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Systematics and Biostratigraphy of Lower Cambrian Trilobites of Western Laurentia

by

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We accept this dissertation as conforming
to the required standard

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Abstract

Medial Lower Cambrian strata from continental shelf deposits of western Laurentia yield abundant, low diversity trilobite faunas. New faunas from the Cranbrook and Eager formations (southeastern British Columbia) and the upper Campito, Poleta, Harkless and Saline Valley formations (southwestern Great Basin, California and Nevada) have yielded: 33 species of Olenellina (20 new); 2 new species of Edelsteinaspidae (Redlichiina); 13 species of Corynexochida (5 new); 4 species of Ptychopariina (1 new); 1 new species of Eodiscina; 1 species of Oryctocephalidae; 1 new species of Protypidae; and 1 possible species of Cheiruroideidae. One new genus, *Wannerellus*, is established and tentatively assigned to the Wanneriidae.

Systematic studies emphasize the importance of early ontogenetic features and ventral morphology in determining supraspecific relationships. Major changes are made to the suprageneric classification of the Olenelloidea: the Wanneriidae is recognized as a family separate from the Olenellidae; the Laudoniinae and Gabriellinae are abandoned and their type genera assigned to the Wanneriidae; the Mesonacinae is characterized as a peramorphic subfamily of the Olenellidae; and the Bristolinae is synonymized with the Biceratopsinae (Olenellidae). The Corynexochidae is also changed in membership to include the Dorypyginae (=Ogygopsidae). Heterochrony is a major pattern of evolutionary change in Lower Cambrian trilobites.

Biostratigraphic division of the medial lower Cambrian comprises 10 new subzones of 4 zones and is the first species-based trilobite zonation for Laurentia. It replaces previous genus-based zonations that are imprecise and questionable in recognition. In ascending order, the zonation includes: the *Nevadia weeksi* and *Nevadia palmeri* subzones of the *Nevadia* Zone; the *Nevadella parvoconica* and *Nevadella eucharis* subzones of the *Nevadella* Zone; the *Elliptocephala stewarti*, *Gabriellus poletensis* and *Wannerellus alcatrazensis* subzones of the *Elliptocephala* Zone; and the *Wanneria logani*, *Wanneria dunnae* and *Proliostracus buelnaensis* subzones of the *Olenellus transitans* Zone. These zones and subzones can be correlated with other successions in western and eastern Laurentia.

Biofacies differentiation of restricted shelf deposits is poorly developed in the *Nevadella* though *Elliptocephala* Zones. For this interval, the *Nevadella* and Wanneriid biofacies are successive

biofacies of restricted shelf deposits and the *Labradoria* and *Ekvipagetia* biofacies are successive biofacies of open shelf deposits. Biofacies differentiation is well developed in the *Olenellus transitans* Zone, with an *Olenellus* Biofacies in clastics; a Wanneriid Biofacies in silty and oolitic carbonates; a *Bonnina* Biofacies in pure carbonates; and an *Ogygopsis* Biofacies in open shelf deposits.

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Special thanks are due to my family and friends, John and Joyce Bohach, Todd Ashton, Margaret Campbell and Terry Russell, who generously volunteered as unpaid field assistants. My parents have always encouraged and stood behind me, even when my endeavors puzzled them. Last but not least, I wish to thank my husband, Todd Ashton, for his loving support, enduring patience and unfailing belief in me.

Dedication

For Clem and Pete,
who introduced me to the joy of desert trilobites.

Chapter 1. Introduction

The Lower Cambrian is a critical time in earth history that marks the early evolution of the Metazoa. This is the time of the Cambrian explosion: the abrupt appearance and diversification of most of the major marine invertebrate phyla. The spectacular soft-bodied faunas from Cambrian lagerstätten have received much attention, however, trilobites are a more commonly preserved Cambrian fossil. It is trilobite zonations that form the basis for relative dating and correlation of younger Lower Cambrian strata in Laurentia. Revision of medial Lower Cambrian trilobite systematics and zonal biostratigraphy are the goals of this project.

While hundreds of species of Lower Cambrian trilobites have been described, suprageneric classifications have either fluctuated from author to author (i.e. the Olenellina) or have been inadequately investigated (i.e. the Corynexochida). Little use has been made of early ontogenetic information or ventral morphology in systematic studies of Lower Cambrian trilobites, yet these are excellent features to use in resolving higher taxonomic relationships. Some of the key trilobite genera, such as *Olenellus* and *Bonnia*, have such a broad attributed morphology that the genera cannot be precisely defined or diagnosed. They have acted as wastebasket taxa for Lower Cambrian species that share some general morphological features. In addition, many species have been oversplit as preservational and ontogenetic differences have not been distinguished from actual taxonomic differences. All of these problems have serious implications when an unstable, poorly defined taxonomy is used in biostratigraphy.

Lower Cambrian trilobite faunas of Laurentia are largely endemic, except for those of deep water or outer shelf to slope deposits. The majority of species belong to the Olenellina and an Olenellian Faunal Realm was described by Kobayashi (1972) and Theokritoff (1979) that includes Laurentia, Avalonia and Baltica. In contrast, a Redlichian Faunal Realm was designated in Gondwana, inclusive of China, Australia and Antarctica. These faunal realms are not mutually exclusive: in Morocco and Siberia, both Olenellina and Redlichacean trilobites are found and a Mixed Realm is recognized. These strong faunal differences make world-wide correlation problematic as almost no species and few genera are shared between faunal realms. Endemism is pronounced even within faunal realms, for example, both Laurentia and Avalonia are part of the Olenellian Faunal Realm, yet no genera of Olenellina are common to both. An additional problem is that strata designated as Lower Cambrian in some parts of the world, correlate to strata designated as Middle Cambrian in other areas

(Geyer and Palmer, 1995). Since the base of the Middle Cambrian has not yet been designated, this problem cannot be resolved.

Palmer (1977) provided a summary of Cambrian biostratigraphic divisions applied in various areas of the world. Laurentian schemes have focused on trilobites, although the small shelly fossil *Salterella* has been described as indicative of the medial Lower Cambrian (Fritz and Yochelson, 1988). The biostratigraphic scheme currently in use for Laurentia was developed by Fritz (1972) on faunas of the Sekwi Formation of the Mackenzie Mountains. There are many problems with this zonal biostratigraphy: first, it is a genus-based zonation. Genera are long-ranging and consequently cannot be used for precise correlation or relative dating. There are also problems with the current taxonomic definitions of many genera. Second, most of the zonal boundaries have not been defined. It might be assumed that the zones are genus-range zones, but it has not been explicitly stated. If they are genus-range zones, then the *Fallotaspis* Zone is particularly problematic since no species of *Fallotaspis* have yet been described from Laurentia. Third, the zones have not been adequately characterized. For example, the *Bonnina-Olenellus* Zone represents a thick stratigraphic interval, yet Fritz (1972) listed only a few genera that are supposed to characterize the upper part of that zone. Fourth, there is no attempt made to account for biofacies restrictions and to integrate the spatial component of biostratigraphy with the time component. All of these factors contribute to a Lower Cambrian biostratigraphy for Laurentia that is imprecise and difficult to apply. What is needed is a species-based zonation.

Development of a species-based zonal biostratigraphy requires three things: a consistent and defensible taxonomy, documentation of biofacies and detailed stratigraphic information on species ranges. To facilitate this investigation, two study areas were identified. The first area, in southeastern British Columbia, was collected from in the fall of 1991 and the spring of 1992. It comprises two fossiliferous Lower Cambrian units: the Cranbrook and Eager formations. Representation of faunas from the middle carbonate belt is good while representation of faunas from the inner detrital belt is fair. These faunas, however, represent only a portion of the Lower Cambrian trilobite succession. An additional study area needed to be identified and other fossiliferous Lower Cambrian strata in British Columbia were either already under investigation by other researchers, or were inaccessible without helicopter support. Nearby deposits in Washington and Idaho were inappropriate for investigation as their Lower Cambrian trilobite faunas are rare and of poor quality. The Great Basin of the western United States was targeted next as a potential study area and A.R. Palmer of the Institute for Cambrian Studies was contacted to determine what areas were available for

study. Palmer invited the author on a tour of the southwestern Great Basin in August of 1992 and provided an introduction to the geology and faunas. At that time, C.A. Nelson, a retired geologist with extensive, undescribed collections from the White-Inyo Mountains, California, and Esmeralda County, Nevada, was introduced to the author. It was agreed that these collections be made available for this study and that the southwestern Great Basin become a second study area for the project. The Poleta, Harkless and Saline Valley formations were identified as the main fossiliferous formations and designated as the stratigraphic units for investigation. Faunas from these strata provided good coverage of both inner detrital and middle carbonate belt deposits while faunas from outer shelf facies have limited representation. Some collections from the Montenegro Member of the Campito Formation were later added when necessary for taxonomic completeness. The stratigraphic succession of the Great Basin is the correlative of the British Columbia succession, but represents a more comprehensive stratigraphic and fossil record.

Field work in the southwestern Great Basin was done in the spring of 1993. All field work in this study emphasized making stratigraphic collections from measured sections and obtaining large samples. A total of 10 sections were measured and collected: four in southeastern British Columbia and six in the southwestern Great Basin. These have been supplemented by collections from 29 spot localities (7 in British Columbia; 22 in the Great Basin) that could be tied into the stratigraphic succession. All collections are of crack-out limestone and shale material that required extensive splitting in the field to make collections. In the lab, material was split further and specimens were prepared using a small chisel and electric engraver. The best specimens were prepared further and photographed. All stages of the photographic process were done by the author.

Goals of the preparatory and systematic work were to discover and describe as much as possible of the whole body morphology (particularly ventral features) and the ontogenetic development of each species. Of the 55 species recognized from the study areas (44 of which are reasonably well-known), hypostomes are illustrated for 26 and ontogenetic stages for 36. Major ontogenetic patterns and hypostomal morphologies can be recognized and used to diagnose families and genera. Recognition of ontogenetic patterns further permits description of heterochrony in the evolution of Lower Cambrian trilobites.

Once a revised and defensible taxonomy is produced, development of a zonal biostratigraphy can proceed. Biofacies analysis is the first step to determine the spatial restrictions on trilobite distributions. Specimen counts were made of all trilobite collections and biofacies

defined based on the predominant genera. Since collections are all of relatively low taxonomic diversity, simple inspection and production of pie diagrams were sufficient to identify and document biofacies patterns. Biofacies are well-developed in the younger strata examined, but *Olenellina* trilobites are found in most shelf deposits and a single zonation scheme is sufficient for deposits of the continental shelf. The species-based zonal biostratigraphy developed here can be related to most shelf sequences described for Laurentia.

Chapter 2. Geology

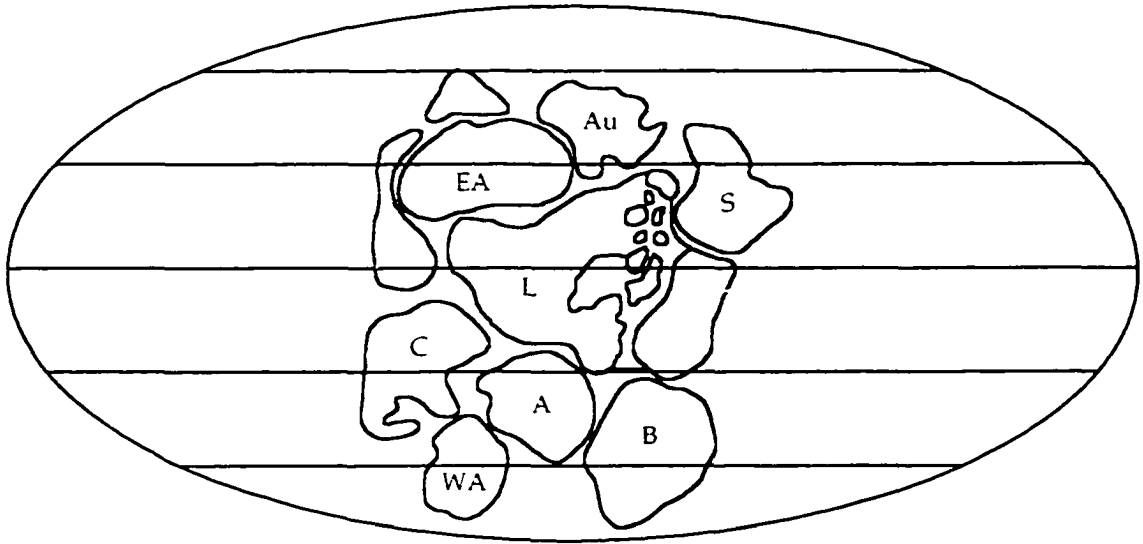
The Cambrian System

The Cambrian System was one of the last chronostratigraphic units to be acceptably defined by 19th century stratigraphers. Adam Sedgwick first proposed the name in 1835 for a package of rocks in North Wales. The name Cambrian, was coined from the Latin name for Wales, Cambria. At the same time as Sedgwick announced the Cambrian System, Roderick Murchison defined his Silurian System. When later field work demonstrated that the upper strata of the Cambrian System and the lower strata of the Silurian System were the same stratigraphic package, definition of both systems became unresolved. This created a bitter conflict between Murchison and Sedgwick, as neither system had priority over the other, and neither geologist would agree to redefine the sequence of rocks assigned to his system. The conflict was not resolved until after the death of both parties, when Lapworth in 1879 proposed the Ordovician System for the disputed strata (Secord, 1986).

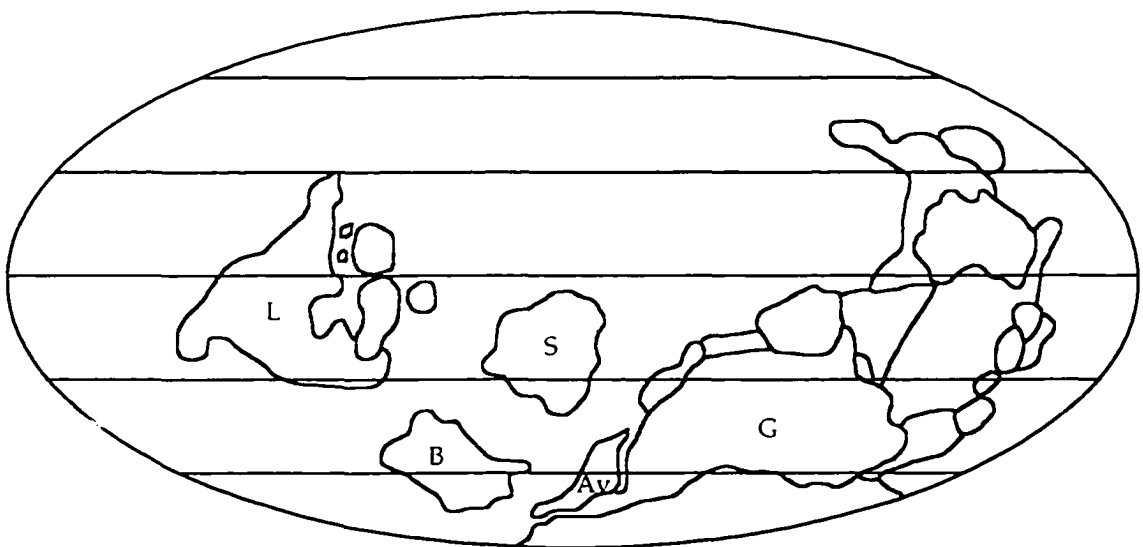
Strata underlying the Cambrian System are commonly referred to as Precambrian and subdivided into an older Archean Eon and a younger Proterozoic Eon (Harland *et al.*, 1990). The term Proterozoic will be used here to refer to the strata and the time interval preceding the Cambrian.

The term Cambrian System did not come into general use in North America until the 1880s with the work of Hunt (1883, 1884) and Walcott (1883). It replaced, in part, the term Taconic System (Emmons, 1844), and similarly the "Primordial Fauna" of various authors (i.e. Barrande, 1861) became, in part, Cambrian. Parts of both the Taconic System and the Primordial Fauna represent strata and fossils now assigned to the Ordovician and Silurian. Walcott (1886) was the first to attempt to subdivide the North American Cambrian rocks into series. Walcott (1886, 1890) initially used the name Georgian Series for the Lower Cambrian, which he later (1912b) replaced with the name Waucoban Series when he decided that it was in bad form to use a formational name (i.e. the Georgia slate of Franklin County, Vermont) as a series name.

Fritz (1991b, 1995) restricted the Waucoban Series to the upper portion of the Lower Cambrian in Laurentia, and applied the name Placentian Series for the lower portion. Recognition and use of the term Placentian for Laurentian strata is here considered problematic since it was defined by Landing (1989) for rocks and fossils in the Avalonian portion of Newfoundland, which was a different continent from Laurentia in the early Cambrian (Text-fig. 2). The base



Text-fig. 1. Reconstruction of the Late Proterozoic supercontinent Rodinia at approximately 700 million years ago (after Hoffman, 1991). A=Amazonia, Au=Australia, B=Baltica, C=Congo, EA=East Antarctica, L=Laurentia, S=Siberia, WA=West Africa



Text-fig. 2. Reconstruction of Early Cambrian continental positions (after McKerrow *et al.*, 1992). Av=Avalonia, B=Baltica, G=Gondwana, L=Laurentia, S=Siberia

of the Placentian Series and the base of the Cambrian System in Avalonia is defined at the base of the *Phycodes pedum* Zone (trace fossil). The top of the Placentian Series equates to the base of the *Callavia* Zone (trilobite). The fossils, and consequently the faunal zones, are different on Avalonia and Laurentia and correlation is speculative at best. Fritz (1991b) defined the boundary between the Placentian and Waucoban series in Laurentia as the boundary between his (Fritz, 1972) *Fallotaspis* and *Nevadella* zones, based on tentative correlation between the *Callavia* and *Nevadella* zones (Fritz, 1972). No trilobite species or genera are shared between these two zones and, accordingly, the two successions cannot be correlated.

Base of the Cambrian

The base of the Cambrian has been placed at different, widely-spaced levels since the middle of the last century, either at the unconformity in most shelf sequences of Precambrian to Cambrian rocks, or at the first appearance of a particular group of skeletal fossils. Starting in 1972, the Precambrian-Cambrian Boundary Working Group began searching for the most appropriate stratotype section and the best interval at which to define the boundary (i.e. see Cowie and Brasier, 1989). In 1992, the controversy was finally resolved when the International Union of Geological Sciences ratified placement of the Lower Cambrian boundary at the base of the *Phycodes pedum* Zone, at a stratotype section of deep-water strata at Fortune Head, Newfoundland (Landing, 1994). This boundary placement was a radical decision in that it used trace fossil rather than body fossil zonation and included in the Cambrian System a thick series of poorly fossiliferous rocks that many authors previously had considered Proterozoic. This boundary is located well below the first appearance of trilobites, but only a short stratigraphic distance below the first small shelly fossils. Only rare and problematic tubular shelly fossils such as *Cloudina* (see McMenamin and McMenamin, 1990) and *Wyattia* (see Taylor, 1966) occur elsewhere in Proterozoic rocks. An age of approximately 544 million years for the boundary has been determined by radiometric dating using uranium-lead zircon data (Bowring *et al.*, 1993), which is considerably less than previous estimates of 570 to 590 million years (i.e. Harland *et al.*, 1990).

In the short time since the *Phycodes pedum* Zone has been chosen as the basal Cambrian zone, there has been little documentation in western Laurentia of the Precambrian-Cambrian boundary. An unconformity has long been recognized at the boundary in many places, especially southern British Columbia (i.e. Walcott, 1910a; Aitken, 1969), and it is unlikely that strata of this age will be found. In northern Canada, Brasier and Cowie (1989) recorded *Phycodes* aff. *pedum* in the Vampire Formation of the Mackenzie and Wernecke Mountains,

while Fritz *et al.* (1983) recorded *P. pedum* from an unnamed map unit immediately below the Vampire Formation. Fritz (1984) also recorded *Phycodes* sp. in the Boya Formation of the Omineca Mountains. In my study area within the Great Basin, Crimes (1989) recorded *Phycodes* and other complex, typically Cambrian trace fossils from the Deep Spring Formation. Recognition of the genus gives little age control on the strata as Crimes (1992) indicated that the range of *Phycodes* extends to the Silurian, but it can be taken as an indication that the strata are at least Cambrian as opposed to Proterozoic in age (Crimes, 1989).

The Lower - Middle Cambrian Boundary

A global stratotype section for the base of the Middle Cambrian is currently undefined (i.e. see Geyer and Landing, 1995). Walcott (1891) considered the Lower Cambrian to be synonymous with the "*Olenellus* Zone": in modern terms, this placed Walcott's boundary at the last occurrence of the *Olenellina*. Many subsequent trilobite workers did not follow Walcott's definition and Resser (1938), Howell *et al.* (1944) and Lochman (1947) all recognized a variably defined post-*Olenellina* Lower Cambrian zone.

Rasetti (1951) recommended a provisional return to Walcott's boundary definition, although he recognized the complications of an unconformity at this interval for most continental shelf deposits and that the disappearance of a group was not likely to be synchronous in all places. Fritz (1991b) accepted Walcott's definition of the boundary without comment and Palmer (1979) suggested that this faunal change might be a biomere boundary¹. The stratigraphic code guidelines state that the top of a stratigraphic interval is by the base of the overlying unit. Accordingly, the Lower - Middle Cambrian boundary should be defined by the lowest fossil zone characteristic of the Middle Cambrian.

Within the study area in British Columbia, Middle Cambrian strata are not preserved and Fritz (1991b) recorded the Upper Cambrian Jubilee Formation unconformably overlying the Lower Cambrian Eager Formation. In the Great Basin, the presence of a unconformity in the basal Middle Cambrian is controversial.

¹ A biomere, according to Palmer (1979, p. 33) is a "regional biostratigraphic unit, bounded by abrupt, non-evolutionary changes in the dominant elements of a single phylum, which were not related to physical discontinuities in the sedimentary record". The biomere concept is controversial. Ludvigsen and Westrop (1985) discounted the attributed uniqueness of a biomere and, instead, proposed that Upper Cambrian biomere boundaries are stadial boundaries.

Regional Tectonic and Depositional Setting

Proterozoic Prelude

The existence of the mid-Proterozoic supercontinent Rodinia has gained wide acceptance (Hoffman, 1992). The consensus for distribution of the continents is that Laurentia occupied a central position within the supercontinent (Text-fig. 1; Hoffman, 1991) with Siberia adjoining the current northwest Laurentian margin (Condie and Rosen, 1994; Pelechaty, 1996), Australia the central western margin (Young, 1992; Idnurm and Giddings, 1995) and east Antarctica the southwestern margin (Moores, 1991; Dalziel, 1991). Timing of the breakup of Rodinia has been variously constrained using evidence from paleomagnetism (Powell *et al.*, 1993), regional stratigraphy (Lickorish and Simony, 1995; Pelechaty, 1996) and tectonic subsidence curves (Bond *et al.*, 1984; Levy and Christie-Blick, 1991). Multiple rifting events were likely involved beginning around 700 million years ago and culminating with final continental separation and initiation of the Paleozoic phase of passive margin subsidence near the Precambrian–Cambrian boundary (Bond *et al.*, 1985; Devlin and Bond, 1988; Ross, 1991). Lower Cambrian strata record the final phase of rifting and the initiation of miogeoclinal sedimentation on a passive margin.

Ross *et al.* (1989), Aitken and McMechan (1991) and Gabrielse and Campbell (1991) provided overviews of Proterozoic sedimentation in eastern British Columbia. Middle Proterozoic rocks consist of the Purcell Supergroup in the southern region which is interpreted to have been deposited in an intracratonic setting as rifting of Rodinia commenced (Gabrielse and Yorath, 1991). A period of deformation and uplift followed, preceding deposition of the Upper Proterozoic rocks of the Windermere Supergroup. Windermere strata, which include glacial deposits, have been tentatively interpreted (Ross, 1991) as a rift to passive margin sequence which predates the rift event associated with initiation of the Cambrian passive margin subsidence.

Stewart (1991) provided an excellent overview of Proterozoic to Cambrian sedimentation in the western United States. He documented a late Proterozoic glacial and volcanic succession followed by a clastic sequence extending through to the Cambrian. In the southwestern Great Basin just south of the thesis area, the mid-Proterozoic Pahrump Group, an intracratonic rift sequence, is unconformably overlain by the Noonday Formation that marks a transition to thermally driven subsidence (Levy and Christie-Blick, 1991). Overlying clastics were interpreted as a possible extensional sequence with subsidence curves indicating final continental separation and initiation of passive margin deposition occurring in this interval.

Lower Cambrian Deposition and Tectonic Setting

Many reconstructions of continental positions have been proposed over the years for the Early Cambrian. One of the most recent is shown in Text-fig. 2. Latitudinal positions of continents are constrained by paleomagnetism, but longitudinal positions are less exact, based largely on faunal similarities between continents. All reconstructions show Laurentia to be an isolated continent located at low latitudes and oriented approximately 90° clockwise compared to the present. This orientation is significant as it means that no large scale latitudinal variations in climate would have influenced faunal distributions of western Laurentia. Baltica and Siberia were also isolated continents positioned between Laurentia and Gondwana.

North (1971) and Fritz (1991b) have both provided excellent overviews of Cambrian geology of eastern British Columbia. The sedimentary record of the Proterozoic-Cambrian boundary is variously preserved. Colpron and Price (1995) suggested that the pericratonic Kootenay Terrane was depositionally linked to and is continuous with typical Laurentian cratonic deposits. The uppermost Proterozoic to Lower Cambrian Hamill Group of this region records the extensional tectonism to passive margin subsidence near the Precambrian-Cambrian boundary (Devlin and Bond, 1988; Devlin, 1989). Another record of this late rifting event is the Gog Group of the Rocky Mountain main ranges (Lickorish and Simony, 1995). In the southernmost portion of the province, Cambrian sedimentation was influenced by Montania (i.e. Deiss, 1941; North, 1971), a tectonically positive area, responsible for a sub-Middle Cambrian unconformity (Norris and Price, 1966; Ross *et al.*, 1989; Colpron and Price, 1995). Within the study area in British Columbia, the Lower Cambrian Cranbrook Formation unconformably overlies Middle Proterozoic strata of the Purcell Supergroup. In the Great Basin, strata of the Proterozoic to Cambrian boundary contain only localized evidence for the Cambrian rift event indicated by the presence of a small amount of volcanic rocks and a minor unconformity (Levi and Christie-Blick, 1991).

Initial deposits on the newly rifted passive margin of western Laurentia consist mainly of thick sandstone and quartzite sequences with minor conglomerates (Gabrielse and Yorath, 1991). The Cranbrook Formation of southeastern British Columbia is an excellent example. The Deep Spring Formation of the southeastern Great Basin has a more mixed lithology of abundant coarse clastics with limestones.

Lithofacies distributions for the Lower Cambrian strata are similar to those described by Palmer (1960) for Upper Cambrian rocks. Three depositional belts can be recognized: a near-shore inner detrital belt, continental shelf middle carbonate belt and offshore outer detrital

belt. These facies belts interfinger as they migrated laterally in response to changes in sea level, subsidence rate and sedimentation. Aitken (1966) recognized that the pattern of sedimentation was cyclic with large scale alterations of predominantly clastic sedimentation followed by predominantly carbonate sedimentation that he called grand cycles. This concept has been applied to Lower Cambrian strata of the Cordillera by Palmer and Halley (1979), Fritz (1975), Mount and Rowland (1981) and Mount *et al.* (1991).

Geology and Historical Paleontology of the Study Areas

Two study areas are targeted in this thesis (Text-fig. 3): one in southeastern British Columbia, the other in the southwestern Great Basin.

Southeastern British Columbia

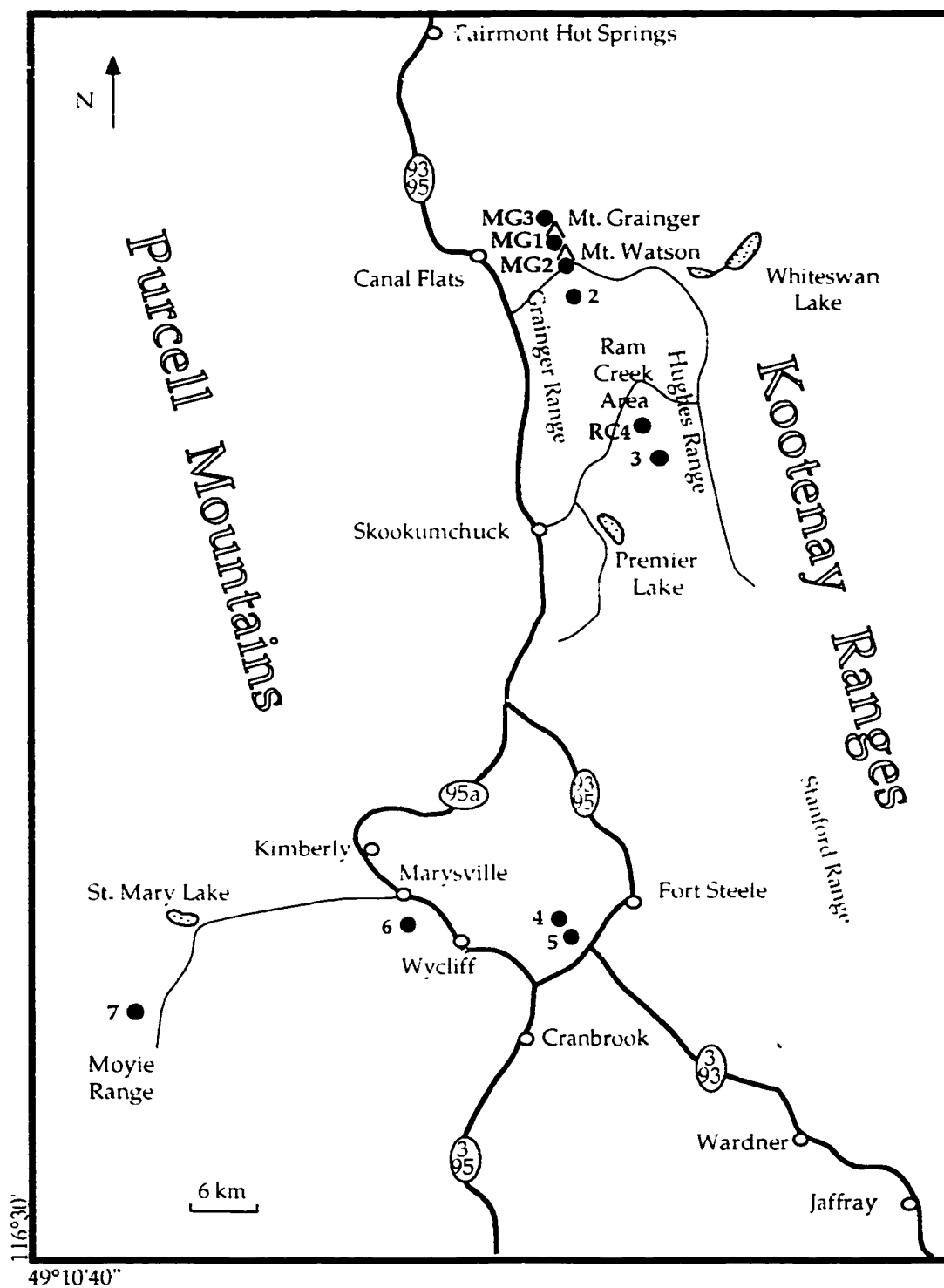
The study area in British Columbia is centered in the Cranbrook to Canal Flats regions (Text-fig. 4) and focuses on the Cranbrook and Eager formations. The generalized stratigraphy for the region is outlined in Text-fig. 5). Early geological exploration of the region was done by Daly (1913), Schofield (1914, 1915, 1922) and Walcott (1924). Walcott (1924, p. 29-30) named Mount Grainger and published a measured section, including a list of fossils collected and previously reported by Schofield (1922, p. 14). Schofield (1921) also announced discovery of Lower Cambrian trilobites near Cranbrook, from what is now known as the Rifle Range locality. Detailed mapping of the Cranbrook region was done by Rice (1937) and Leech (1958a) and mapping of the Canal Flats region by Leech (1954, 1958b).

Cranbrook Formation

As is typical of the lowest Lower Cambrian formations in the south-central Cordillera, the Cranbrook Formation is a coarse clastic deposit separated from underlying Middle Proterozoic strata by an unconformity. The angular unconformity at this contact is graphically demonstrated by the variety of Proterozoic formations of different ages (i.e. Siyeh, Gateway, Purcell intrusives) that underlie the Cranbrook Formation in different localities. Basal deposits of the Cranbrook consist of conglomerates containing clasts of the same lithology as underlying strata. Schofield (1922) first designated the Cranbrook Formation for a series of light coloured quartzites near the city of Cranbrook. The formation has since been recognized in the Purcell Mountains between St. Mary Lake and Creston (Rice, 1941), the Stanford Range of the Rocky Mountains near Fort Steele (Rice, 1937; Leech, 1958a) and north to the area around Canal Flats (Leech, 1954, 1958b).

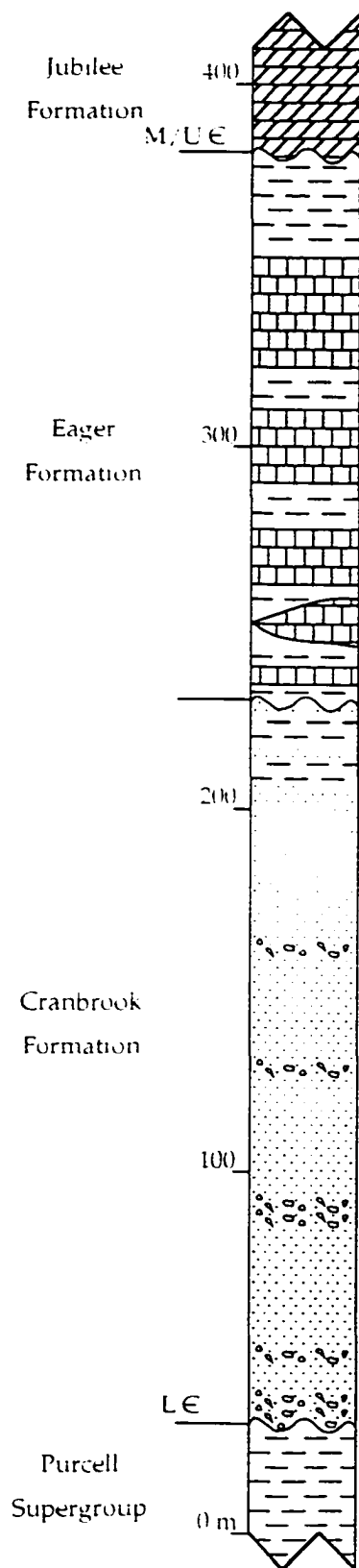


Text-fig. 3. General locality map with studies areas in southeastern British Columbia and the southwestern Great Basin indicated.



Text-fig. 4. Locality map of study area in southeastern British Columbia. Locality numbers correspond to those listed in Appendix A.

Text-fig. 5. Composite Upper Proterozoic to Middle/Upper Cambrian stratigraphic succession in southeastern British Columbia.



Rice (1937) and Leech (1954) have both described the general character of the Cranbrook quartzites and recorded local variations. The quartzites are distinctly bedded with bed thickness ranging from 30 to 180 cm. Most beds are massive. Interbedded pebble conglomerates and grits were also reported by Leech (1954) as well as a less-cemented interval of yellow-weathering sandstones towards the top of the formation. Shale interbeds become common approaching the upper boundary. Schofield recorded a thickness of 180 m in the Cranbrook region, Leech (1954) a thickness of 240 m in the Hughes and Grainger ranges and 75 m at Mount DeSmet (north of Mount Grainger).

Only a single fossil locality is known from the Cranbrook quartzites. G.B. Leech made a large collection of trilobites (see locality 3, Appendix A) from this locality in the Hughes Range, Ram Creek area. The present author was unable to relocate this locality or to find any other fossiliferous Cranbrook strata.

Eager Formation

The Eager Formation is a shale and siltstone, to shale and limestone sequence. Leech (1954) and Schofield (1922) both reported that the lower boundary with the Cranbrook Formation is conformable, while Rice (1937) suggested a minor disconformity. Considering the age disparity between fossils of the upper Cranbrook Formation and those of the lower Eager Formation, a disconformity is probably present. Both Leech (1954) and Fritz (1991b) report a disconformity between the Eager Formation and overlying Upper Cambrian Jubilee Formation.

Schofield (1922), Rice (1937, 1941) and Leech (1954², 1958a, 1958b) have described and delimited the Eager Formation. In the type area near Cranbrook, the Eager Formation consists mainly of a shale and siltstone sequence with minor grit layers (< 1 cm thick) and rare small calcareous lenses. Rice (1937) recorded that the upper Eager Formation strata near Wycliff consist of crystalline limestone. The shales are generally grayish on fresh surfaces but weather to a variety of red and orange hues. Siltstones are generally pink. In the type area, only the basal shales of the formation have yielded fossils. Rice (1937) estimated the total thickness of the Eager Formation as over 1800 m. Over 600 m of strata were measured by the author in an incomplete section in the type area along the highway interchange for Cranbrook, Fernie and Fort Steele.

² In Leech's (1954) preliminary account of the Canal Flats region, he referred to these strata simply as "post-Cranbrook Lower Cambrian strata", though he recognized that they are the lateral equivalent of the Eager and Mount Whyte formations. When Leech (1958b) later published the geological map for the region, he designated these rocks as Eager Formation strata.

The lithology of the Eager Formation in the Hughes and Grainger ranges near Canal Flats is different from the type area near Cranbrook in that it consists of interbedded limestone and shale. The shales are generally cleaved and have not yielded body fossils. One heavily bioturbated shale interval was noted on Mount Watson. The limestones range from marls to pure limestones. The latter tend to be thick-bedded (> 1 m) and include oolites and mudstones. Wackestones, packstones and marls tend to be thin bedded with shaly partings. Many of the limestone beds are lenticular and of a limited extent. Leech (1954) included interbedded sandstones, conglomerates and shales in the lower part of the formation, however, the sandstones and conglomerates should be assigned to the Cranbrook Formation to be consistent with formational designations in the type area (Rice, 1937; Schofield, 1922). The contact between the Cranbrook and Eager formations has never been formally defined. Here it is proposed that the base of the Eager Formation be placed at the top of the highest sandstone or quartzite bed. Approximately 130 m of Eager Formation were measured by the author on Mount Watson, and about 50 m in the Ram Creek area. The base of the Jubilee Formation is taken at the base of the lowest bed of dolostone.

The difference in carbonate content in the Eager Formation strata of the Cranbrook and Canal Flats areas may possibly be attributed to the latter being more offshore deposits. The shoreline during the Early Cambrian was to the east, near the present day British Columbia-Alberta border (Lochman Balk, 1968), but the southern deposits near Cranbrook would have also been under the influence of an additional land mass, Montania. Whether the clastics were transported from the south (Montania) or the east (craton) has yet to be determined, but the former seems likely considering the abundance of inner detrital deposits at Cranbrook versus the mixed inner detrital and carbonate platform deposits near Canal Flats.

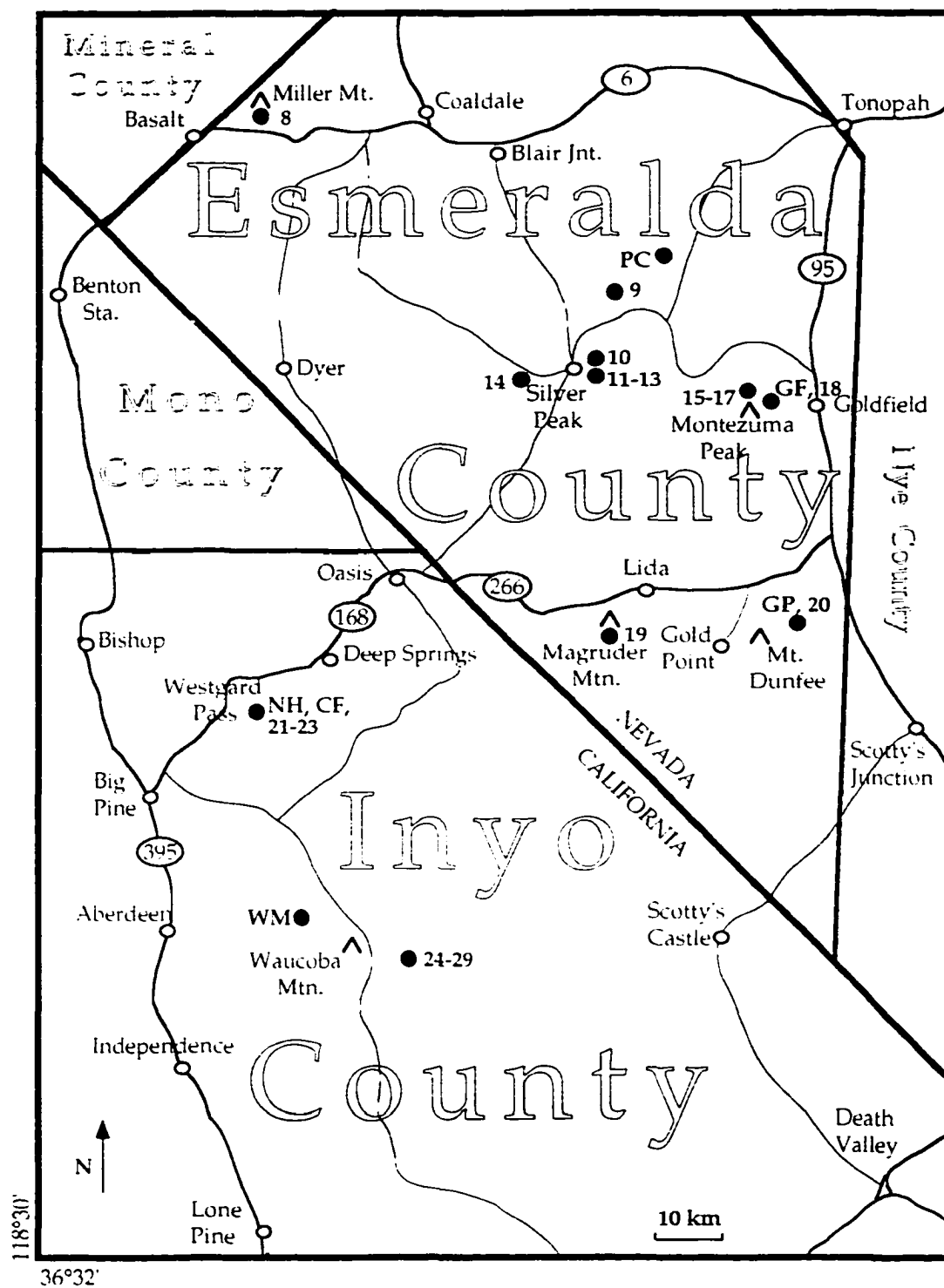
The only previous taxonomic study on trilobites from the Eager Formation is that of Best (1952) on trilobites from the Cranbrook region. Hu (1985) presented an ontogenetic study on one of these species and another on species from material collected near Radium, north of the study area. The strata near Radium may be the Eager Formation, or at least the laterally equivalent. The non-trilobite arthropods *Anomalocaris* and *Tuzoia* have also been described from the Eager Formation near Cranbrook (Resser, 1929; Copeland, 1993).

Southwestern Great Basin

The study area defined in the Great Basin region is centered in what Stewart (1966) and Nelson (1976) referred to as the White-Inyo Facies, and extends through most of Esmeralda County and the northern half of Inyo County (Text-fig. 6). The White-Inyo Facies is a broad spectrum of mostly offshore platform environments that contrasts with the Death Valley Facies to the southeast which represents near-shore environments. Early geological exploration of the western Great Basin was done by Turner (1902), Walcott (1895, 1908) and Kirk (1918). Walcott (1912b) defined the Waucoban Series and proposed that his Barrel Spring and Waucoba Springs sections (Walcott, 1908) be used as standard reference sections. While both of these sections represent nearly complete Lower Cambrian stratigraphic successions, they are structurally complex and only sparsely fossiliferous, and therefore were not sampled for this study. The sections chosen for study were suggested by C.A. Nelson who provided considerable guidance to the geology of this region.

There is an abundance of detailed publications describing the Lower Cambrian geology of the Great Basin study area, with an excellent regional overview given by Palmer (1971). Nelson (1962) was the first to outline the specific stratigraphic succession. Subsequent regional stratigraphic studies have been completed by McKee and Moiola (1962), Albers and Stewart (1962, 1972) and Stewart (1970) in Esmeralda County. McKee (1968) gave an account of the stratigraphic succession in the Magruder Mountain area of California and Nevada. Stewart (1965) described the Proterozoic to Cambrian stratigraphy of the Last Chance Range, California. Sedimentological interpretations of depositional environments were presented by Moore (1976) for the Poleta Formation, and Mount (1982) for the Andrews Mountain Member of the Campito Formation. There are numerous publications on archaeocyathids, brachiopods, trace fossils and small shelly fossils for this area (see summary list in Onken and Signor, 1988a), but few taxonomic studies on trilobites. Walcott included some trilobites from the region in his 1910b monograph. Nelson (1966, 1976) published a series of trilobite photographs with general identifications, but no accompanying taxonomic work. Nelson (1963) recognized that the typical Middle Cambrian *Ogygopsis* ranges into the Lower Cambrian. A tantalizing paper with implications for international correlations was published by Nelson and Hupé (1964) announcing the discovery of Moroccan-type trilobites in California. Palmer (1964) and Fritz (1995) provided the only modern taxonomic studies on Lower Cambrian trilobites from the region.

Nelson (1962, see fig. 3) modernized the stratigraphic terminology of the northern Inyo and Esmeralda regions and replaced the variably-defined Silver Peak Group of previous workers



Text-fig. 6. Locality map of study area in southwestern Great Basin. Locality numbers correspond to those listed in Appendix A.

with a series of formations. Of the remarkably complete Lower Cambrian stratigraphic succession (Text-fig. 7), three formations are targeted in this study: in ascending order, the Poleta, Harkless and Saline Valley formations. Although the underlying Campito Formation has not been studied by the author, some trilobites from these strata are included in this study where necessitated for taxonomic completeness.

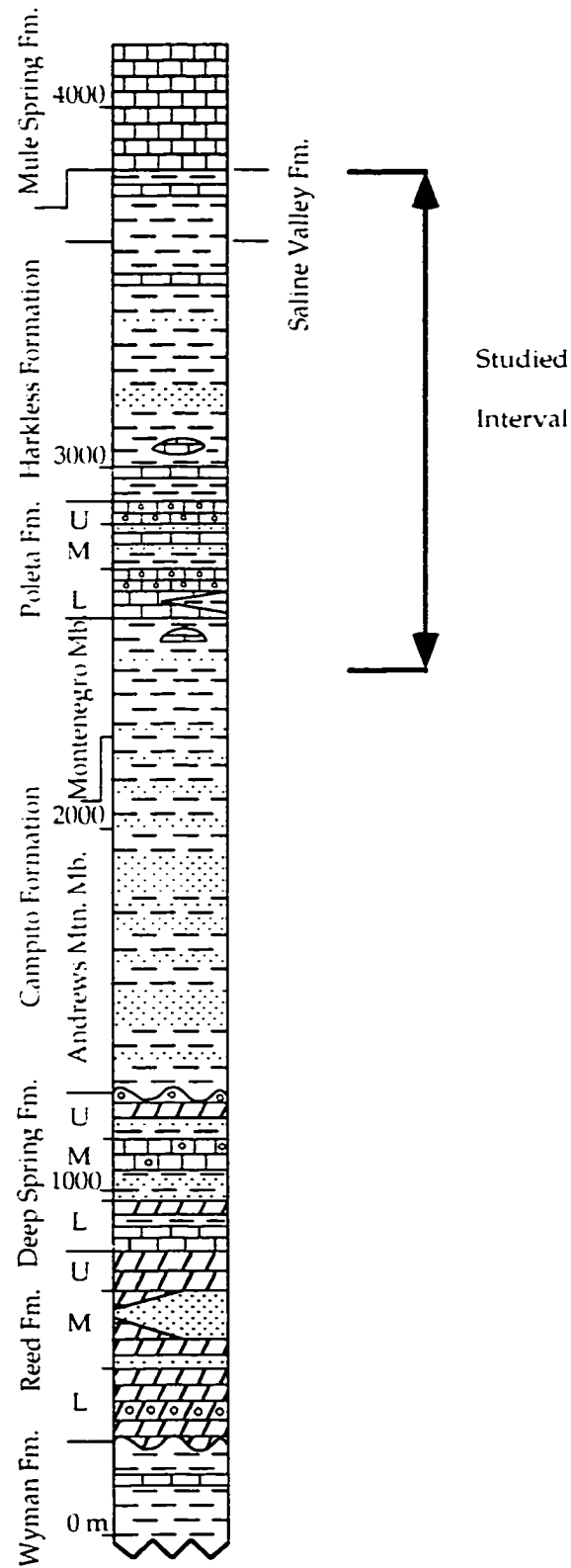
Wyman through Campito formations

General descriptions of the Proterozoic to Cambrian stratigraphic succession are given by Nelson (1962), McKee and Moiola (1962), Stewart (1965), McKee (1968), Albers and Stewart (1972), Stewart (1970) and Ernst (1996). The Proterozoic Wyman Formation is the oldest and is at least 2700 m thick with no exposed base. The lithology is primarily shale and phyllite interbedded with minor limestone and dolostone. Alpert (1977) tentatively identified rare trace fossils from the Wyman Formation as *Planolites?*. Stewart (1966) and Nelson (1976) correlated the Wyman Formation with the Johnnie and lowermost Stirling formations of the Death Valley region, which were interpreted by Levy and Christie-Blick (1991) as the transitional sequences of rifting and continental separation to early passive margin sedimentation. An unconformity separates the Wyman Formation from the overlying Reed Formation (Nelson, 1962; Signor and Mount, 1986: however, see Stewart (1970) and Albers and Stewart (1972) who claim that it is conformable).

The Reed Formation, nearly 500 m thick, is predominantly a dolomitic unit, oolitic in part, with a major clastic tongue developed in the southern exposures. The oldest problematic shelly fossils - calcareous tubes of *Wyattia* (see Taylor, 1966) - are found in this unit. Conformably overlying the Reed Formation is the Deep Spring Formation. It is more than 450 m thick (Nelson, 1962) and is divided into three informal members: a lower limestone, a middle quartzite and limestone, and an upper sandstone and dolostone member. The Deep Spring Formation is, at least in part, Cambrian in age, as it contains the record of the first trace fossils of arthropod grade (*Phycodes* included) (Alpert, 1976a, 1977) and a poorly preserved small shelly fauna (Signor and Mount, 1986).

The contact between the Deep Spring Formation and overlying Campito Formation was initially considered conformable by Nelson (1962), but Mount (1982) interpreted it as disconformable. The Campito Formation is a clastic sequence divided into a lower Andrews Mountain Member of massive quartzite with shale and siltstone interbeds and an upper Montenegro Member primarily of siltstone and phyllite. Moore (1976) interpreted the Montenegro Member strata as tidal flat deposits. Archaeocyathid bioherms occur in localized

Text-fig. 7. Upper Proterozoic and Lower Cambrian stratigraphic succession of the southwestern Great Basin (after Signor and Mount, 1986).



carbonate lenses towards the top (Morgan, 1976). The first occurrence of trilobites in the southeastern Great Basin is in the upper portion of the Andrews Mountain Member (Nelson and Hupé, 1964). These are fallotaspidid trilobites that have not yet been described formally. The overlying Montenegro Member contains more diverse trilobite faunas which were described partially by Walcott (1910) and Fritz (1995). Additional studies on these trilobites are in progress by W.H. Fritz and J.S. Hollingsworth.

Poleta Formation

The Poleta Formation was defined by Nelson (1962) with Walcott's (1908) Waucoba Spring Section as the designated type section. The thickness of this unit averages 365 m in Inyo County and 275 m in north-central Esmeralda County³ (McKee and Gangloff, 1969). A detailed account of the depositional environments of the Poleta Formation was given by Moore (1976), who determined that sediments were derived from a southeastern source and that the depositional basin deepened in a northerly direction. Nelson (1962) proposed a two-fold subdivision of the formation, but the three-fold informal subdivision into lower, middle and upper members used by Moore (1976) and others is preferable.

The lower member of the Poleta Formation is primarily a massive limestone, oolitic in part, with locally abundant archaeocyathids. Moore (1976) interpreted a variety of carbonate bank environments including shoal, back-shoal and shelf margin for this member. In places, the archaeocyathids form bioherms, but they are also a common constituent of bioclastic limestone. The limestone is in part dolomitic and abundant trilobites were only collected at the Gold Point section. The northern localities, such as the Goldfield measured section, have fossiliferous interbeds of shale in the lower part of the member. These shales were interpreted by Moore (1976) as offshore deposits of terrigenous muds that bypassed the carbonate bank complex.

The middle member of the Poleta Formation is predominantly a clastic unit of interbedded shale, limestone and sandstone. Deposition of this unit was suggested by Moore (1976) to have been in intertidal environments in the southern localities, and intertidal to shallow subtidal environments in the northern localities. The basal portion of the member is shale with rare limestone, interpreted by Moore (1976) as mud flats to subtidal deposits. Trilobites are locally

³ Stewart (1970) reported a thickness of 575 m for the Poleta Formation in the Weepah Hills; however, Albers and Stewart (1972) suggested that recognition of the Poleta Formation was problematic and part of the Montenegro Member may be included in this thickness. The latter is probably correct and strata of Poleta lithology are viewed by the author as a thin sequence of outer, carbonate-bank edge deposits in the Weepah Hills.

common in the upper part of these shales and in thin-bedded limestones in this sequence in the Gold Point section. The middle portion of this member is a complex of thin-bedded shale, limestone and quartzite. The more resistant beds stand out in relief giving the sequence a characteristic appearance of many small ledges (hence the name for the Necklace Hill section). Moore (1976) divided this middle portion into a lower sandstone-siltstone unit interpreted as a wave-dominated bar complex and an upper limestone-siltstone unit interpreted as a carbonate bank complex with burrow-mottled back bank deposits to offshore muds. These shales are fossiliferous at all localities. Fossiliferous limestones are best developed at the Gold Point section with exquisite packstones replete with trilobites. The upper portion of the middle Poleta member consists of sandstone and shale beds interpreted by Moore (1976) as foreshore deposits primarily. A massive *Skolithos*-burrowed sandstone occurs at some localities such as the Cedar Flats area.

The upper member of the Poleta Formation in the southern sections is a unit of massive limestone, oolitic in part, representing carbonate bank deposition (Moore, 1976). The northern sections, such as Goldfield, comprise offshore mixed carbonates and clastics that are lensoid in nature. No trilobites have been found in this member.

Harkless Formation

The Harkless Formation conformably overlies the Poleta Formation. Nelson (1962) defined the type locality in the Waucoba Mountain area. The Harkless Formation is a sequence of over 1000 m (Albers and Stewart, 1972) of predominantly fine clastics, that was interpreted by Moore (1976) as tidal flat deposits. The basal layers contain limestone lenses, locally with archaeocyathids, and the Paymaster Canyon section has impressive columnar stromatolites. The bulk of the formation comprises badly cleaved shale with well-preserved trilobites only in the lowest and highest beds. Thin interbeds of limestone and the problematic small shelly fossil *Salterella* occur near the top of the formation.

Saline Valley Formation

The Saline Valley Formation, conformably overlying the Harkless Formation, was named by Nelson (1962) for rocks in the Waucoba Spring area of California. Palmer (1971) reported a thickness of approximately 250 m. Nelson (1962, p. 142) described this formation as "one of the most variable and lenticular units in the succession" while Onken and Signor (1988b, p. 174) called it a "mixed siliciclastic-carbonate platform edge tidalite" based on an unpublished thesis by Crews (1980).

In the type area in California, the lower portion of the Saline Valley Formation is a quartzite capped by limestone. This limestone has a distinctive basal portion with abundant floating quartz grains. It is a regionally persistent unit that can also be recognized in the Gold Point area (Palmer, 1964). The upper portion of the Saline Valley Formation is a series of sandstone, limestone and shale units. Northern localities in Nevada have less limestone and finer clastics than the southern localities. This has led authors such as Nelson (1962) and Stewart (1970) to not formally recognize the Saline Valley Formation in Esmeralda County. The stratigraphically equivalent rocks to those of the Saline Valley Formation in California have been assigned by these authors to the Harkless Formation as they contain abundant shale and are not readily distinguishable from typical Harkless Formation shales. This leads to confusion with equivalent strata called by different names in the two areas. In the Waucoba Mountain region of California, just north of the type area, the basal quartzite unit of the Saline Valley Formation is fine-grained and also difficult to distinguish from the Harkless shales. The base of the Saline Valley Formation is placed at the base of the medium grained clastic unit above the nodular limestone beds bearing *Salterella*. The same criterion is applied in Nevada in the Paymaster Canyon region (section PC), and the boundary between the two formations is placed at the base of Stewart's (1970, p. 158) unit 11.

Post-Saline Valley formations

The Mule Spring Formation, conformably overlying the Saline Valley Formation, was defined by Nelson (1962) for exposures near Waucoba Mountain. Palmer (1971) reported a variable thickness of 300 m in California to only 70 m in Nevada for this largely dolomitized, massive carbonate unit. Nelson (1962) recorded an abundance of algal fossils (*Girvanella*), but trilobites are rare and poorly preserved and consequently have not been collected. Palmer and Halley (1979) recorded a trilobite fauna from the Mule Spring Formation in the Last Chance Range, California that is assignable to the *Bristolia* Zonule.

A shale to limestone sequence called the Monola Formation (Nelson, 1965) conformably overlies the Mule Spring Formation in the White-Inyo Mountains of California. At least the upper member of the Monola Formation is Middle Cambrian in age, based on the presence of the trilobite *Glossopleura* (Palmer, 1971). In Esmeralda County, the Mule Spring Formation is conformably overlain by the Emigrant Formation (Turner, 1902). McKee and Moiola (1962) and Albers and Stewart (1962) provided a modern account of the geology of this formation. It is a thin-bedded succession of siliceous shale, flaggy mudstone, limestone, chert and intraformational breccia considered by Palmer (1971) to be typical of outer detrital deposits. The trilobites of this formation were assigned a Middle Cambrian age by Palmer (reported in

McKee and Moiola, 1962). Nelson (1962), however, reported *Olenellina* from the shaly bottom portion of the Emigrant Formation at Miller Mountain, which suggests that at least part of the formation is Early Cambrian in age⁴.

⁴ Since the base of the Middle Cambrian has not yet been defined, this tentative age assignment is based on the old designation of Walcott (1890) that the top of the Lower Cambrian is equivalent to the termination of the *Olenellina*.

Chapter 3. Lower Cambrian Biostratigraphy

Biostratigraphy is the study of the non-repeating sequences of fossils in strata that change through geological time and vary through geographic space. The concept that fossil assemblages can be used to define and characterize periods of geological time forms the framework for the geological time scale. Early geologists developed the stratigraphic principles of uniformitarianism (Hutton, 1795, 1802; Lyell, 1830-1833) and superposition (Steno, 1669) as basic laws of how the rock record is formed. These concepts were part of necessary framework on which biostratigraphy was developed. Charles Darwin (1859) contributed to biostratigraphy by demonstrating that evolution occurs, giving validity to the concept of faunal succession, formulated first by William Smith in the late 1700's (Berry, 1968). This concept of non-repeating fossil sequence forms the basis for defining the geological periods and for relative dating and biocorrelation.

The temporal aspect of biostratigraphy has been well recognized historically, but the spatial aspect has, until recently, been overlooked or inadequately considered. Fossils are the remains of once living organisms that had definite environmental preferences. Two environments with radically different physical conditions will share few species, even if they are coeval. Ludvigsen *et al.* (1986) formally recognized and defined the dual nature of biostratigraphy and emphasized that fossil distributions are facies dependent. Parallel zonal successions are often required for different facies.

Lower Cambrian biostratigraphy in North America has focused almost exclusively on trilobite successions. While some workers have acknowledged that faunas are facies-specific, there has been little attempt to integrate biofacies into zonal biostratigraphy. Most existing zones are poorly defined and inadequately characterized, making their recognition and correlation between localities imprecise. In addition, zones have mainly been defined on genera rather than on species, which is a problem in two ways: 1. generic concepts have been applied variously by different authors. A species is a more stable and recognizable taxon. 2. genus ranges are longer than species ranges, meaning that zonation and correlation is precise only when based on species. Moreover, genus-defined zones could be biofacies and possibly diachronous. A new species-based zonation with recognition of biofacies is here proposed for the studied Lower Cambrian strata.

Historical Overview

C.D. Walcott provided the first comprehensive Lower Cambrian biostratigraphic framework for North America in 1890. He established the *Olenellus*⁵ Zone, which he considered to represent the entire Lower Cambrian. The base was defined as the level "where the genus *Olenellus*, or the fauna usually accompanying it, first appears" (Walcott, 1890, p. 549). Walcott designated the base of the overlying zone at the first occurrence of the *Paradoxides* fauna, but recognized that this only applies to the Atlantic Province: what is now known as Avalonia. For Laurentia, Walcott (1890, p. 581) stated that "there is a Middle Cambrian fauna more or less distinctly defined, that succeeds the *Olenellus* Fauna, but it is not the typical *Paradoxides* Fauna of the Atlantic Province".

Twenty years later, Walcott (1910b) considerably revised his taxonomy with many new genera of Olenellina, and created a more complex zonal scheme (Table 1). He established four zones, named for genera, but characterized by species. Walcott's scheme was ambitious, but problematic, as it was based on species from both Laurentia (North America and European parts) as well as Avalonia. Walcott's zonal scheme was surprisingly accurate in its species ranges for Laurentia and was an excellent early attempt at biostratigraphic ordering. Unfortunately, it was not followed by subsequent workers and only the *Olenellus* Zone remained in general usage.

Resser (1938) attempted a zonal scheme (Table 2) based on the faunal succession of the southern Appalachians. While his zonal names appear in his correlation table (Resser, 1938, table 1, pp. 20) and are occasionally mentioned in his text, at no point does he define, characterize or directly discuss his zones. His lowest interval, the *Obolella* Zone, is named for a brachiopod and based on the fauna of the Antietam Formation. The formation is quartzite and contains only poorly preserved fossils identified by Resser (1938) as *Olenellus*. Resser's (1938) overlying *Bonnina* and *Kootenia* zones were based on limestone reef faunas of the Shady Formation. Rasetti (1951) pointed out that the stratigraphic position of the faunas is questionable as they occur in isolated fault blocks. Howell *et al.* (1944) built on Resser's (1938) zonation and published a correlation chart that recognized only a *Bonnina* Zone (Table 2). Resser (1938) recognized the *Olenellus* Zone for the fauna of the lower part of the predominately clastic Rome Formation. Rasetti (1951, p. 82) claimed that this zone was likely nothing more than a biofacies typical of shaly strata and stated that "olenellids seem to prevail when the Lower Cambrian is represented by siliceous shales, while *Bonnina* and small, generalized ptychopariid

⁵ It is important to realize that Walcott's (1890) concept of *Olenellus* is equal to the current concept of the Suborder Olenellina.

Table 1. Zonal biostratigraphy of the Lower Cambrian after Walcott (1910b). Zones are given in stratigraphic order with only the Laurentian, North American species listed which were attributed to that zone. All names have been updated to the taxonomy used in this thesis (where the modern taxonomic assignment is uncertain, quotation marks).

D. *Olenellus* or Upper Zone

Fremontella halli (Walcott)
Fremontella canadensis (Walcott)
Mesonacis vermontana (Hall)
Olenellus nevadensis (Walcott)
Olenellus transitans (Walcott)
Olenellus thompsoni Hall
Olenellus gilberti Meek
Peachella iddingsi (Walcott)
Wanneria walcottanus (Wanner)
Wanneria logani (Walcott)

C. *Callavia* Zone

Fremontia fremonti Walcott

B. *Elliptocephala* Zone

Elliptocephala asaphoides Emmons
 ?*Esmeraldina argenta* (Walcott)
 ?"*Olenellus*" *claytoni* (Walcott)
 ?*Nevadella gracile* (Walcott)

A. *Nevadia* or Lower Zone

Esmeraldina rowei (Walcott)
Nevadia weeksi Walcott

Table 2. Zonal biostratigraphy of the Lower Cambrian after Resser (1938) and Howell *et al.* (1944). Genera considered typical of the zones by Howell *et al.* are listed (names have been updated to taxonomy used in this thesis).

Resser, 1938	Howell <i>et al.</i> 1944
Kochiella Zone	Syspacephalus Zone Proliostracus Inglefieldia Kochiella
Olenellus Zone	Olenellus Zone Olenellus Wanneria Protypus
Kootenia Zone	Bonnia Zone Bonnia Olenellus
Bonnia Zone	
Obolella Zone	Obolella Zone no trilobites

trilobites are dominant in limestone or dolomite formations, regardless of age". This was the first explicit recognition of the importance of biofacies in the Lower Cambrian faunal succession. Lochman (1952) recognized that the *Olenellus* Zone represented a huge thickness of strata with great taxonomic diversity that needed to be split into finer divisions.

Resser (1938) recognized a post-Olenellina Lower Cambrian zone for the upper portion of the Rome Formation; the *Kochiella* Zone. This zone was renamed the *Syspacephalus* Zone by Howell *et al.* (1944) and subsequently the *Antagmus-Onchocephalus* Zone by Lochman (1947). Rasetti (1951) rejected a post-Olenellina Lower Cambrian zone and assigned this interval to the Middle Cambrian. As a whole, the zonal scheme outlined by Resser (1938) and modified by Howell *et al.* (1944) was rejected by Rasetti (1951), and has not been subsequently applied. An exception is Lochman (1952) who discussed and tentatively applied the zonal scheme of Howell *et al.* (1944) to Lower Cambrian strata of Sonora, Mexico.

Deiss (1940) named an *Olenellus-Bonnina* Zone based on faunas of the St. Piran Formation in the southern Canadian Rocky Mountains. Rasetti (1951) tentatively applied this name in his description of these faunas, although he inverted the parts of the name to become the *Bonnina-Olenellus* Zone.

Rasetti (1966, 1967) developed a biostratigraphic scheme of successive faunas for the Taconic Region of the northeastern United States (Table 3). This was a significant accomplishment due to the discontinuous nature of the outcrops and poor stratigraphic control. Rasetti built on the earlier work of Lochman (1956), who he claimed had mistakenly combined collections from the two separate *Elliptocephala asaphoides* and *Pagetides* faunas. Most of the trilobites were described by Rasetti as new species and have not been reported elsewhere. This makes correlation to other areas virtually impossible. Little modern revision of Rasetti's taxonomy has been done (with the exception of some taxa of the *E. asaphoides* Fauna). A critical taxonomic comparison between these faunas and other shelf edge to slope deposits of the Sekwi Formation (Fritz, 1972, 1973) and Alaska (Palmer, 1968) may prove that there are some species in common. The majority of the trilobites are eodiscoids; pandemic trilobites characteristic of open ocean environments. Deposition in the Taconic Region was interpreted to have taken place in a shelf margin to slope environment by Lochman (1956) and Theokritoff (1968).

Palmer (*in* Merriam, 1964) produced a brief report on the faunas of the Pioche Formation, Nevada, and recognized two Lower Cambrian biostratigraphic divisions (Table 4). These faunules represent some of the youngest Lower Cambrian assemblages and, based on shared

Table 3. Zonal biostratigraphic scheme developed by Rasetti (1966, 1967) for the Taconic Region. Species names have been updated to taxonomy used in this thesis.

***Pagetides* Fauna**

***Pagetides elegans* Faunule**

<i>Pagetides elegans</i> Rasetti	<i>Leptochilodiscus punctulatus</i> Ras.
<i>Pagetides amplifrons</i> Rasetti	<i>Serrodiscus spinulosus</i> Rasetti
<i>Pagetides leiopygus</i> Rasetti	<i>Bolboparia</i> sp.
<i>Pagetides minutus</i> Rasetti	<i>Oodiscus</i> sp.
<i>Pagetides rupestris</i> Rasetti	<i>Peronopsis</i> sp.
<i>Pagettia bigranulosa</i> Rasetti	<i>Olenellus</i> sp.
<i>Pagettia laevis</i> Rasetti	<i>Bonnia</i> sp.
<i>Analox obtusa</i> Rasetti	<i>Kootenia</i> sp.
<i>Calodiscus lobatus</i> (Hall)	<i>Prozacanthoides</i> sp.
<i>Calodiscus walcotti</i> Rasetti	<i>Protypus</i> sp.

***Neopagetina taconica* Faunule**

<i>Neopagetina taconica</i> Rasetti
<i>Pagetides minutus</i> Rasetti
<i>Peronopsis</i> sp.
<i>Bolboparia</i> sp.
<i>Bonnia</i> sp.
<i>Olenellidae</i> id.

***Acimetopus bilobatus* Fauna**

<i>Acidiscus birdi</i> Rasetti	<i>Oodiscus subgranulatus</i> Rasetti
<i>Acidiscus hexacanthus</i> Rasetti	<i>Oodiscus binodosus</i> Rasetti
<i>Acimetopus bilobatus</i> Rasetti	<i>Oodiscus longifrons</i> Rasetti
<i>Analox bipunctata</i> Rasetti	<i>Serrodiscus subclavatus</i> Rasetti
<i>Bathydiscus dolichometopus</i> Ras.	<i>Serrodiscus spinulosus</i> Rasetti
<i>Bolboparia superba</i> Rasetti	<i>Serrodiscus latus</i> Rasetti
<i>Bolboparia elongata</i> Rasetti	<i>Stigmatiscus stenometopus</i> Rasetti
<i>Calodiscus fissifrons</i> Rasetti	<i>Stigmatiscus gibbosus</i> Rasetti
<i>Calodiscus reticulatus</i> Rasetti	<i>Olenellus</i> sp.
<i>Calodiscus occipitalis</i> Rasetti	<i>Kootenia</i> sp.
<i>Leptochilodiscus punctulatus</i> Ras.	<i>Bonnia</i> sp.
<i>Litometopus longispinus</i> Rasetti	

***Elliptocephala asaphoides* Fauna**

<i>Elliptocephala asaphoides</i> Emmons
<i>Atops trilineatus</i> Emmons
<i>Calodiscus lobatus</i> (Hall)
<i>Calodiscus meeki</i> (Ford)
<i>Serrodiscus speciosus</i> (Ford)
<i>Ekwipagetia marginata</i> (Rasetti)
<i>Rimouskia typica</i> Resser
<i>Bonnia troyensis</i> (Resser)
<i>Fordaspis nana</i> (Ford)

Table 4. Zonal biostratigraphy of the Lower Cambrian portion of the Pioche Formation, after Palmer (*in* Merriam, 1964). All names have been updated to taxonomy used in this thesis.

2. *Olenellus gilberti*-*Olenellus clarki* Faunule

1. *Fremontia fremonti*-*Bristolia bristolensis* Faunule

Table 5. Zonal biostratigraphy of the Lower Cambrian portion of the Cararra Formation, California and Nevada, summarized from Palmer and Halley (1979). All names have been updated to taxonomy used in this thesis (where the modern taxonomic assignment is uncertain, quotation marks are used). *Bolbolenellus euryptaria* was not found in a zonule, but in a poorly fossiliferous interval between zonules.

***Nephrolenellus multinodus* Zonule**

Nephrolenellus multinodus (Palmer)
Olenellus gilberti Meek
Olenellus clarki (Resser)
Olenellus cf. *Fremontia fremonti* Walcott
 "Olenellus" *brachyomma* Palmer

Bolbolenellus euryptaria (Palmer)

***Bristolia* Zonule**

Bristolia bristolensis (Resser) (= *B. fragilis* Palmer)
Bristolia anteros Palmer
Peachella uddingsi (Walcott)
Peachella brevispina Palmer
Olenellus transitans (Walcott) (= *O. puertoblancoensis* Lochman)
Olenellus howelli? Meek
Olenellus clarki (Resser)
Olenellus cf. *Fremontia fremonti* Walcott
Olenellus nevadensis (Walcott)

***Nephrolenellus arcuatus* Zonule**

Nephrolenellus arcuatus (Palmer)
Fremontella cylindricus (Palmer)
Olenellus nevadensis (Walcott)

species, can be correlated to the faunules recognized by Palmer and Halley (1979) for the Cararra Formation, Nevada and California.

The zonal biostratigraphic scheme for Laurentia in use today was proposed by Fritz (1972) (Table 6). The lowest zone of this scheme was defined by Hupé (1953a) in Morocco. Hupé recognized four species-based zones, but Fritz (1972) designated them as subzones of a *Fallotaspis* Zone. Fritz applied the *Fallotaspis* Zone to Laurentia, a move that was premature since formal taxonomic descriptions of any species of *Fallotaspis* have yet to be done. Nelson and Hupé (1964) had reported the presence of the Moroccan trilobites *Fallotaspis* and *Daguinaspis* in California, but without description or illustration. The specimens attributed to *Daguinaspis* have since been recognized as *Cirquella* by Fritz (1993). *Fallotaspis* does occur in the Montenegro Formation, White Mountains of California, as recently confirmed by a modern expert on fallotaspid trilobites (Geyer, 1996). Fritz (1972) reported *Fallotaspis* in the Sekwi and Mural Formations, although he failed to illustrate or describe these critical trilobites. He did describe a new genus, *Parafallotaspis*, which he considered characteristic of the *Fallotaspis* Zone, but, regardless of its name, this trilobite is an archaeaspidid, not a fallotaspidid. Palmer and Repina (1993) recognized the ambiguities of recognition of the *Fallotaspis* Zone in Laurentia and suggested that it be informally applied and considered equal to the range of fallotaspid trilobites. The *Fallotaspis* Zone has been so poorly defined that it is here suggested that the name be abandoned for Laurentia.

The intermediate zone named by Fritz (1972) is the *Nevadella* Zone with a type section designated in the Sekwi Formation of the Mackenzie Mountains. Fritz listed a number of genera that he considered characteristic of this interval (see Table 6). Of these genera, *Judomia* is a misidentification (see discussion under the Nevadiidae) and the genus is not found in Laurentia. *Bradyfallotaspis* ranges into the overlying zone (see Palmer and Repina, 1993, fig. 12) and demonstrates the problem with characterizing a zone using genera. No base was defined for the *Nevadella* Zone, but the overlying zone does have a defined base. Palmer and Repina (1993) suggested that the *Nevadella* Zone is equal to that interval characterized by nevadiid trilobites, with *Nevadia* being a characteristic trilobite of the lower portion. They suggested using the term informally, but the *Nevadella* Zone has been so vaguely defined and poorly characterized that it is of little biostratigraphic use.

Table 6. Zonal biostratigraphy of the Lower Cambrian of Laurentia as proposed by Fritz (1972). Genera listed as characteristic for the zones by Fritz are also given. All names have been updated to taxonomy used in this thesis

Bonnia-Olenellus Zone

(genera listed characteristic only of top of zone)

Bonnia

Olenellus

Proliostracus (= *Antagmus*, *Onchocephalus*)

Nevadella Zone

Nevadella

Bradyfallotasps

Holmiella

Iudomia

Fallotaspis Zone

Fallotasps

Parafallotasps

Fritz (1972) accepted the name *Bonnia-Olenellus* Zone, as used by Rasetti (1951), for his upper Lower Cambrian zone. He formally defined the base at the first occurrence of *Olenellus*⁶ and the top at a regional unconformity, although he declined to name a type area. Fritz (1972) characterized the zone only by listing genera characteristic of the top of the interval. The *Bonnia-Olenellus* Zone as defined by Fritz represents a tremendous thickness of strata (i.e. approximately 1500 m in the White-Inyo Mountains) and great taxonomic diversity. It needs to be subdivided to represent the diversity of faunal successions and the changes in taxonomy of *Olenellus*.

Despite its limitations and problems, Fritz's (1972) zonal scheme has achieved wide acceptance for biostratigraphic division of the Laurentian Lower Cambrian. Palmer and Repina (1993) attempted to salvage the *Fallotaspis* and *Nevadella* zones (as indicated above) and applied the names only informally. While they accepted Fritz's (1972) definition of the *Bonnia-Olenellus* Zone, they reverted to the older name of *Olenellus* Zone for the same interval. This was done because while they accepted that *Olenellus* ranged through the whole zone, they claimed that the distribution of *Bonnia* was restricted in both time and space and not characteristic of the zone as a whole.

Palmer and Halley (1979) similarly used the term *Olenellus* Zone rather than *Bonnia-Olenellus* Zone for the lower Cararra Formation of California and Nevada. They did not state their reasons for doing so, but the near absence of *Bonnia* in the Cararra Formation likely influenced their decision. These strata represent some of the youngest Lower Cambrian assemblages known and correlate, based on shared species, to the Pioche Formation, Nevada (Palmer *in* Merriam, 1964) and the Latham Formation, California (Resser, 1928; Riccio, 1952). Three zonules were established by Palmer and Halley (1979) for the Lower Cambrian portion of the Cararra Formation (Table 5). Species listed in Table X have been subsequently compiled from range charts published by Palmer and Halley. Zonal boundaries have not been biostratigraphically defined, rather the zonules are bounded by barren intervals. Palmer and Halley (1979) noted biofacies restrictions in that certain species of *Olenellus* are restricted to certain facies.

⁶ Fritz's (1972) generic concept of *Olenellus* was broad and included species here assigned to *Elliptocephala*, *Gabriellus* and *Wannerellus*. The first occurrence of *Olenellus*, as here recognized, is stratigraphically considerably above where Fritz (1972, 1992) placed it.

Biofacies Analysis

Ludvigsen (1978) was among the first to deal in a rigorous fashion with trilobite biofacies using Middle Ordovician trilobites from the Mackenzie Mountains. He statistically analyzed the collections using Q- and R-mode cluster analysis and diversity analysis to define repeated associations of dominant genera as biofacies. Ludvigsen's methodology has been applied in subsequent biostratigraphic studies of Upper Cambrian faunas by Ludvigsen and Westrop (1983), Westrop (1986), and Ludvigsen *et al.* (1989). Pratt (1992) also dealt with trilobite biofacies, but did not justify his biofacies statistically since he was dealing with a small number of fossiliferous horizons in which biofacies associations were easily discernible. Biofacies defined here for Lower Cambrian strata are also readily apparent due to the low diversity of the studied assemblages. For example, four common genera is the maximum characteristic of Lower Cambrian biofacies here described (Text-figs. 8-15) compared to Upper Cambrian assemblages where most biofacies have at least five common genera, and some as many as nine (see Pratt, 1992).

All of the collections used in this study are of crack-out limestone and shale material, much of it disarticulated. Over 13 000 specimens from 10 stratigraphic sections and 29 spot localities in 164 collections were studied. Specimen counts for each species were made exclusively on parts, not counterparts. Numbers of individuals for each species were determined by the maximum number of any one unpaired element (cephala/cranidia or pygidia) recorded for that species.

Collection size is an important factor in biofacies analysis. Ludvigsen (1978) used rarefaction curves to illustrate the need for large collections to sample rare species. While biofacies are defined by their common constituent genera, not by rare genera, collection size must still be large enough to obtain a reasonable estimate of generic composition. Ludvigsen (1978) applied rarefaction methodology of Sanders (1968) and others to trilobite biofacies and determined that collections of a minimum of 50-100 individuals are necessary to characterize biofacies diversity. In this study, consequently, only large collections are used for biofacies characterization, and collections of under 50 individuals are given little weight. While every effort was made in the field to obtain large collection sizes, it was not always possible for sparsely fossiliferous biofacies and zones.

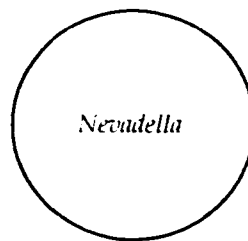
Depositional and preservational factors such as selective preservation (i.e. selective silicification), transportation/mixing of assemblages and size sorting can affect composition of assemblages. For collections studied here, selective preservation is a minor factor. Tiny

specimens generally fossilize poorly in shale assemblages while complete, large specimens are difficult to obtain from crack-out limestone material. Some collections show evidence of size sorting, which is particularly evident where only small specimens of large species are preserved (i.e. collection RC4f, section RC4, see Appendix A). Other collections containing only large specimens and no juvenile material may also be size-sorted. There is no evidence for any significant transportation or mixing of biofacies. Collecting biases were minimized by collecting all identifiable specimens from a horizon, but some collections not made by the author may not have been collected in this fashion. One other bias that interferes with biofacies analysis is when there is a non-random distribution of species through an horizon. One shale collection (collection PC20, section PC, see Appendix A) has individual slabs dominated by different species and cannot be used in biofacies analysis. It is a talus rather than *in situ* collection therefore changing dominance of the assemblage cannot be tied into stratigraphy as the lithology stays the same.

Biofacies determinations were made by inspection. Number counts were made for all collections and dominant genera noted for each. All collections are of relatively low generic diversity and biofacies patterns are readily apparent using pie diagrams (Text-figs. 8-15). Biofacies can be related directly to both lithofacies and depositional belts and indirectly to environment (Text-figs. 16-17). A number of generalizations can be made: first, the *Olenellina* dominate all Lower Cambrian clastic deposits from the inner detrital belt. While the *Olenellina* range spatially across the continental shelf environments of the middle carbonate belt, they are numerically overwhelmed in limestones within the stratigraphic range of *Bonnia*. The *Olenellina* are generally rare in slope deposits. Shelf edge and slope deposits have a higher diversity than inner shelf deposits. Particularly useful is the recognition of pandemic genera as characteristic of slope and shelf edge environments and endemic genera as characteristic of shelf environments (after Fortey and Owens, 1978).

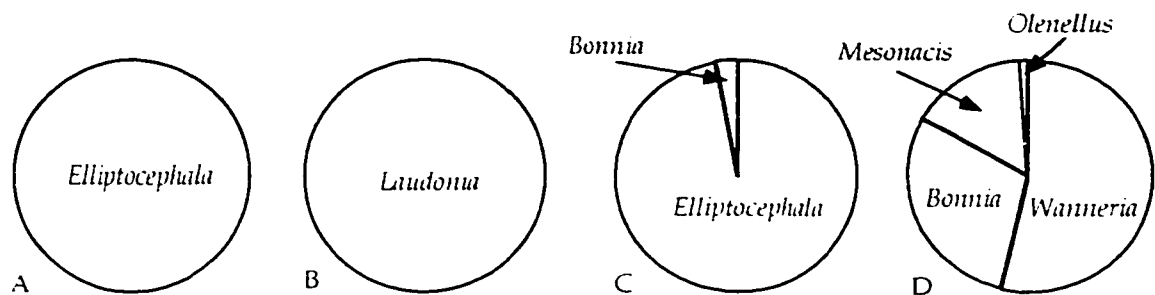
A total of 11 biofacies (Text-figs. 8-15) are defined below for Lower Cambrian strata ranging from the inner shelf to shelf edge. The relationship of biofacies to lithofacies and zonal biostratigraphy is summarized in Text-figs. 16 and 17.

1. *Nevadella* Biofacies (Text-fig. 8) occurs in both inner detrital and middle carbonate belt sediments of the upper Cranbrook and lower - middle Poleta formations in the study areas. Based on 19 collections, these are monotypic to low diversity trilobite assemblages dominated by *Nevadella*. All collections of the low diversity assemblages from the lower Poleta Formation are unfortunately too small (<15 specimens) for significant biofacies



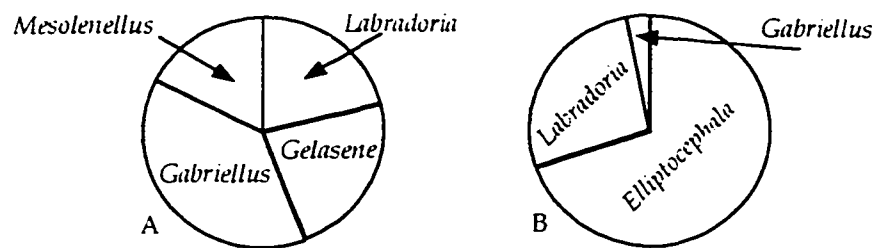
Nevadella Biofacies

Text-fig. 8. Typical distribution of trilobite taxa of the *Nevadella* Biofacies. (GSC collection 023851, Cranbrook Formation, locality 2, 383 individuals)



Wanneriid Biofacies

Text-fig. 9. Typical distribution of trilobite taxa of the Wanneriid Biofacies. (A. LACMIP collection 17049, Poleta Formation, section GP, 196 individuals; B. LACMIP collection 17052, Poleta Formation, section GP, 295 individuals; C. collection MG2a, Eager Formation, section MG2, 98 individuals; D. collection MG3b, Eager Formation, section MG3, 565 individuals)



Labradoria Biofacies

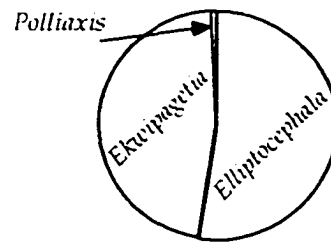
Text-fig. 10. Typical distribution of trilobite taxa of the *Labradoria* Biofacies. (A. collection ICS 1056, Poleta Formation, section GP, 52 individuals; B. LACMIP collections 17081 and 26862, Poleta Formation, locality 22, 241 individuals)

characterization. Outside the study areas, the *Nevadella* biofacies can be recognized in the Mural Formation, Mount Robson area, British Columbia (Fritz, 1992). High diversity, *Nevadella*-bearing limestones of the Sekwi Formation (Fritz, 1972, 1973) belong to a shelf-edge biofacies different from any biofacies described here.

2. Wanneriid Biofacies (Text-fig. 9) has a long stratigraphic range and complex lithofacies distribution. Based on 55 collections, the Wanneriid biofacies is characterized by 54 to 100% of the taxa belonging to genera of the Wanneriidae. In the Poleta to lowermost Harkless Formations, the Wanneriid Biofacies is characterized by monotypic or near monotypic assemblages of early wanneriids such as *Elliptocephala*, *Mesolenellus*, *Gabriellus*, *Mummaspis* and *Wannerellus* that characterize a broad range of lithofacies from the inner detrital to middle carbonate belts (Text-fig. 9a). *Laudonia* is the only early wanneriid with a particular lithofacies association: it dominates in pure carbonate rocks and is only found in small numbers in shales or shaly carbonates (Text-fig. 9b). Similar lithofacies associations of early wanneriids can be found in : the Mural Formation, Mount Robson area, Canadian Rocky Mountains (Fritz, 1992); the Sekwi Formation, Mackenzie Mountains (Fritz, 1972); and the Puerto Blanco Formation of Sonora, Mexico (Lochman, 1952). In the Eager Formation, the Wanneriid Biofacies is expressed as near monotypic assemblages of *Elliptocephala* restricted to oolitic limestones (Text-fig. 9c) and as *Wanneria*-dominated assemblages in shaly carbonates (Text-fig. 9d).

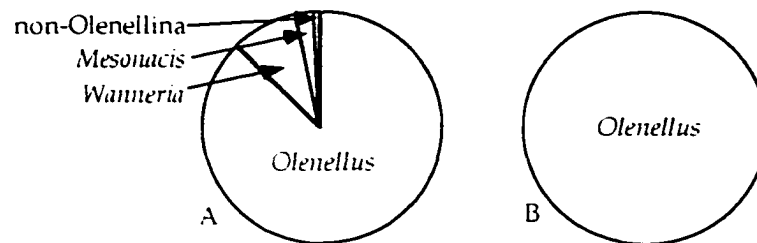
3. *Labradoria* Biofacies (Text-fig. 10) occurs in open shelf to shelf edge shale and carbonate deposits of the middle Poleta Formation. Assemblages of this biofacies are of low to moderate diversity and are characterized by an abundance of specimens of *Labradoria*. Based on 7 collections, *Labradoria* makes up from 21 to 46% of an assemblage. *Labradoria* has a pandemic distribution and is an unusual trilobite in continental shelf deposits of Laurentia. This biofacies can also be recognized in deep-water deposits of the Sekwi Formation (Fritz, 1973). In the Gold Point measured section, *Labradoria* co-occurs with *Gelasene*, a trilobite found in Alaska from what Palmer (1968) described as an assemblage of Siberian aspect.

4. *Ekwipagetia* Biofacies (Text-fig. 11) occurs in shaly limestones of outer-shelf deposition in the Poleta Formation, Gold Point measured section. Based on 3 collections, *Ekwipagetia* makes up 69% of the only collection greater than 50 specimens. *Ekwipagetia* co-occurs with *Elliptocephala* and with *Polliaxis*, a genus originally described by Palmer (1968) from shelf-edge deposits of Alaska. *Ekwipagetia* is an eodiscoid trilobite that has also been described from deep water deposits of the Sekwi Formation, Mackenzie Mountains (Fritz, 1973) where it



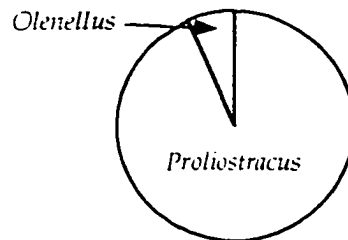
***Ekwipagetia* Biofacies**

Text-fig. 11. Typical distribution of trilobite taxa of the *Ekwipagetia* Biofacies. (LACMIP collections 17054 and 26850, Poleta Formation, section GP, 101 individuals)



***Olenellus* Biofacies**

Text-fig. 12. Typical distribution of trilobite taxa of the *Olenellus* Biofacies. (A. Sutherland collection (U of A), Eager Formation, locality 5, 2185 individuals; B. collections WW"1" and LACMIP 26784, Saline Valley Formation, locality 26, 76 individuals)



***Proliostracus* Biofacies**

Text-fig. 13. Typical distribution of trilobite taxa of the *Proliostracus* Biofacies. (collection MG3g, Eager Formation, section MG3, 106 individuals)

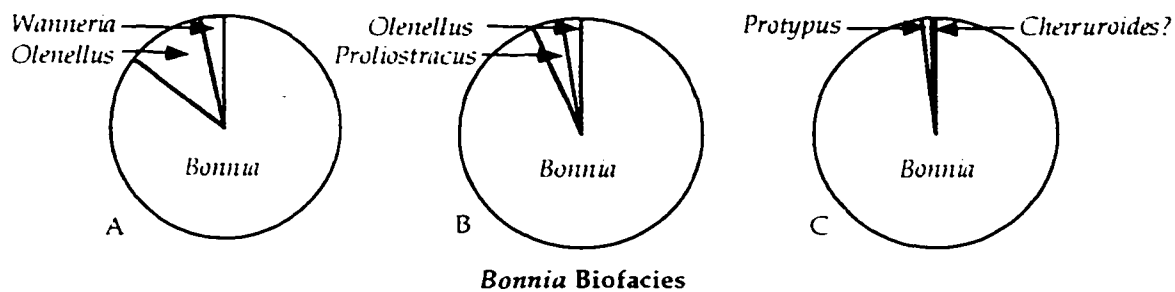
co-occurs with *Labradoria*, and from the Taconic Region (Rasetti, 1967) where it occurs in the *Elliptocephala asaphoides* Faunule (Table 3).

5. *Olenellus* Biofacies (Text-fig. 12) occurs in shales and siltstones of the inner detrital belt of the Eager, Harkless and Saline Valley formations throughout the study areas. These are monotypic to moderate diversity assemblages dominated by *Olenellus*. Based on 12 collections, *Olenellus* makes up 72 to 100% of the assemblages. Outside the study areas, the *Olenellus* Biofacies is well-developed in shales and siltstones of the Kinzers Formation, Pennsylvania (Resser and Howell, 1938); Parker Formation, Vermont (Resser and Howell, 1938); lower Cararra Formation, California and Nevada (Palmer and Halley, 1979); and the Pioche Formation, Nevada (Palmer, submitted).

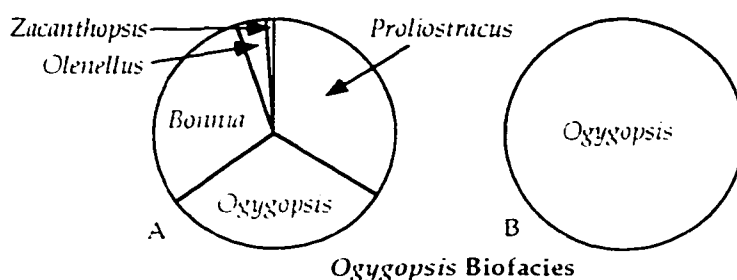
6. *Proliostracus* Biofacies (Text-fig. 13) occurs in lime mudstones of the Eager Formation. These are low diversity assemblages characterized by abundant specimens of *Proliostracus* and minor numbers of *Olenellus*. Based on 6 collections, *Proliostracus* makes up 93% of the only collection greater than 50 specimens. Outside the thesis area, this biofacies can be recognized in: the Sekwi Formation, Mackenzie Mountains (Fritz, 1972); and the Combined Metals Member of the Pioche Formation, Nevada (Palmer, 1957; Palmer *in* Merriam, 1964).

7. *Bonnina* Biofacies (Text-fig. 14) occurs in wackestones and packstones of the Eager Formation, southeastern British Columbia and one limestone bed (collection 26849, section PC) of the Saline Valley Formation, Nevada. These are low to moderate diversity assemblages dominated by *Bonnina* that can include small numbers of *Proliostracus*, *Protypus* and various olenelloids. Based on 11 collections, *Bonnina* makes up from 73 to 97% of the assemblages. The *Bonnina* Biofacies is widespread and is well-developed outside the study areas in: the Illtyd Formation, Wernecke Mountains (Fritz, 1991a); Sekwi Formation, Mackenzie Mountains (Fritz, 1972); limestone conglomerates of the Lévis Formation, Quebec (Rasetti, 1948); and the Shady Formation, southern Appalachians (Resser, 1938).

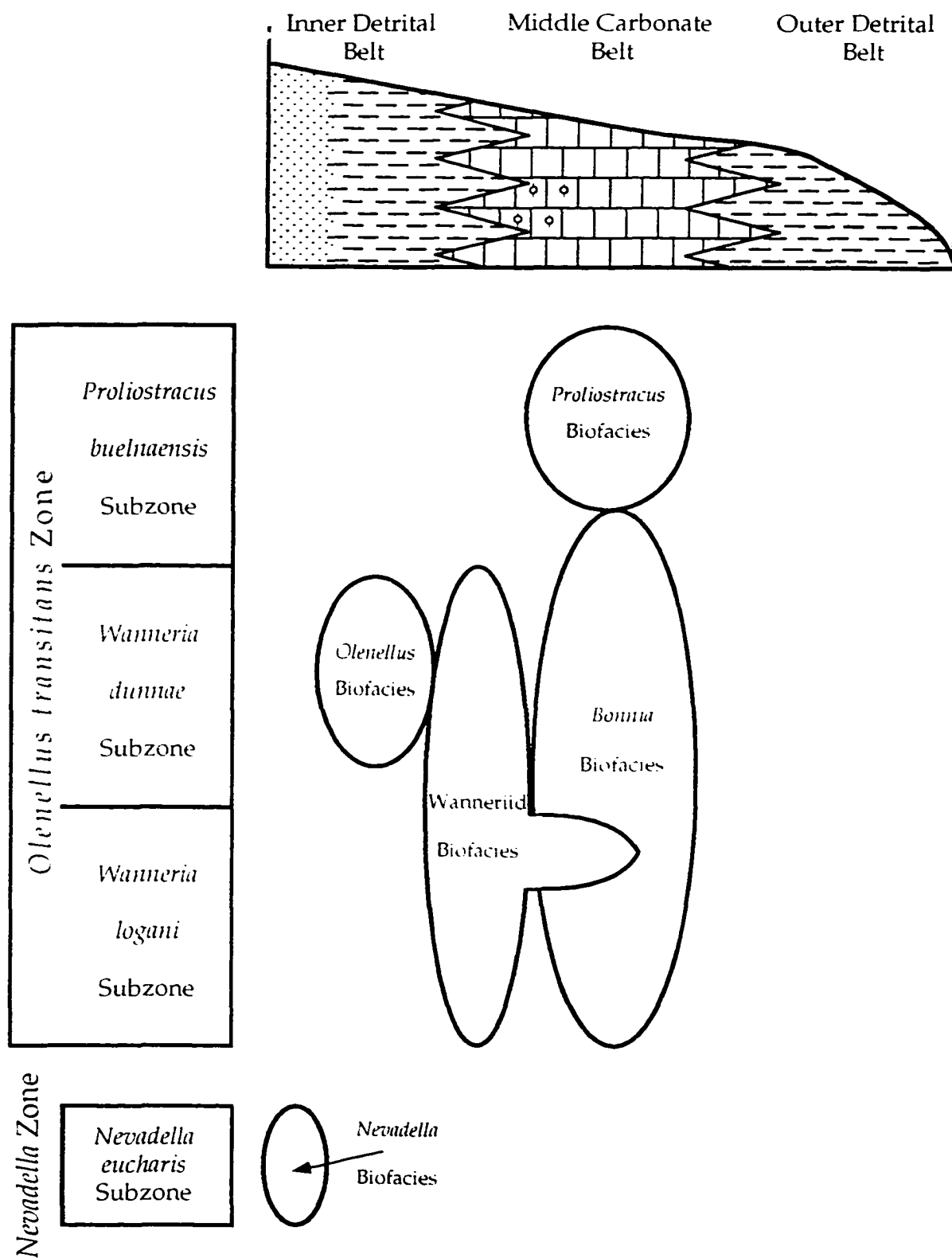
8. *Ogygopsis* Biofacies (Text-fig. 15) occurs in dark shales and limestones of outer shelf deposits of the Saline Valley Formation. These are monotypic to moderate diversity assemblages characterized by an abundance of specimens of *Ogygopsis*. Based on 9 collections, *Ogygopsis* makes up 31 to 100% of the assemblages. *Ogygopsis* is a pandemic, long-ranging genus that has been described from Lower Cambrian outer shelf deposits of Alaska (Palmer, 1968), limestone conglomerates of Quebec (Rasetti, 1948) and the Shady Formation of Virginia (Resser, 1938).



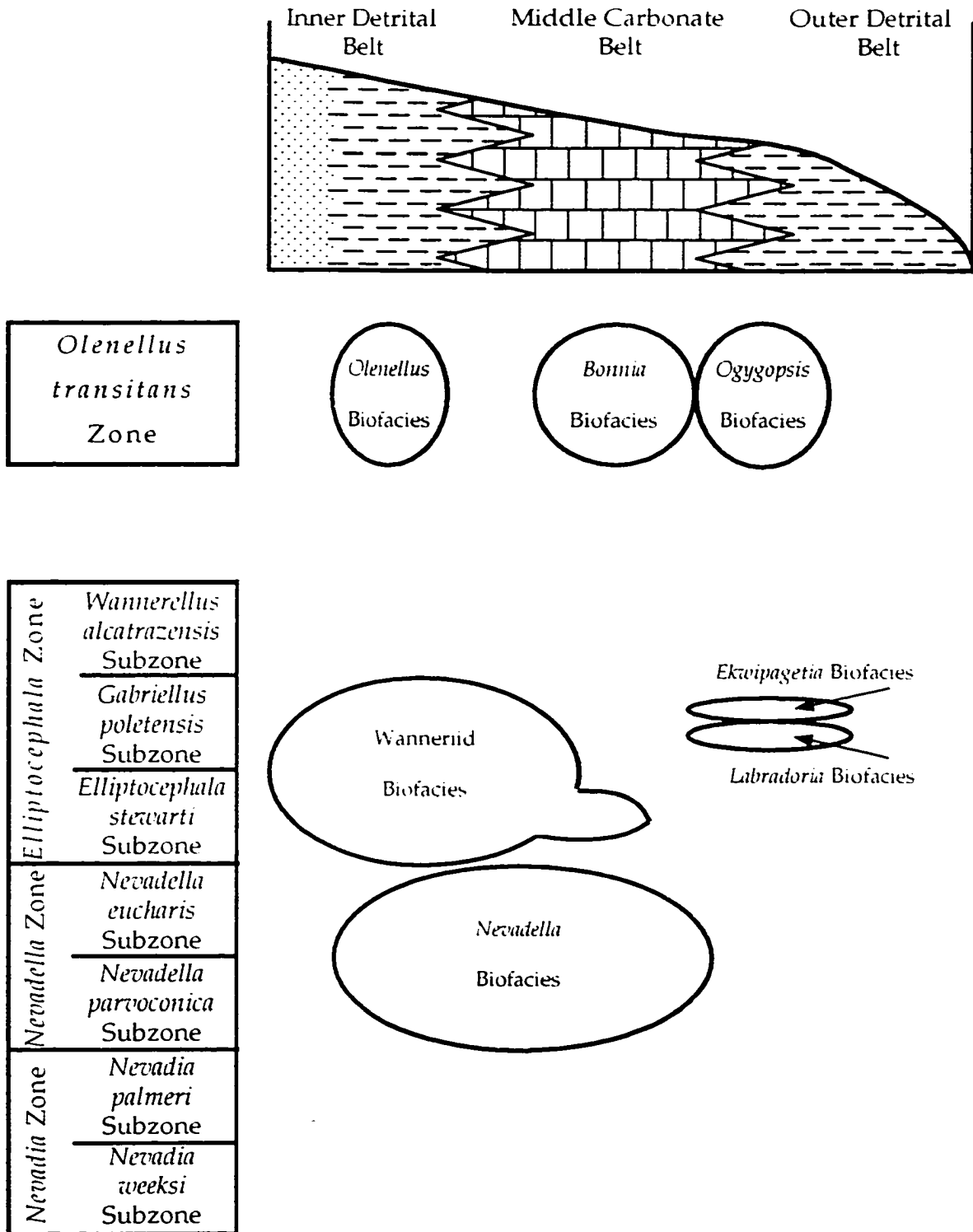
Text-fig. 14. Typical distribution of trilobite taxa of the *Bonnia* Biofacies. (A. collection MG2j, Eager Formation, section MG2, 579 individuals; B. collection MG2d, Eager Formation, section MG2, 286 specimens; C. collection LACMIP 26849, Saline Valley Formation, section PC, 515 individuals)



Text-fig. 15. Typical distribution of trilobite taxa of the *Ogygopsis* Biofacies. (A. collection LACMIP 26877, Saline Valley Formation, locality 9 (horizon 3), 103 individuals; B. LACMIP collections 17085 and 26818, Saline Valley Formation, section WM, 67 individuals)



Text-fig. 16. Relationship between lithofacies, biofacies and biostratigraphic zones expressed in Lower Cambrian strata, southeastern British Columbia.



Text-fig. 17. Relationship between lithofacies, biofacies and biostratigraphic zones expressed in Lower Cambrian strata, southwestern Great Basin.

Zonal Biostratigraphy

The zonal scheme outlined below for the study areas (summarized in Text-figs. 18 and 19) is the first Laurentian Lower Cambrian zonal biostratigraphy defined by species ranges. The interval zoned is the medial Lower Cambrian, with coverage of an estimated 2/3 of the Lower Cambrian trilobite-bearing sequence. Some zonal names have been used by previous authors, but all zones and subzones are newly defined here. Table 7 equates the biostratigraphy of previous authors to the zonal biostratigraphy here proposed.

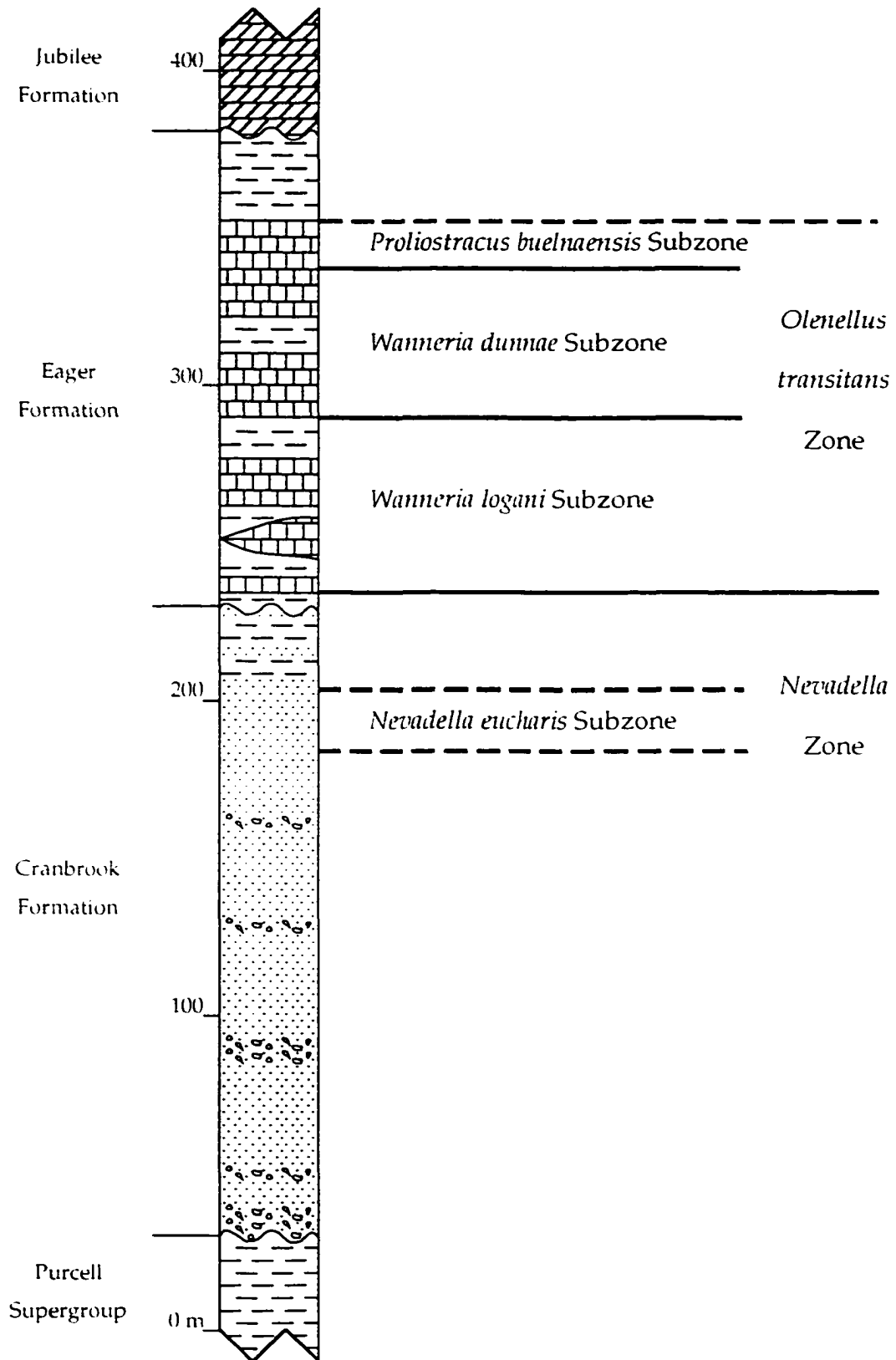
The zonal biostratigraphy may be applied to sequences outside the study areas, but only to continental shelf deposits. Further study is needed to tie in shelf edge and slope deposits (i.e. Fritz, 1973; Palmer, 1968; Rasetti, 1966, 1967) to the shelf sequences. A correlation chart relating the stratigraphic successions of the study areas to other Laurentian localities is given in Table 8.

The general stratigraphic information for the study areas is given in the geology section and Appendix A lists all the locality, stratigraphy and collection information. Text-figs. 16 and 17 relate the zonal biostratigraphy to biofacies.

Nevadia Assemblage Zone. (Estimated thickness: 250 m) The name *Nevadia* Zone was first used by Walcott (1910) as the lowest interval containing *Olenellina* trilobites (Table 1). Walcott did not define a type area and his zonation is a composite based on ranges of *Olenellina* world-wide. The *Nevadia* Zone is here defined on the faunal succession of the Montenegro Member, Campito Formation, localities 16 and 17 in the area of Montezuma Peak, Esmeralda County, Nevada. The base is defined by the base of the *Nevadia weeksi* Subzone. Few collections from this interval were examined in this study, but a distinct faunal succession occurs. All collections were made from shales of the inner detrital zone and biofacies distributions cannot be determined. This interval needs further study, but two subzones can be recognized on the limited data available:

Nevadia weeksi Assemblage Subzone. (Estimated thickness: 65 m) The base of the subzone is defined at the first occurrence of *Nevadia weeksi* Walcott. The Montenegro Member of the Campito Formation at locality 16 in the area of Montezuma Peak, Esmeralda County, Nevada is designated the reference section. This is a low diversity subzone with the only recorded co-occurring species being *Esmeraldina rowei* (Walcott) (see Fritz, 1995). Neither species has been recognized outside of Esmeralda County, Nevada.

Text-fig. 18. Composite Lower Cambrian stratigraphic succession and zonal biostratigraphy in southeastern British Columbia.



Nevadia palmeri Assemblage Subzone. (Estimated thickness: 185 m) The base of the subzone is defined at the first occurrence of *Nevadia palmeri* n. sp. The Montenegro Member of the Campito Formation at locality 17 in the area of Montezuma Peak, Esmeralda County, Nevada is designated the reference section. No species other than *N. palmeri* have been described from this interval. This subzone may be present in the Sekwi Formation, Mackenzie Mountains, because *Nevadella* sp. 1 Fritz (1972) may be conspecific with *N. palmeri*.

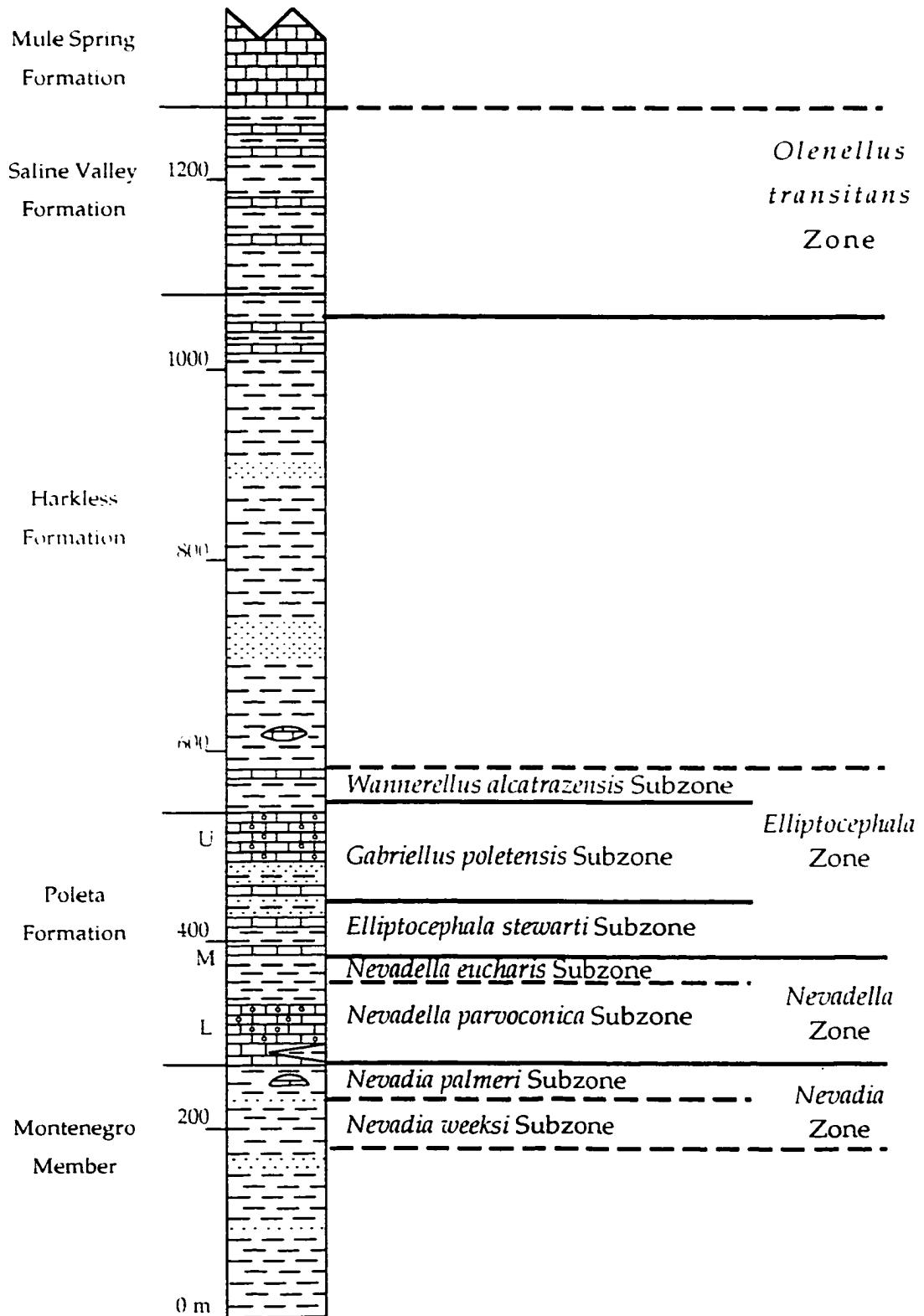
Nevadella Assemblage Zone. (Estimated thickness: 190 m) This zonal name was proposed by Fritz (1972) for shelf margin carbonates of the Sekwi Formation, Mackenzie Mountains. The zone has never been clearly defined: a base was not specified and it was characterized only by listing a few genera considered characteristic of the zone (Table 6). Palmer and Repina (1993, p. 11) used the term *Nevadella* Zone in the sense of a "Nevadiid Zone", which is approximately equivalent to the *Nevadia* and *Nevadella* Zones here defined.

The base of the *Nevadella* Zone is here defined by the base of the *Nevadella parvoconica* Subzone. The Poleta Formation, section CF of the Cedar Flat area, California, is designated the reference section. The subzonal succession described here based on faunas of the Poleta Formation from the study area is equally well-developed in the Mural Formation of the Mount Robson area, Canadian Rocky Mountains (Fritz, 1992).

All faunas are low-diversity, *Nevadella*-dominated assemblages with no apparent biofacies differentiation between inner detrital and middle carbonate belt sediments. Moore (1976b) assigned minor shales occurring in the lower carbonate member of the Poleta Formation at Goldfield to the outer detrital zone, but these sediments contain the same fauna as that found in the limestones. Collection sizes from the lower member of the Poleta Formation where trilobites are sparse are all too low (<15 specimens) for meaningful biofacies analysis.

Nevadella parvoconica Assemblage Subzone. (Estimated thickness: 160 m) The base is defined at the first appearance of *Nevadella parvoconica* (Fritz). The Poleta Formation, section CF of the Cedar Flat area, California, is designated the reference section. These are low-diversity assemblages in which the nominate genus is associated with *Esmeraldina argenta* (Walcott). *N. gracile* (Walcott) and *Cirquella nummularia* Fritz also occur in this zone. Based on the occurrence of *N. parvoconica* (Fritz), the *N. parvoconica* Subzone can also be recognized in the Mural Formation (Fritz, 1992). In the Mural Formation, *N. mountjoyi* Fritz also occurs in this zone. The *N. parvoconica* Subzone can further be recognized in the Donald

Text-fig. 19. Composite Lower Cambrian stratigraphic succession and zonal biostratigraphy in the southwestern Great Basin.



Formation of the Dogtooth Mountains, British Columbia (Fritz, 1993) by the occurrence of *C. nummularia* in these strata.

Nevadella eucharis Assemblage Subzone. (Estimated thickness: 30 m) The base is defined at the first occurrence of *Nevadella eucharis* (Walcott). The Poleta Formation, section CF of the Cedar Flat area, California, is designated the reference section. This subzone is a short interval that has been sparsely collected and poorly constrained in the study areas. In southeastern British Columbia, it is based on a single, monotypic collection from the Cranbrook Formation. It can also be recognized in the middle Poleta Formation of the southeastern Great Basin. No other species have been collected from this interval. The *N. eucharis* Subzone can also be recognized in the Mural Formation, Mt. Robson area, southern Canadian Rocky Mountains (Fritz, 1992).

Overlying the *Nevadella eucharis* Subzone in southeastern British Columbia is a barren interval that may include a disconformity. The next recognizable faunal interval is the *Wanneria logani* Subzone of the *Olenellus transitans* Zone. The typical assemblages dominated by *Elliptocephala*, *Gabriellus*, *Mesolenellus* and *Mummaspis* that overlie the *N. eucharis* Subzone in the Mural and Poleta formations are missing.

Elliptocephala Assemblage Zone. (Estimated thickness: 200 m) This zonal name was first used by Walcott (1910b). Walcott did not define a type area and his zonation is a composite based on ranges of Olenellina world-wide. From the list of species that Walcott considered characteristic of the zone (Table 1), it can be determined that Walcott's usage of the Zone is approximately equivalent to both the *Nevadella* and *Elliptocephala* zones as here defined.

The base of the *Elliptocephala* Zone is here defined in the Poleta Formation at the base of the *E. stewarti* Subzone and section CF of the Cedar Flat area, California is designated as the reference section. This interval records the proliferation of early wanneriids and includes also the *Gabriellus poletensis* and *Wannerellus alcatrazensis* subzones. The *Elliptocephala* Zone is present in: the Mural Formation, Mount Robson area, Canadian Rocky Mountains (Fritz, 1992); Sekwi Formation, Mackenzie Mountains (Fritz, 1972); Cassiar Mountains, British Columbia (W.H. Fritz, in prep.); Ella Island (Poulsen, 1932) and Wulff River (Poulsen, 1958) formations of Greenland; and the "Furoid Beds" of northwest Scotland (Cowie and McNamara, 1978).

Elliptocephala stewarti Assemblage Subzone. (Estimated thickness: 90 m) The base is defined at the first occurrence of *Elliptocephala stewarti* n. sp. in the middle Poleta Formation,

southwestern Great Basin. Section CF of the Cedar Flats area, California is designated the reference section. Little biofacies differentiation exists in this subzone and all assemblages are assigned to the Wanneriid Biofacies. Other species that occur in this interval are: *Bradyfallotaspis repinae* n. sp., *Mesolenellus moorei* n. sp., *Laudonia prima* (Lochman), *L. harringtoni* n. sp. and *Elliptocephala truemani*? (Walcott). The *E. stewarti* Subzone can be recognized in the Puerto Blanco Formation, Sonora, Mexico (Lochman, 1952) based on the occurrence of *L. prima*. Tentative correlation of the subzone in the Mural Formation (Fritz, 1992) is possible based on the occurrence of *E. truemani*.

Gabriellus poletensis Assemblage Subzone. (Estimated thickness: 85 m) The base is defined at the first occurrence of *Gabriellus poletensis* n. sp. in the middle Poleta Formation, southeastern Great Basin. Section CF of the Cedar Flats area, California is designated the reference section. Three biofacies can be recognized in this interval: a Wanneriid Biofacies in clastics to carbonates of the continental shelf, a *Labradoria* biofacies of open shelf to shelf edge deposition and an *Ekwapagetia* Biofacies in shelf-edge shaly carbonates. The *G. poletensis* Subzone can be recognized in the upper middle Poleta to basal Harkless formations. Other species that occur in this subzone are: *Mesolenellus guthi* n. sp., *Elliptocephala nelsoni* n. sp., *Mummaspis albersi* n. sp., *Ekwapagetia rasettii* n. sp., *Labradoria lochmanae* n. sp., *Gelasene aureum* n. sp., and *Polliaxis* sp. 1. *Elliptocephala stewarti*, the nominate species of the underlying subzone, also ranges into the *Gabriellus poletensis* Subzone. All species described from this interval are new and have not been recognized elsewhere. Consequently, none of these species is useful for correlation to other areas.

Wannerellus alcatrazensis Assemblage Subzone. (Estimated thickness: 25 m) The base is defined at the first occurrence of *Wannerellus alcatrazensis* n. sp. This subzone is recognized based on three monotypic collections (localities 12, 14, 21) from the lower Harkless Formation that are not part of measured sections. Locality 21 of the Cedar Flats area, California is designated the reference section. Only inner detrital strata are represented and consequently nothing can be said about biofacies distributions for this interval. *W. alcatrazensis* has not been recognized outside of the Great Basin study area.

Overlying the *Wannerellus alcatrazensis* Subzone in the southwestern Great Basin is a thick, sparsely fossiliferous interval of the Harkless Formation. *Olenellus* has been recorded from this interval (i.e. Waucoba Mountain measured section), but specimens are insufficiently preserved to determine the species. Near the top of the Harkless Formation, identifiable species are preserved, but the bulk of the formation is left unzoned. This has implications for

the *W. alcatrazensis* Subzone which is effectively left unconstrained as the top of a subzone or zone is defined by the base of the overlying interval.

Olenellus transitans Assemblage Zone. (Estimated thickness: 100 m) The base of the zone is defined at the first occurrence of *Olenellus transitans*, which is coincident with the base of the *Wanneria logani* Subzone in the Eager Formation. The Eager Formation, section MG2, Canal Flats area of southeastern British Columbia is designated the reference section. *Olenellus transitans* (Walcott) is a relatively long-ranging species that occurs throughout the Eager, uppermost Harkless and Saline Valley formations. Three subzones are defined for this zone in southeastern British Columbia, but these subzones cannot be recognized in the southwestern Great Basin. The two study areas have few faunal similarities as the former is represented by strata deposited mainly on the inner to middle continental shelf and the latter by strata deposited on the outer shelf. Strong biofacies differentiation is evident and four biofacies are recognized for this interval in British Columbia (Text-fig. 16) and three in the Great Basin (Text-fig. 17).

In the Saline Valley Formation of Nevada, species diversity in the *Olenellus transitans* Zone is relatively high. *O. transitans* (Walcott), *O. cf. thompsoni* (Hall) *Mesonacis? schofieldi* (Best), *Ogygopsis marcoui* (Whitfield), *O. batis* (Walcott) and *W. logani* (Walcott) are some of the widespread species characteristic of this zone that are useful for correlation to other areas. Additionally, species of *Bonnina*, *Protypus*, *Proliostracus*, *Zacanthopsis*, *Zacanthopsina*, *Lancastria* and *Goldfieldia* occur in this zone in the Saline Valley Formation.

Correlation of the *Olenellus transitans* Zone between the two study areas is based on the common occurrence of *O. transitans*, *Wanneria logani* and tentatively, *Mesonacis? schofieldi*. *O. transitans* is a widespread species outside the study areas that permits recognition of the *O. transitans* Zone in the Kinzers Formation, Pennsylvania (Resser and Howell, 1938), Parker Formation, Vermont (Resser and Howell, 1938); Buelna Formation, Sonora, Mexico (Lochman, 1952); Forteau Formation, Newfoundland (Stouge and Boyce, 1983); and the Ella Island Formation, Greenland (Poulsen, 1932). *O. transitans* can also be found in the lower Cararra Formation, California and Nevada (Palmer and Halley, 1979), as well as the upper Sekwi Formation, Mackenzie Mountains (Fritz, 1972) but the associated faunas are different from that seen in the study areas and these faunas likely belong to a different zone. The *O. transitans* Zone can further be recognized in the southern Appalachian Rome and Shady formations (Resser, 1938) based on the occurrence of *O. thompsoni* and *Ogygopsis marcoui*.

	Landing, 1994 Avalonia	Walcott, 1910 world-wide	Resser, 1938 S. Appalachians	Howell et al. 1944 N. America	Palmer in Merriam, 1964 SE Nevada	Rasetti, 1966, 1967 N Y State	Fritz, 1972 Mackenzie Mtns.	Palmer & Halley, 1979 S. Great Basin	Palmer & Repina, 1993 Laurentia	this work SE BC SW Great Basin
Middle Cambrian			Kochiella Zone	Syspacephalus Zone				Pohella lomataspis Zonule		
Lower Cambrian	Acidiscus theristes Zone	Olenellus Zone	Olenellus Zone	Olenellus Zone	O. gilberti-O. clarki Faunule		Bonnia - Olenellus Zone	N. multinodus Zonule	U	
	Protolenus howleyi Zone				Fremontia fremonti- Bristolia bristolensis Faunule			Bristolia Zonule		
								N. arcuatus Zonule		
		Callavia Zone	/? Kootenia Zone Bonnia Zone	— ? — Bonnia Zone		— ? — Pagetides Fauna			M	— ? — Olenellus transitans Zone
	Callavia broeggeri Zone	— ? — Elliptocephala Zone	/? Obolella Zone	— ? — Obolella Zone		— ? — Acmetopus bilobatus Fauna			L	— ? — Elliptocephala Zone
		— ? — Nevadella Zone				— ? — Elliptocephala asaphoides Fauna	Nevadella Zone		"Nevadella " Zone	Nevadella Zone Nevadella Zone
		— ? —					— ? — Fallotaspis Zone		"Fallotaspis " Zone	
	Teichichnus Zone*			— ? — Obolella Zone*						
	Rusophycus avalonensis Zone*			— ? —						
	Phycodes pedum Zone*									

Table 7. Comparison of the relative stratigraphic positions of previous authors biostratigraphic schemes with the zonal biostratigraphy proposed here for Laurentia. The Avalonian zonal biostratigraphy (Landing, 1994) is included to show the relative position of the basal Lower Cambrian zone, but correlation of trilobite zones between the two faunal provinces is not possible. * designates non-trilobitic zones. Abbreviations: O.=Olenellus; N.=Nephrolenellus. 1. Nevadella weeksi Subzone 2. Nevadella palmeri Subzone 3. Nevadella parvocornuta Subzone 4. Nevadella eucharis Subzone 5. Elliptocephala stewarti Subzone 6. Gabriellus poletensis Subzone 7. Wannerellus alcatrazensis Subzone 8. Wanneria logani Subzone 9. Wanneria dunni Subzone 10. Proliostrius buclmaensis Subzone

Southeastern British Columbia Subzones of the *Olenellus transitans* Zone

Wanneria logani Assemblage Subzone (Estimated thickness: 50 m) The base is defined at the first occurrence of the nominate species with the Eager Formation, section MG2, Canal Flats area of southeastern British Columbia designated as the reference section. Two biofacies can be recognized in this subzone in southeastern British Columbia: a Wanneriid Biofacies in shaly and oolitic carbonates and a *Bonnia* Biofacies in pure carbonates. Shale and sandstone assemblages have not been documented for this interval. *Bonnia drysdalea* n. sp. and *B. ornata* n. sp. are characteristic trilobites of the *Bonnia* Biofacies that occur low in the subzone; *B. fritzi* n. sp. and *B. laterispina* Fritz first occur at a higher level, followed by *B. grandis* n. sp. high in the subzone. Other species occurring are *Fremontella ashtoni* n. sp., *F. campbellae*, n. sp., *Mesonacis? leechi* n. sp. and *Olenellus transitans* (Walcott). *Elliptocephala parentalis* n. sp. also occurs in this zone and is found only in oolitic carbonates.

Wanneria logani (Walcott) is a widespread species whose occurrence permits recognition of the *W. logani* Subzone in numerous localities: the Ella Island Formation, Greenland (Poulsen, 1932); the Forteau Formation, Newfoundland (Walcott, 1910b; Stouge and Boyce, 1983), the upper middle Sekwi Formation, Mackenzie Mountains (Fritz, 1972); and the lower middle Illtyd Formation, Wernecke Mountains (Fritz, 1991a). *Bonnia laterispina* Fritz has also been described from the Sekwi (Fritz, 1972) and Illtyd (Fritz, 1991a) formations and *B. fritzi* (= *Bonnia* sp. 1 Fritz) also occurs in the Illtyd.

Wanneria dunnae Assemblage Subzone. (Estimated thickness: 25 m) The base is defined at the first occurrence of the nominate species with the Eager Formation, section MG2, Canal Flats area of southeastern British Columbia designated as the reference section. Three biofacies can be recognized in this subzone in southeastern British Columbia: an *Olenellus* Biofacies in shales, a *Wanneria* Biofacies in shaly carbonates and a *Bonnia* Biofacies in pure carbonates. Other species that occur in this subzone include: *Bonnia laterispina* Fritz, *B. grandis* n. sp., *Bonnaspis fieldensis* (Walcott), *Olenellus schucherti* Resser and Howell, 1938, *O. schofieldi* Best, *O. transitans* (Walcott), *Mesonacis graingerensis* n. sp. and *M. eagerensis* (Best). *Wanneria logani*, the defining species of the base of the underlying subzone, ranges into the lower portion of the *Wanneria dunnae* Subzone.

Several species typical of the *Wanneria dunnae* Subzone of the Eager Formation are found elsewhere. The *W. dunnae* Subzone can be recognized in: the Forteau Formation, Newfoundland

by the occurrence of *Olenellus transitans*, *O. schucherti* and *W. logani*; and in the St. Piran Formation, Alberta (Walcott, 1916b) by the occurrence of *Bonnaspis fieldensis*.

Proliostracus buelnaensis Assemblage Subzone (Estimated thickness: 25 m) The base is defined at the first occurrence of *Proliostracus buelnaensis* (Lochman) with the Eager Formation, section MG2, Canal Flats area of southeastern British Columbia designated as the reference section. Only the *Proliostracus* and *Bonnia* biofacies, both characteristic of carbonate rocks (Text-figs. 13-14), have been described for this interval. Other species that occur in this subzone are: *Bonnia grandis* n. sp., *Olenellus transitans* (Walcott), *O. schucherti*? and *Wenkchemnia*: sp. 1. The *P. buelnaensis* Subzone can also be recognized in the Buelna Formation of Sonora, Mexico based on the occurrence of *P. buelnaensis* and *O. transitans*.

	Trilobite Zonation	Yukon	Northwest Territories	Rocky Mtn. Main Ranges	Southeast BC	Central Nevada	Southwest Great Basin	Southern Great Basin	Sonora, Mexico	Pennsylvania	Southern Appalachians	Labrador, NFL
ME		Slats Creek	Hess River	Chetang		Pioche	Monola	Cararra	Arrojos		Elbrook	March Point
Lower Cambrian				Hota			Mule Spring		Cerro Prieto*	Ledger		Hawk Bay
	— ? — <i>Olenellus transitans</i> Zone	Illtyd			Eager		Saline Valley		Buelna	Kinzers	Rome Shady	Forteau
			Sekwi	Mahto			Harkless	Zabriski	Preveedora*	Antietam	Antietam	Bradore*
	— ? — <i>Elliptocephala</i> Zone					Prospect Mountain						
	<i>Nevadella</i> Zone			Mural			Poleta		Puerto Blanco			
	<i>Nevadella</i> Zone				Cranbrook							
	<i>Nevadella</i> Zone						Campito					
			Vampire	McNaughton*			Deep Spring	Wood Canyon				
PE		Windermere Supergroup			Purcell Supergroup				La Ciénega			

Table 8. Correlation of selected Lower Cambrian formations of Laurentia based on trilobite biostratigraphy. * indicates no faunal data
1. *Nevadella weeksi* Subzone 2. *Nevadella palmerti* Subzone 3. *Nevadella partoconica* Subzone 4. *Nevadella eucharis* Subzone 5. *Elliptocephala stewarti* Subzone 6. *Gabriellus poletensis* Subzone 7. *Wannerellus alcatrazensis* Subzone 8. *Wanneria logani* Subzone 9. *Wanneria dunnae* Subzone 10. *Proliostracus buelnaensis* Subzone

Chapter 4. Trilobite Terminology

General Features

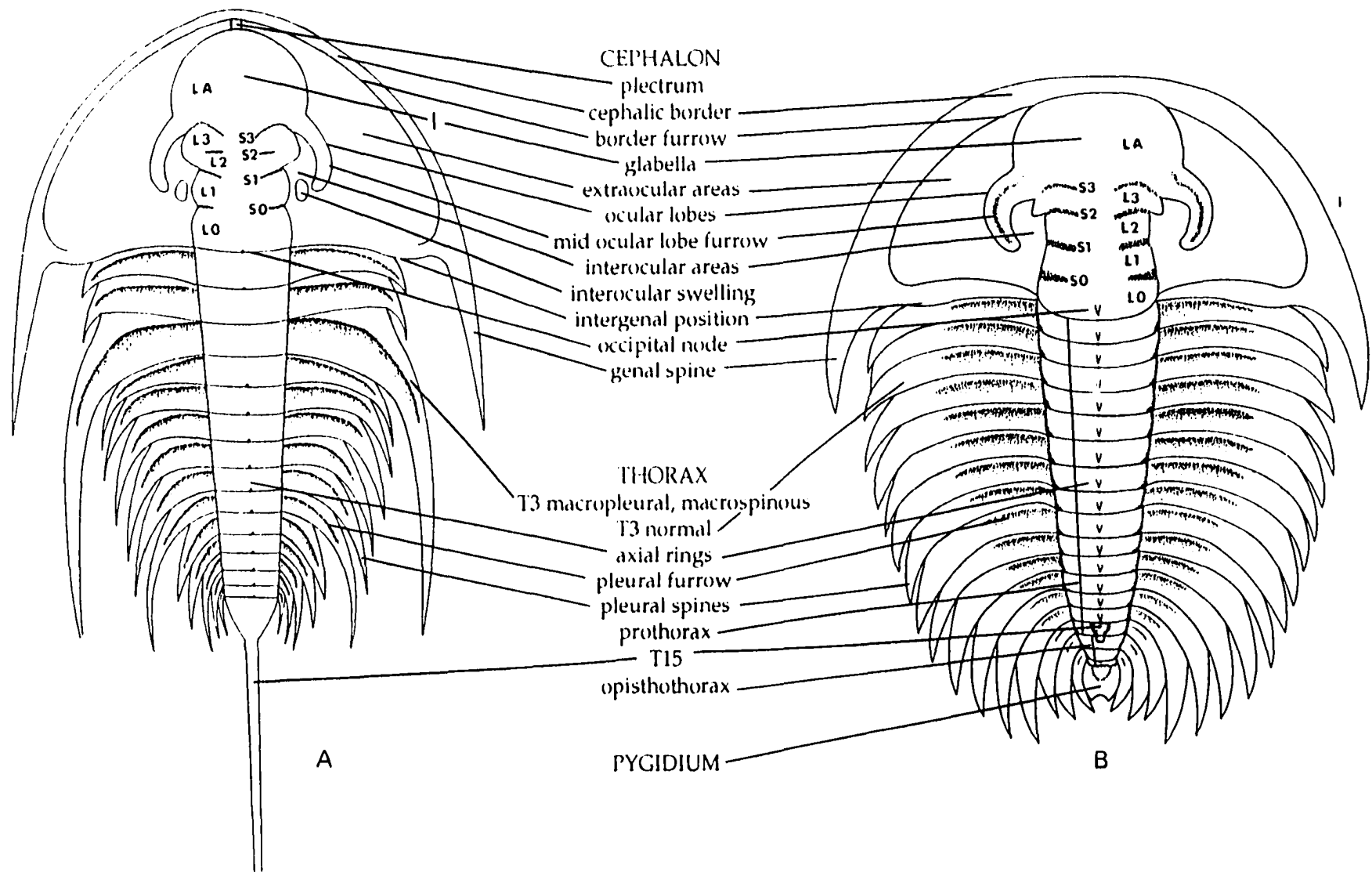
Labeled illustrations for the morphology of the various types of trilobites dealt with in this thesis are given in Text-figs. 20-23. Morphological terms follow those used by Moore (1959), Palmer and Repina (1993) and Jell (1975). Trilobites have three major body divisions: **cephalon**, **thorax** and **pygidium**. The relative size of the pygidium to the cephalon is describe by terms such as **micropygous** (pygidium smaller than cephalon), **isopygous** (pygidium approximately the same size as cephalon) and **macropygous** (pygidium larger than cephalon). Longitudinally, the trilobite is divided into a central **axial region** by the **axial furrows**, and two lateral **pleural regions**. Size of various parts is described by the terms **wide** and **narrow** for transverse directions; **long** and **short** for sagittal and exsagittal directions. Sagittal length of the cephalon, exclusive of any occipital spine, is used as a standard measurement to describe and compare trilobite size.

The external surface of the exoskeleton has a texture that is referred to as **prosopon**. Prosopon is typically a species level characteristic and can be smooth or include such features as pits, reticulate ridges, terrace lines (raised ridges in various patterns), or tubercles. This feature can be complex consisting of a mix of features (ex. "honeycombs" of raised anastomosing ridges with central pits) and can be variable through ontogeny and over different parts of the exoskeleton. Separate from prosopon is the term **effaced** which refers to a "smoothing" of the exoskeleton in which furrows are shallow and indistinct.

Cephalon

The **cephalic border** is delimited by a **border furrow** and consists of **anterior** and **lateral borders**. **Cephalic border pits** are developed in some Olenellina. In eodiscoid trilobites, the anterior border may be subdivided by an **epiborder furrow** with radiating furrows called **scrobicules** occurring posterior to the epiborder furrow. The lateral and posterior borders join at the **genal angle** and may extend into a **genal spine**. The position of the genal spine may be **normal** (on a transverse line with L0), **advanced** (anterior of a transverse line with L0), or **arcuate** (posterior of a transverse line with L0). An **intergenal spine** or **node** may be developed on the posterior border at some point between the genal angle and L0.

A **preglabellar field** is any area that exists between the front of the glabella and the anterior border. Its length varies greatly from wide to non-existent in those trilobites in which LA contacts the anterior border. A **plectrum** is a sagittal ridge found in the Olenellina extending



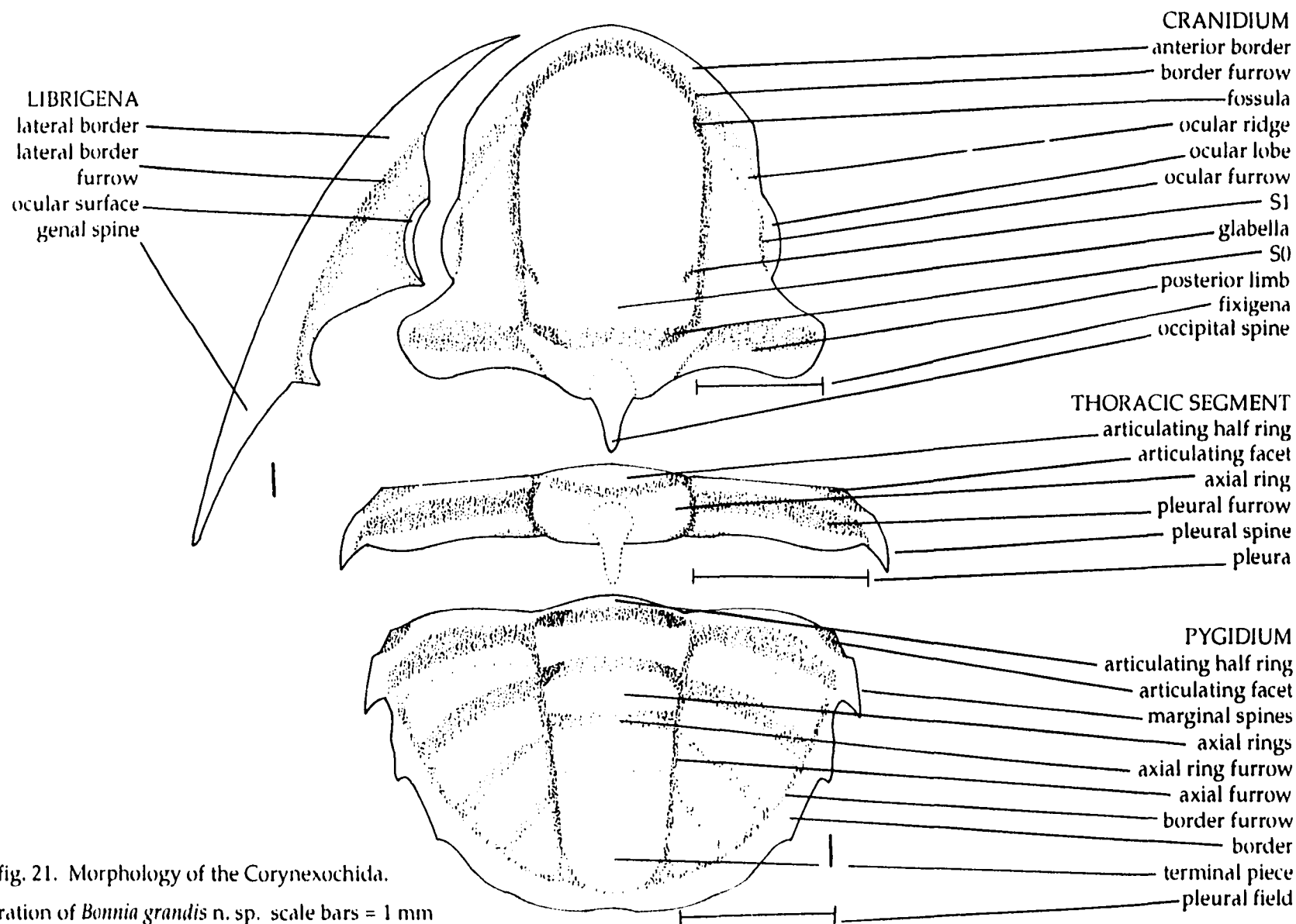
Text-fig. 20. Morphology of the Olenellina. A. *Olenellus ricei* n. sp. (Olenellidae). B. *Wanneria walcottana* (Wanner) (Wanneriidae). scale bar = 1 mm

from the anterior cephalic border at least part way across the preglabellar field. It may be **full** (extending posteriorly to contact LA), **partial** (extending only part ways across the preglabellar field) or **absent**. Eodiscoids and ptychopariids often have a depression in the preglabellar field anterior to the glabella called a **preglabellar depression**.

The cephalon in the majority of trilobites is divided into a central **cranidium** and two lateral **librigenae** by the **facial sutures**. The facial sutures are described as **opisthoparian** (posterior portion of suture cuts the posterior cephalic border medial to the genal angle), **proparian** (posterior portion of the suture cuts the lateral cephalic border anterior to the genal angles) or **gonatoparian** (posterior portion of the sutures bisects the genal angle). Opisthoparian is the only condition exhibited by non-Olenellina trilobites illustrated in this work. The pleural portions of the cranidium are called **fixigenae** which generally extend laterally into **posterior limbs**. In the Corynexochida, **metafixigenal spines** may be developed on the posterior limbs. The facial suture crosses the ocular region of the trilobite separating the lateral **ocular surface** from the medial **ocular lobes**. An **ocular furrow** defines the ocular lobe medially.

The Olenellina lack facial sutures (the cephalon is a single fused tergite) and require a slightly different terminology. The terms **interocular** and **extraocular areas** are approximately equivalent to the terms **fixigenae** and **librigenae** respectively. Measurements of these areas are made along a transverse line from S2. **Interocular swellings**, of unknown significance, are sometimes developed. Olenellina have **ocular lobes**, usually divided longitudinally by an **mid-ocular lobe furrow** into an **inner ocular band** and an **outer ocular band**. Rarely distinguishable is the **ocular surface**, separated from the ocular lobe by the **circumocular suture**. Ocular lobe length varies at the species level and is measured by the relative position of the posterior ocular tips to the glabellar lobes or furrows: in the Olenellina, long ocular lobes have tips opposite or posterior of S0; short ocular lobes have tips opposite or anterior of L1. Trilobites in general have **ocular ridges** extending from the anterior of the ocular lobes to the glabella. Non-Olenellina often have axial pits developed anterior to the point of contact of the ridge to the glabella which are called **fossulae**.

The Olenellina have a series of faint genal "lines" (Geyer, 1996): low ridges that cross the extraocular areas. They can only be distinguished on well-preserved material, and not every type of line can be found in every species. A low **genal ridge** may extend from approximately the midlength of the lateral edge of the ocular lobe to the genal angle. An **intergenal ridge** may run from the interocular area to the intergenal spine or node. An **anterior ocular line** may run from the anterior of the ocular lobe, posterolaterally to the lateral cephalic border. A



Text-fig. 21. Morphology of the Corynexochida.
Illustration of *Bonnia grandis* n. sp. scale bars = 1 mm

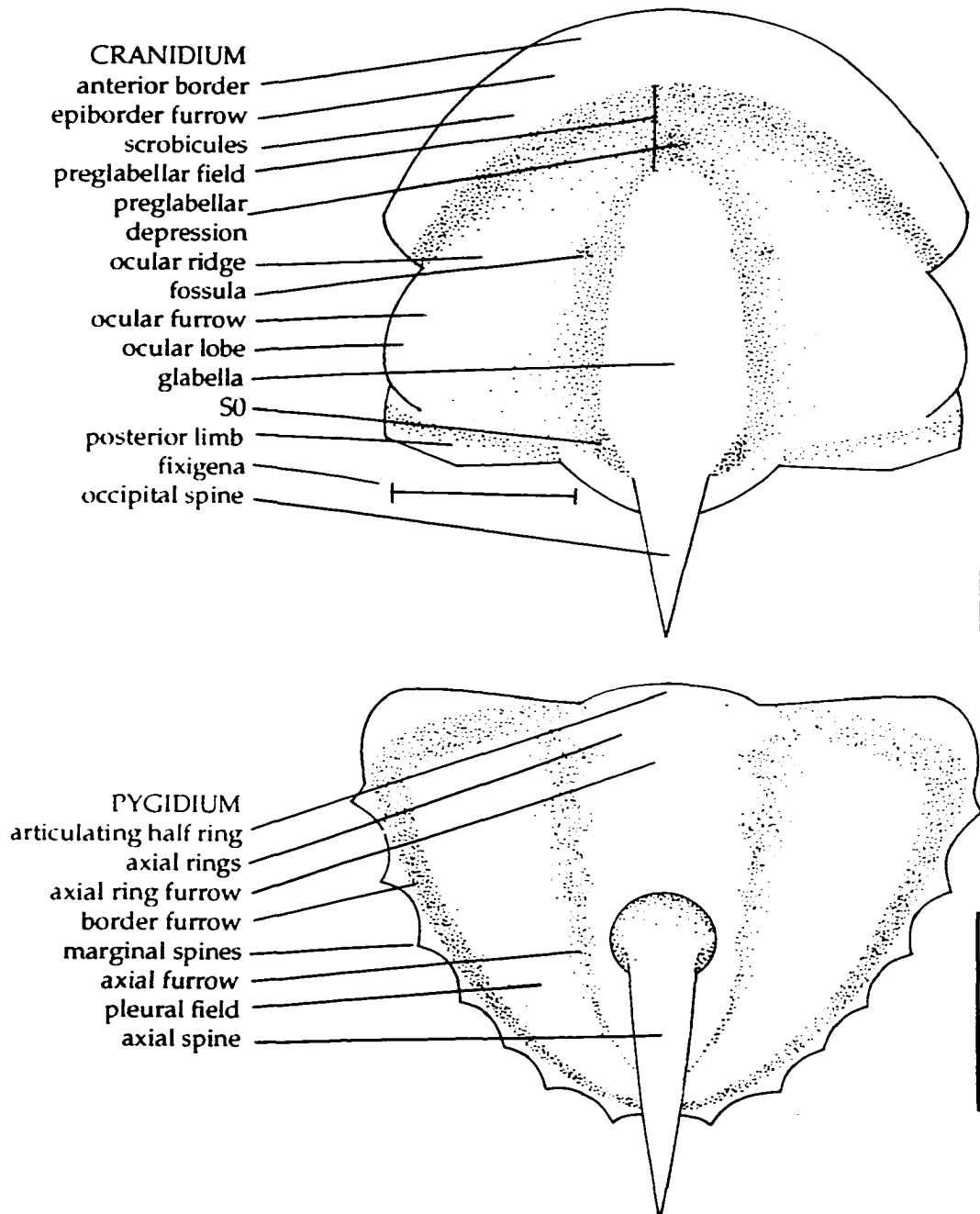
posterior ocular line may run from the posterior tip of the ocular lobe posterolaterally to the posterior border

The **glabella** is the raised axial region of the cephalon generally defined exclusive of L0 (occipital lobe) and bounded posteriorly by S0 (occipital sulcus). L0 may have a median **occipital spine or node**. A useful and diagnostic measure used in this study is the relative length of the glabella plus L0, relative to the cephalic length. For simplicity, this is referred to as **glabellar length**, although the glabella does not technically include L0. Similarly, the term **glabellar stalk** is used for the parallel-sided portion of a clavate glabella, inclusive of L0. Glabellar shape may be **tapering forward** (i.e. *Nevadia*), **corynoid**⁷ (evenly expanding forward, i.e. *Bonnaspis*), **clavate** (club-shaped, i.e. *Wanneria*), **parallel-sided** (i.e. *Bonnina*) or **hourglass-shaped** (constricted at midlength, widening posteriorly and anteriorly, i.e. *Peachella*). **Parafrontal bands** may be present laterally on the anterior glabellar lobe. Glabellar features are numbered starting from the posterior of the glabella. The furrow pairs are S1, S2, and S3 and the glabellar lobes are L1, L2, L3, and LA (anterior lobe). S4 can be distinguished in some trilobites anterior to the attachment point of the ocular ridge to the glabella. In general, the furrow pairs may be **transglabellar** (joined across the glabella) or **marginal** (separate slots near the margins of the glabella). In the Olenellina, S2 may be **marginal and isolated** (separate slots not connected to the axial furrow) or **partially isolated** (deepest medially but continues as a shallow furrow to the axial furrow). S3 may also be partially isolated when the ocular lobe contacts L3 and only a shallow axial furrow remains between them. Furrow orientation may be **straight** (transverse), **oblique** (inclined posteriorly or anteriorly towards the midline) or **curved** (concave posteriorly). Palmer and Repina (1993) used the term **modified** refer to an L3 which is expanded laterally and posterolaterally, wrapping around L2.

Thorax

For the thoracic region, segments are numbered from the anterior to posterior as T1, T2, T3, ... Each segment has a medial axial ring with articulating half-ring, lateral pleurae crossed by **pleural furrows**, and marginal **pleural spines**. In the Olenellina, a **prothorax** of segments gradually diminishing in size towards the posterior is always developed. Some species also have an **opisthothorax** of minute, terminal segments, all the same size. In those species with a large 15th **axial spine**, any segments posterior to the 15th are opisthothoracic. Shape of the pleural spines may be **chelate** (claw-like as in some *Holmia*), **falcate** (sickle-shaped as in *Nevadella*), **sentate** (thorn-like, as the T1 and T2 of *Olenellus*) or **blunt** (rounded as in

⁷ Term coined by Öpik (1982).



Text-fig. 22. Morphology of the Eodiscina.
 Illustration of *Ekvipagetia rasettii* n. sp. scale bars = 1 mm

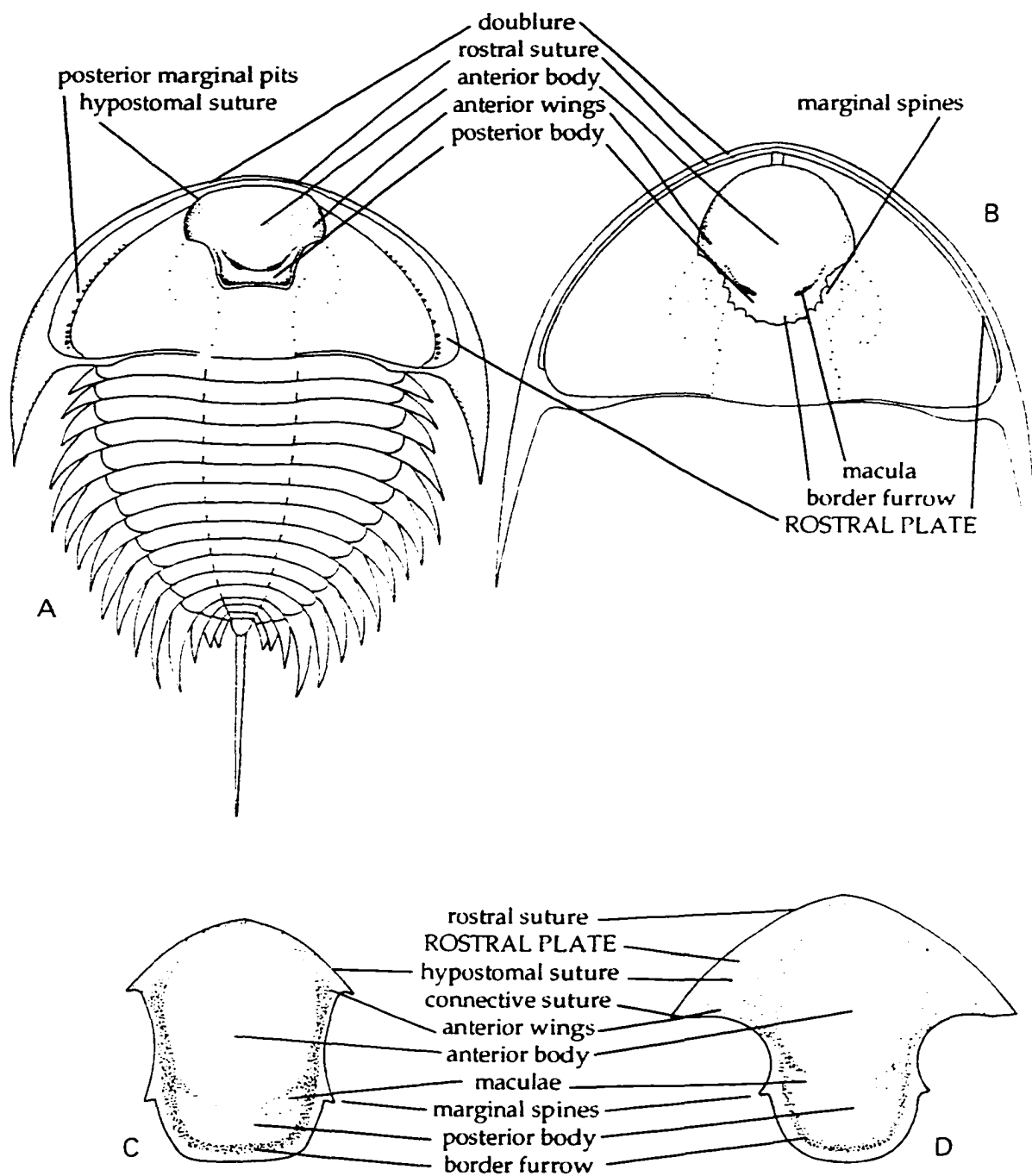
Peachella). Pleural spines may be **pendent** (exsagittally directed), **divergent** or **convergent**. A specialized nomenclature is used in the Olenellina for T3, which often has a different morphology than the preceding and following segments (Text-fig. 20). **Macropleural** refers to segments with a long pleural region (ex. *Olenellus*). **Hyperpleural** refers to T3 segments with greatly elongated lateral pleural regions that distort the surrounding segments (ex. *Peachella*). **Amplipleural** refers to T3s that are slightly enlarged compared to T1 and T2, but not unusually large compared to T4 (ex. *Nevadella*). For the T3 pleural spines, **macrospinous** refers to any spine that is significantly longer than those of adjacent segments. **Dolichospinous** refers to spines that are extremely long and robust compared to adjacent segments (ex. *Peachella*).

Pygidium

The pygidia of trilobites are variably developed from small plates of few segments (i.e. Olenellina, Zacanthoididae) to large, many-segmented tergites (i.e. *Ogygopsis*). Multi-segmented pygidium have a raised axial region divided into **axial rings** by **axial ring furrows**, which may be **transaxial** or **marginal**. An **articulating half-ring** is present anterior to the first axial ring, and rings and furrows are numbered sequentially from anterior to posterior. Medial **axial tubercles** may be present which may extend into **axial spines**. The axis may terminate in an unsegmented **terminal piece** which may be followed by a **post-axial ridge** running sagittally between the axis and border. The pleural regions of the pygidium are referred to as **pleural fields** and are usually crossed by **pleural furrows**, serially homologous to the pleural furrows of the thoracic segments. **Interpleural furrows** that mark the line of fusion between segments may also be present. A **border furrow** and **border** may or may not be present as well as pairs of **marginal spines**.

Ventral Morphology

Most of the ventral portion of trilobites, including the limbs, consisted of uncalcified exoskeleton that is only preserved under exceptional conditions. The margins of the dorsal exoskeleton are curved ventrally and extends a short ways across the ventral surface as the **doublure**. Separate calcified plates of the ventral head region generally include the **rostral plate** and **hypostome** (Text-fig. 23). The rostral plate is joined to the doublure by a **rostral suture**. **Connective sutures** are present, in most trilobites that have rostral plates, to separate the rostral plate from the doublure of the fixigenae. The Olenellina which lack facial sutures, also lack connective sutures and the form of the rostral plate is long and crescentric, extending to the doublure of the genal angles. **Posterior marginal pits** can be seen on the rostral plates of some taxa (i.e. *Wanneria*).



Text-fig. 23. Ventral trilobite morphology. A. *Wanneria dunnae* n. sp.; attached, contaminant hypostome with functional hypostomal suture. B. *Olenellus ricei* n. sp.; natant hypostome. C. *Bonnia grandis* n. sp.; natant? or attached hypostome, rostral plate unknown. D. *Bonnaspis columbensis* (Resser); attached, conterminant hypostome, fused rostral-hypostomal plate.

The **hypostome** is located posterior to the rostral plate to which it may or may not be connected. Terminology to describe the attachment conditions and position of the hypostome follow both that of Whittington (1988a) and Fortey (1990). An **attached** hypostome is in direct contact with the rostral plate via the **hypostomal suture**. The hypostomal suture may be fully functional or may be fused producing a **rostral-hypostomal plate**. Attached hypostomes may be either **conterminant**, lying directly underneath the glabella with the anterior margin corresponding ventrally to the anterior outline of LA; or **impendent**, in which there is no correspondence between the positions of the hypostome and the glabella. A "stalked" hypostome has been found in one species of Olenellina (*Olenellus transitans*) in which a sagittal calcified stalk joins the hypostome to the rostral plate. Hypostomes that are not directly attached to the rostral plate are referred to as **natant** and maintain a position closely corresponding to the glabella. Hypostome attachment conditions may change through ontogeny (i.e. conterminant to natant in some Ptychopariida like *Olenus*; natant to attached, conterminant in some Olenellina like *Wanneria*). Hypostomes have a large, inflated **anterior body** defined posteriorly by a **middle furrow**. A pair of slight protuberances or **maculae** are typically developed posterior to the middle furrow. Anterolaterally the hypostome extends into **anterior wings** that curve dorsally. In natant and conterminant hypostomes, the anterior wing tips are directly below the dorsal fossulae, when developed. The **posterior body** is short with a variably developed **border furrow** and **border**, sometimes bearing **marginal spines**. An additional **posterolateral furrow** may be present (i.e. *Wanneria*) when the posterolateral border is expanded.

Ontogeny

The ontogeny of trilobites can generally be divided into three stages. The smallest is the **protaspid stage**, characterized by the absence of a thorax and the fusion of the pygidium to the cephalon. The intermediate **meraspid stage** has the cephalon and pygidium as separate units, with a variable number (zero to one less the holaspid complement) of thoracic segments in-between. Through meraspid development, thoracic segments are progressively released from the pygidium with each molt. The **holaspid stage** has a thorax with the full complement of thoracic segments characteristic of that species. The meraspid cephalons of the Olenellina typically have well-developed **intergenal spines** that are reduced in size to nodes or short spines in the adult. Considerable growth and morphological development can occur through the holaspid stage.

Much of the material dealt with in this work is disarticulated and the typical stages of trilobite ontogeny are difficult to apply. The ontogeny of *Bonnia* (Corynexochida) is examined

in some detail with small meraspid, large meraspid and holaspid stages recognized and defined in disarticulated material at major changes in glabellar shape (see *Bonnia* discussion). Three cliques are recognized in the presumed holaspids, also based on changes in glabellar shape (see *Bonnia grandis* ontogeny).

Terminology for the ontogeny of the Olenellina, also largely represented by disarticulated material, needs to be revised. Palmer (1957) described a complete ontogenetic sequence of *Olenellus* by defining five stages. The term "stage" is not appropriate here as there are three ontogenetic stages defined for all trilobites, at least two of which (meraspid and holaspid stages) theoretically apply to articulated ontogenies of the Olenellina. In practical application the holaspid stage is difficult to recognize even in articulated material because opisthothoracic segments are minute and typically obscured by the 15th axial spine in the Olenelloidea. For practical purposes, the holaspid stage is recognized by the possession of a long 15th axial spine in articulated material, and by the possession of prominent genal spines in disarticulated cephalae. In this thesis, the ontogeny of the Olenellina is divided into divisions called cliques and described by reference to a standard ontogeny of *Olenellus* (see discussion of *Olenellus*). Seven cliques⁸ labeled A through G are defined to reflect the major changes that occur during growth. Cliques A through D approximately represent the meraspid stage, and cliques E through G approximately represent the holaspid stage. Material representing the protaspid stage has never been described for any species of the Olenellina. Whittington (1989) discussed the possible significance of the apparent absence of this stage.

⁸ The cliques defined here are not equivalent to the "stages" used by Palmer (1957), although the standardized comparative ontogenetic sequence here defined is based on Palmer's material. The cliques reflect the author's views on important ontogenetic changes that are useful in non-silicified material with a poorer quality of preservation, and have a greater emphasis on holaspid development.

Chapter 5 Systematic Philosophy

The past century has seen many changes in how taxonomic decisions are made. Modern approaches emphasize formalized taxonomic procedures and the use of numerical methodologies as justification, where possible. There are currently many competing philosophies on taxonomic thought, each with some merit. Ridley (1986) aptly refers to this "taxonomic controversy" and sums up the source of the problem:

That there should be any controversy at all might, to begin with, seem strange. The principles of classification, considered superficially, might seem too straightforward to be controversial: you simply have to define groups by taxonomic characters.... More and more inclusive groups are defined by more and more general shared characters, to result in the customary hierarchy of species contained in genera, families, orders, classes, phyla.... But classification is controversial. It is controversial because different characters define different groups, which means that taxonomists cannot both naively define groups and agree with each other. The disagreement of characters is both the fundamental source of all taxonomic controversy and the reason why there is more to classification than simple definition of groups. (Ridley, 1986, p. 1-2)

There are three basic schools of evolutionary thought, each of which has a different means of character selection. It is not the purpose here to discuss in detail these competing schools because the relative merits of each have been extensively compared and contrasted by authors such as Wiley (1981), Schoch (1986), Ridley (1986), and Scott-Ram (1990). Phenetics (Sokal and Sneath, 1963) uses as many characters as the taxonomist can distinguish and produces phenograms that are estimates of overall morphological similarity of taxa. Evolutionary systematics (Simpson, 1961; Mayr, 1969) uses subjectively determined homologous characters (Ridley, 1986); its goal is to develop classifications that reflect evolutionary relationships. Cladistics or phylogenetics (Hennig, 1950) uses only synapomorphic characters, that is, only shared derived features. It focuses on determining the branching patterns of evolution and aims to develop classifications according to that branching pattern. Cladistics is the most rigorous of the three methods and it has become the most widespread method. A subset of the cladistic school is the philosophy of transformed cladistics (Platnick, 1979; Scott-Ram, 1990). It uses the same techniques as cladistics, but rejects interpretation of the results in an evolutionary light (Ridley, 1986). The goal of this school is taxonomic classification though the production of unambiguously defined taxa. This philosophy is here rejected since it seems contradictory to

base character selection on synapomorphies, determined in an evolutionary sense, and then to deny that the classification reflects phylogeny. Viewed in this fashion, transformed cladistics becomes another method of performing phenetic analysis that aims to classify based on shared morphology, not shared descent (Ridley, 1986).

An important distinction between cladistics and evolutionary systematics is that the former accepts only monophyletic groups while the latter accepts both paraphyletic and monophyletic groups (Wiley, 1981; Schoch, 1986). Acceptance of paraphyletic groups, defined by sympleisiomorphies (Schoch, 1986), is preferable to the author when dealing with stem groups that have unresolved specific relationships to their descendants (i.e. the Fallotaspidae). A paraphyletic group shares a common ancestor and its members are all closely related, regardless of whether or not some members gave rise to different descendant taxa. Evolutionary systematists also view large morphological gaps as justification for the use of separate higher taxonomic groups (Wiley, 1981). This is the rationale used here for separate status for the Olenellidae and Wanneriidae. One of the most widely accepted examples of these concepts is the separation of Aves from the Reptilia. The reptiles are a paraphyletic group of primitive vertebrates (grade) separated by a large morphological gap from one monophyletic branch of their descendants, the birds (clade). Justification for the Reptilia is simple: reptiles are a group united by common descent and if they had not given rise to morphologically disparate groups such as the birds and mammals, they would be an acceptable monophyletic group.

The author's views on systematic methodology echo those of Fitch (1984):

The field of systematics has been in considerable turmoil as various investigators developed different methods of classification and argued their merits. I guarantee you that no one method or view has all the good points. That is why I commend eclecticism to you; grab the benefit regardless of the label attached. I guarantee you that no method or view is without its blemishes. (Fitch, 1984, p. 247-248)

A cladistic approach with an evolutionary systematic interpretation of results is advocated here for the Olenellina.

Characterization of taxa is done best using homologous, derived features, although it is useful to also note what primitive features are retained in a taxon. Fossils present special problems in character analysis. Typically, observable characters are limited to morphology of hard parts that have a high preservation potential. The process of fossilization can alter the appearance

of features and comparison between material of different preservation types must be done with caution to be sure that differences are taxonomic and not preservational artifacts. The level of taxonomic usefulness of a character must also be considered. Characters that vary at the species level are not informative at the genus or higher level and must be excluded from such analyses. Here, special emphasis is given to ontogenetic and ventral morphological characters as distinguishing features of higher taxonomic groups (discussed below). Numerical methods advocated by cladists are regarded as a useful check to determine if a classification can be supported.

Ventral Morphology

The ventral features of Lower Cambrian trilobites are not well known. Taxonomic studies have often neglected to illustrate aspects of the ventral morphology and even when they have, these features are rarely considered in diagnoses. Every effort has been made to explore the ventral morphology of the described species in this study.

Whittington (1988a, 1988b) and Fortey (1990a) concluded that trilobite ventral morphology and hypostome attachment conditions are important diagnostic features of higher taxa. For example, a natant hypostome was found to be an autapomorphy of the Ptychopariida (Fortey, 1990a) and a median suture an autapomorphy of the Asaphina (Fortey and Chatterton, 1988).

It is, however, important to avoid over-generalization when only a few examples of the ventral morphology are known in a particular group. Rasetti (1951, 1952) and Whittington (1995) used the fused rostral-hypostomal plate (conterminant to impendent condition) as a diagnostic feature of the Corynexochida. Fortey (1990a) concurred and considered the conterminant hypostomal condition to be pleisiomorphic in the Corynexochida. It is demonstrated here in the systematic section that this condition is not a universal feature of the order: *Ogygopsis* (Dorypyginae) and the Horonastinae are accepted taxa of Corynexochida that have a functional hypostomal suture. It is also shown that *Bonnina* and *Olenoides* have either a functional hypostomal suture or a natant hypostome. Since *Bonnina* is one of the oldest members of the Corynexochida, a fused rostral-hypostomal plate is not a primitive feature of the order. It is more likely that the fused rostral-hypostomal plate of Corynexochidae such as *Bonnina*, *Bonnaspis*, *Kootenia* and *Corynexochus* is a derived, pedomorphic feature.

Ventral cephalic morphology is known for only a few Olenellina. Whittington (1988a) summarized much of the known information and showed that *Holmia* has an attached

hypostome with a hypostomal suture that is functional at least part of the time. The same configuration is demonstrated here for large specimens of *Wanneria* (Pl. 7, figs. 4, 6, 8) and *Elliptocephala* (Pl. 9, fig. 7). In a large collection of specimens from the Eager Formation, large hypostomes of *Wanneria* have been found in both states: isolated or attached to a rostral plate. The hypostomal suture was therefore present, though it did not always function in ecdysis. No small hypostomes have been observed in an attached state and it is concluded that small holaspids and meraspids (which also have a preglabellar field) have natant hypostomes. This is an interesting example of a change in hypostome attachment conditions in the holaspid stage. *Wanneria* has a derived hypostomal shape with an indented posterior margin and deep posterolateral furrows.

Olenellus is another member of the Olenellina in which the ventral morphology is reasonably well known. Walcott (1910b, pl. 34, figs. 6, 7) illustrated two specimens of *Olenellus transitans* in which the hypostome is attached to the rostral plate by a narrow stalk (see also Pl. 18, fig. 4 herein). This arrangement has been mistakenly described as the standard condition for *Olenellus* (i.e. Fortey, 1990a). Numerous hypostomes of other species of *Olenellus* have now been illustrated and *O. transitans* is the only species that demonstrably has a stalked hypostome. This delicate stalk has poor preservation potential, but even in finely preserved silicified material of other species of *Olenellus* (see Palmer, 1957), no stalk is evident. Whittington (1988b) made the correct interpretation that some species of *Olenellus* have a stalked hypostome, but not all. A non-mineralized stalk may, however, have been present in other species such as *O. schucherti* (Pl. 20, fig. 5) in which molted hypostomes can sometimes still be found associated in life position with the rostral plate. A stalked hypostome may be a autapomorphy of *Olenellus*, but a mineralized stalk is not.

The rostral plate of the Olenellina in general has a standard morphology, including that of the Fallotaspidae, which Geyer (1996) recently documented. It is crescentic in shape, with the posterior tips located near the genal angles. As Geyer (1996) concluded, the rostral plate position does not correspond to the dorsal cephalic border. A broad plate is the primitive condition in the Olenellina, as exemplified by the Fallotaspidae and Wanneriidae. In at least *Olenellus* of the Olenellidae, the rostral plate is narrow.

In conclusion, hypostome morphology and attachment condition are generally useful diagnostic features of Lower Cambrian genera. The morphology of the rostral plate is significant at the family level or higher.

Ontogeny

Ontogenetic studies on fossil organisms are limited by preservation. Trilobites have an excellent fossil record as a result of their calcified exoskeletons that have a high preservation potential, but small stages are difficult to recover except in silicified material. While ontogeny is the life history of an individual from zygote until death, the embryonic portions of trilobite life histories are not preserved. Trilobite ontogenies are limited to the free-living, calcified, protaspid, meraspid and holaspid stages.

Knowledge of ontogeny is vital information for taxonomic and systematic studies. Many early 20th century taxonomists, such as C. Poulsen and C.E. Resser, took little note of ontogenetic sequences, and consequently named multiple species for different growth stages of a single species. This is one of the problems addressed in the systematics section and a reason why a number of Lower Cambrian species are synonymized. Comparative taxonomic work must also ensure that comparable growth stages of species are compared, otherwise differences noted may be a result of relative maturity, rather than actual taxonomic differences.

The importance of ontogenetic information in systematics is a matter of debate. Von Baer (1828), one of the most influential of the early embryologists, formulated a series of developmental laws, two of which follow:

1. The general features of a large group of animals appear earlier in the embryo than the special features.
2. Less general characters are developed from the more general, and so forth, until finally the most specialized appear. (von Baer, 1828, p. 224; translated in Gould, 1977, p. 56)

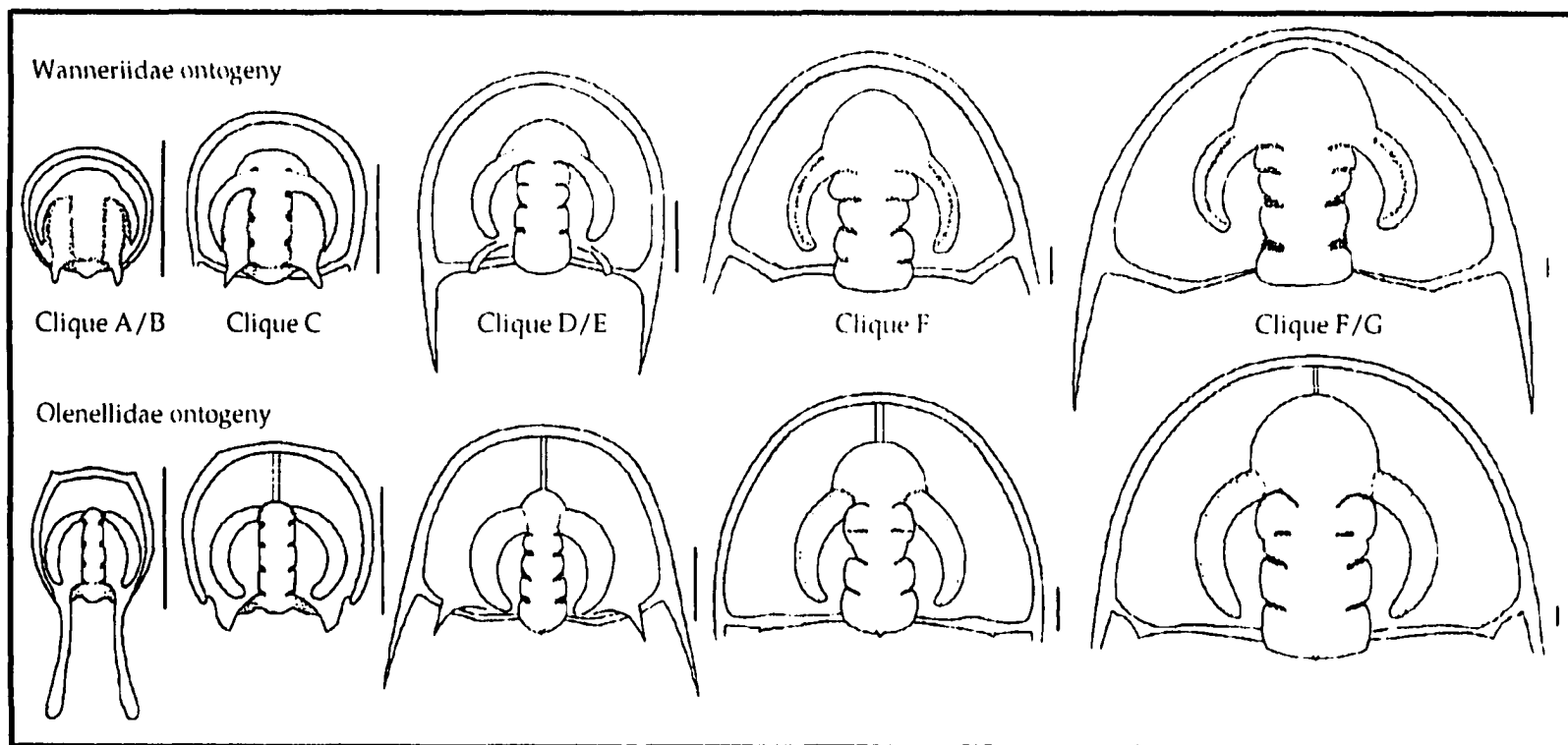
Haeckel (1866) built on von Baer's work and boldly proposed the Biogenetic Law, which is popularly paraphrased as "ontogeny recapitulates phylogeny". This suggests that ancestral morphologies can be read directly from an organism's ontogeny. However, the Biogenetic Law is only valid if evolution proceeds by what Gould (1977, p. 486) called terminal addition, in which "new evolutionary features are added to the end of ancestral ontogenies so that previous adult stages become preadult stages of descendants". There are two problems with this: first, that paedomorphosis is a well-documented and accepted evolutionary process (i.e. see examples in Gould, 1977) that invalidates the law, and second, that evolutionary change can affect any stage of ontogeny (see extensive documentation in Raff, 1996). It is therefore only

under specific evolutionary transformations (terminal addition) that juveniles or descendant taxa resemble ancestral taxa. One clear example of this in the Olenellina is that glibellar morphology of olenelloid meraspids has the parallel-sided to tapering forward shape of holaspid fallotaspidoids, the ancestral group.

While Haeckel's Biogenetic Law has proved untenable, the more basic laws of von Baer have wide applicability. The application of von Baer's laws to cladistics as a way of using ontogeny to polarize a cladogram is discussed in the cladistic section which follows. Gouid (1977) concluded that similarities between early ontogenetic stages are an indication of shared ancestry. For the Trilobita, using shared morphology of early stages as a indication of higher taxonomic relationships has been done for a number of major groups such as the Asaphina (Fortey and Chatterton, 1988), Calymenina (Chatterton *et al.*, 1990) and Encrinuridae (Edgecombe *et al.*, 1988) with more general discussions on ontogeny and phylogeny in the Trilobita provided by Chatterton and Speyer (1990), Whittington (1957a) and Fortey (1990a). Little use has been made of these concepts for systematics of Lower Cambrian trilobites. There has been some work on the Corynexochida and Ptychopariida: Robison (1967) noted that the two orders share a similar protaspid stage and hypothesized that differential growth rates produced the disparate morphologies between the two groups in the holaspid.

This work makes extensive use of early ontogenies in systematic studies on the olenelloids. It is accepted that shared juvenile morphologies are a better indication of relationship than similar adult morphologies. Previous work by the author (Bohach, 1995, 1996) has noted that the Wanneriidae can be diagnosed and differentiated from the Olenellidae on the basis of meraspid morphology. The wanneriid meraspid has a short, wide LA and slender (usually short) intergenal spines. Contrast this with a *Olenellus* meraspid (Text-fig. 24) which has a short, narrow LA and long, baseball bat shaped to cylindrical intergenal spines. The shape of LA in Wanneriidae and the shape of the intergenal spines in the Olenellidae are regarded as synapomorphies of the families⁹. Separation of the Wanneriidae and Olenellidae based on meraspid morphology is supported by certain holaspid features such prosopon, depth of the mid-ocular lobe furrow and position of S2, but these are mainly subtle features and holaspids of the two families can look remarkably similar (Text-fig. 24) with morphologies that have invariably been identified as *Olenellus*. Bohach (1996) argued that this is a result of parallel evolution in the adult morphologies. An alternative suggested here is that it may be an

⁹ Note that the Mesonacinae of the Olenellidae are peramorphically altered and have lost the typical shape of the intergenal spines in the early stages.



Text-fig. 24. Comparative ontogenies of the Wanneriidae and Olenellidae. Wanneriidae illustrations based on the ontogeny of *Elliptocephala parentalis* n. sp. Olenellidae illustrations based on the ontogeny of *Olenellus transitans* (Walcott) (British Columbia material). scale bar = 1 mm

example of conservatism of adult form where major evolutionary changes have occurred in the meraspid stage¹⁰.

Three different applications of ontogeny to taxonomy and systematics have been listed above, although use of ontogeny in cladistics (Kluge, 1985) and in determining higher taxonomic groups is not accepted by all authors (Raff, 1996). At the very least, ontogenetic characters supply additional characters for evaluation of relationships between taxa. Ontogeny can further be used as a check for homology (i.e. Dong-Chan and Chatterton, 1996). One final application of ontogeny is in the recognition of heterochrony in the fossil record. This is discussed in detail in the next section.

Heterochrony

Heterochrony, evolution through changes in developmental timing, was recognized by Gould (1977) as one of two major sources of evolutionary change, the other being innovation. There are two major patterns of heterochrony: paedomorphosis, in which the descendant resembles the juvenile of the ancestor, and peramorphosis, in which the descendant's morphology develops beyond that of the ancestor. In heterochronic change, the elements of growth (size, shape and time), become decoupled (McNamara, 1990). Depending on the type of change involved, six heterochronic processes can be recognized: progenesis, neoteny and post-displacement which can produce paedomorphosis; hypermorphosis, acceleration and pre-displacement which can produce peramorphosis. While the pattern of heterochrony can be readily recognized in fossil material, recognition of the process is more difficult because the element of time cannot be directly measured. Gould (1988) and Jones (1988) both recognized that size data are not always an accurate substitute for time data in growth analysis. Studies here are limited to a recognition of the pattern of heterochronic change.

An excellent introduction to the terminology of heterochrony can be found in McNamara (1990), and a detailed historical account with numerous examples of heterochrony has been published by Gould (1977). McNamara (1988) put heterochronic studies into a paleontological perspective and noted:

¹⁰ Choice between these two alternatives is dependent upon the nature of the relationship between the Olenellidae and Wanneriidae, which is unclear. If the two families are sister groups, then homeomorphy is the likely cause of similarities in holaspid form. If the Wanneriidae gave rise to the Olenellidae, then the similar holaspid morphology between *Olenellus* and some of the early Wanneriidae is likely conservatism of adult form.

If it is possible to compare the ontogenies of species pairs that are both morphologically and phylogenetically closely related and have similar, but not entirely overlapping ranges, then it is possible to assess whether the stratigraphically younger species is a paedomorph or a peramorph. (McNamara, 1988, p. 289)

Comparison of the ontogenies of related taxa is thus put into a stratigraphic context. The two taxa compared do not have to have a demonstrated ancestor-descendant relationship, rather the older of two closely related taxa is assumed to have a morphology that is closer to the ancestral type. It must also be noted that examples of heterochrony are often complex and mosaic evolution is common (i.e. *Olenelloides*).

Heterochrony in Lower Cambrian Trilobites

First, a general description of ontogenetic change is in order for each of the two major groups examined:

Olenelloidea: *Olenelloid* morphology continued to change throughout the trilobite's life history, including during the holaspide stage. Rare fragments of very large individuals are found in many collections suggesting that at least some species had indeterminate growth. The majority of *olenelloid* species show the following general changes throughout their ontogenies:

1. increase in relative width of the extraocular areas and a corresponding decrease in width of the interocular areas
2. decrease in length of the intergenal spines and migration of the intergenal position laterally
3. relative shortening of the ocular lobes
4. increase in the relative length of LA and corresponding decrease in length of the preglabellar field
5. modification of glabellar furrows from the juvenile condition of transverse, marginal slots to a mature configuration (oblique furrows, isolated furrows, etc.) with corresponding modification of L2/L3
7. development of prosopon and mid-ocular lobe furrows
8. loss or migration of medial, marginal hypostomal spines to a lateral position
9. reduction in relative size of T3 compared to the other thoracic segments

Bonnia (Corynexochidae): The only genus of Corynexochida with abundant ontogenetic material described in this study is *Bonnia*. This is a key genus for the Corynexochida since it is one of the oldest members of this order and may be close in morphology to the ancestral type.

The following general changes occur during the ontogeny of *Bonnia*:

1. change in glabellar shape from clavate, to corynoid, to expanding forward, to nearly parallel sided
2. lengthening of the anterior border
3. increase in curvature of the anterior margin of the cranidium and glabella
4. relative shortening of the ocular lobes
5. decrease in relative width of the fixigenae
6. increase in length to width ratio of the pygidium
7. effacement of the interpleural furrows
8. increased curvature of the anterior margin of the hypostome with posterior displacement of the hypostomal wings
9. opening of the hypostomal suture

McNamara (1978, 1982, 1983, 1986) has produced a series of papers on heterochrony in trilobites, many of them dealing with Cambrian species. His olenelloid studies are of particular interest since his results differ from those of Palmer and Repina (1993) and from conclusions reached here through ontogenetic studies. McNamara (1978) is the first paper dealing with olenelloids, focusing on the trilobites from the "Fucoid" beds of Scotland. The trilobites are interpreted by McNamara to show progressive paedomorphosis. The first criticism of this paper is that there is no stratigraphic context: McNamara described the heterochronic pattern as paedomorphic, but it could just as easily be peramorphosis since most of the trilobites co-occur and there is no way of identifying the ancestral type. Second, McNamara has little ontogenetic information; one of his key ontogenetic stages (text-fig. 4d, McNamara, 1978) in the sequence is hypothetical, not real. Third, all of the species belong to the wanneriid *Elliptocephala*, except for *Olenelloides* which is a distantly related mesonacine (Olenellidae) (see systematic section). Thus, *Olenelloides* cannot be part of any transformation series in the Wanneriidae. In conclusion, the paedomorphocline that McNamara (1982, fig. 4; 1986, fig. 6) has produced for olenelloids has no basis in reality.

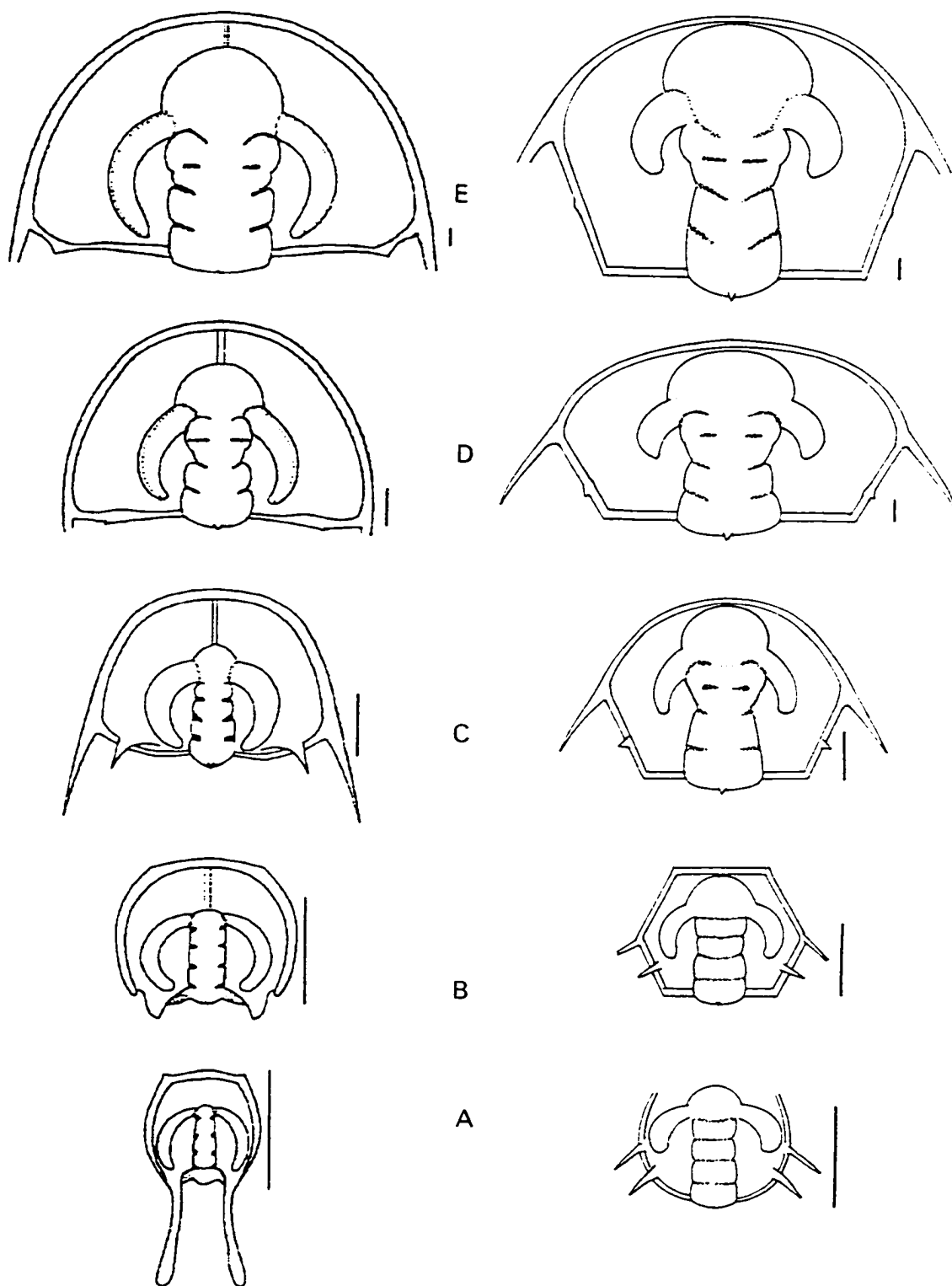
The significance of the morphology of *Olenelloides* is discussed in detail in the systematics section and is briefly summarized here. *Olenelloides* has an unusual morphology for an olenelloid and shows indications that it has evolved by both peramorphic and paedomorphic patterns. Holaspids of *Olenelloides* possess features typically seen only in the larvae of

olenelloid trilobites, such as: narrow extraocular areas, only nine thoracic segments and prominent intergenal and procranial spines. These are paedomorphic features since they are retained in the holaspid. However, even in early ontogeny, *Olenelloides* has short ocular lobes, laterally positioned intergenal spines, almost no preglabellar field and a large LA. These are features that typically do not develop until late in the ontogeny of other species of Olenellidae. These are peramorphic features, typical of the Mesonacinae.

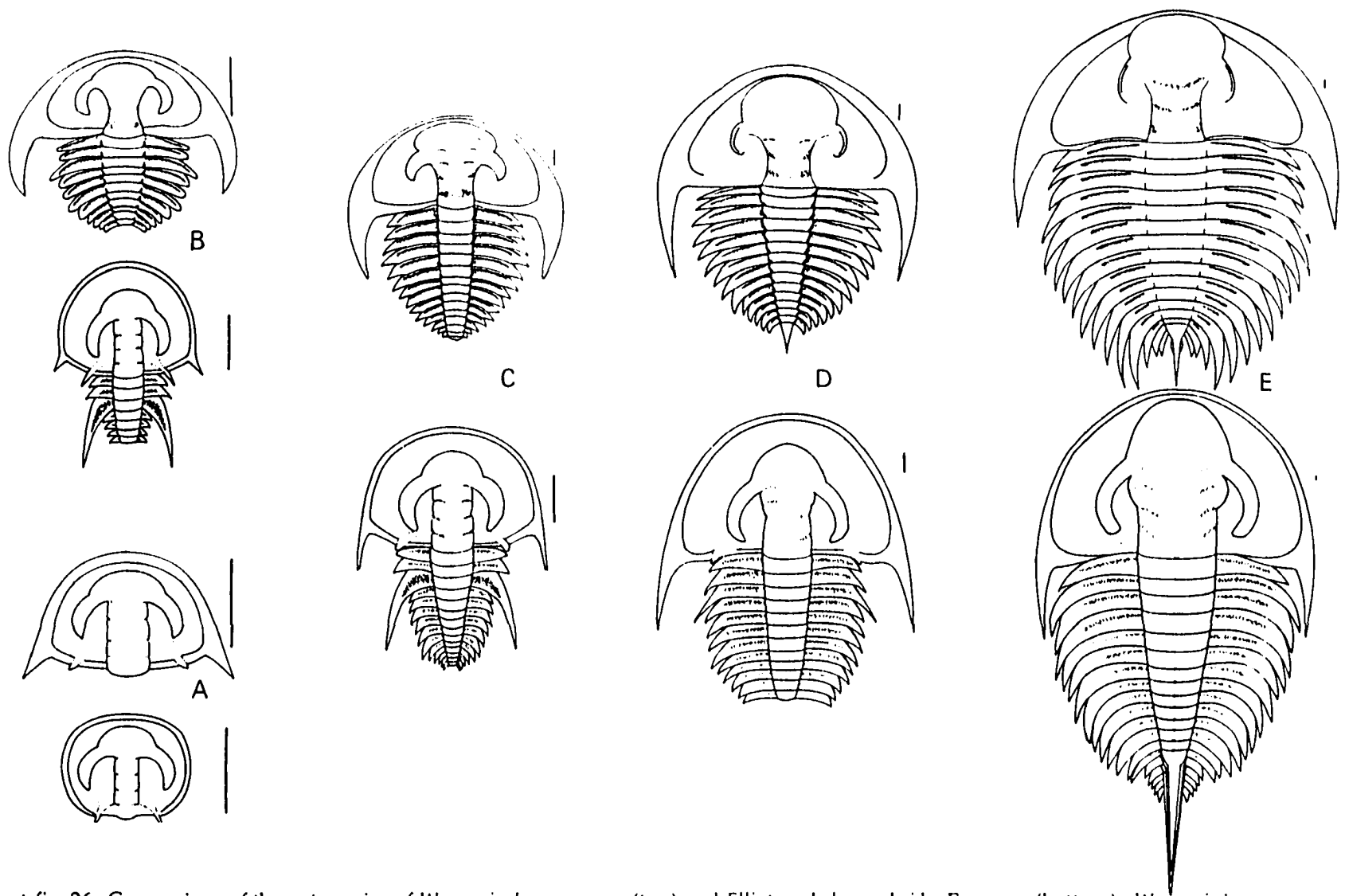
This peramorphic pattern seen in the Mesonacine is graphically illustrated in Text-fig. 25 where the ontogenies of *Mesonacis* and *Olenellus* are compared. *Olenellus* is regarded as the ancestral type: although the species compared here are approximately coeval, *Olenellus* has an earlier first occurrence. Features to note are: the large LA in even the smallest known meraspids of *Mesonacis* compared to the tiny LA in *Olenellus* meraspids that does not become large and subrounded until relatively late in the holaspid ontogeny; corresponding to the size of LA, a preglabellar field is absent in meraspids of *Mesonacis* while it is long in meraspids of *Olenellus* and does not become short until late in the ontogeny; the small size and lateral position of the intergenal spines in the small meraspids of *Mesonacis* where in meraspids of *Olenellus* the intergenal spines are initially long, medially positioned and only shrink and migrate laterally later in the meraspid to early holaspid stages; and the mature configuration of the glabellar lobes and furrows by clique D/E in *Mesonacis* while the glabellar morphology does not mature until late in clique F in *Olenellus*.

A peramorphic heterochronic pattern can also be seen in *Wanneria*, one of the youngest genera of the Wanneriidae. Text-fig. 26 compares the ontogeny of *Wanneria* to the older wanneriid, *Elliptocephala*. Features to note are: the large size of LA and the clavate shape of the glabella by clique C in *Wanneria* which is not even as pronounced in clique G holaspids of *Elliptocephala*; the shortness of the preglabellar field in even the smallest meraspids of *Wanneria* compared to the long preglabellar field that is maintained until at least clique F in *Elliptocephala*; the shortness and lateral position of the intergenal spines in early meraspids (clique B) of *Wanneria* that are similar to about clique E specimens of *Elliptocephala*; *Wanneria* has normal T3's throughout the known ontogeny (at least clique C on) whereas *Elliptocephala* has macropleural T3's early in ontogeny that are progressively reduced and are normal by clique F.

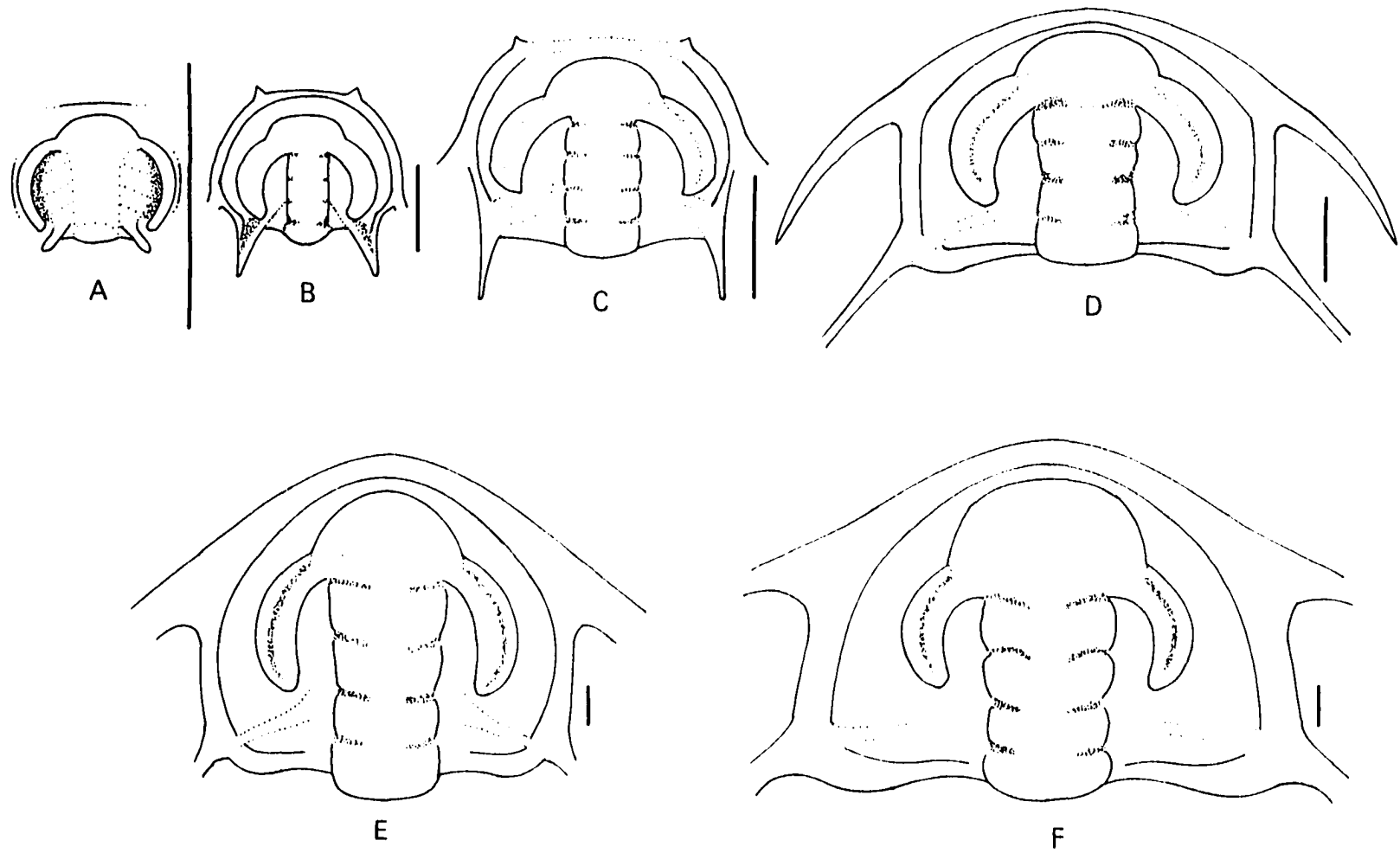
Laudonia is an example of a partially paedomorphic wanneriid, with a single cephalic feature, the long intergenal spines retained in the holaspid stage, that is paedomorphic. With the exception of *Olenelloides*, *Laudonia* is the only Olenellina that has long intergenal spines



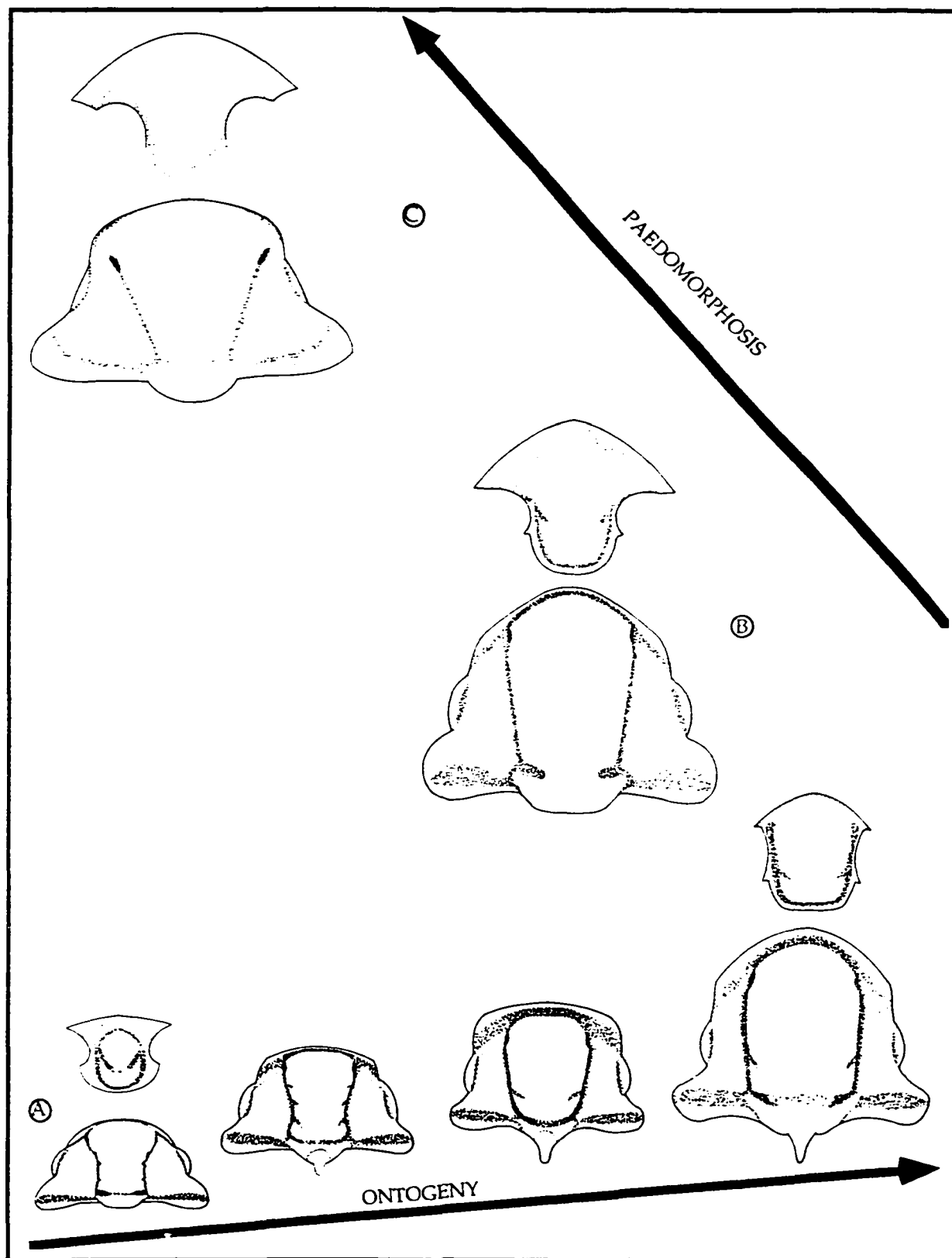
Text-fig. 25. Comparison of the ontogenetic pattern of *Olenellus transitans* (Walcott) (left) and *Mesonacis graingerensis* n. sp. (right). *Mesonacis* is peramorphically altered compared to *Olenellus*.
 A. clique A/B B. clique C C. clique E D. clique F E. clique G scale bars = 1 mm



Text-fig. 26. Comparison of the ontogenies of *Wanneria dunnae* n. sp. (top) and *Elliptocephala asaphoides* Emmons (bottom). *Wanneria* is peramorphic in features compared to *Elliptocephala*. A. clipe B B. clipe D C. clipe E D. clipe F E. clipe G scale bars = 1 mm



Text-fig. 27. Ontogeny of *Laudonia prima* (Lochman). Letters designate cliques. scale bars = 1 mm



Text-fig. 28. Evolution via pedomorphosis in the Corynexochidae. (A) ontogeny of *Ronnia grandis* n. sp. (B) holaspis of *Bonnaspis fieldensis* (Walcott) (C) holaspis of *Corynexochus plumula* Whitehouse.

as a holaspid. *Laudonia* has a morphology that is otherwise closely comparable to contemporaneous wanneriids, except in the autapomorphy of advanced genal spines that become increasingly advanced throughout ontogeny (Text-fig. 27; Pl. 12, figs. 6-13; Pl. 14, figs. 1-8). *Elliptocephala nelsoni* n. sp. (Pl. 11 figs. 1-7) is an unusual species that has minute genal spines in the holaspid stage. This is interpreted as a pedomorphic feature since genal spines develop in the late meraspid stage of most olenelloids and are long by about the time the holaspid stage is reached.

For one final example of heterochrony, the Corynexochidae are examined. Numerous ontogenies of *Bonnia* are illustrated in this study and are significant as *Bonnia* is considered to be close to ancestral morphology for the rest of the family. Text-fig. 28 compares the ontogeny of *Bonnia* (Lower Cambrian) to the holaspid morphology of *Bonnaspis* (upper Lower Cambrian and Middle Cambrian) and *Corynexochus* (Middle and Upper Cambrian) in a pedomorphocline. Compared to the ontogeny of *Bonnia*, the younger genera have an increasing immature configuration of the glabella and anterior border. The hypostome and rostral plate which are fused into a single unit only in meraspids of *Bonnia* are also a single unit in holaspids of the younger genera.

Cladistic Analysis

Cladistic analysis uses mathematical algorithms to find patterns in character state distribution among taxa. The preferred pattern, depicted as a cladogram, is the one that has the smallest number of character state changes with the least amount of homoplasy. This is the principle of parsimony; that is, the cladogram with the least amount of convergence and reversal of characters is taken as the most likely depiction of branching relationships (Kluge, 1984). Detailed discussions of cladistic theory and methodology can be found in Forey *et al.* (1992), Wiley *et al.* (1991), Maddison and Maddison (1992) and Swofford and Begle (1993).

As cladistics is concerned with distinguishing ancestral and derived character states, methodology must be defined for making these distinctions in analyses performed in this work. Many such methods exist. Smith (1994) listed four: commonality, outgroup comparison, ontogeny and stratigraphic sequence. The first method, in which the most common character state is taken as primitive, has been extensively criticized (i.e. Watrous and Wheeler, 1981; Wiley *et al.*, 1991) and is not used here. The fourth method, stratigraphic sequence information, is used here only as a zero weight character for discussion on the resultant cladograms because inadequacies of the fossil record make stratigraphic sequence a less than reliable method of

polarizing data. Outgroup comparison (see Maddison *et al.*, 1984) is a popular method in which a related taxon is compared to the ingroup, and character states shared by both the ingroup and outgroup are taken as plesiomorphic. The sister group, the taxon most closely related to the ingroup, is the preferred outgroup (Wiley *et al.*, 1991). Maddison *et al.* (1984) advocated the use of more than one outgroup to optimize determination of ancestral states. There are problems with outgroup analysis; first, that convergence between the ingroup and outgroup are assumed to be minimal and, second, that some *a priori* knowledge of the phylogeny is needed which adds circularity to the reasoning. Ontogeny analysis is also a popular method for distinguishing primitive and derived character states (Nelson, 1978). The basis for this method is von Baer's (1828) ontogenetic law (see also Gould, 1977), restated in application to cladistics by Nelson (1978, p. 324): "given ontogenetic character transformation, from a character observed to be more general to a character observed to be less general, the more general character is primitive and the less general advanced. Thus character states observed in early ontogenetic stages are ancestral states and those observed in later ontogenetic stages are derived". This is a good general principle, but evolutionary change can affect any stage of ontogeny (Raff, 1996) and innovations can be inserted into early ontogenetic stages too. Rieppel (1993) provided a detailed account of the applicability of von Baer's work to phylogeny interpretation and cladistic methodology. Ridley (1986) concluded that both outgroup and ontogeny analyses are useful though imperfect techniques for estimating ancestral character states. Both are used here.

A number of cladistic analyses were performed in the course of this thesis work. Only the most informative set of results is presented here. This set is designed to illustrate the relationship between the Wanneriidae and Olenellidae, the two families of Olenellina characteristic of the upper Lower Cambrian of Laurentia. Secondly, it provides an indication of the relationships of genera within the families. The most completely known species for each genus of the two families is coded (Appendix B). For some of the key genera examined in this work, an additional species is coded to further characterize the genus, especially where there are missing data. Genera, as such, are not coded; species are. It is not a sound practice to code a generalized morphology for a genus since it may end up with a set of features not exhibited by any species. Further, a species is commonly regarded as the only natural taxonomic category (i.e. Mayr, 1942) with all higher taxa being artificial constructs that are intended to reflect phylogeny.

Character selection focuses on features that are diagnostic of genera and higher taxonomic groups. A strong emphasis is given to ontogenetic features. Ventral morphology features,

though limited, are also included. Cephalic features are well-represented by characters while pygidial features are not characterized due to the paucity of pygidial information. Some characters, such as cephalic border width, have value as higher taxonomic characters for only some taxa and are species-level features for other taxa. Appendix B contains the character list, data matrix and taxon information.

Outgroup selection for the Olenellidae/Wanneriidae clade is problematic due to the uncertainties of relationships between families of the Olenelloidea. In the absence of an obvious sister group, multiple outgroups are used. The Olenellidae and Wanneriidae are united in the Olenelloidea, along with the Holmiidae (Palmer and Repina, 1993), and consequently the best known holmiid, *Holmia kjerulfi* Linnarson, is coded as a potential outgroup. *H. kjerulfi* is a Baltic species, and while a Laurentian species would be preferable, all are inadequately known. As indicated in the taxonomy, the Holmiidae is a group in need of further study to determine their relationship to the Wanneriidae. A potential sister taxon of the Olenelloidea is the Archaeaspididae, which Repina (1979) suggested may be ancestral to the Holmiidae. *Bradyfallotaspis repinae* n. sp. of Laurentia is the best known species. The stratigraphic range of *B. repinae* is coincident with the Wanneriidae. The last "outgroup" identified is a hypothetical ancestor (hyp.ancest) based primarily on ontogenetic character transformation sequences of the Wanneriidae and Olenellidae. The data are supplemented by comparison to the outgroup Archaeaspididae to attempt to determine the most likely primitive character states, following the methodology of Ramsköld and Werdelin (1991). Source of the information for determination of the ancestral character state is indicated for each character in Appendix B. Multiple analyses were run using the outgroups collectively and individually.

Data were processed using PAUP 3.1¹¹ (Swofford, 1993) and cladograms generated using MacClade 3.0 (Maddison and Maddison, 1992). It was not practical to use the algorithms for either exhaustive or branch-and-bound searches and, therefore, heuristic methods were used instead. The following settings for a heuristic search were used in order to optimize results, as recommended by Swofford and Begle (1993). The taxon addition sequence chosen was CLOSEST and results were checked by running a series of randomly generated sequences. In one instance, the randomly generated sequences produced additional trees. Branch swapping was performed using the tree bisection-reconnection algorithm. The MULPARS option was on to save all equally parsimonious trees. The STEEPEST DESCENT option was on requiring all generated trees to be examined and not abandoned when a shorter tree was found. The COLLAPSE option

¹¹ Results from an earlier set of runs were tested using PHYLIP (Felsenstein, 1990) to ensure that no program-generated bias was being created.

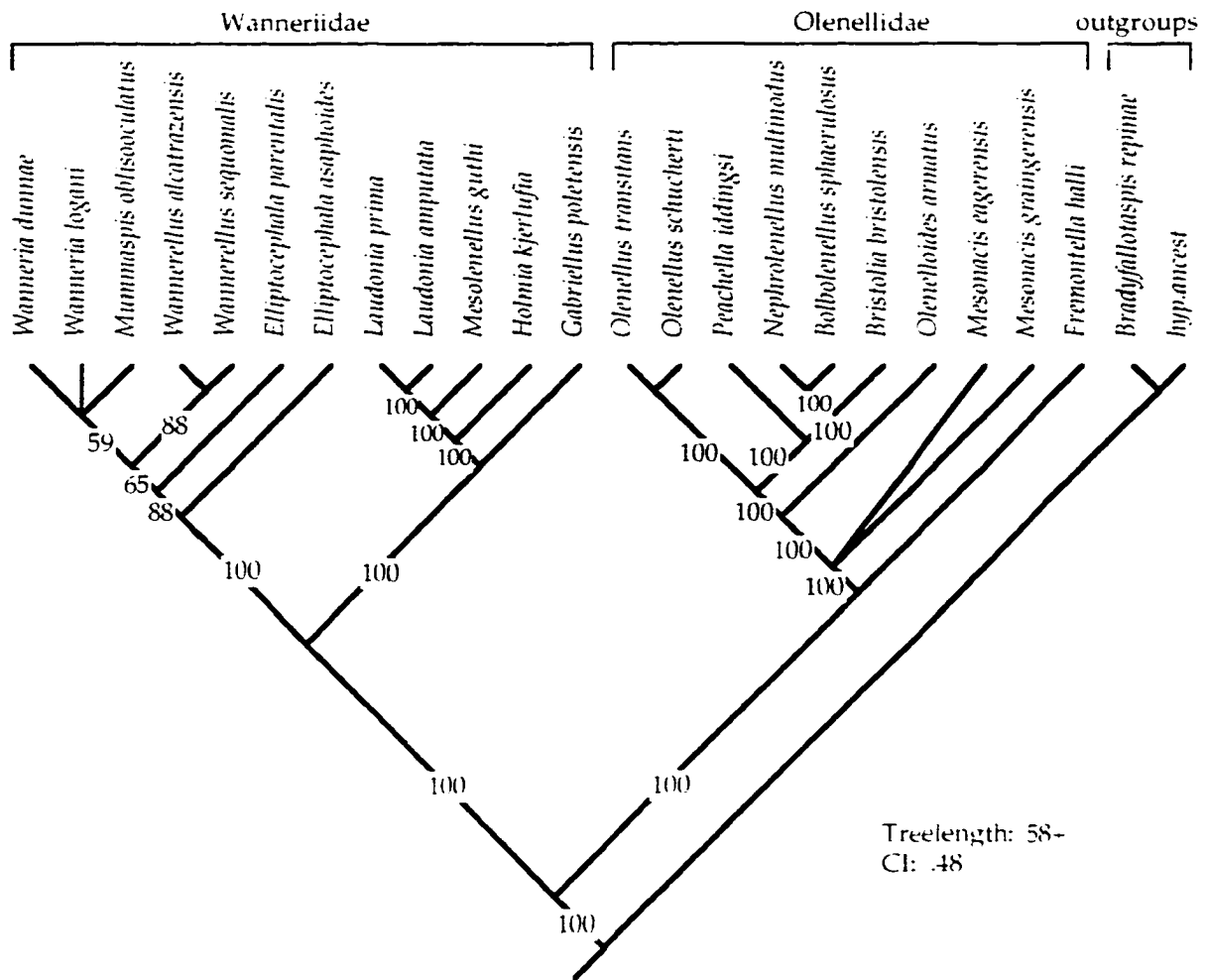
was off to require branch swapping on all dichotomous trees and prevent loss of options at an early stage by swapping on trees with polytomies. The CONDENSE command was given at the end of branch swapping to then remove duplicate trees. Assumptions were minimized by assigning all characters equal weights (except the zero weight character of stratigraphic position) and running characters as unordered.

Results

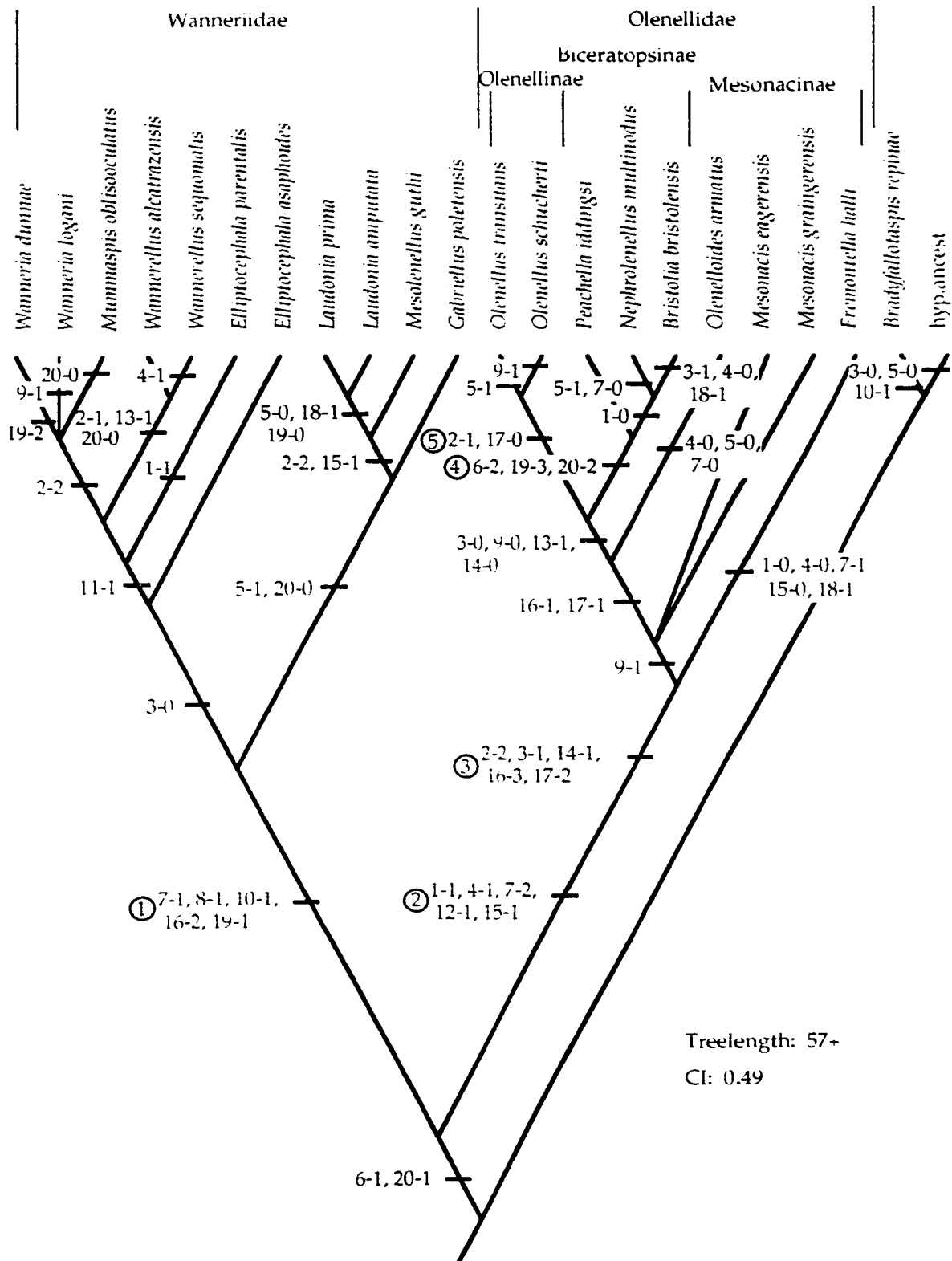
The initial run was made using all three outgroups to produce 51 trees having a treelength of 58 and a consistency index of 0.48. Text-fig. 29 illustrates the configuration of the majority rule consensus tree, which is highly resolved except in configuration of the terminal wanneriid clade. While the outgroups *Bradyfallotaspis repinae* and hyp.ancest were grouped together outside of the ingroup, *Holmia kjerulfi* was placed within the Wanneriidae. This configuration suggests that the Holmiidae shares a closer relationship with the Wanneriidae than with the Olenellidae and that *H. kjerulfi* is a poor choice of outgroup. Cladogram topology supports high-level separation of the Olenellidae from the Wanneriidae in this tree and in most other variations that were run. One surprising taxon arrangement is that *Bolbolenellus sphaerulosus* is placed as a sister taxon to *Nephrolenellus multinodus*, within the Biceratopsinae clade, instead of within the Olenellinae. This is a result of the large amount of missing data for the species and a superficial similarity by sharing the pedomorphic feature of a marginal, straight S2. *Bolbolenellus* lacks the synapomorphies of the Biceratopsinae (described below) as can be demonstrated by a new but as yet undescribed species that is more completely known (Palmer, submitted). Accordingly, *B. sphaerulosus* and *H. kjerulfi* are excluded from the rest of the cladograms.

Exclusion of *Holmia kjerulfi* does not affect the topology of the cladogram when *Bradyfallotaspis repinae* and hyp.ancest are retained as outgroups. Text-fig. 30 illustrates the topology of the consensus tree derived from 51 trees with apomorphies plotted.

Synapomorphies for the higher taxonomic groups are labeled. The major branches for the Wanneriidae and Olenellidae are well-supported by derived features. Major branches within the Wanneriidae are, however, poorly supported by synapomorphies of low significance (i.e. minor differences in intergenal spine length and genal spine position). *Wannerellus* is placed within the Wanneriidae in all analyses that include *Fremontella*, but it should be noted that *Wannerellus* shares some significant synapomorphies with the Olenellinae (demonstrated in the next run).



Text-fig. 29. Cladogram of species within the Wanneriidae and Olenellidae producing a consensus tree (50% majority rule) from 51 trees of equal length using two taxa as outgroups. Percentage of original trees that support this configuration indicated on each branch.



Text-fig. 30. Optimized character distribution for 50% majority rule consensus tree generated using PAUP's "show apomorphies" option. Numbers indicate character and character state as listed in Appendix B. Synapomorphies labeled for the ① Wanneriidae; ② Olenellidae; ③ Mesonacinae; ④ Biceratopsinae; ⑤ Olenellinae.

Fremontella is a key genus that has features of both the Wanneriidae and Olenellidae. By the apomorphy plots (Text-fig. 30) it can be seen that *Fremontella* has mainly sympleisiomorphies in common with the Wanneriidae. *Fremontella* has all the synapomorphies of the Mesonacinae, although it largely lacks the synapomorphies of the Olenellidae. This accounts for the basal position of *Fremontella* and the Mesonacinae within the Olenellidae clade. Each of the Olenellidae subfamilies can be well-characterized by synapomorphies, and the Olenellinae and Biceratopsinae share a number of synapomorphies.

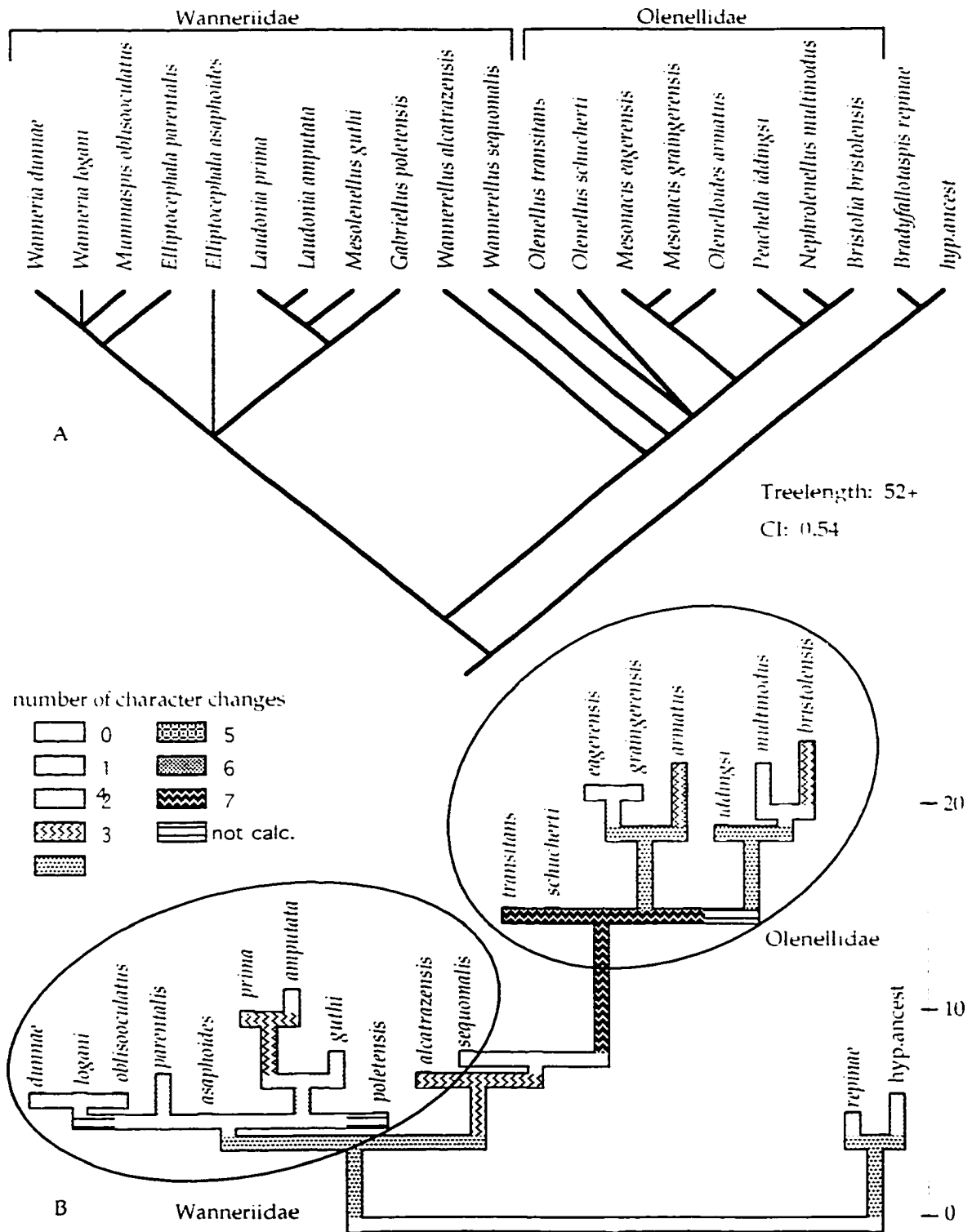
Elimination of *Fremontella* from the analysis produces greater resolution with only six resultant trees. The consensus tree (Text-fig. 31A) has a tree length of 52 and a consistence index of 0.54. Tree topology is changed in some significant ways, namely *Wannerellus* is placed as the basal taxon of the Olenellidae branch. An examination of the apomorphies (Text-fig. 30) however, demonstrates that *Wannerellus* has all the synapomorphies of the Wanneriidae and only two of the synapomorphies of Olenellidae clades. This is confirmed by a plotting of branch lengths¹² (Text-fig. 31B) which shows a large number of changes occurring on the branch between *Wannerellus* and the Olenellidae. In the spirit of an evolutionary systematist rather than a true cladist, *Wannerellus* is considered a member of the Wanneriidae, although it is recognized that the Olenellidae may be more closely related to *Wannerellus* than to the rest of the Wanneriidae.

With *Fremontella* excluded and *Wannerellus* as the closest relative of the Olenellidae, the arrangement of subfamilies within the Olenellidae is also altered. The Olenellinae is placed as the basal clade of the Olenellidae, a position supported by stratigraphy¹³. The Mesonacinae and Biceratopsinae are both well-defined, derived clades of the Olenellidae.

Analyses were run using both *Bradyfallotaspis repinae* and hyp.ancest singly as outgroups. No different taxon configurations were found; however, it was interesting to note that with *Fremontella* excluded, the use of *B. repinae* as outgroup supported the configuration seen in tree 1 (Text-figs. 29-30) and while use of hyp.ancest supported tree 2 (Text-fig. 31A).

¹² Branch length is defined as the number of evolutionary changes that occur along a branch.

¹³ Although both species of *Olenellus* (Olenellinae) coded for this analysis are from the *Olenellus transitans* Zone, species of *Olenellus* do occur lower. Members of the Mesonacinae make their first appearance in the *O. transitans* Zone and members of the Biceratopsinae above this interval. *Olenellus* is therefore the oldest member of the Olenellidae.



Text-fig. 31. A. Consensus tree (strict) from 6 trees of equal length using two taxa as outgroups and excluding *Fremontella halli*. B. Cladogram from A drawn with branch lengths proportional to number of character changes on branch.

Chapter 6. Systematics

Class Trilobita Walch, 1771

Order Redlichiida Richter, 1933

Diagnosis: A micropygous order of Trilobita. Cephalon typically hemicircular, wider than long. Glabella with 4 pairs of lateral furrows. Ocular ridges present. Ocular lobes usually crescentic. Hypostome with large median body, short posterior body. Strong maculae positioned laterally, closer to posterior margin than to anterior margin. Thorax of many segments.

Suborder Olenellina Walcott, 1890

[*nom. transl.* Moore, 1959 *ex* order Olenellida Resser, 1938

Diagnosis: A suborder of Redlichiida lacking dorsal cephalic sutures. Rostral plate long, crescentic. Pygidium minute. Protaspid stage lacking.

Assigned Superfamilies: Olenelloidea Walcott, 1890; Fallotaspidoidea Hupé, 1953a.

Discussion: The suborder Olenellina is an exclusively Lower Cambrian group of redlichiids that lack facial sutures. All have well-developed ocular lobes with the ocular surface facing primarily laterally. The overall convexity of the exoskeleton is moderately low. A curious feature of the group is the apparent absence of protaspids. Even in finely silicified material (Palmer, 1957), the smallest stages found are meraspids. Geyer (1996, fig. 41) recently illustrated a possible protaspid of *Fallotaspis*, but the specimen is poorly preserved and may be a meraspid. It is comparable in size to meraspid cephalae of the Olenelloidea. If it is a protaspid, it may also belong to a redlichiid trilobite that occurs in the same zone. In the absence of more convincing evidence, absence of a protaspid stage is still considered a unique feature of the Olenellina.

Trilobites of the suborder Olenellina are closely comparable in morphology to those of the suborder Redlichiina. Paleogeographic distribution of the two suborders is, for the most part, mutually exclusive. Only Olenellina occur in Lower Cambrian strata of Laurentia¹⁴. Only Redlichiina occur in Lower Cambrian strata of China and Australia. The two suborders do co-occur in rocks of the Siberian Platform and Morocco. Repina (1990, p. 40) noted that on the

¹⁴ Note that one possible exception to this rule is *Churkinia* Palmer, 1968, from offshore Lower Cambrian strata of Alaska. Palmer tentatively assigned this genus to the Redlichiaceae, although he recognized that it did not fit into any established redlichiacean family.

Siberian platform, the Olenellina are the oldest trilobites, and hypothesized that redlichiinids developed from fallotaspidids (the oldest family of Olenellina) by the development of facial sutures. She also noted the close similarity of some genera of redlichiinids and some genera of fallotaspidids, and speculated that members of the Redlichiina may have arisen more than once from different genera of fallotaspidids. This would make the Olenellina a paraphyletic group, and the Redlichiina a polyphyletic group. Revision of the suborder Redlichiina is beyond the scope of this thesis.

The taxonomy of the Olenellina proposed here (Table 9) is different in many details from the most recent comprehensive classification by Palmer and Repina (1993 - see Table 10), however, the basic division of the Olenellina into two superfamilies, proposed by Palmer and Repina, is followed. Geyer (1996) recently challenged this scheme and suggested that the Fallotaspidoidea should be assigned to the Redlichiina rather than to the Olenellina. He claimed that "olenellids and fallotaspidids are offshoots of separate early trilobite groups and represent separate higher taxonomic units" (Geyer, 1996, p. 159). Redlichiids and ptychoparioids therefore represent fallotaspidid descendants. Geyer (1996, p. 159) offered nine points to support his hypothesis. These are discussed below.

1. Lack of dorsal sutures is the only feature uniting the Fallotaspidae and Olenellidae.

While lack of sutures is likely a primitive feature and it is desirable to define taxa based on derived features, the Olenellina *sensu* Palmer and Repina (1993) is the basal clade of the Trilobita. Accordingly, most of their features will be primitive. Further, it is not true that lack of sutures is the only feature they share. Glabellar furrows, ocular lobes, and cephalic spines are comparable between the two groups. Morphology and position of the rostral plate is the same between *Fallotaspis* (Geyer, 1996, fig. 23) and olenelloids such as *Wanneria* (Pl. 5, figs. 2, 5; Pl. 7, figs. 6, 7) and *Elliptocephala* (Pl. 9, fig. 7; Pl. 12, fig. 1). A comparison of detailed features such as the course and origin of genal lines reveals that they are identical in fallotaspidoids and olenelloids (Table 11). A major difference between these groups is the derived form of the glabella in olenelloids. Olenelloid meraspids have a glabellar morphology closely comparable to fallotaspidoid holaspids.

2. *Fallotaspis* and redlichoids have a protaspid stage which olenelloids lack.

As already discussed, the protaspid illustrated for *Fallotaspis* by Geyer (1996, fig. 41) is not convincing.

Table 9. Proposed classification of the suborder Olenellina.

Fallotaspidoidea Hupé, 1953a

Faliotaspididae Hupé, 1953a

Fallotaspidinae Hupé, 1953a

Fallotaspis Hupé, 1953a*Fallotaspidella* Repina, 1961*Profallotaspis* Repina in
Khomentovskii & Repina, 1965*Parafallotaspis* Fritz, 1972*Eofallotaspis* Sdzuy, 1978*Lenallina* Repina, 1990*Pelmanaspis* Repina, 1990

Daguinaspidinae Hupé, 1953a

Daguinaspis Hupé & Abadie, 1950*Choubertella* Hupé, 1953a*Wolynaspis* Chernysheva in Kir'ianov
& Chernysheva, 1967

Archaeaspididae Repina, 1979

Archaeaspis Repina in Khomentovskii
& Repina, 1965*Pseudojudomia* Egorova in Goryanskii
et al., 1964*Bradyfallotaspis* Fritz, 1972*Selindella* Repina, 1979*Repinaella* Geyer, 1996

Neltneriidae Hupé, 1953

Neltneria Hupé, 1953*Judomia* Lermontova, 1951*Bondonella* Hupé, 1953a*Sinskia* Suvorova, 1960*Judomiella* Lazarenko, 1962*Paranevadella* Palmer & Repina, 1993

Nevadiidae Hupé, 1953

Nevadia Walcott, 1910*Nevadella* Raw, 1936*Cirquella* Fritz, 1993

Callaviidae Poulsen (in Moore, 1959)

Callavia Matthew, 1897*Buenellus* Blaker, 1988

Olenelloidea Walcott, 1890

Olenellidae Walcott, 1890

Olenellinae Walcott, 1890

Olenellus Hall, 1861= *Paedeumias* Walcott, 1910*Bolbolenellus* Palmer & Repina, 1993

Mesonacinae Walcott, 1890

Mesonacis Walcott, 1885*Olenelloides* Peach, 1894? *Fremontia* Raw, 1936? *Fremontella* Harrington, 1956

Biceratopsinae Pack & Gayle, 1971

Peachella Walcott, 1910= *Biceratops* Pack & Gayle, 1971*Bristolia* Harrington, 1956*Nephrolenellus* Palmer & Repina, 1993= *Arcuolenellus* Palmer & Repina,
1993

Holmiidae Hupé, 1953a

Holmia Matthew, 1890*Schmidtellus* Moberg in Moberg &
Segerberg, 1906*Kjerulfia* Kiaer, 1917*Esmeraldina* Resser & Howell, 1938= *Palmettaspis* Fritz, 1995*Andalusiana* Sdzuy, 1961*Holmiella* Fritz, 1972*Geraldinella* Fritz, 1993*Cambropallas* Geyer, 1993*Lyouella* Geyer & Palmer, 1995

Wanneriidae Hupé, 1953a

Wanneria Walcott, 1910*Elliptocephala* Emmons, 1844*Laudonia* Harrington, 1956*Mummaspis* Fritz, 1992*Gabriellus* Fritz, 1992*Mesolenellus* Palmer & Repina, 1993= *Olenellus* (*Angustolenellus*)

Palmer & Repina, 1993

? *Wannerellus* n. gen.

Table 10. Palmer and Repina's (1993) taxonomic scheme for the suborder Olenellina.

Fallotaspidoidea

Fallotaspididae

Fallotaspidinae

*Fallotaspis**Eofallotaspis**Lenallina**Parafallotaspis**Pelmanaspis**Profallotaspis*

Daguinaspidinae

*Daguinaspis**Choubertella**Wolynaspis*

Archaeaspididae

*Archaeaspis**Bradyfallotaspis**Fallotaspidella**Geraldinella* (= Genus A)*Selindella*

Judomiidae

*Judomia**Judomiella**Paranevadella**Sinskia*

Neltneriidae

*Neltneria**Bondonella*

Nevadiidae

*Nevadia**Buenellus**Cirquella* (= Genus B)*Nevadella**Pseudojudomia*

Superfamily unassigned

*Poletaevella**Postfallotaspis*

Olenelloidea

Olenellidae

Olenellinae

Olenellus Hall, 1861*Olenellus* (*Olenellus*)*Olenellus* (*Angustolenellus*)*Olenellus* (*Mesolenellus*)*Olenellus* (*Mesonacis*)*Olenellus* (*Paedeumias*)*Fremontella**Mumiaspis*

Biceratopsinae

*Biceratops**Peachella*

Bristoliinae

*Bristolia**Arcuolenellus**Bolbolenellus**Nephrolenellus*

Gabriellinae

Gabriellus

Laudoniinae

*Laudonia**?Olenelloides*

Wanneriinae

Wanneria

Holmiidae

Holmiinae

*Holmia**Andalustana**Elliptocephala**Holmiella**Schmidtellus*

Callaviinae

*Callavia**Kjerulfia*

Table 11. Examples illustrated herein of genal lines observed on Olenelloidea for comparison to homologous structures described for the Fallotaspidae (Geyer, 1996). Note that anterior ocular lines are only observed on meraspids of the Olenelloidea.

ANTERIOR OCULAR LINE <i>Elliptocephala asaphoides</i> <i>Gabriellus poletensis</i> <i>Mesolenellus guthi</i>	Pl. 8, Fig. 9 Pl. 15, Fig. 1 Pl. 16, Fig. 2
POSTERIOR OCULAR LINE <i>Wanneria dunnae</i> <i>Laudonia harringtoni</i>	Pl. 7, Figs. 1, 3 Pl. 13, Figs. 5, 8
INTERGENAL RIDGE <i>Elliptocephala nelsoni</i> <i>Laudonia harringtoni</i> <i>Mummaspis albersi</i>	Pl. 11, Figs. 4-6 Pl. 13, Figs. 1-5, 8 Pl. 15, Figs. 1-5
GENAL RIDGE <i>Elliptocephala asaphoides</i> <i>Wannerellus alcatrazensis</i> <i>Olenellus schucherti</i>	Pl. 9, Figs. 4-7 Pl. 17, Fig. 10 Pl. 21, Fig. 7

3. The Fallotaspidae and Olenellidae have non-overlapping stratigraphic ranges.

Although most Fallotaspidoidea are older than the Olenelloidea, a few fallotaspidoids (i.e. *Bradyfallotaspis*) do overlap in range with the Olenelloidea. It is likely that one of the younger fallotaspidoid families, such as the Archaeaspididae or Nevadiidae, gave rise to the Olenelloidea

4. and 5. *Fallotaspis* has a morphological counterpart in the redlichiid *Lemdadella* and juvenile specimens of *Choubertella* have morphological counterparts in the bigotinids *Pruvostina* and *Bigotinops*.

It is accepted here that some Fallotaspids gave rise to redlichoids. Geyer's evidence supports this claim, but it is not evidence that other fallotaspidoids are not ancestral to olenelloids.

6. Olenelloids have sclerotized hypostomes which fallotaspids lack.

Un-sclerotized hypostomes are an unusual feature for any trilobite and other fallotaspidoids (i.e. at least *Nevadella*, *Cirquella*, and *Callavia* of the North American genera), redlichoids and olenelloids all have sclerotized hypostomes. The absence of this feature in the fallotaspids does not indicate a closer relationship between them and any other group.

7. The site of origin of the genal spine differs between the Fallotaspidae and Olenellidae.

The site of origin of the genal spines is variable in both the Olenellidae and Fallotaspidae. The genal spine can be: advanced and originate from the lateral cephalic border; normal and originate from the posterolateral corners; or arcuate and originate posterolaterally when the posterior borders are angled posterolaterally. The author cannot determine any difference in genal spine origin between the two groups.

8. Pleural articulating facets of *Fallotaspis* differ from those of the Olenellidae.

Details of thoracic articulation have been poorly studied for olenelloids. *Olenellus transitans* (see Whittington, fig. 1) has an articulating flange rather than the fulcral process described for *Fallotaspis* by Geyer (1996, fig. 25). It is not known how much variability there is in this feature for the olenelloids. It is an over-generalization to consider that all olenelloid thoraxes have articulating flanges and to describe this as a major difference between the Fallotaspidoidea and Olenelloidea.

9. Cephalic segmentation differs in the Fallotaspidae and Olenellidae.

Geyer's (1995, p. 116) argument for this difference is unclear. He claimed that the genal ridge is not homologous in the two families, but offers no explanation. Geyer cites Palmer (1957)

as evidence that in the Olenellidae, the ocular lobe segment overrides segment 3 (L1 and the intergenal ridge/spine), a state not seen in the fallotaspidids. While this is typical of long-eyed species of *Olenellus*, it is a state that develops only midway through the meraspid ontogeny (clique C) and does not occur at all in short-eyed species (i.e. *O. ricei*, Pl. 21; also *Laudonia harringtoni*, Pl. 13, figs. 1-5). Even in long-eyed species, Clique A and B meraspids (i.e. *O. transitans*, Pl. 18, fig. 1; Pl. 19, fig. 1) do not have the ocular lobe segment overriding segment 3. Cephalic segmentation is the same in the Olenellidae and Fallotaspididae.

In conclusion, Geyer (1996) failed to demonstrate that the Fallotaspididae shares a closer relationship with the Redlicheoidea than with the Olenelloidea¹⁵. It is likely that the fallotaspidids gave rise to both groups and are a paraphyletic grouping of primitive trilobites. The cladist's solution to this problem would be to abandon the taxon Fallotaspididae and distribute the genera between the Olenelloidea and Redlicheoidea. There is, unfortunately, insufficient data on many fallotaspidids and their relationships to assign them to a particular olenelloid or redlichoid family to which they may be ancestral. Further, if the absence of a calcified hypostome is a unique feature of the Fallotaspididae, it provides support for maintaining the family as a separate taxon.

The question of whether the Olenellina are more closely related to trilobites or chelicerates is of some historical interest. Raw (1925, 1957) and Størmer (1944) contended that the chelicerates arose from an *Olenellus*-like form. This conclusion was based on a presumed homology of the enlarged axial spine on T15 in *Olenellus* and the telson in horseshoe crabs. Lauterbach (1980, 1983, 1989) expanded on this idea and assigned the Olenellina to the Chelicerata, instead of to the Trilobita. This sparked publication of a series of papers rigorously and convincingly defining the Trilobita, inclusive of the Olenellina (Hahn, 1989; Fortey and Whittington, 1989; Fortey, 1990b; Ramsköld and Edgecombe, 1991; see also Whittington, 1989, p. 142-143).

Walcott (1890) suggested that the term "Olenellidae" was appropriate as the name for the higher taxon (= Olenellina) to which *Olenellus* belongs, but recognized that it was too similar to the name for the trilobite family Olenidae Burmeister, 1843. To avoid confusion, Walcott (1890) proposed that the term "Mesonacidae", be used instead, but his first proposed name, Olenellidae, was the one that gained popular usage.

¹⁵ Indeed, Geyer undermines his argument by inconsistent use of taxonomic names and refers in numerous places to fallotaspidid genera as "olenelloids". For example, "olenelloid trilobites that appear to be descendants of the fallotaspidid lineage are the nevadiids" (Geyer, 1996, p. 159). The Nevadiidae are a family of Fallotaspidoidea, which Geyer (1996, p. 159) accepted.

The current form of the suborder name, Olenellina, was first used by Poulsen (*in* Moore, 1959) and subsequently by Palmer and Repina (1993). The assigned rank of the Olenellina has varied from author to author: superfamily Olenelloidea was used by Hupé (1953a,b), Chernysheva (1960), Repina (1979), and Whittington (1989) while order Olenellida was used by Bergström (1973a) and Ahlberg *et al.* (1986). Recent taxonomic treatments of the Olenellina can be found in Palmer and Repina (1993 - summarized in Table 10), Whittington (1989 - focused on type species), and Ahlberg *et al.* (1986 - focused on revision of non-Laurentian taxa). Taxonomic revision herein focuses on Laurentian forms, primarily the superfamily Olenelloidea.

Superfamily Fallotaspidoidea Hupé, 1953a

[*nom. transl.* Repina, 1979, *ex* Fallotaspidinae Hupé, 1953a]

Diagnosis: A superfamily of Olenellina with L4 narrow. Glabella cylindrical to tapering forward. L3 unmodified distally.

Assigned Families: Fallotaspididae Hupé, 1953a; Neltneriidae Hupé, 1953a; Nevadiidae Hupé, 1953a; Callaviidae Poulsen (*in* Moore, 1959); Archaeaspididae Repina, 1979.

Discussion: The Fallotaspidoidea is a large, diverse group that encompasses mostly the older genera of the Olenellina. Uniting features are a tapering to cylindrical glabella where LA and L3 are not expanded transversely.

The membership of the Fallotaspidoidea given in Palmer and Repina (1993) is largely followed here. The configuration of the Fallotaspididae with the subfamilies Fallotaspidinae and Daguinaspidinae is accepted, except for the reassignment of *Fallotaspidella* to the Fallotaspidinae (see discussion under the Archaeaspididae). The Judomiidae of Palmer and Repina differ from the Neltneriidae only in their genal spine position; advanced in the latter but not in the former. This is a character that varies within a genus and is not sufficient to distinguish different families. The name Neltneriidae has priority and herein the genera assigned to the Judomiidae by Palmer and Repina are included in the Neltneriidae. The Neltneriidae can be distinguished by the posterior attachment of the ocular ridges to LA, a cylindrically shaped glabella and ocular lobes situated unusually close to the glabella with a negligible interocular area. The membership of the Archaeaspididae and Nevadiidae are discussed in detail in following sections.

The Callaviidae are here considered to be a family of the Fallotaspidoidea, and to include *Callavia* and *Buenellus*. The family is characterized by a cylindrical to slightly tapered, broad glabella with ocular lobes positioned far from the glabella. Palmer and Repina (1993) gave the callaviids

subfamily status within the Holmiidae. But these trilobites are not olenelloids: *Callavia broeggeri* Matthew, 1891 from the Brigus Formation of Newfoundland, the type species has an LA that is narrow and an L3 that is not or barely modified (see Hutchinson, 1962, pl. 24, figs. 7-14 for unretouched illustrations). *Kjerulfia*, which Palmer and Repina assigned to the callaviids, has a wide LA (basally) and modified L3 and is therefore reassigned to the holmiids. *Buenellus* was assigned by Blaker (1988) and Palmer and Repina to the nevadiids. It has a less tapering, more cylindrically-shaped glabella than the nevadiids and ocular lobes situated far from the glabella. In these features it is closest in appearance to *Callavia* and is reassigned to the callaviids.

Family Archaeaspididae Repina, 1979

Diagnosis: A family of Fallotaspidoidea with glabella tapering forward slightly. Preglabellar field present. LA moderately long; longer than other glabellar lobes. LA narrower than L0. Glabellar furrows transglabellar. Ocular lobes attached to posterior of LA. Parafrontal band present. Ocular lobes located far from glabella: interocular areas wide.

Assigned Genera: *Archaeaspis* Repina in Khomentovskii and Repina, 1965; *Pseudojudomia* Egorova in Goryanskii et al. 1964; *Bradyfallotaspis* Fritz, 1972; *Selindella* Repina, 1979; *Repinaella* Geyer, 1996.

Discussion: The Archaeaspididae are fallotaspidoidea united by the ocular lobes located far from the glabella and the position of the ocular ridges opposite of only the posterior of LA. A parafrontal band connects the ocular ridges to the anterior of LA. This differs from the Fallotaspidae with ocular ridges opposite of the whole of LA, and the Nevadiidae and Neltneriidae (includes Judomiidae of Palmer and Repina, 1993) with long LA's and ocular lobes located close to the glabella.

The membership of the Archaeaspididae given in Palmer and Repina (1993) is accepted with some modifications: *Geraldinella* and *Fallotaspidella* are excluded while *Pseudojudomia* is included. *Geraldinella* Fritz, 1993 (listed as Genus A in Palmer and Repina) from the Dogtooth Mountains southern British Columbia, has a modified L3 that is expanded posterolaterally and the widest point of the glabella is at LA. These are characteristics of the Olenelloidea and *Geraldinella* is reassigned to the Holmiidae. *Fallotaspidella* Repina, 1961 from Siberia and northern Mongolia, has a shorter LA than the other archaeaspidids with the ocular lobes opposite of most of LA. This is the same configuration seen in the fallotaspidid genus *Profallotaspis*. *Fallotaspidella* also has an anterior ocular line: a holaspid feature seen only in the Fallotaspidae. *Fallotaspidella* is

assigned to the Fallotaspidae (subfamily Fallotaspinae), a placement also suggested by Ahlberg *et al.* (1986) and Repina (1979). *Pseudojudomia* Egorova in Goryanskii *et al.* 1964 from the Siberian Platform, was assigned to the Nevadiidae by Repina (1979), Ahlberg *et al.* (1986) and Palmer and Repina (1993). *Pseudojudomia* has ocular lobes that are located far from the glabella, unlike the nevadiids. It has a glabella that is slightly more tapering in shape than the other archaeaspidids, but inclusion in this family is preferable than in the Nevadiidae. The recently described genus *Repinaella* Geyer, 1996 is also accepted as a member of the Archaeaspididae.

Geyer (1996) expanded the Archaeaspididae in membership to include *Archaeaspis*, *Bradyfallotaspis*, *Cirquella*, *Fallotaspidella*, *Lenallina*, *Profallotaspis*, *Selindella* and *Repinaella*. Geyer claimed that these genera are united by their convexity, sharing dome-shaped cephalae in which the glabella and ocular lobes are of comparable elevation and sit at the summit of the dome. Convexity is not a distinguishing feature of the Archaeaspididae, rather it is the general state found in many Olenellina (i.e. see *Olenellus* Pl. 19, figs. 4-5; *Wanneria* Pl. 6, figs. 3, 16) whenever unflattened material is available. Elevation of the ocular lobes compared to the glabella is variable. For example, the archaeaspidid *Bradyfallotaspis* has highly inflated ocular lobes elevated above the glabella in some species (i.e. *B. patula* Fritz, 1972, pl. 6, figs. 1-9, *B. repinae* n. sp. Pl. 1, fig. 7) but standing lower than the glabella in other species (i.e. *B. fusa* Fritz, 1972, pl. 3, figs. 1-7). Geyer's membership and definition of the Archaeaspididae is rejected.

Genus *Bradyfallotaspis* Fritz, 1972

Type Species: *Bradyfallotaspis fusa* Fritz, 1972 from the Sekwi Formation, Mackenzie Mountains, Northwest Territories. (by original designation)

Diagnosis: A genus of Archaeaspididae with highly inflated ocular lobes. Cephalic border wide: subequal in length to L0. Plectrum absent. Glabellar profile uneven: L0, L2-L3 highest points on glabella. L1 widest point on glabella. LA bluntly rounded anteriorly; approximately twice length of L0. S0 deep, transglabellar. S1-S3 transglabellar: deepest laterally, shallow medially. Intergenal position medial. Ocular ridges low. Extraocular areas inflated adjacent to ocular lobes. Intergenal spines weakly developed: posterior border thickens lateral to intergenal position. Genal spines not advanced to slightly advanced. Prosopon of caecae and tubercles well-developed on extraocular areas.

Other Species:

Bradyfallotaspis patula Fritz, 1972, Sekwi Fm., Mackenzie Mtns., NWT.

Bradyfallotaspis sp. 2 Fritz, 1972, Sekwi Fm., Mackenzie Mtns., NWT.

Bradyfallotaspis sp. 3 Fritz, 1973, Sekwi Fm., Mackenzie Mtns., NWT.

Bradyfallotaspis repinae n. sp.; Poleta Fm., Mt. Dunfee area, Nevada.

Discussion: *Bradyfallotaspis* is an archaeaspidid based on the relative position of its ocular ridges to LA. It has the longest LA of any archaeaspidid genus. *Bradyfallotaspis* is unique in its inflated extraocular areas adjacent to the ocular lobes that rapidly flatten out approaching the border furrow. This differs from other genera of Olenellina that typically have the whole extraocular area evenly inflated. *Bradyfallotaspis* has been described only from western Laurentia while all other archaeaspidid genera are Siberian (or northern Mongolian) in distribution.

Fritz (1972) named and described two species of *Bradyfallotaspis* and described but did not name two additional forms represented by single fragmentary cephalons. *Bradyfallotaspis* sp. 1 Fritz is insufficiently preserved to be recognized as distinct from the other species. *Bradyfallotaspis* sp. 2 Fritz, 1972 and *Bradyfallotaspis* sp. 3 Fritz, 1973 probably represent separate species.

Bradyfallotaspis repinae n. sp.

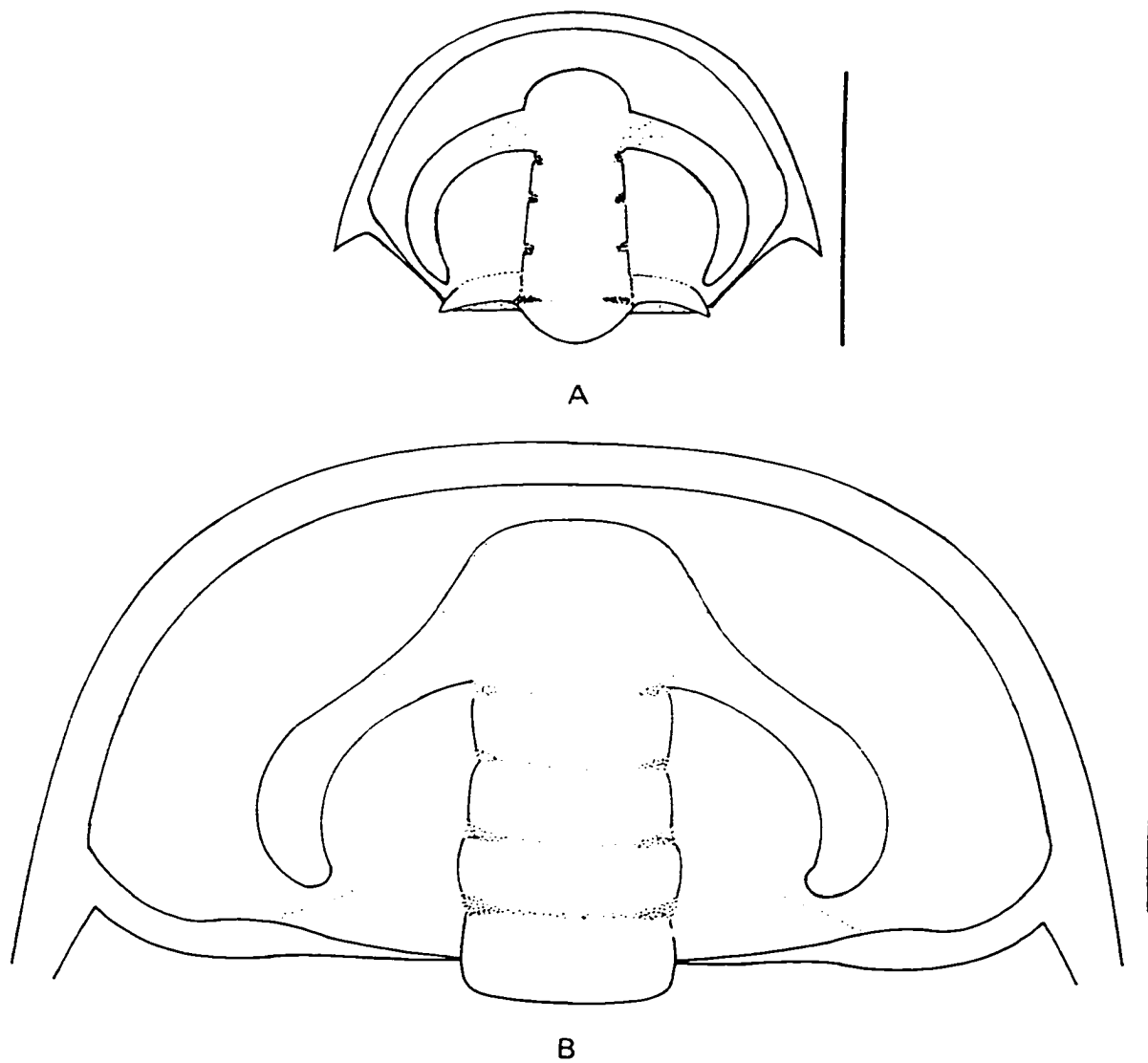
Pl. 1, figs. 1-10; Text-fig. 32

Diagnosis: A species of *Bradyfallotaspis* with ocular lobes moderately short: posterior tips opposite of posterior of L1. Preglabellar field short: less than half length L0. Intergenal ridges distinct. Intergenal spines absent. Posterior border curves anteriorly lateral to intergenal position. Genal spines advanced: opposite of S0. Posterior occipital node minute. Cephalon wide: approximately twice as wide as long. Prosopon on extraocular areas of coarse tubercles, caecae and reticulation: border carries tubercles.

Holotype: A nearly complete cephalon (LACMIP 12509; Pl. 1, fig. 9) from the Poleta Formation, section GP, LACMIP collection 17043, Mt. Dunfee area, 7 km east of Gold Point, Esmeralda County, Nevada. Paratypes: LACMIP 12503, 12506

Etymology: In memory of Lada Repina (1926-1993), for her extensive work on Lower Cambrian trilobites and biostratigraphy.

Occurrences: NEVADA. Poleta Formation, section GP, 7 km east of Gold Point, Esmeralda County.



Text-fig. 32. *Bradyfalloaspis repinae* n. sp. A. cliques B meraspide B. cliques G holaspide
scale bars = 1 mm

Zonal Biostratigraphy: *Elliptocephala stewarti* Subzone, *Elliptocephala* Zone.

Discussion: *Bradyfallotaspis repinae* has more advanced genal spines than the other species of *Bradyfallotaspis*. *B. patula* Fritz, 1972 a straight posterior border while that of *B. fusa* Fritz, 1972 is distally inflected forward slightly in a straight line from the intergenal position. The lateral posterior border is gently curved in *B. repinae* rather than straight as in *B. fusa*. *B. repinae* is closest in morphology to *B. patula* with which it shares moderately short ocular lobes and a wide cephalon. *Bradyfallotaspis* sp. 3 Fritz, 1973 also has a wide cephalon and deep cephalic border pits. The extraocular areas of *B. repinae* have not only the prosopon of caecae and tubercles seen in the other species, but also reticulation. The glabella is insufficiently preserved on all specimens to distinguish prosopon or parafrontal bands.

Ontogeny: Material of *Bradyfallotaspis repinae* is not abundant and consists mostly of holaspis material. The few meraspids that are known have a distinctive glabella: the glabellar stalk is slightly tapered forward and LA is fairly long, extending anterior to the ocular ridges, but it is narrow and does not drape the ocular ridges. Genal spines are more advanced at this early clique than they are later in ontogeny. Migration of the genal spine position posteriorly through ontogeny is also seen in *Nexadella*, and is opposite from the anterior migration of the genal spine position typical of *Laudonia* and *Bristolia*. In the shape of LA, *B. repinae* is closest in morphology to the meraspids of *Olenellus*, but genal spines and lengthening of the cephalon in *Olenellus*, do not develop until a later clique in *Olenellus* sp. A (Text-fig. 41). In general cephalic features, meraspids of *B. repinae* are closely comparable to those of other fallotaspidoids (see Geyer, 1996) and wanneriids (described herein).

Clique B meraspids have no indication of procranial spines. Cephalic border clearly differentiated, extraocular areas narrow. Preglabellar field moderately long. Ocular lobes well-defined, more inflated than ocular ridges, posterior tips opposite of L1. LA moderately short, narrow: extends anteriorly past ocular ridges but does not extend laterally to drape ocular ridges. Glabella parallel-sided to slightly tapering forward. S0 to S3 developed as marginal pits, shallow furrow connects S0 pair. Intergenal spines of unknown size and orientation, located directly posterior to ocular lobes. Genal spines short, advanced: opposite of L2. Cephalon hemicircular in outline: cephalon approximately 1.25 times wider than long. (Pl. 1, figs. 1, 2; Text-fig. 32A)

Family Nevadiidae Hupé, 1953a
[*nom. transl.* Repina, 1979, *ex* Nevadiinae Hupé, 1953a]

Diagnosis: A family of Fallotaspidoidea with glabella tapering forward. Plectrum present if preglabellar field long. LA narrow, tapering, long; usually twice length of L0. Glabellar furrows marginal. Ocular ridges low, attached only to posterior of LA. Ocular lobes close to glabella: narrow interocular and wide extraocular areas. Mid-ocular lobe furrow absent. Intergenal spines absent. Genal spines typically falcate, not advanced. Hypostome long, narrow. Thorax wide, 17 segments or more. Thoracic spines long, broad, falcate. T15 without axial spine. T3 amplipleural. Meraspid cephalon with short, diagonally directed intergenal spines; LA large, bulbous.

Assigned genera: *Nevadia* Walcott, 1910b; *Nevadella* Raw, 1936; *Cirquella* Fritz, 1993.

Discussion: The nevadiids are a family of fallotaspidoids characterized by a tapered glabella with a long LA to which the ocular ridges are attached only to the posterior part. Ocular lobes are positioned close to the glabella, with a narrow but distinct interocular area, equal or greater in width than the width of the ocular lobes. Trilobites of the families Archaeaspididae and Callaviidae differ as their ocular lobes are situated far from the glabella. In addition, members of the Callaviidae also have cylindrical rather than tapering glabellas. Trilobites of the family Neltneriidae (includes family Judomiidae of Palmer and Repina, 1993) have cylindrical glabellas with the ocular lobes situated close to the glabella without an interocular area. Members of the family Fallotaspidae have ocular lobes located far from the glabella and a short LA with the ocular lobes attached to the whole length of LA.

The ventral morphology of nevadiids is poorly known. A single small hypostome of *Nevadella parvoconica* (Pl. 3, fig. 6), less than 1 mm long, has a spinous posterior margin. It is the same as hypostomes of the same size belonging to the Olenellidae and Wanneriidae, suggesting that all small Olenellina hypostomes are of this standard morphology. Larger hypostomes are known for *N. parvoconica* (Pl. 3, fig. 11) and *N. faceta* Fritz (1972, pl. 3, figs. 11, 12) that are proportionately narrower than those of olenelloids and have a distinct posterior furrow. None is sufficiently well preserved to determine if the large hypostomes are spinous. All have a broad, relatively deep furrow connecting the maculae that is deeper than that seen in olenelloid hypostomes.

A distinctive meraspid cephalon characterizes the nevadiids (see *Nevadella parvoconica*, Pl. 3 figs. 3-4; *N. faceta*, Fritz, 1972, pl. 3, fig. 14; *Cirquella nummularia* Fritz, 1993, fig. 6.1; *C. espinata* Fritz,

1993, fig. 9.1). Clique A meraspids have a bulbous LA that is not enclosed within the ocular ridges, as it is in *Olenellus* at this stage (Pl. 19, fig. 1). Intergenal spines are short, laterally directed and positioned posterior to the ocular lobes. The anterior border is strongly curved and without procranial spines. The meraspids of *Cirquella* have a glabella that is less tapered than that of *Nevadella* meraspids. Meraspids attributed with certainty to *Nevadia* are not known. Fritz (1973, pl. 4, figs. 16-18) illustrated three small cephalons that he assigned to *Nevadia*?. Like meraspids of *Nevadella* and *Cirquella*, they have an LA that is not enclosed within the ocular ridges, but it is not bulbous as is seen in the other genera. Their anterior border is strongly curved, without procranial spines and intergenal spines are short and laterally directed. In the absence of any large associated cephalons, assignment of these cephalons to *Nevadia* must remain tentative.

The taxonomic position of the nevadiids has varied greatly. Hupé (1953a,b) gave them subfamily status within the Olenellidae. Poulsen (*in* Moore, 1959) and Bergström (1973a) assigned them subfamily status within the Daguinaspididae. Chernysheva (1960), Repina (1979) and Ahlberg *et al.* (1986) made the nevadiids a high ranking taxon of the Olenellina (or Olenelloidea *sensu* Olenellina, Palmer and Repina, 1993). Repina (1979) and Ahlberg *et al.* (1986) assigned the judomiids and neltneriids subfamily status within the Nevadiidae. As discussed under the Fallotaspidoidea, the judomiids are synonymized with the neltneriids. The nevadiids and neltneriids may be more closely related to one another than to any other fallotaspidoid family as both share a long LA with ocular lobes attached only to the posterior part and ocular lobes situated close to the glabella. However, the neltneriids share with the callaviids a cylindrical glabella as well as a posterior attachment position of the ocular lobes to LA. With this uncertainty of relationship, the approach of Palmer and Repina (1993) is followed and the Callaviidae, Neltneriidae and Nevadiidae are designated separate suprageneric taxa.

The family Nevadiidae is here restricted to three genera from Laurentia. Palmer and Repina (1993) assigned *Pseudojudomia* from Novaya Zemlya, Russia and *Buenellus* from the Siberian Platform and Greenland to this family. These genera both have ocular lobes located far from the glabella (wide interocular areas) which is not characteristic of nevadiids. *Pseudojudomia* has a tapered glabella, like the nevadiids, but this state is also seen in the archaeaspidids which also have ocular lobes situated far from the glabella. On this basis *Pseudojudomia* is assigned to the Archaeaspididae. *Buenellus* has a cylindrical rather than tapered glabella. The most similar genus to *Buenellus* is *Callavia* which also has a cylindrical glabella and ocular lobes placed far from the glabella. On this basis *Buenellus* is assigned to the Callaviidae, which is considered a fallotaspidoid family.

Nevadella effusa Repina, 1974 from the Lena River Section on the Siberian platform has a forwardly tapering glabella like a nevadiid, but lacks interocular areas like species of the Neltneriidae. An associated pygidium has an elongate shape also seen in *Judomia*. This species is assigned to the neltneriid *Paranevadella* which has a tapering glabella and ocular lobes close against the glabella.

Callavia burri Walcott, 1910b, an Avalonian species from Massachusetts, was assigned by Raw (1936) and Fritz (1972) to *Nevadella*. It has a forwardly tapering glabella but the ocular lobes are positioned far from the glabella creating wide interocular areas. Repina (in Palmer and Repina, 1993) suggested that this species belongs to the archaeaspidid genus *Selindella*. *Callavia cartlandi* Raw, in Walcott, 1910b from the Comley Quarry in Shropshire, was assigned by Raw (1936) to *Nevadia*. Walcott's highly retouched reproduction (1910b, pl. 42, figs. 3, 4) is misleading in portraying a highly tapered glabella. The photograph by Raw 1936 (pl. 22, figs. 1, 2) shows that the specimen is poorly preserved, particularly in the anterior glabellar area, and the glabellar shape could easily be interpreted as cylindrical. It is likely a species of *Callavia* as originally designated by Raw (in Walcott, 1910b). In any case, neither *S. burri* nor *C. cartlandi* is a nevadiid, nor are any other Avalonian forms.

Judomia? absita Fritz, 1973 from the Sekwi Formation, Mackenzie Mountains, may be a nevadiid. It does not belong to the neltneriid *Judomia* as it has distinct interocular areas and an LA that is not elongate. Like the archaeaspidids, it has a moderately long LA with ocular lobes attached to the posterior part and a parafrontal band; but it has a cylindrical glabella (like the callaviids and neltneriids), a plectrum and ocular lobes situated close to the glabella (like the nevadiids). The associated meraspid cephalon (Fritz, 1973, pl. 8, figs. 7, 8) have a bulbous LA like that of nevadiids. Compared to meraspids of the nevadiid *Nevadella* (Pl. 3, figs. 3-4; Pl. 4, figs. 2-3) and the archaeaspidid *Bradyfallotaspis* (Pl. 1, figs. 1-2), its interocular areas are narrower like those of *Nevadella*. The hypostome of *Judomia? absita* Fritz (1973, pl. 8, fig. 6) has a distinct posterior border furrow and a broad, moderately deep middle furrow: the same as hypostomes of *Nevadella* (Pl. 3, fig. 11). Based on its ocular lobe position and meraspid and hypostomal forms, *Judomia? absita* Fritz likely represents a new genus of nevadiid with an LA and ocular ridges of archaeaspidid configuration.

Genus *Nevadia* Walcott, 1910b

Type species: *Nevadia weeksi* Walcott, 1910b from Unit 12 of the Silver Peak Group (Montenegro Member of the Campito Formation after Fritz, 1995). Barrel Spring Section (Walcott, 1908, p. 189), 16 km south of Silver Peak, Silver Peak Range, Esmeralda County, Nevada. (by original designation)

Diagnosis: A genus of Nevadiidae with glabella evenly tapering. Cephalic border width narrow to moderately wide. Preglabellar field long: subequal to length of L0. Plectrum present. Parafrontal band distinct. LA subtriangular, widest posteriorly. Prosopon typically of caecae on extraocular areas. Thorax differentiated into prothorax and opisthothorax.

Other species:

Nevadia addyensis Okulitch, 1951; Addy Fm., near Addy, Washington.

Nevadella sp. 2 Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

Nevadia palmeri n. sp., Campito Fm., Montezuma Range, Nevada.

Discussion: It has long been debated whether *Nevadia* and *Nevadella* are synonymous. Only one author (Whittington, 1989) has actually suggested synonymizing the two, but species have alternately been assigned to one or the other genus. McMenamin (1987, p. 740) used ocular lobe length to distinguish the so called "long-eyed" *Nevadia* from the "short-eyed" *Nevadella*. This character is highly variable among species and it is not diagnostic at the generic level. In any case, the type species of *Nevadia* (*Nevadia weeksi*, Pl. 2, figs. 1-4; see also Whittington, 1989, pl. 8, figs. 47,49) is a relatively short-eyed species with the tips of its ocular lobes opposite of L1. Fritz (1992, p. 21) also used ocular lobe length as a distinguishing feature and added that *Nevadia* has "...a wider cephalon, shorter glabella, narrower anterior and lateral borders, a more posteriorly inclined posterior border..." than *Nevadella*. Of these characters, *N. weeksi* does have unusually wide extraocular areas and narrow cephalic borders, but these are species-level characters. The character of a posteriorly inclined posterior border is only seen on some specimens and is likely a result of compaction in shale specimens, rather than a actual feature. The shorter glabella (expressed here as a long preglabellar field) is characteristic of, but not unique to the genus.

The features used herein to distinguish *Nevadia* from *Nevadella* are an evenly tapered glabella and distinct parafrontal band. *Nevadella* has a slightly constricted glabella and LA is widest at midlength rather than posteriorly. The thorax of *Nevadia* is known only for the type species, but it shows a distinct division into a prothorax and opisthothorax, based on an abrupt change

posteriorly in the length of the pleural spines. All species of *Nevadella* with known thoraxes show no such division. *Cirquella* differs from *Nevadia* by lacking genal spines and by having a slightly constricted glabella, relatively narrower cephalon and small overall size.

Nevadia addyensis Okulitch, 1951 was assigned to *Nevadella* by Fritz (1972, p. 22) but later he (Fritz, 1992, p. 21) assigned it back to *Nevadia*. The holotype of *Nevadia addyensis* has an evenly tapered glabella characteristic of *Nevadia*. It is not well-enough preserved to distinguish a parafrontal band. *Nevadella bacculenta* Fritz, 1972 was also later (Fritz, 1992, p. 21) assigned to *Nevadia*. It has a slightly constricted glabella and indistinct parafrontal band, therefore is considered to belong to *Nevadella*. *Nevadella* sp. 2 Fritz, 1972 has an evenly tapered glabella and a parafrontal band, and is assigned to *Nevadia*.

Nevadia weeksi Walcott, 1910b

Pl. 2, figs. 1-4

1908 *Holmia weeksi* Walcott, p. 189 (named in fossil list)

1910b *Nevadia weeksi* Walcott, p. 257, pl. 23, figs. 1-7, text-figs. 14, 15.

1916c *Nevadia weeksi*, Walcott, pl. 14, fig. 1.

1952 *Nevadia weeksi*, Tasch, p. 485, 487, text-fig. 1G.

1959 *Nevadia weeksi*, Poulsen, p. O192, text-fig. 135, no. 3.

1959 *Nevadia weeksi*, Best [unpublished thesis], p. 188-189, text-fig. 6 l.

1989 *Nevadia weeksi*, Whittington, p. 122-125, pl. 7, figs. 41-42; pl. 8, figs. 47, 49; text-figs. 39, 40, 53.

1992 [non] *Nevadia weeksi*, Fritz, p. 22, pl. 1, figs. 1-11, pl. 2, figs. 1-6, text-fig. 7a (= unassigned olenelloid)

1992 *Nevadia weeksi*, Whittington, pl. 59.

1993 *Nevadia weeksi*, Palmer and Repina, fig. 10.1.

1995 *Nevadia weeksi*, Fritz, p. 718, pl. 9, figs. 6-7.

Diagnosis: A species of *Nevadia* with cephalic border narrow: width less than half length L0. Plectrum full to partial. Parafrontal band extends a short distance anteriorly from the ocular ridge. Ocular lobes moderately short; tips opposite midlength of L1. Intergenal ridge distinct; intergenal thickening midwidth on posterior cephalic margins. Prosopon of fine caecae on extraocular areas, glabella smooth. Thorax of 17 prothoracic, 11 opisthothoracic segments. Pygidium simple, hemicircular with a single axial ring.

Lectotype: A complete specimen (USNM 56792b; Walcott, 1910b, pl. 23, fig. 2) designated by Whittington (1989, p. 122, pl. 7, figs. 41, 42, and text-fig. 39). From the Silver Peak Group (Montenegro Member of the Campito Formation after Fritz, 1995), unit 12, Barrel Spring Section (Walcott, 1980, p. 189), 16 km south of Silver Peak, Silver Peak Range, Esmeralda County, Nevada. Paralectotypes: USNM 56792a,c-j.

Occurrences: NEVADA. Montenegro Member, Campito Formation, Esmeralda County: Locality 1f (Walcott, 1910b, p. 260), unit 12, Barrel Spring Section, 16 km south of Silver Peak, Palmetto Mountains (see also Fritz, 1995, p. 718); Locality 174b (Walcott, 1910b, p. 260) north of Red Mountain, 16 km north of Silver Peak; GSC localities 105371 and 105372 (Fritz, 1995, p. 718 and fig. 2), Palmetto Mountains; locality 16, 3 km north of Montezuma Peak summit, near Goldfield.

Zonal Biostratigraphy: *Nevadia weeksi* Subzone, *Nevadia* Zone.

Discussion: The specimens of *Nevadia weeksi* illustrated herein are less distorted than the type material, and were collected from a site about 30 km from the type locality. The specimens closely match the lectotype, differing only in having a slightly wider cephalic border. The pygidium is simple, non-lobate, and appears to have only a single axial ring (Pl. 2, fig. 4). Two axial rings were described by Whittington (1989, p. 124, fig. 40) for the lectotype, but the "first" ring appears to be an opisthothoracic segment in this better preserved material.

Nevadia weeksi can be distinguished from all other species of *Nevadia* by its relatively short ocular lobes, narrow cephalic borders and unusually wide cephalon, reflected in the greater width of its extraocular areas. *N. palmeri* n. sp. and *Nevadella* sp. 2 Fritz, 1972 both have proportionately wider borders. *Nevadia weeksi* has smooth glabellar prosopon while *N. palmeri* has fine tubercles and *Nevadella* sp. 2 Fritz has fine terrace lines, but lacks the caecae on the extraocular areas seen on other species. *N. weeksi* is the only species of *Nevadia* for which the postcephalic morphology is known. The division into prothorax and opisthothorax is designated at T18 where the thoracic spines abruptly decrease in length.

Fritz (1992) described a number of poorly preserved specimens from the Mural Formation that he attributed to *Nevadia weeksi*. The specimens have a wide cephalic border and long ocular lobes (tips opposite of L0) unlike *N. weeksi*. A large cephalon (Fritz, pl. 2, fig. 2) has a modified L3 that curves posterolaterally and an isolated S2, unlike any described species of nevadiid. These specimens are not *N. weeksi*, and are likely an olenelloid of uncertain taxonomic assignment.

Nevadia palmeri n. sp.

Pl. 2, figs. 5-10; Text-fig. 33

1910b [?] *Wanneria?* *gracile* Walcott; pl. 38, fig. 21 only.1972 [?] *Nevadella* sp. 1 Fritz, p. 24, pl. 8, figs. 18-20.

Diagnosis: A species of *Nevadia* with cephalic border moderately narrow: width approximately half length L0. Plectrum full length of prelabellar field. Parafrontal band extending from ocular ridge to plectrum. Ocular lobes moderately long; tips opposite of S0. Interocular ridges indistinct. Intergenal thickening slight; midwidth on posterior cephalic borders. Prosopon granular over total cephalic surface with additional caecae on extraocular areas.

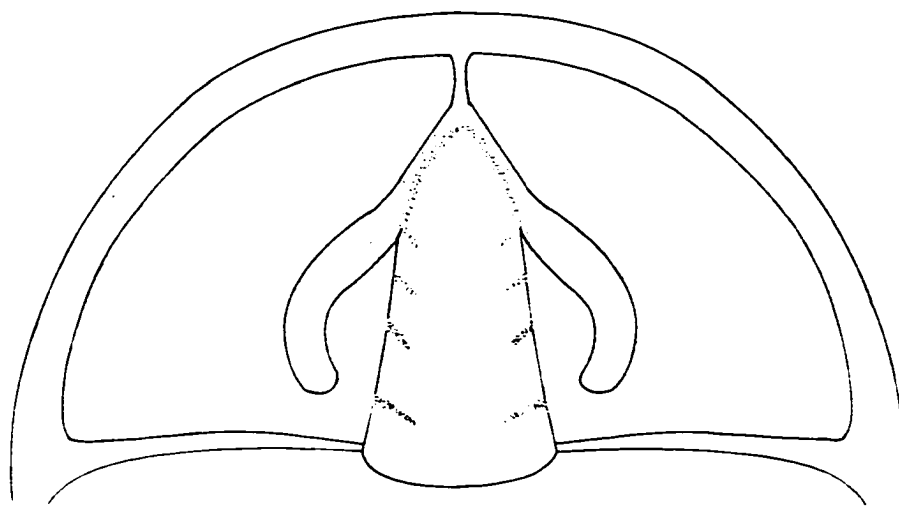
Holotype: A nearly complete cephalon (ICS 1083#2; Pl. 2, fig. 8) from the Montenegro Member of the Campito Formation, locality 17, 3 km north of Montezuma Peak summit, Montezuma Range, Nevada. **Paratype:** ICS 1085#1

Etymology: After A. R. (Pete) Palmer, to honour a lifetime of work on Cambrian trilobites. Pete also collected the type material and generously provided it for description in this thesis.

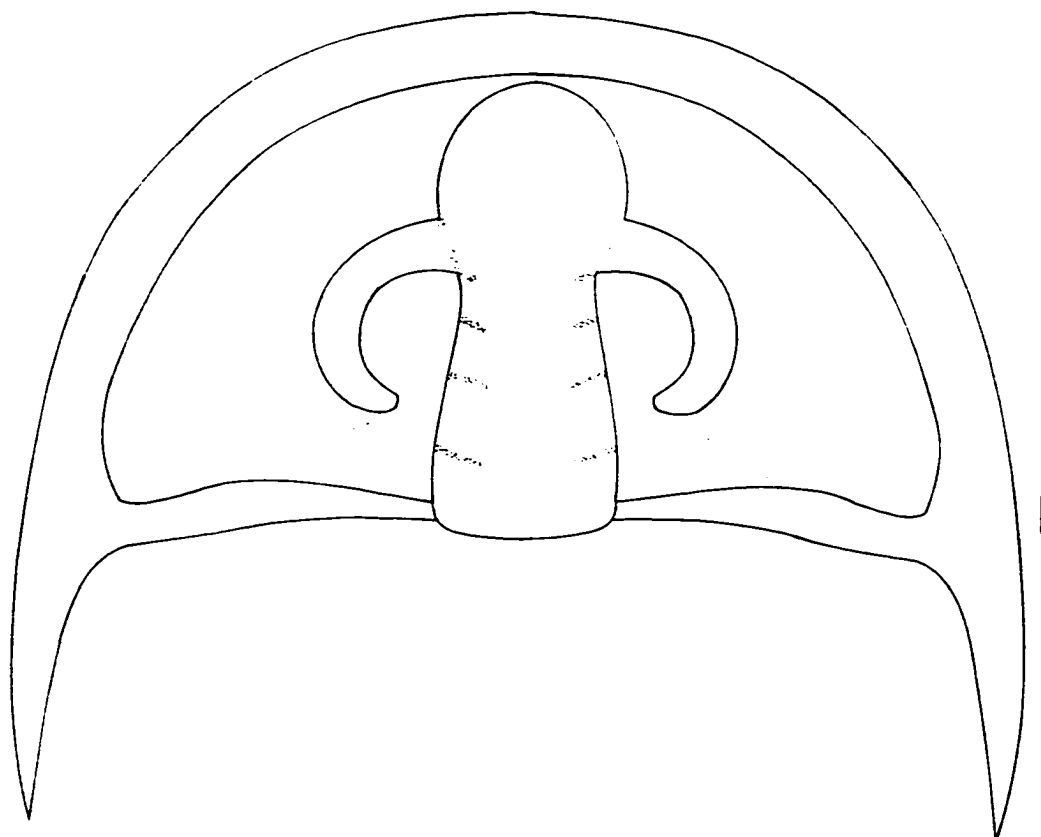
Occurrences: NEVADA. Montenegro Member, Campito Formation, Esmeralda County: locality 17, 3 km north of Montezuma Peak summit, near Goldfield. ?CALIFORNIA. Locality 14p (Walcott, 1910b, p. 300) "from quartzite sandstones near Resting (Fresh Water) Springs, ... on the Amargosa River", Inyo County. ?NORTHWEST TERRITORIES. Sekwi Formation, Mackenzie Mountains (Fritz, 1972).

Zonal Biostratigraphy: *Nevadia palmeri* Subzone, *Nevadia* Zone.

Discussion: *Nevadia palmeri* has the most extensive parafrontal bands of any species of *Nevadia*. The bands extend from the ocular ridges to the plectrum. *N. palmeri* is also unusual in the granular prosopon on its cephalon and it has the longest ocular lobes of any described species of *Nevadia*. *Nevadella bacculenta* is the only other nevadiid species that has a partially granular prosopon. In the Montezuma Peak area, the type specimens of *Nevadia palmeri* occur about 65 m stratigraphically above *N. weeksi*; approximately 185 m below the top of the Campito Formation.



Text-fig. 33. *Nevadia palmeri* n. sp. scale bar = 1 mm



Text-fig. 34. *Nevadella eucharis* (Walcott) n. sp. scale bar = 1 mm

A single specimen preserved as an internal mold in quartzite from the Amargosa River, California, was illustrated as *Wanneria? gracile* by Walcott (1910b, pl. 38, fig. 21) (see synonymy list of *Nevadella gracile* for a full account of Walcott's species). This specimen (Pl. 2, figs. 9-10) closely resembles *Nevadia palmeri*, except that it lacks a plectrum. This lack may be a preservation feature as prosopon is not preserved either.

A fragmentary specimen referred to *Nevadella* sp. 1 Fritz, 1972 (pl. 8, fig. 18-20) may also belong to *Nevadia palmeri*. It has the evenly tapered glabella of *Nevadia*, and the long ocular lobes of *N. palmeri*. The specimen has a short, barely tapering LA and interocular ridges positioned close to the posterior border, characteristic of small holaspid specimens of *N. palmeri*. The prosopon however, appears to be smooth compared to specimens of this size from the type area that have developed a granular prosopon. The plectrum and parafrontal band are indistinguishable.

Ontogeny: A full holaspid ontogeny is known for *Nevadia palmeri*, but no meraspid material. There is shortening of the ocular lobes in the largest holaspids and a general lengthening of the cephalon through ontogeny.

Clique E holaspids have ocular lobes with posterior tips opposite of anterior of L0. Extraocular areas approximately 3 times width of interocular areas. LA tapered, about 1.5 times length of L0. Glabellar furrows transglabellar, deepest laterally. Intergenal spines absent. Cephalon more than twice as wide as long. (Pl. 2, fig. 5)

Clique F holaspids have ocular lobe posterior tips opposite of the anterior of L0. Extraocular areas approximately 3 times the width of the interocular areas. LA approximately twice the length of L0. Glabellar furrows marginal. Cephalon approximately twice as wide as long. (Pl. 2, figs. 6, 7)

Clique G holaspids have ocular lobe posterior tips opposite of S0. Extraocular areas approximately 4 times the width of the interocular areas. LA twice the length of L0. Glabellar furrows marginal. Cephalon less than twice as wide as long. (Pl. 2, fig. 8)

Genus *Nevadella* Raw, 1936

Type species: *Callavia eucharis* Walcott, 1913 from the Mahto Formation (Mural Formation after Fritz, 1992), Mumm Peak, Mount Robson Area, British Columbia (subsequent designation by Whitehouse, 1939, p. 191).

Diagnosis: A genus of Nevadiidae with glabella constricted slightly at L2/L3. Cephalic border wide to moderately wide. Preglabellar field length variable. Parafrontal band absent. LA long, suboval, widest at midlength. Prosopon typically of caecae or terrace lines on extraocular areas. Hypostome with strong posterior border furrow. Middle furrow long, moderately deep. Rostrum a broad, crescentic plate. Thorax not differentiated into prothorax and opisthothorax.

Other species:

Wanneria? gracile Walcott, 1910b, Poleta Fm., Esmeralda County, Nevada.

Nevadella faceta Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT (?= *Nevadia ovalis* McMenamin, 1987; Puerto Blanco Fm., NW Sonora, Mexico).

Nevadella bacculenta Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

Nevadella parvoconica Fritz, 1992; Mural Fm., Mt. Robson Area, BC.

Nevadella mountjoyi Fritz, 1992; Mural Fm., Mt. Robson Area, BC.

Discussion: A unique feature of *Nevadella* is a glabella that is tapered forward, but with an LA distinctly wider than L3, giving the glabella a slightly constricted appearance. A parafrontal band is absent or indistinctly developed (see *Nevadella eucharis*, Pl. 3, figs. 1-2). The hypostome is long and narrow, mirroring the shape of LA, and typically has a moderately deep middle furrow (*N. parvoconica*, Pl. 3, fig. 11; *N. faceta* Fritz, 1972, pl. 3, figs. 11,12). The rostral plate is poorly known and is preserved as an impression on the thin cephalic shell in a handful of specimens (*N. parvoconica*, Pl. 4, fig. 1; see also *N. mountjoyi* Fritz, 1992, pl. 3, fig. 1, 4). It is a wide crescentic band reaching to the genal angle. The ontogeny of *Nevadella* is described in detail under *N. parvoconica* and a comparison of *Nevadella* to *Nevadia* is given under *Nevadia*.

Nevadia ovalis McMenamin, 1987 from the Puerto Blanco Formation, Mexico is tentatively synonymized with *Nevadella faceta* Fritz, 1972 from the Sekwi Formation, Northwest Territories. A poorly preserved, complete cephalon illustrated by McMenamin (1987, fig. 6.1, 6.3) appears to have been photographed at an angle making character determinations difficult and the reconstruction does not match the photograph. The moderately long preglabellar field has a plectrum but the drawing (text-fig. 3) shows an elongated L4 and short preglabellar field. With this new interpretation, all features distinguishable on *N. ovalis* match those seen in *N. faceta* Fritz, 1972.

Nevadella eucharis (Walcott, 1913)

Pl. 3, figs. 1, 2; Text-fig. 34

- 1913 *Callavia eucharis* Walcott, p. 315, pl. 53, fig. 1.
 1913 *Callavia perfecta* Walcott, p. 315, pl. 53, figs. 3, 4, 5.
 1936 *Nevadella eucharis*, Raw, p. 249, 250.
 1936 *Nevadella perfecta*, Raw, p. 249.
 1959 *Nevadella eucharis*, Poulsen, p. O196.
 1959 *Nevadella eucharis*, Best [unpublished thesis], p. 191-192.
 1972 *Nevadella eucharis*, Fritz, p. 22.
 1972 *Nevadella perfecta*, Fritz, p. 22.
 1990 *Nevadella eucharis*, Hunt [unpublished thesis], p. 79-82. pl. 7, fig. 2, pls. 8-11.
 1992 *Nevadella eucharis*, Fritz, p. 24, pl. 4, figs. 1-3, text-fig. 7d.
 1992 *Nevadella perfecta*, Fritz, p. 25, pl. 4, figs. 4-6; pl. 5, figs. 1-5, text-fig. 7e.
 1993 *Nevadella eucharis*, Palmer and Repina, fig. 10.2.

Diagnosis: A species of *Nevadella* with glabella distinctly constricted, narrowest at S3. Cephalic border wide; width subequal to length L0. Cephalic border furrow pits present. Preglabellar field short to absent. Plectrum absent. Ocular lobes moderately short; tips opposite of midlength of L1. Intergenal ridges weakly developed. Prosopon of caecae on extraocular areas, glabella smooth. Thorax of at least 17 segments.

Holotype: A complete articulated specimen (USNM 60079; Walcott, 1913, pl. 53, fig. 1 and Fritz, 1992, pl. 4, fig. 3) from the Mahto Formation (Mural Formation after Fritz, 1992), locality 61K (Walcott, 1913), Mumm Peak, Mount Robson Area, British Columbia.

Occurrences: BRITISH COLUMBIA. Mural Formation, locality 61k (Walcott, 1913), GSC localities 90566 - 90570 (Fritz, 1992), Mumm Peak, Mount Robson area. Cranbrook Formation, locality 3, Ram Creek area, 13 km northeast of Skookumchuck. NEVADA. Poleta Formation, locality 18, Montezuma Range, 7.5 km northwest of Goldfield. ?CALIFORNIA. Poleta Formation: sections CF, NH and locality 23, Cedar Flat area, east of Big Pine, Inyo County.

Zonal Biostratigraphy: *Nevadella eucharis* Subzone, *Nevadella* Zone.

Discussion: The distinctive features of *Nevadella eucharis* are a preglabellar field too short to display a plectrum or absent, relatively short ocular lobes, and wide cephalic borders. *Nevadella*

eucharis differs from *N. parvoconica* which has a moderately long preglabellar field with a partial plectrum, and from *N. mountjoyi* (lectotype selected herein: GSC 98988, illustrated in Fritz, 1992, pl. 3, fig. 1) which lacks a preglabellar field and has an LA that intrudes slightly on the anterior border. These three species share ocular lobes of a similar length.

Nevadella perfecta occurs in the same talus collection (of Walcott, 1913) as specimens assigned to *Nevadella eucharis*. Whether these species are synonyms has been the subject of controversy for nearly 60 years. Raw (1936), Best (1959), Fritz (1972) and Hunt (1990) considered the two to be synonyms, but Fritz (1992) claimed they were separate. They cannot be distinguished using cephalic features: both have a wide cephalic border, ocular lobes of the same length, a short to absent preglabellar field, and a glabella of similar shape and configuration. Fritz (1992) claimed that they could be distinguished based on curvature of various features, position of genal spines, and occurrence of intergenal ridges. All of the material is flattened in shale creating variability in these features, and none can be used to distinguish *N. perfecta* as a distinct species. Fritz (1992) showed a short stratigraphic separation between specimens that he assigned to either species. He also claimed that *N. eucharis* has 23 thoracic segments while *N. perfecta* has 17. Counting the small posterior segments is problematic as examination of the few articulated specimens illustrated in Fritz (1992, pl. 4, fig. 3; pl. 5, figs. 4, 5) demonstrates: pl. 4, fig 3 shows 20; pl. 5, fig. 4 shows 15, pl. 5 fig. 5 shows 17. It is also not known whether *Nevadella* continued to add segments throughout its life as in some other species (for example, *Aulacopleura konincki*, in Hughes, 1994).

Ontogeny: No meraspid material has been illustrated for *Nevadella eucharis*. Fritz (1992) provided many photographs of the holaspid ontogeny that mirror the major changes discussed under *Nevadella parvoconica*.

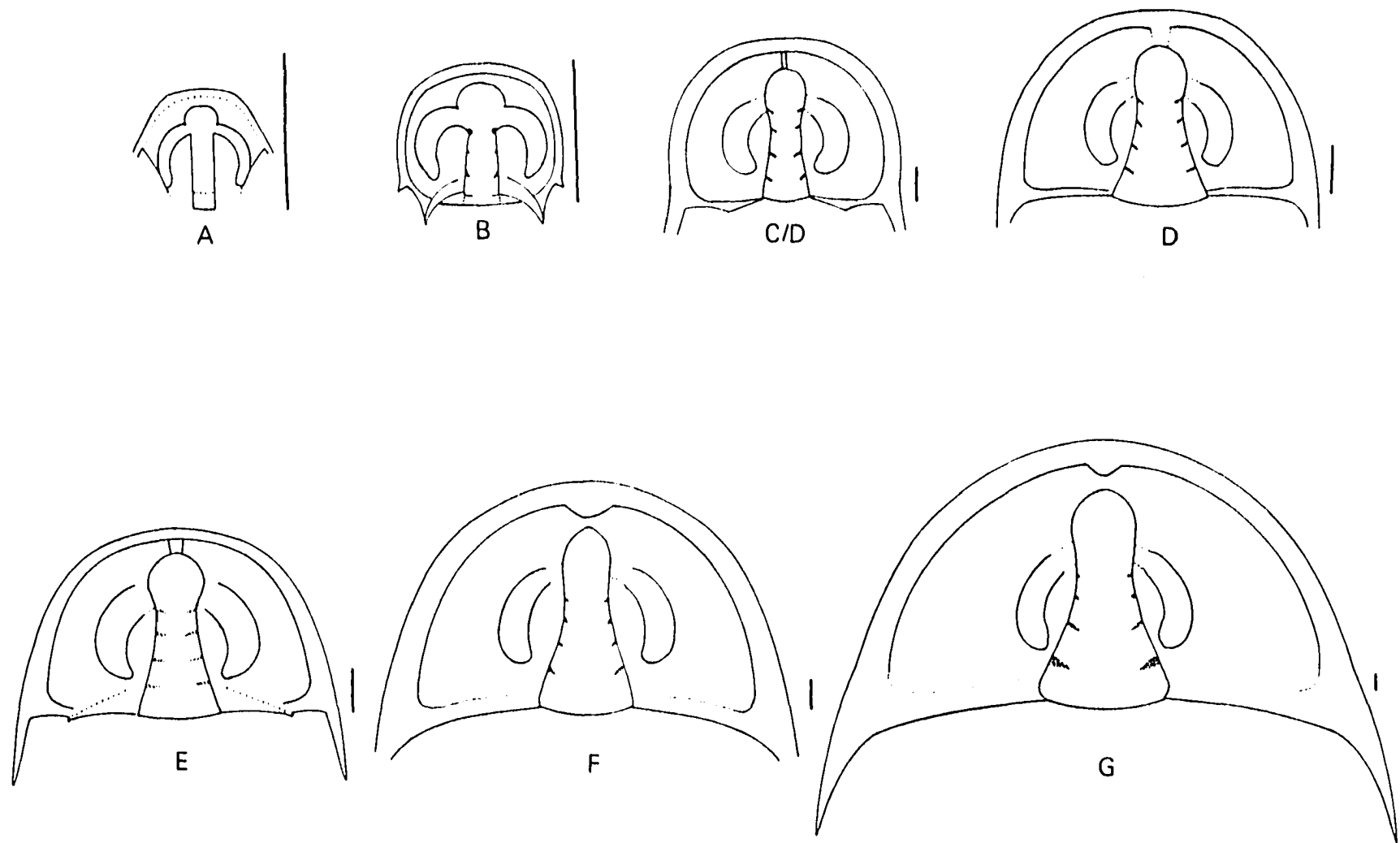
Nevadella parvoconica (Fritz, 1992)

Pl. 3, figs. 3-13; Pl. 4, fig. 1; Text-fig. 35

1910b *Wanneria? gracile* Walcott, pl. 38, figs. 15,16 only.

1992 *Nevadia parvoconica* Fritz, p. 22-24, pl. 2, figs. 7-9, text-fig. 7b.

Diagnosis: A species of *Nevadella* with glabella distinctly constricted, narrowest at S3. Dorsal furrows effaced. Cephalic border moderately wide; width more than half length of L0. Preglabellar field moderately long: more than half length of L0. Plectrum partial. Ocular lobes



Text-fig. 35. Ontogeny of *Nevadella parvoconica* (Fritz). Letters designate cliques. scale bars = 1 mm

moderately short; tips opposite of posterior of L1. Intergenal ridges absent. Prosopon of terrace lines on extraocular areas and border, glabella smooth. Thorax of at least 20 segments.

Holotype: A large partial cephalon (GSC 98987; Fritz, 1992, pl. 2, figs. 7-9) from the Mural Formation, GSC locality 90563 (Fritz, 1992), Mumm Peak, Mount Robson Area, British Columbia.

Occurrences: BRITISH COLUMBIA. Mural Formation, GSC locality 90563, Mumm Peak, Mt. Robson Area (Fritz, 1992). NEVADA. Poleta Formation, Esmeralda County: localities 15, 18 and section GF, Montezuma Range, Goldfield area; section GP, Mt. Dunfee area, 7 km east of Gold Point. CALIFORNIA. Poleta Formation, Cedar Flat area, east of Big Pine, Inyo County: locality 23, sections CF and NH and Walcott's (1910b, p. 300) localities 176, 177 and 178a, .

Zonal Biostratigraphy: *Nevadella parvoconica* Subzone, *Nevadella* Zone.

Discussion: *Nevadella parvoconica* was based on a single large specimen from the Mount Robson area, British Columbia. Abundant material from the Great Basin allows for a better understanding of this species. The type specimen is preserved in limestone and is the same as Great Basin specimens also from limestone. The new specimens have a glabella that is slightly more constricted and the preglabellar field slightly shorter. Both of these characters are variable and the holotype is within the range of variation seen in the Great Basin material. Material preserved in shale displays slightly deeper furrows as a result of compaction.

The distinctive features of *N. parvoconica* are: effacement of the glabellar furrows, distinct constriction of the glabella, and the moderately long preglabellar field. An articulated specimen (Pl. 4, fig. 1) has a thorax of at least 20 segments. It is wide with long, broad thoracic spines; the same morphology as that seen in *Nevadella eucharis* (Walcott, 1913) and *Nevadella mountjoyi* Fritz (1992, pl. 3, figs. 11, 12). The hypostome is also similar to that of *N. faceta* Fritz, 1972. There is a distinct posterior furrow, but the posterior border is poorly known. A long, moderately deep middle furrow connects the maculae. Walcott (1910b, pl. 38, figs. 15,16) illustrated a hypostome and partial thoracic segment under the name of *Wanneria? gracile* that belongs to *N. parvoconica*. Unillustrated material from the same collection includes cephalae of *N. parvoconica*. *N. parvoconica* is closest to *N. eucharis* and *N. gracile* in morphology and comparisons are given under the respective species.

Ontogeny: A nearly complete ontogenetic sequence can now be described for *Nevadella parvoconica* based on material from the Great Basin. The presence or absence of a plectrum cannot be judged any earlier than clique D meraspids due to poor quality of preservation.

Clique A meraspids are not sufficiently well-preserved to determine the presence or absence of procranial spines. Ocular lobe posterior tips opposite of L1. Cephalic border moderately differentiated: extraocular areas narrow, present only anteriorly. LA bulbous. Intergenal and genal spines of unknown extent. Cephalon subcircular in outline: length and width subequal. (Pl. 3, fig. 3)

Clique B meraspids have no indication of procranial spines. Ocular lobes well-defined, posterior tips opposite of L1. Extraocular areas narrow; present over full length of cephalon, narrowest posteriorly. Glabella tapering forward to S3, LA bulbous. S1 deep, marginal. S1 to S3 indistinct, marginal pits. Intergenal spines long, laterally directed, at posterolateral corners. Genal spines minute, advanced: opposite of L1. Cephalon hemicircular in outline: approximately 1.3 times wider than long. (Pl. 3, fig. 4)

Clique C meraspids have ocular lobe posterior tips opposite of S0. Extraocular areas subequal to or slightly wider than interocular areas. Glabella tapering forward to S3, LA bulbous. Glabellar furrows marginal or connected across the glabella by shallow furrows. Intergenal spines minute, medially located on posterolateral borders. Genal spines well-developed, not advanced. Cephalon hemi-circular in outline: approximately 1.4 times wider than long. (Pl. 3, fig. 5)

Clique D specimens have ocular lobe posterior tips opposite of posterior-most portion of L1. Preglabellar area long: plectrum complete. Extraocular areas approximately twice the width of interocular areas. Glabella tapering forward to L3, LA subrounded, furrows marginal to transglabellar as shallow furrows. Intergenal spines minute, genal spines well-developed, not advanced: opposite of posterior-most portion of L0. Cephalon approximately 1.7 times wider than long. (Pl. 3, fig. 7)

Clique E specimens have ocular lobe posterior tips opposite of posterior-most portion of L1. Preglabellar area of moderate length: plectrum complete. Extraocular areas approximately twice the width of interocular areas. Glabella of mature configuration: tapering forward to L3; LA elongate, widest at midlength. Glabellar furrows marginal; S0 pair connected by shallow furrow. Genal spines not advanced: base opposite of T1. Cephalon less than twice as wide as

long. Hypostomes of this clique have a fully spinous margin of at least 6 pairs of spines and a fairly long posterior body. (Pl. 3, fig. 8)

Clique F holaspids have ocular lobe posterior tips opposite of posterior-most portion of L1. Preglabellar area moderately short: plectrum partial. Extraocular areas approximately 3 times the width of interocular areas. S0 marginal. Cephalon nearly twice as wide as long. (Pl. 3, figs. 9, 10)

Clique G holaspids differ from those of clique F in having slightly shorter ocular lobes (posterior tips opposite of midlength of L1), a proportionately shorter plectrum, extraocular areas approximately 4 times the width of the interocular areas, and a cephalon twice as wide as long. (Pl. 3, figs. 12, 13; Pl. 4, fig. 1)

Nevadella gracile (Walcott, 1910b)

Pl. 4, figs. 2-7

1910b *Wanneria gracile* Walcott, p. 298-301, pl. 38, figs. 22, 24 only. [*non*] figs. 15, 16 [= *Nevadella parvoconica*]; figs. 17-20 [= *Elliptocephala truemani*?]; fig. 21 [= *Nevadia palmeri*?]; fig. 23 [= *Cirquella nummularia*].

1936 *Nevadella gracile*, Raw, p. 250.

1959 *Nevadia gracilis*, Best [unpublished thesis], p. 190-191.

Diagnosis: A species of *Nevadella* with glabella distinctly constricted, narrowest at S2. Cephalic border moderately wide; width more than half length L0. Preglabellar field moderately long; more than half length L0. Plectrum partial. Ocular lobes long; tips opposite of anterior of L0. Intergenal ridges absent. Genal spines slightly advanced; opposite of L0.

Lectotype: (selected here) A nearly complete cephalon (USNM 56805a; Walcott, 1910b, pl. 38, fig. 22 and Pl. 4, figs. 6, 7) from the Silver Peak Group, locality IV (Walcott, 1910b, p. 300). From unit 3 of Walcott's Barrel Spring Section (1908, p. 189, which is interpreted herein to be the lower Poleta Formation), "3 miles north of Valcalda Spring and 4 miles northwest of Drinkwater Mine", Silver Peak Range, Esmeralda County, Nevada". Paralectotype: USNM 56804b

Occurrences: NEVADA. Poleta Formation, Esmeralda County: locality IV (Walcott, 1910b, p. 300), Walcott's Barrel Spring Section (1908, p. 189), 16 km south of Silver Peak, Silver Peak Range; ?section GP, Mt. Dunfee area, 7 km east of Gold Point.

Zonal Biostratigraphy: *Nevadella parvoconica* Subzone, *Nevadella* Zone.

Discussion: *Wanneria? gracile* Walcott, 1910b was based on material from four different localities that represents a total of five different species. Most of the material that Walcott illustrated under this name is re-illustrated herein and described. Of Walcott's illustrated specimens (pl. 38, figs 15-24) he referred to fig. 22 as "a cephalon that appears to have the adult characters of the species" and this is chosen as the lectotype. The small cephalon in fig. 24 is a topotype. Walcott's fig. 23, from the same locality lacks genal spines and is reassigned to *Cirquella nummularia*. Reassignments of the other specimens are given under the synonymy list and are discussed elsewhere.

Nevadella gracile is closest in morphology to *N. parvoconica* Fritz, 1992 from which it differs in having longer ocular lobes, slightly advanced genal spines, and in lacking effacement of the glabellar furrows. Prosopon is not preserved. The slightly advanced genal spines are an unusual feature for holaspid nevadiid trilobites. *N. faceta* Fritz, 1972 has ocular lobes of a similar length, but lacks the advanced genal spines of *N. gracile*. Thorax and ventral morphology are unknown for *N. gracile*.

Material from the lower Poleta Formation, near Gold Point, consists of meraspids and a small holaspid that appear to belong to *Nevadella gracile*. The small holaspid has long ocular lobes and slightly advanced genal spines typical of the species. The meraspids are similar in appearance to those described for *N. parvoconica* (Pl. 3, figs. 3, 4) and *N. faceta* Fritz (1972, pl. 3, fig. 14).

Ontogeny: Only a handful of specimens are known for *Nevadella gracile*, but they include meraspid material. From the type material, a clique C meraspid (Pl. 4, fig. 4) is known. Compared to clique C meraspids of *N. parvoconica*, it has longer ocular lobes, a distinct plectrum, more rounded, less bulbous LA and a parallel-sided glabella. A clique C meraspid (Pl. 4, fig. 5) from Gold Point, Nevada, tentatively assigned to *N. gracile*, has distinct intergenal spines and slightly advanced genal spines. Associated clique B meraspids (Pl. 4, figs. 2, 3) from Gold Point are closely comparable to those of *N. parvoconica* except for their longer ocular lobes and barely tapered glabella. These meraspids are of low relief which enables pits (?fossulae) to be distinguished anterior to the junction of the ocular ridges with LA.

Genus *Cirquella* Fritz, 1993

Type species: *Cirquella nummularia* Fritz, 1993, from the Donald Formation, Dogtooth Mountains, southeastern British Columbia (by original designation).

Diagnosis: An genus of Nevadiidae with glabella narrowest at S3. Dorsal surface effaced. Cephalic border moderately wide: width approximately half length L0. Preglabellar field short: one third length L0, typically with preglabellar depression. LA short, subrounded. Genal angles rounded: genal spines absent. Prosopon smooth. Overall size small.

Other species:

Cirquella espinata Fritz, 1993; Donald Fm., Dogtooth Mtns., BC.

Discussion: *Cirquella* was assigned to the Nevadiidae by Fritz (1993) on the basis that it shares a similar glabellar outline and posterior position of ocular lobe attachment to LA with *Nevadia* and *Nevadella*. Palmer and Repina (1993: *Cirquella* listed as Genus B) supported this assignment, but Geyer (1996) assigned *Cirquella* to the Archaeaspididae based on the convexity of the cephalon. However, convexity is not a defining feature of the family (see discussion under Archaeaspididae). *Cirquella* has a small, subrounded LA like *Nevadella*. Meraspids of *Cirquella*, illustrated by Fritz (1993), have a bulbous LA like those of *Nevadella* and unlike the narrow LA of meraspids of the archaeaspidid *Bradyfallotaspis* (Pl. 1, figs. 1, 2). *Cirquella* also shares a superficial similarity with trilobites of the fallotaspid subfamily Daguinaspidinae. The latter also lack genal spines and have a tapered glabella, but differ fundamentally in having ocular lobes attached to the full length of LA and narrower extraocular areas. To conclude, assignment of *Cirquella* to the Nevadiidae is supported by the development and shape of LA and the relationship of the ocular lobes to LA.

Cirquella is an unusual nevadiid in having a depression in the place of a plectrum, lacking genal spines, and having a relatively narrow, rounded cephalon with proportionately narrow extraocular areas. The latter three characters are typical of Olenellina meraspids, and considering the small overall size of these trilobites, *Cirquella* may be a paedomorphic (progenetic) genus.

The general effacement of the cephalon of *Cirquella* creates shallow glabellar furrows, no plectrum, and poorly developed intergenal ridges. The prosopon of *Cirquella* is smooth, though some large specimens of *C. espinata* Fritz, 1993 have terrace lines on the lateral border. A single illustrated hypostome of *C. espinata* (Fritz, 1993, fig. 11.3) has the long, narrow shape also seen in

hypostomes of *Nevadella*. The rostral plate, thorax and pygidium are unknown. Fritz (1993, p. 859) inferred that *Cirquella* has long thoracic pleurae by the lateral position of the intergenal angles.

Cirquella nummularia Fritz, 1993

Pl. 4, figs. 8-10

1910b *Wanneria?* *gracile* Walcott, pl. 38, fig. 23 only.

1990 *Acephalocanthus inyo* nomen nudum Hunt [unpublished thesis], p. 72-74, pls. 3-6.

1993 *Cirquella nummularia* Fritz, p. 859-862, text-fig. 5, pls. 6, 7.

Diagnosis: A species of *Cirquella* with advanced genal angles and minute intergenal spines. Ocular lobes moderately short with tips opposite of L1. Hypostome with shallow posterior furrow.

Holotype: A nearly complete large cephalon (GSC 102330; Fritz, 1993, figs. 7.2-7.4.) from the Donald Formation, Dogtooth Mountains, British Columbia.

Occurrences: BRITISH COLUMBIA. Lower Donald Formation, GSC locality 105119 (Fritz, 1993) Dogtooth Range, near Golden. CALIFORNIA. Wood Canyon Formation (upper member), Titanother Canyon Section II and Daylight Pass Section II (Hunt, 1990), Death Valley Region. NEVADA. Esmeralda County: Locality IV (Walcott, 1910b, p. 300), arenaceous shales 3 miles north of Valcalda (Barrel) Spring, near Silver Peak; Basal Poleta Formation, locality 15, 3 km north of Montezuma Peak summit, near Goldfield.

Zonal Biostratigraphy: *Nevadella parvoconica* Subzone, *Nevadella* Zone.

Discussion: The type material of *Cirquella nummularia* was described in detail by Fritz (1993) and with comparison made to *Cirquella espinata* Fritz, 1993. Material illustrated here consists, in part, of two poorly preserved, partial cephalons that are considered conspecific with those illustrated from the Death Valley Region by Hunt (1990). These specimens from the Great Basin closely match the type specimens from British Columbia, differing only in having slightly shorter ocular lobes (posterior tips opposite of the midlength of L1 instead of the posterior of L1). Fritz (1993 p. 859) similarly assigned Hunt's informally described material to *C. nummularia?*.

A single specimen of *Cirquella nummularia* was illustrated by Walcott (1910b, pl. 38, fig. 23) as *Wanneria? gracile* (see also *Nevadella gracile*). This poorly preserved cephalon (reillustrated in Pl. 4, fig. 9) is identical in its observable features to the type material of *C. nummularia*. The ocular lobes are opposite of the posterior of L1. It is associated with material of *Nevadella gracile* (Walcott, 1910b) and *Esmeraldina argenta* (Walcott, 1910b) in Unit 3 of Walcott's Barrel Spring Section (1910b, p. 298, 300; 1908, p. 189), which is interpreted herein to be the lower Poleta Formation.

Superfamily Olenelloidea Walcott, 1890a

Diagnosis (modified from Palmer and Repina, 1993): A superfamily of Olenellina with L4 enlarged (long and wide); glabella narrowest at L2 or S1. L3 usually modified distally; lateral portion extending posteriorly, wrapping around L2. Ocular lobes connected only to posterolateral part of L4. Thorax of at least 15 segments.

Assigned Families: Olenellidae Walcott, 1890; Wanneriidae Hupé, 1953a; Holmiidae Hupé, 1953a.

Discussion: Palmer and Repina (1993) divided the Olenellina into two superfamilies: the Fallotaspidoidea and Olenelloidea. The Olenelloidea includes all of the youngest taxa of Olenellina. They can be distinguished by possession of a large LA with ocular lobes connected only to the posterior part and a modified L3 that is expanded posterolaterally, wrapping around the anterolateral portion of L2. The concept and composition of the Olenelloidea used here closely follows that of Palmer and Repina (1993). It differs by excluding the Callaviinae (sensu Palmer and Repina, 1993) from the superfamily, as discussed further under the Holmiidae.

Family Holmiidae Hupé, 1953a

[*nom. transl.* Bergström, 1973a, *ex* Holmiinae Hupé, 1953]

Diagnosis: A family of Olenelloidea with glabella widest at LA. S2 curved, marginal. Ocular lobes situated far from glabella: interocular areas wide. Hypostome conterminant in large holaspids: paucidenticate with scalloped posterolateral margins. Thorax not divided into prothorax and opisthothorax. T3 normal or amplipleural. Thoracic spines short, chelate to sentate. T15 without long, posteriorly directed axial spine. Pygidium multisegmented.

Assigned Genera: *Holmia* Matthew, 1890; *Schmidtellus* Moberg in Moberg and Segerberg, 1906; *Kjerulfia* Kiaer, 1917; *Esmeraldina* Resser and Howell, 1938 (= *Palmettaspsis* Fritz, 1995); *Andalusiana* Sdzuy, 1961; *Holmiella* Fritz, 1972; *Geraldinella* Fritz, 1993; *Cambropallas* Geyer, 1993; *Iyouella* Geyer and Palmer, 1995.

Discussion: The Holmiidae is a largely non-Laurentian family outside of the scope of this thesis. The prime uniting features of the holmiids are: the narrow extraocular/wide interocular areas, paucidentulate hypostomes with scalloped posterolateral margins, a normal or amplipleural T3, thoracic spines that are short and chelate to sentate and lack of a long posteriorly directed axial spine on T15. The composition of this family has varied widely as summarized by Palmer and Repina (1993, p. 2-3) and additional changes are made herein. *Elliptocephala* is reassigned from the Holmiidae to the Wanneriidae on the basis of its ontogeny, cephalic proportions, and reinterpreted thoracic structure. *Kjerulfia* is transferred from the Callaviidae to the Holmiidae on the basis that it is much more similar to *Holmia* in its cephalic features than to *Callavia* (see additional comments under the Fallotaspidoidea). *Geraldinella* is removed from the Archaeaspididae and reassigned to the Holmiidae on the basis that it has a wide LA and modified L3. This concept of the Holmiidae agrees closely with the Ahlberg *et al.* (1986) concept of the family, differing only in the inclusion of *Holmiella* and *Esmeraldina* (*Geraldinella*, *Cambropallas* and *Iyouella* were not described at that time). *Esmeraldina* is included in the Holmiidae rather than in the Wanneriidae on the basis of its wide interocular/narrow extraocular areas, chelate thoracic spines, a normal T3 and lack of a long axial spine on T15. *Holmiella* has the olenelloid configuration of LA and the holmiid feature of ocular lobes situated far from the glabella.

The non-Laurentian members of this family (excludes *Esmeraldina*, *Geraldinella* and *Holmiella*) are in need of revision. Several of the genera (i.e. *Holmia*, *Kjerulfia*, *Schmidtellus*) resemble one another so closely that they may all belong to a single genus (if so, *Holmia* has priority). Similarities in hypostomal morphology, ontogenetic development, and glabellar structure in *Holmia kjerulfi* (type species, see Kiaer, 1916) suggests that the holmiids may be most closely related to the wanneriids. The possible relationships of this group are discussed further under the Wanneriidae.

Genus *Esmeraldina* Resser and Howell, 1938

Type Species: *Holmia rowei* Walcott, 1910b from unit 12 of Walcott's Barrel Spring Section (Walcott, 1908, p. 189), 16 km south of Silver Peak, Silver Peak Range, Esmeralda County,

Nevada. (by original designation) Walcott (1908) originally identified *H. rowei* from two intervals in this section, but later (Walcott, 1910b, p. 292, 296) restricted its occurrence to unit 12. Fritz (1992) interpreted these strata to represent the Montenegro Member of the Campito Formation.

Diagnosis: A genus of Holmiidae with glabella expanding forward slightly. Cephalic border wide: width of lateral border subequal to length of L0. S2 marginal. L3 not expanded posterolaterally. Ocular lobes narrow, strongly inclined posteriorly. Mid-ocular lobe furrow shallow. Intergenal ridge faint to absent. Intergenal spines well developed; posterior cephalic border inflected anteriorly lateral to intergenal positions. Genal spines thick, falcate, long; up to twice cephalic length. Occipital spine long, thin. Thorax narrow; pleural spines chelate or sentate.

Other Species:

Olenellus? argenta Walcott, 1910b; lower Poleta Fm., Silver Peak Range, Nevada.

Esmeraldina lidensis Fritz, 1995; Montenegro Mbr., Campito Fm., Silver Peak Range, Nevada.

[?] *Esmeraldina? cometes* Fritz, 1995; Montenegro Mbr., Campito Fm., Silver Peak Range, Nevada.

Palmettaspis consorta Fritz, 1995; Montenegro Mbr., Campito Fm., Silver Peak Range, Nevada.

[?] *Palmettaspis parallela* Fritz, 1995; Montenegro Mbr., Campito Fm., Silver Peak Range, Nevada.

Esmeraldina sp. 1 Fritz, 1995; Cassiar Mtns., B.C.

Discussion: The status of *Esmeraldina* as a genus discrete from *Holmia* has been controversial. Poulsen (*in* Moore, 1959), Fritz (1973) and Palmer and Repina (1993) all synonymized *Esmeraldina* and *Holmia* without discussion. Previously Hupé (1953a,b) and Chernysheva (1960) had recognized *Esmeraldina* as a genus of the Wanneriinae and Olenellinae, respectively. Fritz (1995) gave the first modern treatment of the taxon, recognizing *Esmeraldina* as a holmiid; a reversal from his 1973 position. Fritz (1995, p. 714) noted the following as distinguishing features of *Esmeraldina* from other holmiids; "a general lack of glabellar constriction..., narrow, strap-like ocular lobes, and a lack of differentiation of the third pair of glabellar lobes". Fritz continued by listing how *Holmia* differs from *Esmeraldina* in having a generally longer and rounder LA, more modification of L3, more acute genal angles, fewer thoracic segments, and in lacking a prominent occipital spine. Additional distinguishing features of *Esmeraldina* are the shallow ocular furrows, long and usually broad genal spines and a normal T3.

Table 12. Evaluation of Fritz' (1995) proposed differences
between *Esmeraldina* and *Palmettaspis*.

Proposed Generic Differences	<i>E. rowei</i> ¹⁶	" <i>P.</i> " <i>consorta</i> ¹⁷
shape of glabella (width of LA / width of L0)	1.32	1.26
length of anterior lobe (sag. length LA / sag. length cephalon)	0.29	0.31
inclination of ocular lobes (exsag. length lobe / trans. distance from outer edge of lobe to point where ocular ridge contacts glabella)	2.58	2.42

Fritz (1995) reevaluated Walcott's syntypes of the type species, *E. rowei* (Walcott, 1910b, pl. 29, figs. 1-11), and recognized among them two species, in addition to *E. rowei*, that he assigned to a new genus, *Palmettaspis*. These species were named *P. consorta* (type species) and *P. parallela*. While the split into three separate species can be supported, the features that Fritz used to differentiate the two genera are not distinct. Fritz (1995, p. 718) cited the following features as distinguishing *Palmettaspis* from *Esmeraldina*: narrower, more parallel-sided glabella, longer LA, more steeply inclined ocular lobes, more poorly defined cephalic borders and occipital spines that emanate from a ridge on L0. To evaluate these proposed differences, the first three features are quantified using measurements on the type specimens for the type species of each genus (Table 12). A comparison of the ratios shows that the values differ by less than 8%, a number that is not statistically significant. The last two listed differences are difficult to quantify, but in the illustrations provided by Fritz, there is no appreciable difference in the depth of the border furrows between the two species. Also one specimen of *E. rowei* (Fritz, 1995, pl. 7, fig. 3) appears to show the occipital spine emanating from a ridge; a character that Fritz claimed was characteristic only of *Palmettaspis*. In summary, none of the differences cited by Fritz can be used to support a generic level separation of *Palmettaspis* from *Esmeraldina*.

The generic assignment of *Palmettaspis parallela* Fritz, 1995 is uncertain. It has a more parallel-sided glabella than any other species of *Esmeraldina*, and relatively wider extraocular/narrower interocular areas than most holmiids. While it does have the other features diagnosed for *Esmeraldina*, a questionably assigned partial thorax (Fritz, 1995, fig. 9.5) appears to have a large axial spine on T12, unusual for holmiids (and for the Olenellina in general). *Esmeraldina? cometes*

¹⁶ lectotype USNM 56801c, Fritz, 1995, pl. 6, fig. 6

¹⁷ holotype USNM 476024, Fritz, 1995, pl. 8, fig. 4

Fritz, 1995 also has unusually wide extraocular/narrow interocular areas and may be more closely related to "*P.* *parallela*."

Resser and Howell (1938) placed *Holmia?* *macer* Walcott, 1913 and *Wanneria occidentens* Walcott, 1913 in *Esmeraldina*. Fritz (1973) reassigned the former to *Wanneria*, and the latter became the type for *Mummaspis* (Fritz, 1992). Both lack the narrow ocular lobes with shallow mid-ocular lobe furrows and the long, thick genal spines characteristic of *Esmeraldina*. In addition, both show an expanded L3 uncharacteristic of *Esmeraldina*. These re-assignments are discussed further under their respective genera. Shaw (1962) assigned *Olenellus hermani* Kindle and Tasch, 1948 to *Esmeraldina*. This species with a highly inflated LA is better assigned to *Bolbolenellus* Palmer and Repina (1993).

Esmeraldina is found in south-central Esmeralda County, Nevada, where it occurs in the Montenegro Member of the Campito Formation and the lower Poleta Formation. Outside of this area, the only reported occurrence of this genus is from the Cassiar Mountains of British Columbia (*Esmeraldina* sp. 1 Fritz, 1995).

Esmeraldina argenta (Walcott, 1910b)

Pl. 5, figs. 6-9; Text-fig. 36

1910b *Olenellus?* *argenteus* Walcott, p. 314-315, pl. 40, figs. 12,13,15,16. [non] fig. 14.

1931 *Mesonacis argenteus*, Bell, p. 12, 18, 20.

1956 *Olenellus argenteus*, Harrington, p. 56.

1957 *Esmeraldina?* *argenteus*, Raw, p. 170

1959 *Esmeraldina argenta*, Best (unpublished thesis), p. 182-184, pl. 9, figs. 10-12.

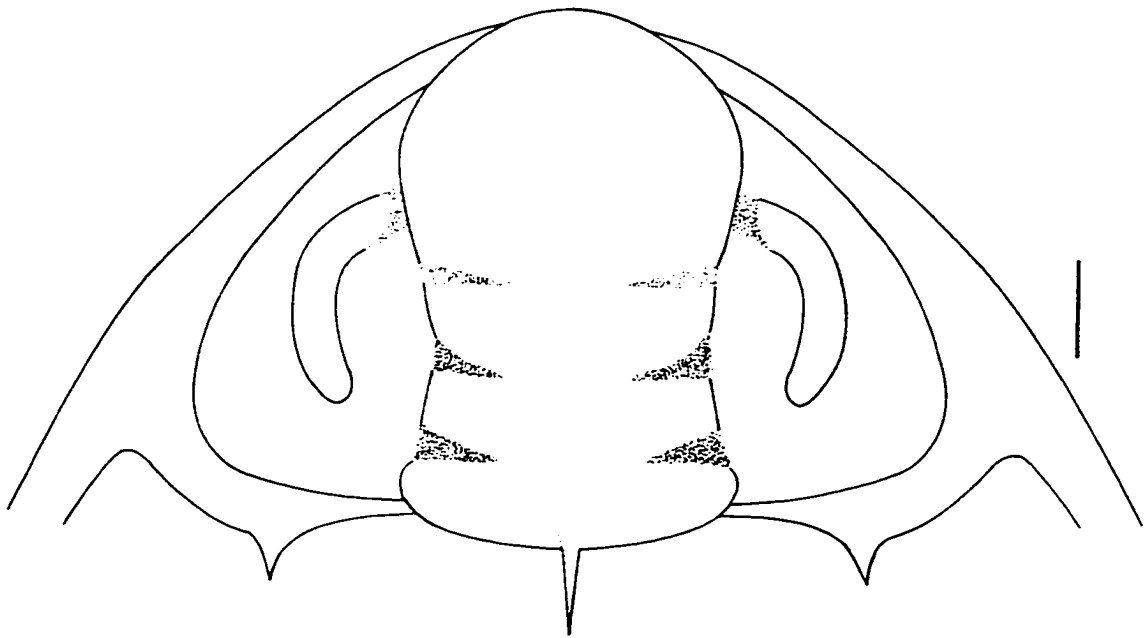
1962 *Esmeraldina argenta*, Shaw, p. 333.

1972 *Holmia?* *argenta*, Fritz, p. 12-13, 25.

1974 *Holmia argenta*, Poulsen, p. 87.

1991a *Holmia?* *argenteus*, Fritz, p. 15.

Diagnosis: A species of *Esmeraldina* with L3-LA highly inflated and S3 effaced. Ocular lobes short; tips opposite anterior part of L1. Ocular ridges effaced. Interocular areas swollen. Intergenital spines located closer to glabella than to genal spines. Base of genal spines opposite of S1. Prosopon of fine tubercles.



Text-fig. 36. *Esmeraldina argenta* (Walcott). scale bar = 1 mm

Lectotype: A complete cephalon (USNM 56812d; Walcott, 1910b, pl. 40, fig. 15) designated by Harrington (1956, p. 56). From unit 3 of Walcott's Barrel Spring Section (1908, p. 189, which is interpreted herein to be the lower Poleta Formation), 16 km south of Silver Peak, Silver Peak Range, Esmeralda County, Nevada. **Paralectotypes:** USNM 56812a,b,e.

Occurrences: NEVADA. Esmeralda County, lower Poleta Formation: Barrel Spring Section (Walcott, 1908, p. 189; 1910b), 16 km south of Silver Peak, Silver Peak Range; locality 18, 7.5 km northwest of Goldfield, Montezuma Range; section GP, Mt. Dunfee area, 7 km east of Gold Point.

Zonal Biostratigraphy: *Nevadella parvoconica* Subzone, *Nevadella* Zone.

Discussion: Based on its occurrence in the lower Poleta Formation, *Esmeraldina argenta* is the youngest known species of *Esmeraldina*. All other described species are from the underlying Montenegro Member of the Campito Formation. A unique feature of *E. argenta* is its enlarged LA, which is highly convex compared to the rest of the glabella, and the effaced S3. *E. argenta* can also be distinguished from all other species by the shortness of its ocular lobes. It shares granular prosopon with *E. rowei* and *Esmeraldina* sp. 1 (of Fritz, 1995). No ontogenetic material was found for this species.

Family Wanneriidae Hupé, 1953a
(*nom. transl.* herein, *ex* Wanneriinae Hupé, 1953a)

Diagnosis: A family of Olenelloidea with glabella slightly to strongly clavate: slightly constricted at S1. LA large, wider than long. S2 curved, marginal. Ocular lobes located close to glabella: extraocular areas wider than interocular areas. Mid-ocular lobe furrow deep. Intergenal position generally far from genal spines. Genal spines long, falcate. Rostral plate robust, wide. T3 normal to macropleural and macrospinous. T15 usually with long axial spine. Prosopon reticulate (at least in part). Early meraspid cephalon with short intergenal spines; spines cross posterior border medial to ocular lobe positions. Meraspid LA short and wide, drapes ocular ridges. Preglabellar field present in meraspid, shortens through ontogeny.

Assigned Genera: *Wanneria* Walcott, 1910b; *Elliptocephala* Emmons, 1844; *Laudonia* Harrington, 1956; *Mummaspis* Fritz, 1992; *Gabriellus* Fritz, 1992; *Mesolenellus* Palmer and Repina, 1993 (= *Angustolenellus* Palmer and Repina, 1993); ?*Wannerellus* n. gen.

Discussion: The Wanneriidae have been misunderstood by previous authors who failed to recognize paedomorphic and homeomorphic taxa. The family is united by and distinguished from the Olenellidae by its unique ontogenetic pattern. The distinctiveness of its ontogeny indicates that it warrants familial status. The Wanneriinae, as originally defined by Hupé (1953a,b), included the genera *Wanneria* and *Esmeraldina*. Most subsequent authors synonymized *Esmeraldina* with *Holmia* (see discussion under *Esmeraldina*) which left the wanneriids as a monotypic subfamily of the Olenellidae (Poulsen *in* Moore, 1959; Repina, 1979; Palmer and Repina, 1993). Alternative arrangements were given by Chernysheva (1960) who included *Wanneria* in the Olenellinae, and Bergström (1973a) who collapsed Hupé's (1953a) subfamilies Wanneriinae, Holmiinae and Elliptocephalinae into a single taxon, the Holmiidae. Ahlberg *et al.* (1986, p. 40) recognized that *Wanneria* was distinct from the Olenellinae based on "the glabellar and palpebral configuration and in the course of the pleural furrows", and that it "should definitely be placed in a discrete subfamily, if not a different family". They further recognized the similarities between *Wanneria* and *Elliptocephala* in hypostome morphology and prosopon, and suggested that the two genera "could be placed in the same family of somewhat holmiid-like trilobites" (p. 40), to which they also tentatively assigned *Holmiella* and *Esmeraldina*. (The latter two are holmiids based on the position of the ocular lobes on the cephalon as well as other features). In this study, *Elliptocephala*, *Laudonia* and *Mummaspis* are included with *Wanneria* in the Wanneriidae based primarily on shared ontogenetic pattern and supplemented by holaspid characters (see diagnosis). The history of classification of each genus is discussed under the respective genera.

The ontogenetic pattern of wanneriids is their prime uniting feature, especially the development of LA as a wide, short lobe early in ontogeny (Text-fig. 24). The intergenal spines are more medially located on the posterior border in the meraspid stage of the Wanneriidae than in the Olenellidae. In the holaspid, S2 is always marginal: it may be deepest medially, but it always continues to the axial margin as at least a shallow furrow. S2 is usually broadly curved, concave posteriorly. All wanneriids have prosopon that is reticulate, at least in part, but this is not a unique feature to this particular family. Kiaer (1916) recorded the prosopon of *Holmia kjerulfi* to be smooth to finely reticulate. A single species of nevadiid, *Nevadella bacculenta* Fritz, 1972 has a partially reticulate prosopon. Some fallotaspidoids, such as *Lenallina lata* Repina, 1990 and *Bradyfallotaspis repinae* n. sp., are also reticulate. The possession of a reticulate prosopon in some species of these older Olenellina may indicate that reticulation is a primitive feature that is particularly well-developed in wanneriids. It is a useful character to distinguish between the Wanneriidae and Olenellidae as the latter never have reticulate prosopon. Development of a

macropleural T3 is variable in the wanneriids: *Wanneria* has a normal T3 throughout its ontogeny; *Laudonia* and *Mummaspis* have a macropleural T3 at all stages of development; *Elliptocephala* has a macropleural T3 in the meraspid that decreases in size through ontogeny. In *E. asaphoides*, large holaspids have regular T3, while in other species of *Elliptocephala* the T3 of the large holaspids is macropleural, but not as strongly macropleural as in the smaller stages. A key point to note is that a macropleural T3 is not a feature exclusive to the Olenellidae (Olenellinae of other authors): it is also seen in the Fallotaspididae, the oldest members of the Olenellina, and therefore may be a primitive feature for the suborder.

The closest relatives of the Wanneriidae may possibly be found in the Holmiidae. Bergström (1973a) and Ahlberg *et al.* (1986) discuss this possible relationship. Illustrations in Kiaer (1916) hint at similarities in ontogeny between *Holmia kjerulfi* (type species of *Holmia*) and wanneriids (note that Kiaer's illustrations are retouched and should be used advisedly). Hypostome morphology in the two families is also broadly similar but where the posterolateral margin is multidenticulate in *Wanneria walcottana*, it is paucidentate with a scalloped margin in *Holmia kjerulfi*. From the available illustrations, it is impossible to resolve whether or not these features are directly comparable with those seen in wanneriids. Bergström (1973a) included *Wanneria* and *Elliptocephala* in the Holmiidae on the basis that they are difficult to delimit from *Holmia*. *Holmia* is very similar to the wanneriids in its glabellar features, deep mid-ocular lobe furrows and reticulate prosopon. It is uncertain whether these similarities are convergent or phylogenetic. One possibly fundamental difference between holmiids and wanneriids proposed by Palmer and Repina (1993, p. 8) is the position of the ocular lobes on the cephalon: near the glabella in the wanneriids (wide extraocular/narrow interocular areas) and far from the glabella in the holmiids (narrow extraocular/wide interocular areas). Ocular lobes far from the glabella is the primitive condition (based on ontogeny and outgroup comparison, i.e. Fallotaspididae), but whether it is primitive or pedomorphic in holmiids is unclear. Further study of the non-Laurentian holmiids is needed.

Genus *Wanneria* Walcott, 1910b

Type Species: *Olenellus (Holmia) walcottanus* Wanner, 1901, from the Kinzers Formation, 3 km northwest of York, Pennsylvania. (by original designation) Junior synonym: *Holmia? macer* Walcott, 1913.

Diagnosis: A genus of Wanneriidae with glabella strongly clavate. Cephalic border width moderate to wide. Anterior border narrows in front of LA. Cephalic border furrow pitted.

Preglabellar field short in small holaspid stage. LA subelliptical (trans.). Ocular lobes strongly curved; approximately equal in width to width interocular area. Intergenal ridges poorly developed. Intergenal spines absent; posterior cephalic border thickened lateral to intergenal position. Genal spines not advanced; base opposite of T1 or posteriormost portion of L0. Hypostome conterminant in large holaspids: posterior margin concave, expanded posterolaterally and delimited by a posterolateral furrow. Inner margin of rostral plate pitted. Rostrum extends to posterior margin and curves medially. T3 normal throughout ontogeny. Thorax wide with long, broad, falcate spines. Pygidium a broad, bifurcate plate. Prosopon reticulate, or reticulate with terrace lines in places. Meraspid cephalon with curved anterior margin, no procranial spines.

Other Species:

Olenellus logani Walcott, 1910b; Forteau Fm., Labrador, NFL (?= *Olenellus? claytoni* Walcott, 1910b; ?Poleta Fm., Silver Peak, Nevada. = *Wanneria nathorsti* Poulsen, 1932 and *W. ellae* Poulsen, 1932; Ella Island Fm., Ella Isl., Greenland).

[?] *Wanneria walcottana buelnaensis* Lochman, 1952, Buelna Fm., NW Sonora, Mexico.

Wanneria mediocris Poulsen, 1958 (= *W. ruginosa* Poulsen, 1958; = *W. subglabra* Poulsen, 1958); Wulff River Fm., Inglefield Land, Greenland.

Olenellus austinvillensis Resser, 1938; Shady Fm., Austinville, Virginia.

Wanneria parvifrons Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

[?] *Olenellus* sp. 3 Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

[?] *Olenellus* sp. 4 Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

Wanneria sp. 1 Fritz, 1992; Illtyd Formation, Wernecke Mtns., Yukon.

Olenellus sp. 2 Fritz, 1992; Illtyd Formation, Wernecke Mtns., Yukon.

Wanneria dunnae n. sp.; Eager Fm. East Kootenay Region, BC.

Wanneria watsonensis n. sp.; Eager Fm. East Kootenay Region, BC.

Discussion: *Wanneria* is the type genus for the Wanneriidae and, as such, the history of its systematic position has been discussed under the family. It is characterized by a wide cephalon, long glabella, a large, subelliptical LA, genal spines that are not advanced, no intergenal spines in the large holaspids, and a T3 that is not macropleural at any stage of development. Two poorly known species, *Wanneria* sp. 1 Fritz, 1992 and *W. walcottana buelnaensis* Lochman, 1952, have advanced genal spines, but in general, unadvanced genal spines are characteristic of *Wanneria*. The ontogenetic development is described in detail for *Wanneria dunnae* n. sp.

The ventral morphology and thoracic structure are well-known and very similar for both *Wanneria walcottana* and *W. dunnae* and likely characterize the genus. The body is wide with long, broad falcate spines. The axial spine on T15 is well developed. Both have the hypostome attached directly to the rostral plate, in large holaspids, via the hypostomal suture. It is inferred from the absence in large collections of any small hypostomes attached to a rostral plate and the longer preglabellar field of small specimens that meraspids and small holaspids have natant hypostomes. The rostral plate is a broad, crescentic plate that extends to the posterior cephalic margin and curves medially a short ways. The inner edge of the rostral plate has a series of marginal pits. Corresponding pits are visible in the border furrow on the dorsal surface of *W. dunnae*, but they are usually only preserved in limestone material. Similar pits have not been observed in the border furrow of *W. walcottana*, which is known only from shale material. These rostral pits are probably typical for the genus as they have been recorded by Fritz (1972) for *W. logani* and *W. parvifrons*, and by Poulsen (1958) for *W. mediocris*. In all known *Wanneria* hypostomes, the posterolateral margin is expanded and usually delimited by a furrow (this furrow is not visible in species such as *W. dunnae* in which the dorsal furrows are effaced).

When he erected *Wanneria*, Walcott (1910b) assigned three species to this genus: *W. walcottana* (type species), *W. halli* Walcott, 1910b and *W.? gracile* Walcott, 1910b. Poulsen (1932, p. 41) noted that "the genotype differs highly from the other species referred to *Wanneria* by Walcott; these species evidently belong to other genera". *W. halli* was designated the type species of *Fremontella* by Harrington (1956), and distinguished from *Wanneria* on the basis of the shape and segmentation of the glabella. This re-assignment is supported here because *W. halli* has an ontogeny similar to the *Mesonacis* (Olenellidae), instead of a wanneriid pattern of development (see further discussion under *Fremontella*). Assignment of *W.? gracile* is a more complex problem as Walcott (1910b, pl. 38, figs. 15-24) illustrated material from four different localities and five species can be recognized in his material: figs. 15, 16 [= *Nevadella parvoconica*]; figs. 17-20; [= *Elliptocephala truemani*?]; fig. 21. [= *Nevadia palmeri*?]; fig. 23 [= *Cirquella nummularia*]. All of these species and Walcott's specimens are discussed under the appropriate species. The lectotype (selected herein, fig. 22: topotype fig. 24) is assigned to *Nevadella gracile* with details provided under a redescription of that species. Only one of the species that can be recognized in this material is a wanneriid: it has reticulate prosopon and a short, wide LA and is assigned to *Elliptocephala truemani*? (see discussion under that species).

Olenellus lundgreni Moberg, 1892 from Sweden is a problematic species that has been assigned to *Holmia* (by Moberg, 1899; Walcott, 1910b), *Kjerulfia*? (by Kiaer, 1916), *Wanneria* and *Holmia* (by Poulsen, 1969, who split Moberg's type material between the two genera) and *Wanneria*? (by

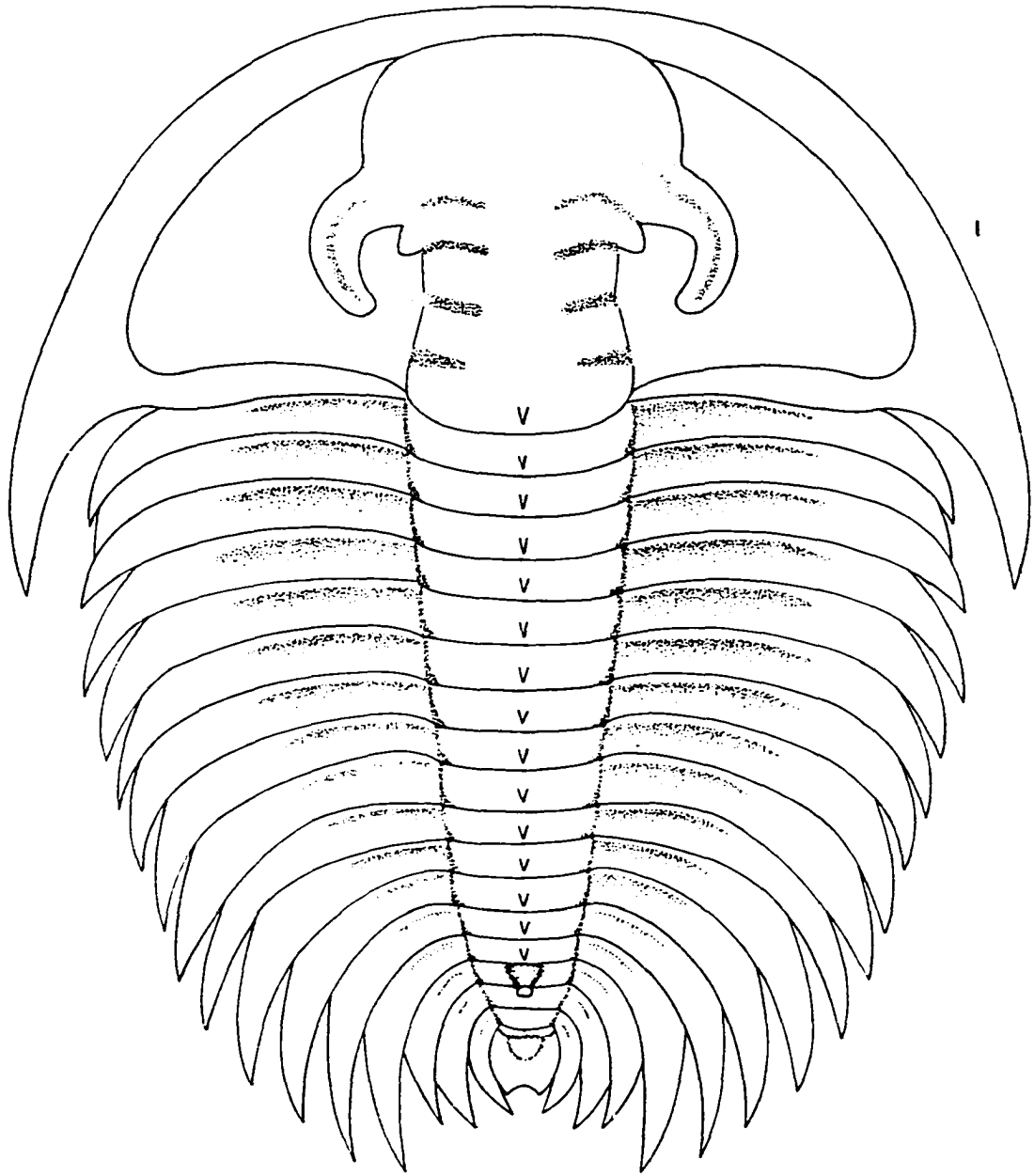
Bergström, 1973a, who assigned it tentatively to *Wanneria*, but found it at least equally similar to *Elliptocephala*). While "*Olenellus*" *lundgreni* has a glabella of wanneriid configuration, unadvanced genal spines and no intergenal spines (like *Wanneria*), it also has narrow extraocular areas and a paucidentate hypostome, that are not seen in wanneriids, but are characteristic of holmiids. "*Olenellus*" *lundgreni* is herein considered a holmiid of questionable generic assignment. *Wanneri?* *pennapyga* Raw, 1936 from Shropshire, Britain was based on a single bifurcate pygidium. This pygidium is long and slender, unlike the broad, subquadrate pygidium of *Wanneria*, and is assigned to the neltneriid *Judomia* which has an elongate, bifurcate pygidium.

Poulsen (1958) described a number of species of *Wanneria* and some problematic forms from the Wulff River Formation of northwest Greenland, but oversplit the species of *Wanneria*: *W. ruginosa* and *W. subglabra* represent intermediate and small holaspid forms respectively of *W. mediocris*, all from the same locality. *W. inermis* Poulsen, 1958 and *W. abnormis* Poulsen, 1958 both have highly inflated LA's and based on their narrow extraocular areas, may represent a new genus of holmiid. *Holmia mirabilis* Poulsen, 1958 was regarded as possibly belonging to *Wanneria* by Bergström (1973a, p. 287). This assignment is regarded as unlikely since "*Holmia*" *mirabilis* has wide extraocular and narrow interocular areas. Fragments described as *Olenellus?* *curvicornis* Poulsen, 1932 from east Greenland may represent the same species. At least some of the Wulff River material is likely to be holmiid as it includes an unassigned quadratodenticulate hypostome similar to that of *Holmia kjerulfi*.

Wanneria walcottana (Wanner, 1901)

Pl. 5, figs. 1-5; Text-fig. 37

- 1901 *Olenellus* (*Holmia*) *walcottanus* Wanner, 1901, p. 267-269, pl. 31, figs 1,2, pl. 32, figs 1-4.
- 1910b *Wanneria walcottanus*, Walcott, p. 302-304, pl. 30, figs. 1-12, pl. 31, figs. 12,13.
- 1913 *Holmia?* *macer* Walcott, p. 313, pl. 54, fig. 1.
- 1916a *Wanneria walcottana*, Walcott, p. 219-220, pl. 38, figs. 1,2.
- 1931 *Wanneria walcottanus*, Bell, p. 2, 4.
- 1932 *Wanneria walcottana*, Poulsen, p. 41,43.
- 1938 *Wanneria walcottana*, Resser and Howell, p. 228, pl. 9, figs. 9,10; pl. 10, figs. 8-10; pl. 11.
- 1938 *Esmeraldina macer*, Resser and Howell, p. 229, pl. 8, figs. 10-12.
- 1952 [non] *Wanneria walcottana*, Best, p. 15 [= *W. dunnae* n. sp.]
- 1952 *Wanneria walcottanus*, Tasch, text-fig. 1h.
- 1956 *Wanneria walcottana*, Harrington, p. 58.
- 1958 *Wanneria walcottana*, Poulsen, p. 16.



Text-fig. 37. *Wanneria walcottana* (Wanner). scale bar = 1 mm

- 1959 *Wanneria walcottana*, Poulsen, in Harrington, p. O197, text-fig. 139.
- 1959 *Wanneria walcottana*, Best [unpublished thesis], p. 153-155, pl. 6, figs. 1-4, 8-10.
- 1959 *Wanneria macer*, Best, p. 158, pl. 6, fig. 11.
- 1973a *Wanneria walcottana*, Bergström, p. 286, 307-309.
- 1964 [non] *Wanneria* cf. *walcottana*, Palmer, p. 4, pl. 1, figs. 11-13, 15. [= *W. logani*?]
- 1989 *Wanneria walcottanus*, Whittington, p. 125-127, pl. 4, fig. 24; fig. 28; pl. 5, figs. 30, 32, 33; pl. 6, figs. 35-38.
- 1993 *Wanneria walcottana*, Palmer and Repina, p. 8, fig. 5.

Diagnosis: A species of *Wanneria* with tips of ocular lobes opposite anterior of L1. Cephalic border wide: width subequal to length L0. Preglabellar field absent. Median occipital spine short. Hypostome with five small, posterolateral marginal spines. Prosopon reticulate over entire dorsal surface. Thorax of 17 segments. Short median axial spines on T1-T14. Pygidium subquadrate, bifurcate.

Lectotype: A complete specimen (USNM 56807a¹⁸; Wanner, 1901, pl. 31, fig. 1) designated by Resser and Howell (1938, p. 228, pl. 10, fig. 9), from the Kinzers Formation, 3 km northwest of York, Pennsylvania. Paralectotypes: USNM 56807e,f,g,m.

Occurrences: PENNSYLVANIA. Kinzers Formation, York County: 3 km northwest of York; 3 km north of Lancaster; near Fruitville; 1.5 km north of Rohrerstown (Walcott, 1910b, p. 304); 0.8 km south of East Petersburg (Resser and Howell, 1938, p. 209).

Discussion: *Wanneria walcottana* is well-known from large, articulated shale specimens with associated hypostomes and rostral plates. It has short ocular lobes and its entire dorsal surface is covered by reticulate prosopon. It compares closely in general body outline with the effaced species, *W. dunnae* n. sp. (see discussion of *W. dunnae* for comparison). Bergström (1973a, p. 286, 307) emphasized a pitted cephalic border furrow as being characteristic of *W. walcottana*. He was possibly referring to a "cast of the underside of the genal spine and the doublure" illustrated by Walcott (1910b, pl. 30, fig. 9). There are a series of bumps beneath where the cephalic border furrow would be that may correspond to pits on the dorsal surface. No specimens of this species illustrated show actual pits in the border furrow. This may be due in part to preservation: well-preserved specimens in limestone of *W. dunnae* have pits in the border furrow that are not visible

¹⁸ The number of the specimen designated as the type is 56807a, not 56807e as listed by Resser and Howell (1938) and by Palmer and Repina (1993, p. 25).

on shale specimens. As discussed under the genus, border pits appear to be a feature of the *Wanneria* but their presence cannot be conclusively demonstrated in the type species.

The species concept of *Wanneria walcottana* has centered on large, highly compacted shale specimens. Walcott (1910b, pl. 30, figs. 3,4) illustrated two small holaspid cephalons from the type locality (Pl. 5, figs. 1, 3), but these specimens were re-assigned to *Holmia? macer* Walcott, 1913 by Resser and Howell (1938), without comment. These specimens have proportionately longer ocular lobes than the type, but since ocular lobe length decreases during ontogeny, as Walcott (1910b, p. 296) himself observed, this is not a valid criterion on which to exclude these specimens from *W. walcottana*. The holotype of *Holmia? macer* Walcott 1913 (also discussed under *Esmeraldina*) is a small, articulated specimen from Pennsylvania, near the type locality of *W. walcottana*. Walcott (1913) emphasized the proportionately large cephalon and narrow thorax of this species, but these are normal features of small holaspids of *Wanneria* (see section on ontogeny of *W. dunnae*). Palmer (1964) suggested that *Holmia? macer* may be conspecific with *W. walcottana* and should not be excluded from *W. walcottana* based on its small size or proportionately longer ocular lobes when the overall specimen size is smaller. *Holmia? macer* is here synonymized with *W. walcottanus* on the basis that it was defined using juvenile features of *W. walcottana*.

Palmer (1964) assigned a handful of small fragmentary specimens from the Saline Valley Formation, near Gold Point, Nevada to *Wanneria cf. walcottana*. The material represents small holaspids in limestone and is difficult to compare to the large holaspids in shale that are known best for *W. walcottana*. Two small holaspid cephalons are known for the latter, but they lack prosopon. The Saline Valley specimens have a proportionately narrower LA and slightly advanced genal spines compared to the small specimens of *W. walcottana* and are considered to perhaps belong to *W. logani*.

Lochman (1952) described a new subspecies, *W. walcottana buelnaensis*, from the Buelna Formation, Mexico. The fragmentary material has strongly advanced genal spines, different from the type and all other species of *Wanneria*. Harrington (1956) assigned this species to *Fremontia*, however, it is a wanneriid based on its prosopon, deep mid-ocular lobe furrows and marginal, curved S2. *W.? buelnaensis* (Lochman) has well-defined border pits and ocular lobes opposite of L1. Small specimens described as *Olenellus truemani* by Hu (1971) are likely referable to this species (see also discussion under *Elliptocephala truemani*).

The ending of the specific portion of *Wanneria walcottana* has been variously cited. Wanner (1901) named the species in honour of C.D. Walcott, but chose to use an adjectival rather than genitive ending. This is acceptable under the Zoological Code (1985, Appendix D, Section IIIa) and as an adjectival ending must agree with the gender of the genus if the species is re-assigned. Therefore *Wanneria walcottana* is the correct form of the name.

Wanneria logani (Walcott, 1910b)

Pl. 6, figs. 1-9

- 1910b *Olenellus logani* Walcott, p. 333-335, pl. 41, figs. 5,6.
 1910b [?] *Olenellus claytoni* Walcott, p. 319-320, pl. 40, figs. 9-11.
 1925 *Olenellus logani*, Dunbar, p. 307.
 1931 *Olenellus logani*, Bell, p. 20.
 1932 *Wanneria nathorsti* Poulsen, p. 40-41, pl. 12, figs. 1-13
 1932 *Wanneria ellae* Poulsen, p. 41-43, pl. 13, figs. 1-9.
 1958 *Wanneria logani*, Poulsen, 1958, p. 16.
 1959 *Wanneria logani*, Best [unpublished thesis], p. 160-161, pl. 7, figs. 1-8.
 1964 [?] *Wanneria* cf. *walcottana*, Palmer, p. 4, pl. 1, figs. 11-13, 15.
 1972 *Wanneria logani*, Fritz, p. 29-30, pl. 14, figs. 1-14; pl. 16, figs. 1-7.
 1991a *Wanneria logani*, Fritz, p. 17-18, pl. 3, figs. 16,17.

Diagnosis: A species of *Wanneria* with posterior tips of ocular lobes opposite of S0. Cephalic border moderately wide: width more than half length of L0. Preglabellar field short to absent. Anterior cephalic border shortens slightly anterior to glabella in large holaspids. Posterior occipital spine short. Hypostome with five pairs small, posterolateral, marginal spines. Prosopon reticulate over posterior glabella, interocular areas, posterior extraocular areas; terrace lines over anterior glabella, middle to anterior extraocular areas.

Lectotype: (selected here) A nearly complete cephalon, (GSC 414b; Walcott, 1910b, pl. 41, fig. 5; Pl. 6, figs. 3, 6 herein), from the Forteau Formation, L'Anse au Loup, Labrador, NFL.

Paralectotype: GSC 414

Occurrences: NEWFOUNDLAND. Forteau Formation, L'Anse au Loup, Labrador (Walcott, 1910b, p. 335). NORTHWEST TERRITORIES. Sekwi Formation, Mackenzie Mountains (Fritz, 1972). YUKON TERRITORY. Illtyd Formation, Wernecke Mountains (Fritz, 1991a). BRITISH COLUMBIA. Eager Formation: section RC4, 13 km northeast of Skookumchuck; sections MG1

and MG2, Mt. Watson, 7 km east-southeast of Canal Flats. ?NEVADA. Saline Valley Formation, Esmeralda County: USGS colln. 37480-CO (Palmer, 1964), 7 km east of Gold Point, Mt. Dunfee area; ?Poleta Formation, Unit 6, Barrel Spring Section (Walcott, 1908, p. 189; 1910b, p. 320), 16 km south of Silver Peak, Silver Peak Range, Esmeralda County.

Zonal Biostratigraphy: *Wanneria logani* to *Wanneria dunnae* subzones, *Olenellus transitans* Zone.

Discussion: The lectotype of *Olenellus logani* Walcott (1910b, pl. 41, figs. 5,6) is reillustrated here (Pl. 6, figs. 3, 6). The prosopon of both reticulation and terrace lines is distinctive for this species. The anterior border narrows only in specimens over 1 cm in length where LA is almost in contact with the border. No cephalic border pits are obvious. Material from the Sekwi Formation (Fritz, 1972) differs slightly in that even small specimens show a shortening of the anterior border compared to the lateral border width. Fritz (1972) also records an occipital tubercle (not obvious in his photographs) and cephalic border pits as being present. The new material from British Columbia agrees more closely with the type material in that it lacks cephalic border pits and an anterior border that shortens early in the holaspid stage. The only difference between the type material and that from British Columbia is that the latter shows interocular swellings of unknown significance on some specimens. Material from the Illtyd Formation (Fritz, 1991a) is too fragmentary for detailed comparison with the type material. It has the typical prosopon and ocular lobe length of *W. logani*. The hypostome illustrated in Fritz (1972, pl. 14, fig. 14) is small and does not clearly show the features of the genus. A large hypostome from British Columbia (Pl. 6, fig. 5) shows the typical expanded posterolateral margin and concave posterior margin of *Wanneria* with a well-developed posterolateral furrow. There are five, small posterolateral spines; the same number as in *W. walcottana*. Smaller hypostomes have at least six spines and show the strong convexity of the anterior body and anterior wings. A pygidium tentatively assigned to this species (Pl. 6, fig. 9) is subquadrate with a bifurcate posterior margin, also closely comparable to *W. walcottana*. *W. logani* differs from the type species in ocular lobe length, prosopon and position of the occipital tubercle. Some of these differences may be size related (*W. logani* is from limestone material and of relatively small size; *W. walcottana* from shale material and of relatively large size). Small holaspids of *W. walcottana* have ocular lobes of the same length as *W. logani*, but the prosopon of these specimens is unknown. Until better small material of *W. walcottana* or larger specimens of *W. logani* are known, the two species are recognized as separate.

Wanneria nathorsti Poulsen, 1932 from eastern Greenland was synonymized by Fritz (1972, p. 29) with *W. logani*. The holotype of *W. nathorsti* is closely comparable to the lectotype of *W. logani*. It

is, however, a small holaspid and slightly larger specimens have shorter ocular lobes and a completely reticulate prosopon: each polygon on the posterior glabella and extraocular areas has a small central tubercle. These are mainly features typical of *W. walcottana* which further suggests that *W. logani* and *W. walcottana* may be synonymous. *W. ellae* Poulsen, 1932 is from the same locality as Poulsen's *W. nathorsti* material and although poorly preserved, is conspecific. Hypostomes are illustrated with this material including a large specimen with seven posterolateral spines. Both *W. nathorsti* and *W. ellae* are here considered junior synonyms of *W. logani*.

Palmer (1964) assigned a handful of small fragmentary specimens from the Saline Valley Formation, near Gold Point, Nevada to *Wanneria* cf. *walcottana*. Additional material of that species is illustrated herein (Pl. 6, fig. 4). These specimens are also small holaspids and species identification is difficult. In glabellar proportions, particularly the size and shape of LA, it is identical to *W. logani*, not to *W. walcottana* which appears to have an unusually wide LA in the small holaspid stage¹⁹. The Saline Valley specimens are similar to those of a similar size of *W. logani* illustrated by Fritz (1972, pl. 14, fig.4), except in having slightly advanced genal spines. In the absence of large holaspids, these specimens are tentatively assigned to *W. logani*.

Walcott (1910b, pl. 40, figs. 9-11) illustrated two specimens as *Olenellus? claytoni* from Unit 6 of the Barrel Spring Section (Walcott, 1908, p. 189), ?Poleta Formation, that are tentatively synonymized with *Wanneria logani*. These specimens are preserved as flattened internal molds in shale. There are no observable features that are different between these specimens and the types of *W. logani*. The stratigraphic horizon is questionable as Walcott (1910b, p. 320) reported that the fossils occur above a mass of andesite suggesting that the stratigraphy is discontinuous. Fritz (1995) reported that this section is structurally complex and judging from Walcott's faunal list, the top part (unit 12 with occurrences of *Nevadia weeksi* and *Holmia rowei*) belongs stratigraphically below unit 3 in the faunal succession. This is important as *Wanneria* has not been observed in any other Poleta strata, rather it occurs in the Saline Valley Formation near Gold Point, stratigraphically far above the Poleta.

Ontogeny: The early development of *Wanneria logani* is only partly known with the best material illustrated by Fritz (1972, pl. 14, figs. 1-4). It is more comparable to the meraspid illustrated for

¹⁹ Preservation may also be a difference in this apparent feature. Due to compaction, shale specimens of *Wanneria dunnae* have a significantly wider LA compared to limestone material of the same species.

W. watsonensis, than to the ontogenetic sequence of *W. dunnae*. A comparative description to the latter follows.

Clique C meraspids are the smallest known for this species. The glabella is not constricted and all furrows are marginal. LA is wide and short. The preglabellar field is moderately long and the genal spines are not advanced. (Fritz, 1972, pl. 14, fig. 1)

Clique D specimens show the first hint of modification of the parallel-sided glabellar stalk: there is a slight constriction at S1 and the furrows are inclined slightly. LA is wide and short. The preglabellar field is moderately short. (Fritz, 1972, pl. 14, fig. 3)

Clique E specimens have a distinct constriction at S1 and a slight modification of L3. LA is wide and moderately short. The preglabellar field is moderately short. Ocular lobes show the earliest indication of mid-ocular lobe furrows. (Fritz, 1972, pl. 14, figs. 2, 4, 5, pl. 16, fig. 1; Pl. 6, figs. 1-2)

Clique F and G specimens are closely comparable to those of *Wanneria dunnae*, except in species-level features. (Pl. 6, figs. 3-4, 6-8).

Wanneria dunnae n. sp.

Pl. 6, figs. 10-18; Pl. 7, figs. 1-8; Pl. 8, figs. 1-2; Text-figs. 26 (top)

1952 *Wanneria walcottana*, Best, p. 15

1959 *Wanneria edentata* Best [unpublished thesis], p. 155-157, pl. 4, figs. 5-13; pl. 5, figs. 1-13
[*nomen nudum*]

1991 *Wanneria walcottana*, Fortey, p.85, unnumbered photograph

Diagnosis: A species of *Wanneria* with tips of ocular lobes opposite anterior of L1. External dorsal furrows effaced. Cephalic border wide: width subequal to length L0. Preglabellar field absent. Anterior border shortens slightly anterior to glabella in large holaspids. Cephalic border furrow pitted. Posterior occipital tubercle tiny. Hypostome with no posterolateral marginal spines. Prosopon finely reticulate over entire dorsal surface. Hypostome with terrace lines on median body, reticulate on posterior body. Thorax of 16 segments. Pygidium subrectangular; posterior margin slightly indented. Glabella strongly constricted in mid-sized meraspids.

Holotype: A complete specimen with associated hypostome and rostral plate (UBC GT507; Pl. 7, fig. 8) from the Eager Formation, locality 5, 6.5 km northeast of Cranbrook, British Columbia.

Paratypes: MG3b#29, MG3b#21, RC4f#4, RBCM EH.997.06.001, UBC GT502

Etymology: After Frances Dunne, an amateur paleontologist from Spillimacheen, British Columbia, who donated a fine collection of specimens of this species to the Geological Survey of Canada.

Occurrences: BRITISH COLUMBIA. Eager Formation: locality 5, 6.5 km northeast of Cranbrook; section RC4, Ram Creek area, 13 km northeast of Skookumchuck; section MG3, Mt. Grainger, 6 km northeast of Canal Flats; section MG2, Mt. Watson, 7 km east-southeast of Canal Flats.

Zonal Biostratigraphy: *Wanneria dunnae* Subzone, *Olenellus transitans* Zone.

Discussion: The most distinctive feature of *Wanneria dunnae* is the effacement of the external furrows of the cephalon: glabellar furrows are shallow and indistinct, no mid-ocular lobe furrow is present and the posterolateral hypostomal furrow is shallow. Effacement does not mean that this trilobite is flat. Limestone material shows that it has considerable relief and the entire cephalon is gently vaulted with swollen ocular lobes and an inflated glabella. Also preserved in the limestone specimens are a series of cephalic border pits that are usually not seen in shale specimens. Specimens from the limestone and shale facies are the same species and differ only in preservational features, such as a more clavate appearance to the glabella and proportionately wider cephalon in shale specimens due to compaction.

In addition to the effacement, *Wanneria dunnae* differs from the type species in having 16 segments instead of 17, a more clavate glabella, no spines on the posterolateral margin of the hypostome as compared to 5 pairs and a more rectangular pygidium with a posterior margin that is only slightly indented as opposed to being subquadrate and strongly bifurcate. The two species are similar in overall body and cephalic outline which can account for the past misidentification of the Cranbrook species by other authors (Best, 1952; Fortey, 1991).

A number of specimens representing molts are present in the illustrated material (Pl. 7, fig. 8; Pl. 8, figs. 1-2). The rostral plate and hypostome were usually shed as a single unit, although the presence of large, isolated hypostomes also in the collections suggests that the hypostomal suture was not fused. From this evidence it can be interpreted that the hypostomal suture was not used to facilitate molting. Many of the molts show the cephalon still articulated to the thorax, with the

hypostome and rostral plate inverted and displaced towards the rear. In the molt scenario, it appears that the marginal suture opened, the trilobite pushed away the hypostome and rostral plate inverting these elements, then crawled forward through the marginal gape, shedding the dorsal exoskeleton as a single unit. A single specimen with the cephalon also inverted and partly covered by the thorax (Pl. 8, fig. 1) shows what may have happened if the trilobite had difficulty freeing itself from its dorsal carapace. It appears that the suture between the cephalon and thorax could also be opened and the cephalic exoskeleton pushed off anteriorly and inverted. The trilobite then crawled forward discarding the thoracic exoskeleton.

Ontogeny: A complete ontogenetic sequence, except for clique A, is known for *Wanneria dunnae*, with specimens from both limestone and shale. Glabellar furrows are effaced in this species and difficult to accurately describe. Articulated specimens are known from shale for cliques C and larger, but the posterior of the thorax is often curled under in small specimens making accurate counts of thoracic segments difficult. Compared to the ontogeny of other species of *Wanneria*, the development of the glabella occurs at an earlier clique. Meraspids of clique C and larger have strongly constricted glabellas, a feature not seen in *Wanneria logani* until clique E.

Clique B meraspids have ocular lobe posterior tips opposite of S1. Extraocular areas slightly narrower than interocular areas. Preglabellar field short. Glabella parallel-sided from L0 to L3. LA short, wide, drapes ocular ridges. Glabellar furrows S1-S3 of shallow, marginal pits; S0 transglabellar. Intergenal spines short, laterally directed, positioned posterior to ocular lobes. Genal spines short, slightly advanced. Cephalon subrectangular in outline, anterior margin of low curvature: approximately 1.6 times wider than long. Prosopon smooth. (Pl. 6, figs. 10-11)

Clique C meraspids have ocular lobe posterior tips opposite of L1 to S1. Extraocular areas are subequal to slightly wider than interocular areas. Preglabellar field short. Glabella clavate, constricted at S1. LA wide, short. Glabellar furrows S1 to S3 marginal, S3 curved, S0 transglabellar. Intergenal spines absent; intergenal position lateral to position of ocular lobes. Genal spines well-developed, moderately long, slightly advanced. Cephalon approximately 1.5 times wider than long, anterior margin of moderate curvature. Thorax of at least 12 segments. (Pl. 6, fig. 12)

Clique D specimens have ocular lobe posterior tips opposite of L1. Extraocular areas wider than interocular areas. Preglabellar field short. Glabella clavate, strongly constricted at S1. LA wide, moderately long. L3 barely modified. Glabellar furrows S1 to S3 marginal, curved, S0 transglabellar. Intergenal position lateral to position of ocular lobes. Genal spines well-

developed, moderately long, slightly to not advanced. Cephalon 1.5 to 2 times as wide as long. Prosopon largely smooth, faint radiating lines on extraocular areas. (Pl. 6, fig. 13)

Clique E specimens have ocular lobe posterior tips opposite of L1. Extraocular areas approximately twice the width of interocular areas. Preglabellar field short to indistinct. Glabella clavate: nearly parallel side posterior to S1, expanding forward anterior to S1. L3 slightly modified. S0 transglabellar, deepest laterally; S1 to S3 marginal. S2 to S3 strongly curved. Intergenal position closer to genal spines than to S0. Genal spines not advanced. Cephalon approximately 1.6 times wider than long. Thorax of 15 segments by 4 mm of cephalic length; 15th axial spine not clearly indicated. (Pl. 6, figs. 14-17)

Clique F holaspids have ocular lobe posterior tips opposite of L1. Extraocular areas at least twice the width of interocular areas. Preglabellar field short to indistinct. Glabella clavate: nearly parallel-sided posterior to S1, expanding forward anterior to S1. L3 modified. S0 transglabellar, deepest laterally. S1 to S3 marginal; S2 to S3 strongly curved. Cephalon approximately 1.7 times wider than long. 15th axial short. Opisthothoracic segments not discernible. Prosopon largely smooth, rare terrace lines on cephalic border. (Pl. 7, figs. 1, 2, 5)

Clique G holaspids have ocular lobe posterior tips opposite of S1 to L2. Extraocular areas more than twice the width of interocular areas. Preglabellar field absent. Glabella clavate: parallel-sided posterior to S1, expanding forward anterior to S1. Glabellar furrows expressed as broad shallow areas. Cephalon almost twice as wide as long. 15th axial spine long, two opisthothoracic segments developed. Prosopon reticulate over total dorsal surface. (Pl. 7, figs. 3, 7-8; Pl. 8, figs. 1-2)

Wanneria watsonensis n. sp.

Pl. 8, figs. 3-5

Diagnosis: A species of *Wanneria* with tips of ocular lobes opposite of L0. Cephalic border moderately wide: width more than half length of L0. Preglabellar field absent. S2 and S3 effaced. Prosopon of terrace lines on extraocular areas.

Holotype: A large partial cephalon (MG1g#3; Pl. 8, fig. 4) from the Eager Formation, section MG1, collection MG1g, Mt. Watson, 7 km east-southeast of Canal Flats, British Columbia.

Paratypes: MG1g#1, MG1g#7

Occurrences: BRITISH COLUMBIA. Eager Formation, section MG1, Mt. Watson , 7 km east-southeast of Canal Flats.

Zonal Biostratigraphy: *Wanneria logani* Subzone, *Olenellus transitans* Zone.

Etymology: For Mt. Watson, on which this species occurs.

Discussion: *Wanneria watsonensis* is known from only a handful of fragmentary specimens from a single horizon on Mt. Watson. It has a moderately wide border comparable to that of *W. logani* (Walcott, 1910b). This species is unique in its long ocular lobes that extend almost to the posterior border and in the effacement of S2 and S3. Effacement is also seen in *W. dunnae* n. sp., where all the glabellar furrows are broad and shallow. The posterolateral furrow of the hypostome in *W. watsonensis* is faint and may also be interpreted as effaced. The single hypostome known is not well-enough preserved to judge whether or not it is spinous. The prosopon is preserved only on a portion of the holotype where terrace lines can be seen on the extraocular areas and lateral border. Similar prosopon can be seen in *W. logani*. A distinct swelling is present in the posterior interocular area of *W. watsonensis*.

Ontogeny: A single meraspid assignable to clique C (Pl. 8, fig. 3) is known for *Wanneria watsonensis*. It is similar to those of clique C of *W. dunnae*, in the size and shape of LA, but differs in having longer ocular lobes (posterior tips opposite of L0), a longer preglabellar field, a parallel-sided glabellar stalk (L0 through L3) with marginal, transverse furrows, tiny intergenal spines located posterior to the ocular lobes and genal spines that are not advanced. In many of these features it is closer to meraspids of *W. logani*.

Genus *Elliptocephala* Emmons, 1844

Type Species: *Elliptocephala asaphoides* Emmons, 1844 from the Greenwich Formation, 1.6 km west of North Greenwich, Washington County, New York. (by monotypy)

Diagnosis: A genus of Wanneriidae with glabella distinctly clavate. Cephalic border width variable. Anterior border usually of equal width to lateral border. Preglabellar field long in small holaspid stage. LA usually short, subpentagonal; narrows anteriorly. Ocular lobes strongly curved. Intergenal ridges distinct. Intergenal spines poorly developed: intergenal position closer to genal spine than to L0. Genal spines not advanced to slightly advanced: opposite of L0 or T1. Hypostome attached in large holaspids. Rostrum terminates anterior of

posterior margin. T3 macropleural and macrospinous through meraspid to early holaspid stages, normal to macrospinous and amplipleural in later holaspid stage. Protopod of caecae on extraocular areas, reticulation on glabella.

Other Species:

Olenellus lapworthi Peach and Horne, 1892; "Furoid" Beds, Allt nan Rìghrean, Scotland.

Olenellus reticulatus Peach, 1894; "Furoid" Beds, Meall a'Ghiubhais, Scotland.

Olenellus truemani Walcott, 1913; Mural Fm., Mt. Robson Area, B.C.

Olenellus svalbardensis Kielan, 1960, Vardepiggen Fm., Spitsbergen.

Olenellus praenuntius Cowie, 1968; Kane Basin Fm., Ellesmere Island.

Olenellus sculptilis Orlowski in Birkenmajer and Orlowski, 1976, Blåstertoppen Dolomite Fm., Spitsbergen.

Olenellus muralensis Fritz, 1992; Mural Fm., Mt. Robson Area, B.C.

Olenellus truncatooculatus Fritz, 1992; Mural Fm., Mt. Robson Area, B.C.

Elliptocephala parentalis n. sp.; Eager Fm., Mt. Watson, B.C.

Elliptocephala nelsoni n. sp.; Poleta Fm., near Gold Point, Esmeralda County, Nevada.

Elliptocephala stewarti n. sp.; Poleta Fm., near Gold Point, Esmeralda County, Nevada.

Discussion: For the over 150 years since its creation, *Elliptocephala*, has remained a monotypic genus based on *E. asaphoides*, from the Taconic Region of New York State. Walcott (1910b, p. 244) viewed *Elliptocephala* as an intermediate stage between *Mesonacis* and *Holmia* in the development of the Olenellina. Hupé (1953a,b) and Poulsen (in Moore, 1959) placed *Elliptocephala* in the Elliptocephalinae, a monotypic subfamily, on equal footing to the Wanneriinae, Olenellinae and Holmiinae. Chernysheva (1960) assigned *Elliptocephala* to the Olenellidae without comment. Bergström (1973a), Repina (1979) and Palmer and Repina (1993) assigned *Elliptocephala* to the Holmiidae. The family diagnosis of Palmer and Repina (1993, p. 25), however, does not fit *Elliptocephala* very well: it does not have wide interocular areas, T3 is macropleural in the small growth stages, and there is a large axial spine on T15 that divides the body into a prothorax and opisthothorax. The latter character has been controversial since Walcott (1890, pl. 90, fig. 1a; 1910b, pl. 24, fig. 1) illustrated a highly reconstructed specimen with large axial spines on segments T14 through T18. Whittington (1989, p. 128) questioned Walcott's reconstruction of a large spine on T14, and reillustrated the type material (pl. 8, figs. 45,46,48). The unretouched photographs do not show a large axial spine on T14. New material from the type locality is illustrated in Pl. 9, fig. 7. The posterior segments of the specimen are slightly displaced, but by the width of the axial region, the segment with the broken, long axial spine is T15. Therefore *Elliptocephala* shows the typical thoracic division into prothorax and opisthothorax, by a long

axial spine on T15, characteristic of olenelloids. Large spines posterior to T15 are inconsequential to this division. Ahlberg *et al.* (1986) also tentatively assigned *Elliptocephala* to the Wanneriidae based on a shared prosopon and similar hypostomal morphology with *Wanneria*.

While the ontogeny of *E. asaphoides* has been intensively studied and illustrated (Ford, 1877, 1878, 1881; Walcott, 1910b; Raw, 1925; Whittington, 1957a,b) the morphology of the holaspis has been poorly known. Walcott illustrated (1890, pl. 90, fig. 1a; 1910b, pl. 24, fig. 1) a large articulated holaspis which Palmer and Repina (1993, p. 26) designated the neotype. Whittington (1989, pl. 8, fig. 48) reillustrated this specimen and showed it to be a much-reconstructed holaspis based on highly-flattened shale material. Lochman (1956) illustrated material of *Elliptocephala asaphoides* from various localities in New York State, but the material is fragmentary and of small individuals. Palmer and Repina (1993, pl. 6, fig. 7) illustrated a small articulated holaspis highly flattened in shale. New material illustrated herein and described under *E. asaphoides* shows the adult morphology of this trilobite.

The ontogenetic development, reticulate prosopon, and marginal S2 identifies *Elliptocephala* as a wanneriid. It differs from *Wanneria* in having a shorter, more tapering LA, prosopon that is usually of caecae on the extraocular areas and reticulation on the glabella, a T3 that is macropleural in the small stages and diminishes in size through ontogeny, a cephalic border that is usually proportionately narrower and genal spines that are often slightly advanced. The hypostome is poorly known for the type species: *E. parentalis* n. sp. and the Scottish *E. reticulatus* (Peach, 1892) have hypostomes with expanded posterolateral margins and a posterolateral furrow: the same morphology as *Wanneria* hypostomes. Species from the Mural Formation (Fritz, 1992) and new species from the Poleta Formation have a posterolateral margin that is only slightly expanded without a distinct posterolateral furrow.

Aside from the large axial spines on T16-T18, *Elliptocephala asaphoides* is not that unusual a trilobite for Laurentia. This feature and the problems of the Taconic Region with its controversial affinities to Laurentia and Avalonia have served to keep *Elliptocephala* a monotypic genus. Lochman (1956) described the fauna of the Taconic Region as transitional between the Atlantic and Pacific provinces with *Elliptocephala asaphoides* occupying a deep water environment off of Laurentia in the Lower Cambrian. Species of *Elliptocephala* are widespread in Laurentia in the lowest part of the "*Bonnia* -*Olenellus*" Zone (as defined by Fritz, 1972, 1992), in Scotland (Cowie and McNamara, 1978), Arctic Canada (Cowie, 1968), Northwest Territories (Fritz, 1972, 1991a), British Columbia (Fritz, 1992, and herein), Nevada (described herein), New York State (Lochman, 1952; Walcott, 1910b) and possibly in Mexico (Lochman, 1952). Most of these species were

originally described as *Olenellus*, based on possession of a macropleural T3, despite the fact that they show a wanneriid style of ontogeny, lack an isolated S2, have deep mid-ocular lobe furrows, and partially reticulate prosopon.

Elliptocephala asaphoides Emmons, 1844

Pl. 8, figs. 6-9; Pl. 9, figs. 1-7; Text-fig. 26 (bottom)

- 1844 *Elliptocephala asaphoides* Emmons, p. 21, figs. 1-3.
 1910b *Elliptocephala asaphoides*, Walcott, p. 269-274, pl. 24, figs. 1-10, pl. 25, figs. 1-18. (synonymy to date)
 1916c *Elliptocephala asaphoides*, Walcott, pl. 14, fig. 3.
 1925 *Elliptocephala asaphoides*, Raw, p. 287,290,291-294,298.
 1927 *Elliptocephala asaphoides*, Raw, p. 138, table II.
 1937 *Elliptocephala asaphoides*, Raw, p. 579,582,586,588.
 1942 *Elliptocephala asaphoides*, Størmer, p. 62-63, text-fig. 3, 5b-d.
 1952 *Elliptocephala asaphoides*, Tash, p. 484-488, text-fig. 1a-d.
 1956 *Elliptocephala asaphoides*, Lochman, p. 1376-1377, pl. 6, figs. 2-21.
 1957a *Elliptocephala asaphoides*, Whittington, p. 935-937, pl. 116, figs. 1-6.
 1957b *Elliptocephala asaphoides*, Whittington, p. 431-434, figs. 3A-D.
 1957 *Elliptocephala asaphoides*, Raw, p. 184, text-fig. 5A.
 1957 *Elliptocephala asaphoides*, Palmer, p. 120.
 1968 *Elliptocephala asaphoides*, Bird and Rasetti, p. 23,25,31,39,41,53,56.
 1973a *Elliptocephala asaphoides*, Bergström, p. 286,307,308.
 1974 *Elliptocephala asaphoides*, Zen, p. 10,76,77,86.
 1978 *Elliptocephala asaphoides*, McNamara, p. 646, fig. 2.
 1979 *Elliptocephala asaphoides*, Theokritoff, p. 281,287-291.
 1981 *Elliptocephala asaphoides*, Theokritoff, p. 228-229, 230.
 1985 [?] *Wanneria*, Theokritoff, p. 283-284, fig. 1.
 1985 *Elliptocephala asaphoides*, Theokritoff, p. 283-285,287,289-291.
 1989 *Elliptocephala asaphoides*, Whittington, p. 128-129, pl. 8, figs. 45, 46, 48; figs. 50, 51.
 1993 *Elliptocephala asaphoides*, Palmer and Repina, p. 26, pl. 6, fig. 7.

Diagnosis: A species of *Elliptocephala* with tips of ocular lobes opposite anterior of L0. Anterior glabellar furrows and mid-ocular lobe furrow effaced. Cephalic border width moderate; width more than half length of L0. Preglabellar field long. LA short. Intergenal spines absent. Posterior border lengthens lateral to intergenal position. Genal spines not advanced. Posterior

occipital spine small. Rostral plate wide, hypostome attached in large holaspids. Thorax of 18 segments: small axial spines on T6-T13; long axial spines on T14-T18. T3 normal in large holaspid. Thoracic spines wide, falcate. Pygidium broad, lobate. Prosopon of fine reticulation on glabella; caecae on extraocular areas. Meraspid cephalon with curved anterior margin, no procranial spines.

Neotype²⁰: A fragmentary whole trilobite, USNM 18350a, (Walcott, 1890, pl. 90, fig. 1a; 1910b, pl. 24, fig. 1; Whittington, 1989, pl. 8, fig. 48) designated by Palmer and Repina (1993, p. 26). From the Greenwich Formation, 1.6 km west of North Greenwich, Washington County, New York.

Occurrences²¹: NEW YORK: Greenwich Formation, various localities in Washington County (Walcott, 1910b, p. 274); Schodack Formation, at Troy, Rensselaer County (Ford, 1877, p. 273; Walcott, 1910b, p. 274); various localities in Cambridge and Hoosick Quadrangles (Lochman, 1956).

Discussion: The neotype, USNM 18350a, was reillustrated by Whittington (1989, pl. 8, fig. 48) and shown to be a highly flattened, fragmentary specimen of a large articulated holaspid. Palmer and Repina (1993, pl. 6, fig. 7) illustrated a small holaspid (Pl. 9, fig. 6 herein) that still retains intergenal spines, a narrow thorax, and short thoracic spines. A limestone specimen (Pl. 9, figs. 3-4) of approximately the same size shows the original convexity of the exoskeleton, which is crushed in the shale specimen, and the actual tapering shape of LA. The anterior glabellar furrows on all specimens are shallow and no mid-ocular lobe furrow is discernible. These features are interpreted as effacement. Caecae are present on the extraocular areas of even the largest specimens, and fine reticulation are present on the glabella of one testate specimen. No intergenal spine is visible on large holaspids, but the posterior border lengthens lateral to the intergenal position. The anterior margin of the hypostome is under the anterior margin of LA (Pl. 9, fig. 7) and attached to the broad rostral plate in large specimens. The details of the posterior morphology of large hypostomes is poorly known. Walcott (1890, pl. 88, fig. 1g) illustrated a small hypostome with a fully spinous posterior border. The rostral plate terminates

²⁰ The original specimens of Emmons (1844) were reported lost by Whittington (1989, p. 128). The specimen Palmer and Repina (1993) selected is an original of Walcott from the type locality of Emmons and not part of Emmon's original collection. Palmer and Repina referred to the type as a "lectotype", but it is actually a neotype.

²¹ Formation names in the Taconic region have been revised by Zen, (1964), however, it is difficult to apply the new names to old locality descriptions and the antiquated names are given here.

anterior of the posterior border, unlike the rostral plate in *Wanneria* that reaches the posterior border and extends a short distance laterally. *Elliptocephala stewarti* n. sp. has a rostral plate of similar extent to *E. asaphoides*.

Elliptocephala asaphoides is unique among the species of *Elliptocephala* with a known thoracic morphology in having axial spines on T16-T18. It is also the only one that completely reduced the macropleural T3 to a normal T3 in the large holaspide stage. *E. muralensis* (Fritz, 1992) shows a reduction in the size of T3 through ontogeny, but it is still amplipleural in the large holaspide stage.

Ontogeny: *Elliptocephala asaphoides* was the first of the Olenellina, and indeed, one of the first trilobites to be described from ontogenetic material as illustrated in the early work of Ford (1877, 1878, 1881). It has remained a focus of attention and been studied by subsequent workers such as Walcott (1910b), Raw (1925), Whittington (1957a,b) and is restudied herein. The close similarity of the small stages of this species to those of *Wanneria* are critical in demonstrating that *Elliptocephala* is a wanneriid, and the ontogeny is described in detail below. Clique B meraspids are the earliest known for this species, but clique A meraspids are described under *E. parentalis*.

Clique B meraspids have ocular lobe posterior tips indistinctly differentiated. Extraocular areas narrow, present over full length of cephalon, narrowest posteriorly. Faint indication of segmentation on interocular areas. Preglabellar field moderately short. Glabellar stalk slightly tapering forward; LA wide, short, drapes ocular ridges. Glabellar furrows marginal, pit-like: S0 slot-like and continued medially as a shallow furrow. Intergenal spines short, laterally direct, cross the posterior border medial to the ocular lobe positions. Genal spines not clearly differentiated. Cephalon subcircular in outline. (Pl. 8, fig. 7)

Clique C meraspids have ocular lobe posterior tips opposite of L1. Extraocular areas about half the width of interocular areas. Preglabellar field moderately long. Glabellar stalk slightly tapering forward; LA wide, short, drapes ocular ridges. Glabellar furrows marginal, pit-like, continued medially as shallow transglabellar furrows. Intergenal spines short, laterally directed, cross the posterior border posterior to the ocular lobes. Genal spines minute, advanced: opposite of L1. Cephalon subcircular in outline. (Pl. 8, fig. 8)

Clique D specimens have ocular lobe posterior tips opposite of the posterior-most portion of L1. Extraocular areas subequal to or slightly more than half the width of interocular areas. Preglabellar field moderately long. Glabellar stalk parallel-sided; LA wide, short, drapes ocular

ridges. Glabellar furrows marginal, slot-like. Intergenal spines narrow, short. Genal spines short, advanced: opposite of S0. Cephalon approximately 1.4 times wider than long. Partial thorax known of 11 segments and T3 macropleural, macrospinous. (Pl. 8, fig. 9; Pl. 9, fig. 1)

Clique E specimens have ocular lobe posterior tips opposite of S0. Extraocular areas approximately twice the width of interocular areas. Preglabellar field moderately long. Glabella barely constricted at S1, L3 slightly modified. LA short, wide. Glabellar furrows marginal, slot-like. Intergenal spines tiny, almost lateral to ocular lobe positions. Genal spines well-developed, advanced: opposite of anterior of L0. Cephalon approximately 1.5 times wider than long. Partial thorax known of at least 15 segments: T3 macropleural, macrospinous; 15th axial spine not clearly developed. (Pl. 9, fig. 2)

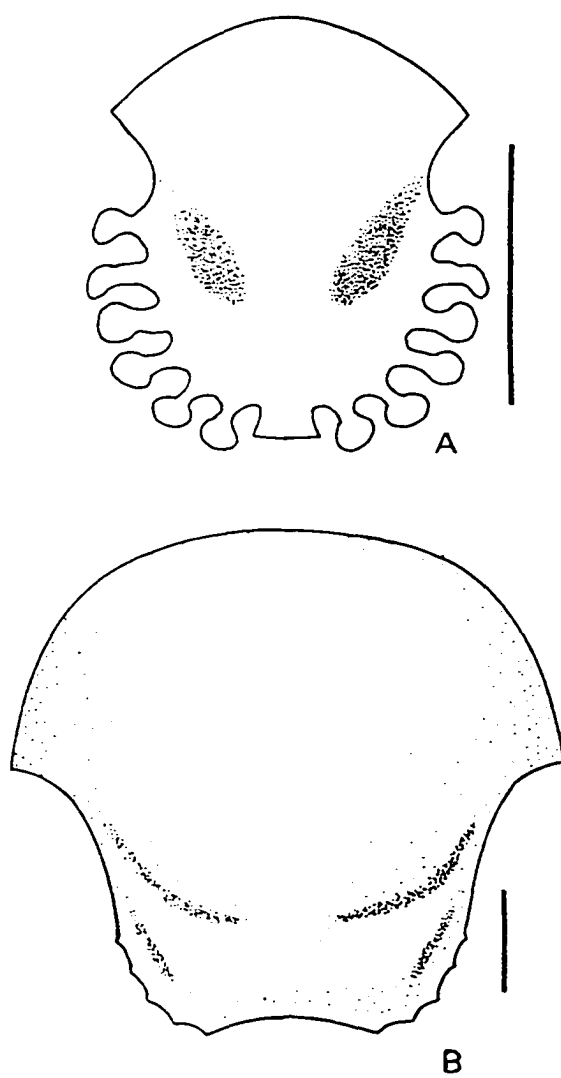
Clique F holaspids have ocular lobe posterior tips opposite of L0. Extraocular areas more than twice the width of interocular areas. Preglabellar field moderately short. Glabella clavate; nearly parallel-sided L0 to S1, expanding forward anterior to S1. L3 modified. LA long, wide, tapering forward. Glabellar furrows marginal, S3 strongly curved. Intergenal spines tiny, positioned lateral to ocular lobe positions. Genal spines long, not advanced. Cephalon more than 1.5 times wider than long. T3 macrospinous. (Pl. 9, figs. 4-6)

Elliptocephala parentalis n. sp.

Pl. 10, figs. 1-15; Text-figs. 24 (top), 38

Diagnosis: A species of *Elliptocephala* with ocular lobe posterior tips opposite of posterior portion of L1. Cephalic border narrow; width less than half length of L0. Preglabellar field short. LA long. Intergenal spines absent. Posterior border lengthens lateral to intergenal position and inflected anteriorly. Genal spines advanced: opposite of posterior of L0. Posterior occipital tubercle small. Hypostome with five pairs of small posterolateral spines, posterolateral furrow, and concave posterior margin. Prosopon coarsely reticulate on glabella, interocular areas, ocular lobes; caecae on extraocular areas faint. Meraspid cephalon with curved anterior margin, no procranidial spines.

Holotype: A complete large cephalon (MG2a#1; Pl. 10, fig. 15) from the Eager Formation, collection MG2a, Mt. Watson, 7 km east-southeast of Canal Flats, British Columbia. Paratypes: MG2a#2, MG2a#6. MG2a#10, MG2a#13-15, MG2a#29



Text-fig. 38. Hypostomes of *Elliptocephala parentalis* n. sp. A. meraspid B. holaspid
scale bar = 1 mm

Occurrences: BRITISH COLUMBIA. Eager Formation, sections MG1 and MG2, Mt. Watson, 7 km east-southeast of Canal Flats.

Zonal Biostratigraphy: *Wanneria logani* Subzone, *Olenellus transitans* Zone.

Etymology: From the Latin adjective "parentalis" meaning "of parents" This species is named in honour of my parents, John and Joyce Bohach, who spent their holidays assisting me in the field. My father collected the holotype of this species.

Discussion: *Elliptocephala parentalis* can be distinguished from most other species by a combination of its long LA, distinctly advanced genal spines, and its hypostomal features. It has a hypostome identical to that of *Wanneria walcottana*. *E. parentalis* is closest in morphology to the Scottish species *E. lapworthi* (Peach and Home, 1892). Both have ocular lobes of the same length, long, tapering LA's, advanced genal spines and glabellas of similar proportions. *E. lapworthi* differs in having a slightly longer preglabellar field, S2 with greater curvature, narrower cephalic border and a posterolateral cephalic border that is curved rather than straight.

Elliptocephala parentalis is only found in a large oolitic bank that extends between two measured sections on Mt. Watson. The preservation is mostly of internal molds that give little indication of prosopon. A single fragmentary specimen with the test (Pl. 10, fig. 10) shows strong reticulation on the central cephalon and deep ocular lobe furrows. Faint caecae can be seen on the holotype. A fragment of a rostral plate is known and possesses marginal pits.

Ontogeny: A complete ontogenetic sequence is known for *Elliptocephala parentalis* that is closely comparable to that of *E. asaphoides*. The major differences are a more parallel-sided glabella in clique B and C meraspids and slightly early modification of the glabella. Clique A meraspids are also known for this species and are described in detail.

Clique A meraspids have ocular lobes indistinctly differentiated posteriorly from the cephalic border, which is itself only well-defined anteriorly. Extraocular areas present only anteriorly. Preglabellar field moderately short. Glabellar stalk parallel-sided, axial furrows indistinct. LA wide, short, drapes ocular ridges. Glabellar furrows not defined: S0 shallow, transglabellar. Intergenal spines short, posteriorly directed, cross the posterior border medial to the ocular lobe positions. Genal spines minute, advanced, opposite of ?L2. Cephalon subcircular in outline. (Pl. 10, figs. 1-2)

Clique B meraspids (Pl. 10, figs. 3-4) are closely comparable to those of *Elliptocephala asaphoides*, except LA is proportionately shorter and the ocular lobes are slightly more medially positioned. Clique C and D meraspids (Pl. 10, figs. 5-6, 11) have variably advanced genal spines and during clique D, LA begins to lengthen, a suggestion of a mid-ocular lobe furrow develops, and the first hint of a modified L3 and constricted glabella appears. Clique E specimens (Pl. 10, fig. 13) have an almost mature glabellar configuration with a well-modified L3, longer LA and shorter preglabellar field. The genal spines are advanced compared to those of *E. asaphoides* at this clique. Clique G holaspids (Pl. 10, figs. 14-15) also have a longer LA, shorter preglabellar field and advanced genal spines compared to *E. asaphoides*.

Elliptocephala nelsoni n. sp.

Pl. 11, figs. 1-7

Diagnosis: A species of *Elliptocephala* with ocular lobe posterior tips opposite posterior of L1. Cephalic border narrow; width approximately one third length of L0. Border shortens anterior of glabella. Preglabellar field absent. LA short. Intergenal spines and intergenal ridges distinct. Genal spines short: advanced, opposite midlength of L0. Posterior occipital tubercle distinct. Prosopon reticulate; each polygon with a tubercle in the center.

Holotype: A nearly complete cephalon (LACMIP 11366; Pl. 11, fig. 6) from the middle Poleta Formation, section GP, Mt. Dunfee area, LACMIP collection 26850, 7 km east of Gold Point, Esmeralda County, Nevada. **Paratypes:** LACMIP 12521, 12524

Occurrences: NEVADA. Middle Poleta Formation, section GP, Mt. Dunfee area, 7 km east of Gold Point, Esmeralda County.

Zonal Biostratigraphy: *Gabriellus poletensis* Subzone, *Elliptocephala* Zone.

Etymology: For Clem A. Nelson, in honour of a lifetime of work in the Cambrian of the southwestern Great Basin. Clem also collected the holotype of this species and provided many of the specimens used in this thesis.

Discussion: *Elliptocephala nelsoni* can be distinguished from all other species of *Elliptocephala* by its remarkable prosopon, reduced genal spines, and shortened anterior border. *E. reticulatus* (Peach, 1894) from Scotland is also anomalous in having its complete dorsal surface reticulate, but lacks the tubercles in the center of each polygon. *Mesolenellus moorei* n. sp., also from Nevada

has reticulate prosopon on its extraocular areas. *E. nelsoni* is the only wanneriid to have reduced genal spines and the only species of *Elliptocephala* to have an anterior border that shortens in front of the glabella. The latter is a typical character of *Wanneria*. *Wanneria inermis* Poulsen, 1958, also has tiny genal spines and an LA that is highly inflated and expanded anteriorly over the frontal border. This species may be a holmiid because its extraocular areas are narrow. In large holaspids of *E. nelsoni*, L1 to L3 have distinct lateral lobes, similar to those seen in *Laudonia prima*.

The hypostome of this species is remarkable in sharing the unusual prosopon of the dorsal surface. The largest (Pl. 11, fig. 7) is under 4 mm in length and shows a slight expansion of the posterolateral margin and up to six pairs of spines.

Ontogeny The limited material does not include meraspids. Like *Elliptocephala asaphoides* and *E. stewarti*, clique E specimens (Pl. 11, figs. 1, 4) of *E. nelsoni* have a nearly parallel-sided glabellar stalk with only a minor constriction at S1 and slight modification of L3. *E. parentalis* has a nearly mature glabellar configuration by this clique. The prosopon of *E. nelsoni* is developing during clique E and is best defined in the central region of the cephalon. In contrast to other ontogenies, the preglabellar field is nearly gone by clique E and clique F specimens have LA intruding on the anterior border. *E. nelsoni* retains intergenal spines through clique F, though not as large as those of *E. stewarti*. Clique G holaspids are not known.

Elliptocephala stewarti n. sp.

Pl. 11, figs. 8-17; Pl. 12, fig. 1

1910b *Olenellus fremonti* Walcott, pl. 37, figs. 3, 22 [only].

Diagnosis: A species of *Elliptocephala* with tips of ocular lobes opposite posterior of L1. Cephalic border width moderate; width more than half length of L0. Preglabellar field short. LA short. Intergenal spines and intergenal ridges distinct. Genal spines advanced: opposite anterior of L0. Posterior occipital spine short. Hypostome with five pairs of posterolateral spines. Meraspid cephalon with curved anterior margin, no procranial spines.

Holotype: A complete cephalon (LACMIP 12533; Pl. 11, Figs 16-17) from the middle Poleta Formation, section GP. LACMIP collection 17049, 7 km east of Gold Point, Esmeralda County, Nevada. **Paratypes:** LACMIP 12526-12528, 12532, 12534

Occurrences: NEVADA. Middle Poleta Formation, Esmeralda County: section GP, Mt. Dunfee area, 7 km east of Gold Point; section GF, Montezuma Range, 7.5 km northwest of Goldfield. CALIFORNIA. Middle Poleta Formation, sections GP and NH, Cedar Flat Area, east of Big Pine, White Mountains, Inyo County.

Zonal Biostratigraphy: *Elliptocephala stewarti* Subzone to possibly the *Gabriellus poletensis* Subzone; *Olenellus transitans* Zone.

Etymology: For John H. Stewart, in honour of his contributions to Lower Cambrian stratigraphy in the Great Basin. John also studied section GP where the type material comes from.

Discussion: *Elliptocephala stewarti* is the most common species of *Elliptocephala* in the Poleta Formation. It can be distinguished from other species of *Elliptocephala* by a combination of features: a moderately wide cephalic border, slightly advanced genal spines, distinct intergenal spines, and moderately long ocular lobes. It is closest in appearance to *Elliptocephala nelsoni* n. sp., also from the Poleta Formation, from which it differs by having longer genal spines, a preglabellar field, wider cephalic border, unusual lateral glabellar lobes and a distinctive prosopon. *E. truemani* (Walcott, 1913) also resembles *E. stewarti* but differs in lacking intergenal spines, having a wider cephalic border and lacking advanced genal spines. *E. muralensis* (Fritz, 1992) has similarly advanced genal spines and cephalic border width, but has an unusually constricted glabella, no intergenal spines, a longer LA, and slightly longer ocular lobes.

The prosopon of *Elliptocephala stewarti* is unknown. Moderately large hypostomes (largest known is 5 mm in length) have five pairs of marginal spines, and a slightly concave posterior margin showing the remnants of a reduced juvenile medial spine. The posterolateral margin is slightly expanded. A single partially articulated molt of a clique D/E specimen (Pl. 12, fig. 1) has a macropleural, macrospinous T3. The hypostome and rostral plate are inverted and displaced toward the rear of the specimen. The hypostome and rostral plate appear to have been shed as a single unit, but there is no evidence for an exoskeletal connection between the two as there is in *Olenellus thompsoni*, nor does the hypostome appear to have been attached as is typical for large holaspids of *Wanneria*. When an image of the rostral plate is repositioned on the cephalon, it does not extend to the posterior margin as it does in *Wanneria walcottana* and *W. dunnae*.

Walcott (1910b, pl. 37, figs. 3, 22) illustrated two specimens from the Cedar Flat area (Deep Spring Valley), that he assigned to *Olenellus fremonti* Walcott, 1910. This name cannot be applied to these specimens since Resser (1928) selected the lectotype of *O. fremonti* Walcott and Palmer (*in* Palmer

and Halley, 1979) restricted the name to that specimen (Walcott, 1910b, pl. 37, fig. 2,) from the Pioche Formation, Eureka County, Nevada. The Cedar Flat specimens belong to *Elliptocephala stewarti*, and are deeply weathered, but retained their original convexity. Unlike specimens of *O. fremonti* Walcott, *E. stewarti* has an almost parallel-sided glabella, small intergenal spines, deep mid-ocular lobe furrows, and a wanneriid ontogenetic pattern.

Ontogeny: A fairly complete ontogeny of *Elliptocephala stewarti* is known beginning with clique B meraspids. It is closely comparable to the ontogeny of *E. asaphoides*. Clique B meraspids (Pl. 11, figs. 8-9) differ in having a glabella distinctly tapering forward to S3 and better developed intergenal spines. Clique C meraspids show the first development of a mid-ocular lobe furrow and a hint of modification of L3 by late in the clique. Modification of the glabella in *E. parentalis* also occurs early, but not until clique D. Clique D meraspids (Pl. 11, figs. 11-12) of *E. stewarti* have a glabella distinctly constricted at S1 and slight modification of L3. *E. stewarti* retains prominent intergenal spines through its ontogeny. Clique G holaspids are not known.

Elliptocephala truemani? (Walcott, 1913)

Pl. 12, figs. 2-5

1910b *Wanneria? gracile* Walcott [in part] pl. 38, figs. 17-20 only.

1913 *Olenellus truemani* Walcott, p. 316, pl. 54, figs. 2, 6(?), 8, *non* figs. 7, 9, 10 [? = *E. muralensis* Fritz].

1916c *Olenellus truemani*, Walcott, pl. 17, figs. 2, 6(?), 8, *non* figs. 7, 9, 10 [? = *E. muralensis* Fritz].

1952 [?] *Olenellus (Olenellus) truemani*, Lochman, p. 89-91, pl. 18, figs. 6-12.

1971 [*non*] *Olenellus truemani*, Hu, p. 76-78, text-fig. 36, pl. 8, figs. 1-26 [= *Wanneria walcottana buelnaensis* Lochman].

1972 [*non*] *Olenellus truemani*, Fritz, p. 16-17, pl. 9, figs. 1-14 [= *E. praenuntius* (Cowie, 1968)]

1992 *Olenellus truemani*, Fritz, p. 15-16, pl. 6, figs. 1-4; pl. 7, figs. 1-6; text-fig. 6b.

Diagnosis: A species of *Elliptocephala* with tips of ocular lobes opposite posterior of L1. Cephalic border width moderate; width more than half length of L0. Preglabellar field long. LA short. Genal spines not advanced; opposite of T1. Prosopon of faint caecae on extraocular areas. Hypostome with at least four pair of posterolateral spines. Meraspid cephalon with straight anterior margin, procranial spines.

Lectotype: A nearly complete articulated specimen (USNM 60084; Walcott, 1913, pl. 54, fig. 2, left) designated by Fritz (1992, p. 15) from the Mural Formation, locality 61k (Walcott, 1913), Mumm Peak, Mount Robson Area, British Columbia.

Occurrences: BRITISH COLUMBIA. Mural Formation, locality 61k (Walcott, 1913; Fritz, 1992), Mumm Peak, Mount Robson area. ?NEVADA. Middle Poleta Formation, Esmeralda County: section GP, Mt. Dunfee area, 7 km east of Gold Point.

Zonal Biostratigraphy: *Elliptocephala stewarti* Subzone, *Elliptocephala* Zone.

Discussion: Poorly preserved material in sandstone from the Poleta Formation, Nevada can possibly be assigned to *Elliptocephala truemani* (Walcott, 1913). These specimens agree with the topotype material (Mural Formation: Fritz, 1992, pl. 6, figs. 1-4; pl. 7, figs. 1-6) in the size and shape of LA, length of the ocular lobes, configuration of the glabella, lateral position of the intergenal angle on the posterior border and in the genal spines which are not advanced. The latter feature distinguishes *E. truemani* from the other species of *Elliptocephala* from the Poleta Formation. The only difference between the Poleta specimens and those from the Mural is the width of the cephalic border. In the topotype specimens, the border width is subequal to the length of L0; in the Poleta specimens border width is just over half the length of L0. This is a minor difference, therefore the Poleta specimens are tentatively assigned to *E. truemani*.

Additional sandstone material from the St. Piran Formation, Vermillion Pass, Alberta, was attributed by Walcott (1910b, pl. 38, figs. 17-20) to *Wanneria? gracile*. These specimens have a smaller, tapering LA than *Wanneria* and are better assigned to *Elliptocephala*. Like *E. truemani*, these specimens have a wide cephalic border, unadvanced genal spines, and ocular lobes opposite of L1. They differ in having reticulate prosopon on the extraocular areas. This is a minor difference, therefore the specimens are assigned to *E. truemani?*.

The smallest illustrated material from the Mural Formation of *Elliptocephala truemani* (Fritz, 1992, pl. 6, fig. 1) is a small holaspid. It agrees closely in morphology with similarly sized specimens from the Poleta, both showing intergenal spines at a lateral position on the posterior border. Large meraspids are known from the Poleta material that have a straight anterior margin and distinct procranial spines.

Fritz (1972, p. 17) synonymized *Elliptocephala praenuntius* (Cowie, 1968) from the Kane Basin Formation, Ellesmere Island, with *E. truemani*, but later (Fritz, 1992, p. 16) he re-established *E.*

praenuntius as a distinct species on the basis of a shorter preglabellar field, longer ocular lobes, more medially placed intergenal spines, and slightly advanced genal spines with a rounded posterolateral cephalic margin. These are all valid criteria, except that the preglabellar field is judged herein to be of equivalent length in *E. praenuntius* and *E. truemani*. Specimens assigned to "*Olenellus*" *truemani* by Fritz (1972) from the Sekwi Formation, Mackenzie Mountains are tentatively assigned to *E. praenuntius*. The specimens from the Sekwi differ from the type material of *E. praenuntius* in having a slightly shorter preglabellar field and ocular lobes. They share the slightly advanced genal spines with the unusual rounded posterolateral margin.

Specimens assigned to "*Olenellus*" *truemani* by Lochman (1952, pl. 18, figs. 6-12) from the Buelna Formation, Mexico, are too fragmentary in the large holaspis stage to be assigned with confidence. The illustrated material was drawn from numerous localities and likely represents a mix of species. For example, the specimen illustrated in Lochman's pl. 18, fig. 12, is from the same locality as her specimens assigned to *Wanneria walcottana buelnaensis* Lochman, and cannot be distinguished from the latter. Hu (1971) illustrated ontogenetic material from the Buelna Formation that he assigned to "*Olenellus*" *truemani*. These specimens appear to be the young stages of *Wanneria? buelnaensis* (Lochman, 1952) as they have advanced genal spines and more medially placed intergenal spines than those of *E. truemani*.

Genus *Laudonia* Harrington, 1956

Type Species: *Laudonia bispinata* Harrington, 1956, from the Mahto Formation (Mural Formation after Fritz, 1995), Mumm Peak, Mt. Robson Area, British Columbia. (by original designation)

Diagnosis: A genus of Wanneriidae with glabella slightly to distinctly constricted at S1. Cephalic border general wide; widest anterolaterally, narrowing medially, narrowest laterally. Preglabellar field short in small holaspis stage. LA subpentagonal. Ocular lobes short. Intergenal ridges strongly developed. Intergenal spines long; base inflected slightly anteriorly from posterior margin. Genal spines posterolaterally directed, strongly advanced; opposite or anterior of L3. Cephalon subpentagonal in outline. Hypostome with rounded posterior margin. T3 macropleural and macrospinous throughout ontogeny. Meraspis cephalon generally with procranial spines. Genal spines migrate anteriorly through ontogeny.

Other Species:

Wanneria mexicana prima Lochman, 1952; Puerto Blanco Fm., NW Sonora, Mexico.

[non] *Laudonia canadensis* Hu, 1971; N of Radium, BC [= *Olenelloides? canadensis*].

Laudonia sp. 1 Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

Laudonia amputata Fritz, 1992; Mural Fm., Mt. Robson Area, BC.

Laudonia harringtoni n. sp.; Poleta Fm., Esmeralda County, Nevada.

Discussion: Harrington (1956) assigned *Laudonia* to the Wanneriinae on the basis that he considered the glabellar shape and segmentation of *L. bispinata* to be closely comparable to that of *Wanneria occidens* Walcott, 1913 (= *Mummaspis*). Fritz (1992) also assigned *Laudonia* to the Wanneriidae, but did not discuss his placement of the genus. Repina (1979) assigned *Laudonia* to the Fremontiinae²², a polyphyletic group defined by the characters of advanced genal spines, long glabellas and short ocular lobes. All of these features developed independently in different taxa. Poulsen (in Moore, 1959), Bergström (1973a) and Ahlberg *et al.* (1986) assigned *Laudonia* to the Olenellinae (-idae) but did not discuss the reason for this placement. Palmer and Repina (1993) erected a new subfamily of Olenellidae for *Laudonia*, the Laudoniinae, to which they also tentatively assigned *Olenelloides*. The main diagnostic features that they cited were (p. 24): strongly advanced genal spines, large intergenal spines, T3 weakly macropleural, and no long T15 axial spine. *Olenelloides* shares an ontogenetic pattern with *Mesonacis*, not with the wanneriids, therefore the similarities between *Laudonia* and *Olenelloides* are likely primitive or convergent.

Laudonia is interpreted herein as a paedomorphic wanneriid genus having large intergenal spines, a barely modified glabella, often narrow extraocular areas, retention of a spiny posterior hypostomal margin to a relatively large size, and a macropleural T3: all of which are juvenile features of other wanneriids. *Laudonia* has a wanneriid ontogenetic pattern (described under *L. prima*) and shares the adult morphological features of a reticulate prosopon, marginal and curved S2 and wide ocular lobes with deep mid-ocular lobe furrows with other members of the family. The cephalic border that shows extreme variations in width in *Laudonia* is a unique feature of the genus. Genal spines that progressively become more advanced throughout ontogeny are a derived feature that may have been independently acquired in *Bristolia* (the latter shows an *Olenellus*-style ontogenetic pattern). Ocular lobes in *Laudonia* are typically short, the longest being those of *L. amputata*, opposite of the anterior of L1. *Laudonia* apparently lacks the long axial spine on T15 that is characteristic of the Olenellidae and Wanneriidae. This may be another paedomorphic feature, or may be a result of lack of preservation in small sample sizes. Only two complete thoraxes have been described for *Laudonia* (*L. bispinata*, Fritz, 1992, pl. 13, fig. 2; pl. 14, fig. 1). Both are internal molds which may not retain the possible dorsal spine on T15. Until

²² Repina (1979) did not follow Fritz (1972) who synonymized *Fremontia* with *Olenellus*.

additional articulated material is found, the apparent lack of an axial spine on T15 in *Laudonia* should be given little weight.

The type species, *Laudonia bispinata*, is based on large specimens flattened in shale. It has extremely short ocular lobes, highly advanced genal spines that originate from the anterolateral border and an highly constricted glabella. *Laudonia* sp. 1 Fritz, 1972 was assigned to the *Bristolia* (Olenellidae) by Fritz (1992, p. 26). That assignment is probably wrong as the specimen shows a wide ocular lobe with an indication of a deep mid-ocular lobe furrow. This feature is characteristic of the Wanneriidae, not the Olenellidae. Only a single, fragmentary cephalon is known which compares most closely with *L. bispinata* of the described species. It differs in having slightly longer ocular lobes. *Laudonia canadensis* Hu, 1971 does not belong to *Laudonia*. It has advanced genal spines and short intergenal spines in the largest illustrated specimen (Hu, 1971, pl. 9, fig. 31; a small holaspis 6 mm in cephalic length), but many olenelloids that lose the intergenal spines in the later holaspis stage still retain intergenal spines at this size, therefore this species may not have large intergenal spines in the later holaspis stage either. This species does not show the ontogenetic pattern, deep mid-ocular lobe furrows, reticulate prosopon, or marginal S2 characteristic of a wanneriid. Instead, it shows an ontogenetic pattern typical of the mesonacine *Olenelloides*.

Laudonia prima (Lochman, 1952)

Pl. 12, figs. 6-13; Pl. 13, figs. 9-11; Text-fig. 27

1952 *Wanneria mexicana prima* Lochman, p. 96-98, pl. 18, figs. 1-3.

1956 *Laudonia prima*, Harrington, p. 56, 60, 61

1972 *Laudonia prima*, Fritz, p. 27

1992 *Laudonia? mexicana*, Fritz, p. 12, 26

Diagnosis: A species of *Laudonia* with glabella slightly constricted at S1, widest at LA. Tips of ocular lobes opposite posterior of L2. Interocular and extraocular areas narrow. L2 and L3 with lateral lobes. Genal spines opposite of S3. Posterior occipital spine short. Cephalon only slightly wider than long. Prosopon reticulate on glabella; reticulate with tubercle in center of each polygon on extraocular areas and lateral cephalic border.

Holotype: Small complete cephalon, USNM 115681 (Lochman, 1952, pl. 18, fig. 3) from the Puerto Blanco Formation, northwestern Sonora, Mexico. Paratypes: USNM 115682-115684.

Occurrences: MEXICO. Puerto Blanco Formation, Proveedora Hills (section 801c of Lochman, 1956), northwestern Sonora, near Caborca. NEVADA. Poleta Formation, Esmeralda County: section GF, Montezuma Range, 7.5 km northwest of Goldfield; section GP, Mt. Dunfee area, 7 km east of Gold Point.

Zonal Biostratigraphy: *Elliptocephala stewarti* Subzone, *Elliptocephala* Zone.

Discussion: The type material of *Laudonia prima* is represented by deeply weathered limestone material that is poorly preserved. New material from Nevada, illustrated herein, can resolve some features that were not discernible in the type specimens. The new material agrees in all respects with Lochman's specimens and shows that this species has a short posterior occipital spine and reticulate prosopon; each polygon with a tubercle in the center on the extraocular areas and cephalic border. *Laudonia prima* is characterized by narrow extraocular and interocular areas and a glabella that is only slightly constricted, expanding forward anterior to S1. Small holaspid cephalons have unusual, distinct lateral lobes on L2-L3.

Lochman (1956, p. 97) stated that undescribed material from locality 61k, Mumm Peak, British Columbia (Mural Formation) was conspecific with *Laudonia prima*. Fritz (1992) later described the Mumm Peak material as a new species, *L. amputata*, without comparing it to *L. prima*. The two species share many features, but are distinguishable: *L. amputata* lacks an occipital spine, has slightly longer ocular lobes and has no tubercles associated with its reticulate prosopon. All of these differences are minor, but collectively are enough to warrant separate species.

The subspecies name of "*prima*" that Lochman (1956) gave this trilobite is used as the species name. From her discussion (p. 97) it is apparent that *Wanneria mexicana* Lochman is an undescribed, poorly preserved form without advanced genal spines that was associated with collections of *L. prima*. Lochman viewed *Wanneria mexicana prima* as a variety of the species with advanced genal spines, therefore the name "*prima*" is used for this species.

Ontogeny: A sparse ontogenetic sequence is known for *Laudonia prima* that is closely comparable in early development of glabellar features to that of *Elliptocephala*, but the holaspid glabella of *Laudonia* remains immature compared to *Elliptocephala*. The intergenal spines are prominent throughout the ontogeny and the genal spines migrate anteriorly.

Clique A meraspid is virtually indistinguishable from those described for *E. parentalis*, including shallow axial furrows early in the clique. Poor preservation makes determining the

shape of the cephalic margin difficult, though it is suggestive of a subcircular outline. (Pl. 12, fig. 6)

Clique B meraspids have procranial spines and a straight anterior margin, comparable to meraspids of *Mesolenellus*. Genal spines are small and advanced opposite of S1/L2. Ocular lobe posterior tips are opposite of S0. (Pl. 12, fig. 7-8)

Clique C meraspids are recognized by the lengthening of LA that occurs at this clique in *E. parentalis*. Ocular lobe posterior tips are opposite of L1. In contrast to described *Elliptocephala* ontogenies, the extraocular areas are still narrow, a deep mid-ocular lobe furrow has already developed and genal spines have migrate forward and are opposite of S2. (Pl. 12, fig. 9)

Clique D specimens retain narrow extraocular areas but a prelabellar field is virtually lost, genal spines are opposite the midlength of L3, and a major widening of the cephalon has occurred. The intergenal spines are long, posterolaterally directed and slightly advanced. The glabellar morphology is closely comparable to that of *Elliptocephala parentalis* with the slightest hint of a constriction at S2 and modification of L3. Lateral glabellar lobes have developed by this clique. Ocular lobe posterior tips are opposite of L1. (Pl. 12, fig. 10)

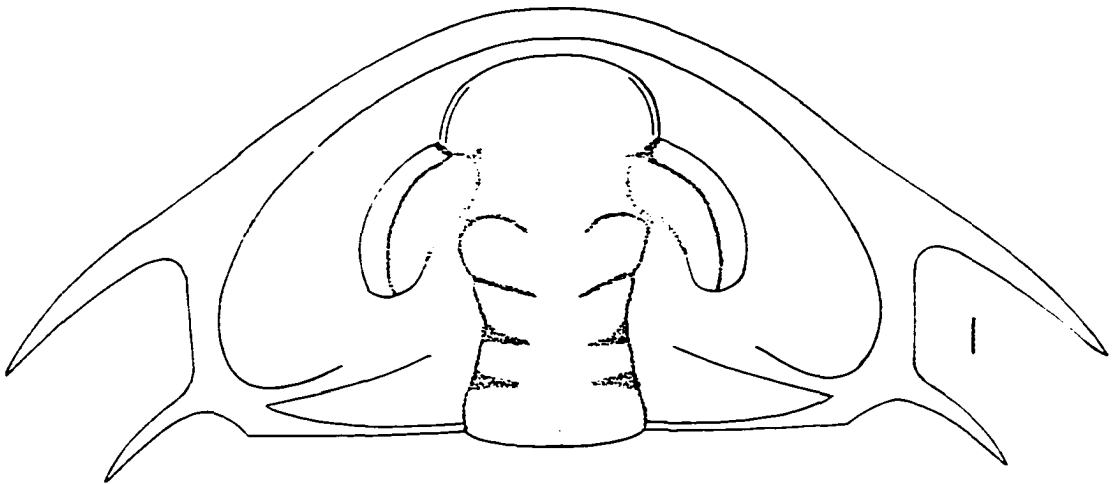
Clique E specimens are little different from those of clique D. The extraocular areas are still narrow, intergenal spines large and the genal spines are still opposite of L3. The ocular lobes have shorten slightly with posterior tips opposite of S1. LA has lengthened and displaces the anterior border forward giving a strong curvature to the anterior margin. Preglabellar furrow deep. (Pl. 12, fig. 11)

Clique F specimens continue the same trends, retaining a barely modified glabella, but the extraocular areas have widened slightly, ocular lobes have shortened with posterior tips opposite of L2 and genal spines are more advanced, opposite of S3. LA is also proportionately longer. Clique G specimens are poorly known. Intergenal spines are still long and genal spines are more advanced, opposite of LA. (Pl. 12, fig. 12)

Laudonia harringtoni n. sp.

Pl. 13, figs. 1-8; Text-fig. 39

Diagnosis: A species of *Laudonia* with glabella slightly constricted at S1, widest at LA. Posterior tips of ocular lobes opposite posterior of L2. Extraocular areas more than twice width interocular



Text-fig. 39. *Laudonia harringtoni* n. sp. scale bar = 1 mm

areas. L2 and L3 with lateral lobes. Genal spines opposite of L3. Posterior occipital tubercle prominent. Cephalon wide: almost twice as wide as long. Prosopon reticulate on glabella, reticulate with tubercle in center of each polygon on cheeks and lateral border.

Holotype: Complete cephalon (LACMIP 12550; Pl. 13, figs. 4-5, 8) from the middle Poleta Formation, section GP, Mt. Dunfee area, LACMIP collection 17052, 7 km east of Gold Point, Esmeralda County, Nevada. Paratypes: LACMIP 12547-12549, 12551

Etymology: After H. J. Harrington, in recognition of his fine contributions to olenelloid taxonomy.

Occurrences: NEVADA. Middle Poleta Formation, Esmeralda County: section GP, Mt. Dunfee area, 7 km east of Gold Point; section GF, Montezuma Range, 7.5 km northwest of Goldfield.

Zonal Biostratigraphy: *Elliptocephala stewarti* Subzone, *Elliptocephala* Zone.

Discussion: *Laudonia harringtoni* has a wide cephalon like *L. bispinata* Harrington that is almost twice as wide as long. *L. prima* (Lochman) and *L. amputata* Fritz have proportionately narrower cephalon, approximately 1.4 times as wide as long. A distinctive feature of *L. harringtoni* is the genal spines which are not as far advanced as in other species. The hypostome is faintly reticulate and retains a fully spinous posterior margin to a large size. *L. harringtoni* shares with *L. prima* the ocular lobes of the same length, reticulate prosopon with tubercles on the extraocular areas and a glabella of very similar shape, including distinct lateral lobes on L2-L3.

Ontogeny: The development of *Laudonia harringtoni* is known for cliques C through G and is closely comparable that of *L. prima*. A major difference is that the extraocular areas widen more through ontogeny and are closer in proportions to those of *Elliptocephala*. A short preglabellar field is maintained throughout ontogeny and while the genal spines also become more advanced through ontogeny, they are not advanced to the same degree as in *L. prima*. Clique G holaspids (Pl. 13, figs. 4-5, 8) are known for this species and they retain the immature glabellar configuration typical of *Elliptocephala* at clique E.

Genus *Mummaspis* Fritz, 1992

Type Species: *Wanneria occidentis* Walcott, 1913 from the Mahto Formation (Mural Formation after Fritz, 1992), locality 61K, Mumm Peak, Mt. Robson Area, British Columbia. (by original designation)

Diagnosis: A genus of Wanneriidae with glabella strongly clavate. Cephalic border wide; width subequal to length L0. Preglabellar field short in small holaspid stage. LA long, subcircular. Ocular lobes strongly inclined posteriorly; width interocular areas less than width ocular lobes. Intergenal ridges distinctly developed. Intergenal spines short to indistinct. Genal spines not advanced to slightly advanced: opposite of T1 or L0. T3 macropleural and macrospinous throughout ontogeny. Thoracic spines long, falcate.

Other Species:

Olenellus simplex Poulsen, 1932; Ella Island Fm., Ella Isl., E. Greenland.

Olenellus paraoculus Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

Mummaspis obliosooculatus Fritz, 1992; Mural Fm., Mt. Robson Area, B.C.

Mummaspis albersi n. sp., Poleta Fm., Esmeralda County, Nevada.

Discussion: Fritz (1992) assigned *Mummaspis* to the Olenellidae, as did Palmer and Repina (1993), on the basis of its macropleural T3 and long 15th axial spine. The latter is also shared with *Wanneria* (of the Wanneriidae), and is not a good basis for assignment of this genus to one family over the other. While a macropleural T3 is found in all genera of Olenellidae but not in *Wanneria*, other wanneriid genera such as *Laudonia* and *Elliptocephala* do have a macropleural T3 (in the small stages only of *E. asaphoides*). The type species, *M. occidentis* lacks known ontogenetic material, but a second species, *M. obliosooculatus* Fritz, 1992 has an ontogenetic sequence (large meraspid to large holaspid) illustrated (Fritz, 1992, pl. 16, figs. 4-7). This species shows a wanneriid style of development of LA. *Mummaspis* is assigned to the Wanneriidae on the basis of this ontogenetic pattern plus the holaspid characters of reticulate prosopon, marginal S2, deep mid-ocular lobe furrows, and large LA.

Wanneria occidentis Walcott, 1913, was erected on the basis of a single specimen from locality 61K in the Mount Robson Area. Resser and Howell (1938) assigned this species to *Esmeraldina*, but did not list what features led them to this decision. This species lacks the narrow extraocular areas of a holmiid and therefore does not belong in *Esmeraldina*. Harrington (1956) suggested that this species was more closely related to *Wanneria walcottanus*, and assigned this species to

Wanneria, stating (p. 61) "The mere presence of a fairly long occipital spine in *W. occidentis* is surely not enough to assign the species to *Esmeraldina*". Lochman (1956) also referred to this species as *Wanneria occidentis*, but did not discuss this generic assignment. Fritz (1992) re-examined Walcott's 61K fauna and recognized this species as belonging to a new genus, *Mummaspis*. The distinguishing features of *Mummaspis* from *Wanneria*, as listed by Fritz (p. 17) are: presence of an intergenal spine in the holaspis, a long occipital spine, a macropleural T3, and a large spine on the 15th axial ring. The last feature listed is not a distinguishing feature: *Mummaspis* shares it with *Wanneria*. The long occipital spine of the type species, *M. occidentis*, appears to be an autapomorphy as it is not seen on any other species of *Mummaspis*. Other distinguishing features of the genus are: steeply inclined ocular lobes that are close to the cephalon (unusually narrow interocular areas) and the large, subcircular LA that is unusually long for olenelloids.

Fragmentary material from east Greenland described as *Olenellus simplex* Poulsen, 1932 can also be assigned to *Mummaspis*. It has the wanneriid features of reticulate prosopon, marginal S2, and deep mid-ocular lobe furrows. The ocular lobes are close to the glabella and LA is long and subcircular in shape, as is typical of species of *Mummaspis*. It has long ocular lobes (tips opposite of L0), no intergenal ridges or spines, and coarse reticulate prosopon; each polygon with a tubercle in the center on the extraocular areas. *Olenellus paraoculus* Fritz, 1972 from the Sekwi Formation, Mackenzie Mountains is an effaced species of *Mummaspis*. It has a clavate glabella with a large LA that intrudes upon the anterior border, a straight posterior margin, and ocular lobes close to the glabella. A full ontogenetic sequence of a wanneriid pattern is illustrated for this species (Fritz, 1972, pl. 15, figs. 8-22).

Mummaspis albersi n. sp.

Pl. 14, figs. 1-5

Diagnosis: A species of *Mummaspis* with genal spines advanced opposite anterior of L0. Ocular lobe posterior tips opposite of midlength of L1. Intergenal spines short. Thorax narrow; pleural spines thin, falcate.

Holotype: Large, complete cephalon (LACMIP 12556; Pl. 14, fig. 3) from the middle Poleta Formation, locality 10, LACMIP collection 26870, Goat Island, Silver Peak area, Esmeralda County, Nevada. **Paratypes:** LACMIP 12557-12558

Etymology: For J. Albers who collected some of the type material of this species with C.A. Nelson.

Occurrences: NEVADA. Middle Poleta Formation, Esmeralda County, Silver Peak Quadrangle: locality 10, Goat Island; locality 13, Alcatraz Island.

Zonal Biostratigraphy: *Elliptocephala poletensis* Subzone, *Elliptocephala* Zone.

Discussion: *Mummaspis albersi* has the most pronounced macropleural development of T3 of any described species of *Mummaspis* and shows a decrease in relative size of T3 through ontogeny. The thorax in both *M. albersi* and *M. occidentis* (Walcott) is narrow with thin thoracic spines while the thorax of *M. obliosooculatus* Fritz is wide with thick thoracic spines. The genal spines in *M. albersi* are also more advanced than in the other species. The ocular lobes of *M. albersi* are equal in length to those of *M. occidentis*, slightly longer than those of *M. obliosooculatus*, and much shorter than those of *M. simplex* (Poulsen). The prosopon and hypostome are not known.

One small holaspis is tentatively assigned to *Mummaspis albersi*. It has strong macropleural development of T3 and a large, well-rounded LA. It is unusual, compared to large holaspids, in having an S2 morphology suggestive of isolated slots and a relatively narrow cephalic border. The absence of a continuous grow series makes it impossible to evaluate whether or not the differences are ontogenetic or specific and the identification of this specimen is consequently tentative.

Genus *Gabriellus* Fritz, 1992

Type Species: *Gabriellus lanceatus* Fritz, 1992, from the Mural Formation, Mumm Peak, Mt. Robson area, British Columbia.

Diagnosis: A genus of Wanneriidae with glabella slightly constricted at S1, LA tapering forward. Cephalic border wide to moderately wide. Anterior border of equal width to lateral border. Preglabellar field present in small holaspis stage. LA long, diamond shaped. Ocular lobes located close to glabella. Intergenal ridges poorly developed. Intergenal spines usually short. Genal spines typically advanced. T3 macrospinous and amplipleural in holaspis. Thoracic pleurae narrow; pleural spines long. Pygidium elongate. Prosopon of caecae on extraocular areas.

Other Species:

Olenellus carinatus Poulsen, 1958; Wulff R. Fm., Blomsterbaekken, NW Greenland (= *Olenellus laevis* Poulsen, 1958; Wulff R. Fm., Blomsterbaekken: *Olenellus troelseni* Poulsen, 1958; Wulff R. Fm., Blomsterbaekken).

Olenellus sp. 3 Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

olenelloid gen. et sp. id. Whittington, 1989, Rossella Fm., Cassiar Mtns. BC (= *Gabriellus* sp. Palmer and Repina, 1993).

Gabriellus poletensis n. sp.; Poleta Formation, Cedar Flat, California.

Discussion: Published material of *G. lanceatus* Fritz, 1992, the only described species of *Gabriellus* that Fritz (1992) recognized, consists of a single cephalon and tentatively assigned thorax. This material is inadequate to provide a rigorous characterization of the genus. Fritz (1992) also referred to a second undescribed species from the Cassiar Mountains on which he partially based his diagnosis of the genus. This species was illustrated by Whittington (1989, pl. 4, figs. 21, 22) and Palmer and Repina (1993, fig. 4.9). The author is grateful to Bill Fritz of the Geological Survey of Canada for providing preprints of unpublished plates illustrating abundant material of two new species from the Cassiar Mountains. They are used to provide critical supplemental information about the genus. A new species from the Great Basin is also described here.

Gabriellus is an unusual olenelloid as it has a glabella tapered forward in general outline, often with a slight widening at L2/L3. Fritz (1992) emphasized narrow interocular areas as a distinctive character of the genus, but this is a variable feature at the species level (i.e. compare Pl. 14, fig. 6 with Pl. 15, fig. 5). In *Gabriellus*, the ocular lobes are generally close to, but not right against the glabella. *Judomia* and other neltneriids also have narrow interocular areas and a cylindrical to tapered glabella, but they lack a modified L3 and the ocular lobes lie against the glabella. *Mummaspis* has ocular lobes in a similar position, but it has a clavate rather than tapered glabella. Along with its distinctive glabellar shape and ocular lobes close to the glabella, *Gabriellus* can be characterized by an elongate, suboval pygidium with sagittal sulcus, narrow thoracic pleurae with long pleural spines, typically advanced genal spines and retention of intergenal spines in the holaspide stage. Fritz (1992) noted an opisthothorax of two segments on the undescribed Cassiar species.

Fritz (1992) suggested that *Gabriellus* is close to *Olenellus* and assigned the genus to the Olenellidae on that basis. Palmer and Repina (1993) also assigned *Gabriellus* to the Olenellidae but emphasized the differences between *Gabriellus* and other members of the Olenellidae and erected a monotypic subfamily for it (Gabriellinae - note that they incorrectly considered that

Gabriellus has an unmodified T3 and lacks an opisthothorax). Here it is determined that *Gabriellus* is a wanneriid based on its marginal S2, deep mid-ocular lobe furrows, partially reticulate prosopon and wanneriid ontogenetic pattern (see *Gabriellus poletensis*)

Poulsen (1958) recognized three species of *Olenellus* from the Wulff River Formation of northwestern Greenland. All are from the same locality and differ only in features that vary through ontogeny such as length of the ocular lobes and length of the prelabellar field. They belong in the same species and *Olenellus carinatus* Poulsen is chosen as the senior synonym of *O. laevis* Poulsen and *O. troelseni* Poulsen. When Poulsen (1958) discussed *Olenellus*, he noted that the Wulff River material has ocular lobes that are only slightly curved which reduces the width of the interocular areas. He considered this to be an unusual feature and suggested that with more complete material, these specimens could possibly be assigned to a new genus. This is a valid observation and the Wulff River species becomes *Gabriellus carinatus*. It is characterized by long ocular lobes, a rather effaced dorsal surface, intergenal thickenings near the genal spines, and an arcuate posterior border. The last feature is unusual for *Gabriellus* which usually has advanced genal spines.

Gabriellus poletensis n. sp.

Pl. 14, fig. 6; Pl. 15, figs. 1-6

Diagnosis: A species of *Gabriellus* with ocular lobe posterior tips opposite anterior of L0. Cephalic border moderately wide; width approximately half length of L0. Preglabellar field short. Parafrontal band faint. Intergenal spines moderately short, posterolaterally located. Genal spines advanced: opposite of S1 to S2. Posterior occipital node small. Thorax of 17 segments: posterior axial nodes on T1-T14. Thoracic spines wide, falcate. Prosopon of caecae on extraocular areas, terrace lines on cephalic border, reticulation on glabella and ocular lobes.

Holotype: A complete specimen (LACMIP B-4030; Pl. 14, fig. 5) from the Poleta Formation, section CF, LACMIP collection BM 39, Cedar Flat area, White Mountains, California. LACMIP 12-263, ICS 1056#9, ICS 1056#11

Etymology: For the Poleta Formation, in which this species occurs.

Occurrences: CALIFORNIA. Poleta Formation, White Mountains: locality 22 and sections CF and NH, , Cedar Flat area, east of Big Pine. NEVADA. Poleta Formation, Esmeralda County:

locality 10, Goat Island, 2 km northeast of Silver Peak; locality 13, Alcatraz Island, 1.5 km southeast of Silver Peak; section GP, Mt. Dunfee area, 7 km east of Gold Point.

Zonal Biostratigraphy: *Gabriellus poletensis* Subzone, *Elliptocephala* Zone.

Discussion: *Gabriellus poletensis* is a widespread species throughout the study area in California and Nevada in sediments of the upper part of the middle member of the Poleta Formation. It has a degree of variability in the position of its genal spines. Preservation may be a factor as all specimens are flattened in shale. The species typically has well-advanced genal spines, moderately large intergenal spines, long ocular lobes, and retains a short preglabellar field in the large holaspide stage. T3 is amplipleural with a long, strongly curved pleural spine. The pygidium closely matches that illustrated for the undescribed Cassiar Mountains species (Whittington, 1989, pl. 4, figs. 21, 22; Palmer and Repina, 1993, fig. 4.9). In both, the pygidium is long, suboval and has appears to have a median furrow running the length of the pygidium. A tentatively assigned hypostome (Pl. 15, fig. 3) has six pairs of posterolateral spines and a slightly expanded posterolateral margin.

Gabriellus poletensis has long ocular lobes like *G. carinatus* and the Cassiar *Gabriellus* sp., but they are not situated as close to the glabella. It is closest in morphology to the Cassiar species with which it shares well-advanced genal spines, moderately short intergenal spines and long thoracic pleural spines. *G. lanceatus* differs as it has short thoracic pleural spines and a posterior border that is inflected anteriorly over its whole length, not only lateral to the intergenal spines.

Ontogeny: The ontogenetic pattern of *Gabriellus poletensis* is nearly identical to that of *Elliptocephala*. Clique C meraspids (Pl. 15, fig. 1) are nearly indistinguishable from those of *E. parentalis*, differing in having a faint indication of the mid-ocular lobe furrow. Clique D and E specimens (Pl. 15, figs. 2, 4) differ in having a narrower LA and larger intergenal spines. In all stages the ocular lobes are longer and intergenal spines are retained even in large specimens. By clique F, the glabella has a mature configuration with a constriction at S1 and a modified L3, but L3 and LA are not appreciably wider than L0, and a general tapering forward appearance is maintained through clique G.

Gabriellus sp. 1

Pl. 15, figs. 7-9

Discussion: Fragmentary material from the Mural Formation, locality 1, Mt. Kerkeslin, British Columbia, can be assigned to *Gabriellus*. It has long ocular lobes (tips opposite of midlength of L0), a moderately long preglabellar field, terrace lines on the glabella and slightly advanced genal spines. It is unclear on the single specimen that has the posterior border preserved whether or not an intergenal spine is present.

Genus *Mesolenellus* Palmer and Repina, 1993(nom. transl. herein, ex *Olenellus* (*Mesolenellus*) Palmer and Repina, 1993)

Type Species: *Holmia hyperborea* Poulsen, 1974, from the Buen Formation, near Børglum Elv, Peary Land, north Greenland.

Diagnosis: A genus of Wanneriidae with glabella slightly constricted at S1; widest at L3/base of LA. Anterior border of equal width to lateral border. Preglabellar field long in small holaspid stage. LA elongate, tapering anteriorly. Ocular lobes strongly curved. Ocular lobes close to glabella but with distinct interocular area. Intergenal ridges distinct. Intergenal spines small, located closer to L0 than to genal spines. Genal spines typically advanced: opposite or anterior of S0. Rostral plate terminates at genal angle. T3 macropleural in small stages, amplipleural in holaspid. Thoracic pleurae narrow, pleural spines long, falcate. Prosopon of caecae on extraocular areas. Meraspid cephalon with straight anterior border and procranial spines.

Other Species:

Olenellus intermedius Peach, 1894; "Furoid" Beds, Meall a'Ghiubhais, Scotland.

Olenellus hamoculus Cowie and McNamara, 1978; "Furoid" Beds, Loch Awe, Scotland.

Mesolenellus guthi n. sp.; Poleta Fm., White Mtns., California.

Mesolenellus moorei n. sp.; Poleta Fm., near Goldfield, Nevada.

Discussion: *Mesolenellus* was erected as a subgenus of *Olenellus* by Palmer and Repina (1993) and diagnosed as having advanced genal spines, a preglabellar field, intergenal spines near L0 and long ocular lobes with tips situated near the glabella. This diagnosis differs from that of *Angustolenellus* Palmer and Repina, 1993 (also erected as a subgenus of *Olenellus*) only in the course and length of the ocular lobes. This feature alone is insufficient to distinguish a different

genus. *Angustolenellus* is here synonymized with *Mesolenellus*. This genus differs from *Olenellus* and other Olenellinae as it lacks isolated S2's, a macropleural T3 and has strongly advanced genal spines and medially positioned intergenal spines. *Mesolenellus* is assigned to the Wanneriidae on the basis of its marginal S2's, an amplipleural T3, and a wanneriid pattern of development of LA.

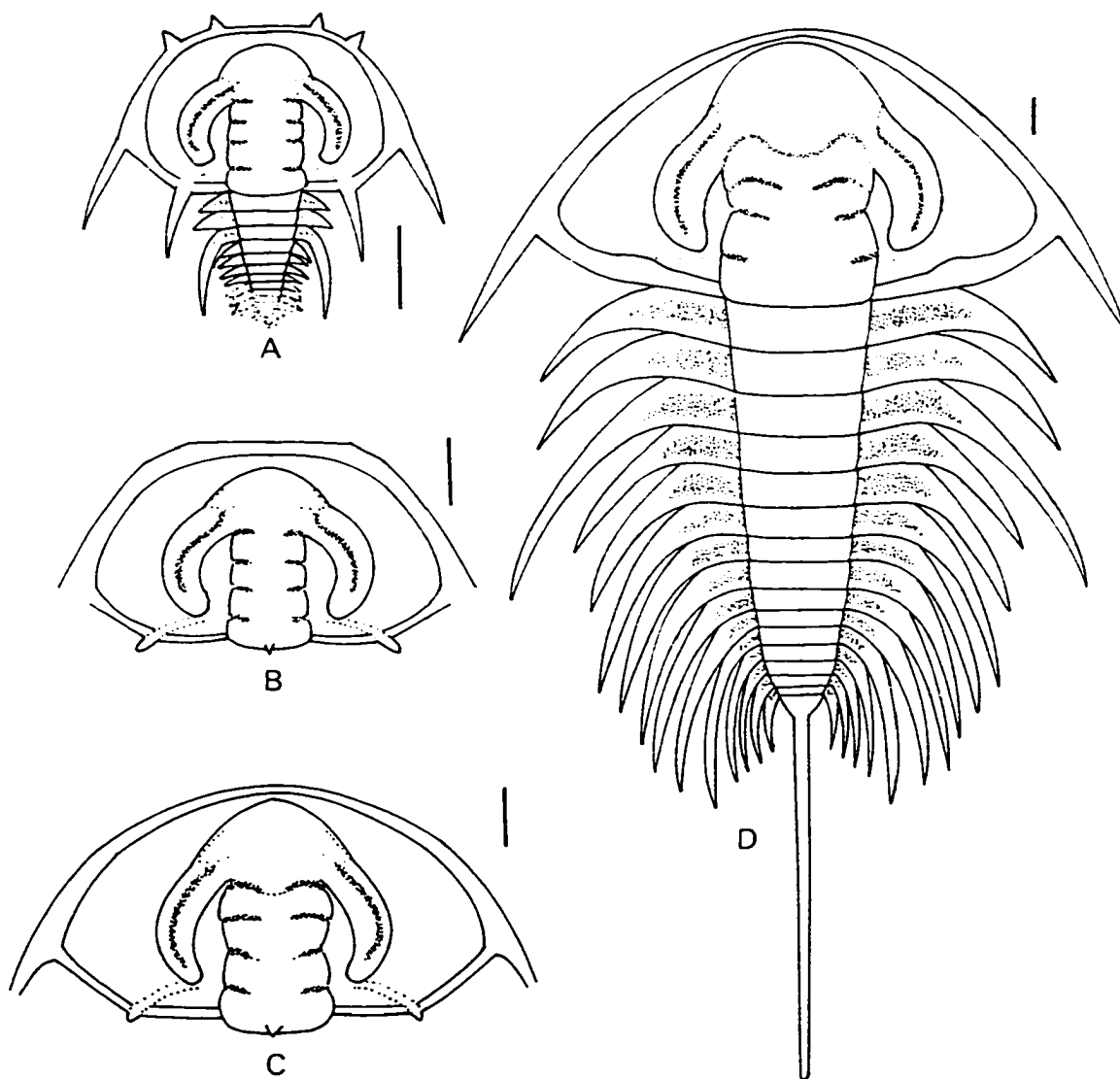
The type species, *Mesolenellus hyperboreus* (Poulsen) was described in detail by Poulsen (1974) and a particularly fine specimen was illustrated by Palmer and Peel (1979, fig. 3) and Palmer and Repina (1993, fig. 1.7). The species was originally attributed to *Holmia* on the basis of its "general glabellar morphology, advanced genal spines, intergenal spines close to the occipital ring, sixteen segments in the thorax which is considerably narrower anteriorly than the cephalon, strongly deflected pleurae, and narrow extraocular genae" (Poulsen, 1974, p. 86). However, *M. hyperboreus* lacks the narrow extraocular areas always seen in holmiids and has long, falcate pleural spines, unlike the short sentate spines of *Holmia*. It has the diagnostic features of wanneriids and is similar in morphology to *Elliptocephala* and *Gabriellus*.

Mesolenellus shares with *Elliptocephala* the same glabellar configuration and ocular lobe positions, but has the advanced genal spines, distinct intergenal spines, narrow thoracic pleurae and an amplipleural T3 characteristic of *Gabriellus*. The intergenal spines in the holaspis are more medially positioned in this genus than in other wanneriids. The ontogeny has been illustrated in detail for the type species (Poulsen, 1974) and is illustrated for two new species here. *Mesolenellus* has a unusual meraspis outline with a straight rather than rounded anterior margin, procranial spines and unusually long intergenal spines. The meraspis intergenal spines are medially positioned and posterolaterally directed like those of *Elliptocephala*, but are long and narrow (note that meraspid of *E. asaphoides* (Pl. 8, figs. 7-9) have similar intergenal spines but the exact length is questionable). Intergenal spines in meraspid of the Olenellinae and Bristoliinae are also long, but they are posteriorly directed and wide: shaped more like a baseball bat.

Mesolenellus guthi n. sp.

Plate 16, figs. 1-9; Text-fig. 40

Diagnosis: A species of *Mesolenellus* with tips of ocular lobes opposite of S0. Cephalic border moderately narrow: less than half length of L0. Preglabellar field absent. Parafrontal band distinct. Intergenal spines small. Genal spines advanced: opposite of L1. Posterior occipital tubercle large. T1-T14 with large axial tubercles. Meraspis cephalon with two pairs of procranial spines, macropleural T3.



Text-fig. 40. Ontogeny of *Mesolenellus guthi* n. sp. A. clique C B. clique D C. clique E
D. clique F scale bars = 1 mm

Holotype: A complete specimen (LACMIP 7397; Pl. 16, fig. 9) from the Poleta Formation, locality 22, LACMIP collection 26862, Cedar Flat, east of Big Pine, White Mountains, California.

Paratypes: LACMIP 12561, ICS 1056#10, ICS 1056#24

Etymology: For Peter L. Guth who donated large collections of superb specimens of this species to the Los Angeles County Museum.

Occurrences: CALIFORNIA. Poleta Formation, Inyo County: locality 22 and sections CF and NH, Cedar Flat area, east of Big Pine, White Mountains. NEVADA. Poleta Formation: section GP, Mt. Dunfee area, 7 km east of Gold Point, Esmeralda County.

Zonal Biostratigraphy: *Gabriellus poletensis* Subzone, *Elliptocephala* Zone.

Discussion: *Mesolenellus guthi* can be distinguished from all other species of *Mesolenellus* by the absence of a preglabellar field in the large holaspide stage. Compared to the type species, *M. guthi* has less advanced genal spines, a larger, broader LA, and two pairs of procranial spines instead of one. Specimens of *M. hyperboreus* also have effaced glabellar furrows. The Scottish species *M. hamoculus* (Cowie and McNamara, 1978) and *M. intermedius* (Peach, 1894) have shorter ocular lobes than *M. guthi*. *M. moorei* n. sp., also from the Poleta Formation, has more advanced genal spines and an unusual set of anterolateral spines on the meraspide cephalon.

Mesolenellus guthi is known from abundant material, including articulated specimens. The thorax is very similar to that of *M. hyperboreus*, including an amplipleural T3, narrow thoracic pleurae and long, falcate thoracic spines. The pygidium and possible opisthothoracic segments are unknown. An articulated meraspide (Pl. 16, fig. 3) has a macropleural T3. Hypostomes associated with this species have straight posterior margins and up to five pairs of posterolateral spines. The posterolateral margin is slightly expanded. A small hypostome has five pairs of long posterior spines, plus a median spine.

Ontogeny: A detailed ontogenetic sequence is available for *Mesolenellus guthi*, except for cliques A and B which are described for *M. moorei*. The ontogenetic pattern is virtually identical to that illustrated for the type species, *Mesolenellus hyperborea* by Poulsen (1974), differing mainly in the possession of two pairs of procranial spines instead of one, and in the rapid loss of a preglabellar field by clique D. All of these ontogenies are so close to that of *Elliptocephala* that only the differences will be described.

Clique C meraspids have a straight anterior margin and two pairs of procranidial spines at the anterolateral corners. Mid-ocular lobe furrows well-developed and a short preglabellar field is present. Both genal and intergenal spines are long. A partial thorax of at least 6 segments is known with a macrospinous T3. (Pl. 16, figs. 1, 3)

Clique D specimens retain a straight anterior margin but have lost the procranidial spines. Intergenal spines are short but well-developed. (Pl. 16, figs. 2, 4)

Clique E specimens develop a rounded anterior margin and LA comes nearly in contact with the anterior border. Lateral glabellar lobes develop at this clique. (Pl. 16, fig. 6)

Clique F holaspids have lost the preglabellar field but still retain intergenal spines. The glabella is distinctly constricted and L3 fully modified. (Pl. 16, figs. 7-9)

Mesolenellus moorei n. sp.

Pl. 16, figs. 10-11; Pl. 17, figs. 1-7

Diagnosis: A species of *Mesolenellus* with tips of ocular lobes opposite S0. Cephalic border moderately wide; width more than half length of L0. Preglabellar field moderately short. LA short. Intergenal spines distinct, slightly advanced. Genal spines advanced opposite posterior of L2. Posterior occipital tubercle distinct. Prosopon reticulate on extraocular areas. Meraspid cephalon with straight anterior margin, procranidial and anterolateral spines.

Holotype: A nearly complete cephalon (GF165#3; Pl. 17, fig. 7) from the middle Poleta Formation, section GF, LACMIP collection 17037, 7.5 km northwest of Goldfield, Esmeralda County, Nevada. **Paratypes:** LACMIP 12564, 12567, 12569

Occurrences: NEVADA. Middle Poleta Formation, Esmeralda County: section GP, Mt. Dunfee area, 7 km east of Gold Point; section GF, Montezuma Range, 7.5 km northwest of Goldfield. CALIFORNIA. Middle Poleta Formation, section NH, Cedar Flat Area, east of Big Pine, White Mountains, Inyo County.

Zonal Biostratigraphy: *Elliptocephala stewarti* Subzone, *Elliptocephala* Zone.

Etymology: For Johnnie N. Moore, in honour of his contributions to Lower Cambrian stratigraphy in the Great Basin. Johnnie also studied the Goldfield area where the type material comes from.

Discussion: *Mesolenellus moorei* has the widest cephalic border of any described species of *Mesolenellus* and is unique in having slightly advanced intergenal spines, and both procranidial and anterolateral spines in the meraspid stage. The anterolateral spines have not been described in any other olenelloid. They are located opposite of LA, midway between the procranidial and genal spines. *Olenelloides armatus* (Peach, 1894) also has a set of spines approximately midlength on the cephalon. These spines are opposite L2 rather than LA and have been interpreted to represent genal spines (Palmer and Repina, 1993, p. 24, 25). The anterolateral spines in *M. moorei* cannot be genal spines as the latter are visible opposite of L1. In comparison, *M. guthi* has a double set of procranidial spines and the more lateral pair are possibly homologous to the anterolateral spines of *M. moorei*.

Mesolenellus moorei has long ocular lobes like those of *M. guthi*, but has a longer preglabellar field, wider cephalic border and more advanced genal spines. The Scottish species of *Mesolenellus* also have distinct preglabellar fields, but have shorter ocular lobes and narrower cephalic borders. The prosopon of *M. moorei* is poorly known, but a single fragmentary specimen shows reticulation on the extraocular areas (Pl. 17, fig. 1). A poorly preserved, clique F holaspid with a partial thorax (Pl. 17, fig. 2) has little indication of a macropleural T3. The pleural spine is not preserved.

Ontogeny: A complete early ontogeny is known for *Mesolenellus moorei*, closely comparable in its glabellar development to *Laudonia*. Specifically, the glabella maintains an immature appearance through clique G holaspids. Clique A meraspids (Pl. 16, fig. 10) are nearly indistinguishable from those of *Elliptocephala parentalis*, except for a slight forward taper to the glabellar stalk. Clique B meraspids (Pl. 16, fig. 11; Pl. 17, fig. 5) have an unusual octagonal cephalic outline with procranidial, anterolateral, genal and intergenal spines. Mid-ocular lobe furrows are already clearly distinguished at this clique. Clique C meraspids (Pl. 17, figs. 3-4) have lost all but the genal and intergenal spines and have a strongly rounded anterior margin. Clique D specimens (Pl. 17, fig. 6) develop a subrounded LA which is maintained through clique F. At clique F (Pl. 17, figs. 2, 7), the intergenal spines become slightly advanced.

Genus *Wannerellus* n. gen.

Type species: *Wannerellus alcatrazensis* n. sp. from the lower Harkless Formation, Alcatraz Island, Esmeralda County, Nevada.

Diagnosis: A possible genus of Wanneriidae with glabella widest at L3 to base of L4. Cephalic border moderately narrow: typically less than half length of L0. Anterior border usually of equal width to lateral border. Preglabellar field moderately long. Plectrum full, of single or multiple ridges. LA triangular; widest at base, tapers anteriorly. Ocular lobes strongly curved. Intergenal ridges and spines poorly developed. Genal spines not advanced to slightly advanced: opposite of L0 or T1. Prosopon of caecae on extraocular areas, reticulation on glabella. Meraspid cephalon with rounded anterior margin, wide, short LA, and long, broad, posteriorly directed intergenal spines.

Etymology: The stem of the generic name *Wanneria* is combined with the suffix of *Olenellus* to emphasize that *Wannerellus* has characteristics of both genera.

Other Species:

Paedeumias tricarinatus Poulsen, 1932; Ella Island Fm., east Greenland.

Paedeumias turmalis Cowie, 1968; Police Post Fm., Ellesmere Island, Arctic Canada.

Olenellus laxocules Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

[?] *Olenellus sequomalus* Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

Wannerellus alcatrazensis n. sp.; Harkless Fm., Alcatraz Island, Nevada.

Discussion: *Wannerellus* has a curious mix of features characteristic of the Olenellidae and Wanneriidae. It is tentatively assigned to the Wanneriidae on the basis of its deep mid-ocular lobe furrows, marginal S2, partially reticulate prosopon, and meraspid with a short, wide LA. However, *Wannerellus* is characterized by a plectrum, often of multiple ridges, and intergenal spines on the meraspid which are long, posteriorly directed and shaped like a baseball bat - both features characteristic of the Olenellidae, particularly *Olenellus*. They have not been noted in any other wanneriid genera. *Wannerellus* is most similar in known morphology to *Elliptocephala* differing only in its unusual Olenellidae features. The post-cephalic morphology is unknown in all assigned species.

Olenellus laxocules Fritz, 1972 and *Olenellus sequomalus* Fritz, 1972, both from the Sekwi Formation, Mackenzie Mountains are assigned to *Wannerellus*. Both have tendencies towards effacement in

their anterior glabellar furrows. *W. sequomalius* is somewhat problematic as it has all the holaspid feature of the genus, but the smallest meraspid (Fritz, 1972, pl. 12, fig. 14) lacks a well-defined wide LA. The large meraspid (Fritz, 1972, pl. 12, fig. 15) has a wider LA typical of wanneriids. A small hypostome (Fritz, 1972, pl. 12, fig. 17) associated with this species has a fully spinous posterior margin bearing seven pairs of spines plus a median spine. A minute hypostome (Fritz, 1972, pl. 11, fig. 12) associated with *W. laxocules* has a fully spinous posterior margin with peg-like spines. This is an unusual species in that its ocular lobes are close to the glabella creating a negligible interocular area; a state characteristic of *Gabriellus*. It differs from *Gabriellus* in lacking the fully tapering glabella and in having a plectrum. The plectrum in *W. laxocules* is not a single ridge, rather at least four separate ridges can be distinguished in the preglabellar field (Fritz, 1972, pl. 11, fig. 19). A similar state is seen in *W. tricarinatus* (Poulsen) from the Ella Island Formation of east Greenland: three ridges can be seen on large holaspids and seven or more on small holaspids. *W. tricarinatus* can also be distinguished from *W. laxocules* as it has a longer preglabellar field and anterior glabellar furrows are deeply impressed. *W. turmalis* (Cowie, 1968) from the Police Post Formation of Ellesmere Island has a glabella that is less evenly tapered than in the other species, deeply impressed glabellar furrows and a plectrum of a single ridge.

Wannerellus alcatrazensis n. gen., n. sp.

Pl. 17, figs. 8-12

Diagnosis: A species of *Wannerellus* with tips of ocular lobes opposite of S0. Preglabellar field long; subequal to length of L0. Plectrum full, developed as a single ridge. Intergenal position moderately close to genal spine. Posterior border thickens lateral to intergenal position, inflected slightly anteriorly. Genal spines slightly advanced: opposite of L0. Posterior occipital tubercle tiny.

Holotype: A complete cephalon (LACMIP 7413; Pl. 17, fig. 10) from the basal Harkless Formation, locality 12, LACMIP collection 26873, Alcatraz Island, Esmeralda County, Nevada.

Paratypes: LACMIP 12571, 11377

Etymology: The species is named for Alcatraz Island, an "island" of rock in the Nevada desert.

Occurrences: NEVADA. Lower Harkless Formation, Esmeralda County: locality 14, south of Coyote Road, 6.5 km west of Silver Peak; locality 12, Alcatraz Island, 1.5 km southeast of Silver Peak. CALIFORNIA. Lower Harkless Formation, Inyo County: locality 21, Cedar Flat area, White Mountains.

Zonal Biostratigraphy: *Wannerellus alcatrazensis* Subzone, *Elliptocephala* Zone.

Discussion: *Wannerellus alcatrazensis* n. gen., n. sp. occurs in basal shales of the Harkless Formation. The meraspid of this species (Pl. 17, fig. 8) has the wide LA typical of wanneriids, combined with long, broad intergenal spines characteristic of the Olenellidae. It has a longer preglabellar field and more advanced genal spines than other species assigned to *Wannerellus*. Most specimens are preserved as internal molds in shale but external molds demonstrate that *W. alcatrazensis* has caecae on the extraocular areas and a parafrontal band. It is closest in morphology to *W. sequomalus* (Fritz, 1972) from the Sekwi Formation, Mackenzie Mountains, with which it shares relatively short ocular lobes and a plectrum of a single ridge. *W. sequomalus* differs as it has a more clavate glabella, arcuate posterior margins, and effaced anterior glabellar furrows. *W. turmalis* (Cowie, 1968) from the Police Post Formation of Ellesmere Island also has a plectrum of a single ridge, but differs from *W. alcatrazensis* in having a less tapered glabella and longer ocular lobes.

Ontogeny: Little ontogenetic material is known for this species except for one slightly distorted clique B meraspid. A long preglabellar field is present and ocular lobes have their posterior tips opposite of L1. The glabellar stalk is nearly parallel-sided and glabellar furrows are shallow marginal pits. LA is short and wide, draping the ocular ridges. Intergenal spines are long, baseball-bat shaped, and located posterior to the ocular lobes. The lateral margins are not sufficiently preserved to judge the presence or absence of genal spines. The anterior cephalic margin is strongly rounded and no procranial spines are developed.

Family Olenellidae Walcott, 1890b

Diagnosis: A family of Olenelloidea with glabella slightly to strongly constricted at S1. LA large, subrounded. S2 usually transversely oriented and isolated. Ocular lobes typically located close to glabella: extraocular areas wider than interocular areas. Mid-ocular lobe furrow shallow to absent. Intergenal spines small or absent in holaspid. Intergenal position generally near genal spines. Hypostome with straight to convex posterior margin; not expanded posterolaterally. Rostral plate generally narrow, delicate. T3 enlarged. T15 typically with long axial spine. Prosopon non-reticulate. Meraspid cephalon with LA short and narrow.

Assigned Subfamilies: Olenellinae Walcott, 1890; Biceratopsinae Pack and Gayle, 1971; Mesonacinae Walcott, 1890.

Discussion: Here the concept of the family Olenellidae is considerable revised and extensively changed in composition from those of previous workers. In the most recent revision, Palmer and Repina (1993) reorganized the family into six subfamilies: Olenellinae, Biceratopsinae, Bristoliinae, Gabriellinae and Laudoniinae. The major change made here is that the Wanneriidae are recognized as a separate family defined by a distinct ontogenetic pattern and holaspid morphology. The Gabriellinae and type genus of the Laudoniinae are considered to be wanneriid taxa. The Bristoliinae shares many synapomorphies with the Biceratopsinae and is synonymized with it. Membership in this combined subfamily closely follows that of Palmer and Repina (1993). The subfamily Olenellinae is also considerable revised in composition from previous classifications.

Olenellus, of course, is the core of all classifications of Olenellidae. Authors have included in the Olenellidae whatever genera they judged to be most closely related to *Olenellus*. But the problem with this approach is that the generic concept of *Olenellus* has been poorly constrained and it has acted as a wastebasket taxon. *Olenellus* is rigorously diagnosed herein and restricted to only those species that are closely comparable to the type species.

All members of the Olenellidae have a meraspid form and ontogenetic pattern that is different from that of members of the Wanneriidae. The general patterns can be observed in the type species of *Olenellus* and *Wanneria*, with details defined using related species with better ontogenetic material. LA in the meraspid stage of all species of Olenellidae is rounded and generally small, in contrast to the short, wide LA that drapes the ocular ridges in species of the Wanneriidae. Initial growth of this lobe is lengthwise, with an increase in width occurring later. Meraspid intergenal spines are typically long and cylindrical to baseball bat shaped with a tapered proximal region. They cross the posterior border posterior lateral to the ocular lobes in clique C and larger cliques (see the Mesonacinae for an account of how this meraspid form can be peramorphically altered). Olenellidae holaspids typically have an isolated S2, ocular lobes either lacking a mid-ocular lobe furrow or having a shallow one, a hypostome with a rounded or straight posterior margin and no expansion of the posterolateral margin, and a thorax with an enlarged T3 and long, hollow axial spine on T15.

The Olenellidae comprises three subfamilies: Olenellinae, Biceratopsinae and Mesonacinae. The first two share a meraspid form but differ in the size of T3 and constriction of the glabella. The Mesonacinae belong to the Olenellidae as they have a small LA in the meraspid stage, a macropleural T3 and ocular lobes without a deep mid-ocular lobe furrow. In other features they

show character states early in ontogeny that are typically only seen in later development of *Olenellus* and appear to be peramorphically altered from an *Olenellus*-like form.

The closest relative of the Olenellidae is likely the Wanneriidae. These families share ocular lobes that are positioned close to the glabella and a basic division of the thorax into a prothorax and opisthothorax by an elongate axial spine on T15. The Holmiidae differ in both these features. Repina (1979) and Palmer and Repina (1993) speculated on the origin of the Olenellidae (which included the Wanneriidae in their classification) and the closest relative of the family. Repina (1979) had proposed both the Nevadiidae and Holmiidae as possibilities, but Palmer and Repina (1993, p. 14-15) favored the Holmiidae as they share with the Olenellidae "a modified L3 of the glabella and an enlarged L4". They further noted that "the ontogeny of olenellids passes through a holmiid stage with regard to relative width of the interocular and extraocular areas". The similarity of the holmiids and wanneriids is noted under these families and the holmiids are accepted as being the likely nearest relatives of the Wanneriidae.

The Olenellidae as here defined may have originated from the Wanneriidae which they stratigraphically follow in first occurrence. *Wannerellus* has a mixture of features of both families and may be a transitional form. Similarities between the Olenellidae and Nevadiidae should also be mentioned. Both have ocular lobes attached only to the posterior part of LA, negligible mid-ocular lobe furrows, ocular lobes positioned near the glabella and a meraspid with a rounded LA. LA is bulbous in nevadiid meraspids (Pl. 3, figs. 3-4), unlike the small, rounded lobe typical of *Olenellus* (Pl. 19, figs. 1-2) but a similar bulbous LA is seen in *Fremontella halli*. These similarities may be convergent as nevadiids have an undifferentiated thorax (does not carry a long axial spine on T15 and T3 is normal to amplipleural, never macropleural), unmodified L3, and a tapered glabella (however, note that in *Nevadella*, the glabella is tapered, but also slightly constricted).

Subfamily Olenellinae Walcott, 1890

Diagnosis: A subfamily of Olenellidae with glabella slightly constricted at S2. Preglabellar field present at least in meraspid stage. T3 macropleural, macrospinous. Meraspid cephalon with long, posteriorly directed intergenal spines; spines cross posterior border immediately behind or lateral to ocular lobe position.

Assigned Genera: *Olenellus* Hall, 1861; *Bolbolenellus* Palmer and Repina, 1993.

Discussion: Membership in the Olenellinae is restricted to *Olenellus* and *Bolbolenellus*. Most previous authors included many more genera. Classifications of Hupé (1953a,b) and Repina (1979) approach the closest in subfamily membership. *Olenellus* and *Bolbolenellus* share a similar configuration of the glabella and the same type of thorax. Meraspids of *Bolbolenellus* have not been described. All Olenellinae have a slightly constricted glabella, isolated or transglabellar S2 and macropleural T3.

The meraspid form seen in the Olenellinae can also be found in the Biceratopsinae. The latter are not classified as Olenellinae because they have a highly derived thorax with an enormous T3 and strong constriction of the glabella. The Mesonacinae have a holaspid form very similar to that seen in the Olenellinae, but lack a preglabellar field and tend to have shorter ocular lobes. The meraspids of mesonacines have similar development of LA compared to meraspids of olenellines, but they lack a preglabellar field and their intergenal spines are short and more laterally positioned. This is interpreted as being peramorphically altered from the olenelline pattern. Both the Biceratopsinae and Mesonacinae could be easily derived from an *Olenellus* type of ontogeny and body plan.

Genus *Olenellus* Hall, 1861

Type Species: *Olenus thompsoni* Hall, 1859, from the Parker Formation, Georgia, Vermont. See Whittington (1989, p. 114) for a discussion of authorship. (By subsequent designation: Walcott, 1886, p. 163.) Junior synonyms listed under discussion of species.

Diagnosis: A genus of Olenellinae with LA subrounded, usually tapering forward slightly from midlength. Cephalic border narrow to moderately narrow: usually less than half length of L0. Preglabellar field present. Plectrum typically present when preglabellar field long. S0, S1 and S3 typically marginal. Intergenal position near genal spines. Genal spines long, falcate, commonly slightly advanced. Thoracic spines long, falcate.

Other Species:

Olenellus gilberti Meek in White, 1874; Pioche Fm., near Pioche, Nevada.

Olenellus howelli Meek in White, 1874; Pioche Fm., near Pioche, Nevada.

Callavia? nevadensis Walcott, 1910b; Prospect Mtn., Nevada.

Paedeumias transitans Walcott, 1910b; Parker Fm., near Georgia, Vermont (= *Paedeumias puertoblancoensis* Lochman, 1952, Buelna Formation, Sonora, Mexico). (and others - see full list under species)

Olenellus thompsoni crassimarginatus Walcott, 1910b; Parker Fm., near Georgia, Vermont (= *Olenellus wanneri* Resser and Howell, 1938 and *Olenellus latilimbatus* Resser and Howell, 1938, both from the Kinzers Fm., Pennsylvania).

Paedeumias robsonensis Burling, 1916; Mural Fm., Mt. Robson Area, BC.

Olenellus clarki Resser, 1928; Latham Fm., Mohave Desert, California.

Olenellus romensis Resser and Howell, 1938; Rome Fm., near Roanoke, Virginia.

Olenellus nodosus Resser and Howell, 1938; Kinzers Fm., Lancaster, Pennsylvania.

Olenellus schucherti Resser and Howell, 1938; Forteau Fm., Bonne Bay, NFL (= *Olenellus terranovicus* Resser and Howell, 1938; Forteau Fm., Bonne Bay, NFL).

Paedeumias granulatus Palmer, 1964; Saline Valley Formation, Gold Point area, Nevada.

Olenellus sp. 2 Fritz, 1972, Sekwi Fm., Mackenzie Mtns., NWT.

Olenellus parvofrontatus Fritz, 1991a, Illtyd Fm., Wernecke Mtns., Yukon.

Olenellus ricei n. sp.; Eager Fm., near Cranbrook, British Columbia.

Species tentatively assigned to *Olenellus*.

Olenellus arcticus Poulsen, 1927, Wulff River Fm., NW Greenland.

Olenellus kentensis Poulsen, 1927, Cape Kent Fm., NW Greenland.

Olenellus mackenziensis Kobayashi, 1936, Clark Mtn., District of Mackenzie.

Paedeumias groenlandicus Poulsen, 1958, Wulff River Fm., NW Greenland.

Olenellus sp. 1 Palmer in Palmer and Halley, 1979, Cararra Fm., California.

Olenellus zondaensis Bordonaro, 1986, La Laja Fm., San Juan, Argentina.

Olenellus sp. 3, Fritz, 1991a, Illtyd Fm., Wernecke Mtns., Yukon.

Olenellus and *Paedeumias* species, Rasetti, 1966, Schodack Fm., North Chatham, New York.

Discussion: *Olenellus* is one of the first established genera of the Olenellina and has acted as a wastebasket taxon for many years. Splitting of *Olenellus* led to the erection of the following genera whose type species were originally assigned to *Olenellus*: *Mesonacis* Walcott, 1985; *Callavia* Matthew, 1897; *Schmidtellus* Moberg in Moberg and Segerberg, 1906, *Peachella* Walcott, 1910b; *Wanneria* Walcott, 1910b; *Nephrolenellus* Palmer and Repina, 1993 and *Bolbolenellus* Palmer and Repina, 1993. The generic concept of *Olenellus* is further refined here by reassignment of approximately 10 species, originally described as *Olenellus*, to *Elliptocephala*. These species have wanneriid features of a marginal S2, reticulate prosopon, and wanneriid pattern of development.

In addition to *Olenellus*, Walcott recognized two other genera: *Mesonacis* Walcott, 1885 and *Paedeumias* Walcott, 1910b. His diagnoses were, however, inadequate and inaccurate, focusing on

the rarely preserved posterior of the body. His summary from (Walcott, 1910b, p. 304) is given below:

Mesonacis has a spine-bearing 15th segment with 10 smaller but typical thoracic segments and a pygidium characterized by postero-lateral spines.

Paedeumias has the 14th segment as a median spine posterior to which there are from 2 to 6 rudimentary segments, and a rudimentary pygidium.

Olenellus has the 15th segment as a terminal telson without segments or pygidium posterior to it.

Paedeumias was based on *Olenellus transitans* which has the 15th segment with a large axial spine (Pl. 18, fig. 6; Pl. 19, figs. 8-9), not the 14th as stated by Walcott. *Olenellus* was based on *Olenellus thompsoni* which has a very broad based axial spine on T15 that obscures the pygidium and any possible opisthothoracic segments. There is no reason to believe that this species lacks a pygidium. Walcott (1910b, p. 304) further stated that "the cephalon and first 14 segments are generically the same in the three genera".

Resser (1928, p. 5) defended the validity of the three genera and expanded on their generic concepts. His characterization of *Mesonacis* included cephalic differences from *Olenellus* of shorter ocular lobes, narrower border, and longer glabella (no preglabellar field). He further emphasized that the opisthothoracic segments of *Mesonacis* had pleurae. Bell (1931) supported Resser's (1928) characterization of *Mesonacis*, but later Resser and Howell (1938) abandoned the genus *Mesonacis* without explanation. Other authors concluded that *Mesonacis* could not be adequately distinguished from *Olenellus*. Raymond (1928), Raw (1936, 1937), Hupé (1953a,b), Poulsen (*in* Moore, 1959), and Chernysheva (1960) synonymized *Mesonacis* with *Olenellus*, but continued to recognize *Paedeumias* as a distinct genus.

Resser (1928, p. 5) diagnosed *Paedeumias* as follows:

Glabella usually tapers forward, never extends forward to rim, with which it is connected by a median ridge. Rim, marginal and epistomal plates, and thorax to the fifteenth segment like *Mesonacis* and *Olenellus*. Intergenal spines present.

Rudimentary segments posterior to the fifteenth *without* pleurae, as in *Olenellus*.

Hypostoma with spines on posterior margin and connected with the rostral or

epistomal plate by a stalk, which probably causes the median ridge on the upper surface of the cephalon.

A critical evaluation of Resser's (1928) characters of *Paedeumias* reveals that: 1. the whole glabella does not taper forward, but LA is tapered in the mid-sided holaspid stage of *Olenellus transitans* 2. the glabella does not "extend to the rim" in the type species of *Olenellus* either, but it is longer (shorter preglabellar field) than the glabella in *Olenellus transitans* 3. presence of intergenal spines is not a distinguishing feature either: short intergenal spines are retained through to the midsize holaspids of *O. transitans*, but are lost in the largest holaspids. It should also be noted that *O. transitans* is the only species that has been demonstrated to possess a stalked hypostome and this is likely a specific characteristic. Thus Resser (1928) failed to provide adequate differentiation of *Paedeumias* from *Olenellus*. Resser and Howell (1938) further revised *Paedeumias* and selected a small holaspid specimen as a lectotype for *Paedeumias transitans* Walcott. Their lengthy diagnosis included many features exhibited by this immature specimen such as a long preglabellar field, plectrum, intergenal spines, and long ocular lobes. These features are modified in larger specimens of the same species and therefore are not useful criteria on which to base a genus. Palmer (1964) further refined the generic concept of *Paedeumias*, but still by using juvenile features and characters of only specific importance (i.e. width of the cephalic border).

Starting in the mid-1950s, with the work of Shaw (1955), Fritz (1972, 1991a), Bergström (1973a), Repina (1979), Palmer (in Palmer and Halley, 1979), Ahlberg *et al.* (1986) and Whittington (1989), the trend was to synonymize both *Mesonacis* and *Paedeumias* with *Olenellus*. In the most recent taxonomic revision of the Olenellina, Palmer and Repina (1993) resurrected both the names *Mesonacis* and *Paedeumias*, but as subgenera of *Olenellus*. *Mesonacis* is recognized here as a genus separate from *Olenellus* based on its glabellar configuration, thoracic shape and ontogenetic pattern. *Paedeumias* is here considered a junior synonym of *Olenellus*.

Palmer and Repina (1993) established two new subgenera of *Olenellus*: *Mesolenellus* and *Angustolenellus*. The type species of *Olenellus* (*Mesolenellus*) is *Holmia hyperborea* Poulsen, 1974. Based on its meraspid form and cephalic configuration (including marginal S2, tapering LA), this species is a wanneriid. *Mesolenellus* is here raised to the level of genus and considered to be a member of the Wanneriidae. Palmer and Repina's (1993) diagnosis of *Olenellus* (*Angustolenellus*)

differed from that of *Mesolenellus* in only a single feature (ocular lobe course and length) of low significance. *Angustolenellus* is considered a junior synonym of *Mesolenellus*.²³

Raw (1936) erected another olenelline genus, *Fremontia*, for "short-eyed" species previously referred to either *Olenellus* or *Mesonacis*. Harrington (1956) provided a diagnosis for the genus and a detailed discussion of the species assigned to it. *Fremontia* was considered a distinct genus by Hupé (1953a,b), Poulsen (in Moore, 1959) and Chernysheva (1960). Fritz (1972, p. 12) synonymized *Fremontia* with *Olenellus* because he claimed that possession of short ocular lobes and slightly advanced genal spines did not effectively separate this genus from *Olenellus*. This synonymy was followed by subsequent workers. The type species of *Fremontia*, *Olenellus fremonti* Walcott, 1910b, is here considered an unusual mesonacine in need of further study (see discussion of species under the Mesonacinae) and *Fremontia* is provisionally accepted as a distinct genus.

An attempt has been made here to evaluate all published species of the Olenellidae and Wanneriidae. Due to the tremendous number of species that have been attributed to *Olenellus* over the past 140 years, there is no attempt made to discuss and review each one. Throughout the systematic text, species are discussed when they are reassigned to different genera. The type species of *Olenellus*, *O. thompsoni* is discussed in detail as well as the associated species, *O. transitans*. Other species of *Olenellus* found within the defined field areas of the thesis are also described.

It is an enormous task to attempt to bring order to the historically poorly constrained genus *Olenellus* with the myriad of species that have been attributed to it. Palmer and Repina (1993) attempted to do so by dividing the genus into five subgenera: *Olenellus* (*Olenellus*), *Olenellus* (*Mesonacis*), *Olenellus* (*Paedeumias*), *Olenellus* (*Angustolenellus*) and *Olenellus* (*Mesolenellus*). They failed, however, to distinguish the wanneriids [*Olenellus* (*Angustolenellus*) and *Olenellus* (*Mesolenellus*), see above] and to recognize that *Olenellus* (*Paedeumias*) was diagnosed by immature features. Ontogenetic pattern and meraspid form have played a key role herein in differentiating taxa and determining relationships. *Olenellus* has a meraspid with a small LA, long preglabellar field, and intergenal spines that are long, posteriorly directed and positioned posterior or posterolateral to the tips of the ocular lobes. In the holaspid, LA is rounded to slightly tapering, the glabella is slightly constricted, S2 is isolated and slot-like, intergenal spines

²³ Note that although *Angustolenellus* has page priority over *Mesolenellus* in Palmer and Repina's (1993) text, *Mesolenellus* is the name selected for the genus, in the interest of stability, since its type species is known from more complete material.

are short or absent and located close to the intergenal spines, T3 is macropleural and T15 has a long axial spine. Typically, the ocular lobes are long with or without a shallow mid-ocular lobe furrow, genal spines are slightly advanced, the thorax has long, falcate pleural spines and the cephalic border is moderately narrow to narrow. The last features are listed only as "typical" as they are particularly prone to heterochronic change as they vary through ontogeny.

Ontogeny: The most complete small ontogenetic sequence known for the Olenellina is that of *Olenellus* sp. A²⁴ from silicified material of the Pioche Formation, Nevada, described by Palmer (1957). The following ontogenetic description will serve as a comparative standard for all Olenellina ontogenies.

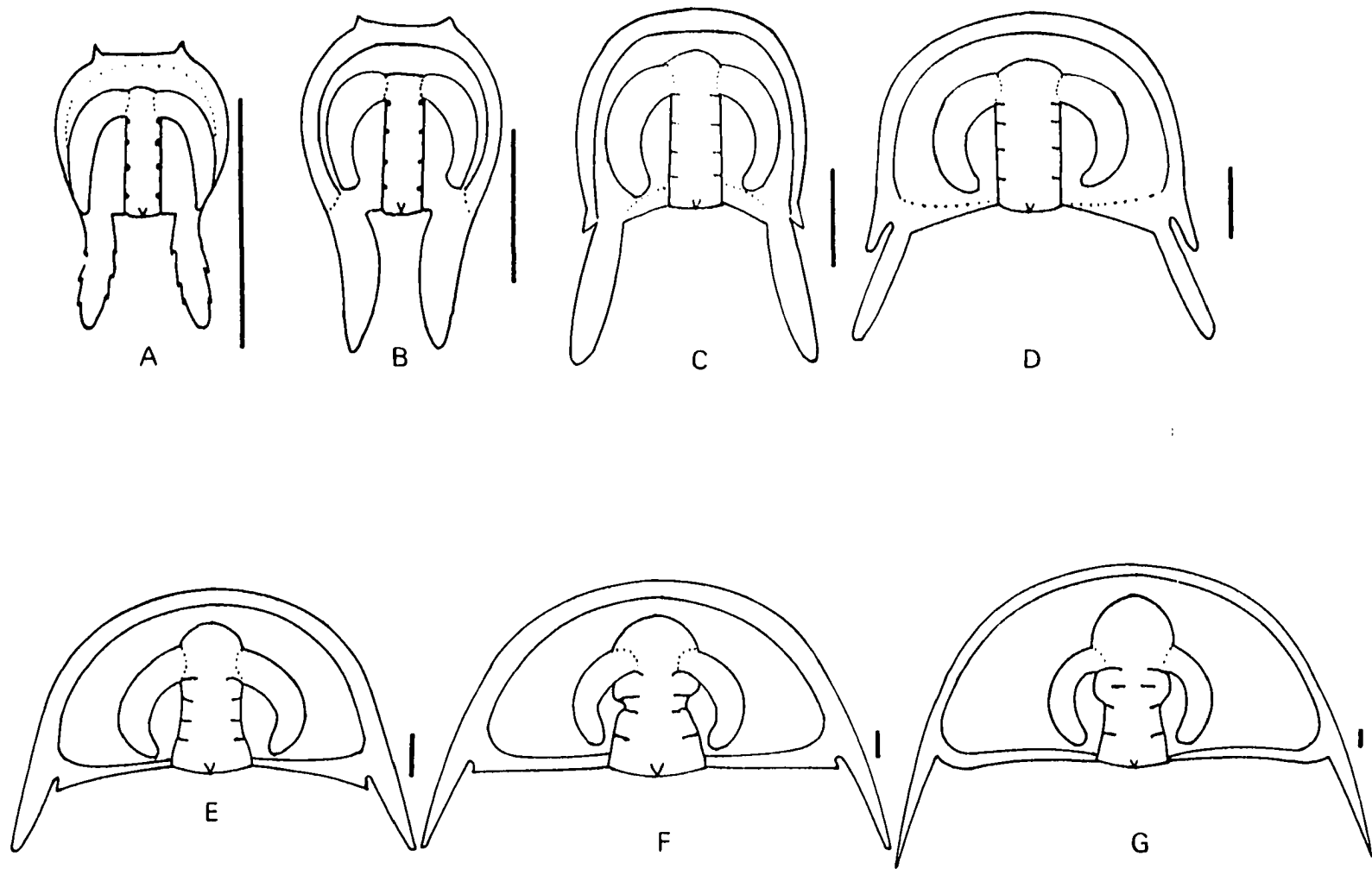
The ontogeny of *Olenellus* sp. A is typical of that of *Olenellus* in most features (Text-fig. 41). One unusual characteristic is that the shortening of the preglabellar field that occurs as LA expands is not pronounced in this species. A plectrum is also absent in the majority of specimens, although this may be a factor of preservation as one meraspid specimen (Palmer, 1957, sp. 19 fig. 12), illustrated in ventral aspect, has a well-defined plectrum. Compared to the ontogeny of carbonate material of *O. transitans* from British Columbia, the anterior expansion of LA occurs at a smaller clique, which also occurs in type material of *O. transitans* and in specimens of *O. ricei* n. sp. from the Eager Formation near Cranbrook. Both of the latter occur in shale. Through comparison with other *Olenellus* ontogenies of articulated specimens, *Olenellus* sp. A probably reached the holaspid stage at a minimum size of 3 mm of cephalic length.

Meraspid Stage

Clique A. 0.5-1 mm. (Text-fig. 41A)

Procranidial spines present. Cephalic border poorly differentiated. Ocular lobes merge into LA and into lateral margin of cephalon. Extraocular areas narrow, present only anteriorly. Glabella parallel-sided; axial furrows shallow, glabellar furrows developed as marginal pits. LA small, contained between anterior termination of ocular ridges. Intergenal spines long, with serrated margins, positioned posterior to the ocular lobes. Genal spines absent. Cephalon subcircular in outline. (approximately equal to Stages I through IIb of Palmer, 1957)

²⁴ This species was originally called *Olenellus gilberti* by Palmer (1957), then designated *Olenellus howelli* by Palmer (in Palmer and Halley, 1979). It is now considered by Palmer (personal communication, March, 1996) to be a new species, which will be named by him in an upcoming paper.



Text-fig. 41. Standard comparative ontogeny for the Olenellina. Ontogeny of *Olenellus* sp. A (to be named by Palmer, submitted). Letters represent cliques. Cliques A through F based on illustrations in Palmer (1957). Clique G based on large holaspid specimen supplied by Palmer. scale bars = 1 mm

Clique B. 1-1.5 mm. (Text-fig. 41B)

Procranial spines present. Cephalic border clearly differentiated. Ocular lobes well-defined, elevated, posterior tips opposite of L0. Extraocular areas narrow; present over full length of cephalon, narrowest posteriorly. Glabella parallel-sided; glabellar furrows developed as marginal pits. LA small, contained between anterior termination of ocular ridges. Intergenal spines long, with smooth edges, positioned posterior to the ocular lobes. Genal spines absent. Cephalon subcircular in outline. (approximately equal to Stages IIc through IIIa of Palmer, 1957)

Clique C. 1.5-2.5 mm. (Text-fig. 41C)

Procranial spines present only in specimens under 2 mm. Ocular lobe posterior tips opposite of L0. Extraocular areas narrower than interocular areas, clearly differentiated over full cephalic length. Glabella parallel-sided; glabellar furrows developed as marginal slots. LA small, subrounded; slightly expanded anterior to position of ocular ridges. Intergenal spines long, positioned posterolateral to the ocular lobes. Genal spines minute. Cephalon subcircular in outline. (approximately equal to Stages IIIb through IVa of Palmer, 1957)

Clique D. 2.5-3 mm. (Text-fig. 41D)

Procranial spines absent. Ocular lobe posterior tips opposite of L0. Extraocular and interocular areas subequal in width. Glabella parallel-sided; glabellar furrows developed as marginal slots, L3 unmodified. LA small, subrounded; slightly expanded anterior to position of ocular ridges. Intergenal spines long. Genal spines short. Cephalon 1.5 times wider than long. (approximately equal to Stage IVb to IVd of Palmer, 1957)

Holaspid Stage²⁵

Clique E. 3-5 mm (Text-fig. 41E)

Ocular lobe posterior tips opposite of L0. Extraocular areas approximately twice width of interocular areas. Glabella slightly constricted at S2, L3 barely modified. Glabellar furrows marginal. LA slightly expanded anterior to position of ocular ridges. Intergenal spines short. Genal spines long. Cephalon approximately twice as wide as long. (approximately equal to Stages IVe through Vb of Palmer, 1957)

Clique F. 5-10 mm. (Text-fig. 41F)

²⁵ The division between the holaspid and meraspid stages is tentatively placed at this point in disarticulated material based on comparison with articulated specimens of other species. Three millimeters is regarded as a minimum size for holaspid *Olenellina*, and specimens of *Olenellus* as small as 2.5 mm with a large 15th axial spine have been observed. A key defining feature of an *Olenellus* holaspid cephalon is relatively large genal and small intergenal spines.

Ocular lobe posterior tips opposite of LO. Extraocular areas approximately 4 times width of interocular areas. Glabella constricted at L2. Glabellar furrows marginal, L3 modified. LA short, subrounded; extends considerably anterior to ocular ridge positions. Intergenal spines short. Genal spines long. Cephalon approximately twice as wide as long. (approximately equal to Stage Vc to Vg of Palmer, 1957)

Clique G. 10+ mm. (Text-fig. 41G)

Ocular lobe posterior tips opposite of anterior of LO to S1. Extraocular areas more than 4 time width of interocular areas. Glabella widest at L2/L3: L3 fully modified, S2 isolated. LA long, subrounded. Intergenal spines absent. Genal spines long. Cephalon more than twice as wide as long. (approximately equal to Stage V+ of Palmer, 1957) Material of this clique is sparsely known to the author and the shorting of the ocular lobes and preglabellar field typical in other species at large size later in this clique cannot be documented here.

Olenellus thompsoni (Hall, 1859)

Plate 18, figs. 8

1859 *Olenus thompsoni* Hall, p. 59, fig. 1.

1910b *Olenellus thompsoni*, Walcott, p. 336-340, pl. 34, fig. 9; pl. 35, figs. 1, 4; pl. 44, fig. 9; [?] pl. 35, figs. 2, 3; [non] pl. 35, figs. 5-7 [= *Olenellus rudis* Resser, 1938]. [synonymy to date]

1910b [?] *Wanneria halli* Walcott, pl. 31, fig. 8 [only].

1925 *Olenellus getzi* Dunbar, p. 307-308, figs. 1, 2.

1925 *Olenellus thompsoni*, Dunbar, p. 305-307.

1928 *Olenellus thompsoni*, Resser, p. 4.

1928 *Olenellus thompsoni*, Raymond, p. 169.

1931 *Olenellus thompsoni*, Bell, p. 2, 4, 5, 10, 12; [non] figs. 1-4 [= *Olenellus transitans*].

1938 *Olenellus buttsi* Resser, p. 52, pl. 5, figs. 9, 19.

1938 *Olenellus rudis* Resser [part], pl. 5, fig. 15 [only].

1938 *Olenellus thompsoni*, Resser and Howell, p. 219-220, pl. 3, figs. 17, 19; [non] fig. 18 [= *Olenellus transitans*].

1938 *Olenellus getzi*, Resser and Howell, p. 221, pl. 5, figs. 1-5.

1938 *Olenellus peculiaris* Resser and Howell, p. 223, pl. 7, fig. 10.

1938 *Olenellus alius* Resser and Howell, p. 224, pl. 7, fig. 7, 8.

1938 *Olenellus agellus* Resser and Howell, p. 223, pl. 9, figs. 11-13.

1938 [?] *Olenellus jonasae* Resser and Howell, p. 222, pl. 8, figs. 5-6; [non] fig. 4 [= *Olenellus transitans*].

- 1938 *Olenellus nitidus* Resser and Howell, p. 224, pl. 8, figs. 7-9.
 1942 *Olenellus thompsoni*, Størmer, p. 68.
 1948 [non] *Olenellus thompsoni*, Kindle and Tasch, p. 135-136, p. 1, fig. 4.
 1954 *Olenellus thompsoni*, Shaw, p. 1040-1042, 1045.
 1955 *Olenellus thompsoni*, Shaw, p. 792-793.
 1962 *Olenellus thompsoni*, Shaw, p. 332.
 1969 *Olenellus thompsoni*, Campbell and Kauffman [part], p. 173-175.
 1989 *Olenellus thompsoni*, Whittington [part], p. 114-120 [non pl. 1, figs. 4-8; pl. 2, figs. 13,15; pl. 3, figs. 17, 19; pl. 5, figs. 29, 31, 34; text-figs. 1-3, 27 = *Olenellus transitans*].
 1993 *Olenellus (Olenellus) thompsoni*, Palmer and Repina, fig. 3.1.

Diagnosis: A species of *Olenellus* with posterior tips of ocular lobes opposite of anterior of L0. Cephalic border moderately narrow: approximately half length of L0. Preglabellar field short. Intergenal position close to genal spines. Posterior border curves slightly anteriorly lateral to intergenal position. Genal spines slightly advanced: opposite of T1. Axial nodes small on T1-T14. T15 axial spine base equals full width of T15 axial ring. Opisthothorax of 3 segments. Posterior thoracic spines short.

Junior Synonyms: *Paradoxides macrocephalus* Emmons, 1860; *Paradoxides brachycephalus* Emmons, 1860; *Olenellus getzi* Dunbar, 1925; *Olenellus buttsi* Resser, 1938; *Olenellus peculiaris* Resser and Howell, 1938; *Olenellus alius* Resser and Howell, 1938; *Olenellus agellus* Resser and Howell, 1938; ? *Olenellus jonasae* Resser and Howell, 1938; *Olenellus nitidus* Resser and Howell, 1938.

Holotype: A complete specimen (AMNH 244) from the Parker Formation, locality 25 (Walcott, 1910b) Parkers Quarry, Georgia, Vermont. This specimen has been reported lost by Resser and Howell (1938, p. 220) and presumably has been lost even longer because Walcott (1910b) did not illustrate the type specimen. A plaster cast of the holotype (plastotype USNM 4795) still exists in the USNM. Illustrated by Hall (1959, fig. 1 - drawing), Resser and Howell (1938, text-fig. 1.1 - copy of Hall's drawing; pl. 3, fig. 19 - photograph of plaster cast of Hall's type specimen).

Occurrences:²⁶ VERMONT. Parker Formation, localities 25 and 25a (of Walcott, 1910b) near Georgia, Franklin County. PENNSYLVANIA. Kinzers Formation: locality 8q (Walcott, 1910b), 3

²⁶ Other localities are listed by Walcott (1910, p. 339-340) but are not included here as no specimens from them were illustrated by Walcott and consequently the species identifications could not be confirmed.

km northwest of York; locality 12x (Resser and Howell, 1989), 1.6 km north of Rohrerstown; locality 22L (Resser and Howell, 1938), 1 km south of East Petersburg. ALABAMA. Rome Formation: locality 141d (Resser, 1938), 2.5 km north of Montevallo; locality 17a (Resser, 1938), 2.5 km west of Montevallo; locality 164c (Resser, 1938), 1.5 km south of Helena.

Zonal Biostratigraphy: *Olenellus transitans* Zone.

Discussion: The species concept of Walcott (1910b) for *Olenellus thompsoni* is followed. Walcott recognized two species of *Olenellus* from the Parker and Kinzers formations of Vermont and Pennsylvania: *Olenus thompsoni* Hall, 1859 and *Paedeumias transitans* Walcott, 1910b. Resser and Howell (1938) restudied these trilobites and divided the two species into nineteen. Campbell and Kauffman (1969) analyzed Resser and Howell's (1938) species from the Kinzers fauna and recognized that they had been greatly oversplit and considered only two species of these species of *Olenellus* to be distinct: *Olenellus thompsoni* and *O. nodosus*. The remainder represent forms produced by deformation, injury or grow stage. It is here proposed that at least four species are present in these two formations: *O. nodosus*, *O. crassimarginatus*, *O. thompsoni* and *O. transitans*. In their analysis, Campbell and Kauffman measured all of Resser and Howell's specimens, and the measurements were statistically compared to measurements of *Olenellus getzi* Dunbar, 1925 (here considered to be *O. thompsoni*). Only one of the criteria used here to distinguish *O. thompsoni* from *O. transitans* was used: length of the cephalic border measured exsagittally. Campbell and Kauffman's (1969) results showed considerable variation in this measurement. This result is understandable considering that exsagittally is a difficult position to accurately measure border length due to crushing of LA forward and backward extension of the border into a plectrum. Measurements of border width (opposite of L3) for *O. transitans* are one third or less the length of L0 while for *O. thompsoni* they are more than half the length of L0. Campbell and Kauffman's measurement of 'glabellar length' (also an indirect measurement of preglabellar field length) is faulty as only the length of LA appears to have been measured. A modern study of the Kinzers and Parker Formation faunas is needed to reconsider in detail the number of species of *Olenellus* that can be distinguished. Until such time as this is done, Campbell and Kauffman's general results are largely accepted and Resser and Howell's (1938) recognized species (other than *O. nodosus*) from the Kinzers and Parker formations are held in synonymy with either *O. thompsoni*, *O. crassimarginatus* or *O. transitans*.

Olenellus thompsoni can be distinguished from *Olenellus transitans* by a shorter preglabellar field, wider cephalic border, shorter posterior thoracic spines, and a broad-based axial spine on T15

that equals the whole width of the axial region. One of Walcott's (1910b, pl. 33, fig. 1) specimens of *Paedeumius transitans* was incorrectly assigned to *O. thompsoni* by Resser (1928) and by Resser and Howell (1938) (and, further, incorrectly included in Campbell and Kauffman's (1969) analysis as *O. thompsoni*). This is an unusually large specimen (re-illustrated in Whittington, 1989, figs. 4-5) that has a relatively short preglabellar field. Preglabellar field length shortens during holaspis ontogeny: in this specimen it is relatively short but still proportionately longer than in smaller specimens of *Olenellus thompsoni*. It also has the narrow cephalic border and long posterior thoracic spines characteristic of *O. transitans*.

Olenellus granulatus (Palmer, 1964) from the Saline Valley Formation near Gold Point, Nevada, has the wide cephalic border, long ocular lobes, short preglabellar field and slightly advanced genal spines characteristic of *O. thompsoni*. The Gold Point material is uncompressed in limestone and has a distinct preglabellar field with plectrum in midsize holaspids and the cephalon has a prosopon of fine granules on the glabella, caecae on the extraocular areas. *O. granulatus* is closely comparable to *O. thompsoni*, but differs in having deeper glabellar furrows and a more pit-shaped S2.

O. thompsoni also occurs in the Rome Formation of Alabama. *Olenellus buttsi* Resser, 1938, collected near Montevallo, Alabama, is indistinguishable from specimens of *O. thompsoni* from the type area. One specimen illustrated as *O. rudis* Resser, 1938 (pl. 5, fig. 15) also from Alabama, can additionally be assigned to *O. thompsoni*. Fragments described as *Olenellus thompsoni* by Kindle and Tasch (1948) from the Monkton Formation of Vermont are too fragmentary for specific assignment. Moreover, they co-occur with a species of *Bolbolenellus*, a genus only found in uppermost Lower Cambrian strata. *O. thompsoni* co-occurs with a species of *Wanneria*, an older genus than *Bolbolenellus*, in the Kinzers Formation.

Ontogeny: Small stages of *Olenellus thompsoni* are poorly known. Moderately small holaspis cephalons (clique F) described as *O. jonasae* and *O. nitidus* by Resser and Howell (1938; pl. 8 figs. 5, 9) have short preglabellar fields and fairly wide cephalic borders and likely belong to *O. thompsoni*. They are closely comparable to clique F holaspids of *Olenellus* sp. A with a short, subrounded LA and constricted glabella without isolated S3. The preglabellar field is short but distinct with no indication of a plectrum. The preglabellar field in clique G holaspids is short and intergenal spines are absent. No meraspids of *O. thompsoni* have been illustrated from the Kinzers or Parker formations.

Olenellus cf. thompsoni

Pl. 18, fig. 7

Occurrences: NEVADA. Saline Valley Formation, Esmeralda County: section PC, Paymaster Canyon, 21 km northeast of Silver Peak.

Discussion: Rare specimens that co-occur with *Olenellus transitans* in the Saline Valley Formation show an affinity to *Olenellus thompsoni*. They differ from topotype material (Pl. 18, fig. 8) of *O. thompsoni* only by having deeper glabellar furrows and a slightly smaller LA. Only cranidia of moderate preservation are known, therefore the identification is tentative.

Olenellus transitans (Walcott, 1910b)

Pl. 18, figs. 1-6; Pl. 19, figs. 1-9; Pl. 20, fig. 1; Text-figs. 24 (bottom), 25 (left)

1910b *Paedeumias transitans* Walcott, p. 305-310, pl. 24, fig. 12; pl. 32, figs. 1-13; pl. 33, figs. 1-5; pl. 34, figs. 1-7; pl. 41, fig. 7; pl. 44, figs. 7, 8; [?] pl. 25, figs. 19-25; [non] pl. 34, fig. 8; .

[synonymy to date]

1925 *Paedeumias transitans*, Dunbar, p. 308.

1928 *Paedeumias transitans*, Raymond, p. 169.

1928 *Paedeumias transitans*, Resser, p. 4.

1931 *Paedeumias transitans*, Bell, p. 2, 4, 5, 13.

1931 *Olenellus thompsoni*, Bell, text-figs. 1-4.

1932 *Paedeumias hansenii* Poulsen, p. 43-45, pl. 11, figs. 4-11.

1938 *Paedeumias transitans*, Resser, p. 53.

1938 *Paedeumias transitans*, Resser and Howell, p. 226, pl. 8, fig. 13.

1938 *Olenellus thompsoni*, Resser and Howell, pl. 3, fig. 18 [only].

1938 *Olenellus similis* Resser and Howell, p. 221, pl. 4, figs. 12-14; [non] fig. 11 [= *Wanneria walcottana*].

1938 *Paedeumias yorkense* Resser and Howell, p. 227, pl. 6, figs. 4, 5; pl. 9, figs. 5-7, pl. 10, figs. 1, 2.

1938 *Olenellus roddyi* Resser and Howell, p. 221-222, pl. 6, figs. 6, 7.

1938 *Paedeumias perkinsi* Resser and Howell, p. 226, pl. 8, fig. 1.

1938 *Paedeumias glabrum* Resser and Howell, p. 226, pl. 8, figs. 2, 3.

1938 *Olenellus jonasae* Resser and Howell, p. 222, pl. 8, fig. 4, [?] figs. 5-6 [?= *Olenellus thompsoni*].

1938 *Paedeumias eboracense* Resser and Howell, p. 227, pl. 8, fig. 14.

1942 *Paedeumias transitans*, Størmer, p. 68.

1952 *Paedeumias puertoblancoensis* Lochman, p. 94-95, pl. 19, figs. 9-16.

- 1954 *Olenellus brachycephalus*, Shaw, p. 1040, 1041, 1044.
 1955 *Olenellus brachycephalus*, Shaw, p. 791-792, pl. 75, figs. 1-3.
 1957 *Paedeumias yorkensis*, Whittington, p. 431, text-fig. 2a-c.
 1962 [non]*Olenellus brachycephalus*, Shaw, p. 332-333, pl. 50, figs. 25-29.
 1972 *Olenellus puertoblancoensis*, Fritz, p. 14-15, pl. 17, figs. 1-7.
 1979 *Olenellus puertoblancoensis*, Palmer in Palmer and Halley, p. 74, pl. 4, figs. 11, 14.
 1983 *Olenellus (Paedeumias) transitans*, Stouge and Boyce, pl. 8, fig. 5.
 1989 *Olenellus thompsoni*, Whittington [part], p. 114-120, pl. 1, figs. 4-8; pl. 2, figs. 13,15; pl. 3, figs. 17, 19; pl. 5, figs. 29, 31, 34; text-figs. 1-3, 27.
 1992 *Olenellus thompsoni*, Whittington, p. 57.
 1993 *Olenellus (Paedeumias) transitans*, Palmer and Repina, fig. 3.3.

Diagnosis: A species of *Olenellus* with posterior tips of ocular lobes opposite anterior of L0. Cephalic border narrow: approximately one third length L0. Preglabellar field long. Intergenal spines small. Intergenal position close to genal spines. Genal spines slightly advanced: opposite of L0. Posterior occipital node small. Hypostome with 6 pairs of marginal spines, straight posterior margin. Hypostome attached to rostral plate by mineralized stalk. Axial nodes small on T8-T14. T15 axial spine base approximately half of T15 axial width. Posterior thoracic spines long. Opisthothorax of 3 to 4 segments. Pygidium roughly rectangular in outline, central axial region inflated. Prosopon of fine terrace lines on dorsal exoskeleton.

Lectotype: Complete specimen (USNM 56808b) from the Parker Formation, locality 25 (Walcott, 1910b), Parkers Quarry, Georgia, Vermont. Designated by Resser and Howell (1938, p. 226). Illustrated by Walcott (1910b, pl. 34, fig. 1); Resser and Howell (1938, pl. 8, fig. 13); Palmer and Repina (1993, fig. 3.3).

Junior Synonyms: *Paedeumias hansenii* Poulsen, 1932; *Olenellus similis* Resser and Howell, 1938; *Paedeumias yorkense* Resser and Howell, 1938; *Olenellus roddyi* Resser and Howell, 1938; *Paedeumias perkinsi* Resser and Howell, 1938; *Paedeumias glabrum* Resser and Howell, 1938; *Paedeumias eboracense* Resser and Howell, 1938; *Paedeumias puertoblancoensis* Lochman, 1952.

Occurrences: VERMONT. Parker Formation, locality 25 (Walcott, 1910b) near Georgia, Franklin County. PENNSYLVANIA. Kinzers Formation: locality 8q (Walcott, 1910b), 3 km northwest of York; locality 12x (Resser and Howell, 1989), 1.6 km north of Rohrerstown; locality 12w (Resser and Howell, 1938), 3.2 km north of Lancaster; locality 22L (Resser and Howell, 1938), 1 km south of East Petersburg. CALIFORNIA. Cararra Formation: USGS colln. 4145-CO (Palmer and

Halley, 1979), Titanother Canyon Section, Grapevine Mountains, Inyo County. Harkless and Saline Valley formations, localities 26 and 28, Waucoba Wash, Inyo Mountains, Inyo County. NEVADA. Saline Valley Formation, Esmeralda County: section PC, Paymaster Canyon, 21 km northeast of Silver Peak. MEXICO. Buelna Formation, localities 801e,f, 807b,c,e, 809a (Lochman, 1956), northwestern Sonora. NEWFOUNDLAND. Forteau Formation, L'Anse au Loup, north shore of the Straits of Belle Isle, Labrador (Walcott, 1910b, p. 310). NORTHWEST TERRITORIES. Sekwi Formation, GSC localities 73068, 73070-73072 (Fritz, 1972), Mackenzie Mountains. BRITISH COLUMBIA. Eager Formation: section RC4, 13 km northeast of Skookumchuck; section MG3, Mt. Grainger, 6 km northeast of Canal Flats; sections MG1 and MG2, Mt. Watson, 7 km east-southeast of Canal Flats; locality 7, 5 km southeast of Mt. Evans summit, Moyie Range. GREENLAND. Ella Island Formation: south coast of Ella Island (Poulsen, 1932, p. 8), east Greenland.

Zonal Biostratigraphy: *Olenellus transitans* Zone.

Discussion: *Paedeumias transitans* Walcott, 1910b, the type species of *Paedeumias*, was proposed by Walcott (1910b) as representative of an intermediate stage in the evolution of *Olenellus*. *Paedeumias* was diagnosed by Walcott using opisthothoracic features, and by Resser (1928) and Palmer (1964) using juvenile features of small holaspids of the species. *Paedeumias* is here considered to be a junior synonym of *Olenellus* (discussed in detail under *Olenellus*).

Olenellus transitans was considered a junior synonym of *Olenellus thompsoni* (Hall) by Raw (1937), Raymond (1928), Størmer (1942), Fritz (1972) and Whittington (1989)²⁷. Part of the confusion in species concepts arose when Resser (1928) and Resser and Howell (1938) mistakenly assigned one of Walcott's (1910b, pl. 33, fig. 1) large specimens of *O. transitans* to *O. thompsoni* (see also discussion under *O. thompsoni*). The species differ in cephalic border width, length of the prelabellar field and length of the posterior thoracic spines and are therefore maintained as separate species of *Olenellus*. Six of the species that Resser and Howell erected from the Kinzers and Parker formations are recognized as junior synonyms of *O. transitans* (see synonymy list).

Olenellus transitans is characterized by long ocular lobes, a long prelabellar field with a plectrum in meraspids (clique C) to mid-sized holaspids (small clique G), a narrow cephalic border less than one third the length of L0, long posterior thoracic spines and three to four opisthothoracic

²⁷ Whittington (1989) also listed Palmer and Halley (1979) as synonymizing the two species. This is incorrect: Palmer (in Palmer and Halley, 1979) accepted *Paedeumias* as a junior synonym of *Olenellus*, but still recognized *O. transitans* as a valid species.

segments. The hypostome has 6 pairs of marginal spines and a straight to gently rounded posterior border without a clearly defined posterior border furrow. The hypostome is attached to the rostral plate by a mineralized stalk (Pl. 18, fig. 4). A stalked hypostome is not known in any other species of *Olenellus*.

Walcott (1910b, p. 41, fig. 7) illustrated a large cephalon from Labrador, Newfoundland that is *Olenellus transitans*. Small cephalons (clique E) from the Rome Formation, Alabama, were also assigned to *Paedeumias transitans* Walcott by Walcott (1910b pl. pl. 25, figs. 19-22). Resser (1938) stated that while these specimens did not belong to *Fremontella hulli*, which also is found in these strata, neither did they belong to *Olenellus transitans*. Species identification of small specimens is difficult. These specimens lack a plectrum, which is well-developed in the type material at this stage, and therefore they are attributed to *Olenellus* sp.

Paedeumias puertoblancoensis Lochman, 1952 from the Buelna Formation of Mexico was considered by Lochman (1952, p. 95) to be closely related to *Olenellus transitans* and to differ from it "only in the more rounded anterior lobe of the glabella and the straight posterior margin of the cephalon. The "roundness" of L4 is the same in both, except that the specimens described as *P. puertoblancoensis* are preserved in limestone and have not been flattened. The specimens are fragmentary, but the holotype of *P. puertoblancoensis* Lochman (1956, pl. 19, fig. 12) has a complete posterior margin that is not straight, but slightly inflected forward distally as in *O. transitans*. *P. puertoblancoensis* is here considered to be a junior synonym of *O. transitans*, and to also include specimens from the Sekwi Formation, Northwest Territories (*O. puertoblancoensis* of Fritz, 1972) and from the Cararra Formation, California (*O. puertoblancoensis* of Palmer in Palmer and Halley, 1979).

Olenellus transitans also occurs in the Saline Valley and Harkless formations of Waucoba Wash, California (Pl. 19, figs. 8-9). These specimens have the long ocular lobes, narrow cephalic border and long preglabellar field characteristic of the species. Their intergenal position is, however, more medially situated without an intergenal spine. Thoracic shape and structure is closely comparable to the type material of *O. transitans* in both small and large nolaspid. There is no indication of an opisthothorax in the California material. A single known hypostome from the California material has 6 pairs of marginal spines and a straight posterior margin.

Material from limestones in southeastern British Columbia (Pl. 18, fig. 3; Pl. 19, figs. 1-7; Pl. 20, fig. 1) is also assigned to *Olenellus transitans*. These specimens from British Columbia differ from the type material of *Olenellus transitans* in minor ways: intergenal spines are slightly more

medially positioned, meraspids have proportionately longer prelabellar fields and smaller LA's and a hypostome with a rounded posterior margin. These differences may be an artifact of preservation as the material has three dimensional preservation in limestone compared to the type material that is crushed and flattened in shale. Poorly preserved articulate material is also known from tectonically distorted phyllites to the south of the British Columbia localities near Hellroaring Creek. Cephalons described as *Paedeumias hansenii* Poulsen, 1932 from the Ella Island Formation of east Greenland are also referred to *O. transitans*. They also have slightly more medially positioned intergenal spines than the type material and have less curved ocular lobes. Otherwise they are identically to the type material of *O. transitans* and the differences are considered subspecific.

Shaw (1954, 1955, 1962) considered the name *Olenellus brachycephalus* (Emmons, 1860) to be a senior synonym of *Paedeumias transitans* Walcott. Emmons (1860) had published the name *Paradoxides brachycephalus* in a geology manual and provided a drawing of a specimen that was subsequently lost. Walcott (1910b) attributed this specimen to *Olenellus thompsoni* (Hall, 1859), a designation that is accepted here. This makes *Paradoxides brachycephalus* a junior synonym of *O. thompsoni*. *O. transitans* is therefore a valid name.

Ontogeny: The ontogeny of *Olenellus transitans* as illustrated by Walcott (1910b) was one of the earliest published ontogenies of the Olenellina. Whittington (1957b, p. 431, fig. 2) and Raw (1925, p. 296-301) discussed Walcott's illustrations and Lochman (1952, p. 94-95, pl. 19, figs. 9-16) illustrated specimens of this species from Mexico under the name *Paedeumias puertoblancoensis*.

Clique A meraspids are unknown however meraspids at the transition from cliques A to B are known. They compare well to the standard ontogeny (*Olenellus* sp. A, p. Text-fig. 41), differing only in having a proportionately longer prelabellar field. Ocular lobe posterior tips are opposite of S0. (Pl. 18, fig. 1; Pl. 19, fig. 1)

Clique B meraspids of the type material have at least 7 thoracic segments and a proportionately longer LA than meraspids of *Olenellus* sp. A. The same long LA is seen in the Mexico material of this clique (Lochman, 1952, pl. 19, fig. 15) but not in the British Columbia material. Interestingly, large individuals of clique B/C from British Columbia (Pl. 19, fig. 2) have large but short intergenal spines. Long intergenal spines are retained in the type material of this species until at least clique C. The Mexican material (Lochman, 1952, pl. 19, fig. 16) also shows an early reduction of the large intergenal spines by clique C. The differences in timing of the loss of the long intergenal spines between localities may be a function of intraspecific variation enhanced by

environmental differences, as the type material is found in shale and the Mexican and British Columbian material is found in limestone. Ocular lobe posterior tips are opposite of S0.

Clique C meraspidids have at least 9 thoracic segments. Compared to *Olenellus* sp. A, the intergenal spines are narrower and LA is slightly longer in the type material of *O. transitans*. Ocular lobe posterior tips are opposite of the anterior of L0. (Pl. 18, fig. 2)

Clique D is poorly known, however, specimens from the type material that are at the transition from cliques C to D are known. They have long, narrow intergenal spines, short genal spines, wider extraocular than interocular areas, a distinct plectrum and at least 12 thoracic segments. Ocular lobe posterior tips are opposite of the anterior of L0. (Pl. 18, fig. 2)

Clique E includes specimens as small as 3.1 mm in cephalic length (from Hellroaring Creek, British Columbia) that have 15 thoracic segments with a long, well-developed 15th axial spine. Compared to specimens of *Olenellus* sp. A of this clique, *O. transitans* has a proportionately longer preglabellar field with well defined plectrum, longer LA, ocular lobes closer to the glabella and a greater cephalic length to width ratio. Hypostomes have a fully spinous posterior margin with at least 5 pairs of marginal spines. Ocular lobe posterior tips are opposite of the midlength of L0. (Pl. 18, fig. 4; Pl. 19, figs. 3-4)

Clique F specimens are closely comparable to those of *Olenellus* sp. A. The preglabellar field is proportionately shorter than in specimens of clique E, LA is larger (both longer and wider), L3 is slightly modified and the cephalon is proportionately wider. Ocular lobe posterior tips remain opposite of the midlength of L0. (Pl. 19, fig. 8)

Clique G specimens can be defined by the same features as those of *Olenellus* sp. A, particularly by the mature configuration of the glabella with a fully modified L3 and isolated S3. Significantly, during this clique there is shortening of the ocular lobes and the preglabellar field in the largest individuals (about 2 cm in cephalic length). Large specimens have ocular lobe posterior tips opposite of the anterior of L0. (Pl. 18, figs. 5-6; Pl. 19, figs. 5-7, 9)

Olenellus cf. *nevadensis* (Walcott, 1910b)

Pl. 20, figs. 2-3, 10-11

Occurrences: NEVADA. Saline Valley Formation, Esmeralda County: locality 19, Magruder Mountain; locality 9, 14 km north-northeast of Silver Peak, Weepah Hills; ?Saline Valley Formation: locality 8, Miller Mountain, Esmeralda County.

Zonal Biostratigraphy: *Olenellus transitans* Zone.

Discussion: *Olenellus nevadensis* (Walcott) was based on three specimens illustrated by Walcott (1910b, pl. 38, figs. 12-14) from three different localities in Nevada. Resser (1928, p. 9) selected the lectotype and restricted the name to only that specimen from Walcott's locality 52 near Prospect Mountain, Eureka District (Walcott, 1910b, pl. 38, fig. 12). Of Walcott's other illustrated specimens, that in fig. 13 is likely *Bristolia bristolensis* based on the advanced, highly curved, genal spines. The small specimen illustrated in fig. 14 has the long preglabellar field typical of *O. nevadensis*, but has short ocular lobes and a straight posterior margin and is of unknown specific assignment. Resser (1928) and Riccio (1952) illustrated specimens of *O. nevadensis* from the Latham Formation of California.

Olenellus nevadensis has the longest preglabellar field of any described species of *Olenellus*, which it retains, along with a plectrum, even in large holaspids. A unique feature of the species is the long, tapering LA that is bullet-shaped. It has moderately long ocular lobes: shorter than those of *O. transitans* and longer than those of *O. clarki* and *O. gilberti*. The genal spines are distinctly advanced and intergenal spines are present even in large holaspids.

Fragmentary material from the Saline Valley Formation of Magruder Mt. and the Weepah Hills, Nevada is assigned to *Olenellus* cf. *nevadensis*. The general proportions of the cephalon, especially the long preglabellar field and tapering LA, are characteristics of *O. nevadensis*. The nature of the ocular lobes in this material differs from that of *O. nevadensis* as the lobes are narrower and lack a mid-ocular lobe furrow. The material is insufficiently preserved to characterize the position of the genal spines and the nature of the intergenal spines.

Highly flattened shale specimens from the Lower Harkless Formation, Miller Mountain, Nevada are also assigned to *Olenellus* cf. *nevadensis*. They have the long preglabellar field with full plectrum, distinctly advanced genal spines, small intergenal spines and ocular lobes opposite of S0 that are characteristic of this species. LA is not as distinctively bullet-shaped as in specimens from the Latham Formation, but these specimens are highly flattened which distorts the shape. Articulated specimens are found with the Miller Mountain material. The thorax is broadly

triangular in outline, like that of *O. transitans*, but the pleural spines are long and straight like those seen in *Mesonacis*. The 15th axial spine is broad like that of *O. thompsoni*.

Olenellus ricei n. sp.

Pl. 20, fig. 5-8, 12; Pl. 21, figs. 1-11; Text-fig. 42

1952 *Olenellus gilberti* Meek; Best, p. 17-18, pl. 1, figs. 13-17.

1959 *Olenellus (Olenellus) garretti* nomen nudum Best [unpublished thesis], p. 95-97, pl. 1, fig. 1.

1985 *Olenellus gilberti*, Hu, p. 125-129, pl. 1, figs. 1-10, 12-23; [non] fig. 11 [= *Mesonacis eagerensis*].

1993 *Olenellus fremonti*, Levi-Setti, pl. 52, 53.

Diagnosis: A species of *Olenellus* with posterior tips of ocular lobes opposite of L1. Cephalic border narrow: approximately one third length L0. Preglabellar field short: less than half length L0. Plectrum partial. Interocular swellings present. Intergenal spines usually absent. Intergenal position close to genal spines. Posterior border curves slightly anteriorly lateral to intergenal position. Genal spines slightly advanced: opposite of L0. Posterior occipital node small. Hypostome with minute spines; posterior margin curved, short. Axial nodes small on T3-T14. T15 axial spine base equals full width of T15. Posterior thoracic pleural spines short. Prosopon of fine caecae on extraocular areas.

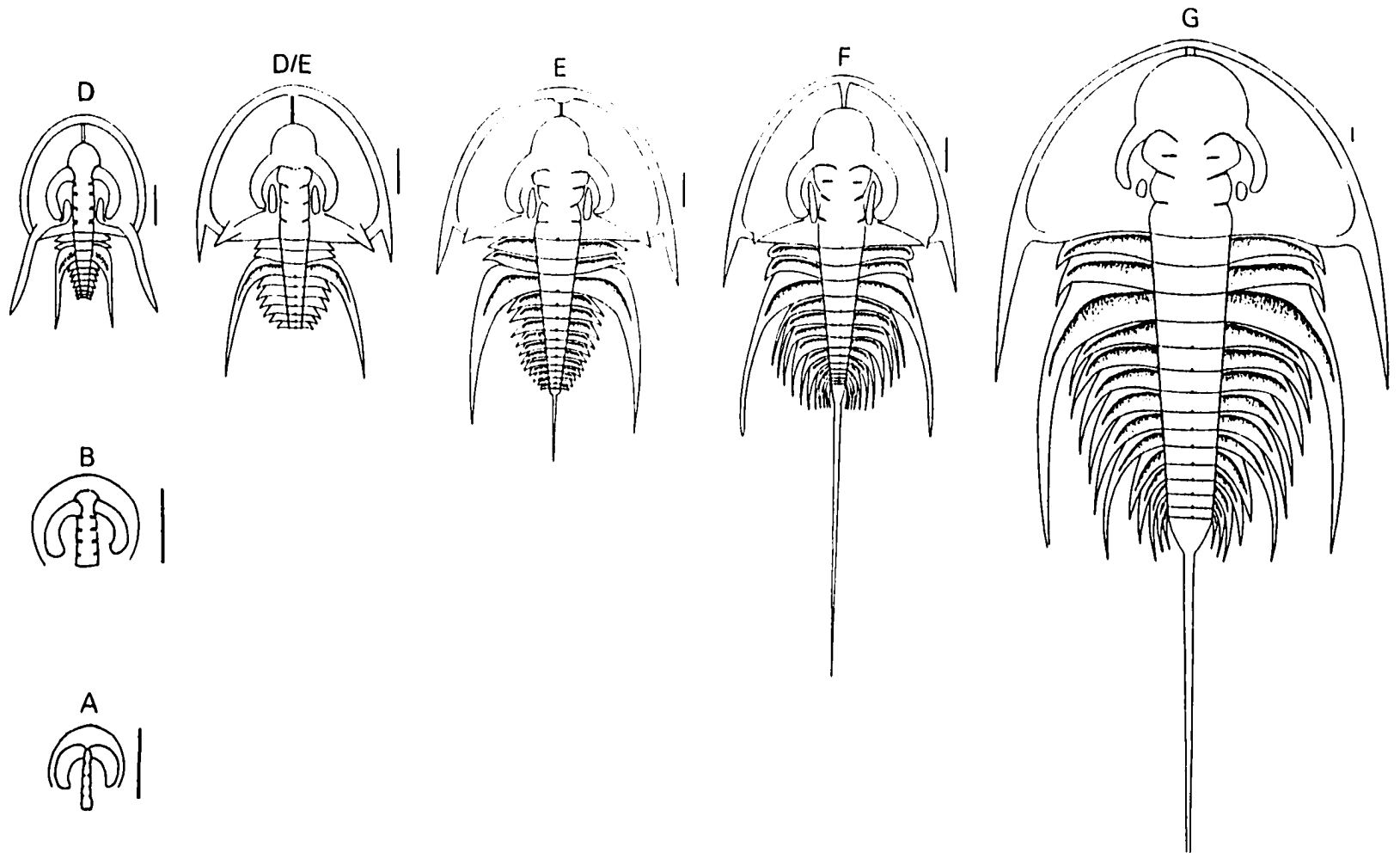
Holotype: A complete specimen (UBC GT352; Pl. 20, fig. 8) from the Eager Formation, locality 5, 6.5 km northeast of Cranbrook, British Columbia. Paratypes: UBC GT302-303, ROM 27414, UA 015

Etymology: For H.M.A. Rice of the Geological Survey of Canada who did much of the early geological mapping in the Cranbrook area.

Occurrences: BRITISH COLUMBIA²⁸. Eager Formation: locality 5, 6.5 km northeast of Cranbrook; locality 4, 2.5 km northeast of St. Eugene Mission, north side of Kootenay River, Kootenay Indian Reserve; section MG3, Mt. Grainger, 6 km northeast of Canal Flats; section MG2, Mt. Watson, 7 km east-southeast of Canal Flats.

Zonal Biostratigraphy: *Wanneria dunnae* Subzone to possibly the *Proliostracus buelnaensis* Subzone; *Olenellus transitans* Zone.

²⁸ Additional localities were listed by Best (1952) and Schofield (1922) but these localities do not exist today due to road-building and extensive quarrying by collectors over the last century.



Text-fig. 42. Ontogeny of *Olenellus ricei* n. sp. Letters designate cliques. scale bars = 1 mm

Discussion: *Olenellus ricei* n. sp. has shorter ocular lobes than most other species of *Olenellus* and unusual interocular swellings. Intergenal spines are general lost in the large holaspids, however, they are retained in rare specimens (Pl. 21, fig. 7). Specimens of *O. ricei* were originally described as *O. gilberti* Meek (*in* White, 1874) by Best (1952), although he acknowledged that they have shorter ocular lobes than the type specimens of *O. gilberti*. In his unpublished thesis, Best (1959) recognized that these specimens were not *O. gilberti*, and described them as a new species, *O. garretti* (nomen nudum). *O. gilberti* is one of the most similar species to *O. ricei*, especially in configuration of the thorax. It differs in having longer ocular lobes (tips opposite of S0 rather than L1), no interocular swellings, a wider cephalic border, and axial tubercles only on the posterior axial segments (see Pl. 20, fig. 4: lectotype²⁹; Pl. 20, fig. 9: articulated specimen courtesy of A. R. Palmer). *O. clarki* (Resser, 1928) is also similar to both species. It has a narrow cephalic border like *O. ricei*, but differs from both *O. ricei* and *O. gilberti* in the thorax with its strongly curved posterior pleural and thoracic spines that lie close against the body.

The Eager Formation material is exquisitely preserved and consists of thousands of specimens housed largely at the University of British Columbia. A full ontogenetic sequence is known as well as details of the ventral morphology. *Olenellus ricei* has a large, subrounded LA that is only slightly tapered. There is no indication of a mid-ocular lobe furrow. Interocular swellings are positioned medial to the tips of the ocular lobes. Genal ridges of unknown significance run asymmetrically from around the midlength of the ocular lobes to the genal angles on many large holaspids. These lines are rarely distinguishable on other species and are likely only seen clearly in this species due to the fine quality of the preservation. The thorax is almost identical to that of *O. gilberti*, differing only in having small axial spines on T3-T14 instead of on T8-14 (compare Pl. 20, fig. 8 with fig. 9). The broad-based axial spine on T15 obscures the pygidium and potential opisthothorax in most specimens, but an indication of two opisthothoracic segments is present on one specimen. Best (1952, p. 18) noted that three opisthothoracic segments could "doubtfully" be observed. The hypostome appears to have been natant (Pl. 21, figs. 3-4, 11) without the mineralized stalk seen in *O. transitans* attaching linking the hypostome to the rostral plate. A soft tissue attachment, however, may have been present as the hypostome and rostral plate are sometimes preserved together in life position, disassociated from the dorsal exoskeleton (Pl. 20,

²⁹ While Palmer (1957, p. 107) recognized that specimens of both *O. gilberti* and *O. clarki* could be recognized in Meek's type collection, he did not assign specific specimens to particular species. Palmer (*in* Palmer and Halley, 1979) listed only one of Meek's (*in* White, 1877, pl. 2 fig. 3a) specimens under the synonymy of *O. gilberti*, however, that specimen illustrated in Meek's fig. 3b is also *O. gilberti*. The latter is the better specimen and is here designated the lectotype (Pl. Fig.), since Palmer (*in* Palmer and Halley, 1979) did not formally select a lectotype. The third of Meek's specimens illustrated in his fig. 3c is likely *O. clarki*.

fig. 5). The posterior margin of the hypostome is poorly preserved and appears to have been thin and short, with possibly up to six pairs of minute, marginal spines. The rostral plate is thin and narrow, and does not extend all the way to the genal angle (Pl. 21, figs. 5, 10).

Material of *Olenellus* from the Forteau Formation, Newfoundland (Resser and Howell, 1938; Stouge and Boyce, 1983) has been inadequately described and illustrated, but shows strong similarities to *O. ricei*. *O. schucherti* Resser and Howell, 1938 (= *O. terranovicus* Resser and Howell, 1938)³⁰ shares with *O. ricei* the same configuration of the cephalon with a moderately narrow border, short prelabellar field, interocular swellings and slightly advanced genal spines. It differs in having slightly shorter ocular lobes and shallower glabellar furrows. *Olenellus brevoculus* Resser and Howell, 1938 (= *O. bonnensis* Resser and Howell, 1938), also from the Forteau Formation, is assigned to *Mesonacis* and can be distinguished from *O. ricei* by its shorter ocular lobes and absence of a prelabellar field.

Ontogeny: The ontogeny of *Olenellus ricei* is well known for cliques D through G, but smaller material is poorly preserved. Compared to the ontogeny of *Olenellus* sp. A, lengthening of LA and reduction of the genal spines occurs at an earlier clique. Reduction of the prelabellar field through ontogeny is dramatic in this species.

Cliques A through C are poorly known. Compared to the ontogeny of *Olenellus* sp. A, the ocular lobes are slightly shorter with the posterior tips opposite of S0 and LA is small but long. A plectrum is present but no procranial spines can be distinguished on clique C meraspids. (Pl. 20, figs. 6-7, 12)

Clique D meraspids have a pentagonal LA, long prelabellar field, extraocular areas approximately twice the width of the interocular areas, and distinct intergenal ridges. In other features, such as glabellar configuration, they are closely comparable to clique C meraspids of *Olenellus* sp. A. The distinct intergenal ridges may be linked to the shorter ocular lobe length of this species as the intergenal ridges are located more posteriorly on long-eyed species and are difficult to distinguish from the posterior border. Ocular lobe posterior tips are opposite of the posterior-most portion of L1. At least 10 thoracic segments are present in this clique. (Pl. 21, figs. 1,2)

³⁰ *Olenellus terranovicus* Resser and Howell, 1938 is synonymized with *Olenellus schucherti* Resser and Howell, 1938 as the holotypes cannot be distinguished from one another. The name *O. terranovicus* has page priority over *O. schucherti*, but the latter is chosen as species name since it was based on considerably better material.

Clique E have long preglabellar fields, shorter ocular lobes (posterior tips opposite of the posterior-most portion of L1) and distinct intergenal ridges compared to those of *Olenellus* sp. A. Specimens of approximately 3 mm of cephalic length have broad but short intergenal spines, short genal spines and at least 11 thoracic segments. Specimens greater than 4 mm cephalic length have proportionately shorter ocular lobes and preglabellar fields, a hint of modification of L3, longer genal spines, smaller intergenal spines and 15 thoracic segments with a broad-based 15th axial spine of unknown length. Hypostomes of this clique have a fully spinous posterior margin with approximately 6 pairs of marginal spines. (Pl. 21, figs. 4, 5)

Clique F cephalae are proportionately longer than cephalae of *Olenellus* sp. A and LA and the preglabellar field are also proportionately longer. Ocular lobe posterior tips are opposite of the posterior of L1. The 15th axial spine is well developed and longer than the rest of the trilobite. Falcate pleural spines develop in this clique. In earlier cliques, pleural spines have been poorly preserved and appear to be poorly developed. Hypostomes have a spinous posterior margin of unusually thin exoskeleton that rarely preserves. (Pl. 21, figs. 5-6)

Clique G holaspids have a large, rounded LA, moderately short preglabellar field with partial plectrum, and ocular lobe posterior tips opposite of the midlength to posterior of L1. In the majority of specimens, intergenal spines are absent. Pleural spines are long and falcate on T5 through T14. Hypostomes have a slightly rounded posterior margin with only a hint of posterolateral marginal spines. (Pl. 20, fig. 6, Pl. 21, figs. 7, 10-11)

Genus *Bolbolenellus* Palmer and Repina, 1993

Type Species: *Olenellus euryptaria* Palmer in Palmer and Halley, 1979, from the Carrara Formation, Eagle Mountain, California. (by original designation)

Diagnosis: A genus of Olenellinae with LA inflated, globose. Cephalic border moderately narrow: typically less than half length of L0. Preglabellar field absent in large holaspids. Glabella slightly constricted at S2. Glabellar furrows transglabellar, deepest laterally. Mid-ocular lobe furrow shallow proximally or absent. Intergenal position near genal spines. Genal spines falcate; not advanced to slightly advanced.

Other species:

Olenellus altifrontatus Fritz, 1972; Sekwi Fm. Mackenzie Mtns., NWT.

Olenellus sphaerulosus Fritz, 1991a; Illtyd fm., Wernecke Mtns., Yukon. [= *Olenellus bufrontis* Fritz, 1991a; Illtyd Fm., Wernecke Mtns., Yukon].

Olenellus hermani Kindle and Tasch, 1948; Monkton Fm., Malletts Bay, Vermont.

Discussion: *Bolbolenellus* was assigned to the Bristoliinae (= Biceratopsinae herein) by Palmer and Repina (1993) on the basis that it has a "narrow-waisted glabella". The glabella is not as highly constricted in *Bolbolenellus* as it is in genera of the Biceratopsinae, but rather it looks narrow-waisted because LA is enormous. Discovery of an articulated species (Palmer, submitted), with a macropleural rather than hyperpleura: T3, confirms that this genus is not a biceratopsine.

Bolbolenellus is here considered to be a genus of Olenellinae with a globose LA and transglabellar furrows. No meraspids have been described to date.

Fritz (1991a) recognized two species assignable to *Bolbolenellus* from the Illtyd Formation, Yukon: *Olenellus sphaerulosus* Fritz, 1991a and *Olenellus bufrontis* Fritz, 1991a. The latter is a junior synonym of *Bolbolenellus sphaerulosus* that was based on small holaspid cephalae. The differences between the two as Fritz described them can be attributed to ontogenetic differences.

Subfamily Biceratopsinae Pack and Gayle, 1971

Diagnosis: A subfamily of Olenellidae with glabella hourglass shaped; strongly constricted at S2. Preglabellar field absent in holaspids, short in clipeus A meraspids. Ocular lobes short. Meraspid cephalae with long, posteriorly directed intergenal spines; spines cross the posterior border immediately behind or lateral to ocular lobe positions. T3 hyperpleural, dolichospinous. Opisthothorax multi-segmented: of at least 10 segments.

Assigned Genera: *Peachella* Walcott, 1910b (= *Biceratops* Pack and Gayle, 1971); *Bristolia* Harrington, 1956; *Nephrolenellus* Palmer and Repina, 1993 (= *Arcuolenellus* Palmer and Repina, 1993).

Discussion: The Biceratopsinae are a morphologically well-constrained subfamily characteristic of the uppermost Lower Cambrian. All have a strongly constricted glabella, extreme development of T3 and a well-developed opisthothorax. They belong to the Olenellidae as they share with *Olenellus* the same meraspid form (see *Bristolia anteros* Palmer in Palmer and Halley, 1979).

The Biceratopsinae was originally erected as a monotypic subfamily of Olenellidae by Pack and Gayle (1971) for the unusual genus, *Biceratops* Pack and Gayle, 1971, that lacks genal spines. Palmer and Repina (1993) later assigned *Peachella* Walcott, 1910b to this subfamily, a genus recognized here as a senior synonym of *Biceratops*. The name Biceratopsinae is retained for the subfamily as under Article 40 of the International Code of Zoological Nomenclature, a valid family-group name with priority cannot be replaced even if the type genus is synonymized. The subfamily Bristoliinae Palmer and Repina, 1993, which included the genera *Bristolia*, *Nephrolenellus*, *Arcuolenellus* and *Bolbolenellus* is thus absorbed into the Biceratopsinae. These genera share many synapomorphies with *Peachella* as listed above, except *Bolbolenellus* which lacks the diagnostic features of the subfamily and is moved to the Olenellinae (see discussion under *Bolbolenellus*). *Arcuolenellus* is synonymized herein with *Nephrolenellus* (see discussion of genus).

Genus *Peachella* Walcott, 1910b

Type Species: *Olenellus iddingsi* Walcott, 1884, from the Pioche Formation, Prospect Peak, Eureka District, Nevada. (by original designation)

Diagnosis: A highly effaced genus of Biceratopsinae. Glabella strongly constricted, usually without dorsal furrows. Ocular lobes short; posterior tips opposite of S1. Narrow interocular areas with ocular lobes close to glabella. Prothorax of 15 segments with long axial spine on T15. Pleural spines of prothorax, except T3, blunt. Opisthothorax of at least 10 segments.

Other Species:

Biceratops nevadensis Pack and Gayle, 1971; Pioche Fm., Frenchman Mt., California.

Peachella brevispina Palmer (in Palmer and Halley, 1979); Carrara Fm., Dubin Hills, California.

Discussion: *Biceratops* is here considered to be a junior synonym of *Peachella*. The only significant difference between the type species of the two genera is their genal regions which bear highly modified genal spines; *Biceratops nevadensis* Pack and Gayle, 1971 lacks the spines completely while *Peachella iddingsi* (Walcott, 1884) has short, swollen genal spines. As Bergström (1973a, p. 306) noted, the genal regions of trilobites are variable at the specific level, therefore there is no need for two genera to contain species that differ only in one feature. The name *Peachella* has priority.

Genus *Nephrolenellus* Palmer and Repina, 1993

Type Species: *Olenellus multinodus* Palmer (*in* Palmer and Halley, 1979), from the Carrara Formation, Pyramid Peak Section, Funeral Mountains, Inyo County, California.

Diagnosis: A genus of Biceratopsinae with glabella distinctly to strongly constricted. S2 marginal. S3 reduced to pits. Ocular lobes short; posterior tips located opposite of L1. Wide interocular areas. Prothorax of 13 segments; opisthothorax of at least 17 segments. No 15th axial spine. Small in overall size.

Other Species:

Olenellus arcuatus Palmer *in* Palmer and Halley, 1979; Carrara Fm., Funeral Mtns., California.

Discussion: The same argument that synonymized *Biceratops* with *Peachella* applies here: *Arcuolenellus* differs from *Nephrolenellus* only in its genal features and therefore is synonymized. Neither generic name has priority over the other. The name *Nephrolenellus* is chosen to represent the genus as its type species is more completely known.

In having only 13 prothoracic segments, ocular lobes situated far from the glabella (i.e. wide interocular areas) and no 15th axial spine, *Nephrolenellus* is an unusual member of the Olenellidae. Both of these features can be found in immature specimens of other genera, and this evidence combined with the small size of this trilobite indicates that it is likely a paedomorphic (progenetic) species. It has the synapomorphies characteristic of the Biceratopsinae such as the constricted glabella and hyperpleural T3.

Genus *Bristolia* Harrington, 1956

Type Species: *Mesonacis bristolensis* Resser, 1928, from the Latham Formation, Marble Mountains, near Cadiz, San Bernardino County, California. (by original designation)

Diagnosis: A genus of Biceratopsinae with glabella distinctly constricted. S2 usually isolated. Genal spines long, falcate, advanced: opposite or anterior of L2. Cephalon subpentagonal in shape. Prothorax of 15 segments with long 15th axial spine. Opisthothorax of at least 17 segments. Meraspid cephalon typically with procranial spines. Genal spines migrate anteriorly through ontogeny.

Other Species:

Bristolia anteros Palmer (in Palmer and Halley, 1979; Carrara Fm., Grapevine Mtns., California.
Mesonacis insolens Resser, 1928; Latham Fm., Mojave Desert, California.

Species in need of re-evaluation:

Paedeumias mohavensis Crickmay, 1933; Latham Fm., Mojave Desert, California.
Bristolia fragilis Palmer (in Palmer and Halley, 1979); Carrara Fm., Grapevine Mtns., California.

Discussion: *Bristolia* is a Biceratopsinae in which the genal spines are highly advanced creating a cephalon that is subpentagonal in shape. It differs from *Peachella* in having a non-effaced glabella and from *Nephrolenellus* in having ocular lobes situated close to the glabella. The ontogeny illustrated in Palmer and Halley (1979) for *Bristolia anteros* matches the ontogenetic pattern seen in *Olenellus*, except for the anterior migration of the genal spines through ontogeny.

There are considerable changes that occur in cephalic shape and genal spine position during ontogeny that has caused some difficulties in species recognition. Based on the published material, specimens of *Paedeumias mohavensis* Crickmay, 1933 are nearly identical to small to medium-size holaspids of *Bristolia bristolensis*. Similarly, *B. fragilis* Palmer (in Palmer and Halley, 1979) overlaps in morphology with specimens illustrated in Palmer and Halley (1979) as *B. bristolensis*. A.R. Palmer (personal communication, August 20, 1997) maintains that all of the described species can be differentiated based on large, new collections that show little variation, but this has yet to be substantiated.

V. Poulsen (1964) redescribed *Olenellus groenlandicus* C. Poulsen, 1927 and *Olenellus kentensis* C. Poulsen, 1927 from the Cape Kent Formation of northwest Greenland, as species of *Bristolia*. This taxonomic assignment was followed by Palmer (in Palmer and Halley, 1979, p. 65). Poulsen (1964) however noted that *Olenellus groenlandicus* Poulsen is similar to *Fremontella* in segmentation of the glabella and in having a less constricted glabella. This species is here assigned to *Fremontella* (see further discussion under that genus). *Olenellus kentensis* Poulsen is represented by a single fragmentary cephalon that has the slightly constricted glabella, long ocular lobes, isolated S2's and rounded LA characteristic of *Olenellus*. It is too fragmentary to assign with certainty to any species, but it differs in no observable features from *O. transitans*.

Subfamily Mesonacinae Walcott, 1890

Diagnosis: A subfamily of Olenellidae with glabella slightly constricted at S2. Ocular lobes typically short; opposite or anterior of L1. Genal spines typically advanced. T3 macropleural, macrospinous. Meraspid cephalon with short, laterally directed intergenal spines; spines cross posterior border lateral to ocular lobe position. Meraspid LA large, subrounded. Preglabellar field absent throughout ontogeny. Genal spines remain in same relative position through ontogeny.

Assigned Genera: *Mesonacis* Walcott, 1885; *Olenelloides* Peach, 1894; *Fremontia* Raw, 1936; ?*Fremontella* Harrington, 1956.

Discussion: The Mesonacinae is a subfamily of Olenellidae characterized by a distinctive ontogenetic pattern: the meraspid LA is small and rounded like that of other Olenellidae, but the intergenal spines are short and laterally located on the posterior border and a preglabellar field is absent throughout ontogeny. The Wanneriidae is also characterized by intergenal spines that are short in the meraspid stage, but these spines are medially located and posteriorly directed. The orientation and position of the intergenal spines is comparable with that seen in the late meraspid to early holaspid stage of other Olenellidae, such as *Olenellus* (i.e. *Olenellus ricei* n. sp.) and *Bristolia*. The general ontogenetic pattern seen in other members of the Olenelloidea is a lengthening of the glabella (the preglabellar field shortens) and a shortening of the ocular lobes. Large holaspids have proportionately shorter preglabellar fields and shorter ocular lobes than small holaspids or meraspids of the same species. In the Mesonacinae, the preglabellar field is absent throughout ontogeny and the ocular lobes are short: features typically only seen late in the ontogeny of other olenelloids. Based on the early development of features typically only seen later in ontogeny of other taxa, the Mesonacinae can be interpreted as peramorphically altered Olenellinae.

The subfamily Mesonacinae is restricted to three genera listed above. When Walcott (1890) originally proposed the name Mesonacidae, he considered it to encompass the whole of the Olenellinae.

An important but problematic mesonacine is *Olenellus fremonti* Walcott, 1910 from the Pioche Formation of Nevada. It has also been described from the Latham Formation of California (Resser, 1928), but all illustrated specimens of the species are highly flattened. No ontogenetic material has been illustrated, not even small holaspids. A restudy of this species is important as

Raw (1936) designated it the type species of his new genus, *Fremontia*. Fritz (1972) synonymized *Fremontia* with *Olenellus*, a decision followed by subsequent workers, but not accepted here. The author has had the opportunity to examine relatively uncompressed material, but it was obtained at a late date from outside the thesis area and is not illustrated at this time. The species does not belong to *Olenellus* because it has a mesonacine ontogenetic pattern combined with short ocular lobes and advanced genal spines in the holaspis. Like species of *Fremontella*, *O. fremonti* Walcott has a wide cephalic border and a highly curved, marginal S2. Relative inflation of the ocular bands cannot be determined. The glabella is more constricted than the typically parallel-sided glabella of *Fremontella*, and closely resembles the glabellar form typical of *Mesonacis*. The intergenal position is slightly anterior of the posterolateral corner, unlike that of *Fremontella* in which it is at the posterolateral corner and unlike that of *Mesonacis* in which it is midway between the posterolateral corner and the genal spine. Ontogenetic development of S2 is unique: in the small holaspis stage, S2 is developed as isolated, transverse slots (like *Mesonacis*) in contrast with large holaspids where S2 is transglabellar and highly curved (like *Fremontella*). This species needs further study with full documentation of the ontogeny, but at this time *Fremontia* must be accepted as a distinct mesonacine genus.

Genus *Mesonacis* Walcott, 1885

Type Species: *Olenus vermontana* Hall, 1859 from the Parker Formation, Georgia, Vermont. (by original designation)

Diagnosis: A genus of Olenellinae with LA pentagonal. Cephalic border narrow: less than one quarter of length L0. S0, S1, S3 marginal, or deepest laterally with shallow transglabellar furrows. Interocular swellings generally developed. Intergenal spines minute. Intergenal position midway between posterolateral corner and genal spine. Genal spines advanced: opposite or anterior of S0. Thoracic pleurae narrow; pleural spines straight.

Other Species:

Olenellus brevoculus Resser and Howell, 1938 (= *Olenellus bonnensis* Resser and Howell, 1938);

Forteau Fm., Labrador, NFL.

Olenellus eagerensis Best, 1952; Eager Fm., near Cranbrook, BC.

[?] *Olenellus schofieldi* Best, 1952; Eager fm., near Cranbrook, BC.

Mesonacis graingerensis n. sp.; Eager Formation, Mt. Grainger, BC.

[?] aff. *Mesonacis? leechi* n. sp., Eager Formation, near Canal Flats, BC.

Discussion: Walcott (1885, 1886) defined the genus *Mesonacis* essentially as an *Olenellus* with an opisthothorax, agreeing in all respects in the cephalon and first 14 thoracic segments with *Olenellus*. Although this definition is erroneous, *Mesonacis* is a distinct genus that can be diagnosed on cephalic and ontogenetic features. It differs from *Olenellus* in lacking a preglabellar field at all stages of its ontogeny, lacking long intergenal spines in the meraspid stage and having a narrow thorax with narrow, straight pleural spines. In addition, species of *Mesonacis* typically have narrower cephalic borders, shorter ocular lobes, narrower extraocular areas and more strongly advanced genal spines than species of *Olenellus*. The intergenal position midway between the genal spines and the anterior inflection of the posterior cephalic border. The opisthothorax is not a unique feature to *Mesonacis* as Walcott claimed, but is also seen in species of *Olenellus* such as *O. transitans* and *O. robsonensis*. When Walcott (1910b) later described the opisthothorax of *O. transitans*, he emphasized that it differed from that of *M. vermontanus* in lacking plural spines on the opisthothoracic segments. Many subsequent authors questioned the distinctiveness of *Mesonacis* as a separate genus from *Olenellus* and a full discussion of the history of *Mesonacis* can be found under *Olenellus*.

Unlike other olenelloid genera that have advanced genal spines (i.e. *Bristolia*, *Laudonia*, *Fremontella*), the genal spines of *Mesonacis* are already advanced in the smallest known meraspids, and remain in approximately the same position relative to the glabella throughout ontogeny. In the other genera, the genal spines migrate anteriorly through ontogeny. This may be another peramorphic feature, as discussed under the Mesonacinae, that is unique to *Mesonacis*.

The type species, *Mesonacis vermontanus* (Hall, 1859) from the Parker Formation of Vermont, is known from only a handful of specimens. Walcott (1886, p. 884-888) provided a detailed description of the species. Unretouched illustrations of a well-preserved, complete topotype specimen can be found in Whittington (1989, pl. 3, figs. 16,18) and Palmer and Repina (1993, fig. 3.2). No meraspids are known for the type species, but meraspids of *M. eagerensis* and *M. graingerensis* are illustrated here. *M. eagerensis* (Best, 1952) is closely comparable to the type species in morphology and is known from many specimens. The most remarkable difference of *M. eagerensis* is the bizarre, long, straight pleural spines found on T13-T14. They are an unusual feature for the Olenellina.

Olenellus mickwitzii Schmidt, 1888 from Estonia and *Olenellus torelli* Moberg, 1892 from Sweden were assigned to *Mesonacis* by Walcott (1910b). The former was designated the type of *Schmidtellus* Moberg (in Moberg and Segerberg, 1906). While *S. mickwitzii* is similar to species of *Mesonacis* in its long glabella (no preglabellar field), narrow thorax with straight spines, and

distinct opisthothorax, it differs in having a marginal S2 and lacking the distinctive intergenal position. It also differs from members of the Olenellidae in having wide interocular areas, characteristic of the Holmiidae. *Olenellus torelli* Moberg was redescribed by Bergström (1973a, p. 296-301) as a subspecies of *S. mickwitzii*. It differs from *Mesonacis* in the same features listed above.

Resser (1928) assigned *Olenellus fremonti* Walcott, 1910b from the Pioche Formation of Nevada and the Latham Formation of California, to *Mesonacis*. This species, unlike species of *Mesonacis*, has a broadly curved, marginal S2, intergenal position near the posterolateral corners, and a broad thorax. It is here considered an unassigned mesonacine in need of further study. Resser (1928) also established the species *Mesonacis bristolensis* and *Mesonacis insolens* from the Latham Formation of California. Harrington (1956) designed the former as the type of *Bristolia* Harrington, 1956, which differs from *Mesonacis* in having a strongly constricted glabella, *Olenellus* type of meraspid, and a hyperpleural, dolichospinous T3. *Mesonacis insolens* Resser differs from *Mesonacis* in a similar fashion and was also assigned to *Bristolia* by Harrington (1956).

Mesonacis egerensis (Best, 1952)

Pl. 22, figs. 1-6; Text-fig. 43

1952 *Olenellus egerensis* Best, p. 19-20, pl. 1, figs. 5-12.

1959 *Bristolia egerensis*, Best, p. 134-135, pl. 2, figs. 1-3.

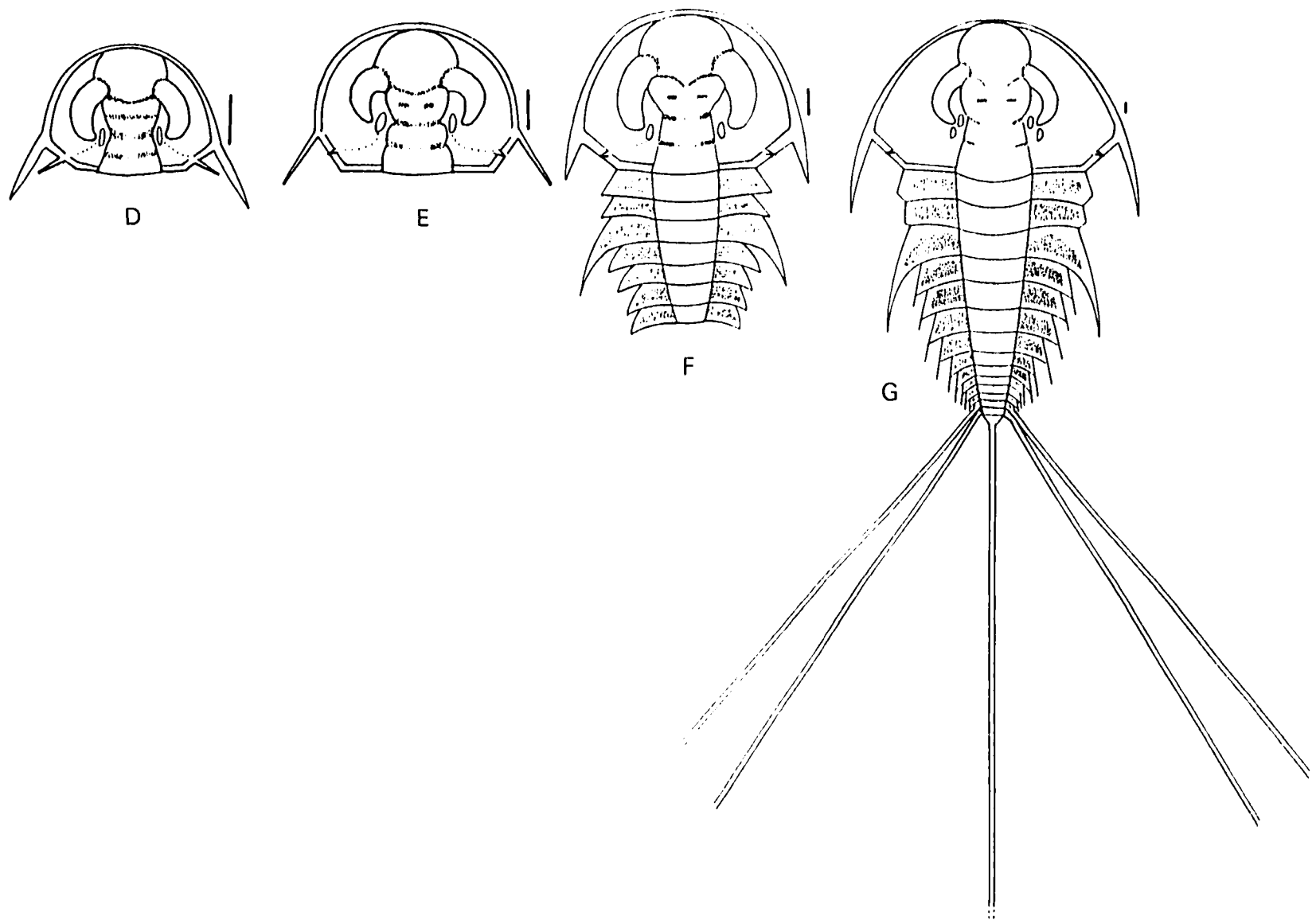
1978 *Olenellus (Olenellus) egerensis*, McNamara, p. 642.

1985 *Olenellus gilberti*, Hu, pl. 1, fig. 11 [only].

Diagnosis: A species of *Mesonacis* with ocular lobe posterior tips opposite of anterior of L1. Cephalic border wire-like: less than one sixth length L0. Interocular swellings elongate. Genal spines advanced: opposite of posterior of L1. Lateral posterior cephalic border inflected anteriorly at obtuse angle. Axial nodes small on T1-T14. T13 - T14 with long, straight, posterolaterally directed pleural spines. Prosopon smooth.

Holotype: Nearly complete specimen (UBC GT101; Best, 1952, pl. 1, fig. 5; Pl. 22, fig. 3 herein) from the Eager Formation, locality 5, near Cranbrook, British Columbia. Paratypes: UBC GT103-104, 110-114.

Occurrences: BRITISH COLUMBIA. Eager Formation, locality 5, 6.5 km northeast of Cranbrook (Best, 1952).



Text-fig. 43. Ontogeny of *Mesonacis egerensis* (Best). Letters designate cliques. scale bars = 1 mm

Zonal Biostratigraphy: *Wanneria dunnae* Subzone, *Olenellus transitans* Zone.

Discussion: *Mesonacis eagerensis* closely resembles the type species, *M. vermontanus*. It differs in having slightly shorter ocular lobes, posterolateral corners that are angular instead of rounded, shorter pleural spines on T4-T12, and unusual, long straight, pleural spines on T12 and T13 that are at least 1.5 times the length of the trilobite. Best (1952) did not illustrate any specimens that showed the rear of the thorax. He claimed that there was an axial spine on T15, but did not comment on any unusual long pleural spines on the rear segments. An exquisite specimen of *M. eagerensis* (Pl. 22, figs. 4-5), recently collected by R. Smith of Cranbrook, displays the full complement of posterior axial and pleural spines. The similarity should be noted between these spines and the elongated pleural spines on the posterior of *Olenelloides armatus* (starting with T6). Nothing further can be add to Best's (1952) description of *M. eagerensis*.

Ontogeny: There are no appreciable differences in the ontogenetic pattern between *Mesonacis eagerensis* and *M. graingerensis*. A significant feature of the former is that the species is known from articulated material. Clique D is described in detail for *M. eagerensis* below as this clique is poorly represented in material of *M. graingerensis*.

Clique D specimens have ocular lobe posterior tips opposite of anterior of L1. Extraocular areas less than twice the width of interocular areas. LA large, subrounded; preglabellar field absent. Glabellar furrows transglabellar. Glabella constricted at S1, L3 slightly modified. Intergenal spines, long, narrow, posterolaterally directed. Genal spines well-developed. Cephalon subcircular in outline, slightly wider than long. (Pl. 22, fig. 1)

Clique E and F specimens are closely comparable to those of *Mesonacis graingerensis*, except in species diagnostic feature. Ocular lobe posterior tips are opposite of anterior of L1. Cephalon approximately 1.4 times wider than long in clique E and partial thoraxes of up to 7 segments are known. Cephalon approximately 1.5 times wider than long in clique F. There are no appreciable differences in morphology between cliques F and G except larger overall size and better development of pleural thoracic spines.

Mesonacis graingerensis n. sp.

Pl. 22, figs. 7-9; Pl. 23, figs. 1-5; Text-fig. 25 (right)

Diagnosis: A species of *Mesonacis* with posterior tips of ocular lobes opposite posterior-most portion of S2. Cephalic border narrow: less than one third length L0. Interocular swellings

elongate. Extraocular areas narrow: about twice the width of interocular areas. Genal spines advanced: opposite of anterior of L2. Posterior cephalic border inflected anteriorly at obtuse angle. Posterior occipital node small. Caecae faint on extraocular areas. Cephalon hexagonal in outline.

Holotype: A complete cephalon (MG3b#3; Pl. 23, fig. 5) from the Eager Formation, section MG3, collection MG3b, Mt. Grainger, British Columbia. Paratypes: MG3b#2, MG3b#25, MG3b#41

Etymology: For Mt. Grainger, on which this species occurs.

Occurrences: BRITISH COLUMBIA. Eager Formation, section MG3, north face of Mt. Grainger, 6 km northeast of Canal Flats.

Zonal Biostratigraphy: *Wanneria dunnae* Subzone, *Olenellus transitans* Zone.

Discussion: *Mesonacis graingerensis* has the most highly advanced genal spines and shortest ocular lobes of any described species of *Mesonacis*. The genal spines are located at about midlength on the cephalon giving the cephalon a hexagonal outline. Interocular swellings are present throughout the known ontogeny. The cephalon is relatively narrow with proportionately narrower extraocular areas than the other species. In glabellar features, *M. graingerensis* is closely comparable to *M. eagerensis* and *M. vermontanus*.

Ontogeny: *Mesonacis graingerensis* has the best known early ontogeny and is described in detail below to act as a comparative standard for the genus. The ontogenetic pattern is identical for *M. eagerensis*.

Clique B is the smallest known ontogenetic stage based on fragmentary material. Presence or absence of procranial spines cannot be determined. Cephalic border clearly differentiated. Ocular lobes well-defined, elevated, posterior tips opposite of midlength of L2. Extraocular areas narrow; present over full length of cephalon, narrowest posteriorly. LA large, rounded, appears to reach anterior border. Glabella parallel-sided L0 through L3, furrows transglabellar. Intergenal and genal spines moderately long, narrow, posterolaterally directed. Cephalon rounded to hexagonal in outline. The main differences at this clique between *Mesonacis graingerensis* and *Olenellus* sp. A are the large size of LA, apparent absence of a preglabellar field, presence of genal spines, and position and shape of the intergenal spines. (Pl. 22, figs. 7-8)

Clique C meraspids have a hint of procranial spines. Ocular lobe posterior tips opposite of S1. Extraocular areas subequal in width to interocular areas. LA large, rounded, reaches anterior border. Glabellar furrows transglabellar, deepest laterally. Glabella slightly constricted at L2/S1. Intergenal spines minute, genal spines well-developed. Cephalon hexagonal in outline. The main differences at this clique between *Mesonacis graingerensis* and *Olenellus* sp. A are the slight constriction of the glabella that heralds the modification of L3, the relative sizes of the spines, the large size of LA and the absence of a preglabellar field. (Pl. 22, fig. 9; Pl. 23, figs. 1-2)

Clique D is not represented among the available specimens of this species and instead is described in detail for *Mesonacis egerensis*.

Clique E has an almost mature configuration of the glabella. Ocular lobe posterior tips are opposite of S1. Extraocular areas wider than interocular areas. LA large, subrounded; preglabellar field absent. Glabella constricted at S1. L3 fully modified. S0 and S1 marginal; S3 isolated, connected medially by a shallow furrow. Intergenal spines minute, genal spines long. Cephalon hexagonal in outline, approximately 1/3 wider than long. The main differences at this clique between *Mesonacis graingerensis* and *Olenellus* sp. A are the highly modified L3, nearly mature configuration of the glabellar furrows, large size of LA, no preglabellar field and relatively narrow cephalon. (Pl. 23, fig. 3)

Clique F holaspids have ocular lobe posterior tips opposite of the posterior-most portion of L2. Extraocular areas approximately twice the width of interocular areas. LA large, subrounded, separated from anterior border by deep furrow. Preglabellar field absent. Glabellar furrows of mature configuration: S3 isolated slots, not connected across glabella. Intergenal spines minute, genal spines long. The main difference at this clique between *Mesonacis graingerensis* and *Olenellus* sp. A is the fully mature configuration of the glabella. (Pl. 23, fig. 5)

Clique G holaspids are little different than clique F holaspids. There is a slight shortening of the anterior border anterior to the glabella. The main differences at this clique between *Mesonacis graingerensis* and *Olenellus* sp. A are the relative narrowness of the cephalon, short ocular lobe length and absence of a preglabellar field. (Pl. 23, fig. 4)

Mesonacis? schofieldi (Best, 1952)

Pl. 23, figs. 6-8

1952 *Olenellus schofieldi* Best, p. 18-19, pl. 1, figs. 1-4.

1959 *Olenellus (Fremontia) schofieldi*, Best, p. 128.

1992 *Olenellus schofieldi*, Fritz, p. 19.

Diagnosis: A possible species of *Mesonacis* with ocular lobe posterior tips opposite of anterior of L1. Cephalic border wire-like: approximately one sixth length L0. Preglabellar field short to absent. LA long, subcircular. Interocular swellings elliptical. Genal spines barely advanced: opposite of posterior of L0. Lateral posterior cephalic border inflected slightly anteriorly. Posterior occipital spine minute. Caecae on extraocular areas. Cephalon hemicircular in shape with wide extraocular areas. T5 through T10? with long, straight pleural spines.

Holotype: A nearly complete specimen with hypostome (UBC GT201; Best, 1952, pl. 1, fig. 1; Pl. 23, fig. 8 herein) from the Eager Formation, near Cranbrook, British Columbia. Paratypes: UBC GT202, 205-206

Occurrences: BRITISH COLUMBIA. Eager Formation: locality B³¹ of Best (1952), just south of the Cranbrook-Fort Steele Road (Schofield, 1922, fig. 2); Mount Whyte Formation: ?Locality 35h (Walcott, 1908, p. 215; 1910b, p. 316), Mt. Bosworth. ?CALIFORNIA. Harkless Formation, localities 24, 25, 28, Waucoba Wash, Inyo Mountains, Inyo County.

Zonal Biostratigraphy: *Wanneria dunnae* Subzone, *Olenellus transitans* Zone.

Discussion: The type material of *Mesonacis? schofieldi* consists of a handful of specimens from the Eager Formation, near Cranbrook, British Columbia. There is no ontogenetic material known and holaspid features are a mix of characters of both *Mesonacis* and *Olenellus*. Specifically, *M.? schofieldi* is midway in morphology between *Olenellus ricei* n. sp. and *M. eagerensis* (Best), both of which are found at the same locality. It has an LA of a similar size and shape as *O. ricei*, as well as a short prelabellar field and broad, hemicircular cephalon. Best (1952) claimed that a prelabellar field was not present in this species, but LA does not contact the anterior border in the holotype (Pl. 23, fig. 8). Its prelabellar field is however, proportionately shorter than that of *O. ricei*. The lateral posterior cephalic border has a slightly inflection anteriorly and an intergenal node midway between the genal spines and the posterolateral corners. *O. ricei* rarely retains intergenal spines through the large holaspid stage, although an exceptional specimen (Pl. 21, fig. 7) has spines located at the posterolateral corners. Like *M. eagerensis*, *M.? schofieldi* has a wire-like cephalic border, intergenal node midway between the genal spine and the posterolateral

³¹ This locality could not be located by the author.

corner, narrow thorax, and straight pleural spines on T5 to the posterior. All three species have interocular swellings. A hypostome associated with the holotype has a rounded posterior margin. Nothing else can be added to Best's (1952) description of the species.

Poorly preserved material from the Waucoba Wash area of California is also tentatively referred to *Mesonacis? schofieldi*. A small holaspid (Pl. 23, fig. 6) is corroded in the anterior of LA, but definitely has a short preglabellar field. A large holaspid lacks a preglabellar field. The ocular lobes are the same length as in the type specimens, and the posterior border is almost straight. Walcott (1910b, pl. 38, figs. 1-11) illustrated a number of specimens as *Olenellus canadensis* from the Mount Whyte Formation of Mt. Bosworth, British Columbia, some of which may be referable to *M.? schofieldi*. The lectotype with its advanced genal spines was referred to *Fremontella* by Harrington (1956) and the name restricted to that single specimen. The other illustrated cephalons have almost straight posterior margins and also share with the type specimens of *M.? schofieldi* ocular lobes of a similar length, interocular swellings, and a similar glabella. Trilobites from Mt. Bosworth need to be restudied, but those illustrated in Walcott (1910b, pl. 38, figs. 4-6) are tentatively referred to *M.? schofieldi*.

No ontogenetic material is known for *Mesonacis? schofieldi*.

aff. *Mesonacis leechi* n. sp.

Pl. 23, figs. 9-12; Pl. 24, fig. 9

Diagnosis: A possible species of *Mesonacis* with ocular lobe posterior tips opposite of L1. Cephalic border narrow: approximately one third length L0. Preglabellar field moderately short. Mid-ocular lobe furrow absent. Interocular swellings absent. Intergenal spines present at posterolateral corners. Genal spines advanced: opposite of posterior of L1. Lateral posterior cephalic border inflected anteriorly at obtuse angle. Prosopon of fine caecae on extraocular areas.

Holotype: A small cephalon (MG2b#19, Pl. 23, figs. 9, 12) from the Eager Formation, section MG2, collection MG2b, 8 km southeast of Canal Flats, British Columbia. Paratypes: MG2b#7, MG2b#16

Etymology: For Geoffrey Leech, geologist with the Geological Survey of Canada, who did the geological mapping in the Canal Flats area and made important fossil collections from Lower Cambrian strata.

Occurrences: BRITISH COLUMBIA. Eager Formation: locality 2, 8 km southeast of Canal Flats; section MG2, Mt. Watson, 7 km east-southeast of Canal Flats.

Zonal Biostratigraphy: *Wanneria logani* Subzone, *Olenellus transitans* Zone.

Discussion: *Aff. Mesonacis leechi* fits poorly into any established genus of Mesonacinae. The material consists of a number of small specimens of unusual morphology plus a tentatively assigned larger specimen. The holaspid morphology is too poorly known to justify erection of a new genus. The species is not a wanneriid as LA is bulbous through the late meraspid stage. The tentatively assigned large specimen (Pl. 24, fig. 9) lacks a mid-ocular lobe furrow and has a S2 morphology that suggests this furrow pair is isolated later in ontogeny. The preglabellar field is moderately long, as in *Olenellus*, and unlike other genera of the Mesonacinae. Clique D though E specimens (Pl. 23, figs. 10-11) have short, laterally directed intergenal spines positioned laterally on the posterior cephalic border. This is the same state as seen in the Mesonacinae. Intergenal spine length increases by clique F (Pl. 23, figs. 9, 12). It is not known how large the intergenal spines were later in the holaspid stage: the single known mid-sized holaspid (clique F) has a broken stub indicating an intergenal spine of unknown length. The large, bulbous LA in the meraspid stage is like that seen in *Fremontella hulli* (see Walcott, 1910b, pl. 31, fig. 5). It should be noted that the nevadiids also have an LA of similar size and shape in the meraspid stage, although this may be a convergent feature. *Aff. M. leechi* has genal spines that remain in the same advanced position relative to the glabella throughout ontogeny, which is a feature characteristic of *Mesonacis*, however, the intergenal spines are at the posterolateral corners. Better holaspid material of this species is needed to determine the generic assignment.

Genus *Olenelloides* Peach, 1894

Type Species: *Olenelloides armatus* Peach, 1894 from the "Fucoid" Beds, Meall a'Ghiubhais, Ross and Cromarty counties, Scotland. (by monotypy)

Diagnosis: A genus of Mesonacinae of small overall size. LA subrounded. Cephalic border narrow. S2 transglabellar, straight. Mid-ocular lobe furrow absent. Extraocular areas narrow. Procranidial, genal and intergenal spines present through to small holaspid stage. Intergenal spines at posterolateral corners. Genal spines advanced: opposite or anterior of S2.

Other Species:

[?] *Laudonia? canadensis* Hu, 1971, near Radium, British Columbia.

Discussion: *Olenelloides* was first proposed by Peach (1894) as a subgenus of *Olenellus*, although he used the name at other places in the text as a genus. Many subsequent workers accepted this taxon: Walcott (1910b, p. 347) as a "degenerate form of the Mesonacidae" (= *Olenellina* herein); Hupé (1953a,b) and Poulsen (*in* Moore, 1959) as a monotypic subfamily of Olenellidae; Chernysheva (1960) as a genus of Olenellinae; Palmer and Repina (1993) as a possible genus of Laudoniinae. Repina (1979) and Ahlberg *et al.* (1986) did not recognize this genus, instead they considered it a larval Olenellidae. Throughout its history, *Olenelloides* has remained a monotypic taxon based on the species *Olenelloides armatus*. A second species is here tentatively recognized.

Olenelloides armatus has been described in detail by Peach (1894), Walcott (1910b), Lake (1938) and in a modern taxonomic treatment by McNamara (1978). The approximately 50 known specimens are preserved as molds in shale from a locality that can no longer be found (see McNamara, 1978, p. 637). *O. armatus* is a small trilobite with the largest known cephalon having a cephalic length under 5 mm. It is closest in morphology to species of *Mesonacis* in the configuration of the glabella, no preglabellar field throughout ontogeny, short ocular lobes, interocular swellings and advanced genal spines. McNamara (1978) demonstrated that the macropleural T6 illustrated by other authors (Raw, 1937; Palmer, 1957) is illusional. T4 and T5 lack pleural spines which emphasizes the spines on T6. T6 is macrospinous, but not macropleural.

Olenelloides armatus possesses features typically seen only in the larvae of the Olenellidae, such as narrow extraocular areas, only nine thoracic segments and retention of intergenal and procranidial spines in the small holaspid. Consequently Hupé (1953b) and McNamara (1978) described it as paedomorphic. However, Palmer and Repina (1993) emphasized that meraspid of *O. armatus* have advanced genal spines and lack preglabellar fields, which are features characteristic of later ontogenetic stages in other olenelloids. They interpreted the development of *O. armatus* as precocious (i.e. peramorphic), not retarded. Both the paedomorphic and peramorphic interpretations are correct. Multiple heterochronic processes have been at work to produce *O. armatus*: it has the peramorphic ontogenetic pattern exhibited by all species of Mesonacinae, overprinted by paedomorphosis.

McNamara (1978, p. 636) stated that although *Olenelloides armatus* "is morphologically very distinct from contemporaneous olenellids from the same horizon, genetically it was probably very closely related to them". He viewed *O. armatus* as the endpoint of paedomorphic evolution of these trilobites, shown graphically in a paedomorphocline (McNamara, 1982, text-fig. 4). His evidence to link this species to the others cannot be substantiated. In his species reconstructions

(1978, text-fig 4), his illustration of the meraspid for "*Olenellus*" *intermedius* (fig. 4d), as a form similar to *Olenelloides armatus*, is purely hypothetical. Also his reconstruction of the *Olenelloides armatus* meraspid (fig. 4b) is faulty in the portrayal of a wide LA, and creates a false sense of similarity between this species and the others illustrated as *Olenellus*. The smallest illustrated meraspid of *O. armatus* (McNamara, 1978, pl. 71, fig. 7) is distorted, but shows no sign of a wide LA; it is instead small and rounded. The other Scottish olenelloids have wide LA's and a wanneriid pattern of development. They are assigned herein to *Elliptocephala*, and are unlikely to be closely related to *Olenelloides*.

Both McNamara (1978) and Palmer and Repina (1993) commented on the similarity between *Laudonia? canadensis* Hu, 1971 from southeastern British Columbia and *Olenelloides armatus*. This species retains an intergenal spine in the holaspid stage, like the wanneriid *Laudonia*, but it has isolated S2's and the ontogenetic pattern is that of the Olenellidae with a small, rounded LA. Like *O. armatus*, it has narrow extraocular areas, no preglabellar field, intergenal spines at the posterolateral corners, strongly advanced genal spines, and procranial spines through the small holaspid stage. Hu (1971) describes the ontogeny of this species in detail, with the largest illustrated cephalon of 6 mm in length. This large cephalon lacks procranial spines and has S2 as isolated slots. In the slightly smaller holaspids, S2 appears transglabellar as in *O. armatus*. It has a hypostome with a narrow, rounded, posterior margin like that of other species of Olenellidae. The posterior margin is fully spinous, which is another juvenile feature. The thorax is unknown. The best generic assignment of *Laudonia? canadensis* Hu is to *Olenelloides*, despite the loss of procranial spines and development of S2 as isolated slots in the largest holaspid specimen. It could be regarded as a less paedomorphically altered species of *Olenelloides* than *O. armatus*. The assignment of these species of *Olenelloides* to the wanneriid subfamily Laudoniinae, proposed by Palmer and Repina (1993), cannot be substantiated as neither shows a wanneriid pattern of development.

Genus *Fremontella* Harrington, 1956

Type Species: *Wanneria halli* Walcott, 1910b from the Montevallo Formation (Rome Formation according to Resser, 1938), near Helena, Shelby County, Alabama. (by original designation)
Junior synonym: *Olenellus alabamensis* Resser, 1938.

Diagnosis: A genus of ?Mesonacinae with glabella expanding forward slightly to clavate. Cephalic border width moderate to wide, of varying width over circumference. LA wide, suboval. S2 transglabellar, deepest laterally, curved. Ocular lobes short: posterior tips opposite

of or anterior to L1. Outer band of ocular lobe strongly inflated compared to inner band. Interocular areas typically with interocular swellings. Intergenal ridges absent. Intergenal position at posterolateral corners. Genal spines long, falcate, advanced: opposite of or anterior to S1.

Other Species:

Olenellus canadensis Walcott, 1910b; Mount Whyte Fm., Mt. Bosworth, BC.

Olenellus groenlandicus Poulsen, 1927; Cape Kent Fm., NW Greenland.

[?] *Wanneria?* sp. Rasetti, 1948, Lévis Fm. conglomerates, Bic, Quebec.

Olenellus cylindricus Palmer in Palmer and Halley, 1979; Carrara Fm., Grapevine Mts., California.

Fremontella campbellae n. sp., Eager Fm., near Canal Flats, BC.

Fremontella ashtoni n. sp., Eager Fm., near Premier Lake, BC.

Discussion: The family assignment of *Fremontella* is problematic as it combines characteristics typical of both the Wanneriidae and Olenellidae. Like the wanneriid *Wanneria*, *Fremontella* has a wide LA, wide cephalic border and marginal S2 in the holaspid stage. The wide LA is likely convergently derived as a result of the extreme length of the glabella where LA intrudes upon the anterior border. Both the wide cephalic border and marginal S2 are primitive features, especially the latter which is expressed in the meraspids of all Olenellina. Unlike the S2 of wanneriids, S2 is transglabellar in *Fremontella*. *Fremontella* is tentatively assigned to the Mesonacinae as it shares with *Mesonacis* and *Olenelloides* a similar meraspid form. The meraspid (of *Wanneria halli* Walcott, 1910b, pl. 31, figs. 5, 6) lacks a preglabellar field, has a short, narrow LA, and short, laterally-directed, marginal intergenal spines. This is different from the wanneriid meraspid form and negates Walcott's assignment of *F. halli* to *Wanneria*.

Unlike *Mesonacis*, the intergenal position in the holaspid of *Fremontella* is at the posterolateral corners, not midway on the posterolateral border. The peculiar interocular swellings common to *Mesonacis*, *Olenelloides* and sometimes seen in *Olenellus*, are also typically developed in *Fremontella*. Its ocular lobes are unusual in having the outer band highly inflated compared to the inner band. The glabella is not constricted at S1 as in most other Olenellidae, but widens forward slightly anterior to S1. The genal spines are highly advanced and migrate anteriorly through ontogeny. This is also seen in *Laudonia* (Wanneriidae) and *Bristolia* (Olenellidae). *Mesonacis* differs by having genal spines that stay in approximately the same relative position to the glabella through ontogeny. *Laudonia* differs from *Fremontella* in having long intergenal spines and a wanneriid pattern of ontogenetic development; *Bristolia* differs in having a constricted glabella and *Olenellus* type of meraspid.

Fremontella was erected by Harrington (1956) as a monotypic genus of Olenellinae with short ocular lobes and advanced genal spines. Harrington (1956, p. 58) considered that *Fremontella* could be "easily distinguished from *Wanneria* in the shape and segmentation of the glabella". It is uncertain exactly what Harrington was referring to because it is in glabellar features (marginal S2 and wide LA) that *Fremontella* most resembles a wanneriid. Part of the discrepancy may be that LA is badly crushed in the lectotype of *F. halli*, especially on the left hand side, which makes LA appear small and tapered, instead of wide as it actually is. Harrington also emphasized that *F. halli* resembles *Olenellus crassimarginatus* (Walcott, 1910b) in the attachment of the ocular lobes to LA, and wide, flat cephalic border. Attachment of the ocular lobes to LA is the same in the Olenellidae and Wanneriidae and is not a distinguishing feature. The cephalic border of *F. halli* is wide for an olenelline, but whether or not it is flat is impossible to judge in shale material. Palmer and Repina (1993) diagnosed the genus on characteristics of only the type species and assigned it to the Olenellinae.

No other species of *Fremontella* has been recognized to date. *Olenellus groenlandicus* Poulsen, 1927 from the Cape Kent Formation of Greenland however, is here assigned to *Fremontella*. It has the advanced genal spines, no intergenal spines, wide LA, transglabellar furrows and inflated outer band of the ocular lobe characteristic of *Fremontella* (see also discussion under *Bristolia*). It is closest in morphology to *F. ashtoni* n. sp. *Olenellus cylindricus* Palmer (in Palmer and Halley, 1979) from the Cararra Formation of California has marginal, curved S2, advanced genal spines, short ocular lobes, a preglabellar field that is short to absent, and small interocular swellings and is therefore also assigned to *Fremontella*.

Walcott (1910b, pl. 38, figs. 1-11) illustrated a varied group of specimens as *Olenellus canadensis*, mostly from the Mount Whyte Formation, Mt. Bosworth, British Columbia. Harrington (1956, p. 58) selected the lectotype, restricting the name to that single specimen with advanced genal spines (pl. 38, fig. 1 of Walcott, 1910b), and assigned the species to *Fremontia*. The other illustrated cephalae of Walcott have a straight posterior margin and Harrington (1956, p. 56) stated that they "obviously belong in a very different species". Herein they are tentatively assigned to *Mesonacis? schofieldi* (Best, 1952). The assemblage needs further study, but the lectotype of *O. canadensis* Walcott is here referred to *Fremontella*. It can be distinguished from other species of *Fremontella* by the extreme shortness of its ocular lobes (tips opposite of midpoint of L2) and slightly advanced genal spines (opposite of posterior of L1). Two new species of *Fremontella* from British Columbia are described below.

Fremontella halli (Walcott, 1910b)

- 1910b *Wanneria halli* Walcott, p. 301-302, pl. 31, figs. 1-7; [non] fig. 8 [= *Olenellus thompsoni*]; [?] figs. 9-11.
- 1938 *Olenellus halli*, Resser, p. 52-53, pl. 5, figs. 7, 8, 18.
- 1938 *Olenellus alabamensis* Resser, p. 53, pl. 5, figs. 16, 17.
- 1956 *Fremontella halli*, Harrington, p. 58, pl. 15, figs. 1-3, 8-9, text-fig. 1c.
- 1959 *Fremontella halli*, Poulsen, in Moore, fig. 133.1.
- 1993 *Fremontella halli*, Palmer and Repina, fig. 3.4.

Diagnosis: A species of *Fremontella* with posterior tips of ocular lobes opposite of midlength of L1. Cephalic border wide: lateral border width subequal to length L0; anterolateral border width greater than length L0. LA intrudes slightly on anterior border. Interocular swellings present. Intergenal spines absent. Intergenal angle approximately 90 degrees. Genal spines advanced: opposite of S2. Posterior occipital node small. Cephalon approximately rectangular in outline.

Lectotype³²: A large partial cephalon (USNM 56806c) from the Rome Formation, 300 m northeast of the town of Helena, Shelby County, Alabama. Designated by Harrington (1956, p. 58). Illustrated by Walcott (1910b, pl. 31, fig. 3); Resser (1938, pl. 5, fig. 7); Harrington (1956, pl. 15, fig. 1); Palmer and Repina (1993, fig. 3.4). **Paralectotypes:** USNM 56806a,b,d-g.

Occurrences: ALABAMA. Rome Formation, localities 56c (300 m northeast of Helena) and 164c (6.4 km south of Helena), Shelby County (Walcott, 1910b, p. 302).

Discussion: The type species, *Fremontella halli* is not illustrated here, but is discussed due to the importance of this species and taxonomic problems associated with it. Walcott (1910b) illustrated two species of olenelloid trilobites from the Rome Formation near Helena, Alabama that he attributed to *Wanneria halli* Walcott and *Paedeumias transitans* Walcott. Resser (1938) described two additional species from these beds: *Olenellus alabamensis* Resser and *O. rudis* Resser. Resser's holotype of *O. alabamensis* was a specimen that Walcott (1910b, pl. 31, fig. 1) illustrated as *W. halli* Walcott, distinguished on the basis that it had more advanced genal spines and shorter ocular lobes than *W. halli* Walcott. There is no difference in ocular lobe length of the two species and

³² A lectotype was also selected by Resser (1938, pl. 5, fig. 8) for this species, but it was not based on one of Walcott's original specimens and is therefore invalid.

only a minor difference in position of the genal spines. *O. alabamensis* Resser is considered a junior synonym of *Fremontella halli*.

Fremontella halli has an unusually wide cephalic border for the Olenellidae that is wider than the border seen in other species of *Fremontella*. Interocular swellings are poorly developed on the lectotype, but distinct on some of the smaller paralectotypes (see Harrington, 1956, pl. 15, figs. 8, 9). The specimens are internal molds in shale and the prosopon is not preserved. The thorax is unknown in this species. The hypostome and thoracic spines that Walcott (1910b, pl. 31, figs. 9-11) illustrated for *Fremontella halli* cannot be attributed with certainty to this species since *Olenellus* also occurs in these strata. One of the meraspids figured by Walcott (1910b, fig. 8) has anomalously long, posteriorly directed intergenal spines compared to the other figured meraspids (figs. 5, 7). It is assigned to *Olenellus* sp.

Ontogeny: A partial ontogenetic sequence can be described based on Walcott's³³ (1910b, pl. 31, figs. 1-7), Resser's (1938, pl. 5, figs. 7, 8, 16-18) and Harrington's (1956, pl. 15, figs. 1-3, 8, 9) illustrations. The ontogeny of *Fremontella halli* is closer to that of *Mesonacis* than *Olenellus* in the timing of glabellar development, transglabellar furrows in early stages, size and position of meraspid intergenal spines and the large size of LA and absence of a preglabellar field throughout ontogeny.

Clique A meraspids are not portrayed as having procranidial spines. Cephalic border moderately well differentiated; ocular lobes lie against the cephalic border posteriorly. Extraocular areas narrow, present only anteriorly. LA well rounded, expanded well anterior to ocular lobes. Intergenal spines short, laterally directed, positioned directly posterior to ocular lobes. Genal spines absent. Cephalon subcircular in outline. (illustrated in Walcott, 1910b, pl. 31, fig. 5).

Clique B meraspids have not been described.

Clique C meraspids are not portrayed as having procranidial spines. Ocular lobe posterior tips opposite of posterior of L1. Extraocular areas slightly wider than interocular areas. LA large, subrounded; preglabellar field absent. Glabella approximately parallel-sided, bulges at LA, L3 unmodified. Glabellar furrows transglabellar. Intergenal spines short, laterally directed, laterally

³³ Walcott's illustrations have been retouched and can be used only as a general indicator of morphology.

positioned. Genal spines not indicated. Cephalon subcircular in outline. (illustrated in Walcott, 1910b, pl. 31, fig. 7).

Clique D meraspids have ocular lobe posterior tips opposite of S0. Extraocular areas almost twice as wide as interocular areas. LA large, rounded. Glabella nearly parallel-sided, L3 slightly modified. Glabellar furrows transglabellar. Intergenal spines, short, laterally directed, located at posterolateral corners. Genal spines moderately long, advanced: opposite of S1. Cephalon almost 1.5 times wider than long. (illustrated in Walcott, 1910b, pl. 31, figs. 4, 6 refigured in Harrington, 1956, pl. 15, figs. 3, 8 respectively).

Clique E specimens have ocular lobe posterior tips opposite of S0. Extraocular areas at least twice as wide as interocular areas. Glabella nearly parallel-sided, L3 slightly modified. Glabellar furrows transglabellar. Intergenal spines unknown. Genal spines long, advanced: opposite of L2. Cephalon almost 1.7 times wider than long. (Illustrated in Walcott, 1910b, pl. 31, fig. 2; refigured in Harrington, 1956, pl. 15, fig. 9).

Clique F holaspids have ocular lobe posterior tips opposite of S0. Extraocular areas at least twice as wide as interocular areas. Glabella nearly parallel-sided, L3 modified, furrows transglabellar. Intergenal spines absent? Genal spines well-developed, advanced: opposite of L2/S2. Cephalon approximately 1.7 times wider than long. (Illustrated in Resser, 1938, pl. 5, fig. 18).

Clique G holaspids have ocular lobe posterior tips opposite of L1. Extraocular areas up to 5 times width of interocular areas. Glabella nearly parallel-sided, L3 fully modified. S0, S1 typically marginal or connect across the glabella by a shallow furrow. S2 transglabellar, broadly curved. Intergenal spines absent, genal spines long. Cephalon up to twice as wide as long. (Illustrated in Walcott, 1910b, pl. 31, figs. 1, 3, reillustrated in Resser, 1938, pl. 5, figs. 7, 17 respectively, figs. 8, 16 additionally, Harrington, 1956, pl. 15, figs. 1, 2).

Fremontella campbellae n. sp.

Pl. 24, figs. 4, 6-8

Diagnosis: A species of *Fremontella* with posterior tips of ocular lobes opposite of anterior of S1. Cephalic border moderately wide: anterolateral border width approximately half length of L0. LA overhangs anterior border. L2 with lateral lobes. Interocular swellings large. Intergenal spines absent. Intergenal angle rounded. Genal spines advanced: opposite of L1. Posterior

occipital node small. Prosopon of fine terrace lines on cephalic border. Cephalon approximately rectangular in outline.

Holotype: A nearly complete cephalon (MG2b#3; Pl. 24, fig. 7) from the Eager Formation, section MG2, collection MG2b, Mt. Watson, 7 km east-southeast of Canal Flats. Paratype: MG2b#4

Etymology: For Margaret Campbell, who assisted with field work in British Columbia, and provided encouragement and helpful discussions throughout the course of this work.

Occurrences: BRITISH COLUMBIA. Eager Formation, section MG2, Mt. Watson, 7 km east-southeast of Canal Flats.

Zonal Biostratigraphy: *Wanneria logani* Subzone, *Olenellus transitans* Zone.

Discussion: *Fremontella campbellae* n. sp. is unique in its extreme development of LA that overhangs the anterior border. The genal spines are less advanced in this species than in most other species of *Fremontella* and the intergenal angles are rounded and gradually curve anteriorly instead of forming a 90 degree angle. A similar condition is seen in the unassigned mesonacine, *Olenellus fremonti* Walcott, 1910b. The interocular swellings are particularly well-developed in *F. campbellae* and are located posterior and slightly medial to the tips of the ocular lobes. Lateral lobes are well-developed on L1 and weakly developed on L2. *F. campbellae* is known from only a handful of holaspid cephalons from limestones in southeastern British Columbia.

Fremontella ashtoni n. sp.

Pl. 24, figs. 1-3, 5

1959 *Fremontella? leechi* Best nomen nudum [unpublished thesis], p. 140-142, pl. 2, figs. 9, 10.

Diagnosis: A species of *Fremontella* with posterior tips of ocular lobes opposite of anterior of L1. Cephalic border moderately wide: lateral border width one third length L0; anterolateral border width two thirds length L0. LA intrudes slightly on anterior border. L2 with lateral lobes. Interocular swellings absent. Intergenial spines minute. Intergenial angle approximately 90 degrees; posterolateral border curves laterally at midlength. Genal spines advanced: opposite of S3. Posterior occipital spine small. Prosopon of faint caecae on extraocular areas. Cephalon approximately trapezoidal in outline.

Holotype: A nearly complete cephalon (RC4c#7; Pl. figs. 3, 5) from the Eager Formation., section RC4, collection RC4c, 13 km northeast of Skookumchuck, southeastern British Columbia.

Paratype: RC4c#8

Etymology: For my husband, Todd Ashton, who assisted with field work in British Columbia and provided support and encouragement throughout this thesis.

Occurrences: BRITISH COLUMBIA. Eager Formation, section RC4, Ram Creek area, 13 km northeast of Skookumchuck.

Zonal Biostratigraphy: *Wanneria logani* Subzone, *Olenellus transitans* Zone.

Discussion: *Fremontella ashtoni* n. sp. has the most highly advanced genal spines of any species of *Fremontella*. As a result, its cephalon is roughly trapezoidal in shape and the extraocular areas are narrow. *F. halli* and *F. campbellae* have wider cephalae that are more rectangular in outline. Unlike the other species, *F. ashtoni* lacks interocular swellings and retains minute intergenal spines at the posterolateral corners in the holaspid stage.

Fremontella groenlandica (Poulsen, 1927) from Greenland is the most similar species to *F. ashtoni*. Both have highly advanced genal spines and ocular lobes of a similar length. However, the posterolateral border bows outward at midlength in *F. ashtoni*, creating the trapezoidal outline of the cephalon, not seen in *F. groenlandica* with its straight posterolateral border. LA in *F. groenlandica* does not intrude on the anterior border and the glabella has deeper furrows, especially medially.

Both *Fremontella ashtoni* and *F. campbellae* have L1 subdivided into distinct lateral lobes and a central depressed area. This condition is not apparent in *F. halli* and may be due to the fact that specimens of this species are preserved flattened in shale. *Laudonia prima* and *L. harringtoni* (see Pl. 12, fig. 10; Pl. 13, figs. 5, 8) also have lateral axial lobes developed. *F. ashtoni* shares a similar cephalic outline with *Olenelloides? canadensis* (Hu, 1971). The latter differs from species of *Fremontella* as it has procranial spines and S2 as isolated slots. *F. ashtoni* is known from only a handful of holaspid cephalae from limestones in southeastern British Columbia.

Suborder Redlichiina Harrington *in* Moore, 1959
 Superfamily Paradoxidacea Huxley and Corda, 1847

Discussion: The Paradoxidacea, as presented by Moore (1959), is a superfamily of large, generally micropygous, multisegmented trilobites with glabella long, either tapering forward or clavate (with a distinct anterior taper). The glabellar furrows tend to be transglabellar. Ocular lobes are generally long and curved and genal spines are well-developed. This superfamily concept is expanded to include the Edelsteinaspidae, which share all the cranidial features of the Paradoxidacea, but have large pygidia. The monotypic Hicksiidae, assigned to the Paradoxidacea by Harrington (*in* Moore, 1959) is an anomalous family that share some similarities with the unassigned Protopygidae.

Family Edelsteinaspidae Hupé, 1953b

Diagnosis: A family of Paradoxidacea with large pygidia. Glabella generally reaching anterior border or margin; tapering forward, or widest near 2/3 length. S1 transglabellar. Three pairs of glabellar furrows. Fixigenae narrow; posterior limbs wide, tapering. Ocular lobes strongly curved. Pygidium vaulted; generally without border or border furrow; margin generally entire. Pygidial axis long, tapering, subterminal; generally with post-axial ridge. Prosopon granular.

Included Genera: *Edelsteinaspis* Lermontova, 1940; ?*Labradoria* Resser, 1936; ?*Granularaspis*³⁴ Babcock and St. John, 1995; *Polliaxis* Palmer, 1968.

Discussion: The Edelsteinaspidae Hupé, 1953b was created as a monotypic family based on the Middle Cambrian *Edelsteinaspis* Lermontova, 1940. Hupé (1953b) tentatively assigned the family to the Corynexochida, a designation followed by Palmer (1968). Moore (1959) did not recognize the family and listed *Edelsteinaspis* among the Middle Cambrian genera of the "Order and Family Uncertain". Other than the large pygidium and long glabella, this family shares no features with members of the Corynexochida. The glabellar furrow arrangement, absence of a preglabellar field and clavate glabellar shape of *Polliaxis* are all features of the Paradoxidacea. The Edelsteinaspidae is regarded here as a family of Paradoxidacea characterized by large pygidia.

³⁴ The name *Granularaspis* was proposed by Babcock and St. John (1995) as a replacement name for *Granularia* Poletaeva (*in* Lermontova, 1951) which is preoccupied by the generic name of a trace fossil, *Granularia* Pomel, 1849.

Polliaxis was assigned to the Edelsteinaspidae by Palmer (1968, p. B49) who noted that both *Polliaxis* and *Edelsteinaspis* have large, multisegmented pygidia and a number of shared cranial features including a "long glabella that has a posterior transglabellar furrow and a relatively large unfurrowed anterior part, narrow fixed cheeks, and long slender posterior limbs". The structure of the pygidia is also similar with both genera having long but subterminal axes, pleural regions with a sigmoidal profile and no border furrow. The sigmoidal profile means that inner and outer portions of the pleurae are nearly flat and the middle portion is strongly downslipping.

Henningsmoen (*in* Moore, 1959) assigned *Labradoria* to "Family Uncertain" in the Redlichiina superfamily Ellipsocephalacea - an inadequately diagnosed superfamily of micropygous trilobites. Chernysheva (1960), Suvorova (1964) and Ivshin (1978) assigned *Labradoria* to the Edelsteinaspidae based on cranial similarities: an assignment that is tentatively followed here. Ivshin (1978) also demonstrated that *Labradoria* has a large pygidium similar to that of other edelsteinaspids.

Granularaspis Babcock and St. John, 1995 of the monotypic family Granularaspidae (= Granulariidae, Poletaeva (*in* Lermontova, 1951)) was originally described as representative of a family of uncertain affinities and Henningsmoen (*in* Moore, 1959) included it under "Order Uncertain". *Granularaspis* has a pygidium that is structurally the same as that of *Edelsteinaspis* and *Polliaxis*, and its glabella has the characteristic shape of the Paradoxidacea. It is unusually in being proparian and in having a preglabellar field. *Granularaspis* is tentatively included in the Edelsteinaspidae, and perhaps could be assigned to a separate subfamily.

Genus *Polliaxis* Palmer, 1968

Type Species: *Polliaxis inflata* Palmer, 1968 from the Adams Formation, Yukon River, east-central Alaska. (by original designation)

Diagnosis: A genus of Edelsteinaspidae with glabella large, widest at 2/3 length. Anterior border well-developed laterally, narrows medially anterior to glabella. S2-S3 marginal when developed. Librigenae with genal spines. Pygidial axis poorly differentiated posteriorly from pleural fields. Pleural furrows deep adaxially, shallow abaxially. Interpleural furrows well-developed, deepest abaxially.

Other Species:

Polliaxis muralensis n. sp.; Mural Fm., Mt. Kerkeslin, B.C.

Polliaxis sp. 1; Poleta Fm., Gold Point, Nevada.

Discussion: *Polliaxis* has a glabella that widens forward, then narrows anteriorly at some point anterior to the midlength, similar to that glabella of *Paradoxides*. Both genera have a tendency towards effacement of anterior glabellar furrows in some species (i.e. compare *Polliaxis muralensis* n. sp. with *Paradoxides pinus* Holm, illustrated in Westergård, 1936, pl. 6). Ocular lobes are inflated and strongly curved in both genera. In contrast, the pygidia of the two genera are different: *Paradoxides* is micropygous whereas *Polliaxis* is approximately isopygous.

The pygidium of *Polliaxis* bears a strong similarity to the pygidium of *Edelsteinaspis* in shape, axial structure and possession of both pleural and interpleural furrows. In *Polliaxis*, pleural furrows are deep only adaxially while interpleural furrows are deep only abaxially. Pygidia of *Edelsteinaspis* typically lack such differentiation in expression of the furrows. Another difference is the typically strong ridge running posteriorly from the pygidial axis in *Edelsteinaspis*, whereas such a ridge is barely distinguishable in *Polliaxis*. Two new species of *Polliaxis* described here demonstrate that the genus was rare but widespread in western Laurentia from Alaska to the Great Basin.

Polliaxis muralensis n. sp.

Pl. 25, figs. 3-8

Diagnosis: A species of *Polliaxis* with S2 and S3 effaced. Glabella highly inflated. Axial tubercle large. Librigenae with long, robust genal spines. Pygidium with median indentation of posterior margin; 7 pairs of pleural furrows. Pygidial axis with 7 axial rings. Prosopon of fine granules.

Holotype: A nearly complete pygidium (GSC 57672#2; Pl. 25, figs. 3, 6) from the Mural Formation, locality 1, GSC collection 57672, Mt. Kerkeslin, Banff-Jasper Highway, British Columbia. Paratypes: GSC 57672#1, #5

Occurrences: BRITISH COLUMBIA. Mural Formation: locality 1, Mt. Kerkeslin, Banff-Jasper Highway.

Discussion: Specimens of *Polliaxis* from British Columbia were first reported by North (1971). W.H. Fritz of the Geological Survey of Canada kindly made these specimens available for this study to allow a more meaningful discussion of the genus. Material of *P. muralensis* is fragmentary, but distinct from the type species, *P. inflata* Palmer, 1968. It has a more inflated

glabella that is wider and has shallower anterior glabellar furrows. The librigenae were not described for *P. inflata*. Only a fragment of the librigenae is known for *P. muralensis* and it consists of the base of a large genal spine. The pygidium has a stronger median indentation than that of *P. inflata*. The sigmoidal shape of the pygidium characteristic of the Edelsteinaspidae is not well developed in *P. muralensis* as the margin remains sloping downward rather than with only a slight flattening out. The granular prosopon on the pygidium is finer than the prosopon on the cranidium. The anterior pygidial margin in small specimens is strongly inclined posteriorly.

Polliaxis sp. 1

Pl. 25, figs. 1-2

Discussion: Only two fragmentary specimens from the Poleta Formation, section GP, can be assigned to *Polliaxis*. The specimens, collected and prepared by C.A. Nelson, consist of a partial pygidium and a glabellar fragment. The pygidium is closely comparable to that of *P. inflata* Palmer, 1968, and differs only in having a slightly longer axis with seven rather than six axial ring furrows and seven rather than six pairs of pleural furrows. Curvature of the pygidium as well as expression and extent of the pleural and interpleural furrows is the same as for *P. inflata*. *P. muralensis* n. sp. has the same number of pygidial furrows as *Polliaxis* sp. 1, but differs in convexity and consequently in the course of the furrows. Although broken, there is no indication of a deep median notch on the posterior border as in *P. muralensis*. The glabellar fragment of *Polliaxis* sp. 1 is too incomplete for detailed comparison. S0-S3 are deep and the glabella does not expand forward as strongly as in other species of *Polliaxis*.

Genus *Labradoria* Resser, 1936

Diagnosis: A genus of ?Edelsteinaspidae with glabella tapering forward. Anterior border and border furrow well-developed. S1 and S2 generally transglabellar. Fixigenae narrow to moderately broad. Pygidial border narrow, well-defined. Pleural furrows deep, interpleural furrows shallow. Pygidial axis long, reaches border.

Type Species: *Conocephalites misera* Billings, 1861 from the Forteau Formation, L'Anse au Loup, Labrador, Newfoundland. (by original designation) Junior synonym: *Labradoria elongata* Resser, 1937a.

Other Species:

[?] *Labradoria cambridgensis* Lochman, 1956; Schodack Fm., Cambridge, N.Y.

Labradora asiatica Repina, 1965; Siberia.

[?] *Edelsteinaspis?* sp. i Fritz, 1973; Sekwi Fm., Mackenzie Mtns., NWT.

Labradora hespera Fritz, 1973; Sekwi Fm., Mackenzie Mtns., NWT.

Labradora angustifrons Ivshin, 1978; Kazakhstan.

Labradora (Labradorina) edrejensis Ivshin, 1978; Kazakhstan.

Labradora lochmanae n. sp.; Poleta Fm., Cedar Flat, Nevada.

Discussion: The affinities of *Labradora* were not discussed when Resser (1936) first named the genus, nor when Resser (1937a) presented a diagnosis and split the type species into two. The history of the type specimens was thoroughly recounted by Resser when he split the type species, but *L. elongata* Resser, 1937a cannot be supported as a separate species from *L. misera* (Billings, 1861). Most of the distinguishing features of *L. elongata* listed by Resser can be accounted for by ontogenetic differences linked to the larger size of the specimens or by preservational differences.

The pygidium of *Labradora*, described here for the first time from Laurentian material, is large. Although *L. lochmanae* n. sp. has a large pygidium like other edelsteinaspids, it has a number of structural differences including: a narrow but well-defined border, a pair of small marginal spines and a long axis that reaches nearly to the border. A post-axial ridge is present as in other edelsteinaspids. The sigmoidal shape of the pleural fields characteristic of *Edelsteinaspis*, *Polliaxis* and *Granularaspis* is not seen in *Labradora*, nor are there deep interpleural furrows as in the first two genera. The pygidium of *Granularaspis* is more similar to that of *Labradora* in having only pleural furrows well-developed and imperfectly preserved material illustrated in Lermontova (1951, pl. 21) has a suggestion of a pygidial border. The cranidium of *Labradora* is comparable to that of *Edelsteinaspis*, but it has marginal S3, and a stronger anterior border furrow. In some features such as the well-developed pygidial border, long pygidial axis, long glabella and hypostomal structure, the morphology of *Labradora* is suggestive of a dorypygine (Corynexochida). The forward tapering glabella is, however, a feature never seen in the Corynexochida, and the transglabellar furrows are never developed in the dorypygines.

Labradora is found both in strata from both Laurentia and the Siberian Platform. *L. asiatica* Repina, 1965 and *L. angustifrons* Ivshin, 1978 are known only from cranidia that are closely comparable to Laurentian species of *Labradora*. Ivshin (1978) established a new subgenus, *Labradora (Labradorina)*, for a species from Kazakhstan with a large pygidium. There are no distinguishing features of the cranidium of *L. (Labradorina) edrejensis* Ivshin, and the pygidium is of comparable morphology to the Laurentian species *Labradora lochmanae* n. sp. A separate

subgenus for the Russian species is not justified and the species should simply be referred to *Labradoria*.

Labradoria lochmanae n. sp.

Pl. 25, figs. 9-14; Pl. 26, figs. 1-10

Diagnosis: A species of *Labradoria* with glabella broadly truncated anteriorly. Anterior border furrow deep, broad. S1 to S3 deep; S1-S2 transglabellar as a shallow furrow; S3 marginal, broadly curved. S4 indistinct. Fixigenae moderately broad. Ocular ridges well-developed. Librigenae narrow with short genal spines. Occipital tubercle large. Thorax of 12 segments, each with median axial tubercle and short pleural spines. Pygidium with narrow, well-defined border, 1 pair of small marginal spines. Pygidial axis connected to border by post-axial ridge; 8 transaxial ring furrows. Pleural furrows wide; 7 pairs, extending to border furrow. Hypostome non-tapering with small anterior wings, poorly-developed maculae. Prosopon of coarse, densely-spaced granules.

Holotype: A complete specimen (LACMIP PLG32-501; Pl. 26, fig. 5) from the Poleta Formation, section CF, LACMIP collection 26866, Cedar Flat area, east of Big Pine, White Mountains, Inyo County, California. **Paratypes:** ICS 1056#4, #7, #12, #14, LACMIP 12579

Etymology: In honour of Christina Lochman, for her work on Cambrian trilobites and biostratigraphy.

Occurrences: CALIFORNIA. Poleta Formation, Inyo County: locality 22 and sections CF and NH, Cedar Flat area, east of Big Pine, White Mountains. NEVADA. Poleta Formation, Esmeralda County: section GP, Mt. Dunfee area, 7 km east of Gold Point.

Zonal Biostratigraphy: *Gabriellus poletensis* Subzone, *Elliptocephala* Zone.

Discussion: *Labradoria lochmanae* has a shorter anterior border furrow, more robust ocular ridges and less rounded glabellar anterior than any other described species of *Labradoria*. S2 are variably connected by a shallow, transglabellar furrow, depending on preservation of the specimens. Small but distinct S4 are present opposite and slightly anterior of the ocular ridges. This is an atypical feature of the edelsteinaspid, although some species of *Paradoxides* also have this pair of furrows developed (i.e. see *P. sjögreni* in Westergård, 1936 pl. 9). *L. hespera* Fritz, 1973 from the Mackenzie Mountains shares with *L. lochmanae* relatively broader fixigenae than those

seen in the type species. *L. cambridgensis* Lochman, 1956 is too poorly known for detailed comparison. It has narrow fixigenae, lengthy ocular lobes, deep axial furrows and a short, bluntly truncated glabellar anterior. Some of its unusual features may be accounted for by the small size of the cranidium.

Labradoria lochmanae is the first species of *Labradoria* to be described from complete specimens. The thorax is broad and non-tapering. The pygidium is of particular interest since it has never been described before for any Laurentian species of *Labradoria*. It is closely comparable to the fragmentary pygidium illustrated for *Edelsteinaspis?* sp. 1 Fritz, 1973, which is tentatively assigned to *Labradoria*. The pygidia are large and have deep, wide pleural furrows and shallow interpleural furrows. A narrow border is clearly defined in *L. lochmanae* but the material of *Edelsteinaspis?* sp. 1 Fritz is too poor to judge the presence or absence of this feature. *L. (Labradorina) edrejsensis* Ivshin, 1978 has a pygidium of closely comparable morphology to that of *L. lochmanae*.

One poorly-preserved (Pl. 26, fig. 10) and two tentatively attributed (Pl. 25, fig. 10) hypostomes are known for *Labradoria lochmanae*. They are similar in general morphology to those illustrated for *Bonnia* with a posterior and anterior body of equal width, poorly defined maculae, small anterior wings and a concave anterior border. A shallow furrow separates the anterior and posterior bodies and a posterior border is well-defined. Small granules are present on the anterior body and posterior border.

Ontogeny: A full ontogenetic sequence of articulated specimens is not known for *L. lochmanae*. Some of the small disarticulated specimens are likely meraspids as the isolated pygidia have a greater number of segments than is typical of larger specimens. The extra segment likely represent an unreleased thoracic segment. The largest pygidium (Pl. 25, fig. 12) with unreleased segments is 1.4 mm and a small cranidium (1.9 mm, Pl. 25, fig. 13) is proportionately the right size to go with it. These are considered large meraspids.

Late Meraspid Stage: Pygidia lack a well-defined border and have a proportionately shorter axis than that seen in the holaspids. The axis is connected to the posterior margin by a long ridge. Nine pairs of pleural furrows are present, the first pair belonging to an unreleased thoracic segment. Cranidia have an almost parallel-sided glabella with only a slight forward taper.

Holaspid Stage: The holaspid ontogeny is conservative. The glabella becomes more tapered and lengthens slightly displacing the anterior border. An anterior border furrow is maintained but

becomes shorter. S3 increases in curvature and a small S4 develops. The pygidium becomes proportionately longer and more hemioval rather than triangular in outline.

Discussion: Ontogenetic material has not been described for any other edelsteinaspid. A feature of particular interest seen in *Labradoria lochmumae* and *L. misera* is a slight shortening of the preglabellar field that corresponds with a lengthening of the glabella. In the Corynexochida, a preglabellar field is generally absent throughout ontogeny. In the Ptychopariida, a preglabellar field is absent early in ontogeny and becomes progressively longer during ontogeny. This corresponds to a shortening of the glabella and is opposite to what occurs in *Labradoria*. The Redlichiida, however, are characterized by a lengthening of the glabella through meraspid ontogeny (see extensive section on the Olenellina) and Westergård (1936, pls. 4, 5) illustrated the same for *Paradoxides*. This is an important piece of information which indicates that the affinities of *Labradoria* are not likely with the Corynexochida or Ptychopariida.

Order Corynexochida Kobayashi, 1935

[*nom. transl.* Moore, 1959 (*ex* Suborder Corynexochida Kobayashi, 1935)]

Diagnosis: An order of Trilobita with hypostome attached to rostral plate throughout ontogeny; usually conterminant. Preglabellar field absent to poorly developed: glabella reaches anterior border or margin. Glabella expanding forward, parallel-sided, suboval or slightly constricted: 4 pairs of glabellar furrows, variably impressed. Pygidium usually with border. Glabella clavate to corynoid from protaspid through meraspid stages.

Assigned "Families": Corynexochidae Angelin, 1854; ?Zacanthoididae Swinnerton, 1915; Dolichometopidae Walcott, 1916b; Albertellidae Hupé, 1953b; Illaenacea Hawle and Corda, 1847.

Discussion: Kobayashi (1935) was the first trilobite taxonomist to group a large number of similar families together under the superfamily Corynexochoidae. Moore (1959) denoted the taxon to ordinal rank and restricted it to Cambrian genera, as Rasetti (1951) had suggested. The fundamental feature uniting this group according to Rasetti (1951, 1952) and accepted by Whittington (1995), is the attached hypostome which is fused to the rostral plate. While this is generally true, a number of genera are demonstrated to have attached hypostomes with a functional hypostomal suture (see *Ogygopsis*, *Bonnia* and discussion under the Dorypyginae). Öpik (1982) also created a subfamily of dolichometopids characterized by hypostomes that are not fused to the rostral plate. While an attached hypostome is common to all Corynexochida, a

fused rostral-hypostomal plate is typical only of some genera. The importance of the fused rostral-hypostomal plate as a diagnostic character of the Corynexochida is further questioned by Fortey (1990a), who proposed that the attached (and conterminant) condition is the primitive hypostomal state in the Trilobita. This would make the attached hypostome in the Corynexochida a sympleisiomorphy, not an autapomorphy, and negate it as a diagnostic characteristic of a monophyletic taxon. All Corynexochida have similar protaspid stages, especially in the clavate glabella. However, this is likely also a sympleisiomorphy as it is shared with ptychopariid trilobites (Robison, 1967). The Corynexochida, as classified by Moore (1959) is likely a grade, rather than a clade, of trilobites.

Classification of early members of any taxon is not an easy task. They are ancestors of later groups, but the exact lineage relationships of these generalized early forms are often unclear. The early soft-bodied arthropods of the Burgess Shale present similar problems (Gould, 1989; McMenamin and McMenamin, 1990). With regards to the Corynexochida, the alternatives are: to recognize the Corynexochida as a paraphyletic group of primitive forms with unresolved ties to later groups or to abandon the use of orders and superfamilies and focus instead on establishing monophyletic families of unresolved relationship to one another. Continued use of the Corynexochida as an acknowledged paraphyletic group is favoured at this time. However, every effort must be made to restrict membership to include only families that are more closely related to one another than to members of the Ptychopariida.

The character of a hypostome attached throughout ontogeny is accepted as a defining feature of the Corynexochida. It may, however, vary from conterminant to impendent, and may not be fused to the rostral plate but have a functionally hypostomal suture. Associated with this feature is the absence of a preglabellar field, although a broad anterior border furrow may be present such as in *Oxygopsis*. Glabellar shape is parallel-sided, expanding forward or suboval: it is never tapering forward as in the Ptychopariida. A pygidial border is generally present, although may it be poorly defined in effaced species. The ontogeny of members of the Corynexochida is distinctive: with some members of the Ptychopariida they share a similar protaspid form with a clavate frontal glabellar lobe, but all known Corynexochida maintain a corynoid glabella through the meraspid stage, a state which is not found in the Ptychopariida.

The suprageneric classification of the Corynexochida in the Treatise on Invertebrate Paleontology (Moore, 1959, summarized in Table 13) is in need of revision. Firstly, diagnoses of the families and subfamilies need to be re-evaluated. The Dolichometopidae Walcott, 1916b, is a heterogeneous family of largely post-Lower Cambrian species that needs re-evaluation. The

Table 13. Previous classifications of the Corynexochida.

Moore (1959)	Suvorova (1964)
Corynexochida	Corynexochoidea
Dorypygidae	Zacanthoididae
<i>Dorypyge</i>	Zacanthoidinae
* <i>Basocephalus</i>	Albertellinae
<i>Bonnaria</i>	Fieldaspinae
<i>Bonnia</i>	Mexicaspinae
<i>Bonniella</i>	*Jakutidae
<i>Bonniopsis</i>	*Jakutinae
* <i>Dorypygina</i>	*Malykaniinae
?* <i>Erbiosis</i>	*Amgaspidae
<i>Fordaspis</i>	Dolichometopidae
<i>Holteria</i>	Dolichometopinae
<i>Kootenia</i>	Ptarmiganiinae
* <i>Notasaphus</i>	Glossopleurinae
?* <i>Paraolenoides</i>	Orrinae
<i>Olenoides</i>	Ogygopsidae
?* <i>Strettonia</i>	*Balangiidae
?* <i>Tolanaspis</i>	Edelsteinaspidae
* <i>Prokootenia</i>	Edelsteinaspinae
?* <i>Tabatopygellina</i>	*Nodiceptinae
?* <i>Kooteniellina</i>	*Laticephalinae
?* <i>Babakovia</i>	Dorypygidae
Ogygopsidae	Dorypyginae
<i>Ogygopsis</i>	Protypinae
† <i>Oryctocephalidae</i>	Holterinae
† <i>Dolichometopidae</i>	*Milaspinae
Corynexochidae	*Hicksiidae
Corynexochinae	Corynexochidae
<i>Corynexochus</i>	Corynexochinae
<i>Bonnaspis</i>	Bonnaspinae
* <i>Corynexochina</i>	*Tiniinae
* <i>Acantheinae</i>	* <i>Corynexochellinae</i>
* <i>Acontheus</i>	* <i>Acantheinae</i>
Zacanthoididae	Vanuxemellinae
<i>Zacanthoides</i>	Oryctocephalidae
<i>Albertella</i>	Oryctocephalinae
<i>Fieldaspis</i>	Oryctocarinae
<i>Mexicaspis</i>	Tonkinellinae
<i>Prozacanthoides</i>	Lancastriinae
<i>Stephenaspis</i>	Cheiruroidinae
<i>Vanuxemella</i>	
<i>Zacanthopsis</i>	
† <i>Dinesidae</i>	

* non-Laurentian taxon

† assigned genera not listed

monotypic Ogygopsidae Rasetti, 1951 is now included in the Dorypyginae Kobayashi, 1935, which is itself reduced in taxonomic level and assigned to the Corynexochidae Angelin, 1854. The Oryctocephalidae Beecher, 1897 is a well-defined family, but it lacks the characteristic ontogeny of the Corynexochida. It may be more closely related to members of the Ptychopariida. The Zacanthoididae are another heterogeneous group, some of which may have closer affinities with members of the Redlichiida, others with members of the Dolichometopidae. The Dinesidae Lermontova, 1940 was questionably considered Corynexochida by Bergström (1973b), but Kobayashi (1942) and Opik (1982) considered it not closely related and Palmer (1968) assigned *Dinesus* to the Ptychopariida. The Illaenacea Hawle and Corda, 1847 (= *Scutelluina sensu* Lane and Thomas, 1983) have all of the defining features of the Corynexochida, including the distinctive ontogeny. The post-Cambrian age of this group is not a justifiable basis for exclusion from the Corynexochida as suggested by Rasetti (1951). The close probably relationship of the Illanacea with the Corynexochida has also been discussed by such authors as Pribyl and Vanek (1971) and Lane and Thomas (1983). Fortey (1990a) suggested assigning the Illanacea to the Corynexochida. This suggestion is followed, although it produces a lopsided taxonomy to have one suborder when all other categories within the Corynexochida are no higher than familial in rank. It is not preferred at this time to group all Cambrian Corynexochida into a separate suborder of equal rank to the Illanacea due to the questionable relationship of some families to the core family, the Corynexochidae. Fortey (1990a) also assigned the Leiestegiacea to the Corynexochida. This superfamily is poorly known to the author and is not commented on. Table 14 summarizes the classification of the Corynexochida developed here.

All taxonomic considerations of the Corynexochida are unfortunately Laurentia-centric. There is an abundance of Russian and Chinese literature, but much of it is not available. The literature that is available can only be examined by the author in a superficial manner due to the language barrier. Suvorova (1964) produced a monograph on the Corynexochida and a summary of her classification is given in Table 13.

Ontogeny: The distinctive pattern of ontogenetic development in the Corynexochida has already been mentioned. Robison (1967) provided a detailed comparison of ontogenies of the Ptychopariida and Corynexochida using *Crassifimbria walcotti* (Resser, 1937b) (described in detail by Palmer, 1958) and *Bathyriscus fimbriatus* Robison, 1964. He concluded that both share a similar protaspid stage in the following features: shape and convexity of the protaspid, possession of three pairs of fixigenal spines, course of the facial suture, attachment of hypostomes, absence of a preglabellar field, forward expansion of the frontal glabellar lobe and large relative size of the protopygidium. Robison (1967) hypothesized that differential growth

Table 14. Laurentia-centric classification of the Corynexochida here proposed.

Order Corynexochida Kobayashi, 1935

Corynexochidae Angelin, 1854

Corynexochinae Angelin, 1854

= Bonnaspininae Suvorova, 1964

Corynexochus Angelin, 1854*Bonnaspis* Resser, 1936= *Bonnaria* Lochman, 1956*Bonnina* Fritz, 1991

†Acontheinae Westergård, 1950

= Trinidae Poletaeva, 1956

= Corynexochellinae Suvorova, 1964

Dorypyginae Kobayashi, 1935

= Ogygopsidae Rasetti, 1951

= Kootenidae Resser, 1939

Dorypyge Dames, 1883*Olenoides* Meek, 1877*Kootenia* Walcott, 1888= *Notusaphus* Gregory, 1903*Ogygopsis* Walcott, 1889= *Taxioura* Resser, 1939= *Wangcunia* Peng *et al.*, 1995*Bonnia* Walcott, 1916= *Bonniella* Resser, 1937*Bonniopsis* Poulsen, 1946*Fordaspis* Lochman, 1956

†Dolichometopidae

?Zacanthoididae

Zacanthoides Walcott, 1888*Prozacanthoides* Resser, 1937b*Zacanthopsis* Resser, 1938*Mexicaspis* Lochman, 1948*Fieldaspis* Rasetti, 1951*Stephenaspis* Rasetti, 1951*Ptarmiganoides* Rasetti, 1951*Parkaspis* Rasetti, 1951*Zacanthopsina* Palmer, 1964*Albertelloides* Fritz, 1968*Albertellina* Palmer (*in* Palmer and Halley, 1979)*Paralbertella* Palmer, (*in* Palmer and Halley, 1979)

Albertellidae Hupé, 1953

Albertella Walcott, 1908*Vanuxemella* Walcott, 1916= *Vistoia* Walcott, 1925*Holteria* Walcott, 1924

Order Unassigned

†Oryctocephalidae Beecher, 1897

+Cheiruroideidae Chang, 1963

* non-Laurentian taxon

† assigned genera not listed

rates are responsible for producing the differences in holaspid form between the two groups (summarized in Table 15), with the Corynexochida retaining many juvenile features. The Corynexochida therefore share a common ancestry with the Ptychopariida.

Ontogenetic stages have been described for a number of species of Corynexochida, listed in Table 16. The most in-depth analysis of ontogeny of a species of Corynexochida was by Robison (1967) for *Bathyriscus fimbriatus* Robison. Using silicified material, he was able to obtain a large number of small stages and to determine possible instars using scatter diagram plots of length versus width. He found marked size groupings for measured cranidia on the scatter diagram and concluded that these represent the first five instars of ontogeny (meraspid degrees 0 through 5). Since the holaspid has nine thoracic segments, either the later instars are missing, or more than one thoracic segment was released during each molt. The former seems more likely as there is a considerable gap in size and morphology between the largest meraspid and smallest holaspid illustrated. It is interesting to note that the long occipital spine present on the holaspid is not present in the meraspids.

A major contribution made in this work is clarification of the ontogeny of *Bonnia*, a dorypygine. It is comparable to that described for other genera of Corynexochida with a meraspid stage characterized by a corynoid glabella. This glabellar shape is not retained in the holaspid and is transformed into an almost parallel-sided to suboval glabella.

Family Dolichometopidae Walcott, 1916b

[*nom. transl.* Hupé, 1953b (ex Dolichometopinae Walcott, 1916b)]

Discussion: Kobayashi (1942, p. 146) first provided a diagnosis of the Dolichometopidae as a "Corynexochidae of large size, elliptical to ovate in outline; eyes mostly large and located close to a glabella; thorax composed of 7 to 12 segments; pygidium with a marginal border". He also provided a detailed account of the early attempts at classification within the group. Poulsen (*in* Moore, 1959) synonymized Bathyriscidae Richter, 1933; Ptarmiganidae Resser, 1935; Orrinae Hupé, 1953b and Glossopleurinae Hupé, 1953b with the Dolichometopidae and provided a broad diagnosis of the family. Only two of Poulsen's listed features have any diagnostic value: anterior area of fixigenae narrow and ocular lobes long and close to glabella anteriorly (facial suture cuts close to the glabella near the contact of the ocular ridges with the glabella). Öpik (1967, p. 177) regarded the Dolichometopidae as a "somewhat artificial division" of the Corynexochida. Öpik (1982) later produced a monograph on the dolichometopid trilobites of Australia, but failed to diagnose the family. He did comment on the incomplete knowledge of the type species

Table 15. Comparison of general holaspid morphology in Corynexochida and Ptychopariida.

	Corynexochida	Ptychopariida
preglabellar field	absent	present
glabellar shape	parallel-sided, suboval, or corynoid	tapering forward
# of glabellar furrows	5	4-5
hypostome	attached	natant
pygidial border	present	absent

Table 16. List of possible Corynexochida species with illustrated ontogenies.

Corynexochinae*Corynexochus felix* Suvorova; Suvorova, 1964*Bonnina semidiscoidea* Fritz; Fritz, 1991*Bonnaspis columbensis* (Resser); Fritz, 1991*Bonnaspis fieldensis* (Walcott); Pl. 27, Figs. 4-11; Pl. 28, Figs. 1-3**Acontheinae***Acontheus burkeanus* Öpik; Öpik, 1961*Clavigellus annulus* Geyer; Geyer, 1994**Dorypyginae***Bonnina laterispina* Fritz; Pl. 28, Figs. 10-19; Pl. 29, Figs. 1-5*Bonnina fritzi* n. sp.; Pl. 29, Figs. 6-13, Pl. 30; Figs. 1-4*Bonnina grandis* n. sp.; Pl. 30, Figs. 5-18; Pl. 31, Figs. 1-6*Bonnina ornata* n. sp.; Pl. 31, Figs. 9-15; Pl. 32, Figs. 1-5*Bonnina drysdalea* n. sp.; Pl. 32, Figs. 6-14; Pl. 33, Figs. 1-3*Bonnina paymasterensis* n. sp.; Pl. 33, Figs. 4-14; Pl. 34, Figs. 1-3*Ogygopsis batis* (Walcott); Pl. 35, Figs. 1-6*Ogygopsis typicalis* (Resser); Pl. 35, Figs. 7-8; Pl. 36, Figs. 1-4*Ogygopsis marcoui* (Whitfield); Pl. 36, Figs. 5-8; Pl. 37, Figs. 1-7**Dolichometopidae***Chilometopus artus* Suvorova; Suvorova, 1964*Glossopleura walcotti* Poulsen; Poulsen, 1964*Bathyriscus fimbriatus* Robison; Robison, 1967*Bathyriscus eboracensis* Rasetti, Rasetti, 1967*Corynexochides? expansus* Rasetti; Rasetti, 1967.*Ptarmingania aurita* Resser; Hu, 1971*Fuchouia fecunda* Öpik, 1982*Glossopleura boccar* (Walcott); Hu, 1985a**Zacanthopsidae***Fieldaspis quadriangularis* Hu; Hu, 1985b*Paralbertella limbata* (Rasetti); Hu, 1985b**Oryctocephalidae***Oryctocara snegirevae* Suvorova; Suvorova, 1964*Oryctocephalops frischenfeldi* Lermontova; Suvorova, 1964*Sandoveria lobata* Shergold; Shergold, 1969*Oryctocephalites sulcatus* Shergold; Shergold, 1969*Oryctocephalites gelasinus* Shergold; Shergold, 1969*Barklyella expansa* Shergold; Shergold, 1969**Cheiruridae***Cheiruroides (Cheiruroides) arcticus* Chernysheva; Suvorova, 1964*Cheiruroides (Inicanella) gracilis* Lermontova; Suvorova, 1964**†Illaenacea***Faillana calva* Chatterton and Ludvigsen; Ludvigsen and Chatterton, 1980*Breviscutellum (Meridioscutellum) sp.*; Feist, 1970*Scutellum calvum*; Chatterton, 1971*Dentaloscutellum hudsoni* Chatterton; Chatterton, 1971*Raymondaspis gregarius* (Raymond); Hu, 1974*Kosovopeltis borealis* (Poulsen); Ludvigsen and Tripp, 1990*Kosovopeltis svobodai* Snajdr; Kácha and Saric, 1991

† selected ontogenies only

producing uncertainty as to some familial concepts. Öpik (1982, p. 7) also stated: "The subfamily Dolichometopinae Walcott is legitimate and valid but its concept remains obscure; its clarification depends on new and informative material regarding its cephalic ventral structure". Three other potential subfamilies were listed, but out of the four subfamilies, only two were diagnosed by Öpik. Suvorova (1964) also dealt with classification of the Dolichometopidae (summarized in Table 13) however, her work has been largely overlooked by western workers.

The Dolichometopidae therefore is poorly defined and in need of revision, but since only one possible member of this family is dealt with in this thesis, such a revision is beyond the scope of this work. Several observations should be recorded at this time: 1. Hypostomes illustrated for some dolichometopids (i.e. Öpik, 1982) share a greater structural similarity with some members of the Redlichiida (i.e. *Holmia* [see Kiaer, 1916, pl. 7, fig. 4], *Wanneria* [Pl. 7, figs. 4, 6], *Paradoxides* [see Nikolaisen and Henningsmoen, 1990, figs. 9c, g] than they do with the Corynexochidae. These similarities include: large, broad anterior wings, and a weakly convex posterior body that is considerably narrower and flatter than the anterior body. Other dolichometopid hypostomes such as that illustrated for *Bathyriscus* (see Robison, 1967, pl. 24, figs. 17-18) are nearly identical to those of the Corynexochidae. 2. Öpik (1982) emphasized that dolichometopids have four pairs of glabellar furrows, but ptychopariids and dorypygines only have three pairs. This is not true: dorypygines often have such shallow glabellar furrows that the furrows can only be distinguished as smooth patches lacking prosopon on the glabella (see illustrations of *Bonnua*). S4 is particularly easy to overlook located adjacent to the fossulae and expressed primarily on the vertical component of the glabella that does not show up well in dorsal photographs. Fritz (1991a) also recorded the presence of S4 in *Bonnua carnata*. The oldest ptychopariids also have four pairs of glabellar furrows (see *Proliostracus*), though three is more typical of younger genera. 3. Most, but possibly not all, described dolichometopid meraspids have a strongly expanding forward glabella, the same as in meraspids of the Corynexochidae. One probable exception is *Glossopleura broccar* (Walcott) illustrated in Hu (1985a). 4. Genera assigned to the Dolichometopidae encompass a wider range of morphologies in size and structure of the pygidium than is found in the Corynexochidae. To conclude, the Dolichometopidae needs to be more rigorously diagnosed and re-evaluated in membership. Subdivision of the family into well-defined subfamilies may provided a partial solution.

Genus *Wenkchemnia* Rasetti, 1951

Type Species: *Wenkchemnia walcotti* Rasetti, 1951 from the Middle Cambrian Mount Whyte Formation, Mt. Whyte, Rocky Mountains, British Columbia. (by original designation)

Diagnosis: (modified from Rasetti, 1951) A micropygous genus of Dolichometopidae with glabella expanding forward. Anterior border and border furrow poorly differentiated: highly reduced anterior to glabella. Glabellar furrows shallow. Ocular lobes short. Posterior limbs of fixigenae long, tapering laterally. Thorax of 9 segments: T9 not enveloping pygidium. Pygidium short, wide. Pygidial axis furrowed, extending most of length of pygidium. Pleural furrows almost straight: interpleural furrows poorly defined. Pygidial border poorly defined.

Other Species:

Wenkchemnia spinicollis Rasetti, 1951; MC Mount Whyte Fm., Mt. Stephen, BC.

Wenkchemnia sulcata Rasetti, 1951; MC Mount Whyte Fm., Mt. Stephen, BC.

Wenkchemnia swasensis Sundberg, 1994; MC Swasey Fm., Drum Mtns., Utah.

[?] *Wenkchemnia? housensis* Sundberg 1994; MC Dome Fm., House Range, Utah.

Discussion: When Walcott (1916b) described *Bathyriscus (Poliella) primus*, he noted that there were specimens of two types in his collections. Resser (1935) restricted the name *Poliella prima* to the form with long ocular lobes, nontapering posterior limbs of the fixigenae, and eight thoracic segments. Rasetti (1951) designated the one specimen from Walcott's original collection that has short ocular lobes, tapering posterior limbs of the fixigenae, and nine thoracic segments to be the type species of *Wenkchemnia*. The two genera, *Poliella* and *Wenkchemnia* share many similarities, but *Poliella* differs in having longer ocular lobes, a posterior limb of the fixigenae that expands rather than tapers laterally, a thorax of anywhere from seven to eleven segments with the most posterior segment enveloping the pygidium and a shorter pygidial axis. Other authors such as Suvorova (1964) have considered *Wenkchemnia* a junior synonym of *Poliella*.

Bathyriscus Meek, 1873 is similar to *Wenkchemnia*, and Robison (1976) suggested that they are synonyms. Rasetti (1951) commented on the similarity but differentiated *Wenkchemnia* as having shallower dorsal furrows, a smaller pygidium and poorly defined interpleural furrows. Sundberg (1994) further noted that *Wenkchemnia* lacks a well-defined pygidial border and argued that this feature, combined with the smaller pygidial size, warrants recognition of *Wenkchemnia* as a separate genus.

Wenkchemnia? sp. 1

Pl. 27, figs. 1-3

Occurrences: BRITISH COLUMBIA. Eager Formation: section MG2, Mt. Watson, 7 km east-southeast of Canal Flats; locality 7, 5 km southeast of Mt. Evans summit, Moyie Range .

Zonal Biostratigraphy: *Proliostracus buelnaensis* Subzone, *Olenellus transitans* Zone.

Discussion: Rare material from the Lower Cambrian of British Columbia is tentatively assigned to the genus *Wenkchemnia*. Two localities separated by more than 80 km are involved, both of which also contain the species *Olenellus transitans*. Material from the Hellroaring Creek locality is poorly preserved in a phyllite, but in all observable features it agrees in morphology with the cranidium in limestone from Mt. Watson. The cranidium has one deeply impressed glabellar furrow (S1), a feature listed by Poulsen (*in* Moore, 1959) as distinctive of *Poliella*. However, the ocular lobes are shorter than those of *Poliella*, extending posteriorly only to opposite of S1, and the posterior limbs of the fixigenae taper laterally. This is characteristic of *Wenkchemnia*. A single, distorted articulated specimen (Pl. 27, fig. 3) has a thorax of nine segments and four to five axial rings plus a terminal piece in the pygidium. The division between the thorax and pygidium is unclear, but is assumed to be at the slight displacement of the axis seen posterior to T9. The margins of the body are unclear but there is no strong posterior curvature of T9 laterally to indicate that the last thoracic segment curves around the anterior of the pygidium as is typical of *Poliella*. If *Wenkchemnia* is accepted as the identification of these specimens, it is the first recorded occurrence of this genus in Lower Cambrian strata.

Family Corynexochidae Angelin, 1854

Diagnosis: A family of Corynexochida of small to large trilobites, isopygous or nearly so. Glabella parallel-sided, expanding forward or suboval. Ocular lobes short. Ocular ridges low to poorly developed. Fossulae deep. Fixigenae typically moderately wide anteriorly. S0 well-impressed, other furrows generally weakly impressed to absent. Thorax typically of 6 to 8 segments. Pygidium with border; border furrow variably defined. Pygidial axis extends to border. First pair of pleural furrows extend to pygidial margin; more posterior pairs extend only to border furrow. Hypostome attached: fused or unfused. Anterior and posterior bodies of approximately equal width and inflation.

Included Subfamilies: Corynexochinae Angelin, 1854; Dorypyginae Kobayashi, 1935; Acontheinae Westergård, 1950).

Discussion: The Corynexochidae has traditionally been considered (Moore, 1959) to consist of two subfamilies, the Corynexochinae and Acontheinae, both characterized by a clavate glabella and absence of an anterior border. Members of these subfamilies bear a remarkable resemblance in their cranidial features to meraspid dorypygine trilobites, such as *Bonnina*. Geyer (1994, p. 1313) remarked on this resemblance and concluded that the defining features of the family were paedomorphic features, rather than "morphological peculiarities", and that the family likely arose by progenesis. This special relationship between the Corynexochidae and Dorypygidae (here used in the sense of Moore, 1959) is not reflected in the traditional taxonomy, therefore it is suggested that the Dorypygidae be redefined as a subfamily of an expanded Corynexochidae. The holaspid of both groups also share a similar pygidial structure.

Hypostome attachment conditions within the Corynexochidae are varied and are used in an attempt to better define subfamilies and genera. The extreme forward extension of the glabella in *Corynexochus*, type genus of the Corynexochidae, was discussed by Fortey (1990a, p. 543) under his section titled "Impendent Hypostomal Condition". Fortey speculated that "it is likely that the rostral plate became extremely narrow (sag.) and impendent attachment was not attained" in this trilobite. This is true for some genera such as *Bonnina* Fritz, 1991a, but the structure of the fused rostral-hypostomal plate of *C. plumula* Whitehouse contradicts this interpretation (see Opik, 1967, pl. 3, fig. 3, 5). The anterior rostral portion is long, and given the coincidence of the front of the glabella with the anterior margin of the trilobite, it is impossible that the anterior of the hypostome coincided with the anterior of the glabella in life position. *Corynexochus* therefore has an impendent hypostome. *Bonnaspis* Resser, 1936, also of the Corynexochinae, likely has an attached, conterminant hypostome approaching the impendent condition seen in *Corynexochus*.

The dorypygine genera *Dorypyge* Dames, 1883 and *Kootenia* Walcott, 1889 both are characterized by attached, conterminant hypostomes. Other genera such as *Ogygopsis* Walcott, 1889; *Olenoides* Meek, 1877; and *Bonnina* Walcott, 1916b, likely have attached but unfused, conterminant hypostomes. There is direct evidence for this in *Ogygopsis* (see *O. marcoui* (Whitfield), Pl. 37, fig. 6). In the latter two genera there is no direct evidence for the existence of a rostral plate and the hypostome is always found as an isolated unit (see discussion under *Bonnina*). It is likely that the hypostome was attached to the rostral plate in life and became disarticulated upon death of the individual through a functional hypostomal suture. The other alternative is that the hypostome was natant in both *Olenoides* and *Bonnina*.

Hypostomal features, regardless of whether the hypostome is fused or unfused to the rostral plate, are remarkably uniform for the family. There is a small pair of anterior wings, well-developed border with deep border furrow, rounded posterior margin, poorly developed maculae, at least one pair of marginal spines that are situated opposite the maculae and a posterior body that is short but of equal width to the anterior body. When the hypostome is fused to the rostral plate, the apparent anterior wings are much larger if the fused hypostomal suture cannot be distinguished. Some taxa have one or more additional pairs of posterior marginal spines and the border can be of varying width between taxa. Deep fossulae on the crania are characteristic of the Corynexochidae and according to Whittington (1988a), indicate the ventral attachment point of the anterior wings of the hypostome to the cranium.

Geyer (1994) recently discussed of the Acontheinae, which he described as progenetic Corynexochidae with proparian facial sutures, or secondarily fused proparian sutures. He also listed the Trinidae Poletaeva, 1956 and Corynexochellinae Suvorova, 1964 as junior synonyms of the Acontheinae. Öpik (1982) provided an alternative view and assigned the Acontheinae to the Dolichometopidae on the basis of pygidial similarities between *Acontheus tenebrarum* Öpik, 1982 and *Fuchouia* Resser and Endo, 1937.

Subfamily Corynexochinae Angelin, 1854

[*nom. transl.* Raymond, 1928 (*ex* Corynexochidae Angelin, 1854)]

Diagnosis: A subfamily of Corynexochidae with glabella expanding forward. Anterior border weak to absent. Fixigenae with minute genal spines or rounded genal angles. Facial sutures opisthoparian. Pygidium with border poorly defined. Pleural furrows shallow. Hypostome attached and fused: conterminant to impendent.

Assigned Genera: *Corynexochus* Angelin, 1854; *Bonnaspis* Resser, 1936; *Bonnima* Fritz, 1991a.

Discussion: As described under the discussion of the family, the Corynexochinae are defined mainly by pedomorphic features. The question must therefore be asked: did pedomorphosis occur once to produce a common ancestor of the corynexochines, or did it occur a number of times in separate lineages each leading to a corynexochine genus? If the latter, then the Corynexochinae represents an artificial grouping of pedomorphic genera that do not share a common ancestor. There is no clear answer to this question, but since all corynexochine genera also have tendencies toward effacement, they are tentatively accepted as a natural group.

The hypostome in the Corynexochinae varies from impendent to conterminant. In the latter state, the fused rostral plate is highly reduced medially to coincide with the slight anterior cephalic border. Such is the case for *Bonnina* Fritz, 1991a, formerly assigned to the Dorypygidae (= Dorypyginae) by Fritz (1991a), and re-assigned here to the Corynexochinae. It shares the paedomorphic features of the subfamily and is highly effaced. *Bonnaspis* Resser, 1936 is considerably expanded in membership to include most species previously assigned to *Bonnina* that have fused rostral-hypostomal plates and weak anterior borders. *Corynexochina* Lermontova, 1940 from Kazakhstan was assigned to the Corynexochinae by Suvorova (1964).

Genus *Bonnaspis* Resser, 1936

Type Species: *Karliia stephenensis* Walcott, 1989 from the Middle Cambrian Stephen Formation, locality 14s (Resser, 1936, p. 6), Mount Stephen, above Field, British Columbia. (by original designation)

Diagnosis: A small genus of Dorypyginae with glabella expanding forward. Anterior border short: strongly constricted by glabella. Anterior border furrow shallow. S0 usually transglabellar, deepest laterally. S1-S4 poorly developed. Ocular ridges low, located close to anterior margin. Anterior course of facial suture subparallel to slightly convergent. Librigenae narrow. Thorax of seven thoracic segments with short to blunt thoracic spines. Pygidium wider than long, typically with shallow border and pleural furrows. Interpleural furrows absent. Pygidial margin entire or with up to 2 pairs of spines. Rostral-hypostomal plate with large apparent anterior wings and long anterior border: one pair small marginal spines opposite of poorly defined maculae. Hypostome conterminant.

Other Species:

Corynexochus (*Bonnina*) *fieldensis* Walcott, 1916b; Mount Whyte Fm., Ptarmigan Pass, Alberta.

Corynexochus brennus Walcott, 1916b; Lévis Fm. conglomerates, Bic, Quebec (= *Bonnina quebecensis* Resser, 1936, Lévis Fm. conglomerates, Bic; and *Bonnina brennoides*, Rasetti, 1948, of the Lévis Fm. conglomerates, Grosses Roches, Quebec).

Corynexochus capito Walcott, 1916b; Parker Fm., Georgia, Vermont. (= *Bonnina lata* Resser, 1936; *B. swantonensis* Resser, 1936; *B. vermontensis* Resser, 1936, all Parker Fm., Georgia Vermont; = *Bonnina wanneri* Resser, 1936 and *Bonnina tumifrons* Resser, 1936, both from the Kinzers Fm., York, Pennsylvania).

Bonnina bicensis Resser, 1936; Lévis Fm. conglomerates, Bic, Quebec.

Bonnina columbensis Resser, 1936; Mount Whyte Fm., Mt. Shaffer, B.C. (= *Bonnua copia* Fritz, 1968; Pioche Fm., Nevada).

Bonnina crassa Resser, 1938; Shady Fm., Austinville, Virginia.

Bonnina tensa Resser, 1938; Shady Fm., Austinville, Virginia.

Bonnaspis acinosa Repina (in Khomentovsky and Repina, 1965); Siberia.

Species Inadequate for evaluation:

Ptychoparia? (Subgenus ?) *clavatus* Walcott, 1887; Taconic Region, Salem, New York (?= *Bonnua salemensis* Resser, 1936, Taconic Region, Salem, New York).

Bonnina sonora Lochman, 1952; Buelna Fm., Sonora, Mexico.

Bonnaspis paleo Suvorova, 1964; Siberia.

Bonnaria shivelikica Suvorova, 1964; Siberian Platform.

Discussion: Walcott (1889, 1916a) assigned two species to the genus *Karlia* Walcott, 1889; *K. minor* Walcott, 1889, from the Manuel Formation, Newfoundland, and *K. stephenensis* Walcott, 1889 from the Stephen Formation, British Columbia. Later however, he (Walcott, 1916b) synonymized *Karlia* with *Corynexochus* Angelin, 1854, without comment. Resser (1936) designated *K. stephenensis* Walcott the type species of *Bonnaspis*. Palmer (1968) provided a detailed discussion of *Bonnaspis* and noted that the type specimens illustrated by Walcott (1916b, pl. 36, figs. 5, 5a-c) and Rasetti (1951, pl. 28, figs. 4-6) included specimens of two different species. Palmer restricted *B. stephenensis* to the "common species" in the collections which included the holotype. The other he referred to a new, unnamed genus.

A summary of the morphology of *Bonnaspis stephenensis* is necessary to help characterize the genus. It has a forwardly expanding glabella separated from a short anterior border by a shallow border furrow. S1 is weakly indicated and S2-S4 are not apparent. The fixigenae are of the same morphology as those of *Bonnina*, and the librigenae are narrow and have a minute genal spine. The thorax has seven thoracic segments with blunt pleural spines. The pygidia are of the same general morphology as those of *Bonnina*, except for the lack of marginal spines and effacement of the border and pleural furrows.

Resser (1936) assigned only the type species, Middle Cambrian in age, to *Bonnaspis* and recognized its close relationship to *Bonnina* by stating (p. 6): "were this a Lower Cambrian form, it is doubtful that a separate genus would be recognized". Lochman (1947) disagreed with the age

division between the two genera and assigned *Ptychoparia?* (Subgenus?) *clavata* Walcott, 1887³⁵ from Lower Cambrian beds of the Taconic Region of New York, to *Bonnaspis*: a species which Resser (1936) had assigned to *Bonnia*. Suvorova (1964) also named three species of *Bonnaspis* from Lower Cambrian strata of Siberia. Material of *B. paleo* Suvorova is poor, but has no features atypical of *Bonnaspis*. *B. orthrios* Suvorova and *B. akaira* Suvorova, however, have poorly developed posterior limbs more typical of *Corynexochella* Suvorova, 1964. *B. acinosa* Repina (in Khomentovsky and Repina, 1965,) also from Siberia, is known only from cranidia, but the cranidia have a morphology typical of *Bonnaspis*. Additional species from Lower Cambrian strata of Laurentia, previously assigned to *Bonnia*, are re-assigned to *Bonnaspis*, and help to complete our understanding of the genus.

Bonnia columbensis Resser, 1936 is a widespread species described from British Columbia (Resser, 1936), Northwest Territories (Fritz, 1972), Yukon (Fritz, 1991a) and Nevada (= *Bonnia copia* Fritz, 1968). It has a well-known morphology (see Pl. 27, figs. 12-13; Pl. 28, figs. 4, 7 for type specimens) that is closer to that of the type species of *Bonnaspis* than to the type species of *Bonnia*. These features include the narrow anterior border with narrow border furrow, forward expansion of the glabella, absence of genal spines, and blunt pleural thoracic spines. This species is consequently assigned to *Bonnaspis* and serves to confirm the diagnostic features of the genus, and to provide information on the morphology of the hypostome which is not known in the type species.

Rostral-hypostomal plates of *Bonnaspis* are illustrated for *B. columbensis* (Pl. 28, figs. 4, 7) and *B. fieldensis* (Walcott, 1916b) (Pl. 27, fig. 10; Pl. 28, fig. 1) and have been previously illustrated for *B. tensa* (Resser, 1938) (see Rasetti, 1948) and *B. bicensis* (Resser, 1936) (see Rasetti, 1948). They have large apparent anterior wings (both long and wide) and a long "anterior border" compared to hypostomes of *Bonnia*, due to the fusion of the rostral plate to the hypostome. The fused suture line is still distinguishable as a change in slope in well-preserved material such as the excellent hypostome of *B. columbensis* illustrated by Fritz (1991a, pl. 8, fig. 18). The cranidium of *B. columbensis* has a minimal anterior border and narrow border furrow. When an image of the rostral-hypostomal plate is superimposed over the cranidium with the tips of the anterior wings placed over the fossulae, the anterior margin of the hypostome is coincident with the anterior margin of the glabella (conterminant condition).

³⁵ Lochman (1947) also synonymized *Bonnia salemensis* Resser, 1936, from a nearby locality in New York, with *Bonnaspis clavata*. Both species were based solely on cranidia.

Bonnaspis is intermediate in some features between *Bonnia* and *Corynexochus*. The glabella of *Bonnaspis* has a stronger forward expansion than that of *Bonnia*, but less than that of *Corynexochus*. The anterior border is narrow in *Bonnaspis*, especially medially, compared to the strong anterior border of *Bonnia* and the absence of an anterior border entirely in most species of *Corynexochus*. Like *Corynexochus*, *Bonnaspis* has seven thoracic segments, and negligible pleural and border furrows on the pygidium. There is also a strong similarity between *Bonnaspis* and *Bonnina* Fritz, 1991a. The latter differs in the extreme effacement of the dorsal furrows, absence of an anterior border and the "semidetached" anterior segment of the pygidium described by Fritz (1991a). The two genera share the same glabellar shape, insignificance of the anterior border, and tendency towards effacement of the pygidial furrows.

Bonnaspis fieldensis (Walcott, 1916b)

Pl. 27, figs. 4-11; Pl. 28, figs. 1-3; Text-fig. 44A

1916b *Corynexochus* (*Bonnia*) *fieldensis* Walcott, p. 327-328, pl. 57, figs. 4, 4a-b.

1947 *Bonnina fieldensis*, Lochman, p. 69.

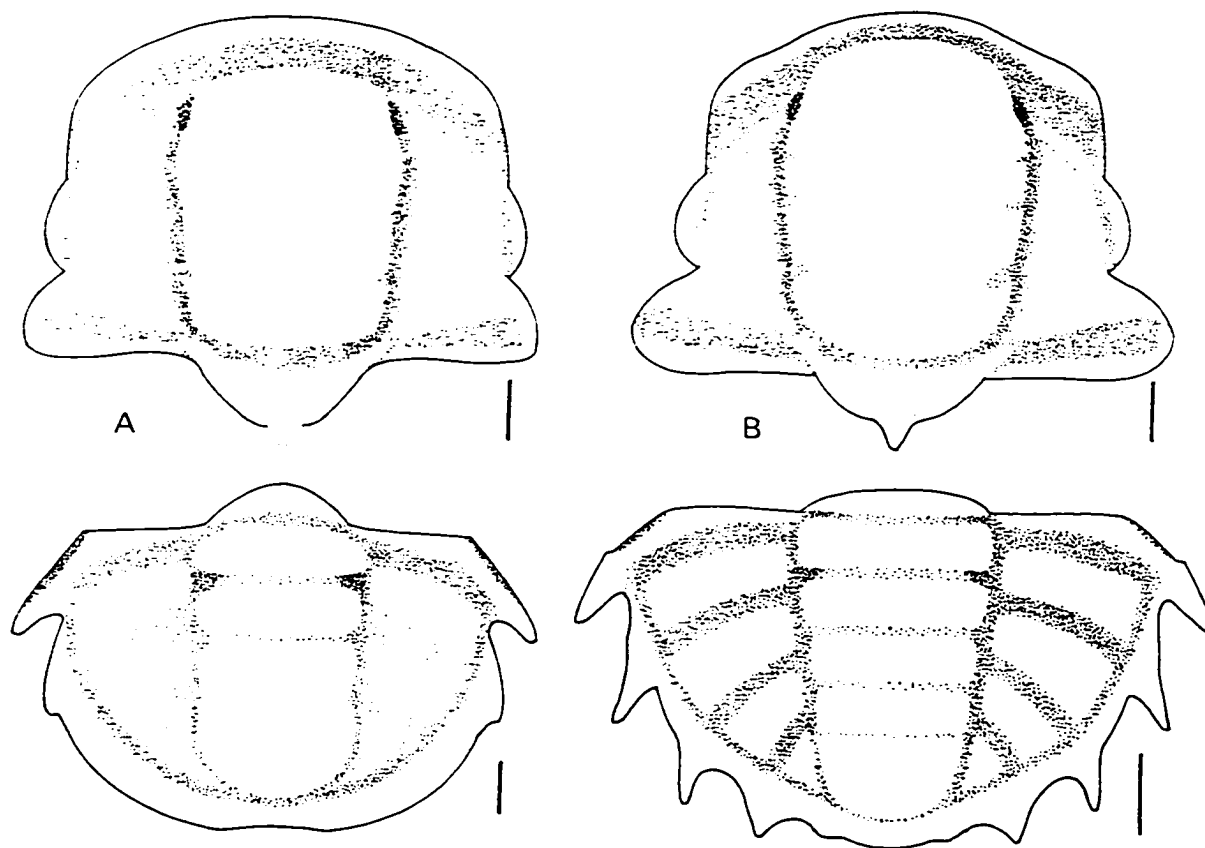
1968 *Bonnina fieldensis*, Fritz, p. 195.

1972 *Bonnina fieldensis*, Fritz, p. 32-33.

Diagnosis: A species of *Bonnaspis* with prosopon of fine pits; external surface nearly smooth. Anterior border strongly constricted anteriorly by glabella, well-developed laterally. Glabella of low relief; nearly parallel-sided, expanding forward slightly. Ocular lobes of low curvature, narrow, short: approximately 1/5 length cranidium. Ocular ridges indistinct. Occipital ring without spine or node. Pygidium with 1-2 pairs of small marginal spines, 1 shallow transglabellar and 1 shallow marginal ring furrows, 3 pairs of shallow pleural furrows. Anterior margin of pygidium inflected posteriorly at 1/2 width of pleural fields. Pygidial axis nontapering. Length/width ratio of pygidium approximately 4:7, triangular in outline.

Holotype: A complete cranidium (USNM 62751; Walcott, 1916b, pl. 57, figs. 4, 4') from the Mount Whyte Formation (reassigned to St. Piran Formation by Rasetti, 1951), south slope of Ptarmigan Pass, head of Corral Creek, 14.4 km north-northeast of Laggan, Alberta. **Paratypes:** USNM 62752-62753.

Occurrences: ALBERTA. St. Piran Formation: locality 35 I (Walcott, 1916b), south slope of Ptarmigan Pass, head of Corral Creek, 14.4 km north-northeast of Laggan. BRITISH COLUMBIA.



Text-fig. 44. A. *Bonnaspis fieldensis* (Walcott) B. *Bonnaspis columbensis* (Resser) scale bars = 1 mm

Eager Formation: section RC4, Ram Creek area, 13 km northeast of Skookumchuck; locality 5, 6.5 km northeast of Cranbrook.

Zonal Biostratigraphy: *Wanneria dunnae* to *Proliostracus buelnaensis* Subzone, *Olenellus transitans* Zone.

Discussion: *Corynexochus (Bonnia) fieldensis* Walcott 1916b is assigned to *Bonnaspis* on the basis of its strongly constricted anterior cranial border and apparent fused rostral-hypostomal plate. It does, however, have a more parallel-sided glabella and shorter anterior border on the rostral-hypostomal plate than is typical for species of this genus. There is no obvious line of fusion to differentiate the rostral plate from the hypostome, as there is in other species of *Bonnaspis*. Based on the cephalic and hypostomal morphology, a conterminant hypostomal condition is suggested and indicates assignment of this species to *Bonnaspis* rather than to *Bonnia*. One to two pairs of small marginal spines are present on the pygidium, the second pair barely distinguishable in most species. The thorax and librigenae of *B. fieldensis* have not been described. Walcott (1916b, p. 328) recognized *B. fieldensis* from a number of localities in the parks region of the Canadian Rocky Mountains, but only illustrated specimens from his Ptarmigan Pass locality. Further evaluation of specimens from Walcott's other localities is need before his identifications can be accepted and these localities added to the list of occurrences.

The history of *Bonnaspis fieldensis* (Walcott, 1916b) is closely tied to that of *B. columbensis* (Resser, 1936), both species from the Canadian Rocky Mountains. Type specimens of the latter are illustrated in Pl. 27, figs. 12-13 and Pl. 28, figs. 4, 7 for comparison (also Text-fig. 44). The two species were considered synonymous by Fritz (1968) and Rasetti (1951). Fritz (1972) later did a detailed study of the type material of both species, and concluded that there were a number of consistent differences between the two species. Fritz's (1972, p. 33) distinguishing features of *B. columbensis* are:

1. glabella expands forward and has steep lateral flanks as opposed to *B. fieldensis* which has a parallel-sided glabella with low lateral flanks
2. facial sutures angle strongly outward from palpebral lobes whereas facial sutures on *B. fieldensis* are directed more steeply back
3. pygidial axis tapers toward rear and has steep lateral flanks in contrast to axis on *B. fieldensis* which is parallel-sided and has low lateral flanks
4. pleural field has low outward dip while field on *B. fieldensis* has low dip near axis but moderate to strong outward dip near border

5. hypostome has wide (sag.) anterior border as opposed to narrow anterior border on *B. fieldensis*
6. test marked by fine granules in contrast to test of *B. fieldensis* which is marked by sparse pits visible even on worn surfaces

Bonnaspis crassa (Resser, 1938) from Virginia and Quebec shares with *B. fieldensis* a similar glabellar shape and pygidial features. It differs in having larger, more curved ocular lobes, narrower anterior fixigenae, and an occipital node. *B. tensa* (Resser, 1938), also from Virginia and Quebec, is similar to both species, but is distinguished by the extreme constriction of the anterior border medially. Its associated hypostome has large anterior wings and a long anterior border.

Subfamily Dorypyginae Kobayashi, 1935

Diagnosis: A subfamily of Corynexochidae with glabella parallel-sided to suboval. Anterior border weak to strong. Librigenae with genal spines. Facial sutures opisthoparian. Pygidium with border general well-defined. Pleural furrows moderately shallow to deep. Hypostome conterminant, attached: fused or unfused to rostral plate.

Included Genera³⁶: *Olenoides* Meek, 1877; *Dorypyge* Dames, 1883; *Kootenia* Walcott, 1889; *Ogygopsis* Walcott, 1889; *Bonnua* Walcott, 1916b; *Bonniopsis* Poulsen, 1946; *Fordaspis* Lochman, 1956.

Discussion: Kobayashi (1935) originally established the Dorypyginae as a subfamily of the Oryctocephalidae. Rasetti (1948) raised the Dorypyginae to family level and included it in the Bathyriscidae Richter, 1933³⁷ claiming that the Dorypygidae were only distantly related to the Oryctocephalidae. Rasetti (1951) was the first to include the Dorypygidae as a family of the Corynexochidae (= Corynexochida) restricted to Cambrian taxa. Hupé (1953b), Moore (1959), Chernysheva (1960) and Suvorova (1964) subsequently accepted this assignment of the Dorypygidae. This suprageneric taxon is here considered a subfamily of the Corynexochidae, to emphasize the close relationship between the Dorypyginae and Corynexochinae, as discussed under the family. Of historical note is the name Kootenidae, proposed, but not discussed or defined, by Resser (1939). Under the heading of this name, Resser described species of *Olenoides*

³⁶ This list includes only genera known from Laurentia. The Russian literature contains a number of additional genera that probably belong to this subfamily, but they are insufficiently known to the author for adequate evaluation at this time.

³⁷ The Bathyriscidae is a superfamily no longer in general use, that consists of the Corynexochidae, Bathyriscidae (= Dolichometopidae), Scutelluidae and Illaenidae.

and *Kootenia*. Both are accepted genera of the Dorypyginae (= Dorypygidae) which has priority over the name Kootenidae.

Kobayashi (1935) originally diagnosed the Dorypyginae as a subfamily with glabella wide, parallel-sided or expanded forward; effaced glabellar furrows; deep fossulae; fixigenae of moderate width; seven to eight thoracic segments; and spinous pygidium of equal size to the cephalon. This list of features is close to the concept of the Dorypyginae here presented, except an expanded forward glabella is considered characteristic of only the Corynexochinae and Acontheinae. Other features such as the effaced glabellar furrows and deep fossulae are characteristic of the Corynexochidae as a whole and are not exclusive to the Dorypyginae.

The original list of genera assigned to the Dorypyginae by Kobayashi (1935) consists of *Olenoides*, *Dorypyge*, *Kootenia*, *Holteria* and questionably *Bonnia*. All are accepted here, except for *Holteria*, which is assigned to the Albertellidae. Poulsen (*in* Moore, 1959) tentatively assigned *Strettonia* Cobbold, 1931 from Avalonia to the Dorypygidae, an assignment recently supported by Geyer (1994). *Oxygopsis* was added by Palmer (*in* Palmer and Halley, 1979). *Bonniopsis* Poulsen, 1946 and *Fordaspis* Lochman, 1956 were originally described as dorypygid (= dorypygine) genera with strongly rounded, oval glabellar outlines. The Laurentian genera *Bonniella* Resser, 1937b and *Bonnaria* Lochman, 1956, attributed to the Dorypyginae, are not considered distinct genera (discussed below). There are a number of possible additional dorypygine genera recognized in the Russian literature (i.e. see Chernysheva, 1960; Suvorova, 1964), mainly described from the Siberian Platform. These genera are insufficiently known to the author for consideration at this time and are omitted.

Palmer (1954) discussed *Holteria* in detail and assigned it to the Dorypygidae on the basis of the close similarity between the cranidia of *Holteria* and *Olenoides*. Palmer claimed that the pygidium of *Holteria* is unlike that of any other trilobite, but at least a superficial resemblance in arrangement of marginal spines can be seen between the pygidia of *Holteria* and the younger genera of the Zacanthoididae. *Vanuxemella* Walcott, 1916a, assigned to the Zacanthoididae by Rasetti (*in* Moore, 1959), is closest in cephalic morphology to *Holteria* with both genera sharing the constricted glabella, absence of an anterior border and small ocular lobes. These features are atypical for the Zacanthoididae. There is some similarity with the Corynexochinae, but the two genera might better be included in a separate family, the Albertellidae Hupé, 1953b with *Albertella*.

The Dorypyginae is characterized by attached hypostomes, but fusion of the hypostome to the rostral plate varies between genera. *Dorypyge* Dames, 1883 (see *D. swaisii* Sundberg, 1994, fig. 13.2) and *Kootenia* Walcott, 1889 (see *K. dawsoni* (Walcott) in Sundberg, 1994, fig. 14.5; *K. burgessensis* Resser, 1942 in Whittington, 1975, pl. 3, figs. 2-4) both have fused rostral-hypostomal plates. A fused hypostomal suture line can still be detected in these examples. *Olenoides* (see *O. serratus* Rominger, 1887 in Whittington, 1975, pl. 1, fig. 3, pl. 15, figs. 1,3, pl. 23, figs. 2,3) was interpreted by Whittington (1975) as having a fused rostral-hypostomal plate comparable to that of *Kootenia*, however, while the hypostome is attached in some of Whittington's illustrations, in others it is clearly disassociated from the rostral plate. A hypostome identified as *Olenoides* sp. by Fritz (1968, pl. 43, fig. 23) has no indication of being fused to a rostral plate. The best interpretation of the ventral morphology of *Olenoides* is that it had an attached hypostome with a functional hypostomal suture. Upon death of the trilobite, this suture opened separating the hypostome from the rostral plate. The same condition is well-known in *Oxygopsis* and is proposed for *Bonnia* (discussed in detail under the genus).

Bonniella Resser, 1937b, listed as a dorypygid (= dorypygine) genus by Poulsen (in Moore, 1959), is not a distinct genus. Lochman (1947) recognized that the cranidia attributed to *Bonniella* by Resser (1938), could not be distinguished from co-occurring cranidia that Resser had assigned to *Bonnia*. Resser (1937b, p. 4) listed the prime distinguishing feature of *Bonniella* as being a "pygidial flange back of the second segment". This is a puzzling feature since in the illustrated specimens (Resser, 1938, pl. 2, figs. 6-8) of the type species, the pygidia appear to be broken and weathered, removing the anterior pygidial border and leaving the anterior pleural ribs standing out in relief. The "pygidial flanges" are nothing more than the unbroken posterior pygidial border emphasized by the incomplete nature of the anterolateral portion of the pygidium. Other than the features caused by incomplete preservation, the pygidia have all the characteristics of *Bonnia*. Resser (1938) named two other species of *Bonniella* based on what appear to be *Bonnia* pygidia in various stages of completeness and two based solely on cranidia. All are now assigned to *Bonnia*.

Bonnaria Lochman, 1956, listed as a dorypygid (= dorypygine) genus by Poulsen (in Moore, 1959), was based on immature specimens and is not a distinct species. Lochman (1956, p. 1385-1386) noted the distinguishing feature of this genus as the shape of the glabella: "the posterior half is narrow, sides nearly parallel, and the anterior half is markedly swollen so that the sides diverge rapidly". This is an accurate description of the corynoid glabella shape typical of meraspids of the Corynexochida in general. Lochman (1956) assigned her small type specimens from New York to *Bonnaria saleimensis* (Resser, 1936), a species that she had previously (Lochman, 1947)

synonymized with the poorly known *Corynexochus clavatus* (Walcott, 1887). The former name is probably redundant, and despite the poor preservation of the holotype of *C. clavatus* Walcott, it is recommended that the latter name be retained as the senior synonym. This species is tentatively referred here to *Bonnaspis* Resser, 1936, as Lochman (1947) originally proposed, with *Bonnaria* tentatively considered a junior synonym of *Bonnaspis*.

Genus *Bonnia* Walcott, 1916b

Type Species: *Bathyrurus parvulus* Billings, 1861 from the Forteau Formation, L'Anse au Loup, on north shore of Straits of Belle Isle, Labrador, Newfoundland. (By original designation) Junior synonyms: *Bonnia matthewi* Resser, 1936; *B. billingsi* Resser, 1937a; *B. westoni* Resser, 1937a; *B. richardsoni* Resser, 1937a, all from the same formation and locality.

Diagnosis: A small genus of Dorypyginae with glabella parallel-sided to suboval. Anterior border well-defined, broad, not constricted by glabella. Anterior border furrow deep. S0 usually transglabellar, deepest laterally. Ocular ridges low, located close to anterior margin. Fixigenae broad. Anterior course of facial suture subparallel to slightly convergent. Librigenae narrow with long pleural spines. Thorax of six segments with short, chelate pleural spines. Pygidium wider than long with well-defined border furrow and wide to moderately wide border. Pleural furrows moderately deep to deep, 3-5 pairs. Interpleural furrows weak to absent. Axis with 2-5 axial ring furrows. Pygidial margin with 1 to 5 pairs of spines, decreasing in size posteriorly. Hypostome not fused to rostral plate.

Other Species:

Bathyrurus senectus Billings, 1861; Forteau Fm., L'Anse au Loup, NFL.

Corynexochus (Bonnia) busa Walcott, 1916b; Lévis Fm. conglomerates, Bic, Quebec.

Corynexochus bubaris Walcott, 1916b; Lévis Fm. conglomerates, Bic, Quebec.

Corynexochus (Bonnia) groenlandicus Poulsen, 1932; Ella Island Fm., East Greenland.

Bonniella virginica Resser, 1938, Shady Fm., Austinville, Virginia.

Bonniella minor Resser, 1938; Shady Fm., Austinville, Virginia. (?= *Bonniella tumida* Resser, 1938;

Bonniella bracteata Resser, 1938; both from same locality as *B. minor*).

Bonnia inflata Lermontova, 1940; Siberia.

Bonnia occipitalis Rasetti, 1948; Lévis Fm. conglomerates, Grosses Roches, Quebec.

Bonnia sculpta Rasetti, 1948; Lévis Fm. conglomerates, Bic, Quebec.

Bonnia similis Rasetti, 1948; Lévis Fm. conglomerates, Isl. of Orléans, Quebec.

Bonnia arctica Poulsen, 1958; Wulff River Fm., northwest Greenland.

Bonnia caperata Palmer, 1964; Saline Valley Fm., Gold Point, Nevada.

Bonnia venefica Khomenkovsky and Repina, 1965; Siberia.

Bonnia titondukensis Palmer, 1968; Hillard Fm., east-central Alaska.

[?] *Kootenia troyensis* Resser, 1937; New York (= *Kootenia diutina* Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT).

Bonnia laterispina Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

Bonnia insueta Ogienko in Ogienko et al., 1974; Siberia.

[?] *Bonnia septenaria* Ergaliev in Ergaliev and Pokrovskaya, 1977; Kazakhstan.

Bonnia carnata Fritz, 1991a; Illtyd Fm., Wernecke Mtns., Yukon.

Bonnia decora Fritz, 1991a; Illtyd Fm., Wernecke Mtns., Yukon.

Bonnia quadrata Fritz, 1991a; Illtyd Fm., Wernecke Mtns., Yukon.

Bonnia fritzi sp.; Eager Fm., near Canal Flats, BC.

Bonnia grandis n. sp. Eager Fm., near Canal Flats, BC.

Bonnia ornata n. sp. Eager Fm., near Canal Flats, BC.

Bonnia drystalea n. sp. Eager Fm., near Canal Flats, BC.

Bonnia paymasterensis n. sp.; Saline Valley Fm., Paymaster Canyon, Nevada.

Inadequate for evaluation:

Olenoides (Dorypyge) desiderata Walcott, 1890; Winoski Fm., Highgate Springs, Vermont.

Bonnia asiatica Pokrovskaya, 1959; Siberia.

Bonnia sisoeae Pokrovskaya, 1959; Siberia.

Bonnia dubia Pokrovskaya, 1959; Siberia.

Bonnia mira Repina, 1964; Siberia.

Bonnia curta Suvorova, 1964; Siberia.

Bonnia venusta Suvorova, 1964; Siberia.

Discussion: *Bonnia* Walcott, 1916b was first established as a subgenus of *Corynexochus* and later elevated to the level of genus by Raymond (1928). Unlike *Bonnia*, the glabella of *Corynexochus* expands forward strongly, no anterior border is present and the pygidium lacks marginal spines. Kobayashi (1935) tentatively assigned *Bonnia* to the *Corynexochinae*, but questioned whether it might better be assigned to the *Dorypyginae*. Subsequent classifications have accepted *Bonnia* as a member of the *Dorypygidae* (= *Dorypyginae*).

Walcott (1916b, p. 325-326) distinguished *Bonnia* as "having a glabella with subparallel sides and only slight traces of glabellar furrows; other parts as far as known are essentially the same as *Corynexochus*." Thus Walcott recognized the close relationship between what are now the

Corynexochinae and Dorypyginae, and acknowledged that *Bonnia* should be restricted to forms with glabellas having subparallel sides. Resser (1936) and Lochman (1947) further refined and expanded the generic concept of *Bonnia* until Rasetti (1948, p. 14) wrote: "The species included in *Bonnia* vary to a considerable extent in the shape of the glabella, distinctiveness of the glabellar furrows, depth of the dorsal furrow, presence or absence of an occipital spine, and other features." Since Rasetti claimed there was a continuous series of morphologies between disparate species, he concluded that there was no basis for splitting the genus. Subsequent authors have accepted this broad generic concept, though Fritz (1991a) made a small improvement by splitting off *Bonnina* from *Bonnia*. This broadly based, poorly defined generic concept must be rejected. Diagnosis of the genus must focus on the type species, *B. parvula* (Billings, 1861). Important features of the type (see species discussion for *B. parvula*) are its robust anterior border, broad anterior border furrow, nearly parallel-sided glabella and well-defined pygidial border. Hypostomes have not been described for this species, but other species that have these same defining dorsal features have a hypostome that is not fused to a rostral plate (further discussion follows). Species previously assigned to *Bonnia* that have expanding forward glabellas, narrow anterior borders, narrow border furrows and fused rostral-hypostomal plates are assigned to *Bonnaspis* Resser, 1936 and *Bonnina*.

Studies of *Bonnia* have focused on cranidia and pygidia, however, important diagnostic features can be found on the hypostomes and librigenae. The hypostomes are of typical morphology for the Corynexochidae, and usually have only a single pair of marginal spines. Many hypostomes of *Bonnia* are illustrated in this work and none, with the exception of a meraspid hypostome (*B. fritz?*, Pl. 30, fig. 3), show any indication of a fused rostral plate. When the outline of the hypostome is superimposed upon the cranidium with the anterior wings contacting the fossulae, the anterior margin of the hypostome is coincident with anterior margin of the glabella, and a considerable space exists between the hypostome and the anterior margin of the trilobite (*Bonnia* has a robust anterior border and broad border furrow anterior to the glabella). This space may have been occupied by a rostral plate that was attached but unfused to the hypostome, as in *Oxygopsis*. Due to the paucity of articulated material of *Bonnia*, no such attached but unfused rostral-hypostomal plate has been described. Neither has isolated rostral plates, but potential rostral plates would be tiny and difficult to distinguish in the predominantly carbonate rocks in which *Bonnia* occurs. However, an interesting comparison is that hypostomes of *Bonnia* are indistinguishable in general morphology from those illustrated as natant by Fortey (1990a, text-fig. 11). Since hypostomes in meraspids likely have a fused rostral-hypostomal plate, opening of the hypostomal suture in adults is likely a derived feature. In conclusion, *Bonnia* likely had a conterminant, attached hypostome that was unfused to a rostral plate, but it is possible that the

hypostome was natant. Librigenae, where known, are narrow with wide borders and long genal spines.

Articulated specimens of *Bonnia* are exceedingly rare given the almost exclusive occurrence of this genus in the hydrodynamically active middle carbonate belt. An enrolled, articulated specimen of *B. bubaris* (Walcott, 1916b) is illustrated in Rasetti (1948, pl. 4, figs. 22-24) and recorded as having eight thoracic segments. This number was also reported by Poulsen (*in* Moore, 1959) as typical for the genus. Careful inspection of Rasetti's photographs reveals that there are only six thoracic segments present in *B. bubaris*, the same number found in *B. paymisterensis* n. sp. (Pl. 34, fig. 1, 2). From the occurrence of six thoracic segments in two species, it is cautiously suggested that six was the typical number of thoracic segments in *Bonnia*.

Resser (1936) provided a detailed discussion of *Bonnia* and named a number of new species by splitting established species. Rasetti (1948) accepted most of Resser's species and illustrated new material from Quebec. Lochman (1947) provided a more critical review of Resser's taxonomy, redefined the genus and synonymized many of Resser's excess species. Rasetti (1948) emphasized the importance of pygidial features and prosopon differences in species determination. He came to the questionable conclusion that the prosopon on the cranidium and pygidium of the same species may be remarkably different. All species in this study show a close correspondence in prosopon between the cranidia and pygidia, although it may vary in nature between axial and pleural regions and between raised and furrowed portions of the exoskeleton. Prosopon varies through ontogeny (see *B. ornata*) and among specimens of a single collection. Palmer (1964) accepted prosopon as the primary distinguishing feature of *Bonnia* species as well as the secondary features of glabellar shape, depth of glabellar furrows, size and shape of L0, depth of pygidial pleural and axial ring furrows and number and length of marginal pygidial spines.

The non-Laurentian species assigned to *Bonnia* are difficult to evaluate due to the general poor quality of illustrations, language difficulties with Chinese and Russian publications, and poor availability of obscure, foreign taxonomic publications. *B. tokunagai* Saito, 1934, from northwest Korea, has the general morphology of *Bonnia* in the configuration of its cephalon and pygidium, however, it has seven thoracic segments. It is illustrated by retouched photographs, and without direct examination of the specimens, the species is best regarded as an unassigned dorypygine. *B. orientalis* Saito, 1934, also from northwest Korea, is illustrated only by drawings. It has the shallow glabellar furrows, rectangular glabella and strong interpleural furrows typical of *Olenoides*, though no marginal spines are illustrated.

Of the Russian species, *Bonnina inflata* Lermontova, 1940, *Bonnina venefica* Repina (in Khomentovsky and Repina, 1965) and *B. insueta* Ogienko in Ogienko et al., 1974 are here accepted as distinct species of *Bonnina*. *B. septenaria* Ergaliev in Ergaliev and Pokrovskaya, 1977 closely resembles *Bonnina*, but has seven thoracic segments; it is tentatively accepted as *Bonnina*. *B. globosa* Tomashpolskaja in Suvorova, 1964 has eight thoracic segments and lacks a robust anterior border, therefore it is considered unlikely to be a species of *Bonnina*. *B. preinflata* Suvorova, 1964 has a pygidium of few segments with a subterminal pygidial axis and is not accepted as a species of *Bonnina*. Species based only on cranidia are considered inadequately known for evaluation and are listed as such under "Other Species". Illustrations of *B. veternosa* Repina, 1964 and *B. arguta* Repina, 1960 have not been seen by the author and these species are not evaluated.

Bonnina is similar in many features to *Kootenia* Walcott, 1889³⁸, and Young and Ludvigsen (1989) questioned whether the two were distinct or actually congeneric. In spite of the similarities in glabella shape, poor development of glabellar furrows and structurally similar cranidia and pygidia, there are a few distinctive features of *Kootenia* that are not characteristic of *Bonnina*. *Kootenia* has seven thoracic segments, relatively weak development of the anterior border and border furrow, a fused rostral-hypostomal plate and a typically fully spinose pygidial margin with spines of equal length or increasing length posteriorly. The spines are a prominent feature that give a scalloped appearance to the pygidial border. *K. diutina* Fritz, 1972 from the Mackenzie Mountains was reassigned to *Bonnina* by Fritz (1991a). This species has a prominent anterior border, wide border furrow, hypostome that is not fused to the rostral plate and a fully spinose pygidial margin of spines that decrease in size posteriorly. All of these features are typical of *Bonnina*, not of *Kootenia*, however, this is a low stratigraphic occurrence for *Bonnina* with a substantial interval between this and the next highest occurrence of the genus. Fritz's (1991a) assignment of the species to *Bonnina* is tentatively followed. Incidentally, *K. diutina* Fritz is indistinguishable from *K. troyensis* Resser, 1937 from New York (see also Lochman, 1956, pl. 7 figs. 1-10), therefore the species should be known by the senior synonym, *Bonnina?* *troyensis*. This

³⁸ The generic concept of *Kootenia* has been explored in detail by Palmer (1968), Fritz (1972) and Sundberg (1994), but no effort has yet been made to revise the approximately 110 species (Palmer in Palmer and Halley, 1979) assigned to this genus. A significant number of the species may be synonymous or belong to other genera (i.e. see *Ogygopsis marcoti* (Whitfield, 1884)). The diagnostic features of *Kootenia* presented here are based mainly on the type species, *Bathyriscus* (*Kootenia*) *datesoni* Walcott, 1889. The Russia literature recognizes a number of *Kootenia*-like forms including *Kooteniella* Lermontova, 1940, *Prokootenia* Lermontova, 1940 and *Kooteniellina* Sivov, 1955 that may be synonymous with *Kootenia*, or may represent distinct genera. If the latter, some of the Laurentian species assigned to *Kootenia* may need to be reassigned to some of the Russian genera. A thorough revision of this predominantly Middle Cambrian genus is beyond the scope of this thesis.

species (listed as *K. diutina* Fritz) has also been recorded from Australia by Jell (in Bengtson *et al.*, 1990).

Ontogeny: Considering the large number of species of *Bonnia* described to date, it is surprising that no juvenile material has been illustrated. One protaspid, possibly of *Bonnia fritzi* n. sp. (Pl. 30, fig. 2), is here illustrated. Disarticulated meraspid cranidia are illustrated for many of the newly described species, but matching these small stages to their respective adults is difficult except in assemblages with only one species. Meraspid pygidia and hypostomes are more poorly known. A meraspid hypostome, possibly of *B. fritzi*, has a suggestion of a fused rostral plate.

The holaspid ontogeny of *Bonnia* is examined in detail, but only sparse meraspid and protaspid material is available. They are insufficient in number for the type of detailed analysis of instars given by Robison (1967) and are arbitrarily divided into an early and late meraspid stage. The early meraspid stage is characterized by a parallel-sided glabellar stalk with only the frontal portion strongly expanding forward. The late meraspid stage is characterized by a more evenly expanding forward glabella. The holaspid stage is impossible to determine with disarticulated material. It is arbitrarily taken at the first sign of a glabella defined by straight rather than curved axial furrows that has lost its rapid forward expansion.

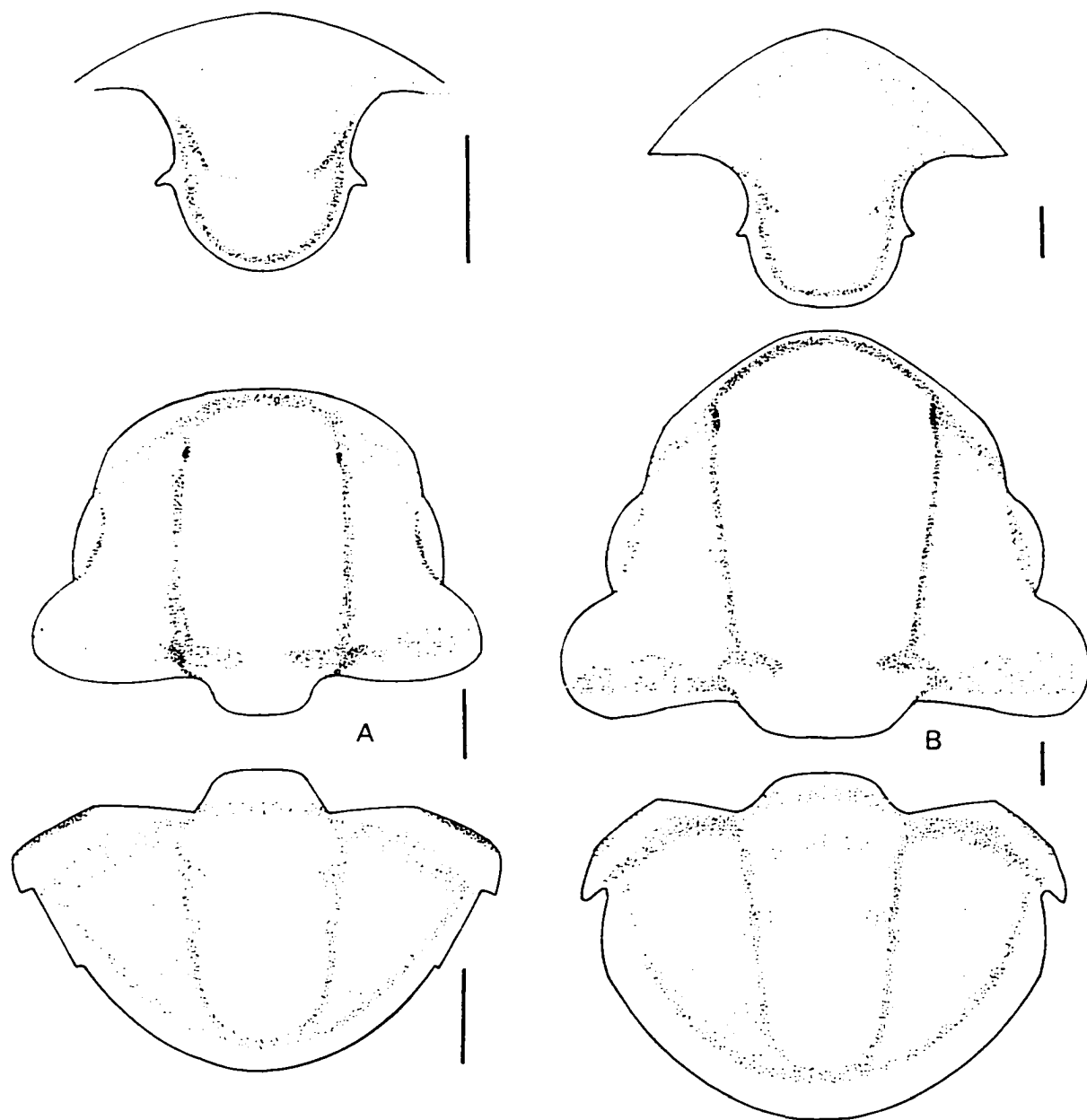
Bonnia grandis n. sp. is one of the most completely known species and description of its holaspid ontogeny serves as the model against which other *Bonnia* ontogenies are compared. Not all species appear to have the three distinct stages of glabellar development characteristic of *B. grandis*. General changes seen through holaspid ontogeny of *Bonnia* are: increased curvature of the anterior border, change in glabellar shape, relative shortening of the ocular lobes, increased development of the prosopon, increase in definition of posterior pleural furrows, loss of interpleural furrows, relative lengthening of the pygidium compared to width, and increased development of the prosopon. Most species have a constant number of marginal pygidial spines throughout their holaspid ontogeny. All ratios given for relative sizes of features in species diagnoses are measured on large holaspid specimens.

Bonnia parvula (Billings, 1861)

Pl. 28, figs. 5-6, 8-9; Text-fig. 45A

1861 *Bathyrurus parvulus* Billings, p. 16, fig. 21.

1916b *Corynexochus (Bonnia) parvulus*, Walcott, p. 328-330, pl. 57, figs. 1, 1b-c; pl. 64, fig. 6, (synonymy to date). 1936 *Bonnia parvula*, Resser, p. 7-8.



Text-fig. 45. A. *Bonnia parvula* (Billings) B. *Bonnia ornata* n. sp. scale bars = 1 mm

- 1936 *Bonnina matthewi* Resser, p. 8.
 1937a *Bonnina parvula*, Resser, p. 45, pl. 8, figs. 1-4.
 1937a *Bonnina matthewi*, Resser, p. 45-46, pl. 8, figs. 5-8.
 1937a *Bonnina westoni* Resser, p. 46, pl. 8, figs. 9-11.
 1937a *Bonnina billingsi* Resser, p. 46-47, pl. 8, figs. 12-15.
 1937a *Bonnina richardsoni* Resser, p. 47, pl. 8, figs. 16-19.
 1947 *Bonnina parvula*, Lochman, p. 69.
 1983 *Bonnina parvula*, Stouge and Boyce, pl. 8, figs. 3, 4.

Diagnosis: A species of *Bonnina* with prosopon of coarse terrace lines on glabella and pygidial axis; anastomosing terrace lines on occipital ring and fixigenae; tubercles on pygidial border; smooth pleural fields. Anterior border separated from glabella by wide border furrow. S1-S4 indistinct. Ocular lobes moderately long: approximately 2/7 length cranidium. Ocular ridges indistinct. Occipital ring with short spine. Pygidium with 2 pairs of small marginal spines, 2 deep and 1 shallow transglabellar ring furrows, 3 pairs of moderately shallow pleural furrows. Anterior margin of pygidium inflected posteriorly at 1/3 width of pleural fields. Pygidial axis non-tapering: terminal piece slightly bulbous. Length/width ratio of pygidium approximately 4:5.

Holotype: A weathered cranidium (GSC 433; Billings, 1861, fig. 21; Pl. 28, fig. 6) from the Forteau Formation, L'Anse au Loup, north shore of Straits of Belle Isle, Labrador, Newfoundland. Pleisio-type: GSC 433a

Occurrences: NEWFOUNDLAND. Forteau Formation, L'Anse au Loup, north shore of Straits of Belle Isle, Labrador.

Discussion: Considerable confusion in the species concept of *Bonnina parvula* (Billings) was created by Resser (1936, 1937a) who restricted the name to the holotype cranidium and associated similarly weathered pygidium. For the other specimens from Forteau Formation collections, Resser established four additional species: *B. matthewi* Resser, 1936; *B. billingsi* Resser, 1937a; *B. westoni* Resser, 1937a; *B. richardsoni* Resser, 1937a. In Lochman's (1947) revision of *Bonnina*, she recognized the first three as junior synonyms of *B. parvula* differing from the holotype primarily in features caused by preservational differences. To Lochman's list must also

be added *B. richardsoni* ³⁹. Resser (1937a) noted the distinguishing features of *B. richardsoni* as a more rounded anterior glabella and stronger prosopon. The type specimen is larger than the others illustrated by Resser (1937a) from the Forteau Formation, which is in keeping with ontogenetic changes that are expressed in greater rounding of the glabella in moderately large specimens (i.e. see *B. grandis* text-fig. X). Prosopon also varies through ontogeny and is highly sensitive to the vagaries of preservation. *B. richardsoni* is therefore another junior synonym of *B. parvula*.

A re-evaluation of the morphology of *B. parvula* as defined above is critical for an understanding of the genus, since *B. parvula* is the type species of *Bonnia*. It has a robust anterior border separated from the glabella by a wide border furrow. The glabella is almost parallel-sided with only the slightest forward expansion. In moderately large specimens the glabella is more rounded. The pygidium has two pairs of marginal spines and moderately impressed border and pleural furrows. The best material illustrated of *B. parvula* is that of Stouge and Boyce (1983, pl. 8, figs. 3,4). No hypostomes or free cheeks of *B. parvula* were available for this study.

The cranidium of *Bonnia parvula* is closely comparable to those of *B. paymasterensis* n. sp. from Nevada and *B. drysdalea* n. sp. from British Columbia. Both species have different pygidia with narrower borders and different segmentation than the pygidium of *B. parvula*.

Bonnia laterispina Fritz, 1972

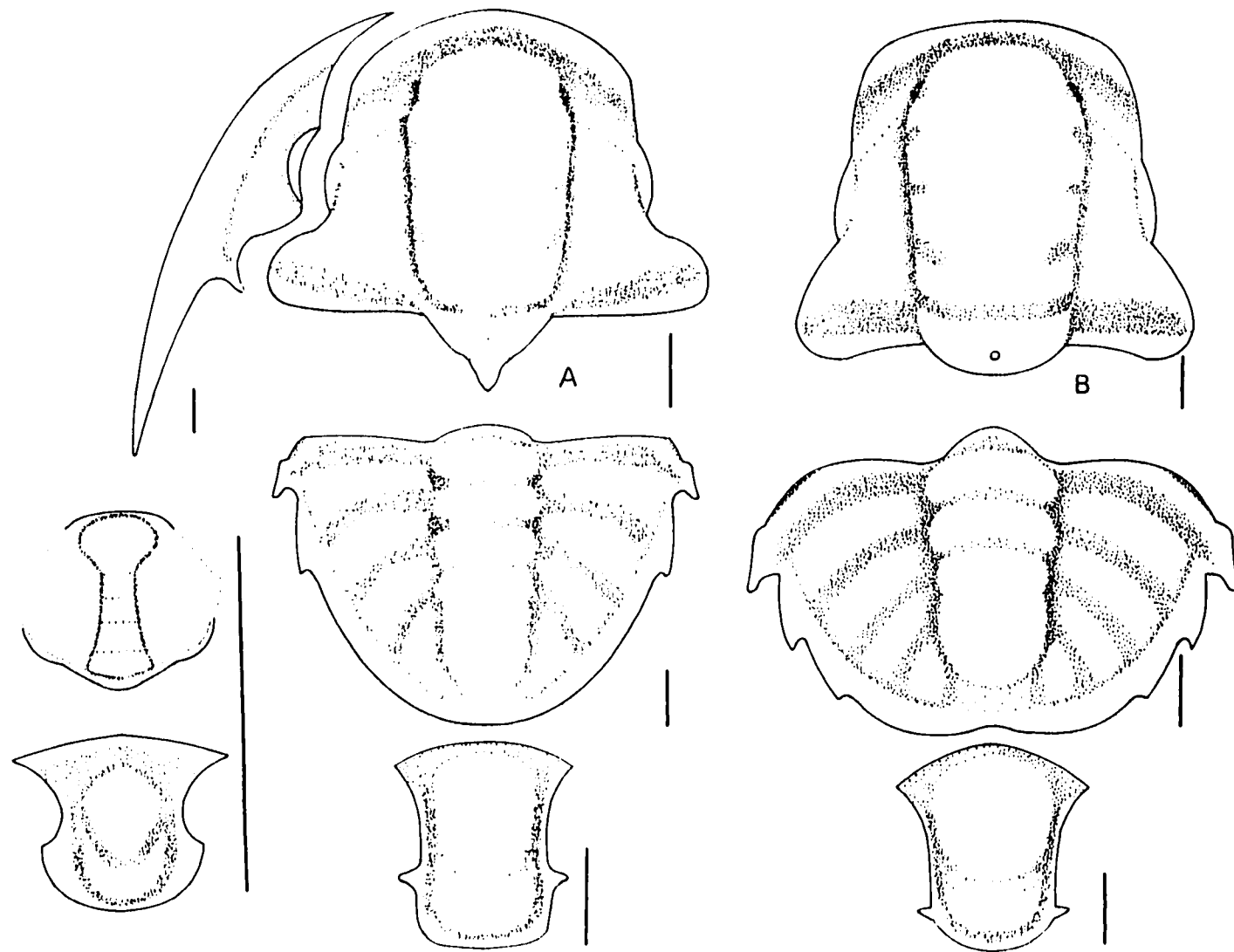
Pl. 28, figs. 10-19; Pl. 29, figs. 1-5; Text-fig. 46B

1972 *Bonnia laterispina* Fritz, p. 33, pl. 15, figs. 1-7.

1991a *Bonnia laterispina*, Fritz, p. 22-23, pl. 3, figs. 7-15, text-figs. 5a, b.

Diagnosis: A species of *Bonnia* with prosopon of fine pits; fine terrace lines on anterior of glabella. Anterior border separated from glabella by moderately narrow border furrow; border constricted slightly anterior to glabella. S1-S4 moderately deep. Ocular lobes wide, slightly curved, moderately short: approximately 1/4 length cranidium. Ocular ridges distinct. Occipital ring with minute node. Pygidium with 3 pairs of small marginal spines, 3-4 transglabellar ring furrows, 3 pairs of pleural furrows. Anterior margin of pygidium inflected posteriorly at 1/3 width of pleural fields. Pygidial axis non-tapering: terminal piece slightly bulbous. Length/width ratio of pygidium approximately 3:5.

³⁹ While Lochman (1947) failed to list *Bonnia richardsoni* as a junior synonym of *B. parvula*, neither did she include it in her list of valid species of *Bonnia*.



Text-fig. 46. A *Bonnia fritzi* n. sp. B. *Bonnia laterispina* Fritz scale bars = 1 mm

Holotype: A partial pygidium (GSC 27384; Fritz, 1972, pl. 15, figs. 3, 4) from the Sekwi Formation, GSC locality 73057, Mackenzie Mountains, Northwest Territories. Paratypes: GSC 27383, 27385-27387.

Occurrences: NORTHWEST TERRITORIES. Sekwi Formation, GSC localities 73057, 73063 (Fritz, 1972), Mackenzie Mountains. YUKON. Illtyd Formation, GSC localities 90658, 90659 (Fritz, 1991a), Wernecke Mountains. BRITISH COLUMBIA. Eager Formation: sections MG1 and MG2, Mt. Watson, 7 km east-southeast of Canal Flats; section MG3, Mt. Grainger, 6 km northeast of Canal Flats; section RC4, Ram Creek area, 13 km northeast of Skookumchuck.

Zonal Biostratigraphy: *Wanneria logani* through *Proliostracus buelnaensis* subzones; *Olenellus transitans* Zone.

Discussion: Fritz (1972, 1991a) recognized *Bonnua laterispina* Fritz, 1972 from both the Mackenzie (NWT) and Wernecke (Yukon) mountains and a degree of variability in morphology can be seen between specimens from the different localities. The Wernecke Mountains specimens have deeper glabellar furrows and a more triangular-shaped pygidium. Specimens from both localities share a pronounced constriction of the anterior border medially, strong development of fossulae, a non-tapering pygidial axis and the same segmentation of the pygidium. A tiny occipital node was recorded for this species by Fritz (1972), but this feature is not apparent in his photographs.

Only a small number of specimens (collections MG2h, MG1c) from southeastern British Columbia are a close match to the type specimens of *Bonnua laterispina*. Specimens from collections MG3b and RC4c have minor but consistent differences that are considered to be intraspecific variation. Their prosopon is variably expressed (perhaps in part due to preservation) from fine pits and granules to deep pits and coarse rugae. Glabellar furrows are also variably defined, but can be strong in mid-sized, testate specimens as they are in the Wernecke Mountains specimens. An occipital node is apparent only on occasional specimens (Pl. 28, figs. 11, 16). A consist feature of specimens from collection MG3b is the presence of only two axial ring furrows, compared to the 3-4 ring furrows typical of specimens from the type locality. Associated hypostomes have a pair of small marginal spines near the posterolateral corners: the small pair of spines opposite of the maculae that is typical of *Bonnua* is difficult to distinguish on these specimens.

Bonnia grandis n. sp. from southeastern British Columbia shares many similarities with *B. laterispina*, but has a few important differences: a long occipital spine, barely constricted anterior border, tapering pygidial axis, four pairs of pleural furrows, and a nearly straight anterior pygidial margin. *B. tatondukensis* Palmer, 1968 from Alaska is similar to *B. laterispina* with a somewhat constricted anterior border and 2-3 pairs of marginal spines, but the prosopon on its cranidia is of variable expressed terrace lines rather than pits and an occipital spine is present. *B. senecta* Billings, 1861 from Labrador and Quebec has deep glabellar furrows like *B. laterispina*, but has a different prosopon, four pairs of well-defined pleural furrows, and only 1-2 pairs of marginal pygidial spines.

Ontogeny: Ontogenetic material of *Bonnia laterispina* from collection MG3b is known from the late meraspid stage to holaspid clique C. Morphology of whole sequence is closely comparable to that described for *B. grandis*. The occipital ring of the late meraspid cranidium bears a small median node, comparable to the node occasionally distinguishable on holaspids. This feature was broken on all meraspids of *B. grandis*, but this suggests that the late meraspid stage may have been the stage at which development of the occipital spine or node first occurred.

Bonnia fritzi n. sp.

Pl. 29, figs. 7-13; Pl. 30, figs. 1-4; Text-fig. 46A

1991a *Bonnia* sp. 1 Fritz, p. 23-24, pl. 3, figs. 3-6.

Diagnosis: A species of *Bonnia* with prosopon of coarse honey-combs to rugae, tubercles in furrows. Anterior border separated from glabella by wide border furrow. S1-S4 generally shallow. Ocular lobes moderately short: less than 1/4 length cranidium. Ocular ridges distinct. Occipital spine short. Pygidium with 2 pairs of small marginal spines, 2 transglabellar plus 2 marginal ring furrows, 4 pairs of wide pleural furrows. Anterior margin of pygidium nearly straight: inflected posteriorly only at lateral edge. Pygidial axis non-tapering: terminal piece slightly bulbous. Length/width ratio of pygidium approximately 4:5.

Holotype: A nearly complete pygidium (MG2j#40; Pl. 29, fig. 8) from the Eager Formation, section MG2, collection MG2j, Mt. Watson, 7 km east-southeast of Canal Flats. Paratypes: MG2j#34, #36, #42

Etymology: In honour of W.H. Fritz, for his extensive contributions on Lower Cambrian trilobites and stratigraphy.

Occurrences: BRITISH COLUMBIA: Eager Formation, sections MG1 and MG2, Mt. Watson, 7 km east-southeast of Canal Flats. YUKON: Illyd Formation, GSC locality 90657 (Fritz, 1991a), Wernecke Mountains.

Zonal Biostratigraphy: *Wanneria logani* Subzone, *Olenellus transitans* Zone.

Discussion: Specimens of *Bonnia fritzi* n. sp. from British Columbia agree well in morphology with specimens illustrated as *Bonnia* sp. 1 by Fritz (1991a) from the Yukon. Key distinguishing features of this species are: two pairs of marginal spines, unusually broad pleural furrows, two transaxial and two marginal ring furrows and a prosopon of a strong honeycomb pattern with granules in the furrows. The prosopon is slightly variable, the "honeycombs" usually appearing as large pits, but sometimes seen as rugae surrounding depressions. Expression of the ring furrows varies with preservation. Fixigenae have wide borders and long genal spines; possibly as long as the length of the cranidium. Hypostomes have a typical morphology for *Bonnia* with faint prosopon of honeycombs to match the dorsal surface.

Bonnia buharis (Walcott, 1916b) also has a pygidium with two pairs of marginal spines and unusually broad pleural furrows, but the pleural furrows taper rapidly approaching the margin, the marginal spines are more widely spaced, the ring furrows are of a different configuration and the anterior pygidial border is wider and strongly inflected posteriorly. *B. decora* Fritz, 1991a from the Yukon has two pairs of marginal pygidial spines, but the pygidium is unusually short with few furrows and a different prosopon. *B. minor* (Resser, 1938) from Virginia shares the unusually wide pleural furrows of *B. fritzi*, but has only one pair of marginal spines and the questionably assigned cranidium has a prosopon of large tubercles.

Ontogeny: Most of the specimens available of *Bonnia fritzi* are of intermediate to large size, probably equivalent to the holaspis cliques B and C recognized for *B. grandis*. The development of the glabella differs from that recorded for *B. grandis* in that the glabella remains parallel-sided with a slight forward expansion throughout the holaspis ontogeny. This is typical of only clique A holaspids of *B. grandis*. Clique A pygidia (Pl. 30, fig. 1) have distinct interpleural furrows and two pairs of marginal spines, the same number found in larger specimens. The pygidium changes in relative proportions in the same fashion as that described for *B. drysdalea*.

Juvenile stages tentatively assigned to *Bonnia fritzi* include the only known *Bonnia* protaspis, a meraspis hypostome, and an early meraspis cranidium (Pl. 30, figs. 2-4). The meraspis

cranidium is of the same morphology described for *B. grandis*. The hypostome is 0.5 mm in length and probably belongs to a late meraspid. Although fragmentary anteriorly, there is an indication of a narrow, fused rostral plate. The anterior border is long and concave and large anterior wings are developed. The pair of marginal spines are developed as large, flat projections. It has a well-defined furrow dividing the anterior body from a wide posterior body, plus a shallow, transverse furrow crossing the posterior of the anterior body. The protaspid stage is described below.

Protaspid Stage: (approximately >0.5 mm) Anterior border barely discernible medially, slightly longer laterally. Anterior border furrow shallow. Glabellar stalk tapering forward, glabella expanding rapidly forward anterior to S4. Anterior of glabella bluntly truncated. Glabellar furrows shallow, transglabellar. Fixigenae wide, approximately 2.5 times wider than glabella. Fixigenal spines cannot be distinguished. (Pl. 30, fig. 2)

Bonnua grandis n. sp.

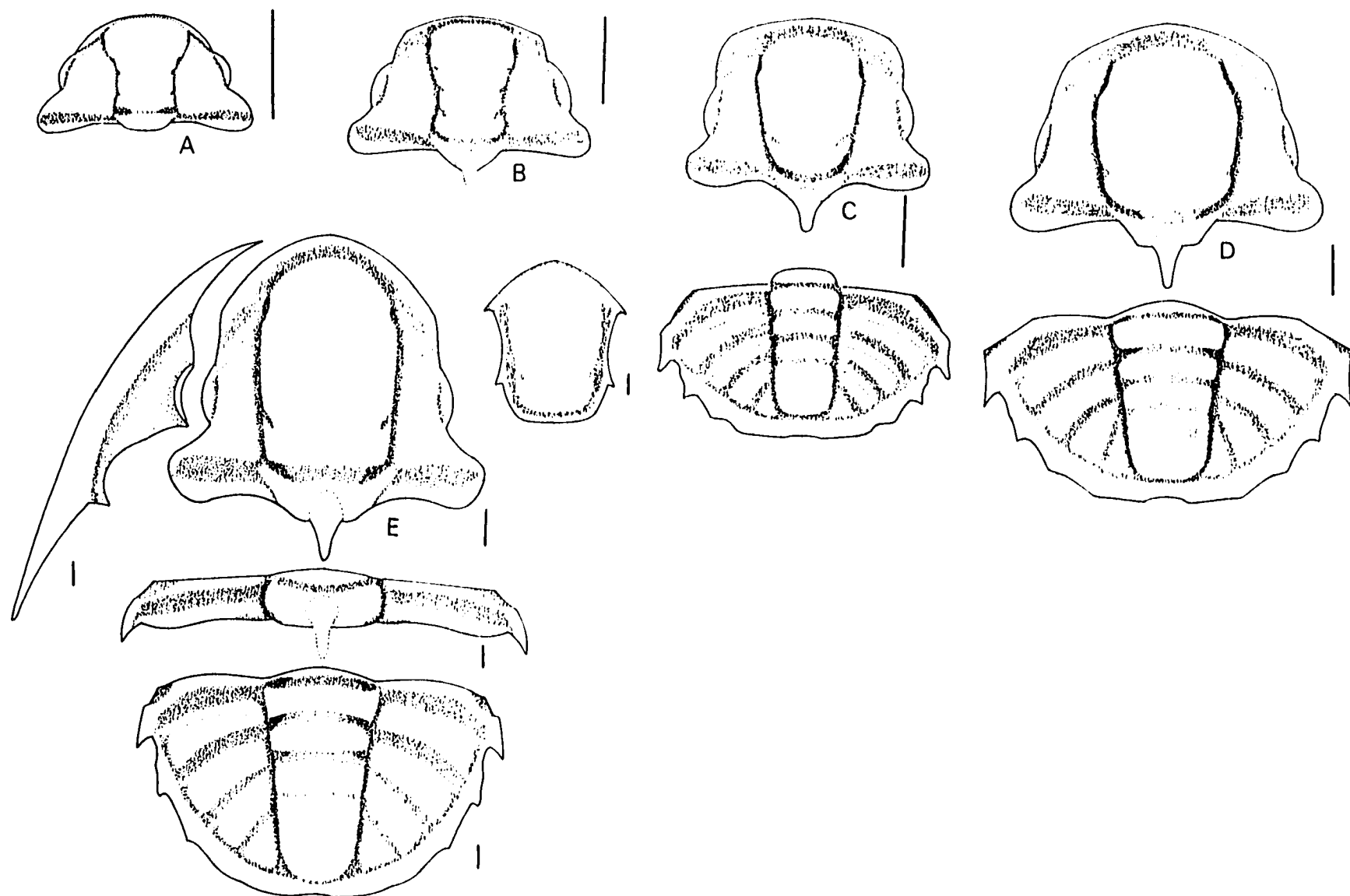
Pl. 30, figs. 5-18; Pl. 31, figs. 1-6; Text-figs. 21, 28A, 47

Diagnosis: A species of *Bonnua* with prosopon of fine honey-combs; tubercles on pygidial border, fixigenal borders, occipital ring and hypostome. Anterior border separated from glabella by moderately wide border furrow. S1 shallow, S2-S4 indistinct. Ocular lobes short: approximately 1/5 length cranidium. Ocular ridges indistinct. Occipital spine long. Pygidium with 3 pairs of marginal spines, 3-4 transglabellar ring furrows, 4 pairs of pleural furrows. Anterior margin of pygidium nearly straight: inflected posteriorly only at corners. Pygidial axis tapered posteriorly. Length/width ratio of pygidium approximately 2:3.

Holotype: A nearly complete pygidium (MG2d#5; Pl. 31, figs. 1-2) from the Eager Formation, section MG2, collection MG2d, Mount Watson, 7 km east-southeast of Canal Flats, British Columbia. Paratypes: MG2b#14, MG2d#2, MG2d#4, MG2d#8, MG3d'#2, MG3d'#4, MG3d'#6, MG3d'#9, MG3d'#12

Etymology: From the Latin adjective "grandis" (feminine, singular) meaning "large, great" for the large size that this species attained.

Occurrences: BRITISH COLUMBIA. Eager Formation: section MG3, Mt. Grainger, 6 km northeast of Canal Flats; sections MG1 and MG2, Mt. Watson, 7 km east-southeast of Canal Flats;



Text-fig. 47. Ontogeny of *Bonnia grandis* n. sp. A. early meraspide B. late meraspide C. clique A D. clique B E. clique C scale bars = 1 mm

section RC4, Ram Creek area, 13 km northeast of Skookumchuck; ?locality 5, 6.5 km northeast of Cranbrook.

Zonal Biostratigraphy: *Wanneria logani* through *Proliostracus buelnaensis* subzones; *Olenellus transitans* Zone.

Discussion: *Bonnia grandis* n. sp. is one of the largest species of *Bonnia* yet described, reaching widths of over 1.5 cm. It has a subtle prosopon of fine pits and tubercles that is also seen on the hypostome. Three pairs of marginal pygidial spines of decreasing size posteriorly are typical with the third pair little more than small nodes. The pygidium is unusually wide for its length even in large specimens. The ocular lobes are narrow bands of low curvature and a large occipital spine is present. A moderately wide border furrow separates the anterior border from the glabella and there is a subtle shortening of the border anterior to the glabella. Librigenae (Pl. 30, fig. 9; Pl. 31, fig. 3) are narrow with a wide border and a long, broad-based gradually tapering genal spine. The hypostome is of standard morphology for *Bonnia* and has the same prosopon as the dorsal exoskeleton. Large hypostomes (Pl. 30, fig. 13) have strongly curved anterior margins comparable to glabellar shape in large cranidia. Thoracic segments (Pl. 31, fig. 6) have short, sentate pleural spines, and may have had an axial spine or tubercle.

Specimens from collections MG2b and MG1g have a slightly different morphology from those of the type collection, MG2d. In these specimens, the glabella has slightly more forward expansion, small holaspids have a deep S1, and instead of a large occipital spine, the occipital ring tapers posteriorly into a small, triangular projection. These differences are minor and are considered to be intraspecific variation.

Bonnia grandis is similar in morphology to *B. laterispina* (comparison given under the latter). *B. tatondukensis* Fritz, 1968 from Alaska shares many similarities with *B. grandis* including an occipital spine, minute third pair of pygidial spines and barely constricted anterior border. It differs in completely lacking S1, having only three pairs of pleural furrows, and in having a prosopon of variably expressed terrace lines rather than pits. Fragmentary material of *B. carnata* Fritz, 1991a from the Yukon has similar cranidial features to *B. grandis*, except for its granular prosopon. Its pygidium has more axial ring furrows and marginal spines as well as a longer, more triangular shape than the pygidium of *B. grandis*.

Ontogeny: *Bonnia grandis* is well-known from abundant material and this description of its ontogeny will serve as the standard of comparison for all *Bonnia* ontogenies. As described under

the genus, meraspid stages are not abundant and are divided simply into an early and late meraspid stage. The protaspid stage is not known for this species, but is described for *B. fitzi*. The holaspid stage cannot be determined with certainty without articulated material, but is considered to be reached when the glabella loses its corynoid shape. Holaspid stages are divided into three cliques defined by glabellar shape. Clique A is the earliest (smallest) and has a parallel-sided glabella with a slight forward expansion. Clique B is intermediate and has a slightly rounded glabella. Clique C is the latest (largest) and has a parallel-sided glabella, broadly curved anteriorly. Pygidia are tentatively assigned to these cliques based on size relative to the cranidia: it is observed in *B. paymasterensis* that in articulated, holaspid material, the pygidial length is equal to cranidial length exclusive of the occipital ring. Numbers of marginal pygidial spines and length of ocular lobes are specific characteristics for this species (species of *Bonnia* typically have a constant number of marginal spines). Ocular lobe length generally decreases through the holaspid ontogeny. Size estimates are based on cranidial lengths, exclusive of occipital spine.

Early Meraspid Stage: (approximately 1 mm and under) Anterior border barely discernible medially, well-developed laterally. Glabellar stalk parallel-sided, glabella expanding rapidly forward anterior to S2. Anterior of glabella bluntly truncated. Glabellar furrows marginal, all shallow except S0. Occipital ring without spine or node. Fixigenae wide, subequal in width to glabella. Ocular lobes long: approximately 1/3 cranidial length. Prosopon smooth. Additional unassigned early meraspid cranidia and pygidia are illustrated in Pl. 31, figs. 7-8. The cranidia have the same morphology already described. The early meraspid pygidia, unknown for *B. grandis*, have six axial ring furrows (more than any holaspid), median tubercles in two of the first ring furrows, a tapering axis, straight posterior margin, length: width ratio 1:2, and a hint of possibly three pairs of marginal spines. (Pl. 30, fig. 5)

Late Meraspid Stage: (approximately 1-2 mm) Anterior border short medially, well-developed laterally. Glabella with gradual forward expansion anterior to S1. Anterior of glabella bluntly truncated. S0 transglabellar, deepest laterally. S1-S4 shallow, marginal. Occipital ring incompletely known. Fixigenae wide, individually subequal in width to glabella. Ocular lobes long: approximately 1/3 cranidial length. Prosopon smooth. (Pl. 30, fig. 6)

Holaspid Stage

Clique A. (approximately 2-4 mm) Anterior border well-developed anteriorly and laterally. Glabella parallel-sided with slight forward expansion, bluntly truncated anteriorly. S0 deep, transglabellar; S1 variably impressed; S2-S4 indistinct. Occipital spine well-developed. Fixigenae slightly narrower than glabella. Ocular lobes approximately 1/4 cranidial length.

Pygidia with distinct interpleural furrows, 3 pairs of marginal spines. Prosopon weakly developed. (Pl. 30, figs. 7-8, 11-12)

Clique B. (approximately 4-6 mm) Anterior border nearly straight to gently curved. Glabella subrounded in outline, bluntly truncated anteriorly. Ocular lobes approximately 1/4 cranial length. Fixigenal width less than half glabellar width. Pygidia with 3 pairs of marginal spines, no interpleural furrows. Prosopon well-developed. (Pl. 30, figs. 14-17)

Clique C. (approximately 6 mm plus) Anterior border broadly curved. Glabella parallel-sided, broadly curved anteriorly. Ocular lobes short; approximately 1/5 cranial length. Fixigenal width less than 2/5 glabellar width. Pygidium with anterior margin nearly straight; 3 pairs of marginal furrows. (Pl. 30, fig. 18; Pl. 31, figs. 1-5)

Bonnia ornata n. sp.

Pl. 31, figs. 9-15; Pl. 32, figs. 1-5; Text-fig. 45B

Diagnosis: A species of *Bonnia* with prosopon of coarse and fine tubercles on fixigenae and occipital ring; tubercles grading anteriorly to terrace lines on glabella; large tubercles arranged in rows on axial rings and pleural ribs; small tubercles on posterior border. Anterior border separated from glabella by wide border furrow. S1 moderately deep, S3-S4 generally shallow. Ocular lobes moderately short: less than 1/4 length cranidium. Ocular ridges distinct. Occipital spine short. Pygidium with 4-5 pairs of marginal spines, 4 transglabellar ring furrows, 4 pairs of wide pleural furrows. Anterior margin of pygidium inflected posteriorly at 1/3 width of pleural fields. Pygidial axis non-tapering: terminal piece slightly bulbous. Length/width ratio of pygidium approximately 4:5.

Holotype: A complete pygidium (MG2j#16; Pl. 31, fig. 15) from the Eager Formation, section MG2, collection MG2j, Mount Watson, 7 km east-southeast of Canal Flats, British Columbia.

Paratypes: MG2j#17-18, #29, #46, #51

Etymology: From the Latin adjective "ornata" (feminine, singular) meaning "decorated, adorned" for the beautiful, complex prosopon of this species.

Occurrences: BRITISH COLUMBIA. Eager Formation: section MG2, Mt. Watson, 7 km east-southeast of Canal Flats; section RC4, Ram Creek area, 13 km northeast of Skookumchuck; locality 5, 6.5 km northeast of Cranbrook.

Zonal Biostratigraphy: *Wanneria logani* Subzone, *Olenellus transitans* Zone.

Discussion: *Bonnina ornata* n. sp. has the most complex prosopon of any species of *Bonnina* with tubercles: there are two rows of tubercles on each axial ring and pleural rib of the pygidium, and the fixigenae have large tubercles widely and regularly spaced with tiny tubercles in between. The large number of marginal spines on the pygidium of *B. ornata* is an unusual feature for the genus. A fully spinose pygidial margin is typical of *Kootenia*, however in *Kootenia*, the marginal spines are all the same length or increase in size towards the rear and the pygidial border has a scalloped appearance. In *B. ornata*, the spines diminish in size towards the rear so that the fifth spine is minute and the pygidial border is of even width over the pygidium, except at the strong constriction opposite of the first pleural furrow. The pleural furrows are wide compared to other species and four, sometimes five, axial ring furrows are usually visible, with the last two becoming increasingly shallow and indistinct. Hypostomes (Pl. 31, fig. 9) tentatively assigned to *B. ornata* have faint granular prosopon and a more rounded posterior margin and slightly longer anterior margin than those tentatively assigned to the co-occurring *B. drysdalen*.

A few specimens (Pl. 32, figs. 1-2) have been found both in the type locality (MG2j) and in a nearby locality (RC4a) that have all the morphological features of *B. ornata*, yet lack the distinctive prosopon. The specimens appear to be testate, yet the external surface is almost smooth with fine granules on the pygidium and a trace of terrace lines on the anterior of the glabella. The specimens are assigned to *B. ornata*? and are regarded as an aberrant variety of the species.

Bonnina carnata Fritz, 1991a based on fragmentary material from the Yukon with four pairs of marginal pygidial spines, is the only species of *Bonnina* to approach *B. ornata* in spininess. Both share a similar segmentation of the pygidium and moderately impressed glabellar furrows, but *B. carnata* has a strongly rounded glabella, simple granular prosopon, and unusual axial nodes on at least the first two axial rings. *B. sculpta* Rasetti, 1948 has similar strong prosopon on the cranidium of tubercles on the occipital ring and fixigenae and terrace lines on the glabella, but the pygidium is almost smooth with only scattered granules⁴⁰. It also differs from *B. ornata* in

⁴⁰ Rasetti (1948) accepted the association of cranidia and pygidia with remarkably different prosopon. The species in this study indicate that while prosopon is variable over the exoskeleton, it is always comparable between cranidia and pygidia. Prosopon is also somewhat variable between specimens and preservation may further exaggerate differences. Large collections are necessary for an appreciation of the prosopon characteristic of any one species.

having a rounder glabella and stronger constriction of the anterior border in specimens of a similar size.

Ontogeny: No meraspids can be assigned to *Bonnina ornata* with certainty, but a full holaspid ontogeny is available. Late meraspid pygidia for *B. ornata* (Pl. 31, fig. 10) have at least four pairs of marginal spines, distinct interpleural furrows, and a non-tapering axis. Unassigned early meraspid pygidia potentially of *B. ornata* are described under *B. grandis*. Holaspids of *B. ornata* have the same ontogenetic pattern described for *B. grandis*, except clique B cranidia do not have particularly rounded glabellas. Clique A holaspids (Pl. 31, figs. 11, 13) have an almost smooth prosopon and pygidia have clearly defined interpleural furrows. Prosopon is fully developed in clique B holaspids, but coarser in clique C holaspids. Interpleural furrows remain discernible throughout ontogeny in this species by virtue of the two rows of large tubercles on the pygidial ribs defining a smooth "furrow" between them. Pygidia show the same relative increase in length through holaspid ontogeny described for *B. drysdalei*.

Bonnina drysdalei n. sp.

Pl. 32, figs. 6-14; Pl. 33, figs. 1-3; Text-fig. 48

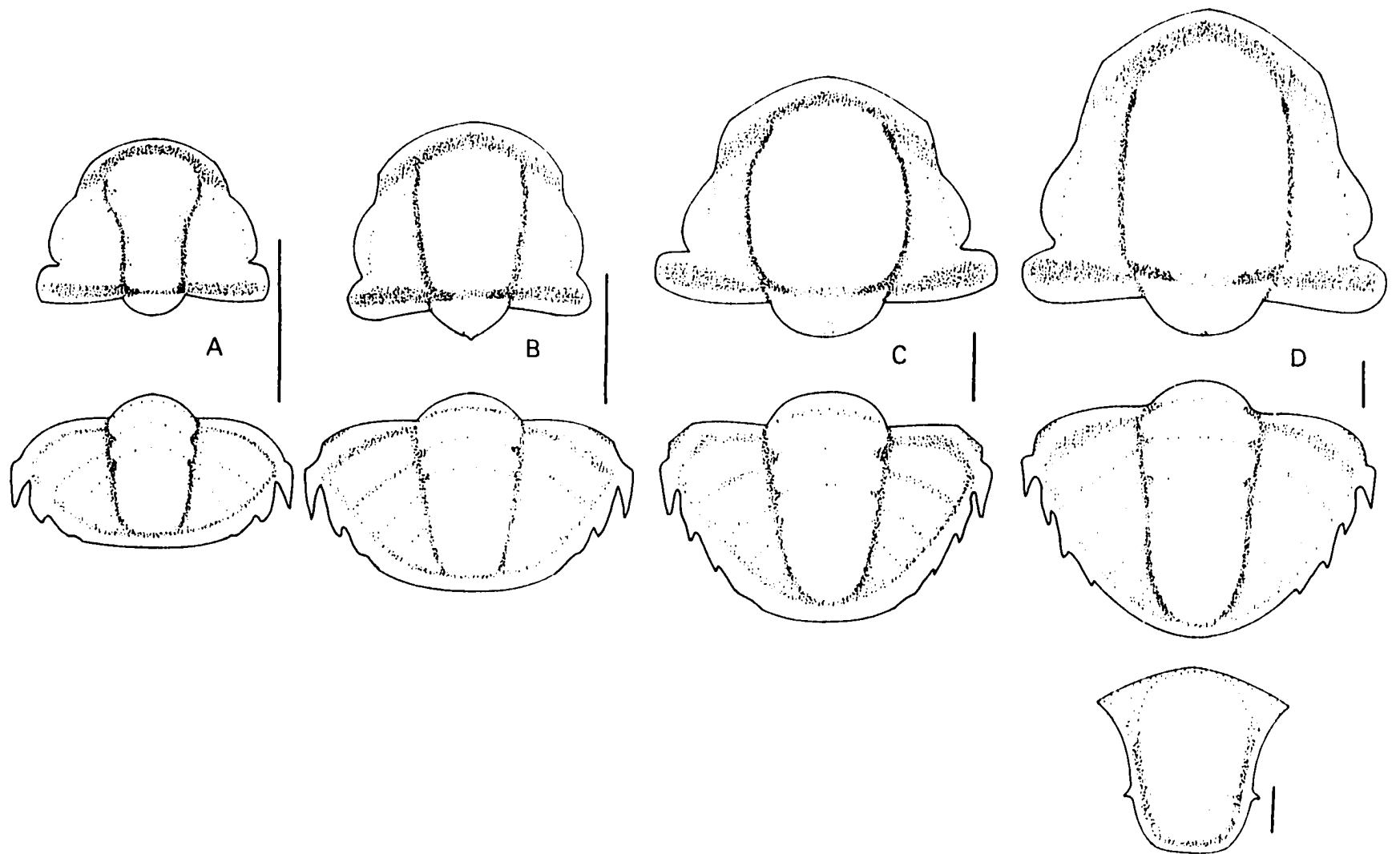
Diagnosis: A species of *Bonnina* with prosopon nearly smooth: fine pits on cranidium and pygidium. Anterior border separated from glabella by wide border furrow: S1-S4 indistinct. Ocular lobes wide, with moderate curvature, long: approximately 1/3 length cranidium. Ocular ridges indistinct. Occipital ring with small posterior node. Pygidium with 3-4 pairs of small marginal spines, 3-4 marginal ring furrows, 4 pairs of pleural furrows. Anterior margin of pygidium inflected posteriorly at 1/2 width of pleural fields. Pygidial axis tapered posteriorly. Length/width ratio of pygidium approximately 3:4.

Holotype: A complete pygidium (MG2j#10; Pl. 33, fig. 3) from the Eager Formation, section MG2, collections MG2j, Mt. Watson, 7 km east-southeast of Canal Flats, British Columbia.

Paratypes: RC4a#6, RC4a#10-11, MG2j#11, MG2j#30-31, MG2j#43, MG2j#48, MG2j#55

Etymology: In memory of Pamela Drysdale (1923-1996) and her family who were early settlers and entrepreneurs in the Skookumchuck area.

Occurrences: BRITISH COLUMBIA. Eager Formation: section MG2, Mt. Watson, 7 km east-southeast of Canal Flats; section RC4, Ram Creek area, 13 km northeast of Skookumchuck.



Text-fig. 48. Ontogeny of *Bonnia drysdalea* n. sp. A. late meraspid B. clique A C. clique B D. clique C scale bars = 1 mm

Zonal Biostratigraphy: *Wanneria logani* Subzone, *Olenellus transitans* Zone.

Discussion: *B. drysdalei* n. sp. is remarkable for its almost smooth external surface with shallow furrows and a prosopon of shallow pits and the paired marginal spines that appear to increase in number from small to large pygidia. This is the only species of *Bonnia* documented that does not have a constant number of marginal spines throughout ontogeny. Association of cranidia and pygidia for this species was made based on prosopon: co-occurring species *B. ornata* n. sp. both has a strong, distinctive prosopon. Because *B. drysdalei* does not occur in any monotypic assemblages, assignment of hypostomes is difficult. It is the most common species in collection RC4a, and the most abundant type of hypostomes in that collection, with a slightly tapered posterior margin, are tentatively assigned to it. One large hypostome (Pl. 32, fig. 10) has a hint of terrace lines and an anterior margin that is strongly curved. This is reflected in the dorsal morphology, as large cranidia (Pl. 33, fig. 2) also have the glabellar anterior strongly curved. No librigenae assignable to *B. drysdalei* have been found.

Bonnia paymasterensis n. sp. from Nevada has a similar morphology to *B. drysdalei*. Both share the rounded outline of the glabella, wide anterior border furrow, tapered pygidial axis, and shallow pleural and axial ring furrows. Differences are listed under the discussion on the former species. *B. quadrata* Fritz, 1991a based on fragmentary material from the Yukon also has a tapered pygidial axis and ?three pairs of marginal spines, but the pygidial furrows are deeper and greater in number than those seen in *B. drysdalei*. All illustrated cranidia of *B. quadrata* are small and bear a strong resemblance to similarly-sized cranidia of *B. drysdalei* in the low, nearly parallel sided glabella with shallow glabellar furrows. Fritz (1991a) recorded that there was no trace of an occipital spine or node in *B. quadrata* compared to the tiny posterior occipital node found in *B. drysdalei*. Differences between the two species are difficult to evaluate because of the fragmentary nature of the specimens of *B. quadrata*, but the two species do appear to be distinct.

Ontogeny: The three holaspid cliques defined for *Bonnia grandis* n. sp. are easily recognizable for *B. drysdalei* as the same changes in glabellar shape can be seen. Development of the cranidium is the same, but three main differences can be seen in the pygidial development. First and second, clique A pygidia have two pairs of marginal spines and length to width ratio of 2:3; clique B three pairs and ratio of 3:2, and clique C four pairs and ratio 3:4. The spines are minute and decrease in size posteriorly which may account for the apparent absence of the more posterior pairs in small specimens. This is the only species of *Bonnia* in which an increase in spine number can be documented for the holaspid ontogeny. The increase in relative length of the pygidium is typical of the genus, but is not well expressed in pygidia of *B. grandis* which remain unusually

wide throughout its ontogeny. Third, there are no interpleural furrows developed in clique A pygidia. This species has shallow pygidial furrows which may account for the complete absence of interpleural furrows, which are generally shallower than the pleural furrows.

Late meraspid (Pl. 32, figs. 6-7) are close in morphology to those described for *Bonnia grandis*. Pygidia have two pairs of marginal spines, a hint of a third pair, and a tapering axis. Unassigned early meraspid potentially of *B. drysdalei* are described under *B. grandis*.

Bonnia paymasterensis n. sp.

Pl. 33, figs. 4-14; Fl. 34, figs. 1-3; Text-fig. 49

Diagnosis: A species of *Bonnia* with prosopon nearly smooth: fine pits on cranium and pygidium; terrace lines on borders. Anterior border separated from glabella by wide border furrow. S1-S4 indistinct. Ocular lobes wide, with moderate curvature, long: approximately 1/3 length cranium. Ocular ridges indistinct. Occipital ring without spine. Pygidium with 1 pair of small marginal spines, 4 marginal ring furrows, 4 pairs of pleural furrows. Anterior margins of pygidium inflected posteriorly at 1/3 width of pleural fields. Pygidial axis tapered posteriorly. Length/width ratio of pygidium approximately 4:5.

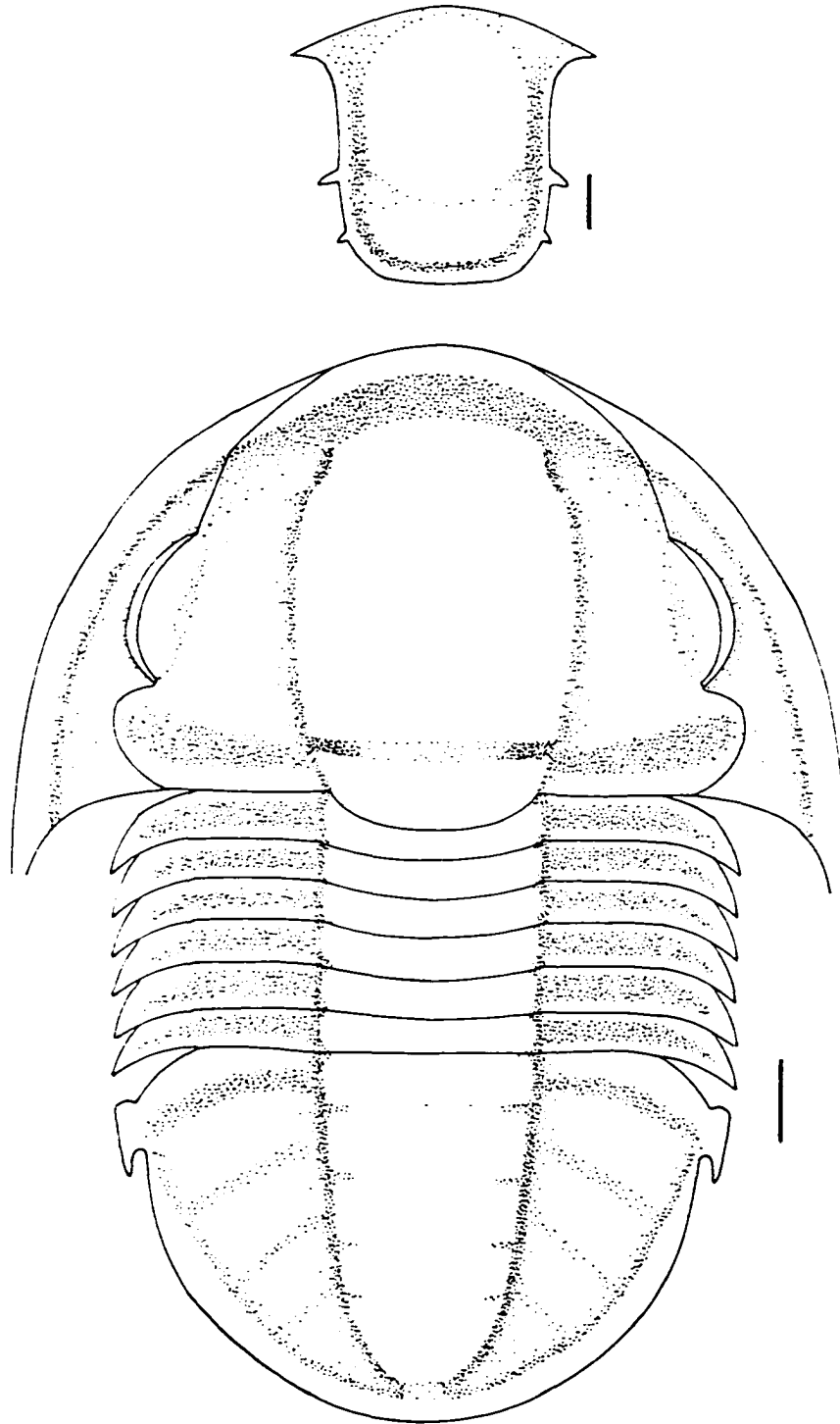
Holotype: A complete pygidium (LACMIP 12585; Pl. 33, fig. 10) from the Saline Valley Formation, section PC, Paymaster Canyon, 21 km northeast of Silver Peak, Esmeralda County, Nevada. **Paratypes:** LACMIP 12581-12583, 12586, 12589, 7427

Etymology: Named for Paymaster Canyon.

Occurrences: NEVADA. Saline Valley Formation, Esmeralda County: locality 9, Weepah Hills, 14 km north-northeast of Silver Peak; section PC, Paymaster Canyon, 21 km northeast of Silver Peak.

Zonal Biostratigraphy: *Olenellus transitans* Zone.

Discussion: Species of *Bonnia* are rare in sediments of the Great Basin, however, *B. paymasterensis* n. sp. is locally abundant in the Weepah Hills, especially in limestones of the Saline Valley Formation. The pygidium of *B. paymasterensis* has only a single pair of marginal spines with a border that is strongly constricted adjacent to the first pair of pleural furrows, and widens gradually posteriorly. It has a tapered axis with shallow furrows and a prosopon of shallow pits



Text-fig. 49. *Bonnia paymasterensis* n. sp. scale bars = 1 mm

also seen on the cranidium. The cranidium has a robust anterior border separated from the glabella by a substantial border furrow. The hypostome of *B. paymasterensis* has a prosopon of anastomosing terrace lines and is atypical of the genus in that it has two pairs of marginal spines; the second set minute and located near the posterolateral corners. A single partial free cheek of the species has been found with a wide border covered in strong terrace lines. A genal spine of unknown length was present. A few articulated specimens of *B. paymasterensis* are also known which have six thoracic segments with tapered pleural spines.

The cranidium of *Bonnia paymasterensis* resembles that of the type species, *B. parvula* Billings, 1861 from Newfoundland, but has a more rounded glabella and no trace of an occipital spine. The pygidia of the two species share few similarities, except both have few pairs of marginal spines and have shallow furrows. *B. drysdalei* n. sp. from British Columbia bears a strong resemblance to *B. paymasterensis* in both pygidium and cranidium, but differs in possession of a small occipital tubercle, three to four pairs of marginal pygidial spines, and a first ring furrow that is deep marginally.

Ontogeny: Holaspide cliques A and B as defined for *Bonnia grandis* can be recognized for *B. paymasterensis*, but clique C is poorly known. Maximum length for well-preserved cranidia is about 6 mm, which is the borderline for cliques B and C in *B. grandis*, and these cranidia have the rounded glabellas typical of clique B.

The few articulated specimens (Pl. 33, figs. 1-3) available for this species provide information on relative size of the pygidium to the cranidium that may be applied to disarticulated material. Pygidial length is approximately equal to length of the cranidium exclusive of the occipital ring. The specimens are clique B/C holaspids and it is unknown if the cranidium:pygidium proportion changed through the holaspide ontogeny. The assumption is made that it stayed the same, for lack of a better way to associate disarticulated cranidia and pygidia.

Bonnia sp. 1

Pl. 34, figs. 4-6

Occurrences: NEVADA. Saline Valley Formation, Esmeralda County: section PC, Paymaster Canyon, 21 km northeast of Silver Peak.

Zonal Biostratigraphy: *Olenellus transitans* Zone.

Discussion: A few unusual pygidia are known from the same limestone collection (LACMIP collection 26849) that yielded abundant specimens of *Bonnia paymasterensis* n. sp. These specimens differ from *B. paymasterensis* in having deep pleural and axial furrows, a second set of tiny marginal spines, a large axial node on the first axial ring, and a small node on the second axial ring. The axial nodes are an unusual feature for *Bonnia*, but are often well developed on species of *Kootenia*. The latter genus, however, typically has a fully spinous pygidial margin with five to seven pairs of marginal spines. The only other species of *Bonnia* described with axial nodes is *B. carnata* Fritz, 1991a, from the Illyd Formation of the Wernecke Mountains. Pygidia of *B. carnata* differ from those of *Bonnia* sp. 1 in having four pairs of marginal spines and a bulbous terminal piece.

Genus *Ogygopsis* Walcott, 1889

Type Species: *Oxygia klotzi* Rominger, 1887 from the Middle Cambrian Stephen Formation, Mount Stephen, Rocky Mountains, British Columbia. (by original designation)

Diagnosis: A large genus of Dorypyginae with glabella parallel-sided to slightly rounded. Anterior border furrow broad. S0 transglabellar, deepest laterally. S1-S4 not apparent. Facial suture slightly to distinctly divergent anteriorly, convergent across anterior border. Fossulae poorly developed. Ocular ridges well-developed. Ocular lobes short. Fixigenae broad: anterior portion moderately long; posterior limbs taper laterally. Posteriorly-directed occipital spine absent. Thorax of 8 segments with short pleural spines. Pygidium longer than wide with shallow border furrow. Axis with 7 or more axial ring furrows. Pleural furrows moderately deep; interpleural furrows shallow to absent.

Other Species:

Dikellocephalus? marcoui Whitfield, 1884; LC Parker Fm., near Georgia, Vermont.

Bathyriscus batis Walcott, 1916b; LCSaline Valley Fm., Miller Mt., Nevada.

Taxioura typicalis Resser, 1939, MCLangston Fm., Wasatch Mtns., Idaho (= *Taxioura elongata* McLaughlin and Enbysk, 1950; MC Metaline Fm., Washington.)

Ogygopsis spinulosa Rasetti, 1951; MC Cathedral Fm., Mount Stephen, BC.

[?] *Kootenia jakutensis* Lermontova, 1951; LC Siberia.

[?] *Kootenia anabarensis* Lermontova, 1951; LC Siberia.

[?] *Kootenia moori* Lermontova in Lazarenko, 1962; LC Siberia.

Ogygopsis antiqua Palmer, 1968; LC Hillard Fm., Tatonduk River area, Alaska.

Wangcunia wangcunensis Peng, Lin and Chen, 1995; MC Huaqiao Fm., Hunan, China.

Discussion: Rasetti (1951) established the monotypic family Ogygopsidae for *Ogygopsis* and noted that (p. 190) "in many respects *Ogygopsis* is intermediate between the Dorypygidae and the Dolichometopidae; the cephalon is like *Kootenia*, the pygidium resembles those of *Orria* and other macropygous Dolichometopidae". Although Rasetti compared *Ogygopsis* to the dolichometopid genera with many-segmented pygidia, there are also Russian dorypygine genera, such as *Erbiopsis*, with many-segmented pygidia. Rasetti (1951) also claimed that the hypostome of *Ogygopsis* was wider posteriorly with shorter anterior wings than in the other two families. These differences cannot be substantiated. Hypostomes illustrated for *O. batis* (Pl. 35, fig. 3) and *O. marcoui* (Pl. 37, fig. 6) have substantial anterior wings and are not appreciably wider posteriorly than in *Kootenia* and other dorypygids. In all dorsal exoskeletal features, *Ogygopsis* is a large dorypygine of moderately low convexity with a many-segmented pygidium. The attached hypostome with functional hypostomal suture was considered a unique feature of the genus that warranted family-level separation from other Corynexochida (Rasetti, 1951; Rasetti *in* Moore, 1959). A detailed examination of the ventral morphology of *Olenoides* and *Bonnia* has demonstrated that both genera also likely have attached hypostomes that are not fused to the rostral plate. A separate family for *Ogygopsis* is unnecessary and *Ogygopsis* is assigned to the Dorypyginae, in agreement with Palmer (*in* Palmer and Halley, 1979).

Ogygopsis is closest in morphology to *Kootenia*. It differs overall in having a lower convexity and in reaching a larger size. Cranidia of *Ogygopsis* differ from those of *Kootenia* only in minor features such as having stronger ocular ridges that are more posteriorly positioned on the frigenae, poorly developed fossulae and an occipital spine that is dorsally directed, if present. The pygidium of *Ogygopsis* is proportionately longer than wide with more axial ring and pleural furrows and the pygidial border furrow is shallow. Spinyness of the pygidium is not a good distinguishing feature between the two genera. *Kootenia* typically has a fully spinous pygidial margin. The type species of *Ogygopsis* has an entire pygidial margin (no spines) but other species have from one (i.e. *O. batis* Walcott, 1916b) to nine (i.e. *O. spinulosa* Rasetti, 1951) pairs of marginal spines.

A number of Siberian species including *Kootenia jakutensis* Lermontova, 1951, *K. anabarensis* Lermontova, 1951 and *K. moori* Lermontova *in* Lazarenko, 1962 may be more closely related to *Ogygopsis* than to *Kootenia*. The best known of these species, *K. jakutensis* Lermontova, has eight thoracic segments and a hypostome with no obviously fused rostral plate (see Suvorova, 1964, pl. 8). All of these species are large, have prominent, dorsally directed occipital spines, large pygidial axial nodes and spinous pygidial margins. With six axial ring furrows, six pairs of

pleural furrows and six to seven pairs of marginal the spines, the pygidia of these species have more segments than is typical of *Kootenia*, but fewer than is typical of *Ogygopsis*. *O. marcoui* (Whitfield) is the most similar species to the Siberian taxa.

Rasetti (1951) synonymized *Taxioura* Resser, 1939 with *Ogygopsis* on the basis that *Taxioura* differed only in lacking any indication of interpleural furrows. This was followed by subsequent authors, except Romanenko (1960). Palmer (1964) provided an in-depth description of *Ogygopsis* and a detailed discussion of the species described to date⁴¹. *Taxioura sibirica* Romanenko, 1960 (see also *Ogygopsis sibirica* in Repina and Romanenko, 1978) from the Lower Cambrian of Siberia, is not a species of *Ogygopsis* as the pygidium is wider than long, has too few segments and a deep border furrow while the cranidium has ocular ridges that are too weakly developed and situated too close to the anterior border. This species is assigned to *Kootenia*. Nelson (1963) concluded that the two South American species attributed to ?*Ogygopsis* by Rusconi (1945, 1952) do not belong to this genus.

Wangcunmia wangcunensis Peng, Lin and Chen, 1995, recently described from Hunan, China, was established as a new, monotypic genus. It was questionably assigned to the Papyriaspidae (of the Ptychopariida) on the basis of its cranidial morphology and multisegmented pygidium. Peng *et al.* (1995) recognized *Wangcunmia* as atypical for this family because of its large, many-segmented pygidium, long, rounded glabella and short preglabellar field. In these features and most other aspects of its morphology, including its attached but unfused hypostome and rostral plate, broad librigenae with genal spine, and fixigenal configuration, *W. wangcunensis* Peng *et al.* is a typical species of *Ogygopsis*. *Wangcunmia* is therefore a junior synonym of *Ogygopsis*. *O. wangcunensis* is distinguishable from other species of *Ogygopsis* by its unusually broad anterior boarder furrow, and by the greater number of segments in its pygidium. It has variably impressed glabellar furrows that are deeper than usual for *Ogygopsis* species, and it has an entire pygidial margin, like the type species, *O. klotzi* (Rominger, 1887). Peng *et al.* (1995) recorded eight thoracic segments in a midsized specimen of *O. wangcunensis*, but regarded this as a minimum number of thoracic segments typical of the species. Since other species of *Ogygopsis* attained eight segments well before reaching maximum growth (see illustrated species, especially *O. batis*) it is likely that Peng *et al.*'s specimen is a holaspide, and that eight is the total complement of thoracic segments in this species, as in other species of *Ogygopsis*.

⁴¹ Palmer (1964) did not recognize *Dikellocephalus? marcoui* Whitfield, 1884 as a species of *Ogygopsis*. Palmer did, however, refer to the spiny specimens from Nevada, that are described here, as a new species of *Ogygopsis*. These specimens are now referred to *O. marcoui*.

Ontogeny: Neither protaspids nor meraspids has been described to date for any species of *Ogygopsis*. One possible meraspid pygidium is illustrated for *O. typicalis* (Pl. 36, fig. 3). Holaspid ontogeny is conservative with no dramatic changes. A considerable increase in size occurred during the holaspids stage, similar to olenellinids. With increasing size, the pygidium becomes proportionately longer and the posterior pleural furrows become more widely separated.

Ogygopsis batis (Walcott, 1916b)

Pl. 35, figs. 1-6; Text-fig. 50A

1916b *Bathyriscus batis* Walcott, p. 337-338, pl. 48, figs. 4, 4a.

1963 *Ogygopsis batis*, Nelson, p. 246, 247.

1964 *Ogygopsis batis*, Palmer, p. F7, pl. 2, figs. 1-6.

1976 [?] *Ogygopsis batis*, Jegorova, p. 94, pl. 16, fig. 16; pl. 21, fig. 15.

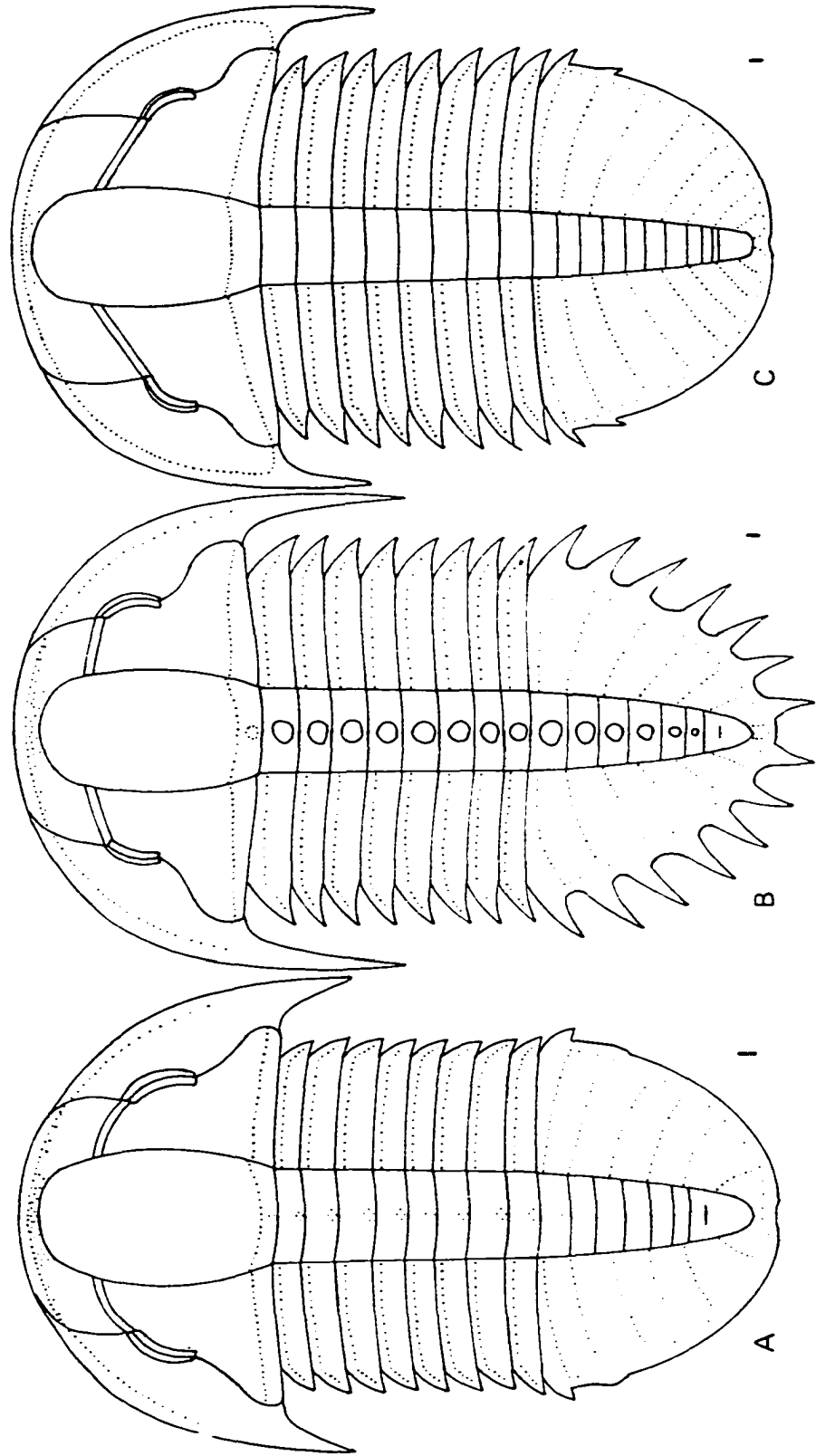
Diagnosis: A species of *Ogygopsis* with a broad, deep anterior border furrow. Facial suture slightly divergent anteriorly. Ocular ridges inclined gently posteriorly. Occipital swelling small. Thorax with small axial nodes, short pleural spines. Pygidium with 5 to 6 well-defined pleural furrows; 6 axial ring furrows plus one partial ring furrow on the terminal piece. Axial swellings minute on each axial ring. Axis terminates short of pygidial border; no ridge connecting axis with border. Pygidial margin with one pair of spines, slight invagination at posterior end. Prosopon of fine honeycombs to fine terrace lines.

Lectotype: (selected here) A nearly complete specimen lacking librigenae (USNM 62653; Walcott, 1916b, pl. 48, fig. 4a right) from the Saline Valley Formation, locality 59p of Walcott (1916b, p. 338), Miller Mountain, 16 km north of Columbus, Esmeralda County, Nevada.

Occurrences: NEVADA Saline Valley Formation, Esmeralda County: locality 59p of Walcott (1916b, p. 338) and locality 8, Miller Mountain, 16 km north of Columbus; USGS colln. 37480-CO (Palmer, 1964), 7 km east of Gold Point, Mt. Dunfee area.

Zonal Biostratigraphy: *Olenellus transitans* Zone.

Discussion: Nelson (1963) was the first to refer *Bathyriscus batis* Walcott, 1916b to *Ogygopsis*. This species lacks the characteristic constriction of the anterior fixigenal region, that is typical of *Bathyriscus*, and has no indication of anterior glabellar or interpleural furrows. New specimens showing the unfused hypostome and rostral plate conclusively demonstrate that this species



Text-fig. 50. A. *Ogygopsis butts* (Walcott) B. *Ogygopsis marconi* (Whitfield) C. *Ogygopsis typicalis* Resser scale bars = 1 mm

belongs to *Ogygopsis*. Superb material of *O. batis* was illustrated by Palmer (1964) from limestones of the Saline Valley Formation near Gold Point, Nevada. The above diagnosis is based primarily on this material. An unusual feature of this species is the axial swellings. These swellings are similar to the axial tubercles seen in *O. marcoui* (Whitfield, 1884) that may be extended into dorsally-directed spines.

Additional specimens of *Ogygopsis batis* from the type locality on Miller Mountain are illustrated. As in the type material, they are highly flattened and are mostly internal molds. One external mold (Pl. 35, fig. 1) shows that this species has small axial tubercles on each thoracic segment. The single marginal spine on the pygidium plus a second slight projection of the margin can be seen. Two hypostomes are illustrated; the first (Pl. 35, fig. 4) with a rostral plate that appears to be displaced over the hypostome, the second (Pl. 35, fig. 3) with a broad anterior wing and moderately well-developed maculae but no distinguishable rostral plate. Rasetti (1951) claimed that the anterior hypostomal wings were poorly developed in *Ogygopsis*. The hypostomes here illustrated contradict that claim.

Ogygopsis typicalis (Resser, 1939)

Pl. 35, figs. 7-8; Pl. 36, figs. 1-4; Text-fig. 50C

- 1939 *Taxionura typicalis* Resser, p. 62-63, pl. 14, figs. 6-14.
- 1939 *Taxionura magna* Resser (part), pl. 14, figs. 1,2 (only).
- 1950 *Taxionura elongata* McLaughlin and Enbysk, p. 470-471, pl. 65, figs. 2, 9.
- 1964 *Ogygopsis typicalis*, Palmer, p. F6, F7.
- 1967 *Ogygopsis* sp. Rasetti, p. 87, pl. 10, fig. 32.
- 1968 *Ogygopsis typicalis*, Fritz, 1968, p. 201.
- 1979 *Ogygopsis typicalis*, Palmer, in Palmer and Halley, p. 82-83, pl. 12, figs. 1-4.
- 1981 [?] *Ogygopsis typicalis*, Gunther and Gunther, p. 48, pl. 34, figs. a, b, c.

Diagnosis: A species of *Ogygopsis* with a shallow anterior border furrow. Ocular ridges inclined strongly posteriorly. Pygidium with 7 to 8 well-defined pleural furrows; up to 10 axial ring furrows. Axis terminates short of pygidial border; ridge connects axis with border. Pygidial margin with two pairs of spines, slight invagination at posterior end. Prosopon of fine terrace lines.

Holotype: An associated pygidium and cranidium (USNM 98565; Resser, 1939, pl. 14, fig. 10) from the Middle Cambrian Langston Formation, Two Mile Canyon, Wasatch Mountains, Idaho.

Occurrences: IDAHO. Langston Formation, locality 54s (Resser, 1939) Two Mile Canyon, 3.2 km (two miles) southeast of Malad, northern Wasatch Mountains. NEW YORK. Taconic Sequence, Columbia County: Collection cs-7/M3 (Rasetti, 1967), boulders from stone walls, Griswold farm, 1.6 km southeast of North Chatham. WASHINGTON. Metaline Formation, Upper Lehigh Quarry, 0.8 km east of Metaline Falls, Pend Oreille County. ?UTAH. Spence Formation: Miners Hollow and Hansen Canyon (Gunther and Gunther, 1981), Wellsville Mountain, near Logan. NEVADA. Cararra Formation,: localities USGS 4436-CO - 4438-CO (Palmer, *in* Palmer and Halley, 1979), Belted Range, Nye County. CALIFORNIA. Saline Valley Formation: section WM, Papoose Flat, Andrews Mountain, Inyo County.

Zonal Biostratigraphy: Within the study are, *Ogygopsis typicalis* occurs in the *Olenellus transitans* Zone.

Discussion: The best preserved material of *Ogygopsis typicalis* (Resser, 1939) is the type material from the Wasatch Mountains of Idaho. The pygidium of *O. typicalis* has the most segments of any described species of *Ogygopsis* with up to ten axial ring furrows clearly visible. *O. klotzi* has up to nine axial ring furrows, but differs in having interpleural furrows in addition to pleural furrows and in lacking marginal spines. Both species have ocular ridges inclined strongly posteriorly. *O. batis* only has six to seven axial ring furrows, but is similar to *O. typicalis* in having one marginal spine plus a hint of a second.

Fritz (1968) considered *Taxionura magna* Resser, 1939 to be a junior synonym of *Ogygopsis typicalis*. Palmer (1964) suggested that the holotype of *T. magna* belongs to *Olenoides maladensis* Resser, but that the pygidia illustrated by Resser (1939) as *T. magna* belongs to *Ogygopsis typicalis*. The latter opinion is accepted. *Taxionura elongata* McLaughlin and Enbysk, 1950 from the Metaline Formation of Washington was synonymized with *O. typicalis* by Palmer (1964). The prime feature used by McLaughlin and Enbysk (1950) to distinguish their species was a long, slender, strongly arched glabella. This feature is a result of deformation. Rasetti (1967) referred a single small pygidium to *Ogygopsis* sp. but was tentative in his assignment because the specimen was wider and shorter than was typical for the genus. The atypical proportions can be accounted for by the small size of the pygidium (2.7 mm) since small specimens are typically proportionately wider than large specimens. It has the large number of pleural and axial ring furrows typical of *O. typicalis* as well as indications of two pairs of marginal spines.

The type material of *Ogygopsis typicalis* from the Wasatch Mountains is Middle Cambrian in age (Resser, 1939) based on its association with typical Middle Cambrian genera such as *Alokistocare*, *Bathyriscus* and *Tonkinella*. The age of the Washington material from the Metakline Formation (McLaughlin and Enbysk, 1950) is less conclusive: it is listed as Middle Cambrian but all of the associated genera range into the Lower Cambrian.⁴² The co-occurrence of *Ogygopsis klotzi* in these rocks suggests that the Middle Cambrian is the likeliest age of the strata. The Taconic material (Rasetti, 1967) is also Middle Cambrian in age. The material from the Saline Valley Formation of California is a monotypic assemblage that is considered to be Lower Cambrian in age (Nelson 1963, p.245). It occurs in strata in close association with a marker bed that elsewhere (Gold Point, Nevada) is associated with specimens of *Olenellus*. Overlying rocks of the Mule Spring Formation contain rare, scrappy material tentatively referred to the Middle Cambrian genus *Alokistocare*. The occurrence of *O. typicalis* in rocks of the Saline Valley Formation is the oldest record of this species.

Ontogeny: A small pygidium (4 mm, Pl. 36, figs. 2-3) of this species may be a meraspis. It is considerably wider than long, but the sample has been tectonically stretched widthwise overemphasizing this aspect. There are six pleural furrows compared to seven or eight in the large holaspids. There are seven axial furrows, compared to up to 10 in the large holaspids. The lack of the full complement of pleural furrows may be an artifact of preservation since the superb small pygidium illustrated by Rasetti (1967, *Ogygopsis* sp., pl. 10, fig. 32) has the full holaspis complement of furrows.

A single small holaspis specimen is known (Pl. 35, fig. 7). It is too poorly preserved to determine numbers of pleural and axial furrows, however, there appear to be fewer than in the large holaspids. The pygidium is also proportionately shorter and wider than in the large holaspids.

Ogygopsis marcoui (Whitfield, 1884)

Pl. 36, figs. 5-8; Pl. 37, figs. 1-7; Text-fig. 50B

1884 *Dikellocephalus? marcoui* Whitfield, p. 150, pl. 14, fig. 7.

1886 *Olenoides? marcoui*, Walcott, p. 186-187, pl. 26, figs 5, 5a,b.

1889 *Dikellocephalus marcoui*, Miller, p. 544.

1889 *Olenoides marcoui*, Lesley, p. 493.

1890 *Olenoides marcoui*, Walcott, p. 642, pl. 94, figs. 2, 2a,b.

⁴² Note that the specimen which McLaughlin and Enbysk (1950) described as *Bathyriscus* sp. is likely a species of *Poliella*.

- 1897 *Dorypyge marcoui*, Matthew, p. 187.
 1937b *Kootenia marcoui*, Resser, p. 16.
 1938 *Kootenia browni* Resser, p. 84, pl. 4, figs. 8-11.
 1938 *Kootenia virginiana* Resser, p. 85, pl. 4, figs. 1-7.
 1938 *Kootenia austinvillensis* Resser, p. 85, pl. 4, figs. 12-15.
 1938 *Kootenia currieri* Resser, p. 85, pl. 4, figs. 33-35.
 1948 *Kootenia* cf. *K. marcoui*, Rasetti, p. 14, pl. 3, fig. 7.
 1955 *Kootenia marcoui*, Shaw, p. 786-787, pl. 74, figs. 1-4.
 1956 [?] *Kootenia* cf. *K. marcoui*, Lochman, p. 1392, pl. 7, figs. 13-18.

Diagnosis: A species of *Ogygopsis* with a broad, deep anterior border furrow. Ocular ridges inclined gently posteriorly. Librigenae wide with long genal spines. Axial swelling on S0. Thorax with short pleural spines, median axial tubercles or dorsally directed spines. Pygidium with 5 to 6 well-defined pleural furrows; 6 axial ring furrows plus one partial ring furrow on the terminal piece. Tubercles or dorsally directed spines on axial rings 1 to 6. Axis terminates short of pygidial border; ridge connects axis with border. Pygidial margin with seven pairs of long spines, slight invagination at posterior end. Prosopon of coarse terrace lines on pygidium.

Holotype: A partial pygidium (AMNH 236; Whitfield, 1881, pl. 14, fig. 7; Shaw (1955, pl. 74, fig. 2) from the Parker Formation, USNM loc. 319g, Parker Quarry, Parker Cobble, near Georgia, Vermont.

Occurrences: VERMONT. Parker Formation, Franklin County (Shaw, 1954, 1955): USNM locality 319g, Parker Quarry, Parker Cobble, near Georgia; USNM locality 25, near Georgia, USNM loc. M-NW-1, 3.2 km west of Georgia Center; loc. SA-C-1, Kelly Quarry, 1 km northeast of Swanton Junction. VIRGINIA. Shady Formation, Wythe County (Resser, 1938): locality 23j, 1.6 km northeast of Austinville; locality 23e, Poplar Camp Road, northeast of Austinville. QUEBEC. Conglomeratic boulders, Matane County: Grosses Roches, about 90 km east of M tis (Rasetti, 1948). NEVADA. Saline Valley Formation, Esmeralda County: locality 9, 14 km north-northeast of Silver Peak, Weepah Hills; section PC, Paymaster Canyon, 21 km northeast of Silver Peak.

Zonal Biostratigraphy: Within the study area, *Ogygopsis marcoui* occurs in the *Olenellus transitans* Zone.

Discussion: Resser (1937b) was the first author to assign *Dikellocephalus? marcoui* Whitfield, 1884 to *Kootenia*; a designation accepted by all subsequent authors. This species has a pygidium with a fully spinous posterior margin, typical of *Kootenia*, but not exclusive to this genus. Most species of *Ogygopsis* have few marginal spines, but *Ogygopsis spinulosa* Rasetti, 1951 has nine pairs. In all other features, such as a shallow pygidial border furrow, long pygidium, strong ocular ridges and absence of an occipital spine⁴³, *D. marcoui* Whitfield is another spiny species of *Ogygopsis*. In addition, a hypostome attached to a rostral plate (Pl. 37, fig. 6) is illustrated for this species from new material from Nevada. The unfused hypostome/rostral unit is an unusual feature for the corynexochid *Ogygopsis*.

In numbers of pleural and axial ring furrows, *Ogygopsis marcoui* is closely comparable to *O. batis* Walcott, 1916b. *O. batis* differs in having only a single pair of marginal spines. *O. spinulosa* has a fully spinous pygidial margin like *O. marcoui*, but differs in having nine pairs of marginal spines, eight to nine pairs of well-defined pleural furrows, and approximately nine axial ring furrows. The single known specimen of *O. spinulosa* is a large internal mold that does not preserve potential axial spines.

New material of *Ogygopsis marcoui* from Nevada includes both internal molds from shale and testate material from limestone. Internal molds do not preserve the axial spines. Development of the marginal pygidial spines is variable: short in shale material, long in limestone material. Part of this variability may be due to preservation, but as Rasetti (*in* Moore, 1959, p. O218) noted for *Kootenia*, marginal spines can vary from "mere scallops to long heavy spines of subequal size in the same species". Undue emphasis on size and shape of the marginal spines led Resser (1938) to recognize four new species from the Shady Formation, Virginia, that are all junior synonyms of *O. marcoui*. One unusual specimen of *O. marcoui* (Pl. 37, fig. 2) from Nevada has eight pairs of marginal spines. It is smaller than other specimens of this species that only have seven pairs of spines and is regarded as aberrant rather than a later developmental stage or a different species.

Ogygopsis marcoui is a widespread species from central eastern North America and Nevada. Type material from Vermont was reillustrated by Shaw (1955) along with new material from nearby localities. One partial articulated specimen from Shaw's collection has axial tubercles on the thorax clearly preserved. Shaw recorded the presence of four axial tubercles on the

⁴³ Shaw (1955, p. 787) noted that the "occipital ring may have borne a node or spine", but there is no evidence for this feature on his specimens. A cranium from Nevada (Pl. 36, Fig. 8) has a hint of an occipital swelling, but there is no evidence that a large, posteriorly-directed occipital spine was present as is typical of many species of *Kootenia*. Well-preserved material from Virginia (Resser, 1938, pl. 4, figs., 1, 2) shows that the central part of S0 was highly inflated.

pygidium. Rasetti (1948) illustrated a moderately small pygidium from Quebec that he tentatively assigned to *O. marcoui*. It has only three well-developed axial tubercles and granular prosopon. Excellently preserved material from Nevada has six axial tubercles of decreasing size on the pygidium and a prosopon of terrace lines. Differences between these and the Quebec specimen may be size and preservation related. Material from Virginia that Resser (1938) named *Kootenia virginiana*, *K. browni*, *K. austinvillensis*, and *K. currieri* belongs to *O. marcoui*. Resser's species differences included many preservation features (ex. material assigned to *K. austinvillensis* has only six spines preserved, but there must have been seven as it is the first pair⁴⁴ that is missing), allometric differences, and minor differences in length, curvature and taper of the marginal spines. Aside from these features, all pygidia have seven pairs of well-developed marginal spines, five to six well-defined pleural furrows and six axial ring furrows. Depending on preservation, up to six axial nodes are preserved and the prosopon is of terrace lines. Resser (1938, pl. 4, fig. 35) illustrated a slab with multiple specimens that includes an isolated thoracic segment preserved in lateral aspect. It has a long, dorsally directed spine on the axis. No other species are preserved on this slab so it is likely that the thoracic segment belongs to *O. marcoui*. It suggests that all of the broken axial "tubercles" that can be seen on the thorax and pygidium of the species may actually be long, dorsally directed spines.

Ontogeny: No meraspids are known for this species⁴⁵ and only a limited amount of the holaspid ontogeny. In the Nevada material, the number of pairs of spines and pleural furrows is constant from the smallest specimens (6 mm, Pl. 36, fig. 5) to the largest (18 mm, Pl. 37, fig. 1). The small pygidia are proportionately wider than long, unlike the proportionately longer large pygidia. The posterior pleural furrows are also better defined in the large pygidia.

?Order Corynexochida Kobayashi, 1935

Family Zacanthoididae Swinnerton, 1915

[*nom. correct.* Richter, 1933 (*pro* Zacanthoidae Swinnerton, 1915)]

Assigned Genera: *Zacanthoides* Walcott, 1888; *Prozacanthoides* Resser, 1937b; *Zacanthopsis* Resser, 1938; *Mexicaspis* Lochman, 1948; *Fieldaspis* Rasetti, 1951; *Stephenaspis* Rasetti, 1951; *Ptarmiganoides* Rasetti, 1951; *Parkaspis* Rasetti, 1951; *Zacanthopsina* Palmer, 1964; *Albertelloides*

⁴⁴ The first pygidial segment in dorypygids always has a marginal spine when more posterior spines are present.

⁴⁵ Lochman (1956, pl. 7, figs. 15-17) illustrated three meraspid cranidia from New York as *Kootenia* cf. *K. marcoui*. The species identification is questionable due to the poor quality of the holaspid material. The glabellas of these specimens have the typical clavate shape of meraspids belonging to the Corynexochida.

Fritz, 1968; *Albertellina* Palmer (in Palmer and Halley, 1979); *Paralbertella* Palmer, (in Palmer and Halley, 1979)

Discussion: The Zacanthoididae was originally assigned to the Mesonacida (= Redlichiida) by Swinnerton (1915), contrary to the more recent practice to assign the family to the Corynexochida. Walcott (1910b, p. 254) had commented on this possible relationship by stating that *Albertella*⁴⁶ and *Zacanthoides* "may be found to have retained some of the characters of the Mesonacidae"⁴⁷. Kobayashi (1935, p. 122) assigned the Zacanthoididae familial status equal to the Redlichiidae and Mesonacidae, but recognized it as a "branch divergent from the Mesonacidae". Richter (1933) gave the Zacanthoididae separate superfamily status. Rasetti (1951) stated that it "seemed impossible" to separate the Zacanthoididae from the Corynexochida, and that the Zacanthoididae were poorly differentiated from the Dolichometopidae. Problems of classification of the Dolichometopidae are discussed elsewhere, and Rasetti did not further discuss the comparative morphology of the Zacanthoididae.

A further examination of the Zacanthoididae in comparison to the Redlichiida and Corynexochida is in order. Kobayashi (1935) listed the similarities of a third macropleural thoracic segment, intergenal spines (= metafixigenal spines?), and an enlarged axial spine shared between some members of the Zacanthoididae and Redlichiida. To this may be added 1. poor differentiation of ocular lobes from ocular ridges 2. simple, micropygous pygidia of the oldest Zacanthoididae genera (i.e. *Zacanthopsis* [see following section], *Prozacanthoides*) that are virtually identical to those of some Redlichiida (i.e. see Opik, 1958, fig. 9 for pygidium of *Redlichia*). 3. short preglabellar fields present in some of the oldest Zacanthoididae genera (i.e. *Zacanthopsis*, *Zacanthopsina*) which are a common feature of Redlichiida, but atypical of the Corynexochida 4. striking similarities in hypostomal morphology between the Zacanthoididae (i.e. *Fichlaspis* see Whittington, 1988a, pl. 54, figs. 1-3) and Redlichiida (i.e. *Paradoxides* see Nikolaisen and Henningsmoen, 1990). Features 3 and 4 are in sharp contrast to the Corynexochida, however, glabellar shape and configuration of the glabellar furrows in the Zacanthoididae are closely comparable to the Corynexochida, not the Redlichiida. The ontogeny of early members of the Zacanthoididae is unknown, but later genera share the corynoid glabella in their meraspid stage with other Corynexochida. It should also be noted that *Paradoxides* (Redlichiina: see *P. pinus* in Westergård, 1936) has a clavate glabella through the early meraspid stage, like the Corynexochida and Ptychopariida, but the glabella becomes parallel-sided rather than corynoid

⁴⁶ Note that Walcott's concept of *Albertella* is considerably broader than that delineated by Palmer (in Palmer and Halley, 1979), which is followed here.

⁴⁷ Mesonacidae as used here is equivalent to Olenellina.

for the rest of the meraspid stage. The Zacanthoididae need further evaluation to determine if these genera should be grouped together in a single family and what is the relationship of these genera to the Redlichiida and Corynexochida.

Rasetti (*in* Moore, 1959) provided a diagnosis of the Zacanthoididae and listed the species described to date (Table 13). Suvorova (1964) discussed the family and subdivided it into four subfamilies. No western author since Rasetti has attempted a detailed re-evaluation of the family, though Palmer (*in* Palmer and Halley, 1979) changed the list of assigned genera, re-assigning *Ptarmiganoides* Rasetti, 1951 from the Dolichometopidae to the Zacanthoididae and creating two new genera: *Albertellina* and *Paralbertella*. An updated list of the genera currently assigned to the Zacanthoididae is given in Table 14.

In a detailed revision of *Albertella*, Palmer (*in* Palmer and Halley, 1979, p. 87) restricted the genus to "generally small-eyed forms with normal pygidial pleura". He questioned whether *Albertella* and *Vanuxemella*, genera assigned to the Zacanthoididae by Rasetti (*in* Moore, 1959) should actually be included in this family, or moved to a separate family or subfamily. A separate family seems most appropriate, and the name Albertellidae Hupé, 1953b is available. It is suggested that the Albertellidae also include *Holteria*, and be diagnosed as having: a slightly constricted glabella, indistinct glabellar furrows, poorly defined anterior border and spinous pygidium lacking a border.

Genus *Zacanthopsis* Resser, 1938

Type Species: *Olenoides levis* Walcott, 1886 from the Lower Cambrian portion of the Pioche Formation, Highland Range, Nevada. (by original designation)

Diagnosis: (modified from Palmer, 1964) A genus of Zacanthoididae with glabella expanding slightly forward. Preglabellar field long, concave. S0 transglabellar, deepest laterally. S1-S4 shallow, marginal. S1 oblique, posteriorly directed. S2 pit-like or developed as a transverse slot. S3 oblique, anteriorly directed. S4 a shallow pit at juncture of ocular ridge with glabella. Ocular ridges well-developed. Ocular lobes long; posterior tips opposite of S0. Fixigenae broad, with short posterior areas without metafixigenal spines. Occipital spine present.

Other Species:

Zacanthopsis virginica Resser, 1938; Shady Fm., near Austinville, Virginia.

Zacanthopsis contractus Palmer, 1964; Saline Valley Fm., near Gold Point, Nevada.

Zacanthopsis strubucus Fritz, 1972: Sekwi Fm., Mackenzie Mtns., NWT.

Zacanthopsis expansa Fritz, 1991a: Iltyd Fm., Wernecke Mtns., Yukon.

Discussion: A detailed discussion of the Lower Cambrian genus *Zacanthopsis* was given in Palmer (1964). *Zacanthopsis* can be distinguished from the Middle Cambrian *Zacanthoides* Walcott, 1888 by its wider fixigenae, ocular lobes that do not directly contact the glabella (ocular ridges are present) and shorter posterior areas of the fixigenae that lack metafixigenal spines. *Zacanthopsina* Palmer, 1964 from the Lower Cambrian of Nevada is also similar to *Zacanthopsis* but can be distinguished by prominent ocular ridges that are undifferentiated from the ocular lobes and merge with the glabella. All three genera possess short but distinct preglabellar fields: an atypical feature for corynexochids.

Species of *Zacanthopsis* have a conservative morphology and vary primarily in relative width of the fixigenae and development of the occipital spine. All share a similar configuration of the glabellar furrows. The pygidium of this genus is only known for the type species (see Resser, 1938, pl. 3 fig. 41; Palmer, 1964, pl. 3, fig. 3) and *Z. expansa* (see Fritz, 1991a, pl. 9, fig. 23). It is short, wide, has two axial rings plus a terminal piece and three to four pairs of marginal spines.

Zacanthopsis contractus Palmer, 1964

Pl. 38, figs. 1-3

1964 *Zacanthopsis contractus* Palmer, p. F10, pl. 3, figs. 4-6.

1972 *Zacanthopsis contractus*, Fritz, 1972, p. 38.

Diagnosis: A species of *Zacanthopsis* with palpebral areas of fixigenae wider than anterior areas. Ocular ridges short: ocular lobes long. L0 posterior margin rounded with short posterior spine. Prosopon of fine granules.

Holotype: A nearly complete cranidium (USNM 144287; Palmer, 1964, pl. 3, fig. 4) from the Saline Valley Formation, 7 km east of Gold Point, Mt. Dunfee area, Esmeralda County, Nevada.

Occurrences: NEVADA. Saline Valley Formation, Esmeralda County: USGS colln. 37480-CO (Palmer, 1964), 7 km east of Gold Point, Mt. Dunfee area (equals locality 20 herein); section PC, Paymaster Canyon, 21 km northeast of Silver Peak.

Zonal Biostratigraphy: *Olenellus transitans* Zone.

Discussion: New specimens of *Zacanthopsis contractus* Palmer, 1964 from stratigraphically equivalent rocks to the north of the type locality add little to the description given by Palmer (1964) for this species. One specimen (Pl. 38, fig. 3) has well-preserved glabellar furrows that are of typical configuration for this genus. *Z. contractus* can be distinguished from other species of this genus by its wide palpebral areas of the fixigenae, short ocular ridges (facial suture cuts closer to the glabella at the anterior of the ocular lobes than in other species), and short occipital spine. *Z. strabus* Fritz, 1972 from the Sekwi Formation is closest in morphology to *Z. contractus* but differs in having longer ocular ridges. *Z. expansa* Fritz, 1991a from the Illtyd Formation shares the wide palpebral areas of the fixigenae, but has a longer preglabellar field and larger occipital spine that originates from the center of L0. *Z. virginica* Resser, 1938 from the Shady Formation is known from a single fragmentary cranidium and shares with *Z. expansa* a long preglabellar field. The material of the *Z. virginica* is inadequate to determine if it is the same species as *Z. expansa*.

Order Ptychopariida Swinnerton, 1915

Diagnosis: An order of Trilobita with hypostome natant. Preglabellar field generally well-developed. Glabella tapering forward; 3-4 pairs of glabellar furrows. Pygidium usually lacking a border. Glabella clavate to corynoid early in ontogeny, becoming parallel-sided, then tapering forward. Glabella shortens during meraspid ontogeny while preglabellar field lengthens. Hypostome attached in protaspid.

Discussion: In the Treatise on Invertebrate Paleontology (Moore, 1959), the Ptychopariida is an enormous order comprising the bulk of the Trilobita. Fortey (1990a) examined the order and restricted membership in the Ptychopariida to those taxa which have the derived character of a natant hypostome. On this basis the Damesellacea, Leiostegiacea, Illaenacea and Calymenacea were excluded by Fortey from the Ptychopariida. He also analyzed the higher taxonomy of the order and concluded that many of the superfamilies are not natural groups (poly- or paraphyletic) and require further study.

The Ptychopariida are generally a small component of Lower Cambrian faunas. The most common are what have been informally called the "small ptychopariids", a generalized, much oversplit group of small size. This group includes the "Antagminae" (Ptychopariidae) which will be examined in detail. The major radiation of the Ptychopariida did not begin until the Middle Cambrian.

Ontogeny: The ontogeny of the Ptychopariina has been well studied by Palmer (1958, 1962), Whittington (1957a, 1957b), Liu (1968, 1971, 1972, 1978, 1979, 1980, 1981, 1983, 1984, 1985a) and Fortey (1990a). Robison (1967) provided a comparison of Ptychopariida and Corynexochida ontogenies. The two orders have similar protaspid and sometimes early meraspid stages (discussed under the Corynexochida), but a different subsequent ontogenetic development. Both start with a long, clavate glabella and no preglabellar field. The Corynexochida retain the long glabella and a corynoid to rounded glabella, while the Ptychopariida progressively shorten the glabella, lengthen the preglabellar field, and develop a tapering forward glabella.

The Ptychopariida and Corynexochida likely share a common origin, based on their early developmental similarities. Fortey (1990a) suggested the Redlichiida as a possible ancestral group. In the ontogeny of *Paradoxides pinus* Holm (see Westergård, 1936, pls. 4-5) (Paradoxidacea, Redlichiida) the protaspid has a long, clavate glabella. The glabella shortens and becomes parallel-sided through the meraspid stage, then lengthens and becomes clavate again during the holaspid stage. In comparison, the Corynexochida retain a *Paradoxides* protaspid to early meraspid glabellar shape and length in the holaspid stage. The Ptychopariida follow the *Paradoxides* ontogeny through the meraspid stage and retain the short glabella in the holaspid. The ontogeny diverges then from that of *Paradoxides* with the glabella modified by widening the occipital ring and rear of the glabella while retaining a nonexpanded glabellar front. This produces a tapering forward glabella in the holaspid.

Suborder Ptychopariina Richter, 1933

Superfamily Ptychopariacea Matthew, 1887

Family Ptychopariidae Matthew, 1887

Discussion: Many discussions have been presented on the difficulties of classifying members of the generalized, mainly Lower Cambrian, Ptychopariidae. Some of these taxa were tentatively collected into the family ?Antagmidae by Hupé, 1953b, which was reduced in rank to subfamily by Rasetti (1955). The Antagminae has been used by some taxonomists, but many modern systematists have not adopted it [i.e. Fritz (1972, 1991a) and Palmer (*in* Palmer and Halley, 1979)], although they have continued to use the many, poorly differentiated genera assigned to it. Fortey (1990a, p. 563) aptly referred to the Antagminae as "ptychopariids sharing only the primitive grade of libristomate organization, and differing only in characters of the most trivial kind".

Lochman (1947, p. 59) was the first to recognize that many of these genera were not adequately defined or distinguishable because of "the establishment of genera without clear-cut generic characters, the careless assignment of species to the genera and the use of fossil material too poor for description". Rasetti (1951) further noted that many taxa were based exclusively on cranidia and preservational differences between shale and limestone specimens made genera based on differently preserved material incomparable.

Lochman (1947, p. 60) stressed the importance of developing a standard set of characters to distinguish genera. She proposed a set of nine diagnostic generic features, each of which is evaluated below. Many of her characters are found to be of lower taxonomic value or of limited usage due to their susceptibility to distortion through preservational biases.

1. Length of ocular lobes and their position with reference to the glabella. In all other genera examined in this study, length of the ocular lobes is a species-level diagnostic feature. Some genera may tend to have either short or long ocular lobes, but the exact length varies among species. Length of the ocular lobe also tends to shorten during ontogeny.

- 2a. Basic shape and convexity of glabella. This is a valid generic feature, but minor variations occur between species.

- 2b. Glabellar furrows: presence/absence, number and direction. These are valid generic features, but strongly influenced by preservation, as Lochman noted. There are also variations in these features between species, especially in effacement of more anterior furrows and in furrow orientation.

3. Proportional width of fixigenae to glabella. In other genera, this is a species-level character, although particular genera or families may be characterized by generally wide or narrow fixigenae.

4. Elevation of the fixigenae. This character is strongly influenced by preservation, and also varies between species.

5. Width and length of the posterior limb. This is a downsloping feature in limestone material and is difficult to compare. Width also varies through ontogeny.

6. General structure of the preglabellar area. This is a valid generic diagnostic feature, although minor variations occur between species.

7. Outline and convexity of the pygidium, and marginal spines. The general shape of the pygidium varies through ontogeny in most genera. Number of marginal spines is a species-level characteristic and nature of the spines is particularly prone to intraspecific variation.

- 8a. Proportion of axial to pleural lobes. A valid generic feature.

- 8b. Presence of a marginal furrow. A valid generic or higher level taxonomic feature. May be influenced by effacement.

8c. Basic character of the marginal border. This is a species-level character.

9. Basic structure of the axial and pleural lobes. These are valid generic features, although number of pygidial segments varies between species.

Rasetti (1951, p. 201-202) criticized Lochman's generic diagnostic characters, particularly the ratios, which he claimed were not diagnostic. He stated that use of Lochman's characters would "lead to an excessively artificial grouping of forms" and pointed out the difficulty of developing meaningful systematics on fossil taxa that have only limited morphological information available. Rasetti (1955; *in* Moore, 1959) supported the use of intergrading genera and the abandonment of stringent generic diagnostic characters. Rasetti's approach to the ptychopariids cannot be supported: a genus that cannot be objectively defined and consistently recognized has no validity and is not useful taxonomically or biostratigraphically.

Shaw (1955, 1962) emphasized the importance of the anterior course of the facial suture in discriminating between Ptychopariidae taxa. Palmer (*in* Palmer and Halley, 1979) questioned the importance of this feature and concluded that it has little value. Considering that the facial sutures will change from anteriorly convergent to divergent through ontogeny⁴⁸, it is agreed that this is not a meaningful taxonomic character and Shaw's taxonomic approach is abandoned. Expression of this feature is also highly affected by preservation.

Each author has redefined the Lower Cambrian Ptychopariidae genera, assigned different species to them, and repressed some generic names while resurrecting others, thus creating an unstable taxonomy. For example, Palmer (1968, p. B74-B75) discussed the problems associated with *Antagmus* and concluded that the name should have been restricted to the holotype, since it was based on unrecognizable material, but refused to do so since the name "is now deeply entrenched in the literature, and *Antagmus* is the nominal genus of a family and subfamily". However, Lochman (1947), Rasetti (1955) and Shaw (1962) each diagnosed the genus differently and assigned different species to it. The genus is therefore meaningless and should be abandoned, along with the family and subfamily (Antagmidae, Antagminae). *Billingsaspis* Resser, 1935, *Periomma* Resser, 1936, *Onchocephalus* Resser, 1937b, *Litocodia* Resser, 1938, and *Sombrerella* Lochman, 1948 are other genera that have been erected based on material too poor for specific or generic identification and have been variously used or abandoned by different authors.

⁴⁸ An excellent example of this change is illustrated for *Syspacephalus obscurus* Palmer (*in* Palmer and Halley, 1979), pl. 7, figs. 6, 8-10.

A different approach to the classification of the Lower Cambrian Ptychopariidae is needed: since the genera intergrade and cannot be objectively defined, many should be synonymized. This is a radical suggestion compared to previous work, but it will create a genus that can be objectively diagnosed and that will be comparable to the generic concept used for post-Cambrian taxa.

Proliostracus Poulsen, 1932 is the name with priority and *Billingsaspis* Resser, 1935, *Antagmus* Resser, 1936, *Syspacephalus* Resser, 1936, *Poulsenia* Resser, 1936, *Periomma* Resser, 1936, *Onchocephalus* Resser, 1937b, *Litocodia* Resser, 1938, *Austinvillia* Resser, 1938, *Crassifimbria* Lochman, 1947, *Piaziella* Lochman, 1947, *Sombrerella* Lochman, 1948, *Luxella* Rasetti, 1955, *Eoptychoparia* Rasetti, 1955, *Eoptychoparia* (*Cyphambon*) Shaw, 1962 and *Illytydaspis* Fritz, 1991a should all be considered junior synonyms. *Illytydaspis* is the only genus synonymized that has been erected in a modern taxonomic study. The primary distinguishing feature of the type species of *Illytydaspis* is a glabella that merges anteriorly with the preglabellar field. All of the "Antagminae" have an anteriorly downsloping glabella. This feature is particularly exaggerated in the type species of *Illytydaspis*, but is not considered of generic importance. Of the genera assigned by Rasetti (*in* Moore, 1959) to the Antagminae, only *Bicella* Rasetti, 1955 is tentatively recognized as a genus separate from *Proliostracus*. Similarly, *Hadrokraspedon* Shaw, 1962 is tentatively recognized. *Ptychoparella* Poulsen, 1927 was restricted to the holotype by Rasetti (1955) and lower Cambrian species from North America that had been assigned to it by Resser (1938), were reassigned by Shaw (1962), and are now assigned to *Proliostracus*. *Elrathina* Resser, 1937b was synonymized with *Syspacephalus* (= *Proliostracus*) by Robison (1976), but has continued to be used in the literature (i.e. see Young and Ludvigsen, 1989). *Elrathina* is judged to be distinct from *Proliostracus* by possession of a well-rounded glabellar anterior. A full discussion of *Proliostracus* as here defined follows.

Numerous species of small ptychopariids have been described from Siberia. Some of the same genera have been used as in Laurentia, but others are names that have been used exclusively for Russian species. Many of these species should also be assigned to *Proliostracus*, but a revision of the Russian literature is beyond the scope of this thesis. For example, *Binodaspis lepida* Pokrovaskaya and Ergaliev *in* Ergaliev and Pokrovaskaya, 1977 is known from both cranidia and pygidia and has all the typical features of a species of *Proliostracus*. *Binodaspis* Lermontova, 1951 is one of the Siberian genera that is a junior synonym of *Proliostracus*.

Genus *Proliostracus* Poulsen, 1932

Type Species: *Proliostracus strenuelliiformis* Poulsen, 1932, from the Ella Island Formation, south coast of Ella Island, East Greenland. (by original designation) Junior Synonyms: *P. rosenkrantzi*

Poulsen, 1932; *P. liostracoides* Poulsen, 1932; *P. noe-nygaardii* Poulsen, 1932, all from the same locality and formation.

Diagnosis: A genus of Ptychopariidae with glabella truncated anteriorly. Anterior border lengthens medially. Anterior border furrow generally deflected slightly posteriorly medially. Preglabellar field generally with depression anterior to glabella. S0 well-defined, transglabellar. Gabellar furrows shallow, nonparallel: S1 oblique, convergent posteriorly, often bifurcate; anterior furrows progressively transverse to oblique, convergent anteriorly. Up to 4 pairs glabellar furrows. Thorax of ?13-18 segments, pleural spines blunt. Pygidium short, wide: of few segments with at least one well-defined axial ring.

Other Species: The list of described species that are now attributed to *Proliostracus* by synonymy of the numerous other genera is long. As the generic concept used here is broader than that adopted by previous workers, so will the species concept be broader. This will likely result in the synonymy of numerous species, which, unfortunately, cannot be undertaken here due to the poor quality of illustrations of many early published species and the low availability of the type material. For example, many of the species established by Resser (1937a, 1938) are likely synonymous, though most of his illustrations of these tiny trilobite are at life size and thus impossible to evaluate.

Shaw (1962) provided an exclusively Lower Cambrian list of 42 Laurentian species which are all (except for *Bicella bicensis* (Resser, 1938) and *Hadrokraspedon crassimarginata* (Rasetti, 1955)) accepted here as belonging to *Proliostracus*, but their validity as separate species cannot be confirmed. Shaw was conservative in accepting species that had been erected based on unrecognizable material, such as *Antagmus typicalis* Resser, 1937a. Since the work of Shaw (1962), several modern taxonomic works have been published and these species are tentatively accepted as distinct, pending comparison with earlier published species. These species of *Proliostracus* are listed below along with Middle Cambrian species described by Rasetti (1951).

Onchocephalus fieldensis Rasetti, 1951; Mount Whyte Fm., Mt. Field, BC.

Onchocephalus depressus Rasetti, 1951; Mount Whyte Fm., Mt. Field, BC.

Onchocephalus maior Rasetti, 1951; Mount Whyte Fm., Mt. Field, BC.

Onchocephalus sublaevis Rasetti, 1951; Mount Whyte Fm., Mt. Field, BC.

Piaziella tuberculata Rasetti, 1951; Mount Whyte Fm., Mt. Stephen, BC.

Syspacephalus gregarius Rasetti, 1951; Mount Whyte Fm., Mt. Stephen, BC.

Syspacephalus laticeps Rasetti, 1951; Mount Whyte Fm., Mt. Stephen, BC.

- Syspacephalus laevigatus* Rasetti, 1951; Mount Whyte Fm., Mt. Stephen, BC.
- Syspacephalus crassus* Rasetti, 1951; Mount Whyte Fm., Mt. Stephen, BC.
- Syspacephalus tardus* Rasetti, 1951; Cathedral Fm., Mt. Stephen, BC.
- Elrathina parallela* Rasetti, 1951; Stephen Fm., Mt. Stephen, BC.
- Luxella socialis* Rasetti, 1963; boulders of the Lévis Fm., Lévis, Quebec.
- Onchocephalus ornatus* Rasetti, 1963; boulders of the Lévis Fm., Lévis, Quebec.
- [non] *Luxella bisulcata* Rasetti, 1963; boulders of the Lévis Fm., Lévis, Quebec.
- [non] *Onchocephalus? limbatus* Rasetti, 1963; boulders of the Lévis Fm., Lévis, Quebec.
- [non] *Eoptychoparia convexa* Rasetti, 1963; boulders of the Lévis Fm., Lévis, Quebec [= *Elrathina*].
- "*Antagmus*" *laminatus* Palmer, 1968; Hillard Fm., Tatonduk River, east-central Alaska.
- Onchocephalus profectus* Palmer, 1968; Hillard Fm., Tatonduk River, east-central Alaska.
- Antagmus arenosus* Fritz, 1968; Pioche Fm., northern Egan Range, Nevada.
- Onchocephalus papulus* Fritz, 1968; Pioche Fm., northern Egan Range, Nevada.
- Eoptychoparia piochensis* Palmer (in Palmer and Halley, 1979); Pioche Fm., Highland Range, Nevada.
- Syspacephalus longus* Palmer (in Palmer and Halley, 1979); Carrara Fm., Belted Range, Nevada.
- Syspacephalus obscurus* Palmer (in Palmer and Halley, 1979); Carrara Fm., Grapevine Mts., California.
- Antagmus truncatus* Fritz, 1972; Sekwi Fm., Mackenzie Mtns, NWT.
- Piaziella pia* Fritz, 1972; Sekwi Fm., Mackenzie Mtns, NWT.
- Piaziella? rara* Fritz, 1972; Sekwi Fm., Mackenzie Mtns, NWT.
- Proliostracus annosus* Fritz, 1972; Sekwi Fm., Mackenzie Mtns, NWT.
- Proliostracus contractus* Fritz, 1972; Sekwi Fm., Mackenzie Mtns, NWT.
- Proliostracus depressus* Fritz, 1972; Sekwi Fm., Mackenzie Mtns, NWT.
- Proliostracus latus* Fritz, 1972; Sekwi Fm., Mackenzie Mtns, NWT.
- Syspacephalus rapidus* Fritz, 1972; Sekwi Fm., Mackenzie Mtns, NWT.
- Antagmus ducketti* Fritz, 1991a; Illtyd Fm., Wernecke Mtns., Yukon.
- Illtydaspis aphylla* Fritz, 1991a; Illtyd Fm., Wernecke Mtns., Yukon.
- Illtydaspis ornata* Fritz, 1991a; Illtyd Fm., Wernecke Mtns., Yukon.
- Illtydaspis quartetensis* Fritz, 1991a; Illtyd Fm., Wernecke Mtns., Yukon.
- Proliostracus ampliatus* Fritz, 1991a; Illtyd Fm., Wernecke Mtns., Yukon.
- Syspacephalus werneckensis* Fritz, 1991a; Illtyd Fm., Wernecke Mtns., Yukon.

Discussion: *Proliostracus* Poulsen, 1932 was established for species from the Lower Cambrian Ella Island Formation of East Greenland. Poulsen (1932) recognized four species of *Proliostracus* in the fauna, including the type species, all from the same locality. *P. rosenkrantzi* Poulsen, *P.*

liostracoides Poulsen and *P. noe-nygaardii* Poulsen were synonymized with *P. strenuelliiformis* Poulsen by Shaw (1959) who demonstrated that all were based on different ontogenetic stages of the same species or features related to differences in preservation. Resser (1938) described two additional species⁴⁹ of *Proliostracus* from the Shady Formation of Virginia, but these species were excluded from the genus by Lochman (1947) and Rasetti (1955), who restricted the genus to the Greenland forms. Subsequently, Fritz (1972) recognized three species of *Proliostracus* from the Sekwi Formation of the Northwest Territories, and one species (Fritz, 1991a) from the Illtyd Formation of the Yukon. Thus *Proliostracus* has been accepted by modern taxonomic workers as occurring in North America, and here the generic concept is considerably expanded to include most of the Laurentian species of the subfamily Antagminae *sensu* Rasetti (*in* Moore, 1959).

Proliostracus is a generalized, small ptychopariid characterized by a truncated glabella, medially lengthening anterior border, preglabellar field with depression and tiny pygidium. The pygidium of *Proliostracus* is known for only a few of the many described species (Table 18), but is consistent in morphology. It is a short, wide plate with a subterminal axis and no border or border furrow. One segment is generally clearly defined (one axial ring furrow and one pair each of pleural and interpleural furrows)⁵⁰ and generally one or two additional poorly defined segments. Up to five poorly defined segments can be seen in *P. obscurus* (Palmer). The thorax is likewise known only for a few species (Table 17), but is also consistent in morphology with a general non-tapering outline (posterior segments becoming abruptly narrower near the pygidium), well-defined pleural furrows and blunt pleural spines. The number of thoracic segments reported for various species has ranged from thirteen to more than eighteen. The pygidium is difficult to distinguish from the thorax in all but the best preserved material, which accounts for some of the variability in the numbers, but in other species the number of segments appears to have varied in the holaspis (see *Elrathina parallela* Rasetti, 1951).

Most of the species characters considered diagnostic by Lochman (1947) are discarded as minor population variations. Characters that are considered of importance are: configuration of preglabellar area (length, depth of preglabellar depression, distinctiveness of anterior border furrow medially), glabellar furrow arrangement, strength of ocular ridge, length and inflation of ocular lobes, relative width of fixigenae to glabella, occipital tubercle (presence/absence, size,

⁴⁹ Lochman (1947) synonymized Resser's species and chose *Proliostracus goodwini* Resser, 1938 as the senior synonym of *P. granulatus*.

⁵⁰ This first segment is likely an unreleased thoracic segment that is retained in the holaspis as noted by Palmer (1958). In specimens that have the test broken, a non-functional articulated half ring can be seen beneath the first axial ring (i.e. *Proliostracus buelnaensis* Pl. Fig. ; *P. obscurus* (Palmer) *in* Palmer and Halley, 1979, pl. 7, fig. 13).

Table 17

List of Laurentian species assigned to *Proliostracus* with known thoraxes.

[15]	<i>Ptychoparella buttsi</i> Resser, 1938, pl. 5, fig. 3.
[18+]	<i>Poulsenia granosa</i> Resser, 1939, pl. 13, figs. 28-29.
[14]	<i>Syspacephalus gregarius</i> Rasetti, 1955, pl. 8, fig. 19.
[13]	<i>Syspacephalus laevigatus</i> Rasetti, 1955, pl. 9, fig. 9.
[13+]	<i>Syspacephalus perola</i> (Walcott), Rasetti, 1955, pl. 9, figs. 17-19.
[15+]	<i>Crassifimbria walcotti</i> (Resser); Palmer, 1958, pl. 25, figs. 19, 23.
[?15]	<i>Eoptychoparia piochensis</i> Palmer, (in Palmer and Halley, 1979), pl. 7, fig. 5.
[15-16]	<i>Syspacephalus longus</i> Palmer, (in Palmer and Halley, 1979), pl. 7, fig. 16.
[13+]	<i>Proliostracus</i> sp. 1, this thesis, Pl. Figs. .

Number in bold preceding species name denotes number of thoracic segments recorded for that species by the author.

Table 18

List of Laurentian species assigned to *Proliostracus* with known pygidia.

<i>Ptychoparella buttsi</i> Resser, 1938, pl. 5, fig. 3.
<i>Poulsenia granosa</i> Resser, 1939, pl. 13, figs. 19-21.
<i>Onchocephalus mexicanus</i> Lochman, 1952, pl. 20, figs. 7-10.
<i>Onchocephalus buelnaensis</i> Lochman, 1952, pl. 20, figs. 18, 21, 22, 26, 27.
<i>Syspacephalus gregarius</i> Rasetti, 1955, pl. 8, fig. 19.
<i>Syspacephalus laevigatus</i> Rasetti, 1955, pl. 9, fig. 9.
<i>Crassifimbria walcotti</i> (Resser); Palmer, 1958, pl. 26, figs. 7-8, 14-24.
<i>Onchocephalus profectus</i> Palmer, 1968, pl. 3, fig. 18.
<i>Onchocephalus papulus</i> Fritz, 1968, pl. 36, fig. 5.
<i>Proliostracus annosus</i> Fritz, 1972, pl. 10, fig. 22.
<i>Eoptychoparia piochensis</i> Palmer, 1979, pl. 7, fig. 5.
<i>Syspacephalus obscurus</i> Palmer, (in Palmer and Halley, 1979), pl. 7, figs. 13, 15.
<i>Syspacephalus longus</i> Palmer, (in Palmer and Halley, 1979), pl. 7, fig. 16.
<i>Syspacephalus</i> sp. Hu, 1985a, pl. 7, fig. 24.
<i>Onchocephalus</i> sp. Hu, 1985a, pl. 9, figs. 21, 22, 25.
<i>Piaziella</i> sp. Hu, 1985a, pl. 2, fig. 28, 31.
<i>Elrathina parallela</i> Rasetti; Young and Ludvigsen, 1989, pl. 9, fig. 7.
<i>Proliostracus buelnaensis</i> (Lochman), this thesis, Pl. Figs.
<i>Proliostracus</i> sp. 2, this thesis, Pl. Figs.

position), number of pygidial segments and prosopon. Palmer (1958) presented a study on intrapopulational variability on *Proliostracus walcotti* (Resser, 1937b) and found that there was an up to 20% variation in measurable cranidial proportions.

Ptychoparia (see type species, *P. striata* (Emmrich, 1839) illustrated in Whittington, 1992, pls. 64, 65) is similar to *Proliostracus*. It differs in having deeper glabellar furrows, sentate pleural spines, a larger pygidium of five well-defined segments and in reaching a considerably larger size. S1 are particularly strong in *Ptychoparia* and are expressed as bold slashes on the posterior of the glabella. Many other Middle Cambrian Ptychopariidae and Alokistocaridae genera such as *Elrathia* Resser, 1937b, *Elrathia Walcott*, 1924, *Caborcella* Lochman, 1948, *Mexicella* Lochman, 1948, etc. are also similar to *Proliostracus*, but differ in features such as a glabella with a rounded anterior, various modifications to the preglabellar area/anterior border and larger pygidia.

Ontogeny: Detailed ontogenetic studies have been presented for species assigned here to *Proliostracus* by Palmer (1958), Shaw (1959) and Hu (1985a). Some species such as *Proliostracus walcotti* (Resser) have a conservative holaspid ontogeny for which Palmer (1958) recorded almost no difference between later meraspid and early holaspid specimens, except for a greater tapering of the glabella. Other species may dramatically increase the medial expansion of the anterior border (see *P. quartetensis* (Fritz, 1991a), pl. 8, figs. 21-28) or radically change the course of the anterior facial suture (see *P. obscurus* (Palmer in Palmer and Halley, 1979), pl. 7, figs. 6, 8-10) through the ontogeny of the holaspid.

Proliostracus buelnaensis (Lochman, 1952)

Pl. 38, figs. 5-6; Pl. 39, figs. 1-15

Onchocephalus buelnaensis Lochman, 1952; p. 104-105, pl. 20, figs. 5, 18-29.

Onchocephalus mexicanus Lochman, 1952; p. 105-107, pl. 20, figs. 6-17.

Diagnosis: A species of *Proliostracus* with S3 developed as isolated, transverse slots. Anterior margin gently rounded. Anterior border furrow shallowest medially, inflected slightly posteriorly. Preglabellar depression shallow. Glabella approximately 7/10 cranidial length. Glabellar furrows indistinct, up to 4 pairs. S1 typically bifurcate. S2 marginal, inclined slightly posteriorly. S4 minute, isolated: slightly oblique, convergent anteriorly. Occipital tubercle well-developed, posterior. Fixigenae moderately wide: each approximately 3/5 width of glabella. Ocular ridges generally indistinct. Ocular lobes minute: narrow, short, midpoint located opposite slightly less than 2/3 glabellar length. Facial suture convergent anteriorly. Librigenae

with wide, well-defined border, moderately short genal spine. Posterior limbs moderately long, wide, tapering laterally. Pygidium tapering laterally; 2-3 pairs of pleural furrows. Posterior margin with slight indentation. Pygidial axis short, stubby; two axial ring furrows. Prosopon of fine granules, faint radiating ridges on fixigenae.

Holotype: A complete cranidium (USNM 115724; Lochman, 1952, pl. 20, figs. 19, 23) from the Buelna Formation, Buelna Hills, 15 km northwest of Caborca, Sonora, Mexico.

Occurrences: MEXICO: Buelna Formation, Sonora (Lochman, 1952): locality 807c, Buelna Hills, 15 km northwest of Caborca; localities 809a,b, Prieto Hill, 2.5 km southwest of Caborca; locality 801f, Proveedora Hills, north side of Puerto Blanco, 10-11.5 km west of Caborca. BRITISH COLUMBIA. Eager Formation: section MG2, Mt. Watson, 7 km east-southeast of Canal Flats; section MG3, Mt. Grainger, 6 km northeast of Canal Flats; ?section RC4, Ram Creek area, 13 km northeast of Skookumchuck; ?locality 7, 5 km southeast of Mt. Evans summit, Moyie Range.

Zonal Biostratigraphy: *Proliostracus buelnaensis* Subzone, *Olenellus transitans* Zone.

Discussion: Lochman (1952) illustrated two species from the Buelna Formation of Mexico which she attributed to *Onchocephalus*: *O. buelnaensis* Lochman and *O. mexicanus* Lochman. Lochman (1952, p. 106-107) distinguished the latter from the former by "the steeper descent of the brim and continued down-slope of the border of the cranidium, and the steep slope of the pleural platforms of the pygidium". These are minor differences easily accommodated by intraspecific variation, and none of them is readily apparent in Lochman's illustrations. Both species co-occur in all but one of Lochman's reported occurrences and are considered synonymous. Since both species are adequately illustrated, *Proliostracus buelnaensis* is chosen as the senior synonym based on page priority.

Material of *Proliostracus* from the Canal Flats region of British Columbia closely matches that illustrated by Lochman (1952) for *P. buelnaensis* from Sonora, Mexico in proportions of cranidial features and arrangement of the pygidial features. Lochman's illustrations are inadequate to fully evaluate the glabellar furrows in the type material. The furrows are barely discernible, however, the holotype (see Lochman, 1952, pl. 20 figs. 19, 23) appears to have isolated S3 at least on the left side, although Lochman recorded this furrow pair as marginal and did not mention the presence of S4. On the best preserved specimens from near Canal Flats, S3 is clearly developed as a pair of transverse slots, isolated on the glabella and closer to the midline than to the glabellar margin. Minute S4 are developed approximately midway between S3 and the

ocular ridges. The largest cranidia (> 5mm long) have broader, shallower glabellar furrows. The ocular lobes of this species are small and inclined dorso-laterally. Pygidia from two different collections near Canal Flats are nearly identical except that the ones from MG2e are smaller and have a slightly lower proportion of width of the pleural to axial regions. The difference is likely due to ontogenetic changes and the same trend of increasing width of the pleural regions is seen in *Proliostracus walcotti* (Resser) illustrated in Palmer (1958, pl. 26). The smaller pygidia are identical to those illustrated by Lochman (1952) from the type area.

Material from the Hellroaring Creek area of British Columbia is tentatively assigned to *Proliostracus buelnaensis*. These rocks are stratigraphically equivalent to those of the Canal Flats region and share the same fauna. The material agrees in all observable features with *P. buelnaensis*, but is too badly deformed for accurate species identification. An articulated specimen has at least ten thoracic segments and the gradually tapering outline typical of the genus.

Proliostracus buelnaensis can be readily distinguished from most other Lower Cambrian species by the isolated S3 that are located closer to the midline than the glabellar margin. *Poulsenia* sp. 2 Fritz, 1991a from the Iltyd Formation, Yukon, is another Lower Cambrian species that shares this feature. It differs in having narrower fixigenae, a longer glabella, longer ocular lobes, deeply bifurcate S1, and S3 that are not so medially situated. *Ptychoparia thia* Walcott, 1917⁵¹ from the St. Piran Formation, Mt. Bosworth, British Columbia is closely comparable to *Proliostracus buelnaensis*. It differs in having more posteriorly positioned ocular lobes and wider fixigenae. The exact nature of its glabellar furrows cannot be determined using illustrated material (see Rasetti, 1951, pl. 8, figs. 1, 2.)

Proliostracus sp. 1

Pl. 39, figs. 17-18

Discussion: Rare, poorly preserved cranidia from the Eager Formation, locality 5, can be assigned to *Proliostracus*, but are too poor for specific identification. The material is preserved as flattened internal molds in shale. The cranidia are not of *P. buelnaensis* (Lochman), which occurs nearby at Canal Flats, as they have a longer preglabellar field, wider fixigenae and shorter anterior border. Glabellar furrows are not preserved well enough to be described.

⁵¹ This species was based on a single badly worn and broken cranidium by Walcott (1917, pl. 12, fig. 6). Lochman (1947) redescribed the species using unfigured paratype material. *Ptychoparia thia* Walcott was used as the type species of *Onchocephalus* by (Resser, 1937). Here it is considered a species of *Proliostracus*.

Proliostracus sp. 2

Pl. 38, figs. 4, 7-14; Pl. 39, fig. 16

Occurrences: NEVADA. Saline Valley Formation, Esmeralda County: locality 9, Weepah Hills, 14 km north-northeast of Silver Peak; section PC, Paymaster Canyon, 21 km northeast of Silver Peak.

Zonal Biostratigraphy: *Olenellus transitans* Zone.

Discussion: Abundant material, including articulated species, is available for *Proliostracus* sp. 2, but the level of preservation is low. Specimens are preserved as internal molds and many features used in species identification cannot be distinguished. Comparisons to testate species preserved in limestone are inconclusive as the same features can appear quite different.

There are at least thirteen thoracic segments in *Proliostracus* sp. 2. The pygidium is difficult to distinguish from the thorax in most specimens. Small holaspids (Pl. 38, fig. 7) may be partly enrolled with the pygidium curled beneath the thorax as was illustrated by Palmer (1958, pl. 25, figs. 19, 23) for *P. walcotti* (Resser, 1937b). The pygidium is poorly known and appears to have two poorly defined axial ring furrows, and two pairs of pleural furrows. Librigenae have a wide, well-defined border and likely have only a tiny genal spine (Pl. 38, figs. 4, 11). A tentatively assigned hypostome has a slightly posteriorly tapering shape. The posterior body is short and is separated from the anterior body by a deep furrow.

Proliostracus sp. 2 has at least a general resemblance to *P. angustifrons* (Rasetti, 1955) from Quebec in its anterior border with minimal medial expansion, small ocular lobes, and other proportions of the cranidial features, but S3 are transverse in *Proliostracus* sp. 2 and oblique (converging anteriorly) in *P. angustifrons*. *P. gregarius* (Rasetti, 1951), from Middle Cambrian strata of the Canadian Rocky Mountains, is also closely comparable to *Proliostracus* sp. 2, but differs in having a slightly longer preglabellar field without a distinct depression and narrower posterior limbs. It shares the same glabellar furrow configuration with *Proliostracus* sp. 2, except S4 cannot be distinguished in *P. angustifrons*. The thorax and pygidium are also similar in both species with *P. angustifrons* having 14 thoracic segments.

Family Unassigned
Genus *Gelasene* Palmer, 1968

Type Species: *Gelasene acanthinos* Palmer, 1968 from the Adams Formation, Yukon River, east-central Alaska. (by original designation)

Diagnosis: (modified from Palmer, 1968) A micropygous genus of Ptychopariacea. Anterior border well developed. Anterior border furrow broad. Glabella well-defined; axial furrows deep. S0 transglabellar, deepest laterally. S1-S3 deep; oblique, convergent posteriorly, subparallel. Fixigenae broad. Fossulae deep. Ocular ridges low. Ocular lobes medially situated, moderately small, curved. Facial suture convergent anteriorly. Posterior limbs broadly tapering. Librigenae broad with wide border and laterally inflected genal spines. Thorax with straight thoracic segments, short pleural spines. Pygidium minute, subrounded. Pygidial axis large, poorly defined, with at least two axial rings. Prosopon of broad-based spines, interspersed with fine granules.

Other Species:

Gelasene? sp. Fritz, 1972; Sekwi Fm., Mackenzie Mtns., NWT.

Gelasene aureum n. sp.: Poleta Fm., Gold Point, Nevada.

Discussion: *Gelasene* is a large, spiny Ptychopariina with deep glabellar furrows, broad cheeks and a minute pygidium. It has deep fossulae which is an unusual feature for Ptychopariida, but is typical of Corynexochida, especially dorypygines. The minute pygidium with broad, poorly defined axis and marginal spines is closely comparable to that of *Redlichia* (i.e. see Öpik, 1958, fig. 9), though in most other features these trilobites are dissimilar. *Keeleaspis*⁵² Fritz, 1972 is another granular Ptychopariina similar to *Gelasene* in cranidial features. It differs in having a proportionately larger and wider pygidium, longer ocular lobes, nonparallel glabellar furrows and no fossulae and is similar to *Proliostracus*.

Gelasene is closely comparable in morphology to *Atops* Emmons, 1844. The genera differ primarily in the course of the facial suture: opisthoparian in *Gelasene*; proparian in *Atops*. As a proparian Ptychopariida, *Atops* has been assigned to the Conocoryphacea (Conocoryphidae). Fortey (1990a) concluded that the Conocoryphacea is not a natural group, and is merely a

⁵² The types species of *Keeleaspis* was designated by Fritz (1972) as "*K. gratia* sp. nov.", however, no species by this name was described by Fritz. *K. stupenda* Fritz, 1972 is the best known of the two species of *Keeleaspis* that Fritz did describe, and is here designated the type species.

polyphyletic collection of blind ptychopariaceans adapted to deep water environments. The type genus, *Conocoryphe*, was compared to *Ptychoparia* by Whittington (1992) who stated that the former may have been derived from the latter. *Atops* and *Gelasene* differ from these trilobites in having three pairs of deep, subparallel glabellar furrows (exclusive of S0), well-developed genal spines, a long glabella, and minute, narrow pygidium with a large, poorly defined axis.

Gelasene Palmer, 1968 was originally assigned to the Solenopleuridae (superfamily Solenopleuracea) by Palmer (1968). Fortey (1990a, p. 563) also dismissed the Solenopleuridae as an unnatural group and claimed that it encompasses "only primitive ptychoparioid morphologies"⁵³. The Solenopleuridae is a waste-basket taxon for Ptychopariina with a granular or tuberculose prosopon. The type genus, *Solenopleura* Angelin, 1854, differs from *Gelasene* but is similar to *Proliostracus* in having an anterior border that lengthens medially, shallow glabellar furrows, minute genal spines, blunt thoracic spines and a short, wide pygidium with narrow axis.

The higher taxonomy of the Ptychopariina needs to be re-evaluated before *Gelasene* can be assigned to a particular family or superfamily. It differs fundamentally from both *Conocoryphe* and *Solenopleura* and it is unlikely that its affinities lie with either of the type genera of the polyphyletic superfamilies discussed above.

Gelasene aureum n. sp.

Pl. 40, figs. 1-11

Diagnosis: A species of *Gelasene* with glabella broadly rounded anteriorly. Anterior border broadly curved. Genal spine short, broad based, rapidly tapering. Pygidium with two axial rings plus terminal piece, two pairs minute marginal spines.

Holotype: A nearly complete cranidium (ICS 1056 #1; Pl. 40, figs. 3, 6, 8) from the Poleta Formation, section GP, ICS collection 1056, Mt. Dunfee Area, 7 km east of Gold Point, Esmeralda County, Nevada. Paratypes: ICS 1056#2, 6, 8

Etymology: From the Latin adjective "aureum" (neuter, singular) meaning "golden". Named for the ghost town of Gold Point, near the type locality of the species.

⁵³ For an alternative treatment of the Solenopleuridae, see Ahlberg and Bergström (1978), who assigned many other ptychopariinids to an expanded Solenopleuracea, instead of disbanding the family and assigning its genera to other groups as is done here.

Occurrences: NEVADA. Poleta Formation: section GP, Mt. Dunfee Area, 7 km east of Gold Point, Esmeralda County, Nevada.

Zonal Biostratigraphy: *Gabriellus poletensis* Subzone, *Elliptocephala* Zone.

Discussion: *Gelasene aureum* n. sp. is a highly spinous trilobite. Most specimens have only the bases of these robust spines preserved, but the spines must have been of considerable length judging by the partial spines illustrated in Pl. 40, fig. 8. The spines are larger and less numerous than those found on *G. acanthinos* Palmer, 1968. *G. aureum* also differs from *G. acanthinos* in having a less pointed glabella, narrower anterior border furrow and shorter genal spines. *G. acanthinos* has occipital and fixigenal spines as well as secondary thoracic pleural spines. None of these spines can be detected on *G. aureum* due to fragmentary material. The pygidium is better preserved in *G. aureum* and can be demonstrated to have a spinous margin and the same spinous prosopon found on all other parts of the dorsal exoskeleton. No hypostomes can be attributed with certainty to *Gelasene*, however, the hypostomes tentatively assigned to *Labradoria lechmanae* n. sp. (Pl. 25, fig. 10) might belong to *G. aureum*, as both trilobites occur in the same collection.

Suborder Eodiscina Kobayashi, 1939

Family Eodiscidae Raymond, 1913 (emend. Jell, 1975)

Diagnosis: See Jell (1975).

Discussion: Some of the classic studies of trilobite taxonomy such as Jaekel (1909), Whitehouse (1936), and Hupé (1953b), favored a division of the Trilobita into two major groups: miomerans, trilobites with only two to three thoracic segments, and polymerans, trilobites with more than three thoracic segments. The miomerans include the eodiscoids and agnostoids. These subdivisions were never accepted by most North American trilobitologists and recent work by Shergold (1991) using comparative ontogeny demonstrated that the eodiscoids and agnostoids are not closely related. Shergold suggested that the eodiscoids be included in the Ptychopariida, and the agnostoids in a separate order. Babcock (1994) using cladistic methods also concluded that agnostoids and eodiscoids do not share a close common ancestor. Babcock further suggested that the eodiscoids arose via mosaic heterochrony and that they may be a paraphyletic or even polyphyletic group.

Eodiscoids can be distinguished from the agnostoids by: a well-developed glabella without basal lobes and usually with an occipital furrow and a pygidium with normal segmentation.

Eodiscoids typically have inflated posterior fixed cheeks, tubercles, pits or radial scrobicules on the cephalic rim, and a pygidium with up to 15 axial rings. The superfamily has traditionally been divided into two families based on the presence (Family Eodiscidae) or absence (Family Pagetiidae) of ocular lobes (see Rasetti⁵⁴ in Moore, 1959). Jell (1975) suggested that some genera without ocular lobes are closer phylogenetically to some genera with ocular lobes than they are to each other. He suggested that the presence or absence of ocular lobes is not a character of primary significance and used cluster analysis to reorganize the superfamily into two families based on a broad, flexible diagnosis. The family Eodiscidae as used by Jell (1975) includes all of the genera with ocular lobes that were previously assigned to the Pagetiidae, plus the blind genera *Eodiscus*, *Dawsonia*, *Calodiscus*, *Chelediscus* and *Opsidiscus*. Descriptive terminology for the eodiscids is modified from Jell (1975) and summarized in Text-fig. 22.

Genus *Ekwipagetia* Fritz, 1973

Type Species: *Ekwipagetia plicofimbria* Fritz, 1973 from the Sekwi Formation, Mackenzie Mountains, Northwest Territories. (by original designation)

Diagnosis: A highly convex genus of Eodiscidae with glabella tapering anteriorly. Anterior border long, of equal length medially and laterally. Epiborder furrow present. Scrobicules poorly developed to absent. Preglabellar field long: equal or greater than length of border. Ocular ridges low. Ocular lobes well-developed. Glabellar furrows poorly developed: S0 marginal, deep. Occipital spine long, posteriorly directed. Pygidium with minute marginal spines, deep border furrow, narrow border. Axis inflated; well-defined by deep axial furrows, terminates slightly anterior to posterior border. Axial ring furrows poorly developed: 3-4 pairs typically developed as marginal indentations. Axial spine non-terminal, long, dorsoposteriorly directed. Pleural fields unfurrowed.

Other Species:

Hebediscus marginatus Rasetti, 1967; Washington County, New York.

Ekwipagetia rasettii n. sp.; Poleta Formation, near Gold Point, Nevada.

⁵⁴ Note that the authorship of the eodiscoid families in the Treatise on Invertebrate Paleontology was incorrectly attributed to B.F. Howell.

Discussion: Fritz (1973) established *Ekvipagetia* as a large eodiscoid that resembles *Pagetides*. In addition to the type species, Fritz assigned *Hebediscus marginatus* Rasetti, 1967 from the Taconic Region of New York to the genus. Here is added a new species from Nevada, *E. rasettii*. Rasetti (1972, p. 46) discussed some of Siberian eodiscoids, originally described as species of *Hebediscus* Whitehouse, 1936, and described them as being "somewhat intermediate between *Hebediscus* and *Hebediscina*". Fritz (1973, p. 10) also drew attention to these Siberian eodiscoids that resemble *Ekvipagetia*. The Russian eodiscoid literature is unavailable for study, but based on Fritz's observations, assignment of these species to *Hebediscina* Rasetti, 1972 is a possibility..

The cranidium of *Ekvipagetia* closely resembles that of *Pagetides* except that the latter has a deep furrow running the length of the preglabellar field and has an anterior border that lengthens medially. Unlike *Ekvipagetia*, the pygidium of *Pagetides* lacks axial and marginal spines, and has a well-segmented axis, though both genera typically have unfurrowed pleural fields. *Pagetia* is another genus that closely resemble *Ekvipagetia*. It differs in having strongly developed scrobicules, a terminal axial spine on the pygidium that is posteriorly directed, no marginal pygidial spines and typically a well-furrowed pygidial axis and often pleural furrows. *Ekvipagetia* is very similar in cephalic morphology to *Hebediscina* differing only in lack of well-defined ocular ridges. The pygidium of *Hebediscina* has the same general outline and marginal spines as seen in *Ekvipagetia*, but has deep transaxial and pleural furrows, small axial nodes, and no large axial spine. *Hebediscus*⁵⁵ is a highly effaced genus that lacks occipital, axial and marginal spines, as well as a wide, well-defined anterior border.

Ekvipagetia rasettii n. sp.

Pl. 40, figs. 12-20; Pl. 41, figs. 1-2; Text-fig. 22

Diagnosis: A species of *Ekvipagetia* with glabella long and narrow. Scrobicules weakly developed. Preglabellar field with depression anterior to glabella. Ocular furrow shallow. Pygidium with 7 pairs of marginal spines. 1st axial ring furrow deep marginally, shallow medially; 2nd through 4th ring furrows developed only as marginal indentations. Axial spine originates on the 3rd to 4th axial rings.

⁵⁵ Shaw (1950) synonymized the type species of *Hebediscus* Whitehouse, 1936 with the type species of *Diapharus* Clark, 1923. The latter was erected on a meraspid cephalon from a pebble found on Revere Beach, Massachusetts. It is questionable whether both species are from the same horizon, and if the immature cephalon belongs to the holaspids attributed to *Hebediscus*. *Diapharus* is therefore an unrecognizable eodiscid, and the name *Hebediscus* is valid. This is comparable to the taxonomy followed by Fritz (1973), Rasetti (1972) and Jell (1975)

Holotype: A complete pygidium (LACMIP 12672; Pl. 40, figs. 15, 19) from the Poleta Formation, section GP, LACMIP collection 17674, Mt. Dunfee area, 7 km east of Gold Point, Esmeralda County, Nevada. Paratypes: LACMIP 12620, 12622-12623

Etymology: In honour of Franco Rasetti, for his extensive contributions on Cambrian trilobites.

Occurrences: NEVADA. Poleta Formation, section GP, Mt. Dunfee area, 7 km east of Gold Point, Esmeralda County.

Zonal Biostratigraphy: *Gabriellus poletensis* Subzone, *Elliptocephala* Zone.

Discussion: *Ekwipagetia rasettii* is the only eodiscoid known from the thesis area. It occurs in a single studied section (near Gold Point, Nevada) but has also been observed by the author to the north in the Fish Lake Section of W.H. Fritz (work in progress), near Dyer. *E. rasettii* differs from the type species in having: a longer, narrower glabella; faint scrobicules on the anterior cephalic border; a shallow ocular furrow; a first axial ring furrow on the pygidium that crosses the axis, and a more anteriorly positioned pygidial axial spine. The axial spine position is somewhat variable with the anterior portion of the spine base originating on the third to fourth axial ring. *E. marginata* (Rasetti, 1967), from the Taconic sequence of New York, is known from only a single cranidium that shares with *E. rasettii* a long slender glabella and depression in the preglabellar field immediately anterior to the glabella. It differs in having deep ocular furrows and a slightly shorter anterior cephalic border that lacks scrobicules.

Neocobboldia spinosa Palmer, 1968 has a pygidium that is closely comparable to that of *Ekwipagetia rasettii* in having a single axial ring furrow that crosses the axis, a large axial spine originating from segments three and four, and no pleural furrows. The pygidium differs from that of *E. rasettii* in being proportionately shorter and having only three pairs of marginal spines that are posterolaterally positioned. The cranidium also has a tapered glabella with a long occipital spine and marginal S0's, but has more evenly inflated fixigenae and a cephalic border that is short, lacks an epiborder furrow and is not inflated. The type species of *Neocobboldia*, *N. dentata* (Lermontova, 1940) lacks an occipital spine, pygidial axial spine, and has a furrowed pygidial axis and pleural field. *N. spinosa* Palmer has characteristics of both *Neocobboldia* and *Ekwipagetia* and is herein considered of uncertain generic assignment.

Order Unassigned

Family Oryctocephalidae Beecher, 1897

[*nom. transl.* Rasetti, (*in* Moore, 1959) (*ex. Oryctocephalinae* Beecher, 1897)]

Diagnosis: (after Rasetti (*in* Moore, 1959) and Whittington (1995)) A family of Corynexochida with S1 though S3 developed as isolated pits. Preglabellar field absent. Glabella parallel-sided to expanding forward slightly. S0 transglabellar. Fixigenae typically wide. Ocular ridges typically well-developed. Thorax of 5 to 18 segments. Micropygous to isopygous. Pygidium lacks border and border furrow: pleural and interpleural furrows extend to pygidial margin.

Included Subfamilies: Oryctocephalinae Beecher, 1897; Oryctocarinae Hupé, 1955.

Discussion: In most of the recent taxonomic treatments, oryctocephalid trilobites have been classified as Corynexochida as they share the characteristic of a fused rostral-hypostomal plate. Bergström (1973b, p. 38) however, questioned assignment of the oryctocephalids to the Corynexochida on the basis that they were "habitually dissimilar from other corynexochids and may have (had) a different origin". Palmer (*in* Palmer and Halley, 1979) noted that oryctocephalids were as different from other Corynexochida as they were from Ptychopariida. Opik (1982) claimed that like the Ptychopariida, oryctocephalids have only three pairs of glabellar furrows, while there are four pairs in dolichometopids. This cannot be substantiated. Like dorypygines, oryctocephalids have an S4 pair that are small, marginal and easy to overlook in many species.

Corynexochids and ptychopariids share a similar ontogeny (Robison, 1967), but glabellar shape differs between members of the two groups in the meraspid stage. Meraspids of oryctocephalids (Table 16) do not have the characteristic corynoid glabella seen in other Corynexochida.

Oryctocephalids also have a different hypostomal structure (see examples in Shergold, 1969) than other corynexochids: they have strong rather than weak maculae, no pair of spines opposite of the maculae and consequently no constriction anterior to the spines with a resultant different overall shape. Fusion of the hypostome to the rostral plate in oryctocephalids may therefore be a sympleisiomorphic character with corynexochids, rather than a synapomorphy. At least some Oryctocephalids may have also had fused connective sutures (Rasetti, 1952; Shergold, 1969). In conclusion, oryctocephalids share features with both the Corynexochida and Ptychopariida, and more detailed comparison of oryctocephalid morphology with that of other Corynexochida is needed for resolution of relationships.

Whittington (1995) is followed for subdivision of the oryctocephalids into two subfamilies: the Oryctocephalinae that have genal and pleural spines and the Oryctocarinae that lack such spines. See Shergold (1969) and Chang (1980) for an alternative subdivision of the Oryctocephalidae into additional subfamilies.

Subfamily Oryctocephalinae Beecher, 1897

Diagnosis: (after Whittington, 1995) A spiny subfamily of Oryctocephalidae with pleural thoracic spines, marginal pygidial spines and genal spines. Facial sutures opisthoparian.

Assigned Genera: *Oryctocephalus* Walcott, 1886; ?*Tonkinella* Mansuy, 1916; *Oryctocephalites* Resser, 1939; *Oryctocephalina* Lermontova, 1940; *Lancastria* Kobayashi, 1935; *Oryctocephalops* Lermontova, 1940; ?*Goldfieldia* Palmer, 1964; *Protoryctocephalus* Zhang *et al.*, 1980.

Discussion: Only two genera of oryctocephalids are known from the thesis area. *Goldfieldia* (see Palmer, 1964) is known only from cranidia making subfamily assignment tentative. *Lancastria* is assigned to the Oryctocephalinae following Whittington (1995) instead of to the Lancastriinae Kobayashi, 1935. One of the prime uniting features of the Lancastriinae as diagnosed by Shergold (1969) was a micropygous pygidium. As is demonstrated below, the type species, *L. rodlyi*, has a multisegmented pygidium with a low degree of fusion of the segments. The Lancastriinae is therefore invalidated as a micropygous subfamily and synonymized with the Oryctocephalinae. The Oryctocephalinae are all spiny trilobites that share similar cephalic features.

Genus *Lancastria* Kobayashi, 1935

Type Species: *Olenopsis rodlyi* Walcott, 1912a from the Kinzers Formation, near Fruitville, Lancaster County, Pennsylvania. (by original designation)

Diagnosis: A genus of Oryctocephalinae with glabella expanding forward slightly. Cephalic border narrow. S1-S3 typically developed as deep slots rather than pits. S1 transglabellar as a shallow furrow. S4 developed close to glabellar furrow. Ocular ridges strong. Ocular lobes long. Thorax of 12 or more segments. Pygidium multisegmented with low degree of fusion.

Other Species:

Oryctocephalites incertus Chernysheva, 1960; Siberian Platform.

[?] *Oryctocephalops frischenfeldi* Lermontova (in Vologdin, 1940); Siberian Platform.

Discussion: *Lancastria* was erected as a monotypic genus of the family Lancastridae (order unknown) by Kobayashi (1935, p. 129) who considered that *Lancastria* "has a cephalon of the Oryctocephalidae and a thorax and pygidium of the Paradoxidae". The resemblance to the Paradoxidae is superficial. The type species of *Lancastria* actually has a large, poorly fused pygidium, as demonstrated by Whittington (1995), in which the anterior segments closely resemble thoracic segments. *Lancastria* is remarkable in its glabellar furrows that are more slot-like rather than pit-like than those of most other genera of Oryctocephalinae. The pygidium is poorly developed, either as a small plate or as a larger structure of poorly fused segments.

Oryctocephalites incertus Chernysheva 1960 from the Siberian Platform is here assigned to *Lancastria*. It is closely comparable in cranidial features to *L. roddyi* and has a pygidium of three poorly fused segments plus a terminal piece (see Chernysheva, 1962, pl. 3, figs. 7-10). *Oryctocephalops frischenfeldi* Lermontova (in Vologdin, 1940) is tentatively assigned to *Lancastria*. It has the same cranidial features as *L. roddyi* and *L. incertus*, 12 thoracic segments and a small pygidium of one segment plus a terminal piece. Articulating half rings are visible for all 12 segments plus the pygidium (see Chernysheva, 1962, pl. 3, fig. 14). If *Oryctocephalops frischenfeldi* Lermontova, the type species of *Oryctocephalops*, is accepted as a species of *Lancastria*, then the genus *Oryctocephalops* becomes a junior synonym of *Lancastria*. *Oryctocephalina lancastrionides* Shergold, 1969 was assigned by Whittington (1995) to *Lancastria*. This species is closely comparable to *L. roddyi* in thoracic shape with 14 thoracic segments and three thoracic-like segments plus a terminal piece incorporated into the pygidium⁵⁶. Its glabellar furrows are different from those of *Lancastria* as they are pit-like instead of slot-like. The type species of *Oryctocephalina*, *O. reticulata* from Siberia, also has glabellar furrows that are pit-like, but the thorax and pygidium are unknown. *Oryctocephalina* is regarded as a closely related genus to *Lancastria* that differs in the nature of the glabellar furrows. The original generic designation of *O. lancastrionides* is preferred.

Lancastria roddyi (Walcott, 1912a)

Pl. 41, figs. 3, 6

1912a *Olenopsis roddyi* Walcott, p. 244-246, pl. 36, fig. 1.

⁵⁶ Shergold (1969) interpreted the pygidium as containing only the terminal piece, but in pl. 12, figs. 1, 2 (of Shergold) axial rings are not visible for the last two segments. The axial ring associated with the third from last segment is interpreted as the pygidial axial ring.

- 1935 *Lancastria roddyi*, Kobayashi, p. 129.
 1938 *Lancastria roddyi*, Resser and Howell, p.229, pl. 10, fig. 3.
 1959 *Lancastria roddyi*, Rasetti (in Moore, 1959), O220, text-fig. 162.4.
 1969 *Lancastria roddyi*, Shergold, p. 46-47, pl. 11, fig. 4.
 1995 *Lancastria roddyi*, Whittington, p. 552-555, pl. 3, figs. 1-5, text-fig. 1.

Diagnosis: A species of *Lancastria* with wide fixigenae. Ocular lobes large. Posterior limbs narrow. Genal spines long. Thorax likely of 12 segments with long pleural spines. Pygidium of up to 7 diffusely fused segments plus a terminal piece.

Holotype: A nearly complete specimen (USNM 58363; Walcott, 1912a, pl. 36, fig. 1; Whittington, 1995, pl. 3, figs. 2,5) from the Kinzers Formation, 3.2 km north of Lancaster, Lancaster County, Pennsylvania.

Occurrences: PENNSYLVANIA. Kinzers Formation, Lancaster County: locality 12w (Walcott, 1912a, p. 246), 3.2 km north of Lancaster; 800 m south of East Petersburg and Donnerville Quarry (Whittington, 1995, p. 554). NEVADA. Saline Valley Formation: section PC, Paymaster Canyon, 21 km northeast of Silver Peak, Esmeralda County.

Zonal Biostratigraphy: *Olenellus transtans* Zone.

Discussion: Whittington (1995) provided a detailed description of *Lancastria roddyi* and little can be added from the two, highly flattened cranidia from Nevada. They are morphologically indistinguishable from the type material and have the characteristic broad fixigenae of the species. These Nevada specimens are significant as they are the first recorded occurrence of this species outside of the Kinzers Formation of Pennsylvania. Campbell and Kauffman (1969) noted that *L. roddyi* is very rare in the Kinzers Formation and the same is true in the Saline Valley Formation.

Whittington (1995) reillustrated the holotype of *Lancastria roddyi* in addition to two new specimens. Walcott (1912a) and Shergold (1969) considered there to be 19 thoracic segments and a small pygidium, but Whittington (1995) observed that traces of articulating half rings could only be observed on segments 1-12. Whittington concluded that the first 12 segments likely made up the thorax and the rest were part of the pygidium. This means that the pygidium in this species is not a small plate, as previous authors had thought, but rather is a large, diffusely fused plate with long pleural spines as in the thorax. The two articulated specimens that Whittington

(1995, pl. 3) illustrated have different numbers of segments in the pygidial region: 7 plus a terminal piece in the holotype; 4 plus a terminal piece in the other. The specimens are approximately the same size and Whittington did not comment on the significance of these differing numbers of segments in specimens of the same species.

Order Unassigned

Family Cheiruroideidae Chang, 1963

Genus *Cheiruroides* Kobayashi, 1935

Type Species: *Atops orientalis* Resser and Endo (in Kobayashi, 1935) from the Manto Formation of Jinxian, Liaodong Peninsula, China.

Discussion: *Cheiruroides* was initially assigned by Kobayashi, 1935 to the Pagodiidae, but was included in the Oryctocephalidae by Rasetti (in Moore, 1959), Chernysheva (1960, 1962), Suvorova (1964) and Shergold (1969). Chang (1963) did a detailed comparison of *Cheiruroides* with other trilobites assigned to the Oryctocephalidae. He found significant differences and established a separate family for *Cheiruroides* and related genera (see also Chang, 1980). Chang and Jell (1987) provided a detailed discussion of the genus and reviewed the species assigned to it.

Cheiruroides? sp. 1

Pl. 41, figs. 4-5

Occurrences: NEVADA. Saline Valley Formation, Esmeralda County: section PC, Paymaster Canyon, 21 km northeast of Silver Peak.

Zonal Biostratigraphy: *Olenellus transitans* Zone.

Discussion: Three fragmentary cranidia from the Saline Valley Formation, section PC (LACMIP collection 26849), Nevada are tentatively assigned to *Cheiruroides*. Superficially, these specimens resemble dorypygine trilobites in the long, parallel-sided glabella, but the glabellar furrows are deep, and S1 is transglabellar. S2 to S3 are marginal and S1 are connected by a moderately deep furrow. Only three pairs of glabellar furrows can be distinguished. This is typical of the arrangement of glabellar furrows in *Cheiruroides*. The cranidia are covered with large tubercles evenly interspersed with small tubercles.

Order Unassigned
Family Protypidae
Genus *Protypus* Walcott, 1886

Type Species: *Angelina hitchcocki* Whitfield, 1884 from the Parker Formation, Parker's Quarry, near Georgia, Franklin County, Vermont. (by original designation) Illustrated in Shaw (1955, pl. 74, fig. 9).

Diagnosis: (modified from Rasetti *in* Moore, 1959) A genus of unassigned micropygous Trilobita with glabella large, inflated, pear-shaped to suboval. Anterior border well-developed.

Preglabellar field absent: glabella reaches anterior border or furrow. S0 transglabellar. S1-S4 not apparent. Occipital ring short. Fixigenae moderately narrow. Ocular ridges low. Ocular lobes of low convexity, curved. Facial sutures divergent to parallel anteriorly. Posterior limbs moderately long, broad, downsloping. Thorax of 12 segments with blunt pleural spines. Pygidium short, wide, with short axis and no border.

Other Species:

Solenopleura?? tumida Walcott, 1887; Schodack Fm., ?North Greenwich, N.Y.

Bicaspis typica Resser, 1938; boulders in Lévis Fm., Bic, Quebec.

Bicaspis austincillensis Resser, 1938; Shady Fm., Austinville, Virginia.

Protypus marginatus Rasetti, 1948; boulders in Lévis Fm., Bic, Quebec.

Protypus reticulatus Rasetti, 1948; boulders in Lévis Fm., Bic, Quebec.

Protypus acquabilis Suvorova, 1964; Siberia.

Protypus inflatus n. sp.; Saline Valley, Fm., Paymaster Canyon, Nevada.

Species Inadequate for evaluation:

Protypus orientalicus Repina *in* Okuneva and Repina, 1973; Primorye, Russia.

Discussion: *Protypus* is an unusual trilobite that seems to have a dorypygine cranidium and a small ptychopariid pygidium. There is no question that the two parts are correctly associated since the type species is based on an articulated specimen. Rasetti (*in* Moore, 1959) described the glabella as "pear-shaped": it is strongly rounded, widest at about 1/3 to 1/2 the glabellar length and narrows anteriorly. This is different from the glabellar form of *Bonnia* which is nearly parallel-sided in large specimens. Other parts of the exoskeleton are poorly known. A single poorly-preserved hypostome was illustrated for *P. typicalus* (Resser, 1938, pl. 2, fig. 19). It is a large, tumid plate with large anterior wings, typical of the type found in dorypygines with fused

rostral-hypostomal plates. Unlike the hypostomes of dorypygines, it tapers posteriorly. No ontogenetic material is known for this genus to determine if it retained a corynoid glabella through the meraspid stage. Hupé (1953b) assigned *Protypus* to the monotypic family Protypidae of the Corynexochida. Rasetti (in Moore, 1959) listed *Protypus* under the "Order and Family Uncertain", though he stated that it was possibly related to the Ellipsocephalidae. There is a general similarity between *Protypus* and *Hicksia*, a Lower Cambrian genus from Portugal of the monotypic family Hicksiidae, superfamily Paradoxidacea. Both genera have a rounded, unfurrowed glabella, a small, wide pygidium and many thoracic segments, but these similarities are of unknown significance. *Protypus* is best regarded as a genus of unknown affinities that may be part of a basal Corynexochida/Ptychopariida clade.

Protypus hitchcocki (Whitfield, 1884), the type species, is known only from the holotype, a complete articulated specimen, from the Parker Formation of Vermont. Resser and Howell (1938) criticized the accuracy of Walcott's (1886, pl. 31, fig. 4) illustration of the holotype, but did not provide a photograph. Shaw (1955, pl. 74, fig. 9) provided an unretouched photograph of a cast of the holotype. The holotype is listed as missing (Rasetti, 1948; Shaw, 1955), but a cast of the specimen (USNM 15424) is retained by the USNM.

Bicaspis Resser, 1938 was established by Resser (1938, p. 61-62) for "peculiar trilobites... with a tumid cranidium, a peculiar short pygidium and a peculiar hypostoma" with *B. typica* Resser, 1938 from limestone boulders in the Lévis Formation, Quebec, as the type species. Rasetti (1948) synonymized *Bicaspis* Resser, 1938 with *Protypus* on the basis that "allowing for the different manner of preservation, there is no significant difference in the cranidial and pygidial features" between the type species of each genus.

Solenopleura?? tumida Walcott, 1887 from ?New York was assigned to *Fordaspis* by Lochman (1956) who provided a detailed history of the species. It is known from only the holotype specimen, which is strongly rounded in glabellar shape, like that of *Protypus*, and unlike the parallel-sided glabella of the type species of *Fordaspis*. It also lacks a preglabellar field, like *Protypus*, and unlike the type species of *Fordaspis*. It is most likely a species of *Protypus* and shares a highly inflated glabella with *P. inflatus* n. sp. *Fordaspis* differs from *Protypus* in having a large pygidium typical of that of the Dorypyginae.

Protypus can also be found outside of Laurentia in Lower Cambrian strata of the Siberian Platform. *P. aequabilis* Suvorova, 1964 is closely comparable to Laurentian species of *Protypus*. *P. tyrginicus* Repina, 1964 and *P. orientalicus* Repina in Okuneva and Repina, 1973 are based on

material too poor for evaluation. Illustrations of *P. carus* Repina, 1960, *P. tyrginicus* Repina, 1964 and *P. rotundatus* Repina, 1964 were not available to the author and are not discussed. All Siberian specimens of *Protypus* are based exclusively on cranidia.

Protypus inflatus n. sp.

Pl. 41, figs. 7-11

Diagnosis: A species of *Protypus* with glabella highly inflated. Anterior border furrow deep. Ocular lobes tilted dorsally, long: more than 1/4 length cranium. Occipital ring possibly with median spine or node. Prosopon of terrace lines on glabella, fine tubercles on fixigenae.

Holotype: A fragmentary cranidium (LACMIP 12632; Pl. 41, fig. 7) from the Saline Valley Formation, section PC, LACMIP collection 26849, Paymaster Canyon, Esmeralda County, Nevada. Paratype: LACMIP 12633

Etymology: From the Latin word "inflatus" (masculine, singular) meaning "swollen, puffed up", for the extreme inflation of the glabella in this species.

Occurrences: NEVADA. Saline Valley Formation: section PC, Paymaster Canyon, 21 km northeast of Silver Peak, Esmeralda County.

Zonal Biostratigraphy: *Olenellus transiens* Zone.

Discussion: *Protypus inflatus* n. sp. has the most strongly inflated glabella of any species of *Protypus*. The glabella of *P. tumidus* (Walcott, 1887) approaches it in convexity, but is more evenly inflated. The glabella of *P. inflatus* reaches maximum inflation at about midlength. The ocular lobes of *P. inflatus* are long and curved as well as flat, as is typical for the genus, but they are tilted strongly dorsally giving a false impression of convexity. The prosopon of this species is well-developed, similar to, though different in nature from, *P. reticulatus* Rasetti (1948). Most other species have a smooth external surface. This is the first record of *Protypus* from western North America.

Chapter 7. Conclusions

Through the course of this work, new trilobite faunas are described from southeastern British Columbia and the southwestern Great Basin. Many changes are made to the taxonomy of Lower Cambrian trilobites. The changes are summarized below along with the major evolutionary and systematic observations resultant from ontogenetic studies.

- Ontogenetic features and ventral morphology are important diagnostic characters of suprageneric taxa. Distinctive meraspid forms characterize families of Olenellina. Hypostome attachment conditions vary between genera of the Corynexochidae.
- The Wanneriidae is distinguished from the Olenellidae based on ontogenetic pattern and select holaspid features. *Laudonia*, *Mummaspis*, *Gabriellus*, *Mesolenellus* and *Elliptocephala*, genera previously assigned to other families, are here assigned to the Wanneriidae. A new genus *Wannerellus*, is established for species that have the diagnostic features of the Wanneriidae, but have some unusual features typical of *Olenellus*.
- The generic concept of *Olenellus* is re-evaluated and restricted to those species closely comparable to the type. Many of the older species previously assigned to *Olenellus* are reassigned to the wanneriids *Elliptocephala* and *Wannerellus*.
- The Biceratopsinae is considerably revised. The Bristolinae is synonymized with the Biceratopsinae and of the assigned genera: *Biceratops* is synonymized with *Peachella*; *Arcuolenellus* is synonymized with *Nephrolenellus*; and *Bolbolenellus* is assigned to the Olenellinae.
- The Mesonacinae is a peramorphic subfamily of the Olenellidae.
- The Dorypygidae (= Ogygopsidae) is reduced in taxonomic rank to subfamily and assigned to the Corynexochidae. The Corynexochinae are paedomorphically altered compared to the Dorypyginae.
- A fused rostral-hypostomal plate is not a diagnostic feature of the Corynexochida: it is a paedomorphic feature characteristic of many younger families of Corynexochida and some genera of the Corynexochidae.

- Heterochrony is a major pattern of evolutionary change in Lower Cambrian trilobites. Peramorphosis is documented in the Mesonacinae and in *Wanneria*; paedomorphosis is documented in *Laudonia* and in the Corynexochinae.
- Membership in the Antagminae, a subfamily of small, primitive ptychopariids, comprises genera that are so similar morphologically that they cannot be diagnosed or objectively distinguished one from another. The Antagminae is abandoned (genera assigned to the Ptychopariidae) and most of the previously assigned genera are placed in synonymy with the senior synonym, *Proliostracus*.

Four successive biostratigraphic zones are described for the medial Lower Cambrian of Laurentia, each subdivided into new species-based subzones. All zones are newly-defined, despite previous usage of some names. These zones and subzones can be correlated with shelf successions throughout Laurentia. This is the first usage of species-based, explicitly defined subzones and zones, that is intended to replace the genus-based zonation of Fritz (1972).

Lower Cambrian trilobite assemblages of the continental shelf are of low taxonomic diversity. All shelf deposits contain Olenellina and a single biostratigraphic scheme focused on the Olenellina is applicable for all Lower Cambrian shelf facies of Laurentia. Biofacies differentiation is minimal in the *Nevadella* and *Elliptocephala* zones. The *Gabriellus poletensis* Subzone has an incursion of pandemic trilobites, atypical of the endemic faunas of the continental shelf. These biofacies are interpreted as deposits of an open rather than restricted shelf. The *Olenellus transitans* Zone has strong biofacies differentiation. Olenelloids are present in most shelf facies, but in carbonate rocks, *Bonnia* is overwhelmingly abundant. Outer shelf or open shelf deposits are characterized by higher diversity faunas and the presence of *Ogygopsis*.

Literature Cited

- AHLBERG, P. and BERGSTRÖM, J. 1978. Lower Cambrian ptychopariid trilobites from Scandinavia. *Sveriges Geologiska Undersökning*, 49. 41 pp.
- , ----- and JOHANSSON, J. 1986. Lower Cambrian olenellid trilobites from the Baltic Faunal Province. *Geologiska Föreningens i Stockholm Förhandlingar*, 108(1), pp. 39-56.
- AITKEN, J.D. 1966. Middle Cambrian to Middle Ordovician cyclic sedimentation, southern Rocky Mountains of Alberta. *Canadian Petroleum Geology Bulletin*, 14, pp. 405-441.
- 1969. Documentation of the sub-Cambrian unconformity, Rocky Mountains main ranges, Alberta. *Canadian Journal of Earth Sciences*, 6(2), pp. 193-200.
- and MCMECHAN, M.E. 1991. Chapter 5. Middle Proterozoic assemblages. *In* Gabrielse, H. and Yorath, C.J. (eds.). *Geology of the Cordilleran Orogen in Canada*. Geological Survey of Canada, *Geology of Canada*, 4, pp. 97-124.
- ALBERS, J.P. and STEWART, J.H. 1962. Precambrian (?) and Cambrian stratigraphy in Esmeralda County, Nevada. *United States Geological Survey Professional Paper*, 450-D. 24 pp.
- and ----- 1972. *Geology and mineral deposits of Esmeralda County, Nevada*. Nevada Bureau of Mines and Geology Bulletin, 78. 80 pp.
- ALPERT, S.P. 1976a. Trilobite and star-like trace fossils from the White-Inyo Mountains, California. *Journal of Paleontology*, 50(2), pp. 226-239.
- 1976b. Trace fossils of the White-Inyo Mountains. *Pacific Coast Paleogeography Field Guide 1*. Society of Economic Paleontology and Mineralogy, pp. 43-48.
- BABCOCK, L.E. 1994. Systematics and phylogenetics of polymeroid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Grønlands Geologiske Undersøgelse Bulletin*, 169, pp. 79-127.
- BAER, K.E. von. 1828. *Entwicklungsgeschichte der Thiere: Beobachtung und Reflexion*. Bornträger, Königsberg. 264 pp.
- BARRANDE, J. 1861. Documents anciens et nouveaux sur la faune primordiale et le Systeme Taconique en Amérique. *Geological Society of France Bulletin*, ser. 2, 13, pp. 203-321.
- BELL, G.K. 1931. The disputed structures of the Mesonacidae and their significance. *American Museum Novitates*, 475, pp. 1-23.
- BENGTSON, S., CONWAY MORRIS, S., COOPER, B.J., JELL, P.A. and RUNNEGAR, B.N. 1990. Early Cambrian fossils from South Australia. *Association of Australasian Palaeontologists Memoir*, 9, Brisbane, Australia. 364 pp.
- BERGSTRÖM, J. 1973a. Classification of olenellid trilobites and some Balto-Scandian species. *Norsk Geologisk Tidsskrift*, 53(3), pp. 283-314.
- 1973b. Organization, life, and systematics of trilobites. *Fossils and Strata*, 2. 69 pp.

- BERRY, W.B.N. 1968. Growth of a Prehistoric Time Scale. W.I. Freeman and Co., San Francisco, California. 158 pp.
- BEST, R.V. 1952. Two new species of *Olenellus* from British Columbia. Transactions of the Royal Society of Canada, 46(3), pp. 13-22.
- 1959. Taxonomic revision of North American olenellid trilobites. Unpublished Ph.D. dissertation, Princeton University, Princeton, New Jersey.
- BLAKER, M.R. 1988. A new genus of nevadiid trilobite from the Buen Formation (Early Cambrian) of Peary Land, central North Greenland. Grønlands Geologiske Undersøgelse Rapport, 137, pp. 33-41.
- , NELSON, C.A. and PEEL, J.S. 1996. *Perissopyge*, a new trilobite from the Lower Cambrian of Greenland and North America. Journal of the Czech Geological Society, 41(3/4), pp. 209-216.
- BOHACH, L.L. 1995. A revision of the Lower Cambrian trilobite family Wanneriidae. Program and Abstracts, Geological Association of Canada/Mineralogical Association of Canada. Annual Meeting, Victoria, May 17-19, p. A-8.
- 1996. Homeomorphy in Lower Cambrian olenelloid trilobites. Program and Abstracts, International Symposium on the Relationships of Major Arthropod Groups, Natural History Museum, London, England, April 17-19, p. 25.
- BOND, G.C., CHRISTIE-BLICK, N., KOMINZ, M.A. and DEVLIN, W.J. 1985. An early Cambrian rift to post-rift transition in the Cordillera of western North America. Nature, 315, pp. 742-746.
- , NICKESON, P.A. and KOMINZ, M.A. 1984. Breakup of a supercontinent between 625 Ma and 555 Ma: new evidence and implications for continental histories. Earth and Planetary Science Letters, 70, pp. 325-345.
- BOWRING, S.A., GROTZINGER, J.P., ISACHSEN, C.E., KNOLL, A.H., PELECHATY, S.M. and KOLOSOV, P. 1993. Calibrating Rates of Early Cambrian Evolution. Science, 261, pp. 1293-1298.
- BRASIER, M.D. and COWIE, J.W. 1989. Other areas: northwest Canada; California, Nevada, and Mexico; Morocco, Spain and France. In Cowie, J.W. and Brasier, M.D. (eds.). The Precambrian-Cambrian boundary. Clarendon Press, Oxford, England. pp. 105-114.
- CAMPBELL, L. and KAUFFMAN, M.E. 1969. *Olenellus* fauna of the Kinzers Formation, southeastern Pennsylvania. Proceedings of the Pennsylvania Academy of Science, 43, pp. 172-176.
- CHANG, W.T. 1963. Classification of the Lower and Middle Cambrian trilobites from north and northwestern China, with descriptions of new families and new genera. Acta Palaeontologica Sinica, 11(4), pp. 447-491.
- 1980. On the Miomera and Polymera (Trilobita). Scientia Sinica, 23(2), pp. 223-234.
- and JELL, P.A. 1987. Cambrian Trilobites of North China: Chinese Cambrian trilobites housed in the Smithsonian Institution. Science Press, Beijing, China. 459 pp.

- CHATTERTON, B.D.E., SIVETER, D.J., EDGECOMBE, G.D. and HUNT, A.S. 1990. Larvae and relationships of the Calymenina (Trilobita). *Journal of Paleontology*, 64(2), pp. 255-277.
- and SPEYER, S.E. 1990. Applications of the study of trilobite ontogeny. *In* Culver, S.J. (ed.). *Arthropod paleobiology. Short Courses in Paleontology 3*, The Paleontological Society, pp. 116-136.
- CHERNYSHEVA, N.E. (editor) 1960. Chlenistonogie, Trilobitoobraznye i Rakoobraznye (Arthropoda: Trilobitomorpha and Crustacea). *Osnovy Paleontologii* (Fundamentals of Paleontology). Akademiia Nauk SSR Ministerstvo Geologii i Okhrang Nedr SSSR, Moscow. 515 pp. [in Russian]
- 1962. Kembriyskie trilobity semeistva Oryctocephalidae. (Cambrian trilobites of the family Oryctocephalidae). *In* Shvedov, N.A. (ed.). *Problems of oil and gas occurrence in the Soviet Arctic, paleontology and biostratigraphy*, 3. *Trudy Nauchnoissledovatel'skii Geologii Institut Arktiki (NIIGA)*, 127, pp. 1-64. [in Russian]
- COLPRON, M. and PRICE, R.A. 1995. Tectonic significance of the Kootenay terrane, southeastern Canadian Cordillera: an alternative model. *Geology*, 23(1), pp. 25-28.
- CONDIE, K.C. and ROSEN, O.M. 1994. Laurentia-Siberia connection revisited. *Geology*, 22(2), pp. 168-170.
- COPELAND, M.J. 1993. *Anomalocaris* (of unknown affinity) and *Tuzoia* (a possible arthropod) from the Lower Cambrian Eager Formation, near Cranbrook, British Columbia. *Contributions to Canadian Paleontology, Geological Survey of Canada Bulletin*, 444, pp. 1-5.
- COWIE, J.W. 1968. Lower Cambrian faunas from Ellesmere Island, District of Franklin. *Geological Survey of Canada Bulletin*, 163, pp. 3-27.
- and BRASIER, M.D. (eds.) The Precambrian-Cambrian Boundary. *Oxford Monographs on Geology and Geophysics*, 12. Clarendon Press, Oxford, England. 213 pp.
- and MCNAMARA, K.I. 1978. *Olenellus* (Trilobita) from the Lower Cambrian strata of north-west Scotland. *Palaeontology*, 21(3), pp. 615-634.
- CREWS, A.L. 1980. Sedimentology of a Lower Cambrian marine shelf sequence: Zabriskie Quartzite, Saline Valley Formation, and related strata, southern Great Basin, U.S.A. Unpublished Ph.D. dissertation, University of California, Los Angeles, California. 152 pp.
- CRIMES, T.P. 1989. Trace fossils. *In* Cowie, J.W. and Brasier, M.D. (eds.). *The Precambrian-Cambrian Boundary*. Clarendon Press, Oxford, England, pp. 166-185.
- 1992. Changes in the trace fossil biota across the Proterozoic-Phanerozoic boundary. *Journal of the Geological Society of London*, 149, pp. 637-646.
- DALY, R.A. 1913. North American Cordillera, 49th parallel. *Geological Survey of Canada Memoir*, 38.
- DALZIEL, I.W.D. 1991. Pacific margins of Laurentia and east Antarctica-Australia as a conjugate rift pair: evidence and implications for an Eocambrian supercontinent. *Geology*, 19(6), pp. 598-601.

- DARWIN, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. J. Murray, London, England.
- DEISS, C. 1940. Lower and Middle Cambrian stratigraphy of southwestern Alberta and southeastern British Columbia. Geological Society of America Bulletin, 51, pp. 731-794.
- 1941. Cambrian geography and sedimentation in the central Cordilleran region. Geological Society of America Bulletin, 52, pp. 1085-1116.
- DEVLIN, W.J. 1989. Stratigraphy and sedimentology of the Hamill Group in the northern Selkirk Mountains, British Columbia: evidence for latest Proterozoic - Early Cambrian extensional tectonism. Canadian Journal of Earth Sciences, 26, pp. 515-533.
- and BOND, G.C. The initiation of the early Paleozoic Cordilleran miogeocline: evidence from the uppermost Proterozoic - Lower Cambrian Hamill Group of southeastern British Columbia. Canadian Journal of Earth Sciences, 25, pp. 1-19.
- DONG-CHAN, L. and CHATTERTON, B.D.E. 1996. Terminology of glabellar lobes in trilobite larvae based on homology. Journal of Paleontology, 70(3), pp. 439-442.
- EDGECOMBE, G.E., SPEYER, S.E. and CHATTERTON, B.D.E. 1988. Protaspid larvae and phylogenetics of encrinurid trilobites. Journal of Paleontology, 62(5), pp. 779-799.
- EMMONS, E. 1844. The Taconic System. Albany, New York. 67 pp.
- 1860. Manual of Geology. Second Edition, New York. New York.
- ERNST, W.G. 1996. Petrochemical study of regional/contact metamorphism in metaclastic strata of the central White-Inyo Range, eastern California. Geological Society of America Bulletin, 108, pp. 1528-1548.
- FELSENSTEIN, J. 1990. PHYLIP: phylogeny inference package. Version 3.3. University of Washington. (computer program and manual)
- FITCH, W.M. 1984. Cladistic and other methods: problems, pitfalls and potentials. In Duncan, T. and Stuessy, T.F. (eds.). Cladistics: perspectives on the reconstruction of evolutionary history. Columbia University Press, New York, New York. pp. 221-252.
- FORD, S.W. 1877. On some embryonic forms of trilobites from the primordial rocks at Troy, New York. American Journal of Science, 113, pp. 265-273.
- 1878. Note on the development of *Olenellus usaphoides*. American Journal of Science, 115, pp. 129-130.
- 1881. On additional embryonic forms of trilobites from the primordial rocks of Troy, New York, with observations on the genera *Olenellus*, *Paradoxides* and *Hydrocephalus*. American Journal of Science, 122, pp. 250-259.
- FOREY, P.L., HUMPHRIES, C.J., KITCHING, I.L., SCOTLAND, R.W., SIEBERT, D.J. and WILLIAMS, D.M. 1992. Cladistics. A Practical Course in Systematics. The Systematics Association Publication, 10, Clarendon Press, Oxford, England. 191 pp.
- FORTEY, R.A. 1990a. Ontogeny, hypostome attachment and trilobite classification. Palaeontology, 33(3), pp. 529-576.

- 1990b. Trilobite evolution and systematics. *In* Mikulic, D.G. (ed.). Arthropod paleobiology. Short Courses in Paleontology, 3, pp. 44-65.
- 1991. Fossils: the key to the past. Harvard University Press, Cambridge, Massachusetts. 187 pp.
- and CHATTERTON, B.D.E. 1988. Classification of the trilobite suborder Asaphina. *Palaeontology*, 31(1), pp. 165-222.
- and OWENS, R.M. 1978. Early Ordovician (Arenig) stratigraphy and faunas of the Carmarthen District, south-west Wales. *British Museum of Natural History Bulletin, Geology Series*, 30, pp. 225-294.
- and WHITTINGTON, H.B. 1989. The Trilobita as a natural group. *Historical Biology*, 2, pp. 125-138.
- FRITZ, W.H. 1968. Lower and early Middle Cambrian trilobites from the Pioche Shale, east-central Nevada, U.S.A. *Palaeontology*, 2(2), pp. 183-235.
- 1972. Lower Cambrian trilobites from the Sekwi Formation type section, Mackenzie Mountains, northwestern Canada. *Geological Survey of Canada Bulletin*, 212. 58 pp.
- 1973. Medial Lower Cambrian trilobites from the Mackenzie Mountains, northwestern Canada. *Geological Survey of Canada Paper*, 73-24. 43 pp.
- 1984. Uppermost Precambrian and Lower Cambrian strata, northern Omineca Mountains, north-central British Columbia. *Current Research, Part B, Geological Survey of Canada Paper*, 84-B, pp. 245-254.
- 1991a. Lower Cambrian trilobites from the Iltyd Formation, Wernecke Mountains, Yukon Territory. *Geological Survey of Canada Bulletin*, 409. 77 pp.
- 1991b. Cambrian Assemblages. *In* Gabrielse, H. and Yorath, C.J. (eds.). *Geology of the Cordilleran Orogen in Canada*. Geological Survey of Canada, *Geology of Canada*, 4, pp. 155-184.
- 1992. Walcott's Lower Cambrian olenellid trilobite collection 61K, Mount Robson Area, Canadian Rocky Mountains. *Geological Survey of Canada Bulletin*, 432. 65 pp.
- 1993. New Lower Cambrian olenelloid trilobite genera *Cirquella* and *Geraldinella* from southwestern Canada. *Journal of Paleontology*, 67(5), pp. 856-868.
- 1995. *Esmeraldina rowei* and associated Lower Cambrian trilobites (1f fauna) at the base of Walcott's Waucoban Series, southern Great Basin, U.S.A. *Journal of Paleontology*, 69(4), pp. 708-723.
- , NARBONNE, G.M. and GORDEY, S.P. 1983. Strata and trace fossils near the Precambrian-Cambrian boundary, Mackenzie, Selwyn and Wernecke mountains, Yukon and Northwest Territories. *Current Research, Part B, Geological Survey of Canada Paper*, 83-1B, pp. 365-375.
- and YOCHELSON, E.L. 1988. The status of *Salterella* as a Lower Cambrian index fossil. *Canadian Journal of Earth Sciences*, 25, pp. 403-416.

- GABRIELSE, H. and CAMPBELL, R.B. 1991. Chapter 6. Upper Proterozoic assemblages. *In* Gabrielse, H. and Yorath, C.J. (eds.). *Geology of the Cordilleran Orogen in Canada*. Geological Survey of Canada, *Geology of Canada*, 4, pp. 125-150.
- and YORATH, C.J. Chapter 18. Tectonic synthesis. *In* Gabrielse, H. and Yorath, C.J. (eds.). *Geology of the Cordilleran Orogen in Canada*. Geological Survey of Canada, *Geology of Canada*, 4, pp. 677-705.
- GEYER, G. 1994. Cambrian corynexochid trilobites from Morocco. *Journal of Paleontology*, 68(6), pp. 1306-1320.
- 1996. The Moroccan fallotaspide trilobites revisited. *Beringeria*, 18, pp. 89-199.
- and LANDING, E. (eds.) 1995. Morocco '95. The Lower-Middle Cambrian Standard of western Gondwana. Introduction, Field Guide, Abstracts and Proceedings of the First Conference of the Lower Cambrian Stage Subdivision Working Group and I.G.C.P. Project 366 Ecological Aspects of the Cambrian Radiation. *Beringeria Special Issue 2*, Würzburg. 269 pp.
- and PALMER, A.R. 1995. Neltneriidae and Holmiidae (Trilobita) from Morocco and the problem of early Cambrian intercontinental correlation. *Journal of Paleontology*, 69(3), pp. 459-474.
- GOULD, S.J. 1977. *Ontogeny and Phylogeny*. Belknap Press of Harvard University Press, Cambridge, Massachusetts and London, England. 501 pp.
- 1988. Chapter 1. The uses of heterochrony. *In* McKinney, M.L. (ed.). *Heterochrony in evolution: a multidisciplinary approach*. Plenum Press, New York, New York and London, England, pp. 1-13.
- 1989. *Wonderful Life. The Burgess Shale and the Nature of History*. W.W. Norton and Company, New York, New York, and London, England. 347 pp.
- HAECKEL, E. 1866. *Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie*. Georg Reimer, Berlin, Germany.
- HAHN, G. 1989. Reconstruction of the phylogenetic relationships among the higher taxa of trilobites. *Abhandlungen Naturwissenschaftlicher Verein in Hamburg*, 28, pp. 187-199.
- HARLAND, W.B., ARMSTRONG, R.L., COX, A.V., CRAIG, L.E., SMITH, A.G. and SMITH, D.G. 1990. *A Geological time Scale 1989*. Cambridge University Press, Cambridge, England and New York, New York. 263 pp.
- HARRINGTON, H.J. 1956. Olenellidae with advanced cephalic spines. *Journal of Paleontology*, 30(1), pp. 56-61.
- HENNIG, W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin, Germany.
- HOFFMAN, P.F. 1991. Did the breakout of Laurentia turn Gondwanaland inside-out? *Science*, 252, pp. 1409-1412.

- 1992. Supercontinents. *Encyclopedia of Earth System Sciences*, 4, Academic Press Incorporated, San Diego, California, pp. 323-327.
- HOWELL, B.F., BRIDGE, I., DEISS, C.F., EDWARDS, I., LOCHMAN, C., RAASCH, G.O. and RESSER, C.E. 1944. Correlation of the Cambrian formations of North America. *Geological Society of America Bulletin*, 55, pp. 993-1003.
- HU, C.-H. 1968. Notes on the ontogeny and sexual dimorphism of Upper Cambrian trilobites of the *Welleraspis* faunule from Pennsylvania. *Journal of the Nanyang University*, 2, pp. 321-357.
- 1971. Ontogeny and sexual dimorphism of Lower Paleozoic Trilobita. *Palaeontographica Americana*, 7(44), pp. 31-155.
- 1972. Ontogeny of three *Cedaria* Zone trilobites from the Upper Cambrian, Montana. *Transactions and Proceedings of the Palaeontological Society of Japan*, new ser., 85, pp. 245-259.
- 1978. Ontogenies of four Upper Cambrian trilobites from the Bonnetterre Dolomite, Missouri. *Transactions and Proceedings of the Palaeontological Society of Japan*, new ser., 111, pp. 348-357.
- 1979. Ontogenetic studies of a few Upper Cambrian trilobites from the Deadwood Formation, South Dakota. *Transactions and Proceedings of the Palaeontological Society of Japan*, new ser., 114, pp. 49-63.
- 1980. Ontogenies of a few Upper Cambrian trilobites from the Deadwood Formation, South Dakota. *Transactions and Proceedings of the Palaeontological Society of Japan*, new ser., 119, pp. 371-387.
- 1981. Studies on the ontogenetic and phylogenetic development of two Upper Cambrian trilobites from south Dakota. *Transactions and Proceedings of the Palaeontological Society of Japan*, new ser., 123, pp. 159-167.
- 1983. Ontogenetic and phylogenetic development of two Upper Cambrian trilobites from the Nolichucky Formation, Tennessee. *Transactions and Proceedings of the Palaeontological Society of Japan*, new ser., 129, pp. 26-34.
- 1984. Ontogenesis of *Ehmaniella burgessensis* Rasetti (Trilobita) from Burgess Shale, Middle Cambrian, Yoho Park, British Columbia. *Transactions and Proceedings of the Palaeontological Society of Japan*, new ser., 135, pp. 395-400.
- 1985a. Ontogenetic development of Cambrian Trilobites from British Columbia and Alberta, Canada (Part 1). *Journal of Taiwan Museum*, 38(2), pp. 121-158.
- 1985b. Ontogenies of two Middle Cambrian corynexochid trilobites from the Canadian Rocky Mountains. *Transactions and Proceedings of the Palaeontological Society of Japan*, new ser., 138, pp. 138-147.
- HUGHES, N.C. and CHAPMAN, R.E. 1995. Growth and variation in the Silurian proetide trilobite *Aulacopleura konincki* and its implications for trilobite palaeobiology. *Lethaia*, 28, pp. 333-353.

- HUNT, D.L. 1990. Trilobite faunas and biostratigraphy of the Lower Cambrian Wood Canyon Formation, Death Valley Region, California. Unpublished MSc. thesis. University of California, Davis, California. 104 pp.
- HUNT, T.S. 1883. The Taconic question in geology. Part I. Transactions of the Royal Society of Canada, 1(4), pp. 217-270.
- 1884. The Taconic question in geology. Part II. Transactions of the Royal Society of Canada, 2(4), pp. 125-157.
- HUPÉ, P. 1953a. Contribution a l'étude du Cambrien inférieur et du PréCambrien III de l'Anti-Atlas Marocain. Notes et Memoires du Division Géologiques. Service Géologiques, 103. 402 pp.
- 1953b. Classe des trilobites. In Piveteau, J. (ed.). Traité de Paléontologie. Masson et C, Paris, France. pp. 44-216.
- HUTCHINSON, R.D. 1962. Cambrian stratigraphy and trilobite faunas of southeastern Newfoundland. Geological Survey of Canada Bulletin, 88, 156 pp.
- HUTTON, J. 1785, 1802. Theory of the earth, with proofs and illustrations: 1 & 2: W. Creech, Edinburgh, England (1795); 3: Cadell and Davies, London, England (1802).
- IDNURM, M. and GIDDINGS, J.W. 1995. Paleoproterozoic-Neoproterozoic North America-Australia link: new evidence from paleomagnetism. Geology, 23(2), pp. 149-152.
- IVSHIN, N.K. 1978. Biostratigraphiya i Trilobity Nizhnego Kembriya tsentral'nogo Kazakhstana. (Biostratigraphy and trilobites of the lower Cambrian of central Kazakhstan). Kazakhstan Academy of Sciences, Nauk, Alma Ata.
- JAEKEL, O. 1909. Ueber die Agnostiden. Zeitschrift deutsche geologische Gesellschaft, 61, pp. 380-401.
- JELL, P.A. 1975. Australian Middle Cambrian eodiscoids with a review of the superfamily. Palaeontographica Abt. A, 150, pp. 1-97.
- and REPINA, L.N. 1992. Botomian olenellid trilobites from the Siberian Platform. Paleontological Journal, 26(1), pp. 156-160.
- JONES, D.S. 1988. Sclerochronology and the size versus age problem. In McKinney, M.L. (ed.). Heterochrony in evolution: a multidisciplinary approach. Plenum Press, New York, New York and London, England, pp. 93-108.
- KIAER, J. 1916. The Lower Cambrian *Holmia* fauna at Tømten in Norway. Videnskapsselskapets Skrifter 1. Matematisk-Naturvidenskapelig Klasse, 10. 140 pp.
- KINDLE, C.H. and TASCH, P. 1948. Lower Cambrian fauna of the Monkton Formation of Vermont. The Canadian Field-Naturalist, 62(5), pp. 133-139.
- KIRK, E. In A. Knopf. 1918. A geological reconnaissance of the Inyo Range and the eastern slope of the southern Sierra Nevada, California, with a section on the stratigraphy of the Inyo Range by Edwin Kirk. United States Geological Survey Professional Paper 110. 130 pp.

- KLUGE, A.G. 1984. The relevance of parsimony to phylogenetic inference. *In* Duncan, T. and Stuessy, T.F. (eds.). *Cladistics: perspectives on the reconstruction of evolutionary history*. Columbia University Press, New York, New York. pp. 24-38.
- 1985. Ontogeny and phylogenetic systematics. *Cladistics*, 1(1), pp. 13-27.
- KOBAYASHI, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen. *Palaeontology*. pt. III. The Cambrian faunas of South Chosen with a special study on the Cambrian trilobite genera and families. *Journal of the Faculty of Science, Imperial University of Tokyo*. II, 4(2), pp. 49-344.
- 1942. On the Dolichometopinae. *Journal of the Faculty of Science, Imperial University of Tokyo*. Section II, 6(10), pp. 141-206.
- 1972. Three faunal provinces in the early Cambrian Period. *Proceedings of the Japan Academy*, 48, pp. 242-247.
- LAKE, P. 1937. A monograph of the British Cambrian trilobites. pt. X. *Palaeontographic Society*.
- LANE, P.D. and THOMAS, A.T. 1983. A review of the trilobite suborder Scutelluina. *Special Papers in Palaeontology*, 30, pp. 141-160.
- LANDING, E. 1994. Precambrian-Cambrian boundary global stratotype ratified and a new perspective of Cambrian time. *Geology*, 22, pp. 179-182.
- LAUTERBACH, K.-E. 1980. Schlüsselereignisse in der evolution des grundplans der Arachnata (Arthropoda). *Abhandlungen Naturwissenschaftlicher Verein in Hamburg*, 23, pp. 163-327.
- 1983. Synapomorphien zwischen Trilobiten-und Cheliceraten-Zweig der Arachnata. *Zoologischer Anzeiger*, 210, pp. 213-238.
- 1989. Trilobites and phylogenetic systematics: a reply to G. Hahn. *Abhandlungen Naturwissenschaftlicher Verein in Hamburg*, 28, pp. 201-211.
- LEECH, G.B. 1954. Preliminary account, Canal Flats, British Columbia. *Geological Survey of Canada Paper*, 54-7. 32 pp.
- 1958a. Fernie map-area, west half, British Columbia. *Geological Survey of Canada Paper*, 58-10. 40 pp.
- 1958b. Canal Flats, Kootenay District, British Columbia. *Geological Survey of Canada, Map*, 24-1958.
- LERMONTOVA, E.V. 1951. Nejnekembriyskei trilobity i brahiopody Vostochnoy Sibiri. (Lower Cambrian trilobites and brachiopods from eastern Siberia). *Gesgeolizdat, Moskva*. 222 pp. [in Russian]
- LEVI-SETTI, R. 1993. *Trilobites*. Second Edition. University of Chicago Press, Chicago, Illinois and London, England. 342 pp.
- LEVY, M. and CHRISTIE-BLICK, N. 1991. Tectonic subsidence of the early Paleozoic passive continental margin in eastern California and southern Nevada. *Geological Society of America Bulletin*, 103, pp. 1590-1606.

- LICKORISH, W.H. and SIMONY, P.S. 1995. Evidence for late rifting of the Cordilleran margin outlined by stratigraphic division of the Lower Cambrian Gog Group, Rocky Mountain main ranges, British Columbia and Alberta. *Canadian Journal of Earth Sciences*, 32, pp. 860-874.
- LOCHMAN, C. 1947. Analysis and revision of eleven Lower Cambrian trilobite genera. *Journal of Paleontology*, 21(1), pp. 59-71.
- 1952. Trilobites. In Cooper, G.A., Arellano, A.R.V., Johnson, J.H., Okulitch, V.J., Stoyanow, A., and Lochman, C. *Cambrian stratigraphy and paleontology near Caborca, northwestern Sonora, Mexico*. Smithsonian Miscellaneous Collections, 119(1), pp. 60-161.
- 1956. Stratigraphy, paleontology, and paleogeography of the *Elliptocephala asaphoides* strata in Cambridge and Hoosick Quadrangles, New York. *Geological Society of America Bulletin*, 67, pp. 1331-1396.
- LOCHMAN-BALK, C. 1968. Cambrian paleoenvironments on the craton of the United States. *Proceedings of the IPU, XXIII International Geological Congress*. pp. 267-282.
- LUDVIGSEN, R. 1978. Middle Ordovician trilobite biofacies, southern Mackenzie Mountains. In Stelck, C.R. and Chatterton, B.D.E. (eds.) *Western and Arctic Canadian Biostratigraphy*. Geological Association of Canada Special Paper, 18, pp. 1-37.
- and WESTROP, S.R. 1983. Trilobite biofacies of the Cambrian-Ordovician boundary interval in northern North America. *Alcheringa*, 7, pp. 301-319.
- and ----- 1985. Three new upper Cambrian stages for North America. *Geology*, 13, pp. 139-143.
- , ----- and KINDLE, C.H. 1989. Sunwaptan (Upper Cambrian) trilobites of the Cow Head Group, western Newfoundland, Canada. *Palaeontographica Canadiana*, 6, 175 pp.
- , -----, PRATT, B.R., TUFFNELL, P.A. and YOUNG, G.A. 1986. Dual biostratigraphy: zones and biofacies. *Paleoscene 3*, Geoscience Canada, 13(3), pp. 139-154.
- LYELL, C. 1830-1833. *Principles of Geology*. J. Murray, London, England. (1: 1830; 2: 1832; 3: 1833).
- MADDISON, W.P., DONOGHUE, M.J. and MADDISON, D.R. 1984. Outgroup analysis and parsimony. *Systematic Zoology*, 33, pp. 83-103.
- and MADDISON, D.R. 1992. *MacClade: Analysis of phylogeny and character evolution*. Version 3.0. Sinauer Associates, Sunderland, Massachusetts. (computer program and manual)
- MAYR, E. 1942. *Systematics and the origin of species*. Columbia University Press, New York, New York. 334 pp.
- *Principles of Systematic Zoology*. McGraw-Hill, New York, New York. 428 pp.
- MCKEE, E.H. 1968. *Geology of the Magruder Mountain area, Nevada-California*. United States Geological Survey Bulletin, 1251-H. 40 pp.

- and MOIOLA, R.J. 1962. Precambrian and Cambrian rocks of south-central Esmeralda County, Nevada. *American Journal of Science*, 260, pp. 530-538.
- and GANGLOFF, R.A. 1969. Stratigraphic distribution of archaeocyathids in the Silver Peak Range and the White and Inyo Mountains, western Nevada and eastern California. *Journal of Paleontology*, 43(3), pp. 716-726.
- MCKERROW, W.S., SCOTSE, C.R. and BRASIER, M.D. 1992. Early Cambrian continental reconstructions. *Geological Society of London Journal*, 149, pp. 599-606.
- MCLAUGHLIN, K.P. and ENBYSK, B.B. 1950. Middle Cambrian trilobites from Pend Oreille County, Washington. *Journal of Paleontology*, 24(4), pp. 466-471.
- MCMENAMIN, M.A.S. 1987. Lower Cambrian trilobites, zonation, and correlation of the Puerto Blanco Formation, Sonora, Mexico. *Journal of Paleontology*, 61(4), pp. 738-749.
- and MCMENAMIN, D.L.S. 1990. *The emergence of animals: the Cambrian breakthrough*. Columbia University Press, New York, New York. 217 pp.
- MCNAMARA, K.J. 1978. Paedomorphosis in Scottish olenellid trilobites (early Cambrian). *Palaeontology*, 21(3), pp. 635-655.
- 1982. Heterochrony and phylogenetic trends. *Paleobiology*, 8(2), pp. 130-142.
- 1983. Progenesis in trilobites. *Special Papers in Paleontology* 30, pp. 59-68.
- 1986. The role of heterochrony in the evolution of Cambrian trilobites. *Biological Reviews*, 61, pp. 121-156.
- 1988. The abundance of heterochrony in the fossil record. *In* McKinney, M.L. (ed.). *Heterochrony in evolution: a multidisciplinary approach*. Plenum Press, New York, New York and London, England. pp. 287-325.
- 1990. Chapter 2.4. Heterochrony. *In* Briggs, D.E.G. and Crowther, P. R. (eds.). *Palaeobiology: a synthesis*. Blackwell Scientific Publications, London, England and Boston, Massachusetts. pp. 111-119.
- MERRIAM, C.W. 1964. Cambrian rocks of the Pioche Mining District, Nevada. *Geological Survey Professional Paper*, 469, 59 pp.
- MOBERG, J.C. 1899. Sveriges älsta kända trilobiter. *Geologiska Föreningens i Stockholm Förhandlingar*, 21(4), pp. 309-348.
- MOORE, J.N. 1976a. The Lower Cambrian Poleta Formation: a tidally dominated, open coastal, and carbonate bank depositional complex, western Great Basin. Unpublished Ph.D. dissertation, University of California, Los Angeles, California.
- 1976b. Depositional environments of the Lower Cambrian Poleta Formation and its stratigraphic equivalents, California and Nevada. *Brigham Young University Geology Studies*, 23(2), pp. 23-38.
- MOORE, R.C. (ed.) 1959. *Treatise on invertebrate paleontology*, pt. O, Arthropoda 1. Geological Society of America Incorporated and University of Kansas Press. Boulder, Colorado, and Lawrence, Kansas. 560 pp.

- MOORES, E.M. 1991. Southwest U.S. - east Antarctic (SWEAT) connection: a hypothesis. *Geology*, 19(5), pp. 425-428.
- MORGAN, N. 1976. The Montenegro bioherms: their paleoecology, relation to other archaeocyathid bioherms and to Early Cambrian sedimentation in the White and Inyo Mountains, California. *Pacific Coast Paleogeography Field Guide 1*. Society of Economic Paleontology and Mineralogy, pp. 13-18.
- MOUNT, J.F. 1982. Storm-surge-ebb origin of hummocky cross-stratified units of the Andrews Mountain Member, Campito Formation (Lower Cambrian) White-Inyo Mountains, eastern California. *Journal of Sedimentary Petrology*, 52, pp. 941-958.
- , HUNT, D.L., GREENE, L.R. and DIENGER, J. 1991. Depositional systems, biostratigraphy and sequence stratigraphy of Lower Cambrian grand cycles, southwestern Great Basin. *In* Cooper, J.D. and Stevens, C.H. (eds.). *Paleozoic paleogeography of the western United States - II*. 1. Pacific Section, Society Economic Paleontologists and Mineralogist, 67, pp. 209-229.
- and ROWLAND, S.M. 1981. Grand Cycle A (Lower Cambrian) of the southern Great Basin: a product of differential rates of relative sea level rise. *In* Taylor, M.E. (ed.). *Short papers for the Second International Symposium on the Cambrian System*. United States Geological Survey Open-File Report, 81-743, pp. 143-146.
- NELSON, C.A. 1962. Lower Cambrian-Precambrian succession, White-Inyo Mountains, California. *Geological Society of America Bulletin*, 73, pp. 139-144.
- 1963. Stratigraphic range of *Ogygopsis*. *Journal of Paleontology*, 37(1), pp. 244-248.
- 1976. Late Precambrian-Early Cambrian stratigraphic and faunal succession of eastern California and the Precambrian-Cambrian boundary. *Pacific Coast Paleogeography Field Guide 1*. Society of Economic Paleontology and Mineralogy, pp. 31-42.
- 1978. Late Precambrian-Early Cambrian stratigraphic and faunal succession of eastern California and the Precambrian-Cambrian boundary. *Geological Magazine*, 115(2), pp. 121-126.
- 1978. Ontogeny, phylogeny, paleontology and the Biogenetic Law. *Systematic Zoology*, 27, pp. 324-345.
- and HUPÉ, P. 1964. Sur l'existence de *Fallotaspis* et *Daguanaspis*, trilobites marocains, dans le Cambrien inférieur de Californie, et ses conséquences. *Comptes Rendues de Academie de Science*, 258, pp. 621-623.
- NIKOLAISEN, F. and HENNINGSMOEN, G. 1990. Lower and Middle Cambrian trilobites from the Digermul Peninsula, Finnmark, northern Norway. *Norges Geologiske Undersøkelse Bulletin*, 419, pp. 55-95.
- NORRIS, D.K. and PRICE, R.A. 1966. Middle Cambrian lithostratigraphy of southwestern Canadian Cordillera. *Canadian Petroleum Geology Bulletin*, 14, pp. 385-404.
- NORTH, F.K. 1971. The Cambrian of Canada and Alaska. *In* Holland, C.H. (ed.). *Cambrian of the New World*. John Wiley and Sons, London, England and Toronto, Ontario, pp. 219-324.

- OKULITCH, V.J. 1951. A Lower Cambrian fossil locality near Addy, Washington. *Journal of Paleontology*, 25(3), pp. 405-407.
- ONKEN, B.R. and SIGNOR, P.W. 1988a. Lower Cambrian stratigraphic paleontology of the southwestern Great Basin (White-Inyo Mountains of eastern California and Esmeralda County, Nevada). *Southern California Paleontological Society Bulletin*, 20, pp. 131-150.
- and ----- 1988b. *Lidaconus palmettoensis* n. gen. and sp.: an enigmatic early Cambrian fossil from western Nevada. *Journal of Paleontology*, 62(2), pp. 172-180.
- OPIK, A.A. 1958. The Cambrian trilobite *Redlichia*: organization, and generic concept. Commonwealth of Australia, Department of National Development and Energy, Bureau of Mineral Resources, Geology and Geophysics Bulletin, 42. 50 pp.
- 1967. The Mindylian Fauna of North-Western Queensland. Commonwealth of Australia, Department of National Development and Energy, Bureau of Mineral Resources, Geology and Geophysics Bulletin, 74. 404 pp.
- 1982. Dolichometopid trilobites of Queensland, Northern Territory, and New South Wales. Commonwealth of Australia, Department of National Development and Energy, Bureau of Mineral Resources, Geology and Geophysics Bulletin, 175. 85 pp.
- PACK, P.D. and GAYLE, H.B. 1971. A new olenellid trilobite, *Biceratops nevadensis*, from the Lower Cambrian near Las Vegas, Nevada. *Journal of Paleontology*, 45(5), pp. 893-898.
- PALMER, A.R. 1954. An appraisal of the Great Basin Middle Cambrian trilobites described before 1900. United States Geological Survey Professional Paper, 264-D, pp. 55-85.
- 1957. Ontogenetic development of two olenellid trilobites. *Journal of Paleontology*, 31(1), pp. 105-128.
- 1958. Morphology and ontogeny of a Lower Cambrian ptychoparioid trilobite from Nevada. *Journal of Paleontology*, 32(1), pp. 154-170.
- 1960. Some aspects of the early Upper Cambrian stratigraphy of White Pine County, Nevada, and vicinity. *Intermountain Association of Petroleum Geologists Guidebook*, pp. 53-58.
- 1962. Comparative ontogeny of some opisthoparian, gonatoparian and proparian Upper Cambrian trilobites. *Journal of Paleontology*, 36(1), pp. 87-96.
- 1964. An unusual Lower Cambrian trilobite fauna from Nevada. U.S. Geological Survey Professional Paper 483-F. 13 pp.
- 1968. Cambrian Trilobites of East-Central Alaska. U.S. Geological Survey Professional Paper 559-B. 115 pp.
- 1971. The Cambrian of the Great Basin and adjacent areas, western United States. In Holland, C.H. (ed.). *Cambrian of the New World*. John Wiley and Sons, London, England and Toronto, Ontario, pp. 1-78.
- 1977. Biostratigraphy of the Cambrian System - a progress report. *Annual Review of Earth and Planetary Sciences*, 5, pp. 13-33.

- 1979. Biome boundaries re-examined. *Alcheringa*, 3, pp. 33-41.
- submitted. Terminal Early Cambrian extinction of the Olenellina. *Journal of Paleontology*.
- and CAMPBELL, D.P. 1976. Biostratigraphic implications of trilobite biofacies: *Albertella* Zone, Middle Cambrian, western United States. *Brigham Young University Geology Studies*, 23(2), pp. 39-50.
- and HALLEY, R.B. 1979. Physical stratigraphy and trilobite biostratigraphy of the Carrara Formation (Lower and Middle Cambrian) in the southern Great Basin. *Geological Survey Professional Paper*, 1047. 131 pp.
- and PEEL, J.S. 1979. New Cambrian faunas from Peary Land, eastern North Greenland. *Rapport Grønlands Geologiske Undersøgelse*, 91, pp. 29-36.
- and REPINA, L.N. 1993. Through a glass darkly: taxonomy, phylogeny and biostratigraphy of the Olenellina. *University of Kansas Paleontological Contributions*, new ser., 3. 35 pp.
- PEACH, B.N. 1894. Additions to the fauna of the *Olenellus*-zone of the northwest Highlands. *Geological Journal*, 50, pp. 661-676.
- PENG, SHAN-CHI, LIN, HUAN-LING and CHEN, YONG-AN. 1995. New polymerid trilobites from Middle Cambrian Huaquiao Formation of western Hunan. *Acta Palaeontologica Sinica*, 34(3), pp. 277-300.
- PELECHATY, S.M. 1996. Stratigraphic evidence for the Siberia-Laurentia connection and early Cambrian rifting. *Geology*, 24(8), pp. 719-722.
- PLATNICK, N.I. 1979. Philosophy and the transformation of cladistics. *Systematic Zoology*, 28, pp. 537-546.
- POULSEN, C. 1927. The Cambrian, Ozarkian and Canadian faunas of northwest Greenland. *Meddelelser om Grønland*, 70(2), pp. 233-343.
- 1932. The Lower Cambrian faunas of east Greenland. *Meddelelser om Grønland*, 87(6). 66 pp.
- 1946. Notes on Cambro-Ordovician fossils collected by the Oxford University Ellesmere Land Expedition 1934-5. *Quarterly Journal of the Geological Society of London*, 102, pp. 299-337.
- 1958. Contribution to the palaeontology of the Lower Cambrian Wulff River Formation. *Meddelelser om Grønland*, 162(2). 25 pp.
- 1969. The Lower Cambrian from Slagelse no. 1, Western Sealand. *Danmarks Geologiske Undersøgelse*, II. Raekke, 93, 1-27.
- POULSEN, V. 1964. Contribution to the Lower and Middle Cambrian paleontology and stratigraphy of northwest Greenland. *Meddelelser om Grønland*, 164(6). 105 pp.
- 1974. Olenellacean trilobites from eastern north Greenland. *Bulletin of the Geological Society of Denmark*, 23, pp. 79-101.

- POWELL, C.McA., McELHINNY, M.W., MEERT, J.G. and PARK, J.K. 1993. Paleomagnetic constraints of timing of the Neoproterozoic breakup of Rhodinia and the Cambrian formation of Gondwana. *Geology*, 21(10), pp. 889-892.
- PRATT, B.R. 1992. Trilobites of the Marjuman and Steptoean stages (Upper Cambrian), Rabbitkettle Formation, southern Mackenzie Mountains, northwest Canada. *Palaeontographica Canadiana*, 9, 179 pp.
- PRIBYL, A. and VANEK, J. 1971. Studie über die familie Scutelluidae Richter et Richter (Trilobita) und ihre phylogenetische entwicklung. *Acta Universitatis Carolinae - Geologica*, 4, pp. 361-394.
- RAFF, R.A. 1996. The shape of life: genes, development, and the evolution of animal form. The University of Chicago Press, Chicago, Illinois and London, England. 520 pp.
- RAMSKOLD, L. and EDGECOMBE, G.D. 1991. Trilobite monophyly revisited. *Historical Biology*, 4, pp. 267-283.
- and WERDELIN, L. 1991. The phylogeny and evolution of some phacopid trilobites. *Cladistics*, 7, pp. 29-74.
- RASETTI, F. 1948. Lower Cambrian trilobites from the Conglomerates of Quebec. *Journal of Paleontology*, 22(1), pp. 1-24.
- 1951. Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains. *Smithsonian Miscellaneous Collections*, 116(5). 270 pp.
- 1952. Ventral cephalic sutures in Cambrian trilobites. *American Journal of Science*, 250, pp. 885-598.
- 1955. Lower Cambrian ptychopariid trilobites from the conglomerates of Quebec. *Smithsonian Miscellaneous Collections* 128(7). 35 pp.
- 1963. Middle Cambrian ptychoparioid trilobites from the conglomerates of Quebec. *Journal of Paleontology*, 37(3), pp. 575-594.
- 1966. New Lower Cambrian trilobite faunule from the Taconic sequence of New York. *Smithsonian Miscellaneous Collections*, 148(9), 52 pp.
- 1967. Lower and Middle Cambrian trilobite faunas from the Taconic sequence of New York. *Smithsonian Miscellaneous Collections*, 152(4). 111 pp.
- 1972. Cambrian trilobite faunas of Sardinia. *Atti Della Accademia Nazionale dei Lincei Memoire*, ser. 8. 11 pp.
- RAW, F. 1925. The development of *Leptoplastus salteri* (Callaway) and of other trilobites (Olenidae, Ptychopariidae, Conocoryphidae, Paradoxidae, Phacopidae, and Mesonacidae. *Quarterly Journal of the Geological Society of London*, 81, pp. 223-324.
- 1936. Mesonacidae of Comley in Shropshire, with a discussion of classification within the family. *The Quarterly Journal of the Geological Society of London*, 92, pp. 236-293.
- 1937. Systematic position of the Olenellidae (Mesonacidae). *Journal of Paleontology*, 11(7), pp. 575-597.

- 1957. Origin of chelicerates. *Journal of Paleontology*, 31(1), pp. 139-192.
- RAYMOND, P.E. 1928. Two new Cambrian trilobites. *American Journal of Science*, 5th ser., 15, pp. 309-313.
- REPINA, L.N. 1979. The dependence of morphological features upon the living conditions of trilobites and an evaluation of their importance in the classification of the superfamily Olenelloidea. *Trudy Instituta Geologii i Geofiziki*, 431, pp. 11-30.
- 1990. Evolution of trilobites in the beginning stages of their historical development. *In*: Environment and life in the geologic past: aspects of evolution of organisms and environment. Institute for Geology and Geophysics, Siberian Section, *Trudy*, 764, pp. 34-44. [translated by A.R. Palmer]
- RESSER, C.E. 1928. Cambrian fossils from the Mohave Desert. *Smithsonian Miscellaneous Collections*, 81(2). 14 pp.
- 1929. New Lower and Middle Cambrian Crustacea. *Proceedings of the United States National Museum*, 76(9), 18 pp.
- 1935. Nomenclature of some Cambrian trilobites. *Smithsonian Miscellaneous Collections*, 93(5). 46 pp.
- 1936. Second contribution to nomenclature of Cambrian trilobites. *Smithsonian Miscellaneous Collections*, 95(4). 29 pp.
- 1937a. Elkanah Billings' Lower Cambrian trilobites and associated species. *Journal of Paleontology*, 11(1), pp. 43-54.
- 1937b. Third Contribution to nomenclature of Cambrian trilobites. *Smithsonian Miscellaneous Collections*, 95(22). 29 pp.
- Cambrian System (restricted) of the southern Appalachians. *Geological Society of America Special Papers*, 15. 140 pp.
- 1939. The *Ptarmigania* strata of the northern Wasatch Mountains. *Smithsonian Miscellaneous Collections*, 98(24). 72 pp.
- 1942. Fifth contribution to nomenclature of Cambrian fossils. *Smithsonian Miscellaneous Collections*, 101(15). 58 pp.
- and ENDO, R. 1937. Description of the fossils. *In* Endo, R. and Resser, C.E. The Sinian and Cambrian formations and fossils of southern Manchoukuo. *Manchurian Science Museum Bulletin*, 1, pp. 103-301.
- and HOWELL, B.F. 1938. Lower Cambrian *Olenellus* Zone of the Appalachians. *Geological Society of America Bulletin*, 49, pp. 195-248.
- RICCIO, J.F. 1952. The Lower Cambrian Olenellidae of the southern Marble Mountains, California. *Bulletin of the Southern California Academy of Science*, 51, pp. 25-49.
- RICE, H.M.A. 1937. Cranbrook map-area, British Columbia. *Geological Survey of Canada Memoir*, 207. 67 pp.

- 1941. Nelson map-area, east half, British Columbia. Geological Survey of Canada Memoir, 228. 86 pp.
- RICHTER, R. 1933. Crustacea. *In*: Handwörterbuch der Naturwissenschaften, Second Edition, pp. 840-864.
- RIDLEY, M. 1986. Evolution and classification: the reformation of cladism. Longman Group Limited, London, England and New York, New York. 201 pp.
- RIEPPPEL, O. 1993. The conceptual relationship of ontogeny, phylogeny and classification. *Evolutionary Biology*, 27, pp. 1-32.
- ROBISON, R.A. 1967. Ontogeny of *Bathyriscus fimbriatus* and its bearing on affinities of corynexochid trilobites. *Journal of Paleontology*, 41(1), pp. 213-221.
- Middle Cambrian trilobite biostratigraphy of the Great Basin. *Brigham Young University Geology Studies*, 23(2), pp. 93-110.
- ROMANENKO, E.V. 1960. Otesany trilobitov. Biostratigrafia Paleozoa Sayano-Altaeskoj gornoy oblasti 1. Novosibirsk. Trudy. 436 pp.
- ROSS, G.M. 1991. Tectonic setting of the Windermere Supergroup revisited. *Geology*, 19(11), pp. 1125-1128.
- , McMECHAN, M.E. and HEIN, F.J. 1989. Chapter 6. Proterozoic history: the birth of the miogeocline. *In* Ricketts, B.D. (ed.). Western Canada sedimentary basin. Canadian Society of Petroleum Geologists, pp. 79-104.
- RUSCONI, C. 1945. Nuevos trilobites del Cámbrico de Mendoza. *Boletín Paleontológico de Buenos Aires*, 19.
- 1952. Fósiles Cámbrico del Cerro Aspero, Mendoza. *Museo Historia Natural de Mendoza (Argentina)*, Revista, 6, pp. 63-122.
- SAITO, K. 1934. Older Cambrian Trilobites and Conchostraca from north-western Korea. *Japanese Journal of Geology and Geography*, 11(3-4), pp. 211-237.
- SANDERS, H.L. 1968. Marine benthic diversity - a comparative study. *American Naturalist*, 102, pp. 243-282.
- SCHOCH, R.M. 1986. Phylogeny reconstruction in paleontology. Van Nostrand Reinhold Company, New York, New York. 353 pp.
- SCHOFIELD, S.J. 1914. The Pre-Cambrian (Beltian) rocks of southeastern British Columbia and their correlation. *Canada Department of Mines Museum Bulletin*, 2, Geological ser., 16. 13 pp.
- 1915. Geology of the Cranbrook map-area, British Columbia. Geological Survey of Canada Memoir, 76. 245 pp.
- 1921. The discovery of *Olenellus* fauna in southeastern British Columbia. *Science*, 54, pp. 666-667.

- 1922. Relationship of the Precambrian (Beltian) terrain to the Lower Cambrian strata of southeastern British Columbia. Geological Survey of Canada Museum Bulletin, 35. 15 pp.
- SCOTT-RAM, N.R. 1990. Transformed cladistics, taxonomy and evolution. Cambridge University Press, Cambridge, Massachusetts and New York, New York. 238 pp.
- SECORD, J.A. 1986. Controversy in Victorian Geology: the Cambrian-Silurian Dispute. Princeton University Press, Princeton, New Jersey. 363 pp.
- SHAW, A.B. 1950. A revision of several early Cambrian trilobites from eastern Massachusetts. Journal of Paleontology, 24(5), pp. 577-590.
- Lower and Middle Cambrian faunal succession in northwestern Vermont. Geological Society of America Bulletin, 65, pp. 1033-1046.
- Paleontology of northwestern Vermont V: the Lower Cambrian fauna. Journal of Paleontology, 29(5), pp. 775-805.
- Quantitative trilobite studies III: *Proliostractus strenuelliiformis* Poulsen, 1932. Journal of Paleontology, 33(3), pp. 474-487.
- Paleontology of northwestern Vermont IX. Fauna of the Monkton Quartzite. Journal of Paleontology, 36(2), pp. 322-345.
- SHERGOLD, J.H. 1969. Oryctocephalidae (Trilobita: Middle Cambrian) of Australia. Commonwealth of Australia, Department of National Development and Energy, Bureau of Mineral Resources, Geology and Geophysics Bulletin, 104, 66 pp.
- 1991. Protaspid and early meraspid growth stages of the eodiscoid trilobite *Pagetia ocellata* Jell, and their implications for classification. Alcheringa, 15, pp. 65-86.
- SIGNOR, P.W. and MOUNT, J.F. 1986. Position of the Lower Cambrian boundary in the White-Inyo Mountains of California and in Esmeralda County, Nevada. Newsletters in Stratigraphy, 16(1), pp. 9-18.
- SIMPSON, G.G. 1961. Principles of animal taxonomy. Columbia University Press, New York, New York. 247 pp.
- SMITH, A.B. 1994. Systematics and the fossil record: documenting evolutionary patterns. Blackwell Scientific Publications, Oxford, England. 223 pp.
- SOKAL, R.R. and SNEATH, P.H.A. 1963. The principles of numerical taxonomy. W. H. Freeman and Company, San Francisco, California. 573 pp.
- STEWART, J.H. 1965. Precambrian and Lower Cambrian formations in the Last Chance Range area, Inyo County, California. In Cohee, G.V. and West, W.S. (eds.). Changes in stratigraphic nomenclature by the United States Geological Survey, 1964. United States Geological Survey Bulletin, 1224-A, pp. A60-A70.
- 1966. Correlation of Lower Cambrian and some Precambrian strata in the southern Great Basin, California and Nevada. United States Geological Survey Professional Paper, 550-C, pp. 66-72.

- 1970. Upper Precambrian and Lower Cambrian strata in the southern Great Basin, California and Nevada. United States Geological Survey Professional Paper, 620. 206 pp.
- 1991. Latest Proterozoic and Cambrian rocks of the western United States - an overview. *In* Cooper, J.D. and Stevens, C.H. (eds.). Paleozoic Paleogeography of the Western United States - II. 1. Pacific Section, Society Economic Paleontologists and Mineralogists, 67, pp. 13-38.
- STØRMER, L. 1942. Studies on trilobite morphology. pt. II. The larval development, the segmentation and the sutures, and their bearing on trilobite classification. *Norsk Geologisk Tidsskrift*, 20, pp. 50-163.
- 1944. On the relationship and phylogeny of fossil and recent Arachnomorpha. A comparative study on Arachnida, Xiphosura, Eurypterida, Trilobita, and other fossil Arthropoda. *Norske Videnskaps-Akademi i Oslo, Matematisk-Naturvidenskapelig Klasse. Skrifter*, 5, 158 pp.
- STOUGE, S. and BOYCE, W.D. 1983. Fossils of northwestern Newfoundland and southeastern Labrador: conodonts and trilobites. Mineral Development Division, Department of Mines and Energy, Government of Newfoundland and Labrador Report, 83-3. 55 pp.
- SUNDBERG, F.A. 1994. Corynexochida and Ptychopariida (Trilobita, Arthropoda) of the *Ehmaniella* Biozone (Middle Cambrian), Utah and Nevada. Natural History Museum of Los Angeles County, Contributions in Science, 446. 137 pp.
- SUVOROVA, N.P. 1964. Trilobity korineksokhoidy i ikh istoricheskoe razvitiye. (Corynexochid trilobites and their historical development). *Trudy Palaeontologicheskii Instituta*, 103. 319 pp. [in Russian]
- SWINNERTON, H.H. 1915. Suggestions for a revised classification of trilobites. *Geological Magazine*, 52, pp. 487-496, 538-545.
- SWOFFORD, D.L. 1993. PAUP: phylogenetic analysis using parsimony. Version 3.1. Laboratory of Molecular Systematics, Smithsonian Institution. (computer program)
- and BEGLE, D.P. 1993. PAUP: phylogenetic analysis using parsimony. User's Manual for Version 3.1. Laboratory of Molecular Systematics, Smithsonian Institution.
- TAYLOR, M.E. 1966. Precambrian mollusc-like fossils from Inyo County, California. *Science*, 153, pp. 198-201.
- THEOKRITOFF, G. 1968. Cambrian biogeography and biostratigraphy in New England. *In* Zen, E., White, W.S., Hadley, J.B. and Thompson, J.B. Jr. (eds.). *Studies of Appalachian Geology; Northern and Maritime*. Wiley-Interscience, New York, New York, pp. 9-22.
- THEOKRITOFF, G. 1979. Early Cambrian provincialism and biogeographic boundaries in the North Atlantic region. *Lethaia*, 12, pp. 281-295.
- TURNER, H.W. 1902. A sketch of the historical geology of Esmeralda County, Nevada. *American Geology*, 29, pp. 261-272.
- WALCOTT, C.D. 1883. The Cambrian system in the United States and Canada. *Philosophical Society of Washington Bulletin*, 6, pp. 98-102.

- 1885. Paleozoic notes: new genus of Cambrian trilobite, *Mesonacis*. American Journal of Science, ser. 3, 29, pp. 328-330.
- 1886. Second contribution to the studies on the Cambrian faunas of North America. United States Geological Survey Bulletin, 30. 369 pp.
- 1889. Description of new genera and species of fossils from the Middle Cambrian. Proceedings of the United States National Museum, 11, pp. 441-446.
- 1890. The fauna of the Lower Cambrian or *Olenellus* Zone. In 10th Annual Report of the Director of the U.S. Geological Survey for 1888-1889, pt. 1, pp. 509-774.
- 1895. Lower Cambrian rocks in eastern California. American Journal of Science, 149, pp. 141-144.
- 1908. Cambrian sections of the Cordilleran area. Smithsonian Miscellaneous Collections, 53(5), pp. 167-230.
- 1910a. Abrupt appearance of the Cambrian fauna on the North American continent. Smithsonian Miscellaneous Collections, 53(1), pp. 1-16.
- 1910b. *Olenellus* and other genera of the Mesonacidae. Smithsonian Miscellaneous Collections, 53(6), pp. 231-422.
- 1912a. The Sardinian Cambrian genus *Olenopsis* in America. Smithsonian Miscellaneous Collections, 57(8), pp. 239-249.
- 1912b. Group terms for the Lower and Upper Cambrian series of formations. Smithsonian Miscellaneous Collections, 57(10), pp. 305-307.
- 1913. New Lower Cambrian subfauna. Smithsonian Miscellaneous Collections, 57(11), pp. 309-327.
- 1916a. Cambrian Geology and Paleontology III, Cambrian trilobites. Smithsonian Miscellaneous Collections, 64(3), pp. 157-258.
- 1916b. Cambrian Geology and Paleontology III, Cambrian trilobites. Smithsonian Miscellaneous Collections, 64(5), pp. 303-456.
- 1916c. Evidences of primitive life. Smithsonian Institution, Annual Report (1915), pp. 235-255.
- 1917. Fauna of the Mount Whyte Formation. Smithsonian Miscellaneous Collections, 67(3), pp. 61-114.
- 1924. Geological Formations of Beaverfoot-Brisco-Stanford Range, British Columbia, Canada. Cambrian Geology and Paleontology V. 1. Smithsonian Miscellaneous Collections, 75(1). 56 pp.
- WANNER, A. 1901. A new species of *Olenellus* from the Lower Cambrian of York County, Pennsylvania. Proceedings of the Washington Academy of Sciences, 3, pp. 267-272.
- WATROUS, L.E. and WHEELER, Q.D. 1981. The out-group comparison method of character analysis. Systematic Zoology, 31, pp. 1-11.

- WESTERGÅRD, A. H. 1936. *Paradoxides oelandicus* beds of Öland, with the account of a diamond boring through the Cambrian at Mossberga. Sveriges Geologiska Undersökning, ser. C, 30(1). 66 pp.
- 1950. Non-agnostidean trilobites of the Middle Cambrian of Sweden II. Sveriges Geologiska Undersökning, ser. C, 43(9). 56 pp.
- WESTROP, S.R. 1986. Trilobites of the Upper Cambrian Sunwaptan Stage, southern Canadian Rocky Mountains, Alberta. *Palaeontographica Canadiana*, 3. 179 pp.
- WHITE, C. A. 1877. United States geographical surveys west of the one hundredth meridian report. 4, Paleontology.
- WHITEHOUSE, F.W. 1936. The Cambrian faunas of north-eastern Australia. *Memoirs of the Queensland Museum*, 11(1), pp. 59-112.
- 1939. The Cambrian Faunas of north-eastern Australia. pt. 3: The polymerid trilobites - with supplement 1. *Memoirs of the Queensland Museum*, 11(3), pp. 179-282.
- WHITTINGTON, H.B. 1957a. Ontogeny of *Elliptocephala*, *Paradoxides*, *Sao*, *Blainia*, and *Triarthrus* (Trilobita). *Journal of Paleontology*, v. 31(5), pp. 934-946.
- 1957b. The ontogeny of trilobites. *Biological Reviews*, v. 32, pp. 421-469.
- 1975. Trilobites with appendages from the Middle Cambrian Burgess Shale, British Columbia. In Martinsson, A. (ed.). *Evolution and morphology of the Trilobita, Trilobitoidea, and Merostomata*. *Fossils and Strata*, 4, pp. 97-136.
- 1988a. Hypostomes and ventral cephalic sutures in Cambrian trilobites. *Palaeontology*, 31(3), pp. 577-609.
- 1988b. Hypostomes of post-Cambrian trilobites. *New Mexico Bureau of Mines and Mineral Resources Memoir*, 44, pp. 321-339.
- 1989. Olenelloid trilobites: type species, functional morphology and higher classification. *Philosophical Transactions of the Royal Society of London. Biological Sciences*, 324(1221), pp. 111-147.
- 1992. *Trilobites*. Boydell Press, Woodbridge, England. 145 pp.
- 1995. Oryctocephalid trilobites from the Cambrian of North America. *Palaeontology*, 38(3), pp. 543-562.
- WILEY, E.O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. John Wiley & Sons. New York, New York and Toronto, Ontario. 439 pp.
- , SIEGEL-CAUSEY, D., BROOKS, D.R. and FUNK, V.A. 1991. *The complete cladist. a primer of phylogenetic procedures*. The University of Kansas Museum of Natural History Special Publication 19, Lawrence, Kansas. 158 pp.
- YOUNG, G.A. and LUDVIGSEN, R. 1989. Mid-Cambrian trilobites from the lowest part of the Cow Head Group, western Newfoundland. *Geological Survey of Canada Bulletin*, 392. 49 pp.

- YOUNG, G.M. Late Proterozoic stratigraphy and the Canada-Australia connection. *Geology*, 20(3), pp. 215-218.
- ZEN, E-AN. 1964. Taconic stratigraphic names: definitions and synonymies. United States Geological Survey Bulletin, 1174. 95 pp.

Appendix A

Locality Information and Collection Data

Trilobite collections described in this thesis come from a variety of sources and locations. The bulk of the collections were made by the author from stratigraphic sections, but these are supplemented by many other undescribed trilobite collections made by mapping geologists, professional collectors and amateur and professional paleontologists. In particular, many collections from the Great Basin were collected or acquired by C.A. Nelson. Material from the Cranbrook Rifle Range locality in British Columbia is well represented at various institutions such as the University of Alberta, University of British Columbia and the Geological Survey of Canada. When the locality has not been visited by the author, the collector's locality information is given, as provided, enclosed in quotation marks. Repositories for collections used in this study are various. The author's collections from the Great Basin will be housed by the Los Angeles County Museum of Invertebrate Paleontology (LACMIP), California. The author's and P. Ransom's collections from the Cranbrook (localities 4-6) and Hellroaring Creek areas (locality 7) will be housed by the Royal British Columbia Museum (RMCM). All other collections made by the author from British Columbia will be housed by the Geological Survey of Canada (GSC), Ottawa. Other collections have repositories as indicated and their abbreviations are given on the frontispiece to the plates (p. 410).

Locality information for measured stratigraphic sections is listed first and coded with letter or letter/number designations. Localities that represent individual collections or associated collections are listed second and designated by sequential numbers. All locality information is presented following the occurrence of localities geographically from north to south. General locality maps (Text-figs. 4 and 5) are provided with all stratigraphic sections and localities plotted.

Trilobite species found in each collection are indicated along with counts of numbers of individuals of each species. Species names preceded by a ? are tentative identifications. Non-trilobite genera from the collections are also listed but without number counts. Except in the small collections, counts were made based only on parts, not counterparts, to obtain a better estimate of numbers of individuals for biofacies analysis. Collections from measured stratigraphic sections are listed in descending stratigraphic order.

Part I Measured Stratigraphic Sections
British Columbia

MG3 - Mount Grainger Measured Section

Lat. 50°09'06" Long. 115°44'01"

Eager Formation

Northeast face of Mount Grainger, 6 km northeast of Canal Flats, overlooking the J2 Ranch at approximately 4700 feet. (Text-fig. 51)

Collector: L.L. Bohach

Lithology: interbedded limestones and shales.

See stratigraphic section (Text-fig. 52) for stratigraphic position of specific collections, lithology and species ranges.

Collection MG3i (above fault, not tied into section) (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, *Proliostracus* Biofacies)

Lithology: grey limestone (wackestone)

Fauna:	<i>Proliostracus buelnaensis</i> (Lochman)	21
	<i>Olenellus</i> sp.	3

Collection MG3h (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, *Proliostracus* Biofacies)

Lithology: grey limestone (wackestone)

Fauna:	<i>Proliostracus buelnaensis</i> (Lochman)	12
	<i>Olenellus</i> sp.	numerous fragments

Collection MG3g (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, *Proliostracus* Biofacies)

Lithology: grey limestone (mudstone to wackestone)

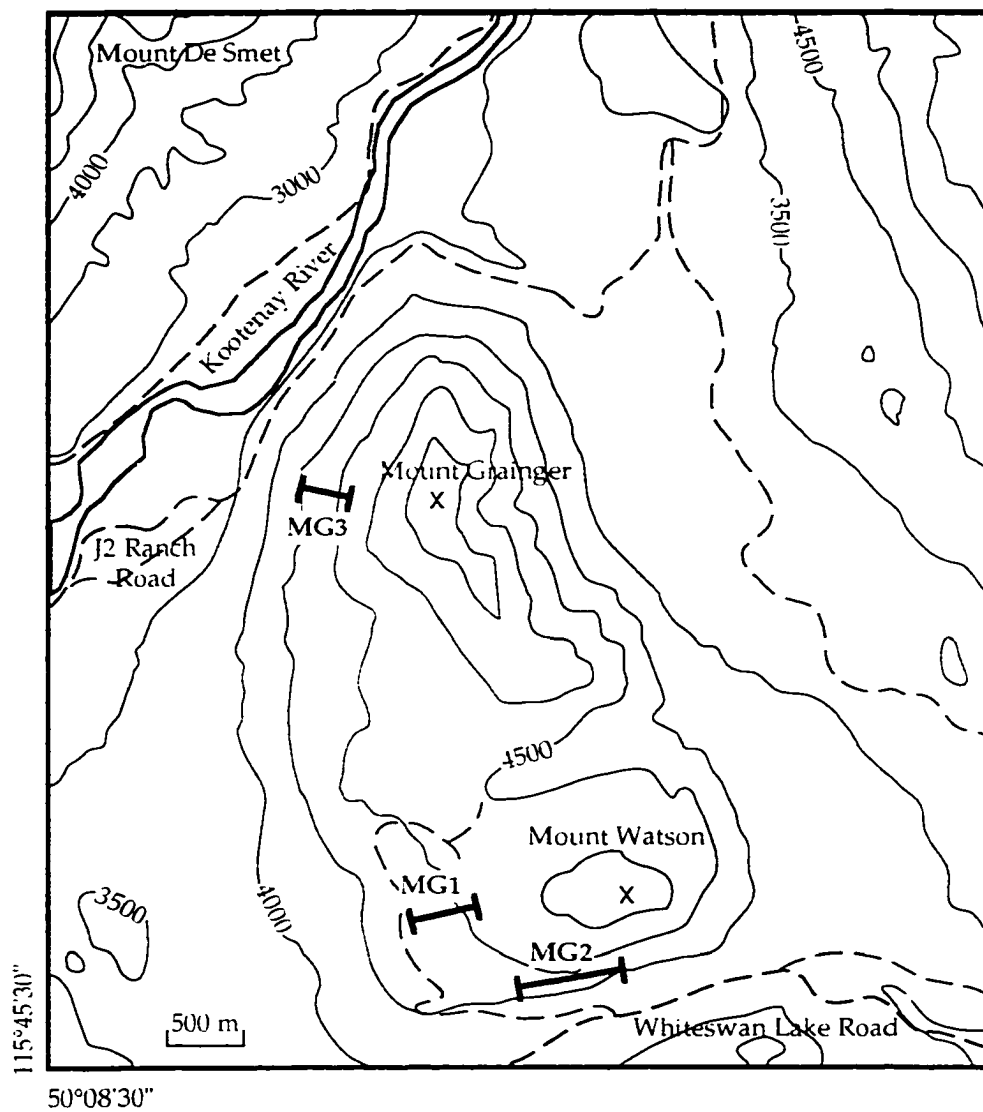
Fauna:	<i>Proliostracus buelnaensis</i> (Lochman)	99
	<i>Olenellus transitans</i> (Walcott)	7
	<i>Scenella</i> (Gastropoda?)	

Collection MG3f (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, *Proliostracus* Biofacies)

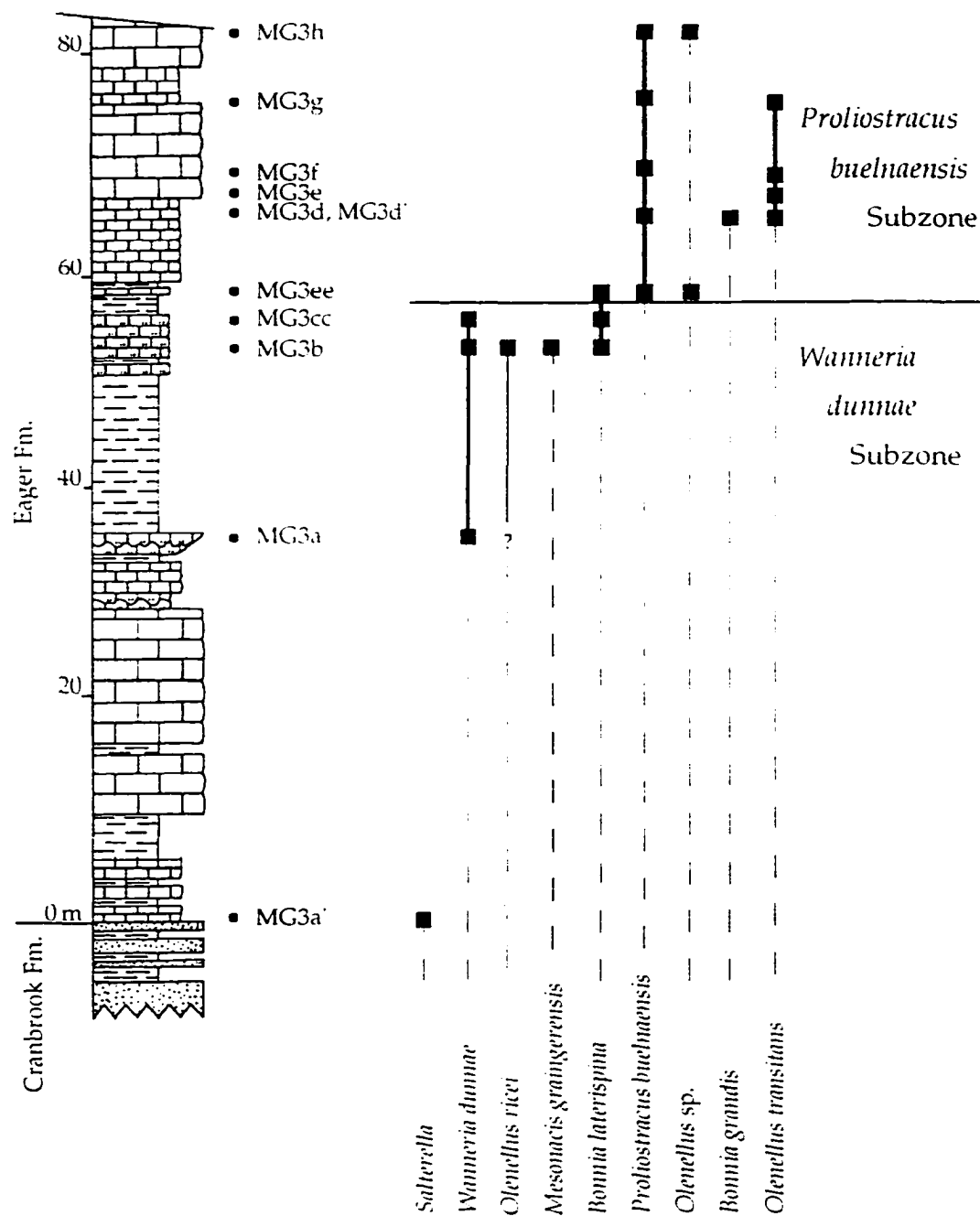
Lithology: grey limestone (mudstone to wackestone)

Fauna:	<i>Proliostracus buelnaensis</i> (Lochman)	29

Text-fig. 51. Location map for measured sections of the Canal Flats area. Sections MG1, MG2, MG3. (topography based on Canal Flats topographic map, 82 J/4, edition 2, 1977, 1:50 000, Surveys and Mapping Branch, Department of Energy, Mines and Resources, 1977) contour interval: 500 feet



Text-fig. 52. Stratigraphy and species ranges for the Mount Grainger measured section (MG3). (measured by author)



<i>Olenellus transitans</i> (Walcott)	3 plus numerous fragments
<i>Scenella</i> (Gastropoda?)	

Collection MG3e (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, Biofacies unassigned)

Lithology: grey to brown limestone (mudstone)

Fauna:	<i>Olenellus transitans</i> (Walcott)	6

Collection MG3d' (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, *Bonnia* Biofacies)

Lithology: light grey limestone (packstone)

Fauna:	<i>Bonnia grandis</i> n. sp.	77
	<i>Proliostracus buelnaensis</i> (Lochman)	39
	<i>Olenellus transitans</i> (Walcott)	3

Collection MG3d (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, Biofacies unassigned)

Lithology: grey limestone (mudstone)

Fauna:	<i>Bonnia grandis</i> n. sp.	5
	<i>Proliostracus buelnaensis</i> (Lochman)	2

Collection MG3ee (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, Biofacies unassigned)

Lithology: grey to red limestone (wackestone)

Fauna:	<i>Proliostracus buelnaensis</i> (Lochman)	15
	<i>Bonnia laterispina</i> Fritz	4
	<i>Olenellus</i> sp.	fragments

Collection MG3cc (*Olenellus transitans* Zone, *Wanneria dunnae* Subzone, Biofacies unassigned)

Lithology: brown-grey limestone (wackestone)

Fauna:	<i>Bonnia laterispina</i> Fritz	12
	<i>Wanneria dunnae</i> n. sp.	4

Collection MG3b (= MG3c) (*Olenellus transitans* Zone, *Wanneria dunnae* Subzone, *Wanneriid* Biofacies)

Lithology: grey to brown shaly limestone (packstone)

Fauna:	<i>Wanneria dunnae</i> n. sp.	303
	<i>Bonnia laterispina</i> Fritz	166
	<i>Mesonacis graingerensis</i> n. sp.	90
	<i>Olenellus ricei</i> n. sp.	6
	<i>Stenethecoides</i> (Gastropoda)	
	<i>Kutorgina</i> (Brachiopoda)	

Collection MG3a (*Olenellus transitans* Zone, *Wanneria dunnae* Subzone, Biofacies unassigned)

Lithology: grey to brown shaly limestone (wackestone)

Fauna:	<i>Wanneria dunnae</i> n. sp.	3
	? <i>Olenellus ricei</i> n. sp.	4
	wanneriid sp.	1

Collection MG3a' (*Olenellus transitans* Zone, Subzone unassigned, Biofacies unassigned)

Lithology: limestone (wackestone to packstone)

Fauna: *Salterella* (small shelly fossil)

MG1 - Mount Watson Measured Section I

Lat. 50°08'04" Long. 115°43'05"

Cranbrook and Eager formations

East face of Mount Watson, 7 km east-southeast of Canal Flats, along logging road at approximately 4300 feet. (Text-fig. 51)

Collector: L.L. Bohach

Lithology: interbedded limestones and shales.

See stratigraphic section (Text-fig. 53) for stratigraphic position of specific collections, lithology and species ranges.

Collection MG1t (talus block, not tied into section, specimens not counted)

Lithology: grey limestone

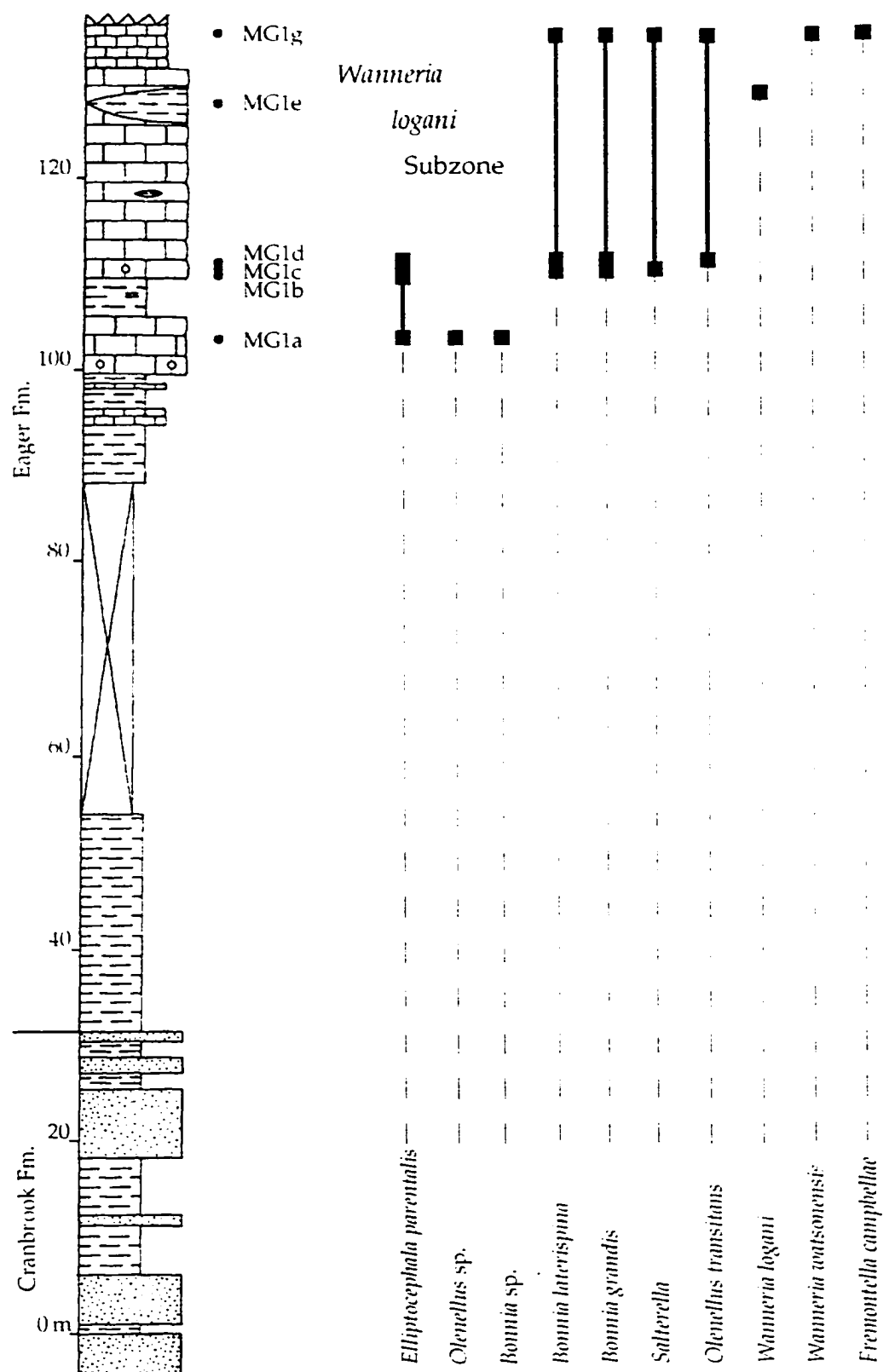
Fauna: *Bonnia fritzi* n. sp.

Collection MG1g (*Olenellus transitans* Zone, *Wanneria logani* Subzone, *Bonnia* Biofacies)

Lithology: grey to red limestone (wackestone to packstone)

Fauna:	<i>Bonnia grandis</i> n. sp.	13
	<i>Bonnia laterispina</i> Fritz	5

Text-fig. 53. Stratigraphy and species ranges for the Mount Watson measured section I (MG1). (measured by author)



<i>Bonnia</i> sp.	40
<i>Fremontella campbellae</i> n. sp.	9
<i>Wanneria watsonensis</i> n. sp.	7
<i>Olenellus transitans</i> (Walcott)	6
<i>Salterella</i> (small shelly fossil)	
<i>Stenethecoides</i> (Gastropoda)	
helcionellids (Gastropoda)	
shelly tubes	

Collection MG1e (*Olenellus transitans* Zone, *Wanneria logani* Subzone, Biofacies unassigned)

Lithology: light brown platy limestone (mudstone)

Fauna:	<i>Wanneria logani</i> (Walcott)	1

Collection MG1d (*Olenellus transitans* Zone, *Wanneria logani* Subzone, Biofacies unassigned)

Lithology: grey limestone (wackestone to packstone)

Fauna:	<i>Bonnia laterispina</i> Fritz	6
	<i>Bonnia grandis</i> n. sp.	3
	<i>Elliptocephala parentalis</i> n. sp.	2
	<i>Olenellus transitans</i> (Walcott)	2
	<i>Kutorgina</i> (Brachiopoda)	
	<i>Nisusia</i> (Brachiopoda)	

Collection MG1c (*Olenellus transitans* Zone, *Wanneria logani* Subzone, Biofacies unassigned)

Lithology: grey limestone, oolitic in part (mudstone to wackestone)

Fauna:	<i>Elliptocephala parentalis</i> n. sp.	15
	<i>Bonnia grandis</i> n. sp.	3
	<i>Bonnia laterispina</i> Fritz	4
	<i>Bonnia</i> sp.	29
	<i>Salterella</i> (small shelly fossil)	
	<i>Kutorgina</i> (Brachiopoda)	
	<i>Scenella</i> (Gastropoda?)	

Collection MG1b (*Olenellus transitans* Zone, *Wanneria logani* Subzone, Biofacies unassigned)

Lithology: brown platy limestone with shale partings (mudstone)

Fauna:	<i>Elliptocephala parentalis</i> n. sp.	3

Kutorgina (Brachiopoda)
Scenella (Gastropoda?)
 helcionellids (Gastropoda)

Collection MG1a (*Olenellus transitans* Zone, *Wanneria logani* Subzone, ?Wanneriid Biofacies)

Lithology: grey limestone, oolitic in part (mudstone to wackestone)

Fauna: *Elliptocephala* *parentalis* n. sp. 3
Bonnia sp. 2
Olenellus sp. 1
Kutorgina (Brachiopoda)
Scenella (Gastropoda?)
 helcionellids (Gastropoda)

MG2 - Mount Watson Measured Section II

Lat. 50°08'05" Long. 115°45'09"

Eager Formation

South face of Mount Watson, 7 km east-southeast of Canal Flats, along first section of logging road climbing Mount Watson at approximately 4000 feet. (Text-fig. 51)

Collector: L.L. Bohach

Lithology: interbedded limestones and shales.

See stratigraphic section (Text-fig. 54) for stratigraphic position of specific collections, lithology and species ranges.

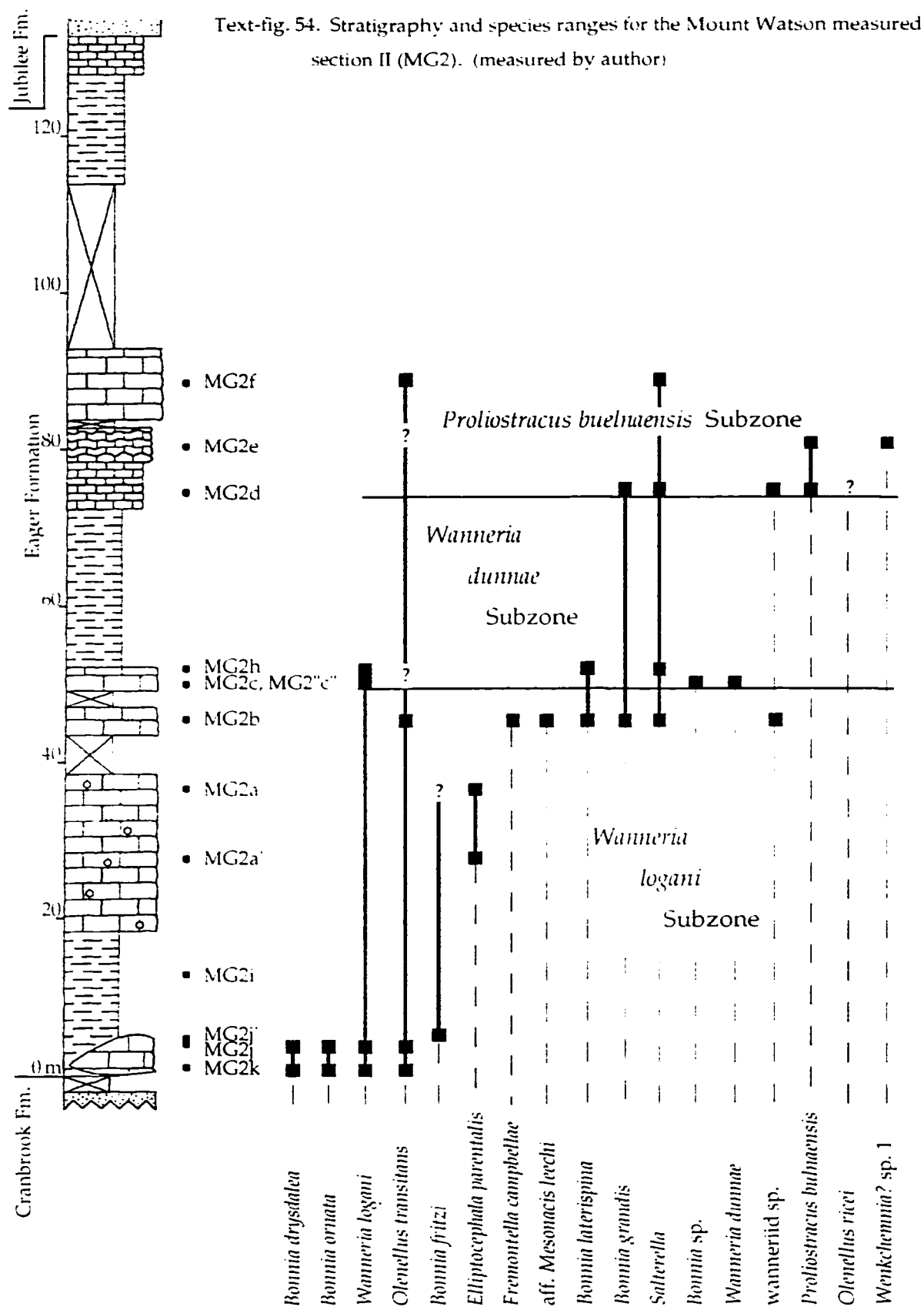
Collection MG2f (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, Biofacies unassigned)

Lithology: white to light grey limestone (mudstone to packstone)

Fauna: *Olenellus transitans* (Walcott) 7
Salterella (small shelly fossils)
Scenella (Gastropoda?)
Stenethecoides (Gastropoda)
Kutorgina (Brachiopoda)

Collection MG2e (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, *Proliostracus* Biofacies)

Lithology: light grey limestone (mudstone to wackestone)



Fauna:	<i>Proliostracus buelnaensis</i> (Lochman)	33
	? <i>Olenellus transitans</i> (Walcott)	7 plus many fragments
	<i>Wenckhemnia?</i> sp.	1
	<i>Scenella</i> (Gastropoda?)	
	<i>Stenethecoides</i> (Gastropoda)	

Collection MG2d (*Olenellus transitans* Zone, *Proliostracus buelnaensis* Subzone, *Bonnia* Biofacies)

Lithology: grey limestone (packstone to grainstone)

Fauna:	<i>Bonnia grandis</i> n. sp.	268
	<i>Proliostracus buelnaensis</i> (Lochman)	2
	? <i>Olenellus ricei</i> n. sp.	5
	wanneriid sp.	2 plus fragments
	<i>Salterella</i> (small shelly fossils)	
	<i>Stenethecoides</i> (Gastropoda)	
	helcionellids (Gastropoda)	
	sponge spicules	

Collection MG2h (*Olenellus transitans* Zone, *Wanneria dunnae* Subzone, *Bonnia* Biofacies)

Lithology: mottled (salt and pepper) limestone (wackestone to packstone)

Fauna:	<i>Bonnia laterispina</i> Fritz	15
	<i>Wanneria logani</i> (Walcott)	3
	<i>Salterella</i> (small shelly fossils)	

Collection MG2"c" (from top of bed containing MG2c) (*Olenellus transitans* Zone, *Wanneria dunnae* Subzone, Biofacies unassigned)

Lithology: mottled grey, white and black limestone with shaly partings (mudstone)

Fauna:	<i>Bonnia</i> sp.	18
	<i>Wanneria logani</i> (Walcott)	3
	<i>Wanneria dunnae</i> n. sp.	1
	<i>Olenellus</i> sp. 1	2

Collection MG2c (*Olenellus transitans* Zone, ?*Wanneria dunnae* Subzone, Biofacies unassigned)

Lithology: cream limestone (mudstone)

Fauna:	<i>Olenellus</i> sp. 1	2

Collection MG2b (*Olenellus transitans* Zone, *Wanneria logani* Subzone, Biofacies unassigned)

Lithology: light grey to purple limestone (mudstone)

Fauna:	<i>Bonnia grandis</i> n. sp.	7
	<i>Bonnia laterispina</i> Fritz	8
	<i>Bonnia</i> sp.	18
	<i>Fremontella campbellae</i> n. sp.	18
	<i>Olenellus transitans</i> (Walcott)	9
	aff. <i>Mesonacis leechi</i> n. sp.	6
	wanneriid sp.	6
	<i>Salterella</i> (small shelly fossils)	
	<i>Stenethecoides</i> (Gastropoda)	
	helcionellids (Gastropoda)	

Collection MG2a (*Olenellus transitans* Zone, *Wanneria logani* Subzone, Wanneriid Biofacies)

Lithology: grey limestone, oolitic in part (mudstone to wackestone)

Fauna:	<i>Elliptocephala parentalts</i> n. sp.	95
	? <i>Bonnia fritzi</i> n. sp.	3
	<i>Kutorgina</i> (Brachiopoda)	
	<i>Nisusia</i> (Brachiopoda)	
	helcionellids (Gastropoda)	

Collection MG2j (*Olenellus transitans* Zone, *Wanneria logani* Subzone, *Bonnia* Biofacies)

Lithology: grey limestone (wackestone)

Fauna:	<i>Bonnia fritzi</i> n. sp.	32

Collection MG2j (*Olenellus transitans* Zone, *Wanneria logani* Subzone, *Bonnia* Biofacies)

Lithology: white to grey limestone (packstone to grainstone)

Fauna:	<i>Bonnia drysdalea</i> n. sp.	288
	<i>Bonnia ornata</i> n. sp.	164
	<i>Bonnia</i> sp.	52
	<i>Olenellus transitans</i> (Walcott)	66
	<i>Wanneria logani</i> (Walcott)	19

Collection MG2k (*Olenellus transitans* Zone, *Wanneria logani* Subzone, *Bonnia* Biofacies)

Lithology: white to light brown limestone (wackestone to packstone)

Fauna:	<i>Bonnia drysdalea</i> n. sp.	66
	<i>Bonnia ornata</i> n. sp.	9
	<i>Wanneria logani</i> (Walcott)	3
	<i>Olenellus transitans</i> (Walcott)	1

RC4 - Ram Creek Measured Section

Lat. 50°00'30" Long. 115°37'00"

Cranbrook and Eager formations

On west facing unnamed ridge, Hughes Range, Ram Creek area, at about 7000 feet. About 13 km north-northeast of Skookumchuck. (Text-fig. 55)

Collector: L.L. Bohach

Lithology: interbedded limestones and shales.

See stratigraphic section (Text-fig. 56) for stratigraphic position of specific collections, lithology and species ranges.

Collection RC4f (many meraspids, all specimens small) (*Olenellus transitans* Zone, *Wanneria dunnae* Subzone, ?Wanneriid Biofacies)

Lithology: grey to brown shaly limestone (packstone to grainstone)

Fauna:	<i>Bonnaspis fieldensis</i> (Walcott)	192
	? <i>Olenellus transitans</i> (Walcott)	49
	<i>Wanneria dunnae</i> n. sp.	29
	<i>Bonnia laterispina</i> Fritz	5

Collection RC4e (*Olenellus transitans* Zone, *Wanneria logani* Subzone, Biofacies unassigned)

Lithology: grey limestone (mudstone)

Fauna:	wanneriid sp.	2

Collection RC4c (*Olenellus transitans* Zone, *Wanneria logani* Subzone, ?*Olenellus* Biofacies)

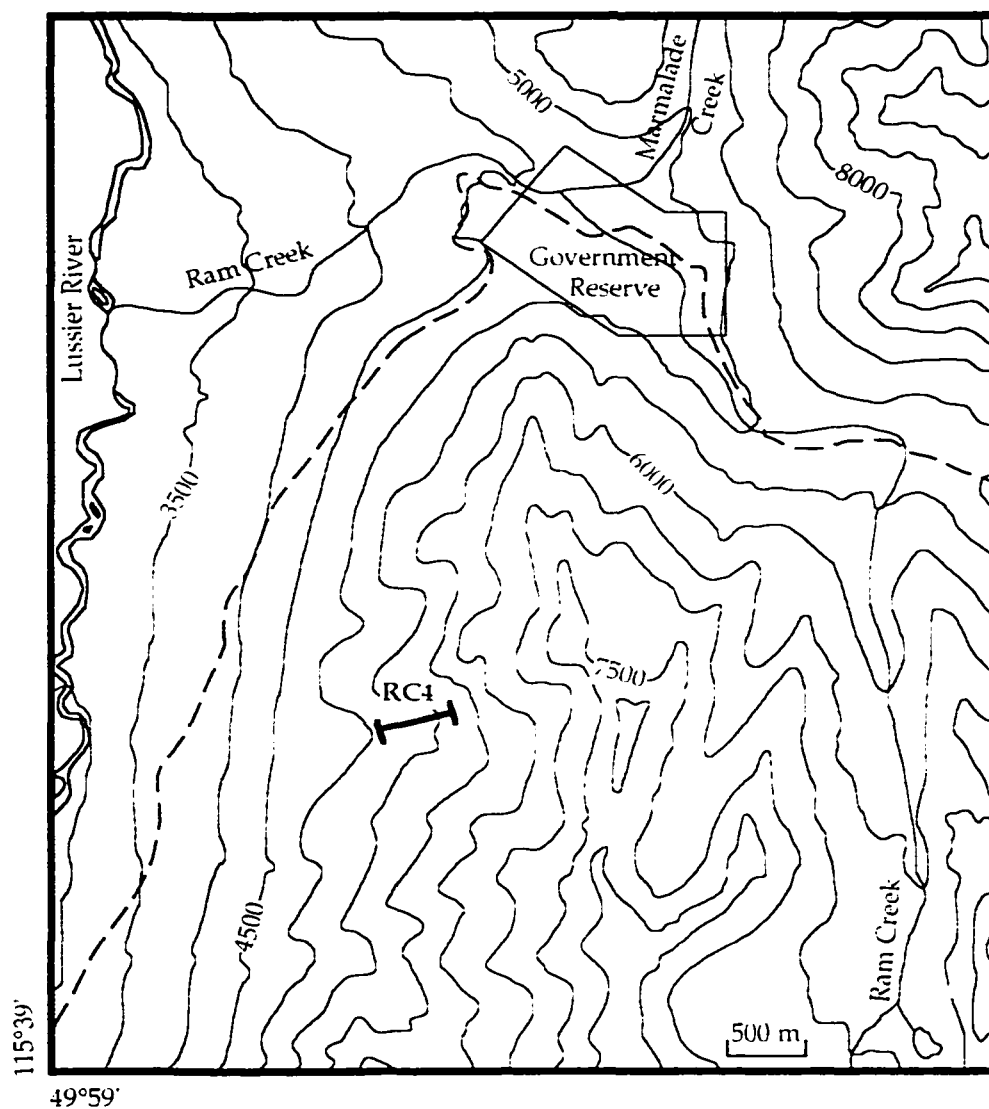
Lithology: grey limestone with shaly partings (packstone to grainstone)

Fauna:	<i>Olenellus transitans</i> (Walcott)	70
	<i>Fremontella ashtoni</i> n. sp.	10
	<i>Wanneria logani</i> (Walcott)	7
	<i>Bonnia laterispina</i> Fritz	9
	<i>Proliostracus</i> sp.	1
	helcionellids (Gastropoda)	

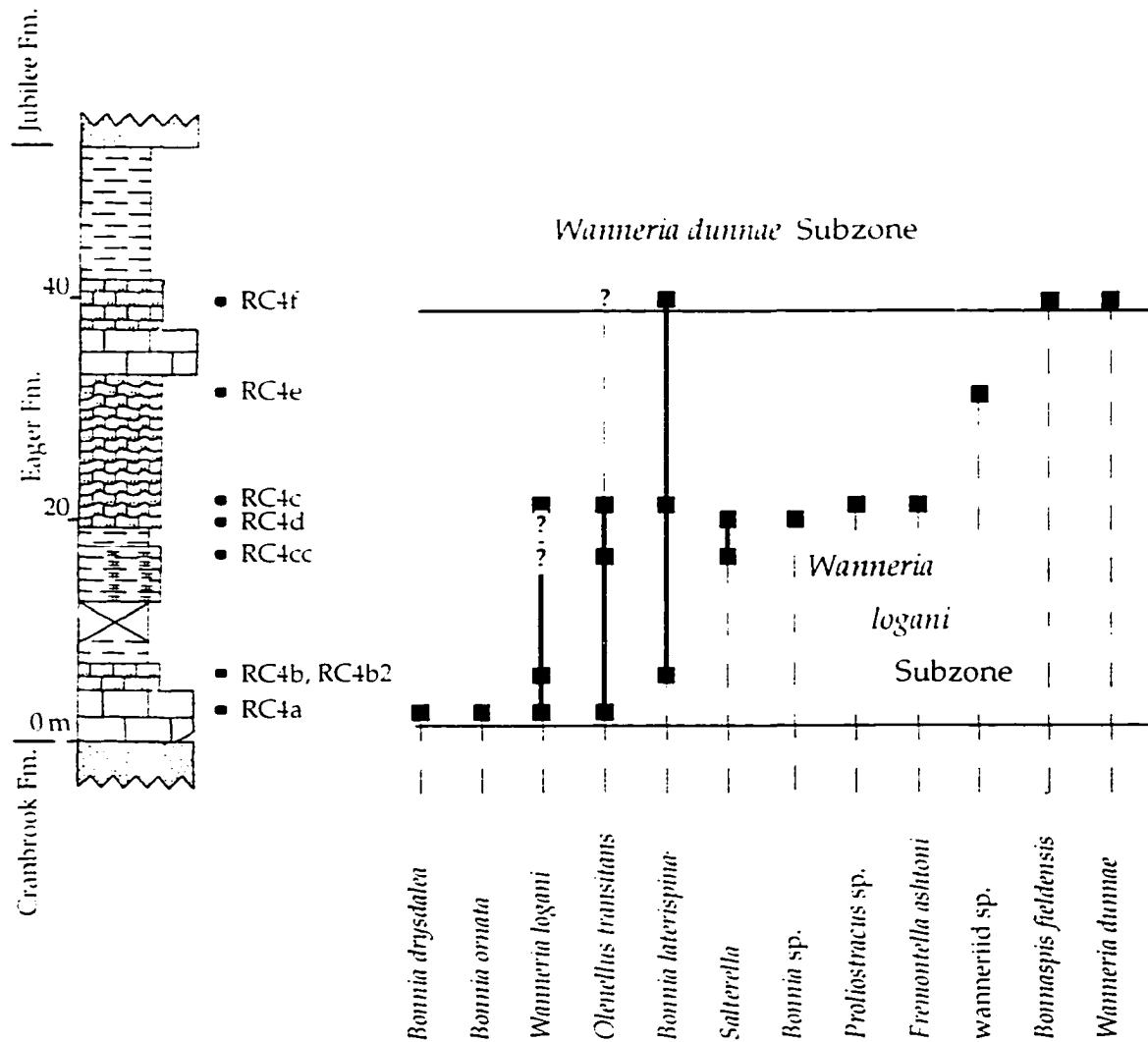
Text-fig. 55. Location map for the Ram Creek measured section (RC4).

(topography based on Canal Flats topographic map, 82J/4, edition 2, 1977 and Skookumchuk topographic map, 82G/13, edition 3, 1980; 1:50 000, Surveys and Mapping Branch, Department of Energy, Mines and Resources)

contour interval: 500 feet



Text-fig. 56. Stratigraphy and species ranges for the Ram Creek measured section (RC4).
(measured by author)



Collection RC4d (*Olenellus transitans* Zone, *Wanneria logani* Subzone, Biofacies unassigned)

Lithology: grey shaly limestone (wackestone)

Fauna:	<i>Bonnia</i> sp.	1
	? <i>Wanneria logani</i> (Walcott)	1
	<i>Salterella</i> (small shelly fossils)	abundant

Collection RC4cc (*Olenellus transitans* Zone, *Wanneria logani* Subzone, Biofacies unassigned)

Lithology: grey to brown limestone with shaly partings (wackestone)

Fauna:	<i>Olenellus transitans</i> (Walcott)	2
	? <i>Wanneria logani</i> (Walcott)	1
	<i>Salterella</i> (small shelly fossils)	abundant

Collection RC4b2 (lateral equivalent of RC4b) (*Olenellus transitans* Zone, *Wanneria logani* Subzone, ?*Bonnia* Biofacies)

Lithology: grey to yellow-brown limestone (packstone)

Fauna:	<i>Bonnia laterispina</i> Fritz	10
	<i>Wanneria logani</i> (Walcott)	3 plus fragments

Collection RC4b (*Olenellus transitans* Zone, *Wanneria logani* Subzone, Wanneriid Biofacies)

Lithology: grey to yellowish brown shaly limestone (wackestone)

Fauna:	<i>Wanneria logani</i> (Walcott)	38
	<i>Bonnia</i> sp.	1

Collection RC4a (*Olenellus transitans* Zone, *Wanneria logani* Subzone, *Bonnia* Biofacies)

Lithology: white limestone (packstone to grainstone)

Fauna:	<i>Bonnia drysdalea</i> n. sp.	65
	<i>Bonnia ornata</i> n. sp.	27
	<i>Bonnia</i> sp.	52
	<i>Olenellus transitans</i> (Walcott)	19
	<i>Wanneria logani</i> Walcott)	14

Great Basin: Nevada and California
Esmeralda County, Nevada

PC - Paymaster Canyon Measured Section
(includes old LACMIP localities 26849-26852)

Lat. 37°54'45" Long. 117°28'45"

Harkless and Saline Valley formations

"1.3 miles southwest of 7700' peak, Goldfield 1:250,000 AMS sheet, in sec. 25 and 26 (uns) T1N, R40E, Esmeralda County"

Fossiliferous portion of measured stratigraphic section is in a saddle on the Weepah Hills ridge system, south wall of Paymaster Canyon, 14 km north-northeast of Silver Peak, just north of Paymaster mine (Text-fig. 57). This is Stewart's (1970) locality 44, Weepah Hills No. 2 published section.

Collectors: C.A. Nelson (LACMIP collections 26849-26852), L.L. Bohach (LACMIP collections 17019-17023)

Lithology: interbedded limestones, shales and siltstones.

See stratigraphic section (Text-fig. 58) for stratigraphic position of specific collections, lithology and species ranges.

LACMIP Collection 17023 (= unit 16 of Stewart, 1970, p. 157) (*Olenellus transitans* Zone, Subzone unassigned, *Olenellus* Biofacies)

Lithology: pink to brown siltstone to very fine grained sandstone

Fauna:	<i>Olenellus transitans</i> (Walcott)	10
	<i>Bonnia</i> sp.	1

LACMIP Collection 26852 (= unit 16 of Stewart, 1970, p. 157) (*Olenellus transitans* Zone, Subzone unassigned, *Olenellus* Biofacies)

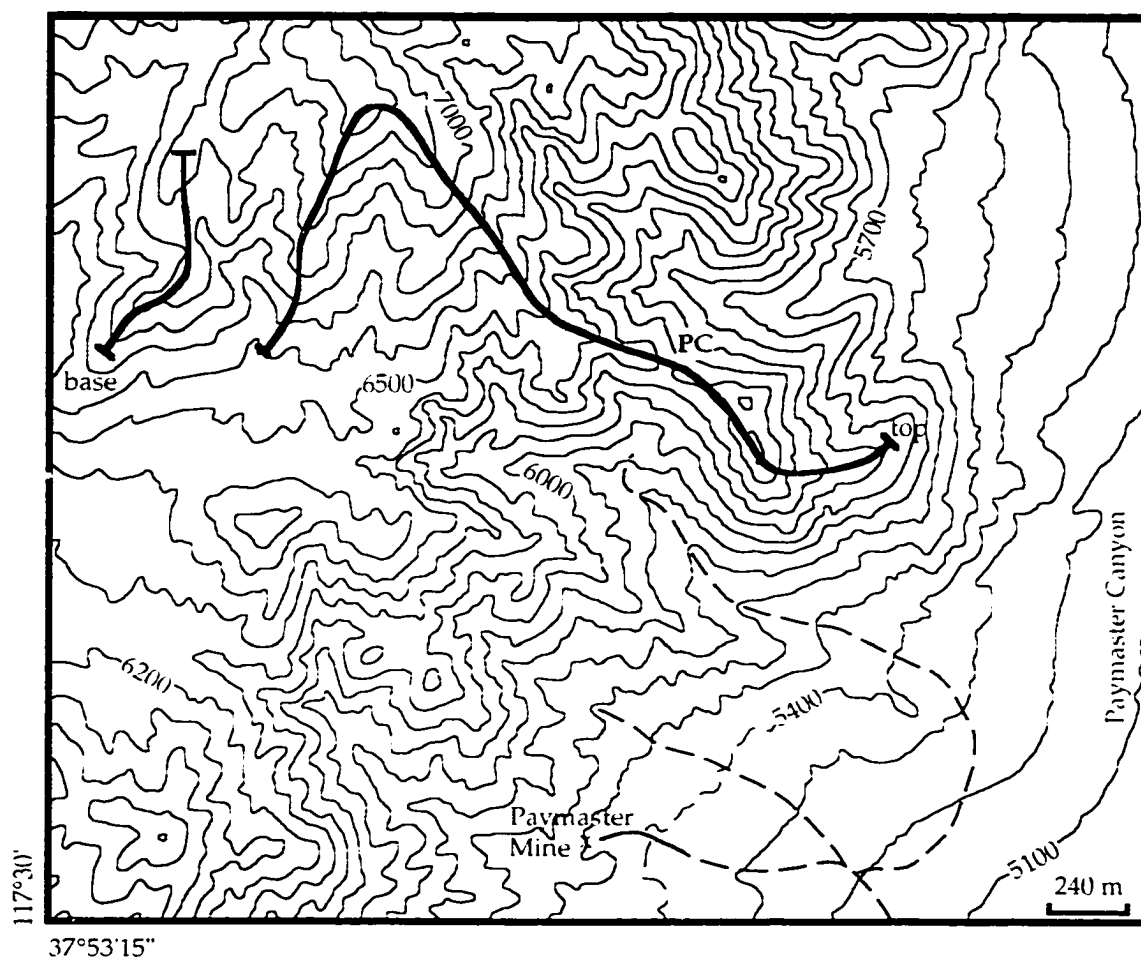
Lithology: pink to brown siltstone to very fine grained sandstone

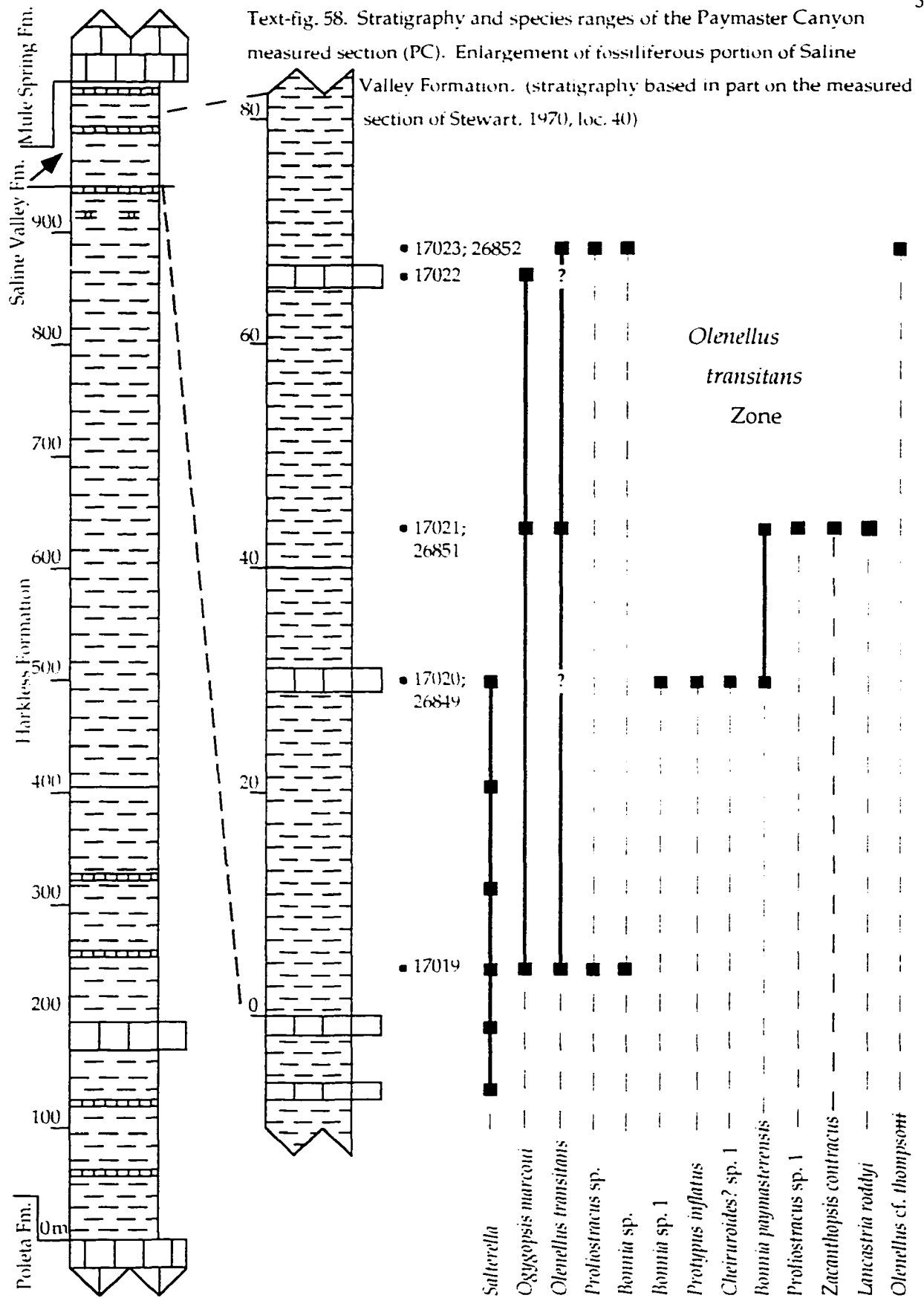
Fauna:	<i>Olenellus transitans</i> (Walcott)	46
	<i>Olenellus</i> cf. <i>thompsoni</i> (Hall)	3
	<i>Proliostracus</i> sp.	4
	<i>Bonnia</i> sp.	1

LACMIP Collection 17022 (= unit 15 of Stewart, 1970, p. 157) (*Olenellus transitans* Zone, Subzone unassigned, ?*Ogygopsis* Biofacies)

Lithology: dark grey limestone (wackestone)

Text-fig. 57. Location map for the Paymaster Canyon measured section (PC).
(topography based on Paymaster Canyon Quadrangle map, Nevada-Esmeralda County, 7.5
minute topographic series, 1:24 000, United States Department of the Interior, Geological
Survey, 1970) Contour interval: 100 feet





Fauna:	<i>Ogygopsis marconi</i> (Whitfield)	4
	<i>Proliostracus</i> sp.	4
	<i>Olenellus transitans</i> ? (Walcott)	1

LACMIP Collection 17021 (= unit 14 of Stewart, 1970, p. 157) (*Olenellus transitans* Zone, Subzone unassigned, ?*Ogygopsis* Biofacies)

Lithology: dark grey shale with cubic cavities

Fauna:	<i>Proliostracus</i> sp. 1	273
	<i>Olenellus transitans</i> (Walcott)	28
	<i>Bonnia paymasterensis</i> n. sp.	20
	<i>Ogygopsis marconi</i> (Whitfield)	19
	<i>Zacanthopsis contractus</i> Palmer	13
	<i>Lancastria roddyi</i> (Walcott)	2
	echinoderm plates	

LACMIP Collection 26851 (= unit 14 of Stewart, 1970, p. 157) (*Olenellus transitans* Zone, Subzone unassigned, ?*Ogygopsis* Biofacies)

Lithology: dark grey shale with cubic cavities

Fauna:	<i>Proliostracus</i> sp. 1	266
	<i>Olenellus transitans</i> (Walcott)	24
	<i>Bonnia paymasterensis</i> n. sp.	40
	<i>Ogygopsis marconi</i> (Whitfield)	32
	<i>Zacanthopsis contractus</i> Palmer	11
	echinoderm plates	

LACMIP Collection 17020 (= unit 12 of Stewart, 1970, p. 157) (*Olenellus transitans* Zone, Subzone unassigned, *Bonnia* Biofacies)

Lithology: grey to light brown limestone (wackestone)

Fauna:	<i>Bonnia paymasterensis</i> n. sp.	49
	<i>Olenellus</i> sp.	numerous fragments
	<i>Bonnia</i> sp. 1	1
	<i>Salterella</i> (small shelly fossils)	

LACMIP Collection 26849 (= unit 12 of Stewart, 1970, p. 157) (*Olenellus transitans* Zone, Subzone unassigned, *Bonnia* Biofacies)

Lithology: white to light grey limestone (packstone to grainstone)

Fauna:	<i>Bonnia paymasterensis</i> n. sp.	505
	<i>Bonnia</i> sp. 1	19
	<i>Protypus inflatus</i> n. sp.	7
	<i>Cheiruroides?</i> sp. 1	3
	<i>Olenellus</i> sp.	fragments

LACMIP Collection 17019 (= base of unit 11 of Stewart, 1970, p. 157) (*Olenellus transitans* Zone, Subzone unassigned, ?*Ogygopsis* Biofacies)

Lithology: dark grey shale

Fauna:	<i>Ogygopsis marcoui</i> (Whitfield)	12
	<i>Olenellus transitans</i> (Walcott)	3
	<i>Proliostracus</i> sp.	1
	<i>Bonnia</i> sp.	1

GF - Goldfield Measured Section

Lat. 37°43'20" Long. 117°19'20"

Poleta Formation

North slope of Indian Springs Canyon, just north of Dago Joe Spring, Montezuma Range, approximately 7.5 km northwest of Goldfield. (Text-fig. 59)

Collector: L.L. Bohach (LACMIP collections 17024-17041)

Lithology: interbedded shales, limestones and sandstones

See stratigraphic section (Text-fig. 60) for stratigraphic position of specific collections, lithology and species ranges.

LACMIP Collection 17041 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: grey to orange mottled limestone (packstone)

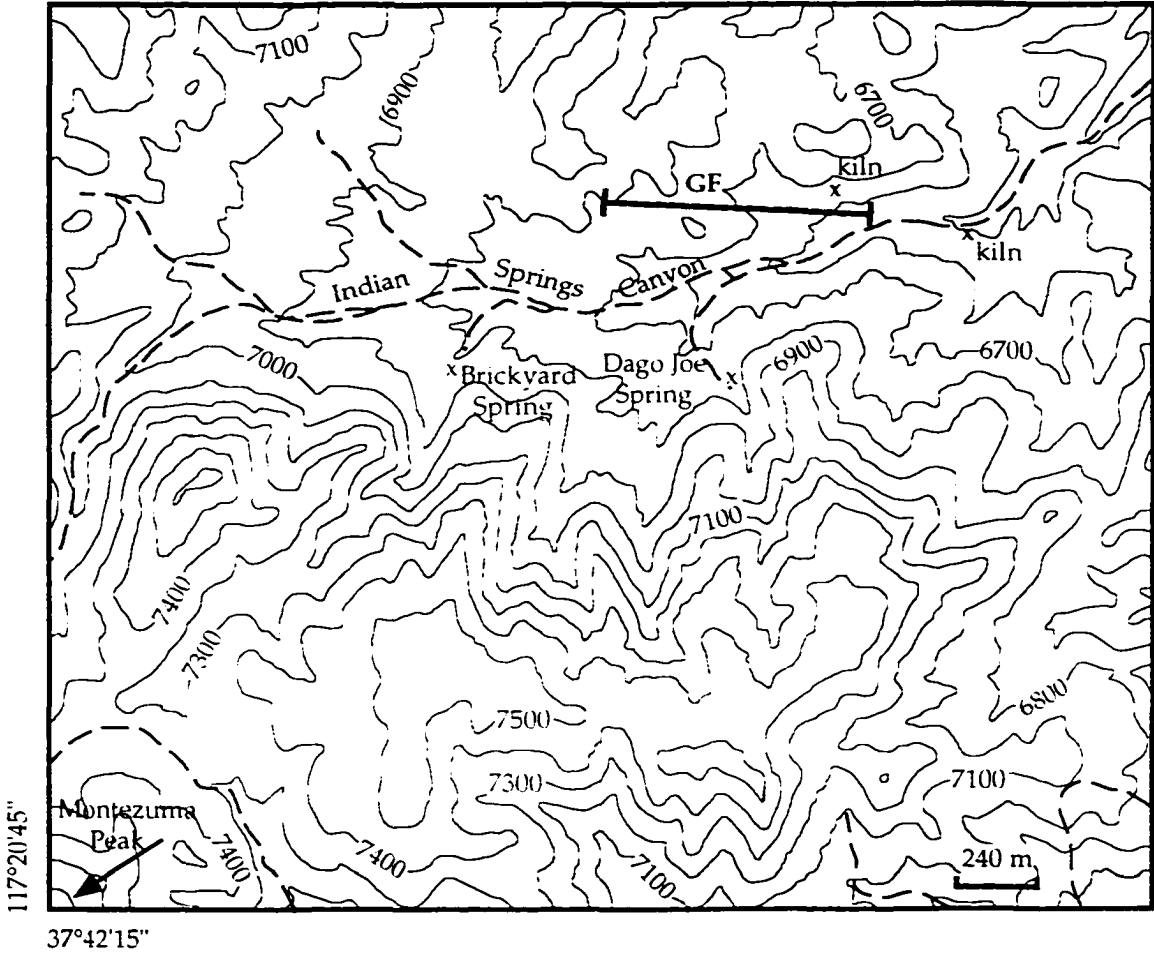
Fauna:	<i>Laudonia prima</i> (Lochman)	4
	<i>Elliptocephala</i> sp.	1
	fragments	abundant

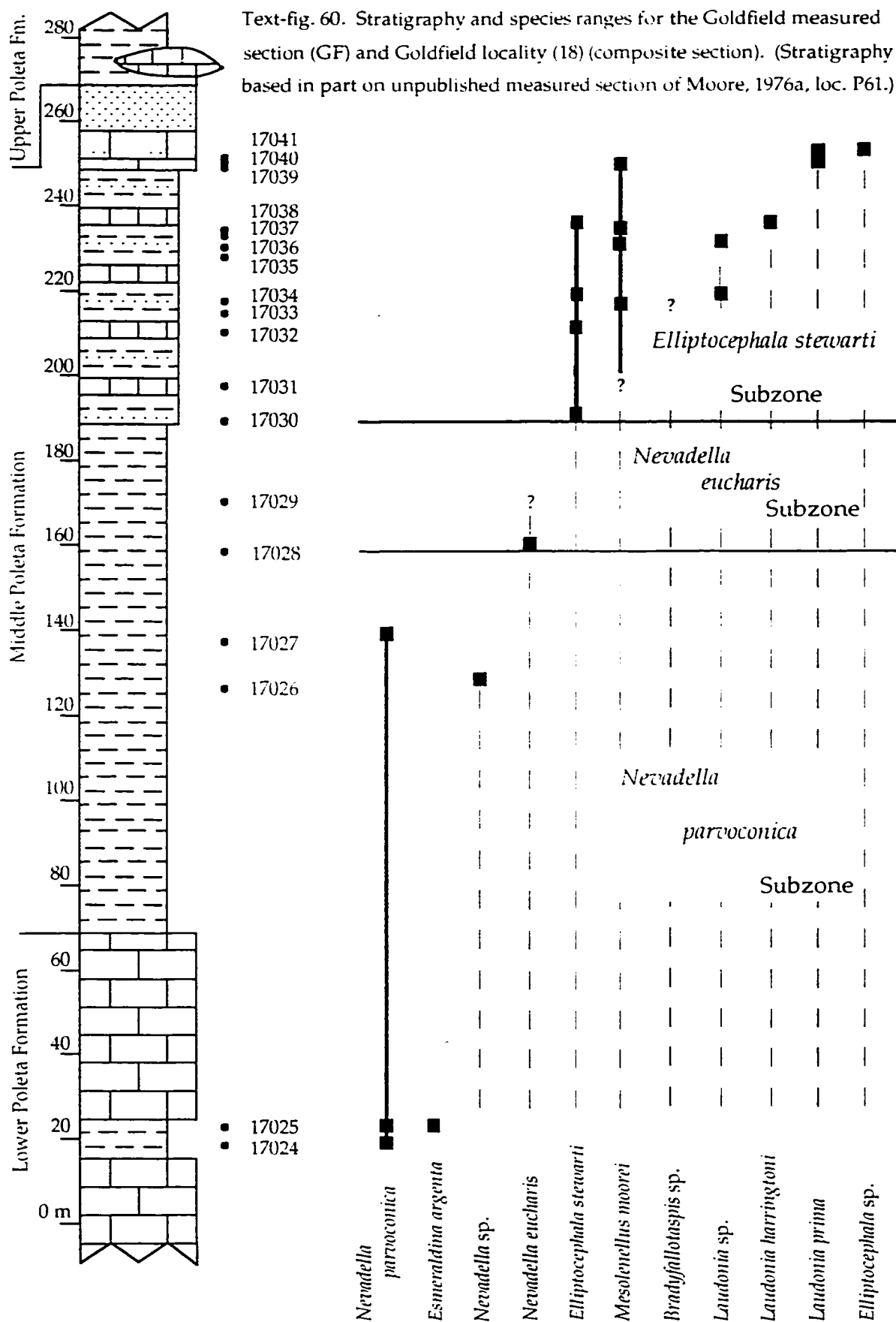
LACMIP Collection 17040 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: cream-colored limestone (mudstone)

Fauna:	<i>Laudonia prima</i> (Lochman)	1

Text-fig. 59. Location map for the Goldfield measured section (GF). (topography based on Montezuma Peak Quadrangle, Nevada-Esmeralda County, 7.5 minute topographic series, 1:24 000, United States Department of the Interior Geological Survey, 1970) contour interval: 100 feet





LACMIP Collection 17039 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: light yellow to brown limestone (wackestone)

Fauna:	<i>Laudonia prima</i> (Lochman)	12
	<i>Mesolenellus moorei</i> n. sp.	2
	fragments	abundant

LACMIP Collection 17038 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: olive green shale with red-purple bands

Fauna:	<i>Laudonia harringtoni</i> n. sp.	8
	<i>Elliptocephala stewarti</i> n. sp.	6

LACMIP Collection 17037 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: dark grey limestone (mudstone to packstone)

Fauna:	<i>Mesolenellus moorei</i> n. sp.	71

LACMIP Collection 17036 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: brown limestone with interbedded shale

Fauna:	<i>Mesolenellus moorei</i> n. sp.	77
	<i>Laudonia</i> sp.	1

LACMIP Collection 17035 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: yellow-brown shale with red-purple bands

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	26

LACMIP Collection 17034 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: orange to brown shale with fine limestone interbeds

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	52
	<i>Laudonia</i> sp.	1

LACMIP Collection 17033 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: cream colored quartzite with mica

Fauna:	<i>Mesolenellus moorei</i> n. sp.	1
	? <i>Bradyfallotaspis</i> sp.	1

LACMIP Collection 17032 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: multi-colored shale to siltstone

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	9

LACMIP Collection 17031 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: olive brown shale with reddish limestone layer (grainstone)

Fauna:	<i>Mesolenellus moorei</i> n. sp.	19

LACMIP Collection 17030 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: fine-grained shaly limestone (mudstone to wackestone)

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	24

LACMIP Collection 17029 (*Nevadella* Zone, *Nevadella eucharis* Subzone, *Nevadella* Biofacies)

Lithology: light brown to orange shale

Fauna:	? <i>Nevadella eucharis</i> (Walcott)	4

LACMIP Collection 17028 (*Nevadella* Zone, *Nevadella eucharis* Subzone, *Nevadella* Biofacies)

Lithology: light brown to orange shale

Fauna:	<i>Nevadella eucharis</i> (Walcott)	11

LACMIP Collection 17027 (*Nevadella* Zone, *Nevadella parvoconica* Subzone, *Nevadella* Biofacies)

Lithology: light brown to orange shale

Fauna:	<i>Nevadella parvoconica</i> (Fritz)	1

LACMIP Collection 17026 (*Nevadella* Zone, *Nevadella parvoconica* Subzone, *Nevadella* Biofacies)

Lithology: light brown to orange shale

Fauna: *Nevadella* sp. abundant fragments

GP - Gold Point Measured Section

(includes old LACMIP localities 26849-26850; ICS localities 1052-1057)

Lat. 117°16'48" Long. 37°21'18"

Poleta and Harkless formations

"Five miles N15°E of Gold Point, in NE1/4, sec. 33 and NW1/4 sec. 34, T6S, R42E, Goldfield 1:250,000 AMS sheet, Esmeralda Co., Nevada"

In canyon carved in north facing slope of Slate Ridge, opening to Lida Valley, 7 km east of Goldpoint. Almost the same locality was measured as that of Stewart (1970; locality 52), except that he measured the crest and the author measured the base of the canyon. (Text-fig. 61) Collections by Nelson and Palmer are integrated into the composite section.

Collectors: A.R. Palmer (ICS collections 1052-1057); C.A. Nelson (LACMIP collections 26849-26850); L.L. Bohach (LACMIP collections 17042-17055)

Lithology: interbedded shales, limestones and sandstones

See stratigraphic section (Text-fig. 62) for stratigraphic position of specific collections, lithology and species ranges.

ICS Collection 1057 (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, Wanneriid Biofacies)

Lithology: brown sandstone to siltstone

Fauna: *Gabriellus poletensis* n. sp. 2
Elliptocephala stewarti n. sp. 1

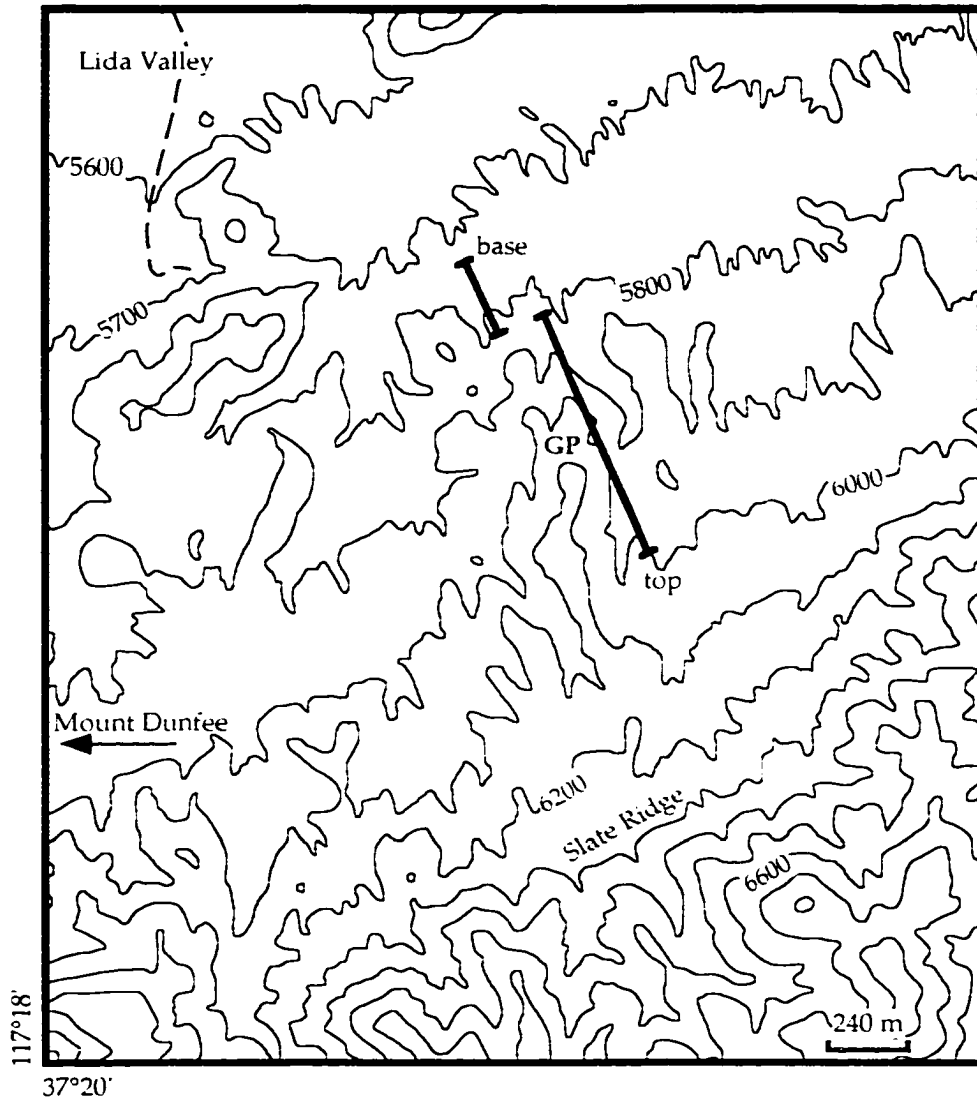
LACMIP Collection 17055 (along strike to GP9) (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, *Ekvipagetia* Biofacies)

Lithology: grey to brown limestone (mudstone to wackestone)

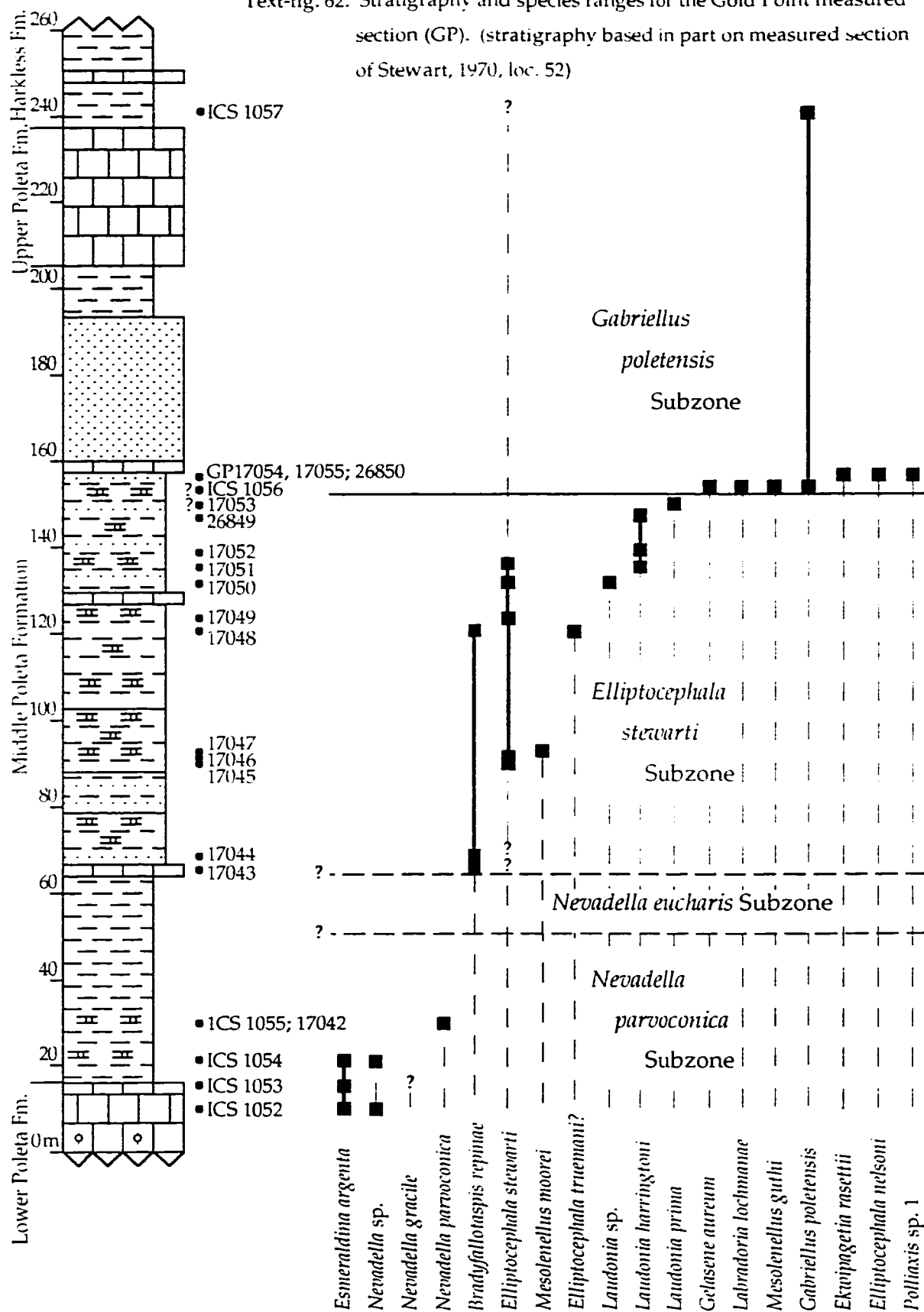
Fauna: *Elliptocephala nelsoni* n. sp. 14
Ekvipagetia rasettii n. sp. 2

LACMIP Collection 17054 (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, *Ekvipagetia* Biofacies)

Text-fig. 61. Location map for the Gold Point measured section (GP).
(topography based on Gold Point Quadrangle map, Nevada-Esmeralda County,
7.5 minute topographic series, 1:24 000, United States Department of the Interior,
Geological Survey, 1968) contour interval: 100 feet



Text-fig. 62. Stratigraphy and species ranges for the Gold Point measured section (GP). (stratigraphy based in part on measured section of Stewart, 1970, loc. 52)



Lithology: dark grey limestone with shaly partings (mudstone to wackestone)

Fauna:	<i>Ekwipagetia rasettii</i> n. sp.	40
	<i>Elliptocephala nelsoni</i> n. sp.	18

LACMIP Collection 26850 (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, *Ekwipagetia* Biofacies)

Lithology: limestone with shaly partings (mudstone to wackestone)

Fauna:	<i>Elliptocephala nelsoni</i> n. sp.	21
	<i>Ekwipagetia rasettii</i> n. sp.	5
	<i>Polliaxis</i> sp. 1	1

ICS Collection 1056 (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, *Labradoria* Biofacies)

Lithology: grey limestone (wackestone)

Fauna:	<i>Gabriellus poletensis</i> n. sp.	13
	<i>Gelasene aureum</i> n. sp.	12
	<i>Labradoria lochmanae</i> n. sp.	11
	<i>Mesolenellus guthi</i> n. sp.	6
	unassigned wanneriids	10

LACMIP Collection 17053 (talus collection) (*Elliptocephala* Zone, ?*Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: light grey limestone (packstone)

Fauna:	<i>Laudonia prima</i> (Lochman)	38

LACMIP Collection 26849 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: brown limestone (wackestone to grainstone)

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	649
	<i>Laudonia harringtoni</i> n. sp.	46

LACMIP Collection 17052 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: brown limestone (packstone to grainstone)

Fauna:	<i>Laudonia harringtoni</i> n. sp.	295

LACMIP Collection 17051 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies,

Lithology: yellow to brown limestone with interbedded pink shale

Fauna:	<i>Laudonia harringtoni</i> n. sp.	44
	<i>Elliptocephala stewarti</i> n. sp.	4

LACMIP Collection 17050 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: pink shale

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	19
	<i>Laudonia</i> sp.	3

LACMIP Collection 17049 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: light grey limestone (packstone to grainstone)

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	196

LACMIP Collection 17048 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: cream-colored quartzite with mica and calcareous cement

Fauna:	<i>Elliptocephala truemani?</i> (Walcott)	48
	<i>Bradyfallotaspis reptinae</i> n. sp.	8
	brachiopods	

LACMIP Collection 17047 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: red to yellow limestone (wackestone)

Fauna:	<i>Mesolenellus moorei</i> n. sp.	41

LACMIP Collection 17046 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: red to yellow limestone (wackestone)

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	5

LACMIP Collection 17045 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: red to yellow limestone (wackestone)

Fauna: *Elliptocephala stewarti* n. sp. 3

LACMIP Collection 17044 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, ?Wanneriid Biofacies)

Lithology: light grey limestone (wackestone)

Fauna: *Elliptocephala stewarti* n. sp. 7

Bradyfallotaspis repinae n. sp. 3

LACMIP Collection 17043 (*Elliptocephala* Zone, ?*Elliptocephala stewarti* Subzone, Biofacies unassigned)

Lithology: grey limestone (mudstone to wackestone)

Fauna: *Bradyfallotaspis repinae* n. sp. 7

Elliptocephala stewarti n. sp. 2

small shelly fossils

LACMIP Collection 17042 (*Nevadella* Zone, *Nevadella parvoconica* Subzone, *Nevadella* Biofacies)

Lithology: thinly interbedded yellow-brown shale and limestone

Fauna: *Nevadella parvoconica* (Fritz) 23

brachiopods

ICS Collection 1055 (*Nevadella* Zone, *Nevadella parvoconica* Subzone, *Nevadella* Biofacies)

Lithology: thinly interbedded yellow-brown shale and limestone

Fauna: *Nevadella parvoconica* (Fritz) 23

ICS Collection 1054 (*Nevadella* Zone, *Nevadella parvoconica* Subzone, ?*Nevadella* Biofacies)

Lithology: thin-bedded shale and limestone

Fauna: *Nevadella* sp. 7

Esmeraldina argenta (Walcott) 1

helcionellids (Gastropoda)

phosphatic tubes

ICS Collection 1053 (*Nevadella* Zone, *Nevadella parvoconica* Subzone, ?*Nevadella* Biofacies)

Lithology: grey and orange mottled limestone (wackestone)

Fauna:	<i>Nevadella gracile</i> (Walcot.)	4
	<i>Esmeraldina argenta</i> (Walcott)	1
	unassigned trilobite meraspid	2
	archaeocyathids	abundant

ICS Collection 1052 (*Nevadella* Zone, *Nevadella parvoconica* Subzone, Biofacies unassigned)

Lithology: grey and orange mottled limestone (mudstone to wackestone)

Fauna:	<i>Esmeraldina argenta</i>	7
	<i>Nevadella</i> sp.	2
	helcionellids (Gastropoda)	
	archaeocyathids	

Northern Inyo County, California

CF - Cedar Flat Measured Section

(includes old LACMIP localities 26777, 26783, 26826, 26866)

Lat. 37°17'38" Long. 118°07'48"

Poleta Formation

Along a NE-SW trending ridge, Cedar Flat region, Westgard Pass, approximately 2 km northeast of junction for Highway 168 and Ancient Bristle Cone Pine Forest Road. (Text-fig. 63)

This area has been intensively collected by Nelson, Guth and others, and the collections are tied into the stratigraphic section.

Collectors: L.L. Bohach (LACMIP collections 17056-17066); C.A. Nelson (LACMIP collections 26783, 26826); C.A. Nelson and B. Akpati (LACMIP collection 26780b); G.W. Stuckey (LACMIP collection 26777), P.L. Guth (LACMIP collection 26866)

Lithology: interbedded shales, limestones and sandstones

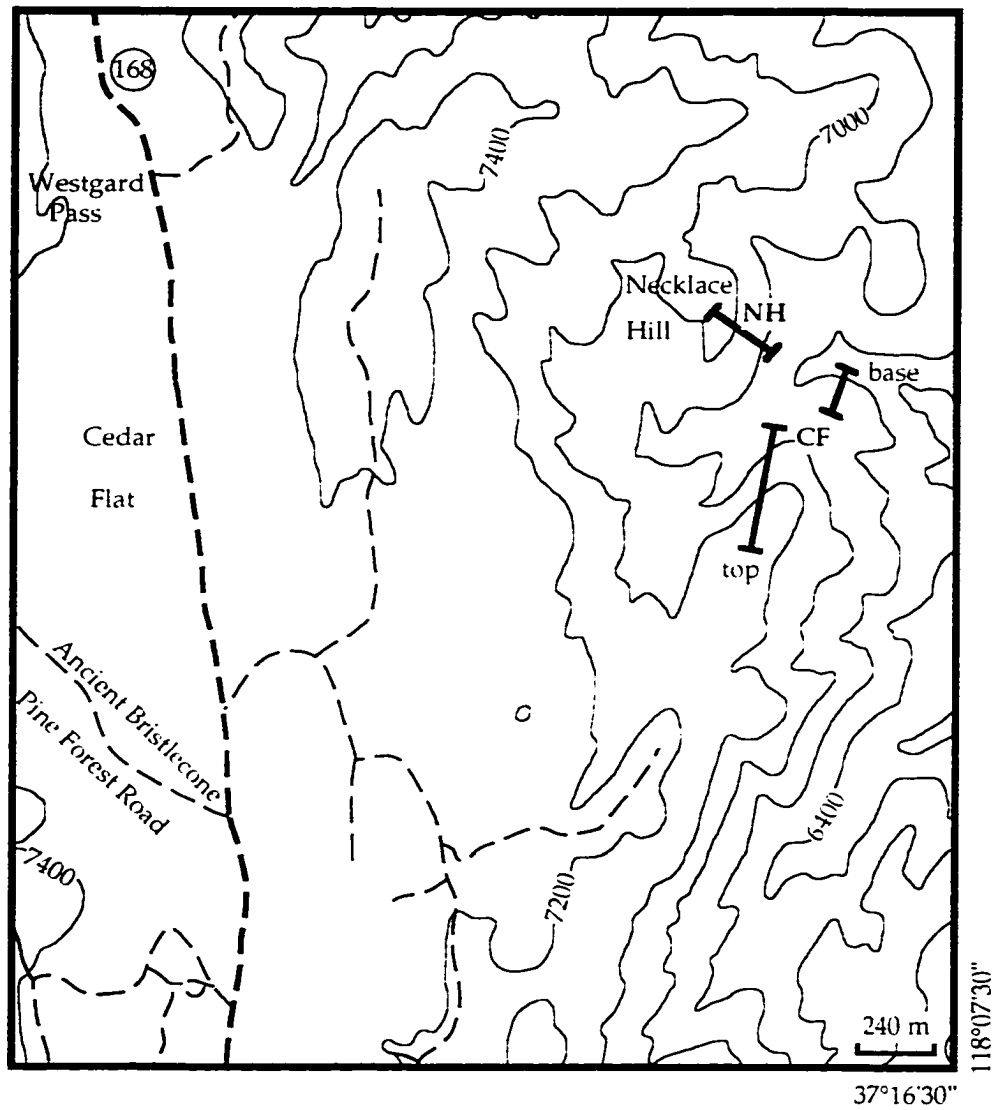
See stratigraphic section (Text-fig. 64) for stratigraphic position of specific collections, lithology and species ranges.

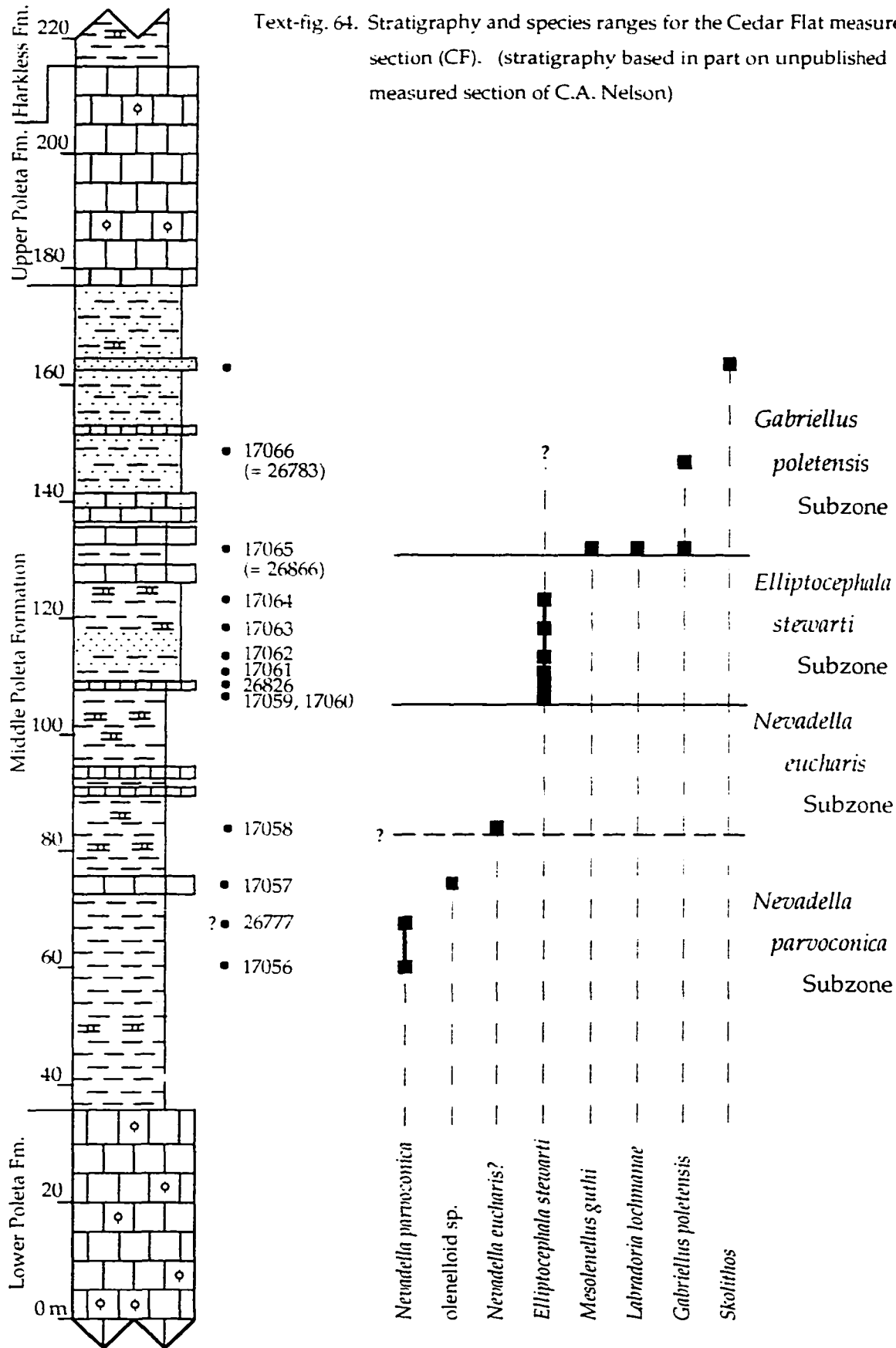
LACMIP Collection 17066 (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, Wanneriid Biofacies)

Lithology: light brown to green siltstone

Fauna:	? <i>Elliptocephala stewarti</i> n. sp.	4
	<i>Gabriellus poletensis</i> n. sp.	2

Text-fig. 63. Location map for measured sections of the Cedar Flat area. Sections NH, CF. (topography based on Westgard Pass Quadrangle, California-Inyo County, 7.5 minute topographic series, 1:24 000, United States Department of the Interior, Geological Survey, 1987) contour interval: 200 feet





LACMIP Collection 26783 (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, Wanneriid Biofacies)

Lithology: light brown to green siltstone

Fauna:	<i>?Elliptocephala stewarti</i> n. sp.	13
	<i>Gabriellus poletensis</i> n. sp.	1

LACMIP Collection 17065 (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, *Labradoria* Biofacies)

Lithology: light green-grey shale

Fauna:	<i>Mesolenellus guthi</i> n. sp.	18
	<i>Labradoria lochmanae</i> n. sp.	8
	<i>Gabriellus poletensis</i> n. sp.	1

LACMIP Collection 26866 (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, *Labradoria* Biofacies)

Lithology: light green-grey shale

Fauna:	<i>Labradoria lochmanae</i> n. sp.	1

LACMIP Collection 17064 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: light green shale

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	29

LACMIP Collection 17063 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: olive green to yellow shale

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	49

LACMIP Collection 17062 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: light green shale to brown siltstone

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	67

LACMIP Collection 17061 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: light grey to green siltstone

Fauna: *Elliptocephala stewarti* n. sp. 7

LACMIP Collection 26826 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: grey limestone (wackestone), rough textured at top of bed: "elephantide limestone"

Fauna: *Elliptocephala stewarti* n. sp. 7

LACMIP Collection 17060 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: light grey to green shale

Fauna: *Elliptocephala stewarti* n. sp. 2

LACMIP Collection 17059 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: dark grey shale

Fauna: *Elliptocephala stewarti* n. sp. 4

LACMIP Collection 17058 (*Nevadella* Zone, ?*Nevadella eucharis* Subzone, *Nevadella* Biofacies)

Lithology: dark olive green shale

Fauna: ?*Nevadella eucharis* (Walcott) 1

LACMIP Collection 26777 (exact stratigraphic horizon unknown) (*Nevadella* Zone, *Nevadella parvoconica* Subzone, *Nevadella* Biofacies)

Lithology: dark green to grey shale

Fauna: *Nevadella parvoconica* (Fritz) 1

LACMIP Collection 17057 (*Nevadella* Zone, *Nevadella parvoconica* Subzone, Biofacies unassigned)

Lithology: white laminated limestone (mudstone)

Fauna: *Olenellina* sp. 1 (thoracic segment)

LACMIP Collection 17056 (*Nevadella* Zone, *Nevadella parvoconica* Subzone, *Nevadella* Biofacies)

Lithology: dark green to grey shale

Fauna: *Nevadella parvoconica* (Fritz) 13

NH - Necklace Hill Measured Section
(includes old LACMIP localities 26780a,b, BM 39)
(locality 22 tied into section)

Lat. 37°17'47" Long. 118°07'55"

Poleta Formation

One east side of Necklace Hill (elevation 7083 feet), facing Cedar Flat section, Cedar Flat area, Westgard Pass, east of Big Pine. (Text-fig. 63)

Collectors: L.L. Bohach (LACMIP collections 17067-17080); P.L. Guth (LACMIP collection 26780a); C.A. Nelson and B. Akpati (LACMIP collection 26780b)

Lithology: interbedded shales, limestones and sandstones

See stratigraphic section (Text-fig. 65) for stratigraphic position of specific collections, lithology and species ranges.

LACMIP Collection 17080 (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, Wanneriid Biofacies)

Lithology: light brown siltstone

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	15
	<i>Gabriellus poletensis</i> n. sp.	7

LACMIP Collection BM 39 (exact locality not specified) (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, Wanneriid Biofacies)

Lithology: light brown to green siltstone

Fauna:	<i>Gabriellus poletensis</i> n. sp.	1

LACMIP Collection 26780b (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, Wanneriid Biofacies)

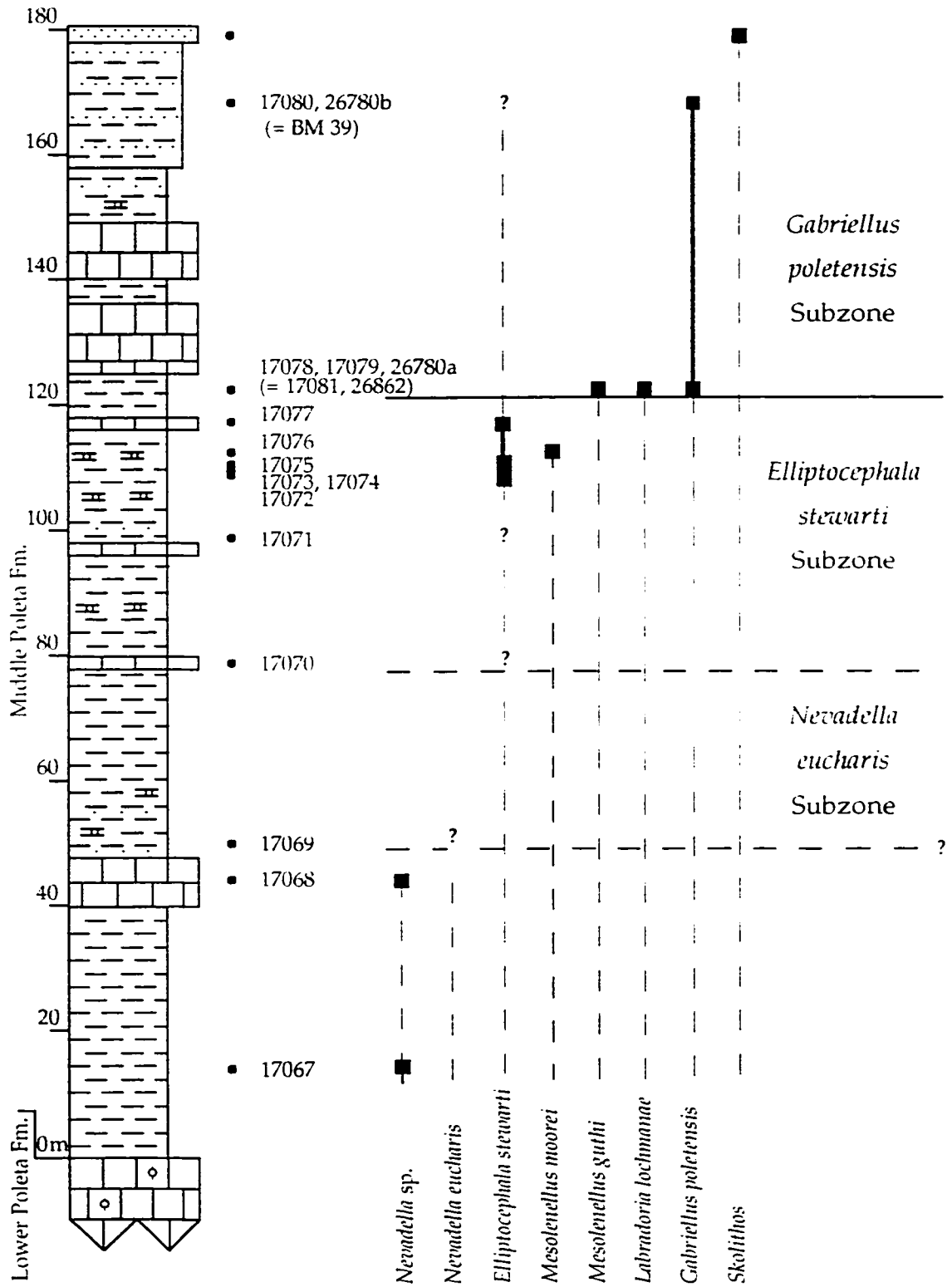
Lithology: light brown siltstone

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	3
	<i>Gabriellus poletensis</i> n. sp.	1

LACMIP Collection 17079 (collected near summit of hill, where section begins to repeat)
(*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, *Labradoria* Biofacies)

Lithology: green to grey shale

Text-fig. 65. Stratigraphy and species ranges for the Necklace Hill measured section (NH)
with locality 22 collections tied into section. (measured by author)



Fauna:	<i>Mesolenellus guthi</i> n. sp.	11
	<i>Labradora lochmanae</i> n. sp.	10

LACMIP Collection 17078 (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, *Labradora* Biofacies)

Lithology: green-grey shale

Fauna:	<i>Mesolenellus guthi</i> n. sp.	37
	<i>Labradora lochmanae</i> n. sp.	20

LACMIP Collection 26780a (*Elliptocephala* Zone, *Gabriellus poletensis* Subzone, *Labradora* Biofacies)

Lithology: green to grey shale

Fauna:	<i>Mesolenellus guthi</i> n. sp.	43
	<i>Labradora lochmanae</i> n. sp.	14
	<i>Gabriellus poletensis</i> n. sp.	3

LACMIP Collection 17077 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: light green-grey shale

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	28

LACMIP Collection 17076 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: light yellow-brown sandstone

Fauna:	<i>Mesolenellus moorei</i> n. sp.	18

LACMIP Collection 17075 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: green-grey shale

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	8

LACMIP Collection 17074 (from uppermost part of bed yielding NH 9) (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: cream-colored sandstone

Fauna:	<i>Elliptocephala stewarti</i> n. sp.	30

LACMIP Collection 17073 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: cream-colored sandstone/quartzite

Fauna: *Elliptocephala stewarti* n. sp. 80

LACMIP Collection 17072 (*Elliptocephala* Zone, *Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: light green-brown shale

Fauna: *Elliptocephala stewarti* n. sp. 3

LACMIP Collection 17071 (*Elliptocephala* Zone, ?*Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: white sandstone/quartzite

Fauna: ?*Elliptocephala stewarti* n. sp. 1

LACMIP Collection 17070 (*Elliptocephala* Zone, ?*Elliptocephala stewarti* Subzone, Wanneriid Biofacies)

Lithology: green to grey shale

Fauna: ?*Elliptocephala stewarti* n. sp. many fragments

LACMIP Collection 17069 (*Nevadella* Zone, ?*Nevadella eucharis* Subzone, *Nevadella* Biofacies)

Lithology: olive green shale

Fauna: ?*Nevadella eucharis* (Walcott) 5

LACMIP Collection 17068 (*Nevadella* Zone, Subzone unassigned, *Nevadella* Biofacies)

Lithology: white limestone (mudstone)

Fauna: *Nevadella* sp. 1

LACMIP Collection 17067 (*Nevadella* Zone, Subzone unassigned, *Nevadella* Biofacies)

Lithology: dark green to grey shale

Fauna: *Nevadella* sp. 5

WM - Waucoba Mountain Measured Section
(includes old LACMIP localities 26772, 26809, 26810, 26818, 26915)

Lat. 37°04'35" Long. 118°06'50" (at about middle of section)

Harkless and Saline Valley formations

Section is measured west and northwest of Andrews Mountain, at end of Hines Road, climbing onto Papoose Flat. (Text-fig. 66)

Collectors: L.L. Bohach (LACMIP collections 17082-17085); C.A. Nelson (LACMIP collections 26772, 26809, 26810, 26818, 26915)

See stratigraphic section (Text-fig. 67) for stratigraphic position of specific collections, lithology and species ranges.

LACMIP Collection 17085 (all collected along line of strike) (*Olenellus transitans* Zone, Subzone unassigned, *Ogygopsis* Biofacies)

Lithology: light silvery-grey slate

Fauna: *Ogygopsis typicalis* (Resser) 45

LACMIP Collections 26772, 26809, 26810, 26818, 26915 (*Olenellus transitans* Zone, Subzone unassigned, *Ogygopsis* Biofacies)

Lithology: light silvery-grey slate

Fauna: *Ogygopsis typicalis* (Resser) 33

LACMIP Collection 17084 (*Olenellus transitans* Zone, Subzone unassigned, Biofacies unassigned)

Lithology: nodular limestone

Fauna: *Salterella* (small shelly fossils)

LACMIP Collection 17083 (?*Olenellus transitans* Zone, Subzone unassigned, ?*Olenellus* Biofacies)

Lithology: green slate

Fauna: *Olenellus* sp. 1

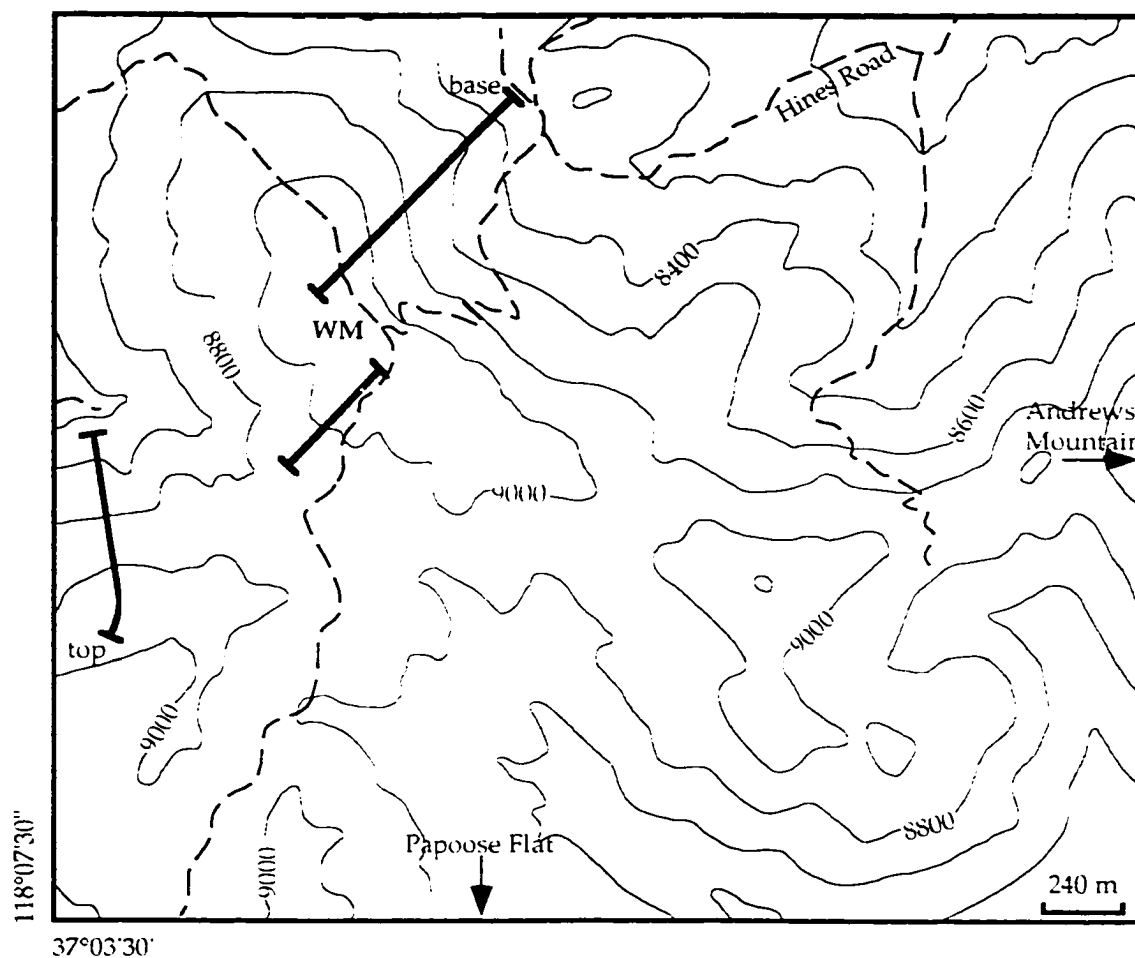
LACMIP Collection 17082 (?*Olenellus transitans* Zone, Subzone unassigned, ?*Olenellus* Biofacies)

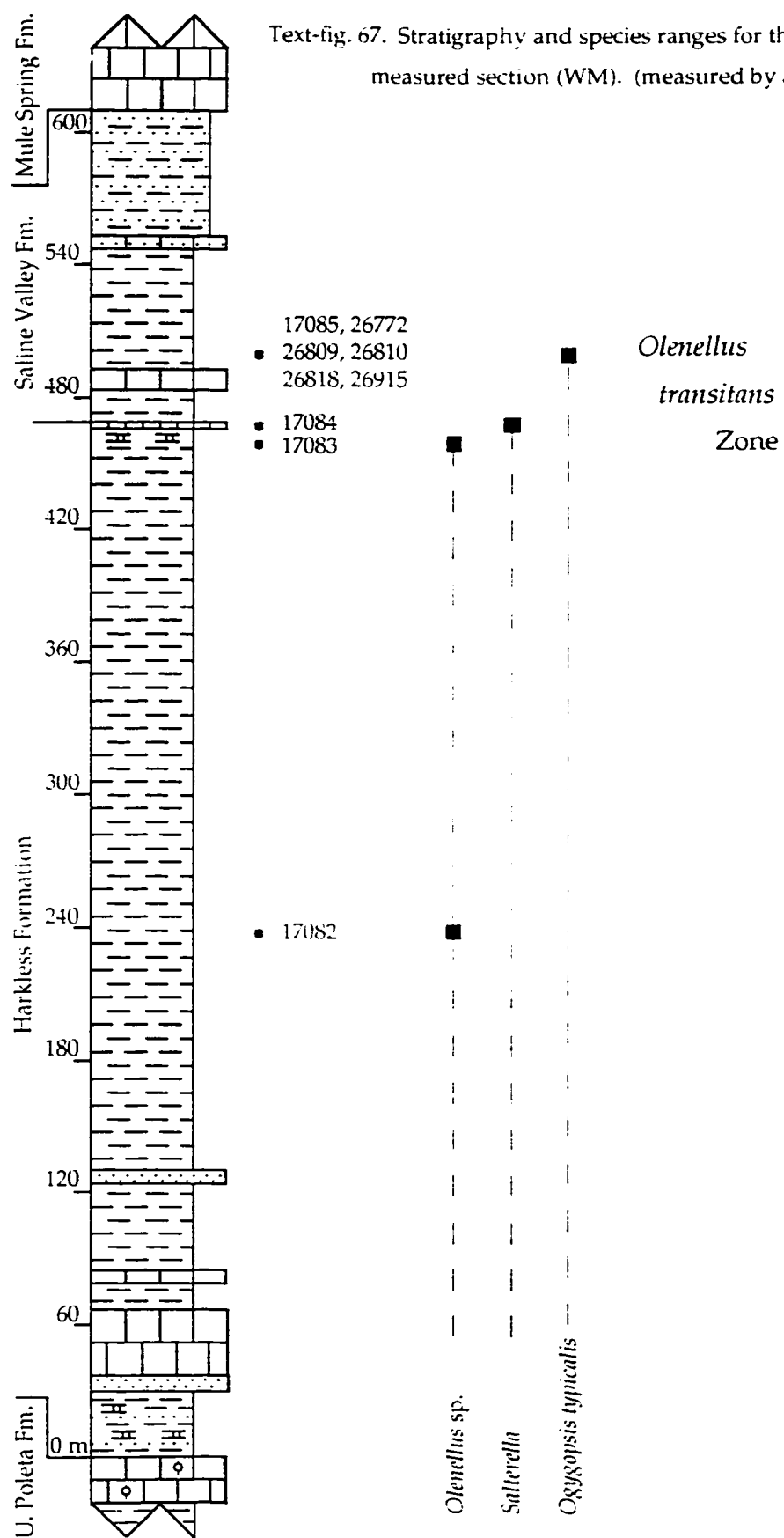
Lithology: brown slate

Fauna: *Olenellus* sp. 9

Text-fig. 66. Location map for the Waucoba Mountain measured section (WM).

(topography based on Waucoba Mountain Quadrangle map, California-Inyo County, 7.5 minute topographic series, 1:24 000, United States Department of the Interior Geological Survey, 1987)
contour interval: 200 feet





Part II Localities without Measured Sections
British Columbia

1. Mt. Kerkeslin Locality (GSC locality 57672)

Lat. 52°39'N Long. 117°50'W

Mural (Tah) Formation

Mount Kerkeslin, Jasper National Park, Banff-Jasper highway, section AC-99 at 149-152 feet in section. (GSC report C-2-1965)

collector: J.D. Aitken, 1963

Lithology: medium to coarse-grained mottled grey and white limestone

Fauna:	<i>Polliaxis muralensis</i> n. sp.	2
	<i>Gabriellus</i> sp. 1	4
	ptychopariid id.	9
	wanneriid new genus	5
	<i>Labradoria</i> sp.	2
	<i>Bonnina</i> sp.	1
	<i>Paterina</i> (Brachiopoda)	
	<i>Stenethecoides</i> (Gastropoda)	

Only the first two species are described in this work as a supplement to collections of similar species from the field areas.

2. Grainger Range Locality (GSC locality 23916)

Olenellus transitans Zone, ?*Wanneria logani* Subzone, Biofacies unassigned
at approximately Lat. 50°03' Long. 115°43'

Eager Formation

"at 11, 200⁵⁷ on Brg. 92° from Mud Creek at highway"

Interpreted to be on unnamed mountain ridge directly south of Mount Watson, approximately 8 km southeast of Canal Flats at about 5000 feet.

Collector: G.B. Leech

Lithology: coarse grained purple to white limestone

(*Olenellus transitans* Zone, ?*Wanneria logani* Subzone, Biofacies unassigned)

Fauna:	aff. <i>Mesonacis leechi</i> n. sp.	10
	wanneriid sp.	2

⁵⁷ This locality description given by Leech is problematic since the highest point along this bearing is approximately 6500 feet. The latitude and longitude cited are estimates based on where the Eager Formation is mapped along this bearing.

Bonnaspis fieldensis (Walcott) 100
Stenethecoides (Gastropoda)
 helcionellids (Gastropoda)

3. Hughes Range Locality (GSC locality 23851)

Nevadella Zone, *Nevadella eucharis* Subzone, *Nevadella* Biofacies

"at 7400 feet on Brg. 110° from Lat. 50°00' Long. 115°37'30"

Cranbrook Formation

Hughes Range, about 14 km northeast of Skookumchuck.

Collector: G.B. Leech

Lithology: cream colored, fine grained sandstone, well-cemented

(*Nevadella* Zone, *Nevadella eucharis* Subzone, *Nevadella* Biofacies)

Fauna: *Nevadella eucharis* (Walcott) 383

4. St. Eugene Mission Locality

Olenellus transitans Zone, ?*Wanneria dunnae* Subzone, *Olenellus* Biofacies

Lat. 49°35'20" Long. 115°43'50"

Eager Formation

At side of road on north bank of the St. Mary River, 2.5 km northeast of St. Eugene Mission, Kootenay Indian Reserve.

Collector: L.L. Bohach

Lithology: cleaved shales

Fauna: *Olenellus ricei* n. sp. 52

5. Cranbrook Rifle Range Locality

Olenellus transitans Zone, *Wanneria dunnae* Subzone, *Olenellus* Biofacies

Lat. 49°35'20" Long. 115°42'30"

Basal Eager Formation

On crown land leased to the Cranbrook Rifle Club, 6.5 km northeast of Cranbrook, just south of the St. Mary River. Best (1952) and Schofield (1922) list other localities nearby, but this was the only one of their localities that the author was able to locate .

Collectors: various, including G. Sutherland, F. Dunne, R. Smith, D. Ferguson, L.L. Bohach and collections compiled by R. Best, University of British Columbia.

Lithology: multicolored shales with thin grit layers

(specimen counts from Sutherland, U of A collection)

Fauna: *Olenellus ricei* n. sp. 1965

<i>Wanneria dunnae</i> n. sp.	198
<i>Mesonacis eagerensis</i> (Best)	37
<i>Bonnina ornata</i> n. sp.	1
? <i>Bonnina grandis</i> n. sp.	
<i>Bonnaspis fieldensis</i> (Walcott)	21
<i>Proliostracus</i> sp. 1	
<i>Anomalocaris</i> (Arthropoda)	3
<i>Tuzoia</i> (crustacean)	9

6. Marysville Locality

Olenellus transitans Zone, ?*Wanneria dunnae* Subzone, Biofacies unassigned

Lat. 49°36'50" Long. 115°56'25"

Eager Formation

On south bank of the St. Mary River, approximately 2 km south-southeast of town of Marysville.

Collector: P. Ransom

Lithology: cleaved and tectonically deformed shale

Fauna: *Mesonacis eagerensis* (Best) 2

7. Hellroaring Creek Locality

Olenellus transitans Zone, ?*Proliostracus buelnaensis* Subzone, ?*Proliostracus* Biofacies

Lat. 49°30'48", Long. 116°16'24"

Eager Formation

Approximately 5 km southeast of Mt. Evans summit, Moyie Range, Purcell Mountains.

Collector: P. Ransom

Lithology: low-grade phyllite Fossils, including articulated material, retain much of their original convexity, but have been highly distorted.

Fauna: ?*Olenellus transitans* (Walcott) 20

?*Proliostracus buelnaensis* (Lochman) 12

Wenkchemnia? sp. 1 5

Great Basin: Nevada and California
Esmeralda County, Nevada

8. Miller Mountain Locality (LACMIP locality 24411)

Olenellus transitans Zone, Subzone unassigned, *Ogygopsis* Biofacies

stratigraphic horizon questionable - probably Upper Harkless Formation.

At Miller Mountain, in Esmeralda County, Nevada, near border with Mineral County, California, north of Highway 8.⁵⁸

Collector: C.A. Nelson

Lithology: dark grey shale

Fauna:	<i>Ogygopsis batis</i> (Walcott)	92
	<i>Perissopyge triangulata</i> Blaker <i>et al.</i> , 1996 ⁵⁹	85
	<i>Olenellus cf. nevadensis</i> (Walcott)	45
	<i>Helicoplacus</i> (Echinodermata)	
	sponge spicules	
	brachiopods	

9. Weepah Hills Locality (LACMIP locality 26877)

Lat. 37°52' Long. 117°33'58"

Saline Valley Formation

Southern Weepah Hills, 14 km north-northeast of Silver Peak

Collector: C.A. Nelson

Lithology: interbedded shales and limestones:

1. greenish shales, immediately underlying Mule Spring Limestone

Olenellus transitans Zone, Subzone unassigned, ?*Olenellus* Biofacies

Fauna:	<i>Olenellus cf. nevadensis</i> (Walcott)	1

2. first limestone bed underlying Mule Spring Limestone, dark grey, 8-10' bed

Olenellus transitans Zone, Subzone unassigned, *Ogygopsis* Biofacies

Fauna:	<i>Ogygopsis marcoui</i> (Whitfield)	18
	<i>Proliostracus</i> sp.	1

3. grey phyllitic shale underlying limestone bed (laterally equivalent to unit 14 of Paymaster Canyon section)

Olenellus transitans Zone, Subzone unassigned, *Ogygopsis* Biofacies

⁵⁸ This is the only locality information that can be determined from map provided by collector.

⁵⁹ This trilobite is not described as it was already being studied by others. It has now been published by Blaker, Nelson and Peel, (1996).

Fauna:	<i>Proliostracus</i> sp. 2	35
	<i>Ogygopsis marcoui</i> (Whitfield)	32
	<i>Bonnina paymasterensis</i> n. sp.	31
	<i>Olenellus</i> cf. <i>nevadensis</i> (Walcott)	4
x	<i>Zacanthopsis</i> id.	1

10. Goat Island Locality

(LACMIP localities 26869, 26870)

Elliptocephala Zone, *Gabriellus poletensis* Subzone, Wanneriid Biofacies

Lat. 37°45'29" Long. 117°36'40"

Poleta Formation

"Northwest tip of Goat Island, NE1/4, sec. 14, T2S, R39E, Silver Peak 30' Quad., Esmeralda Co., Nevada."

On "island" of rock in Clayton Valley, Goat Island, 2 km northeast of Silver Peak.

Collectors: C.A. Nelson and R. Moiola (26869); C.A. Nelson and J. Albers (26870)

Lithology and Fauna:

1. olive green shale, 15 feet above *Skolithos* quartzite (26870)

Fauna:	<i>Mummaspis albersi</i> n. sp.	17
	<i>Gabriellus poletensis</i> n. sp.	8

2. olive green to grayish shale, just below *Skolithos* quartzite (26869)

Fauna:	<i>Gabriellus poletensis</i> n. sp.	44
	<i>Mummaspis albersi</i> n. sp.	10

11. Alcatraz Island Locality #1 (LACMIP locality 26872)

Elliptocephala Zone, *Gabriellus poletensis* Subzone, Wanneriid Biofacies

approximately Lat. 37°45' Long. 117°37'

basal Harkless Formation, no more than 50-75 feet above base of formation

"North Side of Alcatraz Island, south edge of sec. 23, T2S, R39E, Silver Peak 30' quad., Esmeralda Co., Nevada."

On "island" of rock in Clayton Valley, Alcatraz Island, 1.5 km southeast of Silver Peak.

Collector: C.A. Nelson

Lithology: grey shale

Fauna:	<i>Mummaspis</i> sp.	2

12. Alcatraz Island Locality #2 (LACMIP locality 26873)

Elliptocephala Zone, *Wannerellus alcatrazensis* Subzone, Wanneriid Biofacies

approximately Lat. 37°45' Long. 117°37'

basal Harkless Formation, approximately 175-200 feet above base of formation

"Alcatraz Island, south edge of sec. 23, T2S, R39E, Silver Peak 30' quad., Esmeralda Co., Nevada."

On "island" of rock in Clayton Valley, Alcatraz Island, 1.5 km southeast of Silver Peak.

Collector: C.A. Nelson

Lithology: grey shale

Fauna: *Wannerellus alcatrazensis* n. sp. 14

13. Alcatraz Island Locality #3 (LACMIP locality 26868)

Elliptocephala Zone, *Gabriellus poletensis* Subzone, Wanneriid Biofacies

approximately Lat. 37°45' Long. 117°37'

Poleta Formation, above *Skolithos* quartzite?

"Central part of Alcatraz Island, south edge of sec. 23, T2S, R39E, Silver Peak 30' quad., Esmeralda Co., Nevada."

On "island" of rock in Clayton Valley, Alcatraz Island, 1.5 km southeast of Silver Peak.

Collector: C.A. Nelson

Lithology: multicolored brown and purple shale

Fauna: *Gabriellus poletensis* n. sp. 19

Mummaspis alberst n. sp. 14

14. Coyote Road Locality (LACMIP locality 27297)

Elliptocephala Zone, *Wannerellus alcatrazensis* Subzone, Wanneriid Biofacies

Lat. 37°45'20" Long. 117°42'08"

Basal Harkless Formation, approximately 5 feet above Upper Poleta Limestone.

"Immediately south of Coyote Road, at 5920' contour in basal shales of Harkless Formation, NE1/4, SW1/4, NE1/4 sec. 24, T2S, R39E, "T" sheet of Silver Peak 15' quadrangle, Esmeralda Co., Nevada."

6.5 km west of Silver Peak, Silver Peak Range.

Collector: C.A. Nelson.

Lithology: shale

Fauna: *Wannerellus alcatrazensis* n. sp. 8

15. Montezuma Ridge Locality (LACMIP locality 26770)

Nevadella Zone, *Nevadella parvoconica* Subzone, *Nevadella* Biofacies

Poleta Formation

"Northwest Montezuma Range, NE1/4, Se. 34, T2S, R41E, Montezuma Peak 7 1/2 quad., Esmeralda Co., Nevada." This locality is part of a unpublished section measured by Moore (1976a, locality P68).

Collector: J.N. Moore.

1. Lithology: Lower Poleta Formation, shale to platy siltstone (26770b), 14 m thick, 40 m above base of Poleta.

Fauna: *Cirquella nummularia* Fritz 2

2. Lithology: Middle Poleta Formation, shale and siltstone (26770c), 20 m+ thick, approximately 70 meters above base of section.

Fauna: *Nevadella parvoconica* (Fritz) 23

16. Montezuma Peak Horizon 1

(ICS localities 1084, 1086, 1087, 1093)

Nevadia Zone, *Nevadia weeksi* Subzone, Biofacies unassigned

Montenegro Member, Campito Formation, about 250 m below base of Poleta Formation

"NE1/4, NE1/4, NE1/4 sec. 34 and adjoining SE1/4, SE1/4, SE1/4 sec. 27; T2S, R41E, Montezuma Peak 7.5' quadrangle". This is approximately 3 km north of Montezuma Peak, near Goldfield.

Collector: A.R. Palmer

Lithology: slightly deformed shale

Fauna: *Nevadia weeksi* Walcott 5

17. Montezuma Peak Horizon 2

(ICS localities 1083, 1085, 1089)

Nevadia Zone, *Nevadia palmeri* Subzone, Biofacies unassigned

Montenegro Member, Campito Formation, about 185 m below base of Poleta Formation

"NE1/4, NE1/4, NE1/4 sec. 34, T2S, R41E, Montezuma Peak 7.5' quadrangle". This is approximately 3 km north of Montezuma Peak, near Goldfield.

Collector: A.R. Palmer

Lithology: slightly deformed shale

Fauna: *Nevadia palmeri* n. sp. 4

18. Goldfield Locality

(includes old LACMIP locality 26886)

Part of repeated section, measured by Moore (1976a; locality P61), immediately east of Goldfield measured section (GF) studied in detail by the author .

Poleta Formation

"Just west of Kiln on road and extending NW along slope, NW1/4, sec. 31, T2S, R42E and NE1/4 sec. 36, T2S, R41E, Montezuma Peak 7 1/2' quad., Esmeralda Co., Nevada."

1. Collector: L.L. Bohach (LACMIP collections 17024-17025)

Lithology: lowest minor shale interval in Lower Poleta limestone

Nevadella Zone, *Nevadella parvoconica* Subzone, *Nevadella* Biofacies

Nevadella parvoconica (Fritz) 14

Esmeraldina argenta (Walcott) 2

2. Collectors: J.N. Moore and C.A. Nelson (LACMIP collection 26886)

Lithology: reddish-brown shale from lower shale of middle Poleta member (probably an interval collection)

Nevadella Zone, Subzone unassigned, *Nevadella* Biofacies

Fauna: *Nevadella parvoconica* (Fritz) 15

Nevadella eucharis (Walcott) 6

not identifiable to species 8

19. Magruder Mountain Locality (LACMIP locality 26854)

Olenellus transitans Zone, Subzone unassigned, Biofacies unassigned

Saline Valley Formation, "about 58 m below base of Mule Spring Formation"

"On east facing slope at 7840', directly east of closed contour (8160'), in SE1/4, NW1/4, NW1/4 sec. 5, T6S, R40E, Magruder Mtn. quadrangle, Esmeralda Co., Nevada."

Collector: T. McKee

Lithology: shale

Fauna: *Proliostracus* id. 8

Olenellus cf. *nevadensis* (Walcott) 4

20. Mt. Dunfee Locality (LACMIP locality 26142)

Olenellus transitans Zone, ? *Wanneria logani* Subzone, Biofacies unassigned

Saline Valley Formation

"Thin-bedded dark gray limestone exposed on ridge top trending NE-SW, approximately 7200' north and 6100' west from the SE corner of Mt. Jackson quadrangle, T6S, R41E."

Gabriellus poletensis n. sp.

8

23. Deep Spring Lake Localities (LACMIP localities 26855, 26858)

Nevadella Zone, Subzone unassigned, *Nevadella* Biofacies

Lat. 37°15'51" Long. 118°05'58" (location for summit of hill of elevation 6363 feet, Deep Spring Lake 7.5' quadrangle)

Poleta Formation

"locality 26855 on south flank of hill 6363; locality 26858 on northwest flank of hill 6363: in SW1/4, NE1/4, SE1/4, sec. 11, T8S, R35E, Blanco Mtn. 15' quadrangle, White-Inyo Mtns., Inyo Co., California"

In hills immediately west-southwest of Deep Spring Lake.

Collector: P.L. Guth

Lithology: dark green to grayish shales, some tectonic deformation (probably interval collections)

Fauna:	<i>Nevadella parvoconica</i> (Fritz)	117
	? <i>Nevadella eucharis</i> (Walcott)	6
	not assigned to species	11

24. Waucoba Wash Locality 1 (LACMIP locality 26833)

Olenellus transitans Zone, Subzone unassigned, Biofacies unassigned

upper Harkless Formation

"On SW side of draw at 5600 feet, NW1/4, SE1/4, NE1/4, sec. 14, T11S, R37E, Waucoba Wash quadrangle, Inyo Mtns., Inyo Co., California."

Collector: K.M. Scott

Lithology: olive-brown shale

Fauna:	? <i>Mesonacis? schofieldi</i> (Best)	3

25. Waucoba Wash Locality 2 (LACMIP locality 26834)

Olenellus transitans Zone, Subzone unassigned, Biofacies unassigned

uppermost Harkless Formation

"One east side of SSW canyon, at 5440 feet, in SW1/4, SW1/4, NE1/4, sec. 15, T11S, R37E, Waucoba Wash quadrangle, Inyo Mtns., Inyo Co., California."

Collector: K.M. Scott

Lithology: light grey siltstone

Fauna:	? <i>Mesonacis? schofieldi</i> (Best)	9

26. Waucoba Wash Locality 3 (LACMIP locality 26784)

Olenellus transitans Zone, Subzone unassigned, *Olenellus* Biofacies

uppermost Saline Valley Formation

"SE1/4, NW1/4, sec. 27, T11S, R37E, Waucoba Wash quadrangle, White-Inyo Range, Inyo Co., California."

West side of Waucoba Wash, on west facing side of outcrop.

Collectors: L.L. Bohach (WW"1"); C.A. Nelson (26784)

Lithology: brown shale

Fauna: *Olenellus transitans* (Walcott) 73

27 Waucoba Wash Locality 4 (LACMIP locality 26838)

Olenellus transitans Zone, Subzone unassigned, *Olenellus* Biofacies

uppermost Saline Valley Formation

"Just northeast of Waucoba Wash, just below 0 in 5053, in SE1/2, NE1/4, SW1/4, sect. 23, T11S, R37E, Waucoba Wash quadrangle, Inyo Mtns., Inyo Co., California."

Collectors: C.A. Nelson and K.M. Scott

Lithology: olive to brown shale

Fauna: *Olenellus transitans* (Walcott) 2

28. Waucoba Wash Locality 5 (LACMIP locality 26878)

Olenellus transitans Zone, Subzone unassigned, ?*Olenellus* Biofacies

uppermost Harkless Formation

"On east side of wash, at 5450 feet, in NE1/4, NW1/4, sec. 15, T11S, R37E, Waucoba Wash quadrangle, Inyo Co., California.

Collectors: C.A. Nelson and J. Albers.

Lithology: light grey siltstone

Fauna: *Olenellus transitans* (Walcott) 1

?*Mesonacis? schofieldi* (Best) 2

29. Waucoba Wash 6 (LACMIP locality 26896)

Olenellus transitans Zone, Subzone unassigned, *Olenellus* Biofacies

uppermost Saline Valley Formation

"Just west of crest of northwest trending ridge, at 5240 feet, NW1/4, SE1/4, SW1/4, sec. 15, T11S, R37E, Waucoba Wash quadrangle, Inyo Co., California."

Collector: C.A. Nelson

Lithology: light colored shale and siltstone

Fauna: *Olenellus transitans* (Walcott) 2

Appendix B Cladistic Data

Characters for cladistic analysis of the Wanneriidae and Olenellidae

Holaspid Characters. Assessed on clique F or G specimens.

1. Width of cephalic border (ratio of width of border to length of L0; border measured perpendicular to cephalic margin, opposite of L2):

- 0 wide (>0.5)
- 1 narrow (≤ 0.5)

Ancestral state interpreted as wide based on ontogeny of both the Wanneriidae and Olenellidae, (cephalic border proportionately wider in meraspids) and supported by outgroup comparison (archaeaspidids).

2. Plectrum (Note that this character is dependent on possession of a prelabellar field. Assessed on clique D-F cephalae.):

- 0 prelabellar field without plectrum
- 1 prelabellar field with plectrum
- 2 prelabellar field absent to short

Ancestral state interpreted as absent due to appearance of this feature late in meraspid stage of *Olenellus*.

3. Genal spine position (position of base of genal spines relative to glabellar lobes / furrows):

- 0 slightly advanced to not advanced (base of genal spines posterior of S0)
- 1 strongly advanced (base of genal spines opposite or anterior of S0)

Ancestral state interpreted as slightly advanced according to ontogeny and outgroup comparison (archaeaspidids).

4. Intergenal position

- 0 far from genal spine
- 1 adjacent to genal spine

Ancestral state interpreted as far from genal spine based on ontogeny of wanneriids and *Olenellus* and supported by outgroup comparison.

5. Intergenal spine length:

- 0 longer than L0
- 1 shorter than L0
- 2 absent

Ancestral state interpreted as long based on ontogenies of both the Wanneriidae and Olenellidae in which spine size typically decreases through ontogeny.

6. Glabellar shape:

- 0 parallel-sided to tapering forward
- 1 slightly constricted at S1
- 2 strongly constricted at S1

Ancestral state interpreted as parallel-sided to tapering forward based on ontogenies of both wanneriids and olenellids and supported by outgroup comparison (archaeaspidids).

7. S2 position and course:

- 0 marginal, transverse to oblique
- 1 marginal, curved
- 2 isolated, transverse

Ancestral state interpreted as marginal based on both wanneriid and olenellid ontogenies and supported by outgroup comparison (archaeaspidids).

8. Mid-ocular lobe furrow:

- 0 shallow or absent
- 1 deep

Coded as missing (?) on effaced species.

Ancestral state interpreted as shallow based on ontogeny of the Wanneriidae and Olenellidae and supported by outgroup comparison (archaeaspidids).

9. Interocular swellings:

- 0 absent
- 1 present

Ancestral state cannot be interpreted based on ontogeny because those species that have interocular swellings have them from the smallest known stages and those that lack such swellings, lack them at all stages of their ontogeny. Ancestral state interpreted as absent based on outgroup comparison (archaeaspidids).

10. Prosopon:

- 0 non-reticulate
- 1 reticulate (at least in part)

Ancestral state interpreted as non-reticulate as meraspids of both Wanneriidae and Olenellidae are smooth.

Holaspid Ventral Morphology Characters (using hypostomes of at least 5 mm in length)

11. Posterior margin of hypostome:

- 0 rounded to straight; not expanded posterolaterally
- 1 indented, expanded posterolaterally

Ancestral state interpreted as rounded based on morphology of small hypostomes in all Olenellina.

12. Rostral plate:

- 0 robust, wide
- 1 delicate, slender

Ancestral state interpreted as robust based on proportionally large rostral plates in meraspids of *Olenellus*.

Meraspid Characters (assessed on clique A/B cephalae)

13. Nature of the intergenal spines:

- 0 short or long, narrow, and obliquely oriented,
- 1 long, posteriorly oriented, baseball bat-shaped

Unable to interpret ancestral state.

14. Intergenal spine position:

- 0 medial, approximately posterior of ocular lobes
- 1 lateral, at posterolateral corners

Ancestral conditional interpreted as medial based on ontogeny of wanneriids, *Olenellus* and *Bristolia* and supported by outgroup comparison (archaeaspidids).

15. Procranial spines:

- 0 absent
- 1 present

Unable to interpret ancestral state.

Ontogenetic Pattern Characters (based on development of a feature from meraspid through holaspid stages)

16. LA:

0 LA short and narrow in meraspid, extends anterior of ocular ridges in early meraspid stage; lengthens through ontogeny to a long, narrow lobe

1 LA short and narrow, contained between ocular ridges in early meraspid stage; lengthens in late meraspid to early holaspid stages; remains subcircular through holaspid stage, slightly wider than long

2 LA short and wide, drapes ocular ridges in early meraspid stage; late meraspid to early holaspid stage lobe remains short and wide; lengthens through holaspid stage to a subrounded lobe, slightly wider than long

3 LA large and subrounded from early meraspid stage on
Unable to interpret ancestral state.

17. Preglabellar field:

0 present through meraspid stage, shortens during ontogeny

1 present only in earliest meraspids (cliques A, B)

2 absent at all stages

Ancestral state interpreted as present through ontogeny based on ontogeny of the Wanneriidae and *Olenellus* and supported by outgroup comparison (archaeaspidids).

18. Genal spine position through ontogeny:

0 remains approximately constant

1 migrates anteriorly

Ancestral state taken as constant position for genal spines based on outgroup comparison (archaeaspidids).

19. T3:

0 macropleural throughout ontogeny

1 macropleural through early holaspid stage, decreases in relative size in cliques E/F, amplipleural to regular in clique G holaspids

2 not macropleural at any stage in ontogeny

3 hyperpleural and dolichospinous, at least in holaspid stage

Ancestral state macropleural based on ontogeny of *Elliptocephala*.

20. stratigraphic position (zero weight character)

0 *Elliptocephala* Zone1 *Olenellus transitans* Zone2 above *Olenellus transitans* Zone

Ancestral state taken as the lowest zone.

Table X. Data for cladistic analysis. Missing data coded as "?".

character #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
dunnae	0	2	0	0	2	1	1	?	0	1	1	0	0	0	0	2	0	0	2	1
logani	0	2	0	0	2	1	1	1	1	1	1	?	?	0	0	2	0	0	?	1
asaphoides	0	0	0	0	2	1	1	?	0	1	0	0	0	0	0	2	0	0	1	?
parentalis	1	0	0	0	2	1	1	1	0	1	1	0	0	0	0	2	0	0	?	1
prima	0	2	1	0	0	1	1	1	0	1	0	?	0	0	1	2	0	1	?	0
amputata	0	2	1	0	0	1	1	1	0	1	?	0	?	?	?	?	?	1	0	0
obliosooculatus	0	2	0	0	2	1	1	1	0	1	?	0	0	0	0	2	0	0	1	0
poletensis	0	0	1	0	1	1	1	1	0	1	0	0	0	0	0	2	0	0	1	0
guthi	1	2	1	0	1	1	1	1	0	?	0	?	0	0	1	2	0	0	1	0
alcatrazensis	0	1	0	0	2	1	1	1	0	?	?	?	1	0	0	2	0	0	?	0
sequomalus	0	1	0	1	2	1	1	1	0	1	?	?	?	?	0	0	2	0	?	0
transitans	1	1	0	1	1	1	2	0	0	0	0	1	1	0	1	1	0	0	0	1
schucherti	1	1	0	1	2	1	2	0	1	0	0	1	1	0	?	1	0	0	0	1
eagerensis	1	2	1	1	2	1	2	0	1	0	?	1	?	?	?	3	2	0	0	1
graingerensis	1	2	1	1	2	1	2	0	1	0	?	?	0	1	?	3	2	0	?	1
halli	0	2	1	0	2	1	1	?	0	0	?	?	0	1	0	3	2	1	?	1
armatus	1	2	1	0	0	1	0	0	1	?	0	?	0	1	1	1	1	0	0	?
iddingsi	1	2	0	1	2	2	2	?	0	0	?	?	?	?	?	?	?	0	3	2
multinodus	0	2	0	1	1	2	0	0	0	0	?	?	?	?	?	?	?	0	3	2
bristolensis	0	2	1	0	2	2	2	0	0	0	?	1	1	0	1	1	1	1	3	2
sphaerulosus	0	2	0	1	1	1	0	0	0	0	?	?	?	?	?	?	?	0	?	2
repinae	0	0	1	0	2	0	0	0	0	1	?	?	0	0	0	0	0	0	?	0
kjerulfi	0	2	1	0	1	1	1	1	0	1	0	0	0	0	0	?	0	0	?	?
hyp.ancest	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	0	0	0	0

Taxa and Material used in Cladistic Analysis

Wanneriidae

Wanneria dunnae n. sp. Eager Formation, British Columbia: Pl. 6, figs. 10-18; Pl. 7, figs. 1-8.

Wanneria logani (Walcott). Forteau Formation Newfoundland: Pl. 6, figs. 3, 6; Eager Formation, British Columbia: Pl. 6, figs. 1-2, 5, 7-9; Sekwi Formation, Mackenzie Mountains, Northwest Territories: Fritz (1972), pl. 14, figs. 1-14; pl. 16, figs. 1-7.

Elliptocephala asaphoides Emmons. Type species of *Elliptocephala*. Schodack Formation, New York: Pl. 8, figs. 6-9; Pl. 9, figs. 1-7; Walcott (1910b), pl. 24, figs. 1-10; pl. 25, figs. 1-18; Ford (1877), figs. 1-10; Ford (1881), figs. 1-3.

Elliptocephala parentalis n. sp. Eager Formation, British Columbia: Pl. 10, figs. 1-15.

Laudonia prima (Lochman). Poleta Formation, Nevada: Pl. 12, figs. 6-13; Puerto Blanco Formation, Sonora, Mexico: Lochman (1952), pl. 18, figs. 1-3.

Laudonia amputata Fritz. Mural Formation, Mount Robson Area, southern Canadian Rocky Mountains: Fritz (1992), pl. 11; pl. 12, figs. 1-3.

Mummaspis oblioculatus Fritz. Mural Formation, Mount Robson Area, southern Canadian Rocky Mountains: Fritz (1992), pl. 16, figs. 4-7; pl. 17, figs. 1-5.

Gabriellus poletensis n. sp. Poleta Formation, California and Nevada: Pl. 14, fig. 6; Pl. 15, figs. 1-6.

Mesolenellus guthi n. sp. Poleta Formation, California and Nevada: Pl. 16, figs. 1-9.

Wannerellus alcatrazensis n. sp. Type species of *Wannerellus*. Poleta Formation, California and Nevada: Pl. 17, figs. 8-12.

Wannerellus sequomalus Fritz. Sekwi Formation, Mackenzie Mountains, Northwest Territories: Fritz (1972), pl. 12, figs. 14-25.

Olenellidae

Olenellus transitans (Walcott). Kinzers Formation, Pennsylvania: Pl. 18, figs. 1-2, 3, 6. Eager Formation, British Columbia: Pl. 18, fig. 3; Pl. 19, figs. 1-7. Saline Valley Formation, California and Nevada: Pl. 18, figs. 5; Pl. 19, figs. 8-9.

Olenellus schucherti Resser and Howell. Eager Formation, near Cranbrook, British Columbia: Pl. 20, figs. 5-8, 12; Pl. 21, figs. 1-11.

Mesonacis eagerensis (Best). Eager Formation, near Cranbrook, British Columbia: Pl. 22, figs. 1-6.

Mesonacis graingerensis n. sp. Eager Formation, near Canal Flats, British Columbia: Pl. 22, figs. 7-9; Pl. 23, figs. 1-5.

Fremontella halli (Walcott). Type species of *Fremontella*. Rome Formation, near Helena, Alabama: Walcott (1910b), pl. 31, figs. 1-7; Resser (1938), pl. 5, figs. 7, 8, 16-18; Harrington (1956), pl. 15, fig. 1-3, 8, 9.

Olenelloides armatus Peach. Type species of *Olenelloides*. "Furoid Beds", northwest Scotland: McNamara (1978), pl. 71; Palmer and Repina (1993), fig. 4-8.

Peachella iddingsi (Walcott). Type species of *Peachella*. Cararra Formation, Nevada and California: Palmer and Halley (1979), pl. 5, figs. 4-9; Palmer and Repina (1994), fig. 4.2.

Nephrolenellus multinodus (Palmer in Palmer and Halley, 1979). Type species of *Nephrolenellus*. Cararra Formation, Nevada: Palmer and Halley (1979), pl. 4, figs. 1-9.

Bristolia bristolensis (Resser). Type species of *Bristolia*. Cararra Formation, Nevada: Palmer and Halley (1979), pl. 1, figs. 14-19; pl. 2, figs. 1-6 = *B. fragilis*. Latham Formation, California: Palmer and Repina (1993), fig. 4.5; Riccio (1952), pl. 7, figs. 1, 2, 5; pl. 8; Resser (1928), pl. 2, figs 5-8.

Bolbolenellus sphaerulosus (Fritz). Iltyd Formation, Wernecke Mountains Yukon: Fritz (1991a), pl. 10.

Outgroups

Holmia kjerulfii (Linnarsson). *Holmia* shales, Tømten, Norway: Kiaer (1916), pls. 6-8. Kiaer is the only author who has illustrated the ontogeny of a holmiid, however, the illustrations are from a time when retouching of photographs was common and they must be used with caution.

Bradyfallotaspis repinae n. sp. Poleta Formation, Goldpoint, Nevada: Pl. 1, figs. 1-10.

Hypothetical ancestor (Hyp.ancestor). Based on consideration of ontogenetic development, plus outgroup comparison to the Archaeaspididae. Details for each character are given under character list.

PLATES

Specimens were blackened with black watercolor paint then whitened with ammonium chloride prior to photography, except where noted. Counterparts were generally cast using liquid latex and the latex photographed (indicated by L).

Plates have been reduced by a factor of 80% from the indicated magnifications.

Locality, stratigraphic section and collection numbers correspond to designations in Appendix A. Repositories for collections used in this study are various. The author's collections from the Great Basin will be housed by the Los Angeles County Museum of Invertebrate Paleontology, California. The author's and P. Ransom's collections from the Cranbrook (localities 4-6) and Hellroaring Creek areas (locality 7) will be housed by the Royal British Columbia Museum. All other collections made by the author from British Columbia will be housed by the Geological Survey of Canada, Ottawa. Other collections have repositories as indicated and their abbreviations are given below.

Ontogenetic stages are designated as cliques. The comparative ontogenetic standard for the *Olenellina* is described under the taxonomy of *Olenellus* (p.) and the standard for *Bonnia* is described under the taxonomy of *B. grandis* (p.).

Abbreviations:

GSC	Geological Survey of Canada, Ottawa
ICS	Institute for Cambrian Studies, Boulder, Colorado
LACMIP	Los Angeles County Museum of Invertebrate Paleontology, California
NHM	Natural History Museum, London, England
NYSM	New York State Museum, Albany
RBCM	Royal British Columbia Museum, Victoria
ROM	Royal Ontario Museum, Ottawa
UA	University of Alberta, Edmonton
UBC	University of British Columbia, Vancouver
USNM	United States National Museum (Smithsonian Institution), Washington, DC

Plate 1

Figs. 1-9. *Bradyfallotaspis repinae* n. sp. Poleta Formation, section GP, Mt. Dunfee area, Nevada. Figs. 1-4, 6, 10: LACMIP collection 17043; Figs. 5, 7-9: LACMIP collection 17048.

1. Cephalon (L) (meraspid, Clique B), LACMIP 12502, x20
2. Cephalon (meraspid, Clique B), LACMIP 12503, **Paratype**, x20
3. Glabella, LACMIP 12504, x8
- 4, 10. Genal region and prosopon enlargement (L), LACMIP 12505, x15, x6
5. Cephalon, LACMIP 12506, **Paratype**, x10
6. Cephalon, LACMIP 12507, x6
- 7-8. Cephalon (L), LACMIP 12508, x9
9. Cephalon, LACMIP 12509, **Holotype**, x9

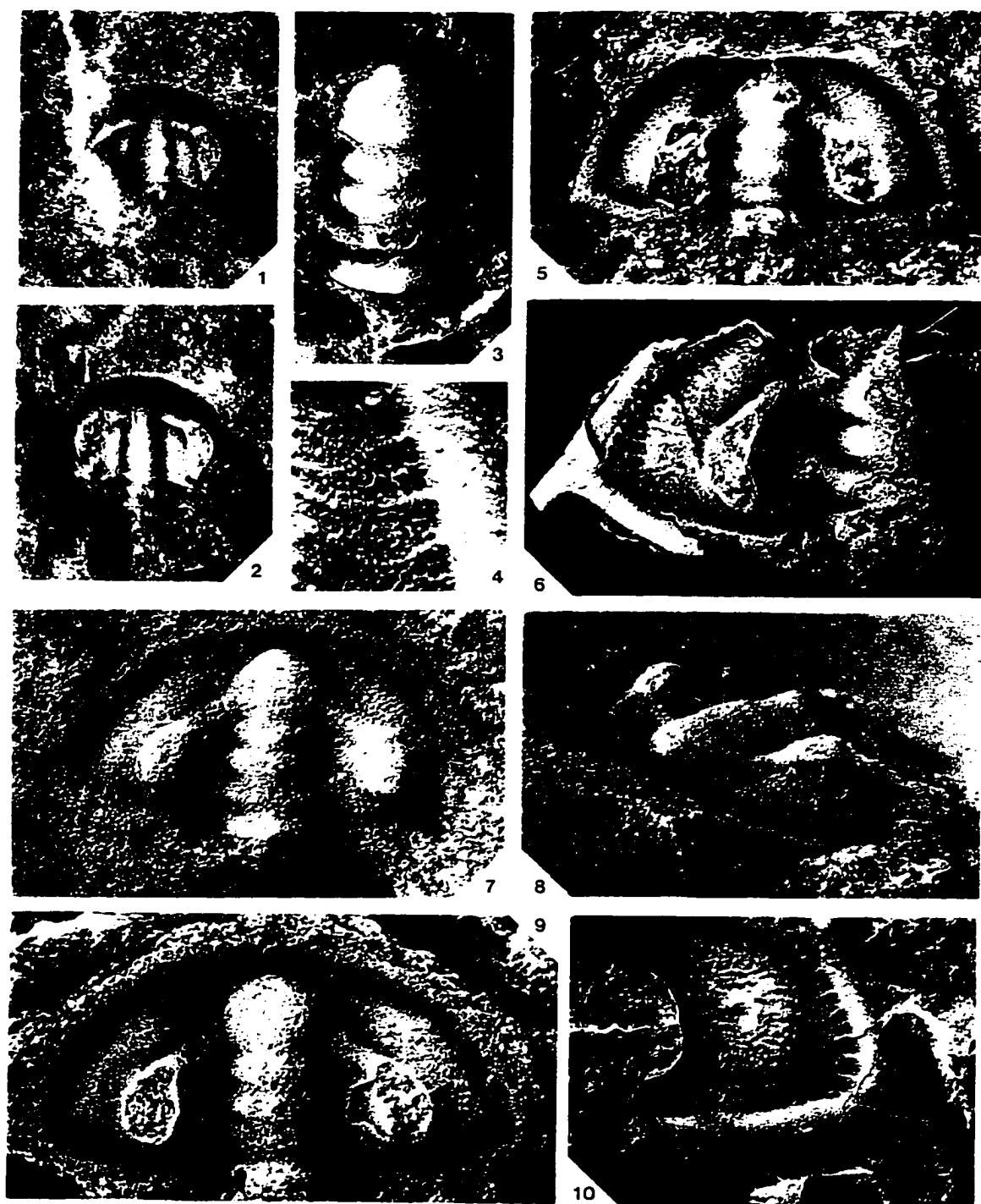


PLATE 1

Plate 2

Figs. 1-4. *Nevadia weeksi* Walcott, 1910b. Montenegro Member, Campito Formation, locality 16, Montezuma Range, Nevada. Fig. 1: ICS collection 1093; Fig. 2: ICS collection 1081; Fig. 3: ICS collection 1086.

1. Cephalon (L), ICS 1093#1, x2
2. Cephalon, ICS 1081#1, x1.25
- 3-4. Thorax with pygidium, ICS 1086#1, x1.25, x5

Figs. 5-10. *Nevadia palmeri* n. sp. All Montenegro Member, Campito Formation, locality 17, Montezuma Range, Nevada. Figs. 5, 8: collection ICS 1083; Fig. 6: collection ICS 1085; Fig. 7: collection ICS 1089. Except Figs. 9-10 (tentatively attributed), Quartzitic sandstones, locality 14p of Walcott (1910b, p. 300), Resting Springs, California.

5. Cephalon (L) (Clique E), ICS 1083#1, x4
6. Cephalon (L) (Clique F), ICS 1085#1, **Paratype**, x3.5
7. Cephalon (L) (Clique F), ICS 1089#1, x3.5
8. Cephalon (L) (Clique G), ICS 1083#2, **Holotype**, x3.5
- 9-10. Cephalon, USNM 56804a, x2

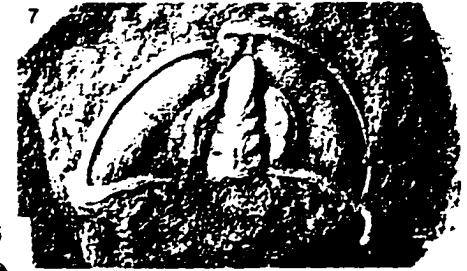
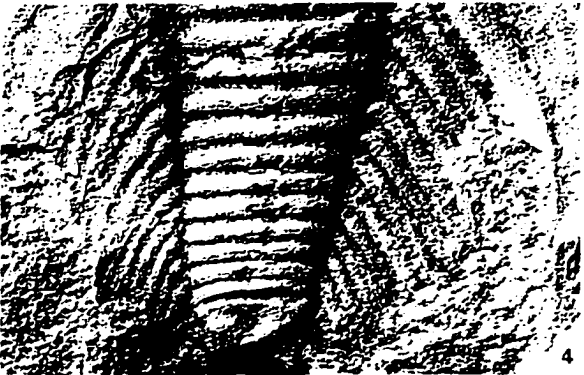
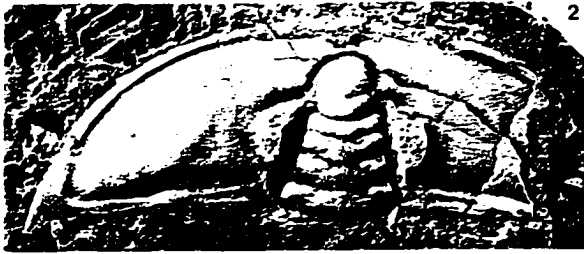
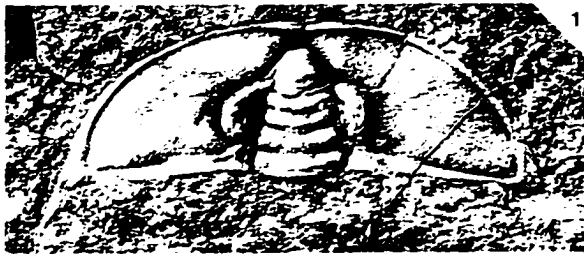


PLATE 2

Plate 3

Figs. 1, 2. *Nevadella eucharis* (Walcott, 1913). Fig. 1: Poleta Formation, locality 18, LACMIP collection 26866, near Goldfield, Nevada. Fig. 2: Cranbrook Formation, locality 3, GSC collection 23851, Ram Creek Area, British Columbia.

1. Cephalon, LACMIP 12510, x3
2. Cephalon, GSC 23851B, x3

Figs. 3-13. *Nevadella parvoconica* (Fritz, 1992). All Poleta Formation. Figs. 3, 7, 9: locality 15, LACMIP collection 26770, Cedar Flat area, California; Figs. 4-6, 10: section GP, LACMIP collection 17042, Mt. Dunfee area, Nevada; Figs. 8, 12-13: section GP, collection ICS 1055, Mt. Dunfee area, Nevada; Fig. 11: locality 177 of Walcott (1910b, p. 300), Cedar Flat area, California.

3. Cephalon (L) (meraspid, Clique A), LACMIP 12511, x20
4. Cephalon (meraspid, Clique B), LACMIP 12512, x20
5. Cephalon (meraspid, Clique C/D), LACMIP 12513, x9
6. Hypostome, LACMIP 12514, x20
7. Cephalon (Clique D), LACMIP 12515, x7
8. Cephalon (Clique E), ICS 1055#5, x7
9. Cephalon (L) (Clique F), LACMIP 12516, x5.5
10. Cephalon (Clique F), LACMIP 12517, x5
11. Hypostome, USMN 56802a, x5
- 12-13. Cephalon (L) (Clique G), ICS 1055#4, x3

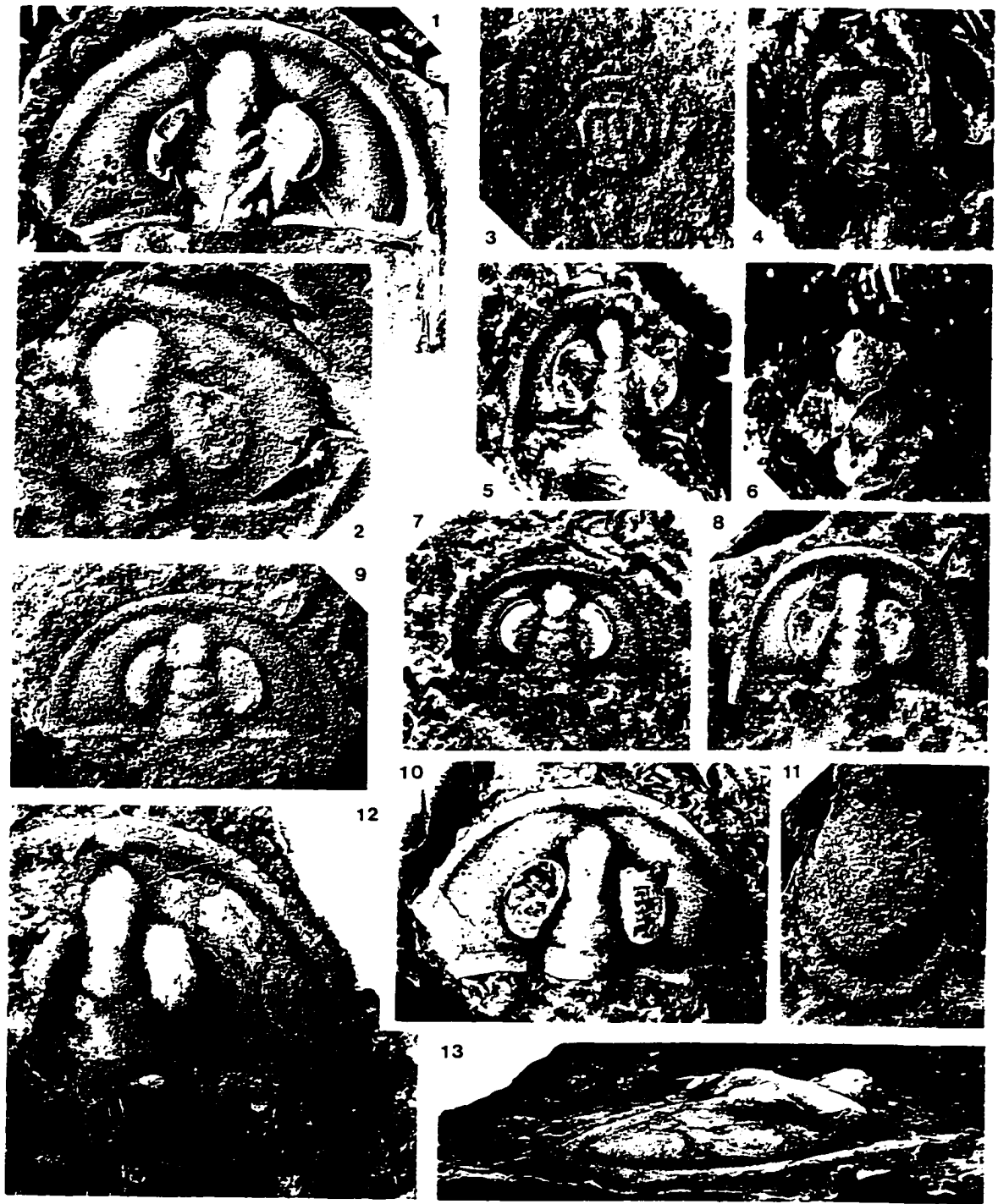


PLATE 3

Plate 4

Fig. 1. *Nevadella parvoconica* (Fritz, 1992). Poleta Formation, section CF, LACMIP collection 26777, California.

1. Articulated specimen (Clique G), LACMIP 11340, x2.5

Figs. 2-7. *Nevadella gracile* (Walcott, 1910b). All Poleta Formation. Figs. 2-3, 5 (tentatively attributed): section GP, ICS collection 1053, Mt. Dunfee area, Nevada; Figs. 4, 6: locality IV (of Walcott, 1910b, p. 300), Barrel Spring, Nevada.

2. Cephalon (meraspid, Clique B), ICS 1053#5, x20
3. Cephalon (meraspid, Clique B), ICS 1053#6, x20
4. Cephalon (meraspid, Clique C), **Paralectotype**, USNM 56804b, x10
5. Cephalon (meraspid, Clique C), ICS 1053#4, x10
- 6-7. Cephalon (Clique F), USNM 56805a, **Lectotype**, x4

Figs. 8-10. *Cirquella nummularia* Fritz, 1993. Poleta Formation, locality 15, LACMIP collection 26770b, Montezuma Range, Nevada, except Fig. 9: locality IV of Walcott (1910b, p. 300) Barrel Spring, Nevada.

8. Cephalon (L), LACMIP 12518, x7
9. Cephalon, USMN 56805b, x6.5
10. Cephalon, LACMIP 12519, x3.5



PLATE 4

Plate 5

Figs. 1-5. *Wanneria walcottana* (Wanner, 1901). Kinzers Formation, York County, Pennsylvania. Figs. 1, 3: locality 8q of Walcott (1910b, p. 304); Figs. 2, 4: original of Wanner (1901), 5 km northwest of York; Fig. 5: locality 22L of Resser and Howell (1938, p. 209).

1. Cephalon (Clique F), USMN 56807d, x3
2. Hypostome and rostral plate, USMN 56807e, x1.5 (photographed uncoated and unblackened)
3. Cephalon (Clique E), USMN 56807c, x4
4. Posterior of hypostome (from Fig. 2), USMN 56807e, x4 (photographed submerged in water)
5. Articulated specimen (L) (Clique G), USMN 85357, x1.25

Figs. 6-9. *Esmeraldina argenta* (Walcott, 1910b). Poleta Formation, section GP, Mt. Dunfee area Nevada. Figs. 6, 8, 9: ICS collection 1052; Fig. 7: ICS collection 1053.

6. Genal region, ICS 1052#3, x6
7. Cephalon (L), ICS 1053#1, x8
- 8-9. Cephalon, ICS 1052#2, x8

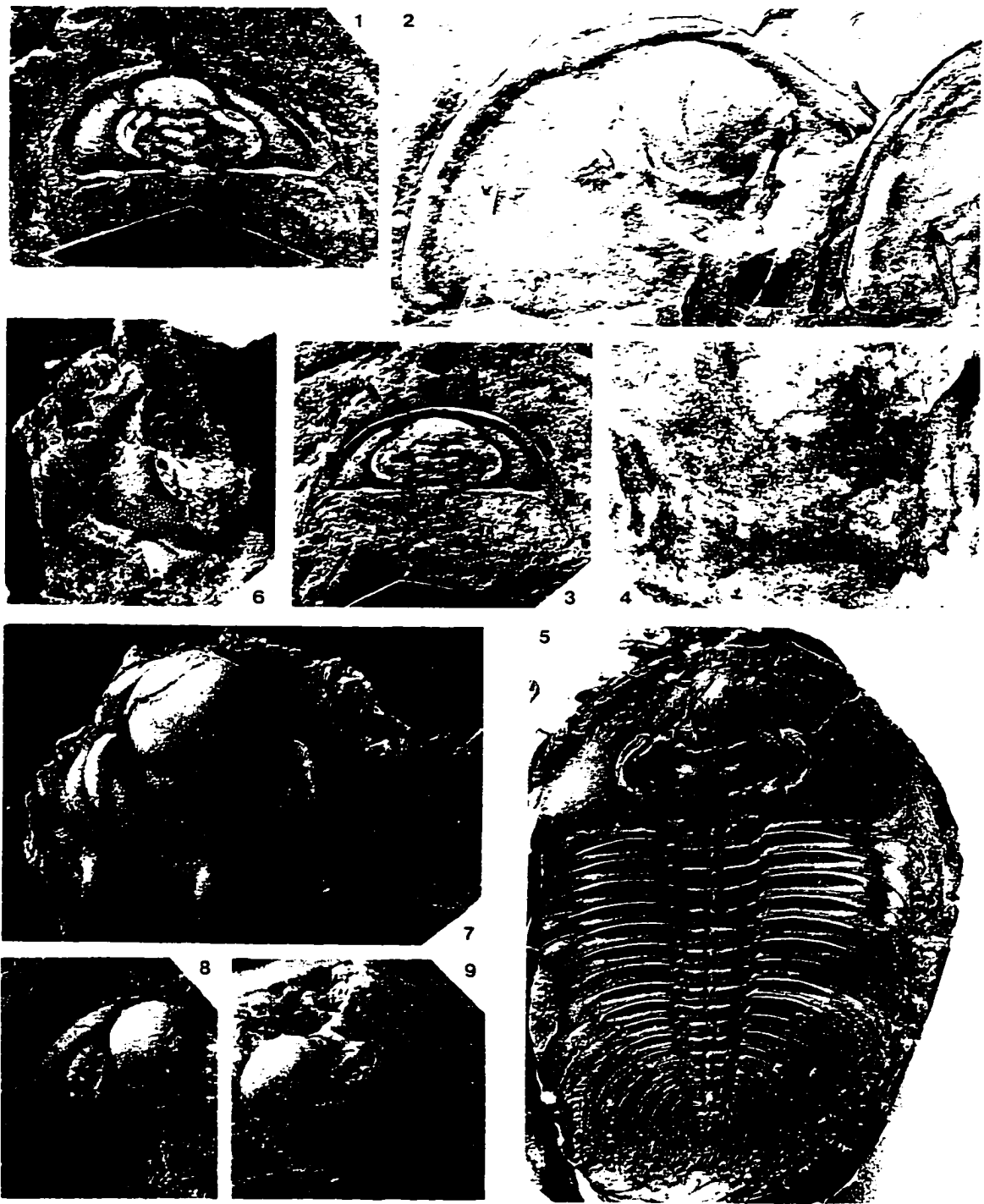


PLATE 5

Plate 6

Figs. 1-9. *Wanneria logani* (Walcott, 1910b). Figs. 1-2, 5, 8: Eager Formation, section RC4, collection RC4b, Ram Creek area, British Columbia; Figs. 3, 6: Forteau Formation, L'Anse au Loup, Labrador; Fig. 4 (tentatively attributed): Saline Valley Formation, locality 20, LAMIP collection 26142, Mt. Dunfee area, Nevada; Fig. 7: Eager Formation, section MG2, collection MG2j, Canal Flats area, British Columbia; Fig. 9 (tentatively attributed): Eager Formation, section MG2, collection MG2b, Canal Flats area, British Columbia.

1. Cephalon (L) (Clique E), RC4b#5, x7
2. Cephalon (Clique E), RC4b#1, x7
- 3, 6. Cephalon (Clique F), GSC 414b, **Lectotype**, x6
4. Cephalon (Clique E/F), LACMIP 12520, x5.5
5. Hypostome, RC4b#7, x6
7. Cephalon (Clique F), MG2j#22, x5
8. Cephalon (L) (Clique G), RC4b#3, x3.75
9. Pygidium, MG2b#17, x4

Figs. 10-18. *Wanneria dunnae* n. sp. Eager Formation, section MG3, collection MG3b, Canal Flats area, British Columbia, except Figs. 12, 14, 17: locality 5, Cranbrook area.

10. Cephalon (meraspid, Clique B), MG3b#26, x15
11. Cephalon (meraspid, Clique B), MG3b#29, **Paratype**, x15
12. Articulated meraspid (L) (Clique C), RBCM EH.997.06.001, **Paratype**, x7.5
13. Cephalon (meraspid, Clique D), MG3b#31, x8
14. Articulated specimen (Clique E), UBC GT505, x5
- 15-16. Cephalon (Clique E), MG3b#39, x5
17. Cephalon and associated thorax (Clique E), UBC GT502, **Paratype**, x3
18. Pygidium, MG3b#21, **Paratype**, x10

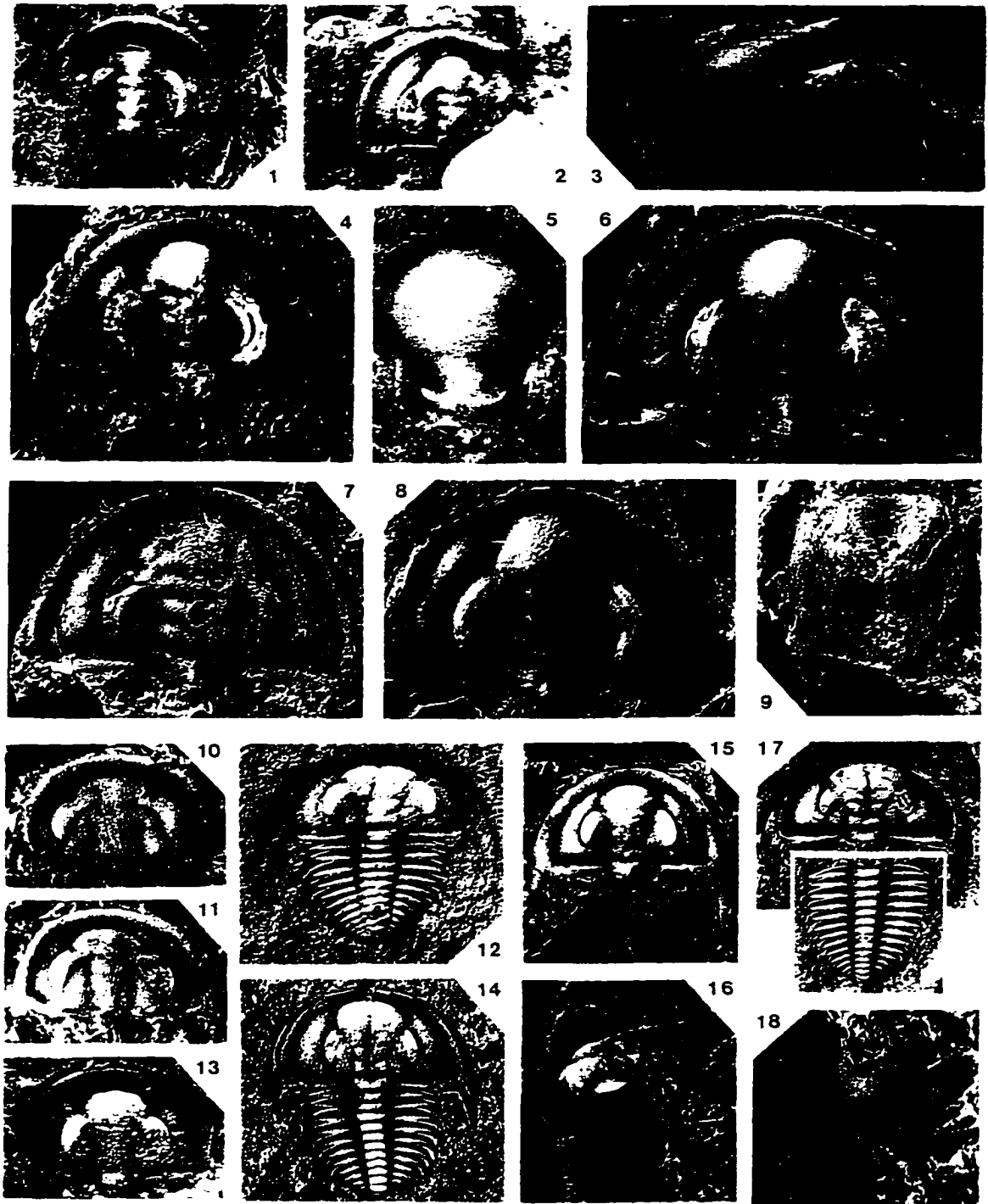


PLATE 6

Plate 7

Figs. 1-8. *Wanneria dunnae* n. sp. Eager Formation, locality 5, Cranbrook area, British Columbia, except Figs. 2, 5: section RC4, collection RC4f, Ram Creek area; and Fig. 7: section MG3, collection MG3b, Canal Flats area.

1. Articulated specimen (Clique F), UBC C13-21, x2.5
- 2, 5. Cephalon (Clique F), RC4f#4, **Paratype**, x5
3. Articulated specimen (Clique G), GSC 105234#1, x2
4. Hypostome and partial rostral plate, GSC 105234#2, x1.5
6. Hypostome and rostral plate (L), GSC 105234#3, x1.5
7. Cephalon (Clique G), MG3b#8, x2.5
8. Articulated specimen with molted hypostome and rostral plate (L) (Clique G), UBC GT507, **Holotype**, x2

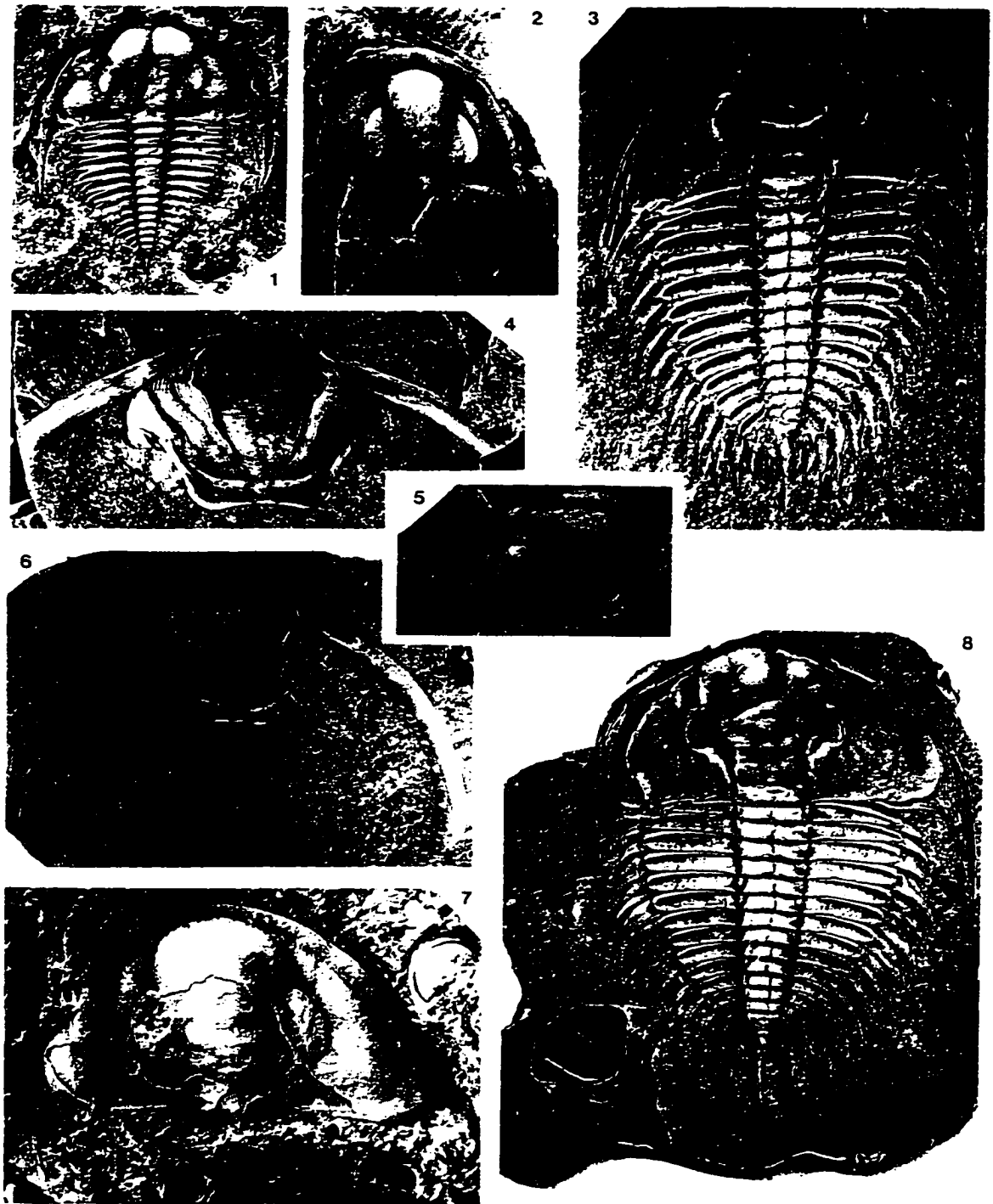


PLATE 7

Plate 8

Figs. 1-2. *Wanneria dunnae* n. sp. Eager Formation, locality 5, Cranbrook area, British Columbia

1. Articulated specimen, molt configuration with inverted cephalon (Clique G), GSC 105234#4, x1.2
2. Articulated specimen, molt configuration with displaced cephalon (L) (Clique G), GSC 105234#5, x1.5

Figs. 3-5. *Wanneria watsonensis* n. sp. Eager Formation, section MG1, collection MG1g, Canal Flats area, British Columbia.

3. Cephalon (meraspid, Clique C), MG1g#7, **Paratype**, x10
4. Cephalon (Clique G), MG1g#3, **Holotype**, x4.5
5. Hypostome, MG1g#1, **Paratype**, x6

Figs. 6-9. *Elliptocephala asaphoides* Emmons, 1844. All Schodack Formation, Troy, New York. Fig. 6: locality Y-13 of Lochman (1956, p. 1376); Figs. 7-8: Ford collection, NYSM; Fig. 9: locality Y-II a of Lochman (1956, p. 1376).

6. Hypostome, USNM 125712, x7.5
7. Cephalon (meraspid, Clique B), NYSM 4595, x22
8. Cephalon (meraspid, Clique B/C), NYSM 4594, x20
9. Cephalon (meraspid, Clique D), USNM 125707, x15

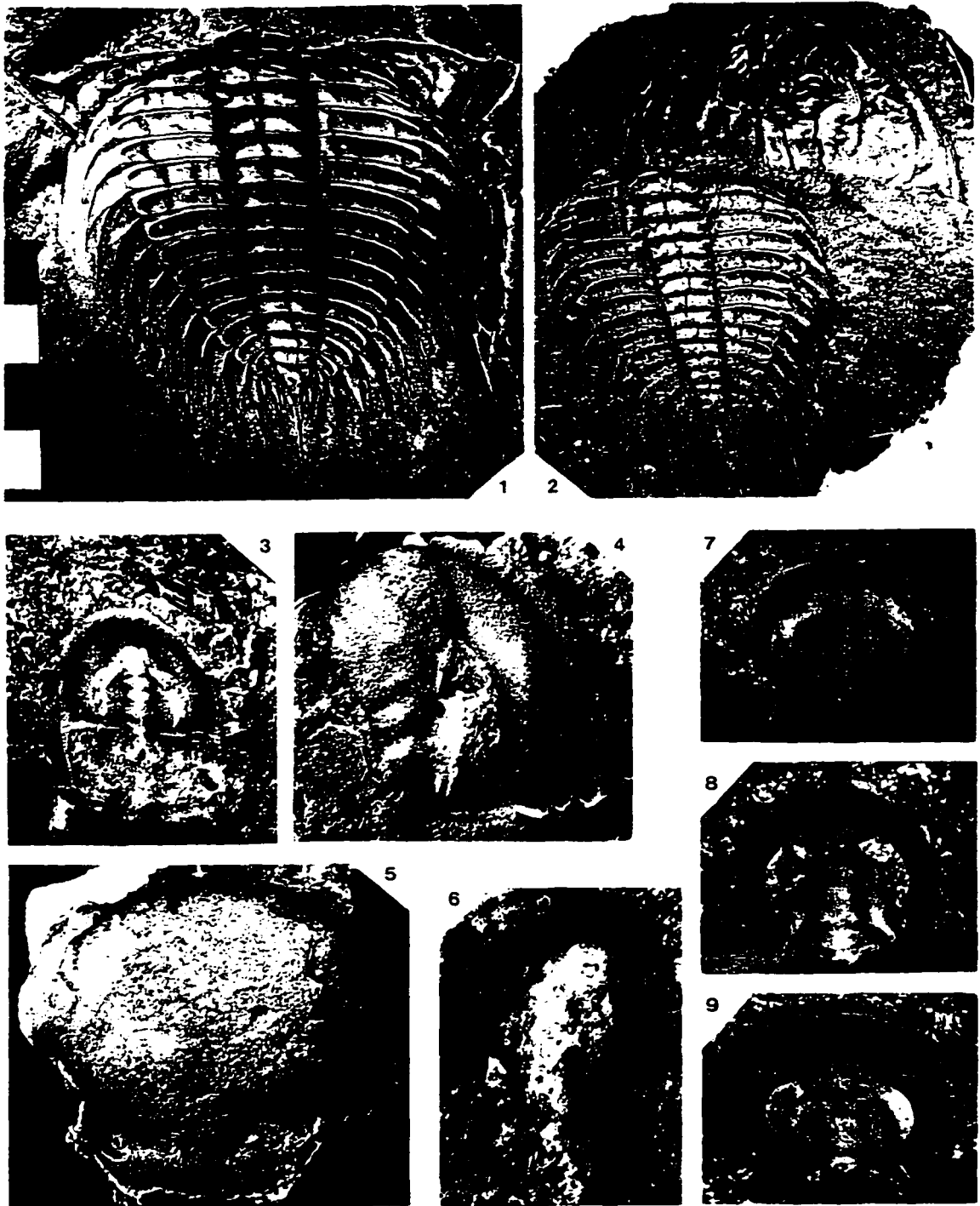


PLATE 8

Plate 9

Figs. 1-7. *Elliptocephala asaphoides* Emmons, 1844. All Schodack Formation, Troy, New York (Figs. 1, 2, 6: Ford collection, NYSM; Figs. 3-5: Rasetti collection, NHM), except Fig. 7 (Greenwich Formation, Washington County, New York, Walcott collection, NHM).

1. Articulated specimen (Clique D), NYSM 4604, x15
2. Articulated specimen (Clique E), NYSM 4605, x12.5
3. Cephalon (Clique G), NYSM 2568#3, x4
- 4-5. Cephalon (Clique F), NHM IT5513-5, x5.5
6. Articulated specimen with displaced, inverted hypostome (Clique F), NYSM 4598, x5.5
7. Articulated specimen, note rostral plate (Clique G), NHM I1585, x1



PLATE 9

Plate 10

Figs. 1-15. *Elliptocephala parentalis* n. sp. Eager Formation, section MG2, collection MG2a, Canal Flats, British Columbia, except Fig. 12 (section MG1, collection MG2d).

1. Cephalon (meraspid, Clique A), MG2a#15, **Paratype**, x22
2. Cephalon (meraspid, Clique A), MG2a#16, x22
3. Cephalon (meraspid, Clique B), MG2a#29, **Paratype**, x22
4. Cephalon (meraspid, Clique B), MG2a#25, x20
- 5-6. Cephalon (meraspid, Clique C), MG2a#13, **Paratype**, x17
7. Hypostome, MG2a#24, x20
- 8-9. Hypostome, MG2a#10, **Paratype**, x8.5
10. Prosopon (ocular lobe), MG2a#4, x5.5
11. Cephalon (Clique D), MG2a#14, **Paratype**, x11
12. Rostral plate, MG1d#1, x7
13. Cephalon (Clique E/F), MG2a#6, **Paratype**, x7.5
14. Cephalon (Clique G), MG2a#2, **Paratype**, x3.5
15. Cephalon (Clique G), MG2a#1, **Holotype**, x3.5

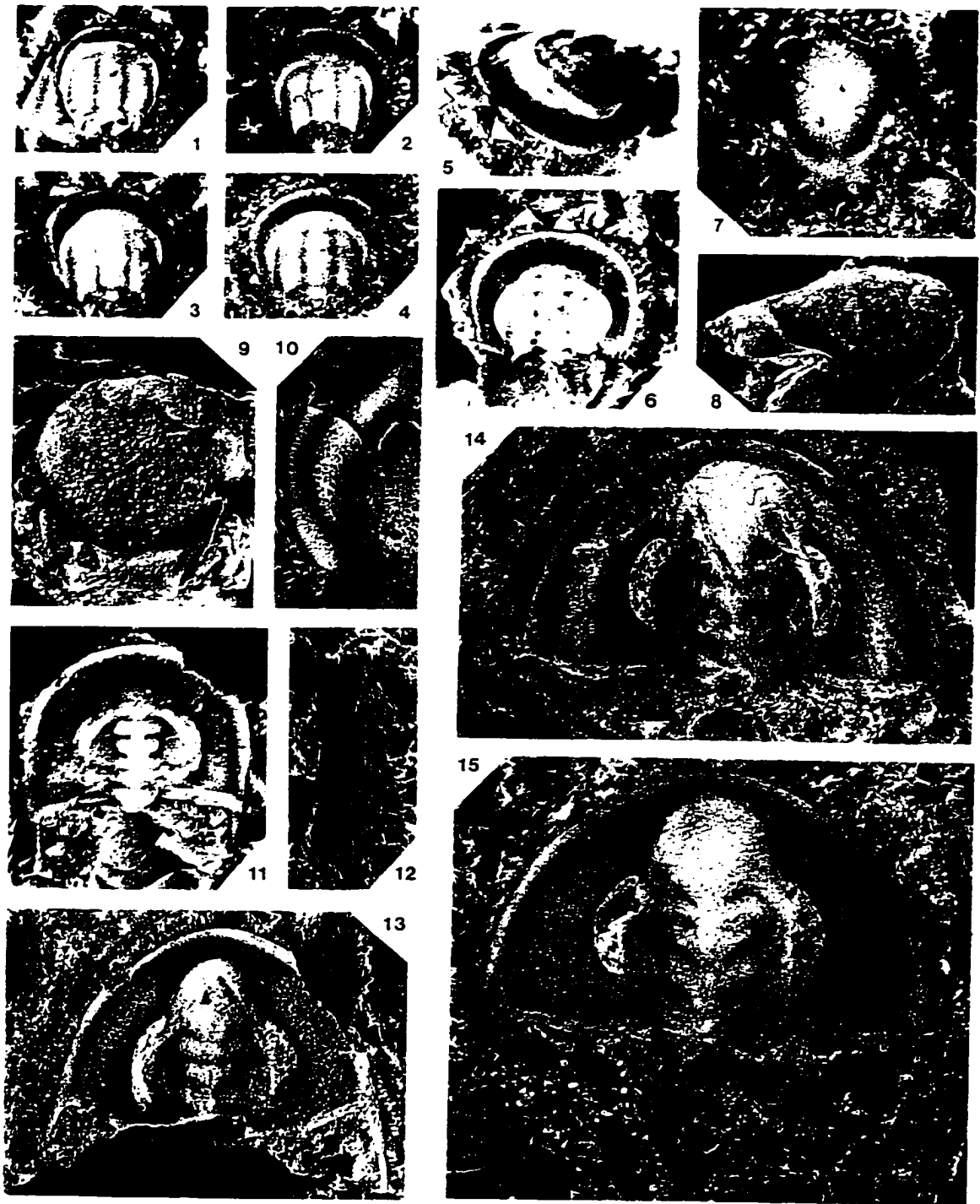


PLATE 10

Plate 11

Figs. 1-7. *Elliptocephala nelsoni* n. sp. Poleta Formation, section GP, Mt. Dunfee area, Nevada. Figs. 1, 4: LACMIP collection 17055; Figs. 2-3, 7: LACMIP collection 17054; Figs. 5-6: LACMIP collection 26850.

- 1, 4. Cephalon (Clique E), LACMIP 12521, **Paratype**, x7
2. Hypostome, LACMIP 12522, x10
3. Hypostome, LACMIP 12523, x10
5. Cephalon (Clique F), LACMIP 11366, x6
6. Cephalon (Clique F), LACMIP 11368, **Holotype**, x5
7. Hypostome, LACMIP 12524, **Paratype**, x10

Figs. 8-17. *Elliptocephala stewarti* n. sp. Poleta Formation, section GP, LACMIP collection 17049, Mt. Dunfee area, Nevada.

8. Cephalon (Clique B), LACMIP 12525, x15
9. Cephalon (Clique B), LACMIP 12526, **Paratype**, x15
10. Cephalon (Clique C), LACMIP 12527, **Paratype**, x10
11. Cephalon (L) (Clique D), LACMIP 12528, **Paratype**, x9
12. Cephalon (Clique D), LACMIP 12529, x7
13. Cephalon (Clique F), LACMIP 12530, x5
14. Hypostome, LACMIP 12531, x15
15. Hypostome, LACMIP 12532, **Paratype**, x7
- 16-17. Cephalon (L) (Clique F), LACMIP 12533, **Holotype**, x5

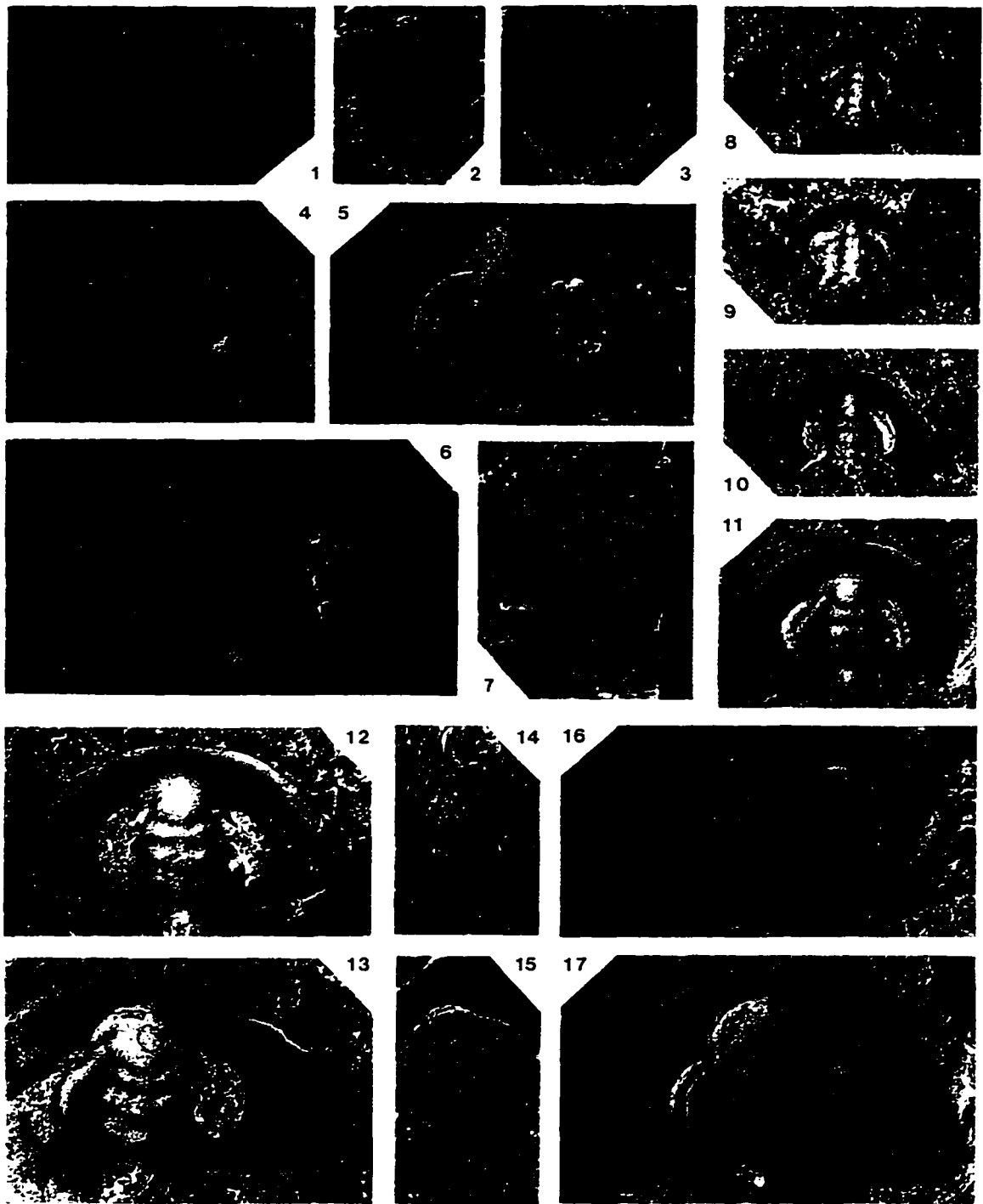


PLATE II

Plate 12

Fig. 1. *Elliptocephala stewarti* n. sp. Poleta Formation, section CF, LACMIP collection 17063, Cedar Flat area, California.

1. Articulated specimen, molt configuration, with inverted hypostome and rostral plate, LACMIP 12534, **Paratype**, x7

Figs. 2-5. *Elliptocephala truemani?* (Walcott, 1913). Poleta Formation, section GP, LACMIP collection 17048, Mt. Dunfee area, Nevada.

2. Cephalon (meraspid, Clique D), LACMIP 12535, x12
3. Cephalon (Clique E), LACMIP 12536, x10
4. Hypostome, LACMIP 12537, x8
5. Cephalon (Clique G), LACMIP 12538, x4.5

Figs. 6-13. *Laudonia prima* (Lochman, 1952). Poleta Formation, section GP, LACMIP collection 17053, Mt. Dunfee area, Nevada, except Figs. 11-13 (section GF, Goldfield area; Fig. 11: LACMIP collection 17039; Figs. 12-13: LACMIP collection 17041).

6. Cephalon (meraspid, Clique A), LACMIP 12539, x20
7. Cephalon (meraspid, Clique A/B), LACMIP 12540, x15
8. Cephalon (meraspid, Clique B), LACMIP 12541, x10
9. Cephalon (meraspid, Clique C), LACMIP 12542, x10
10. Cephalon (Clique D), LACMIP 12543, x9.5
11. Cephalon (Clique E), LACMIP 12544, x7
12. Cephalon (Clique F), LACMIP 12545, x5
13. Cephalon (Clique G), LACMIP 12546, x2

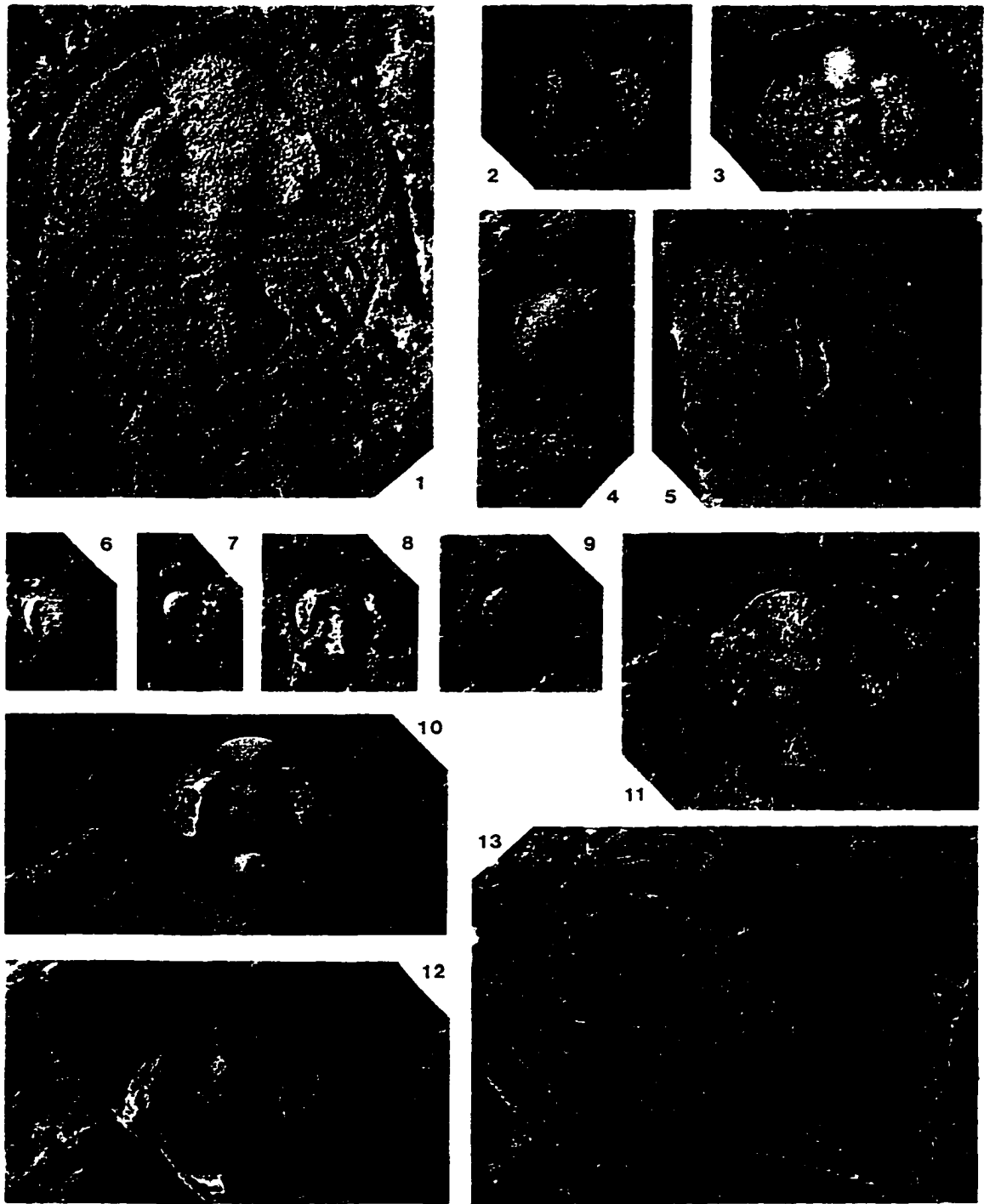


PLATE 12

Plate 13

Figs. 1-8. *Laudonia harringtoni* n. sp. Poleta Formation, section GP, LACMIP collection 17052, Mt. Dunfee area, Nevada.

1. Cephalon (meraspid, Clique C), LACMIP 12547, **Paratype**, x10
2. Cephalon (L) (Clique D), LACMIP 12548, **Paratype**, x10
3. Cephalon (Clique F), LACMIP 12549, **Paratype**, x5.5
- 4-5. Cephalon (L) (Clique G), LACMIP 12550b, counterpart, **Holotype**, x4.5
- 6-7. Hypostome, LACMIP 12551, **Paratype**, x5
8. Cephalon (Clique G), LACMIP 12550a, part, **Holotype**, x4.5

Figs. 9-11. *Laudonia prima* (Lochman, 1952). Poleta Formation, section GP, LACMIP collection 17053, Mt. Dunfee area, Nevada.

9. Prosopon (extraocular area), LACMIP 12552, x10
10. Hypostome, LACMIP 12553, x10
11. Hypostome, LACMIP 12554, x4.5

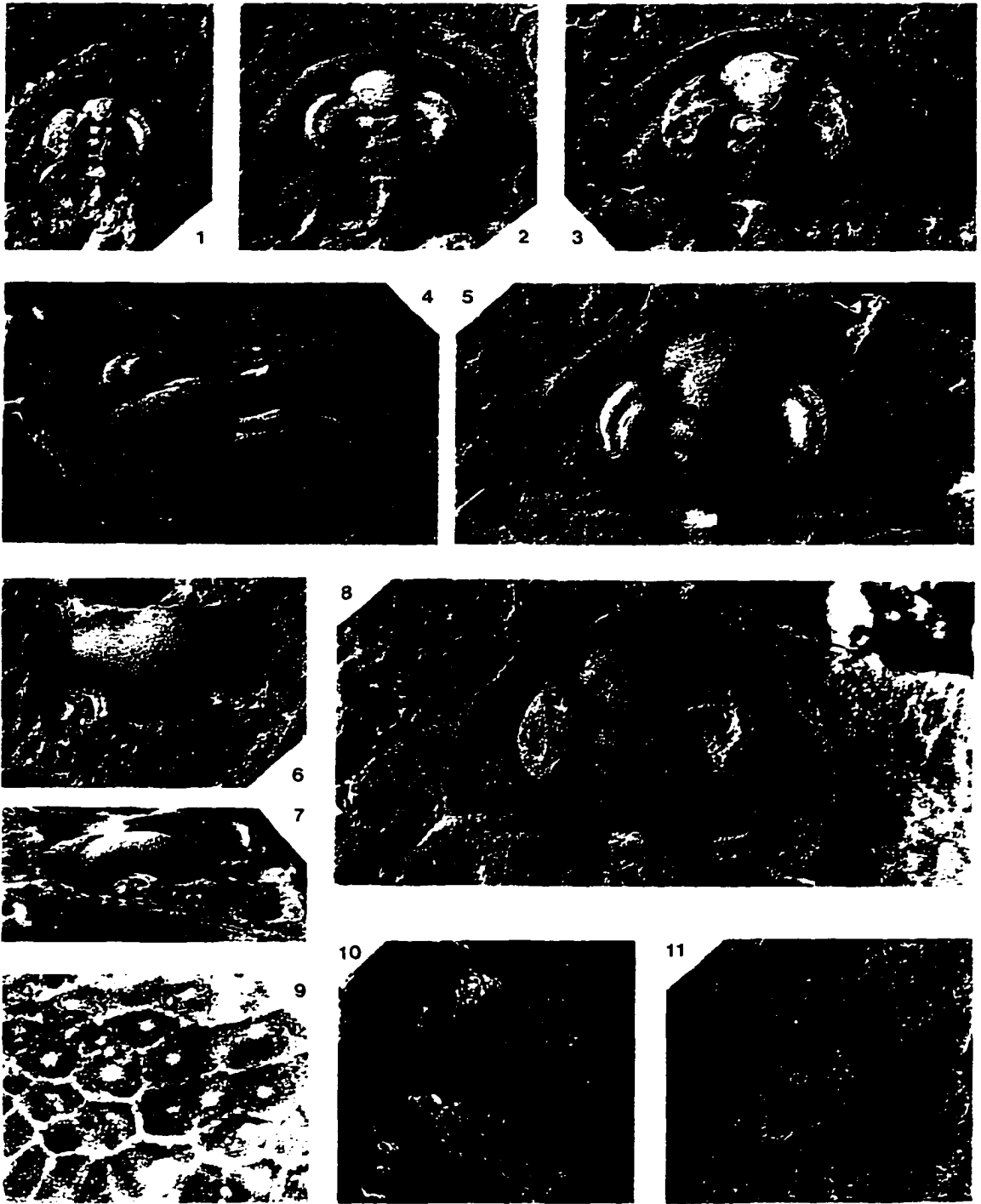


PLATE 13

Plate 14

Figs. 1-5. *Mummaspis albersi* n. sp. Poleta Formation, locality 10, LACMIP collection 26870, Goat Island, Nevada, except Fig. 1 (LACMIP collection 26869).

1. Articulated specimen, LACMIP 11358, x7.5
2. Cephalon, LACMIP 12555, x4.5
3. Cephalon, note rostral plate (L), LACMIP 12556, **Holotype**, x3.5
4. Articulated specimen (L), LACMIP 12557, **Paratype**, x3.5
5. Articulated specimen, note rostral plate (L), LACMIP 12558, **Paratype**, x7

Fig. 6. *Gabriellus poletensis* n. sp. Poleta Formation, locality 10, LACMIP collection 26869, Goat Island, Nevada.

6. Cephalon (L) (Clique G), LACMIP 12559, **Paratype**, x2.25



1



2



3



5



4



6

PLATE 14

Plate 15

Figs. 1-6. *Gabriellus poletensis* n. sp. All Poleta Formation. Figs. 1, 4: (section GP, ICS collection 1056, Mt. Dunfee area, Nevada; Fig. 2: locality 22, LACMIP collection 26862, Cedar Flat area, California; Figs. 3, 6 (3 is tentatively attributed): locality 10, LACMIP collection 26869, Goat Island, Nevada; Fig. 5: LACMIP locality BM-39, Cedar Flat area, California.

1. Cephalon (meraspid, Clique C), ICS 1056#11, **Paratype**, x10
2. Cephalon (Clique D), LACMIP 12-263, **Paratype**, x9.5
3. Hypostome, LACMIP 12560, x2.5
4. Cephalon (Clique E), ICS 1056#9, **Paratype**, x8
5. Articulated specimen with pygidium (Clique G), LACMIP B-4030, **Holotype**, x2
6. Articulated specimen, note rostral plate (Clique G), LACMIP 7393, x2

Figs. 7-9. *Gabriellus* sp. 1. Mural Formation, locality 1, GSC collection 57672, Mt. Kerkeslin, British Columbia.

7. Cephalon (L), GSC 57672#9, x3.5
8. Glabella and ocular lobe, GSC 57672#1, x6
9. Glabella and ocular lobe, GSC 57672#10, x4

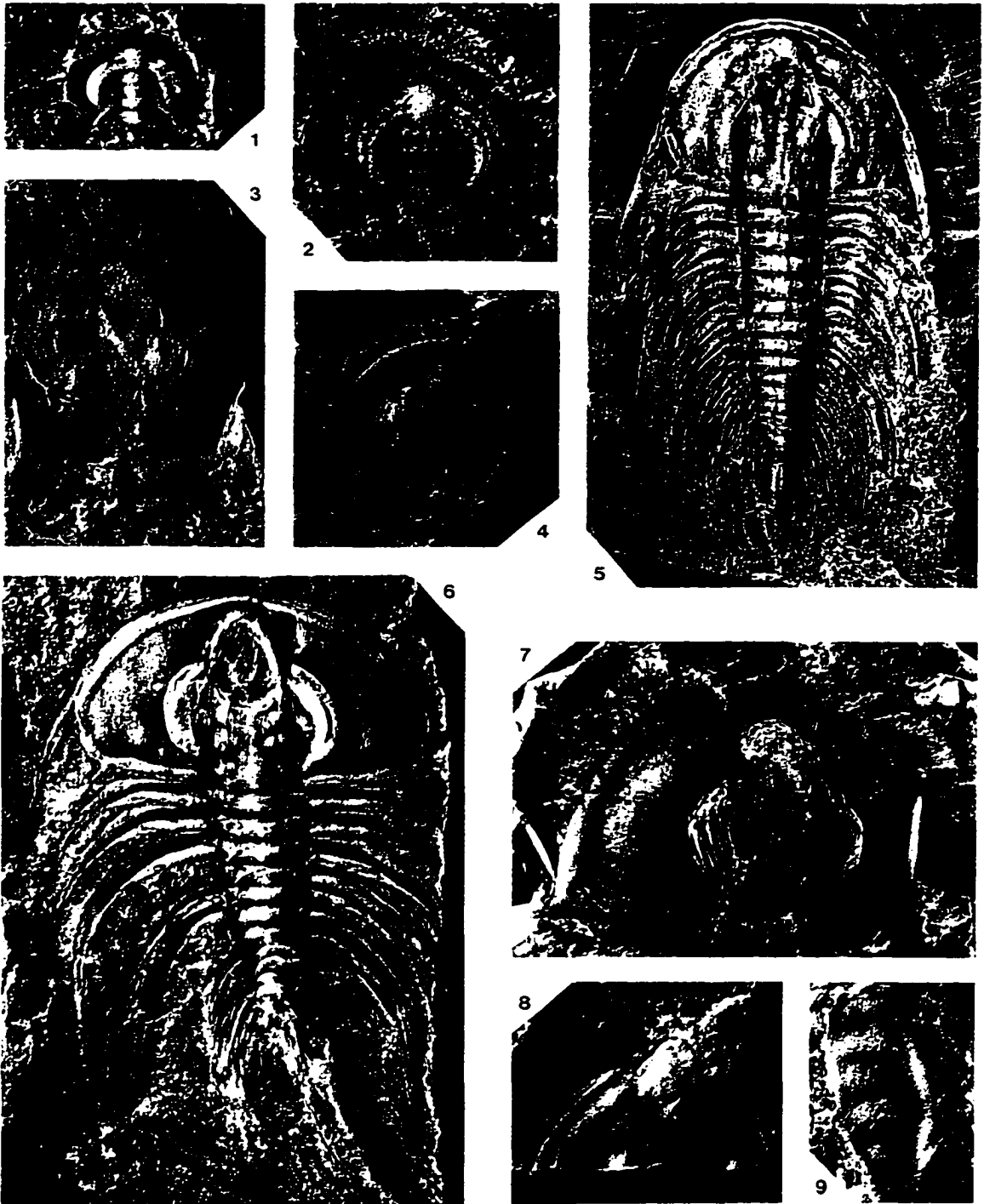


PLATE 15

Plate 16

Figs. 1-9. *Mesolenellus guthi* n. sp. All Poleta Formation. Figs. 1, 3, 5, 7-9: Cedar Flat area, California: Figs. 1, 9: locality 22, LACMIP collection 26862; Fig. 3: locality 22, LACMIP collection 17081; Figs. 5, 8: section NH, LACMIP collection 26780a; Fig. 7: section CF, LACMIP collection 17065. Figs. 2, 4, 6: section GP, collection ICS 1056, Mt. Dunfee area, Nevada.

1. Cephalon (L) (meraspid, Clique C), LACMIP 12-278a, x10
2. Cephalon (Clique D), ICS 1056#20, x10
3. Articulated specimen (L) (meraspid, Clique C), LACMIP 12561, **Paratype**, x15
4. Cephalon (Clique D), ICS 1056#24, **Paratype**, x8
5. Hypostome, LACMIP 11-221, x6
6. Cephalon (Clique E), ICS 1056#10, **Paratype**, x7
7. Cephalon (Clique F), LACMIP 12562, x4.5
8. Articulated specimen (L) (Clique F), LACMIP 11-527, x4.5
9. Articulated specimen (Clique F), LACMIP 7397, **Holotype**, x4.5

Figs. 10-11. *Mesolenellus moorei* n. sp. Poleta Formation, section GF, LACMIP collection 17037, Goldfield area, Nevada.

10. Cephalon (meraspid, Clique A/B), LACMIP 12563, x15
11. Cephalon (meraspid, Clique B), LACMIP 12564, **Paratype**, x12

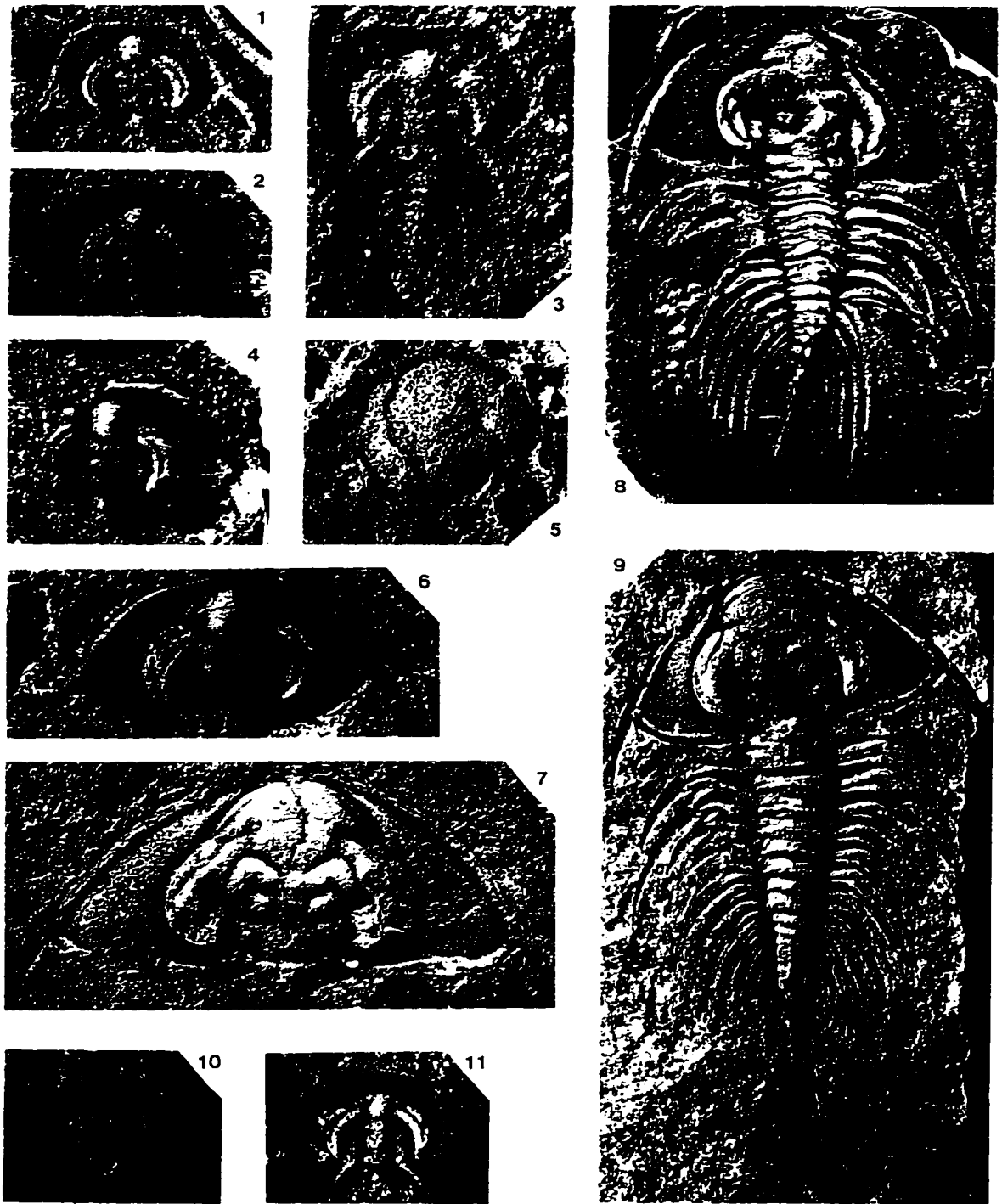


PLATE 16

Plate 17

Figs. 1-7. *Mesolenellus moorei* n. sp. Poleta Formation, section GF, LACMIP collection 17037, Goldfield Area, Nevada, except Fig. 1 (LACMIP collection 17033).

1. Cephalon with prosopon (Clique G), LACMIP 12565, x2.25
2. Articulated specimen (Clique F), LACMIP 12566, x4
3. Cephalon (meraspid, Clique C), LACMIP 12567a, part, **Paratype**, x12
4. Cephalon (L) (meraspid, Clique C), LACMIP 12567b, counterpart, **Paratype**, x12
5. Cephalon (L) (meraspid, Clique B), LACMIP 12568, x12
6. Cephalon (L) (Clique D), LACMIP 12569, **Paratype**, x10
7. Cephalon (L) (Clique F), LACMIP 12570, **Holotype**, x4

Figs. 8-12. *Wannerellus alcatrazensis* n. gen., n. sp. Harkless Formation, locality 12, LACMIP collection 26873, Alcatraz Island, Nevada, except Figs. 8, 12: locality 14, LACMIP collection 27297, east of Silver Peak.

8. Cephalon (meraspid, Clique B), LACMIP 12571, **Paratype**, x18
9. Cephalon (Clique F), LACMIP 11377, **Paratype**, x3.5
10. Cephalon (Clique G), LACMIP 7413, **Holotype**, x2.5
11. Cephalon (L) (Clique G), LACMIP 12572, x3
12. Cephalon (Clique F), LACMIP 11379, x4

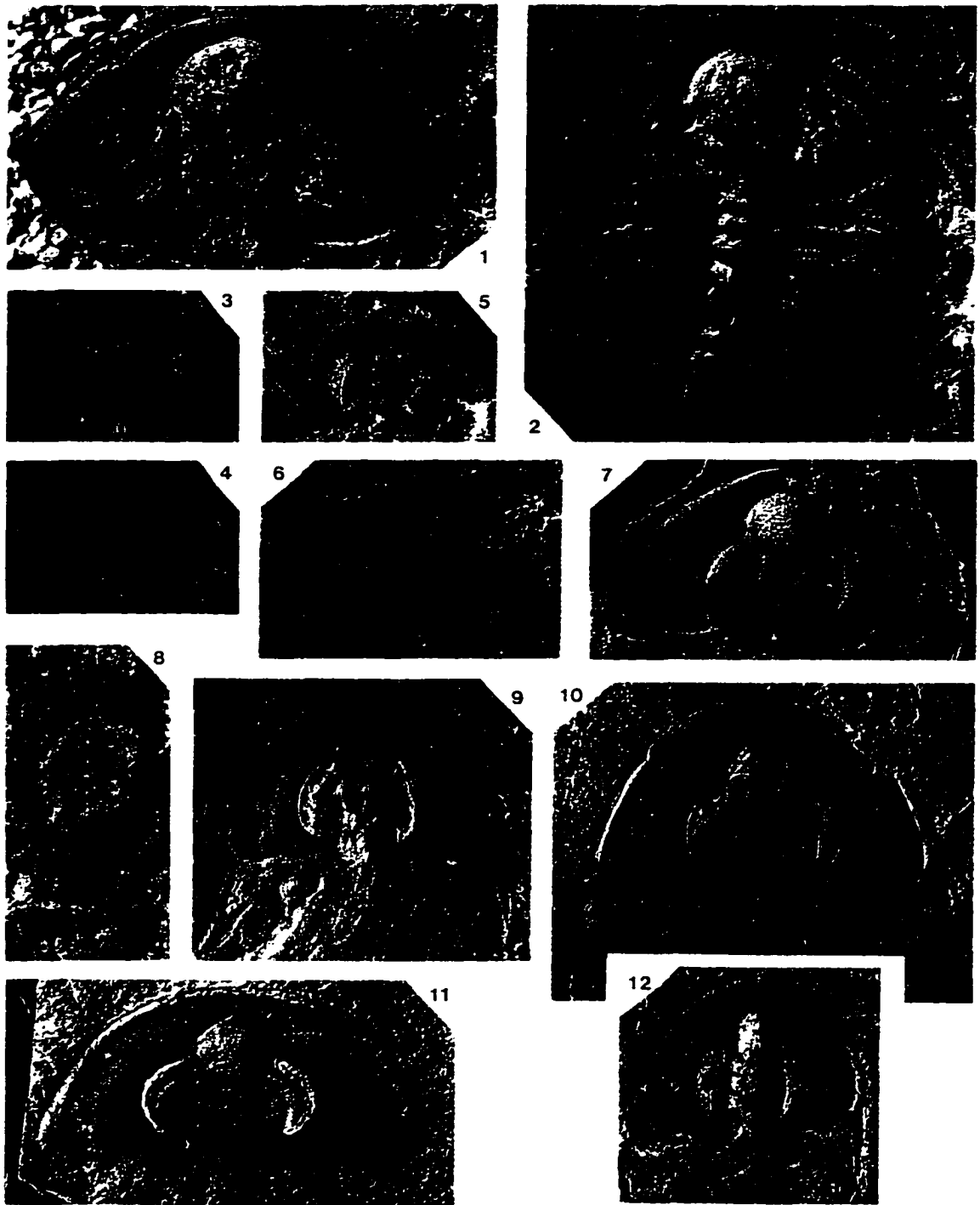


PLATE 17

Plate 18

Figs. 1-6. *Olenellus transitans* (Walcott, 1910b). Kinzers Formation, locality 8q (of Walcott, 1910b, p. 310), York, Pennsylvania, except Fig. 3 (Eager Formation, section RC, collection RC4c, Ram Creek area, British Columbia) and Fig. 5 (Saline Valley Formation, section PC, LACMIP collection 26851, Paymaster Canyon, Nevada).

1. Articulated meraspid (Clique A/B), USNM 56810b, x20
2. Articulated meraspid (Clique C/D), USNM 56810a, x10
3. Hypostome, RC4c#18, x12
4. Cephalon, molt configuration, with inverted hypostome and rostral plate (Clique E), USNM 56810u, x5
5. Cephalon (Clique G), LACMIP 7426, x1.8
6. Articulated specimen with opisthothorax, pygidium and inverted rostral plate (Clique G), USNM 56810j, x1.75

Fig. 7. *Olenellus cf. thompsoni*. Saline Valley Formation, section PC, LACMIP collection 26852, Paymaster Canyon, Nevada.

7. Cephalon (Clique G), LACMIP 11406, x1.25

Fig. 8. *Olenellus thompsoni* (Hall, 1859). Parker Formation, locality 25 of Walcott (1910b, p. 339), Georgia, Vermont.

8. Articulated specimen (L) (Clique G), USNM 15418a, *Topotype*, x2

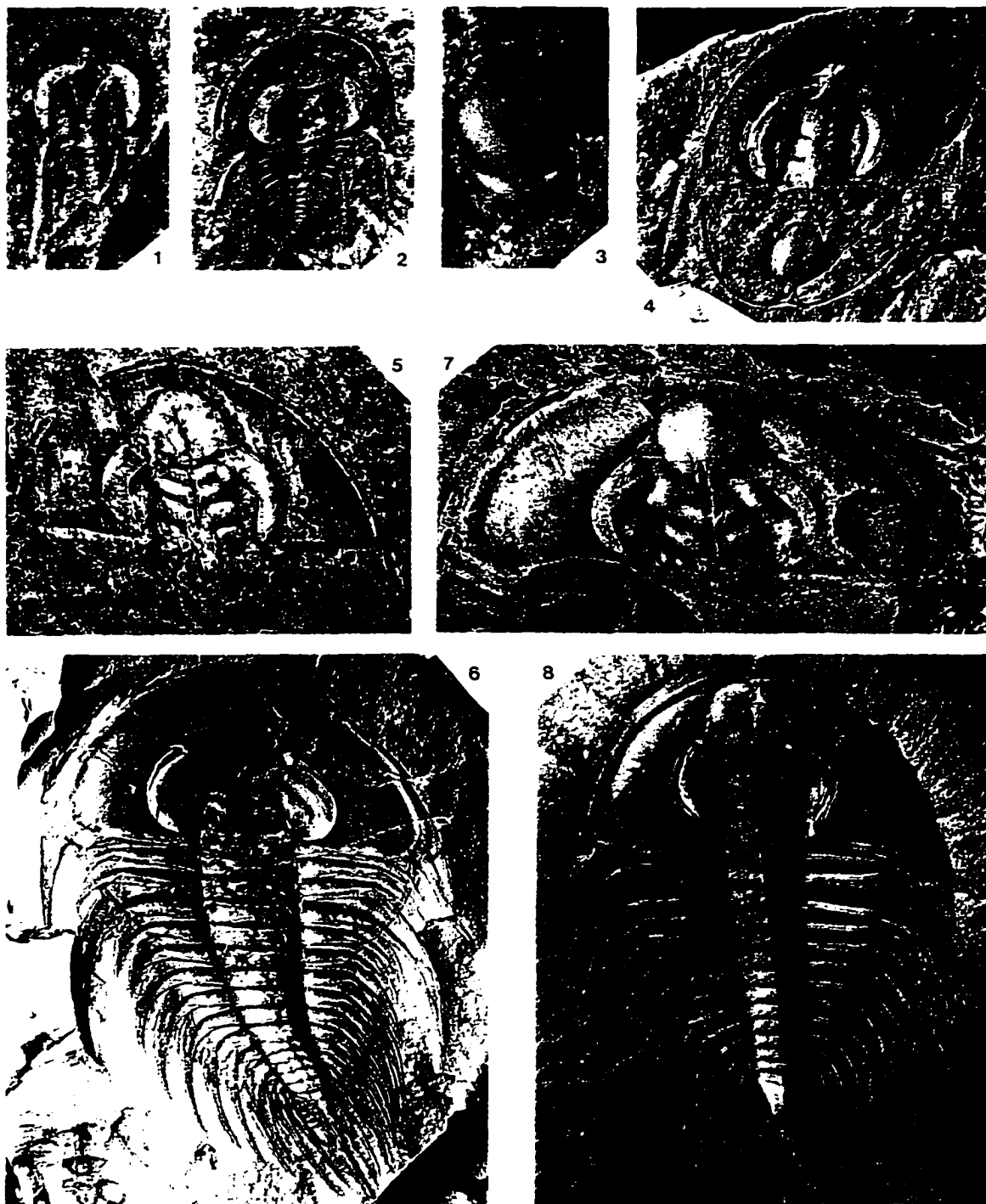


PLATE 18

Plate 19

Figs. 1-9. *Olenellus transitans* (Walcott, 1910b). Eager Formation, section RC, collection RC4c, Ram Creek area, British Columbia; except Figs. 8-9: Saline Valley Formation, locality 26, LACMIP collection 26784, Waucoba Wash, California.

1. Cephalon (meraspid, Clique A/B), RC4c#24, x24
2. Cephalon (meraspid, Clique B/C), RC4c#25, x20
- 3-4. Cephalon (Clique E), RC4c#16, x9
- 5-6. Cephalon (Clique G), RC4c#12, x3.5
7. Cephalon (Clique G), RC4c#11, x3
8. Articulated specimen (Clique F), LACMIP 11416, x3
9. Articulated specimen (L) (Clique G), LACMIP 11408, x1.5

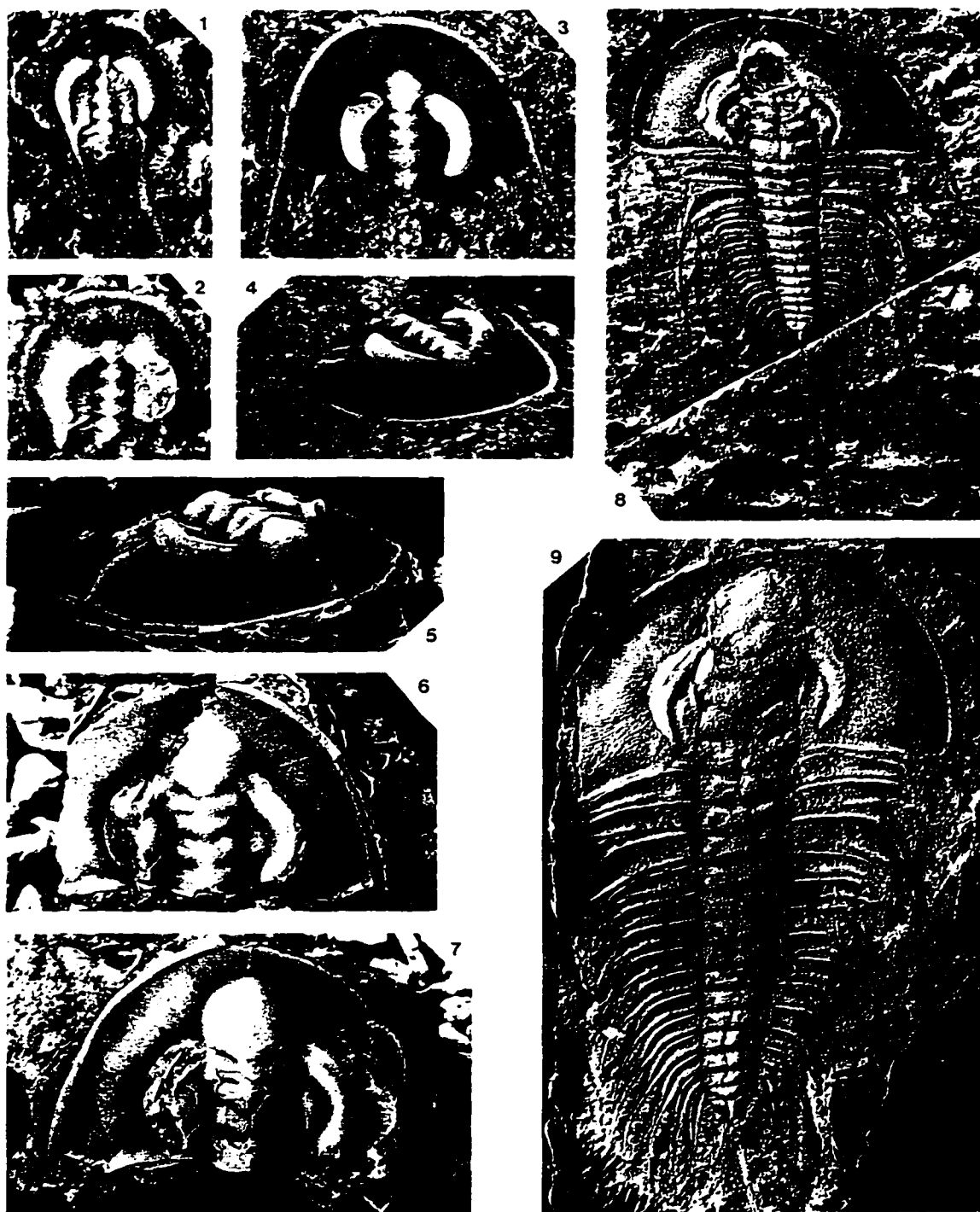


PLATE 19

Plate 20

Fig. 1. *Olenellus transitans* (Walcott, 1910b). Eager Formation, section RC, collection RC4c, Ram Creek area, British Columbia.

1. Hypostome, RC4c#17, x5

Figs. 2-3, 10-11. *Olenellus cf. nevadensis* (Walcott, 1910b). Figs. 2, 10: Saline Valley Formation, locality 19, LACMIP collection 26854, Magruder Mountain, Nevada; Fig. 3 : ?Harkless Formation, locality 8, LACMIP collection 24411, Miller Mountain, Nevada; Fig. 11: Saline Valley Formation, locality 9, LACMIP collection 26877, Weepah Hills, Nevada.

2. Cephalon, (Clique G), LACMIP 12573, x3.5
3. Articulated specimen, LACMIP 12574, x2
10. Cephalon, (Clique G), LACMIP 12575, x3
11. Cephalon, (Clique F/G), LACMIP 12576, x3.5

Figs. 4, 9. *Olenellus gilberti* Meek in White, 1874. Pioche Formation, Nevada: Fig. 4: Pioche Hills, near Pioche; Fig. 9: Chief Range, southwest of Pioche and northwest of Caliente .

4. Cephalon, USNM 15411a, Lectotype, x2
9. Articulated specimen (L), ICS RW1, x2

Figs. 5-8, 12. *Olenellus ricei* n. sp. Eager Formation, locality 5, Cranbrook area, British Columbia.

5. Hypostome and rostral plate (L), RBCM EH.997.06.002, x5
6. Cephalon (Clique A) UBC C1-19, x10
7. Cephalon (Clique A/B) UBC C13-42, x10
8. Articulated specimen (Clique G), UBC GT352, **Holotype**, x2
12. Cephalon (Clique C) UA 036, x10

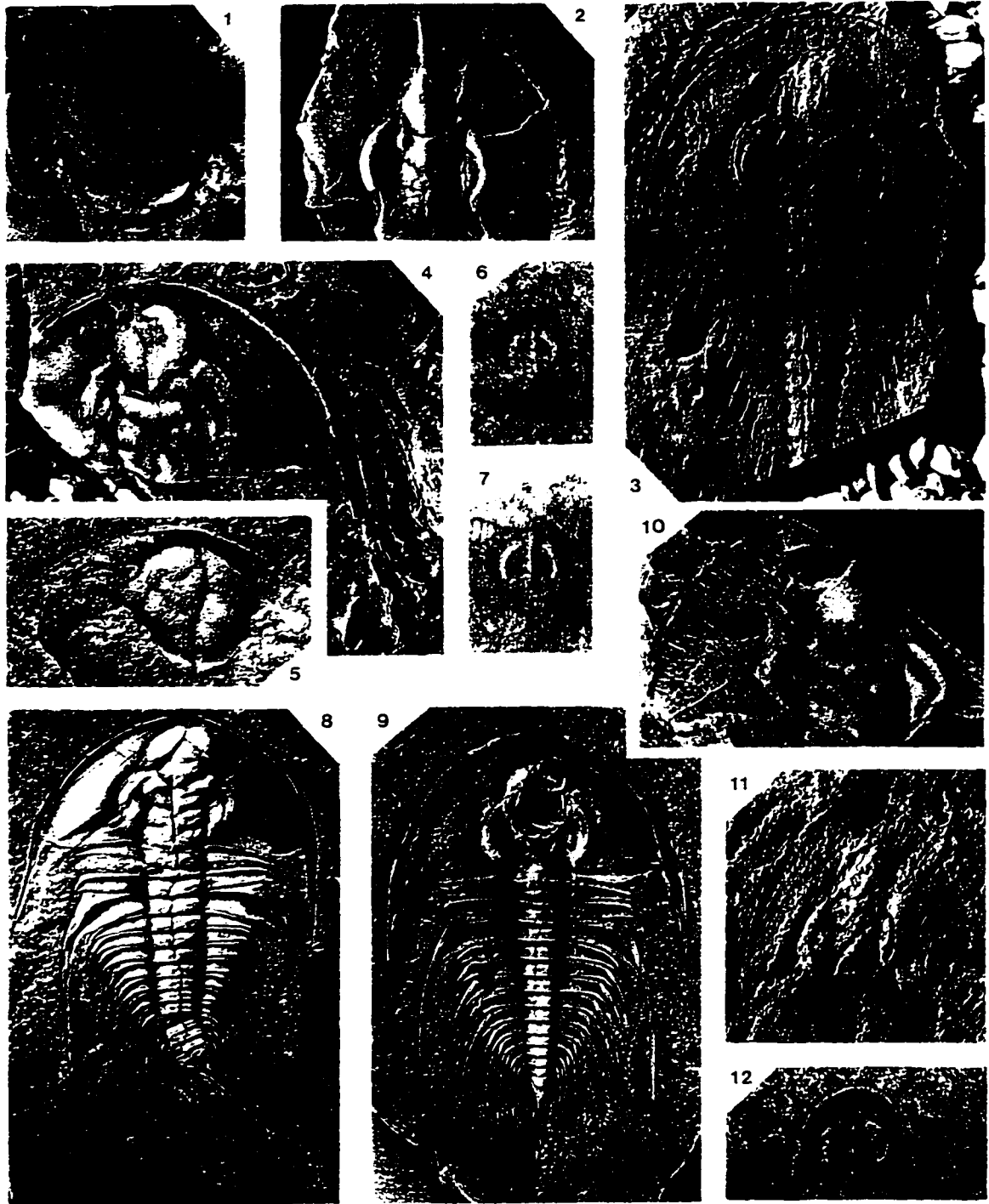


PLATE 20

Plate 21

Figs. 1-11. *Olenellus ricei* n. sp. Eager Formation, locality 5, Cranbrook area, British Columbia.

1. Cephalon (Clique D), RBCM EH.997.06.003, x10
2. Articulated meraspid (Clique D), UBC GT302, **Paratype**, x10
3. Hypostome (L), UA 008, x7.5
- 4, 11. Articulated specimen, molt configuration, with hypostome (Clique G), ROM 27414, **Paratype**, x5, x2.5
5. Articulated specimen with rostral plate (L) (Clique F), UBC GT303, **Paratype**, x5
6. Articulated specimen with hypostome in place (Clique F), UBC C6-34, x4
7. Cephalon (Clique G), UA 011, x3
8. Articulated specimen (L) (Clique D/E), UA 035, x7.5
9. Articulated specimen (L) (Clique E), UA 015, **Paratype**, x5
10. Cephalon with rostral plate (Clique G), UA 027, x3.5

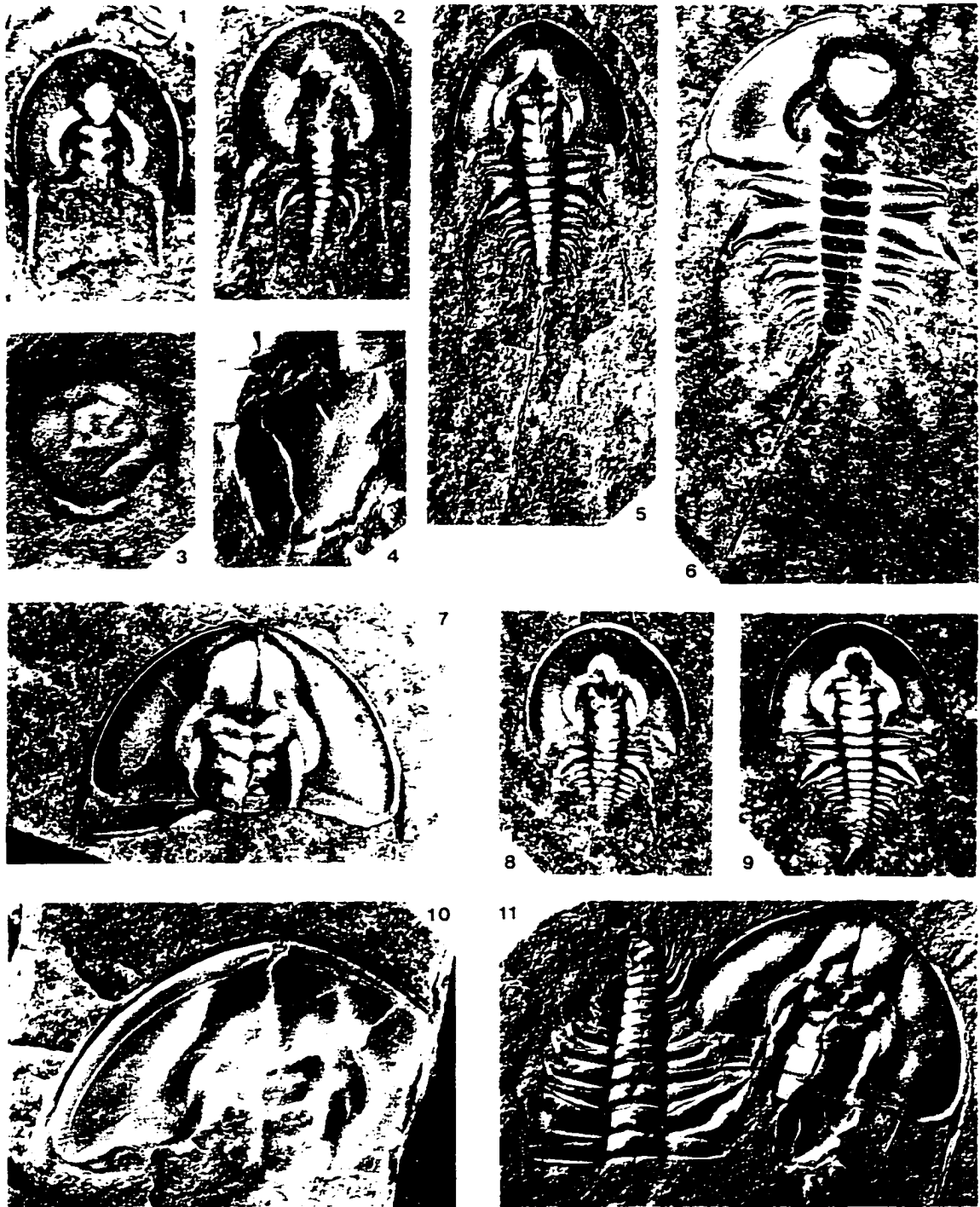


PLATE 21

Plate 22

Figs. 1-6. *Mesonacis eagerensis* (Best, 1952). Eager Formation, locality 5, Cranbrook area, British Columbia.

1. Cephalon (Clique D), UA 024, x10
2. Cephalon (Clique E), UBC C3-115, x6
3. Articulated specimen (Clique G), **Holotype**, UBC GT101, x2
- 4-5. Articulated specimen (L) (Clique F/G), RBCM EH96.05.0001, x3, x7
6. Articulated specimen (Clique G), UA 013, x2

Figs. 7-9. *Mesonacis graingerensis* n. sp. Eager Formation, section MG3, collection MG3b, Canal Flats area, British Columbia.

7. Cephalon (Clique B), MG3b#25, **Paratype**, x15
8. Cephalon (Clique B), MG3b#30, x15
9. Cephalon (Clique C), MG3b#24, x10

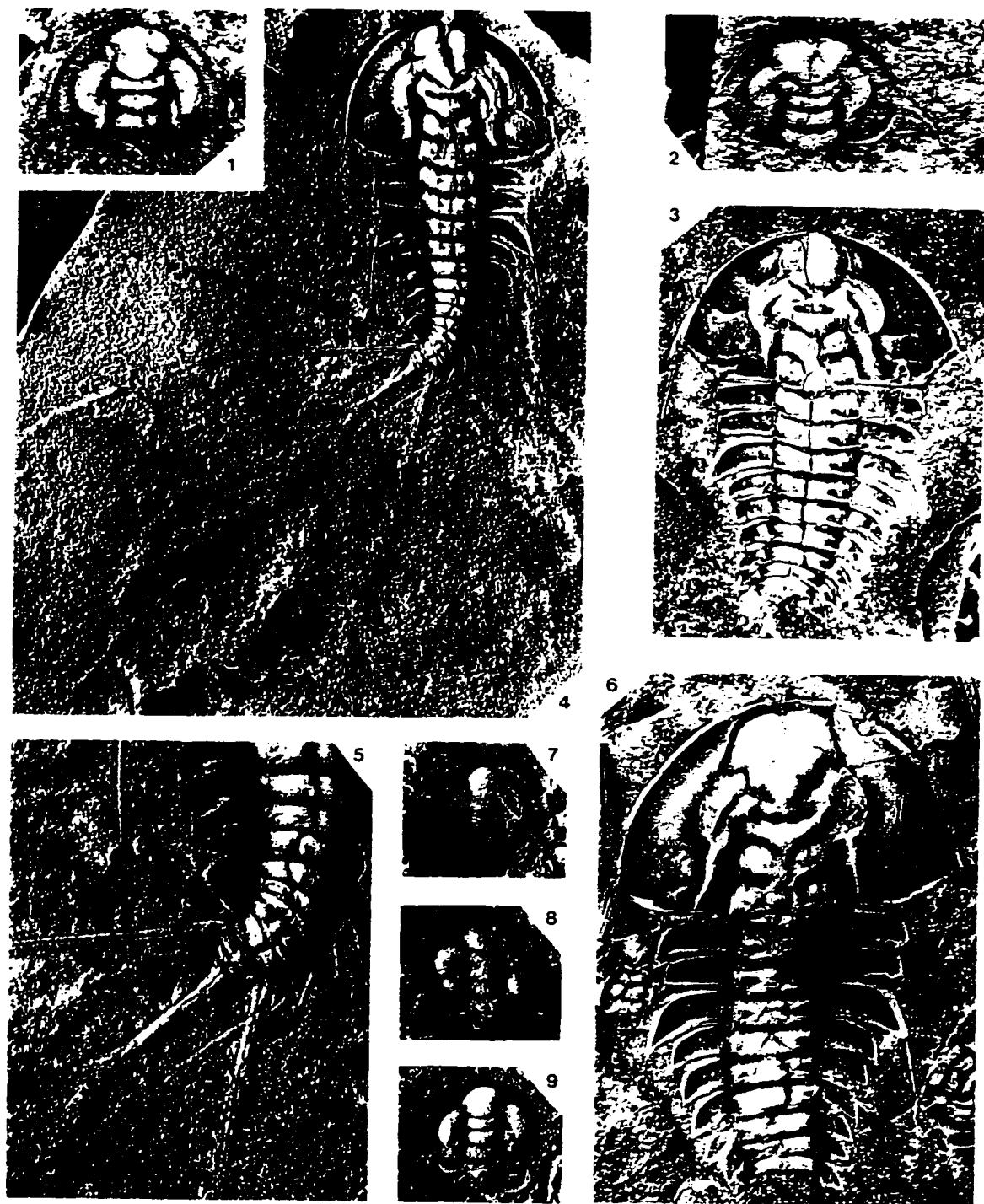


PLATE 22

Plate 23

Figs. 1-5. *Mesonacis graingerensis* n. sp. Eager Formation, section MG3, collection MG3b, Canal Flats area, British Columbia.

- 1-2. Cephalon (Clique C), MG3b#32, x10
3. Cephalon (Clique E), MG3b#41, **Paratype**, x7
4. Cephalon (Clique G), MG3b#2, **Paratype**, x3
5. Cephalon (L) (Clique F), MG3b#3, **Holotype**, x3

Figs. 6-8. *Mesonacis? schofieldi* (Best, 1952). Fig. 6 (tentatively attributed): Harkless Formation, locality 25, LACMIP collection 26834, Waucoba Wash, California; Figs. 7-8: Eager Formation, locality B of Best (1952, p. 13), Cranbrook area, British Columbia.

6. Cephalon, LACMIP 11396, x3.5
7. Cephalon, UBC GT205, **Paratype**, x2
8. Articulated specimen with associated hypostome, UBC GT201, **Holotype**, x3

Figs. 9-12. aff. *Mesonacis leechi* n. sp. Eager Formation, section MG2, collection MG2b, Canal Flats area, British Columbia.

- 9, 12. Cephalon (Clique E/F), MG2b#19, **Holotype**, x8
10. Cephalon (Clique D) , MG2b#16, **Paratype**, x12
11. Cephalon (Clique E), MG2b#7, **Paratype**, x8



PLATE 23

Plate 24

Figs. 1-3, 5. *Fremontella ashtoni* n. sp. Eager Formation, section RC4, collection RC4c, Ram Creek area, British Columbia.

1. Cephalon, RC4c#9, x5.5
2. Cephalon, RC4c#8, **Paratype**, x5.5
- 3, 5. Cephalon, RC4c#7, **Holotype**, x5.5

Figs. 4, 6-8. *Fremontella campbellae* n. sp. Eager Formation, section MG2, collection MG2b, Canal Flats area, British Columbia.

- 4, 6. Cephalon, MG2b#4, **Paratype**, x6
7. Cephalon, **Holotype**, MG2b#3, x6
8. Cephalon, MG2b#5, x6

Figs. 9. aff. *Mesonacis leechi* n. sp. (tentatively attributed) Eager Formation, locality 2, GSC collection 23916, Canal Flats area, British Columbia.

9. Cephalon (L), GSC 23916a, x8

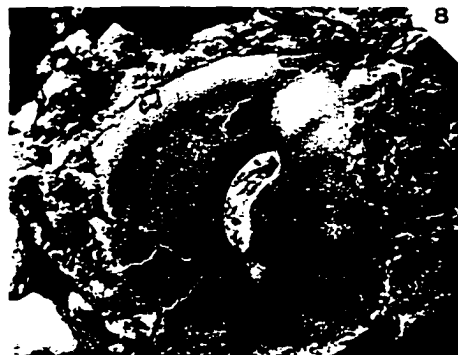


PLATE 24

Plate 25

Figs. 1-2. *Polliaxis* sp. 1 Poleta Formation, section GP, LACMIP collection 26850, Mt. Dunfee area, Nevada.

1. Pygidium, LACMIP 12577, x4
2. Glabellar fragment, LACMIP 12578, x6

Figs. 3-8. *Polliaxis muralensis* n. sp. Mural Formation, locality 1, GSC collection 57672, Mt. Kerkeslin, British Columbia.

- 3, 6. Pygidium, GSC 57672#2, **Holotype**, x4
- 4, 7. Cranidium, GSC 57672#1, **Paratype**, x3.5
5. Librigena fragment, GSC 57672#6, x2
8. Pygidium, GSC 57672#5, **Paratype**, x7.5

Figs. 9-14. *Labradoria lochmanae* n. sp. Poleta Formation, section GP, ICS collection 1056, Mt. Dunfee area, Nevada (Fig. 10 tentatively attributed).

9. Pygidium, ICS 1056#14, **Paratype**, x10
10. Hypostome, ICS 1056#29, x20
11. Pygidium, ICS 1056#13, x10
12. Pygidium, ICS 1056#20, x10
13. Cranidium, ICS 1056#15, x10
14. Cranidium, ICS 1056#12, **Paratype**, x10

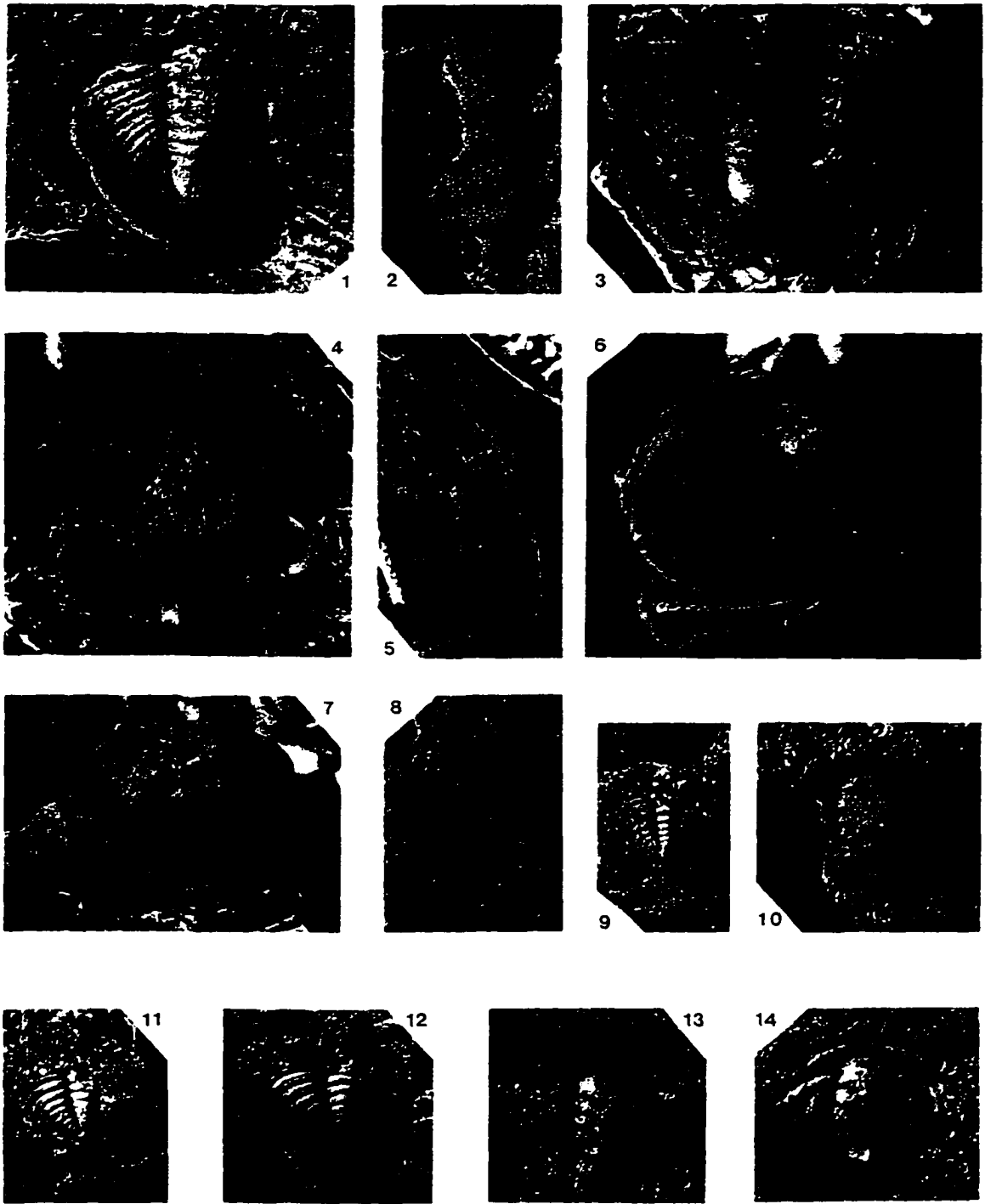


PLATE 25

Plate 26

Figs. 1-10. *Labradoria lochmanae* n. sp. All Poleta Formation. Figs. 1-4, 6-7: section GP, ICS collection 1056, Mt. Dunfee area, Nevada; Fig. 5: section CF, LACMIP collection 26866, Cedar Flat area, California; Figs. 8, 10: locality 22, (Fig. 8: LACMIP collection 26862; Fig. 10: LACMIP collection 17081), Cedar Flat area, California; Fig. 9: section NH, LACMIP collection 17078, Cedar Flat area, California.

1. Pygidium, ICS 1056#21, x8
- 2, 4. Pygidium, ICS 1056#7, **Paratype**, x6
- 3, 6. Cranidium, ICS 1056#22, x6
5. Articulated specimen, LACMIP 32-501, **Holotype**, x5
7. Cranidium, ICS 1056#4, **Paratype**, x5
8. Articulated specimen (L), LACMIP 12-515, x5
9. Cranidium (L), LACMIP 12579, **Paratype**, x5
10. Hypostome (L), LACMIP 12580, x8

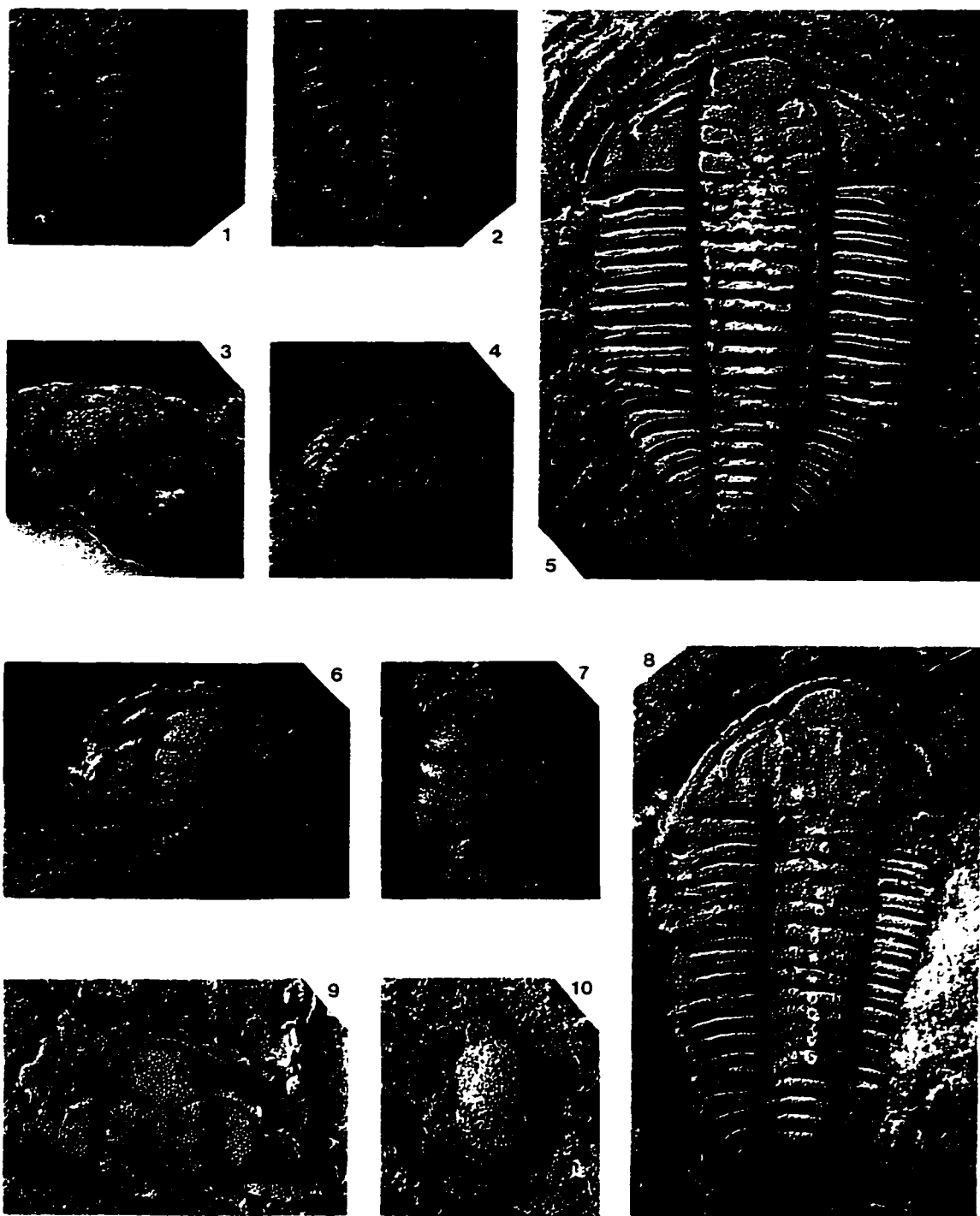


PLATE 26

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Figs. 1-3. *Wenkchemnia?* sp. 1. All Eager Formation. Fig. 1: section MG2, collection MG2e, Canal Flats area, British Columbia; Figs. 2-3: locality 7, Purcell Mountains, British Columbia.

1. Cranidium, MG2e#3, x10
2. Cranidium, RBCM EH.997.06.004, x10
3. Articulated specimen lacking librigenae, RBCM EH.997.06.005, x9

Figs. 4-11. *Bonnaspis fieldensis* (Walcott, 1916b). Eager Formation, section RC4, collection RC4f, Ram Creek area, British Columbia, except Fig. 11 (locality 5, Cranbrook area).

4. Cranidium, RC4f#14, x9
5. Pygidium, RC4f#19, x10
- 6, 8. Cranidium, RC4f#1, x8
- 7, 9. Pygidium, RC4f#15, x9
10. Hypostome, RC4f#8, x14
11. Cranidium, U.A. 044, x7.5

Figs. 12-13. *Bonnaspis columbensis* (Resser, 1936). Mount Whyte Formation, locality 61d of Walcott (1916, p. 319), Mount Shaffer, British Columbia.

12. Pygidium, USNM 62723, **Paratype**, x5
13. Cranidium, USNM 62722, **Holotype**, x5



PLATE 27

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Figs. 1-3. *Bonnaspis fieldensis* (Walcott, 1916b). Eager Formation, section RC4, collection RC4f, Ram Creek area, British Columbia.

1. Hypostome, RC4f#7, x14
2. Pygidium, RC4f#17, x11
3. Pygidium, RC4f#16, x9

Figs. 4, 7. *Bonnaspis columbensis* (Resser, 1936). Mount Whyte Formation, locality 61d of Walcott (1916, p. 319), Mount Shaffer, British Columbia.

4. Hypostome, USNM 62725, **Paratype**, x6
7. Hypostome, USNM 62726, **Paratype**, x6

Fig. 5-6, 8-9. *Bonnia parvula* (Billings, 1861). Forteau Formation, L'Anse au Loup, north shore of Straits of Belle Isle, Labrador.

5. Cranidium, GSC 433g, x6
6. Cranidium, GSC 433, **Holotype**, x6
8. Pygidium, GSC 427, x6
9. Pygidium, GSC 433a, **Pleisiotype**, x9

Figs. 10-19. *Bonnia laterispina* Fritz, 1972. Eager Formation, section MG3, collection MG3b, Canal Flats area, British Columbia, except Fig. 16 (section MG1, collection MG1c) and Fig. 17 (section RC4, collection RC4c, Ram Creek area).

10. Cranidium (late meraspid), MG3b#61, x12
11. Cranidium (late meraspid), MG3b#60, x12
12. Cranidium (Clique A), MG3b#54, x10
- 13, 18. Cranidium (Clique A), MG3b#51, x9.5
14. Hypostome, MG3b#20, x8
15. Pygidium (L) (Clique A), MG3b#59, x10
16. Cranidium (Clique A), MG1c#5, x8
17. Pygidium (Clique A), RC4c#23, x12
19. Cranidium (Clique A), MG3b#50, x9.5

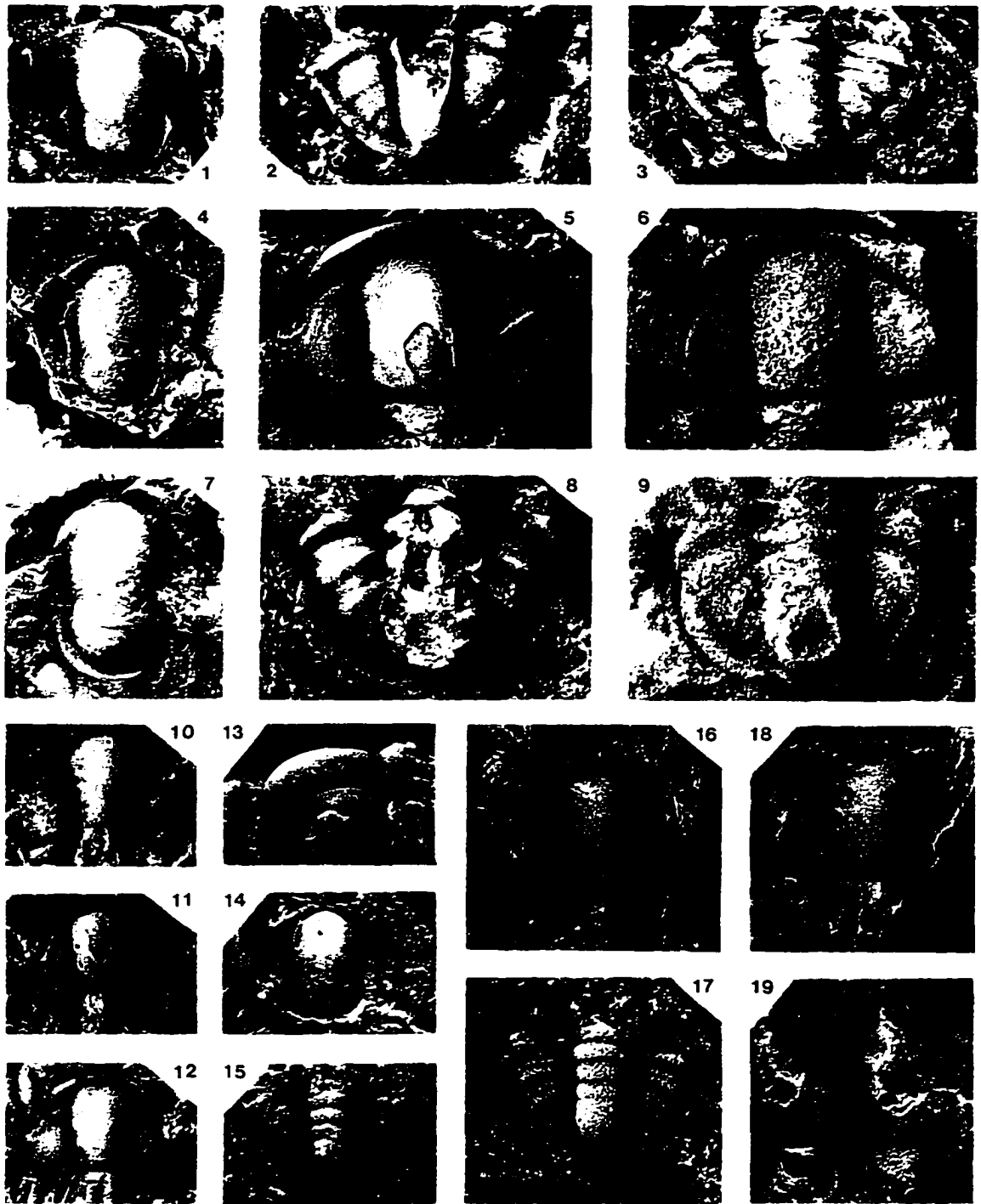


PLATE 28

Plate 29

Figs. 1-5. *Bonnia laterispina* Fritz, 1972. Eager Formation, section MG3, collection MG3b, Canal Flats area, British Columbia.

1. Cranidium (Clique A), MG3b#49, x9.5
2. Cranidium (Clique B), MG3b#48, x8
3. Cranidium (Clique C), MG3b#47, x7
- 4-5. Pygidium (Clique C), MG3b#45, x8

Figs. 6-13. *Bonnia fritzi* n. sp. Eager Formation, section MG2, collection MG2j', Canal Flats area, British Columbia, except Fig. 13 (section MG1, collection MG1t).

- 6-7. Cranidium (Clique B), MG2j'#34, **Paratype**, x9
8. Pygidium (Clique C), MG2j'#40, **Holotype**, x8
9. Pygidium (Clique C), MG2j'#38, x8
10. Cranidium (Clique C), MG2j'#36, **Paratype**, x8
11. Hypostome, MG2j'#42, **Paratype**, x10
12. Hypostome, MG2j'#41, x10
13. Librigena (L), MG1t#5, x8

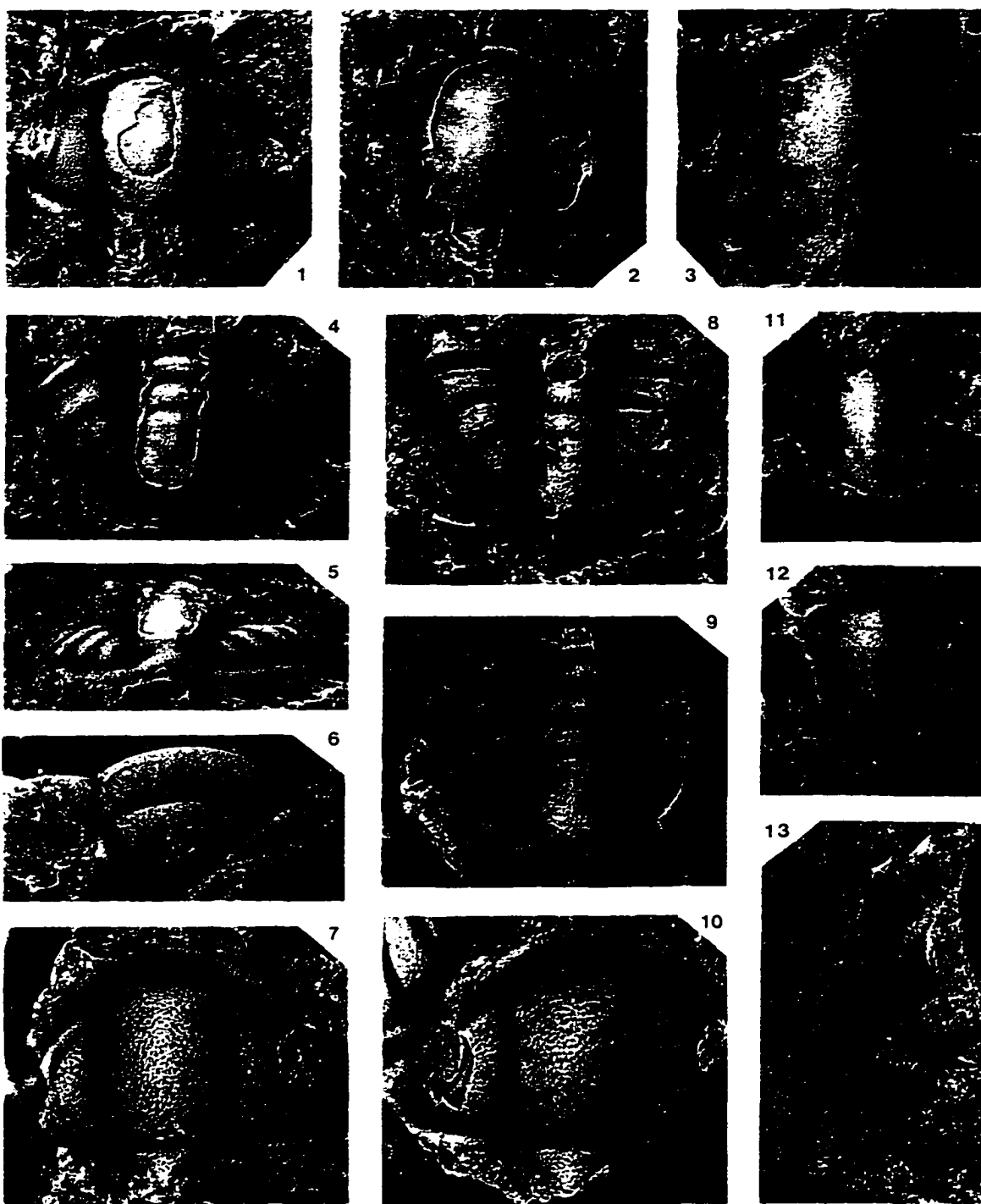


PLATE 29

Plate 30

Fig. 1-4. *Bonnia fritzi* n. sp. All Eager Formation. Fig. 1: section MG2, collection MG2j', Canal Flats area, British Columbia. Figs. 2-4 (tentatively attributed): collection MG2a.

1. Pygidium (Clique A), MG2j'#13, x10
2. Protaspid, MG2a#21, x40
3. Hypostome, MG2a#32, x40
4. Cranidium (early meraspid), MG2a#31, x25

Figs. 5-18. *Bonnia grandis* n. sp. All Eager Formation. Figs. 5, 7: section MG2, collection MG2b, Canal Flats area, British Columbia; Figs. 6, 8, 12-14, 16: section MG3, collection MG3d'; Figs. 9-10, 15, 17-18: section MG2, collection MG2d; Fig. 11: section MG2, collection MG2c.

5. Cranidium (early meraspid), MG2b#14, **Paratype**, x18
6. Cranidium (late meraspid), MG3d'#12, **Paratype**, x18
7. Cranidium (Clique A), MG2b#12, x12
8. Cranidium (Clique A), MG3d'#6, **Paratype**, x10
9. Librigena, MG2d#9, x6
10. Hypostome, MG2d#1, x9
11. Pygidium (Clique A), MG2c#7, x8
12. Pygidium (Clique A), MG3d'#4, **Paratype**, x10
13. Hypostome, MG3d'#9, **Paratype**, x5
14. Cranidium (Clique B), MG3d'#5, x8
- 15, 17. Cranidium (Clique B), MG2d#2, **Paratype**, x6
16. Pygidium (Clique B), MG3d'#2, **Paratype**, x7
18. Cranidium (Clique C), MG2d#8, **Paratype**, x6

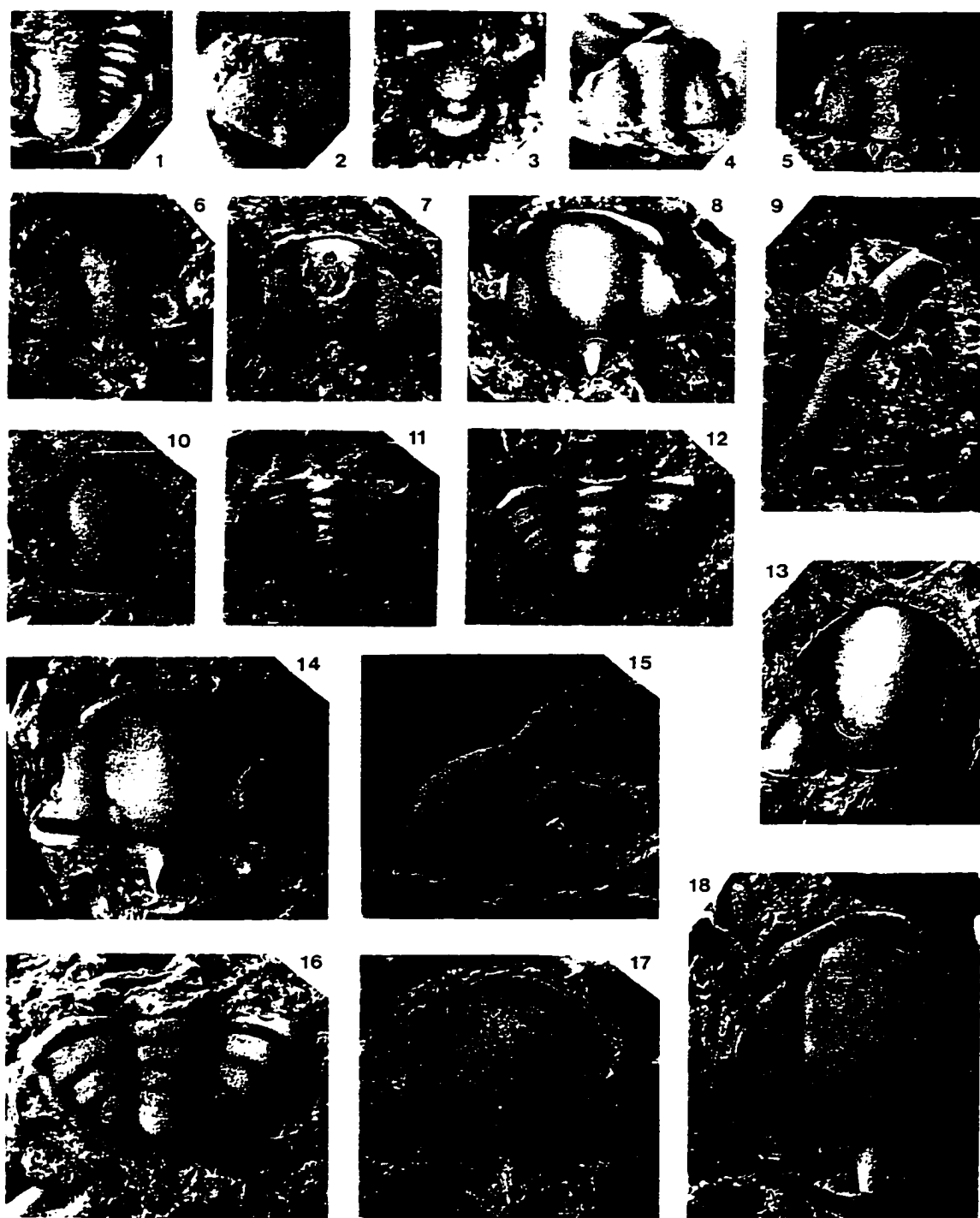


PLATE 30

Plate 31

Figs. 1-6. *Bonnia grandis* n. sp. Eager Formation, section MG2, collection MG2d, Canal Flats area, British Columbia, except Figs. 5-6 (section MG3, collection MG3d').

- 1-2. Pygidium (Clique C), MG2d#5, **Holotype**, x5
3. Librigena, MG2d#4, **Paratype**, x5
4. Pygidium (Clique C), MG2d#6, x5
5. Cranidium (Clique C), MG3d'#3, x6
6. Thoracic segment, MG3d'#11, x4.5

Figs. 7-8. Unassigned small stages, possibly of *Bonnia ornata* n. sp. or *B. drysdalea* n. sp. Eager Formation, section MG2, collection MG2j, Canal Flats area, British Columbia.

7. Cranidium (early meraspid), MG2j#54, x15
8. Pygidium (early meraspid), MG2j#57, x20

Figs. 9-15. *Bonnia ornata* n. sp. Eager Formation, section MG2, collection MG2j, Canal Flats area, British Columbia (Fig. 9 tentatively attributed).

9. Hypostome, MG2j#20, x8
10. Pygidium (late meraspid), MG2j#51, **Paratype**, x15
11. Cranidium (Clique A), MG2j#46, **Paratype**, x10
12. Pygidium (L) (Clique B), MG2j#5, x8
13. Pygidium (Clique A), MG2j#17, **Paratype**, x10
14. Cranidium (Clique B), MG2j#18, **Paratype**, x8
15. Pygidium (Clique B), MG2j#16, **Holotype**, x9

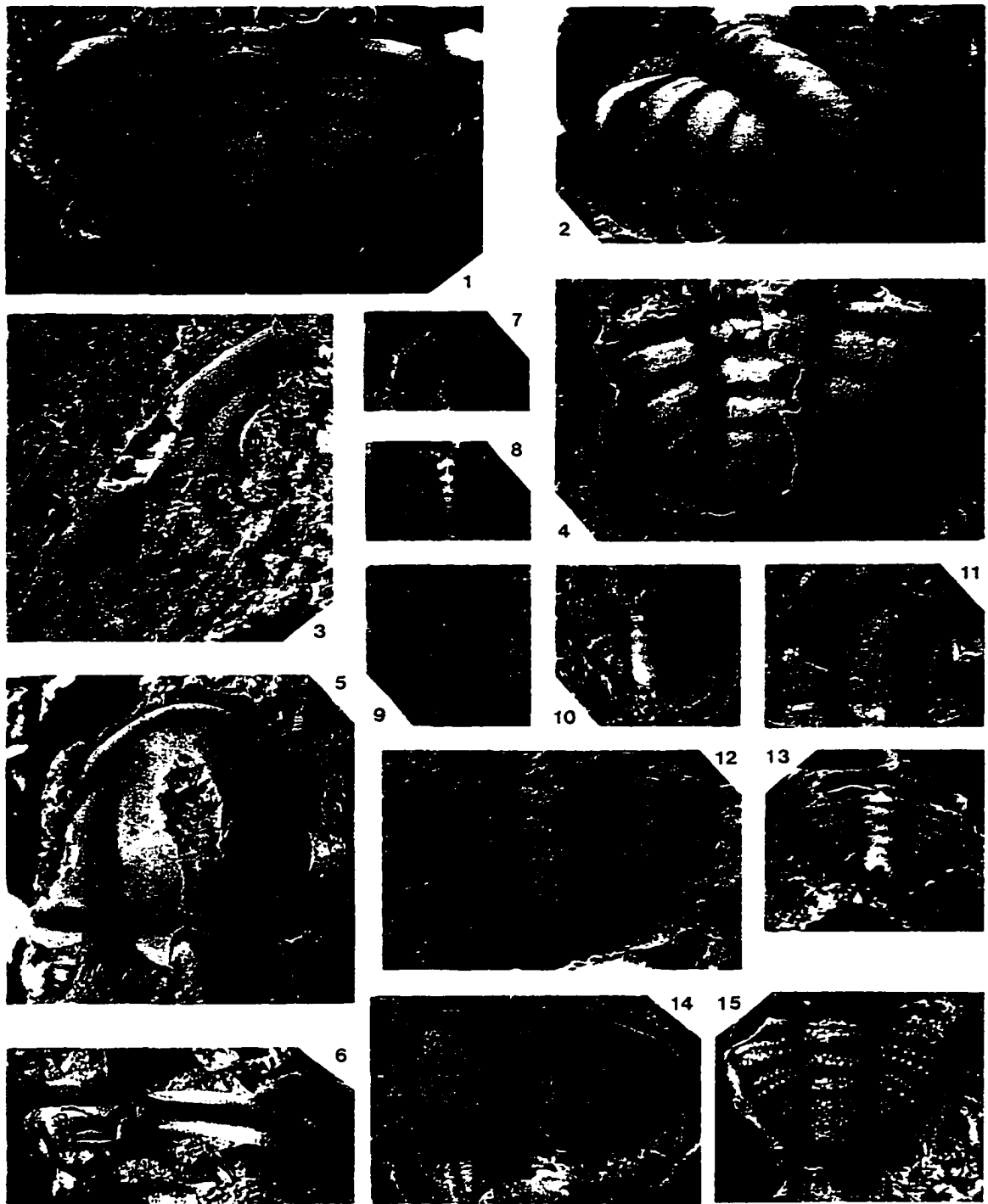


PLATE 31

Plate 32

Figs. 1-5. *Bonnia ornata* n. sp. Eager Formation, section MG2, collection MG2j, Canal Flats area, British Columbia (Figs. 1-2 tentatively attributed).

1. Cranidium (Clique C), MG2j#28, x8
2. Pygidium (Clique C), MG2j#7, x7
3. Cranidium (Clique C), MG2j#29, **Paratype**, x8
- 4-5. Cranidium (Clique C), MG2j#19, x7

Figs. 6-14. *Bonnia drysdalea* n. sp. All Eager Formation. Figs. 6-7, 10, 13: section RC4, collection RC4a, Ram Creek area, British Columbia (Figs. 10, 13 tentatively attributed); Figs. 8-9, 11-12, 14: section MG2, collection MG2j, Canal Flats area, British Columbia.

6. Cranidium (late meraspid), RC4a#10, **Paratype**, x15
7. Pygidium (late meraspid), RC4a#11, **Paratype**, x15
8. Cranidium (Clique A), MG2j#48, **Paratype**, x12
9. Pygidium (Clique A), MG2j#55, **Paratype**, x12
10. Hypostome, RC4a#5, x8
11. Cranidium (Clique A), MG2j#30, **Paratype**, x10
12. Pygidium (Clique A/B), MG2j#43, **Paratype**, x9
13. Hypostome, RC4a#6, **Paratype**, x8
14. Cranidium (Clique B), MG2j#31, **Paratype**, x8

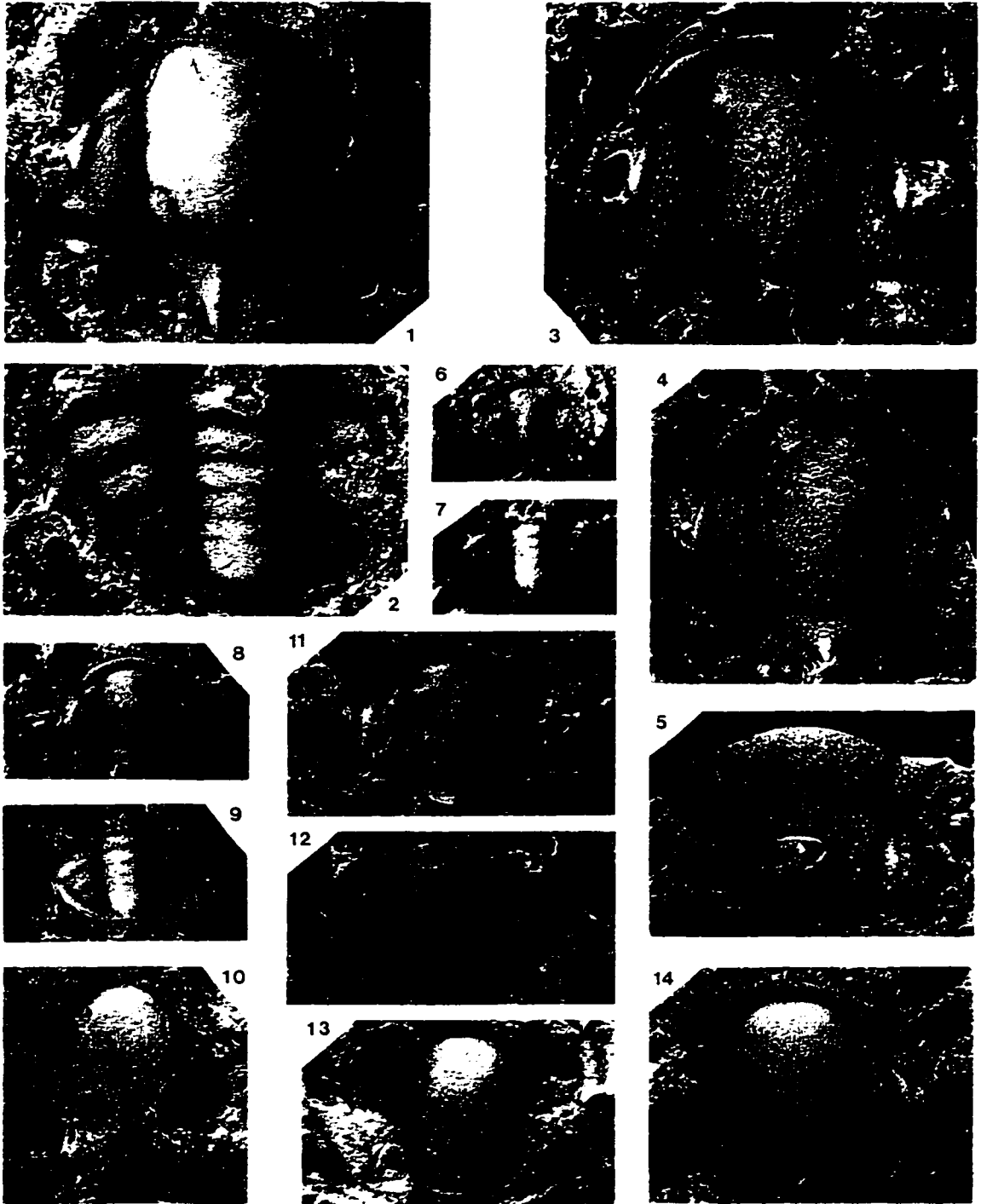


PLATE 32

Plate 33

Figs. 1-3. *Bonnia drysdalea* n. sp. Eager Formation, section MG2, collection MG2j, Canal Flats area, British Columbia.

1. Cranidium (Clique B), MG2j#33, x8.5
2. Cranidium (Clique C), MG2j#11, **Paratype**, x7
3. Pygidium (Clique C), MG2j#10, **Holotype**, x7

Figs. 4-14. *Bonnia paymasterensis* n. sp. Saline Valley Formation, section PC, LACMIP collection 26849, Paymaster Canyon, Nevada.

- 4-5. Pygidium (Clique C), LACMIP 12581, **Paratype**, x8
- 6-7. Cranidium (Clique B), LACMIP 12582, **Paratype**, x8
8. Cranidium (Clique C), LACMIP 12583, **Paratype**, x7
9. Pygidium (Clique C), LACMIP 12584, x8
10. Pygidium (Clique B), LACMIP 12585, **Holotype**, x9
11. Cranidium (Clique A), LACMIP 12586, **Paratype**, x12
12. Cranidium (Clique A), LACMIP 12587, x10
13. Librigena fragment and hypostome, LACMIP 12588, x4
14. Hypostome, LACMIP 12589, **Paratype**, x8

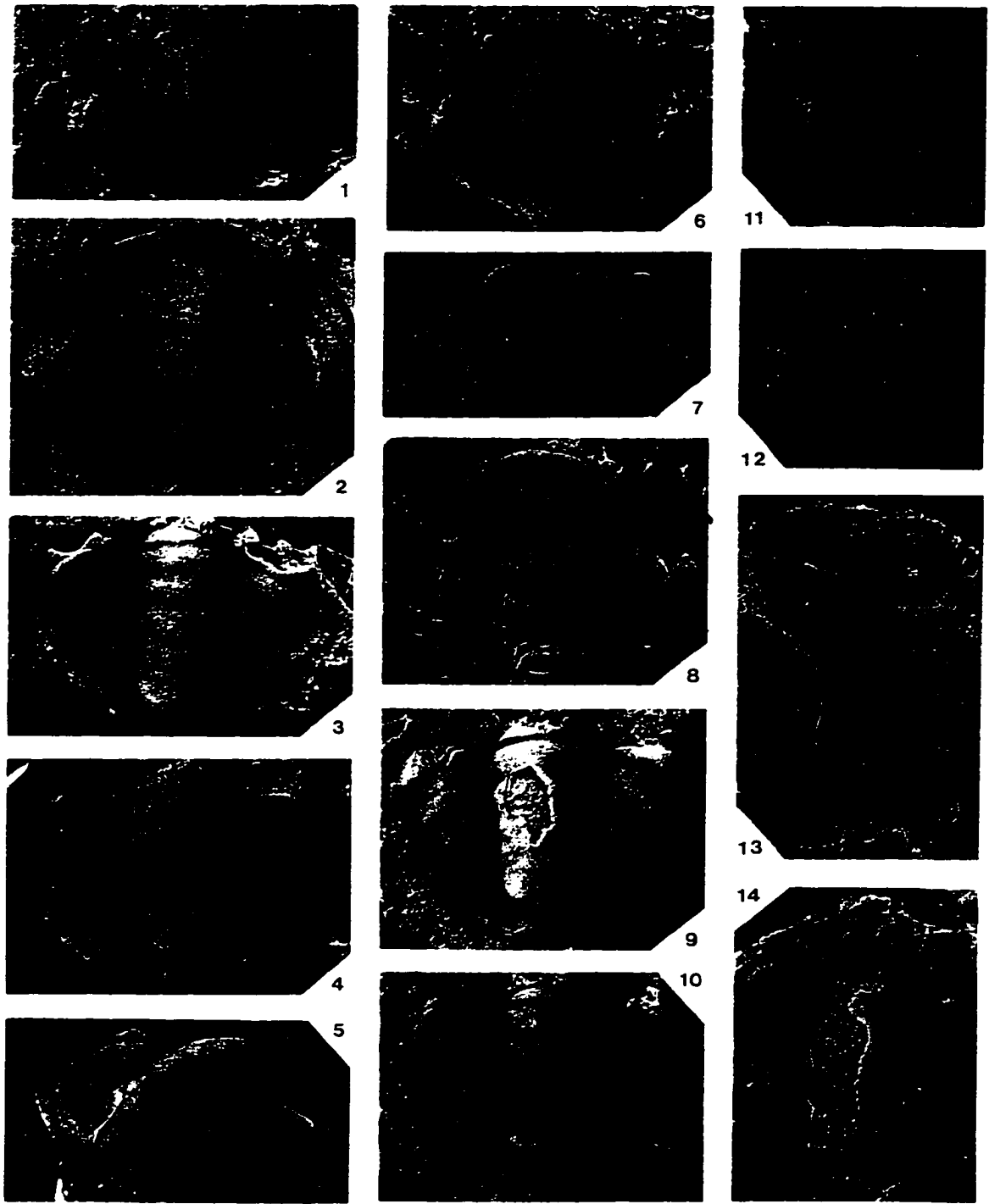


PLATE 33

Plate 34

Figs. 1-3. *Bonnia paymasterensis* n. sp. Saline Valley Formation, locality 9, LACMIP collection 26877, Weepah Hills, Nevada.

- 1, 3. Articulated specimen, exclusive of librigenae (Clique B/C), LACMIP 7427, Paratype, x7
2. Articulated specimen, exclusive of librigenae (Clique B), LACMIP 12590, x7

Figs. 4-6. *Bonnia* sp. 1. Saline Valley Formation, section PC, LACMIP collection 26849, Paymaster Canyon, Nevada.

- 4, 6. Pygidium (Clique C), LACMIP 12591, x6
5. Pygidium (Clique C), LACMIP 12592, x6

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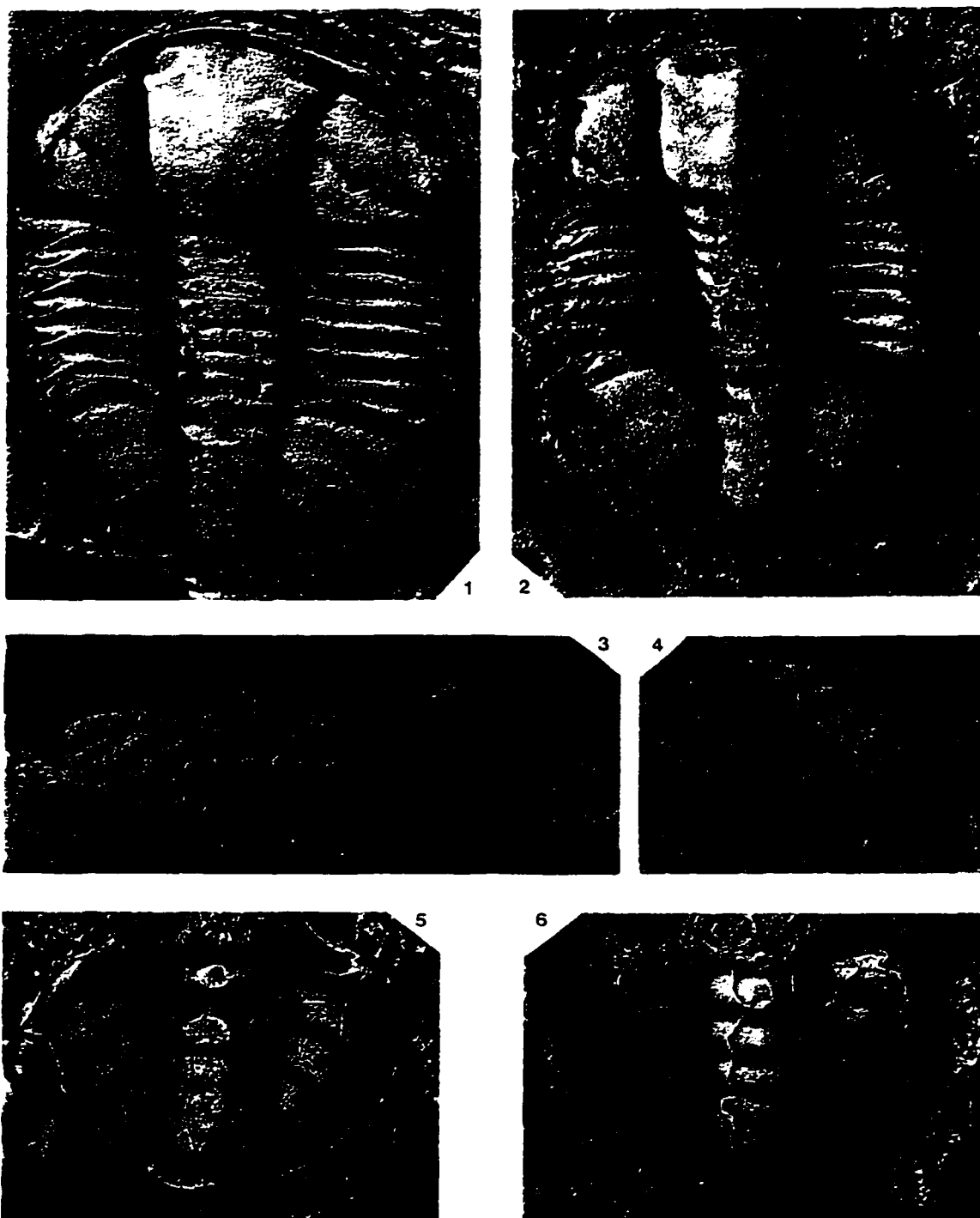


PLATE 34

Plate 35

Figs. 1-6. *Ogygopsis butis* (Walcott, 1916b). Saline Valley Formation, locality 8, LACMIP collection 24411, Miller Mountain, Nevada.

1. Articulated thorax and pygidium (L), LACMIP 12593, x3
2. Articulated specimen, exclusive of librigenae (L), LACMIP 12594, x6
3. Hypostome (L), LACMIP 12595, x6
4. Hypostome and rostral plate, LACMIP 12596, x6
5. Articulated specimen, exclusive of librigenae, LACMIP 7411, x2.5
6. Pygidium, LACMIP 12597, x4.5

Figs. 7-8. *Ogygopsis typicalis* (Resser, 1939). Saline Valley Formation, section WM, Waucoba Mountain, California. Fig. 7: LACMIP collection 26818; Fig. 8: LACMIP collection 26809.

7. Articulated specimen, exclusive of librigenae, LACMIP 11386, x5.5
8. Partial articulated specimen with associated hypostome and librigenae, LACMIP 11389a, x2



PLATE 35

Plate 36

Figs. 1-4. *Ogygopsis typicalis* (Resser, 1939). Saline Valley Formation, section WM, Waucoba Mountain, California; Fig. 1: LACMIP collection 26809; Figs. 2-3: LACMIP collection 26810; Fig. 4: LACMIP collection 17085.

1. Pygidium and partial thorax, LACMIP 11389b, x2
2. Articulated specimen, exclusive of librigenae and with small pygidium, LACMIP 7425a&b, x2.5
3. Pygidium, LACMIP 7425b, x5
4. Articulated specimen, exclusive of librigenae, LACMIP 12598, x2

Figs. 5-8. *Ogygopsis marconi* (Whitfield, 1884). All Saline Valley Formation, Nevada. Figs. 5-6: locality 9, LACMIP collection 26877, Weepah Hills; Fig. 7: section PC, LACMIP collection 26851, Paymaster Canyon; Fig. 8: section PC, LACMIP collection 17021, Paymaster Canyon.

5. Pygidium, LACMIP 12599, x5
6. Articulated specimen, exclusive of librigenae (L), LACMIP 12600, x2.5
7. Librigena (L), LACMIP 12601, x3
8. Cranidium, LACMIP 12602, x3.25

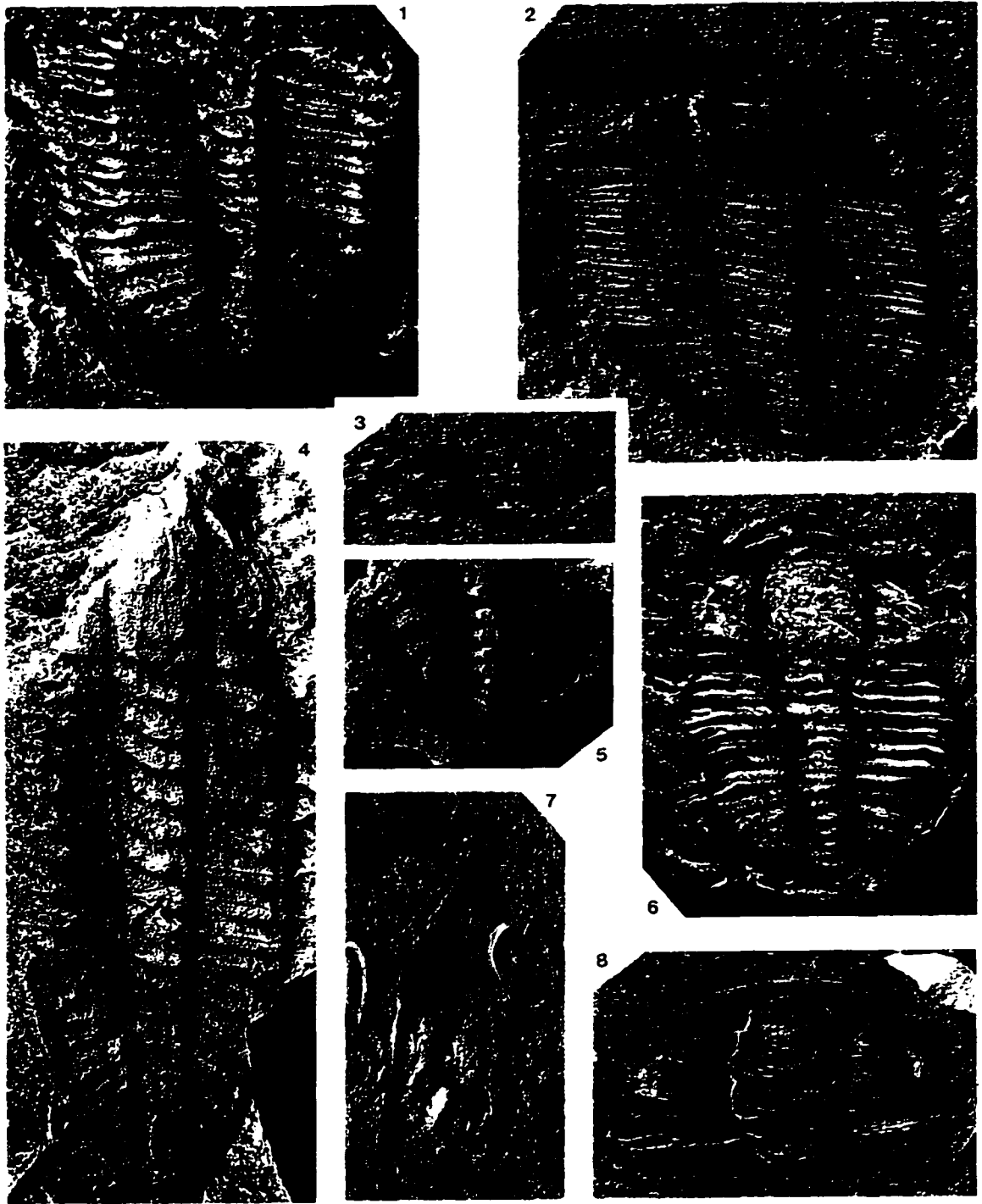


PLATE 36

Plate 37

Figs. 1-7. *Ogygopsis marcoui* (Whitfield, 1884). All Saline Valley Formation, Nevada. Figs. 1-2: locality 9, LACMIP collection 26877, Weepah Hills; Fig. 3: section PC, LACMIP collection 26851, Paymaster Canyon; Figs. 4-5. section PC, LACMIP collection 17022, Paymaster Canyon; Figs. 6-7: section PC, LACMIP collection 17021, Paymaster Canyon.

1. Pygidium, LACMIP 7428, x3
2. Cranidium and pygidium (L), LACMIP 12603, x3
3. Pygidium (L), LACMIP 12604, x3
- 4-5. Pygidium (L), LACMIP 12605, x3
6. Hypostome and rostral plate (L), LACMIP 12606, x4
7. Articulated specimen, exclusive of fixigenae, LACMIP 12607, x2

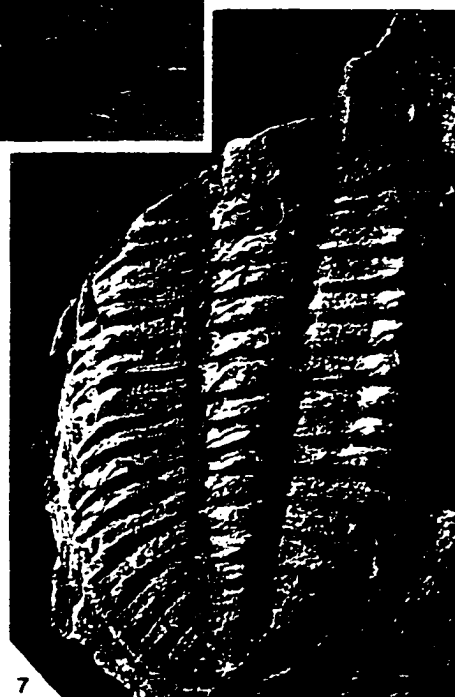
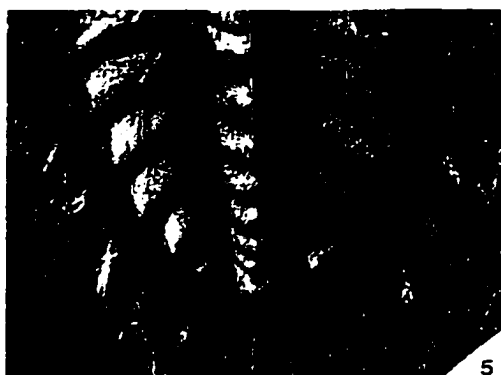


PLATE 37

Plate 38

Figs. 1-3. *Zacanthopsis contractus* Palmer, 1964. Saline Valley Formation, section PC, LACMIP collection 17021 (except Fig. 2: LACMIP collection 26851), Paymaster Canyon, Nevada.

1. Cranidium, LACMIP 12608, x7
2. Cranidium, LACMIP 7431, x7
3. Cranidium, LACMIP 12609, x8

Figs. 4, 7-14. *Proliostracus* sp. 2. Saline Valley Formation, section PC, Paymaster Canyon, Nevada, Figs. 4, 7-9, 14: LACMIP collection 17021; Figs. 10-13: LACMIP collection 26851.

4. Librigena (L), LACMIP 12610, x12
7. Articulated specimen, LACMIP 12611, x10
8. Pygidium (L), LACMIP 12612, x12
9. Articulated specimen, LACMIP 12613, x12
10. Articulated specimen (L), LACMIP 12614, x9
11. Librigena, LACMIP 12615, x12
- 12-13. Articulated specimen (L), LACMIP 12616, x8.5
14. Hypostome, LACMIP 12617, x10

Figs. 5-6. *Proliostracus buelnaensis* (Lochman, 1952). (tentatively attributed) Eager Formation, locality 7, Purcell Mountains, British Columbia.

5. Articulated specimen, RBCM EH.997.06.006, x10
6. Cranidium, RBCM EH.997.06.007, x5.5

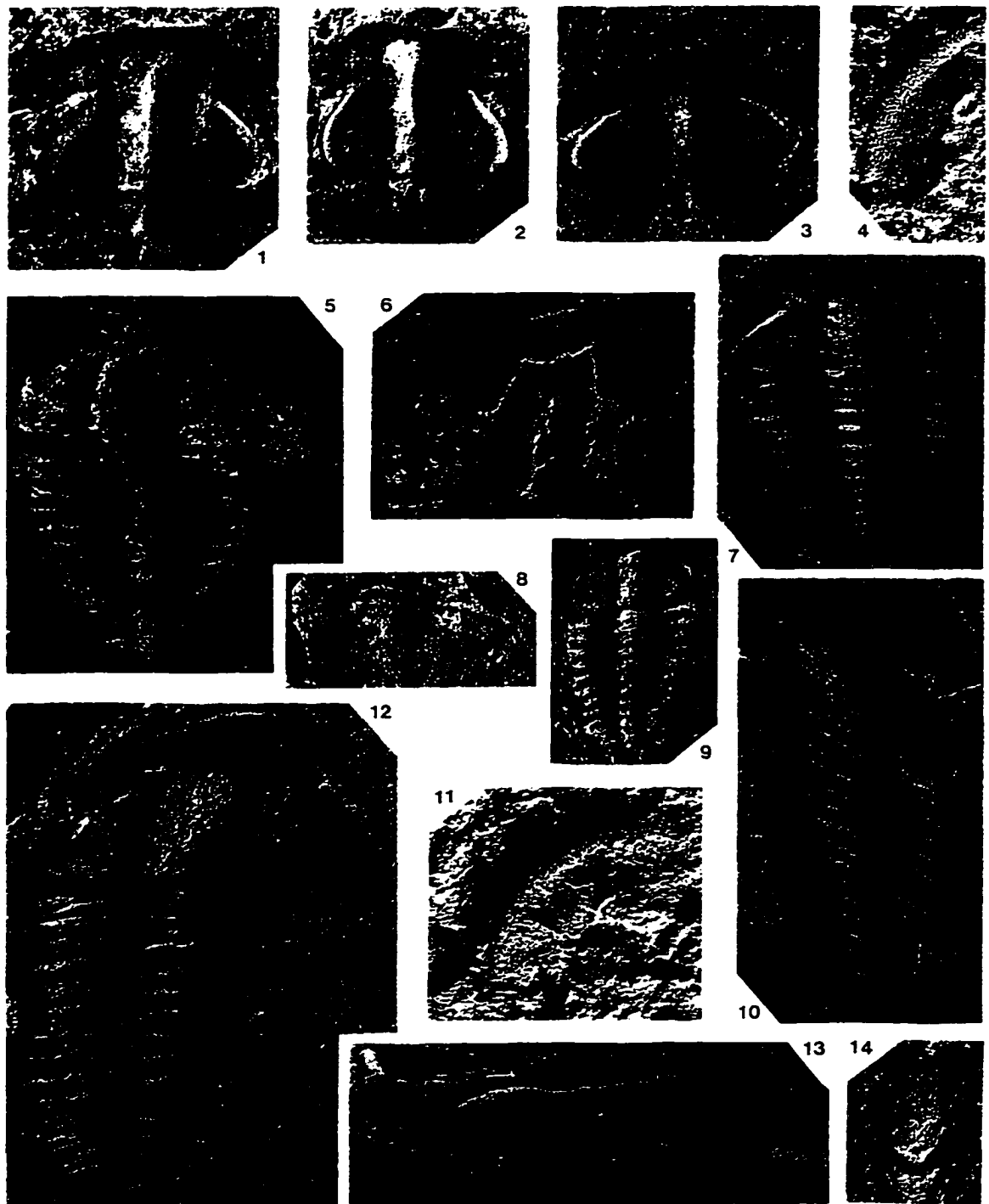


PLATE 38

Plate 39

Figs. 1-15. *Proliostracus buelnaensis* (Lochman, 1952). All Eager Formation, Canal Flats area, British Columbia. Figs. 1-3, 15: section MG2, collection MG2d; Figs. 4, 11: section MG3, collection MG3d'; Figs. 5-6, 8-9: section MG2, collection MG2e; Figs. 7, 10, 12-14: section MG3, collection MG3g.

1. Cranidium (meraspid), MG2d#14, x22
- 2-3. Cranidium, MG2d#10, x12
4. Cranidium, MG3d'#10, x10
5. Librigena, MG2e#7, x10
6. Cranidium, MG2e#5, x12
7. Cranidium, MG3g#2, x10
8. Librigena, MG2e#6, x9
9. Pygidium, MG2e#9, x15
10. Cranidium, MG3g#1, x9
11. Cranidium, MG3d'#8, x10
- 12-13. Pygidium, MG3g#4, x15
14. Pygidium, MG3g#5, x15
15. Cranidium, MG2d#12, x9

Fig. 16. *Proliostracus* sp. 2. Saline Valley Formation, section PC, LACMIP collection 17021, Paymaster Canyon, Nevada.

16. Cranidium, LACMIP 12618, x12

Figs. 17-18. *Proliostracus* sp. 1. Eager Formation, locality 5, Cranbrook area, British Columbia.

17. Cranidium, RBCM EH.997.06.008, x7.5
18. Cranidium (L), RBCM EH.997.06.009, x7.5

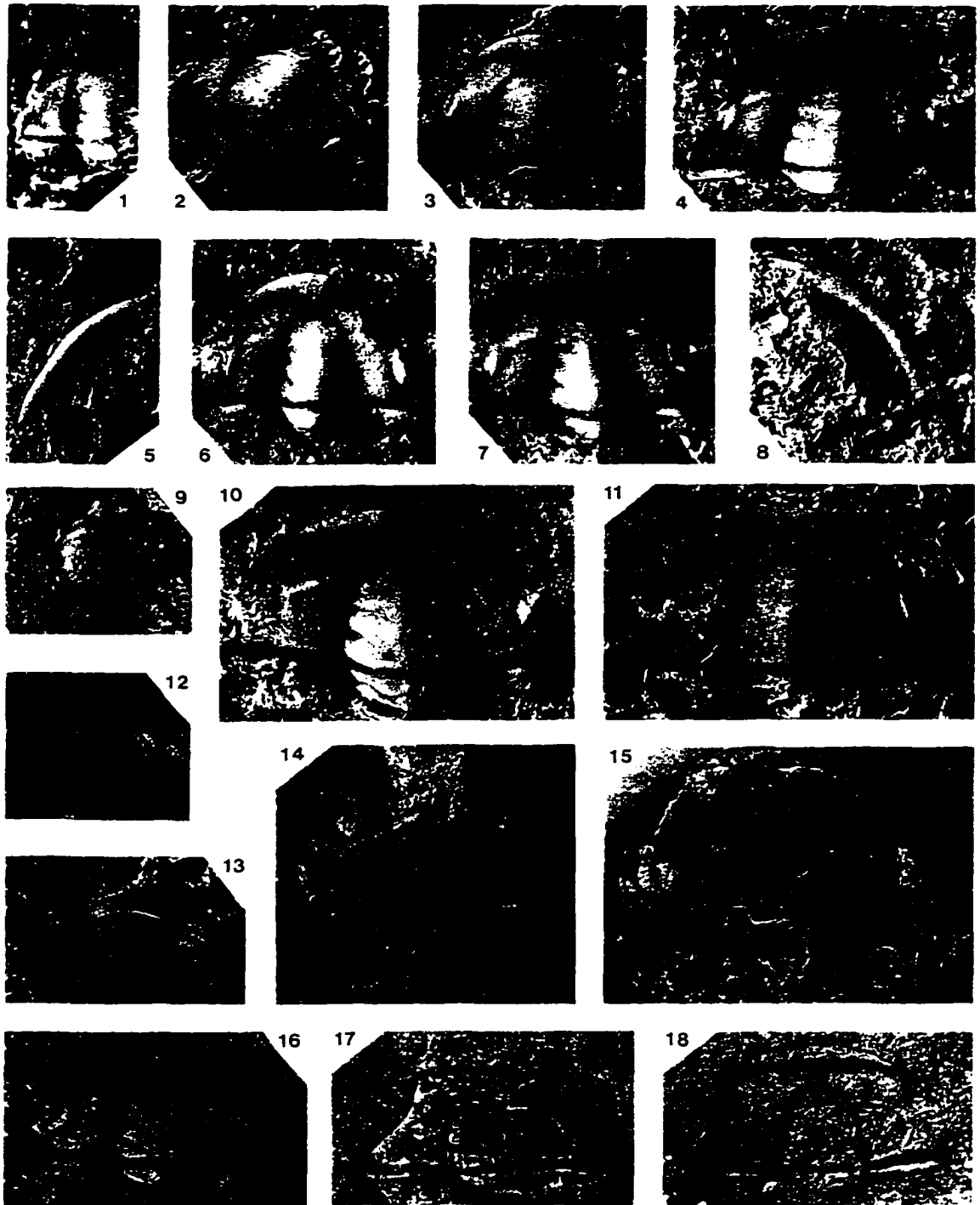


PLATE 39

Plate 40

Figs. 1-11. *Gelasene aureum* n. sp. Poleta Formation, section GP, ICS collection 1056, Mt. Dunfee area, Nevada.

1. Librigena, ICS 1056#6, **Paratype**, x5
2. Cranidium, ICS 1056#18, x6
- 3, 6, 8. Cranidium and enlargement of border spines, ICS 1056#1, **Holotype**, x5, x15
- 4, 9. Cranidium and prosopon enlargement, ICS 1056#2, **Paratype**, x5, x10
5. Pygidium, ICS 1056#8, **Paratype**, x20
7. Thoracic segment, ICS 1056#19, x8
10. Cranidium, ICS 1056#3, x5
11. Librigena, ICS 1056#5, x5

Figs. 12-20. *Ekwiipagetia rasettii* n. sp. Poleta Formation, section GP, Mt. Dunfee area, Nevada. Figs. 12, 14-15, 18-19: LACMIP collection 17054; Figs. 13, 16-17, 20: LACMIP collection 26850.

12. Cranidium, LACMIP 12619, x15
- 13, 17. Pygidium, LACMIP 12620, **Paratype**, x12
14. Pygidium, LACMIP 12621, x20
- 15, 19. Cranidium, LACMIP 12622, **Paratype**, x15
16. Cranidium, LACMIP 12623, **Paratype**, x10
18. Pygidium, LACMIP 12624, x12
20. Cranidium, LACMIP 12625, x10

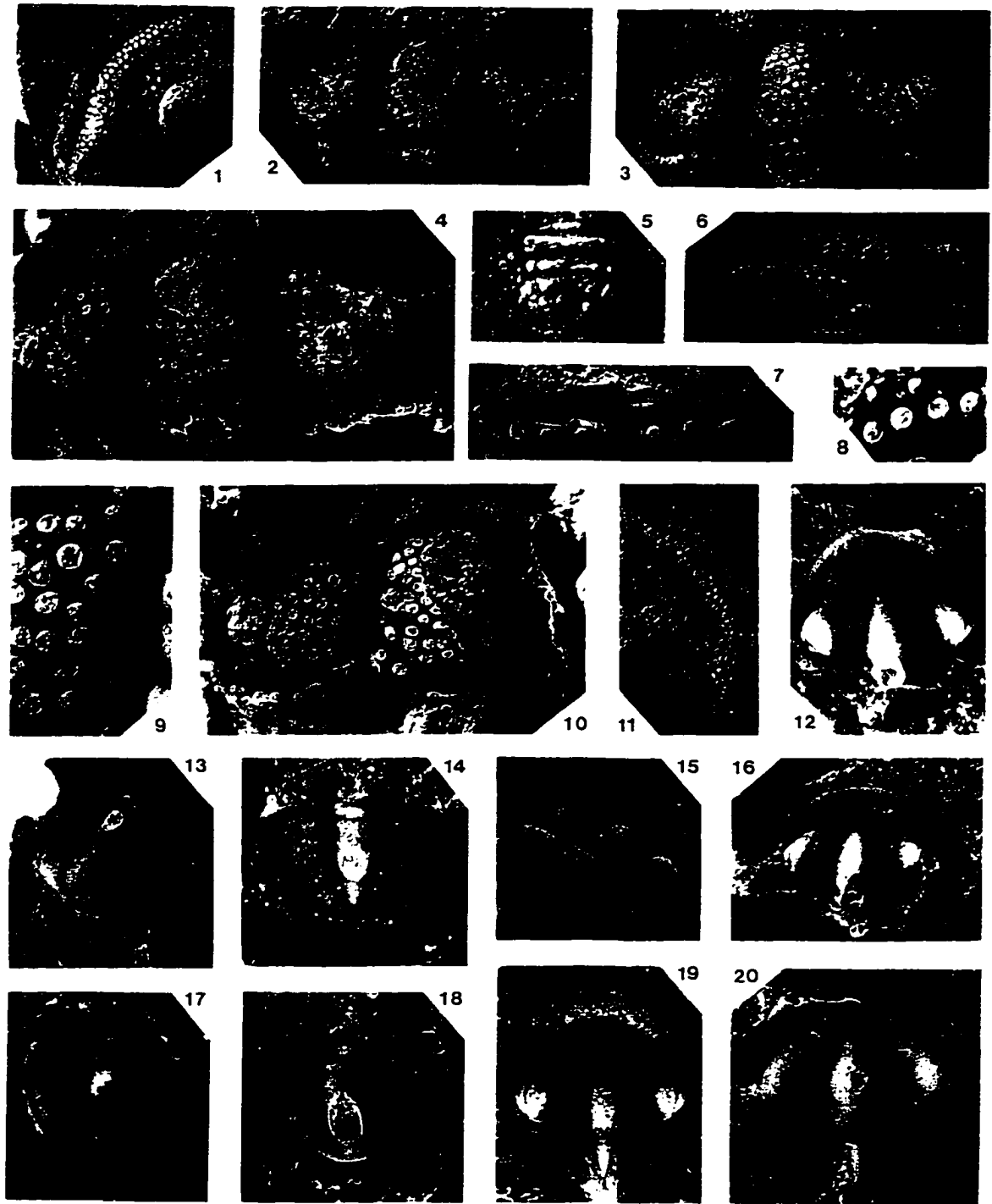


PLATE 40

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Figs. 1-2. *Ekwipagetia rasettii* n. sp. Poleta Formation, section GP, LACMIP collection 17054, Mt. Dunfee area, Nevada.

1. Pygidium, LACMIP 12626, x20
2. Pygidium, LACMIP 12627, **Holotype**, x12

Fig. 3, 6. *Lancastria roddyi* (Walcott, 1912a). Saline Valley Formation, section PC, LACMIP collection 17021, Paymaster Canyon, Nevada.

3. Cranidium, LACMIP 12628, x8
6. Cranidium, LACMIP 12629, x8

Figs. 4-5. *Cheiruroides?* sp. 1. Saline Valley Formation, section PC, LACMIP collection 26849, Paymaster Canyon, Nevada.

4. Cranidium, LACMIP 12630, x7
5. Cranidium, LACMIP 12631, x7

Figs. 7-11. *Protypus inflatus* n. sp. Saline Valley Formation, section PC, LACMIP collection 26849, Paymaster Canyon, Nevada.

7. Cranidium, LACMIP 12632, **Holotype**, x5.25
- 8-9. Cranidium, LACMIP 12633, **Paratype**, x6.5
10. Cranidium, LACMIP 12634, x4.5
11. Cranidium, LACMIP 12635, x3.5

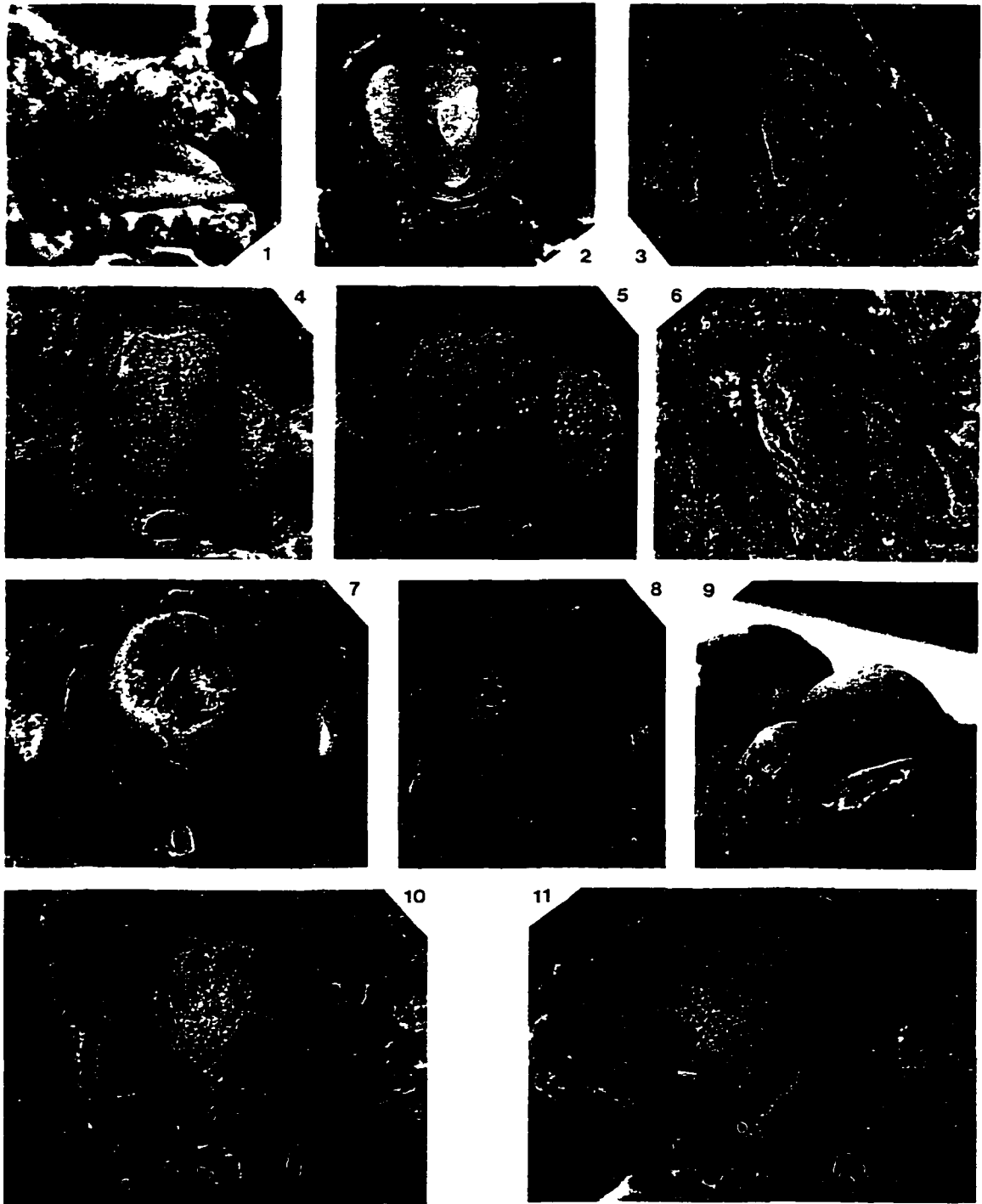


PLATE 41