UNIVERSITY OF ALBERTA

SYSTEMATICS OF SILURIAN LICHID TRILOBITES FROM THE MACKENZIE MOUNTAINS, CANADA

BY

MARGARET CAMPBELL ©

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Margaret Campbell

3619 - 114 Street

Edmonton, Alberta, T6J 1L7

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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 Lichid Trilobites from the Mackenzie Mountains, Canada** submitted by Margaret Campbell in partial fulfilment of the requirements for the degree of Master of Science.

B.D.E. Chatterton (Supervisor)

Richard C. Fox

R. Fox

B. Jones

M.V.H. Wilson

Date August 31, 1994

ABSTRACT

Lichids are uncommon members of a silicified trilobite fauna from the Llandovery and Wenlock horizons of the Avalanche Lake sections in the central Mackenzie Mountains, Canada. Seventeen species of lichids, 16 of them previously undescribed, belong to 7 genera in 3 subfamilies: *Dicranopeltis*, subfamily Lichinae; *Platylichas*, subfamily Homolichinae; *Acanthopyge*, *Borealarges*, *Dicranogmus*, *Radiolichas* and *Richterarges*, subfamily Trochurinae.

Borealarges is the best represented and most diverse of the genera with 7 species, *Dicranogmus* the second with 3 species. The Avalanche Lake sections represent a transition from shelf carbonates to deep water shales, but, in terms of lichid distribution, there is little difference between the most distal (AV5) and most proximal sections (AV2). The lichid population distribution is remarkably uniform in the Wenlock sections.

Three species represent the earliest recorded occurrence of their genus: *Acanthopyge* (*Lobopyge* s. l.) *pristinus* n. sp.; *Radiolichas* n. sp. A; and *Richterarges facetus* n. sp. Evidence of evolutionary relationships is seen in: *Richterarges facetus* n. sp. which retains characters associated with *Borealarges*; in *Dicranogmus* n. sp. A which provides evidence that *Dicranogmus* and *Radiolichas* are sister taxa; and in *Acanthopyge* (*Lobopyge* s. l.) *pristinus* n. sp. which illustrates the connection between *Hemiarges* and *Acanthopyge* (*Lobopyge*).

Platylichas has recently been divided into 2 subgenera (Thomas and Holloway, 1988) but *Platylichas* (*Rontrippia*) *infimus* n. sp. has morphological features of both, suggesting the concept of 2 subgenera requires reexamination.

A phylogenetic analysis of *Borealarges* shows it to be a monophyletic clade, separate and distinct from *Hemiarges* and *Richterarges*.

Protaspides and meraspides that can be assigned to 5 genera, *Dicranopeltis*, *Platylichas*, *Borealarges*, *Dicranogmus*, and *Radiolichas*, are described. This nearly doubles the previously described lichid ontogenies. The ontogenetic sequences provide support for ideas regarding onset of development and homologies of cranidial lobes, new information about relationships between taxa, and raise questions about current lichid classifications.

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CHAPTER I

INTRODUCTION
Order Lichida (Trilobita)

The Lichida are a group of trilobites distinguished by their unusual glabellar lobation. In the nineteenth century, lichids were best known from Europe and eastern North America. Exciting 20th century discoveries of lichids in Australia, Africa, eastern and northern North America and, although few in number, in China, Japan, Kazakhstan and South America, have greatly expanded our knowledge of the diversity of lichids and their geological and stratigraphical distribution.

Lichids are not common and their thin exoskeletons are usually poorly preserved. Some species are based on a fragment or a single body part. Convergence occurs frequently in lichid evolution.

A recent comprehensive review of the Order Lichida by Thomas and Holloway (1988) illustrates some of the difficulties that arise in attempts to classify the lichids. Thomas and Holloway gave a detailed summary of the history of classification of lichids and, building on the work of Tripp (1957), retained the ordinal status of the whole group, with a division into two families. In the larger of the two families, the Lichidae, there are 4 sub-families, and in the smaller, older family, the Lichakephalidae, there are no subdivisions. Tripp (1957) judged the structure of the hypostome to be the most important feature for the division of the Lichidae into subfamilies. The glabellar structure, and to a lesser degree, librigenal and, rarely, pygidial structures have been used to define membership in a genus. Because convergence is common, Thomas and Holloway stressed the importance of considering several features of the exoskeleton in order to assign specimens to a genus, with emphasis placed on "relative size, orientation and degree of inflation of the glabellar lobes, relative size of pygidial axis and presence or absence of border". They agreed (p.184) with previous workers (Tripp, 1957; Warburg, 1939) that the presence of spines or other protuberances on the cranidium and pygidium are not important taxonomic features. Ontogenetic studies have shown that certain tubercles can be followed through ontogeny (Chatterton, 1971, p. 39), which suggests that some notice must be paid to these features.

Purpose and Scope of the Study

The purpose of this project is to study the lichids, an uncommon component of the silicified fauna from the Avalanche Lake Area of the southern Mackenzie Mountains. Fossil preservation at this site is exceptional; silicification of most of the fauna has occurred and extremely small organisms have been preserved in three-dimensional detail. The identification and distribution of lichids in the study area are determined. Ontogenetic sequences of lichids are studied and the ontogeny, where possible, is related to phylogeny. Studies based on material from the Mackenzie Mountains (this work) and the Canadian Arctic (Adrain, in preparation) will considerably expand our knowledge of the ontogeny and phylogeny of lichids.

Location, Geology and Paleontology of Study Area

The study area (Fig. 1), in southwestern Northwest Territories, is located about 10 km east of Avalanche Lake (Glacier Lake map-area) on the north limb of the Avalanche Syncline. The sections studied are on the slope from the Redstone Arch into the Selwyn Basin, an area of transition between shelf carbonates and deep water shales (Gabrielse et al., 1973a; 1973b).

Information from conodont distribution and sulphur isotope studies suggest that the Selwyn Basin was restricted during the Late Ordovician and Early Silurian, with a faunal turnover/extinction just below the Ordovician-Silurian Boundary, and returned to ventilated open ocean conditions in the Wenlock (Wang et al., 1993; Nowlan et al., 1988; Goodfellow and Jonasson, 1984).

The Whittaker Formation consisting of, at this location, argillaceous limestone and shale, is Ordovician and Llandovery in age. The Road River Formation, predominantly shale and calcareous shale, and the Delorme Group, generally recessive limestones and dolomites, are Wenlockian (Chatterton et al., 1990). In this area, the Road River Formation and the Delorme Group interfinger as shown on the geological map of the Glacier Lake map area (Gabrielse et al., 1973a, map 1314A; 62°23'N, 127°02'W).

Sections in the study area extend from the latest Ordovician to the Wenlock, including a well exposed section of Ordovician-Silurian boundary strata. Three of the sections, AV1, AV2 and AV4, are located close together, AV5 is farther to the east (see map, Fig. 1). AV1 and 2 are the most shoreward of the sections, and AV4 (and 4B), and 5, are progressively more basinward, with increasing water depth (Fig. 2)

The Ordovician-Silurian boundary, as defined by conodonts and ostracods, was placed at AV4B 111.3 m above datum (Over and Chatterton, 1987; Nowlan et al., 1988; Copeland, 1989). Graptolite information recently available (Wang et al. 1993) suggests that this previously defined boundary is actually at the base of the *Glyptograptus persculptus* Zone, the time of the latest Ordovician extinctions/faunal turnover, and the Ordovician-Silurian boundary, defined as occurring at the base of the *Akidograptus acuminatus* zone, should be placed one metre higher than previously recognized. The trilobites collected from this 1 metre interval, previously thought to be earliest Silurian, occur after the Late Ashgill extinction, and are of Silurian aspect but now considered latest Ordovician in age. One trilobite species of Silurian aspect from this 1 metre interval is described in this study. In addition, one Ordovician trilobite species which appears well below the extinction event in the same section is included in the interests of comparison.

A few specimens, collected by B.D.E. Chatterton and D.G. Perry in 1979, from the Delorme range (notation DR), on the eastern side of the Mackenzie Mountains are discussed. This site (62°46'N, 125°15'W) in the Root Basin is shown on the locality map (Fig. 1). The Root Basin was an area of intra-shelf sediment accumulation (Morrow, 1991). The Delorme Range section has been correlated with the Avalanche Lake sites using conodonts and trilobites (Chatterton and Perry, 1983; Chatterton and Perry, 1984; Johnston and Chatterton, 1983). DR 91.44, the locality from which all the specimens in this study were collected, is approximately equivalent to AV4 126 m.

The stratigraphy, description of individual rock units, environment of deposition and conodont zonations of the Avalanche lake sections have been well described in previous work (Chatterton and Perry, 1983; Over and Chatterton, 1987; Chatterton et al. 1990). The sections record the presence of 3 sedimentary cycles, each with a lower deep water portion of carbonates and shales, and a higher portion of shallower carbonates. The lithology and faunal composition of the sections reflect major and minor trangressions and regressions as well as indicators of depth and energy levels. The substrate surface was probably a "soft" carbonate mud as indicated by lithology, presence of sedimentary structures and organisms such as *Lingula*.

Changes in sea level, degree of oxygenation, salinity, temperature, food, energy, local substrate connditions and seafloor contours produced both large- and small-scale changes in the environment that affected faunal composition in a given setting. During the Llandovery there was a major transgression and regression with minor smaller-scale pulses. The first part of the Wenlock, the time of deposition of most of the Avalanche Lake sections studied, was a time of shallowing.

Studies of lichids in other localities indicate they were inhabitants of the middle to outer shelf, living in moderately deep water (Chatterton and Ludvigsen, 1976; Thomas, 1981). This is in general agreement with observations made at the Avalanche Lake sites. The lichids appear in these sections during periods representing the shallower part of the sequences, and disappear in periods of deeper water.

Most of the major trilobite groups of this fauna, with the exception of the lichids, proetids, illaenids and styginids, have already been described; odontopleurids (Chatterton and Perry, 1983), cheirurids (Chatterton and Perry, 1984), encrinurids (Edgecombe and Chatterton, 1987; 1992; 1993; Edgecombe et al., 1988), calymenids (Siveter and Chatterton, in press); aulacopleurids (Adrain and Chatterton, 1994; Adrain and Chatterton, in press). Studies on non-trilobite members of this fauna include rostroconchs (Johnston and Chatterton, 1983); conodonts (Over and Chatterton, 1987; Nowlan et al., 1988), ostracodes (Copeland, 1989), bryozoans (Bolton and Ross, 1985), brachiopods (Lenz, 1977; Over, 1988) and fish (Soehn and Wilson, 1990)

Although many lichids are large in size, and some such as the Ordovician *Uralichas* and the Devonian *Terataspis* are among the largest known trilobites, very few large sclerites belonging to lichids were recovered from the Avalanche Lake sites. The presence of a few fragments of very large trilobites indicates large adults were present in the original communities. This suggests a preservational bias towards the small and juvenile end of the scale, a bias that has been seen in other members of this fauna and is typical, in general, of silicified faunas.

Methods

Bulk samples of fossiliferous limestone were collected from each section, and from as many horizons as possible within each section. The sampling location for each specimen is described by the section number followed by the height in metres above a datum (e.g., AV4 126 m or DR 91.44 m). If the notation (T) is included, it means the material was talus found in this area, indicating an ooriginal occurrence at or above the horizon where the sample was collected.

The lichids forming the basis of this study were extracted from samples collected in 1978 and 1979 by B. D. E. Chatterton and D. G. Perry; in 1983 by Chatterton and D.J. Over; in 1986 by Chatterton, G. D. Edgecombe, J. Qian, P. A. Tuffnell; and in

1990 by Chatterton, J. Adrain, L. Bohach, M. Caldwell and the writer. Efforts were made to examine material from all sections and at all horizons.

To extract silicified material, rock samples (limestone) are dissolved in 10% hydrochloric acid, the residue sieved and the required specimens picked from this residue (Cooper and Whittington, 1965). Many of the specimens were found by others, especially by B. D. E. Chatterton, in the course of other studies.

Holaspides and larger meraspides were photographed by standard photographic methods. The individual specimens were painted with black watercolour paint and mounted on blackened toothpicks, using gum tragacanth. Each specimen was whitened with a sublimation of ammonium chloride, which provided visual relief, and photographed. Small meraspides and protaspides were photographed on the Scanning Electron Microscope (SEM).

All specimens illustrated in this work are housed in the University of Alberta Paleontological Type collections, except where otherwise indicated, and are identified by Universty of Alberta (UA) numbers.

Species and subspecies

The concept of species is continually discussed in the literature and even the recent accessibility of molecular data for extant groups has not settled the species concept debate. In paleontology, one is usually dealing with information found in hard parts, with little or no input from soft tissues or behavioural patterns. In this project, the interpretation of a species is based on the exoskeletal morphology, and sclerites assigned to one species must be morphologically distinct from those assigned to another.

The question of subspecies in paleontological systematics is an interesting one. If specimens differ sufficiently that they can be distinguished one from the other, even though they are strongly connected because of similarities in one body part (sclerite), should they be classified as members of separate species or of subspecies? The *Hemiarges turneri* group may be used as an example of differing viewpoints on the subject of subspecies. Tripp and Evitt (1981) decided that trilobites from the Edinburg Formation of Virginia was closely related to *H. turneri* Chatterton and Ludvigsen, 1976 from the Esbatoattine of the southern Mackenzie Mountains and named it *H. turneri rasetti*. Rudkin et al. (in press) decided *H. t. turneri*, *H. t. rasetti* plus two more, *H. t. amiculus* and *H. t. elassouothos*, should be considered subspecies of *H. turneri* in spite of being widely separated geographically and chronostratigraphically. The holaspid cranidia of all 4 are similar, but the pygidium of each differs considerably. Two of the proposed subspecies, *H. t. turneri* and *H. t. amiculus*, are from the Esbataottine Formation of the Mackenzie Mountains and the Crown Point Formation of the Chazy of eastern North America respectively, roughly contemporaneous but widely separated geographically. A third subspecies, *H. t. rasetti* from the Edinburg Formation of Virginia, is Blackriveran in age, and the fourth, *H. t. elassouothos*, occurs in the Trentonian of the Whittaker Formation of the Mackenzie Mountains.

A comparison of *H. turneri turneri* and *H. turneri rasetti* at equivalent ontogenetic stages shows that each is distinct from the other from the earliest stages of development. The characters compared are ones readily visible in photographs (Chatterton and Ludvigsen, 1976, pl. 1, figs. 1 - 23; Tripp and Evitt, 1981, pl. 1, figs. 1 - 13; pl. 2, figs. 1 - 6, 17 - 21; this work, Table 1 and Fig. 3). Even in the protaspid period, *Hemiarges turneri turneri and H. turneri rasetti*, while sharing similarities in overall appearance, are different, although Tripp and Evitt (1981) said these differences are not important. Apart from more distinct ornamentation, which may or may not be taxonomically significant, the spines projecting from the protopygidia of *H. turneri rasetti* are longer, narrower and freer, even in the "three-spine" stage, than those of *H. turneri turneri*. If both occurred in the same locality, could one distinguish between them? A comparison of photographs (Chatterton pl. 17; figs 1 - 4 and Tripp and Evitt pl. 1; figs 1 - 13) suggests that the answer is yes. Ontogenetic sequences are not available for the other two subspecies, but, considering holaspid morphological differences, one could anticipate a similar result.

In consideration of consistent and persistent morphological differences through ontogeny of two of the four proposed subspecies of *Hemiarges turneri*, as well as differences in geographical and stratigraphical distribution, and the morphological distinctiveness of holaspides of all 4, it seems reasonable to consider the 4 previously designated subspecies to be individual species of *Hemiarges*, i.e. *H. turneri*, *H. rasetti*, *H. amiculus* and *H. elassouothos*. In this text, all are treated below as separate species.

Terminology

The terminology applied to trilobites as used in this paper follows the definitions presented in the Treatise of Invertebrate Paleontology, Part O, Arthorpoda 1 (Harrington et al., 1959). The following are exceptions or additions to Treatise definitions, based on a new understanding of morphology.

<u>Bullar lobe</u>. This term was proposed by Temple (1972) to replace the formerly used terms such as lateral lobe, anterolateral lobe and bicomposite lobe. The use of the term

"lateral" implies homology with the lateral lobes of other trilobite groups. Ontogenetic studies in lichids have shown the lobes in question are glabellar in origin and develop by expanding forward from S1, rather than backward from the S3 furrow (Temple, 1969; Chatterton, 1971).

Cranidial furrows. The longitudinal furrow defines the lateral margins of the median glabellar lobe; the axial glabellar furrow outlines, partially or completely, the lateral extent of the glabellar lobes. S1 defines the posterior boundary of the bullar lobe, extending laterally partially or completely from the longitudinal furrow to the axial furrow. S3 defines the anterior boundary of the bullar lobe and curves laterally from the longitudinal furrow to the axial furrow. S2 may be marked by a deflection of the longitudinal furrow between S1 and S3, but, in many cases, it is not apparent.

Cranidial lobes. Nomenclature follows that shown in Thomas and Holloway (1988, figure 2, facing p. 188).

Cranidial tubercles. A notational system for tubercles found on the protocranidium of lichid protaspides was developed by Chatterton (1971, p. 34 - 35, fig 9). This notation has been revised, so that the numbering of the tubercles on the glabella corresponds to the lobe on which they are found (Fig. 4). In the revised system, the numbering of tubercles begins with 0, assigned to the tubercle on the occipital ring. Through ontogeny, there may be loss of tubercles and the addition of others, and allometric changes can make it difficult to follow specific tubercles through all stages. For these reasons, it is not always possible to apply this notation to cranidial tubercles of holaspides.

Eye stalk. This term is used to describe the situation where the medial half of the librigenal field stands at an angle approaching 90° to the external half. This term is not entirely satisfactory, but will be used until a more appropriate term is devised.

Posterior area of fixigena. This is the area of the fixigena posterior to an imaginary line drawn transversely from the posterior corner of the palpebral lobe to the axial furrow. It may be very limited in size, or it may be expanded.

Terms of nomenclature.

Abbreviations

sag. and exsag. for sagittal and exsagittal

tr. transverse

"3 spine" and "5 spine". used to describe protasid stages with, respectively, 3 pairs and 5 pairs of protopygidial marginal spines.

sp. species (singular), used when a specimen is identifed as a belonging to a particular genus but cannot be identified at the species level.

n. sp. new species.

n. sp. A etc. used when specimens belong to a new species, but the species remains unnamed because there are insufficient specimens or material is fragmented or lacking in well-preserved detail.

aff. *affiinis*, having affinity with but not identical with, used to identify a group of specimens with morphological affinities to a named taxa.

? used when there is a high probability a group of specimens are members of a given taxon, but for a variety of reasons (e.g., lack of preserved detail, teratological specimen) there is not a precise fit.

s.l. *sensu lato* , in the broad sense, used, in this thesis, where the "best fit" for a group of specimens is in a given taxon, but the specimens do not meet all the diagnostic criteria for that taxon.

CHAPTER II

ONTOGENY OF LICHIDS: A LITERATURE REVIEW

This (development and embryology) is one of the most important subjects in history........ It has already been stated that various parts in the same individual which are exactly alike during an early embryonic period, become widely different and serve for widely different purposes in the adult stage. So again it has been shown that generally embryos of the most distinct species belonging to the same class are closely similar, but become, when fully developed, widely disimilar. .....

Darwin; Origin of Species. Sixth Edition, 1872 (Reprint, 1962)

The life cycle of a trilobite is divided into three major periods; protaspid (larval); meraspid (juvenile) and holaspid (adult). Trilobites, like other arthropods, grow in increments with the addition of segments associated with the periodic loss of the exoskeleton (moulting) and the development and remineralization of a new cuticle. Information on the ontogeny of the trilobite and on the morphology of the various instars is preserved in the discarded moults. Holaspides and possibly late meraspides are the most frequently represented in most described trilobite faunas, a situation that reflects preservational biases but that may also be influenced by collecting and preparation practices. Most faunas containing well-preserved protaspid and early meraspid specimens are silicified.

The protaspid period is the larval phase, in which the protocranidium and the protopygidium are fused and there is no transverse joint. This is the earliest mineralized stage.

Protaspid larvae fall into one of two main body plans: the nonadult-like and the adult-like (Speyer and Chatterton, 1989). The nonadult-like protaspides are three dimensional with spines that point in all directions and are believed, on the basis of morphology, to have had a planktonic life mode. The adult-like protaspides are flatter, more two-dimensional in appearance, and have features that can be traced through developmental stages. These larval forms are thought to have had a benthic life mode. Chatterton and Speyer (1989) formulated four developmental strategies. A few taxa, such as the Calymenidae, Scutelluidae and Styginidae have an early nonadult-like protaspid form and a later adult-like form. Most taxa have an adult-like protaspides, but it is possible that, for these taxa, an earlier, poorly or non-calcified nonadult-like stage existed.

There are general patterns of morphological change with growth that appear to hold true for all adult-like protaspides. The glabella expands. Eyes, which in the protaspis are positioned at the anterolateral margin of the cranidium move backwards and outwards (laterally) with cranidial development. The character of overall prosopon may change considerably. In some taxa, it may be possible to follow the position of certain key tubercles through ontogeny: for example, pairs of tubercles on the glabella, certain tubercles on the fixed cheek and on the posterior margin of the cranidium, as well as those on the axis and on the pleural lobes of the pygidium. However, in many cases, some or all of these tubercles will disappear during ontogeny. Frequently, there are marginal spines in the protaspid and meraspid periods, many or all of which have disappeared in the adult stages. The hypostome initially has blunt marginal spines or the margin subdivided by perpendicular slits. Axial furrows may deepen and other evidence of increased muscle attachments appear.

The second major phase in development is the meraspid period. This encompasses a number of instars, ranging from the first appearance of the transverse joint between the cranidium and the pygidium, to the stage where the adult number of thoracic segments less one has been released from the transitory pygidium. The meraspid degrees are defined by the number of thoracic segments that have been released.

Whittington (1957) reviewed the ontogeny of trilobites, and recommended the value of information from protaspides and meraspides in determining phylogenetic history. There is a problem in determining the homology of ontogenetic features that must be addressed whenever a comparative study is being done. If one cannot tell whether developmental stages, which appear similar in different taxa, are homologous or not, it is difficult to compare apparently homologous features. For example, a notational system for describing protaspid cranidial spines was developed for odontopleurids by Whittington (1956b, fig. 1) which then was adapted by Chatterton (1971, fig. 9C) to describe the protaspid cranidial spines of lichids, but at no time was it suggested that, between the two groups, spines with similar notation are homologous.

Edgecombe (1992, p. 156) suggested that characters from early stages are useful in "filtering out some of these highly derived characters and in recognizing more general similarities .....". Information from early ontogenetic stages has been used to determine relationships, evolutionary patterns and the monophyletic nature of taxa. Because radical morphological changes may occur in ontogeny, characters present only in larvae may be helpful in determining membership in higher taxa. Monophyly of groups can often be determined by the study of the protaspides. This has been done successfully with odontopleurids (Whittington, 1956b), asaphids (Fortey and Chatterton, 1988), calymenids (Chatterton et al., 1990), encrinurids (Edgecombe et al., 1988), lichids (Chatterton, 1971; Chatterton, 1980; Hu, 1974; Tripp and Evitt, 1981; Whittington, 1956a).

The lichid protaspis has a characteristic appearance regardless of the subfamily to which it belongs. Lichids have also been closely allied to the odontopleurids on the basis of protaspid characters (Edgecombe, 1992). Some illaenid and styginid protaspides have, on occasion, been identified incorrectly as lichids (e.g. Shaw, 1968, pl. 3:10; text-fig. 12).

Lichid protaspides are adult-like (Speyer and Chatterton, 1989), have an opisthoparian facial suture, a distinct anterior border, a defined axial region, a flaring outwards of the lateral margin immediately posterior to the palpebral lobe, and a median tubercle on the occipital ring. In addition to the large median occipital tubercle, a distinctive pattern of tubercles can be seen on the fixigena, fixigenal posterior border, the glabella and protopygidium. The tubercles vary somewhat in their arrangement according to the taxon to which the protaspis belongs. All known lichid protaspid specimens fall into one of 2 stages, the "three spine" stage (3 pairs border spines, 3 spines on each side) and the "five spine" stage (5 pairs border spines) (Chatterton, 1980; Tripp and Evitt, 1981). No protaspides with 4 pairs of spines have ever been found, which suggests that the known stages represent two successive instars, between which is a moult in which two pygidial segments are added. The protaspid hypostome is subrectangular in shape, longer (sag.) than wide, and has four slits in the lateral margin.

Chatterton and Speyer (in press) suggested that there might be an earlier planktonic, nonadult-like protaspid stage for the lichids, which is discussed in the section on *Acanthopyge* (*Jasperia*) *bifida*.

Lichid meraspides are beginning to assume more adult characteristics. In most lichids, cranidial lobes begin developing on the sides of the glabellar lobe in the early meraspid period. During successive moults, there are qualitative and quantitative changes in prosopon, increasing inflation and expansion of cranidial lobes, especially the glabella, and allometric changes, including the movement of the eye backwards and outwards, leading to the final holaspid form. The nature and timing of these changes can provide important phylogenetic information.

The proportions of the hypostome change during the meraspid period, from the early meraspid form, in which the length is greater than the width, to latest meraspid hypostome, with the width just slightly less than the length (sag.). During this period the lateral margin slits become less pronounced.

Ontogenetic sequences of 4 genera belonging to 3 subfamilies, 3 genera from the Ordovician and one from the Devonian, have been reported in the literature.

Subfamily LICHINAE Hawle & Corda, 1847

Species *LICHAS LACIANATUS* (Wahlenburg, 1818)

Temple (1969) found meraspid specimens of *Lichas lacianatus* in the Lower Llandovery Limestone at Keisley, Westmoreland in northern England. Of interest from the viewpoint of ontogeny are a series of 12 cranidia. The cranidial sagittal lengths range from 1.1 mm to >5.25 mm. The smallest has a small bullar lobe developing between the level of S2 and S1. Temple plotted the length of the developing bullar lobe against the sagittal length of the preoccipital glabella (1969; p. 215, fig. 3) and found the relationship between the two was linear, with the x axis being intercepted at 0.45 mm. In other words, according to his calculations, the bullar lobe development begins after the preoccipital glabellar length is greater than 0.45 mm. Temple interpreted these data as showing the bullar lobe developed by growing forward rather than by backward development of the S3 furrow.

Subfamily TETRALICHINAE Phleger, 1936

Genus *AMPHILICHAS* Raymond, 1905

Chatterton (1980) discussed the ontogeny of two species of *Amphilichas*, *A. conradi* Chatterton and Ludvigsen, 1976 and *A.* aff. *A. aspratilis* (Bradley, 1930) from two sections of the Middle Ordovician Esbataottine Formation of the Mackenzie Mountains. The ontogenetic sequences are represented by several specimens of the "three-spine" protaspid stage, meraspides and holaspides for *A.* aff. *A aspratilis* and early meraspid to holaspid stages of *A. conradi*. Attribution of protaspides and meraspides to a species was possible because, for each of the two sections, holaspides of one species were more common than those of the other. The characters found to differ between the two species in the early stages (a difference in concavity of the anterior margin, length (sag.) of anterior border and depth of the longitudinal glabellar furrow opposite L1 in early meraspid stages) might not have been as useful in separating the two species if the distribution of holaspides had not also been different.

While there are no signs of bullar lobe development in the protaspid period, one can see, in the earliest meraspid cranidia, small lobes developing in front of S1. They are defined by an inwardly and posteriorly directed furrow beginning at the S2 position on the adaxial side of the axial furrow (Chatterton 1980, text fig 12D, E). As the bullar lobe develops with forward expansion, Chatterton suggested it incorporated, rather than displaced, L3 and L4. Early meraspid cranidia have distinctive spinose tubercles that can be identified and traced through to holaspid cranidia

The series of meraspides provides information regarding allometric changes as well as the development of lobes and changes in ornamentation. Some of the ontogenetic changes include: expansion of the glabella laterally at the expense of fixed cheeks; appearance in early meraspides of bullar lobes with subsequent forward growth and increased size; expansion forward of the median lobe of the glabella; change in the shape of the anterior margin from concave to strongly convex forward; decrease in size of tubercles and increase in their number; decrease in the relative length (sag.) of the anterior border; migration inward of the posterior branch of the facial suture so that ω is directly behind the palpebral lobe in the holaspis; and increasing depth of axial and pleural furrows on the pygidium.

Tripp and Evitt (1981, pl. 1, figs. 14 - 27; pl. 2, figs. 22 - 32) found numerous protaspides and meraspides attributable to *Amphilichas* from the Middle Ordovician of Virginia. There are, in all probability, several species represented in this sample, based on morphological variations in the pygidium, size differences an' ornamentation. Numerous protaspides of both the "three-spine" (37 specimens) and the "five-spine" (22 specimens) stages were found. The two instars could not be clearly separated on the basis of morphometric measurements. Tripp and Evitt demonstrated the forward growth of the bullar lobe, using a method similar to that of Temple (1969).

A late protaspis specimen showed the development of a fixigenal spine (pl. 1, figs. 22 - 27), which they suggest indicates a strong similarity between lichid and odontopleurid protaspides. It should be noted that this fixigenal spine is not evident on any of the protaspides belonging to other genera.

The protaspides found in the Edinburg Formation can be distinguished from those from the Esbataottine Formation in that the latter have a more concave (forward) anterior margin, an anterior border that is narrower medially and a different arrangement of tubercles.

Hu (1974) also described *Amphilichas* from the Middle Ordovician of Virginia. Many of Hu's specimens attributed to *Amphilichas* belong to *Hemiarges* (Hu 1974, p. 357 - 363, pl. 49: figs. 1, 5 - 14, 19 - 30; Chatterton, 1980; Tripp and Evitt, 1981). The remaining specimens are correctly identified as *Amphilichas* (Hu, 1974, pl. 49, figs. 2 -

4, 15 - 17, 18? and 31). Drawings (Hu, 1974; text fig. 2) illustrating a growth sequence of *Amphilichas* are misleading and not useful since both *Hemiages* and *Amphilichas* are represented, and a certain idealization of features appears to have occurred, showing them as they should be, rather than as they are.

Chatterton and Speyer (in press) illustrated some early growth stages of *Amphilichas*: protaspides of *Amphilichas* sp. from the lower Edinburg Formation of Virginia (fig. 44E) and *Amphilichas minganensis* ? from the Crown Point Formation, New York (fig. 44H, I); and a meraspid cranidium of *A. conradi* from the Esbataottine Formation of northwestern Canada

Subfamily TROCHURINAE Phleger, 1936

Genus *ACANTHOPYGE* Hawle & Corda, 1847

Beecher (1893) was the first to describe a lichid protaspis which he named *Phaëthonides* sp. In 1895, he (Beecher, 1895) re-assigned it to *Arges consanguinea* (Clarke, 1894), now *Acanthopyge (Lobopyge) consanguinea* (Clarke, 1894). This single silicified protaspis from the Lower Devonian of New York was redescribed by Whittington (1956a, text-figure 1A, B and pl. 131, figs. 1 - 6).

The most complete ontogenetic sequence of a lichid, that of *Acanthopyge (Mephiarges) bifida* Edgell, 1955, the type species of *Acanthopyge (Jasperia)*, was reported by Chatterton (1971) from the Lower Devonian of Yass, New South Wales.

Approximately 200 protaspides of *A.(J.) bifida* were collected, all of which fell into two distinct growth stages. The smaller stage, designated as the "3 spine" stage (Chatterton, 1971; fig 9A, B and plate 7, figs. 1 - 4), has dimensions of approximately 0.9 mm long by 1.0 mm wide. There are 3 small pairs of spines projecting from the posterior protopygidial border and a characteristic pattern of spines and tubercles on the dorsal surface of both the protocranium and protopygidium.

The second protaspid stage, the "five spine" stage (Chatterton, 1971; figs. 9C, D, F and pl. 7, figs. 5 - 7), is slightly larger (1.2 mm long by 1.5 mm wide) and has 5 border spines, suggesting the addition of two more segments. In the late protaspis, there are signs of the initial stages of a lateral glabellar lobe opposite glabellar spine pair 3. Chatterton determined that the lobe develops from the side of the glabella in the region of the axial furrow and so the unusual lobation characteristic of the lichids is mainly (or entirely) of glabellar origin. Temple (1972) has suggested the term "bullar" to describe these lobes since to use the term "lateral" would imply homology with lateral lobes in other groups. Thomas and Holloway (1988) agree that the bullar lobe develops in a central position within the furrow, but they feel one cannot tell if the bullar lobes are derived from the glabella or the fixigena. An internal view of the protaspis (Chatterton 1971, pl. 7, figs. 6a, b), shows greater growth on the adaxial side of the furrow, supporting the idea that the bullar lobe is of glabellar origin rather than fixigenal. The earlier timing in development of the bullar lobe in *A.* (*J.*) *bifida* suggests a heterochronic change.

The hypostome is similar for both protaspid stages, being longer than wide and only slightly inflated. The major characteristics of interest are the four slits along the lateral border (Chatterton, 1971, fig 9A; pl. 8, figs. 6 - 10).

The two protaspid stages *Acanthopyge* (*Jasperia*) *bifida* are very large relative to protaspides of other species found at Yass, the smaller stage 0.9 mm long and the larger, 1.2 mm long. Chatterton speculated that smaller stages of this lichid should have been found but were not because: a) the earlier developmental stages were completed in the egg (Størmer, 1942) or b) the earlier stages lacked a mineralized exoskeleton. Chatterton and Speyer (in press) later suggested that an earlier planktonic (non-adult-like) growth stage was, in fact, preserved, and these specimens had been incorrectly assigned to *Apocalymene quadrilobata* (see Chatterton 1971; text-figs. 18 H, I and pl. 19, figs. 8 - 10, pl. 21, figs. 1 - 3). No nonadult-like protaspides have been found for any other lichids. The reasons for the proposed association have not been presented and the identification remains uncertain.

Meraspid cranidia and transitory pygidia show important morphological changes. The continuing development of the cranidial lobes can be followed. The small glabellar lobe, the bullar lobe, which appears in the late protaspis, grows forward and laterally, until it is opposite spine pairs 3, 4 and 5. Chatterton suggested that these spine pairs on the glabella represent lobes L2, L3 and L4 and that the bullar lobe must therefore be tricomposite. The posterolateral lobes appear in the earliest meraspid cranidia along the axial furrow opposite the preoccipital glabellar lobe L1, and gradually grow outwards with increasing inflation. Initially the growing lobe appears to displace spine A1, but eventually this spine is incorporated into the lobe, suggesting the posterolateral lobes are derived from both glabella and fixigena (see pl. 7, figs. 8 - 15).

Between the last protaspid and earliest meraspid stages, the free cheek develops a large genal spine with a deep subgenal notch. With growth, the genal spine projects more transversely.

With many specimenˢ representing an almost complete sequence of transitory pygidia from M0 - M10, it is possible to analyse, by tracking ornamentation on the spines, the development and release of thoracic segments. The area of segment proliferation appears to lie in a zone between the posterior part of the axis and the posterior margin of the transitory pygidium close to the mmedian plane.

During meraspid development, the hypostome changes from its early form in which the length is greater than the width, to one in which the width is greater than the length. The anterior lobes of the middle body become larger than the posterior lobe. Ornamentation appears first on the anterior lobe, then on the posterior lobe and finally on the lateral borders. In late meraspid stages, the lateral borders are ornamented with terrace lines parallel to the margins. The characteristic median concavity on the posteromedian part of the doublure appears late. The lateral slits seen on the protaspid and early meraspid hypostome become small shallow indentaations on the margin, often with small furrows crossing the lateral borders in line with the indentations. Eventually these disappear.

Genus *HEMIARGES* Gürich, 1901

Chatterton (1980, pl. 17, figs. 1 - 23; text-fig. 12 F - K) described protaspid and meraspid stages of *Hemiarges turneri* Chatterton and Ludvigsen 1976 from the Middle Ordovician Esbataottine Formation of the Mackenzie Mountains, Northwest Territories, Canada. Protaspides (two stages) were described as well as meraspid cranidia and transitory pygidia. Although this ontogenetic series is not as complete as that of *Acanthopyge (Jasperia) bifida* (Edgell, 1955), allometric changes in the free cheek, cranidium, hypostome and pygidium can be followed. The bullar lobes begin to develop as glabellar lobes at the L2 position in the earliest meraspid stage, as is seen in *Amphilichas,* but not in *A. (J.) bifida* in which this occurred in the latest protaspid instar.

Tripp and Evitt (1981, pl. 1, figs. 1 - 13; pl. 2, figs. 7 - 16) described two protaspid stages, meraspid cranidia and transitory pygidia which are ascribed to *Hemiarges rasetti* Tripp and Evitt, 1981 (pl. 1, figs. 1 - 13; pl. 2, figs. 1 - 6, 17 - 21; text-figs. 1, 1 - 5, text-fig. 2, 1a - d), and to *Hemiarges* sp. (pl. 2, figs 7 - 16) from the Middle Ordovician of Virginia. The developmental pattern of this species of *Hemiarges* is similar to that reported by Chatterton. In *H. rasetti,* Tripp and Evitt determined that the small "occipital" lobe developed from the posterior slope of L1 during late meraspis, thus making it a posterolateral swelling of the glabella and not an occipital lobe. Hu (1974) illustrated specimens from the Middle Ordovician of Virginia, which he identified as

Amphilichas. A number of these have been reassigned to *Hemiarges* by Chatterton and Ludvigsen (1976) and to *H. rasetti* by Tripp and Evitt (1981) although there is some discrepancy between the two papers as to which specimens were incorrectly identified. It appears that of the specimens photographed for Plate 49 of Hu (1974), those in figs. 1, 5 - 14, 19 - 30 should be assigned to *Hemiarges*. This includes protaspides and meraspides.

Tripp (1979, pl 40, fig. 25) illustrated a *Hemiarges* protaspid from the Ordovician limestones of Girvan, possibly *H. inghami*. Tripp, 1979. Little detail is apparent in the extremely small photograph.

Shaw (1968) illustrated one protaspid, several meraspid cranidia and transitory pygidia from the Chazy which he identified as *Amphilichas*. The meraspides and some holaspides (Shaw, 1968, pl 3, figs. 8, 11, 14 - 22, 24) were reassigned to *Hemiarges* by Chatterton (1980) and later placed by Rudkin et al. (in press) in a new subspecies, but here considered a species, *Hemiarges amiculus* (see subspecies question discussed in Introduction). The protaspis (see Shaw, 1968; pl. 3, fig. 10) is believed by Chatterton (1980; p.23, text-fig. 4B) to be an illaneid or styginid protaspis.

Chatterton and Speyer (in press) illustrated a growth series from the Crown Point Formation, New York, identified as *H.* aff. *H. turneri* (fig. 44A -G). Also from the Crown Point Formation is a protaspis of *Hemiarges* sp. (cf. *H. turneri* Chatterton and Ludvigsen, 1976) illustrated by Speyer and Chatterton (1989, fig. 4 D, E). This specimen is remarkable because the free cheeks and hypostome are still present.

CHAPTER III

ONTOGENY OF SILURIAN LICHIDS FROM THE MACKENZIE MOUNTAINS

The Avalanche Lake trilobite fauna includes lichids belonging to 7 genera, which are described in this section. Most of the lichids belong to 5 genera in the subfamily Trochurinae (*Acanthopyge, Borealarges, Dicranogmus, Radiolichas, Richterarges*), and there is one genus from each of the subfamilies Lichinae (*Dicranopeltis*) and Homolichinae (*Platylichas*). The occurrence of lichid holaspides is unusual, that of protaspides and meraspides even more so. The present collection of early growth stages is the result of setting aside specimens over many years of trilobites studies, with many of the specimens being found by B.D.E. Chatterton. The previously undescribed ontogeny of 5 of the 7 genera is discussed.

The similarities between lichid protaspides of different genera can make identification difficult. In this work, assignment of early growth stages to a particular genus was done on the basis described by Chatterton (1980): 1) morphological transition through developmental stages; 2) co-occurrence of different stages in the same horizon; 3) previously published growth stages of similar taxa; 4) assumption of orderly increase in size through various stages. There may be major changes in morphology during ontogeny which can make association difficult. If certain key elements such as cranidial tubercles show a continuity of pattern, association is facilitated.

Similar criteria are involved in identifying disassociated holaspid sclerites to the species level. As will be seen, there was little stratigraphic separation in some taxa, which made the task more difficult. In this work, association of individual sclerites was done on the basis of: 1) co-occurrence of different sclerites and/or growth stages; 2) similarities in morphology, e.g., inflation of glabella and pygidial axis or nature of pygidial and cephalic spines; 3) similarities in ornamentation; 4) comparison with published lichids from other localities.

Attribution of early growth stages is made at the genus level. Some differences seen within morphologically similar protaspid and meraspid stages may be attributed to species differences (as is seen for *Hemiarges*, Table 1 and Fig. 3).

Descriptions of holaspides, which provide the basis of species identifications, are included in this section on ontogeny since holaspides are the final stage of development in the ontogenetic sequence.

Systematic Paleontology

Order LICHIDA Moore, 1959

Family LICHIDAE Hawle and Corda, 1847

Subfamily LICHINAE Hawle and Corda, 1847

Genus *DICRANOPELTIS* Hawle and Corda, 1847

{Objective synonym: *Trachylichas* Gürich, 1901

Subjective synonyms: *Dicranopeltoides* Phleger, 1936; *Raymondarges* Phleger, 1937, *Tsunyilichas* Chang, 1974 }

Type species. Lichas scabra Beyrich, 1845 from the Liten Formation (Wenlock), Czech Republic. Holotype pygidium figured by Beyrich 1845, fig. 16 (also Thomas and Holloway, 1988, pl. 2, fig. 36).

Stratigraphical range. Ashgill - Ludlow.

Geographical range. Canada (Newfoundland, Ontario, Québec, Northwest Territories - Mackenzie Mountins and Canadian Arctic), United States (Arkansas, Illinois, New York, Wisconsin; Ireland, England, Scotland, Sweden, Germany, Czech Republic (Bohemia); Kazakhstan, Tadzhikistan, China (Guizhou Province).

Diagnosis. Glabella strongly convex anteriorly. Bullar lobe fully circumscribed; L1a and L1b usually present, may be confluent abaxially. If longitudinal furrow extends posterior to S1, it is very shallow and does not disturb prosopon. Axial furrow extends to occipital furrow or L1a. Librigena with deep subgenal notch. Pygidium with three pairs of marginal spines. Pygidial axis about one third of pygidium length, long post axial band which narrows posteriorly, and axial furrows that do not meet.

DICRANOPELTIS n sp. A

(Plate 1, figures. 1 - 16; Plate 2, figures. 1 - 10)

Material. Cranidia UA 9762, 9763, 9767, librigenae UA 9765 - 9773, hypostomes UA 9764, 9768 - 9770.

Stratigraphical interval. AV1 588 and AV1 590 m; AV4 126 (T) m; AV2 256 m; AV5 58 - 60 m.

Description. Cranidium. Glabella fairly flat posteriorly, curving downwards anteriorly. Longitudinal furrow distinct anterior to S1, not continuing posterior to S1. Axial furrow, narrow and distinct, continues from posterolateral border of bullar lobe to lateral corner of occipital ring. Furrow defining Lla shallow, most distinct adaxially (Lla not present in cranidium UA 9763 from AV1 588 m). Palpebral lobes semicircular, bisected by short (tr.) slit. Occipital ring moderately long (sag.) and wide (tr.). Prosopon bimodal. Paired tubercles on glabella, row of tubercles along posterior edge of occipital ring.

Free cheeks robust with long (exsag.) curved eye. Eye stalk at right angles to librigenal field. Large subgenal angle. Librigenal spine large, wide (tr.) with rounded termination. Tubercles aligned along length of eye platform. Prosopon bimodal, consisting of large tubercles and much smaller ones. Doublure plain except for long subparallel terrace lines on lateral margin. In dorsolateral view, fine terrace lines visible along lateral margins.

Hypostome. Width greater than length. Posterior border broad (sag.), lateral borders slightly less broad (tr.). Shoulders opposite mid-length (sag.) of hypostome. Pronounced anterior wings and large, ventrally inflated antennal notch. Middle body divided into anterior and posterior lobes by middle furrow which meets lateral furrow at level of anterior wing and is obliquely, posteromedially directed, adaxial portion of furrow approaches posterior border furrow and is non-bifurcating; anterior lobe considerably larger than posterior lobe, posterior lobe is swollen laterally. Small maculae present at adaxial end of middle furrow. Lateral border furrow deep, with extensions beyond posterior border furrow. Anterior lobe and central part of posterior lobe pitted, shallower pits on lateral portions of posterior lobe. Tubercles present to greater or lesser degree on anterior portion of anterior lobe. Wavy terrace lines subparallel to lateral margins on full extent of lateral border, anastomose posterior to antennal notch. Medial portion of posterior border lacks ornament. Posterior margin curved with curved median reentrant. Doublure plain, narrowest sagittally, extending anteriorly over half distance from posterior margin reentrant to posterior border furrow. Anterior border of doublure forms inflated lip medially anterior to small median depression.

Discussion of Species

The sclerites assigned to *Dicranopeltis* n. sp. A. show wide distribution, being found in all the sections sampled for this study. There is, however, a paucity of specimens, and considerable difference in relative size of parts, with the hypostomes and free cheeks being considerably larger than the complete holaspid cranidia found.

The hypostome is assigned to *Dicranopeltis* n. sp. A. on the basis of the unusual nature of the middle furrow, which meets the lateral furrow opposite the anterior wing and proceeds posteriorly in an oblique and transverse direction, a characteristic of lichine hypostomes, and particularly that of *Dicranopeltis*.

Ontogeny

Protaspid period (Plate 1, figures 1, 2).

Material. Protaspis UA 9757, "5 spine" stage.

Stratigraphical interval. AV4 126 (T) m.

Description. Large protaspis, 1.7 mm long; maximum width slightly greater than length. Protocranidium about 55% sagittal length of protaspis. Axial furrows well defined, moderately deep and wide, subparallel with slight adaxial deflection at approximately L2. Glabella inflated, protruding slightly into anterior border. Anterior border broken, details not available. Palpebral lobes large, long (20-25% sagittal body length), semi-circular, moderately swollen and projecting laterally. Eye ridge present. Posterior to palpebral lobes, genal area flares outward perpendicular to exsagittal plane to form large rounded genal lobe. Transverse demarcation of cranidium from protopygidium more apparent on inner surface than on external. Axis of protopygidium narrows to small rounded point. Axial furrows shallow. Four axial rings and terminal piece in axis, first three rings defined posteriorly by ring furrows, fourth ring furrow faintly. Four pleural bands plus undifferentiated median area (seen most clearly on internal surface). First and second posterior pleural bands slightly inflated. Interpleural furrows deeper than pleural furrows. Doublure narrow with small anterior sharp projection medially, continuous anteriorly with that of cranidial posterior margin of genal lobe. Five pairs of spines project from posterior margin, spines are broken, anterior spines appear to be long and slender (based on appearance of third spine), fifth pair small and triangular, projecting posteriorly.

Prosopon of external surface shows very small, evenly distributed, overall granules. Anterior border has transverse row of tubercles. Large medial tubercle on occipital ring. Glabellar tubercles 2 and 4, large, single and medial, possible smaller paired tubercles, probably pairs 1, 3 and 5 (see internal surface, Pl. 1, fig. 2). Very small tubercles anterior to glabellar tubercle pair 5, arranged in triangular fashion with apex forward. Fixigenal tubercles A1 and A2, two small tubercles on posterior border (B, C), palpebral tubercles and very small eye ridge tubercle present. (In Pl. 1, fig. 1, large tubercle on right side of glabella, probably teratological). Small tubercles are arranged in row (tr.) along each protopygidial axial ring. Single large tubercle is present on each posterior pleural band that line up to form curve ending with tubercle C on the posterior margin of the cranidium.

Meraspid period (Plate 1, figures 3 - 7).
Material. Cranidia UA 9759, 9760, transitory pygidium UA 9758 (7 pairs free spines), late meraspid transitory pygidium UA 9761 (5 pairs of spines).
Stratigraphical interval. AV4 126 (T) m, AV1 588 m.
Description. Cranidium 1.6 mm long. Long (sag.) anterior border, length greatest at anterolateral corners. Glabella inflated, median lobe widened, with increased inflation anteriorly. Bullar lobes forming on either side of glabella anterior to S1, separated from medial glabellar lobe by longitudinal furrow. Slight inflation of L1 medially. Palpebral lobes large, semicircular, projecting outward. Eye ridge present. Genal angle projects laterally well beyond palpebral lobe. Occipital ring with width (tr.) equal to width of glabella across bullar lobes.

Prosopon of fine granules. Small tubercles arranged in row on anterior border. Large medial tubercle on occipital ring with smaller tubercles flanking it. Glabellar tubercles pattern not clear but apparently similar to protocranidium described above. Tubercles A1 and A2 on fixigena, tubercles B and C on posterior margin, two larger tubercles and one smaller tubercle on rim of palpebral lobe, and 3 small tubercles along eye ridge.

Transitory pygidium. Length (sag.) 1.02 mm. Six well-defined axial rings and terminal piece, ring furrows distinct, axial furrows narrow and distinctly impressed. Axis narrows to small rounded termination some distance from the posterior margin. Furrows more visible on internal surface. Six pleurae, each defined posteriorly by an interpleural furrow, fifth and sixth interpleural furrows incomplete abaxially, the sixth shallower than the fifth. Seventh pleura medial and undifferentiated. Pleural furrows shallower than interpleural furrows and more distinct on more anterior pleurae Posterior bands of pleurae 1, 2 and 3 are longer (exsag.) than the anterior bands. Seven pairs of marginal spines, pair 1 projects laterally, pairs 2, 3, 4 project progressively more posteriorly, pair 5 projects directly backward, 6 and 7 posteromedially. Spines 1 - 6 are long, slender and slightly curved, spine 7 is short and conical in shape. Prosopon of granules distributed uniformly. Paired small tubercles on axial rings 1 - 4, one larger, median tubercle on axial ring 5. Three tubercles on posterior band of first pleura, distal one largest. Pleurae 2 and 4 have two pairs of tubercles on posterior bands, abaxial tubercle larger. Pleura 3 has one small tubercle on the posterior band midway between axial furrow and margin. No tubercles on pleura 5, and one each on pleurae 6 and 7. Large tubercles on posterior band of pleurae 1, 2, 4, 6 and 7 form curve, as in protaspis.

Late meraspid transitory pygidium. Length (sag.) 2.5 mm. First two axial rings defined by deep axial ring furrows, third axial ring furrow shallow. Axial furrows firmly impressed, convergent posteriorly to meet at posterior margin. Five pairs of pygidial marginal spines, broad and flat. Pleurae separated by firmly impressed interpleural furrows. Pleurae 1 - 4 have pleural furrows, anterior and posterior bands subequal in length (exsag.) with anterior band increasing in length (exsag.) abaxially as spine, which is continuous with pleura, forms and curves posterolaterally. Pairs of enlarged tubercles, part of row of tubercles aligned (tr.) along axial ring found on 5 axial rings, sixth ring or terminal piece marked by single tubercle. Enlarged tubercles found on both anterior and posterior pleural bands, largest of these tubercles occurs on each of the posterior pleural bands at outer edge of pleura.

Discussion of ontogeny

The size of the protaspis is large relative to those of other genera. No "3-spine" protaspides were found. It should be noted that in the case of *Acanthopyge* (*Jasperia*) *bifida* which also has exceptionally large protaspides, the "3-spine" protaspis is as large as or larger than many of the "5-spine" stage protaspides of other genera (Chatterton, 1971). Thus, the "3 spine" protaspis of this species could be expected to be large.

The meraspid cranidium and the protocranidium of the protaspis are similar in the shapes of the palpebral lobe and genal lobe, and in the arrangement of enlarged tubercles. Paired tubercles, present on the holaspid median glabellar lobe, are extremely small or absent on the protaspid and meraspid glabella. The two large median tubercles, so visible in the protaspis, disappear during the meraspid period. It is unfortunate that no later meraspid cranidia were found to show transitional stages. The relation between protopygidium and the smaller of the two transitory pygidia is also clear. The spines of the later transitory pygidium have flattened and broadened, assuming a more adult-like morphology, the axis has lengthened and the axial furrows meet at the posterior margin. Further growth must bring an expansion of the axis, until the adult form is reached in which the axial furrows do not meet and sometimes diverge. From early to later meraspid stages, there has been a change in the axis morphology from an axis with 6 axial rings visible to one in with 2-3 distinct axial rings. At the later stage, the pygidium proportions are still immature with the width approximately twice the length.

The holaspid cranidia from these sections are incomplete. The single medial glabellar tubercles have been lost and there are at least 4 pairs of tubercles visible.

Discussion of genus

This is a widespread genus, both geographically and stratigraphically. Most of the known species were discovered and described in the 1800's and early 1900's, many of them too poorly illustrated to use for comparative purposes. The holaspid material from the Avalanche Lake sections is widely distributed but not common, and the ontogenetic material in this study, however sparse, gives us previously unavailable information on the protaspid and meraspid periods.

The holaspid cranidia of *Dicranopeltis* n. sp. A have clearly defined paired glabellar tubercles and there is evidence, although not consistent, of paired glabellar tubercles at all stages of development. The fact that paired tubercles are not always readily observable in the protaspid or meraspid specimens suggests their development occurs late in ontogeny. *D. salteri* (Thomas, 1981, pl. 19, fig. 11) and *D. salteri?* (Siveter, 1989 pl. 23, figs.1, 2, 3, but probably not 8) have paired tubercles. Siveter (1989) reported that paired tubercles are also found on some specimens from Bohemia attributed to *D. scabra and D. scabra propinqua* (see Vanek 1959, fig. 13 for the latter) while other specimens (Thomas and Holloway, pl. 2, fig. 32) are lacking them. Siveter suggested these species need revision in order to clarify some of these problems.

Subfamily HOMOLICHINAE Phleger, 1936
{*nom. correct.* Tripp 1957 ex Homolichadinae Phleger, 1936}

Genus *PLATYLICHAS* Gürich, 1901

Type species. Lichas margaritifer Nieszkowski, 1857

Subgenus *PLATYLICHAS (RONTRIPPIA)* Thomas and Holloway, 1988

Type species. Lichas grayii Fletcher, 1850, from the Wenlock of England and Gotland.
Stratigraphical range. Caradoc?, Ashgill - Wenlock, Ludlow?.

Geographical range. Canada (Northwest Territories, Quebec?), United States (Illinois?) Greenland, Wales, England, Sweden (Gotland), Ireland? Estonia?.

Diagnosis. Platylichas with pygidium up to twice as wide anteriorly as long (sag.) Axis half or more of sagittal pygidial length, distinctly constricted or gradually narrowing posteriorly. Two complete ring furrows, third and fourth increasingly discontinuous adaxially. Third pleural furrow describing a loop posteriorly and confluent with furrow bounding postaxial band (emended diagnosis based on Thomas and Holloway, 1988; p. 212, 213).

PLATYLICHAS (RONTRIPPIA) INFIMUS n. sp.

(Plate 3, figures 1 - 21)

Material. Holotype pygidium UA 9774, paratypes UA 9774 - 9790.

Stratigraphical interval. AV1 95.5 m (Llandovery).

Etymology. infimus (L), lowest: Found at the base of the Silurian.

Diagnosis. Pygidium axis length more than half pygidium length (sag.), axial band narrowing gradually posterior to fourth axial ring, third pleural furrow forming loop, posterior part of loop partially incomplete; hypostome length equal to or slightly less than width; free cheek long (exsag.), narrow with long (exsag.) eye socle and short blunt genal spine.

Description. Cranidium slightly wider than long, width (tr.) of median and bullar lobes similar at S2, median lobe slightly elevated above bullar lobes. In lateral profile, median glabellar lobe overhangs, very slightly, the anterior border; little independent inflation of bullar lobes. Anterior border short (sag.), separated from glabella by well-defined preglabellar furrow. L1a lobes clearly defined, furrow defining anterior margin of L1a lobes slightly shallower than posterior and occipital furrows. Occipital ring wider (tr.) than median lobe at S1. Longitudinal furrows meet occipital furrow at adaxial boundary of L1a lobes, are displaced laterally by expanded median glabella at L1 and then converge slightly forward towards S1; longitudinal furrows diverge from S1 to S3 curving laterally around anterior of bullar lobe, meeting axial furrow lateral to S3. S1 deep, curves anterolaterally, meeting axial furrow near palpebral lobe with bullar lobe completely circumscribed. Anterior edge of palpebral lobe opposite S2. Prosopon of small, dense, bimodal tubercles, uniformly covering cranidium. Slightly enlarged tubercles along posterior of occipital ring, median tubercle slightly forward of posterior margin.

Librigena long and narrow with very long (exsag.) eye that protrudes outward (laterally), eye socle distinguished from rest of librigena by break in slope and by diminished overall prosopon and moderately sized tubercles arranged in more or less linear fashion. Field has fine overall bimodal tubercular prosopon. Lateral margin relatively straight, doublure with long subparallel terrace lines, lateral portions of which are visible from dorsolateral view as anterior lateral margin curls slightly upward. On internal surface, terrace lines curve backward adaxially, are subparallel and transverse across librigenal spines; librigenal spine slightly concave on adaxial margin.

Hypostome. Maximum width (tr.) equal to or slightly greater than length. Shape of hypostome and of middle body sub-trapezoidal, broad posterior border (sag.) and moderately broad (tr.) lateral borders, small anterior wings, shoulders at mid-length (exsag.) of hypostome, slightly behind middle furrow. Middle body divided into anterior and posterior lobes by middle furrow which runs inward transversely and adaxially a short distance, furrow incomplete medially. Both lobes are wider than long with anterior lobe larger than posterior lobe and with slight swelling of both lobes on laterally. Maculae in posterior lobe small, slightly inflated. Slight extension of lateral furrow into posterior border beyond posterior furrow. Prosopon of fine even granules (obscured by poor preservation). Posterior margin curved, with median reentrant, the transverse inner margin of which is straight to convex.

Thoracic segment. Incomplete segment only. Pleural furrow present, runs obliquely from close to anterior edge near axial furrow to midpoint (exsag.) about 1/3 width (tr.) abaxially, then continues laterally to distal region of pleura.

Pygidium. Width (tr.) greater than length, with three pairs of broad, spatulate pleura, ending in broad, flat, backward-directed marginal spines, no posterior border. First and second pleural furrows slightly curved posteriorly, and extending to margin, third pleural furrow curves posteriorly and then medially and anteriorly to meet axial furrow, forming well-defined loop. Axial furrow deep and narrow. Four axial rings and a terminal piece, first three axial rings completely defined by ring furrows, third axial ring being almost effaced adaxially and fourth ring defined posteriorly by a ring furrow which disappears adaxially. Axis narrows gradually posterior to fourth axial ring. Prosopon bimodal, of fine tubercles. May be pairs or row of slightly larger tubercles on axial rings (details uncertain). Doublure wide, with long terrace lines approximately parallel to margin with some anastomosis of terrace lines.

Ontogeny

Protaspid period (Plate 3, figures 17, 20, 21).

Material. Protaspides, "5 spine" stage, UA 9791, 9792.

Stratigraphical interval. AV1 95.5 m.

Description. Protocranidium 60-65% of total length (sag.) of 1.06 mm. Glabella bounded laterally by subparallel axial furrows. Occipital ring defined by shallow occipital furrow; median occipital tubercle (visible from internal surface). Anterior border relatively straight (tr.) and of constant length (sag.) across transverse width. Palpebral lobe slightly swollen, eye ridge present; fixed cheek between palpebral lobe and glabella inflated. Cranidium and protopygidium delineated transversely by marginal furrow. Protopygidium axis terminates in a point separated from posterior margin by 15% of total sagittal length. Three axial rings and terminal piece separated by shallow ring furrows. Three pleura with inflated posterior pleural bands, the remainder of protopygidium undifferentiated. Five marginal spines projecting from posterior margin of protopygidium, first two pairs projecting slightly lateral of backward direction, third pair projects posteriorly and farther back than others, pairs 4 and 5 project posteromedially, fifth pair medial and partly fused. External surface rough probably due to overall prosopon (details not clear); cranidial tubercles present but pattern not clear.

Discussion of genus

The only lichid which has been found in the AV1 95.5 m horizon is *Platylichas (Rontrippia) infimus* and this is the basis of the identification of the protaspides.

The appearance of this protaspis is very similar to that of *Borealarges* (compare Pl. 3, figs. 17, 20, 21 to Pl. 21, figs. 13 - 19). The *Platylichas* protaspis tends to be wider and more rounded, and differs in the inflation of the fixed cheek area, the lack of glabellar waisting, and the character of the protopygidial marginal spines, which are longer and freer than those of *Borealarges*.. If both *Platylichas* and *Borealarges* occurred in the same horizon, it could prove difficult to distinguish the protaspides of one from those of the other, and it does lead one to question whether or not this protaspis is correctly identified. At present, there are no known species of *Borealarges* from the Llandovery with the possible exception of *Hemiarges rolfei* Lamont, 1965, which was assigned by Thomas and Holloway (1988) to *Richterarges* and by Adrain (in press), tentatively to *Borealarges*.

Discussion of subgenus

Thomas and Holloway (1988) created two subgenera of *Platylichas*; *Platylichas (Platylichas)* Gürich, 1901 and *Platylichas (Rontrippia)* Thomas and Holloway, 1988, the division being based on the fact that while cranidia of each are similar, there are two morphologically distinct pygidia. The two differ in the proportions of width to length and the shape of the marginal spines but the major defining feature for *Platylichas* (*Rontrippia*) is the loop formed by the third pleural furrow. The stratigraphical range of *Platylichas* (*Platylichas*) is Caradoc to Llandovery, that of *Platylichas* (*Rontrippia*) overlaps and extends beyond the former, to the Wenlock, and possibly the Ludlow. Thomas and Holloway have assigned two species to *Platylichas* (*Rontrippia*) and several more tentatively because they are known from only the cranidium. The cranidia of most members of the genus *Platylichas* are conservative in their morphology with only minor differences being diagnostic for the two subgenera.

P. (*R*.?) *parvulus* Cooper and Kindle, 1936 (p. 368, pl. 15, fig. 16, 22) from the Upper Ordovician Whitehead Formation of Percé, Québec, is, unfortunately, illustrated by very small photographs of a cranidium which show little detail. The longitudinal furrow posterior to L1 appears to be convex with respect to the sagittal plane (that of *P*. (*R*.) *infimus* is concave). *P*.(*R*.?) *telleri* (Weller, 1907) from the Niagaran Limestone near Chicago is illustrated by drawings (Weller, 1907, pl. 22, figs. 8, 9) which Thomas and Holloway (1988) found, on comparison with the actual specimens, to be somewhat inaccurate with regard to the placement of the axial furrow. Norford (1981, p. 12; pl. 7, figs. 11, 12) assigned a hypostome to the genus *Platylichas* based on the similarity of its shape to the sketch of the outline of the hypostome of the type (Tripp, 1957, fig. 4p). The illustration shows a heavily granulated hypostome, the prosopon of which is quite unlike any of the illustrated hypostomes of *Platylichas*. Unfortunately the posterior margin of Norford's specimen is broken, eliminating an important source of information, but the pattern of granulation and the overall shape suggests this is a hypostome of *Dicranogmus* (see Pl. 31).

Platylichas (*Rontrippia*) *infimus*, from the Llandovery, occurs towards the middle of the stratigraphic range occupied by *Platylichas* (*Rontrippia*).

The holaspid sclerites of *P*. (*R*.) *infimus* are similar to those of *Platylichas* sp. A. from the Llandovery of Washington Land, North Greenland, illustrated by Lane (1979, pl. 6, figs 10 - 14, 17). Details of the cranidial morphology of *Platylichas* sp. A are difficult to discern from the published illustrations. The hypostome has width/length proportions similar to that of *P*. (*R*.) *infimus*. The shape of the pygidial axis of both the

Greenland and Mackenzie Mountain species is similar in that there is a gradual narrowing of the postaxial band rather than an abrupt narrowing immediately posterior to the axis seen in *P.* (*R.*) *grayii* (Thomas and Holloway, 1988, fig. 182). On Lane's specimen, there is a knoblike protuberance on the terminal piece of the axis, a feature not discernible on the axis of *P.* (*R.*) *infimus* since this area is broken in both specimens available (Pl. 3, figs. 1, 2), but breakage at this point could be due to the presence of a protuberance. The pygidium of *P.* (*R.*) *infimus* has a partially defined fourth axial ring which does not appear to be the case in *Platylichas* sp. A. The proportions of pygidial width/length and of axial width/pygidial width are slightly different between the two species.

The hypostome and the pygidium of *P.* (*R*) *infimus* have features that fall between those described for each of the 2 subgenera.

The proportions of the hypostome are intermediate between those illustrated by Thomas and Holloway (1988, fig.173, 187) for *P.* (*P.*) *nasutus* (Wigand, 1888) and *P.* (*R*) *grayii* (Fletcher, 1850). However, if one compensates for the anterior expansion of the hypostome of *P.* (*P*) *nasutus*, the proportions of the hypostome of *P.* (*R*) *infimus* are more similar to that than they are to *P.* (*R.*) *grayii*.

The morphological characters of the pygidium of *P.* (*R.*) *infimus* and of *Platylichas* sp. A, which appear to be intermediate between those of *P.* (*P.*) *nasutus* and *P.* (*R.*) *grayii* , are seen in the third pleural furrow and in the axis. The loop formed by the third pleural furrow, the main feature diagnostic of the subgenus *Platylichas* (*Rontrippia*), is incomplete for a short distance in the posterior loop in *P.*(*R.*) *infimus*. The pygidium of Lane's *Platylichas* sp. A. also has an incomplete posterior portion of the loop. The axis of *P.*(*R.*) *infimus* is not "distinctly constricted posteriorly" as the diagnosis of Thomas and Holloway states (1988, p. 213), but narrows gradually, as does that of *Platylichas* sp. *A.*. The axis of both species differs from the diagnosis of each subgenus by having a length greater than one half the pygidial length. In spite of these differences, these two species belong in *Platylichas* (*Rontrippia*) and therefore the diagnosis of the subgenus has been emended to include the differences.

There are questions regarding the validity of the subgenera of *Platylichas*. One could make the suggestion that the 2 subgenera reflect morphoclinal variation with one end member being *Platylichas* (*Platylichas*) *nasutus* from the Ashgill and the other *Platylichas* (*Rontrippia*) *grayii* from the Wenlock. At present there is insufficient information to support this contention. In an Appendix to their monograph on the lichids, Thomas and Holloway (1988) discussed the possibility that *Metaleiolichas*, a genus erected by Kobayashi and Hamada (1987), based on one incomplete cranidium, might be a senior synonym for *Platylichas* (*Rontrippia*). For the moment it is convenient to retain the two subgenera as proposed by Thomas and Holloway, with the hope, common to most paleontological questions, that the discovery of more material will help resolve the question.

Subfamily TROCHURINAE Phleger, 1936
{=Argetinae Gürich, 1901; Euarginae Phleger, 1936;
Acanthopyginae Erben, 1952; Ceratarginae Tripp, 1957}
Genus *ACANTHOPYGE* Hawle and Corda,1847

Type species. Lichas Haueri Barrande, 1872

Thomas and Holloway (1988) recognized four subgenera of *Acanthopyge* based mainly on differences in pygidial morphology, but united at the genus level by similar cranidial morphology. Included in the diagnosis of the genus is the presence, on the cranidium, of L1 with a very short medial portion which is depressed and bears a prominent tubercle

Subgenus *ACANTHOPYGE (LOBOPYGE*) Přibyl & Erben, 1952

Type species. Original designation; *Lichas branikensis* Barrande, 1872, (p. 43), Dvorce-Prokop Limestone (Pragian), Bohemia.

Stratigraphical range. Late Ordovician?, Wenlock - Eifelian, Givetian?.

Geographical range. Canada (Mackenzie Mountains, Baillie-Hamilton Island, Ontario), United States (New York), Bolivia, England, Wales, Sweden (Gotland), Germany, Czech Republic, Turkey, former U.S.S.R. (central Kazakhastan, Kuznetsk Basin), China (Ghuizhou Province), Australia (New South Wales, Victoria).

Diagnosis. Cranidium has greatest width across posterior part of fixigena. Medial portion of L1 short, depressed and bearing large tubercle. Pygidium with three major pairs of relatively short marginal spines, slightly flattened in cross section, and projecting backwards; a pair of secondary spines may be present between successive pairs of major ones. Two pairs of pleural furrows, not meeting pygidial margin, pleural and interpleural furrows curving backwards abaxially. Excluding marginal spines, length of pygidium approximately 65% of width; axis width 40-50% of maximum pygidium width, and axis length 65-75% pygidial sagittal length (adapted from Thomas and Holloway, 1988; p. 225).

ACANTHOPYGE (*LOBOPYGE*) n. sp. A

(Plate 4, figures 1 - 3)

Material. Partial cranidia UA 9794, 9795; pygidium UA 9793.

Stratigraphical interval. AV2 274-279 m (Wenlock).

Description. Cranidium with short (sag.), depressed Ll, with median pair of tubercles, and complete S1. Cranidial prosopon bimodal, with 2 sizes of large tubercles. Paired tubercles present at approximately S2 position on median glabellar lobe, large tubercles present at possible A1 and A2 positions of posterior lobe and at least one large tubercle towards posterior of bullar lobe. Large median tubercle present towards posterior of occipital ring, flanked by smaller tubercles. Margins of palpebral lobe and posterior branch of facial suture lined with small tubercles. Fixigenal spine fairly long, projecting laterally and slightly posteriorly. Length of pygidium is about 75% of the width. Axis width is approximately 45-50% of pygidial width and axis length 75% of pygidial length. Anterior and posterior bands of first and second pleura are equal in length (exsag.), and posterior bands inflated. First two marginal spines are continuous with posterior bands, but receive contributions from anterior bands. No posterior border. Interpleural and pleural furrows stop short of margin. Details of axial structure are not available, although it appears that first axial ring furrow deep and probably complete. Short postaxial ridge stops short of margin at distance similar to that of pleural furrows. Prosopon of large tubercles is sparsely distributed.

Discussion of species

This is a new species, but it was not formally named because the specimens available were incomplete and the number limited (2 cranidial fragments, 1 small pygidium).

Most Silurian species of *Acanthopyge* (*Lobopyge*) have pygidia with pronounced posterior borders (see discussion below). The specimens identified as *Acanthopyge* (*Lobopyge*) n. sp. A are very small (pygidium 1.85 mm long) and appear to be in the late meraspid to early holaspid stages of development. Since these specimens are close to maturity, the absence of a pygidial border is unlikely to be a reflection of the stage of development. These specimens represent an early (Wenlock) member of a predominantly Devonian clade.

ACANTHOPYGE (*LOBOPYGE* s.l.)*PRISTINUS* n. sp.

(Plate 5, figures 1 - 27)

Type and other material. Holotype cranidium UA 9796, paratypes UA 9797 - 9813.

Stratigraphical interval. AV4B 111 m, (Llandovery).

Etymology. pristinus (L.), early, primitive, with reference to the early occurrence of this species.

Diagnosis. Cranidium relatively flat; small, fully circumscribed bullar lobe, anterior border of moderate length (sag.). Free cheek with moderately curved subgenal notch. Pygidium width slightly greater than length, with three pairs of free marginal spines that are long, tapered, and flattened in cross section, well-developed postaxial ridge, marginal border.

Description. Cranidium. Anterior border moderate length (sag.), inflated, and curved convex anteriorly, fairly deep preglabellar furrow. Anterior branches of facial suture subparallel to divergent. Palpebral lobe small, semicircular, with suggestion of pit in centre. Sharp deflection laterally of posterior branch of facial suture immediately behind palpebral lobe. Posterior area of fixigena short (tr.). Longitudinal furrow faintly impressed across L1, deeply impressed and divergent for length of bullar lobe (S1 - S3), curving outward and backward to meet axial furrow. Small pit present at this point. S1 curves sharply anteriorly to meet axial furrow a short distance behind point where longitudinal furrow meets axial furrow. Axial furrow very short (exsag.). Bullar lobe is small and fully circumscribed. Minimal dorsal-ventral curvature of bullar lobes allows entire circumscription of bullar lobe to be visible in dorsal plan view. Median glabella lobe broad, slightly wider than bullar lobes (tr.), increases in width (tr.) anterior to bullar lobe. Glabella lobe does not overhang anterior border. Prosopon bimodal and evenly distributed. No paired glabellar tubercles. Occipital ring (L0) slightly longer (sag.) than anterior border.

Librigena elongate, broad lateral and posterior border furrows meet on surface of genal spine. Librigenal field moderately deep. Prosopon of field bimodal, evenly distributed tubercles; few tubercles present on lateral and posterior borders. Genal spine of moderate length with gently curved, subgenal notch.

Rostral Plate. Length (sag.) and width (tr.) similar to that of anterior border, anterior margin convex, posterior margin concave; details of lateral projections not available.

Hypostome gently inflated, subtrapezoidal, sagittal length about 85-90% maximum width. Anterior border rounded, convex anteriorly. Anterior wings minimal. Broad, barely indented lateral notch. Posterior and laterai border furrows narrow, moderate depth separating middle body from lateral and posterior border. Posterior border about 30% of total sagittal length, broader than lateral border, re-entrant medially. Length of anterior lobe about 65% (sag.) of length of middle body, middle furrow present abaxially. Middle body, posterior and lateral borders with bimodal, uniformly distributed granules, lateral border has faint terrace lines subparallel to margin. Doublure full width of posterior border. Dorsal median concavity, median doublure margin posteriorly turned to form small lip with three small posteriorly directed spines, median one largest.

Pygidium. Pygidium maximum width slightly greater than length (excluding half ring and marginal spines); with three pairs marginal spines. First anterior pleural band slightly longer (exsag.), than posterior pleural band, second anterior band is almost twice the length (exsag.) that of posterior band. First and second posterior bands inflated. Posterior border distinct, interrupted by border spines Well-developed postaxial ridge extends to merge with border, length about 25% of total pygidial length (sag.). First axial ring furrow deep and probably complete, second axial ring furrow shallow abaxially. (Axis incomplete in all specimens). Marginal spines free, project posteriorly, taper to point and fairly long, in cross section flattened oval shape. Space between median spines V-shaped.

Discussion of subgenus

Acanthopyge (*Lobopyge*) is a predominantly Devonian genus, with several reported occurrences in the Wenlock and Upper Silurian. *Acanthopyge* (*Lobopyge*) n. sp. A conforms to the diagnosis of the subgenus, but *A*. (*L*. s.l.) *pristinus*, found in the Late Ordovician just above the last Ordovician faunal turnover, in the *persculptus* Zone, presents some difficulties in its identification.

A. (*L*. s.l.) *pristinus* has a pygidium that most closely resembles *Acanthopyge* (*Lobopyge*), and a cranidium which is very *Hemiarges* - like. In this horizon, only one lichid cranidium and one lichid pygidium are found, and it is on this basis the two are associated. The sclerites assigned to this species are compatible with respect to size, prosopon and preservation.

The cranidium of *A*. (*L*. s.l.) *pristinus* is very like that of *Hemiarges diadayma* Rudkin, Tripp and Ludvigsen (in press) from the lower Whittaker Formation (Middle

Ordovician), Funeral Range, Mackenzie Mountains (see Ludvigsen, 1978, pl. II, fig.16), but *A.* (*L.* s.l.) *pristinus* does not have a Lla lobe. A new species of *Hemiarges*, *H. avalanchensis* (described in this work), is geographically closest to *A.* (*L.* s.l.) *pristinus*, occurring in same section, at AV 4B 16.5 m (and possibly up to AV 4B 43), but its morphology resembles that of *H. paulianus* (Rudkin et al., in press, pl. 1, figs. 1, 2; pl. 2, figs. A - J; pl. 3, figs. C, D, E, H; pl.4, C, G - H) and is distinctly different from either *H. diadayma* or *A.* (*L* s.l.) *pristinus*, as can be seen in Figure 5.

The cranidium of *A.* (*L.* s.l.) *pristinus* shows an almost equal number of *Hemiarges* -like and *Acanthopyge* -like characters. The Ll differs from the diagnosis of the genus *Acanthopyge* in that it is not short (exsag.) and depressed and does not bear a prominent tubercle. There is, however, a complete S1 extending from the longitudinal furrow to the axial furrow, which is characteristic of *Acanthopyge*, but may also occur in some species of *Hemiarges*, including *H. diadayma*. There is a posteromedial extension of S1 (faintly impressed in this case), characteristic of *Acanthopyge* but also sometimes seen in *Hemiarges*, e.g. *H. maccullochi* (Thomas and Holloway, 1988, pl. 15, figs. 322, 323, 327). The librigena of *A.* (*L.* s.l.) *pristinus* has a moderate, subgenal notch.

The pygidia of *A.* (*L.* s.l.) *pristinus*, *H. diadayma* and *H. avalanchensis* are quite different (see Fig. 5). The pygidium of *A.* (*L.* s.l.) *pristinus* has 3 pairs of marginal spines, the pygidia of *H. diadayma* and *H. avalanchensis* have 4 pairs of marginal spines, although the pygidium of *H. diadayma* appears to be losing its third marginal spine which is located on the abaxial edge of the median fourth pair. In both *H. diadayma* and *H. avalanchensis*, the second and fourth spines are the largest. *H. avalanchensis* and *A.* (*L.* s.l.) *pristinus* have a posterior border, *H. diadayma* does not.

The pygidium of *A.* (*L.* s.l). *pristinus* resembles a pygidium from the Canadian Arctic illustrated by Perry and Chatterton (1977, pl. 5, fig. 17) in that it has three marginal spine pairs, a posterior border and an expanded second anterior pleural band. It differs in that the marginal spines of *A.* (*L.* s.l) *pristinus* are shorter, project backwards rather than posterolaterally, and the median space between the third pair of spines is V shaped rather than U shaped. The specimen illustrated by Perry and Chatterton was included by them in their new species, *Hemiarges rohri*, now known as *A.* (*L.*) *rohri* , but the morphology appears to be distinct from that of the holotype (pl. 5, fig. 4). Both pygidia have a posterior marginal border.

A posterior marginal border is not present in the Devonian members of *Acanthopyge* (*Lobopyge*) but is found in many Silurian species presently assigned to *Acanthopyge* (*Lobopyge*). In addition to the Mackenzie Mountains and Arctic material, pygidial borders are found in other Silurian material. A species from the Upper Silurian of southwest China, *A.* (*L.*) *orientalis* Wu 1977, appears to have a border. *A.* (*L.*) *pusilla* (Angelin, 1854) from Gotland, Sweden is reported to have a border (Thomas and Holloway, 1988, p. 226).

Posterior marginal borders are present in some, but not all, of the specimens assigned to *A.* (*L.*) *hirsuta* (Fletcher, 1850) from the Wenlock of England (pl. 6, figs. 1 - 3; Thomas and Holloway 1988, pl. 15, fig. 301; Thomas 1981, fig. 17, pl. 20, fig. 2; Reed, 1903, pl. 1, fig. 4). There is considerable morphological variation, in addition to the presence or absence of a pygidial marginal border, in specimens assigned to *A.* (*L.*) *hirsuta*. Thomas (1981) considered these variations morphoclinal. It is more probable that collections have been made without proper stratigraphical constraints, and that there are, in fact, several species represented in the illustrated material of this taxon.

A. (*L.* s.l) *pristinus* may be considered a very late *Hemiarges*, a very early *Acanthopyge* or a member of a sister group to *Acanthopyge*. With only a small number of specimens available, the decision was made to place them, until the problem can be resolved, in *Acanthopyge* (*Lobopyge*) *sensu lato*.

The subgenus *Acanthopyge* (*Lobopyge*), a predominantly Devonian clade, is widely distributed around the globe. Thomas and Holloway (1988) give the stratigraphical range of *Acanthopyge (Lobopyge)* as Wenlock to Eifelian. If *Acanthopyge* (*Lobopyge* s.l) *pristinus* is properly placed in *Acanthopyge* (*Lobopyge*), the stratigraphical range of the subgenus would extend back in time to the Late Ordovician and would make this the oldest known member of both the subgenus *Acanthopyge* (*Lobopyge*) and the genus *Acanthopyge*.

Genus *BOREALARGES* Adrain, in press

Type species. Borealarges reedi Adrain, in press; from Cape Phillips Formation (late Wenlock), northwestern Cornwallis Island, central Canadian Arctic.

Stratigraphic range. Upper Llandovery?, Wenlock - Eifelian.

Geographic range. Canada (Arctic, Mackenzie Mountains), United States (California) England,Scotland, China, Japan, .

Diagnosis. Trochurine with short anterior border; bullar lobe circumscribed anteriorly; anterolateral corners of cranidium often with small projections; cranidial ornament of relatively coarse tubercles with paired median glabellar tubercles retained, often prominent in large holaspides; S1 strongly anteriorly directed and with considerable posterior convexity; hypostomal suture usually describing gentle continuous arc with no abrupt posterior deflection; hypostomal middle body with ornament of fine to moderately coarse pits and tubercles anteriorly; pygidium with basic pattern of two pairs of pleural spines, two pairs marginal spines, and single posteriomedian spine (sometimes secondarily lost); pygidium with length (sag.), usually with 7 - 8 discernible axial rings; postaxial ridge prominent but short (adapted from Adrain, in press).

BOREALARGES FRITILLUS n. sp.

(Plate 7, figures 1 - 15)

Material. Holotype pygidium UA 9816 from AV2 256 m, paratypes UA 9814, 9815, 9817, 9820.

Stratigraphical interval. AV1 583 and 590 m; AV2 256 and 274 - 279 m.

Etymology. fritillus (Latin), spotted, referring to appearance of tubercles on cranidium and pygidium.

Diagnosis. Cranidium with slight anterolateral projections. Curvature of bullar lobes and median glabellar lobe similar. Large central tubercle on each bullar lobe and posterolateral lobe. Paired tubercles on median glabellar lobe at approximately S2 and S3. Moderately dense bimodal prosopon. Pygidial marginal spines flattened; spines 1, 2 and 3 elongate triangular, spines 4 and 5 small triangle shapes.

Description. Cranidium with small to slight subangular anterolateral projections where anterior branch of facial suture intersects anterior margin. Anterior branches of facial sutures convergent where they intersect anterior margin. Glabella overhangs border slightly. Palpebral lobe small semi-circular projection with central transverse slit-like pit oriented. Posterior area of fixigena of moderate length (tr.), extends slightly posterolaterally. Longitudinal furrows between occipital furrow and S1 shallow and broad, between S1 and S3 (along length of bullar lobe) narrower and slightly deeper, with deflection laterally at S2 position; shallowing as curving laterally at S3 towards axial furrow; small pit at point where longitudinal furrow meets axial furrow, point of articulation with anterior wing of hypostome. Curvature of bullar lobes similar to that of median glabellar lobe but median glabellar lobe slightly higher. Ornamentation moderately dense and bimodal, ratio of small to large tubercles 3:1. Two pairs of tubercles on glabella (glabellar tubercle pairs 3 & 5?). Ll medially depressed with 4 - 6 larger tubercles, roughly arranged in 2 rows, posterior row with pair of large tubercles flanking 1 or more smaller tubercles and anterior row variable. Occipital ring ornamented with row of five larger tubercles.

Pygidium. First and second pleurae defined by interpleural furrows; anterior and posterior bands of first pleura similar in length (exsag.); anterior band of second pleura expanded; first and second posterior pleural bands inflated. Pleural field of third pleura long (exsag.), undifferentiated. Five pairs of marginal spines, fifth median fused pair, spines slightly upturned. Third pair of spines largest, elongate subtriangular, extending short distance beyond fourth and fifth spines. First two axial rings defined by deep broad ring furrows. Details of axial structure obscured or missing. Short, well-defined postaxial ridge. Prosopon sparse, with few large and many small tubercles. Large tubercles widely spaced along posterior margin border; 3 to 4 large tubercles aligned along posterior pleural bands. Large tubercles scattered on pleural field of undifferentiated third pleura.

BOREALARGES FRITILLUS ?

(Plate 7, figures 14, 15)

Discussion. A single large pygidium from AV5 58 - 60 m resembles *B. fritillus* n. sp. in the shape and arrangement of the posterior marginal spines. It is wider with respect to length when compared to the holotype pygidium of *B. fritillus*. No other sclerites were found that could contribute to the identification of this pygidium.

BOREALARGES PATULUS n. sp.

(Plate 8, figures 1 - 20; Plate 9, figures 1 - 20)

Material. Holotype pygidium UA 9821 from AV4 240 m, and paratypes UA 9822 - 9843.

Stratigraphical interval. AV2 256 and 274-279 m; AV4 231, 234 - 238, 240 and 245 m.

Etymology. patulus (L), meaning spread out, broad, wide open, with reference to the spacing of the spines on the flattened posterior margin of the pygidium.

Diagnosis. Borealarges with flat (rather than curved) posterior pygidial margin. Nine marginal spines, fourth pair of spines small, immediately adjacent to large third pair, with considerable space between fourth pair and median fifth spine; two axial rings defined by complete ring furrows. Cranidium with small anterolateral projections, paired tubercles on median glabella present but often masked by prosopon.

Description. Cranidium with short anterior border and small anterolateral projections. Anterior branches of facial suture slightly convergent at intersection with anterior margin. Small, elevated palpebral lobes bisected by transverse pit. Posterior area of fixigena moderate length. Longitudinal furrows shallow between occipital ring and S1, more deeply impressed between S1 and S3, curves anterolaterally at S3, with small pit marking point at which it meets axial furrow. Occipital ring defined by deep occipital furrow. Paired tubercles present on median glabellar lobe, often masked by bimodal prosopon of large and medium sized tubercles.

Pygidium with sagittal length 60 - 70% width. Two axial rings defined by complete ring furrows, rings 3 - 7 discernible with ring furrows present abaxially on rings 3 and 4, subsequent rings marked by presence of tubercles. Tubercles aligned along first axial ring. Tubercle pattern on subsequent axial rings variable, but usually consists of pairs of tubercles on axial rings, with closely spaced pairs of larger tubercles (3 pairs) alternating with more widely spaced smaller tubercle pairs. Axis narrows fairly abruptly to short postaxial ridge. First anterior pleural band short (exsag.); second anterior pleural band expanded; first and second posterior pleural bands inflated, row of 2 - 3 large tubercles along posterior bands. Third pleural field with several large tubercles on background of smaller one, largest tubercle near centre of field. Pleural spines appear to be formed mainly from posterior pleural band with some contribution from anterior band. Third spine pair largest, elongate flattened triangle, posteriorly directed, projecting beyond fourth pair of spines and median spine. Fourth pair of spines small, located medial and immediately adjacent to third pair. Median spine small. Median spines (fourth and fifth) spaced far apart. Posterior marginal border defined by shallow border furrow, ornamented by few large tubercles; border interrupted by second and first pleural spines. Pygidial posterior margin flattened and relatively straight (tr.) between third pair of spines. Doublure ornamented with terrace lines which coarsen distally and, close to margin, become rows of small triangular shaped tubercles which also extend onto ventral surface of marginal spines.

Discussion of species

The pygidial morphology of *Borealarges patulus*, particularly with respect to the posterior margin and marginal spines, is sufficiently distinct from that of other species of *Borealarges* to support it being identified as a separate species.

In *B. patulus*, there are two main patterns of pygidial axis tubercle arrangements, involving large, closely spaced pairs and smaller, more widely spaced pairs. These patterns occur with similar frequency and similar stratigraphic distribution. The larger more closely spaced pairs are usually found on either rings 2, 5, 7 or rings 3, 5, 7 and the smaller, more widely spaced tubercles on rings 1, 4, 6 or 2, 4, 6, respectively, so the variation in the tubercle arrangement occurs on axial rings 1, 2 and 3. There is usually a row of tubercles on axial ring 1 and occasionally a row of tubercles on ring 2, but on ring 2 it is more common to see a pair of tubercles, either the large, close pair or small, widely spaced pair; if it is the small widely spaced pair, the pair can be slightly enlarged tubercles in a row of tubercles. It would be interesting to know what the thoracic segments of these trilobites looked like. If the thoracic segments have rows of tubercles, the first to third axial rings of the holaspid pygidium could be showing a developmental transition from pairs to rows of tubercles. A variation in the pattern of tubercle distribution has also been seen in *B. variabilis*.

The cranidium assigned to *B. patulus* bears a strong resemblance to that of *Richterarges facetus*. *B. patulus* differs in the presence of anterolateral projections, shorter (tr.) posterior area of the fixigena and the presence of paired median glabellar tubercles. There is also a stratigraphic separation with cranidia of *B. patulus* being found only in the high AV4 horizons and pygidia at the high AV4 horizons plus AV2 256 m; and *R. facetus* at AV5 57.7 - 60 m.

BOREALARGES RENODIS n. sp.

(Plate 10, figures 1 - 15; Plate 11, figures 1 - 24; Plate 12, figures 1 - 12)

Material. Holotype pygidium UA 9844 from AV4 126 (T) m, paratypes UA 9845 - 9857, UA 9984 - 9993.

Stratigraphical interval. AV1 590 m, AV2 256, 255-260 and 274-279 m, AV4 126 (T) m, AV5 58-60 m.

Etymology. *renodis* (L) unbound, loose, free, referring to pygidial marginal spines which, for a species of *Borealarges*, are unusually long and free.

Diagnosis. *Borealarges* with median glabellar lobe of cranidium showing great dorsal convexity, particularly opposite S2, elevated above lateral glabellar lobes; two pairs glabellar tubercles enlarged; weak anterolateral cranidial projections; anterior fixigenal field expanded, anterior border defined by strong anterior border furrow; elevated eye, usually not as high as maximum height of bullar lobe; free cheek broad field (tr.), eye high and at angle to field; genal spine curved, long, and flattened cylindrical in cross-section, large semi-circular subgenal notch; pygidium with 3 pairs of long, slender, curved cylindrical spines and 3 much smaller medial spines.

Description. Cranidium. Anterior border moderate length (sag.), defined by strong anterior border furrow, weak anterolateral projections; anterior branches of facial suture sub-parallel to convergent. at point of intersection with anterior margin. Anterior fixigenal field expands anteriorly. Palpebral lobe elevated, semicircular, lined with tubercles, and with transverse slit at midpoint of circumference. Longitudinal furrow very shallow from occipital furrow to S1, parallel and strong from S1 to S3, and furrow laterally deflected at S2. S1 extends adaxial to longitudinal furrow. Median lobe of glabella dorsally inflated at S2, convexity independent of that of bullar lobes which are only slightly inflated, and much less elevated than median lobe. Prosopon bimodal, with coarse larger tubercles. Two pairs enlarged tubercles (glabellar tubercles 3 and 4?) on median glabella, at point of maximum inflation. Occipital ring with median tubercle sometimes obscured by ornamentation; occipital furrow and posterior border furrow deep.

Librigena. Large librigenal field with inner half of field bent upwards at right angles to outer part (see Pl. 10, fig. 23); lateral border broad, with large evenly spaced tubercles along border, and small closely spaced tubercles along outer edge; posterior border narrower with several evenly spaced large tubercles along border; librigenal spine long, narrow, curved backward, flattened in cross-section and dorsally grooved proximally; broad, semicircular subgenal notch. Eye length short (exsag.); eye socle semicircular, lined with closely but irregularly placed tubercles, largest tubercle at anterior end of platform. Bimodal prosopon, with numerous small tubercles and fewer large tubercles scattered evenly over surface.

Pygidium with three pairs long, curved, free marginal spines and 3 small medial spines; first anterior and posterior pleural bands short (exsag.) and subequal, the posterior band inflated; second pleura with expanded anterior band and inflated posterior band. Three larger tubercles aligned along both first and second posterior pleural bands. Third pleural band undifferentiated. First and second marginal spines appear continuous with posterior pleural bands; first three spines about equal in length; the fourth spine, small, on margin halfway between third spine and small median spine; first 3 spines often flexed upwards. Posterior border defined by shallow, broad furrow. Axis width, anteriorly, about 40% total pygidial width; first axial ring most inflated, first and second rings defined by complete axial ring furrows; subsequent rings defined abaxially by partial ring furrows and/or by presence of tubercles on rings; pairs of larger tubercles often on rings 1, 3, 5 and 7; smaller tubercles pairs more closely spaced on rings 2, 4, 6 and possibly 8; arrangement of tubercles less clear on larger specimens. Short postaxial ridge. Inner margin of doublure "V" shaped, forming almost straight line from near anterolateral corner to point just anterior to termination of axis; doublure widest opposite second spine. Fine terrace lines parallel to margin, coarsening to parallel rows of small tubercles towards margin. Ventral surface of spines with rows of triangular shaped spines, apex outwards similar to those on outer doublure.

Discussion of species

Borealarges renodis n. sp. is one of the more widely distributed species of the Mackenzie Mountain *Borealarges*, appearing in all 4 sections, and in all horizons with the exception of the high AV4 levels.

B. renodis shares some characters with *B. tuckerae* Adrain, in press. In both, the median glabellar lobe is highly convex and inflated, with prominent paired tubercles, although, in *B. tuckerae*, these tubercles are much larger, tending towards spinosity. The anterolateral projections on the cranidium of *B. tuckerae* are much more distinct than are those in *B. renodis*. The librigena of both have a broad librigenal field and similar ornamentation along the eye socle. The pygidium of *B. tuckerae* has long free spines which are straight, with the third spine being markedly longer than the others. In *B. renodis*, the pygidial spines are curved, the second and third spines are similar in length and the first spines only slightly shorter.

BOREALARGES TUCKERAE Adrain, in press

(Plate 13, figures 1 - 21; Plate 14, figures 1 - 10)

Material: Cranidia UA 9994 - 9996; librigena UA 9997, 9998; pygidia UA 9999, 100000. 10002 - 10004; transitory pygidium UA 10001.

Horizons. AV1 586 m; AV2 256 and 255-260 m; AV4 240 m; AV5 57 and 58-60 m, DR 91.44 m.

Discussion. The holaspides have been described by Adrain (in press). The transitory pygidium (Plate 14, figs. 2 - 5) with 6 pairs of pygidial marginal spines shares, in common with the holaspid pygidium, elongate cylindrical spines, and in the axis, an abrupt transition from a horizontal plane to a steep downward slope terminating in the postaxial ridge.

The free cheeks of *B. tuckerae* are interesting for the pattern of tubercles seen on the eye socle (see Pl. 13, figs. 15, 16). One extremely large tubercle is found at the anterior edge of the socle. Two rows of smaller tubercles are aligned parallel to the eye socle margin posterior to the large tubercle. This feature is not discussed in the original description of the species, although one figure shows the presence of tubercles on the eye socle (Adrain, in press, pl. 10, fig. 25), but the tubercle arrangement in this specimen is not as regular as that seen in the specimens from the Avalanche Lake area.

This is the only species of *Borealarges* that is found in both the Arctic and the Mackenzie Mountains. *B. tuckerae* is found in the Cape Phillips Formation, Baillie Hamilton Island (sections BH 1 164.5 - 204 m and BHI 1 92 m) central Canadian Arctic.

BOREALARGES sp. aff. *B. TUCKERAE*

(Plate 15, figures 1 - 9)

Material. Cranidium UA 10005, pygidium UA 10006.

Horizon. AV5 57 and 58-60 m.

Discussion. The median glabellar lobe of the cranidium is slightly inflated and has enlarged tubercles protruding at S2. There is a resemblance between this cranidium and that of *B. tuckerae* . On the median glabellar lobe, *B. tuckerae* has two pairs of enlarged tubercles, and a third pair, the posterior pair, just anterior to approximately the S1 position. In *B.* sp.aff. *B. tuckerae*, the tubercle pairs are enlarged but lack the spinosity seen in *B. tuckerae*, and the posterior pair of tubercles is only slightly larger than background ornamentation. The anterolateral projections of the crandium are similar in both. *B.* sp.aff. *B. tuckerae* lacks the pronounced hump of the median glabellar lobe and the spinose tubercles of *B. tuckerae.*

The pygidium assigned to *B.* sp.aff. *B. tuckerae* has curved spines ornamented with numerous elongate tubercles, unlike the straight spines ornamented with small tubercles of *B. tuckerae.* The third spine is largest in both species. The nature of the other spines of *B.* sp.aff. *B. tuckerae* is unknown. *B.* sp.aff. *B. tuckerae* lacks the pronounced and abrupt change in slope of the posterior pygidial axis seen in *B. tuckerae.*

The cranidium and pygidium of *B.* sp.aff. *B. tuckerae* were associated because the sclerites were found in only one section and in essentially the same horizon, and both are morphologically similar to equivalent sclerites of *B. tuckerae.* The cranidium and pygidium do not fit into any existing species and appear to be a new species. Clarification of this taxon must wait until more material becomes available.

BOREALARGES VARIABILIS n. sp.

(Plate 16, Figures 1 - 16; Plate 17, figures 1 - 18)

Material. Holotype pygidium UA 10007 from AV4 126 (T) m, paratypes UA 10008 - 10021

Stratigraphical interval. AV1 587 and 590 m; AV2 256, 255 - 260 and 274 - 279 m; AV4 126 (T), 238 and 260 m; DR 91.44 m.

Etymology. *variabilis* (L) changeable, referring to the varying arrangement of tubercles on the axis of the pygidium

Diagnosis. *Borealarges* with small anterolateral projections; narrow median glabellar lobe; L1 portion of glabella depressed; indistinct paired tubercles on glabella; longitudinal furrows subparallel between S1 and S3 with slight lateral deflection at S2; posterior area of fixigena of moderate length (tr.). Pygidium with marginal spines that increase in length from spine 1 to spine 3. Third spine long, broad, flattened subtriangular shape; three medial spines small and usually evenly and fairly closely spaced between third pair, all spines posteriorly directed; two complete axial ring furrows, 3 sets paired axial tubercles variously arranged.

Description. Cranidium with small anterolateral projections. Anterior border short medially, convex forward. In lateral view, glabella does not overhang border. Palpebral lobe small blunt lateral projection with central transverse slit-like pit; posterior branch of facial suture continues approximately in line with anterior branch of suture; small posterior area of fixigena projects slightly posterolaterally. Longitudinal furrows from occipital furrow to S1 shallow and broad, from S1 - S3 subparallel, narrow and deep with slight deflection laterally at S2; become shallower as curving laterally at S3 towards axial furrow; small pit at point where longitudinal furrow meets axial furrow, this being point of articulation with anterior wing of hypostome. From anterior view, bullar lobes and median glabellar lobe show uniform curvature from side to side. Slight elevation of eyes, but remain at or below height of bullar lobe. Prosopon bimodal, consisting of large and small tubercles relatively uniformly distributed. Large tubercles most dense on medial aspects of bullar lobes and on median glabellar lobe between S1 and S3; indistinct paired tubercles on median glabellar lobe, characteristic but occasionally variable, pattern of large tubercles on depressed L1 of median glabellar lobe with three larger tubercles to the posterior and one median tubercle to the anterior. Occipital ring ornamented with several medium sized tubercles against background of small ones. Occipital furrow strong.

Pygidium wider than long, sagittal length excluding spines approximately 67% maximum width; pleurae defined by interpleural furrows, anterior and posterior bands of first pleura approximately equal in length (sag.); anterior band of second pleura expanded; posterior pleural bands of first two segments inflated, and 3 (sometimes 4) tubercles aligned along bands; 9 marginal spines, fifth spine medial, spine pairs 1 - 4 broad elongate triangle, third spine pair longest and largest. Median spines 4 and 5, smaller, usually equally spaced between third spine pair. First two axial rings completely defined by distinct ring furrows, third ring furrow almost complete, subsequent rings partially defined abaxially. Short postaxial ridge. Prosopon mainly small tubercles with some larger tubercles present. Row of tubercles along first axial ring, some variability in size. Three patterns of tubercles present on axis: a) pairs of large tubercles on axial rings 2, 5 and 7 (Pl. 16, fig. 1); b) pairs of large tubercles on rings 1?, 3, 6 and 8 (Pl. 16, fig. 7); c) pair of tubercles on ring 2 and pattern on rest of axis variable (Pl. 16, fig. 6). Doublure widest at posteromedian point, inner edge reaching termination of axis. Outer doublure ornamented distally with fine parallel lines consisting of small tubercles which also appear on ventral surface of posterior marginal spines. Terrace lines increasingly fine proximally.

Discussion of species

Variability of tubercle patterns on pygidial axial rings is not restricted to this species. It is also seen in *B. patulus*, where the variation in tubercle arrangements appears to be restricted to the first 3 axial rings. In the case of *B. variabilis*, there are 3 patterns of tubercle distribution on the axial rings (see above).

The cranidium of *B. variabilis* resembles, in some respects, that of *B. morrisoni* Adrain, in press. The similarities are ones of proportion, degree of curvature and inflation of bullar lobes and median glabellar lobe, length and projection of fixigenal spine, character of tubercles of median portion of L1 lobe, glabellar tubercle arrangement and ornamentation. But there are differences. The anterolateral projections of *B. variabilis* are minimal whereas those of *B. morrisoni* are fairly extreme. The palpebral lobe of *B. variabilis* is posterior to S1 whereas that of *B. morrisoni* is opposite a point slightly anterior to S1 meeting the longitudinal furrow. There are few specimens of the pygidium of *B. morrisoni*, and the resemblance between them and the pygidia of *B. variabilis* is what one would expect of members of the same genus. The pygidium of *B. variabilis* shows a greater resemblance to some of the pygidia attributed by Adrain to *B.* s.l. *calei*. (see Adrain, in press, pl. 1, fig 1). However, in *B. variabilis*, the axis is narrower, the postaxial ridge longer and the pygidial marginal spines are more posteriorly directed.

BOREALARGES sp.

(Plate 18, figures 1 - 18)

Material. Cranidia UA 10022 - 10025.

Horizon. AV1 590 m; AV2 256 and 274 - 279 m; AV4 126 (T) m.

Discussion. These 4 cranidia could not be assigned, with confidence, to any of the known species. There is a resemblance to *B. variabilis* (see Plate 17) in terms of anterior border shape and anterolateral projections, but the overall proportions of the cranidium are quite different, with *B. variabilis* being rather long with respect to width, and *Borealarges* sp. short. There is also a resemblance to the cranidia assigned to *B. patulus* (see Plate 7), but again there is a difference of proportion and of tubercle arrangement. Although *B. patulus* is found mainly in the high AV 4 horizons, a few specimens have been found from AV2 256 and 274 - 279 m horizons which means the cranidia of *Borealarges* sp. could not be excluded on the basis of stratigraphy. For the present, it seems best to identify these cranidia as *Borealarges* sp.

Librigenae of *Borealarges*

(Plate 19, figures 1 - 11, 13 -19, 21, 22)

While it was possible to identify some librigena to the species level, it was not possible in all cases. Those librigena unidentified at the species level were divided into two main groups: Group A from the high AV4 horizons (Pl. 19, figs. 1 - 12) and Group B (Pl. 19, figs. 12 - 19, 21, 22) from all other horizons. In both groups, but particularly in Group B, it is evident there is more than one species represented. There is morphological overlap between the two groups.

Group A librigena have a broad librigenal field and a gently curved lateral margin. The prosopon is bimodal, with numerous fine tubercles and a few larger ones, and with a slight increase in concentration of larger tubercles close to eye. The eye platform is ornamented with small, closely packed tubercles. The posterior facial suture is long. The lateral and posterior borders are broad, separated from the field by a change in slope. Fine parallel terrace lines are visible on the dorsal surface of lateral margin. Slightly enlarged tubercles line the posterior margin. The genal spine is fairly long and broad. The subgenal notch is long and gently concave. All of the doublure is ornamented with fine terrace lines, laterally parallel to the lateral margin and curving adaxially on the genal spine.

Group B differs from Group A in that lateral margins are less convex ("flatter") and bimodal prosopon varies from very few larger tubercles as seen in Group A to densely distributed larger tubercles.

Hypostomes of *Borealarges*

(Plate 20, figures 1 - 22)

It was not possible to assign hypostomes to individual species. No articulated specimens with the hypostome in place were found and there is no good stratigraphic separation of species in the Avalanche Lake sections, where most horizons contain at least 2 species of *Borealarges* and usually more (see Table 2 for distribution of lichids). Morphologically similar hypostomes appear in all sections and there are fewer types of hypostome than there are species of *Borealarges*, all but one of which are new species. The hypostomes were separated into 2 very general and overlapping groups on the basis of morphology, with the proportions (length/width ratios) and the degree of convexity (forward) of the anterior margin of end members of Group A (Pl. 20, figs. 1 - 8) differing from those of Group B (Pl. 20, figs. 9 - 22).

Hypostome of both groups have: anterior lobe longer (sag.) than posterior lobe of middle body; pits on the middle body and coarse tubercles on the anterior portion of the anterior lobe; pits on the lateral portions of the posterior border; terrace lines subparallel to the lateral margin; and similar morphology of the doublure. Group A hypostomes are subtrapezoidal with an average length to width ratio of.0.87. The ratio of the middle body length (sag.) to the hypostome length (sag.) is 0.55. The anterior margin is convex forward. Group B hypostomes are shallower, having a ratio of length (sag.) to maximum width 0.73 and a ratio of middle body length (sag.) to hypostome length of 0.58. Rarely seen in Group A, but present and noticeable in Group B, are small tubercles close to and distributed parallel to the lateral border furrow. The anterior margin is relatively flat to slightly convex forward.

Ontogeny of *Borealarges*

(Plates 21, figures 1 - 19; Plate 22, figures 1 - 18; Plate 23, figures 1 - 10; Plate 24, figures 1 - 13; Plate 25, figures 1 - 18)

Protaspid and meraspid specimens are identified at the generic level. Meraspid cranidia and transitory pygidia, particularly in the later stages, show a differentiation of features but it is still difficult, except in the case of a few late meraspid transitory pygidia, to identify sclerites at the species level. There is no attempt to associate meraspid cranidia and transitory pygidia. *Borealarges* is a widely distributed genus in the Avalanche Lake Area sections and rarely is a species restricted to one locality. Furthermore, although a species may be restricted to one locality, it will not be the only species of *Borealarges* present. Distribution of lichids, and the problems this poses for identification of sclerites are discussed in the final chapter.

Protaspid period (Plate 21).

Material. "3 spine" protaspides UA 10059, 10060; "5 spine" protaspides UA 10061 - 10077.

Stratigraphical interval. AV1 587 m; AV4 126 (T) and AV4 240 m; AV5 58-60 m.

Description: "3 spine" protaspides. Small protaspides with three pairs of spines; 0.89 mm long, slightly longer than wide; narrow protocranidium and wider protopygidium, protocranidium approximately 60% of total length (sag.). Glabella slightly inflated, axial furrows narrow and shallow, subparallel; occipital furrow faint; anterior border length (sag.) about 10% total length (sag.); palpebral lobe slightly swollen, adjacent to lateral base of anterior border. Small eye ridge. Slight swelling of fixed cheek. No demarcation of protocranidium from protopygidium abaxially. Three pairs of free marginal spines projecting posteriorly from margin of protopygidium; pygidial axis slightly inflated, axial furrows not well-defined, converge medially and disappear some distance from posterior margin (about 20% body length, sag.). One axial ring faintly defined. Tubercles poorly defined. Tubercles A1, A2 and D on fixed cheek. Suggestion of palpebral tubercles and eye ridge tubercles. Poorly defined pairs of tubercles on glabella (up to 4 pairs). Single large median occipital tubercle. Tubercles B and C on posterior margin of protocranidium.

"5 spine" protaspis. Shape more elongate than "3-spine" stage; length 0.88 - 1.14 mm; increased distance between anterior border and palpebral lobe (eye has "moved backwards"); from posterior margin of palpebral lobe, fixed cheek flares outward and posteriorly at an angle oblique (>90°) to the anterior branch of the facial suture; eye ridge from palpebral lobe to anterolateral corner of glabella. Anterior border length (sag.) remains about 10% of total length, border gently convex forward. Demarcation of anterior border by change of slope rather than by presence of distinct furrow. Cranidium, including occipital ring, about 55-65% total sagittal length. Glabella inflated, slightly waisted, bounded by subparallel axial furrows; occipital furrow defined by change in slope; demarcation of protocranidium and protopygidium almost complete, but indistinct.

Row of tubercles on anterior margin of anterior border. Distal corner of posterior area of fixigena subangular but not spinose (just in front of first pair of protopygidial spines).

Axis of protopygidium narrows to a rounded termination some distance (about 20% body length) anterior to posterior margin. Three axial rings and terminal piece defined by shallow ring furrows. Slight inflation of posterior pleural bands. Five pairs protopygidial marginal points; pairs one and two project in posterolateral direction, third pair points backward, and fourth pair projects posteromedially. Fifth pair is small, partially fused. Width of doublure on posterior margin half the distance from posterior margin to termination of axis. Doublure longer (sag.) postermedially, with small angular median projection. One marginal ridge or terrace line visible on distal part of pygidial doublure.

Prosopon of fine granules. Row of 6 -7 tubercles along anterior part of anterior border. Large median occipital tubercle; 4 pairs of glabellar tubercles (glabellar tubercles 1 - 4) and two medial glabellar tubercles, usually one between tubercles 1 and 2, the other between tubercles 3 and 4 (tubercles not well defined). Three tubercles (spines) on each fixed cheek in positions A1, D, A2. Palpebral lobe tubercle and possibly small eye ridge spine, Er, anterior to palpebral lobe. On protopygidium, pairs of tubercles on axial rings 1 and 3, and single tubercle located on each posterior pleural band, all aligned in gentle curve from posterior to anterior.

Meraspid period (Plates 22 - 25).

Material. Cranidia UA 10078 - 10098; librigena UA 10100 - 10108; hypostomes UA 10130 - 10139; transitory pygidia UA 10109 - 10129.

Stratigrapahical interval. AV2 250 - 260 and 274 - 279 m; AV4 126 (T), 126 - 127, 230 - 240, 231, 234, 234 - 237, 238, 240 and 240 - 246 m; AV5 58 - 60 m.

Description. Smallest cranidium 0.74 mm long. Glabella inflated, axial furrows subparallel. Glabella intrudes slightly into border. Bullar lobe present as minute sliver anterior to S1 along lateral edge of glabella. Long (sag.) anterior border. Row of 6 - 8 tubercles aligned along front of anterior border. Tubercles D, A2, Pr, Er, and glabellar tubercles present.

With growth, anterior glabella greatly enlarged, expands into anterior border, anterior border tubercles more numerous, less pronounced. Bullar lobe expands forward and outward, posterolateral lobes inflated. In late meraspides, morphological variation includes degree of inflation of median glabellar lobe, ornamentation and presence of paired and spinose tubercles.

Librigena can be divided into 2 general groups, A and B. Group A (Pl. 23, figs. 13, 15 - 19) has uniform bimodal ornamentation on free cheeks, broad genal spine with slight to no subgenal notch. Group B (Pl. 23, figs. 11, 12, 14, 20) has bimodal ornamentation, a row of enlarged tubercles along lateral margin, a curved subgenal notch and a narrow, fairly short genal spine.

Hypostome. Smallest hypostome 0.58 mm (sag.) long, longer than wide, anterior margin straight, anterior wings projecting, lateral notch long (exsag.), 4 slits in lateral margin; middle body longer than wide, anterior lobe twice length (sag.) of posterior lobe. With growth, hypostome becomes adult-like, wider than long, last and very short, faint signs of lateral slits present at hypostome length of 0.93 mm. Ornamentation in form of tubercles on anterior part of anterior lobe, and terrace lines on lateral border developing.

Transitory pygidium. Several stages of transitory pygidia present, with 6 - 10 pairs of spines. Spines cylindrical, slightly tapering, fairly long, and free. Axial rings defined by axial ring furrows. Some axes have enlarged tubercles arranged on four subsequent rings in characteristic pattern of pair of tubercles, single tubercle, pair of tubercles, pair of more widely spaced medium sized tubercles. Posterior pleural bands also show pattern of enlarged tubercles, with pleural bands associated with axial rings carrying enlarged tubercle pairs having enlarged tubercle on distal half of pleura. Late meraspid transitory pygidia assume more adult-like appearance.

Discussion of ontogeny

The distribution of early growth stages (Table 3) probably does not reflect their distribution in life. At the protaspid level, there appears to be a preservational bias, with the majority of protaspid specimens coming from one horizon (AV4 126 m). Among the protaspides illustrated, there are some minor morphological variations which could be indicative of separate species of *Borealarges*. Some of the differences include presence or absence of tubercles on anterior border, the shape of the protopygidium and the arrangement of pygidial tubercles.

Meraspid specimens are more widely distributed, but are still few in number. These specimens are beginning to show definite morphological differences, but, in most cases, remain difficult to identify to the species level. Several meraspid cranidia from AV4 230 - 240 (Pl. 23, figs. 11, 13, 14 and 12, 15, 16) most closely resemble holaspid cranidia identified as *B. renodis and B. tuckerae*; however, no adult members of these species were found in these horizons.

Meraspid cranidia from AV5 58-60 m (Pl. 22, figs. 11, 12) could be referred to *Richterarges facetus*. These cranidia share a number of features with the holaspid cranidium of *R. facetus* including the lack of a pair of tubercles on the median glabellar lobe, uniform ornamentation and the shape and the direction of extensions of the posterior area of the fixigena. It is interesting to note that 2 specimens from the high AV4 horizons share some of these characteristics. The specimen illustrated in Pl. 23, fig. 1 differs from the specimens from AV5 58-60 in the nature of the anterior border, but with respect to the fixigenal spine and prosopon, they are quite similar. A second specimen, illustrating internal morphology (Pl. 23, fig. 2) has a long, laterally directed posterior area of the fixigena and longitudinal furrows showing no lateral deflection at S2. Holaspid cranidia of *B. patulus* have been found only in the high AV4 horizons and, as discussed previously, they are similar, in many ways, to the holaspid cranidia of *R. facetus*, found only in AV5 58-60.

Transitory pygidia show, with growth, a transition towards adult-like morphology, but in most cases, it is still difficult to identify them to the species level. The specimens that are the exception to this situation are illustrated under the description and discussion of that species, e.g. *B renodis*. At least one of the transitory pygidia from the high AV 4 sections (see Pl. 25, fig. 2) is probably that of *B. patulus*.

Distinguishing features such as segment-specific enlarged tubercle patterns were visible on only a few transitory pygidia so the determination of meraspid degrees was not possible.

Discussion of genus.

Thomas and Holloway (1988) resolved some of the ambiguities that existed in the *Hemiarges* group by establishing two new genera, *Richterarges*, a Silurian genus and *Uripes*, a Late Ordovician to Ludlow genus, each containing former members of *Hemiarges*. Adrain (in press) contributed to a further resolution, particularly with respect to *Richterarges*, by erecting the genus *Borealarges*, a predominantly northern Laurentia taxon. Included in the genus *Borealarges* are two species, *B. mikulicorum* and *B. bucklandi*, formerly members of *Richterarges*, and before that, of *Hemiarges*. Within *Borealarges*, Adrain believes there are two species groups, *Borealarges* sensu stricto and *Borealarges* sensu lato (*B.* s.l. *calei* and *B.* s.l. *bucklandi*).

In the Mackenzie Mountains, as in the Arctic, the majority of trochurines are members of *Borealarges*, but the species are distinct from those of the Arctic with one exception, *B. tuckerae*, found at both localities.

Phylogenetic analysis of *Borealarges*

A phylogenetic analysis was undertaken with the intent of answering several questions including: 1) is *Borealarges* a monophyletic taxon? 2) are there two species groups within *Borealarges* as discussed by Adrain? 3) is *Richterarges facetus* properly assigned as to genus?

The analysis was carried out using PAUP 3.1.1 (Swofford, 1993) and MacClade 3.0 (Maddison and Maddison, 1992) and included all known and adequately illustrated species of *Borealarges*, 3 species of *Richterarges* and 2 species of *Hemiarges*. Sixteen taxa were included in the analysis and coded from photographs: *Borealarges reedi*, *B. mikulicorum*, *B. morrisoni*, *B.* s.l. *calei*, *B. fritillus*, *B. patulus*, *B. renodis*, *B. tuckerae*, *B.* cf. *B. tuckerae*, *B. variabilis*, *B.* s.l. *bucklandi*, *Richterarges aquilonius*, *R. ptyonurus*, *R. facetus*, *Hemiarges turneri* and *H. avalanchensis* (for species and sources, see Table 4).

In a cladistic analysis, the choice of an outgroup or sister group is of critical importance. The use of the outgroup is one method for understanding the polarity of the characters, of determining whether a character is primitive or derived. The outgroup may include several taxa, including the sister group, closely related to the ingroup. The ingroup, presumed to be monophyletic, is defined as such by the presence of synapomorphies. These apomorphies or shared derived characters can only be recognized if they can be shown to be derived and not primitive, a primitive character being one that is shared with other groups, particularly the outgroup.

The use of an outgroup has been the subject of discussion in the literature (Colless, 1985, Ramsköld, 1991, Adrain and Chatterton, 1990). One can argue the choosing of an outgroup involves circular reasoning in that the choice requires prior knowledge of phylogeny, but the purpose of the cladistic analysis is to gain a knowledge of phylogeny. However, circular reasoning is already involved in choosing the taxa belonging to the ingroup, the basis of which is usually an existing classification scheme. Often, an analysis based on an existing classification scheme can be helpful in assessing the validity of that scheme.

In this analysis of *Borealarges*, two species of *Hemiarges* were included in the outgroup, the chosen outgroup *Hemiarges turneri* Chatterton and Ludvigsen 1976, an early member of *Hemiarges*, found in the Middle Ordovician (Chazyan) Esbataottine Formation of the southern Mackenzie Mountains, and *H. avalanchensis* n. sp., found just below the Ordovician - Silurian boundary in the Avalanche Lake sections. It is probable that a species of *Hemiarges* was ancestral to *Borealarges*. Thomas and Holloway (1988) believe that *Hemiarges*, the earliest occurring of the trochurines, is the "rootstock" of all trochurines. Such an analysis, however, only requires that the outgroup is made up of taxa closely related to the ingroup being analysed and that, preferably, it includes a sister species.

The selection of characters is the most important and the most difficult part of the analytical procedure. Characters should be homologous between taxa, unambiguous, well defined and, in this case, visible on the exoskeleton. Only holaspid sclerites were used in this analysis and character selection was restricted to the external morphology of the cranidium and the pygidium. Useful characters from the hypostome and free cheek were unavailable from the Mackenzie Mountain material because of a lack of articulated specimens, and the difficulty in identifying sclerites to the species level. A set of 20 characters was chosen (see Table 5). The morphology of the internal surface, visible in silicified specimens, but not usually in calcareous ones, was useful in confirming external morphology but, with one exception (character 20), was not used as a source of characters.

Some explanation of the selected characters and the methods of coding them are given, since some of the characters might be difficult to understand from the one line descriptions given in Table 5. The development of characters during ontogeny and a comparison to all stages of the outgroup are examined for information regarding possible polarity and ordering of characters. However, the analysis was conducted on unordered, unpolarized characters.

1. Anterolateral projections on cranidium. The projections are considered to be the portion of the anterior area of the fixigena that project beyond an imaginary line formed by the lateral curving of the anterior margin of the cranidium. The size and definition of the anterolateral projections vary from absent (State 0) through small, well or less well defined (State 1) to large (State 2). Those of *B. morrisoni* are considered large (2), *B. renodis* small (1), and *B.* s.l. *calei* absent (0). Projections are not present during ontogeny and do not appear until possibly the latest meraspid stages (see Pl. 22, fig. 16; Pl. 23, figs. 4, 9). Outgroup comparison suggests absence of projections (0) is primitive.
2. Direction of anterior branches of facial suture at anterior margin. This character can be difficult to code. Some error can be introduced since orientation of the specimen when photographed is important. The anterior branches of the facial suture can be parallel to subparallel (State 0), divergent (State 1) or convergent

(State 2). This feature in meraspid cranidia and in the outgroup is generally convergent anteriorly, and this state (2) is probably primitive.

3. Paired glabellar tubercles on median glabellar lobe at S2. Paired tubercles at the S2 position are usually clearly defined, both with respect to pairing and with position. Three states were identified: absent (0); present and enlarged (1); present and spinose (2). An enlarged pair of tubercles at S2 (State 1) is found in most protocranidia and meraspid cranidia of *Borealarges*, in holaspid cranidia of most species of *Borealarges*, and in the outgroup, *Hemiarges*, and is therefore considered plesiomorphic.
4. Length of posterior area of fixigena expressed as a ratio of length (tr.) of area to length (tr.) of occipital ring. Three states were recognized: ratio less than 0.80 (State 0); ratio 0.81 - 1.05 (State 1); ratio greater than 1.15 (State 2). The distinction between states was based on the natural divisions seen in the ratios calculated from measurements. The distinction between State 1 and 2 is the greatest. Considerable allometric change in the cranidia occurs during the meraspid period and, for both *Hemiarges* and *Borealarges*, the ratio appears to decrease with growth. Both representatives of the outgroup genus have a low ratio. *Richterarges* has a high ratio. The primitive state is equivocal.
5. S1 incomplete (State 0) or complete (State 1) behind bullar lobe. This trait separates members of the ingroup from those of the outgroup. Most species of *Hemiarges* have an incomplete S1 (State 0), more derived members of *Hemiarges*, e.g. *H. diadayma* possess a complete S1. (There is the question of whether or not the genus *Hemiarges*, as it presently exists, is monophyletic). The incomplete S1 is considered primitive.
6. S1 extends adaxially across median glabellar lobe. If S1 is present adaxially, but not strong, it can be difficult to determine if it is incomplete or shallow and complete (State 1). However, the other two states, absence of furrow (0) and presence of strong furrow, are easily determined (2). The furrow is absent in the outgroup and is also absent in early meraspid cranidia of *Borealarges* but can be seen in later meraspis. The absence of S1 adaxially is primitive.
7. Longitudinal furrows between S1 and S3 are parallel or subparallel to each other (State 0); divergent anteriorly (State 1); convergent anteriorly (State 2). Both meraspid cranidia of *Borealarges* and the outgroup exhibit divergent (anteriorly) longitudinal furrows and this is considered to be primitive.

8. Deflection of longitudinal furrows laterally at S2. The deflection is often easier to see on the internal surface of the cranidium since the curvature of the median glabellar lobe or the prosopon at that position can obscure the deflection. The deflection may be absent (State 0) or present (State 1). Both the meraspid cranidia of *Borealarges* and the outgroup lack the deflection suggesting absence is the primitive state.
9. Expansion of anterior fixigenal field between axial furrow and anterior branch of facial suture. The degree of expansion does not include the portion of the field involved in the anterolateral projections and is independent of the presence or absence of projections. The three states for this character are: little or no expansion (State 0); some expansion (State 1); greater expansion (State 2). The more expanded anterior fixigenal field (State 2) is probably primitive since it is found in the outgroup, *Hemiarges turneri* as well as in meraspid cranidia of *Borealarges*. Absence of expanded anterior fixigenal field can be seen in *B. morrisoni* or *B. bucklandi*.
10. Height of the median glabellar lobe. Height equal to or greater than that of bullar lobe is state 0, height much higher than bullar lobe, State 1. Nearly all the species included in this analysis exhibit State 0, as do the meraspid cranidia. State 0 is plesiomorphic.
11. Axial ring dominance. If one ring is dominant (State 0), it may be that either only one ring is defined by a ring furrow, or that the first ring is larger and more pronounced than any others. This is an uncommon situation, and in this study is seen in *B. renodis* and *H. turneri*, but not *H. avalanchensis*. State 1 occurs when the first two rings are equal or subequal, and both are more distinct than the others. State 2 is seen when the axial ring dominance and definition decrease from the anterior to posterior of the axis. The axis of the transitory pygidia of *Hemiarges* and of *Borealarges* have many well defined rings, as does the holaspid pygidium of *Richterarges*. Developmentally, the pattern is to move from many defined axial rings to a few, usually 2, dominant and subequal rings. The primitive state is equivocal.
12. The position of the first pygidial marginal spine taken at the point of contact of the anterior part of the adaxial margin of the spine with the pygidium, relative to the axis. This is an effort to express allometric differences seen in pygidia. State (0), where the point of contact is opposite the postaxial ridge, is found in the

outgroup, and is considered primitive. If the point of contact is opposite axial rings 6 - 8, it is coded State 1 and if opposite axial rings 1 - 5, State 2.

13. Direction of projection of first pygidial marginal spine. The angle of the projection is measured from the posterior of the spine relative to the exsagittal plane. An angle of 45° or greater is State 0; 10° to 45°, State 1; less than 10°, State 2. The outgroup and several of the ingroup exhibit State 1, which is regarded as plesiomorphic.

14. Relative sizes of marginal spines. Four states are coded: all spines, whether large or small, are similar in size (State 0); second spine is largest (State 1); third spine is largest (State 2); other, for example second and fourth spines largest (State 3). In late meraspid transitory pygidia of both *Hemiarges* and *Borealarges*, spines are similar in length. In the holaspid pygidium of *H. turneri*, State 1 is seen, and, in *H. avalanchensis*, State 3. The primitive state is equivocal.

15. Ratio of axial width to axial length. The length is the sagittal length of the axis excluding the articulating half ring and post axial ridge. Ratios fall into 3 groups: greater than 0.95 (State 0); 0.7 - 0.9 (State 1); less than 0.7 (State 2). Most holaspid pygidia and transitory pygidia of *Borealarges*, holaspid pygidia of *H. avalanchensis* and transitory pygidia of *H. turneri* (but not its holaspid pygidia), exhibit State 1. This suggests State 1 is probably primitive.

16. Direction of axial furrows at position of axial rings 1 and 2 relative to direction of furrow posterior to this. In transitory pygidia there is a steady increase in width (tr.) of axial rings from posterior to anterior such that the axial furrows are relatively straight. In the latest meraspid transitory pygidia of *Borealarges* and in pygidia of most species of *Borealarges* and *Hemiarges* the width of the first or first 2 rings has increased so that the axial furrow is deflected laterally at this point. A straight axial furrow is coded State 0 and a discontinuous furrow, State 1. With development during ontogeny, there is a change from State 0 to State 1. The outgroup and most of the ingroup exhibit State 1, and *Richterarges* State 0. The primitive state is equivocal, although if only the holaspid pygidium is considered, then State 1 would be plesiomorphic.

17. Number of marginal spines. The 8 marginal spines of *Hemiarges* (State 0) is considered primitive but the 8 spines in *R. ptyonurus* represents a secondary loss of the medial spine. The presence of nine marginal spines, seen in all members of *Borealarges*, is coded State 1.

18. Length of postaxial ridge relative to length of pygidium (sag.) exclusive of marginal spines, expressed as a ratio. *Richterarges* is distinguished from the other two groups by its long postaxial ridge with a ratio of >0.35 (State 2), *Hemiarges* by its short ridge, ratio 0 - 0.18 (State 0). State 1 is coded when the ratio is between 0.20 and 0.30. Species of *Borealarges* have an intermediate length of postaxial ridge and are split between State 0 and State 1. The postaxial ridge does not develop until late in the meraspid period. A short postaxial ridge is probably primitive.
19. The separation of pygidial marginal spines 2 and 3. These 2 spines are clearly separate and distinct, but with no pygidial margin or border between them in *Hemiarges* (State 0). This is also the situation in transitory pygidia of all species and is considered to be the plesiomorphic condition. In State 1, the anterior edge of spine 3 meets the margin at an oblique angle extending to the posterior adaxial point of contact of the second spine. If spines 2 and 3 are separated by the pygidial margin border with the anterior edge of the third spine meeting the border at an angle close to 90°, this is coded State 0.
20. The shape of the inner margin of doublure medially. If the inner margin is rounded or a rounded V shape this is State 0; if there is anteriorly directed angular projection this is State 1. State 1 is uncommon. State 0 is considered plesiomorphic.

Homoplasy is a persistent problem with lichids. To a certain extent it can be limited in but not eliminated from the analysis. Trying to determine homoplasies without a tree can induce mental paralysis, but after an initial phylogenetic analysis, homoplasies may become more evident. The Consistency Index (C.I.) is an indicator of homoplasy with a C.I. of 1 indicating no homoplasy for the tree being considered and a low C.I. indicating higher homoplasy. A Homoplasy Index (H.I.) is determined by (C.I. - 1).

A number of characters used in initial analyses were discarded for various reasons. Some were complex characters, some were difficult to code consistently, some morphometric ratios were continuous and lacked breaks or clustering of data, and some uninformative (autapomorphic). Some apparently obvious characters had to be eliminated because one could not show homology of characters between taxa or it was difficult to determine which of several features were homologous. For example, the use of certain median glabellar tubercle pairs caused problems because some are difficult to identify as a pair, some are enlarged, some are not, some are only slightly larger than background ornamentation and not all are placed precisely at an identifiable point. Some of the discarded characters were: morphometric ratios such as ratio of pygidial length to pygidial width, axial width to pygidial width; length (sag.) of anterior border relative to either the cranidial length or the occipital ring length; shape of anterior border; relative curvatures of the bullar lobe and median glabellar lobe; height of palpebral lobes relative to bullar lobes; nature of anterior longitudinal furrows; position of L1 lobes relative to the bullar lobe; and the arrangement of medial pygidial marginal spines.

The character matrix, using the above characters, is seen in Table 6. Initially, minimal length trees were generated in PAUP 3.1.1, using the heuristic approach which, with this data set, took several minutes to complete. Branch-and-bound search methods, which took several hours to complete, generated the same tree topology as the heuuristic methods. Although the PAUP 3.1.1 algorithm finds only binary trees, a COLLAPSE option is available, which will collapse dichotomies into polytomies when internal branches with a maximum length of zero are present. According to the authors of PAUP 3.1.1 (Swofford, 1993, p.45), "When the data are insufficient to determine fully resolved trees, trees containing polytomies may be preferable to binary trees containing one or more branches of zero length". The COLLAPSE option was utilized in these analyses.

Several rooting options were explored. The outgroup method using *Hemiarges turneri* as the selected outgroup was the final choice, but other avenues explored involved using a hypothetical ancestor and midpoint rooting. Using the hypothetical ancestor made no difference in the organization of the trees since its coded characters were very similar to those of the selected outgroup. Midpoint rooting roots the tree at "the midpoint of the longest path connecting any pair of taxa" (Swofford, 1993).

Analysis and results. The initial runs, using the heuristic approach, produced 12 minimal length trees with a tree length of 64 and a Consistency Index of 0.531.

In PAUP 3.1.1, it is possible to reweight characters *a posteriori*, according to the Consistency Index obtained during the initial analysis. In other words, *a posteriori* weighting is based on the degree of homoplasy, with more weight accorded the characters exhibiting the smallest degree of homoplasy. This "successive approximations" method avoids the problems of clique analysis because it retains and uses all the characters. When this approach was applied using characters reweighted to a base of 10, the number of trees was reduced from 12 to 6 (length 376, C.I. 0.572), but consensus trees for the 6 were identical to those for the original 12 trees. A second reweighting did not change the tree form or number of trees but did shorten the tree length to 342 and increased the

Consistency Index to 0.582. Subsequent reweightings did not change topology or any of the parameters.

Six trees were obtained, using *Hemiarges turneri* as the outgroup (Fig. 6). Because Tree # 4 (Fig. 8) has the same topology as all 4 consensus trees (see Fig. 7), it was used for analysis of character states. The cladograms show a separation of the 3 genera, *Richterarges*, *Borealarges* and *Hemiarges*.

Is *Borealages* monophyletic? In all analyses, including the final one, *Borealarges* remained distinct from the other 2 genera. The species of *Borealarges* from the Avalanche Lake sections are separated from those of the Arctic, with the exception of *B. tuckerae* which occurs in both localities and falls in with the Avalanche Lake species on the cladogram. *B. renodis*, the sister species of *B. tuckerae* is probably also present in the Arctic (Adrain, personal communication). In one configuration only (tree # 2, Fig. 6), *B. calei*, an Arctic species, falls into the the Avalanche Lake group.

Although the Arctic and Avalanche Lake species together form a distinct clade, there is considerable ambiguity within this clade. *B. morrisoni*, *B. mikulicorum*, and *B. reedi* (the type species) remain outside the polytomy affecting the remaining species. All but one of the 6 trees exhibit a polytomy, and the species involved in the polytomy vary. Within the species involved in a polytomy, certain relationships remain robust. *B. calei*, *B. variabilis* and *B.* cf. *B tuckerae* are one grouping, *B. renodis and B. tuckerae* are a second, and *B. fritillus* and *B. patulus* are a third.

An interesting difference between the Arctic and Avalanche Lake species is the matter of stratigraphic separations. The Arctic species are apparently confined to one graptolite zone, those of the Avalanche Lake sections more widely distributed through time. Although graptolite zonation is not available for the Avalanche Lake sections, a tentative correlation of this site with the Arctic has been done (Adrain, personal communication). *B. tuckerae*, found in the *Crytograptus perneri - Monograptus* aff. *munchi* zone of the Arctic, occurs above and below this zone in the Mackenzie Mountains.

Adrain (in press) proposed two species groups within *Borealarges* Adrain (in press) and placed *bucklandi*, a British lichid, formerly in the genus *Richterarges*, into *Borealarges sensu lato*, along with *calei*.. In this analysis, the 2 species assigned to *Borealarges sensu lato* are well separated, suggesting the *sensu stricto / sensu lato* distinctions may not be valid.

The position of *bucklandi*, the only species from outside of northern Canada included in this analysis, is somewhat ambiguous. If *Hemiarges turneri* is used as the outgroup, *bucklandi* appears as the nearest relative to all other *Borealarges* and is included in the *Borealarges* clade. When the trees are rooted by the midpoint rooting method, (rooting at midpoint of longest path), rooting occurs between *bucklandi* and the northern Canadian *Borealarges* species (Fig. 9). If *Hemiarges* is excluded from the analysis and *Richterarges ptyonurus* is used as the sister group (Fig. 10a), *bucklandi* falls into the *Richterarges* clade, as it does if midpoint rooting is used (Fig. 10b). On examination of photographs (Thomas and Holloway, 1988; pl. 15, figs. 318 - 321, 324), intuitively it would seem that *bucklandi* is more appropriately placed in *Borealarges* (see Adrain, in press, for discussion) than in *Richterarges* (Thomas and Holloway,1988, pl. 15, figs. 325, 325, 330 - 333, 336, 337). Thomas (1981), in discussing *bucklandi*, refers to its resemblance to *B. mikulicorum*. However, the illustrated specimens of the species show considerable variation (Thomas, 1981, pl. 20, fig. 18 vs. fig 28), which suggests further work needs to be done with the specimens assigned to this species. For the present, this species will be left in *Borealarges*.

Richterarges facetus is assigned to the correct genus according to this analysis and becomes the earliest known member of this genus.

Synapomorphies, characters which unite a clade, are of interest. Unambiguous character changes have been mapped onto the chosen tree, tree # 4, using MacClade 3.0 (Fig. 11). In tracing changes in characters, problems arise when 2 character states are present above a node, one of which appears on another part of the tree. There are problems then in interpretation of the character state distribution. Did that character arise only once and then disappear, or did that character arise twice independently? Table 8 lists all apomorphies, determined by PAUP 3.1.1, which are greater in number than the unambiguous changes mapped by MacClade. Fig. 11, with some reference to Table 8, is the basis for the following discussion.

Richterarges and *Borealarges* are separated from *Hemiarges* by 5 unambiguous characters; the nature of S1 behind bullar lobe, the lateral deflection of the longitudinal furrow at S2, the position of the first pygidial marginal spine, the number of marginal spines and the relationships of marginal spines 2 and 3. *Richterarges* is separated from *Borealarges* by 2 unambiguous changes, the length of the posterior fixigenal area relative to the occipital ring, and the direction of the first pygidial marginal spine; and by 2 other changes, axial ring dominance and relative size of pygidial marginal spines. The most highly derived members of *Borealarges*, based on number of character state changes, are *B. fritillus*, *B. patulus*, *B renodis* and *B. tuckerae*, and *Richterarges*, *R. aquilonius* and *R. ptyonurus*.

In conclusion, *Borealarges*, particularly the Arctic and Mackenzie Mountain species, form a monophyletic clade, with *B. bucklandi* probably a member in this clade. The existence of 2 clades within *Borealarges* is questionable. *Richterarges facetus* is correctly assigned with respect to genus, is less derived than its sister taxa, *R. aquilonius* and *R. ptyonurus*, and represents the earliest known *Richterarges*.

Genus *DICRANOGMUS* Hawle and Corda, 1947

{Objective synonym: *Liparges* Gürich, 1901}

Type species. Dicranogmus pustulatus Hawle and Corda, 1847 from the Kopanina Formation (Ludlow), Czech Republic.

Stratigraphical range. Ashgill - Ludlow.

Geographical range. Canada (Arctic, Mackenzie Mountains) Greenland, Sweden, Czech Republic, China (Guizhou Province and Inner Mongolia).

Diagnosis. Trochurine with strongly convex (sag., exsag.) glabella overhanging anterior border. Median and bullar lobes may or may not have independent convexity. Longitudinal furrows subparallel in front of S1, usually dying out between S2 and S3, may extend behind S1 as poorly defined depressions not interrupting exoskeletal granulation; S1 strong, curves antero-laterally behind bullar lobe, may be present medially as weak, concave-forward depression not interrupting exoskeletal granulation and extending towards occipital furrow on sagittal line. Maximum width of bullar lobe almost equal to width of median lobe. L1a usually clearly circumscribed; occipital ring very wide (tr.). Hypostome subtrapezoid in shape, wider than long, broad lateral and posterior borders, long shallow antennal notch, posterior margin gently concave with slightly convex median portion. Pygidium with three broad, flat pleural lobes terminating in minimal to slightly protruding spines, first two pleurae with pleural furrows, posterior pleural bands may or may not be inflated, one axial ring defined, axis gently narrowing to point at or just short of posterior margin. (Diagnosis emended from that of Thomas and Holloway, 1988, and expanded to include pygidium)

DICRANOGMUS LEPIDUS n. sp.

(Plate 26, figures 1 - 13; Plate 27, figures 1 - 17; Plate 28, figures 1 - 12; Plate 31, figures 1 - 8, 12)

Material. Holotype cranidium UA 10140 from AV4 126 (T) m,. paratypes UA 10141 - 10172, 10191 - 10196.

Stratigraphical inteval. AV1 590 and 591 m; AV2 256, 255 - 260 and 274 - 279 m; AV4 117 (T), 126 (T) and 234 - 238 m; AV5 58 - 60 m; DR 91.44 m (Delorme Range).

Etymology. *lepidus* (L) agreeable, neat, elegant, with reference to its morphology.

Diagnosis. *Dicranogmus* with large, well defined cranidial Lla lobe; longitudinal furrows parallel, deep and narrow between S1 and S2, becoming shallow between S2 and S3, disappearing close to S3, may or may not continue in postero-medial direction posterior to S1; width of median glabellar lobe similar to that of bullar lobes; median glabellar lobe higher than bullar lobes with increasing curvature in larger specimens, forming pronounced hump just in front of S1; anterior border widest anterolaterally, ornamented with row of tubercles; cranidial ornamentation bimodal, with larger tubercles forming possible pattern of pairs on the median glabellar lobe. Pygidium with 3 pairs of slightly projecting marginal spines, first and second posterior pleural bands inflated, first axial ring with row of tubercles (tr.) defined by deep axial ring furrow.

Description. Cranidium wider than long, width (tr.) of median glabellar lobe and lateral lobes similar. Median glabellar lobe elevated above lateral lobes, with increasing elevation leading to pronounced hump in glabellar lobe just in front of S1 in largest cranidia. Lla lobes large circumscribed ovals at lateral ends of occipital ring, depressing anterior margin of ring somewhat; occipital ring wide (tr.), extending laterally a distance equivalent to lateral margin of bullar lobes In lateral profile, anterior slightly inflated, barely overhanging anterior border. Longitudinal furrows subparallel, deepest at S1, becoming shallower anteriorly and fading out in front of S2, behind S1, furrows may or may not continue for short distance in posteromedial direction. S1 deep, separate bullar lobes from posterior lateral lobes, extending in anterolateral direction to meet axial furrows opposite S2. Anterior border narrow (sag.) separated from glabella by well defined preglabellar furrow. Occipital furrow deep, occipital ring wide (tr.) forming broad, high arch. Prosopon bimodal. Larger tubercles on median glabellar lobe, with suggestion of being organized into pairs. Anterior border ornamented with tubercles on outer edge.

Librigena with broad genal spine narrowing to blunt point, slightly curved genal notch, Ornamentation complex, with a few large tubercles close to eye socle, and others aligned parallel to lateral margin. Bimodal prosopon of smaller tubercles on librigenal field. Row of larger tubercles parallel to lateral margin. Parallel rows of medium sized tubercles along lateral margin and edge. On doublure, terrace lines curving from lateral margin to adaxial margins.

Hypostome and middle body both subtrapezoidal. Posterior and lateral borders wide. Very short middle furrow visible on internal surface only. Posterior border inflated medially. Prosopon bimodal, round distinct tubercles distributed on middle body, lateral border and lateral part of posterior border. Posterior margin fairly flat with medial embayment with central convex portion. Doublure broad posteriorly and laterally, narrowing at shoulders. Shallow antennal notch. Wide (tr.) rectangular shaped medial concavity with small medial spine projecting posteriorly from rolled lip on anterior margin of doublure.

Pygidium wider than long, with three broad pleura. First and second pleura have sharply defined posterior interpleural furrows and pleural furrows which extend almost to pygidial margin. Posterior pleural bands inflated, almost as large as anterior bands. Axis has one well-defined axial ring with strong axial ring furrows separating ring anteriorly from articulating half ring and posteriorly from rest of axis, which is poorly differentiated. Axis narrows gradually until, just posterior to point where second interpleural furrow meets axial furrow, narrows more abruptly for short distance, two axial furrows approach sagittal plane just anterior to posterior margin, but do not meet. No posterior border but increased concentration of tubercles found along margin. Prosopon bimodal. Larger tubercles arranged in rows along axial ring and along posterior pleural bands. Doublure about 1/2 length (sag.) of pygidium, discontinuous terrace lines parallel to, tubercles along posterior margin of doublure.

Discussion of species

The unemended diagnosis of *Dicranogmus* states that the bullar lobes and median glabellar lobe lack independent convexity (Thomas and Holloway, 1988). In *D. lepidus*, there is a difference in convexity between the two, yet this species clearly belongs in the genus *Dicranogmus*. Therefore, the diagnosis has been emended to include independent convexity. In addition, the diagnosis has been expanded to include the pygidium. There can be no question that known pygidia are correctly associated with cranidia of *Dicranogmus*.

The hypostomes were tentatively assigned to *D. lepidus* on the basis of their resemblance to the hypostome from the Delorme Range site since there is only one species of *Dicranogmus*, *D. lepidus*, found in this horizon (compare Pl. 26, figs 20, 22 to Pl. 31, figs. 1 - 8, 12). For comparison with *D. wilsoni* n. sp. see discussion under that species.

DICRANOGMUS WILSONI n. sp.

(Plates 29, figures 1 - 19; Plate 30, figures 1 - 12; Plate 31, figures 9 - 11, 13 - 18)

Material. Holotype cranidium UA 10173 from AV4 126 (T) m, paratypes UA 10174 - 10190, 10197 - 10202.

Stratigraphical interval. AV1 590; AV2 256, 255 - 260 and 274 - 279 m; AV4 126 (T) m.

Etymology. After the late J. Tuzo Wilson, eminent Canadian geologist.

Diagnosis. Cranidium with small L1A lobe and very slight indentation of occipital ring; longitudinal furrows converge slightly anteriorly and die out between S1 and S2. In lateral profile, relatively flat, gently rounded, glabella slightly overhanging anterior border. In transverse profile, bullar lobes and median glabella in gentle continuous curve; no independent curvature of median and lateral lobes. Prosopon bimodal, evenly distributed over entire cranidium. Librigena with fine bimodal granulation on field, several rows tubercles parallel to lateral margin, innermost row tubercles largest. Pygidium with three broad pleural lobes, with minimal to slightly projecting spines, posterior bands flat; ornamentation tending to be small and evenly distributed.

Discussion of species

Dicranogmus wilsoni n. sp. differs from *D. lepidus* n. sp. in the following ways: a) smaller L1a lobe; b) lateral and median glabellar lobes lack independent convexity; c) slight convergence of longitudinal furrows; d) prosopon of bimodal tubercles distributed more evenly over entire cranidium; e) pygidium does not have inflated posterior pleural band; f) pleural furrows extend only approximately 50% of pleural length; g) pygidial axial furrows meet posteriorly

Because there is no stratigraphic separation between the *D. lepidus* and *D. wilsoni* , the assignment of hypostomes and free cheeks is difficult. The hypostomes of *D. wilsoni* (Pl. 31, figs. 9 - 11, 13 - 18) are similar to those assigned to *D. lepidus*, but the ornamentation, although distributed in the same areas, differs in that the tubercles are less well defined and appear flattened and misshapen in comparison to the clear distinct tubercles of the former. The free cheeks were assigned to *D. wilsoni* on the basis of their prosopon, which is similar to but finer than that of free cheeks assigned to *D. lepidus*.

Ontogeny of *Dicranogmus*

(Plate 32, figures 1 - 12; Plate 33, figures 1 - 13; Plate 34, figures 1 - 12)

The ontogenetic sequences will be described at the generic level because, although there may be more than one species represented by the protaspides and meraspides, identification to the species level is not possible.

Protaspid period (Plate 32).

Material. "5 spine" protaspides UA 7905, UA 10203 - 10212.

Stratigraphical interval. AV2 248.8 m, AV4 126 (T) m.

Description. Protaspis shape, including missing free cheeks, oval; with width/length ratios of 0.9 - 1.1, protocranidium about 60% total length. Glabella inflated and bounded laterally by axial furrows of moderate depth; slight narrowing of glabella in front of S1, width (tr.) of axis greatest across L1 and L0, internal surface shows shallowing of axial furrow opposite L1. Glabella intrudes slightly into border, making border longer (sag.) anterolaterally than medially. Anterior border straight, and long (sag.), about 10% of body length, delineated by shallow anterior border in form of change in slope and ornamentation. Palpebral lobe short and slightly inflated; weak eye ridge present anterior to palpebral lobe; lateral margin flares outwards posterior to palpebral lobe. Occipital ring distinct, occipital furrow usually well-defined; transverse demarcation of cranidium from protopygidium distinct with inflated posterior border and sharp marginal furrow. Axis of protopygidium narrows gently to a rounded point at a distance from the posterior margin of 15-20% total body length; 3 axial rings and a terminal piece visible, with definition of axial ring furrows decreasing from anterior to posterior; 4 pleura plus fifth undifferentiated; anterior and posterior pleural bands of pleura 1 and 2 subequal in size, with the posterior band somewhat inflated; slight inflation of third posterior band; 5 pairs free spines projecting, fifth small, short and sometime partially fused; spines 1 & 2 project posterolaterally, 3 posterolaterally to posteriorly, 4 postero-medially. Protopygidial doublure narrow and showing signs of terrace line development near margin. Entire surface of protaspis covered with tubercles. Anterior border has 6 or more tubercles in a row; occipital ring has one large median tubercle (tubercle 0) flanked by a smaller one on each side; glabellar tubercles arranged in pairs, usually pairs 2 - 5 present; A2, D, and sometimes A1 present on fixed cheek; palpebral tubercle and often eye ridge tubercle present (slight inflation of eye ridge gives background tuberculation an appearance of alignment); tubercles B and C (plus smaller tubercles) on posterior border of cranidium; axial rings of protopygidium have same tubercle arrangement as occipital ring, one large medial tubercle flanked by two smaller; posterior pleural bands may have row of tubercles, with one larger one present on outer half; large pleural band tubercles aligned with cranidial tubercles to form a curved line; small tubercles present on anterior pleural bands. Free cheek, hypostome and rostral plate not known.

Meraspid period (Plates 33, 34).
Material. Cranidia UA 10213 - 10220; very late meraspid or earliest holaspid cranidum UA 10221; hypostomes UA 10222, 10223; librigena UA 10224, 10225; transitory pygidia UA 10226 - 10236.
Stratigraphical inteval. AV4 126 (T) m.
Cranidia. Earliest meraspid cranidium (0.70 mm long) similar in shape to protocranidium but differs mainly in size and more sharply defined features. Axial furrows narrow, deep and parallel, with shallowing of furrow opposite L1. Occipital furrow distinct. Anterior glabella slightly inflated, protrudes into anterior border. Occipital ring tubercle and glabellar tubercles 1 - 4. Fixigenal tubercles D and A2 present as well as posterior margin tubercles B and C, and palpebral tubercle. Anterior margin of anterior border lined with small regularly spaced tubercles. On internal surface (Pl. 33, fig. 1), but not yet visible on external surface, first sign of bullar lobe, very small enclosed sliver, bulging laterally, on adaxial side of axial furrow anterior to S1 position.

With growth, allometric changes include considerable expansion (tr.) of anterior lobe of glabella, broadening of glabella generally, increase in width of glabella just anterior to the occipital ring, apparent movement backward of the palpebral lobe, expansion of bullar lobe forward to approximately S3 position. Axial furrow which defines abaxial margin of the bullar lobe deepest anteriorly and weakens considerably as furrow curves inwards posteriorly. Longitudinal furrow effaced opposite L1 with some expansion and slight inflation of the glabella laterally starting development of posterolateral lobes. Change in slope of area where L1a found in adult. Three pairs of glabellar tubercles (2, 3, and 4), fourth pair less clear, possibly due to expansion of anterior glabella. All other tubercles remain.

With continued growth, shape becomes more adult-like. Anterior border begins to curve convexly forward, bullar lobe expands. L1a fully circumscribed, L1b inflated, may have incorporated some fixigenal tissue.

Free cheeks. Free cheeks simple, with gently curved lateral margin, 8 - 10 enlarged tubercles arranged in row along margin. Librigenal spine short narrow, with slight subgenal notch.

Hypostomes. Two late meraspid hypostomes, both with adult proportions, one still with 4 slits along each lateral margin, other with slits barely visible, and ornamentation adult-like.

Transitory pygidia. Several stages represented. Shape of smaller transitory pygidia consistent with shape of protaspid protopygidium. Each axial ring ornamented with single large median tubercle, flanked by 2 or more smaller tubercles. Both anterior and posterior pleurae have row of tubercles, usually consistent in size and extending full length of band, larger tubercle toward periphery of posterior pleural band, just inside fulcrum, all of which line up in gentle curve (also seen in protaspides). Gradual widening of pygidium with respect to length. Axis width 27-37% pygidial width. Shape of spines protaspis-like.

Latest meraspid transitory pygidium adult-like. Pleural furrow shorter stopping at point equivalent to position of border in other trochurines, furrow deepens, anterior band becomes more distinct and posterior band, in *D. lepidus*, but not in *D. wilsoni*, slightly inflated. Ornamentation of posterior band more distinct than that of anterior band, but distinction enhanced with inflation of band.

Discussion of ontogeny

The timing of the development of the glabellar and cranidial lobes can be determined in ontogenetic studies if sufficient stages of development are represented. Temple (1969) was able to show, by measuring the distances from the anterior margin to the occipital furrow and of the posterior margin of the bulla from the occipital furrow and plotting these measurements against the preoccipital glabellar length that the bullar lobe grew forward from approximately the S2 position, rather than backwards from S3, and that bullar lobe development began at a preoccipital glabellar length of 0.48 mm. A similar study of the development of the bullar lobe in meraspides of *Dicranogmus* is shown in Fig. 6. In this case, preoccipital cranidial length rather than preoccipital glabellar length was used. Also plotted is the length of the bullar lobe. Regression lines for each plot were calculated. The point at which the lines intersect indicates the preoccipital cranidial length at which the bullar lobe begins to develop. In *Dicranogmus*, bullar growth begins when the preoccipital cranidial length is approximately 0.53 mm. Chatterton (1971) showed that in the Devonian *Acanthopyge* (*Jasperia*) *bifida*, bullar lobe development is visible in the latest protaspid stage, but in all other genera for which we have specimens, all of which are Ordovician and Silurian in age, the bullar lobe does not appear until the early meraspid stages. The change of timing of cranidial lobe formation could be evidence of heterochrony.

In this collection of meraspides, there is a gap between non-holaspid-like and holaspid-like transitory pygidia. We cannot see the transition of the transitory pygidial axis to the adult form of the axis. The arrangement of the axial rings and the pattern of the tubercles on the rings has changed by the latest meraspid stage. In the protopygida and most meraspid stages, there are defined axial rings, each ring has a central enlarged tubercle flanked by smaller ones, with the size of the large tubercle decreasing from anterior to posterior rings. In the larger transitory pygidia (Pl. 43, fig. 10), the median tubercles of the anterior 3 rings are clearly visible and much larger than adjacent tubercles; those of the more posterior rings are much diminished. In the latest meraspid specimen (Pl. 34, fig. 11), which has 4 spine pairs, there are two axial rings defined, the first of which belongs to the last, unreleased thoracic segment, and the tubercle pattern has changed. The median tubercle is smaller than the two immediately adjacent to it and it now appears there are pairs of tubercles along the axis. (In the holaspid form, there is only one defined axial ring, and the arrangement of tubercles varies).

During the meraspid period, new segments, first thoracic and then pygidial, are being produced, and thoracic segments released. The number of transitory pygidial segments represents a balance between these two processes. In these specimens of *Dicranogmus,* the smallest transitory pygidium has 6 spines, presumably a M0 transitory pygidium. The remaining specimens can be subdivided on the basis of size, number of axial rings and number of spines and could represent 5 meraspid degrees, possibly M1, M2, M3, M4 and M5. The most mature transitory pygidium would be a M10 if *Dicranogmus* is like other lichids in having 11 thoracic segments.

DICRANOGMUS n. sp. A

(Plate 35, figures 1 - 20)

Material. Cranidium UA 10251.

Stratigraphical interval. AV2 15 m (Late Llandovery).

Description. Cranidium slightly wider than long. Median glabellar lobe elevated above and wider (tr.) than bullar lobes. Anterior border short, separated from glabella by distinct anterior border furrow, not overhung by median glabellar lobe. Lla lobes present. Occipital ring wide (tr.), lateral margins of ring slightly adaxial to lateral margins of bullar lobes. Longitudinal furrows subparallel between S1 and S3, do not extend posterior to S1. Palpebral lobes narrow and bisected by laterally directed slit, elevated above bullar lobes Prosopon overall, bimodal, with many small distinct tubercles and few large tubercles. Large tubercles on median glabellar lobe, some in pairs.

Ontogeny

Protaspid period (Plate 35, figures 1 - 4).

Material. Protaspides UA 10238 - 10240.

Stratigraphical interval. AV 2 15m.

Description. Protaspis 1.22 mm long (body length (sag.) excluding spines); protocranidium 60-65% total length. Glabella bounded laterally by distinct axial furrow. Shallowing of furrow at S1 - S2. Glabella inflated anteriorly into large spine. Prominent spines project anterolaterally from anterolateral corners of anterior margin of protocranidium. Protocranidium and protopygidium delineated by transverse marginal furrow. Axis of protopygidium terminates at point separated from posterior margin by approximately 15% of body length and includes 3 axial rings and terminal piece, separated by shallow ring furrows. Three pleura with pleural furrows, anterior and posterior bands subequal; posterior band not inflated; remainder of protopygidium undifferentiated. Five pairs of marginal spines, long, tapering slightly distally. Spine pair 4 (and possibly spine pair 3) project slightly above and backwards. Prosopon numerous small distinct tubercles. Enlarged tubercles on glabella, distribution not known; large single median occipital tubercle, fixigenal tubercles A2, D and tubercle B on posterior margin of protocranidium; single enlarged tubercle flanked by small uniform tubercles on axial rings of protopygidium.

Meraspid period (Plate 35, figures 5 - 14).

Material. Cranidium UA 10241; transitory pygidia UA 10242, 10243, 10245; librigena UA 10246 - 10250.

Stratigraphical interval. AV2 15 m; AV1 320 and 413 m.

Description. Cranidium length similar to that of protocranidium. Axial furrows broad, "waisting" at S2. Glabella wider (tr.) than protaspid glabella. Anterior glabella inflated into forward projecting spine. Sliver of bullar lobe present on adaxial side of axial furrow at S2. L1 inflating laterally. Anterolateral spines present on border. Palpebral lobe elevated, has palpebral spine (not tubercle). Ornamentation overall small tubercles. Prosopon on glabella appears fairly uniform. Tubercles A2 and D (probably) present on fixigena. Large median tubercle flanked by smaller tubercles on occipital ring.

Free cheeks. Free cheek long, narrow with elevated semicircular eye socle. Long genal spine. Broad subgenal notch. Lateral margins with 2-3 large spines projecting laterally. Overall ornamentation spinose tubercles. With growth, lateral spines and spinose tubercles moderate and disappear. Along ventral surface of lateral margin, tubercles aligned along margin.

Transitory pygidium. Similar in appearance to transitory pygidia of Wenlockian *Dicranogmus* described above but marginal spines slightly more tubular and background ornament of tubercles slightly denser and coarser.

Discussion of species

The only holaspid found was a cranidium. To erect a new species on the basis of one cranidium is difficult, although, in the literature this has been done, usually to the disadvantage of those trying to understand lichid systematics and phylogeny. The unusual protaspid and meraspid sclerites provide evidence of the validity of saying this is a new species. However, to name a species using an early growth stage with an unusual morphology, which is lost during ontogeny, as a type specimen, seems irresponsible. Ontogenetic sequences are rare and found at few localities, and in this instance, the holaspid morphology cannot be predicted from the meraspid sclerites available.

The sclerites assigned to this species have been associated, in part, on the basis of their being the sole lichids found in AV2 15 m (with the exception of a small late meraspid transitory pygidium that is distinctly different). The holaspid cranidium resembles others assigned to *Dicranogmus*, and the pygidium also resembles those of *Dicranogmus*. The protaspides, meraspid cranidium and meraspid free cheeks are spinose and quite different in this respect from other known early growth stages of

Dicranogmus. Regardless of the unusual morphology of the protaspid and early meraspid cranidia there is considerable similarity to those stages seen in *Dicranogmus* particularly with respect to the pygidium.

The holaspid cranidia of *Dicranogmus* and of *Radiolichas* share a similar morphology with respect to bullar lobes, L1a lobes, and longitudinal furrows. The major differences are ones of proportion and of ornamentation. It is interesting to note that similarities to both *Dicranogmus* and *Radiolichas* are present in the protaspides and meraspides of *Dicranogmus* n. sp. *A* as can be seen in Table 8.

Dicranogmus has a stratigraphical range from the Ashgill to the Ludlow. The earliest known member of *Radiolichas* is the Wenlock species found in the Mackenzie Mountains. Given the similarities between the 2 genera, it is likely that *Dicranogmus* n. sp. A with its interesting resemblances in early ontogeny to both *Radiolichas* and *Dicranogmus*, is very close to the ancestor of *Radiolichas*.

Discussion of genus

The specimens of *Dicranogmus* from the Wenlock horizons of the Avalanche Lake sites have been assigned to two different species, each with cranidia, free cheeks, hypostomes and pygidia. In some respects, the morphology of the sclerites suggests morphoclinal variation. The separation into two species was based mainly on cranidial morphology with shape and size of L1a lobes, independent vs. dependent curvature of bullar lobes and median glabellar lobes being the major distinguishing features. Prosopon and tubercle arrangement is quite distinct in each of the type specimens, but variation is apparent in other specimens assigned to each of the two species. The pygidia were assigned to each species on the basis of the inflation or not of the posterior pleural bands, marginal spine morphology, and the course of the axial furrows; with the posterior band inflation being the most consistent feature. Prosopon was also a factor in assigning pygidia to one species or the other, as was the case with free cheeks. The hypostomes, which are illustrated separately (Pl. 31, figs. 1 - 18). have been tentatively identified to the species level, but again the only basis for this identification is ornamentation, with those hypostomes resembling the hypostome from DR 91.44 m, a horizon which contains only one species of *Dicranogmus*.

On a world-wide basis, *Dicranogmus* is known mainly from the cranidium or cephalon. Perry and Chatterton (1977, pl. 6, figs. 16 - 21), studying material from the Canadian Arctic, were the first to assign a pygidium and hypostome to *Dicranogmus*.

Lane and Owens (1982, p. 56; pl. 5, fig. 4, 6, 7) working with material from Greenland, also assigned a pygidium to *Dicranogmus*.

Thomas and Holloway (1988, p. 231) argued that the pygidia would be more correctly associated with lichine or tetralichines, suggesting that if these sclerites are properly associated, then the question of where *Dicranogmus* best fits in the classification of lichids would have to be reassessed. As a result of this study, there seems little doubt that the pygidium, regardless of its *Amphilichas* - like appearance, is correctly identified as *Dicranogmus*. Both cranidia and pygidia have been found in a number of horizons which eliminates the possibility of chance association. Only a few fragments of *Dicranopeltis* (a lichine), and none of any tetralichines (normally from the Ordovician) have been found in these horizons.

To continue with the concerns of Thomas and Holloway (1988), should *Dicranogmus* be considered a trochurine? The hypostome is of major importance at the subfamily level. The hypostome assigned to *Dicranogmus* is definitely trochurine, with affinities to that of *Radiolichas*. The hypostome is wider than long, has a circumscribed middle body with a very short, narrow transverse middle furrow, and a broad, shallow medial embayment in the posterior margin. The cranidium has always been considered of primary importance for identification at the generic level. The cranidium of *Dicranogmus* seems more trochurine than lichine, particularly with respect to S1 which is deep behind the bullar lobe. The pygidium of *D. lepidus* has inflated posterior pleural bands, giving the pygidium a trochurine appearance. The pygidium of *D. wilsoni* lacks the inflated bands, but in other respects is similar to the former. *Dicranogmus* is not a typical trochurine but it seems most at home in this subfamily.

Genus HEMIARGES Gürich 1901

Type species. Lichas (Arges) Wesenbergensis Schmidt, 1885 from the Rakvere Limestone (Caradoc), Estonia.

Stratigraphical range. Llanvirn - Ashgill

Geographical range; Canada (District of Mackenzie, Ontario), United States (Illinois, Kentucky, New York, Minnesota, Missouri, Virginia), Scotland, Norway, Estonia.

Diagnosis. Trochurine with posteriorly converging longitudinal furrows becoming weak or obsolete posterior to bullar lobe. S1 usually incomplete behind bullar lobe. Posterior lobes and possible L1a lobe. Pygidium width greater than length, with 4 pairs marginal spines, of which second is usually largest (adapted from Thomas and Holloway, 1988).

HEMIARGES AVALANCHENSIS n. sp.

(Plate 36, figures 1 - 15)

Material. Holotype pygidium UA 10254; and paratypes UA 10252 - 10256.

Stratigraphical interval. AV4B 16.5 to AV4B 43 m.

Etymology. *avalanchensis* referring to Avalanche Lake locality.

Diagnosis. Cranidium wider than long. Bullar lobes oblique, diverging anteriorly, bimodal tuberculation, enlarged "pairs" of tubercles on median glabellar lobe, anterior border strongly convex forward, posterior lobes postero-lateral to bullar lobes. Pygidium with 4 pairs marginal spines, pairs 2 and 4 largest.

Description. Cranidium width greater than length, convex sagittally but glabella does not overhang border. Anterior border strongly convex forward, longest (exsag.) anterolaterally. Longitudinal furrows convergent posteriorly, deep and narrow between S3 and S1, becoming indistinct to absent between S1 and occipital furrow. Median glabellar lobe becoming wider, more inflated and more convex anteriorly. Bullar lobes oblique to exsagittal plane. Posterolateral lobes posterolateral to bullar lobe, independently inflated. No L1a lobes. Occipital ring defined by deep occipital furrow. Prosopon bimodal, with larger tubercles forming a pattern of poorly symmetrical "pairs" on median glabellar lobe. Enlarged tubercle present on bullar lobe, and another (A1?) on postero-lateral lobe. Several enlarged tubercles on occipital ring.

Hypostome. Width almost twice that of length. Anterior margin gently convex forward. Middle body subtrapezoidal. Short middle furrow distinct abaxially. Posterior and lateral borders wide. Posterior margin with medial embayment. Posterior lobe of middle body and posterior borders unornamented. Enlarged tubercles on anterior portion of anterior lobes of middle body, and adaxial portions of lateral borders. Doublure is plain, without terrace lines, with slight concavity behind shoulders. Elongate (tr.) medial concavity with rolled lip on anterior margin of doublure. Shallow antennal notch.

Pygidium maximum width about 1.5 times that of length. Axis with two slightly inflated axial rings defined posteriorly by distinct, complete ring furrows. Axial furrows subparallel for approximately 2/3 pygidial length, then narrowing to form postaxial ridge. Pleurae 1 and 2 divided into anterior and posterior bands by pleural furrows. Second anterior pleural band expanded slightly. First and second posterior bands inflated. Third pleura undifferentiated. Four pairs marginal spines, spine pairs 2 and 4 largest, spine pair 3 smallest. Posterior margin border distinct, interrupted by second and first posterior pleural bands. Ornamentation bimodal. Three to 5 enlarged tubercles aligned along posterior pleural bands. Tubercle arrangement on axis variable; with two pair of large tubercles, first pair on rings 1, 2 or 3, second pair on ring 6. Pairs of smaller tubercles may or may not be present. Enlarged tubercles on posterior border. Doublure moderate width, inner margin of which is subparallel to posterior margin; fine terrace lines, not well defined, parallel to posterior margin on distal portion, becoming subparallel with some anastomoses on proximal portion, extension of fine subparallel terrace lines on inner surface of spines.

Discussion of species

Hemiarges avalanchensis belongs to the group of species of *Hemiarges* that includes the type species, *H. wesenbergensis* (Schmidt, 1885) (Thomas and Holloway, 1988, fig. 214, 218, 219), *H. turneri* Chatterton and Ludvigsen, 1976 (pl. 19, fig.1 - 41), *H. rasetti* Evitt and Tripp, 1981 (pl. 2, figs. 1 - 6, 17 - 21) and *H. paulianus* (Clarke, 1894) (Rudkin et al., in press, pl. 1 A - H; Pl. 2, A - H; pl. 3, C - I; pl. 4, C - G; fig. 1; Ludvigsen, 1979, fig 33a - c). If ordered by age, *H. turneri* is the oldest (Chazy), then *H. rasetti* (Blackriveran), *H. paulianus* (Franklinian), *H. wesenbergensis* (Caradoc) and finally *H. avalanchensis* (Ashgill), the youngest. These all share a similar cranidial morphology, including convex bullar and medial glabellar lobes, incomplete S1, and enlarged glabellar tubercles. Rather more variation is seen in the pygidium, particularly with respect to the pygidial marginal spines (size and shape of spines).

The pygidium of *H. avalanchensis* is very similar to that of *H. paulianus*. Both have enlarged second and fourth spines and a well defined postaxial ridge. The pygidial border of *H. paulianus* is possibly more swollen and enhanced. The axis of each has 2 axial rings defined by complete ring furrows, and a third ring partially defined. The tubercle arrangement on the axis of *H. avalanchensis* is distinct and perhaps more similar to that seen on *H. turneri*, with enlarged tubercles aligned along the first and sometimes second rings, a pair of tubercles on the second or third rings and another distinct pair of tubercles on the terminal part of the axis.

The morphology of the cranidium of *H. avalanchensis* is closest to that of *H. turneri*, with similar curvature of glabellar lobes, oblique bullar lobes, similarities of cranidial tubercle arrangement and a lack of L1a.

H. avalanchensis is sufficiently distinct from other members of *Hemiarges* to be considered a new species. Although this work is devoted to Silurian lichids, a description of this late Ordovician lichid has been included because: a) it occurs just before the late Ordovician extinction event (as determined by occurrences of other trilobites), and other lichids, such as *Acanthopyge (Lobopyge) pristinus*, an Ordovician trilobite of Silurian aspect, occur just after the event; b) in the phylogenetic analysis of *Borealarges*, it was useful to include this species along with the designated outgroup, *H. turneri*, in the analysis.

Genus *RADIOLICHAS* Reed, 1923
{Subjective synonyms: *Diplolichas* Phleger, 1936 ;
?*Septidenta* Maksimova in Mennera, 1975 }

Type species. Lichas aranea Holzapfel, 1895, p. 32 from the Massenkalk Limestone (Givetian), West Germany.

Stratigraphical range. Wenlock to Middle Devonian

Geographical range. Canada (Mackenzie Mountains and Canadian Arctic), West Germany, England, Kazakhstan and Mongolian Altai.

Diagnosis. Trochurine, moderately convex glabella (sag., exsag.), not overhanging anterior border; median glabellar lobe with slight or no elevation above bullar lobe. Longitudinal furrows subparallel from S1 - S3, diverge anterior to S3, posterior to S1 may continue to occipital furrow. L1 absent or very short (exsagittal length less than or equal to that of occipital ring) behind posterior extremity of bullar lobe; L1a may or may not be defined. Prominent tubercle in subtriangular depressed region at intersection of S1 and occipital and longitudinal furrow. Librigena with subgenal notch, genal spine laterally to posteral-laterally directed. Hypostome wider than long, coarse tubercles on anterior of middle body and on lateral borders immediately adjacent to middle body. Pygidium with seven long spines, flat in cross section, radiating from pleural region, fairly constant width along length, or broader at tips than at base; median posterior spine. Axis triangular to subrectangular, with one distinct ring. Postaxial ridge poorly defined.

RADIOLICHAS n. sp. A
(Plate 37 figures 1 - 13; Plate 38, figures 1 - 20)

Material. Cranidia UA 10261, 10262; librigena 10273; hypostomes UA 10269, 10272; thoracic segments (partial) UA 10276, 10277; pygidia UA 10259, 10260, 10271.

Stratigraphical interval. AV1 590 m; AV2 256, 255 - 260 and 274 - 279 m; AV4 126 (T) m.

Description. Cranidium. Anterior border length (sag.) short, convex forward, defined by strong preglabellar furrow, border slightly overhung by median glabellar lobe. Palpebral lobe height less than bullar lobe, semi-circular to almost rectangular in shape with narrow end projecting laterally, palpebral lobe almost bisected by laterally directed central elongated slit.. L1 very short (exsag.) with enlarged tubercle just behind junction of S1 with longitudinal furrow. At S3 longitudinal furrow becomes less distinct and curves anterolaterally to meet axial furrow. Median glabellar lobe slightly higher than bullar lobes. Occipital ring wider (tr.) than median glabellar lobe, defined by distinct short (sag.), deep occipital furrow. Prosopon bimodal, small tubercles fill space between large tubercles. Large tubercles on glabella may be arranged in pairs (although other, randomly arranged, large tubercles obscure this pattern). Tranverse row of large tubercles on posterior margin of occipital ring, less dense, scattered smaller tubercles on anterior portion.

Librigena with broad librigenal field. Ornamentation overall elongated tubercles of pointing posteriorly, large tubercles in centre of field and on librigenal spines. Smaller tubercles towards anterior and antero-lateral portions. Small row of tubercles along eye socle. Anteriorly, lateral margin slightly indented, showing pattern of long, subparallel terrace lines. Fairly large subgenal notch, librigenal spine ends in blunted point. Doublure robust with considerable space between upturned proximal portion of doublure and external surface. Most of doublure plain and unornamented, terrace lines present along more horizontal distal portions.

Hypostome. Subrectangular, length (sag.) short relative to width. Anterior wing small, lateral notch long. Lateral margin inflated outwards over notch; posterior margin broad (sag.). Posterior margin broad (sag.) with broad shallow reentrant, median portion of reentrant convex posteriorly. Middle body subrectangular, large anterior lobe separated from posterior lobe by short middle furrow present abaxially and directed from lateral furrow obliquely posteriorly. Ornamented with large tubercles along anterior margin of anterior lobe of middle body and on lateral border adjacent to posterior lobe. Small pits on anterior lobe posterior to large tubercles.

Thoracic segment (partial). Axial region of segment plain, with row of small, widely spaced tubercles arranged transversely. Pleura with three rows of large tubercles arranged transversely. Termination of pleura blunt.

Pygidium with 7 marginal spines. Length approximately equal to width. Spines expand slightly distally, terminating either in blunt rounded point or expanding on posterior margin of spine to form blunt triangular terminations. Axis occupies most of pygidium, very wide relative to width of pygidium anteriorly, and posteriorly, extending into median spine or terminating to rounded poorly defined point. Axial furrows deep. One axial ring, defined by deep axial ring furrow. Axial ring with row of tubercles transversely (similar to axis of thoracic segment). Axis posterior to axial rings covered with large tubercles. Posterior to axis tubercles arranged in a fashion suggesting postaxial ridge. No pygidial border, pleural area small. Tubercles on pleurae arranged in 3 - 6 rows, including two rows of larger tubercles which continue onto spines. Doublure wide, almost reaching edge of axis, narrows slightly anteriorly, unornamented except for a few widely spaced terrace lines towards posterior margi: .

Remarks. The larger pygidium has retained one thoracic segment, and its morphology appears to be teratological. The axial ring furrow of the first pygidial axial ring is incomplete and misshapen. Pygidial spines 2, 3 and 4 are curled and the proximal ends expanded and distorted.

Ontogeny

Protaspid period (Plate 38, figures 1 - 4).

Material. "3 spine" protaspis UA 10259; "5 spine" protaspides UA 10260, 10261.

Stratigraphical interval. AV 4 126 (T) m.

Description. "Three-spine" stage protaspis incomplete, with protocranidium and 3 pairs of spines broken. Demarcation of protocranidium and protopygidium; median occiptital tubercle present. Pleural and interpleural furrows shallow and narrow. Small tubercles uniformly distributed. No enlarged tubercles on protopygidal pleura. Tubercle pair on axial ring.

"Five-spine" protaspis with protocranidium approximately 60% of total length. Glabella inflated, bounded by narrow, deep axial furrows. Glabella width narrowest opposite A2 tubercle, widening anteriorly and posteriorly, with the anterior part being wider and more inflated. Glabella overhangs anterior border medially. Anterior border very short (sag.) medially, slightly longer laterally. Palpebral lobe ve.y small. Eye ridge not very distinct. Occipital ring defined by changes in slope. Transverse demarcation of cranidium-protopygidium. Axis of protopygidium narrows to rounded point some distance (about 16% of body length) anterior to posterior margin. Four axial rings defined by faint furrows. Three pleura well defined, fourth faintly defined, fifth small and undifferentiated. Posterior pleural bands slightly inflated. Five pairs free spines projecting from protopygidial margin. Spines long, non-tapering, very slightly curved. Overall ornamentation of small tubercles. Forward projecting tubercle (spines?) on anterolateral corners of cranidium. One large tubercle with smaller flanking tubercles on occipital ring; 9 pairs tubercles on median glabellar lobe, with arrangement of pairs alternating between being far apart and closer together, and with anterior pair projecting forward. Tubercles D and A 2 on fixed cheek; palpebral tubercle. Eye ridge three small tubercles (similar in size to background tubercles and may appear more prominent because of slight inflation of eye ridge). One large (B) and several smaller tubercles on posterior margin of protocranidium. Paired tubercles on axial rings 1 - 3 of protopygidium. Two large tubercles on posterior pleural bands 1 - 3, 1 on fourth, the outer of the pair forming a line curving from posterior forward through B, D and A2. Small tubercles arranged in a row on spines. Posterior margin of doublure lined with tubercles.

Meraspid period (Plate 38, figures 5 - 7, 9).

Material. Transitory pygidia.UA 10266 - 10268, 10270.

Stratigraphical interval. AV4 126-127 m, AV5-7 m.

Description. Transitory pygidia with 7 spine pairs have 6 axial rings and a terminal piece; one with 5 spine pairs, 4 rings and terminal piece. Width of axis at anterior axial ring is one half total pygidial width. Axis tapers to rounded point. Four pleurae bounded by interpleural furrows, the fifth pleura has incomplete posterior interpleural furrow, the sixth and seventh undifferentiated by furrows. Posterior bands of pleurae 1 and 2 inflated, that of 3 - 5 decreasingly so. Pleura 6 & 7 indicated by presence of single tubercle. Marginal spines long, relatively straight and non-tapering, extension of posterior pleural band with minor contribution from anterior band. Spine 1 projects almost laterally, subsequent spine projections are progressively more posteriorly directed until spine 5 which points directly backward, followed by spines 6 & 7 which are posteromedially directed. On axial rings 1 - 5, 2 large tubercles flank slightly smaller medial tubercle, small tubercles in a row lateral to each of the two large tubercles. Two enlarged tubercles present on posterior pleural bands 1 - 5, larger tubercle outermost, close to margin. Row of tubercles on each spine, smaller tubercles line spine margins.

Discussion of ontogeny

The shape and ornamentation of the pygidial marginal spines are similar throughout the complete ontogeny. The similarities between the protaspides and meraspides of *Radiolichas* and *Dicranogmus* n. sp. A are striking. These similarities are the basis of discussion on the identity of *Dicranogmus* n. sp. A and of the possible relationships of the genus *Radiolichas* (see discussion of *Dicranogmus* n. sp. A and below).

Discussion of genus

Radiolichas is not a well known genus, with only a few species from the Devonian of Germany, England, and possibly Kazakhstan and the Mongolian Altai. *Radiolichas* n. sp. A from the Wenlock of the Mackenzie Mountains is considerably older than any of the previously reported species, with the exception of material from Baillie Hamilton Island in the Canadian Arctic (Perry and Chatterton, 1977). Because of a) limited holaspid material and b) teratological and incomplete sclerites, this new species of *Radiolichas* has not been named.

Thomas and Holloway (1988) consider that, within the Trochurinae, *Radiolichas* may have been derived from *Acanthopyge* (1988; fig. 363, p. 251; fig. 365, p. 252) because it resembles *Acanthopyge* in having a reduced L1 with medially placed large tubercles near the position of the longitudinal furrow, which may or may not be present, and because both have large subgenal notches. In the literature (Thomas and Holloway, 1988), *Radiolichas* is considered a Devonian genus and *Acanthopyge* predominantly Devonian with some Wenlock representatives. However, the Mckenzie Mountain material, as well as that from the Canadian Arctic (Perry and Chatterton, 1977), shows that *Radiolichas* was present and well developed in the Wenlock. *Radiolichas* not only occurs in these areas far earlier than previously reported, it also shares many characters with *Dicranogmus*. This evidence suggests a reexamination of *Radiolichas* and its relationships within the Trochurinae is required.

Perry and Chatterton (1977; p.302, pl. 7, figs. 1 - 9) found some specimens from the Wenlock of Baillie Hamilton Island in the Canadian Arctic, which they identified as Lichid n. gen. n. sp. Their schematic reconstruction of the lichid which was hampered by the lack of the anterior portion of the cranidium, does not resemble either *Radiolichas* or *Dicranogmus* (p. 303, fig. 3). Rather than being members of a new genus, these specimens belong to *Radiolichas*. The cranidium (of which there are 2 partial specimens), has a very distinct L1a lobe, and a very short (exsag.) L1 on which is located a large tubercle. The cranidia were associated, on the basis of ornamentation, co-occurrence and preservation, with hypostomes, free cheeks and pygidal fragments that are consistent with identification as *Radiolichas*. The fragments of cranidia (Pl. 6, figs. 13 - 15) show a resemblance to *Dicranogmus* but differ from the cranidia of *Dicranogmus* found in the same locality in terms of the S1 furrow, longitudinal furrow, length (exsag.) of L1, possession of large tubercle on L1 and ornamentation.

Radiolichas n. sp. A appears to have a small Lla, although the details are well-hidden by the surface ornamentation. The hypostome of *Radiolichas* (Pl. 38, figs 8, 11) resembles that of *Dicranogmus* (Pl. 31) in the overall shape as well as morphology of the lateral border, particularly in the region of the lateral notch, and of the posterior border.

The resemblance of protaspides and meraspides of *Radiolichas* to those of *Dicranogmus* n. sp. A. is striking. The protaspides of *Radiolichas* and the Wenlockian *Dicranogmus* are also similar to each other with respect to: a) the shape of the glabella, with that of *Radiolichas* being more extreme in both inflation and expansion of anterior and posterior portions; b) the arrangement of glabellar tubercles; c) the arrangement of the occipital ring tubercles; d) tubercles of the pleural bands of the protopygidia and e) the free pygidial spines. The two differ in: a) the anterior border where *Dicranogmus* has a deep (sag.) anterior border lined with tubercles, and *Radiolichas* a narrow border, obscured medially by the inflated glabella and anterolaterally has possible spiny projections; b) a single median enlarged tubercle flanked by smaller tubercles on the axial rings of the protopygidium of *Dicranogmus* vs. paired enlarged tubercles flanked with smaller ones in *Radiolichas*; c) the relatively straight, non-tapering marginal spines of the protopygidium of *Radiolichas*.

The strongest confirmation of a close relationship between *Radiolichas* and *Dicranogmus* lies in the protaspides and meraspides of *Dicranogmus* n. sp. A from the Llandovery. All of these factors support the idea that *Radiolichas* and *Dicranogmus* are sister taxa.

Genus *RICHTERARGES* Phleger, 1936

Type species. Lichas (Dicranogmus) ptyonurus Hall & Clarke, 1888, p. 86, Cobleskill Limestone (upper Pridoli), New York.

Stratigraphical range. Wenlock - Pridoli.

Geographical range. Canada (Mackenzie Mountains, Arctic), Greenland, United States (New York).

Diagnosis. Trochurine with long anterior border (up to one eighth cranidial length, sag.). Longitudinal furrow subparallel between S1 and S3, very weak to effaced in front of bullar lobe, usually extends back to occipital ring. S1 complete behind bullar lobe. No L1a. Subgenal notch shallow to absent. Pygidial length 70-80% width. 7-11 axial rings defined by ring furrows, decreasing in definition from anterior to posterior. Short pygidial spines, 8 or 9 major marginal spines, occasionally secondary spines present (adapted from Thomas and Holloway, 1988).

RICHTERARGES FACETUS n. sp.

(Plate 39, figures 1 - 21; Plate 40, figures 1 - 16)

Material. Holotype pygidium UA 10278, paratypes UA 10279 - 10284, 10290 - 10297.

Stratigraphical interval. AV5 58-60 m.

Etymology. facetus (L) meaning fine, elegant, well made, with respect to the morphology of, in particular, the pygidium

Diagnosis. Cranidium with rounded, relatively short (sag.) anterior border defined by deep anterior border furrow. Pygidium with 3 pairs backward projecting short marginal spines, and three median marginal spines. Postaxial ridge of moderate length. Pygidium ornamentation bimodal, with larger tubercles uniformly and more sparsely distributed.

Description. Cranidium. Anterior border short for genus, rounded anterolaterally, anterior border furrow deep. Palpebral lobe small, semicircular in outline, elevated. Row of tubercles lines rim of lobe and continues posteriorly along posterior branch of facial suture. Anterior branches of facial sutures slightly convergent forward, posterior branches strongly divergent immediately posterior to palpebral lobe. Posterior area of fixigena wide (tr.), projects laterally. Longitudinal furrows weak between occipital furrow and S1, strongly impressed and slightly divergent through length of bullar lobe, anterior to S3 slightly shallower, defining anterior of bullar lobe, meeting axial furrow at point well back from anterolateral "corner" with small pit at this point. Occipital ring moderate width (tr.) and highly arched, occipital furrow distinct. Prosopon of bimodal tubercles, uniformly distributed, with no enlarged tubercles present.

Librigena elongate, lateral and posterior borders wide. Prosopon fine bimodal tubercles, with increased proportion of larger tubercles towards eye; eye socle with row of small tubercles and possible larger one at anterior of socle; small tubercles closely spaced along inner edge of lateral border; outer part of border with fine subparallel lines which continue a short way onto lateral margin area of doublure. Broad doublure with weak terrace lines subparallel to lateral margin curving so as to be transverse across genal spine. Between eye and beginning of librigenal spine, long posterior facial suture. Librigenal spine moderate in length and width; subgenal notch shallow and gently curved.

Pygidium with sagittal length (excluding half ring) approximately 63% of width. Strong pleural furrows on first and second pleurae. First anterior band slightly longer (exsag.) than posterior pleural band; second anterior band greatly expanded; both posterior pleural bands inflated with row of tubercles. Third pleura undifferentiated, broad field. Prosopon bimodal on anterior bands and pleural field, larger tubercles sparsely distributed. Axis width approximately 70% of axis length (excluding articulating half ring). Two axial rings defined by distinct axial rings furrows, third and subsequent axial rings progressively less defined by furrows and by arrangement of tubercles. Five to seven tubercles aligned along axial rings 1 and 2; fewer tubercles (5 or less) on subsequent rings, sometimes with slightly enlarged pairs. Postaxial ridge well developed, slightly narrower than posterior border, ornamented with tubercles similar in size to larger ones on pleural field. Tubercles distributed evenly along posterior border. All p sterior marginal spines project backwards, pairs one and two short, third pair slightly longer and broader than first and second. Fourth pair small and close to third pair, fifth, median small and triangular. Posteromedian part of doublure projects anteriorly with median part forming subangular projection, apex of which is at widest part of doublure and touches base of axis. Ornamentation of outer part of doublure consists of subr allel lines formed of small asymmetrical tubercles which extend outwards onto spine d decrease in size and width towards middle part of doublure. Inner part devoid of ornamentation.

Ontogeny

Meraspid period (Plate 39, figures 14 - 21).

Material. Transitory pygidia UA 10285 - 10289.

Transitory pygidium. Appearance similar to holaspid pygidium. Three transitory pygidia with 7 posterior marginal spine pairs (penultimate meraspid degree) and two with 6 (last meraspid degree). Axis elongate triangular in shape, with small "proto" postaxial ridge.

Discussion of species

The cranidia and pygidia assigned to *Richterarges facetus* have been found only in AV 5 58 - 60. In spite of apparent discrepancies in size and ornamentation, the association of the two was made on the basis of co-occurrence and on the strong resemblance of each to the species of *Richterarges*. In the specimens found, the cranidia are small relative to the pygidia. This could be the result of taphonomic bias, since known articulated specimens of other species of *Richterarges* do not exhibit such a size discrepancy, or it could be just that our small number of specimens are not representative of the original population. However, in other genera, some articulated specimens of lichids such as *Dicranopeltis scabra* Beyrich, 1845 have cranidia that are much smaller than the pygidia (Kowalski, 1992, fig. 152). The cranidium and pygidium of *R. facetus*

n. sp. are not similar with respect to ornamentation but neither are they incompatible. As can be seen in specimens of *R. ptyonurus* (Thomas and Holloway, 1988, pl. 15, figs 331, 336, 337), this dissimilarity is not always a barrier to association.

The difficulty with respect to this species was deciding in which genus it should be placed. Is it a member of *Richterarges* or of *Borealarges*?

The holaspid sclerites of this species have been found only in AV 58-60, and the sclerites (particularly the pygidium illustrated in Pl. 39, fig. 9) resemble those of *Richterages ptyonurus* (see Thomas and Holloway, 1988, Pl. 15: 331, 336). The posterior marginal spines of *Richterarges facetus* are small and tucked in close to the pygidial margin in a manner similar to that seen in *Richterarges*.

The cranidium has a long (tr.) posterior area of fixigena, laterally directed and very uniform ornamentation, and lacks antero-lateral projections and paired tubercles on the median glabella, all of which are features quite consistent with membership in *Richterarges*. The anterolateral corners are very rounded and the anterior part of the fixigena is fairly wide (tr.). Although *B. calei* Adrain, in press, lacks anterolateral projections, the cranidia of these two species are quite dissimilar. *B. calei* has a posterior area of the fixigena of moderate length (tr.), coarse ornamentation and well defined paired tubercles on the median glabella. The cranidia of *B. patulus* also share some characters with *R. facetus* (see discussion of *B. patulus*).

R. facetus differs from the diagnosis of the genus in that: a) the anterior border is not long (but is close to that seen in *R. ptyonurus*); and b) there is a well defined S3 defining the anterior boundary of the bullar lobes.

Table 9 analyses the morphological features seen in the pygidia of *Richterarges*, *R. facetus*, and *Borealarges*. Average values of morphometric parameters of pygidia of 2 species of *Richterarges*, 8 species of *Borealarges* (3 from the Arctic and 5 from the Mackenzie Mountains) and *R. facetus* were recorded. The pygidia of *Borealarges* from the Arctic and the Mackenzie Mountains are similar, and *R. facetus* is most like these in the proportions of: a) pygidial length and width; b) axis length to pygidial length. *R. facetus* resembles *Richterarges* in the proportions of the axis and in the nature of the posterior marginal spines, but differs from both *Richterarges* and *Borealarges* in the length of the postaxial ridge, which is intermediate between postaxial ridge lengths of the other 2 taxa.

A cladistic analysis (reported in the discussion of *Borealarges*) quite clearly separates *R. facetus* from other members of *Borealarges* and aligns it with *Richterarges*. Characters separating *Richterarges from Borealarges* in this analysis are the absence of paired tubercles at S2 on the crandium, the position of the first pygidial marginal spine relative to the axis, the direction of projection of the first pygidial marginal spine and the ratio of the length of the postaxial ridge to the pygidial length.

R. facetus is the oldest species of *Richterarges* yet to be reported and it is the only species of *Richterarges* to be found in the Avalanche Lake sections.

DISCUSSION AND CONCLUSION

The Avalanche Lake sections show a rich diversity of lichids, but, paradoxically, are poor in actual numbers of lichid sclerites. Seven genera of Silurian lichids belonging to 3 subfamilies are represented: *Dicranopeltis* (1 species), *Platylichas* (1 species), *Acanthopyge* (2 species), *Borealarges* (7 species), *Dicranogmus* (3 species), *Radiolichas* (1 species), and *Richterarges* (1 species). All are from the Wenlock with the exceptions of *Acanthopyge* (*Lobopyge* s.l.) *pristinus* from the Late Ordovician (*persculptus* zone), and *Platylichas* (*Rontrippia*) *infimus* and *Dicranogmus* n. sp A. from the Llandovery.

Lichids from two sites outside the main study area were included, which provided some assistance in understanding the nature of the Avalanche Lake lichids. The first site was an Ordovician horizon in the Avalanche Lake sections, AV4B 16.5 to 43 m, which is below the extinction and faunal turnover event in the late Ashgill. One lichid, *Hemiarges avalanchensis*, was recovered from these horizons and was useful for comparing lichid composition of horizons before and after the extinction/faunal turnover event. It was also included in the cladistic analysis of *Borealarges*, as a member of the outgroup, along with the Middle Ordovician *H. turneri*. The other site was in the Delorme range (DR 91.44 m), from which 3 species of lichids, belonging to 2 genera, *Borealarges tuckerae*, *B. variabilis* and *Dicranogmus lepidus* were extracted. Individual sclerites of these 3 species were sufficiently different each from the other, that it allowed species-level associations, which supported or assisted in association of sclerites in the Avalanche Lake sections.

Identification and association of sclerites of the Wenlock lichids became a complex puzzle when it became apparent that there was little or no stratigraphic separation of species, that in each horizon there could be from 1 to 8 species of lichids represented, that each species could be found in up to 7 horizons (Table 2) and that, for each species, relatively few sclerites were available. Adding to the complexity of the puzzle was the fact that of 17 species identified, 16 are new species. *Borealarges* was the major challenge. It is the best represented genus in the Avalanche Lake sections, and up to 4 species could be found in a given horizon.

Protaspid and meraspid stages occur in all sections and most horizons (see Table 3). The richest horizon, in terms of both genera and abundances, is AV4 126 m where protaspides and meraspides of 4 genera are represented.

The diversity of lichid species for a given horizon, particularly that of the best represented genus, *Borealarges*, is high relative to the diversity seen for other trilobite groups from these same sections. Chatterton and Perry (1983) found 12 species of odontopleurids belonging to 7 genera in one horizon (AV4 126 m), which included 2 species of *Ceratophalina*, 2 of *Ceratophala*, 2 of *Dudleyaspis* and 2 of *Leonaspis*. In a study of cheirurids, Chatterton and Perry (1984) found 10 species belonging to 6 genera in AV4 126 m, with 4 of the genera being represented by 2 species each. Curiously, AV4 126 m, which is the richest of the AV horizons for cheirurid and odontopleurid diversity, is slightly less so for lichids.

Chatterton and Perry (1983, 1984) found certain cheirurids and odontopleurids occurring in each of AV1 587-598 m, AV2 250-279 m, AV4 126-136 m; this collection they termed Faunal Assemblage j. The high AV4 horizons (165 - 248.5 m) contained a different assemblage, designated Faunal Assemblage k. The former fell into what Chatterton and Perry described as the third episode (beginning of a regressive phase) of the third Grand Cycle, the latter into the fourth episode (continuing of regressive phase). With lichids, one does not see a distinction comparable to the j and k faunal assemblages of Chatterton and Perry. None of the lichids found is unique to the high AV4 (230-260 m) sections, site of the k assemblage. Lichids found in the high AV4 horizons are also found in the lower horizons, and in other sections. Only one horizon, AV5 58 - 60 m, in a deep water section, has unique occurrences of lichids, of which there are 2, *Richterarges facetus* and the poorly represented *B*. sp. aff. *B. tuckerae*. In terms of lichids, the faunal uniformity of the Wenlock horizons is impressive.

In the Arctic, the only other known locality with a great diversity of lichids, Adrain (in press) found 6 species of *Borealarges* that are fairly well separated stratigraphically, with a maximum of three species being found in one locality and fewer than 3 in all other localities.

As noted in the discussion of the phylogenetic analysis, the stratigraphic separation of species of *Borealarges* in the Arctic is in direct contrast to the lack of separation in the Mackenzie Mountains. The reasons for this difference in distribution patterns could be related to paleoecological factors.

The paleoenvironment of the Avalanche Lake sites has been explored by Chatterton and co-workers (e.g. Chatterton et al., 1990). The horizons, from which the samples were collected, were deposited during a regressive phase (Chatterton and Perry 1983, 1984). In regressive phases there can be a displacement of benthic assemblages outward, which particularly affects outer platform assemblages, forcing them onto the slope. There may also be migration of species to more favourable environments, separate from the downward shifting. Chatterton et al. (1990, Table 2) set out some criteria to be used in determining whether or not a clade had become extinct or had emigrated elsewhere, but these are not helpful with respect to the lichids. There is no evidence presently available to support migration. In addition, to regression, there is evidence of slumping, or debris flows, at this site. This means that material collected from a horizon of a given section may have originated, not from there, but from a location up slope. However, there is a consistency in the composition of the lichid asssemblages in all Wenlock sections from most proximal (AV2) to most distal (AV5), and the presence, in most sections, of ontogenetic sequences. All of this suggests the findings reflect paleo-community composition.

In the Silurian, trilobites, including lichids, were recovering from at least 3 extinction events in the Upper Ordovician. In the Avalanche Lake sections, there was a major faunal turnover, probably the last of the Ordovician extinctions that, in terms of trilobites and conodonts, occurred within a <60 cm interval (Wang et al., 1993), of which the upper limit is AV4B 111.3 m. Trilobites of a Silurian aspect are found just above this horizon, and one species, *Acanthopyge* (*Lobopyge* s.l.) *pristinus* occurs in this interval between the faunal turnover and the Ordovician-Silurian boundary, at approximately AV4B 112 m.

The Selwyn Basin is thought to have been restricted during the Late Ordovician - early Silurian time period (Wang et al., 1993; Goodfellow and Jonasson,1984), and to have opened up to less restricted oceanic circulation during the Llandovery. It is not hard to imagine that, with basin circulation pattern changes, sea level changes, possible temperature changes, and recovery from extinctions, conditions existed which would contribute to speciation. There is some evidence of speciation occurring in this area.

Dicranogmus n. sp A, from the Llandovery (AV2 15m, AV1 320 - 413 m), has an interesting morphology which suggests it had to be closely related to the ancestor of *Radiolichas*. The earliest known *Radiolichas*, previously considered a Devonian clade, has been found widely distributed in the Wenlock (AV1 591 m, AV2 255 - 279 m, AV4 126 m and AV5 7 m) and in the Arctic (Perry and Chatterton, 1977). The Wenlock ontogeny of *Dicranogmus* has similarities to that of *Radiolichas* and the holaspid cranidia of each genus give evidence of a close relationship, even though, by the Wenlock, the 2 genera have diverged.

Acanthopyge (*Lobopyge* s.l.) *pristinus* is the earliest reported member of that clade, which is known from the Wenlock to Devonian. There are suggestions *A.* (*L.* s.l.) *pristinus* and some Wenlock species could constitute a sister taxon to *Acanthopyge* (*Lobopyge*). There is a strong similarity of appearance, both in cranidial and pygidial morphology, between *A.* (*L.* s.l.). *pristinus* and some species of *Hemiarges*, particularly

Hemiarges diadayma (Fig. 5), but not with *H. avalanchensis*, which occurs in the same section, just below the faunal turnover (*persculptus*) zone.

A third species, *Richterarges facetus*, is also the earliest reported member of that genus. Here, the morphology suggests a close relationship to *Borealarges*, and the phylogenetic analysis (Fig. 6) supports this.

Two of the 3 earliest reported occurrences, *Acanthopyge* (*Lobopyge* s.l.) *pristinus* and *Richterarges facetus* exhibit morphology "intermediate" between possible ancestral groups and well developed later groups. Another species, *Platylichas* (*Rontrippia*) *infimus*, has features intermediate between those considered diagnostic of 2 recently erected subgenera (Thomas and Holloway, 1988), indicating a need for reassessment of the subgenera question, if and when, more (probably Northern Laurentian) material becomes available.

Lichid ontogeny: a comparative look

The Avalanche Lake sections are unusual in that the depositional and preservational conditions were such that many very small, fragile organisms were preserved. In the case of the trilobites, we find intact 3-dimensional silicified forms of protaspides and meraspides. Material such as this can contribute to the understanding of various trilobite groups (Speyer and Chatterton, 1989, and references therein).

Lichid protaspides and meraspides representing 5 genera were identified in these sections. As discussed earlier (Table 3), protaspid and meraspid specimens were found in all sections; but one horizon, AV4 126 m, was richer than all other horizons in both number of genera represented and in frequency of occurrence.

It is evident from ontogenetic sequences reported in the literature and in this work, that the earliest protaspides are already morphologically distinct. At the "3-spine" stage, distinctive characters such as the shape of protopygidial marginal spines is visible. There is a continuity of morphology between the "3 spine" and the "5 spine" stages.

One of the surprises in the protaspides of the Avalanche Lake sections was the degree of individuality seen in the protaspides of different genera (Fig. 13). *Borealarges* and *Platylichas* almost seem to be "no-name brands" relative to those of *Radiolichas*, *Dicranopeltis* and *Dicranogmus*.

If, as a general rule, closely related organisms are more similar in their juvenile stages than less closely related forms, and if juvenile forms are more "general": and adult forms more derived, what does this new material tell us?

If the protaspides of *Platylichas* are correctly identified (see text), their resemblance to those of *Borealarges* is one that crosses subfamily boundaries and is closer than that seen between species in the Subfamily Trochurinae. This similarity could be explained by convergence, a common feature of lichid evolution, but if this identification were to be supported by future finds of protaspid material, a reexamination of lichid classification would be in order. Within the Trochurinae, *Borealarges* is most like the Ordovician, and probable ancestral *Hemiarges*, with *Dicranogmus* and *Radiolichas* becoming more extreme.

Some features are seen in early ontogeny and then disappear; others remain thoughout ontogeny. A unique feature of protaspides and early transitory pygidia of *Dicranogmus* is the single large median tubercle on each of the pygidial axial rings. This feature has disappeared in the late meraspid stages. An extreme example of morphological individuality is seen in the protaspis of *Dicranogmus* n. sp. A, a Llandovery species. The protaspis is graced with an elongated, forwardly projecting median glabellar lobe. The glabellar projection continues into the early meraspid stages but is lost in later stages, and the holaspid cranidium is very like those of Wenlock members of *Dicranogmus*, an excellent example of a highly derived early ontogenetic morphology and a more general adult morphology. Examples of retention of characters can be seen in *Radiolichas* and *Dicranopeltis*. *Radiolichas* has, in the holaspid pygidium, non-tapering pygidial marginal spines, a feature which is retained from the protaspid period. The protaspis of *Dicranopeltis* has very large palpebral lobes and a pronounced genal flare, features which are modified, but evident in the holaspid cranidium.

The present work greatly expands the knowledge of the ontogeny of lichids. Two stages of lichid protaspides are found, the "3 spine" stage and the "5 spine" stage. The "3 spine" stage is now known for 5 genera: *Acanthopyge*, *Amphilichas* and *Hemiarges* reported in the literature (see Chapter 2 for an account), *Borealarges* and *Radiolichas* (this work). The "5 spine" stage is known for all of the above and *Dicranopeltis*, *Platylichas* and *Dicranogmus* (this work).

Meraspid sclerites provide glimpses of the transition to the adult form and can often be identified to the species level. They are valuable in understanding the homologies of such features as the lobes on the cranidium.

The definite and different morphologies of the protaspides, with even the "3 spine" stages exhibiting strong morphological distinctiveness raise questions regarding ontogenetic development. It is evident that considerable morphological differentiation has occurred prior to the "3 spine" protaspid stage. Chatterton and Speyer (in press) have proposed the existence of an earlier mineralized, planktonic larval form. There is also the possibility of early non-mineralized larval instars. This matter, too, remains unresolved.

In most cases, the protaspid - meraspid - holaspid transition goes from the primitive to more derived with the exception of the already discussed *Dicranogmus* n. sp. *A*.

Unresolved questions based on observations such as have been recorded in this work are useful and can be compared to threads running through the background of various projects, with the hope that information from diverse sources will bring some of the threads together, providing some answers.

Future work

Future studies should include a closer look at Llandovery horizons of the Avalanche Lake sections. The Llandovery was a time period during which a lot happened in the lichid story. This was a time of recovery from the extinctions of the Late Ordovician and a time sealevel change with major and minor transgressions and regressions, with the highstand occurring in the mid-Llandovery (Chatterton et al., 1990). In the Avalanche Lake sections the time of maximum transgression is represented by horizons AV1 150 - 320 m. The Llandovery - Wenlock boundary occurs in the region of AV 1 460 m or AV2 157 m. Although three sections from this locality contain Llandovery material (section AV1 is available through the Llandovery, AV2, the later Llandovery and AV4B, the early Llandovery), very little collected Llandovery material was available for this study. The Llandovery specimens came from horizons deposited during the transgressive phase.

The evidence from this study suggests the Llandovery is a time period critical to the understanding of lichid evolution, biodiversity and biogeography.

Table 1: Comparison of *Hemiarges turneri* Chatterton and Ludvigsen, 1976 and *Hemiarges rasetti* Tripp and Evitt, 1981 through ontogeny (See also Fig. 3).

MORPHOLOGY	*H. TURNERI*	*H. RASETTI*
PROTASPIS, "3 SPINE"		
Posterior margin spines	triangular, projections close to pygidium	elongate, triangular, project freely, well-defined
Ornamentation	indistinct	pronounced, well-defined
PROTASPIS, "5 SPINE"		
Posterior margin spines	triangular, broad- based, extend outwards farther than 3 spine stage, but still close to body	spines elongate, uniform in width (tr.) for entire length, all terminate at a point equidistant to a line drawn perpendicular to median spine
TRANSITORY PYGIDIUM		
Curvature posterior margin	highly convex posteriorly	relatively flat curvature convex posteriorly
Pygidium Length/Width	71%	63%
Spines	triangular	"cylindrical"
Cranidium	glabella fairly flat	glabella inflated
HOLASPID, PYGIDIUM		
Axial rings	1	2
Axial furrows	subparallel, converge abruptly ("sigmoidal")	convergent, straight (axis triangular)
Post axial ridge	present	small to non-existent
Posterior margin border	present, well-defined	absent
Marginal spines	2nd longer than 3rd	2nd not longer than 3rd
Spine size	2nd spine larger in all dimensions	fairly uniform, not long, project to similar distance posterior to median spine
Paired tubercles near termination of axis	present	absent
HOLASPID CRANIDIUM		
Occipital ring tubercles	tubercles in addition to median tubercle	median tubercle only

Table 2. Distribution of lichids collected from Mackenzie Mountain sites.

INTERVALS	*H. avalenchensis*	*A(L.s.l.) pristinus*	*P.(R.) infimus*	*Dicranogmus n. sp. A*	*Dicranopeltis sp.*	*A.(L.) n.sp. A*	*Borealarges fruillus*	*B. patulus*	*B. renodis*	*B. tuckerae*	*B.sp. aff. tuckerae*	*B. variabilis*	*Borealarges sp.*	*Dicranogmus lepidus*	*D. wilsoni*	*Radiolichas n.sp. A*	*Richterarges facetus*	#Genera	# Species
DR 91.44 m										X		X		X				2	3
AV5 58-60 m					X				X	X	X			X			X	4	6
AV4 230-260 m								X		X		X		X				2	4
AV4 117-126 m					X				X			X	X	X	X	X		4	7
AV2 274-279 m						X	X	X	X			X	X	X	X	X		4	9
AV2 250-260 m					X			X	X	X		X	X	X	X	X		4	9
AV1 587-598 m					X		X		X	X		X	X	X	X	X		4	9
AV2 15 m				X														1	1
AV1 95.5 m			X															1	1
AV4B 111 m		X																1	1
AV4B 16.5-43 m	X																	1	1

Table 3. Distribution of lichid protaspides and meraspides from Mackenzie Mountain sites.

INTERVAL	*Platylichas*	*Dicranogmus n. sp. A*	*Dicranogmus*	*Dicranopeltis*	*Borealarges*	*Radiolichas*	# Genera (P)	# Genera (M)
AV5 58-60 m					P, M	M	1	1
AV5 7 m								1
AV4 230-260 m			P		P, M		2	1
AV4 124-127 m			P, M	P, M	P, M	P, M	4	4
AV2 274-279 m					M			1
AV2 250-260 m					M			1
AV1 587-598 m				M	P, M		1	2
AV1 413 m		M						1
AV2 15 m		P, M					1	1
AV1 95.5 m	P						1	

Table 4 - Taxa included in cladistic analysis (Plate #, without reference, refers to plates in this work)

Borealarges fritillus n.sp., Wenlock, Mackenzie Mountains
Plate 7: 1 - 15.

Borealarges patulus n.sp., Wenlock, Mackenzie Mountains
Plates 8: 1 - 20; 9: 1 - 20.

Borealarges renodis n.sp., Wenlock, Mackenzie Mountains
Plates 10: 1 - 15; 11:1 - 24; 12: 1 - 12.

Borealarges sp. aff. *B. tuckerae*, Wenlock, Mackenzie Mountains
Plate 15: 1 - 6.

Borealarges variabilis n.sp., Wenlock, Mackenzie Mountains
Plate 16: 1 - 15; 17: 1 - 18.

Borealarges mikulicorum (Perry and Chatterton, 1977), Wenlock, Canadian Arctic
Perry and Chatterton (1977, Plate 5: 5, 22 - 25; Pl. 6: 1 - 6).
Adrain (in press, Plate 3: 1 - 25; Pl. 4: 5, 8 - 17).

Borealarges morrisoni Adrain, in press, Wenlock, Canadian Arctic
Adrain (in press, Plates 8: 1 - 23; 9: 1 - 3, 5, 6, 8, 10).

Borealarges reedi Adrain, in press, Wenlock, Canadian Arctic
Adrain (in press, Plates 4: 1 - 4, 7; 5: 1 - 27)

Borealarges tuckerae Adrain, in press, Wenlock, Canadian Arctic
Adrain (in press) Plates 9: 4, 7, 9, 11 - 16, 18; 10: 1 - 10, 25).
Borealarges tuckerae Adrain, in press, Wenlock, Mackenzie Mountains
Plates 13: 1 - 21: 14: 1 - 9.

Borealarges s.l. *calei* Adrain, in press, Wenlock, Canadian Arctic
Adrain (in press, Plates 6: 1 - 22; 7: 1 - 23).

Borealarges s.l. *bucklandi* (Milne Edwards, 1840), Wenlock, Dudley, England
Thomas and Holloway (1988, Plate 15: fig. 318-321, 324).

Hemiarges turneri Chatterton and Ludvigsen, 1976, M. Ord., S. Mackenzie Mtn.
Chatterton and Ludvigsen (1976, Plate 18: 3 - 16, 21, 22 - 24, 35 - 38).

H. avalanchensis n.sp., Late Ordovician, Mackenzie Mountains
Plate 36: 1 - 13.

Richterarges aquilonius (Whittington, 1961), Ludlow, Canadian Arctic
Thomas and Holloway (1988, Pl. 15, fig. 330, 333)
Whittington (1961, Plate 56: 19, 25)

Richterarges ptyonurus (Hall and Clarke, 1888), Pridoli, New York State, U.S.A.
Thomas and Holloway (1988, Plate 15: fig. 331, 336, 337).
Whittington (1961, Plate 55: 1 - 4, 5 - 7, 8, 9, 11).

Richterarges facetus n.sp., Wenlock, Mackenzie Mountains
Plates 39, 40.

Table 5 Characters used in phylogenetic analysis of *Borealarges* (Character states unordered, unpolarized).

Cranidial characters

1. Anterolateral projections on cranidium: (0) absent; (1) small; (2) large.
2. Direction of anterior branches of facial suture as they meet anterior margin: (0) parallel; (1) divergent; (2) convergent.
3. Paired glabellar tubercles on median glabella at S2: (0) absent; (1) enlarged; (2) spinose.
4. Length of posterior area of fixigena (tr.) expressed as a ratio of length (tr.) of posterior area of fixigena to length (tr.) of occipital ring: (0) short, less than 0.80; (1) moderate 0.81-1.05; (2) long, greater than 1.15.
5. Nature of S1 behind bullar lobe: (0) incomplete; (1) complete.
6. S1 extends adaxially across median glabellar lobe: (0) not present; (1) partial, and/or shallow furrow present; (2) strong furrow extends full width.
7. Longitudinal furrows between S1 and S3 are: (0) parallel or subparallel to each other; (1) divergent anteriorly; (2) convergent anteriorly.
8. Deflection laterally of longitudinal furrows at S2: (0) absent; (1) present.
9. Expansion of anterior fixigenal field between axial furrow and anterior branch of facial suture: (0) little or no expansion; (1) some expansion; (2) greater expansion.
10. Height of the median glabellar lobe is: (0) equal to or slightly higher than the height of the bullar lobe; (1) much higher than the bullar lobes.

Pygidial characters

11. Axial ring dominance: (0) first ring dominant; (1) first and second rings equal or subequal; (2) axial ring dominance decreases gradually from anterior to posterior.
12. The position of the first pygidial spine taken at the point of contact of the anterior part of the adaxial margin of the spine with the pygidium, relative to the axis. Point of contact opposite: (0) post-axial ridge; (1) axial rings 6-8; (2) axial rings 1-5.
13. Direction of projection of first pygidial spine expressed as a posteriorly projected angle relative to the exsagittal plane: (0) posterolaterally at 45° or more to exsagittal plane; (1) less than 45° to exsagittal plane; (2) posteriorly.
14. Relative sizes of pygidial marginal spines: (0) all spines similar; (1) second spine largest; (2) third spine largest; (3) other (e.g. second and fourth spines largest).
15. Ratio of axial width to axial length: (0) ratio greater than 0.95; (1) ratio of 0.7 - 0.9; (2) ratio less than 0.7.
16. Direction of axial furrows at position of axial rings 1 and 2 relative to direction posterior to this: (0) continuous, no change in direction; (1) discontinuous, change in direction.
17. Number of marginal spines: (0) 8 spines; (1) 9 spines (2) 6 spines.
18. Length of postaxial ridge relative to length of pygidium exclusive of marginal spines, expressed as a ratio: (0) 0 - 0.18; (1) 0.20 - 0.30; (2) greater than 0.35.
19. Separation of second and third pygidial marginal spines: (0) spines clearly separated by posterior marginal border; (1) third spine blends into marginal border between second and third spines; (2) second and third spines not separated by marginal border.
20. Shape of internal margin of doublure (0) rounded, convex anteriorly; (1) convex anteriorly with medial anterior projection.

Table 6. Data matrix for analysis of *Borealarges*, *Richterarges* and *Hemiarges*.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	R. facetus	0	2	0	2	1	0	1	1	2	0	2	2	2	0	1	1	1	1	1	1
2	B. frutillus	1	2	1	1	1	1	1	1	1	0	1	1	2	2	2	1	1	0	1	0
3	B. patulus	1	2	0	1	1	1	1	1	2	0	1	1	0	2	1	1	1	0	0	1
4	B. renodis	1	2	1	1	1	1	1	1	2	1	0	1	0	0	1	0	1	0	0	0
5	B. tuckerae	1	1	2	1	1	1	0	0	1	1	1	2	0	2	0	0	1	0	0	0
6	B. cf. B. tuckerae	1	2	1	1	1	1	0	1	1	0	1	2	1	2	1	1	1	1	0	0
7	B. variabilis	1	2	1	1	1	1	0	0	1	0	1	1	1	2	1	1	1	1	1	0
8	B. calei	0	2	1	1	1	1	0	1	1	0	1	1	0	2	1	1	1	1	0	?
9	B. mikuliceorum	1	2	1	0	1	1	1	1	0	0	1	2	0	2	1	?	1	1	0	0
10	B. morrisoni	2	1	1	?	1	1	1	1	0	0	?	?	1	2	1	1	1	?	1	0
11	B. reedi	1	2	1	0	1	2	1	1	1	0	1	2	0	2	1	1	1	0	0	0
12	B. bucklandi	0	2	0	1	1	1	2	1	0	0	2	2	1	2	1	0	1	1	1	?
13	R. aquilonius	0	2	0	2	1	0	0	1	2	0	2	1	2	0	2	0	1	2	1	?
14	R. ptychonotus	0	2	0	2	1	0	0	1	1	0	2	1	2	0	2	0	0	2	1	?
15	H. avalanchensis	0	2	1	0	0	0	1	0	2	0	1	0	1	3	1	1	0	1	2	0
16	H. turneri	0	2	0	0	0	0	1	0	2	0	0	0	1	1	0	1	0	0	2	0

Table 7. List of apomorphies on cladogram number 4, from PAUP 3.1.1 analysis.

Branch	Character	Steps	CI	Change
B.turneri --> node_25	11	1	0.500	0 --> 1
	14	1	[illegible]	1 --> 0
	15	1	0.500	0 --> 1
	18	1	0.500	0 --> 1
node_[illegible] --> node_[illegible]	5	1	1.000	0 --> 1
	8	1	0.333	0 --> 1
	11	1	0.500	1 --> 2
	12	1	0.400	0 --> 2
	17	1	[illegible]	0 --> 1
	19	1	0.500	2 --> 1
node_[illegible] --> node_[illegible]	4	1	0.667	0 --> 2
	13	1	0.500	1 --> 2
	20	1	0.500	0 --> 1
node_[illegible] --> node_[illegible]	7	1	0.500	1 --> 0
	12	1	0.400	2 --> 1
	15	1	0.50[illegible]	1 --> [illegible]
	16	1	[illegible]	[illegible]
	18	1	[illegible]	[illegible]
node_[illegible] --> B.pty[illegible]	9	1	0.4[illegible]	[illegible]
	17	1	[illegible]	[illegible]
node_[illegible] --> node_24	6	1	1.0[illegible]	[illegible]
	9	1	[illegible]	[illegible]
	14	1	[illegible]	[illegible]
node_24 --> node_[illegible]	1	1	[illegible]	[illegible]
	3	1	[illegible]	[illegible]
	11	1	[illegible]	[illegible]
node_[illegible] --> node_[illegible]	13	1	[illegible]	[illegible]
	19	1	[illegible]	[illegible]
node_[illegible] --> node_[illegible]	9	1	[illegible]	[illegible]
	18	1	[illegible]	[illegible]
node_[illegible] --> node_[illegible]	4	1	[illegible]	[illegible]
	12	1	0.4[illegible]	[illegible]
node_[illegible] --> B.[illegible]	13	1	[illegible]	[illegible]
	15	1	[illegible]	[illegible]
	19	1	[illegible]	[illegible]
node_[illegible] --> B.[illegible]	3	1	[illegible]	[illegible]
	9	1	[illegible]	[illegible]
	20	1	[illegible]	[illegible]
node_[illegible] --> node_[illegible]	10	1	1.0[illegible]	[illegible]
	16	1	[illegible]	[illegible]
node_[illegible] --> B.[illegible]	9	1	[illegible]	[illegible]
	11	1	[illegible]	[illegible]
	14	1	[illegible]	[illegible]
node_[illegible] --> B.tuckerae	2	1	[illegible]	[illegible]
	3	1	[illegible]	[illegible]
	7	1	[illegible]	[illegible]
	8	1	[illegible]	[illegible]
	12	1	0.4[illegible]	[illegible]
	15	1	[illegible]	[illegible]
node_[illegible] --> node_19	7	1	[illegible]	[illegible]
	18	1	[illegible]	[illegible]
node_19 --> node_18	13	1	[illegible]	[illegible]
node_18 --> B.cf.B.tuckerae	12	1	0.4[illegible]	[illegible]
node_18 --> B.variabilis	8	1	[illegible]	[illegible]
	19	1	[illegible]	[illegible]
node_19 --> B.[illegible]	1	1	0.667	[illegible]
node_[illegible] --> B.reedi	6	1	1.0[illegible]	[illegible]
node_[illegible] --> B.morrisoni	1	1	[illegible]	[illegible]
	2	1	[illegible]	[illegible]
node_24 --> B.bucklandi	4	1	[illegible]	[illegible]
	7	1	[illegible]	[illegible]
	16	1	[illegible]	[illegible]
node_[illegible] --> B.[illegible]	3	1	[illegible]	[illegible]
	14	1	[illegible]	[illegible]

Table 8. Comparison of morphology of protaspides and meraspides of *Dicranogmus*, *Dicranogamus* n.sp. A and *Radiolichas* (those of *Dicranogmus* and *Radiolichas* identified to genus level only).

Morphology	***Dicranogmus* n.sp.A**	***Radiolichas***	***Dicranogmus***
Protaspis, "5-spine"			
Length	1.2 mm	1.07-1.16 mm	0.85-1.08 mm
Ant. glabellar spine	yes	no	no
Anterolateral spines	yes	probable	no
Pygidial spines	slight taper	uniform width	tapered
Axial (pyg.) tubercles	single	pair	single
Pleural tubercles	none enlarged	enlarged pairs	single enlarged
Meraspid cranidium			
Ant. glabellar spine	yes	no	no
Transitory pygidium			
Axis width/pyg. width	30%	45%	27-37%
Overall appearance	*Dicranogmus*	*Radiolichas*	*Dicranogmus*
Meraspid free cheeks	*Radiolichas*-like		

Table 9. Comparison of morphology of *Richterarges*, *R. facetus* and *Borealarges*

CHARACTER	*RICHTERARGES* (2 species)	*R. FACETUS*	*BOREALARGES*((Mackenzie Mtns) (5 species)	*BOREALARGES* (Arctic.) (3 species)
Pyg. length/width	0.77	0.65	0.66	0.62
Axis length/pyg. length	0.59	0.71	0.73	0.79
Axis width/pyg. width	0.3	0.29	0.35	0.38
# Axial rings	7 - 11	7 - 9	7 - 8	7 - 8
Pygidial spines	short, flat	short, flat-cylindrical	longer, cylindrical	longer, cylindrical
Anterolateral projections	no	no	yes	yes
Anterior border (sag.)	long	short	short	short
S3 furrow	partially effaced	weak	strong	strong
Paired glabellar tubercles	no	no	yes	yes

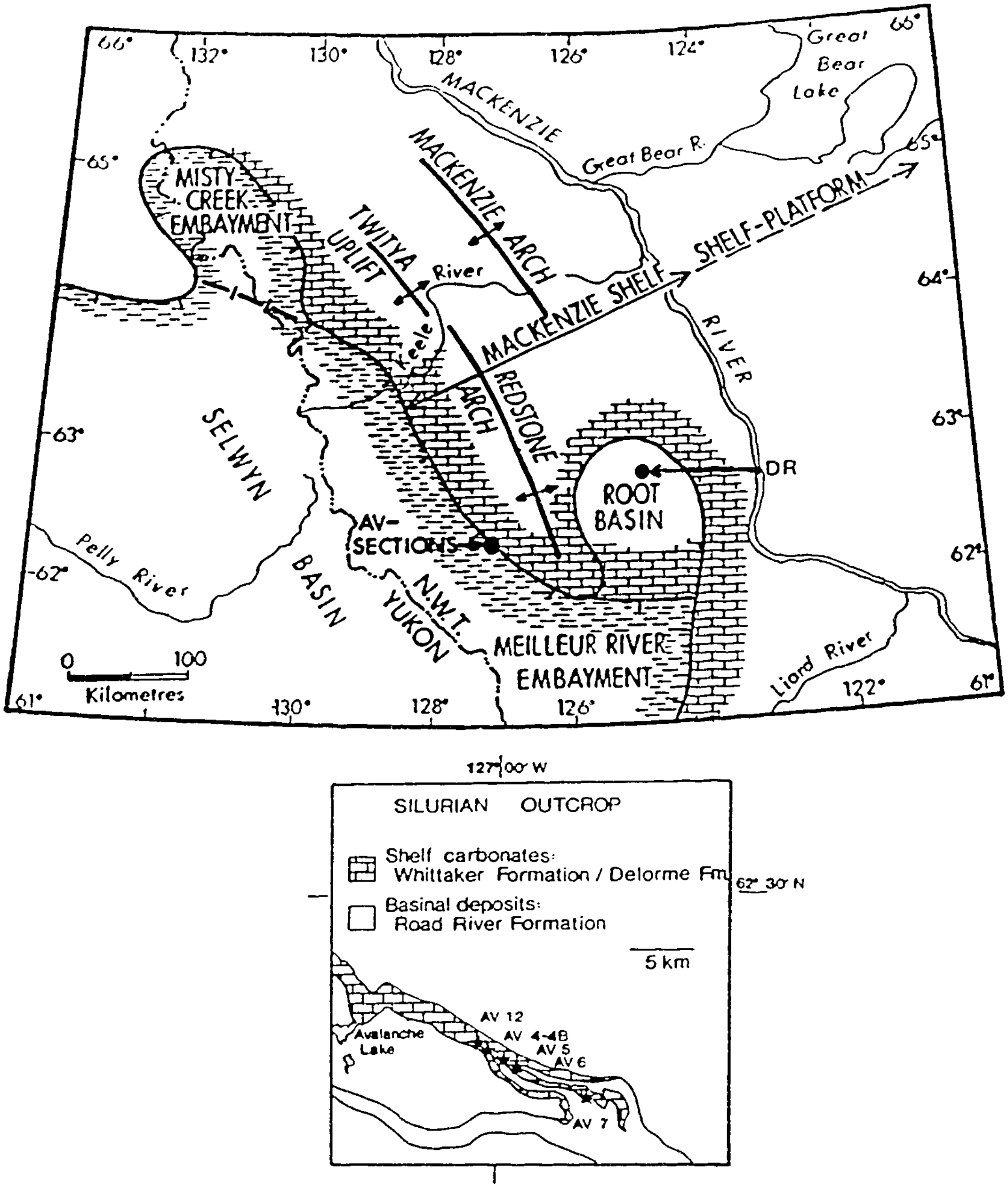


Fig. 1. Map of study area. A. Late Ordovician - Early Silurian lithofacies and the location of the Avalanche Lake (AV) sections and the Delorme (DR) section (after Wang et al., 1993). B. Detail map showing distribution of AV sections and interfingering of Whittaker Formation / Delorme Formation and Road River Formation (after Over and Chatterton, 1987).

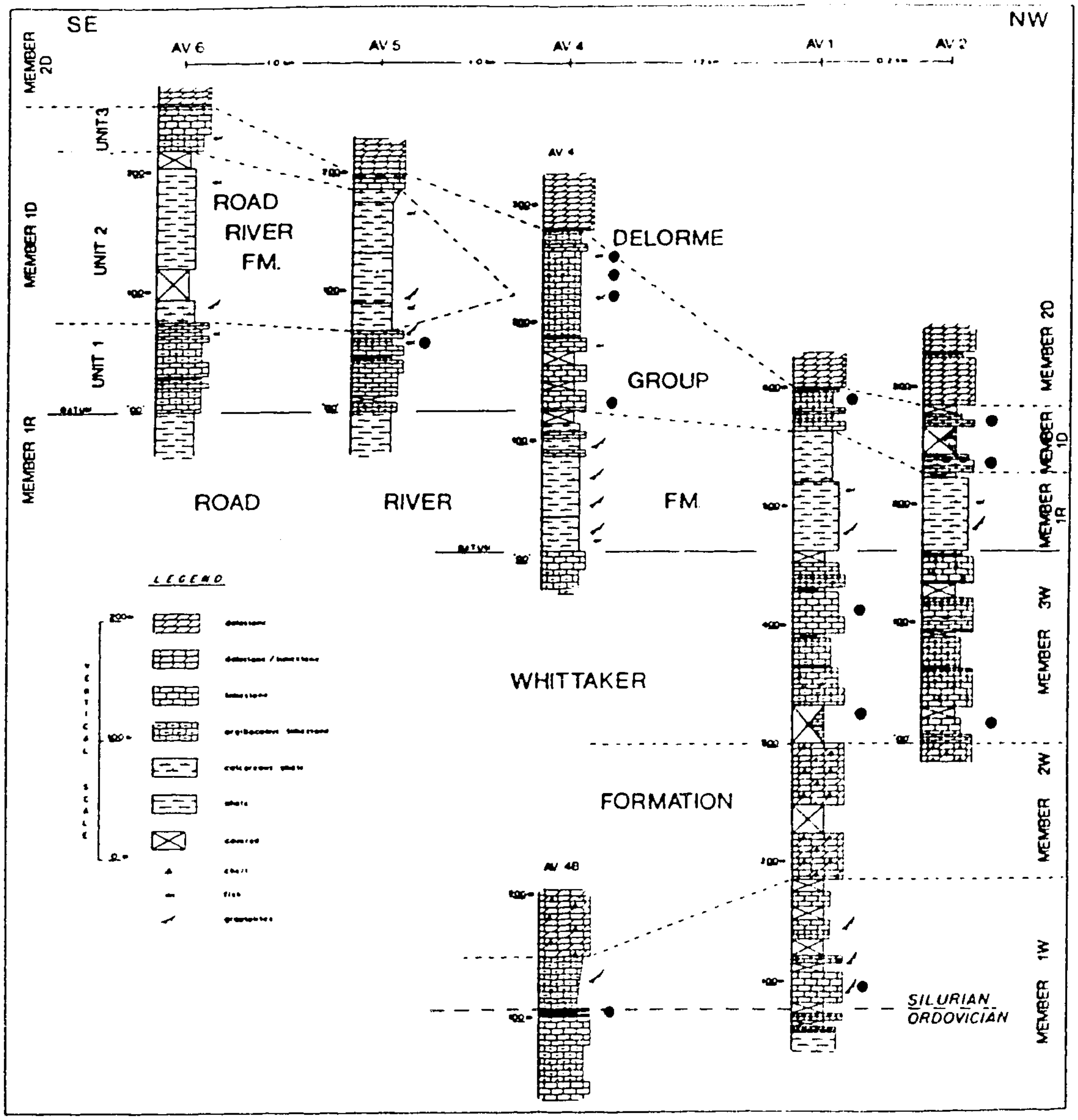


Fig. 2. Lithological correlation of Avalanche Lake sections (from Over and Chatterton, 1987). Small circles (•) mark horizons where lichids have been found.

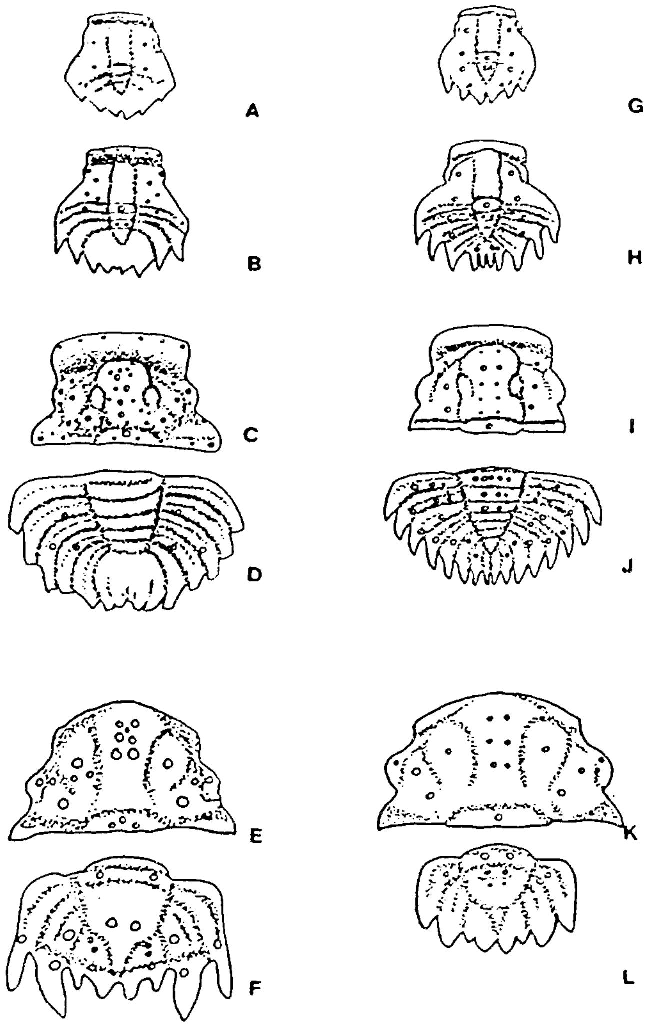


Fig. 3.Comparison of morphology during ontogeny of *Hemiarges turneri* (A - F) and *H. rasetti* (G - L). A & G, dorsal view of "3 spine" protaspis; B & H, dorsal view of "5 spine" protaspis; C & I, dorsal view of meraspid cranidium; D & J, dorsal view of transitory pygidium; E & K, dorsal view of holaspid cranidium; F & L, dorsal view of holaspid cranidium.

Magnification: A. x25; B. x26; C. x33; D. x29; E. x19; F. x21; G, H, I, J. x9; L. x6.
Drawings of *H. turneri* (A - F) based on photographs (Pl. 17:1, 2, 12,1 9, 21) and drawings (Fig. 12:H) from Chatterton and Ludvigsen, 1976. Drawings of *H. rasetti* based on photographs (Pl. 2:17, 21) and drawings (Text-fig. 1, 2, 4a and 4b) from Tripp and Evitt, 1981.

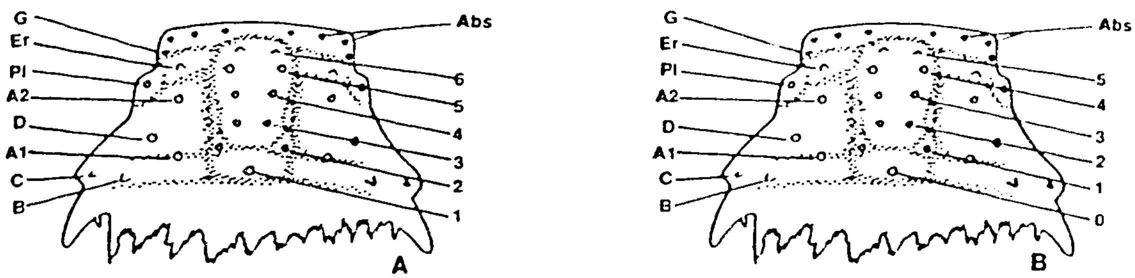


Fig. 4. Cranidial tubercle notation for lichid protaspides A. Cranidial tubercle notation of Chatterton (1971). B. Revised cranidial tubercle notation. Note that revision affects glabellar tubercle notation only, with new numbering reflecting probable glabellar lobe on which lobe is located.

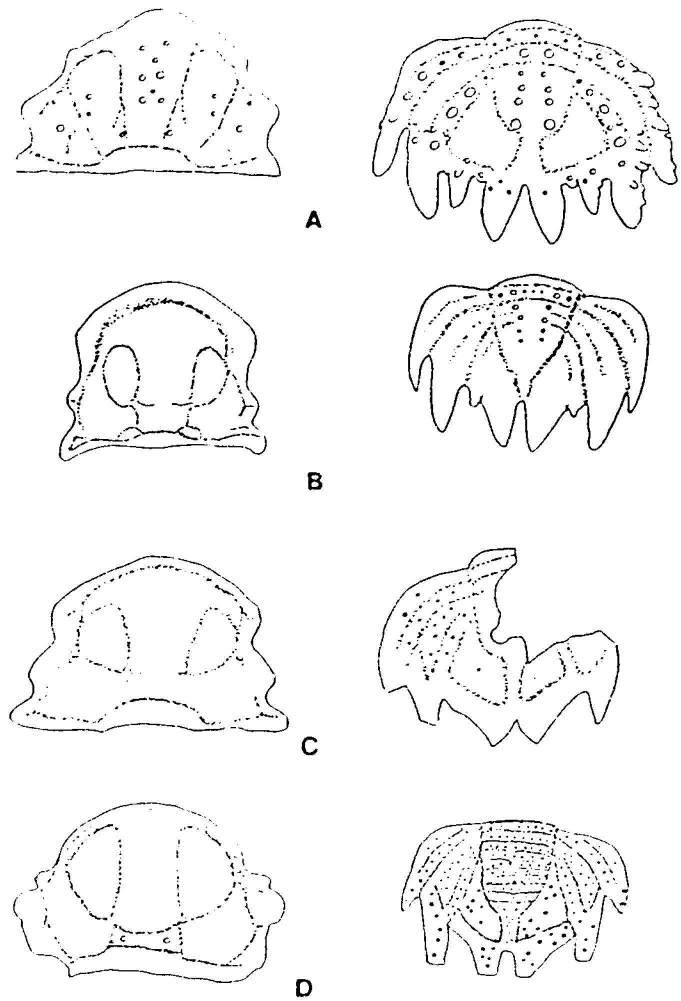


Figure 5. Comparison of morphology of A. *Hemiarges avalanchensis* n.sp., B. *H. diadayma* Rudkin et al., in press; C. *Acanthopyge* (*Lobopyge*) s.l. *pristinus* n.sp.; and D. *A* (*L.*) *hirsuta* (Fletcher, 1850).

Magnification. A. cranidium x6, pygidium x7.9; b. cranidium x6, pygidium x8; C. cranidium and pygidium x8.3; D. cranidium x3, pygidium x2.3.

Drawings of: *Hemiarges avalanchensis*, based on Pl. 36, figs. 4, 11; *H. diadayma*, Ludvigsen, 1978, Fig. 16; *A.* (*L.*) s.l. *pristinus*, Pl. 5, figs. 1, 13; of *A.* (*L.*) *hirsuta* , Thomas and Holloway, 1988, Fig. 301, 302.

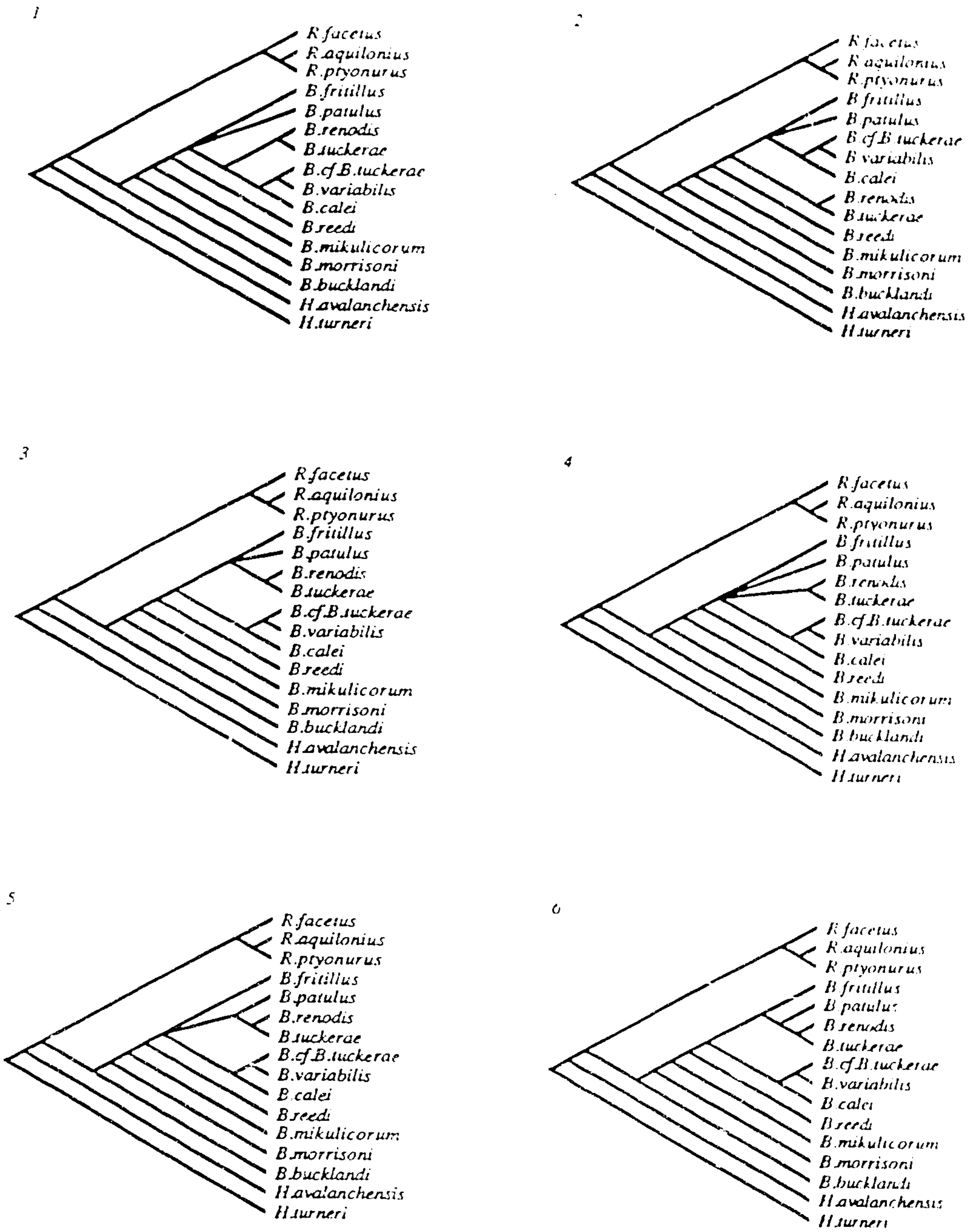


Fig. 6. Six minimum length trees (length 342, C.I. 0.582) generated by PAUP 3.1.1 from data set (Table 6), characters unordered, all reweighted (see text discussion). Rooted by outgroup method, *Hemiarges turneri* selected outgroup.

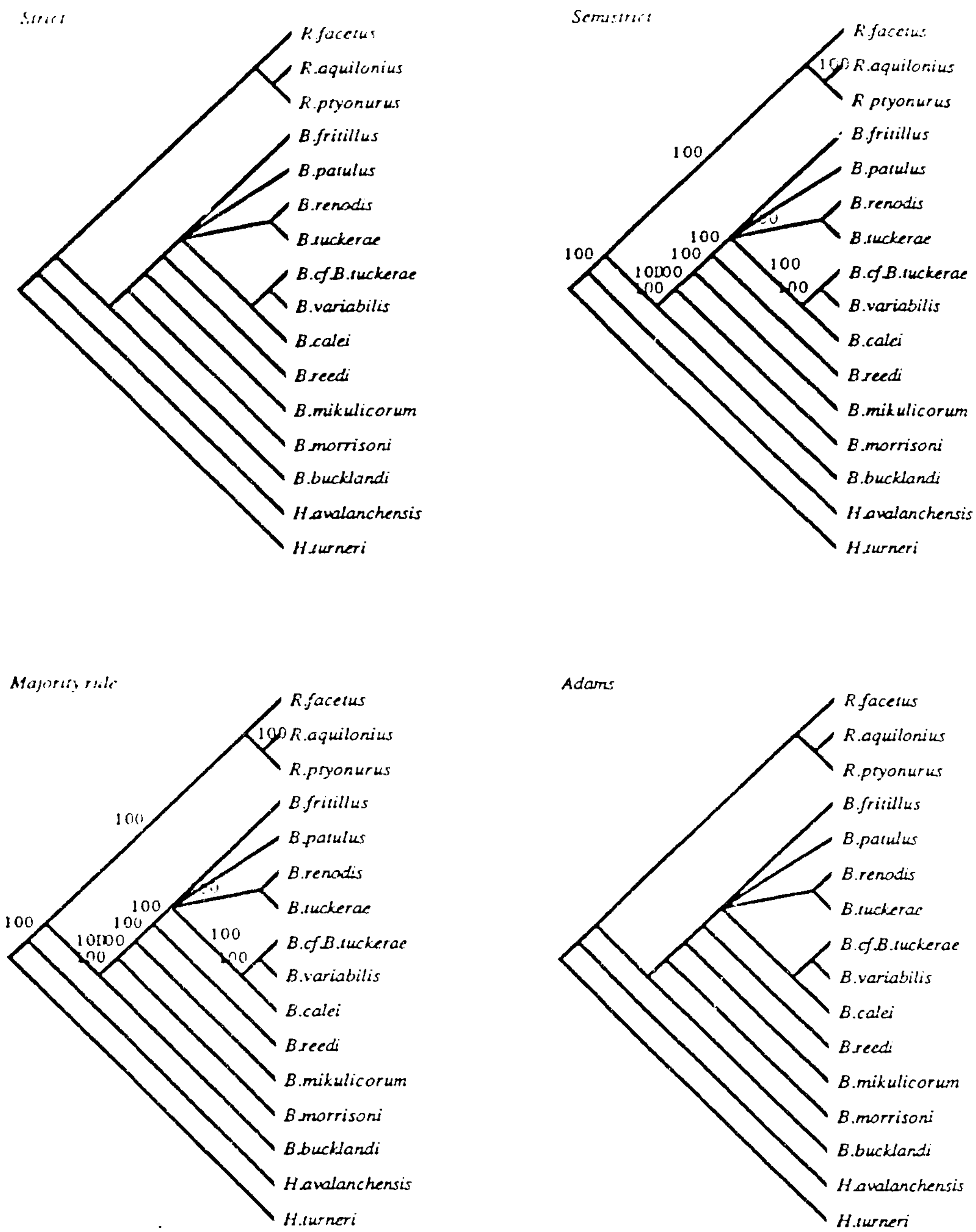


Fig. 7. Consensus trees of 6 minimal length trees from Fig. 6.

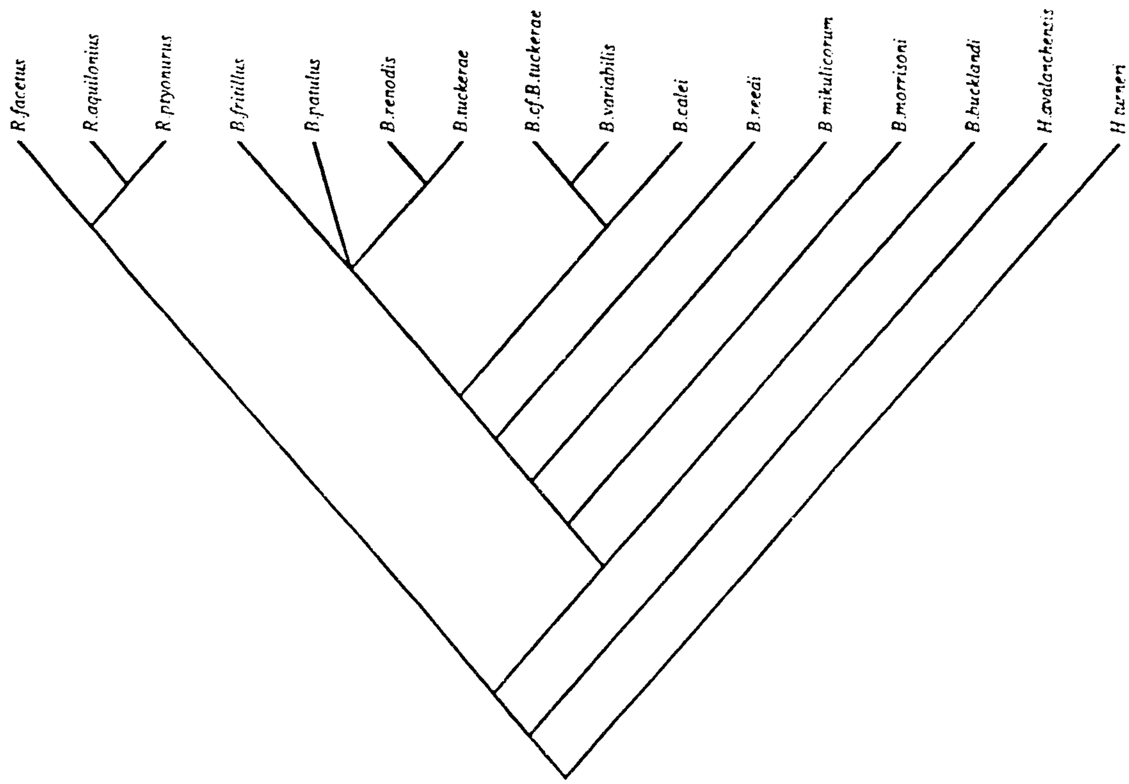


Fig. 8. Cladogram number 4 (of 6 minimal length cladograms, Fig. 6) selected for analysis of character state distribution.

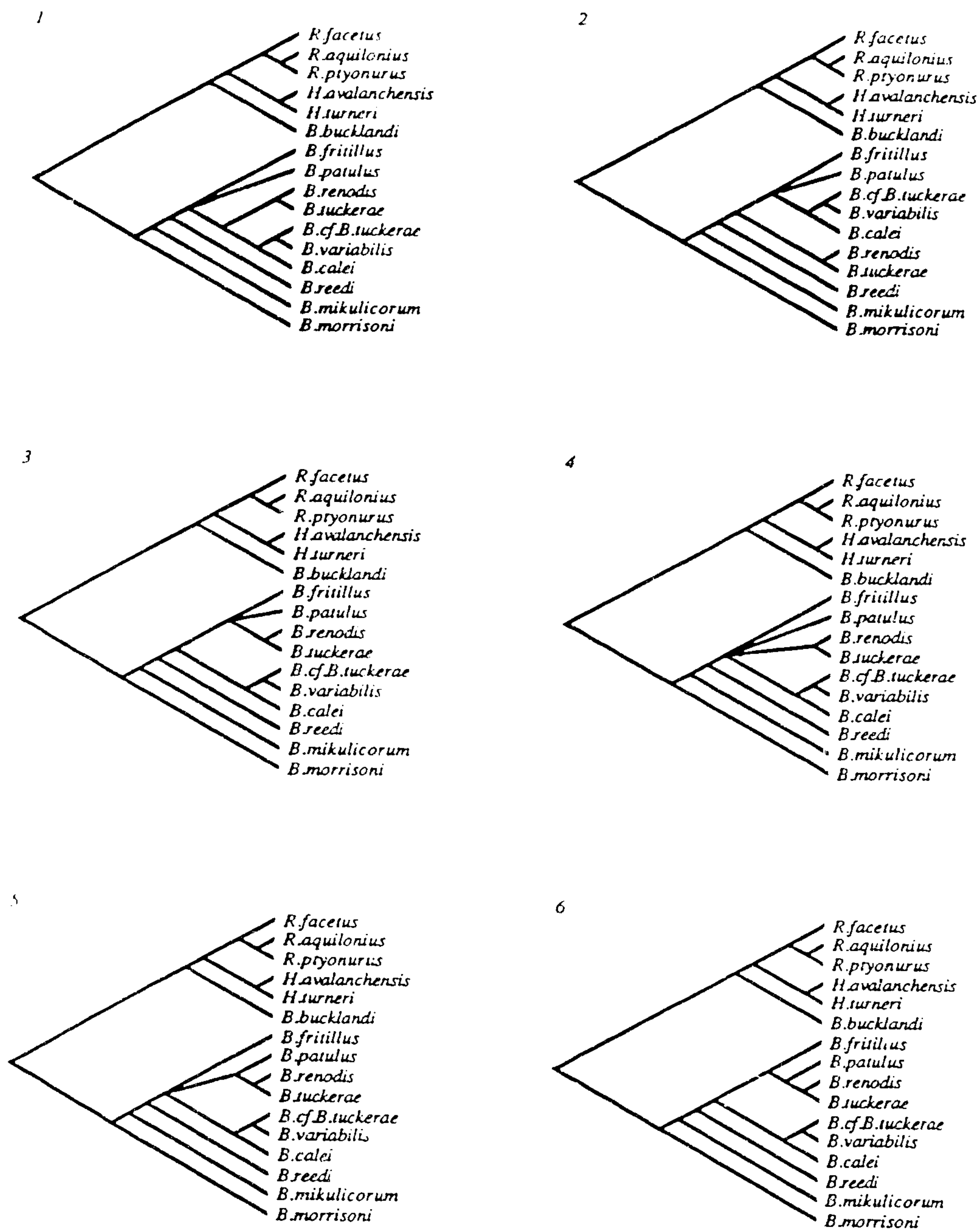
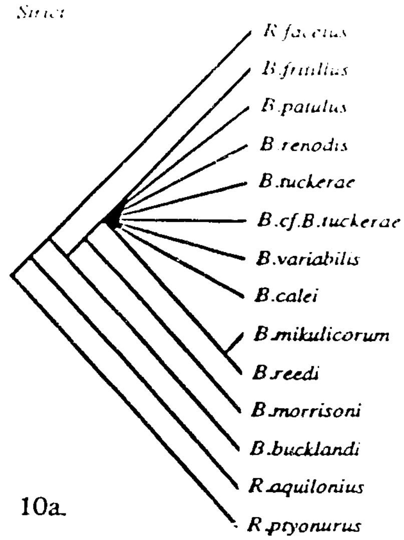
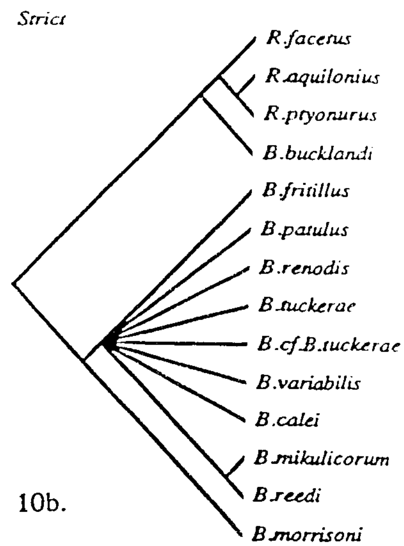


Fig. 9. Six minimum length trees (length 342, C.I. 0.582) generated by PAUP 3.1.1 from data set (Table 6), characters unordered, all reweighted (see text discussion). Midpoint rooting.



10a.



10b.

Fig. 10. Phylogenetic analysis of data set (Table 6)with *Hemiarges turneri* and *H. avalanchensis* removed from data set, characters unordered, reweighted as for cladograms in Fig. 6. Minimal tree length tree length 270, C.I. 0.607, 16 trees.

Fig. 10a. Strict consensus tree, outgroup *Richterarges ptyonurus*.

Fig. 10b. Strict consensus tree, midpoint rooting.

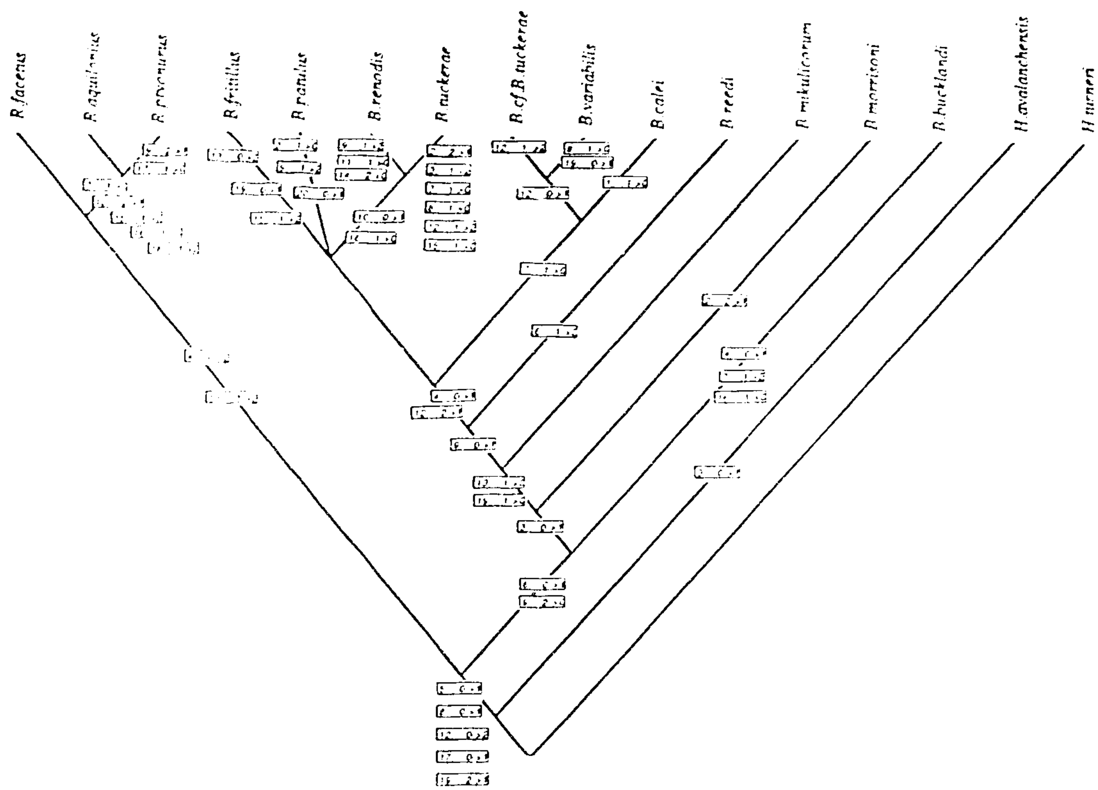


Fig. 11. Distribution of unambiguous characters mapped onto cladogram number 4 (from Fig. 6), using MacClade 3.0.

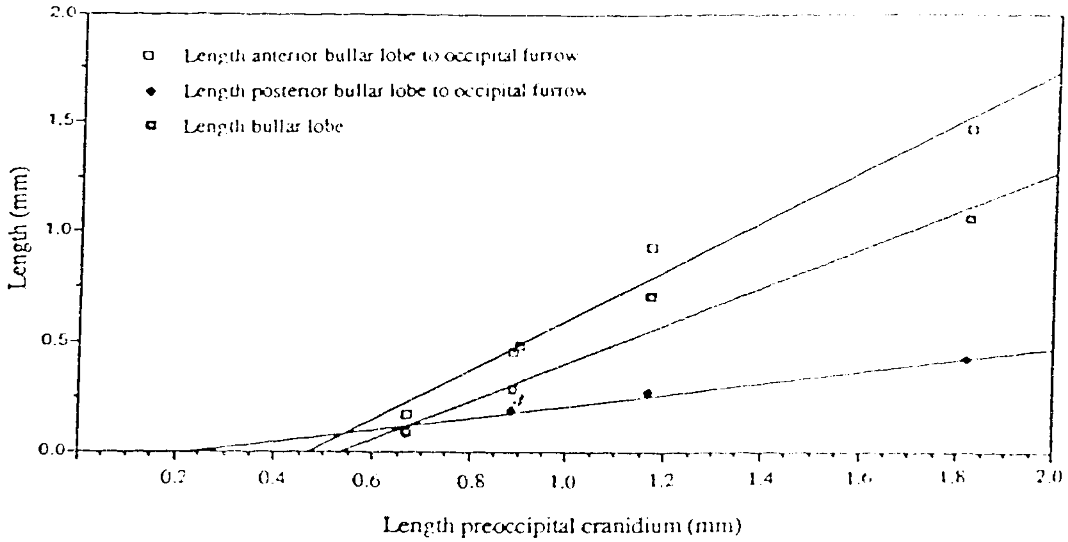


Fig. 12. Growth of bullar lobe in *Dicranogmus*. Bullar lobe appears when preoccipital cranidial length is 0.53 mm.

Plate 1

Figs. 1 - 16.	*Dicranopeltis* n. sp. A from Avalanche Lake sections AV1 588 and 590 m, AV2 256 m, AV4 126 m, AV5 58 - 60 m. Magnification x10 unless otherwise stated.
1, 2.	Dorsal (x25) and ventral (internal) views (x23) of protaspis UA 9757, AV4 126 m.
3, 6.	Dorsal and ventral (internal) views of transitory pygidium UA 9758, mag. x23, AV4 126-127 m.
4.	Dorsal view of meraspid cranidium UA 9759, x32.5, AV 4 126 (T) m.
5.	Dorsal view of meraspid cranidium UA 9760, x31.25, AV4 126 m.
7.	Dorsal view of transitory pygidium UA 9761, AV1 588 m.
8, 9.	Dorsal and anterior views of cranidium UA 9762, AV4 126(T) m.
10 -12.	Posterior-to-dorsal, dorsal, and anterior views of cranidium UA 9763, AV1 588 m.
13, 14.	Ventral and dorsal (internal) views of hypostome UA 9764, AV2 256 m.
15, 16.	Dorsal and ventrolateral views of right librigena UA 9765, AV1 590 m

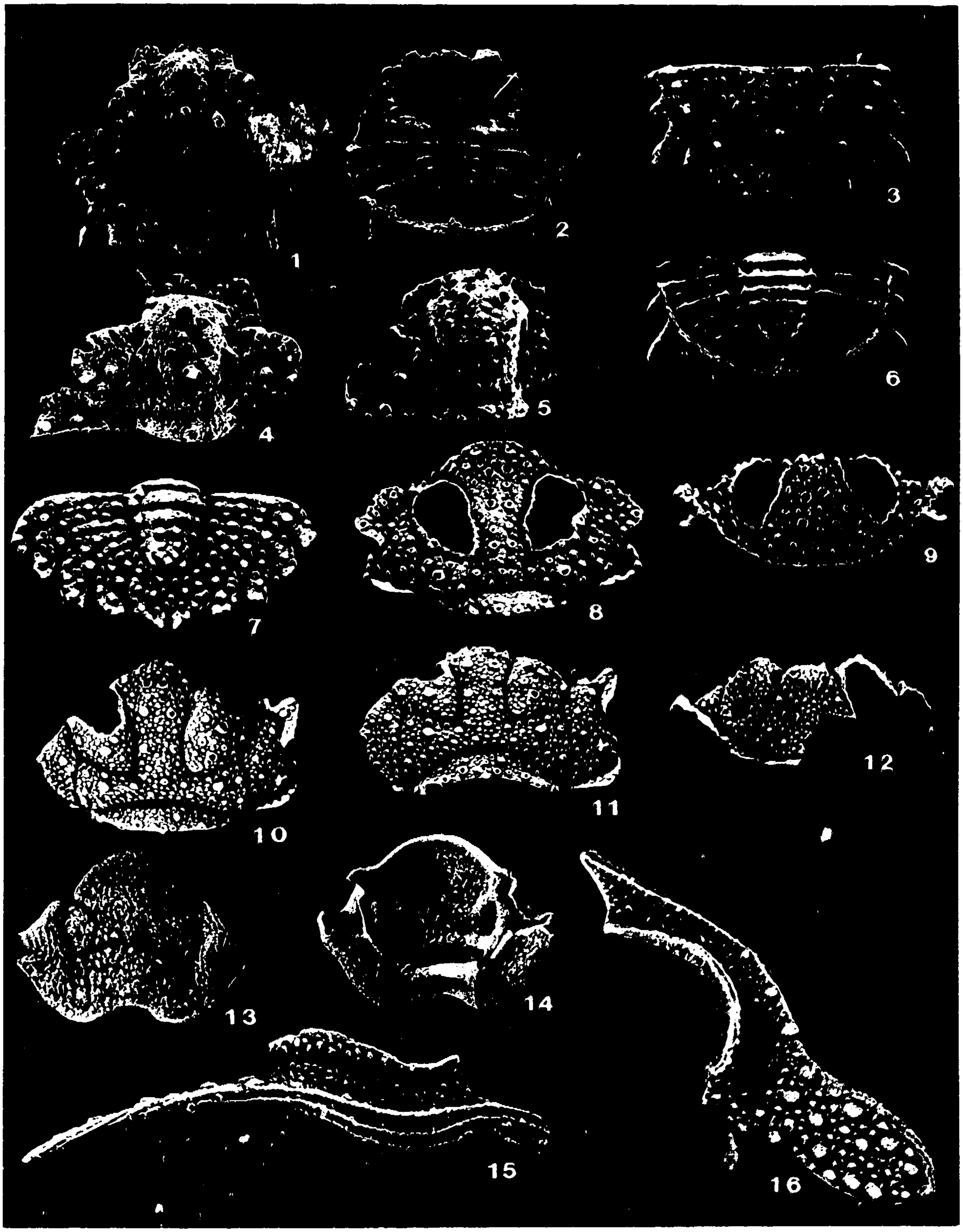

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Plate 2

Figs. 1 - 10.	*Dicranopeltis* n. sp. A from Avalanche Lake sections AV1 583 and 590 m, AV2 256 m, AV4 126 m, AV5 58-60 m. Magnification x10 unless otherwise stated.
1.	*Dicranopeltis*?. Dorsal view of pygidium UA 9766, AV4 126 (T) m, x17.5. (Compare to transitory pygidium,Pl. 1, fig. 7).
2.	Dorsal view of partial cranidium UA 9767, x7.5, AV4 126 m.
3.	Ventral view of hypostome UA 9768, AV2 256 m.
4, 5.	Ventral and dorsal (internal) views of hypostome UA 9769, AV5 58-60 m.
6.	Ventral view of hypostome UA 9770, AV2 256 m.
7, 8.	Oblique-dorsal and dorsal view of left librigena UA 9771, x7.5, AV5 58-60.
9.	Dorsal view of right librigenal fragment UA 9772, AV2 256 m.
10.	Ventral view of right librigena UA 9773, AV1 583 m.

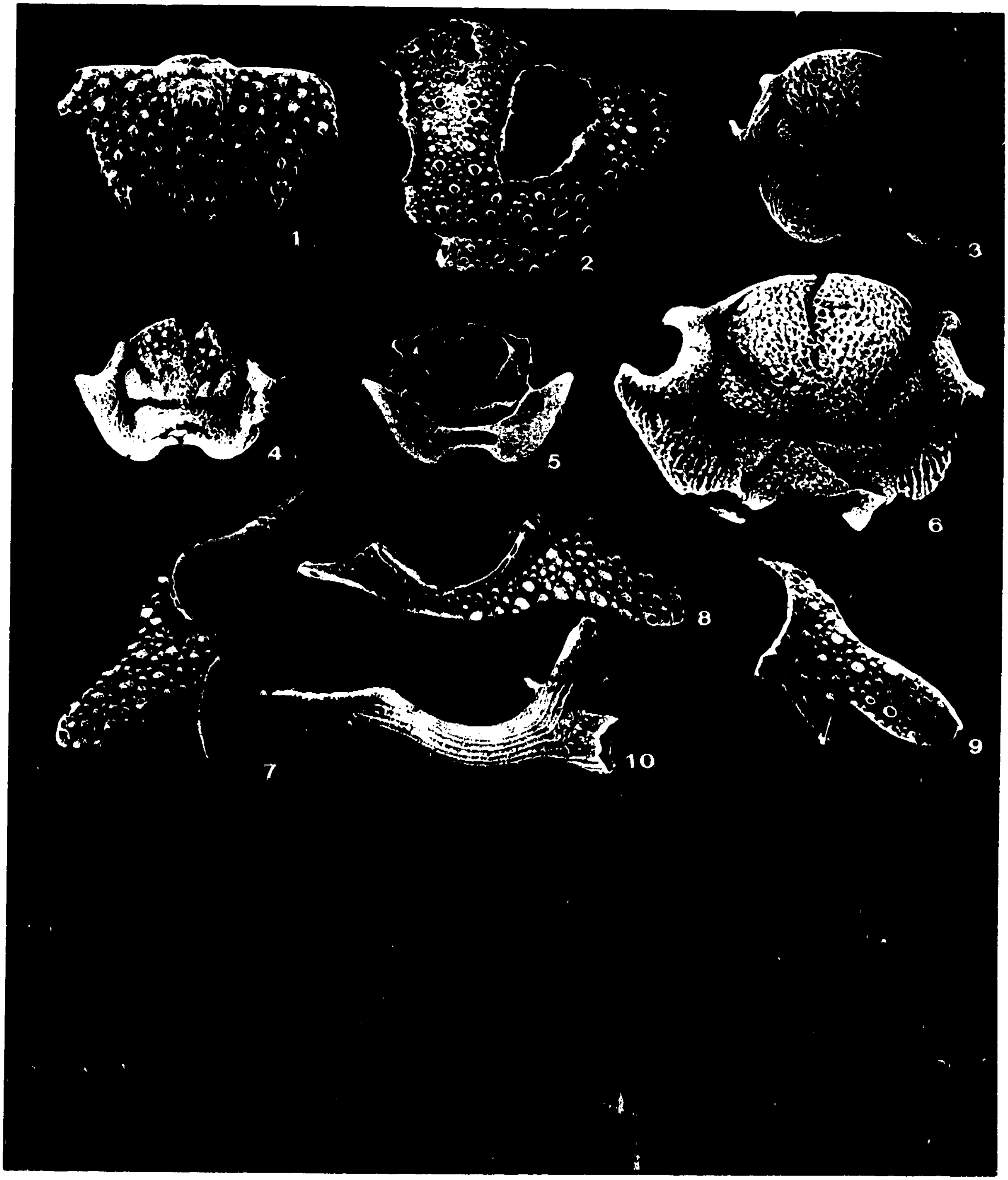
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Plate 3

Figs. 1 - 21.	*Platylichas* (*Rontrippia*) *infimus* n. sp. from Avalanche Lake section AV1 95.5 m (Llandovery). Magnification x10 unless otherwise stated.
1.	Dorsal view of holotype pygidium UA 9774.
2.	Dorsal view of partial pygidium UA 9775, x4.
3, 4, 6.	Dorsal, anterior and left lateral views of cranidium UA 9776, x3.
5.	Dorsal view of fragment of cranidium UA 9777.
7.	Ventral view of hypostome UA 9778, x5.
8.	External view of left librigena UA 9779.
9.	Dorsal view of left librigena UA 9780.
10.	Dorsal view of partial cranidium UA 9781.
11.	Dorsal view of partial cranidium UA 9782.
12.	Dorsal view of partial cranidium UA 9783.
13.	Dorsal view of fragment of thoracic segment UA 9784.
14.	Internal view of right librigena UA 9785.
15.	Lateral view of left librigena UA 9786.
16.	Ventral view of hypostome UA 9787.
17.	Dorsal view of protaspis UA 9788, x38.75
18.	Lateral view of left librigena UA 9789.
19.	Lateral view of right librigena UA 9790.
20.	Dorsal view of protaspis UA 9791, x37.5
21.	Internal view of protaspis UA 9792, x38.75

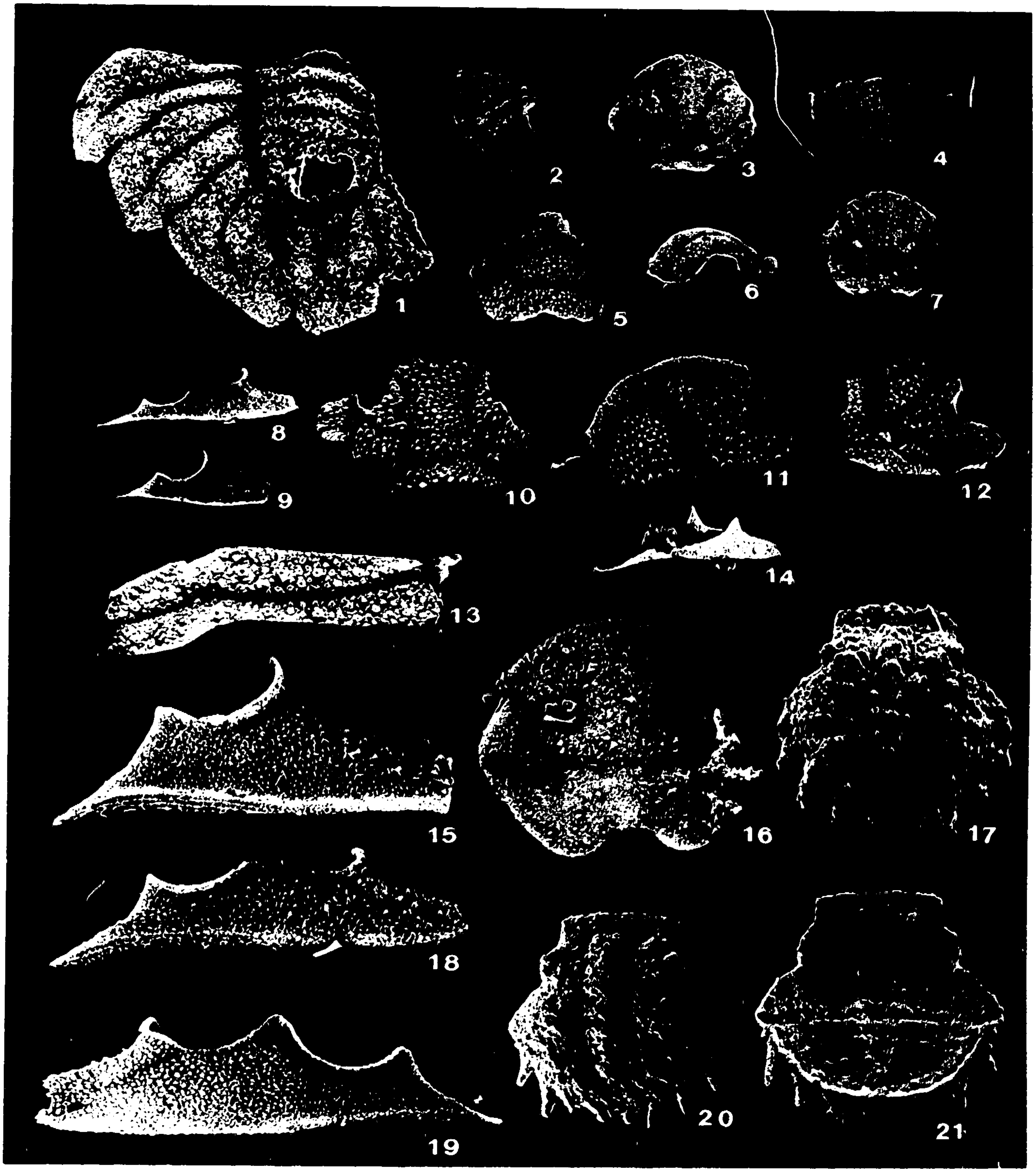
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Plate 4

Figs. 1 - 3. *Acanthopyge (Lobopyge)* n.sp. A from Avalanche Lake section AV2 274 - 279 m.

1. Dorsal view of pygidium UA 9793, x19.
2. Dorsal view of partial cranidium UA 9794, x20.
3. Dorsal view of partial cranidium UA 9795, x20.

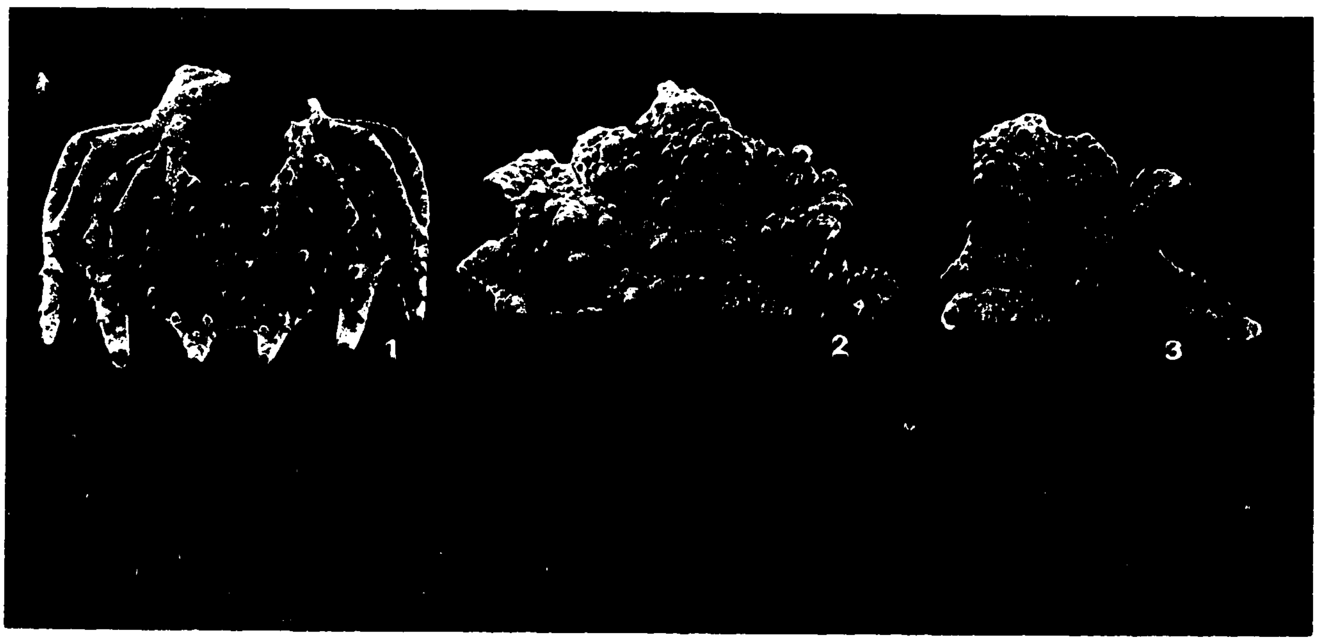
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Plate 5

Figs. 1 - 27.	*Acanthopyge* (*Lobopyge* s.l.) *pristinus* n. sp. from Avalanche Lake section AV 4B 111 m. (Latest Ordovician, post faunal turnover). Magnification x10, unless otherwise stated.
1, 3, 4, 7 11.	Dorsal, anterior, lateral, posterior and internal views of holotype cranidium UA 9796.
2.	Dorsal view of right librigena UA 9797.
5, 6, 10.	Dorsal, lateral and posterior views of cranidium UA 9798.
8, 9.	Dorsal and posterior views of cranidium UA 9799.
12.	External view of right librigena UA 9800.
13.	Dorsal view of partial pygidium.UA 9801.
14, 15.	Dorsal and ventral (internal) views of partial cranidium UA 9802.
16.	External view of right librigena UA 9803.
17.	Dorsal view of partial pygidium UA 9804.
18, 19.	Ventral and dorsal (internal) views of hypostome with attached rostral plate UA 9805.
20.	External view of right librigena UA 9806.
21.	Internal view of right librigena UA 9807.
22.	Ventral view of hypostome UA 9808.
23.	Ventral view of hypostome UA 9809.
24.	Ventral view of hypostome UA 9810
25.	External view of left librigena UA 9811.
26.	Dorsal (internal) view of hypostome UA 9812.
27.	Dorsal (internal) view of hypostome UA 9813.

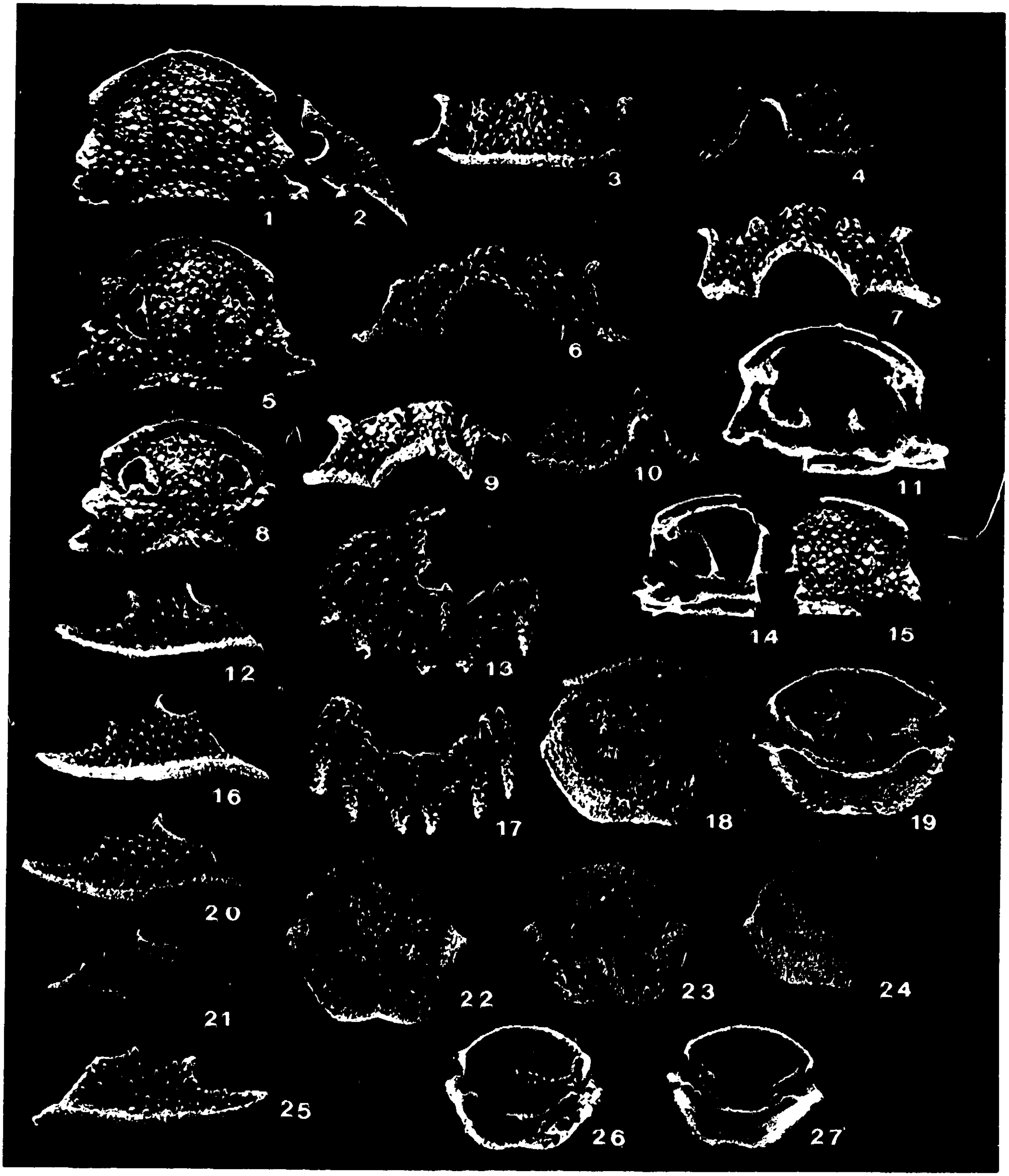
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Plate 6

Figs. 1 - 3. Species of *Acanthopyge* (*Lobopyge*) from Much Wenlock Limestone Formation, Dudley, Britain (Wenlock). Specimens from British Museum.

1. Dorsal view of *A*. (*L.*)*hirsuta* (Fletcher 1850) BM 59001, x2.9. (British Museum label *Lichas hirsutus* (Fletcher, 1850). Figured by Reed (1903) Pl. 1, fig. 4; and by Thomas (1981) Pl. 20, fig. 8.
2. Dorsal view of *A*. (*L.*) *hirsuta* (Fletcher 1850) I 1485a, x5.7. (British Museum label *Trochurus hirsutus tuberculatus* (Reed). Figured by Thomas (1981) Pl 20, fig. 5. (Collection number given as BM It15444)
3. Dorsal view of *A*. (*L.*) *hirsuta* (Fletcher, 1850) I 1485, x5.2 (British Museum label *Lichas hirsutus* Fletcher var. *tuberculatus* Reed cf. *hirsutus tuberculatus*) Figured in Thomas (1981), Pl. 20, fig.6. (Collection number given by Thomas as BM It15445)

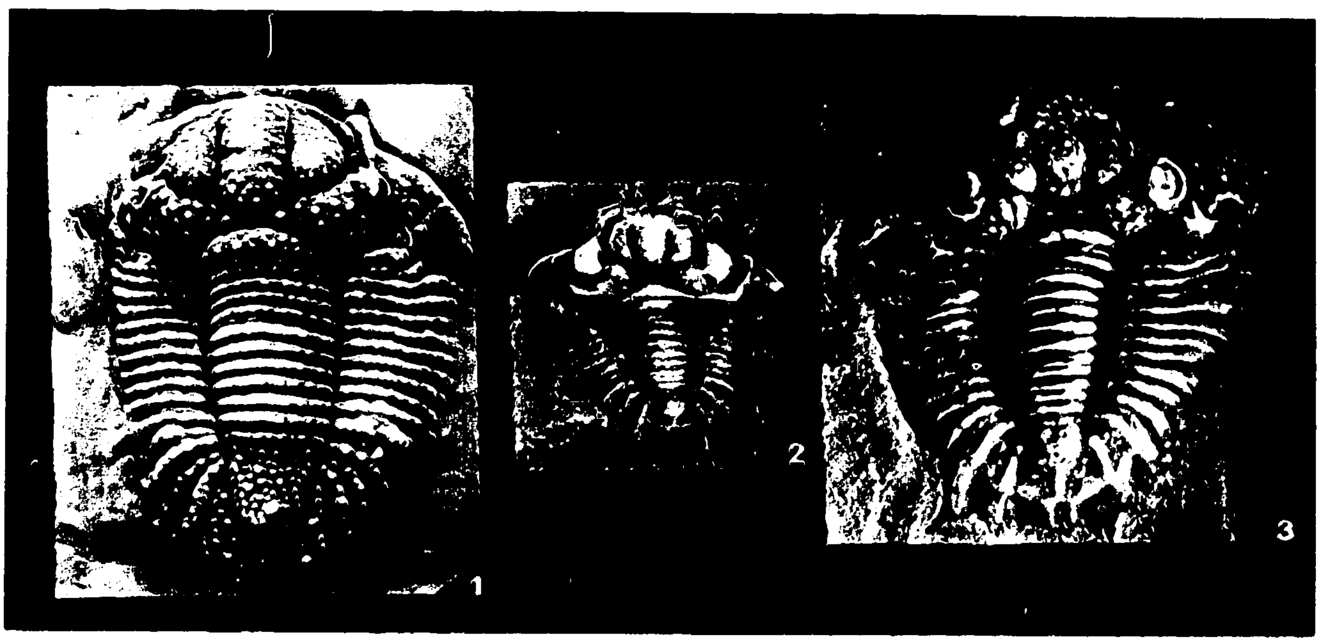
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Plate 7

Figs. 1 - 15.	*Borealarges fritillus* n. sp. from Avalanche Lake sections AV1 583, 590 and 596 m, AV2 256 m. *B. fritillus* ? from AV5 58 - 50 m. Magnification x10 unless otherwise stated.
1, 2.	Dorsal and lateral views of cranidium UA 9814, AV1 590 m.
3.	Dorsal view of cranidium UA 9815, AV1 590.
4, 8, 9.	Dorsal, internal and posterior views of holotype pygidium UA 9816, AV2 256 m, x7.5.
5, 6, 7.	Dorsal, lateral and posterior views of pygidium UA 9817, AV1 583.1 m, x7.5.
10.	Dorsal view of pygidium UA 9818, AV2 256 m.
11 - 13.	Dorsal, left lateral and posterior views UA 9819, AV2 274 - 279, x7.5.
14, 15.	*B. fritillus*?. Dorsal and internal views of pygidium UA 9820 AV5 58 - 60, x7.5.

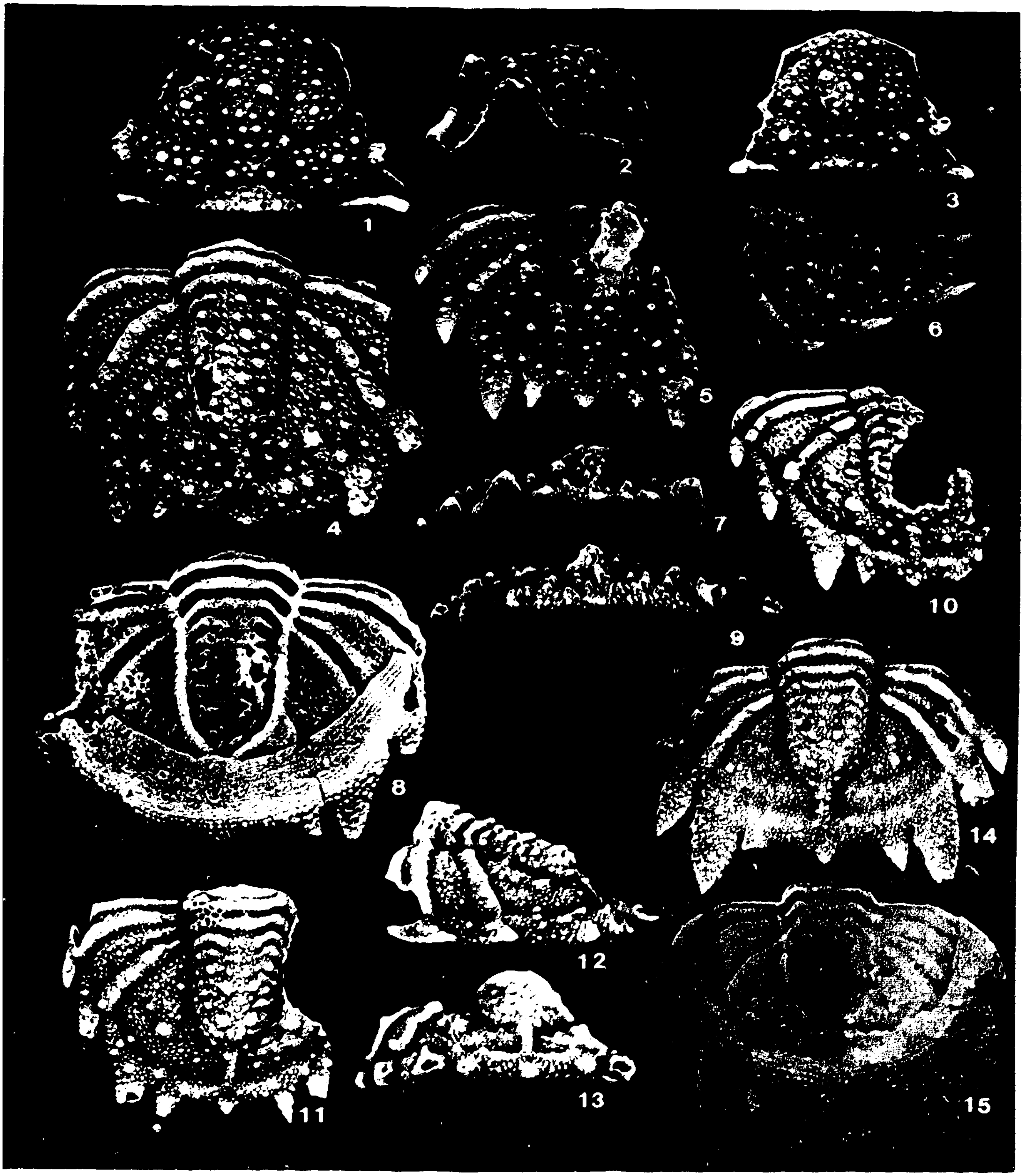
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Plate 8

Figs. 1 - 20.	*Borealarges patulus* n. sp. from Avalanche Lake sections AV2 256 and 274-279 m, AV4 234, 234-238, 240, 245 and 260 m. Magnification x10 unless otherwise indicated.
1.	Dorsal view of holotype pygidium UA 9821 AV4 240 m.
2.	Dorsal view of pygidium UA 9822, AV2 274 - 279 m.
3.	Dorsal view of pygidium UA 9823, AV4 234 - 237 m..
4.	Dorsal view of pygidium UA 9824, AV4 240 m, x7.5.
5.	Dorsal view of pygidium UA 9825, AV4 240 m.
6, 10, 14, 17.	Internal, dorsal, left lateral and posterior views of pygidium UA 9826, AV2 256 m.
7.	Dorsal view of pygidium UA 9827, AV4 238 m.
8.	Dorsal view of pygidium UA 9828, AV4 234 - 238 m.
9.	Dorsal view of pygidium UA 9829, AV2 256 m, x5.
11.	Dorsal view of pygidium UA 9830, AV2 256 m.
12.	Internal view of transitory pygidium UA 9831, AV4 238 m.
13.	Dorsal view of transitory pygidium 9832, AV4 240.
15, 16.	Dorsal and ventral (internal) views of partial pygidium UA 9833 AV4 260 m, x7.5.
18.	Dorsal view of partial pygidium UA 9834, AV4 234 (T) m.
19	Dorsal view of pygidium UA 9835, AV4 245 m, x7.5.
20.	Dorsal view of partial pygidium UA 9836, AV4 240 m.

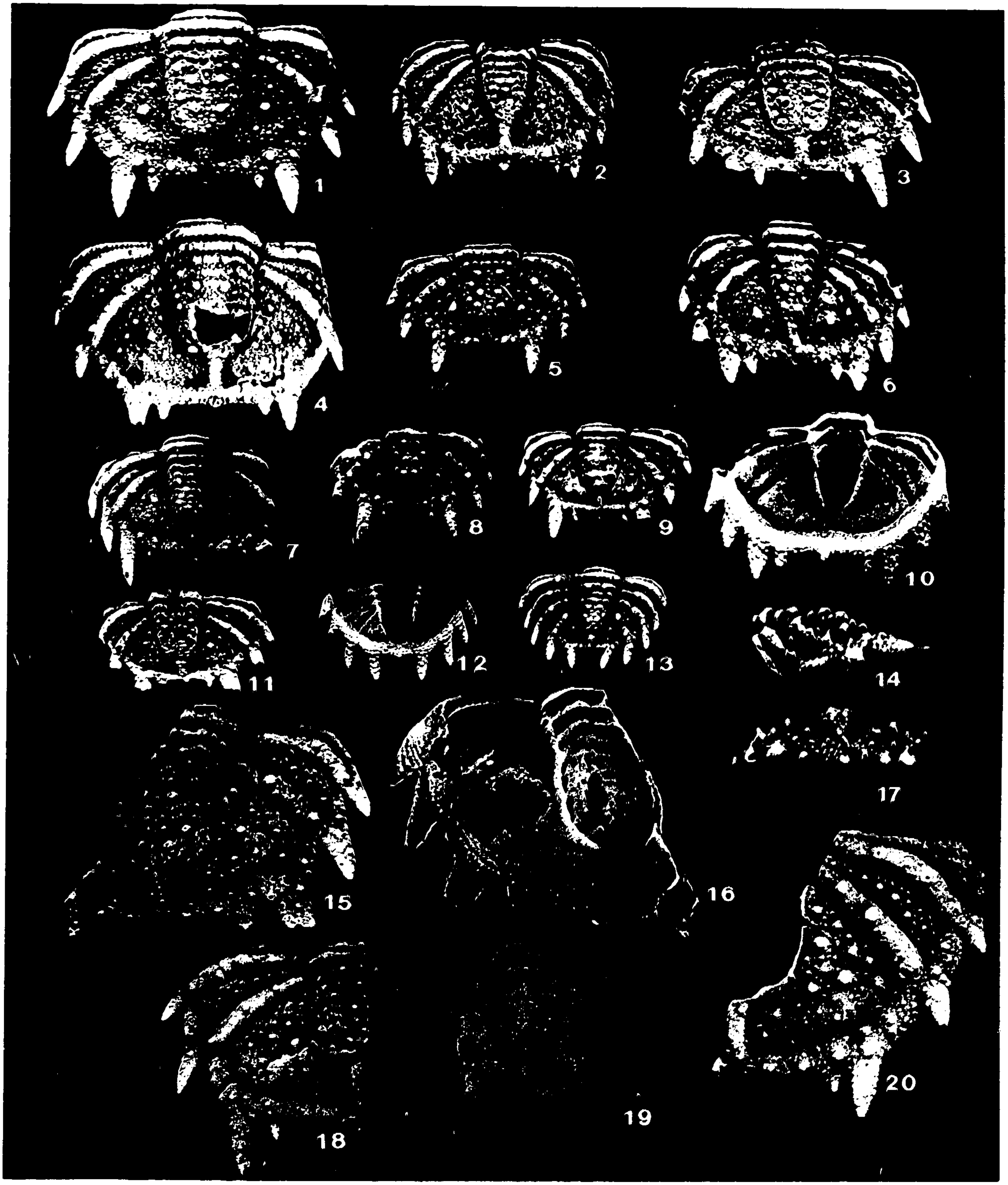
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Plate 9

Figs. 1 - 20.	*Borealarges patulus* n.sp. from Avalanche Lake sections AV4 231, 234, 238, and 240 m. Magnification x10 unless otherwise stated.
1 - 3.	Dorsal, anterior and internal views of cranidium UA 9837, AV4 231 (T) m.
4 - 7.	Dorsal, anterior to dorsal, posterior and left lateral views of cranidium UA 9838, AV4 238 m.
8 - 11.	Dorsal, posterior, left lateral and internal views of cranidium UA 9839, AV4 238 m.
12.	Dorsal view of cranidium UA 9840, AV4 240 m.
13.	Dorsal view of cranidium UA 9841, AV4 240 m.
14, 15.	Dorsal and left lateral views of cranidium UA 9842 AV4 240 m.
16 - 20.	Posterior-to-dorsal, internal, dorsal, anterior and posterior views of cranidium UA 9843, AV4 238 m.

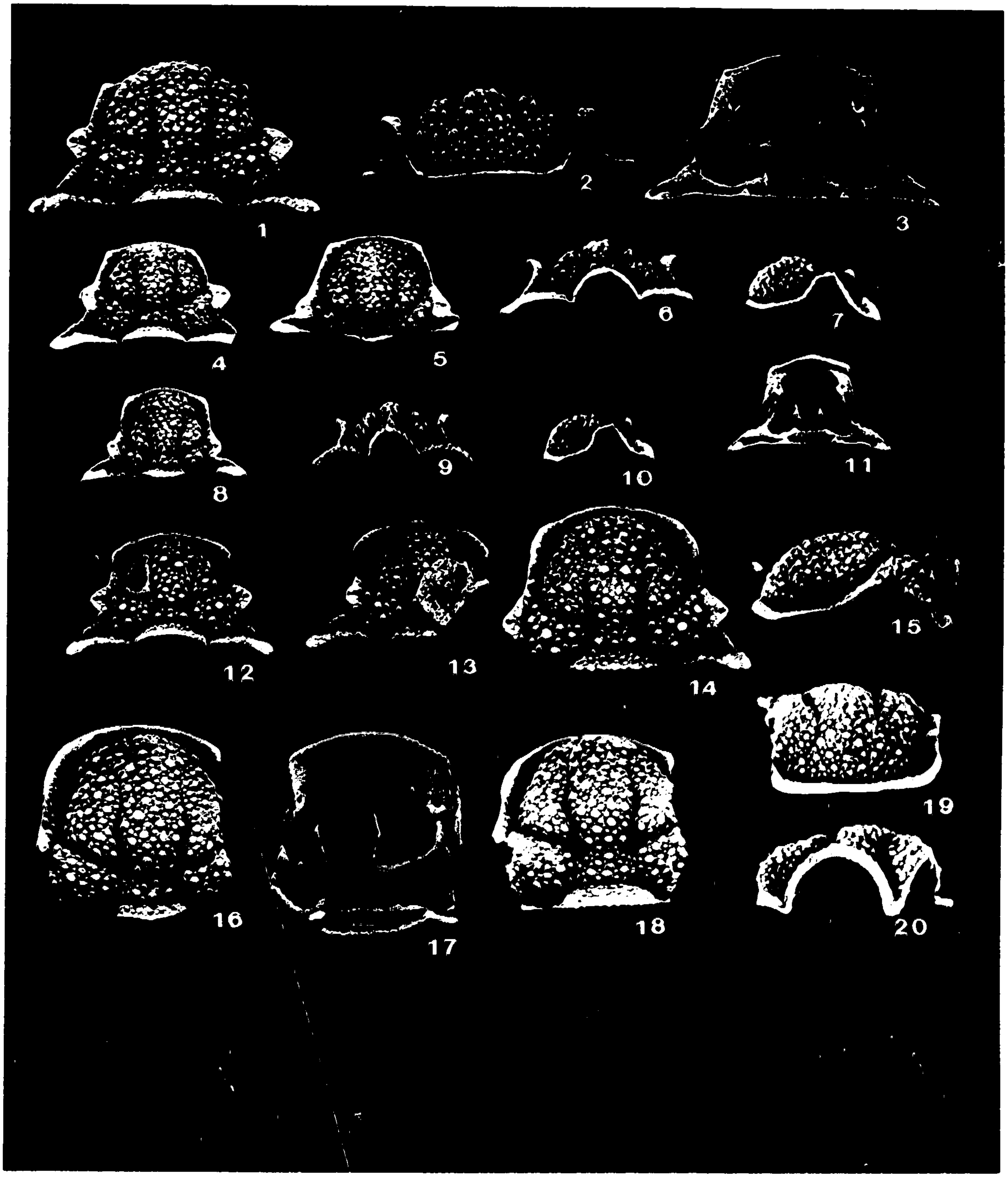
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Plate 10

Figs 1 - 15.	*Borealarges renodis* n.sp. from Avalanche Lake sections AV1 590 m, AV2 256, 255 - 260 and 274 - 279 m, AV4 126 (T) m. Magnification x10 unless otherwise stated.
1, 2, 3.	Dorsal, posterior and internal views of holotype pygidium UA 9844, AV4 126 (T) m.
4.	Dorsal view of pygidium UA 9845, AV2 274 - 279 m.
5.	Dorsal view of pygidium UA 9846, AV1 590 m.
6.	Dorsal view of pygidium UA 9847, AV4 126 (T) m.
7.	Dorsal view of pygidium UA 9848, AV4 126 (T) m.
8.	Dorsal view of pygidium UA 9849, AV2 274 - 279 m.
9.	Dorsal view of partial pygidium UA 9850 AV 2 274 - 279 m.
10, 11.	Dorsal and anterior views of partial pygidium UA 9851, AV2 274 - 279 m.
12.	Dorsal view of partial pygidium UA 9852 AV2 255 - 260 m.
13.	Dorsal view of pygidium UA 9853, AV4 126 (T) m.
14.	Dorsal view of transitory pygidium UA 9854, AV4 126 (T) m, x19.
15.	Dorsal view of transitory pygidium UA 9855, AV4 126 (T) m, x20.

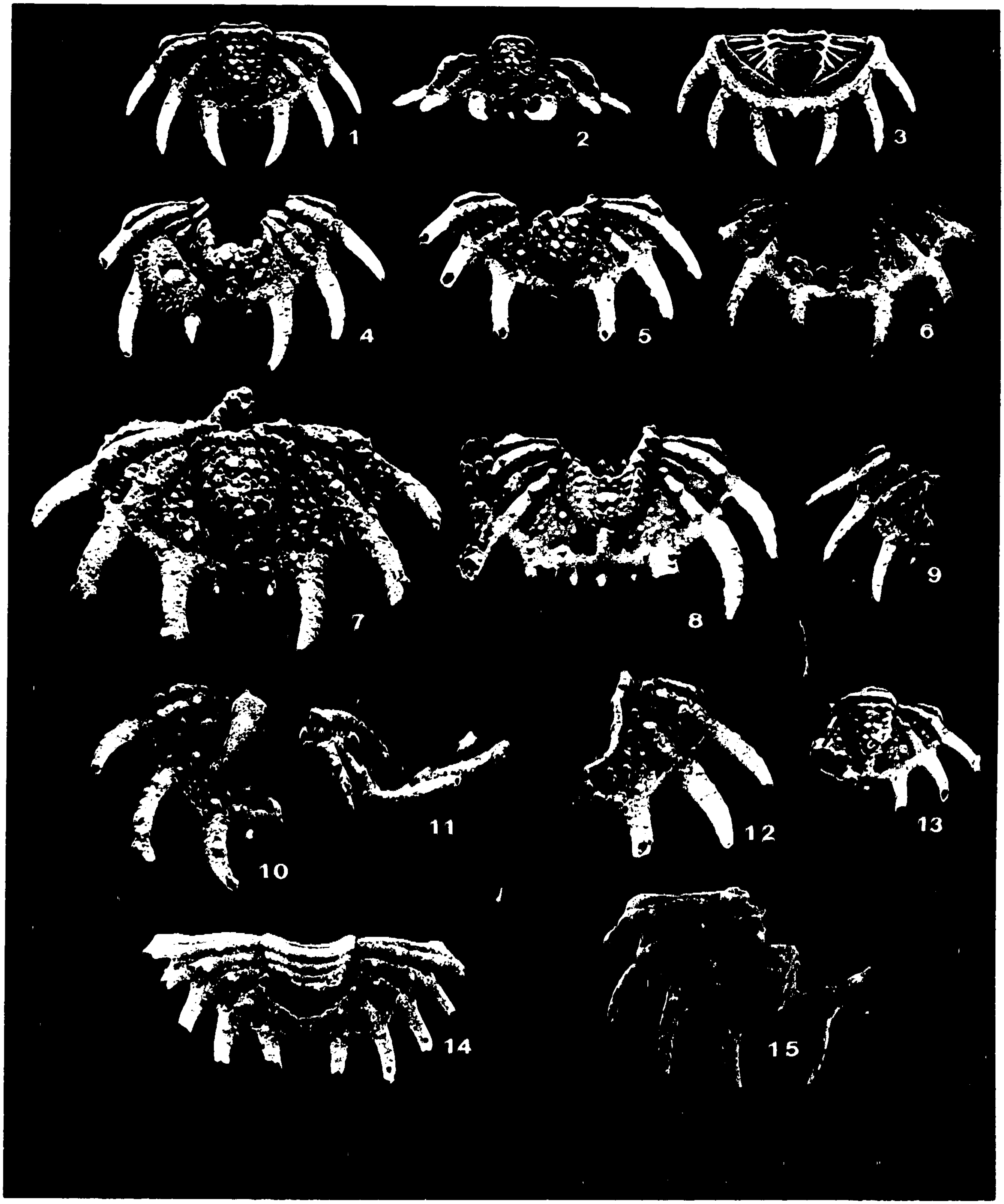
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Plate 11

Figs. 1 - 24.	*Borealarges renodis* n.sp. from Avalanche Lake sections AV1 590 m, AV2 256 and 274 - 279 m, AV4 126 m, AV5 58 - 60 m. Magnification x10 unless otherwise stated.
1 - 6.	Dorsal, posterior-to-dorsal, internal, anterior, right lateral and posterior view of cranidium UA 9856, AV2 256 m, x7.5.
7, 8, 11.	Dorsal, anterior, and right lateral views of cranidium UA 9857, AV4 126 (T) m, x15.
9, 10, 12 - 14.	Posterior-to-dorsal, dorsal, left lateral, anterior and internal views of cranidium UA 9984, AV2 274 - 279 m.
15, 16.	Dorsal and right lateral views of cranidium UA 9985 AV1 590 m.
17, 18.	Dorsal and right lateral views of cranidium UA 9986, AV1 590 m.
19, 20.	Dorsal and left lateral views of cranidium UA 99857 AV1 590 m.
21.	External view of left librigena UA 9988. AV4 126 (T) m.
22 - 24.	Dorsal, anterior and lateral views of librigena UA 9989, AV5 58 - 50 m.

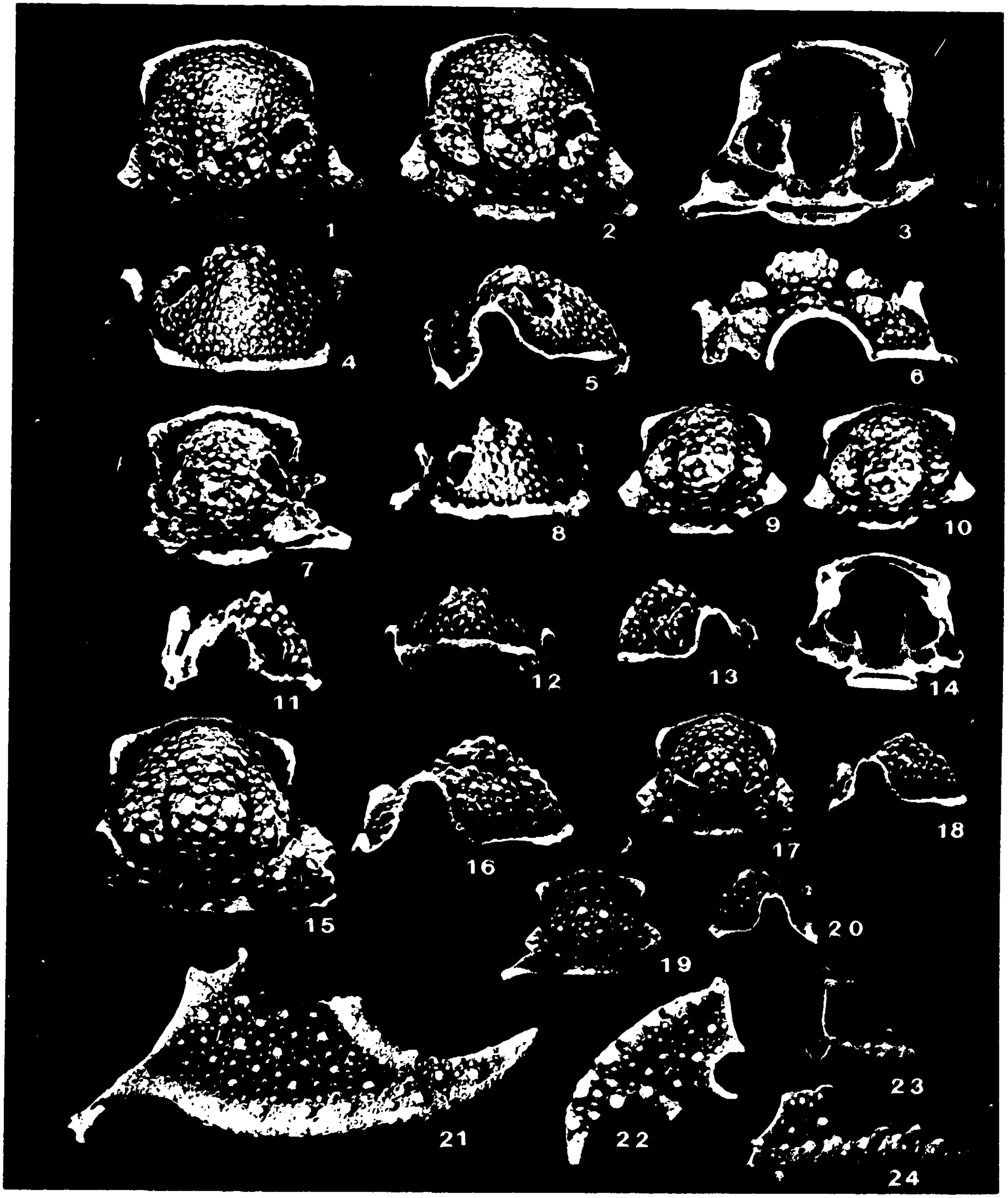
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Plate 12

Figs. 1 - 12.	*Borealarges renodis* n.sp. from Avalanche Lake sections AV1 588 m, AV2 274 - 279 m, AV4 126 (T) m, AV5 58 - 60 m. Magnification x10 unless otherwise stated.
1 - 5.	Dorsal, anterior-to-dorsal, right lateral, posterior, and anterior views of cranidium UA 9990 AV4 126 (T) m, x7.5.
6 - 10.	Anterior, posterior -to-dorsal, dorsal, right lateral and posterior views of cranidium UA 9991 AV1 588 m.
11.	External view of right librigena UA 9992, AV4 126 (T) m.
12.	External view of right librigena UA 9993, AV2 274 - 279 m.

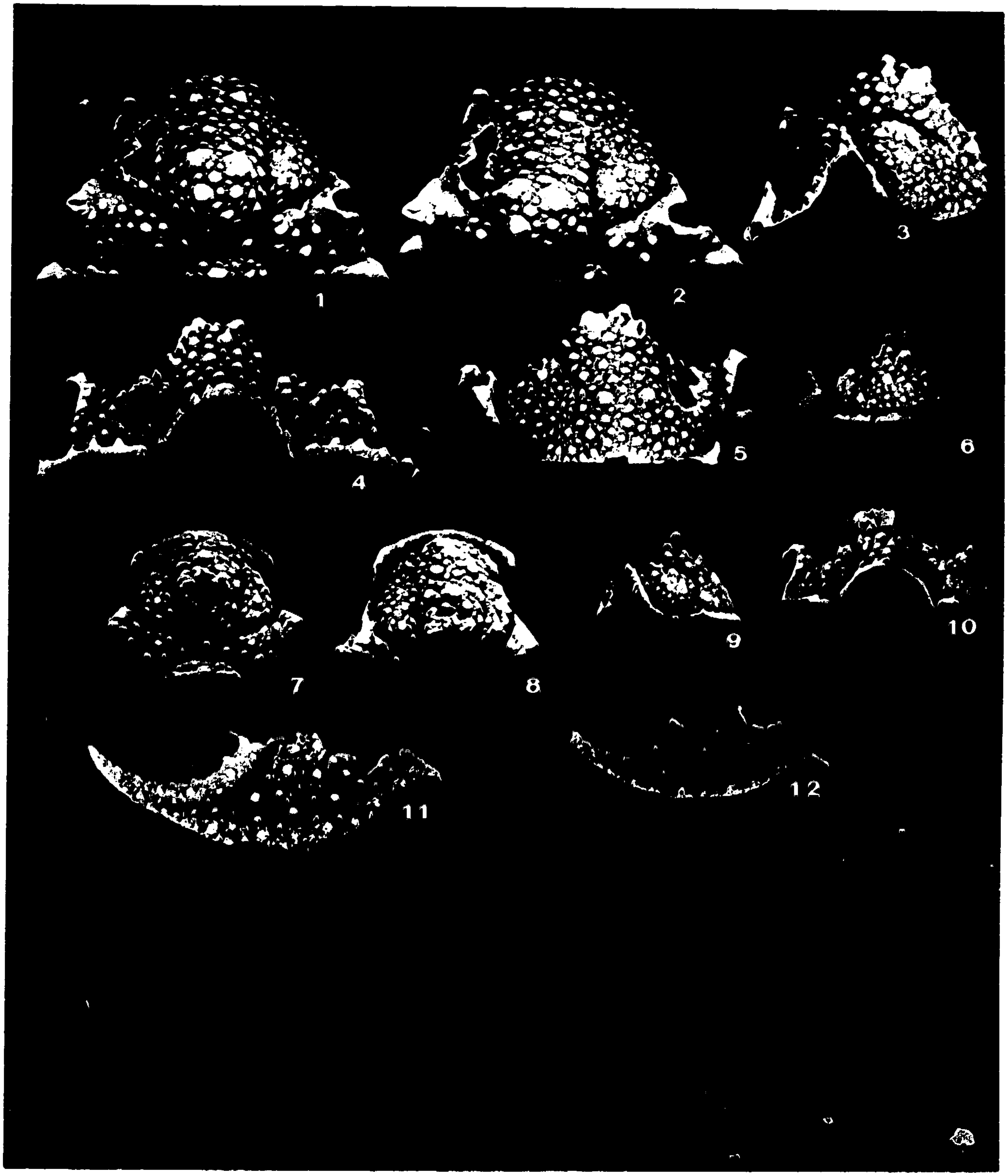
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Plate 13

Figs. 1 - 22.	*Borealarges tuckerae* Adrain, in press, from Avalanche Lake sections AV1 586 m, AV2 256 and 255 - 260 m, AV4 240 m, AV5 57 and 58 - 60 m; and from the Delorme range, section DR 91.44 m. Magnification x10 unless otherwise stated.
1 - 6.	Posterior-to-dorsal, dorsal, anterior-to-dorsal, anterior, posterior and right lateral views of cranidium UA 9994, AV5 58 - 60 m.
7 - 9.	Posterior, dorsal and right lateral views of cranidium UA 9995, AV2 256 m, x7.5.
10 - 13.	Dorsal, anterior, left lateral, posterior views of cranidium UA 9996 DR 91.44 m.
14, 15, 17, 18.	External view, detail of tubercle pattern (x15), internal and ventro-lateral views of left librigena UA 9997 AV5 58 - 60 m.
16, 19.	Detail of tubercle pattern (x7.5) and external view (x5) of left librigena UA 9998, AV5 58 - 60 m.
20 - 22.	Dorsal, posterior and left lateral view of pygidium UA 9999, AV2 255 - 260 m, x7.5.

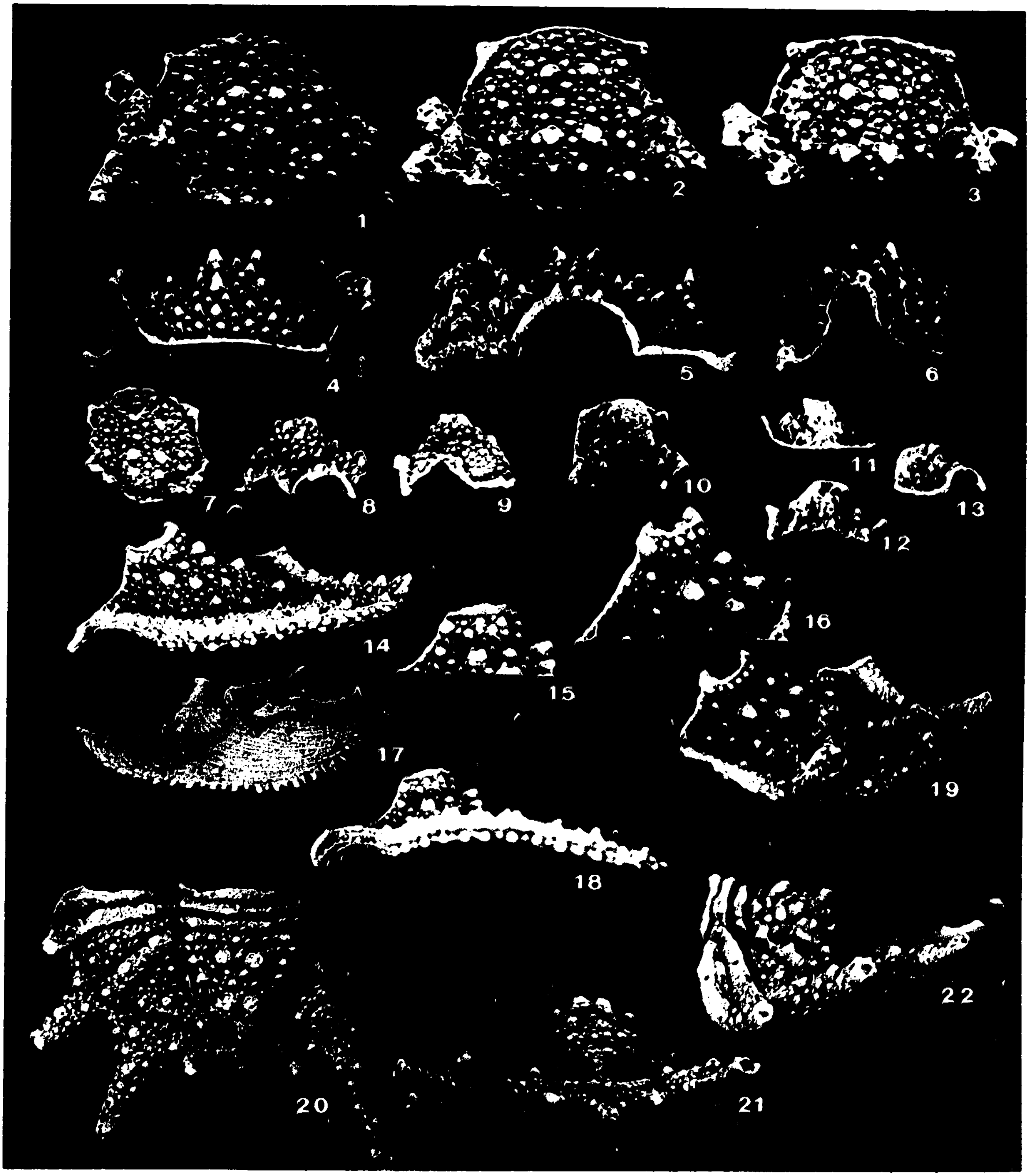
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Plate 14

Figs. 1 - 10.	*Borealarges tuckerae* Adrain, in press from Avalanche Lake sections AV1 586 m, AV4 260 m, AV5 57 m; and from the Delorme Range, DR 91.44 m. Magnification x10, unless otherwise stated.
1.	Dorsal view of pygidium UA 100000, AV5 57 m.
2 - 5.	Dorsal, left lateral, internal and posterior views of transitory pygidium UA 10001, AV1 586 m.
6, 8.	Dorsal and left lateral views of pygidium UA 10002, DR 91.44 m.
7.	Dorsal view of partial pygidium UA 10003, AV4 260 m.
9, 10.	Dorsal and right lateral views of partial pygidium UA 10004, DR 91.44 m.

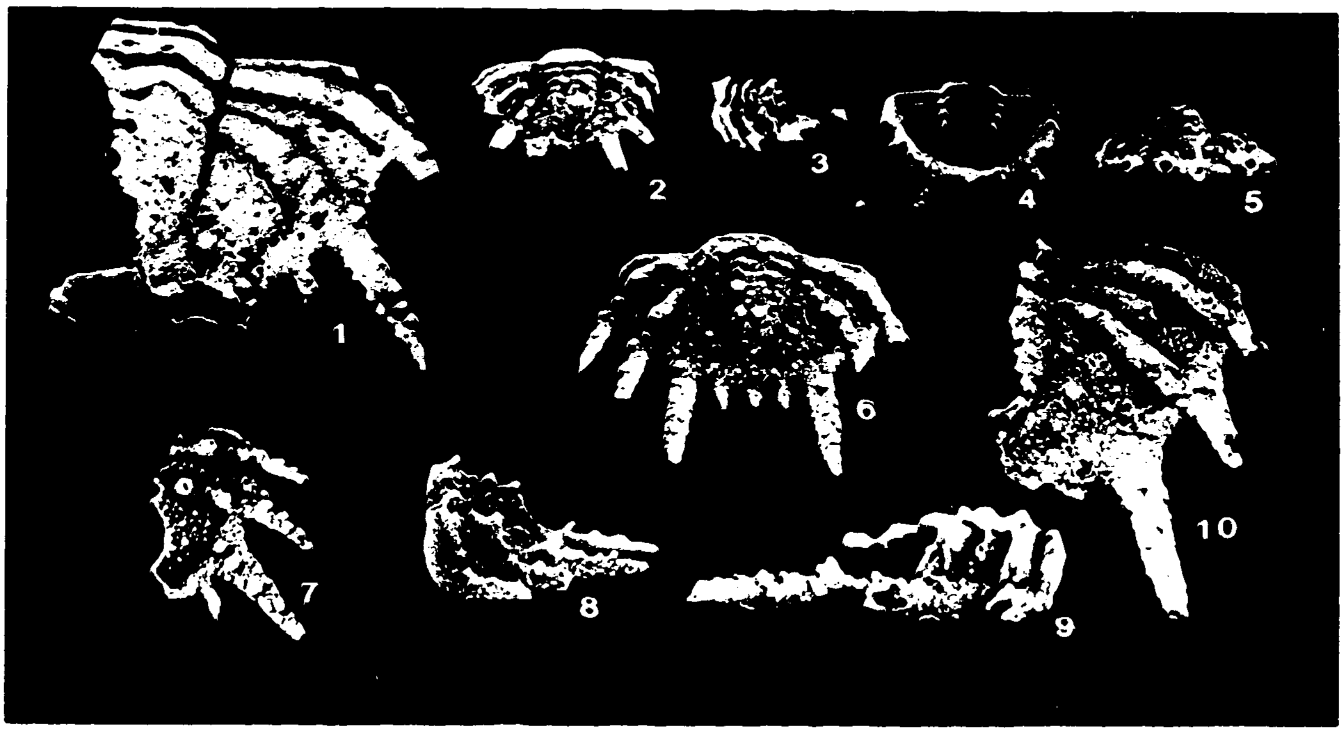
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Plate 15

Figs. 1 - 9.	*Borealarges* sp. aff. *B. tuckerae* from Avalanche Lake section AV5 58 - 60 m. Magnification x10 unless otherwise stated
1 - 7.	Posterior-to-dorsal, dorsal, anterior-to-dorsal, anterior, right lateral, posterior and internal views of cranidium UA 10005, x7.5.
8, 9.	Dorsal and internal view of pygidium UA 10006.

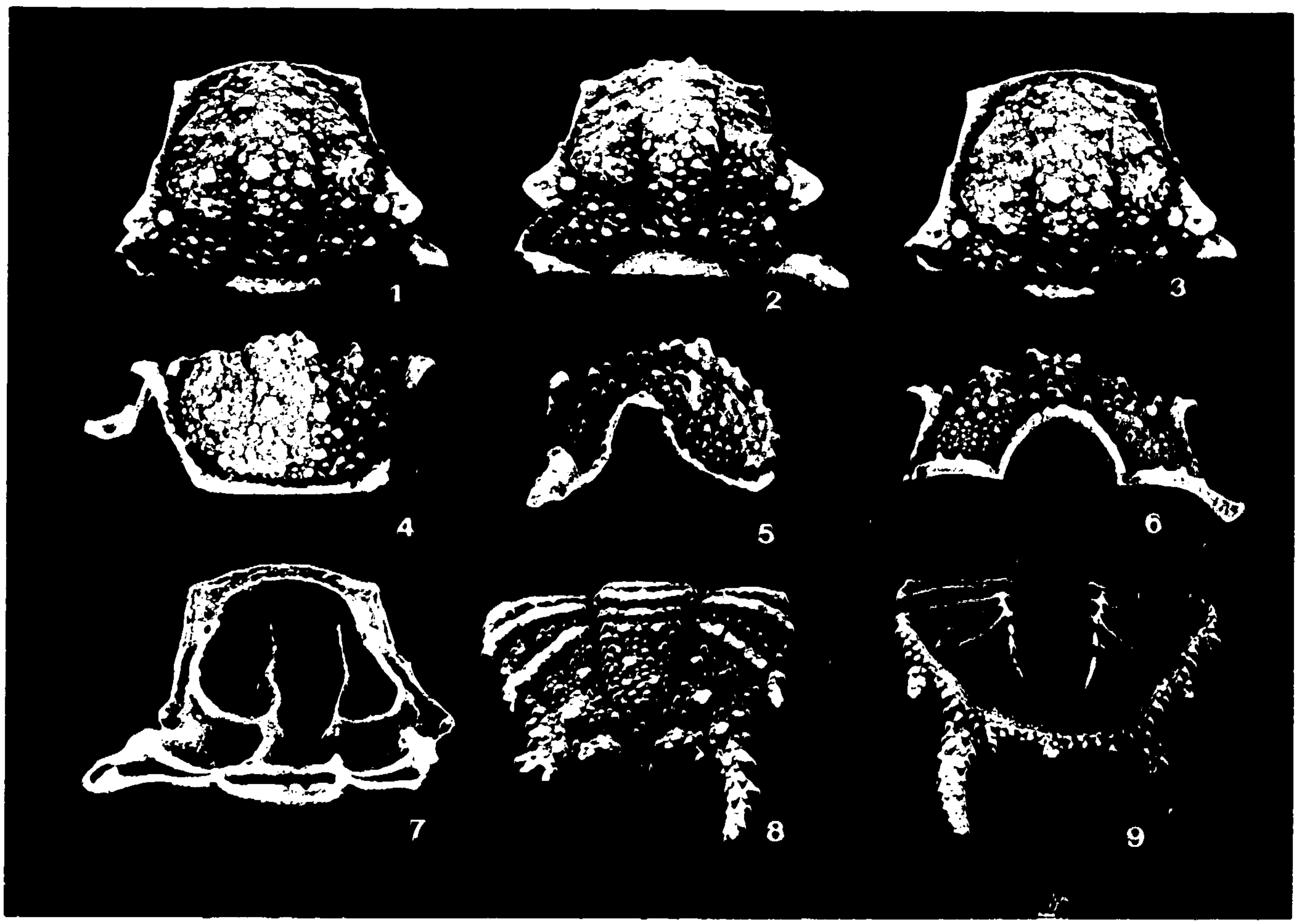
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Plate 16

Figs 1 - 15.	*Borealarges variabilis* n.sp. from the Avalanche Lake sections AV1 590 and 596 m, AV2 256, 255 - 260, 274 - 279 m, AV4 126, 238, 260 m, and from the Delorme range, section DR 91.44 m. Magnification x10 unless otherwise stated.
1 - 3.	Dorsal, internal and right lateral views of holotype pygidium UA 10007, AV4 126 m.
4, 5.	Dorsal and left lateral view of pygidium UA 10008, AV2 255 - 260 m, x7.5.
6.	Dorsal view of partial pygidium UA 10009, DR 91.44 m.
7.	Dorsal view of pygidium UA 10010, AV2 274 - 279 m.
8, 9.	Dorsal and internal view of pygidium UA 10011, AV2 255 - 260 m.
10.	Dorsal view of pygidium UA 10012, AV4 238 m, x5.
11, 12.	Dorsal and right lateral view of pygidium UA 10013, AV2 274 - 279 m.
13.	Dorsal view of pygidium UA 10014 AV2 256 m.
14.	Dorsal view of pygidium UA 10015 AV4 260 m.
15.	Dorsal view of transitory pygidium UA 10016, AV1 596 m.

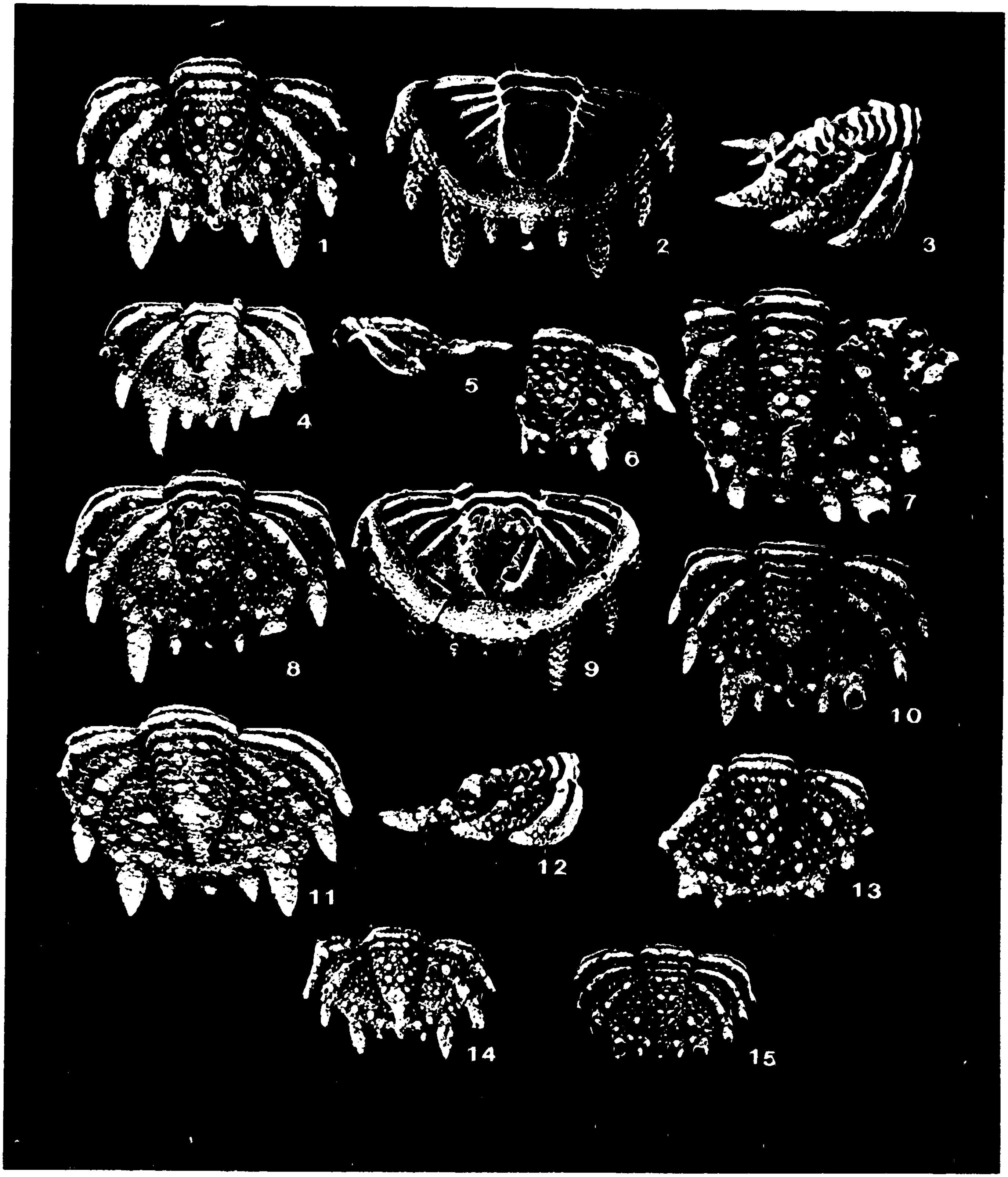
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Plate 17

Figs. 1 - 19.	*Borealarges variabilis* n.sp. from Avalanche Lake sections AV1 587 m, AV2 256, 255 - 260 and 274 -279 m.
1, 2, 4, 5, 7.	Posterior-to-dorsal, anterior, dorsal, right lateral and posterior views of cranidium UA 10017, AV2 274 - 279 m, x7.5.
3, 6.	Dorsal and anterior views of cranidium UA 10018, AV2 255 - 260 m, x5.
8, 9.	Dorsal and internal views of partial cranidium UA 10019, AV1 587 m, x7.5.
10 - 13, 15.	Posterior-to-dorsal, dorsal, anterior, right lateral and posterior views of cranidium UA 10020, AV2 256 m, x7.5.
14, 16 - 19.	Anterior, dorsal, posterior and left lateral views of cranidium UA 10021, AV2 255 - 260 m, x7.5.

Plate 18

Figs. 1 - 13.	*Borealarges* sp. from Avalanche Lake sections AV1 590 m, AV2 256 and 274 - 279 m, AV4 126 (T) m.
1 - 4.	Dorsal, posterior-to-dorsal, anterior and left lateral views of cranidium 10022 AV1 590 m, x7.5.
5 - 7.	Dorsal, posterior and left lateral views of cranidium UA 10023 AV2 256 m, x7.5.
8, 9.	Dorsal and anterior views of cranidium UA 10024, AV2 274 - 279 m, x7.5.
10 - 13.	Anterior, dorsal, left lateral and posterior views of cranidium UA 10025, AV4 126 (T) m, x10.

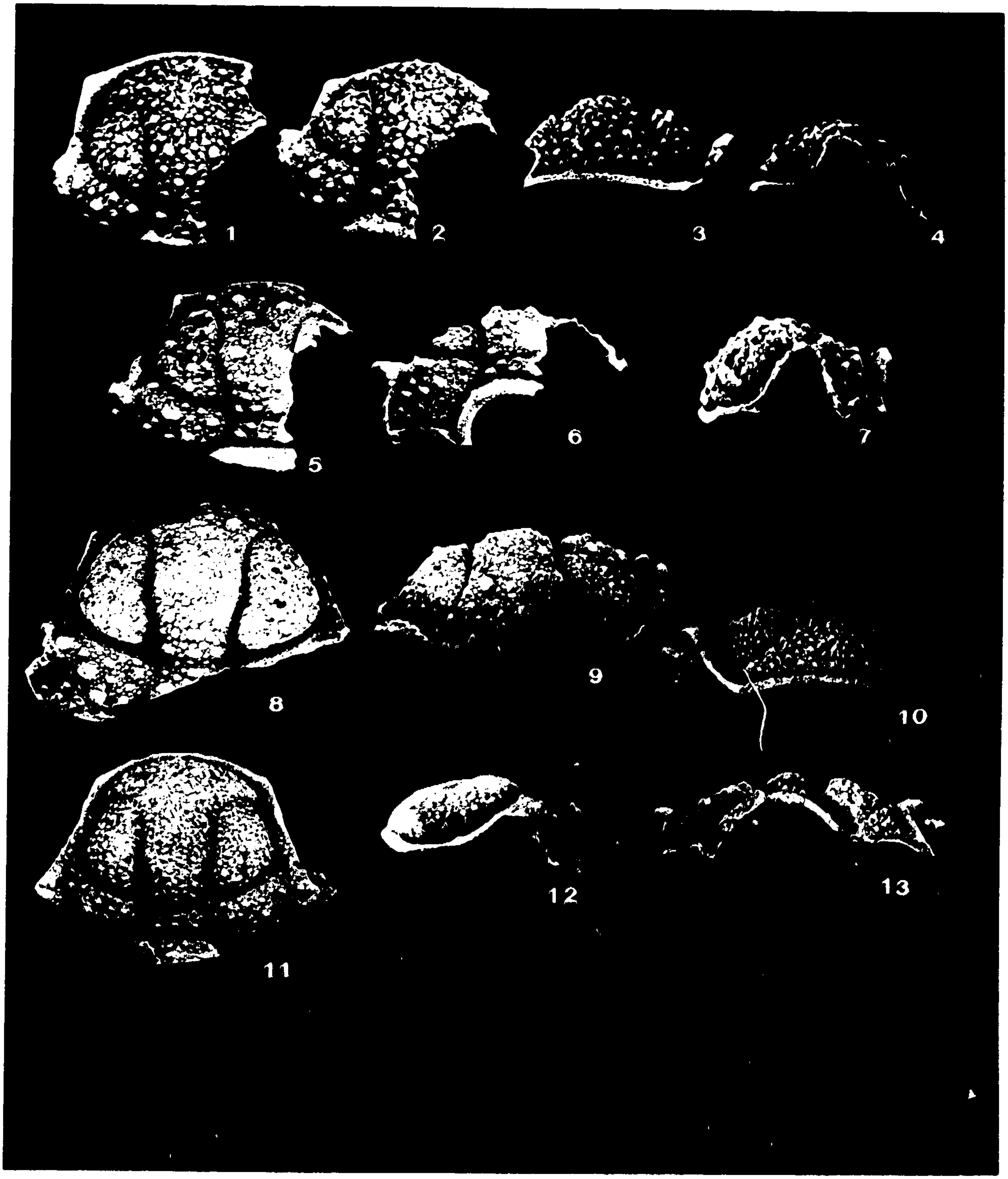
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Plate 19

Figs. 1 - 19, 21, 22.	Librigenae and thoracic segment of *Borealarges* from Avalanche Lake sections AV2 256 and 274 - 279 m, AV4 126 (T), 231, 234, 240 and 245 m, and from the Delorme range, section 91.44 m. (Group A, Figs. 1 - 12; Group B, Figs. 13 - 21).Magnification x10 unless otherwise stated.
1, 3.	External and internal views of right librigena UA 10026 AV4 231 m.
2, 4.	External and internal views of right librigena UA 10027, AV4 245 m.
5 - 8.	External, anterior, lateral and dorsal views of left librigena UA 10028, AV4 240 m.
9.	External view of left librigena UA 10029, AV4 231 (T) m.
10.	Dosolateral view of right librigena UA 10030, AV 4 231 (T) m, x5.
11.	External view of right librigena UA 10031 AV4 231 (T) x5.
12.	Dorsal view of partial thoracic segment UA 10032 showing part of axial ring and pleura , AV4 231 (T) m, x5.
13.	External view of left librigena UA 10033, DR 91.44.
14.	External view of right librigena UA 10034, AV2 274 - 279 m.
15, 18.	External and internal views of left librigena UA 10035, AV2 256 m.
16.	External view of right librigena UA 10036, AV2 274 - 279.
17.	External view of right librigena UA 10037, AV2 274 - 279 m.
19, 22.	Internal and external views of left librigena UA 10038, AV2 256 m.
21.	External view of left librigena UA 10040, AV4 126 (T) m.
20, 23.	*Dicranogmus* sp. External and dorsal views of librigena UA 10039, AV2 256 m.

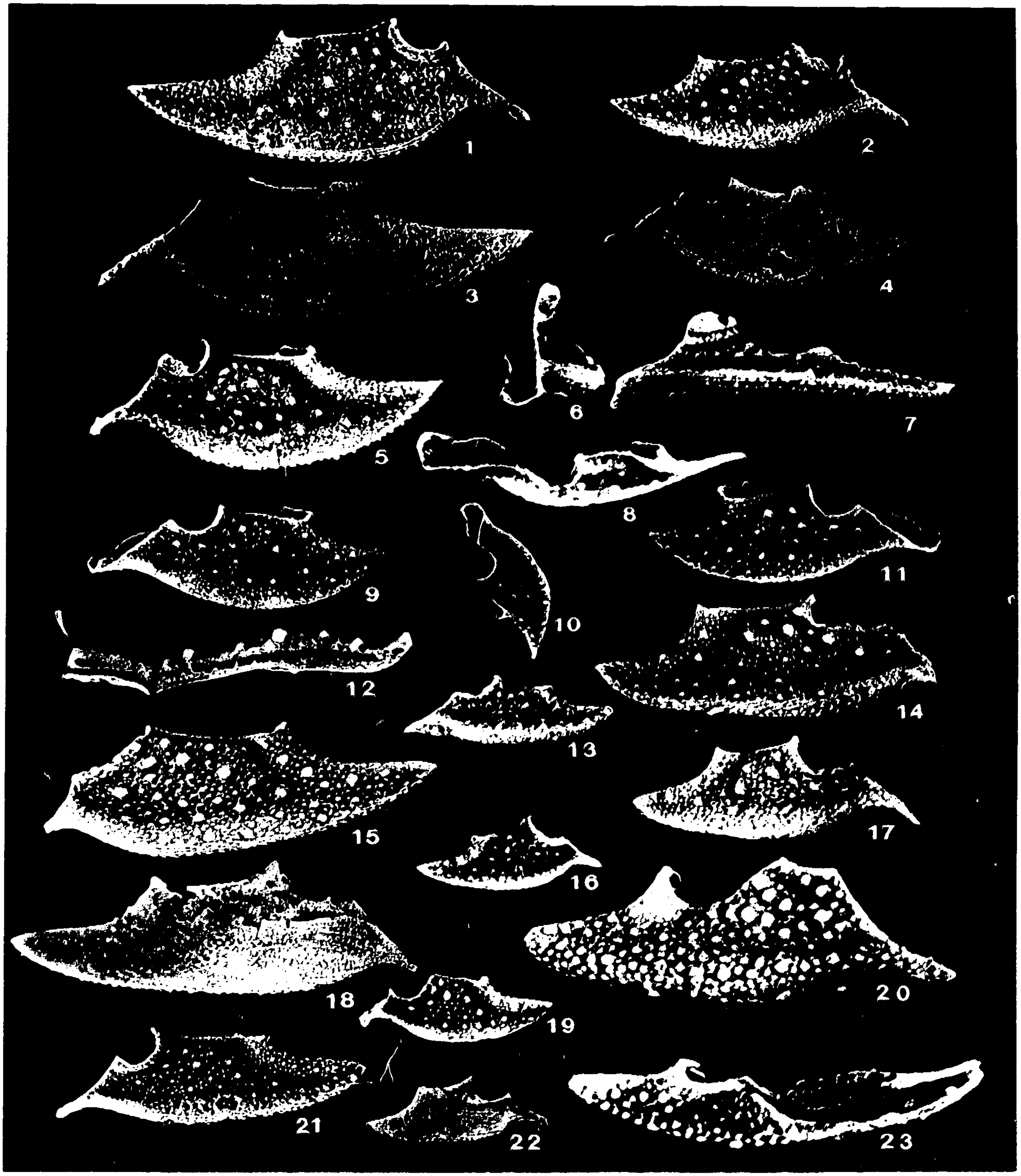
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Plate 20

Figs. 1 - 22. Hypostomes of *Borealarges* from Avalanche Lake sections AV2 255 - 260 and 256 m, AV4 231, 238 and 240 m, and AV5 58 - 60 m. Magnification x10 unless otherwise stated. (Group A, Figs. 1 - 8; Group B, Figs. 9 - 22)

1.	Ventral view of hypostome UA 10041, AV5 58 - 60 m.
2.	Ventral view of hypostome UA 10042 AV4 240 m.
3.	Ventral view of hypostome UA 10043, AV2 255 - 260 m.
4.	Dorsal (internal) view of hypostome UA 10044, AV2 255 - 260 m.
5, 6.	Ventral and lateral views of hypostome UA 10045, AV2 256.
7, 8.	Ventral and dorsal (internal) views of hypostome UA 10046, AV2 255 - 260 m.
9.	Ventral view of hypostome UA 10047 AV4 231 m.
10.	Dorsal (internal) view of rostral plate UA 10048, AV2 256 m.
11.	Ventral view of hypostome UA 10049, AV2 256 m.
12.	Ventral view of hypostome UA 10050, AV4 238 m.
13.	Dorsal (internal) view of hypostome UA 10051, AV5 58 - 60 m.
14.	Dorsal (internal) view of hypostome UA 10052, AV5 58 - 60 m.
15.	Ventral view of hypostome UA 10053, AV4 231 m.
16.	Ventral view of hypostome UA 10054, AV2 255 - 260 m.
17, 18.	Ventral and dorsal views of hypostome UA 10055, AV4 231 m.
19.	Ventral view of hypostome UA 10056, AV2 256 m, x7.5.
20, 21.	Ventral and dorsal views of hypostome UA 10057, AV4 240 m.
22.	Dorsal (internal) view of hypostome UA 10058, AV4 238 m.

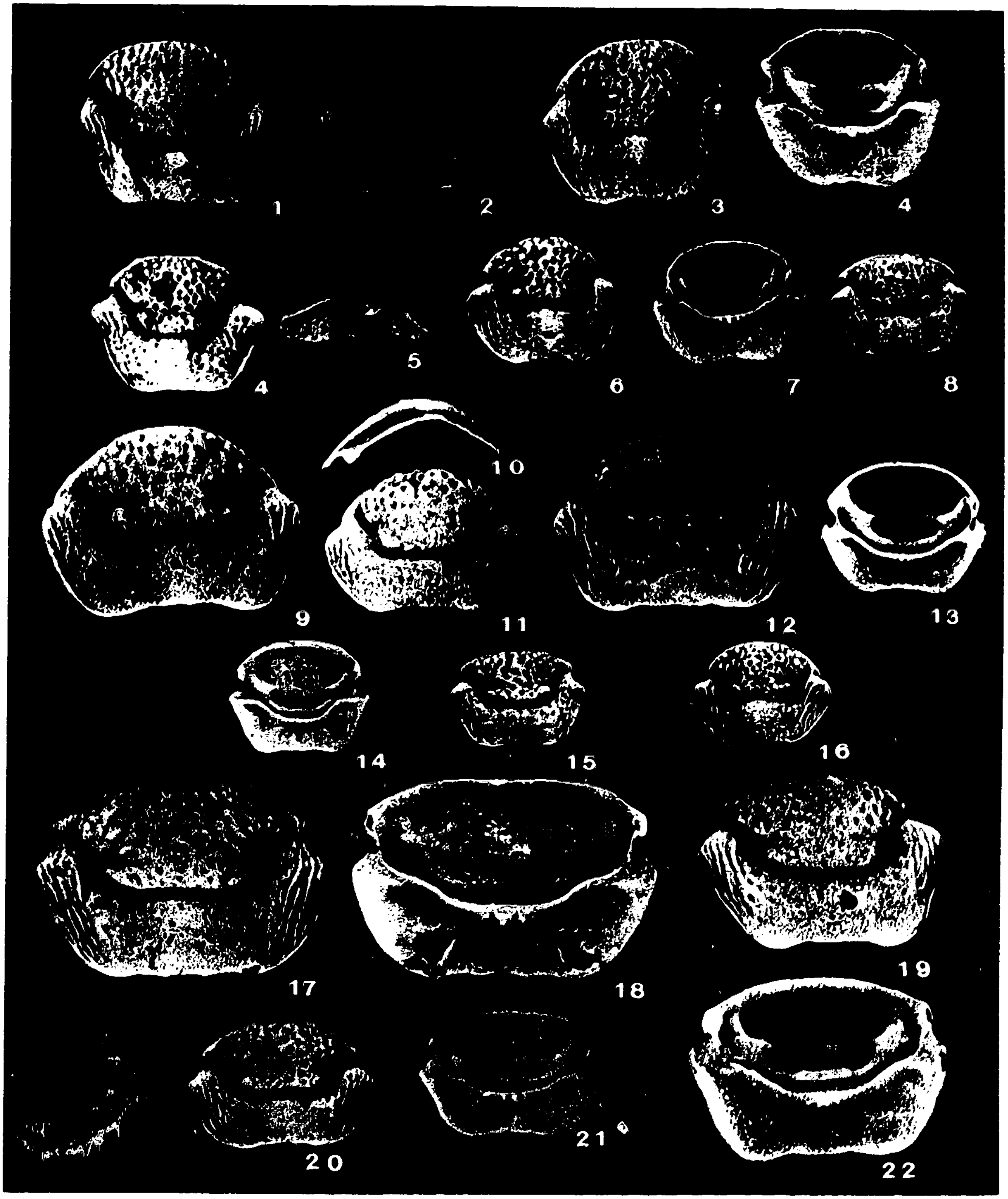
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Plate 21

Figs. 1, 2. "3-spine" protaspides of *Borealarges* from Avalanche Lake section AV4 126 (T) m.

1. Dorsal view of protaspis UA 10059, x31.25.
2. Dorsal view of protaspis UA 10060, x41.25.

Figs. 3 - 19. "5-spine" protaspides of *Borealarges* from Avalanche Lake sections AV1 587 m, AV4 126 (T) and 240 m, AV5 58 - 60 m.

3. Dorsal view of protaspis UA 10061, AV4 240 m, x40.
4. Dorsal view of protaspis UA 10062, AV4 126 (T) m, x35.
5. Ventral (internal) view of protaspis UA 10063, AV4 126 (T) m, x31.25.
6. Dorsal view of protaspis UA 10064, AV4 126 (T) m, x31.25.
7, 8. Dorsal and dorsolateral views of protaspis UA 10065, AV4 126 (T) m, x31.25.
9. Dorsal view of protaspis UA 10066, AV4 126 (T) m, x31.25.
10. Dorsal view of protaspis UA 10067, AV4 126 (T) m, x31.25.
11. Dorsal view of protaspis UA 10068, AV4 126 (T) m, x32.5.
12. Ventral (internal) view of protaspis UA 10069, AV4 126 (T) m, x31.25.
13. Dorsal view of protaspis UA 10070, AV4 126 (T) m, x36.25.
14. Dorsal view of protaspis UA 10071, AV4 126 (T) m, x31.25.
15. Dorsal view of protaspis UA 10072, AV4 126 (T) m, x31.25.
16. Ventral (internal) view of protaspis UA 10073, AV4 126 (T) m, x31.25.
17. Dorsal view of protaspis UA 10074, AV5 58 - 60 m, x35.
18. Dorsal view of protaspis UA 10076 AV5 58 - 60 m, x31.25.
19. Dorsal view of protaspis UA 10077, AV5 58 - 60 m, x40.

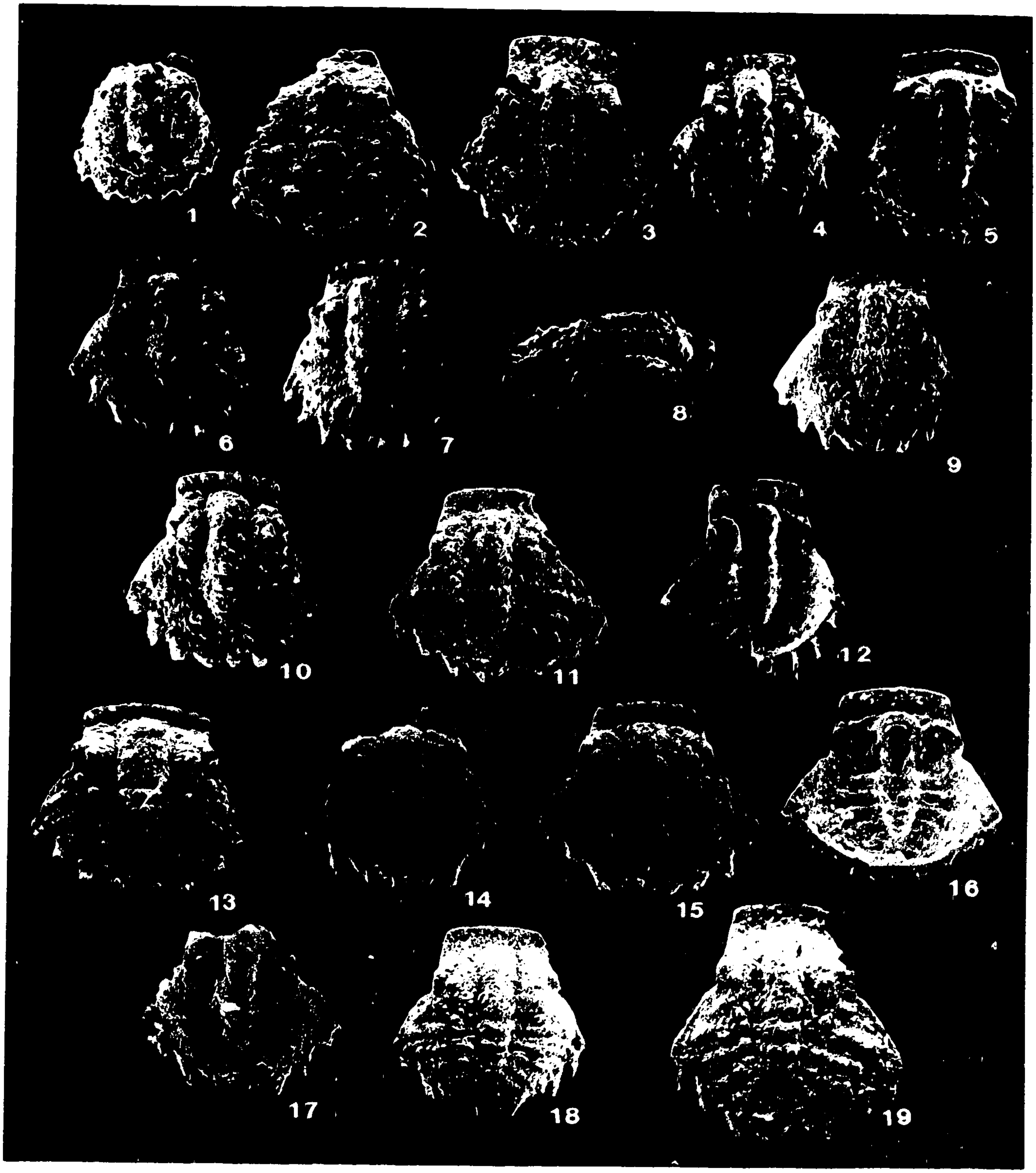
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Plate 22

Figs. 1 - 18. Meraspid cranidia of *Borealarges* from Avalanche Lake sections AV4 126 (T) and 230 - 240 m, AV5 58 60 m.. Note early development of bullar lobe in Figs. 1 - 7.

1. Dorsal view of small cranidium UA 10078, AV2 126 (T) m, x32.5.
2. Ventral (internal) view of small cranidium UA 10079, AV4 126 (T) m, x31.25.
3. Ventral (internal) view of cranidium UA 10080, AV5 58 - 60, x35.
4. Dorsal view of cranidium UA 10081, AV4 126 (T) m, x31.25,
5. Dorsal view of cranidium UA 10082, AV4 126 (T) m, x32.5.
6. Ventral (internal) view of cranidium UA 10083, AV4 126 (T) m, x31.25.
7. Dorsal view of cranidium UA 10084, AV4 126 (T) m, x31.25.
8. Dorsal view of cranidium UA 10085, AV4 126 (T) m, x26.25.
9. Dorsal view of cranidium UA 10086 AV5 58 - 60, x35.
10. Dorsal view of cranidium UA 10087 AV4 126 (T) m, x26.25.
11. Dorsal view of cranidium UA 10088, AV5 58 - 60, m, x35.
12. Dorsal view of cranidium UA 10089, AV5 58 - 60, m x35.

13 - 15. Dorsal (x47.5), anterior (x50.5) and left lateral (x40) views of cranidium UA 10090, AV4 234 m.

16 - 18. Dorsal (x27.5), anterior (x32.5) and left lateral (x25) views of cranidium UA 10091, AV4 240 m.

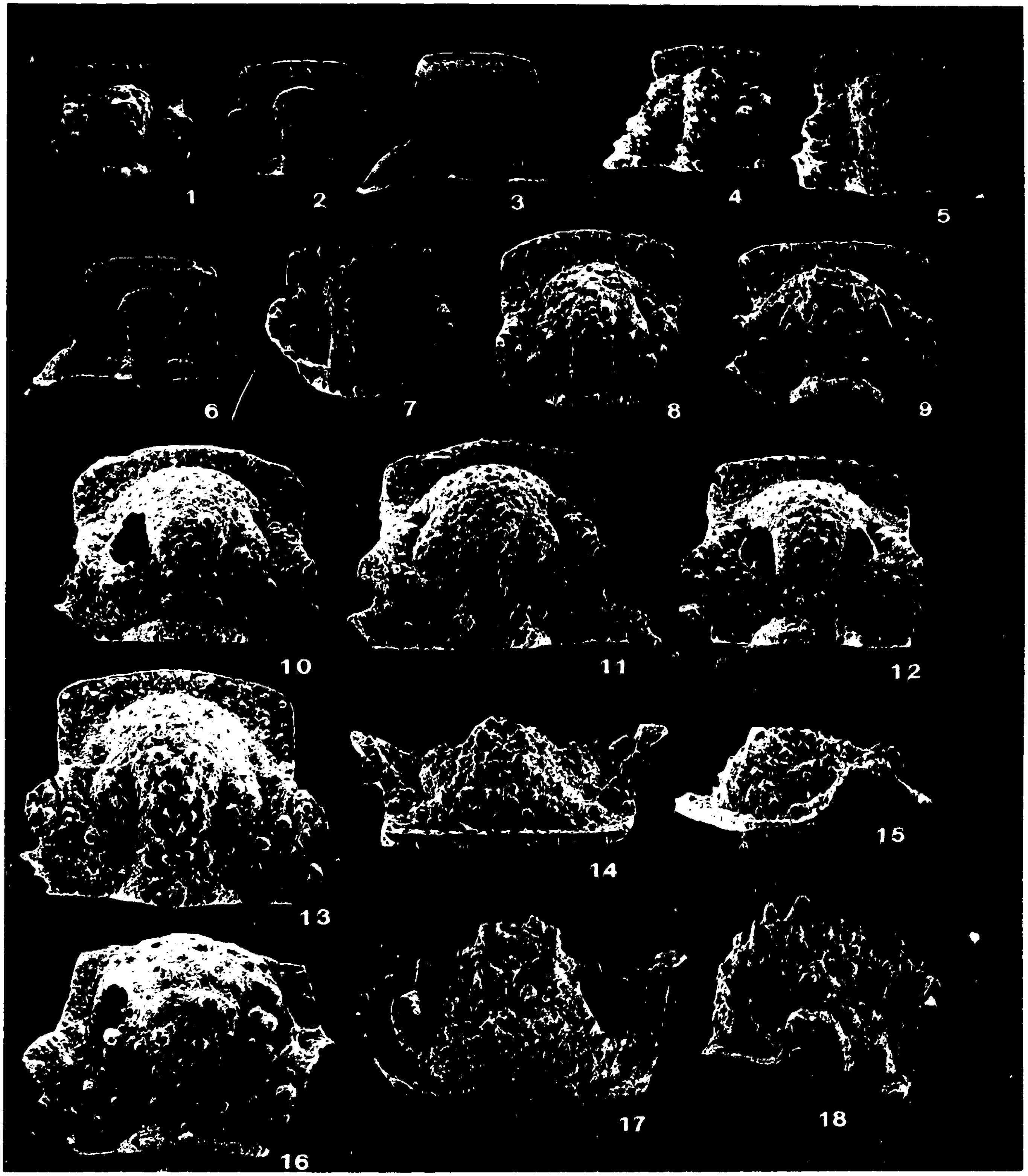
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Plate 23

Figs 1 - 10. Meraspid cranidia of *Borealarges* from Avalanche Lake sections AV2 274 - 279 m, AV4 230 - 246 m and AV5 58 - 60 m.

1. Dorsal view of cranidium UA 10092, AV4 240 - 246 m, x20.
2. Ventral (internal) view of cranidium UA 10093, AV4 240 m, x26.25.
3. Dorsal view of partial cranidium UA 10094, AV5 58 - 60 m, x20.

4, 8. Dorsal and anterior views of cranidium UA 10095, AV4 230 - 240 m, x20.

5 - 7 Right lateral, dorsal and anterior views of cranidium UA 10096, AV4 230 - 240 m, x20.

9. Dorsal view of partial cranidium UA 10097, AV2 274-279, x20.
10. Dorsal view of cranidial fragment UA 10098, AV2 274 - 279 m, x20.

Figs. 11 - 20. Meraspid librigena of *Borealarges* from Avalanche lake sections AV4 126 (T), 234 and 240 - 246 m.

11. Dorsolateral view of small left librigena UA 10099, AV4 126 (T) m, x31.25.
12. External view of right librigena UA 10100, AV4 126 (T) m, x31.25.
13. External view of left librigena UA 10101, AV4 234 - 237, x35.
14. External view of left librigena UA 10102, AV4 126 (T) m, x20.
15. External view of right librigena UA 10103, AV4 240 - 246 m, x20.
16. Internal view of right librigena UA 10104, AV4 240 - 246 m, x20.
17. External view of left librigena UA 10105, AV4 234 m, x35.
18. External view of right librigena UA 10106, AV4 240 - 246 m, x20.
19. External view of left librigena UA 10107, AV4 240 - 246 m, x20.
20. External view of left librigena UA 10108 AV4 126 (T) m, x20.

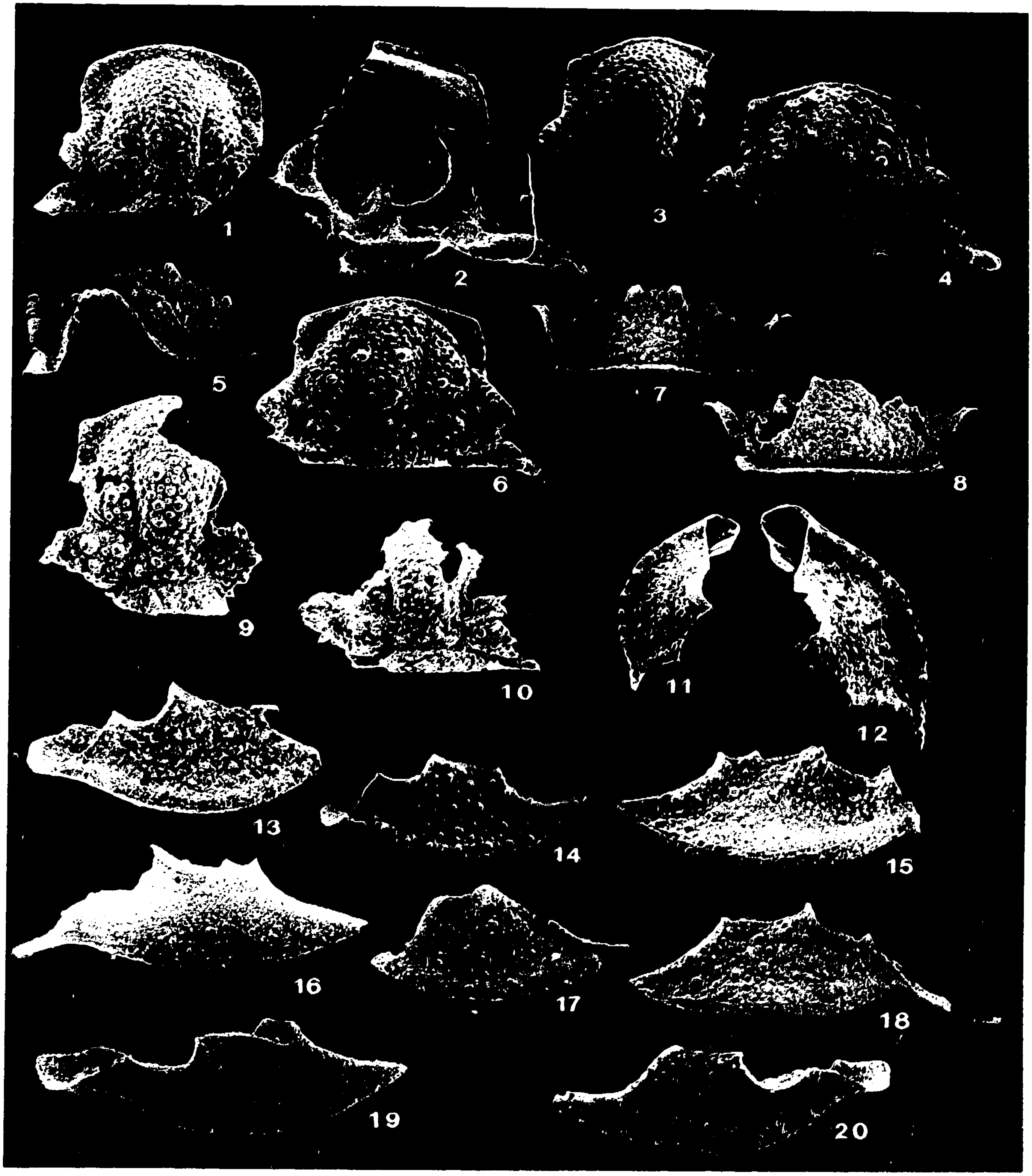
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Plate 24

Figs 1 - 13. Transitory pygidia of *Borealarges* from Avalanche Lake sections AV2 250 - 260 and 274 - 279 m, AV4 126 - 127 m.

1. Dorsal view of transitory pygidium UA 10109, AV4 126 - 127 m. x31.25.
2. Dorsal view of transitory pygidium UA 10110, AV4 126 - 127 m, x19.
3. Dorsal view of transitory pygidium UA 10111, AV2 274 - 279 m, x30.
4. Dorsal view of partial transitory pygidium UA 10112, AV4 234 - 237 m, x20.
5. Dorsal view of transitory pygidium UA 10113, AV4 126 - 127.
6. Dorsal view of transitory pygidium UA 10114, AV4 126 (T) m, x46.25.
7. Dorsal view of transitory pygidium UA 10115, AV4 126 - 127 m. x31.25.
8. Dorsal view of transitory pygidium UA 10116, AV4 126 - 127 m, x 31.25.
9. Dorsal view of transitory pygidium UA 10117, AV4 126 - 127 m, x32.5.
10. Dorsal view of transitory pygidium UA 10118 AV4 126 - 127, x22.5.
11. Dorsal view of transitory pygidium UA 10119, AV4 238 m, x20.
12. Dorsal view of transitory pygidium UA 10120, AV2 250 - 260 m, x26.25.
13. Dorsal view of transitory pygidium UA 10121, AV2 274 - 279 m, x20.

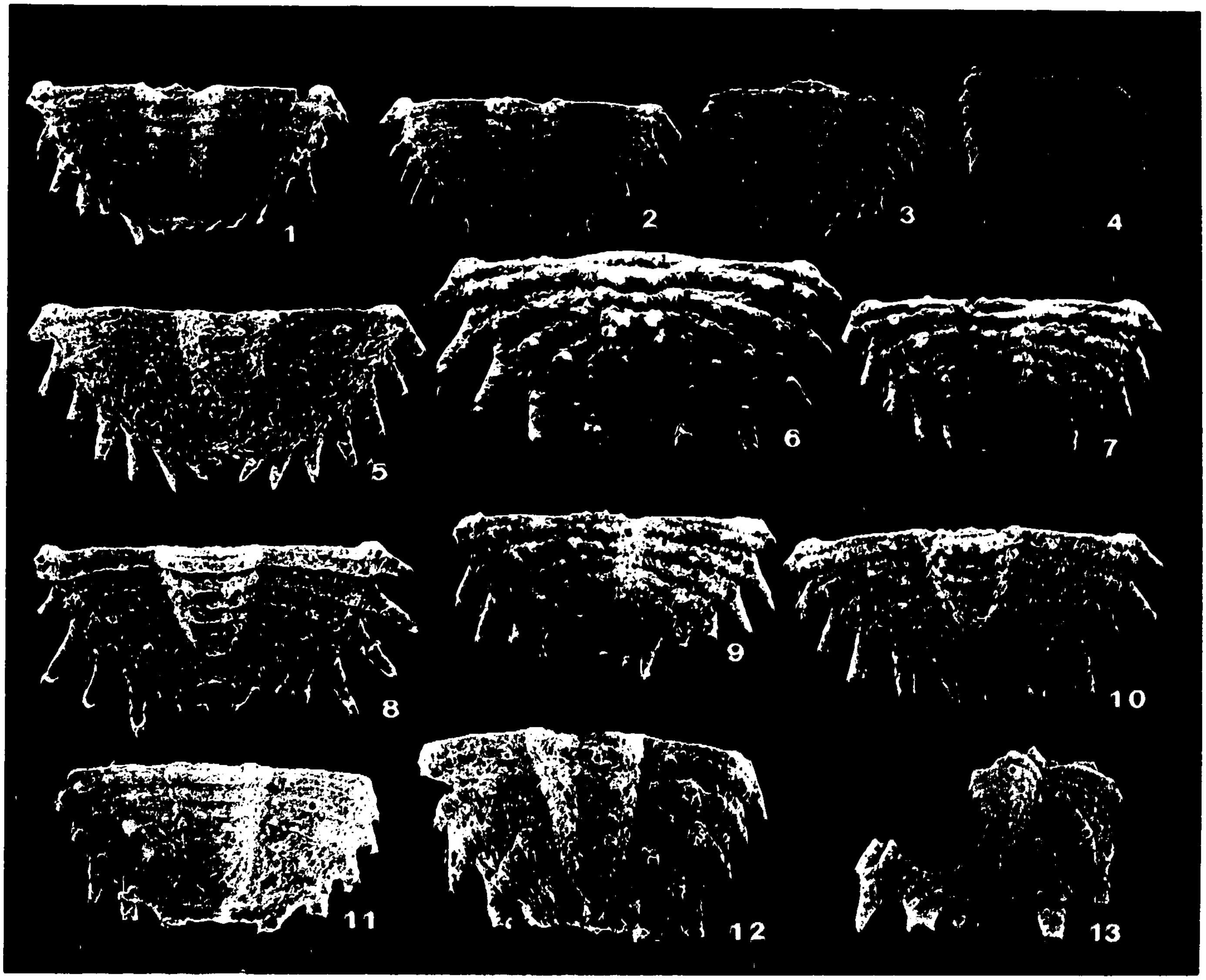
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Plate 25

Figs.1 - 8.	Transitory pygidia of *Borealarges* from Avalanche Lake sections AV2 274 - 279 m, AV4 230 - 246 m.
1.	Dorsal view of transitory pygidium UA 10122 AV4 240 - 246 m, x20.
2.	Dorsal view of transitory pygidium UA 10123, AV2 274 - 279, x20.
3.	Dorsal view of transitory pygidium UA 10124, AV4 240 - 246 m, x21.25.
4.	Dorsal view of transitory pygidium UA 10125, AV4 230 240 m, x20.
5.	Dorsal view of transitory pygidium UA 10126, AV4 238, x21.25.
6.	Dorsal view of transitory pygidium UA 10127, AV4 240 - 246 m, x26.25.
7.	Dorsal view of transitory pygidium UA 10128, AV4 231, x20.
8.	Dorsal view of transitory pygidium UA 10129 AV4 231, x20.
Figs 9 - 18.	Meraspid hypostomes of *Borealarges*. from the Avalanche Lake sections. Note presence of slits in lateral margins and their gradual decrease in size with growth.
9.	Ventral view of hypostome UA 10130, AV 126 - 127 m, x42.5.
10.	Ventral view of hypostome UA 10131, AV4 126 - 127 m, x31.25.
11.	Ventral view of hypostome UA 10132, AV4 126 m, x23.75.
12.	Ventral view of hypostome UA 10133, AV5 58 - 60 m, x35.
13.	Dorsal (internal) view of hypostome UA 10134, AV5 58 - 60 m, x35.
14.	Ventral view of hypostome UA 10135, AV4 240 - 246 m, x30.
15.	Ventral view of hypostome UA 10136, AV 4 234, x 35.
16.	Ventral view of hypostome UA 10137, AV4 126 m, x23.75.
17.	Dorsal view of hypostome UA 10138, AV4 126 m, x23.75.
18.	Ventral view of hypostome UA 10139, AV2 274 - 279, x30.

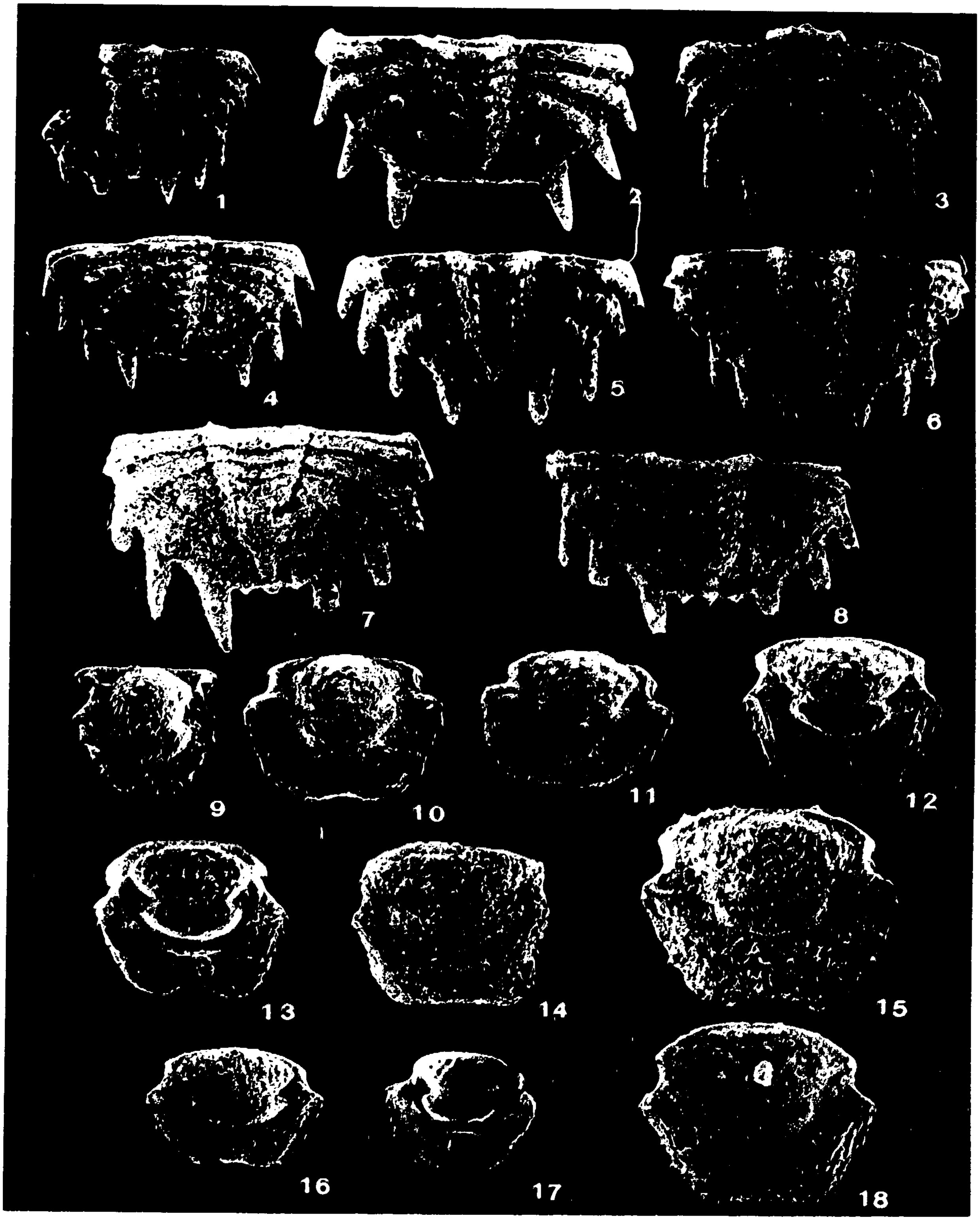
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Plate 26

Figs. 1 - 23.	*Dicranogmus lepidus* n. sp. from Avalanche Lake sections AV1 598 m and AV4 126 m. Magnification x10, unless otherwise stated.
1 - 6.	Posterior-to-dorsal, dorsal, left lateral, internal, posterior and anterior views of holotype cranidium UA 10140, AV4 126 m, x3.
7 - 12.	Dorsal, anterior-to-dorsal, posterior, right lateral, anterior and internal views of cranidium UA 10141, AV1 598.
13, 17 - 19.	Dorsal, right lateral, posterior and anterior views of cranidium UA 10142, AV4 126 m.
14.	Dorsal view of partial cranidium UA 10143, AV4 126 m, x3.
15.	Posterior-to-dorsal view of partial cranidium UA 10144, AV4 126 (T) m.
16, 21, 23.	Posterior-to-dorsal, anterior-to-dorsal and left lateral views of cranidium UA 10145, DR 91.44 m.
20.	Ventral view of hypostome UA 10146, DR 91.44 m.
22..	Ventral view of hypostome UA 10147, DR 91.44 m.

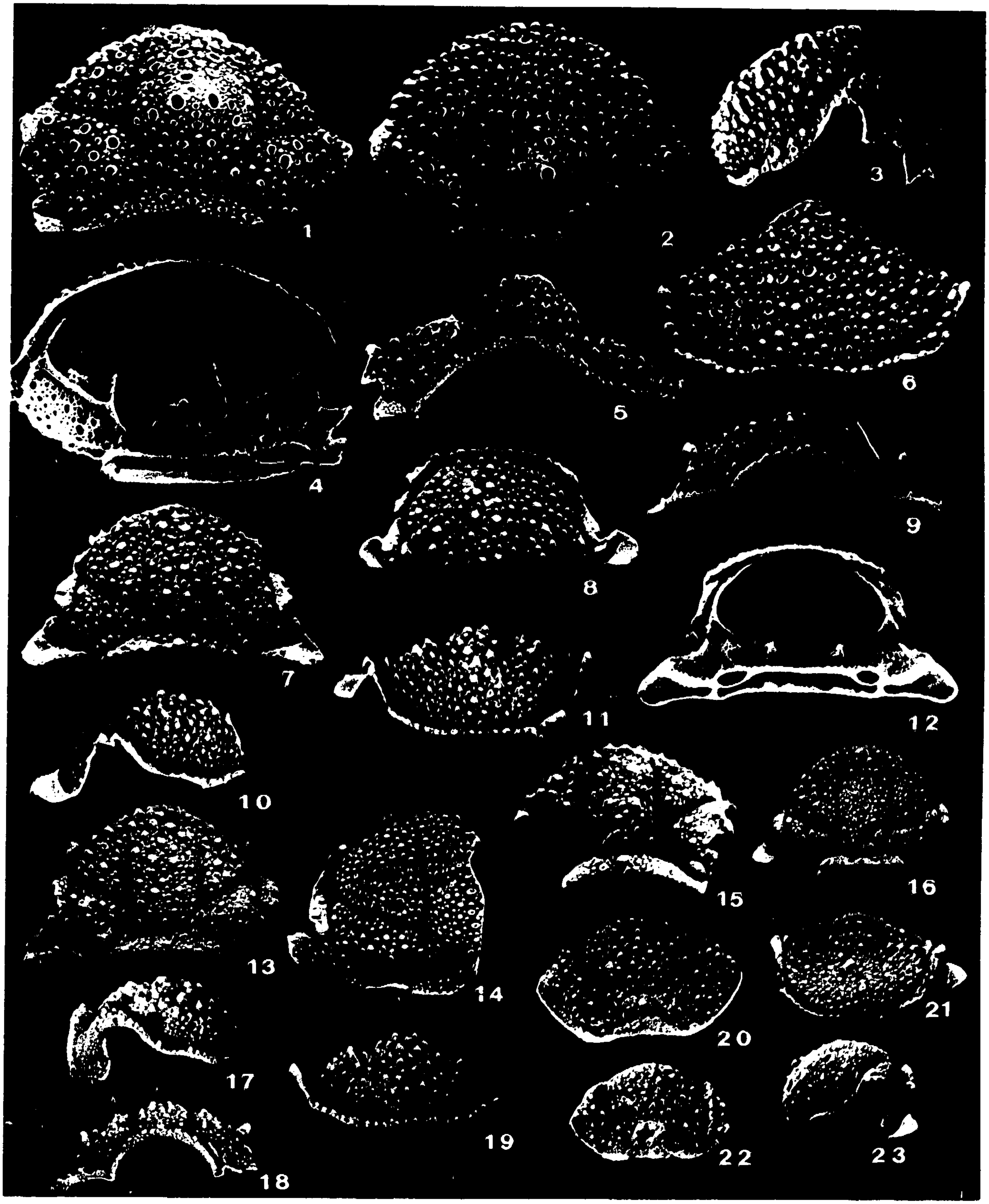
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Plate 27

Figs. 1 - 17. Pygidia of *Dicranogmus lepidus* n.sp. from Avalanche Lake sections AV1 590 - 591 m, AV2 250 - 260 and 274 - 279 m, AV4 126 (T) m. Magnification x10, unless otherwise stated.

1.	Dorsal view of pygidium UA 10148, AV1 591
2, 3.	Dorsal and ventral (internal) views of pygidium UA 10149, AV4 117 m.
4.	Dorsal view of pygidium UA 10150, AV4 126 (T) m.
5, 6.	Dorsal and ventral (internal) views of pygidium UA 10151, AV1 590 m.
7.	Dorsal view of partial pygidium, UA 10152, AV5 58 - 60 m.
8.	Dorsal view of pygidium UA 10153, AV2 256 m.
9.	Dorsal view of pygidium UA 10154, AV2 274 - 279 m, x5.
10.	Dorsal view of partial pygidium UA 10155, AV4 126 (T) m
11, 12.	Ventral (internal) and dorsal views of partial pygidium UA 10156, AV2 255 - 260 m.
13.	Dorsal view of partial pygidium UA 10157, AV1 590 m, x3.
14.	Dorsal view of partial pygidium UA 10158, AV5 58 - 60.
15.	Dorsal view of partial pygidium UA 10159, AV2 274 - 279 m, x5.
16.	Dorsal view of partial pygidium UA 10160 AV2 274 - 279 m, x5.
17.	Dorsal view of partial pygidium UA 10161, AV4 240 m.

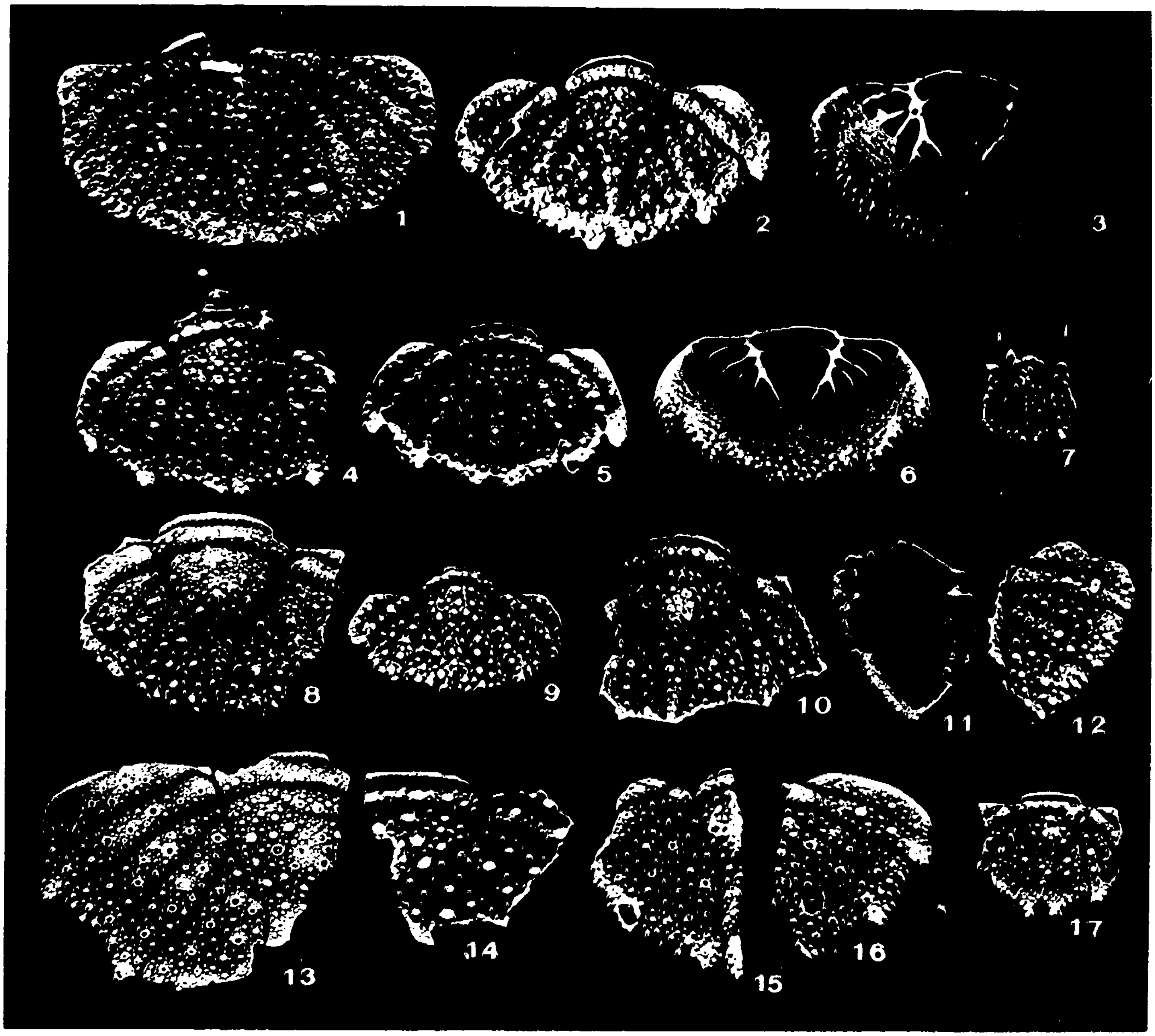
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Plate 28

Figs. 1 - 12. *Dicranogmus lepidus* n. sp.from Avalanche Lake sections AV1 590 m, AV2 256 m, AV4 126 - 127 m. Magnification x10, unless otherwise stated.

1.	External view of left librigena UA 101602 AV4 126 - 127 m.
2.	External view of left librigena UA 10163, AV4 126 - 127 m.
3.	Internal view of left librigena UA 10164, AV4 126 - 127 m.
4, 5.	External and internal views of librigena UA 10165, AV4 126 (T) m.
6.	Internal view of left librigena UA 10166, AV4 126 - 127 m.
7.	External view of left librigena UA 10167, AV1 590 m, x5.
8.	Internal view of librigena UA 10168, AV4 126 - 127 m.
9.	Lateral view of librigena UA 10169, AV 4 126 (T) m.
10.	External view of librigena UA 10170, AV2 256 m, x7.5.
11.	Ventrolateral view of librigena UA 10171, AV1 590 m.
12	Dorsal view of pleura UA 10172, AV2 256 m.

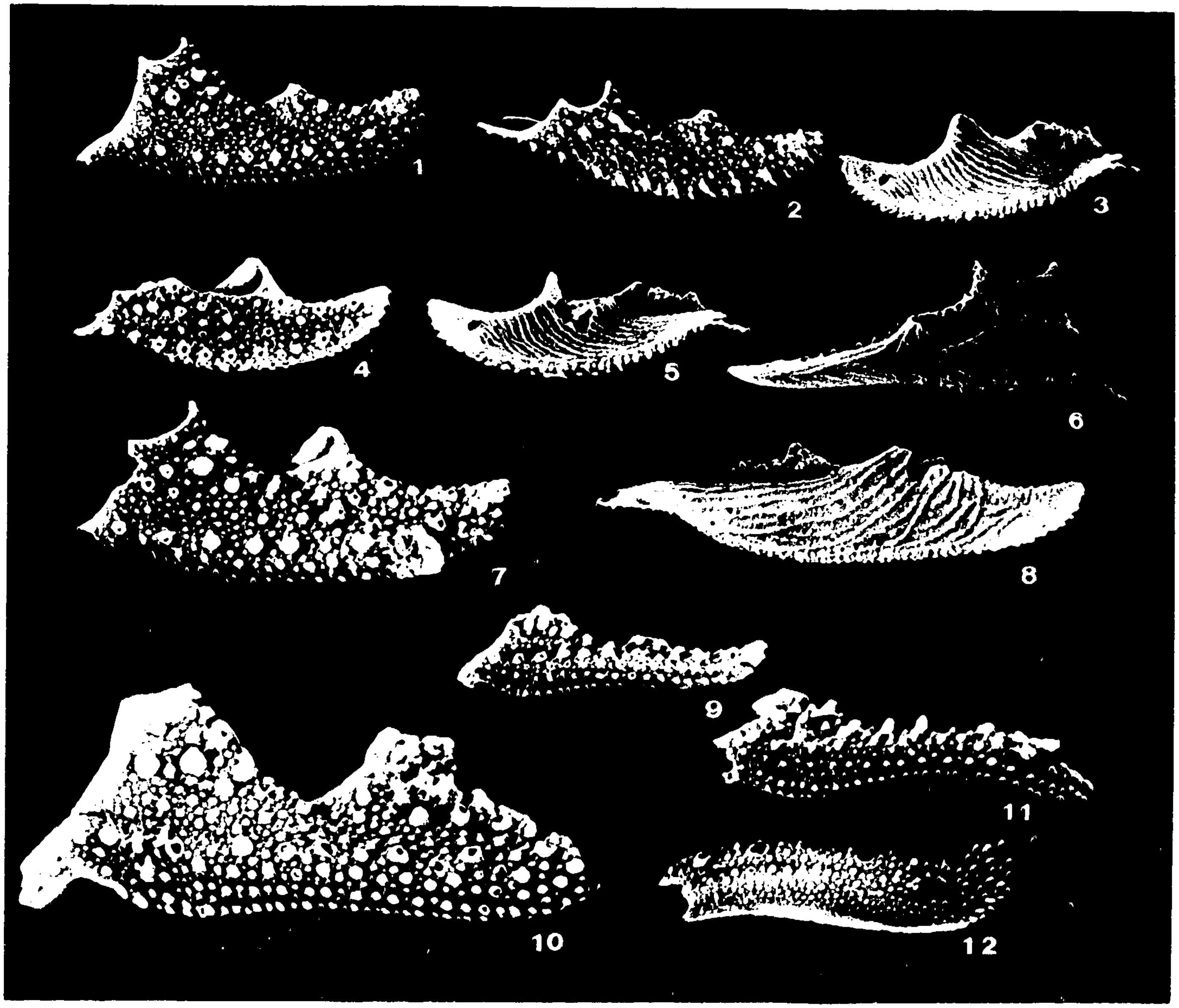

Plate 29

Figs. 1 - 19. *Dicranogmus wilsoni* n. sp. from Avalanche Lake sections AV1 590 m, AV2 256 m, AV4 126 (T) m. Magnification x10, unless otherwise stated.

1 - 6.	Posterior-to-dorsal, dorsal, anterior-to-dorsal, posterior, right lateral and anterior views of holotype cranidium UA 10173, AV4 126 (T) m, x10.
7.	Internal view of cranidium UA 10174, AV2 256 m.
8, 9.	Dorsal and ventral (internal) views of cranidium UA 10175, AV2 256 m.
10	Dorsal view of partial cranidium UA 10176, AV4 126 (T) m..
11.	Dorsal view of partial cranidium UA 10177, AV4 126 (T) m.
12.	Dorsal view of partial cranidium UA 10178, AV1 590 m, x7.5.
13 - 18.	Dorsal, anterior-to-dorsal, anterior, right lateral, internal and posterior views of cranidium UA 10179, AV4 126 (T) m.
19.	Dorsal view of cranidium UA 10180, AV4 126 (T) m.

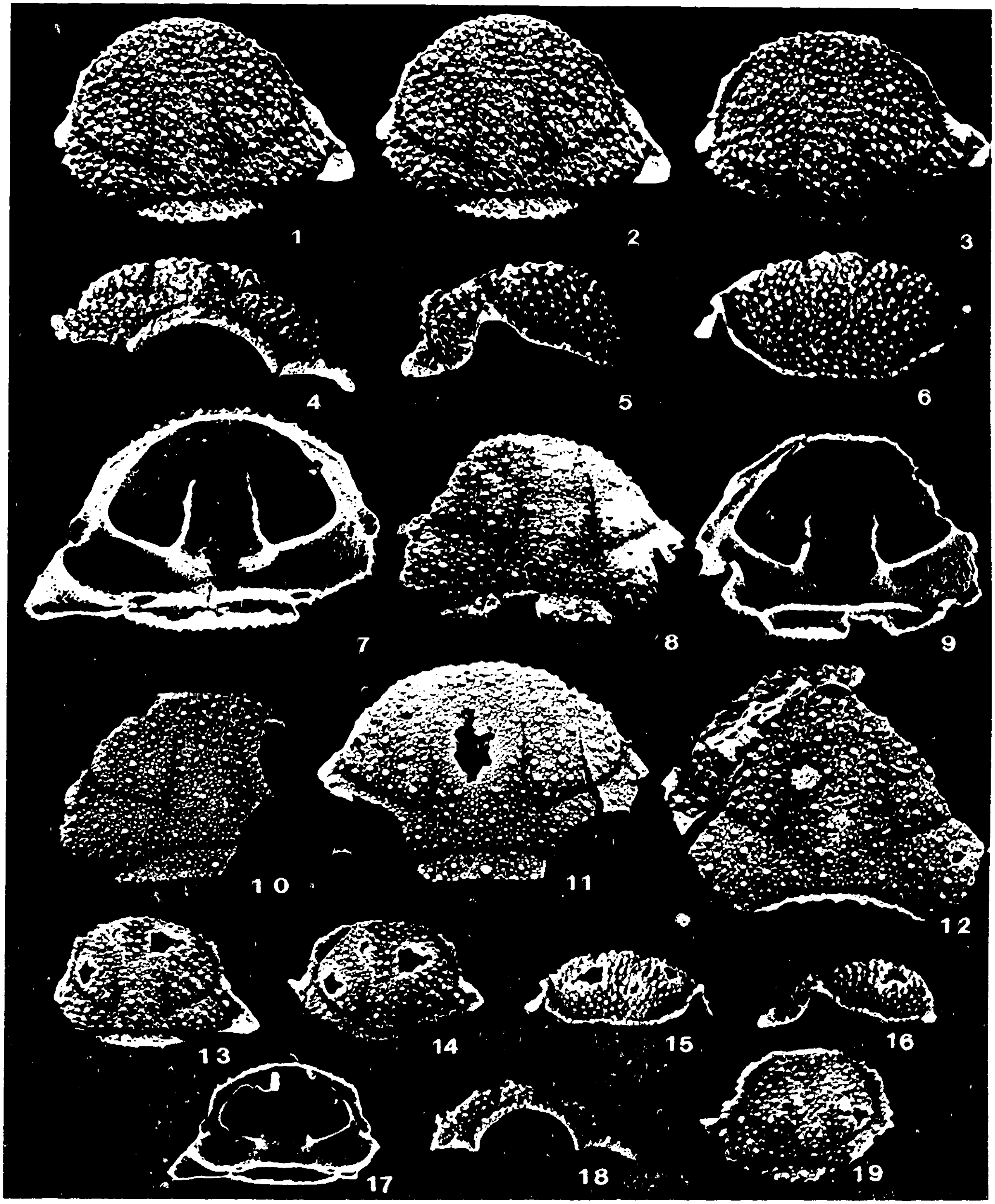
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Plate 30

Figs. 1 - 12.	*Dicranogmus wilsoni* n. sp. from Avalanche Lake sections AV1 590 m, AV2 274 - 279 m, AV4 126 (T) m. Magnification x10, unless otherwise stated.
1.	Dorsal view of pygidium UA 10181 AV2 274 - 279 m.
2.	Dorsal view of pygidium UA 10182, AV2 255 - 260 m.
3.	Dorsal view of pygidium UA 10183, AV4 126 (T) m.
4.	External view of right librigena UA 10184, AV1 590 m.
5.	Dorsal view of partial pygidium UA 10185, AV2 274 - 279 m, x6.
6, 9.	Dorsal and ventral (internal) views of partial pygidium UA 10186, AV2 274 - 279 m, x3.
7.	External view of right librigena UA 10187, AV4 126 (T) m.
8.	External view of right librigena UA 10188, AV4 126 (T) m.
10.	Ventral (internal) view of partial pygidium UA 10189, AV2 274 - 279 m.
11, 12.	External and ventrolateral views of right librigena UA 10190, AV4 126 (T) m.

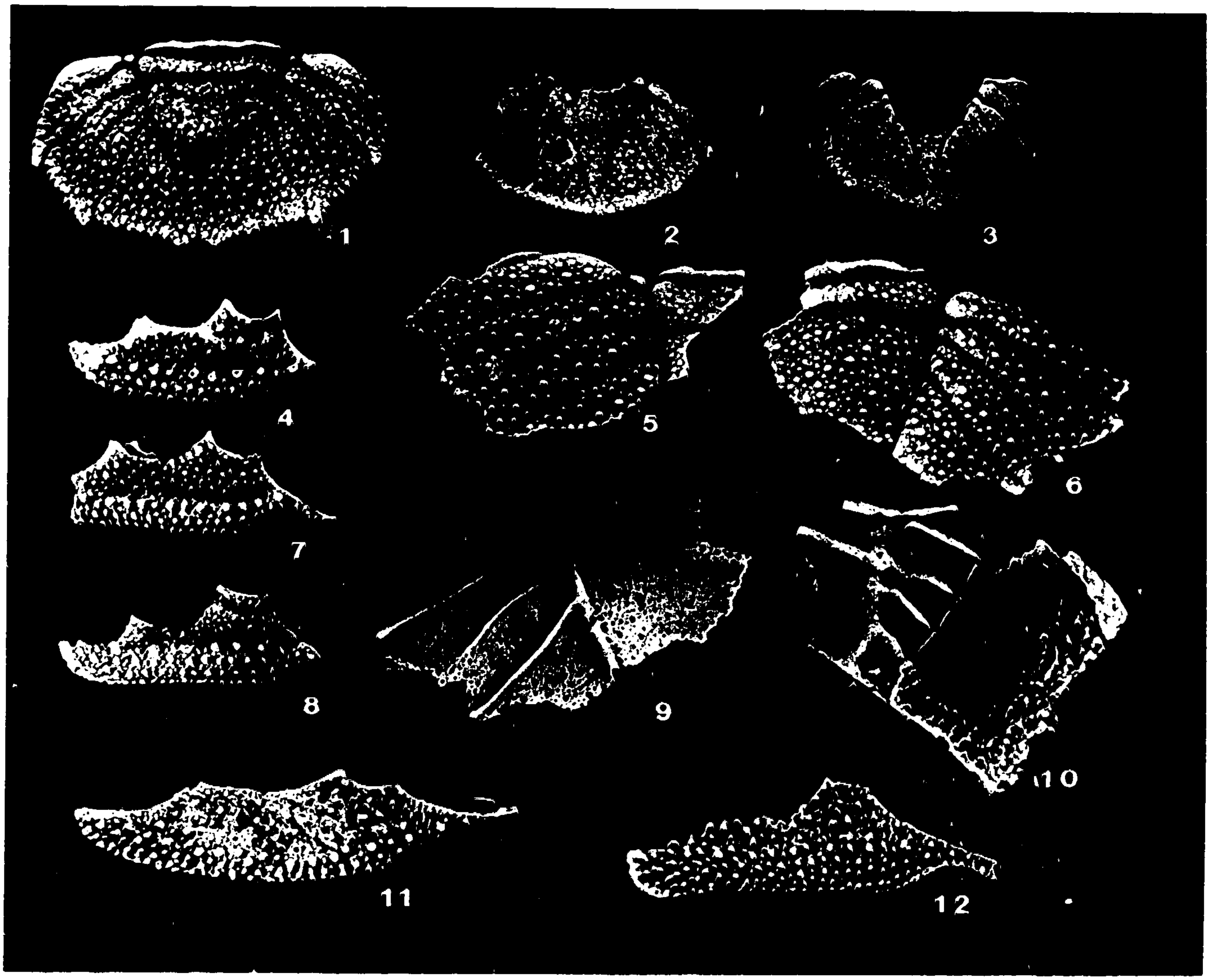

Plate 31

Figs. 1 - 18.	Hypostomes of *Dicranogmus* from Avalanche Lake sections AV1 590 m, AV2 256, 255 - 260 and 274 - 279 m, AV4 126 (T) and 234 m. Magnification x10, unless otherwise stated. (Figs 1 - 8, probably *D. lepidus*. For comparison, refer to Pl. 26, figs. 20, 22).
1, 4.	Ventral and dorsal (internal) views of hypostome UA 10191, AV1 590 m.
2.	Ventral view of hypostome UA 10192, AV2 256 m.
3, 6.	Ventral and dorsal (internal) views of hypostome UA 10193 AV2 255 - 260 m.
5.	Ventral view of partial hypostome UA 10194, AV2 274 - 279 m.
7, 11.	Ventral and dorsal (internal) views of hypostome UA 10195, AV2 256 m.
8, 12.	Ventral and dorsal (internal) views of hypostome UA 10196, AV4 126 (T) m.
9, 13.	Ventral and dorsal (internal) views of hypostome UA 10197, AV2 274 - 279.
10.	Ventral view of hypostome UA 10198, AV2 274 - 279.
14.	Ventral view of hypostome UA 10199, AV1 590.
15, 16.	Ventral and dorsal (internal) views of hypostome UA 10200, AV2 274 - 279 m.
17.	Dorsal view (internal) view of hypostome UA 10201, AV4 126 (T) m.
18.	Ventral view of hypostome UA 10202, AV4 234 m.

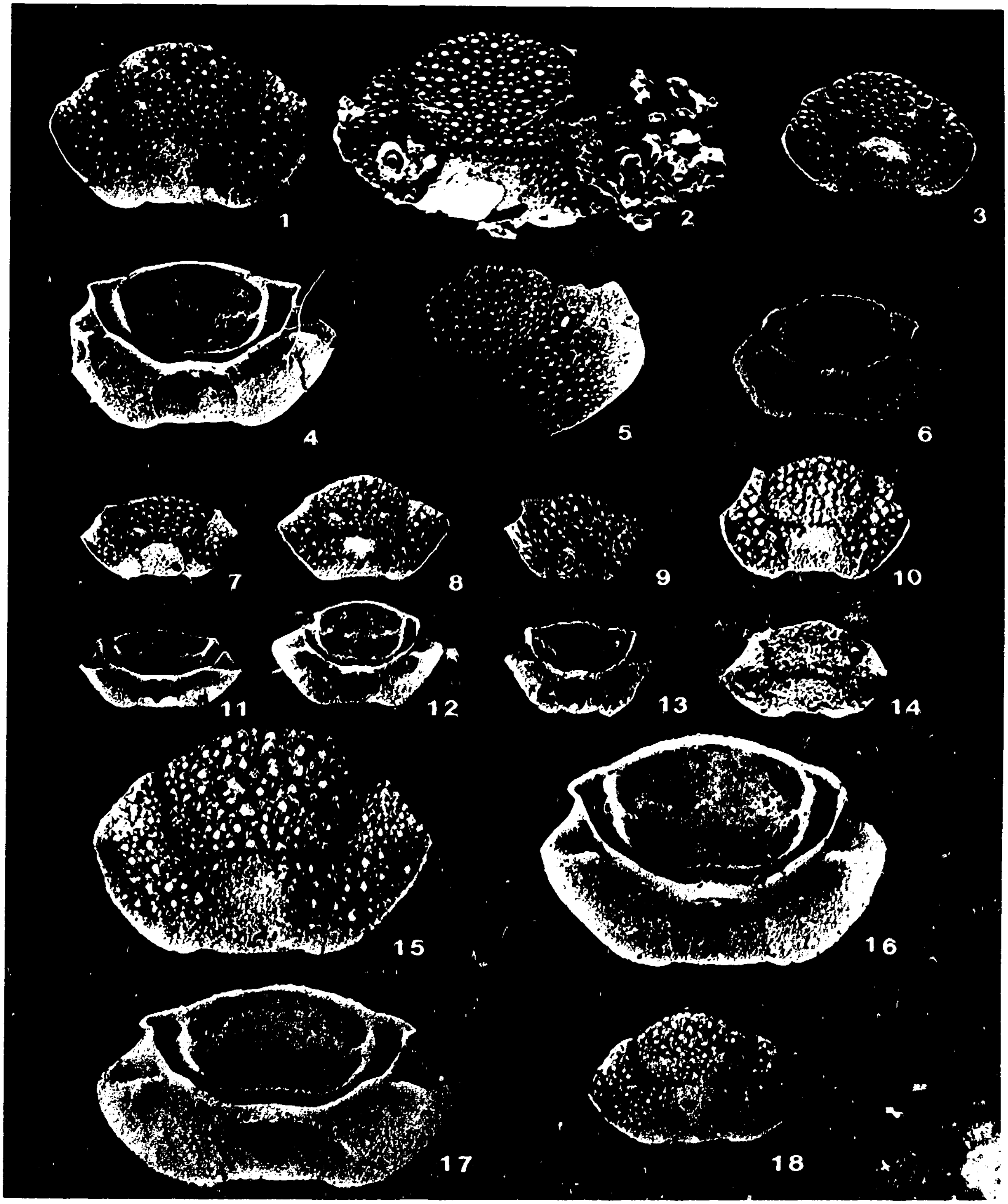
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Plate 32

Figs. 1 - 12.	Protaspides of *Dicranogmus* from the Avalanche Lake sections AV2 248.8 and 249 m, AV4 126 (T) and 126 - 127 m.
1.	Dorsal view of protaspis UA 7905, AV4 126 - 127 m, x31.25. (figured by Speyer and Chatterton, 1989, fig. 10B)
2.	Dorsal view of protaspis UA 10203 AV4 126 - 127 m, x31.25.
3.	Internal view of protaspis UA 10204, AV4 126 -127 m, x31.25.
4.	Dorsal view of protaspis UA 10205, AV4 126 (T) m, x31.25.
5, 6.	Dorsal and ventral (internal) views of protaspis UA 10206, AV4 126 (T) m, x32.5.
7.	Dorsal view of protaspis UA 10207, AV4 126 - 127 m, x36.25.
8.	Ventral (internal) view of protaspis UA 10208, AV4 126 - 127 m, x31.25.
9.	Dorsal view of protaspis UA 10209, AV4 126 - 127 m, x36.25.
10.	Dorsal view of protaspis UA 10210, AV2 248.8 m, x36.25.
11.	Ventral (internal) view of protaspis UA 10211, AV2 249 m, x36.25.
12.	Dorsal view of protaspis UA 10212, AV4 126 (T) m, x41.25.

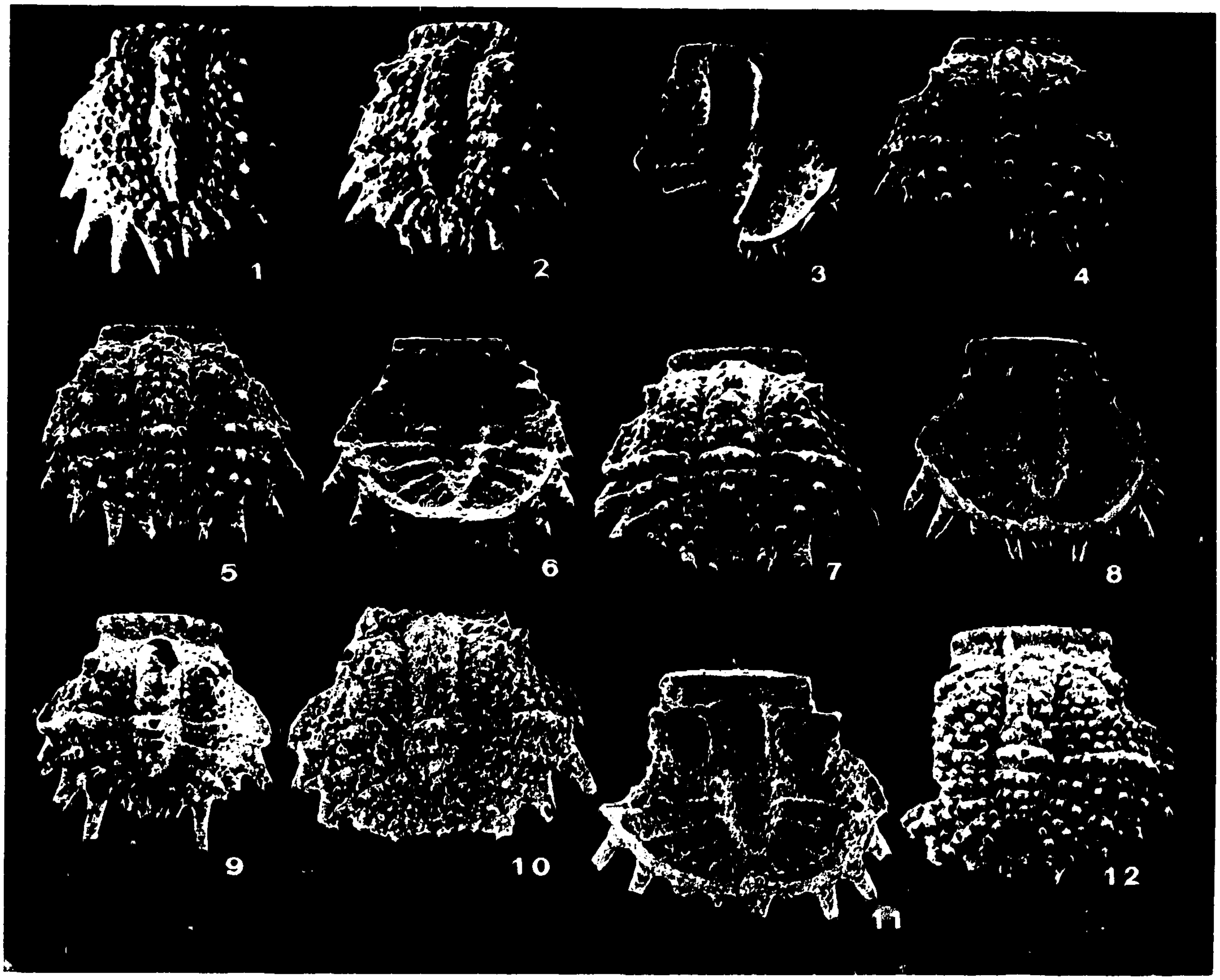
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Plate 33

Figs. 1 - 13. Meraspid sclerites of *Dicranogmus* from Avalanche Lake sections AV4 126 (T) m, unless otherwise stated.

1. Ventral (internal) view of cranidium UA 10213, AV4 126 (T) m, x31.25.
2. Dorsal view of cranidium UA 10214, x31.25.
3. Dorsal view of cranidium UA 10215, x31.25.
4. Dorsal view of cranidium UA 10216, x32.5.
5. Dorsal view of cranidium UA 10217, x31.25.
6. Dorsal view of cranidium UA 10218, x19.
7. Dorsal view of cranidium UA 10219, x22.
8. Dorsal view of cranidium UA 10220, x22.
9. Dorsal view of cranidium UA 10221, x10.
10. Ventral view of hypostome UA 10222, x31.25.
11. Ventral view of hypostome UA 10223, x20.
12. Dorsolateral view of librigena UA 10224, AV2 274 - 279 m, x32.5.
13. Dorsolateral view of librigena UA 10225, x41.75.

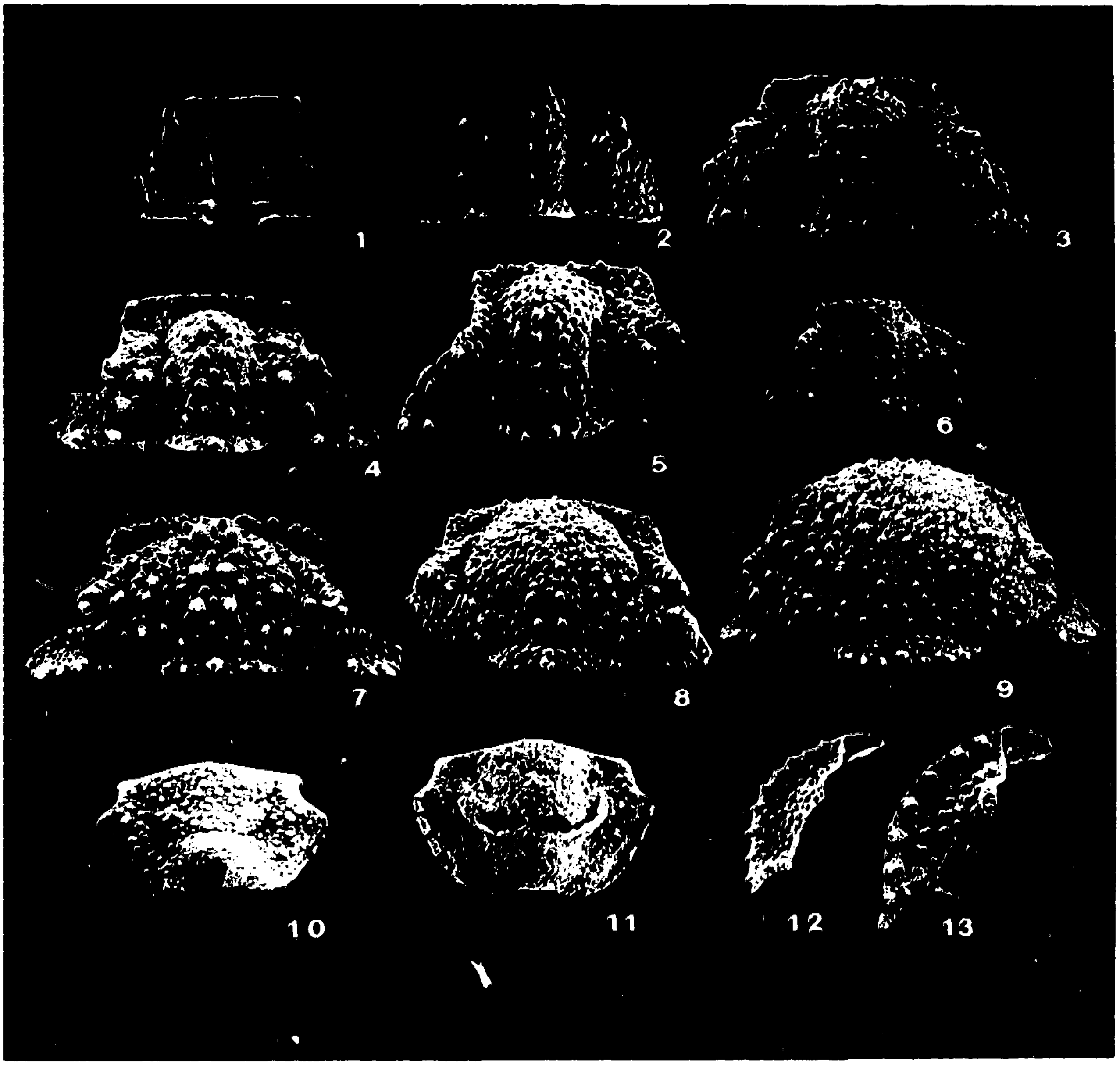
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Plate 34

Figs. 1 - 12. Transitory pygidia of *Dicranogmus* from the Avalanche Lake section AV4 126 (T) m.

1. Dorsal view of transitory pygidium UA 10226, x31.28.
2. Dorsal view of transitory pygidium UA 10227, x25.
3. Dorsal view of transitory pygidium UA 10228, x31.25.
4. Dorsal view of transitory pygidium UA 10229, x31.25.
5. Dorsal view of transitory pygidium UA 10230, x31.25.
6. Dorsal view of transitory pygidium UA 10231, x31.25.
7. Dorsal view of transitory pygidium UA 10232, x31.25.
8. Dorsal view of transitory pygidium UA 10233, x31.25.
9. Dorsal view of transitory pygidium UA 10234, x31.25.
10. Dorsal view of transitory pygidium UA 10235, x31.25
11. Dorsal view of transitory pygidium UA 10236, x10.
12. Dorsal view of pygidium UA 10237, x16.

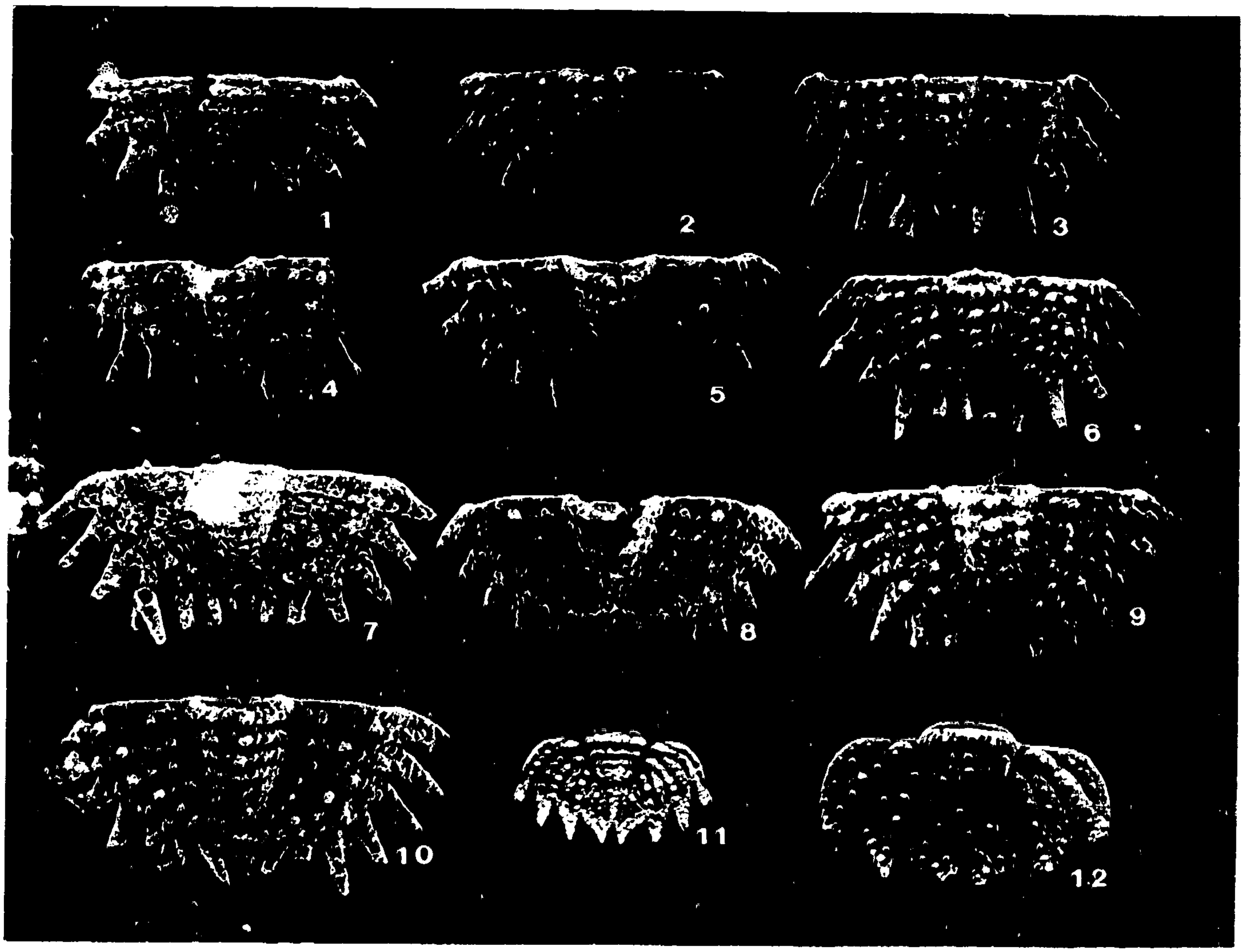
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Plate 35

Figs. 1 - 20.	*Dicranogmus* n. sp. A from Avalanche Lake section AV2 15 m (Llandovery) unless otherwise stated.
1.	Dorsal view of protaspis UA 10238, x31.25.
2, 3.	Posterodorsal and dorsal views of protaspis UA 10239, x30.
4.	Dorsal view of partial protaspis UA 10240, x30.
5.	Dorsal view of meraspid cranidium UA 10241, x31.25.
6.	Dorsal view of transitory pygidium UA 10242, AV1 320 m, x30.
7.	Dorsal view of transitory pygidium UA 10243, x30.
8.	Ventral view of librigena UA 10244, x31.25.
9.	Dorsal view of transitory pygidium UA 10245, x25.
10.	Dorsal view of left meraspid librigena UA 10246, x31.25.
11.	Dorsal view of left meraspid librigena UA 10247, x31.25.
12.	Dorsal view of right meraspid librigena UA 10248, x30
13.	Dorsal view of right meraspid librigena UA 10249, AV1 413, x25.
14.	Dorsal view of right meraspid librigena UA 10250, AV1 413, x25.
15 - 20.	Posterior-to-dorsal, dorsal, anterior-to-dorsal, left lateral, anterior and posterior views of holaspid cranidium UA 10251, x10.

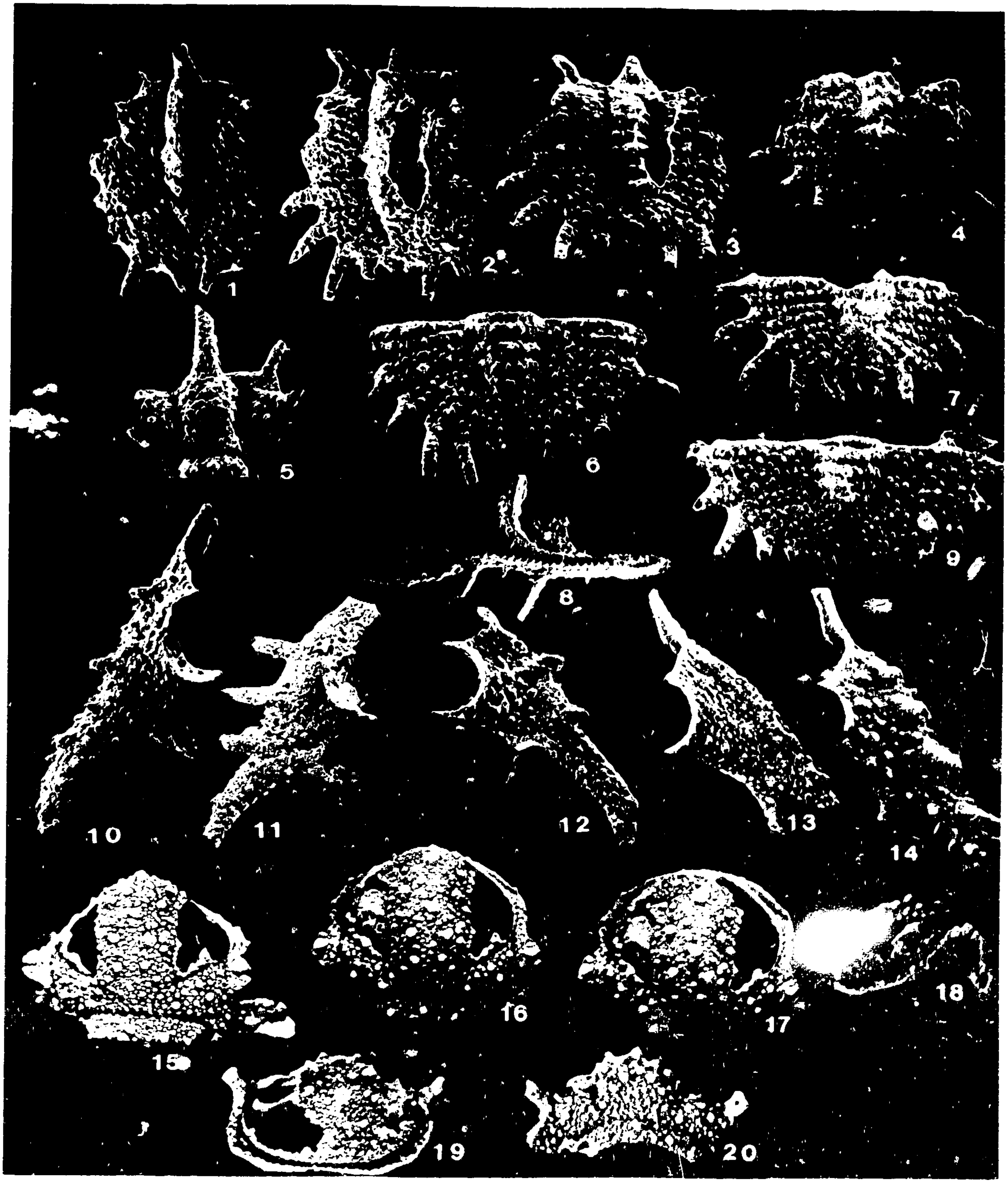
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Plate 36

Figs. 1 - 15.	*Hemiarges avalanchensis* n. sp. from Avalanche Lake section AV4B 16.5 m (Late Ordovician, post-faunal turnover) Magnification x10
1 - 3, 5, 6.	Posterior-to-dorsal, anterior-to-dorsal, anterior, right lateral and posterior views of cranidium UA 10252
4, 7 - 10.	Dorsal, anterior-to-dorsal, posterior-to-dorsal, left lateral and posterior views of cranidium UA 10253.
11.	Dorsal view of holotype pygidium UA 10254.
12.	Dorsal view of pygidium UA 10255.
13.	Dorsal view of pygidium UA 10256.
14.	Ventral view of hypostome UA 10257.
15.	Ventral view of hypostome UA 10258.

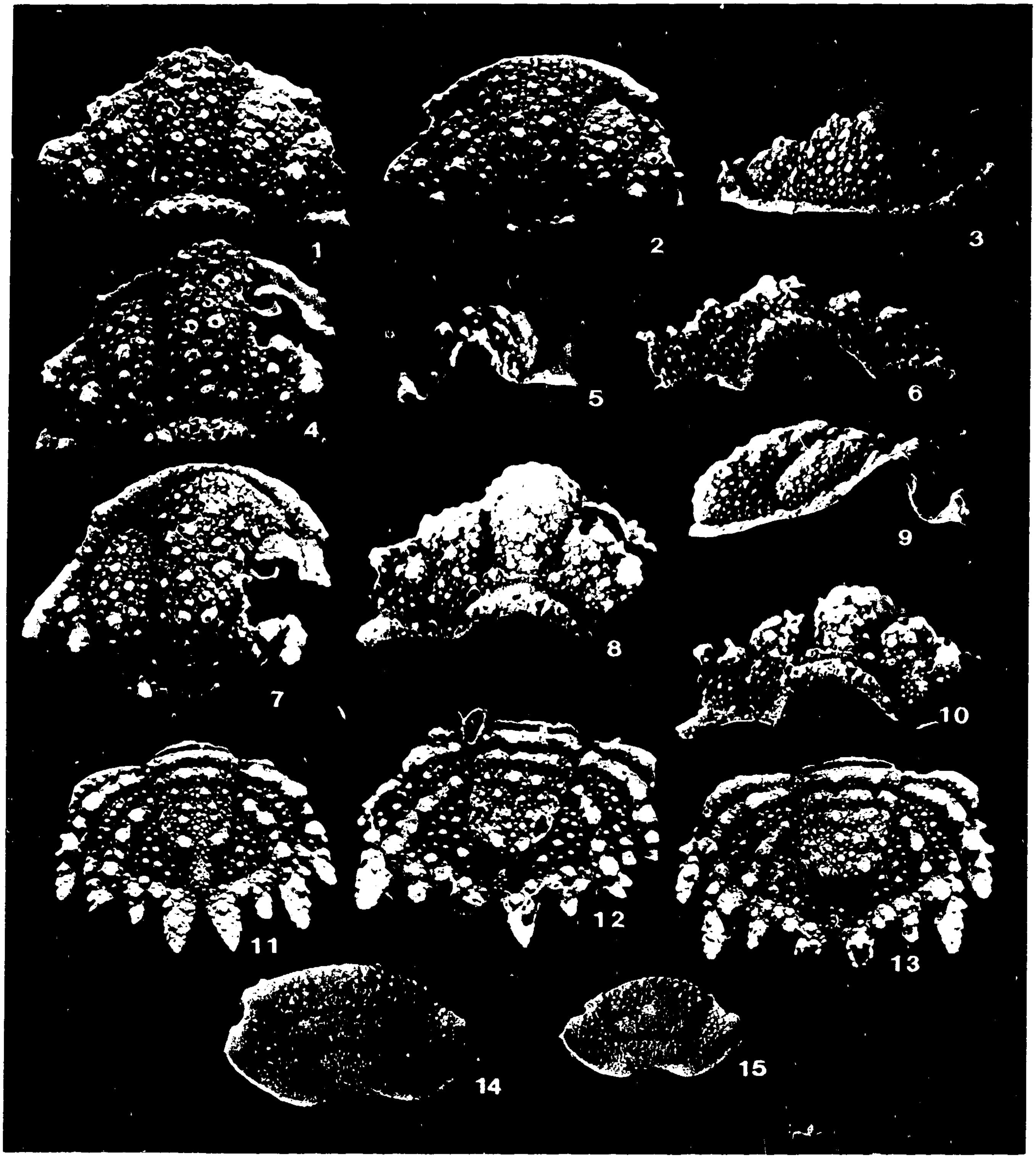
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Plate 37

Figs. 1 - 13.	*Radiolichas* n. sp. A from Avalanche Lake Sections AV1 591 m, AV2 274 - 279 m, AV2 126 (T) m. Magnification x10 unless otherwise stated.
1, 2, 3.	Dorsal, ventral (internal) and lateral views of pygidium UA 10259, AV1 591 m, x5.5.
4.	Dorsal view of pygidium UA 10260, AV2 274 - 279 m.
5 - 9.	Anterior-to-dorsal, dorsal, anterior, right lateral and posterior views of cranidium UA 10261, AV4 126 (T) m, x15.
10 - 13.	Anterior, anterior-to-dorsal, dorsal, posterior-to-dorsal views of cranidium UA 10262, AV 1 595.

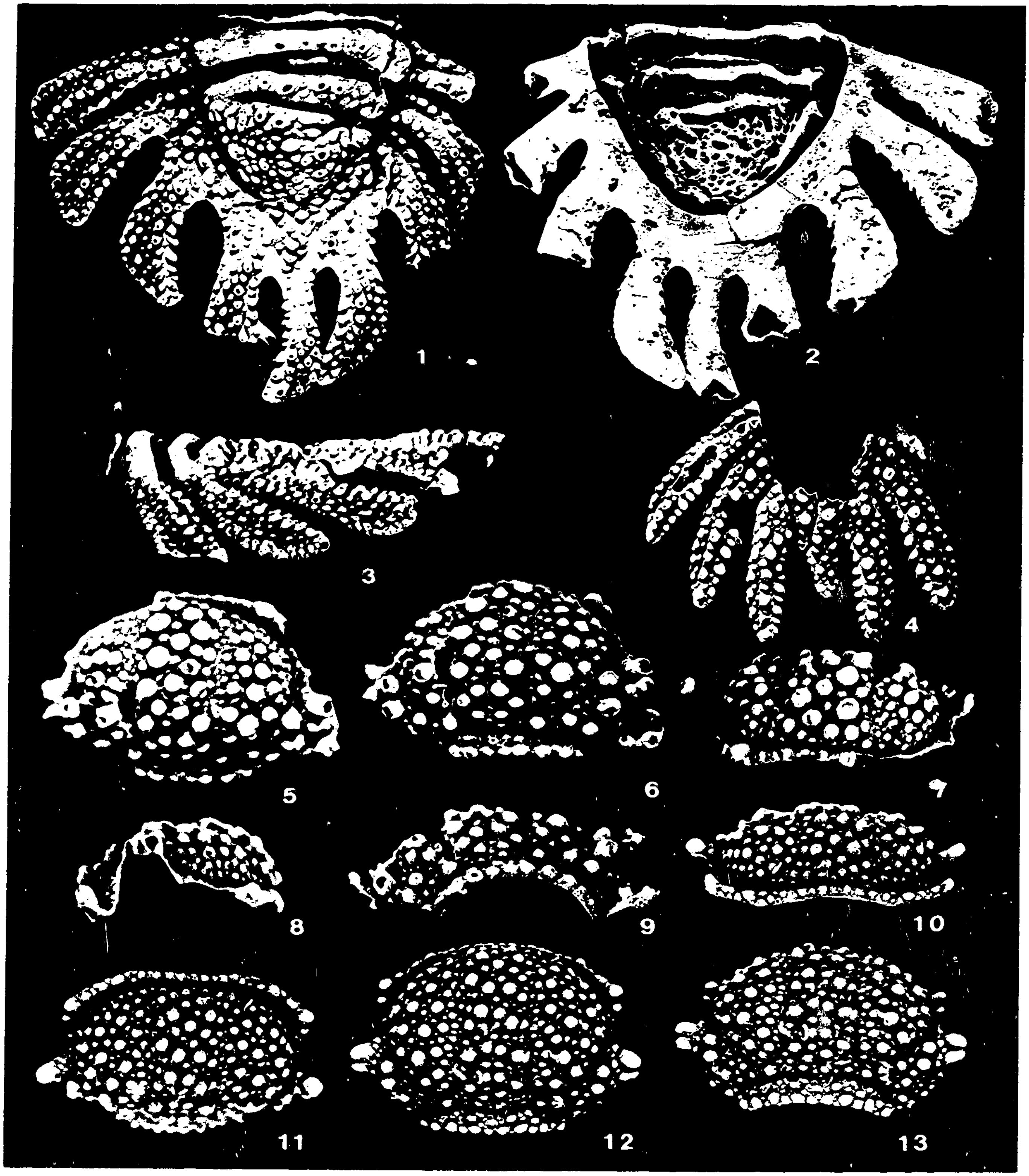
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Plate 38

Figs. 1 - 20.	*Radiolichas* n.sp. A from Avalanche lake sections AV2 256 m, AV2 255 - 260 m, AV4 126 (T) m, AV5 7 m.
1.	Dorsal view of "3 spine" protaspis UA 10263, AV4 126 (T) m, x32.5.
2.	Dorsal view of "5 spine" protaspis UA 10264, AV4 126 (T) m, x35.
3, 4.	Dorsal (x37.5) and ventral (internal) (x31.25) views of "5 spine" protaspis UA 10265, AV 4 126 (T) m.
5.	Dorsal view of partial transitory pygidium UA 10266, AV4 126 (T) m, x 25.
6.	Dorsal view of transitory pygidium UA 10267, AV4 126 (T), x16.5.
7.	Dorsal view of transitory pygidium UA 10268, AV5 7 m, x10.
8.	Ventral view of holaspid hypostome UA 10269, AV2 274 - 279 m, x10.
9.	Dorsal view of fragment of transitory pygidium UA 10270, AV4 126 (T) m, x60.
10.	Dorsal view of pygidium UA 10271, AV4 126 - 127 m, x19.5.
11.	Ventral view of holaspid hypostome UA 10272, AV1 590 m, x10.
12, 13, 16, 17, & 19.	External, lateral (showing terrace lines at margin), internal, dorsal and ventral views of right holaspid librigena UA 10273, AV2 255 - 260, x4.
14.	Dorsal view of left meraspid librigena UA 10274, AV4 126 (T) m, x31.25.
15.	Dorsal view of right meraspid librigena UA 10275, AV4 126 (T) m, x31.25.
18.	Dorsal view of fragment of axial region of holaspid thoracic segment UA 10276, AV1 589 m, x10.
20.	Dorsal view of fragment of axial region and pleura of holaspid thoracic segment UA 10277, AV2 256 m, x7.5.

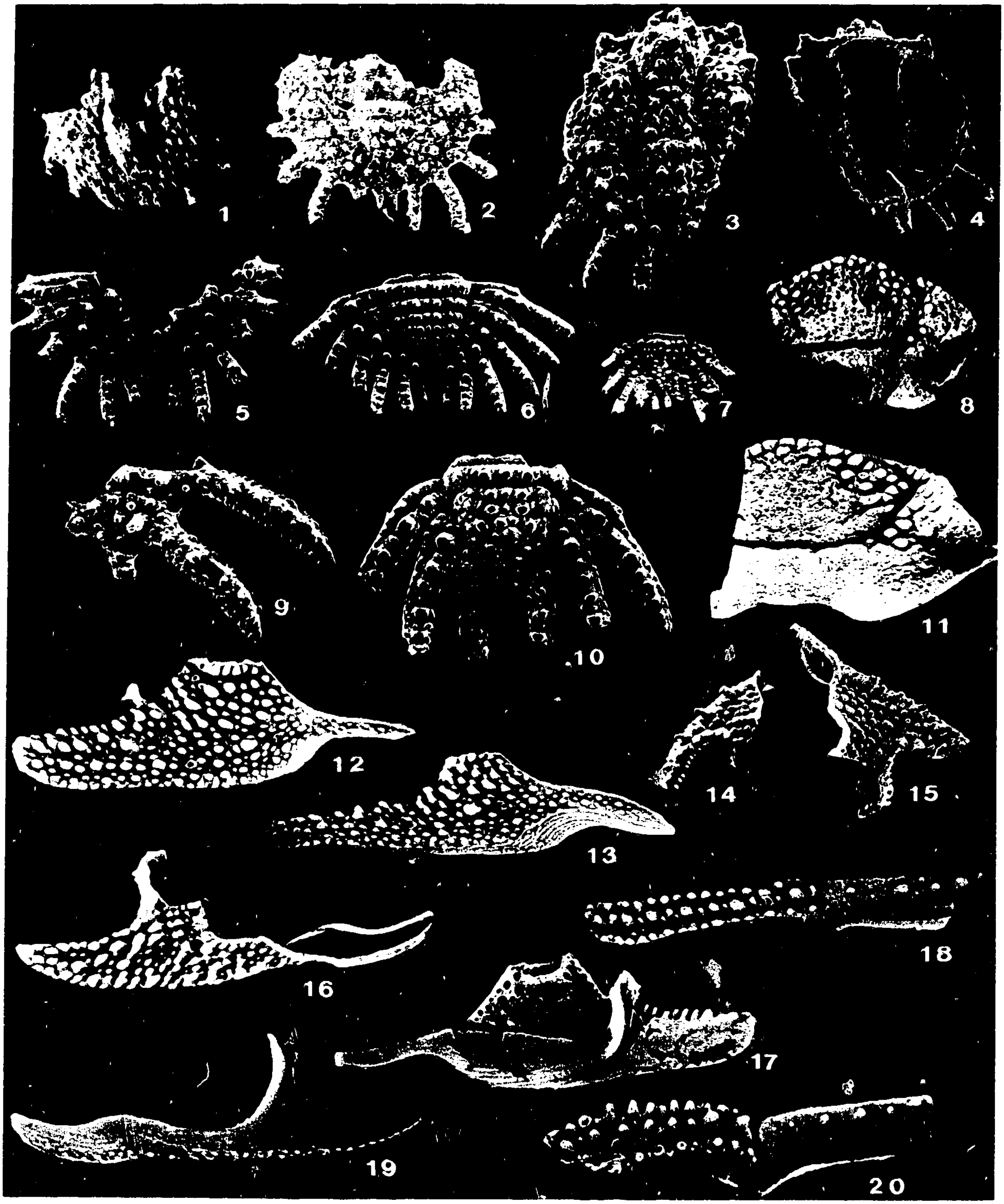
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Plate 39

Figs. 1 - 21

Richterarges facetus n. sp. from the Avalanche Lake sections AV5 57 and 58 - 60 m. Magnification x10, unless otherwise stated.

1, 2, 4.	Dorsal, right lateral and posterior views of holotype pygidium UA 10278, AV5 58 - 60, x7.5.
3.	Dorsal view of pygidium UA 10279, AV5 57.5 m.
5 - 8.	Dorsal, ventral (internal) right lateral and posterior views of pygidium UA 10280, AV5 58 - 60 m.
9.	Dorsal view of partial pygidium UA 10281, AV5 58 - 60, x7.5.
10.	Dorsal view of partial pygidium UA 10282, AV5 58 - 60.
11, 12.	Dorsal and ventral (internal) view of partial pygidium UA 10283, AV5 58 - 60 m.
13.	Dorsal view of partial pygidium UA 10284, AV5 58 - 60.
14 - 16.	Dorsal, ventral (internal) and left lateral view of transitory pygidium UA 10285, AV5 58 - 60 m.
17.	Dorsal view of transitory pygidium UA 10286, AV5 58 - 60 m.
18, 19.	Dorsal and ventral (internal) views of transitory pygidium UA 10287, AV5 58 - 60 m.
20.	Dorsal view of transitory pygidium UA 10288, AV5 58 - 60.
21.	Dorsal view of partial transitory pygidium UA 10289, AV5 58 - 60 m.

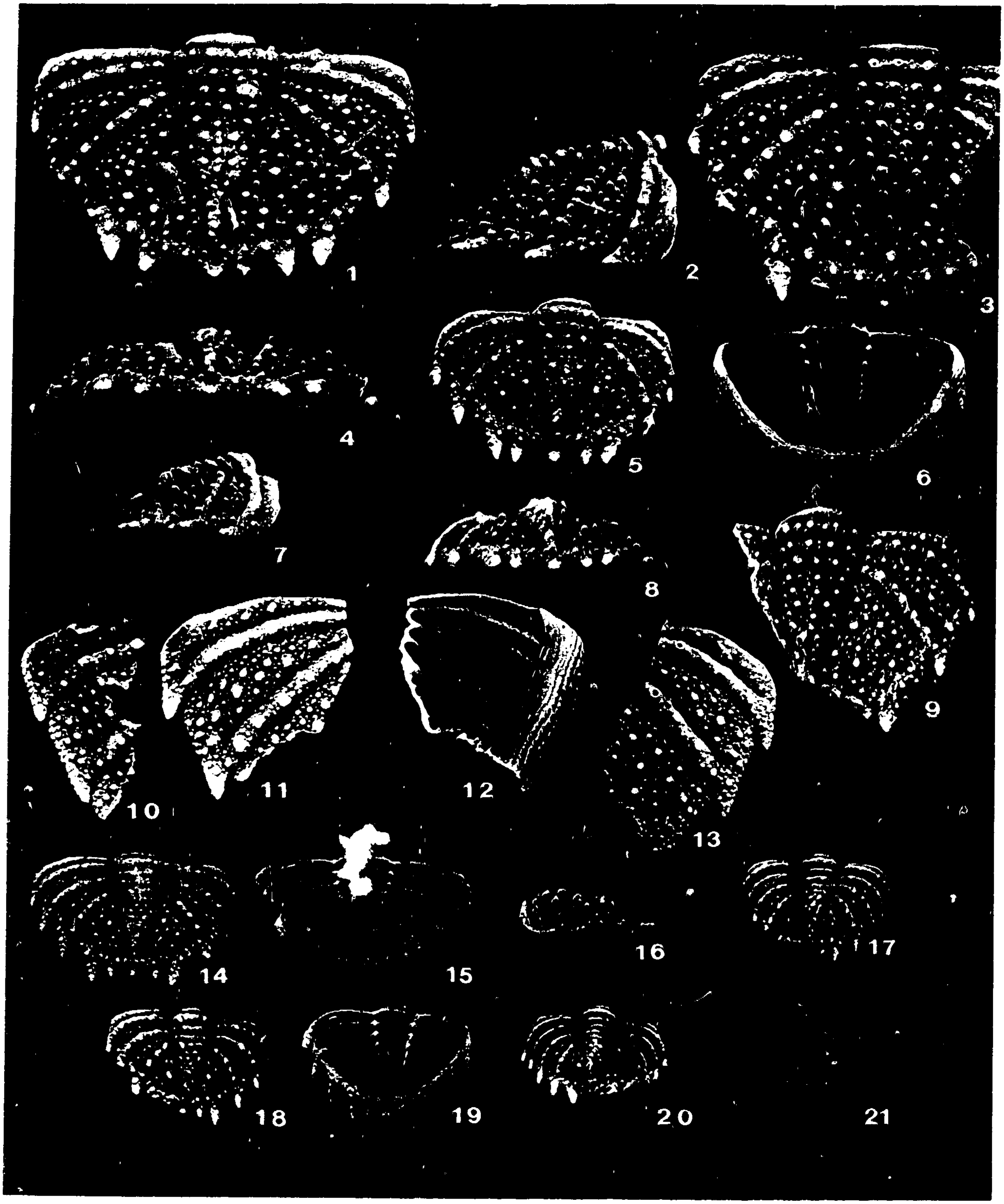
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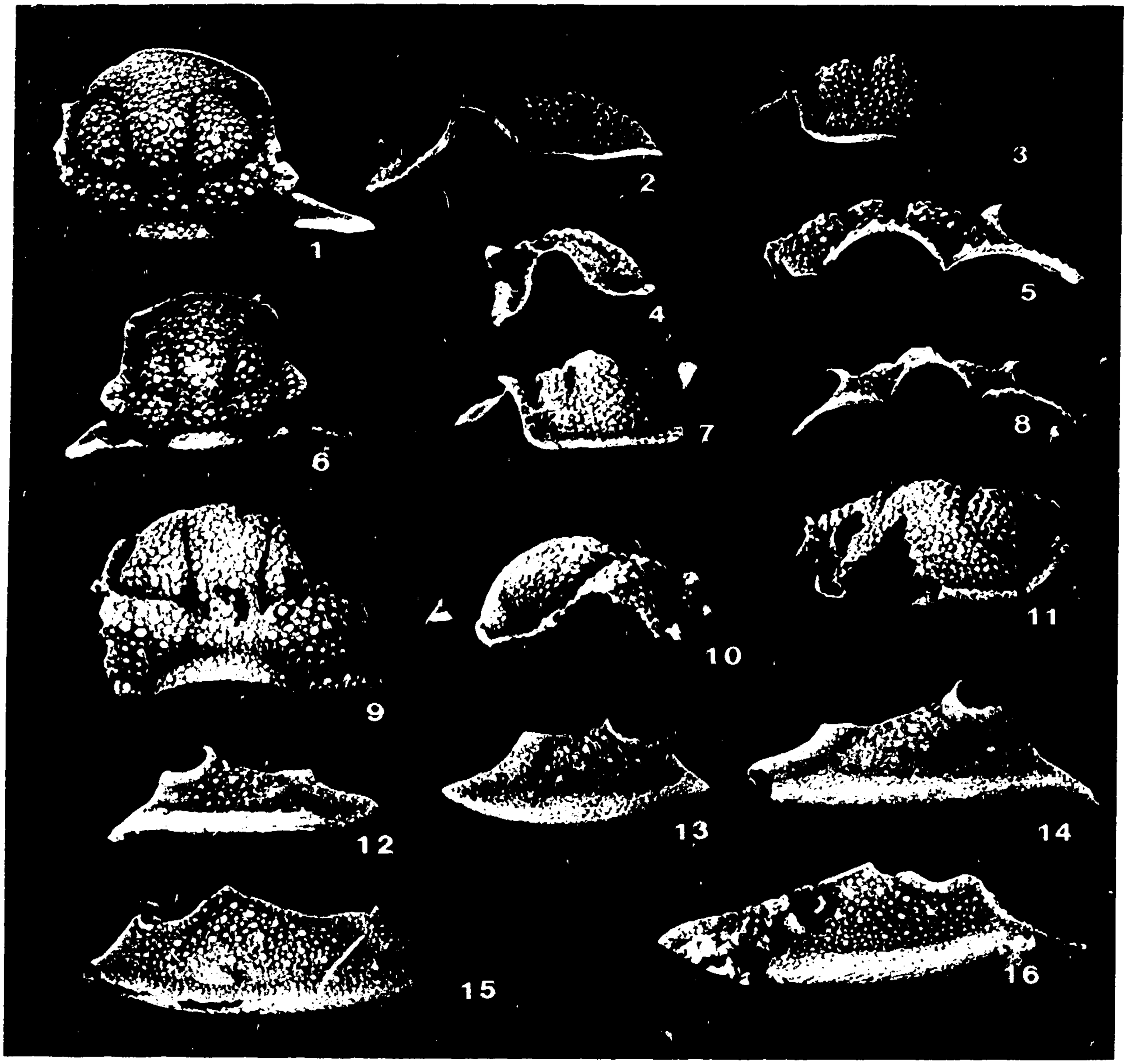
Plate 40

Figs. 1 - 16.	*Richterarges facetus* n. sp. from Avalanche Lake section AV5 58 - 60 m. Magnification x10 unless otherwise stated.
1 - 3, 5.	Dorsal, right lateral, anterior and posterior views of cranidium UA 10290.
4, 6 - 8.	Right lateral, dorsal, anterior and posterior views of cranidium UA 10291, x15.
9 - 11.	Dorsal, left lateral and anterior views of cranidium UA 10292.
12.	External view of left librigena UA 10293.
13.	External view of right librigena UA 10294.
14.	External view of right librigena UA 10295.
15.	External view of left librigena UA 10296.
16.	External view of right librigena UA 10297.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