSTRALIA

INTRODUCTION

THIS PAPER is third in a series describing the aulacopleurid trilobites of the upper Whittaker Formation and Delorme group of the central Mackenzie Mountains, Northwest Territories, Canada. Adrain and Chatterton (in press) have dealt with the genus *Otarion* Zenker, 1833, and Adrain and Chatterton (submitted) with the subfamily Aulacopleurinae Angelin, 1854.

Following Thomas and Owens (1978), the genus *Maurotarion* Alberti, 1969, has been considered a synonym of *Harpidella* M'Coy, 1849, by most workers. The present study aims to demonstrate that *Maurotarion* is a separate and valid taxon, not particularly similar to *Harpidella*; to provide a species list for each; to describe new species of these genera from the Ashgill to Wenlock of northwestern Canada; and to revise several previously described species from other parts of the world.

Locality information for Canadian material follows Chatterton and Perry (1983, 1984) and Over and Chatterton

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[1] A version of this chapter has been submitted for publication. Adrain, J. M., and Chatterton, B. D. E. Journal of Paleontology.

(1987). Only Harpidella kurrii n. sp., H. greggi n. sp., and Maurotarion messieri n. sp. are given extended written descriptions. The remainder of species treated have either been previously described or are similar enough to described species that they can be dealt with through differential diagnoses.

SYSTEMATIC PALEONTOLOGY

Repository.--Illustrated material is housed in the paleontological collections of the Department of Geology, University of Alberta (UA), the National Museum of Ireland, and the National Museum of Natural History (USNM).

Family AULACOPLEURIDAE Angelin, 1854

Subfamily OTARIONINAE Richter and Richter, 1926

Discussion.--Adrain and Chatterton (in press) have given a diagnosis and list of included genera.

Genus HARPIDELLA M'Coy, 1849

Rhinotarion WHITTINGTON AND CAMPBELL, 1967, p. 458.

?Malimanaspis BALDIS AND LONGOBUCCO, 1977, p. 148.

Type species.--Harpes? megalops M'Coy, 1846, from the upper Llandovery of Ireland.

Other species.--Format of this list follows that for Otarion given by Adrain and Chatterton (in press).

akkae Alberti, 1969; Otarion (Otarion); Pragian, Morocco; single cranidium.

?bowningensis Mitchell, 1888; Cyphaspis; Lochkovian, Elmside Formation, New South Wales, Australia; dorsal exoskeleton; see Chatterton (1971, p. 96, Pl. 24, figs. 8-10).

greggi n. sp.; *Harpidella*; Wenlock (Sheinwoodian), Delorme Group, northwestern Canada; all sclerites.

?*gruanum* Alberti, 1969; *Otarion* (*Otarion*); Pragian, Morocco; two cranidia.

isoplates Tripp, 1954; *Otarion*; Caradoc, Craighead Limestone, upper Ardwell Group, Girvan district, Scotland; see also Tripp, 1980b, Pl. 1, figs. 13, 14; a librigena and a pygidium assigned by Tripp (1980b, Pl. 1, figs. 15, 16) may not belong; five cranidia.

kurrii n. sp.; *Harpidella*; Ashgill, Whittaker Formation, northwestern Canada; all sclerites.

lacrymosa Price, 1980; *Harpidella* (*Harpidella*); Ashgill, Sholeshook Limestone Formation, Wales; dorsal exoskeleton.

magnificum Alberti, 1967; *Otarion* (*Otarionella*); Pragian, Morocco; cranidia and right librigena.

sentosum Whittington and Campbell, 1967; *Rhinotarion*; probably Ludlow, Hardwood Mountain Formation, Baker Pond, Maine; cephalon, thoracic segments; hypostome and pygidium likely among illustrated but unassigned sclerites.

spinafrons Williams in Cooper and Williams, 1935; *Otarion*; Givetian, Tully Formation, New York State; cephala.

stephanophora Hall, 1888; *Cyphaspis*; Lower Devonian, New

York State; cephala; unrevised in modern era.

?taganon Chatterton, Johnson, and Campbell, 1979; Otarionella; late Lochkovian or Pragian, Garra Formation, New South Wales, Australia; cranidia, librigena.

tikkaneni n. sp.; Harpidella; Llandovery (Rhuddanian), Whittaker Formation, northwestern Canada; cranidia, librigenae, pygidia.

trilobus Hu, 1975; Otarion; Caradoc, Edinburg Formation, Virginia; cranidia, librigenae, hypostomes, thoracic segments, pygidia.

validum Alberti, 1969; Otarion (Otarion); Pragian, Morocco; single cranidium.

Diagnosis.--Otarionines with L1 large and with prominent lateral displacement from remainder of glabella; cranidium with strong, even dorsal convexity; preglabellar field typically short, glabella and occipital ring occupying about 70 percent of sagittal length of cranidium in dorsal view; anterior border short (sag., exsag.), with strong and even dorsal convexity, and similar in length medially and laterally; palpebral lobes of moderate size; lateral and posterior librigenal borders usually of nearly equal width; genal spine long; eye socle prominent and usually bilobate; thoracic axial spine present; pygidium small, even for subfamily, with as few as 2, most commonly 3, and as many as 5 axial rings.

Discussion.--As outlined by Adrain and Chatterton (in press), aulacopleurids were rather indiscriminately referred to *Cyphaspis* Burmeister, 1843, in the late nineteenth and early twentieth centuries, and to *Otarion* in the period following Richter and Richter's (1926) placement of *Cyphaspis* in its synonymy. Whittington and Campbell (1967) refigured material of the type species of both *Harpidella* and *Otarion*, and gave reasons for considering the genera synonymous. Thomas and Owens (1978) argued that both *Cyphaspis* and *Harpidella* were valid taxa, generically distinct from *Otarion*. Adrain and Chatterton (in press) have given a species list and new diagnosis for *Otarion* and a differential diagnosis with *Cyphaspis*, including both genera, along with *Namuropyge* Richter and Richter, 1939, in a monophyletic tribe Otarionini.

Unfortunately, *Harpidella* has remained poorly understood, and has essentially been treated as a wastebasket for most otarionine trilobites not belonging to either *Otarion* or *Cyphaspis*. In fact, the popular concept of *Harpidella* in recent years seems to have been centered on species which are herein placed in a separate genus, *Maurotarion* (e.g. *M*. *aitholix* (Thomas, 1978)). This is perhaps due to the following reasons. First, the type material of *H*. *megalops* is rather coarsely preserved. Second, until now, it has been known only from internal molds of cranidia. Third, and most importantly, until now very few closely similar species have been described. With knowledge of the new Canadian species, it becomes evident that *Harpidella* represents a distinctive and long-ranging group of trilobites, with quite different general morphology from that of species assigned to *Maurotarion* (see differential diagnosis under discussion of that genus below). The genera were both established by the Caradoc, and there is every reason to believe that both groups are monophyletic.

As is the case with *Otarion* (see Adrain and Chatterton, in press), diagnosis of *Harpidella* is complicated by its long stratigraphic range and the variety of novel morphologies developed within it. *Harpidella tikkaneni*, for example, is a "stretched" species in which many parts of the dorsal exoskeleton have become lengthened relative to other members of the genus. Other species (*H. sentosa*, *H. greggi*, *H. spinafrons*, etc.) develop varieties of axial, occipital, and marginal spines. Nevertheless, the large, laterally displaced L1, distinctive cranidial profile, and short, convex anterior border, taken together, immediately identify members of the genus and serve to separate them from members of other clades (cf. Figure IX-1.1, IX-1.3 with Figures IX-2.1, IX-3.1, IX-5.1, IX-6.2, IX-8.1, IX-8.5). Although the type species is known only from coarse mold material, these features are all obvious (Figure IX-1), and leave little doubt about the generic makeup.

Apart from their respective generic apomorphies, *Harpidella* and *Maurotarion* are also distinguished from members of the Otarionini by their juvenile cephalic spine array, which Adrain and Chatterton (in press) interpreted as plesiomorphic relative to that of members of Otarionini. Every single species of *Harpidella* and *Maurotarion* for which information is available has spine pairs G1-G3 almost evenly spaced (as opposed to G2 and G3 crowded near the front of the glabella in Otarionini), has Fx1-Fx4 of similar size (as opposed to Fx2 and Fx3 suppressed), and has two major palpebral spines (as opposed to one). Almost all have a single row of cephalic border spines, as opposed to a universal two in Otarionini. The single exception is *H. spinafrons*, which has the typical robust laterally directed row retained in the holaspid, but has also added a small, ventrally directed row (see particularly Figure IX-8.15). This can safely be considered a parallelism with Otarionini, as *H. spinafrons* is the stratigraphically youngest and arguably most derived member of *Harpidella*, and conforms in all other respects to the morphology of that genus. Finally, while the cephalic spine array is nearly identical in *Harpidella* and *Maurotarion*, its condition is interpreted as the primitive state for most of Otarioninae (the genus *Beggaspis* Pribyl and Vanek, 1981, is problematic, as it lacks glabellar spine pairs; there are several ways to interpret this and the genus is the subject of a separate forthcoming work by us). If this is correct, the similarity cannot be taken as evidence that the genera together form a clade (i.e. that they are sister groups).

Hence, at present, the subfamily Otarioninae has three major, at least moderately diverse, components to which the great majority of described species belong: the tribe Otarionini, Harpidella, and Maurotarion. Each is a well-supported monophyletic group, but their relationship to one another is not yet clear.

The only feature possessed by Harpidella sentosa (Whittington and Campbell, 1967), that is unknown in other members of the genus is the prong-like median extension of its anterior border and rostral plate. Recognition of monotypic genera based on autapomorphic species is phylogenetically uninformative and creates paraphyly. If more diversity is found it may eventually prove possible to subdivide Harpidella into constituent monophyletic groups. For the present, however, Rhinotarion is considered a junior subjective synonym.

Baldis and Longobucco (1977) erected Malimanaspis for a single poorly known species from the Middle Devonian of Argentina. The species is certainly distinct from Maurotarion dereimsi (Kozlowski, 1923) (see below), and is similar to two poorly preserved internal molds from Bolivia established as Malimanaspis angustilimbata Pek and Vanek, 1991. Additional and better material from Bolivia, which will be described in a forthcoming work by J.M.A. and G.D. Edgecombe, indicates that Malimanaspis may prove to be a junior subjective synonym of Harpidella.

The otarionine material described by Chatterton et al. (1979, Pl. 105) may represent as many as four separate species, one of which may belong to Harpidella. With the benefit of improved knowledge from the Canadian silicified material, it is possible to revise the association of sclerites as follows, although more material would be necessary to be certain of many of the assignments. Most of the material assigned to Otarion listron Chatterton, Johnson, and Campbell, 1979, including the holotype, has features indicating that the species belongs to Cyphaspis. These include an inflated, densely tuberculate glabella with very small L1, librigenae with a robust genal spine, and thorax with a very long axial spine. In addition, a small cheek assigned by Chatterton et al. (1979, Pl. 105, fig. 19) to their Otarionella taganon has two border spine rows with small accessory spines typical of juvenile librigenae of members of Otarionini (see Adrain and Chatterton, in press), and likely belongs to C. listron. The only problematic feature of the species is its relatively long preglabellar field, which is unusual in Cyphaspis. We tentatively assign the specimens illustrated by Chatterton et al., 1979, Pl. 105, figs. 5-13, and 19 to C. listron. The cranidium illustrated in their Pl. 105, figs. 1-3 was interpreted as a juvenile of C. listron, but the ontogenetic changes required for this to be the case (especially the development of coarse tubercles on the preglabellar field and anterior part of the glabellar late in ontogeny and an increase in ontogeny of the size of L1) have not been observed in any other species, and the cranidium possibly belongs to a species of Otarion. Nevertheless, a cranidium illustrated by Chatterton et al. (1979, Pl. 105, figs. 7, 25) could conceivably be interpreted as a morphological intermediate. Specimens illustrated in Chatterton et al.'s Pl. 105, figs. 4, 21, and 22 all belong to a species of Maurotarion. Differences in preservation (silicified versus poorly preserved calcareous) between these specimens and a paratype of M.? struszi (Chatterton et al., 1979, Pl. 105, figs. 23, 26, 27) make accurate comparisons difficult, but the silicified cranidia do seem at least to have less subrectangular glabellae. Finally, a single librigena and two cranidia (Chatterton et al., 1979, Pl. 105, figs. 14-18, 20), including the holotype of Otarionella taganon, are possibly referable to Harpidella. The large holotype cranidium seems to show the typical large, laterally displaced L1, but has a long preglabellar field. The smaller cranidium, however, has smaller L1. Much more material would be required to determine the affinity of the species with confidence.

HARPIDELLA MEGALOPS (M'Coy, 1846)

Figure IX-1

Harpes? megalops M'COY, 1846, p. 54, Pl. 4, fig. 5.

Harpidella megalops (M'Coy); THOMAS AND OWENS, 1978, p. 71.
PRIBYL AND VANEK, 1981, p. 169, Pl. 1, figs. 1, 2;
MORRIS, 1988, p. 105 (with synonymy). TOMCZYKOWA,
1991, p. 17, fig. 4a.

Otarion megalops (M'Coy). WHITTINGTON AND CAMPBELL, 1967, p.
461, Pl. 19, figs. 1-14, 16.

Diagnosis.--Harpidella with very broad interocular fixigena; preglabellar field slightly longer than usual for the genus; L1 exsagittally elongate; median occipital node small, paired spines absent; librigena with narrow (tr.) field.

Discussion.--This species has heretofore been known only from internal molds of cranidia (Whittington and Campbell, 1967, Pl. 19, figs. 1-14, 16). The type specimens occur on small blocks of sandstone. Further inspection of these blocks revealed a small number of external molds, together with a single internal mold of a pygidium, all of which are illustrated in Figure IX-1. Harpidella megalops is most similar to H. tikkaneni, with which it shares a relatively long preglabellar field, elongate L1, and interocular fixigenae that are broader than in any other members of the genus. The species differ in the more extreme elongation of the cranidium of H. tikkaneni, its much broader librigenal field, and pygidium with a greater number of segments (usually five as opposed to three). The only species with a librigenal field comparably narrow to that of H. megalops is H. triloba (see below).

Temple (1969, p. 221, Pl. 5, figs. 1-5, 7-13, 15-22) referred Ashgill material (described as Llandovery, but see Ingham and Wright in Williams et al., 1972; Cocks and Price, 1975) to Harpidella megalops, but these specimens are clearly not conspecific. Of Temple's illustrated material, his Pl. 5, fig. 22, seems to be referrable to Panarchaegonus Öpik, 1937 (Pribyl and Vanek, 1981, p. 170). The remainder likely represent a distinct, new, species. While several of the cranidial specimens are reminiscent of the morphology of Harpidella, they are difficult to evaluate because of their rather coarse, internal mold, preservation. Nevertheless, if the pygidia assigned to the species are correctly associated (Temple, 1969, Pl. 5, figs. 5, 13), an assignment to Harpidella, or any other currently recognized otarionine, is ruled out, as they have many more axial rings than is usual. The species Harpidella (Harpidella?) helenae Lane, 1979, from the Llandovery of North Greenland, is very similar to Temple's (1969) material in cranidial features. It, too, is associated with a pygidium with many axial rings and well-impressed pleural bands. If the assocations are confirmed by further occurrences, it is possible that these and similar species (e.g. Otarion cf. megalops of Cocks and Price, 1975; Harpidella (s.l.) sp. B of Owen and Bruton, 1980, Pl. 5, figs. 16, 17) belong to a separate, new, otarionine genus. They are otherwise difficult to interpret.

HARPIDELLA TRILOBA (Hu, 1975)

Figure IX-2

Otarion trilobus HU, 1975, p.115, Pl. 1, figs. 2-16, 18?, 19, 20 (non Pl. 1, figs. 1, 17, 21-26).

Mesotaphraspis acris HU, 1976, partim, Pl. 27, figs. 16, 22, 25, 27-29.

Diagnosis.--Harpidella with anterior sections of facial suture only very slightly anteriorly divergent to slightly anteriorly convergent; preglabellar field, interocular fixigena, and glabella with sculpture of very fine granules and moderately dense, coarse tubercles; occipital node low and faint; librigena with inflated eye socle of dorsal continuous band and ventral anterior and posterior lobes; librigenal field narrow (tr.), with sculpture of dense caecal pits and evenly scattered coarse tubercles; posterior border furrow and lateral border furrow uniting to run along dorsal aspect of genal spine; posterior librigenal border with two or three coarse tubercles on dorsal aspect; pygidium with two or three axial rings.

Discussion.--When erected, cranidia and librigenae of this species were incorrectly associated with pygidia belonging to Panarchaegonus (see Hu, 1975, Pl. 1, figs. 21-26). Hu later described the Panarchaegonus species (as

Mesotaphraspis acris Hu, 1976). Work in progress has shown that pygidia assigned by Hu (1976) to *P. acris* include some that belong to *Harpidella triloba* and some belonging to "*Phaseolops*" *conus* Hu, 1971 (to which cornuproetine pygidia belonging to *Stenoblepharum strasburgensis* (Cooper, 1953) were originally misassigned), but none that are actually conspecific with the *Panarchaegonus* cranidia. The separate pygidial morphologies were considered "male" and "female" morphs. A protaspid assigned to *Harpidella triloba* (Hu, 1975, Pl. 1, fig. 1) is an encrinurine (Edgecombe et al., 1988, p. 793-794). Finally, a specimen comprising several articulated thoracic segments assigned to the species (Hu, 1975, Pl. 1, fig. 17) has a broad axial lobe, segments with preannuli and pleurae that seem to taper to a point distal to the fulcrum. All of these features are at odds with the typical morphology of otarionine thoracic segments, and with other specimens confidently associated with this species (Hu, 1975, Pl. 1, fig. 19; Figure 2.16), and the specimen is likely a proetid, probably *Stenoblepharum strasburgensis*.

Harpidella triloba is the oldest well known member of the genus, and resembles various contemporaneous species from the Caradoc of Scotland, including *H. isoplates* (Tripp, 1954), and others described in open nomenclature (e.g. Tripp 1976, Pl. 4, figs. 12, 13; 1980a, Pl. 2, figs. 21, 23, 24). Most of the Scottish material, however, is in the form of somewhat distorted internal molds, making exact comparisons difficult. Harpidella triloba differs from the Ashgill H. kurrii n. sp. in its more expanded L1, anteriorly convergent or slightly divergent as opposed to prominently divergent anterior sections of the facial sutures, more laterally protruded palpebral lobe, cephalic sculpture of more robust tubercles, particularly on the librigenal field, shorter occipital ring, and narrower pygidium.

Material.--Illustrated specimens UA 9025-9043, all from the Edinburg Formation (Blackriver/Caradoc) near Strasburg, Virginia. Most of the illustrated material is from a block purchased by the Australian National University in the late 1960s from a commercial geological specimen company. The precise Edinburg locality from which it is derived is unknown. The remainder of the specimens are from Locality Four of Whittington and Evitt (1954), and were collected by B.D.E.C. and Derek J. Siveter.

HARPIDELLA KURRII n. sp.

Figures IX-3, IX-4

Diagnosis.--Harpidella with anterior sections of facial sutures strongly divergent; glabella long; L1 narrow for genus; interocular fixigena narrow; occipital ring long; dorsal cranidial sculpture of closely scattered, moderately coarse tubercles; librigenal field lacking tubercles; pygidium with three or four axial rings.

Description.--Cranidium with width across midlength (exsag.) of palpebral lobes equal to or slightly less than length (sag.); width across maximum divergence of anterior sections of facial suture 88-93 percent width across palpebral lobes; anterior border (sag., exsag.) two thirds length (sag.) of occipital ring; preglabellar field subequal in length (sag.) to anterior border; anterior border furrow sharply incised, short (sag., exsag.); preglabellar field and frontal area with sculpture of densely scattered moderate to fine tubercles; similar tuberculate sculpture continued on interocular fixigena; Fx1-Fx4 sometimes discernible in holaspides; interocular fixigena narrow, but with some independant swelling; very faint palpebral furrow present; palpebral lobe mainly defined by break in slope and sculpture; palpebral lobe similar in length (exsag.) to L1, narrow, with small, centrally placed, pit; palpebral tubercles suppressed in large holaspides; eye set at about one third height of glabella; glabella with maximum width across basal part of L1 subequal to length (sag.); preglabellar furrow with strong anterior convexity; L1 elongate, less laterally protruded than in most congenerics; axial furrow deep, subparallel to slightly anteriorly convergent in front of L1; S1 deep, of similar depth along entire course, communicating posteriorly with S0; S2 a shallow notch; S3 not obvious; L1 with densely scattered tubercles, slightly finer than those on interocular fixigena; median glabellar lobe with densely but evenly scattered tubercles, similar in size to those on L1 but somewhat less densely scattered; occipital ring longest medially, lacking scattered tubercles or with very few, low, scattered tubercles and with very low occipital node slightly behind sagittal midlength; posterior border furrow deep; posterior border shorter than occipital ring, smooth and lacking in tuberculate sculpture.

Width (tr.) of librigenal field at midlength of eye about one half maximum length (exsag.) in front of genal angle; eye socle bilobate, with anterior lobe larger; field lacking tuberculate ornament, with fine, close-set caecal pits; librigenal trunk not discernible on most specimens; lateral and posterior borders of similar width; posterior border furrow somewhat deeper than lateral border furrow; lateral border furrow shallowing in front of genal angle; posterior border furrow not shallowing, uniting with lateral border furrow to run along dorsal aspect of genal spine; genal spine long, longer than remainder of librigena including anterior doublural projection; doublure narrow, increasing slightly in width anteriorly.

Hypostome with width across shoulder approximately 83 percent sagittal length; middle furrow set two thirds distance posteriorly (sag.); anterior wings relatively long (exsag.), protruded laterally only slightly past shoulder, with blunt lateral aspect; anterior margin slightly ventrally flared; lateral border furrow shallow anteriorly, deepening posteriorly to grade into posterior border furrow;

anterior lobe of middle body narrow, posterior lobe wider; shoulders coming to sharp lateral point; posterior spines somewhat spatulate; doublure very narrow anteriorly, widening slightly posteriorly.

Thoracic segments with axis about 30 percent of total width; axial furrow relatively shallow, communicating weakly with pleural furrow; ring furrow describing very shallow "W" shape; articulating half ring lozenge shaped; axial ring lacking sculpture; thoracic axial spine present, seemingly long; fulcrum set at slightly less than half width of pleural lobe; anterior and posterior pleural bands subequal in length (exsag.); pleural furrow deeper than axial furrow, effacing proximal to pleural tip; pleural tip blunt, with several small tubercles, dorsal articulating facet on anterior band; doublure developed into facet distally, with small vincular notch in posterior part; ventral part of posterior pleural band proximal to fulcrum developed into very short (exsag), groove-like facet for articulation with leading edge of anterior pleural band.

Pygidium with sagittal length including articulating half-ring slightly less than one half maximum width; three or possibly four axial rings; three pleural segments defined, becoming progressively indistinct posteriorly; axial furrows converging rapidly and shallowing posteriorly, nearly effaced behind axis; only first ring furrow well defined, posterior furrows becoming increasingly indistinct;

pleural and interpleural furrows terminating distally at distinct border; border wider anteriorly than posteriorly; posterior margin with row of very fine tubercles or denticles; doublure moderately broad (for subfamily), wider anteriorly, with several very fine terrace lines running subparallel to margin.

Ontogeny.--Some smaller growth stages of this species have been recovered, including a single, very poorly preserved, protaspid (Figure IX-4.29). Transitory pygidia (particularly Figure IX-4.30) agree well with similar-sized sclerites of Otarion huddyi Adrain and Chatterton, in press, Fig. 7.7, 7.9,, except for the absence in Harpidella kurrii of the proto-fulcral spines seen on the pleural field of the former. Small thoracic segments (Figure IX-4.15, IX-4.16) retain short spines on the distal part of the posterior pleural band. The fulcral spines are lost in mature individuals, while the distal pleural spines are reduced to small tubercles (Figures IX-3.6, IX-4.22). The smallest hypostomes (Figure IX-4.23) have, in addition to the posterior spines typical of the subfamily, a pair of short, posterolaterally directed, spines on the shoulder. These spines are lost in more mature specimens (Figure IX-4.14). Small librigena show the single row of border tubercles typical of primitive juvenile otarionines (Figure IX-4.11). These are completely suppressed in mature holaspides of H. kurrii (Figures IX-

3.9, IX-3.11, IX-4.2). No very small cranidia were recovered, but the smallest available are likely still meraspides (Figure IX-4.12, IX-4.13). In contrast to younger members of the genus (see H. greggi below), it appears that a long occipital spine is not present in the early ontogeny of either this species (Figure IX-4.12), H. triloba (Figure IX-2.20, IX-2.21), or possibly H. tikkaneni (Figure IX-5.10). Harpidella kurrii does display the general, primitive, juvenile cephalic spine array of a single P1, fully expressed Fx1-Fx4, evenly spaced G1-G3, and single row of border tubercles. In both H. kurrii and H. triloba, the juvenile features are very small tubercles, in contrast to their development in younger species as prominent tubercles or short spines (e.g. Figure IX-7.1, IX-7.2).

Discussion.--Harpidella kurrii most closely resembles H. tikkaneni n. sp., and is compared with that species below. A comparison with H. triloba is given above.

Material.--Holotype cranidium UA 9045; paratypes UA 9044, 9046-9076, all from the Whittaker Formation, section Avalanche Lake One, 53.5-54 m above base (Ashgill), central Mackenzie Mountains, Northwest Territories, Canada.

Etymology.--After Jari Kurri.

HARPIDELLA TIKKANENI n. sp.

Figure IX-5

Diagnosis.--Harpidella with preglabellar field, median lobe of glabella, and L1 elongate (sag., exsag.); S2 prominent as a deep notch and S3 a faint but distinct furrow; preglabellar furrow with strong anterior convexity; preglabellar field with sculpture of fine, dense, caecal pits, lacking tubercles; glabellar sculpture of sparse, low tubercles restricted to posterior part of median lobe and all of L1; eye socle a single, continuous, narrow band; librigenal field wide, with dense fine caecal pits but lacking tubercles; genal spine very long; pygidium long relative to width (for genus), with five axial rings.

Discussion.--Some of the morphological features of Harpidella tikkaneni (e.g. length of preglabellar field; length of L1; number of pygidial axial rings) might at first seem atypical of the genus. These anomalies, however, seem to be related to a single development: H. tikkaneni is "stretched" as compared with related species. On one-to-one comparison, many features are simply longer (sag., exsag.) than their congeneric homologues, and H. tikkaneni can be distinguished from all other members of the genus on this basis.

Harpidella tikkaneni is most closely comparable to H. kurrii n. sp. The species share a similar cranidial sculpture, similarly widely divergent anterior sections of the facial sutures, and a complete absence of tubercles on the librigenal field. In addition to the differences resulting from the sagittal and exsagittal elongation of H.

tikkaneni, the latter species is distinct from H. kurrii in its more deeply dorsally impressed S2 and non-lobate eye socle which is reduced to a single, narrow band.

Material.--Holotype cranidium UA 9078; paratypes UA 9077, 9079-9099, all from the Whittaker Formation, section Avalanche Lake One, 95.5-97.5 m above base (lower Llandovery), central Mackenzie Mountains, Northwest Territories, Canada.

Etymology.--After Esa Tikkanen.

HARPIDELLA GREGGI n. sp.

Figures IX-6, IX-7

Otarion sp., PERRY AND CHATTERTON, 1979, p. 581, Pl. 70, figs. 23-25.

Diagnosis.--Harpidella with long median occipital spine; single pair of small spines on occipital ring and each thoracic axial ring, sometimes with smaller, abaxial, pair; anterior sections of facial sutures only slightly anteriorly divergent; cranidium with dorsal sculpture of moderate to densely spaced moderate to coarse tubercles; fixigenal, glabellar, and anterior border major juvenile spines usually retained in holaspid; librigenal caecal trunk inflated into broad girder that interrupts lateral border furrow and connects to base of genal spine; librigenal doublure flat and ventrally concave, rimmed laterally by a row of very small, serrate tubercles.

Description.--Cranidium with length (sag., excluding occipital spine) 93 percent of width across palpebral lobes; width across maximum divergence of anterior sections of facial sutures 83 percent of width across palpebral lobes; anterior sections of facial sutures slightly anteriorly divergent; anterior border very short, retaining juvenile border spines as small tubercles; anterior border furrow gently and evenly arcuate, deep; preglabellar field short; interocular fixigena and frontal area with sculpture of moderately sized tubercles, with finer tubercles interspersed, and nearly obscured, very fine caecal pitting; interocular fixigena very narrow; palpebral lobe set off from fixigena by very abrupt change in slope, protruded adaxially at midlength and moderately wide, with small pit set at midlength and nearer to lateral margin and single very small tubercle set slightly behind and adaxial to pit; glabella with sagittal length (excluding occipital ring) 90 percent maximum width across base of L1; L1 large; S1 deep, shallowing somewhat posteriorly near to communication with S0; S2 a subdued notch; S3 not distinct; axial furrows with strong anterior convergence; preglabellar furrow with only weak anterior convexity; L1 with two to four larger tubercles and numerous smaller tubercles; median glabellar lobe with G1-G3 sometimes distinct in mature holaspides, interspersed with moderate to fine, weakly to densely scattered tubercles; occipital node extended into long, posteriorly (not dorsally) directed spine; pair of small spines set behind and just adaxial to posterior termination of S1; often a second, very small pair of spines set behind adaxial half of L1; occipital ring otherwise lacking tubercles; posterior border furrow deep; posterior border with small tubercle at fulcrum.

Librigena with bilobate eye socle, anterior lobe slightly larger; field with width (tr.) at midlength (exsag.) of eye one half field length, sculpture of fine caecal pits and moderately large tubercles interspersed with several smaller tubercles; lateral border narrow, similar in width to posterior border, both with fine granular sculpture; lateral border furrow shallow; posterior border furrow deeper; genal trunk very infated, so as to seem like extension onto field of genal spine base; genal spine tubular, long, not rapidly tapering distally, about same width at base as lateral border; ventrolateral aspect of lateral border changing slope (tr.) abruptly at contact with flattened doublure; row of small denticles running along lateral edge of doublure; doublure slightly ventrally concave, lacking terrace lines; anterior doublural projection of similar width posteriorly and anteriorly.

Rostral plate unknown, but triangular, based on shape of connective sutures.

Mature hypostomes not assigned.

Thorax with long axial spine; each segment with pair of small axial spines; axial lobe about 30 percent width of given segment; ring furrow shallow; axial furrows shallow; pleural furrow deep; anterior and posterior pleural bands of similar length (exsag.); posterior band with three spines, one on proximal part, one on fulcrum, and one on distal part; fulcrum set at two thirds width of pleural lobe.

Pygidium very small; length (sag; including articulating half-ring) 45 percent of width; only one ring and pleural furrow well defined; one or two axial rings very poorly defined posteriorly; pair of small spines set distal to fulcrum on first posterior pleural band; doublure broad, widening slightly anteriorly.

Ontogeny.--Harpidella greggi occurs with Otarion huddyi Adrain and Chatterton, in press, and an undescribed species of Cyphaspis and caution must hence be exercised in assigning growth stages. All very small (i.e. early meraspid degree) otarionine transitory pygidia are similar, and none can be assigned with confidence to H. greggi. Small hypostomes are assigned (Figure IX-7.12, IX-7.13), but these could also belong to the cooccurring otarionine species. Stage one protaspids (Figure IX-7.24, IX-7.25) are illustrated, but these could also belong to various other members of the Order Proetida occurring with H. greggi. There is considerable confidence in the assignment of the remainder of illustrated growth stages.

Last-stage protaspides are notable for the full development of the cephalic spine array as short spines, and posterior pleural band spines are present in all segments of even the smallest transitory pygidium assigned. Transitory pygidia of this species are notable also for the degree to which the pleural tips of protothoracic segments protrude laterally (cf. Figure IX-7.23 and Figures IX-2.27, IX-4.28, IX-5.26). Small cranidia (Figure IX-7.1, IX-7.2, IX-7.6) are very similar to those of other members of the genus, with the exception of the development of the juvenile spine array into relatively long spines, versus subdued tubercles in older species (cf. Figure IX-2.20, IX-2.21, IX-4.12). These spines are reduced in size through ontogeny, but can usually still be distinguished in the holaspid as the most prominent of cranidial tubercles.

Discussion.--The Wenlock Harpidella greggi, the Pragian H. magnifica (Alberti, 1967), and the Givetian H. spinafrons (Williams in Cooper and Williams, 1935; see below) are united by their retention in the holaspid of juvenile anterior border tubercles, development of the median occipital node into a short to long spine flanked by one or two pairs of very short spines, and the inflation of the librigenal trunk into a girder that interrupts the lateral border furrow. In additional, G1-G3 can often be discerned in large holaspids (Figures IX-6.13, IX-8.1, IX-8.5, IX-8.12; Alberti, 1969, Pl. 35, fig. 3a). These features serve genus. The presence of anterior border tubercles or spines, retention in the holaspid of G1-G3, and the long occipital spine can be interpreted as paedomorphic retentions of features seen in the early ontogeny of many otarionines (Figures IX-7.2, IX-10.10; Adrain and Chatterton, in press, Fig. 7.1).

Within this small group, *Harpidella greggi* differs from *H. magnifica* in its sparser tuberculate cranidial sculpture, longer median occipital spine, anterior border tubercles that are retained but not developed into short spines in the holaspid, and more inflated librigenal trunk. It differs also from *H. spinafrons* in several of these features (sparser sculpture, anterior border tubercles as opposed to spines), but shares a similar librigenal sculpture and a similarly long median occipital spine.

Material.--Holotype cranidium UA 9101; paratypes UA 9100, 9102-9152, from the Delorme Group, section Avalanche Lake Four, 126 m above base, and section Avalanche Lake Two, 242.5-249 m above base (Wenlock, Sheinwoodian), central Mackenzie Mountains, Northwest Territories, Canada.

Etymology.--After Randy Gregg.

HARPIDELLA SPINAFRONS (Williams in Cooper and Williams, 1935)

Figure IX-8

Otarion spinafrons WILLIAMS IN COOPER AND WILLIAMS, 1935, p.

835, Pl. 66, figs. 7, 19, 22.

Diagnosis.--Harpidella with long occipital spine; G1-G3 prominent in holaspid; moderately inflated librigenal trunk; and double row of cephalic border spines in holaspid.

Discussion.--Williams (in Cooper and Williams, 1935) compared H. spinafrons with "Cyphaspis" craspedota Hall, 1888. A more significant comparison might be with "Cyphaspis" stephanophora Hall, 1888 (Pl. 34, figs. 2-6), which shares the retention of the cephalic border spines in the holaspid, and may even have the autapomorphic second row seen in H. spinafrons. The species has not been revised and is unknown from photographic illustrations, but it does appear to belong to the H. greggi-H. spinafrons group (see discussion under H. greggi above). Harpidella stephanophora differs from H. spinafrons in its shorter occipital spine. H. spinafrons was compared with H. greggi above. It differs from H. magnifica (Alberti, 1969) in its double border spine row, longer occipital spine, and coarser glabellar tuberculation.

Material.--Holotype cephalon USNM 89751; paratype USNM 89751a, topotypes USNM 89751b, c, all from the Tully Formation, West Brook Member (Givetian), West Brook, three miles south of Sherburne, New York State.

Genus MAUROTARION Alberti, 1969

Tricornotarion CHATTERTON, 1971, p. 74.

Nomenclatural note.--Cyphaspis dereimsi Kozlowski, 1923, [illegible] type species of *Harpidella* (*Branisella*) Pribyl and Vanek, 1981. The species is an autapomorphic representative of *Maurotarion* (see species list below), and as such *Branisella* would fall into junior subjective synonymy of *Maurotarion*. The generic name *Branisella*, however, was previously established by Hoffstetter (1969) for an Oligocene primate, and *Branisella* Pribyl and Vanek is therefore a junior objective homonym.

Type species.--*Harpidella maura* Alberti, 1967, from the Ludlow of Morocco.

Other species.--

aitholix Thomas, 1978; *Harpidella* (*Harpidella*); Wenlock, England; all exoskeletal parts; Thomas (1978) referred other material from the Coalbrookdale Formation (Thomas, 1978, Pl. 8, figs. 11, 12, 15, 17) to the North African *Maurotarion maura* (Alberti, 1967), but did not state how he considered this material to differ from that assigned to *M. aitholix*, nor did he provide a differential diagnosis for the species. There do not seem to be any obvious differences between the two sets of material figured by Thomas (1978), and all should likely be referred to *M. aitholix*. This species is very similar to *M. maura*, and a more satisfactory contrast might be possible if material other than cranidia were known for the latter. Alberti (1969, Pl. 46, fig. 19) assigned a pygidium, but Thomas (1978, p.

34) pointed out that it did not agree with that of M. aitholix, and indeed it is probably referrable to a species of Cyphaspis. Cranidia of M. maura do appear to differ from those of M. aitholix in the wider anterior divergence of the anterior sections of the facial sutures (cf. Alberti, 1969, Pl. 36, figs. 1-3 with Thomas, 1978, Pl. 8, figs. 1, 3, 12, 15, 17), tubercles restricted to posterior edge of occipital ring versus scattered forward on ring in most specimens of M. aitholix, and generally more subdued tuberculate sculpture on the median glabellar lobe of M. maura.

axitiosum Campbell, 1977; Otarion; Lochkovian, Oklahoma; dorsal exoskeleton.

christyi Hall, 1854; Cyphaspis; Wenlock, Waldron Shale, Waldron, Indiana; dorsal exoskeleton; see Fortey and Owens (1979, Fig. 2G, 2H) and Johnson (1985, p. 137).

cimex Haas, 1968; Harpidella; Eifelian, Gebze Formation, northwestern Turkey; single cranidium.

dereimsi Kozlowski, 1923; Cyphaspis; the lectotype (designated by Wolfart in Wolfart and Voges, 1968, p. 56) is from the Upper Belén Formation (Eifelian? or Givetian; see Racheboeuf, 1992) at Tarabuco, Chuquisaca Department, Bolivia; many specimens similar to the type are known from the Icla Formation (Emsian) at Padilla, and also from the Schaphiocoelia Zone (base of Icla Formation, upper Pragian to lower Emsian) at Presto El

Peral; this stratigraphic range has not been observed in any other trilobite species in the sequence (G.D. Edgecombe, personal commun.), and it is possible that further study will reveal that more than one species is involved. The species is an autapomorphic representative of Maurotarion, differing from typical congenerics mainly in its widened and flattened librigenal lateral borders and genal spines. See nomenclatural note regarding Branisella above.

distincta Pribyl and Vanek, 1981; Harpidella (Harpidella); Pragian, Vinarice Limestone, Bohemia; single fragmentary cranidium; nomen dubium.

elegantulum Loven, 1846; Proetus; upper Wenlock, Mulde Marl, Gotland, Sweden; all exoskeletal parts; see Haas (1968, Pl 28, figs. 11-13); Schrank (1972, Pl. 7, fig. 1); Fortey and Owens (1979, Fig. 2A-2F); material from German glacial erratics assigned to the species by Schrank (1972, Pl. 7, figs. 2-7) is not conspecific and probably represents a new species, differing most obviously in the possession of a thoracic axial spine on the sixth segment and much denser tuberculate cranidial sculpture.

hama Šnajdr, 1984; Conoparia; Ludlow, Kopanina Formation, Bohemia; single cranidium; nomen dubium.

?infrequens Pribyl, Vanek, and Hörbinger, 1985; Harpidella (Harpidella); Ludlow, Kopanina Formation, Bohemia;

single cranidium; nomen dubium.

institita Whittington and Campbell, 1967; *Otarion*; probably Ludlow, Hardwood Mountain Formation, Baker Pond, Maine; cephalon, undetermined hypostomes, thoracic segments, and pygidia.

kobayashii Pribyl and Vanek, 1981; *Harpidella* (*Harpidella*); Emsian, Chýnice Limestone, Bohemia; two cranidia.

?*lodenicensis* Pribyl, Vanek, and Hörbinger, 1985; *Harpidella* (*Harpidella*); Wenlock, Liten Formation, Bohemia; two cranidia; nomen dubium.

messieri n. sp. *Maurotarion*; Llandovery (Rhuddanian), Whittaker Formation, central Mackenzie Mountains, Northwest Territories, Canada; cranidia, librigenae, hypostomes, thoracic segments?, pygidia.

?*munroei* Strusz, 1964; *Otarion*; late Lochkovian or Pragian, Garra Formation, New South Wales, Australia; two poorly preserved cephala; see Chatterton et al. (1979, Pl. 105, figs. 23, 26, 27) for illustrations of the paratype.

neptis Alberti, 1967; *Harpidella*; Pragian, Morocco; two cranidia.

?*newlandensis* Begg, 1950; *Cyphoproetus*; Llandovery, Newlands Formation, Scotland; three cranidia; see Howells (1982, p. 22, Pl. 6, figs. 12-14); nomen dubium.

obnoxium Šnajdr, 1978; *Otarion*; Llandovery, near Hýskov, Bohemia; two cranidia, pygidium doubtfully belonging;

nomen dubium.

?occidentalis Owen, 1981; Harpidella (s.l.); Ashgill, Oslo region, Norway; cranidia.

periergum Haas, 1969; Otarion (Otarion); Pragian, Nevada; cranidia, librigenae, thoracic segments, pygidium.

plana Tomczykowa, 1991; Harpidella; lower Pridoli, Poland; two cranidia.

plautum Whittington and Campbell, 1967; Otarion; probably Ludlow, Hardwood Mountain Formation, Baker Pond, Maine; cephala, undetermined hypostomes, thoracic segments, and pygidia.

struszi Chatterton, 1971; Otarion (Tricornotarion); Emsian, Taemas Formation, New South Wales, Australia; cranidia, librigenae.

tantula Pribyl and Vanek, 1981; Harpidella (Harpidella); Pragian, Dvorce-Prokop Limestone, Bohemia; five cranidia.

?tantuliformis Pribyl, Vanek, and Hörbinger, 1985; Harpidella (Harpidella); Lochkovian, Lochkov Formation, Bohemia; two cranidia; nomen dubium.

thomasi Clarkson and Howells, 1981; Harpidella (Harpidella); Llandovery (Telychian), Upper Reservoir Formation, Scotland; counterpart molds of anterior part of single exoskeleton.

zlichovensis Pribyl and Vanek, 1981; Harpidella (Harpidella); Emsian, Zlíchov Limestone, Bohemia;

coarsely preserved molds of articulated individual and fragmentary exfoliated cranidium; nomen dubium.

Diagnosis.--Otarionine trilobites with glabella low and weakly inflated, deviating little from the sagittal profile of the entire cranidium; L1 variably sized, but lacking significant lateral protrusion from outline of glabella; anterior border furrow describing shallow, inverted "V"; anterior border long, with posterior two thirds usually flattened, longer medially than laterally; palpebral lobes large, long, and protruding laterally; librigena with lateral border typically inflated and broader than posterior border, and with field typically narrow (tr.); thoracic axial spine present only in some species.

Discussion.--*Maurotarion* differs from *Harpidella* in its much less inflated, usually less sculptured, glabella; typically longer preglabellar field; universally much longer anterior border that is longer medially than laterally; anterior border furrow which describes a shallow, anteriorly directed "V", versus evenly arcuate; much larger, more laterally protruded palpebral lobes and correspondingly larger eyes; librigenal field that is typically shorter and usually with very subdued sculpture; librigenal lateral border that is wider than posterior border, often inflated, with shallow lateral border furrow; and genal spine that often has an inflated base, with a rapid taper distally.

Chatterton (1971) erected *Tricornotarion* for a single species from the Emsian of Australia. Maurotarion struszi (Chatterton, 1971; see below) is very unusual in its possession of a long occipital spine in the adult, fusion of juvenile spine pairs G1-G3 into single median spines, and development of P1 and P2 into dorsally directed spines. Its pygidium is unknown. Despite their unique fusing and shape, the juvenile spines correspond exactly to the Harpidella/Maurotarion pattern. Furthermore, the librigenae (Figure IX-10.5 to IX-10.7) are typical of Maurotarion, with narrow, unsculptured field, shallow lateral border furrow, and somewhat inflated lateral border. The species seems to be an autapomorphic member of Maurotarion. As mentioned above, there is nothing to be gained from recognizing autapomorphic, monotypic genera, except the creation of a paraphyletic group, in this case Maurotarion. Hence, Tricornotarion is regarded herein as a junior subjective synonym.

Despite the range of morphologies developed, most members of the genus are immediately distinguished by their low, subquadrate glabellae and very large palpebral lobes. The existence of a group thus characterized has long been recognized (e.g. Haas, 1969, p. 646), but the uncertain composition of Harpidella has meant that in recent years (e.g. Pribyl and Vanek, 1981), these trilobites have generally been assigned to that genus. With the demonstration of the rather different morphology of

Harpidella, and its taxonomic restriction above, it becomes evident that a separate monophyletic group is represented, of which Maurotarion maura is a typical member.

MAUROTARION MESSIERI n. sp.

Figures IX-9, IX-10.18 to IX-10.20, IX-10.22 to IX-10.25

Diagnosis.--Maurotarion lacking cephalic tuberculate sculpture; interocular fixigenae and glabella smooth, and lacking any sculpture whatever; interocular fixigena broad and slightly inflated; S2 very prominently impressed (for subfamily); S1 long (exsag.), with prominent deep middle part; median occipital node extremely small; anterior lobe of hypostomal middle body long, with middle furrow set posteriorly.

Description.--Cranidium with length (sag.) approx. 80 percent of maximum width across posterior part of fixigena, 88 percent of width across palpebral lobes, and subequal to width across maximum point of divergence of anterior sections of facial suture; anterior sections of facial sutures strongly anteriorly divergent, reaching maximum divergence prior to anterior border furrow, opposite midlength of preglabellar field; anterior border subequal to length of occipital ring sagittally, shortening rapidly exsagittally; anterior border most convex anterodorsally, sloping evenly posteroventrally over posterior two thirds, lacking sculpture; anterior border furrow with more or less sharp break in curvature sagittally, of moderate depth;

preglabellar field long, about two and a half times as long (sag.) as occipital ring, with densely scattered fine caecal pits; bicomposite eye ridge moderately well expressed in large holaspides, more strongly expressed in proximal part; preglabellar furrow with gentle anterior convexity, deep; axial furrows converging slightly anteriorly to run smoothly into arc of preglabellar furrow; interocular fixigenae broad, slightly inflated, lacking sculpture; palpebral lobes large, protruding laterally past maximum divergence of anterior sections of facial suture, subequal in length (exsag.) to L1, with small but prominent central pit set only slightly lateral to midwidth and with P1-2 fully suppressed in holaspid; L1 large, slightly more than half as broad as long, lacking sculpture; S1 deep anteriorly, shallowing posteriorly; S2 a deep, short, transverse notch; L2 with no independant inflation; S3 not evident; median glabellar lobe low, broad, and smooth, lacking sculpture; occipital ring relatively short (sag., exsag.), lacking sculpture except for very small, subdued median occipital node set just behind midlength (sag.); posterior border short (exsag.), unsculptured.

Librigenal field with sculpture of fine caecal pits similar to that on preglabellar field; librigenal trunk distinct but not inflated; field with width (tr.) under midlength of eye slightly less than half length (exsag.); eye with very subdued, indistinct, socle; lateral border about same width as posterior border immediately in front of genal spine, but broadening significantly anteriorly, lacking sculpture; lateral border furrow shallow; posterior border furrow deeper; lateral and posterior border furrows unite to run along dorsal aspect of genal spine as very faint furrow that effaces distally; genal spine tapering rapidly to sharp point, slightly longer than remainder of librigena, excluding anterior doublural projection; doublure of similar width posteriorly and anteriorly, with several very subdued terrace lines running subparallel to lateral margin.

Hypostome with length (sag.) subequal to or slightly shorter than maximum width across anterior wings; width across shoulders 71-72 percent width across anterior wings; anterior lobe of middle body very long, middle furrow set at about 80 percent of hypostomal length (sag.) posteriorly; anterior wing with tiny wing process bearing small ventral pit and dorsal boss; anterior margin flared ventrally; lateral border furrow deep, not impressed anteriorly opposite wings, running smoothly into middle furrow, but interrupted immediately behind middle furrow by lateral protrusion of posterior lobe of middle body; lateral border furrow resuming behind lateral extent of posterior lobe of middle body to run into evenly arcuate posterior border furrow; posterior lobe of middle body very short (sag., exsag.), describing shallow "U"; lateral border narrow, broadest anteriorly, not protruded strongly laterally at shoulder; posterior spines small, tubular, directed slightly posteromedially; entire hypostome with moderate ventral convexity.

Thoracic segments not definitely assigned (see discussion below).

Pygidium with length (sag., excluding articulating half-ring) about 40 percent width; first axial ring and ring furrow well expressed, posterior rings and furrows progressively effaced; three to four rings present; only anteriormost pleural furrow deep, remainder more or less effaced; pleura slightly dorsally convex proximally, dorsally concave distally in front of border; axial furrows deeper anteriorly, deepening at contact with each ring furrow, nearly effaced but meeting posteriorly to fully define axis; axis with weak dorsal convexity (sag.); border broad, of similar width posteriorly and anteriorly; doublure narrow posteriorly, broadening anteriorly; dorsal surface of pygidium entirely lacking tuberculate sculpture.

<u>Ontogeny</u>.--A few very coarsely preserved protaspides have been recovered (Figure IX-10.22 to IX-10.25). These were collected from a horizon at which <u>Aulacopleura</u>? <u>ranfordi</u> Adrain and Chatterton, submitted, also occurs. That species is considerably less common, but some of the protaspides could well belong to it. Transitory pygidia are quite distinct, and the similarity of those assigned to

Maurotarion messieri to those of other otarionines indicates considerable confidence in the association. Small cranidia of M. messieri (Figure IX-9.19 to IX-9.21, IX-9.39 to IX-9.45) show that, early in ontogeny, the primary spines are the sole large tubercles developed. They are progressively shrunk and completely suppressed in the holaspid. The median occipital spine, contrary to the situation in other otarionine species (particularly Otarion, see Adrain and Chatterton, in press), is never very large, even in early ontogeny. It, too, becomes smaller and is nearly indistinct in the holaspid. Small librigenae (Figure IX-9.28) have a characteristic granular sculpture on the field and prominent lateral border tubercles, features seen also in younger members of the genus (cf. Figures IX-9.28 and IX-10.15, IX-10.16).

Discussion.--There are no obvious very close comparisons for Maurotarion messieri among described species. This is certainly due to the near absence of well known Upper Ordovician and Llandovery members of the genus. The species can be distinguished from most of its congenerics in its nearly total lack of any dorsal tuberculate sculpture.

Illustrated thoracic segments (Figure IX-9.16 to IX-9.18, IX-9.24, IX-9.25) may belong to Harpidella tikkaneni. All species of Harpidella for which definite information is available possess a thoracic axial spine, whereas the occurrence of the feature is variable within Maurotarion, although most species lack a spine.

There is likewise some uncertainty about assignment of hypostomes. Only one obvious type was recovered, and specimens are assigned to Maurotarion messieri mainly on the basis of that species' more common occurrence. The available specimens also have a much more posteriorly placed middle furrow than hypostomes definitely assigned to Harpidella species (Figures IX-2.18, IX-2.19, IX-4.14).

Material.--Holotype cranidium UA 9153; paratypes UA 9154-9173, 9565-9571, 9588-9594, from section Avalanche Lake One, 95.5-98.5 m above base, and Avalanche Lake FourB, 131.3 m above base.

Etymology.--After Mark Messier.

MAUROTARION STRUSZI (Chatterton, 1971)

Figure IX-10.1 to IX-10.9, IX-10.12

Discussion.--The morphology of this species, and its assignment to Maurotarion, was discussed above. A single protaspid has been recovered, along with some transitory pygidia. The assignment of the specimen illustrated in Figure IX-10.8 may be doubtful, as it bears protofulcral spines, unknown in other members of the genus.

Material.--Topotype specimens UA 9572-9579 from the Emsian Taemas Formation, locality A of Chatterton (1971), New South Wales, Australia.

MAUROTARION INSTITA (Whittington and Campbell, 1967)

Figure IX-10.10, IX-10.11, IX-10.13 to IX-10.17, IX-10.21

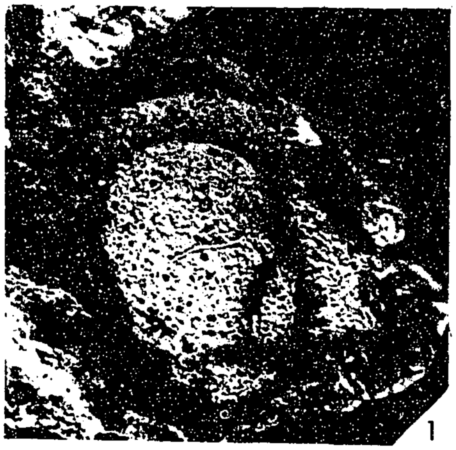
Discussion.--Study of topotype material (collected by B.D.E.C and S.E. Speyer) from the Baker Pond locality has led to the following emendations of the treatment by Whittington and Campbell (1967).

In addition to *Harpidella sentosa* (Whittington and Campbell, 1967), Whittington and Campbell considered that three additional aulacopleurid species were present, two of which they formally named, and one of which they described in open nomenclature. Allowing for the considerable distortion of the Baker Pond specimens, the latter material (Whittington and Campbell, 1967, Pl. 5, figs. 7, 8, 12, 17, 19-26) agrees in all substantial respects (e.g. length of anterior border and preglabellar field, glabellar outline, size of L1, size of eye, length of genal spine) with *Maurotarion plautum* (Whittington and Campbell, 1967), and we consider it referrable to that species. Secondly, one cranidium assigned to *M. plautum* (Whittington and Campbell, 1967, Pl. 7, figs. 8, 11, 12) differs from others of that species in its glabella with axial furrows subparallel versus anteriorly convergent, very small L1, and dense tuberculate sculpture. It resembles *M. instita* in all of these features and almost certainly belongs to that species.

Whittington and Campbell illustrated light photographs of a range of small aulacopleurid sclerites. Micrographs of additional examples are illustrated to allow better comparison. With three species occurring in the fauna, all of which can be expected to have small growth stages with similar spine patterns, there is considerable ambiguity in associations; we have assigned the illustrated material to *Maurotarion* *instita* because it is by far the most common of the species in the samples from which the material was derived.

Material.--Illustrated specimens UA 9580-9587, probably Ludlow, Hardwood Mountain Formation, Baker Pond, Maine.

FIGURE IX-1--*Harpidella megalops* (M'Coy, 1846), from the Llandovery (Telychian) of Cong, County Galway, Ireland. Figs. 1-4 are latex casts from external molds; fig. 5 is an internal mold; all magnifications are x10. 1, 2, dorsal and right lateral views of cranidium; 3, dorsal view of cranidium; 4, external view of left librigena; 5, dorsal view of internal mold of pygidium.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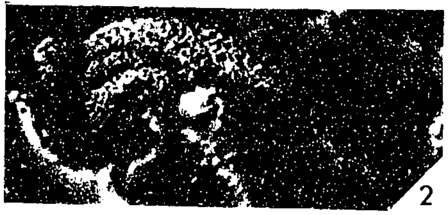
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FIGURE *IX-2*--*Harpidella triloba* (Hu, 1975), from the Edinburg Formation (Caradoc), near Strasburg, Virginia. Specimens in figs. 1-15 and 17 were derived from a block purchased by the Australian National University; the exact Edinburg locality from which it was collected is not known. The remainder of the specimens are from Locality Four of Whittington and Evitt (1954). Magnifications x20 except where otherwise noted. *1*, *4*, *8*, *12*, cranidium UA 9025, dorsal, left lateral, anterior, and posterodorsal views; *2*, *5*, *11*, cranidium UA 9026, dorsal, left lateral, and ventral views; *3*, *6*, cranidium UA 9027, dorsal and left lateral views; *7*, *17*, left librigena UA 9028, external and internal views; *9*, *10*, cranidium UA 9029, dorsal and left lateral views; *13*, left librigena UA 9030, external view; *14*, right librigena UA 9031, external view; *15*, right librigena UA 9032, external view; *16*, thoracic segment UA 9033, dorsal view; *18*, hypostome UA 9034, ventral view, x20, SEM; *19*, hypostome UA 9035, ventral view, x28, SEM; *20*, cranidium UA 9036, dorsal view, x40, SEM; *21*, cranidium UA 9037, dorsal view, x40, SEM; *22*, pygidium UA 9038, dorsal view, x38, dorsal view; *23*, *24*, pygidium UA 9039, dorsal and posterior views, x20; *25*, transitory pygidium UA 9040, dorsal view, x40, SEM; *26*, transitory pygidium UA 9041, dorsal view, x40, SEM; *27*, pygidium UA 9042, dorsal view, x40, SEM; *28*, pygidium UA 9043, dorsal view, x38, SEM.

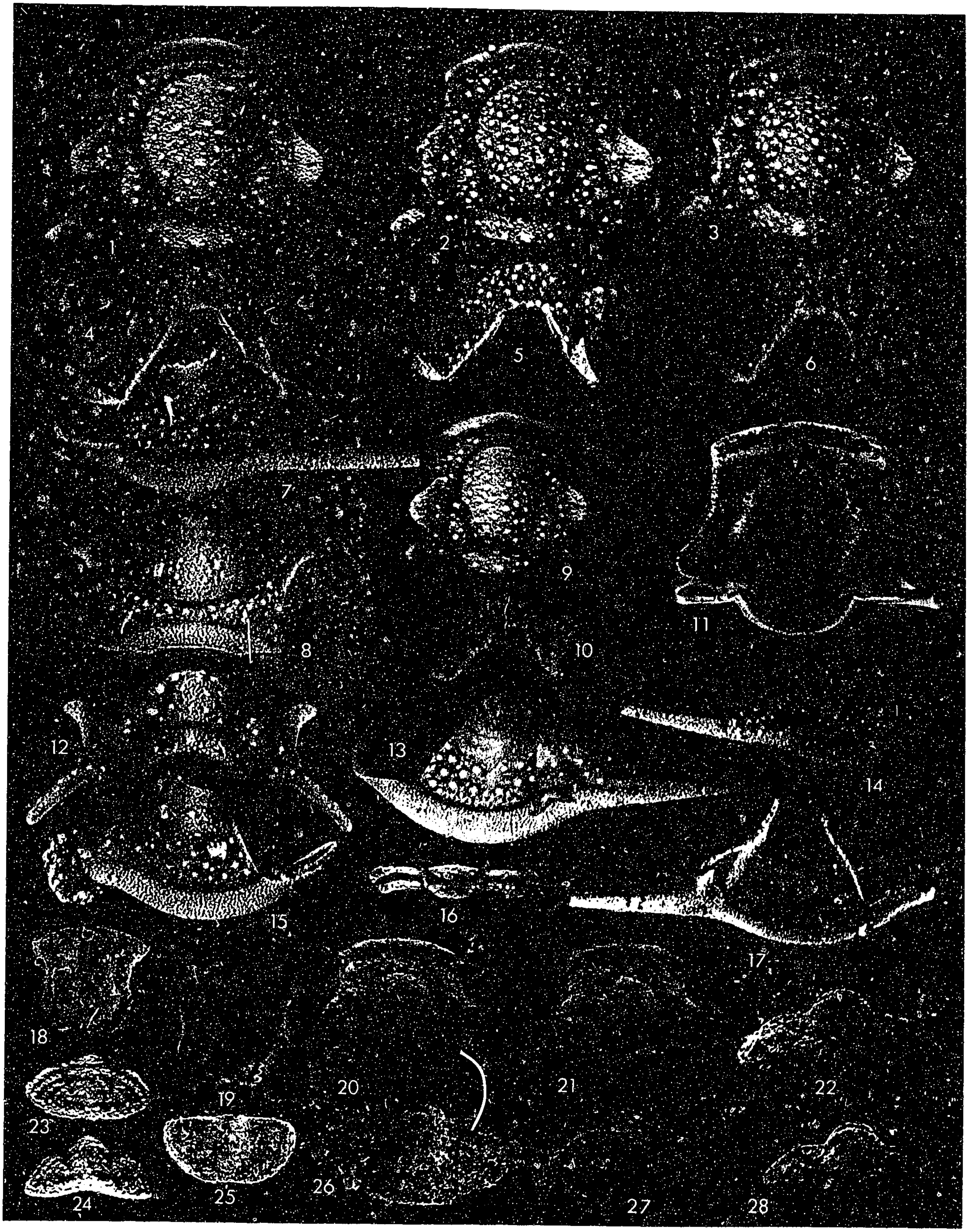
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FIGURE IX-3--*Harpidella kurrii* n. sp., from section Avalanche Lake One, 53.5 m above base, Whittaker Formation (Ashgill), central Mackenzie Mountains, Northwest Territories, Canada. All magnifications x15. 1, 5, 12, cranidium UA 9044, dorsal, left lateral, and anterior views; 2, 7, 13, holotype cranidium UA 9045, dorsal, left lateral, and anterior views; 3, cranidium UA 9046, dorsal view; 4, 10, cranidium UA 9047, dorsal and left lateral views; 6, 14, thoracic segment UA 9048, dorsal and left lateral views; 8, pygidium UA 9049, dorsal view; 9, right librigena UA 9050, external view; 11, right librigena UA 9051, external view; 15, right librigena UA 9052, external view.

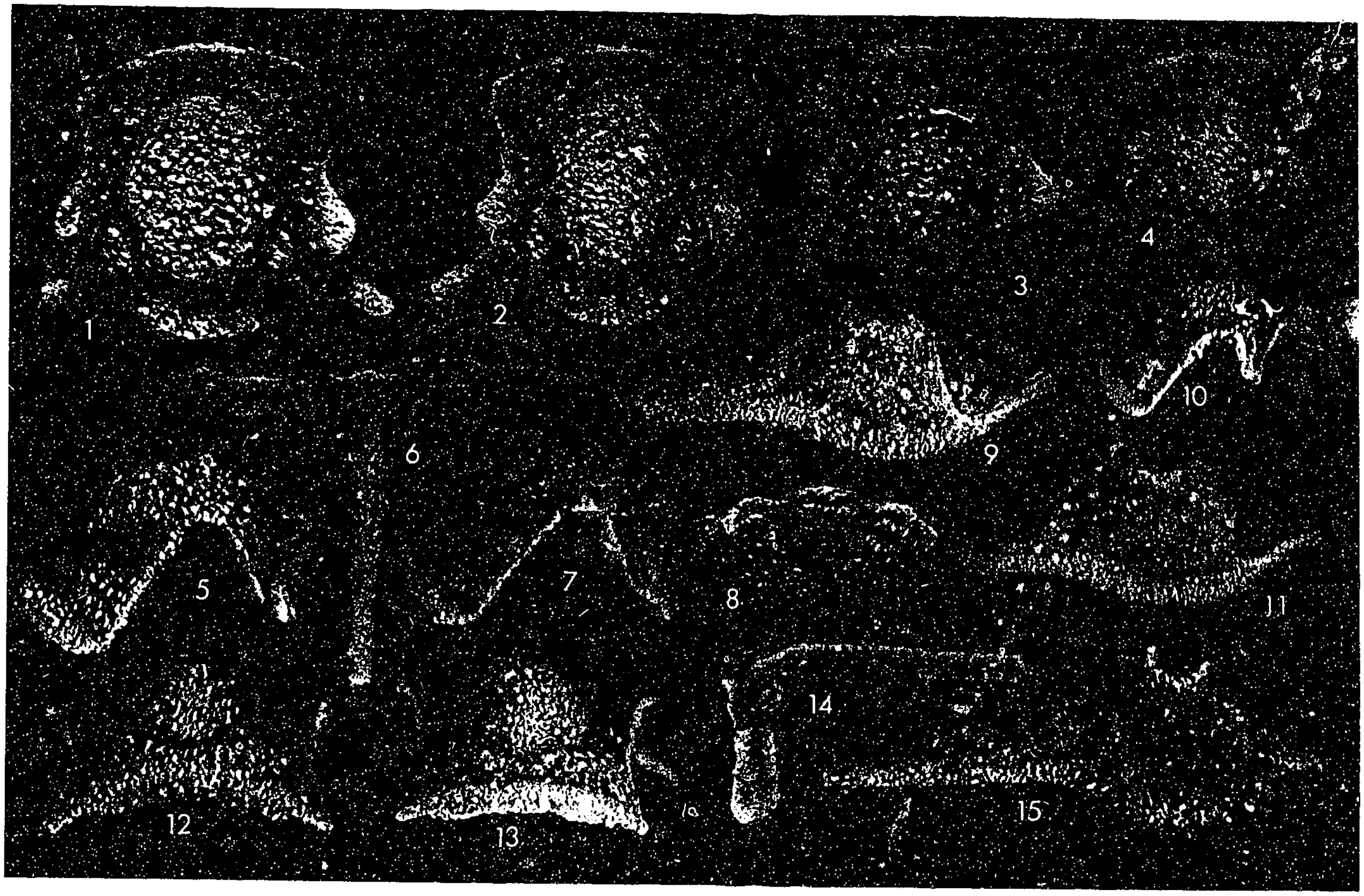
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FIGURE <u>IX-4</u>--<u>Harpidella</u> <u>kurrii</u> n. sp., from section Avalanche Lake One, 53.5-54 m above base, Whittaker Formation (Ashgill), central Mackenzie Mountains, Northwest Territories, Canada. All figures are scanning electron micrographs. <u>1</u>, <u>4</u>, <u>17</u>, cranidium UA 9053, left lateral, dorsal, and anterior views, x15, x12, and x15; <u>2</u>, left librigena UA 9054, external view, x16; <u>3</u>, cranidium UA 9055, dorsal view, x15; <u>5</u>, <u>8</u>, cranidium UA 9056, ventral and dorsal views, x24 and x20; <u>6</u>, <u>10</u>, left librigena UA 9057, internal and external views, x28; <u>7</u>, cranidium UA 9058, anterodorsal view, x15; <u>9</u>, cranidium UA 9059, left lateral view, x15; <u>11</u>, left librigena UA 9060, dorsal view, x28; <u>12</u>, cranidium UA 9061, dorsal view, x56; <u>13</u>, cranidium UA 9062, dorsal view, x56; <u>14</u>, <u>19</u>, hypostome UA 9063, ventral and dorsal views, x38 and x45; <u>15</u>, <u>16</u>, thoracic segment UA 9064, dorsal and posterior views, x30; <u>18</u>, left librigena UA 9065, external view, x18; <u>20</u>, <u>21</u>, pygidium UA 9066, dorsal and ventral views, x38 and x33; <u>22</u>, <u>27</u>, thoracic segments UA 9067, dorsal and ventral views, x40 and x38; <u>23</u>, hypostome UA 9068, ventral view, x38; <u>24</u>, hypostome UA 9069, ventral view, x38; <u>25</u>, pygidium UA 9070, dorsal view, x38; <u>26</u>, pygidium UA 9071, ventral view, x38; <u>28</u>, transitory pygidium UA 9072, dorsal view, x38; <u>29</u>, protaspis UA 9073, dorsal view, x56; <u>30</u>, transitory pygidium UA 9074, dorsal view, x75; <u>31</u>, transitory pygidium UA 9075, dorsal view, x 56; <u>32</u>, pygidium UA 9076, dorsal view, x55.

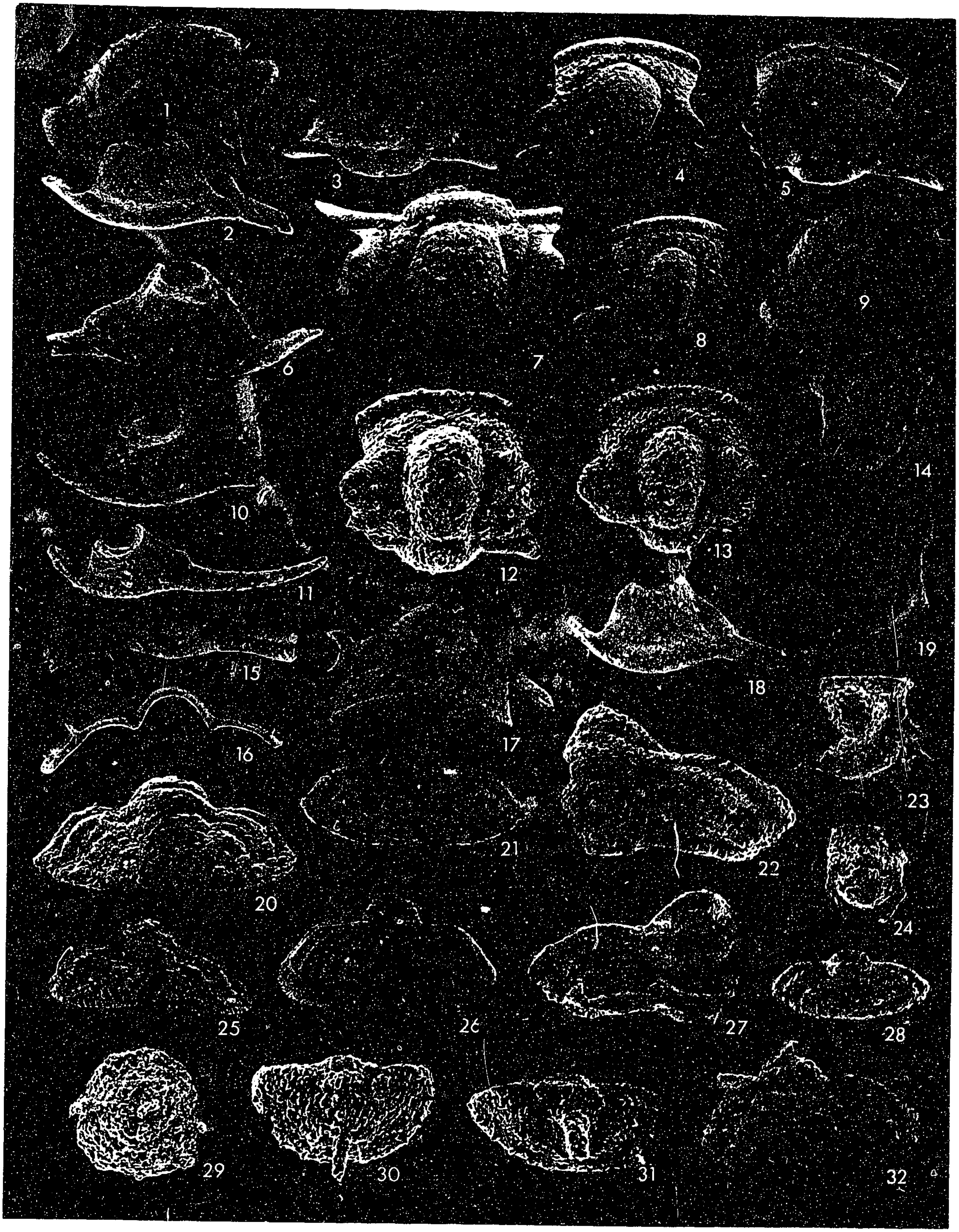
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FIGURE *IX-5*, *Harpidella tikkaneni* n. sp., from section Avalanche Lake One, 95.5 m, Whittaker Formation (Llandovery, Rhuddanian), central Mackenzie Mountains, Northwest Territories, Canada. Magnifications x10 except where otherwise noted. *1*, *5*, cranidium UA 9077, dorsal and left lateral views; *2*, *7*, *8*, *14*, holotype cranidium UA 9078, dorsal, left lateral, anterior, and ventral views; *3*, cranidium UA 9079, dorsal view; *4*, *9*, cranidium UA 9080, dorsal and left lateral views; *6*, *12*, left librigena UA 9081, external and dorsal views; *10*, *11*, cranidium UA 9082, dorsal and left lateral views; *13*, cranidium UA 9083, dorsal view; *15*, *16*, *18*, left librigena UA 9084, internal, ventrolateral, and external views; *17*, left librigena UA 9085, external view; *19*, right librigena UA 9086, external view; *20*, pygidium UA 9087, ventral view; *21*, *22*, pygidium UA 9088, ventral and dorsal views; *23*, pygidium UA 9089, ventral view; *24*, *29*, pygidium UA 9090, right lateral and dorsal views; *25*, transitory pygidium UA 9091, dorsal view, scanning electron micrograph, x25; *26*, transitory pygidium UA 9092, dorsal view, scanning electron micrograph, x30; *27*, pygidium UA 9093, dorsal view; *28*, pygidium UA 9094, dorsal view; *30*, transitory pygidium UA 9095, dorsal view, scanning electron micrograph, x55; *31*, transitory pygidium UA 9096, dorsal view, scanning electron micrograph, x30; *32*, small pygidium UA 9097, dorsal view, x20; *33*, pygidium UA 9098, dorsal view; *34*, *35*, pygidium UA 9099, dorsal and posterior views.

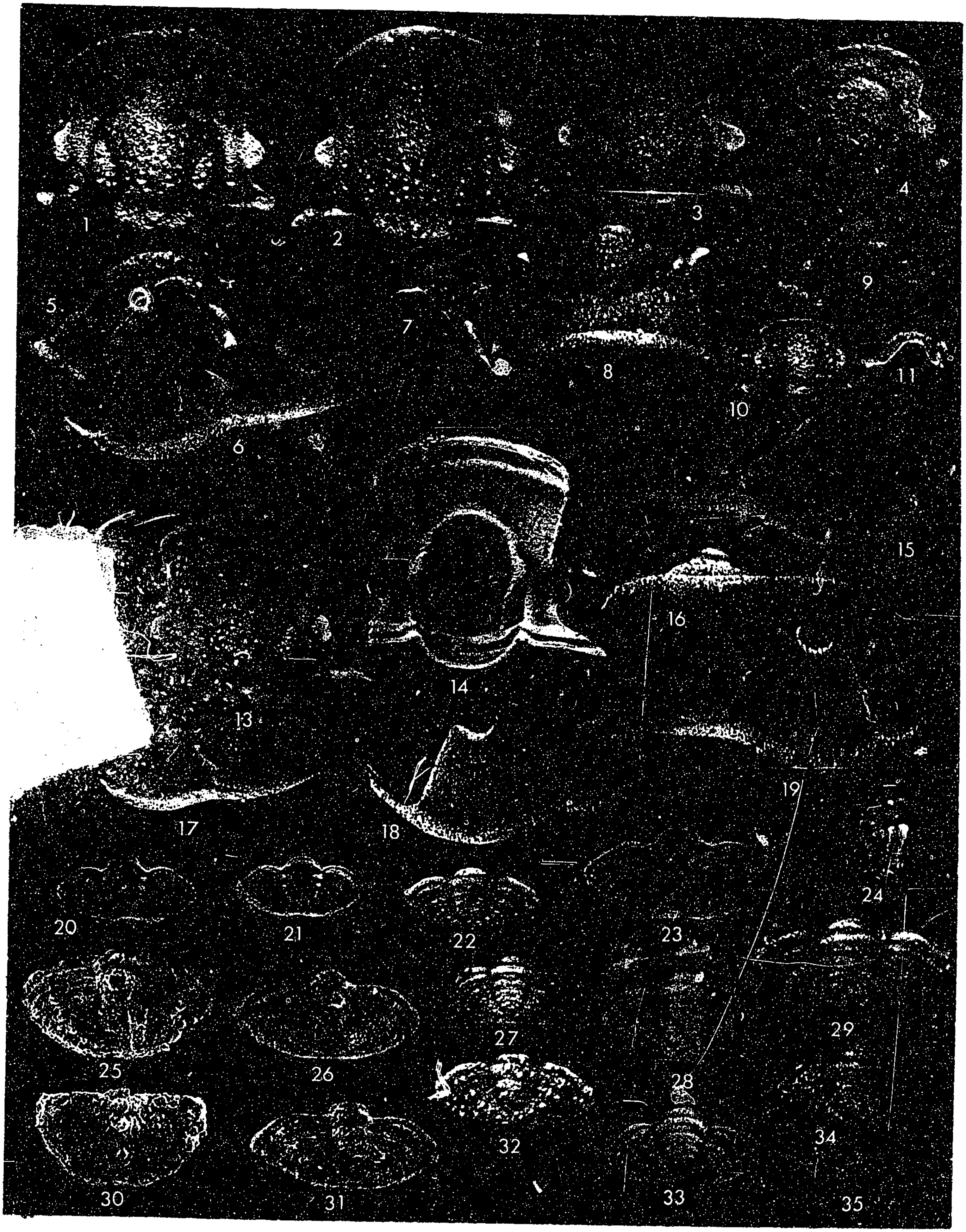
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FIGURE *IX-6*--*Harpidella greggi* n. sp., from section Avalanche Lake Four, 126 m above base and section Avalance Lake Two, 242.5-249 m above base, Delorme Group, Wenlock (Sheinwoodian; probably *Cyrtograptus* aff. *rigidus*-*Monograptus* aff. *riccartonensis* Zone). All magnifications x15, except where noted otherwise. *1*, *9*, dorsal and external views of left librigena UA 9100 (AV 4 126 m); *2*, *6*, dorsal and right lateral views of holotype cranidium UA 9101 (AV 4 126 m); *3*, dorsal view of cranidium UA 9102 (AV 4 126 m); *4*, *10*, dorsal and right lateral views of cranidium UA 9103 (AV 4 126 m); *5*, ventral view of cranidium UA 9104 (AV 4 126 m); *7*, external view of right librigena UA 9105; *8*, external view of left librigena UA 9106, x20 (AV 2 249 m); *11*, external view of right librigena UA 9107 (AV 4 126 m); *12*, internal view of right librigena UA 9108 (AV 4 126 m); *13*, *17*, *18*, dorsal, right lateral, and anterior views of cranidium UA 9109 (AV 4 126 m); *14*, *19*, dorsal and posterodorsal views of cranidium UA 9110 (AV 4 126 m); *15*, dorsal view of cranidium UA 9111 (AV 4 126 m); *16*, dorsal view of posterior thoracic segments UA 9112, x20 (AV 2 242.5 m); *20*, dorsal view of cranidium UA 9113 (AV 4 126 m); *21*, dorsal view of thoracic segment UA 9114, x20 (AV 2 242.5 m); *22*, *23*, *26*, anterior, dorsal, and left lateral views of cranidium UA 9115, x20 (AV 2 242.5 m); *24*, external view of right librigena UA 9116, x20 (AV 2 242.5 m); *25*, external view of left librigena UA 9128, x20 (AV 2 242.5 m).

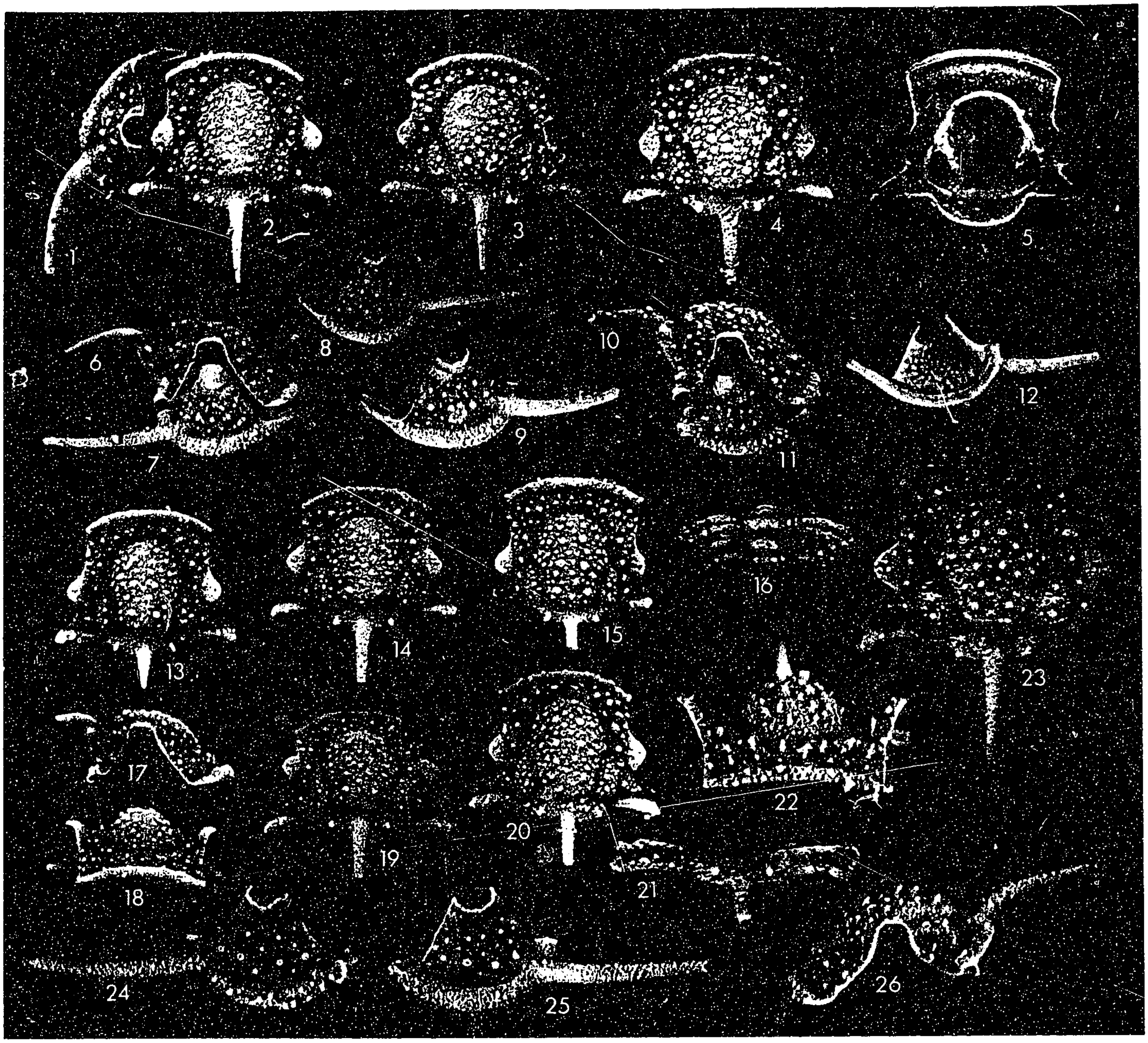
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FIGURE *IX-7*--*Harpidella greggi* n. sp., from section Avalanche Lake Two, 242.5-249 m above base and section Avalanche Lake Four, 126 m above base (Wenlock; Sheinwoodian). All illustrations are scanning electron micrographs. *1*, cranidium UA 9129, dorsal view, x39 (AV 2 249 m); *2*, cranidium UA 9130, dorsal view, x38 (AV 2 248.8 m); *3*, right librigena UA 9131, external view, x28 (AV 2 242.5 m); *4*, *5*, thoracic segment UA 9132, right lateral and dorsal views, x30 (AV 2 248.8); *6*, cranidium UA 9133, dorsal view, x57 (AV 2 249 m); *7*, thoracic segment UA 9134, anterodorsal view, x22 (AV 2 248.8 m); *8*, right librigena UA 9135, external view, x24 (AV 4 126 m); *9*, thoracic segment UA 9136, dorsal view, x30 (AV 2 249 m); *10*, pygidium and attached thoracic segments UA 9137, dorsal view, x45 (AV 2 248.8 m); *11*, thoracic segment UA 9138, dorsal view, x27 (AV 2 249 m); *12*, hypostome UA 9139, ventral view, x95 (AV 2 248.8 m); *13*, hypostome UA 9140, ventral view, x95 (AV 2 248.8 m); *14*, pygidium UA 9141, ventral view, x30 (AV 2 248.8 m); *15*, protaspid UA 9142, dorsal view, x100 (AV 2 248.8 m); *16*, protaspid UA 9143, left lateral view, x120 (AV 2 249 m); *17*, pygidium UA 9144, dorsal view, x38 (AV 2 249 m); *18*, *21*, *22*, *26*, protaspid UA 9145, anterior, dorsal, left lateral, and right oblique dorsolateral views, x120, x105, x120, and x120 (AV 2 249 m); *19*, pygidium UA 9146, dorsal view, x28 (AV 2 248.8 m); *20*, protaspid UA 9147, dorsal view, x100 (AV 2 248.8 m); *23*, transitory pygidium UA 9148, dorsal view, x45 (AV 2 242.5 m); *24*, early protaspid UA 9149, dorsal view, x140 (AV 2 248.8 m); *25*, early protaspid UA 9150, dorsal view, x160 (AV 2 248.8 m); *27*, transitory pygidium UA 9151, dorsal view, x39 (AV 2 249 m); *28*, transitory pygidium UA 9152, dorsal view, x38 (AV 2 242.5 m).

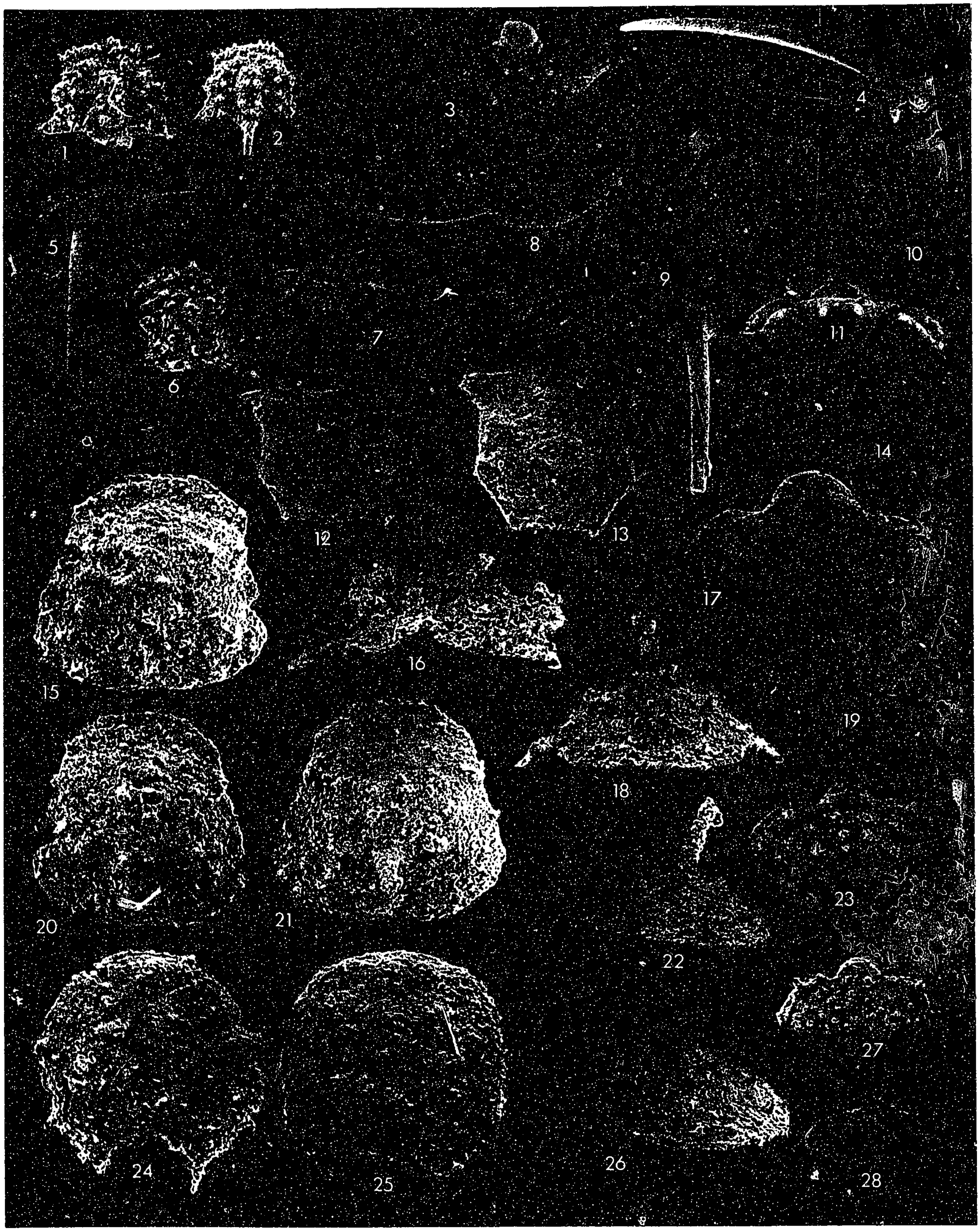
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FIGURE IX-8--*Harpidella spinifrons* (Williams in Cooper and Williams, 1935), from the Tully Formation (Givetian), New York State. All magnifications are x10; all figures are of latex casts from external molds, except figures 4 and 7, which are latex casts from internal molds. 1-4, cranidium and partial left librigena USNM 89751b, dorsal, left dorsolateral, anterior, and ventral views; 5, 6, 9, 11, cranidium and left librigena USNM 89751c, dorsal, oblique dorsolateral, left lateral, and anterior views; 7, right librigena USNM 89751, internal view; 8, 13, holotype cranidium and right librigena USNM 89751(holotype), oblique dorsolateral and right lateral views (specimen is dorsolaterally flattened); 10, 12, 14, 15, cranidium and right librigena USNM 89751a, posterodorsal, dorsal, anterior, and right lateral views.


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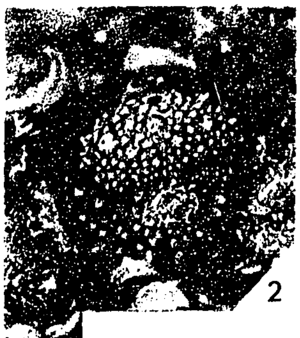
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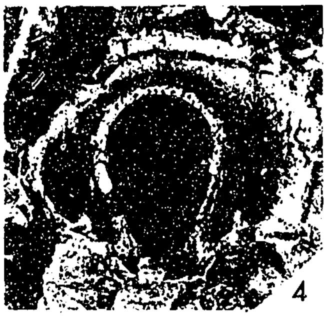
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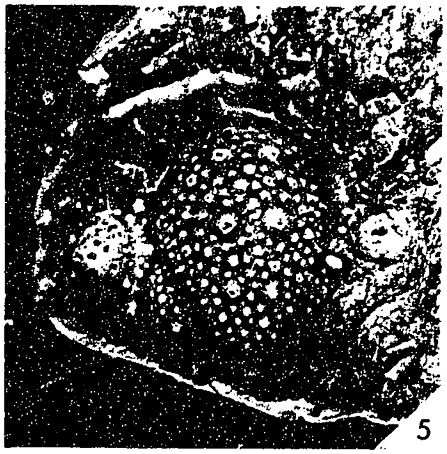
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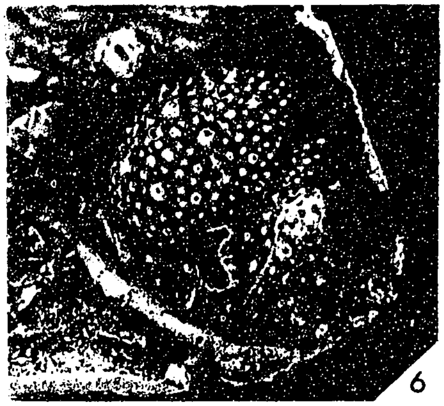
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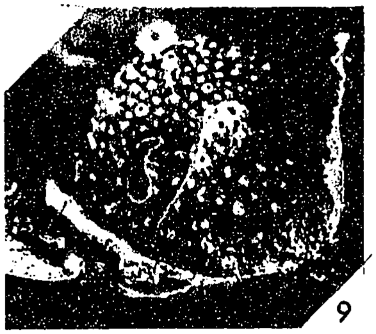
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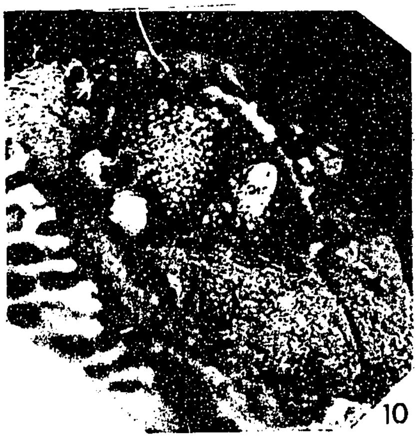
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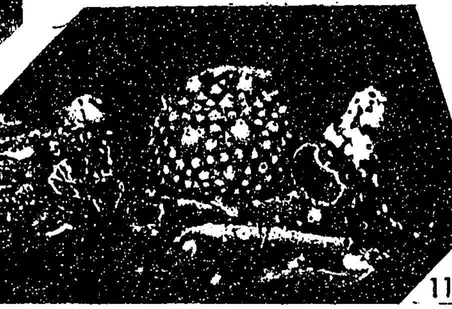
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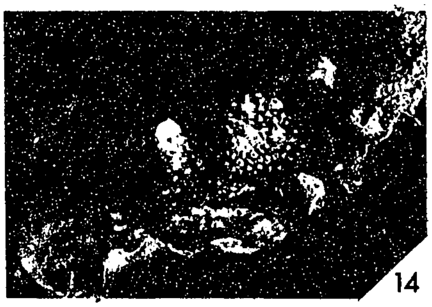
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FIGURE *IX-9*--*Maurotarion* *messieri* n. sp., from section Avalanche Lake One, 95.5-98.5 m above base. Magnifications x10 except where otherwise noted. *1*, *5*, *15*, holotype cranidium UA 9153, dorsal, left lateral, and ventral views; *2*, *6*, *7*, cranidium UA 9154, dorsal, left lateral, and anterior views; *3*, cranidium UA 9155, dorsal view; *4*, cranidium UA 9156, dorsal view; *8*, *9*, cranidium UA 9157, dorsal and left lateral views; *10*, right librigena UA 9158, internal view; *11*, left librigena UA 9159, external view; *12*, right librigena UA 9160, external view; *13*, *14*, right librigena UA 9161, external and ventrolateral views; *16*, *17*, *25*, thoracic segment UA 9162, dorsal, left lateral, and anterior views; *18*, thoracic segment UA 9163, dorsal view; *19*, *20*, *21*, cranidium UA 9164, dorsal, left lateral, and anterior views, x15; *22*, hypostome UA 9165, ventral view; *23*, hypostome UA 9166, ventral view; *24*, thoracic segment UA 9167, dorsal view; *26*, *27*, *29*, *30*, pygidum UA 9168, posterior, left lateral, ventral, and dorsal views; *28*, right librigena UA 9169, external view, x30, SEM; *31*, pygidium UA 9170, dorsal view; *32*, *33*, hypostome UA 9171, ventral and right lateral views, x20, SEM; *34*, pygidium UA 9172, dorsal view; *35*, *40*, cranidium UA 9173, left lateral and dorsal views, x27, SEM; *36*, pygidium UA 9565, dorsal view, x20; *37*, pygidium UA 9566, dorsal view; *38*, pygidium UA 9567, dorsal view; *39*, cranidium UA 9568, dorsal view, x27, SEM; *41*, cranidium UA 9569, dorsal view, x55, SEM; *42*, *43*, cranidium UA 9570, dorsal and anterior views, x20; *44*, *45*, cranidium UA 9571, dorsal and left lateral views, x20.

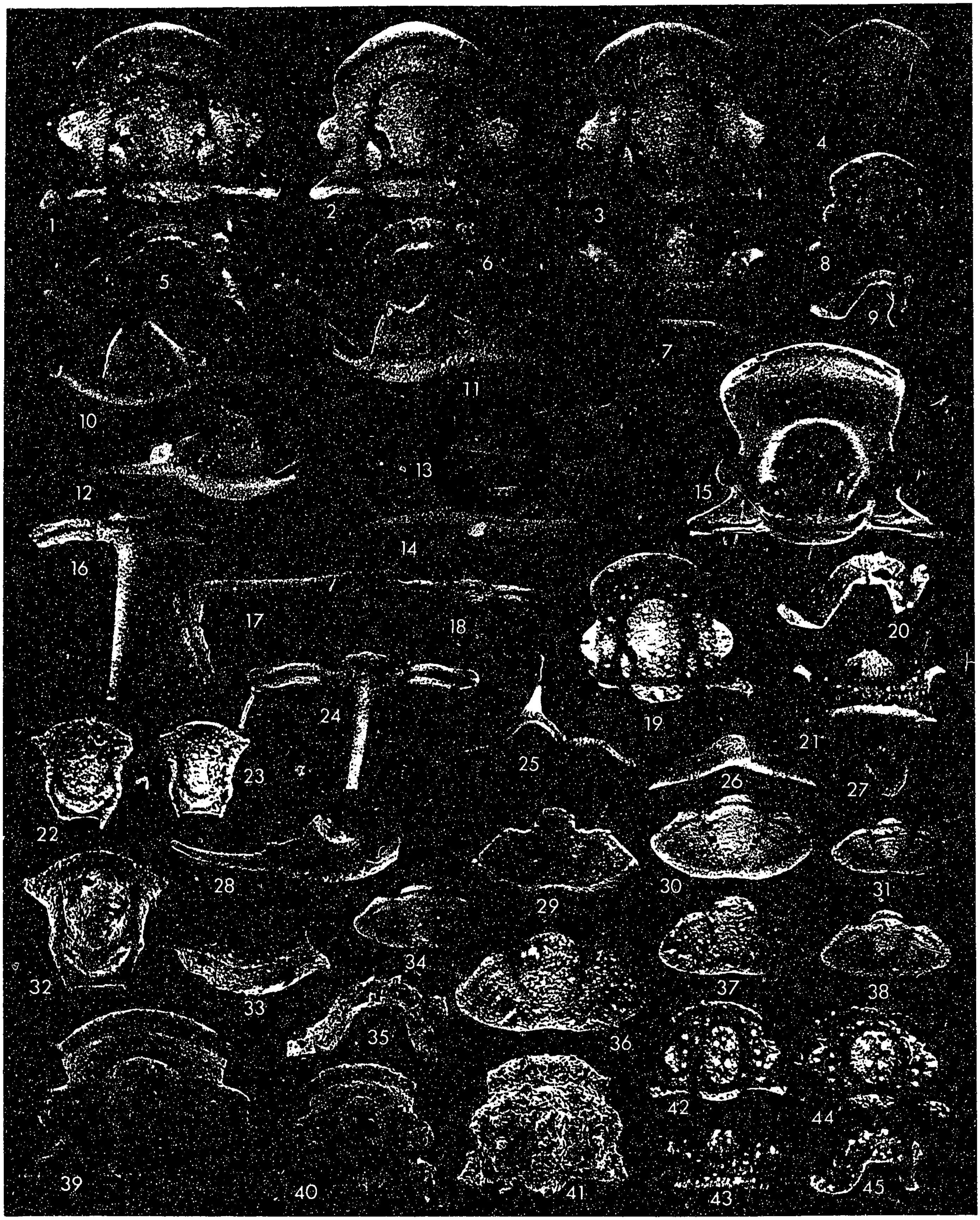
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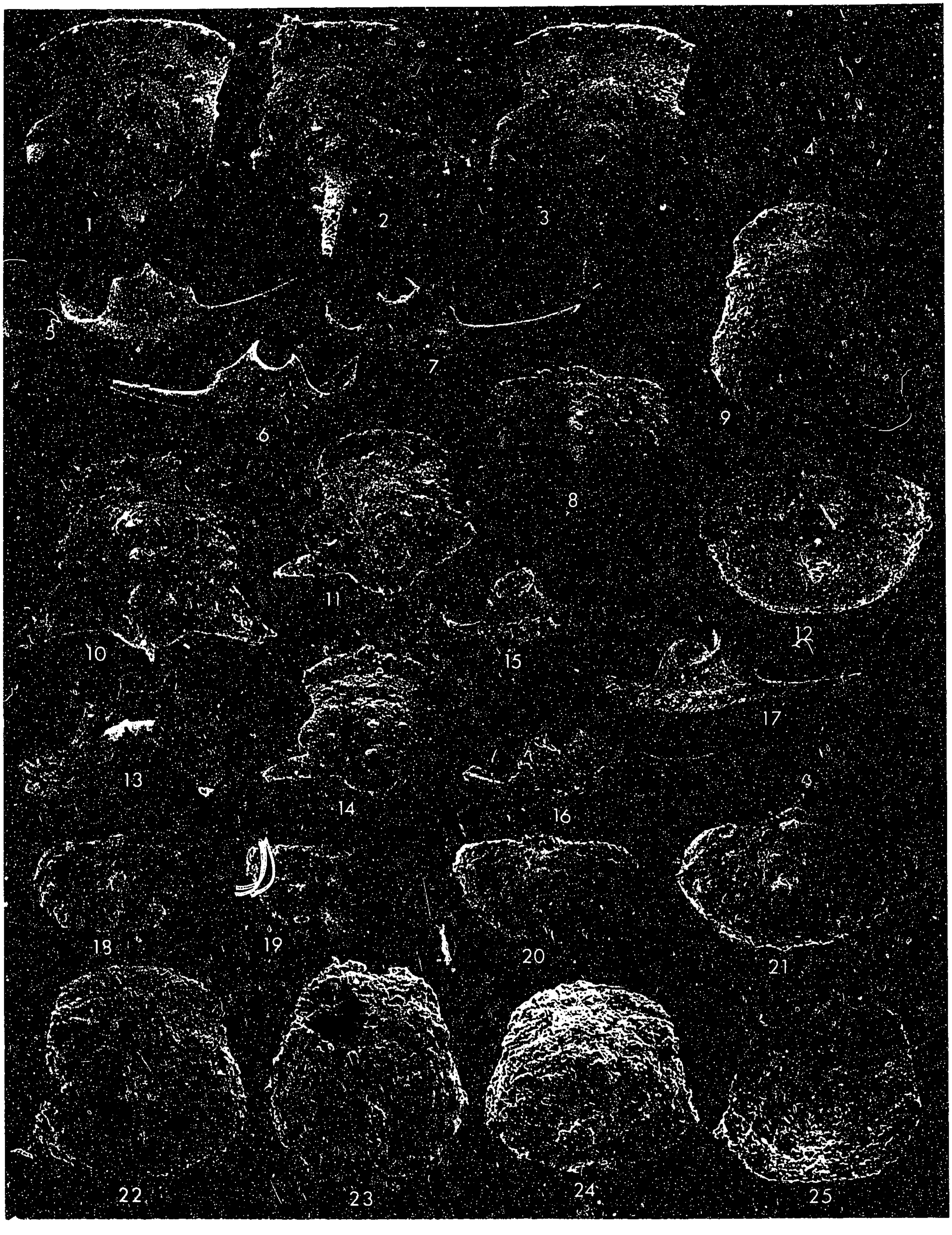
FIGURE *IX-10*--All figures are scanning electron micrographs. *1*-*9*, *Maurotarion struszi* (Chatterton, 1971), Emsian, Taemas Formation, New South Wales, Australia; *1*, cranidium UA 9572, dorsal view, x38; *2*, cranidium UA 9573, dorsal view, x38; *3*, *4*, cranidium UA 9574, dorsal and left lateral views, x38; *5*, left librigena UA 9575, external view, x21; *6*, right librigena UA 9576, external view, x20; *7*, left librigena UA 9577, external view, x20; *8*, transitory pygidium UA 9578, dorsal view, x90; *9*, protaspis UA 9579, dorsal view, x90. *10*-*17*, *21*, *Maurotarion instita* (Whittington and Campbell, 1967), probably Ludlow, Hardwood Mountain Formation, Baker Pond, Maine; *10*, *13*, cranidium UA 9580, dorsal and left lateral views, x90; *11*, cranidium UA 9581, dorsal view, x40; *12*, transitory pygidium UA 9582, dorsal view, x90; *14*, cranidium UA 9583, dorsal view, x40; *15*, left librigena UA 9584, external view, x30; *16*, left librigena UA 9585, external view, x55; *17*, left librigena UA 9586, external view, x28; *21*, transitory pygidium UA 9587, dorsal view, x95. *18*-*20*, *22*-*25*, *Maurotarion messieri* n. sp., from Section Avalanche Lake Four-B, 131.3 m above base (Llandovery; Rhuddanian), Whittaker Formation, central Mackenzie Mountains, Northwest Territories, Canada; *18*, transitory pygidium UA 9588, dorsal view, x55; *19*, transitory pygidium UA 9589, dorsal view, x55; *20*, transitory pygidium UA 9590, dorsal view, x55; *22*, protaspis UA 9591, dorsal view, x90; *23*, protaspis UA 9592, dorsal view, x90; *24*, protaspis UA 9593, dorsal view, x90; *25*, protaspis UA 9594, ventral view, x90.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CHAPTER X

GENERAL DISCUSSION

SYNTHESIS

THE WORKS gathered in this thesis represent the contribution of the writer to date to knowledge of the Silurian trilobite faunas of northern Laurentia.

Chapters III, VI, and IX are integrated parts of an overall revision of the Family Aulacopleuridae Angelin, 1854. Thus far, two monophyletic subfamilies, Aulacopleurinae Angeline, 1854, and Otarioninae, Richter and Richter, 1926, have been diagnosed, and their constituent genera listed. In addition, an attempt has been made to recast the genera _Otarion_ Zenker, 1833, _Aulacopleura_ Hawle and Corda, 1847, _Songkania_ Chang, 1974, _Harpidella_ M'Coy, 1849, and _Maurotarion_ Alberti, 1969, as monophyletic groups. Most of the systematic ideas presented were made possible by the vast advances in knowledge resulting from study of the superb Mackenzie Mountains silicified material. Works on the genus _Cyphaspis_ Burmeister, 1843, and on several new taxa are in progress, as are systematic descriptions of the Silurian aulacopleurids of the Canadian arctic, of the Bolivian Devonian, and of the classic Silurian sequence on the island of Gotland, Sweden.

Chapters II, V, and VII represent treatments of more limited scope, each of which have their own special interest. Chapter II was the writer's first published scientific paper. A new species was described and a genus comprehensively revised.

Chapter V described a superbly preserved Ludlow trilobite from the Canadian Arctic. The surprising aspect of this species was that its familial affinity was not obvious. There are by now many modern works on Silurian trilobites from most parts of the world, and at least a broad consensus on familial classification. Finding a trilobite difficult to classify to this level, particularly one for which virtually all dorsal exoskeletal features are well known, is extremely rare. The hypothesis that Goodsiraspis packardi belongs to the aulacopleuroidean family Rorringtoniidae Owens (a taxon only named in 1990) developed from the ongoing aulacopleurid revision of Chapters III, VI, and IX, and might not otherwise have been possible.

Chapters IV and VIII are, in a way, the tip of an iceberg. The summer of 1991 was spent prospecting for Ordovician and Silurian trilobites in the central Canadian Arctic. The impetus was silicified collections made by A. J. Boucot and R. Thorsteinsson (described by Perry and Chatterton, 1977), and by B. D. E. Chatterton on several trips in the late 1970s. The results of the 1991 fieldwork far exceeded expectations. Platform carbonates of the Douro Formation yielded an unexpectedly diverse fauna, far in excess of what had previously been reported (Thomas and Narbonne, 1979). Better still, the Cape Phillips Formation silicified faunas of the early Wenlock to early Ludlow interval were revealed to be the most numerous and diverse known from anywhere in the world. Fieldwork continued in 1992 and is planned for 1993; the scope of the project is immense, and grows as more sections are measured and sampled. Chapters IV and VIII represent the first of what should be many published results.

All told, it is hoped that the studies grouped herein reflect a unity of purpose (if an evolving one). It is an absolutely fundamental responsibility of the invertebrate palaeontologist to produce descriptive works of the highest quality possible. All systematic, biostratigraphic, palaeoecological, and palaeobiogeographical hypotheses depend upon descriptive palaeontology for their basic data. The quality of such work cannot exceed the quality of those data.

TAXONOMIC APPROACH: DEVELOPMENT AND PRESENT OUTLOOK

As mentioned in Chapter I, the studies grouped in this volume are presented in sequential fashion, with no internal "updating", and reflect both a developing body of knowledge and a developing systematic outlook. This is a strength of the paper-format thesis: new data, new ideas, and exposure to different ways of thinking lead to ever-changing attitudes to our previously published work. Using this format, these attitudes and the manner in which they have changed can be documented and commented upon. This luxury is not available to writers of traditional-format theses, who must present their work in final form from a unified point of view, which may not reflect their outlook at the time many parts of the study were produced. Nevertheless, the function of the present chapter is to draw together the enclosed studies, and hence it is profitable to describe the manner in which the writer's systematic practice evolved, and to outline its current state.

<u>Constrained</u> <u>congruency</u>.--Chapter II presented a method of computer-based systematic analysis. The ideas grew from a literature survey and a long period of thinking about how best to do taxonomy. In the end, the guiding principles turned out to be objectivity and parsimony. Thus, the data were supposed to "speak for themselves" and trees were supposed to "fall out" with as little subjective human manipulation as possible, through application of strict parsimony to an unordered data set. Trees were supposed to root themselves through maximal internal consistency.

This was all well and good, but it wasn't cladistics. Cladistics is grouping by special similarity, and nothing more. It is no more or less objective than any other method of generating hypotheses of relationship, and it depends not at all upon parsimony. Its great and lasting advantage is an insistence on grouping on the basis of shared evolutionary novelties. Strictly applied, this at least means that our classificatory entities are attempts to specify things created by nature (monophyletic groups), not more or less arbitrary human decisions (taxa based on "overall similarity", "ancestral" higher taxa, etc.).

Current approach.--Systematic palaeontology is fundamentally subjective. Among workers who have invested much time and effort studying a particular group, a cladist is no more likely to have a good idea of the general pattern of relationship than an "evolutionary taxonomist" (whatever that means and assuming equal talent). The approach currently taken, however, is cladistic, for the reasons given above. The goal is to approximate real things, not things that we find "convenient" or "useful".

Every time we create a taxonomic character (see Chapter II), we formulate an hypothesis of relationship. The more characters we create, the more hypotheses we generate. Ideally, if we are correct more often than not, most of the hypotheses should agree and suggest a limited number of possible patterns of relationship. As the number of characters increases, however, conflict often arises, and the subtles and implications of the data set become impossible to evaluate without electronic assistance. What computers help us to do is to order our assumptions and assess their combined meaning. There are several ways of doing this, but the most widely used is the concept of parsimony. Here, the pattern of relationship favoured is that which requires the fewest number of character-state transformations (or "evolutionary steps") to have taken place.

There exists, by now, a vast literature on the subtleties and complexities of computer-based parsimony analysis. This is all valuable work, although most busy taxonomists will not have time to assess a lot of it, never mind incorporate it into their own studies. The point that bears emphasis here is that all of these algorithms and assumptions are not being applied to some sort of universal codification of any group of organisms. Rather, for all their developing grace and power, cladistic parsimony procedures can only help us make the best internal sense of our own ideas. The real work in cladistics, as in any other remotely worthwhile taxonomic approach, is creating sound characters.

THE RELEVANCE OF SYSTEMATICS

As noted above, systematic palaeontology is fundamentally important to virtually all other palaeontological endeavour. Geology can be carried out treating fossils as clasts, but palaeontology is about organisms, and to support inferences based on them, it is necessary that the organisms be classified. Systematic analysis forms the basic premisses upon which hypotheses about palaeoecology, biostratigraphy, palaeobiogeography, etc., stand or fall.

In the example of the Douro Formation (see Chapters I and VIII), it has already been noted that detailed taxonomic study has shown previously unreported (and apparently unsuspected) trilobite diversity to exist. Phylogenetic analysis reveals also some very interesting aspects of the Douro trilobites. Perirehaedulus, for instance, is the only representative of its subfamily known outside the Chinese Llandovery. Waigatchella, Palaeodechenella, and Frammia all occur in only one other unit in the world, on Waigatch Island in the Russian Arctic. Some of the trilobites are closely related to older (i.e., early Ludlow) platform margin forms from the Cape Phillips Formation. Many of the trilobite groups one would expect to find, however, are absent, and several usually rare clades dominate the assemblages. Why all of this is so is a very good question. Palaeoecological and palaeobiogeographical analysis can now be brought to bear to help find answers. The point is, without (hopefully) competent and detailed systematic analysis of the trilobites, no one would know that these "quirks" even exist.

The value of systematics is further illustrated by the Alaskan trilobites described in Chapter VII. When initially forwarded for study, the United States Geological Survey had formed the preliminary opinion (R. B. Blodgett, personal commun.) that the stratigraphic interval from which they were derived was Upper Silurian (Ludlow-Pridoli), and that its faunas had Uralian affinities. It is some measure of the rapidly developing state of knowledge of northern Laurentian Silurian trilobites that it was possible to determine, with some confidence and solely through study of the trilobites, that the fauna was Telychian and had firm northern Laurentian affinities. Without specialized knowledge and detailed study of trilobite relationships, these conclusions would not have been possible.

The independence of systematics.--The point cannot be made often enough that systematic analysis depends on one element only: the morphology of the organisms to be classified. Relationships should be deduced solely by reference to presumptive shared evolutionary novelties. Relative stratigraphic or geographic position, together with the sedimentological character of the rocks from which the fossils were derived, is irrelevant.

Take the case of stratigraphic proximity. When two or more species occur in stratigraphic sequence in the same place, relationship and even an ancestral-descendant lineage are often hypothesized. If the species were a sponge, a bryozoan, and a chimpanzee, this would not be the case. "Yes," is the reply, "but it only works on closely related species." How does one know the species are closely related? Because they look like one another; notions of phylogeny depend upon morphology. The same reasoning applies to other applications. It is sometimes held, for example, that without allowing palaeoecological analysis to contribute to phylogenetic analysis, one cannot hope to detect ecophenotypes. But this is backwards. Nobody would wonder whether the chimpanzee and the sponge are ecophenotypes. The possibility has only been suggested because of primary systematic palaeontology based on morphology. Perhaps ecophenotypes exist in a particular example, but the problem should be addressed in the form of a phylogenetic hypothesis which can be tested by sedimentological and palaeoecological work. If such data are allowed to enter into the initial phylogenetic hypothesis, using the classificatory units thus produced as the basis for further palaeocological inference is circular and worthless.

IMPLICATIONS

While there is still much taxonomic work to be done on northern Laurentian Silurian trilobites, what has been produced thus far by the writer and others, coupled with knowledge of works in progress, has begun to suggest several interesting implications of the descriptive data.

Palaeobiogeography.--New data reveal that the taxonomic composition of the Wenlock-Ludlow trilobite biota of northern Laurentia differs in many striking aspects from that of the southeastern region. In addition to various plexi that are essentially northern Laurentian endemics during this time, there are many generic and familial taxa that are widespread through most of the world, represented in southern Laurentia, but rare or completely absent in northern Laurentia. Most important is the complete absence of dalmanitids, acastids, homalonotids, staurocephalids, and phacopidellines. In addition, phacopines are known from a single rare undescribed species in the northern Laurentian Wenlock, while they are common and widespread in the southern Laurentian Wenlock-Ludlow. Further differences are the high diversity of the genus Encrinurus in the south in contrast to its rarity in the north and the widespread occurrence of Calymene s.s. in the south versus its complete absence in the north. These differences cannot be dismissed as undersampling of shallow water facies in northern Laurentia. While certain absentees (e.g., acastids and homalonotids) are typically most abundant in nearshore, often clastic, environments in the Wenlock, these groups and others missing from the northern Laurentian record range into shelf limestones and offshore shale belts in coeval faunas elsewhere (Thomas, 1980).

Such profound differences in taxonomic makeup indicate the presence of a significant barrier to dispersal and faunal interchange between the northern and southern areas of the Laurentian landmass during the Wenlock and Ludlow. This pattern is attributable to the influence of the Transcontinental Arch. Rigby and Chatterton (1989) reached a similar conclusion to account for the disjunct distribution of sponges in the two areas.

As the picture emerges, it is becoming more evident that the northern Laurentian faunas have more in common with those of Baltica than southern Laurentia.

Biostratigraphy.--The lower Wenlock to lower Ludlow of the Cape Phillips Basin has yielded an unparallelled number of high-diversity trilobite faunas. In fact, the rocks contain the highest number of distinct faunas in stratigraphic sequence known from this interval worldwide. As such, this is the most highly resolved record of Wenlock trilobites known. Once taxonomic description is advanced, the trilobites should provide the basis for a shelly fossil biostratigraphy applicable across northern Laurentia. Preliminary results show that trilobite correlations across the Cape Phillips Basin are no less resolved, and in some intervals more highly resolved, than the graptolite zonation. Integration of the shelly fossil and graptolite data might potentially result in a highly calibrated dual zonation scheme.

Biotic events.--Silurian trilobites have not generally been considered in light of biotic turnovers, due probably to the lack until very recently of an adequately described record. Trilobite faunas from the Cape Phillips Basin, and their correlates in the central Mackenzie Mountains, have thus far revealed at least one prominent and previously undetected extinction event.

It has long been recognized that graptolites experienced one of the most significant mass extinctions in their history (the *ludensis* event) in the upper Wenlock (Rickards, 1989; Quinby-Hunt and Berry, 1991). Previously, however, this event has not been detected amongst benthic shelly fossils.

At section Abbott River One on northwestern Cornwallis Island (see Chapter IV), the graptolite turnover (between the *Cyrtograptus lundgreni*-*Monograptus testis* Zones and *Pristiograptus ludensis* Zones of Lenz and Melchin, 1990) occurs between 10 and 12 metres. Silicified trilobite faunas occur at 9 and 13.5 m. Recorded in this section, and in correlative sections in the Cape Phillips Basin, is the worldwide extinction across this interval of the acanthoparyphine *Hyrokybe*, the proetid *Thebanaspis*, a related, unnamed proetid, an unnamed calymenid, and an unnamed odontopleurine. Additionally, the overall aspect of faunas above and below the extinction level is radically different. Many taxa which do not become extinct worldwide do disappear forever from the northern Laurentian record (all calymenids, most proetines, several lichids). Finally, the odontopleurine genus *Acanthalomina* makes its worldwide first appearance immediately above the extinction level.

As is obvious from the above lists, formal description of the trilobite extinction must await publication of the many works in progress on descriptive palaeontology, as most of the key taxa involved are undescribed. The fact that this extinction has not been detected in other parts of the world is surely a reflection of a less highly resolved shelly fossil record for the interval.

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