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THROUGH A GLASS DARKLY: TAXONOMY, PHYLOGENY, AND
BIOSTRATIGRAPHY OF THE OLENELLINA

Allison R. Palmer and Lada N. Repina

Institute for Cambrian Studies, 445 N. Cedarbrook Road, Boulder, Colorado 80304, and Institute for Geology and Geophysics,
Siberian Section, Russian Academy of Sciences, Novosibirsk, Russia 630090

“For now we see through a glass, darkly; but then face to face . . .”
1 Corinthians 13:12 (The Bible, King James Version).

Abstract.—The Olenellina is an exclusively Early Cambrian trilobite suborder that dominates the later Early Cambrian trilobite faunas of Laurentia and constitutes a lesser component of the trilobite faunas of Siberia, Baltica, Avalonia, and the western sector of Gondwana/peri-Gondwana (Morocco, Spain, and eastern Germany). The classification of the Olenellina presented here will appear in the revised edition on Trilobita of the *Treatise on Invertebrate Paleontology*.

Two superfamilies, 7 families, 10 subfamilies, 45 genera, and 5 subgenera are distinguished primarily on characters of the cephalon. Major revisions from previous usage primarily involve the Laurentian Olenellidae. New taxa in this family include Bristoliinae, Gabriellinae, Laudoniinae, *Arcuolenellus*, *Bolbolenellus*, *Nephrolenellus*, *Olenellus* (*Angustolenellus*), and *Olenellus* (*Mesolenellus*). One new taxon, *Paranevadella*, is added to the Judomiidae. The previously synonymized genera *Mesonacis* and *Paedeumias* are revived as subgenera of *Olenellus*.

Intercontinental correlation of Lower Cambrian strata is hampered by high endemism of genera and species, especially among the Olenellina. Biostratigraphic and biogeographic analysis of the Olenellina suggests increasing geographic isolation of Laurentia during Early Cambrian time and that Laurentian Olenellidae are mostly younger than the Olenellina of the other Cambrian continents.

Morphologic and stratigraphic considerations suggest derivation of the Olenellidae from some element of the Holmiidae and the Holmiidae from some element of the Archaeaspididae.

INTRODUCTION

All fossils represent some degree of success in survivorship. Taxonomy in paleontology is a human effort to make order out of this survivorship. The challenge is to detect a phylogenetically meaningful pattern of relationships among groups of organisms, many of which are extinct, based on incomplete information about anatomical features, environmental preferences, ethology, and distribution in time and space. Biochemical and genetic information is almost completely lacking, the principal source of information being the preserved morphology of the shell or skeleton. The success of any taxonomy is the degree to which it is viewed as a constructive representa-

tion of evolutionary relationships among organisms. The Olenellina provide a rich taxonomic challenge.

The Olenellina is a distinctive suborder of the trilobite order Redlichiida (Moore, 1959) restricted to and characteristic of rocks of later Early Cambrian age. Fifty genera or subgenera and their associated higher taxa are recognized here (Table 1). These taxa form the principal basis for biostratigraphic subdivisions of the later Lower Cambrian rocks of Laurentia and are major indices for the later Lower Cambrian biostratigraphy of Baltica, Avalonia, Siberia, and the Moroccan sector of Gondwana (Fig. 1).

One of the many mysteries regarding the Olenellina is their complete absence from Lower Cambrian rocks of the Asiatic sector of Gondwana/peri-Gondwana (Australia,

Table 1. Comparison of historical classifications of the Olenellina with the classification proposed in this paper.

Hupé, 1953	Moore, 1959	Chernysheva, 1960	Bergström, 1973b
OLENELLOIDEA	OLENELLIDAE	OLENELLOIDEA	OLENELLACEA
OLENELLIDAE	OLENELLINAE	OLENELLIDAE	OLENELLIDAE
OLENELLINAE	Olenellus	OLENELLINAE	Olenellus
Olenellus	Bristolia	Olenellus	Biceratops
Fremontia	Fremontella	Elliptocephala	Bristolia
Paedeumias	Fremontia	Esmeraldina	Fremontella
WANNERIINAE	Laudonia	Fremontia	Laudonia
Wanneria	Paedeumias	Olenelloides	?Olenelloides
Esmeraldina	Peachella	Paedeumias	Peachella
HOLMIINAE	OLENELLOIDINAE	Peachella	HOLMIIDAE
Holmia	Olenelloides	Wanneria	Holmia
Bondonella	WANNERIINAE	HOLMIINAE	Elliptocephala
?Callavia	Wanneria	Holmia	Esmeraldina
Kjerulfia	HOLMIINAE	Bondonella	?Judomiella
ELLIPTOCEPHALINAE	Holmia	Callavia	Schmidtiellus
Elliptocephala	Bondonella	Choubertella	Wanneria
FALLOTASPIDINAE	Schmidtiellus	Cobboldus	DAGUINASPIDIDAE
Fallotaspis	CALLAVIINAE	Daguinaspis	DAGUINASPIDINAE
NEVADIINAE	Callavia	Fallotaspis	Daguinaspis
Nevadia	Judomia	Judomia	Choubertella
Nevadella	Kjerulfia	Kjerulfia	?Wolynaspis
NELTNERIINAE	ELLIPTOCEPHALINAE	Neltneria	FALLOTASPIDINAE
Neltneria	Elliptocephala	NEVADIINAE	Fallotaspis
DAGUINASPIDAE	FALLOTASPIDINAE	Nevadia	?Andalusiana
Daguinaspis	Fallotaspis	Nevadella	Bradyfallotaspis
(Daguinaspis)	DAGUINASPIDIDAE		Fallotaspidella
(Eodaguinaspis)	Daguinaspis		Parafallotaspis
(Epidaguinaspis)	Choubertella		NEVADIINAE
Choubertella	NEVADIINAE		Nevadia
	Nevadia		Judomia
	Nevadella		Nevadella
	NELTNERIINAE		NELTNERIINAE
	Neltneria		Neltneria
			?Kjerulfia
			CALLAVIINAE
			Callavia
			?Bondonella
			?Holmiella

Repina, 1979	Ahlberg et al., 1986		This paper
OLENELLOIDEA	OLENELLIDA	OLENELLOIDEA	FALLOTASPIDOIDEA
OLENELLIDAE	OLENELLIDAE	OLENELLIDAE	FALLOTASPIDIDAE
OLENELLINAE	Olenellus	OLENELLINAE	FALLOTASPIDINAE
Olenellus	Biceratops	Olenellus	Fallotaspis
?Peachella	Bristolia	(Olenellus)	Eofallotaspis
BICERATOPSINAE	Fremontella	(Angustolenellus)	Lenallina
Biceratops	Fremontia	(Mesolenellus)	Parafallotaspis
FREMONTIINAE	Laudonia	(Mesonacis)	Pelmanaspis
Fremontia	?Peachella	(Paedeumias)	Profallotaspis
Bristolia	WANNERIIDAE	Fremontella	DAGUINASPIDINAE
Fremontella	Wanneria	Mummaspis	Daguinaspis
Laudonia	?Bondonella	BICERATOPSINAE	Choubertella
WANNERIINAE	?Elliptocephala	Biceratops	Wolynaspis
Wanneria	?Esmeraldina	Peachella	ARCHAEASPIDIDAE
HOLMIIDAE	?Holmiella	BRISTOLIINAE	Archaeaspis
HOLMIINAE	HOLMIIDAE	Bristolia	Bradyfallotaspis
Holmia	Holmia	Arcuolenellus	Fallotaspidella
Andalusiana	Andalusiana	Bolbolenellus	Genus A
Bondonella	Kjerulfia	Nephrolenellus	Selindella
Elliptocephala	Schmidtiellus	GABRIELLINAE	JUDOMIIDAE
?Holmiella	CALLAVIIDAE	Gabriellus	Judomia
Kjerulfia	ARCHAEASPIDINAE	LAUDONINAE	Judomiella
Schmidtiellus	Archaeaspis	Laudonia	Paranevadella
CALLAVIINAE	Bradyfallotaspis	?Olenelloides	Sinskia
Callavia	Selindella	WANNERIINAE	NELTNERIIDAE
ARCHAEASPIDIDAE	CALLAVIINAE	Wanneria	Neltneria
Archaeaspis	Callavia	HOLMIIDAE	Bondonella
Bradyfallotaspis	DAGUINASPIDIDAE	HOLMIINAE	NEVADIIDAE
Selindella	Daguinaspis	Holmia	Nevadia
DAGUINASPIDIDAE	Choubertella	Andalusiana	Buenellus
Daguinaspis	Wolynaspis	Elliptocephala	Genus B
Choubertella	FALLOTASPIDINAE	Holmiella	Nevadella
Wolynaspis	Fallotaspis	Schmidtiellus	Pseudojudomia
FALLOTASPIDIDAE	Fallotaspidella	CALLAVIINAE	SUPERFAMILY UNASSIGNED
Fallotaspis	Parafallotaspis	Callavia	Poletaevella
Fallotaspidella	?Poletaevella	Kjerulfia	Postfallotaspis
Parafallotaspis	Postfallotaspis		
?Poletaevella	Profallotaspis		
Postfallotaspis	NEVADIIDAE		
Profallotaspis	NEVADIINAE		
NEVADIIDAE	Nevadia		
NEVADIINAE	Nevadella		
Nevadia	Pseudojudomia		
Nevadella	JUDOMIINAE		
Pseudojudomia	Judomia		
JUDOMIINAE	Judomiella		
Judomia	Sinskia		
Judomiella	?NELTNERIINAE		
Sinskia	Neltneria		
NELTNERIINAE			
Neltneria			

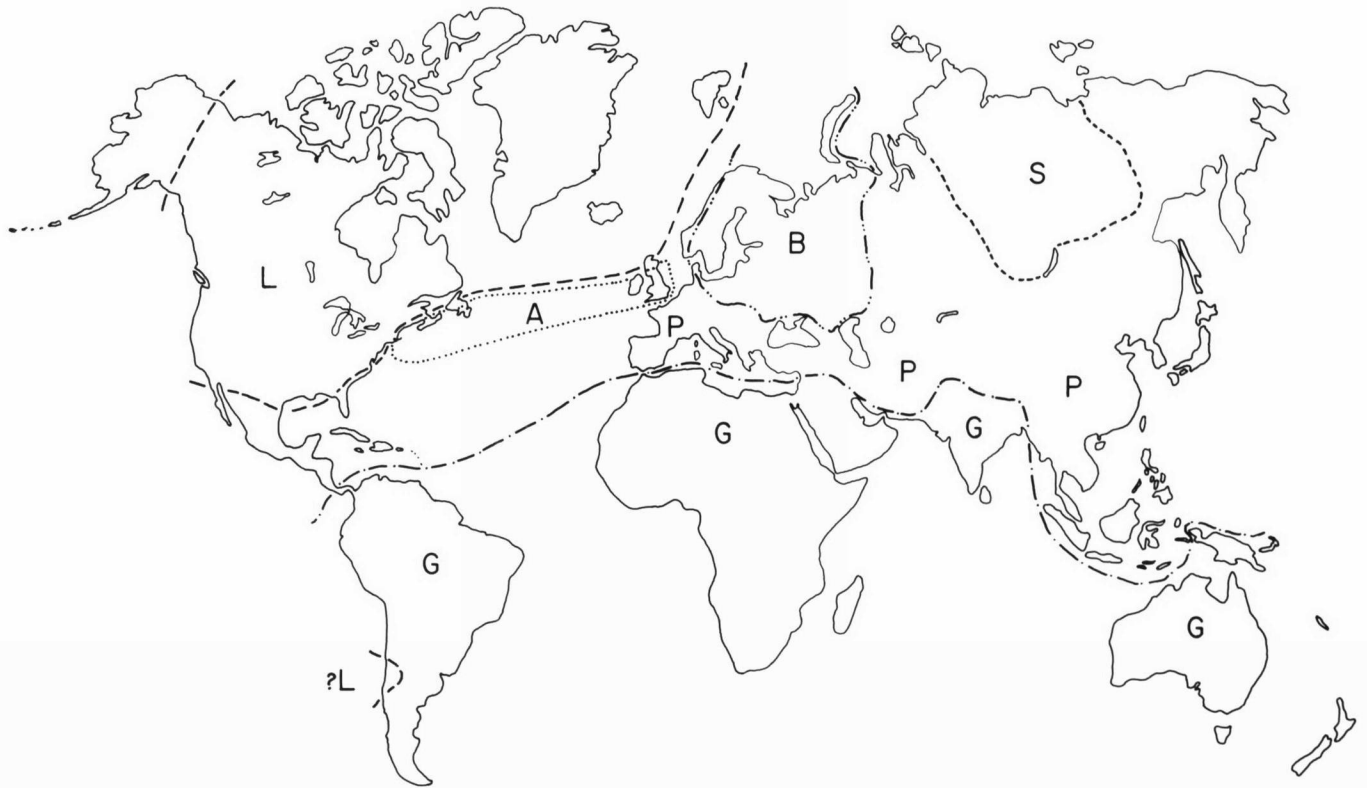


Fig. 1. Sketch map showing present distribution of major Early Cambrian paleogeographic regions. A, Avalonia; B, Baltica; G, Gondwana; L, Laurentia; P, peri-Gondwana; S, Siberia (new).

Antarctica, India, and southeastern Asia), where the characteristic Early Cambrian trilobites are Redlichiina. This has been traditionally expressed in an Early Cambrian biogeography that consists of an olenellid realm or province and a redlichiid realm or province (e.g., Richter & Richter, 1941b; Cowie, 1971; Chang, 1989). Olenellina and Redlichiina coexisted in the Moroccan sector of Gondwana, in the epicontinental seas of southern Siberia, and in areas now included in some central Asian orogens. In these areas of coexistence, the earliest Olenellina may be direct ancestors of the earliest Redlichiina (Repina, 1990a). Perhaps their subsequent geographic segregation resulted from some kind of environmental or competitive control of dispersal to the more peripheral parts of the Cambrian world.

Subsequent to the classical review of all Olenellina by Walcott (1910), most classifications other than the summaries in the *Treatise* (Moore, 1959) and the *Osnovy Paleontologii* (Suvorova in Chernysheva, 1960) have been provincial (Table 1) with strengths primarily in the geographic regions of each author. A comprehensive modern review of Laurentian Olenellina has not previously been attempted. This paper is the result of a review of all Olenellina for the revised edition of the *Treatise on Invertebrate Paleontology*. It is an attempt to improve understanding of the classification, phylogeny, and stratigraphic utility of this important and complex group of trilobites. The review has been aided by a collection of several hundred replicas of most of

the illustrated Olenellina and some undescribed forms that have been accumulated by Palmer over the past 30 years from all major Early Cambrian regions, as well as by excellent photographs of additional specimens generously supplied by colleagues. Only taxa based on published species or on species known to be in press in 1992 are incorporated in this review. The coauthors collaborated on the classification presented here, which was worked out during conferences in Novosibirsk, Russia (1990), and Boulder, Colorado (1991).

General morphology and principles of classification.—Olenellina are a morphologically varied and highly diverse group of generally micropygous trilobites that share a primary absence of dorsal ecdysial sutures, a presence of well-developed eyes at all developmental stages, and an ontogeny in which the first mineralized stages are already early meraspid (Palmer, 1957).

Ancestry of the Olenellina can only be speculative. They first appear as fully developed and morphologically diverse trilobites in the early, but not earliest, part of the shelly fossil record and are the oldest trilobites known (Repina, 1990a). The principal phylogenetic trend within the Olenellina involves the relationship between the ocular lobe and the anterior segment (L4, Fig. 2) of the glabella (Repina, 1990a). In all of the earliest Olenellina, which include genera from Siberia, Laurentia, and the Moroccan sector of Gondwana, the glabella has parallel sides or tapers forward, L4 is short, and the ocular lobe is attached along

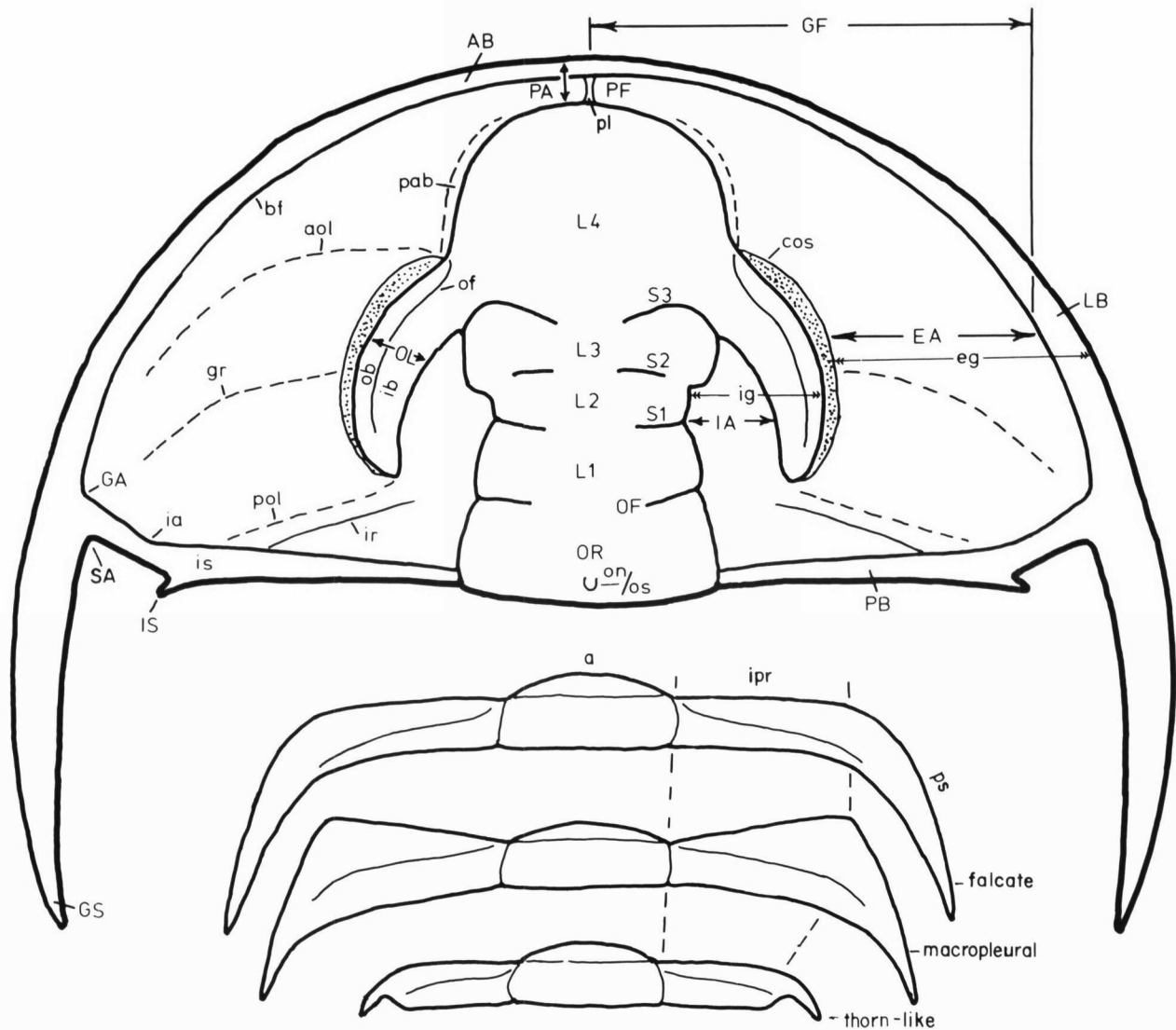


Fig. 2. Nomenclature for parts of the cephalon and thorax of *Olenellina*. Abbreviations: a, axis; AB, anterior border; aol, anterior ocular line; bf, border furrow; cos, circumlocular suture; EA, extraocular area; eg, extraocular gena; GA, genal angle; GF, genal field; gr, genal ridge; GS, genal spine; IA, interocular area; ia, intergenal angle; ib, inner band (of ocular lobe); ig, interocular gena; ipr, inner pleural region; ir, intergenal ridge; IS, intergenal spine; is, intergenal swelling; LB, lateral border; L1 to L4, glabellar segments; ob, outer band (of ocular lobe); OF, occipital furrow; of, ocular furrow; OL, ocular lobe; on/os, occipital node or occipital spine; OR, occipital ring; PA, preglabellar area; pab, parafrontal band; PB, posterior border; PF, preglabellar field; pl, plectrum; pol, posterior ocular line; ps, pleural spine; SA, genal spine angle; S1 to S3, glabellar furrows (new).

the entire margin of L4 (see Figs. 7, 9, 1, 9, 2). In later genera, L4 first becomes elongate so that the ocular lobes connect only to its posterior part and then generally expands laterally, and the glabella as a whole expands anteriorly from the level of S1 (Figs. 3–6). L4 in these genera is also commonly inflated. Accompanying this modification of L4, the distal parts of L3 extend laterally and posterolaterally and encroach on L2, commonly isolating the S2 furrows (Figs. 3–6), and L3 takes on a broad M-shape (Fig. 3, 3).

This phylogenetic trend is shown in the proposed classification. Within the Fallotaspidoidea, all Fallotaspididae (Figs. 7, 8, 1–3; the earliest family of the Olenellina) have the ocular lobe attached along the entire margin of L4 and

an unmodified L3, and the anterior end of L4 does not project forward of a line tangent to the anterolateral margin of the ocular lobe. In the remaining, generally younger families of the Fallotaspidoidea (Figs. 9–11), the anterior end of L4 projects forward of the junction with the anterior margin of the ocular lobe, but L3 remains unmodified. All Olenelloidea (Figs. 3–6), which includes the youngest *Olenellina*, have the ocular lobe attached to the posterior part of L4 and have a modified L3.

Within the superfamilies of the Olenellina, morphological changes of taxonomic value at the family level follow different patterns. The principal character distinguishing families in the Olenelloidea is the relationship between the extraocular area and the interocular area.

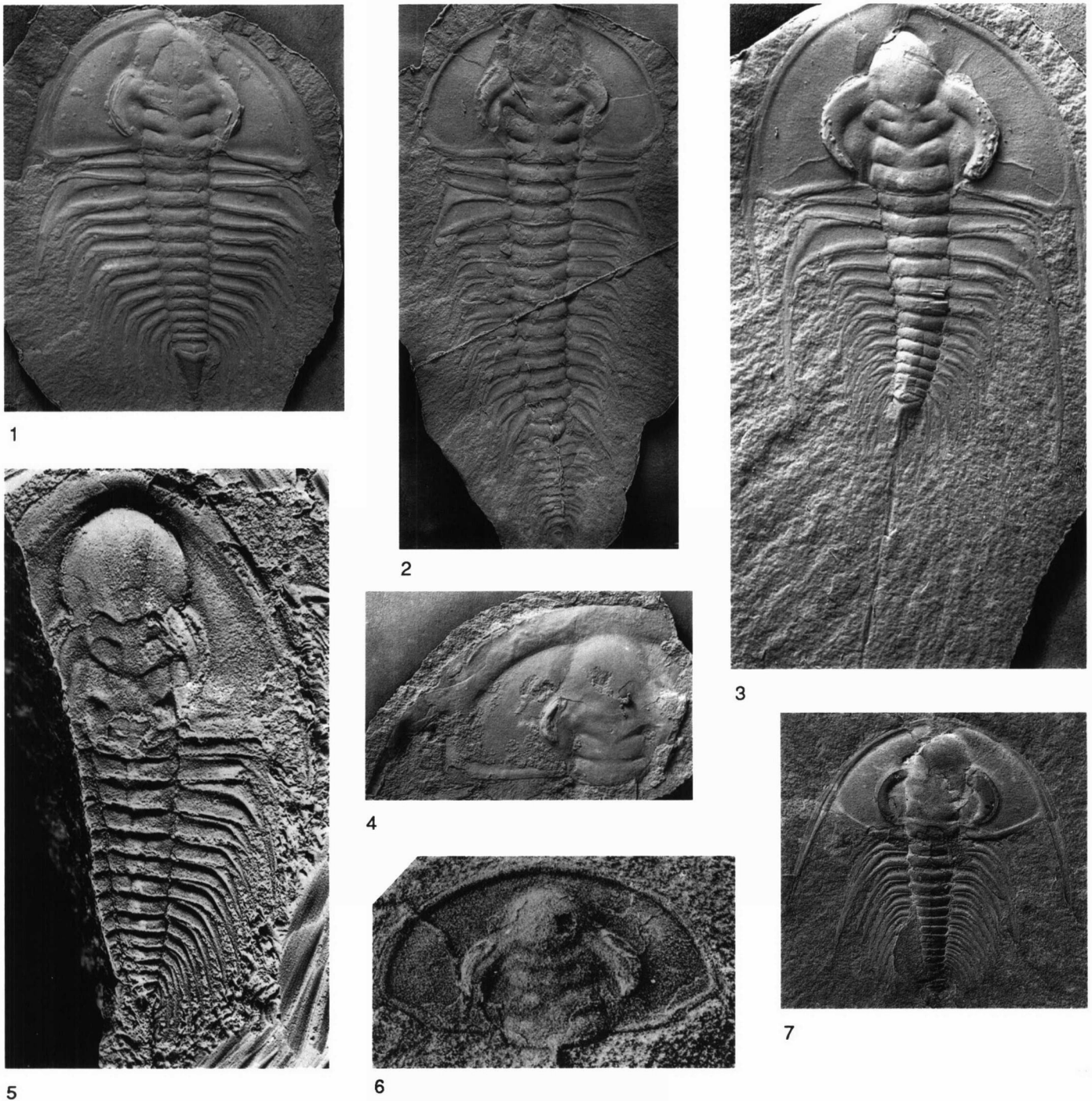
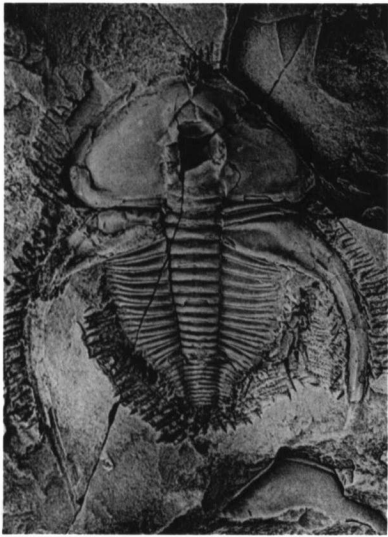
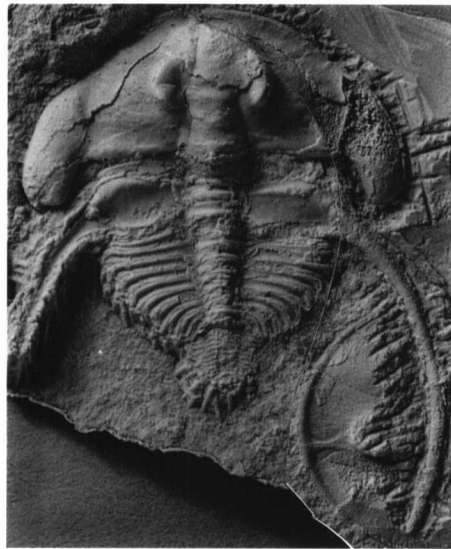


Fig. 3. Olenellidae, Olenellinae; 1, *Olenellus (Olenellus) thompsoni*, complete individual, topotype, USNM 15418a, $\times 2$ (new); 2, *O. (Mesonacis) vermontanus*, complete individual, topotype, USNM 15399a, $\times 1.3$ (new); 3, *O. (Paedeumias) transitans*, complete individual, lectotype, USNM 56808b, $\times 3$ (new); 4, *Fremontella halli*, cephalon, lectotype, USNM 56806c, $\times 1.25$ (new); 5, *Mummaspis occidens*, complete individual, topotype, USNM 443745, $\times 4$ (Fritz, 1992); 6, *O. (Angustolenellus) hamoculus*, cephalon, holotype, GSE 13302, $\times 3$ (Cowie and McNamara, 1978); 7, *O. (Mesolenellus) hyperborea*, complete individual, topotype, MGUH 13.945 from GGU 184219, $\times 4$ (Peel, unpublished.)

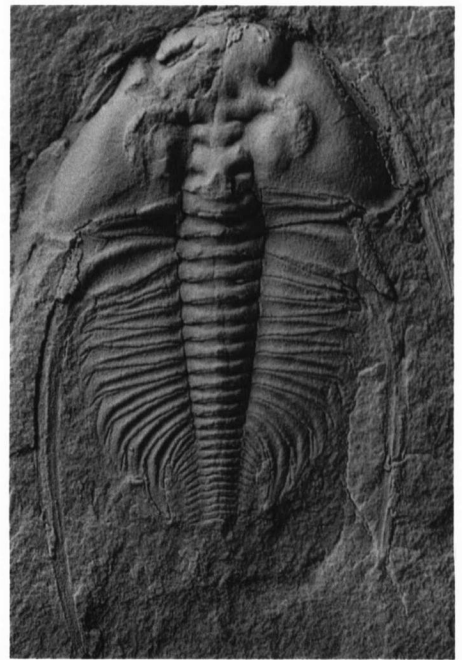
Fig. 4. Olenellidae.—1, 2, Biceratopsinae; 1, *Biceratops nevadensis*, complete individual, holotype, USNM 168225, $\times 3$ (Pack and Gayle, 1971); 2, *Peachella iddingsi*, nearly complete individual, LACMIP 11621, $\times 2.5$ (new).—3, 5–7, 10, Bristoliinae; 3, 6, *Nephrolenellus*; 3, *Nephrolenellus* sp., nearly complete individual, USNM 466536, $\times 3$ (new); 6, *N. multinodus*, cephalon, holotype, USNM 177225, $\times 5$ (Palmer and Halley, 1979); 5, *Bristolia bristolensis*, nearly complete individual, UCR 10/7, $\times 1$ (new); 7, *Arcuolenellus arcuatus*, cephalon, holotype, USNM 177200, $\times 6$ (Palmer and Halley, 1979); 10, *Bolbolenellus evryparia*, cephalon, holotype, USNM 177204, $\times 2$ (Palmer and Halley, 1979).—4, 8, Laudoniinae; 4, *Laudonia amputata*, cephalon and partial thorax, USNM 443754, $\times 2$ (Fritz, 1992); 8, *Olenelloides armatus*, cephalon, holotype, GSE 472, $\times 8$ (McNamara, 1978).—9, Gabriellinae; *Gabriellus* sp., complete individual, GSC 104195, $\times 1.7$ (Fritz, unpublished).



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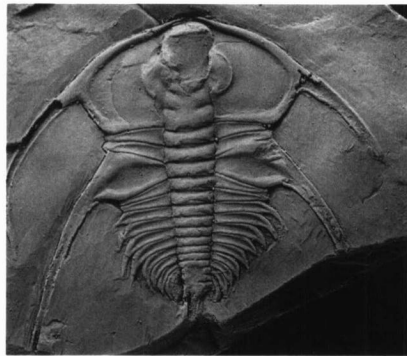
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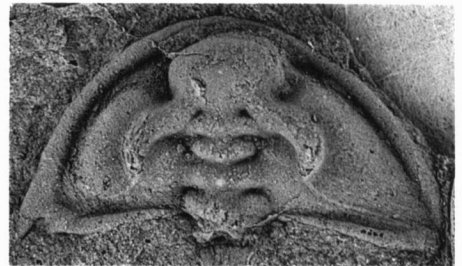
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Fig. 4. (Explanation on facing page.)

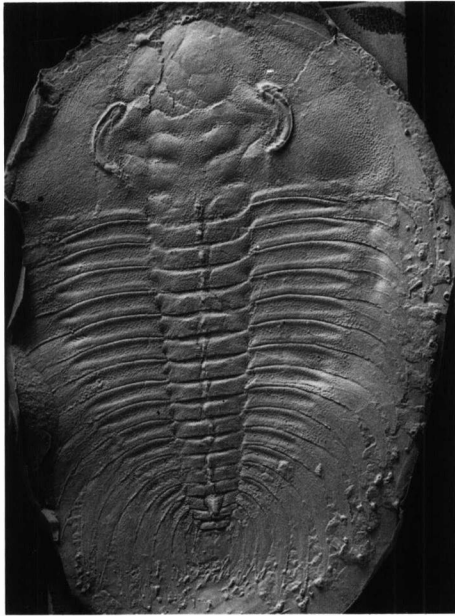


Fig. 5. Olenellidae, Wanneriinae, *Wanneria walcottana*; complete individual, totopype, USNM 85357, $\times 1$ (new).

The Holmiidae (Fig. 6) all have a narrow extraocular area that is less than twice the width of the interocular area. With minor exceptions (*Olenelloides* and some undescribed Laurentian forms), the Olenellidae (Figs. 3–5) have a wide extraocular area that is more than twice the width of the interocular area. In the Fallotaspidoidea (Figs. 7–11), the relationship between the ocular lobe and L4, the shape of the glabella (parallel-sided versus tapered), and outline of the cephalon distinguish families.

Subfamilies of the Olenellidae (Figs. 3–5) are discriminated by the shape of the glabella and form of the thorax. Subfamilies of the Holmiidae (Fig. 6) are discriminated by general form of the thorax, by presence or absence of a preglabellar field, and by relative positions of the genal and intergenal spines.

At the generic and subgeneric level, all taxonomically useful characters represent parts of continuous trends, including exsagittal shortening of the ocular lobes, changes in width of the interocular area, modification in sagittal length of the preglabellar field, position of the genal spines relative to the posterior cephalic margin, elaboration of the third thoracic segment, loss of genal spines, and position and degree of development of the intergenal spines. These characters are thus difficult to define precisely. Nevertheless, within-population variability of these charac-

ters is low (Riccio, 1952; Cowie and McNamara, 1978; McNamara, 1978), and their various combinations generally distinguish groups of species. Particular combinations of characters that are useful at generic and lower taxonomic levels are mentioned below in the discussion of each major taxon.

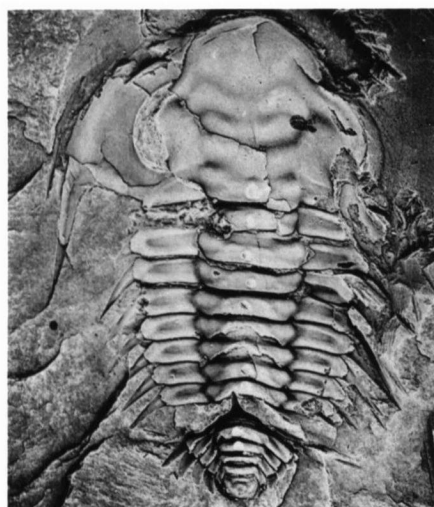
The relatively narrow extraocular area of some adults has biogeographic and perhaps also ecologic and biostratigraphic significance in the superfamily Olenelloidea. This feature, typical of the Holmiidae, is present in all Olenelloidea of Baltica, Avalonia, and the western sector of Gondwana/peri-Gondwana (Morocco, Spain, and eastern Germany). In Laurentia, it is found only in some Olenelloidea from open-shelf or slope environments, including all Laurentian Holmiidae and some rare and unusual younger Olenellidae. Most paleogeographic reconstructions for Early Cambrian time indicate relatively high latitudes and thus cooler-water habitats for the non-Laurentian Holmiidae. Similar cool habitats have been postulated for the waters around the margins of Laurentia (Taylor and Forester, 1979) where Holmiidae occur. Thus, width of the extraocular area in the adult may reflect some aspect of generally cool-water habitats. However, except for *Elliptocephala* and some undescribed taxa, all Olenelloidea with narrow extraocular areas (primarily the rest of the Holmiidae) seem to be from beds older than those bearing the Olenellidae. Therefore, widening of the extraocular area may be a phylogenetic change rather than an ecological control.

BIOSTRATIGRAPHY OF THE OLENELLINA

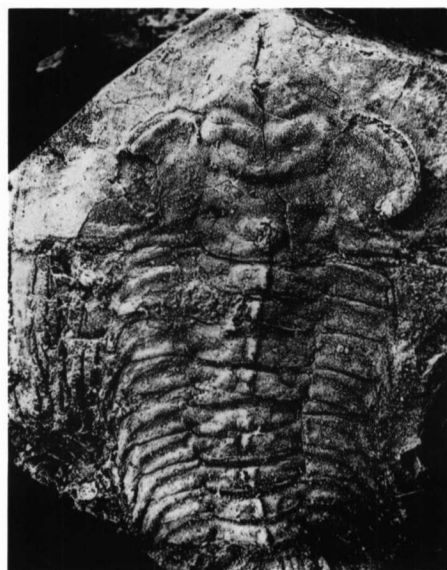
Any attempt to develop an integrated range chart for the genera and subgenera of the Olenellina is complicated because there is no international agreement on either correlation of subdivisions within the Lower Cambrian or on the biostratigraphic level of the upper boundary of this series. Data on stratigraphic ranges of Olenellina in measured sections are also limited. Furthermore, endemism is so strong within the Olenellina that there are no species and only a few genera that ranged between the major Cambrian continents.

An additional complication results from the observation that regional similarity among the Olenellina, limited at best, diminished during the Early Cambrian. Similar genera of the Fallotaspidoidea are present in the basal part of the trilobite record in North America, Morocco, and Siberia. In the medial part of the trilobite-bearing Lower

Fig. 6. Holmiidae.—1–4, 6, 7, Holmiinae; 1, *Holmia kjerulfi*, nearly complete individual, paratype, PMO 74283, $\times 1.5$ (Whittington, 1990); 2, *Schmidtellus reetae*, cephalon and partial thorax, holotype, GIT 2590a, $\times 1.4$ (Mannil in Bergström, 1973b); 3, *Andalusiana* sp., cephalon, IGR 19613, $\times 2$ (Geyer, unpublished); 4, 6, *Holmiella preancora*; 4, cephalon, paratype, GSC 27240, $\times 4$ (Fritz, 1972); 6, pygidium, holotype, GSC 27241, $\times 5$ (Fritz, 1972); 7, *Elliptocephala asaphoides*, cephalon and partial thorax, NYSM 4598, $\times 5$ (new).—5, 8–10. Callaviinae; 5, 8, *Callavia*; 5, *C. crosbyi*, complete individual, paratype, USNM 56798g, $\times 4$ (new); 8, *C. broeggeri*, cephalon, totopype, USNM 462671, $\times 1$ (new); 9, 10, *Kjerulfia lata*; 9, cephalon, lectotype, PMO 61376, $\times 0.8$ (new); 10, partial thorax, paratype, PMO 73170, $\times 0.8$ (new).



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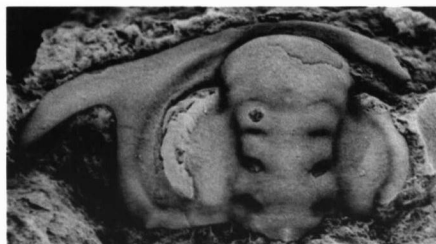
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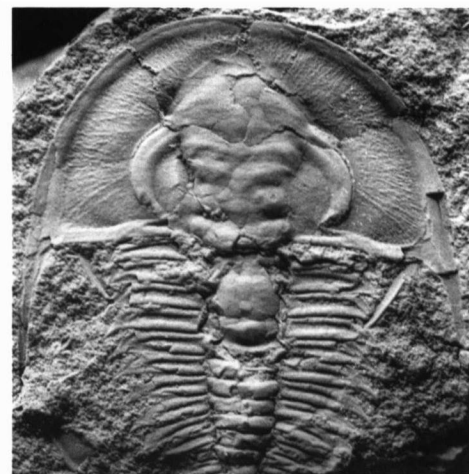
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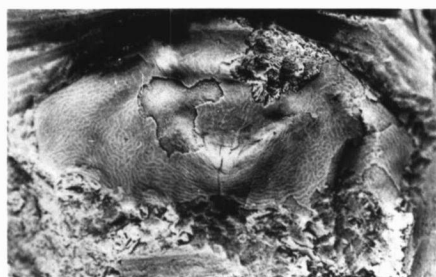
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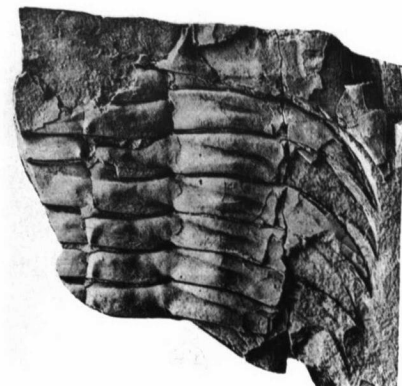
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Fig. 6. (Explanation on facing page.)

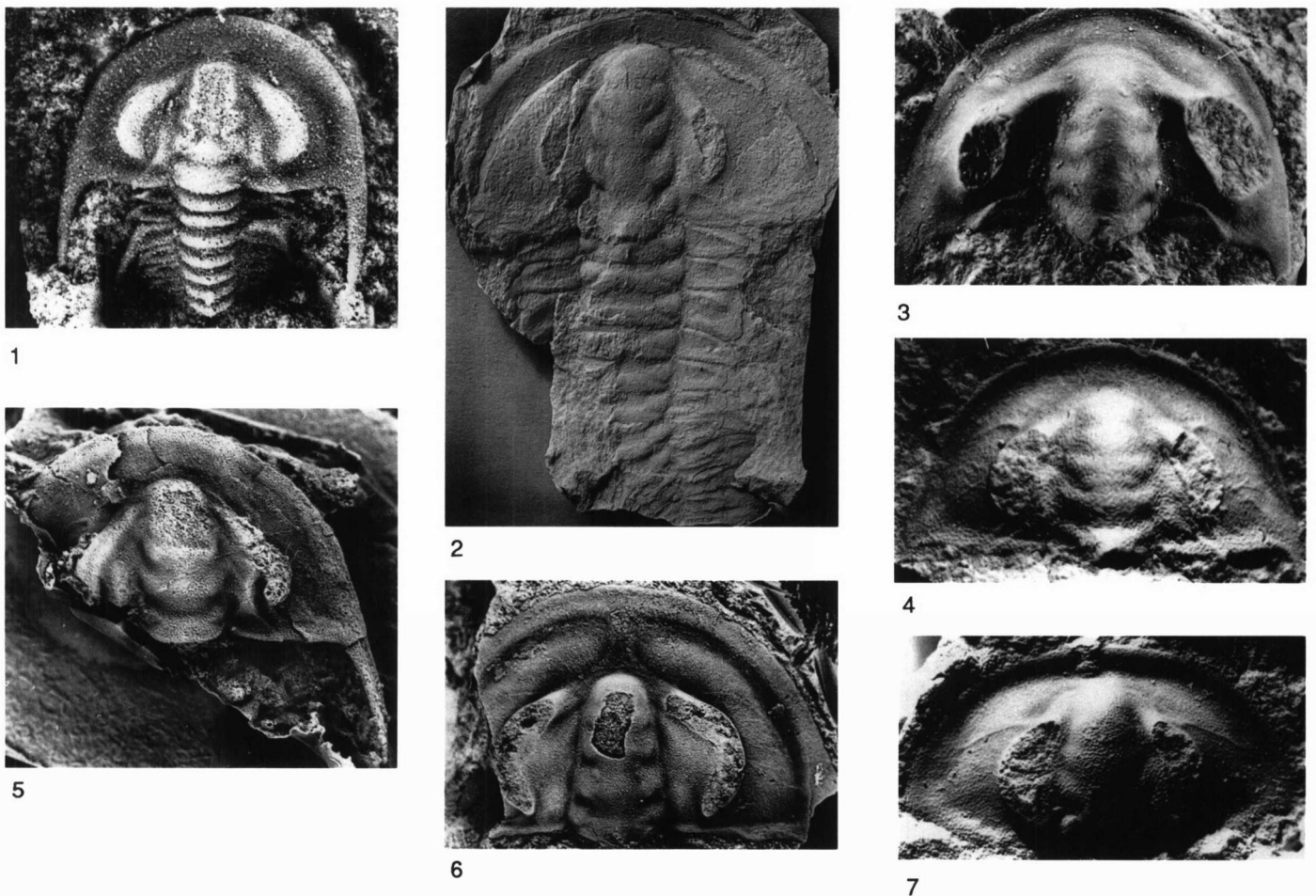


Fig. 7. Fallotaspididae, Fallotaspidinae; 1, 5, *Eofallotaspis tioutensis*; 1, cephalon and partial thorax, SMF 41984, $\times 10$ (Sdzuy, 1981); 5, cephalon, holotype, SMF 28567, $\times 5$ (Sdzuy, 1978); 2, *Fallotaspis typica*, cephalon and partial thorax, holotype, MNN G.26, $\times 2$ (new); 3, *Profallotaspis jakutensis*, cephalon, paratype, TsGM 265/13, $\times 7$ (Repina in Khomentovskii and Repina, 1965); 4, *Pelmanaspis jurii*, cephalon, holotype, TsGM 902/15, $\times 6$ (Repina, 1990a); 6, *Parafallotaspis grata*, cephalon, holotype, GSC 27202, $\times 3$ (Fritz, 1972); 7, *Lenallina lata*, cephalon, holotype, TsGM 902/1, $\times 6$ (Repina, 1990a).

Cambrian, Judomiidae dominate faunas of the Siberian Platform; Holmiidae dominate faunas of Baltica, Avalonia, and the western sector of Gondwana/peri-Gondwana; and Nevadiidae dominate faunas of Laurentia. In upper Lower Cambrian strata, the principal Olenellina seem to belong to the Olenellidae, which occur only on Laurentia [including northwestern Scotland and probably the Occidentalia terrane (Dalla Salda *et al.*, 1992) of Argentina]; some Judomiidae range into the lower part of this interval in Siberia. This pattern of diminished regional similarity and reduced geographic distribution among the Olenellina may have resulted from increasing isolation of Laurentia and separation of the other Cambrian continents during Early Cambrian time, following the putative breakup of a late Proterozoic supercontinent. The problems of intercontinental correlation in the uppermost Lower Cambrian, which largely involve nonolenellids outside of Laurentia, were discussed by Repina (1986).

As a result of all of these complications, we have chosen to show the ranges of olenellinid genera separately for five

geographic regions (Fig. 12): Laurentia, Siberia, Baltica, Avalonia, and the western sector of Gondwana/peri-Gondwana. Problems within each area and possible correlative intervals are discussed below.

In Laurentia (Fig. 12.A), the looseness of the biostratigraphic nomenclature needs to be understood before ranges can be discussed. Previously, three trilobite zones have been recognized, in ascending order: *Fallotaspis*, *Nevadella*, and *Bonnia-Olenellus* (Fritz, 1972).

Although *Fallotaspis* seems to be present in the White-Inyo region of California, the only record of its presence elsewhere on Laurentia is as *Fallotaspis* sp. in a faunal list by Fritz (1980) from the Cassiar Mountains of northern British Columbia. It is not present in the stratigraphic sections of northern Canada where the name was first used, and the stratigraphic relationship between *Parafallotaspis* in Canada and the fallotaspid of California is not precisely known. The zonal name is currently used in Laurentia in the sense of the interval with Fallotaspididae and is thus enclosed in quotation marks on Figure 12.A.

Similarly, *Nevadella* is found only in the upper part of the *Nevadella* Zone throughout the Cordilleran region; *Nevadia* characterizes the lower part of the zone. Thus, the zonal name has conventionally been used for the interval with Nevadiidae that is found between beds with Fallotaspidae and those with Olenellidae; it is also enclosed with quotation marks here (Fig. 12,A). The Nevadiidae terminate abruptly below the first Olenellidae in western Canada (Fritz, 1992) and seem to show a similar abrupt termination in California and Nevada.

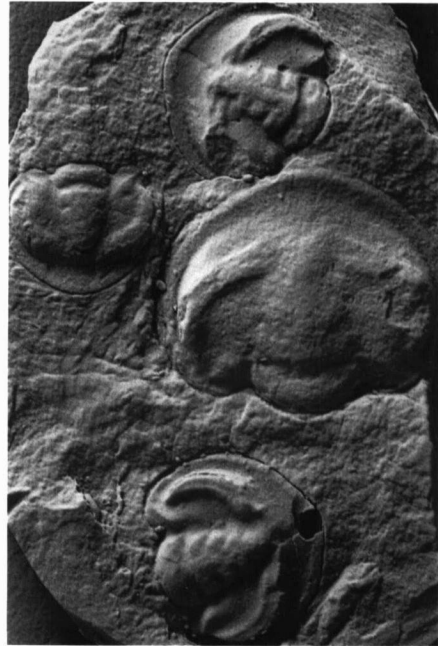
In this paper, the uppermost Lower Cambrian zone is the *Olenellus* Zone, defined by the full range zone of *Olenellus*. *Bonnia* is found in only a part of the *Olenellus* Range Zone, and it is common principally in open-shelf, carbonate deposits; it is not characteristic of the whole zone either geographically or stratigraphically. The *Olenellus* Zone occupies a thick stratigraphic interval, and it can be divided into three parts by the limited range of *Wanneria*, which is confined to an informal middle part.

Reasonably accurate ranges of most of the described Laurentian genera and subgenera can be worked out by integration of data in monographs and stratigraphic reports by Fritz (1972, 1973, 1976, 1978, 1979, 1992) and Palmer and Halley (1979) on the Cordilleran region of western North America. This has been supplemented by the less precisely controlled data in undescribed material of C. A. Nelson for the White-Inyo region, for which only a generalized stratigraphic column and plates without descriptions have been published (Nelson, 1976).

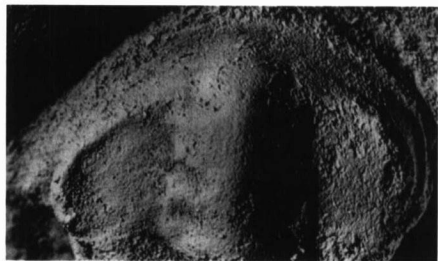
Data from the Appalachian and Arctic regions of North America and from northwestern Scotland are integrated into the range chart by inferred correlations. There are no published measured sections for these areas that include precise faunal data, and evidence for a hiatus of some kind involving loss of the uppermost Lower Cambrian beds abounds (the Hawke Bay event of Palmer and James, 1979). The Scottish Olenellidae, which occur within the range of *Salterella*, are assumed to be from the middle *Olenellus* Zone because *Salterella* is found primarily in the *Wanneria* interval in the middle *Olenellus* Zone in western Canada and also in western Newfoundland (Fritz and Yochelson, 1988). *Buenellus*, from beds in north Greenland below those with *Olenellus*, is placed in the "*Nevadella*" Zone on the basis of stratigraphic position and because the Nevadiidae, to which it is assigned, is represented elsewhere in Laurentia only in that Zone. *Fremontella* is assigned a position in the middle part of the *Olenellus* Zone



1



2



3



4

Fig. 8. 1–3. Fallotaspidae, Daguinaspidinae; 1, *Choubertella spinosa*, cephalon, holotype, MNN G.230, $\times 3$ (new); 2, *Daguinaspis ambroggii*, cephalon, holotype (at top), MNN G.200, $\times 3$ (new); 3, *Wolynaspis unica*, cephalon, holotype, GMU 1731/8, $\times 2$ (Chernysheva in Kir'ianov and Chernysheva, 1967).—4. Superfamily unassigned; *Poletaevella baljutica*, cephalon, holotype, BGU 0213/11, $\times 13$ (Dalmatov and Repina, 1971).

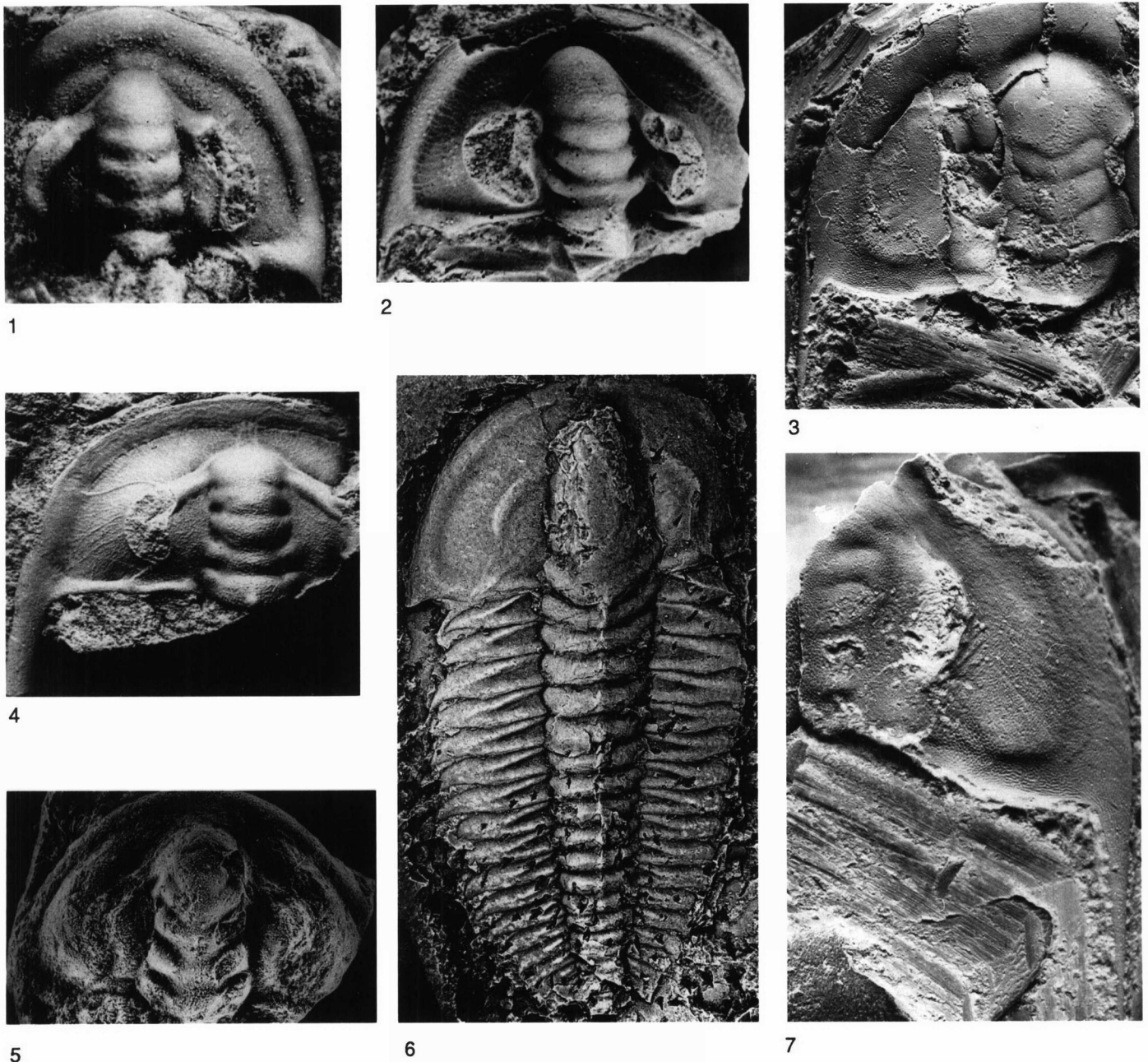


Fig. 9. 1–5, 7. Archaeaspididae; 1, *Archaeaspis hupei*, cephalon, holotype, TsGM 265/146, $\times 15$ (Repina in Khomentovskii and Repina, 1965); 2, *Bradyfallotaspis fusa*, cephalon, holotype, GSC 27226, $\times 6$ (Fritz, 1972); 3, 7, *Genus A species A*; 3, cephalon, holotype, GSC 102363, $\times 4$ (Fritz, 1993, in press); 7, cephalon, paratype, GSC 102355, $\times 7$ (Fritz, 1993, in press); 4, *Fallotaspidella musatovi*, cephalon, topotype, TsGM 3556/1020, $\times 4$ (Repina, unpublished); 5, *Selindella gigantea*, cephalon, holotype, TsGM 560/1, $\times 1.2$ (Repina, 1979).—6. Nevadiidae; *Buenellus higginsii*, complete individual, paratype, MGUH 17.589, $\times 3$ (Blaker, 1988).

because it is from beds that precede or reflect the Hawke Bay event in the southern Appalachian region. *Elliptocephala* is assigned to the middle part of the *Olenellus* Zone because it is associated with *Discinella micans* (Billings), which is abundant in the *Wanneria*-bearing beds of western Newfoundland and Labrador.

Hard data on stratigraphic ranges of most Siberian *Olenellina* (Fig. 12, B) comes from the Siberian Platform (Egorova and Savitskii, 1969; Repina, 1979, 1990a; Repina

et al., 1974; see also summary in Rozanov and Sokolov, 1984). Zonal and stage nomenclature is also from Rozanov and Sokolov (1984). *Fallotaspidella* is the only genus found outside of the Siberian Platform. It occurs in the *Sajanaspis-Kameshkoviella* Zone of the Kameshkov Horizon in the Sayan-Altay fold region, which is correlated with the upper part of the Atdabanian Stage (Rozanov and Sokolov, 1984). Occurrences of *Paranevadella*, in both Siberia and the cordillera of North America, provide support for an ap-

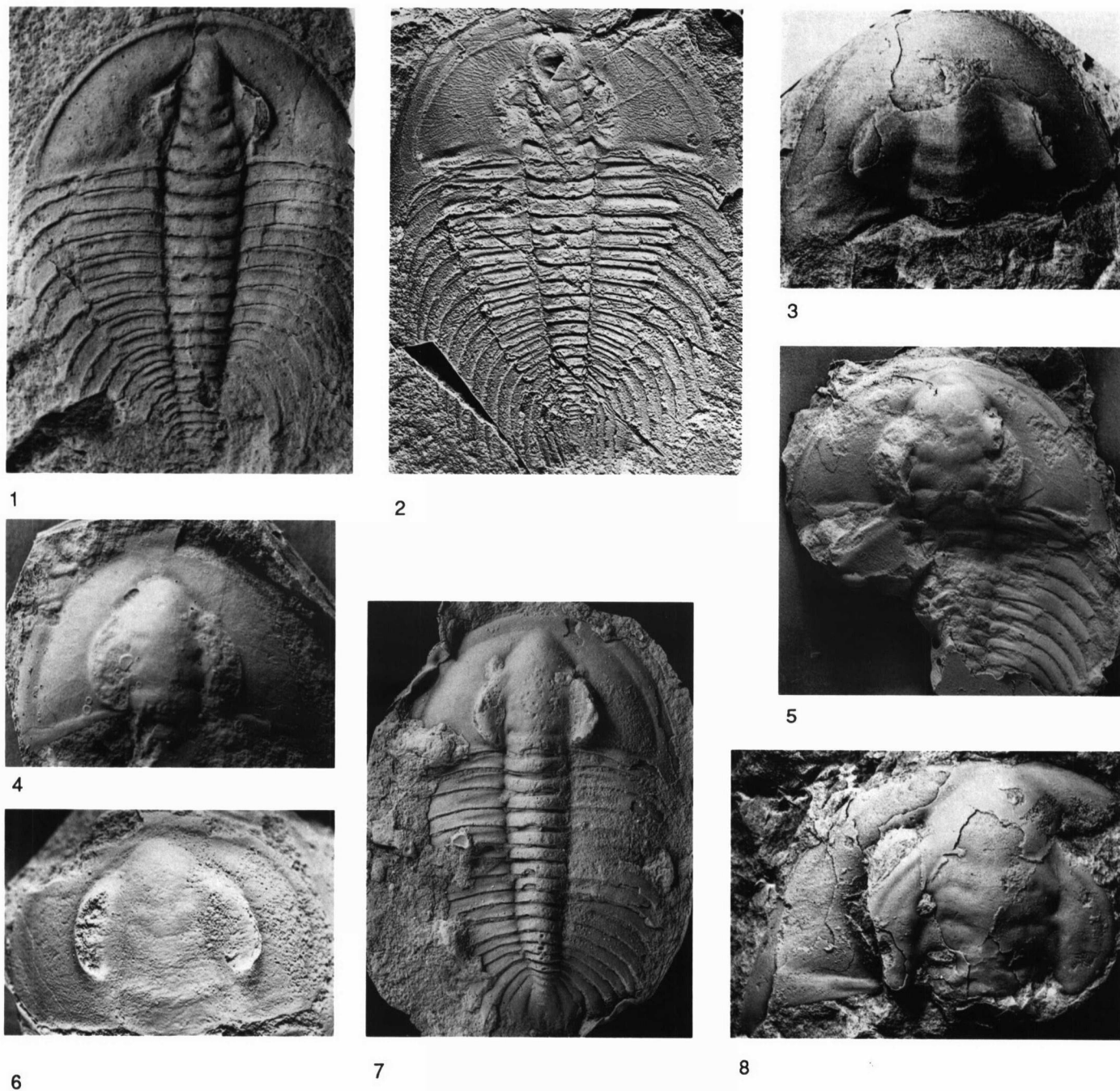


Fig. 10. 1–4, 6. Nevadiidae; 1, *Nevadia weeksi*, complete individual, topotype, LACMIP 7376, $\times 3$ (Nelson, unpublished); 2, *Nevadella eucharis*, complete individual, holotype, USNM 60079, $\times 2$ (new); 3, *Pseudojudomia egregia*, cephalon, holotype, CNIGR 8363/15, $\times 1.5$ (Egorova and Savitskii, 1969); 4, *Paranevadella subgroenlandicus*, cephalon, holotype, TsGM 265/174, $\times 3$ (new); 6, *Genus B species A*, cephalon, holotype, GSC 102330, $\times 7$ (Fritz, 1993, in press).—5, 7, 8. Judomiidae; 5, *Sinskia optabilis?*, cephalon and partial thorax, TsGM 452/500, $\times 1.5$ (new); 7, *Judomia tera*, complete individual, TsGM 659/50, $\times 2$ (new); 8, *Judomiella heba*, cephalon, TsGM 659/55, $\times 1.5$ (Repina, unpublished).

proximate correlation between Laurentia and Siberia. *Paranevadella* occurs in the upper part of the *Pagetiellus anabarus* Zone of Siberia and in the lower part of the “*Nevadella*” Zone on Laurentia. *Holmia* also occurs at these same levels in both Siberia and Laurentia.

Ranges of Olenellina from the western sector of Gondwana/peri-Gondwana (Fig. 12,C) have been pieced

together by integrating data from stratigraphic charts and section descriptions of Hupé (1953), Sdzuy (1978), and Geyer (1990a, with discussions in Geyer, 1990b). In addition, photos of stratigraphically located Olenellina in undescribed collections of Hupé were provided by Geyer (personal communication, 1991). The zonal nomenclature is that proposed by Geyer (1990a). Geyer (1990b)

discussed the problem of identifying *Fallotaspis* and recognizing a *Fallotaspis* Zone outside of Morocco. He stated that most of the material of Hupé (1953) was flattened and slightly distorted in shales and indicated the need for a complete reevaluation of the species assigned to this genus both in and outside of Morocco. Pending a revision, *Fallotaspis* is listed on Figure 12 as it has been identified in various areas. The unpublished material from Geyer includes a species of *Andalusiana* (Fig. 6,3), which permits this genus, originally described from badly distorted material in Spain by Sdzuy (1961), to be placed in context with the other Olenellina of the western sector of Gondwana/peri-Gondwana. Repina (1986) discussed the evidence for correlation of beds with the earliest Olenellina in North Africa and Siberia.

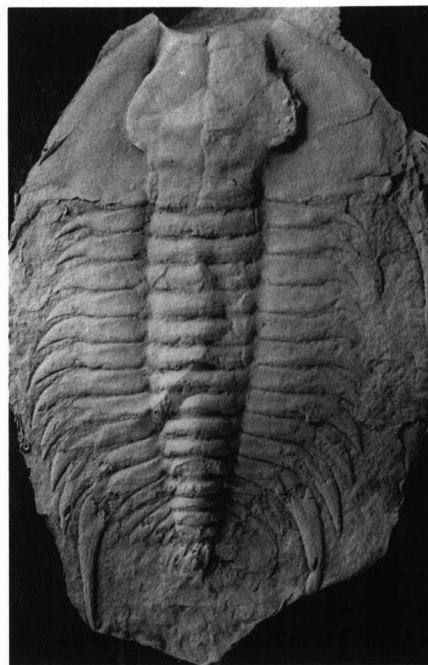
The principal genus of the Olenellina from Avalonia is *Callavia*. Based on associated eodiscoids in the Comley section of England (*Triangulaspis*, *Delgadella*, *Serrodiscus bellimarginatus*), the stratigraphic position of this genus has been placed by Repina (1986) as shown on Figure 12,D. These eodiscoids also assist correlation of the Siberian sections with those of North Africa. Consistent with the medial Lower Cambrian position of *Callavia* are suggested identifications of associated species of *Andalusiana* (suggested here by Palmer for *Kjerulfia? granulata* Raw) at Comley, England and *Selindella* (suggested here by Repina for *Callavia burri* Walcott) from the Boston area in the United States. Hupé (1953) has suggested that *Kjerulfia? lungreni* (Raw, 1936) from pre-*Callavia* beds at Comley is a fallotaspid, a suggestion that we tentatively accept.

The ranges of Olenellina within Baltica have been synthesized from scattered occurrences in Norway, Sweden, Estonia, and southern Poland and integrated into the regional lithostratigraphy by Ahlberg *et al.* (1986) and Ahlberg (1991). Occurrences of undescribed specimens referable to *Kjerulfia* in North Africa and to *Holmia* in Siberia and the presence of *Holmia rowei* Walcott and *H. argenta* (Walcott) in the western North American cordillera (Walcott, 1910) are the basis for the suggested position of the Baltic Holmiidae in the medial part of the trilobite-bearing Lower Cambrian on the integrated range chart of Figure 12,E.

PHYLOGENETIC QUESTIONS

As with any group for which morphologic, stratigraphic, and biogeographic information is substantially incomplete, development of an overall phylogeny is a highly speculative activity. Suggestions of a full phylogenetic picture have been presented by Repina (1979, 1990b). Here we discuss only some attractive trends within certain parts of the classification that seem to have phylogenetic importance. These comments will also illuminate some of the reasons for the title of this paper.

Origin of the Olenellidae.—The largest and most diverse taxonomic group of Olenelloidea is the Olenellidae, which is almost exclusively a Laurentian family and is the phylo-



1



2

Fig. 11. Neltneriidae; 1, *Neltneria jacqueti*, complete individual, ICS 122, $\times 2$ (new); 2, *Bondonella typica*, complete individual, holotype, MNN R50865, $\times 3$ (new).

genetically terminal group of the suborder. At present, it seems most likely that the Olenellidae evolved from some element of the Holmiidae. Repina (1979) recognized the Holmiidae as one of two possible sources, the alternative being the Nevadiidae.

The occurrence of *Holmia* and other undescribed Holmiidae within the "*Nevadella*" Zone, well below the

earliest Olenellidae, indicates that the Holmiidae preceded the Olenellidae on the Laurentian Cordilleran margin. Shared, high-level taxonomic characters include a modified L3 of the glabella and an enlarged L4. In addition, the ontogeny of olenellids passes through a holmiid stage with regard to relative widths of the interocular and extraocular areas. Also, two subgenera of *Olenellus*, *O. (Angustolenellus)* and *O. (Mesolenellus)*, as well as *Laudonia* and *Olenelloides*, all from the lower or middle *Olenellus* Zone, have the intergenal spines on the cephalon well inside the genal spines, as in *Holmia*. Furthermore, among other Holmiidae, *Callavia* has a prominent intergenal spine near the genal spine in a configuration very similar to some species of *Olenellus* (*Olenellus*), and prominent axial spines on posterior prothoracic segments are present in the Olenellinae, Biceratopsinae, and most Bristolinae, as well as in *Holmia*, *Kjerulfia*, and *Schmidtellus*.

In contrast, Nevadiidae, which are associated with Holmiidae in western Laurentia, share few significant morphologic convergences with Olenellidae. Judomiidae seem to be ruled out as possible ancestors to Olenellidae because of their highly modified pygidium and the distinctive development of long ocular lobes close to the glabella. However, the youngest observed species of *Judomia*, *J. rossae* (Jell and Repina, 1993, in press), shows slight development of an anteriorly expanded glabella, thus trending toward olenellid morphology. The straight to gently curved posterior cephalic margin of *O. (Olenellus) truemani* (Walcott, 1913), one of the earliest species of *Olenellus* (Fritz, 1992), and of species of the Wanneriinae is a morphological character shared with the Nevadiidae. Thus, the choice of Holmiidae over Nevadiidae as the ancestral group for the Olenellidae is not without problems.

With regard to the origin of the Holmiidae, Repina (1979) has suggested that the family was derived from the Archaeaspididae, based on the characters shared with *Holmia* of wide interocular cheeks, prominent glabellar furrows, anteriorly rounded L4, and intergenal spines widely separated from the genal spines. This is supported by Genus A (Fritz, 1993, in press), which is assigned to the Archaeaspididae because of the relations between L4 and the ocular lobe but has a slight development of the modified L3 glabellar segment characteristic of the Holmiidae and Olenellidae (Fig. 9,7). Other members of the Holmiidae have different configurations of the genal and intergenal spines and less prominent glabellar furrows. If the hypothesis of Repina (1979) is correct, a primitive character—intergenal spines widely separated from the genal spines—persists from the earliest Fallotaspididae, through Archaeaspididae and Holmiidae, to Olenellidae. Other configurations within the Nevadiidae, Holmiidae, and Olenellidae, with intergenal spines close to the genal spines, would then be independent and later developments in several families. This alternative seems to be preferable to a classification in which genal and intergenal spine relations are primary determinants of lineages. Such

a structure would split the Holmiidae and Olenellidae as presently constituted and would destroy the usefulness of the ratio between the widths of the extraocular and interocular cheeks as a grouping character, which seems to have biogeographic as well as possible ecologic and biostratigraphic significance. Perhaps a cladistic analysis using biostratigraphic and biogeographic data along with morphologic data might resolve this murky situation.

Problems with intrafamilial suprageneric classification.—Although the broadest aspects of phylogeny in the Olenellina can be surmised, most attempts to determine the derivation of individual genera from other genera and even to identify the genus from which a family or subfamily might have originated are exercises in frustration. Detection of defensible phylogenetic trends at these taxonomic levels is limited for many species by inadequate information about the entire olenellid exoskeleton; by limited biostratigraphic, biogeographic, and paleoecologic information; and by the fact that the Lower Cambrian is still inadequately sampled. Almost every new locality yields new forms, and very few stratigraphic sequences have been sampled thoroughly, so sections that seem to be well known still regularly yield new forms as well. The net result of this inadequate information base is a classification at lower taxonomic levels that attempts to group related genera without an adequate basis for defending the relationships. There are, for example, problems even with seemingly straightforward suprageneric taxa.

Within the Olenellidae, the subfamily that seems best constrained in both morphology and the time-space context is the Biceratopsinae. This subfamily contains only two described genera, *Peachella* and *Biceratops*. Both genera are characterized by narrow-waisted glabellas with nearly effaced glabellar furrows and short ocular lobes located close to the glabella (Figs. 4,1,2); they have extreme macropleural development of the third thoracic segment; and they occur only in southern Nevada where *Peachella* is present in the medial part of the upper *Olenellus* Zone and *Biceratops* is present in only the uppermost beds of the zone. *Peachella* has unusual, swollen, genal spines in normal position at the posterolateral cephalic corners, and *Biceratops* lacks any vestige of genal spines. The stratigraphic and biogeographic context plus the combination of unusual thoracic and glabellar characters support the association of these quite distinct forms in a single suprageneric taxon.

A recently discovered, undescribed species associated with *Peachella* has the glabellar and thoracic characters of the Biceratopsinae but is distinguished by having strongly advanced genal spines and a cephalic outline that is more pentagonal than semicircular. These differences complicate the simple scenario above. The cephalic outline of the new form is very similar to some species of *Bristolia* from approximately coeval beds in the same region. However, *Bristolia* (Fig. 4,5), which has well-developed glabellar furrows on its narrow-waisted glabella, distinct ocular lobes

A. LAURENTIA	"FALLOTASPIS"	"NEVADELLA"		OLENELLUS		
		lower	upper	lower	middle	upper
<i>Fallotaspis</i>	-----? █████					
<i>Parafallotaspis</i>	-----? █████					
<i>Cirquella</i>	-----? █████					
<i>Geraldinella</i>	----- █████ ?					
<i>Holmia</i>	----- █████ ?					
<i>Paranevadella</i>	----- █████ ?					
<i>Nevadia</i>	----- █████					
<i>Holmiella</i>	----- █████			 ?	
<i>Bradyfallotaspis</i>	----- █████					
<i>Buenellus</i>	----- █████ ?					
<i>Nevadella</i>	----- █████					
<i>Laudonia</i>	----- █████			 ?	
<i>Mummaspis</i>	----- █████ ?					
<i>Gabriellus</i>	----- █████ ?					
<i>Olenelloides</i>	----- █████ ?					
<i>Olenellus (Angustolenellus)</i>	----- █████					
<i>Olenellus (Olenellus)</i>	----- █████					
<i>Olenellus (Paedeumias)</i>	----- █████					
<i>Olenellus (Mesolenellus)</i>	----- █████ ?					
<i>Olenellus (Mesonacis)</i>	----- █████					
<i>Wanneria</i>	----- █████					
<i>Elliptocephala</i>	----- █████ ?					
<i>Fremontella</i>	----- █████ ?					
<i>Bristolia</i>	----- █████ ?					
<i>Bolbolenellus</i>	----- █████ ?					
<i>Arcuolenellus</i>	----- █████					
<i>Peachella</i>	----- █████					
<i>Nephrolenellus</i>	----- █████					
<i>Biceratops</i>	----- █████					

Fig. 12. Ranges of Olenellina within the principal paleogeographic regions of the Early Cambrian world; A, Laurentia; B, Siberia; C, Gondwana/peri-Gondwana; D, Avalonia; E, Baltica (new).

well separated from the glabella, and a somewhat less dramatic macropleural development of the third thoracic segment, is interpreted here to be the representative genus for the new subfamily Bristoliinae. Also, in this region, but only in the highest beds of the *Olenellus* Zone, a species here assigned to the new genus *Nephrolenellus* (Fig. 4,3) has the dramatic development of the third thoracic segment like *Peachella* and *Biceratops*, a glabellar structure and configuration of the ocular lobes like some species of *Bristolia*, and a normal development of the genal spine at the posterolateral corners of a semicircular cephalon. It is assigned to the Bristoliinae because of the structure of the glabella and ocular lobes.

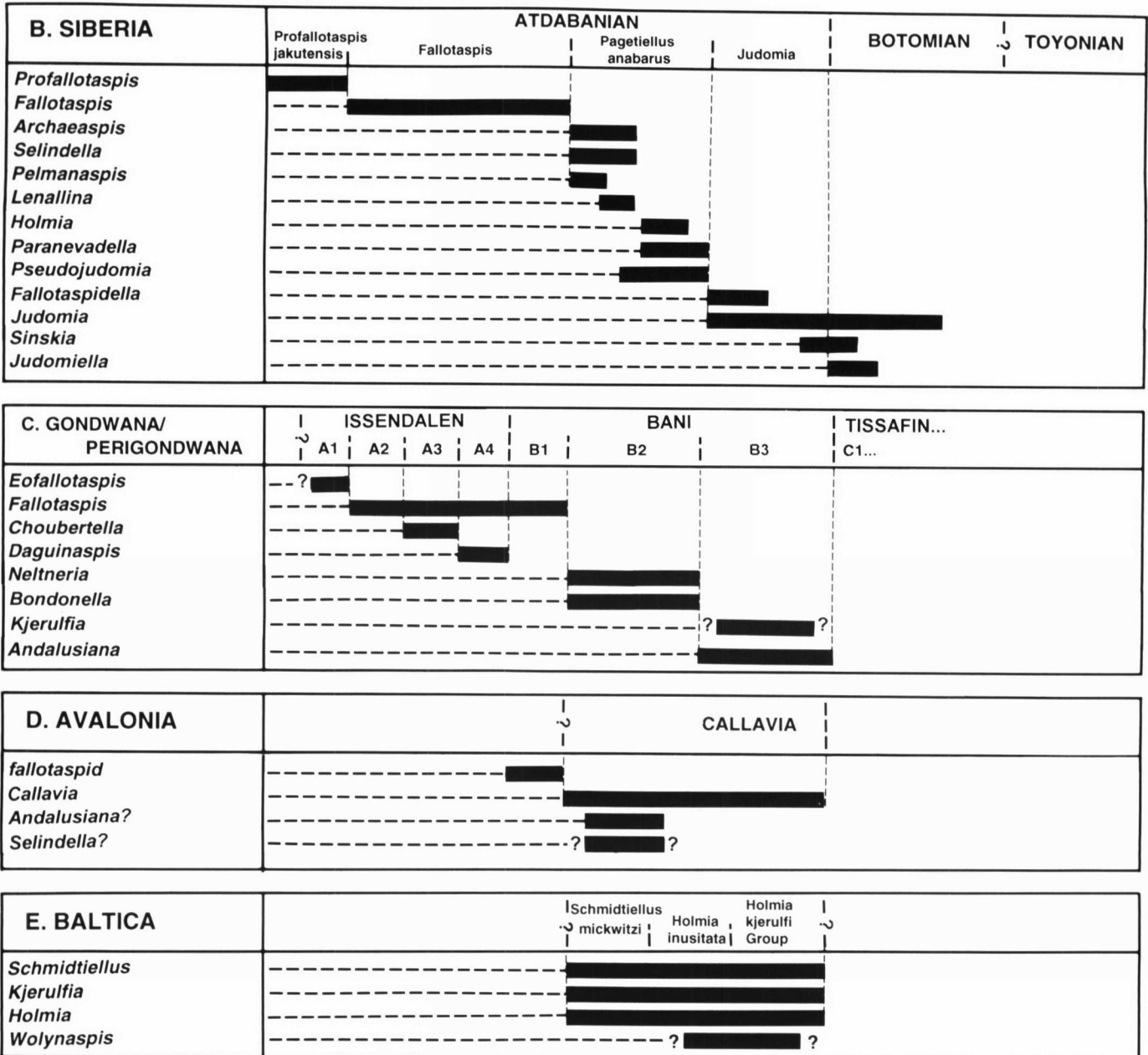
All species of the Biceratopsinae and Bristoliinae for which a thorax is known share with associated species of *Olenellus* a well-developed opisthothorax. In addition, they are all found in clay shales of the inner shelf in a limited part of the upper Lower Cambrian in the same geographic region.

Cephalic morphology is usually the only information consistently available for classification. In the Biceratopsinae and Bristoliinae, additional information about the thorax shows a common, extreme, macropleural development of the third thoracic segment, not known for any

other olenellids, on several genera with dramatically different cephalic structures. Thus, the Biceratopsinae, which seemed like a straightforward suprageneric taxon, and the Bristoliinae become less straightforward as the knowledge base expands.

Neoteny and the problem of Olenelloides.—McNamara (1978) reevaluated *Olenelloides armatus* Peach in the context of associated Scottish olenellids, and he interpreted the species as a paedomorph that retains immature characters in the adult through the process of progenesis. Therefore he concluded that *Olenelloides* deserves a taxonomic rank no higher than subgenus within *Olenellus*. However, although the relatively narrow extraocular area is a character of immature olenellids, it is also an ancestral feature within the Olenelloidea. Problems with the progenetic interpretation have led us to conclude that *Olenelloides* should be treated as a valid but peculiar genus within the Olenellidae, questionably assigned to the new subfamily Laudoniinae.

The problems with the progenetic explanation (the descendant adult, *O. armatus*, retaining ancestral juvenile characters) concern the absence of a preglabellar field and the presence of advanced genal spines on the cephalon of *O. armatus*. These are not immature features. Olenellids



without a preglabellar field either have no preglabellar field throughout their ontogeny (*Laudonia?* Hu, 1971; *Bristolia* Palmer and Halley, 1979) or lose the preglabellar field during ontogeny, as in *Olenellus paraoculus* (Fritz) and *Wanneria logani* Walcott (Fritz, 1972). In no known instances do preglabellar fields develop during ontogeny. Also, during ontogeny genal spines of forms with advanced adult positions either move forward from normal immature positions (Palmer and Halley, 1979, pl. 1, figs. 1–9, 11 for *Bristolia anteros* Palmer) or are advanced throughout ontogeny (Hu, 1971, pl. 9, figs. 20–31 for *Laudonia? canadiensis* Hu). The strongly advanced genal spines of *O. armatus* (opposite L3 in the smallest forms; opposite S2 in the largest forms) are more advanced than in any of the proposed ancestral forms. Thus, in the Scottish series illustrated by McNamara (1978, text-fig. 6), these key fea-

tures are not in a stage of arrested development compared to the other species in the series, and no interpretation of either neoteny or progenesis for the origin of *Olenelloides* is warranted.

The fact that the genal spines of *O. armatus* Peach are advanced at all growth stages suggests a closer relationship to *L.? canadiensis* Hu than to any species of *Bristolia*. This possible relationship, also suggested by Hu (1971), is supported by the fact that the Scottish trilobites are found in beds within the range of *Salterella*, which characterizes the middle part of the *Olenellus* Zone, and thus are approximately correlative with the beds bearing *L.? canadiensis* Hu in the North American cordillera. Rather than a retention of ancestral characters, both the absence of a preglabellar field and the strong advancement of the genal spines are phylogenetically derived characters, and the development

of *O. armatus* is more likely to be precocious than retarded. Further knowledge of ontogenies of advanced-spined olenellids with relatively narrow extraocular areas on the cephalon may help clarify the taxonomic and phylogenetic affinities of *Olenelloides*.

Trends within the Fallotaspidae.—Repina (1990a) has provided a detailed account of the stratigraphic succession of the earliest Olenellina from two sections in the south-eastern part of the Siberian Platform: one adjacent to the Lena River, the other in the Uchur-Maya region. Flat-lying beds exposed in river bluffs provide continuous undisturbed exposures and clear evidence for the trilobite succession. The oldest trilobites represent *Profallotaspis*. These trilobites have a nearly parallel-sided glabella with a short L4 engulfed by the anterior end of a broad, laterally directed ocular lobe. In successively higher strata, L4 becomes better defined and longer, the ocular lobes become more posterolaterally directed, and the slight anterior taper of the glabella increases. In Siberia, the succession proceeds stratigraphically from *Profallotaspis* through *Fallotaspis* to *Pelmanaspis* and *Lenallina*, both derived from a different species of *Fallotaspis*. In Morocco, a parallel succession proceeds through several species of *Eofallotaspis* (Sdzuy, 1978). Repina compared the earliest species of *Eofallotaspis* to *Profallotaspis* and later species of *Eofallotaspis* with Siberian forms assigned to *Fallotaspis*. Geyer (1990a) disagreed with the identification of *Fallotaspis* in Siberia, but the succession of morphologic changes is remarkably similar between Morocco and Siberia regardless of the taxonomic nomenclature applied.

Repina (1990b) also suggested that fallotaspid genera may be ancestral to the earliest genera of the Redlichina, represented by *Bigotina* (*Bigotinella*) in Siberia and *Hupetina* in Morocco. This possible phylogenetic relationship, which seems to involve each genus of the Fallotaspidae with a morphologically similar, suture-bearing genus of the Redlichina, is being developed in a paper by Jell, Chang, and Repina (in preparation).

Comments on the taxonomic significance of some cephalic features.—Many of the early Olenellina have low, threadlike ridges emanating from the margins of the eye and extending onto or across the preglabellar field or extraocular area (Fig. 2). A nomenclature for these features was provided by Hupé (1953). The anteriormost ridge is the **parafrontal band**, which skirts the lateral margins of L4 as a continuation of the outer band of the ocular lobe and continues in some specimens around the front of the glabella or continues into the plectrum between L4 and the border. A second ridge, the **anterior ocular line**, develops from the anterior margin of the eye and continues outward and backward in a curve across the extraocular area to the vicinity of the genal angle. Hupé considered this to be a possible fused suture from an ancestral form that possessed ecdysial sutures. A similar narrow ridge, the **posterior ocular line**, extends from the tip of the ocular lobe to the posterior margin distal but close and parallel to

the intergenal ridge and was also interpreted as a possible fused ecdysial suture. On younger olenellids, a narrow ridge (the **genal ridge**) may extend from the lateral margin of the eye to the vicinity of the genal angle and may be homologous with the anterior ocular line.

Repina (1990a) presented stratigraphic evidence that ecdysial sutures are a derived feature, which suggests that the anterior and posterior ocular lines have some other explanation. Some olenellids from the *Olenellus* Zone with well-preserved genal caecae have more prominent caecae in the positions of the parafrontal band, genal ridge, and posterior ocular lines (Fig. 13). This suggests that features such as the anterior and posterior ocular lines and the genal ridge reflect major but conservative anatomical features common to all Olenellina and variably expressed in the exoskeleton. Thus presence or absence of such features may be useful only at lower taxonomic levels.

CHANGES TO PREVIOUS OLENELLINID CLASSIFICATIONS

The classification presented here provides a considerable elaboration of the previous (and perhaps still) confusing complex of the Olenellidae and some minor updating and reassignment of genera in the Holmiidae and Fallotaspidoidea. Development of the classification began with an attempt to create a key to identification of genera of the Olenellina by Palmer during the 1980s. As this evolved through a number of iterations, insights were gained about the ranking of characters that grouped species geographically and stratigraphically. These insights were tested with all material available and the result is a fairly robust system for identification that seems to reflect geologically and phylogenetically meaningful taxonomic groupings. Table 1 includes several of the more recent classifications, beginning with the classification of Hupé (1953), for comparison with the classification proposed here. So many new taxa have been created in the past 40 years that earlier classifications are of historical interest



Fig. 13. Cephalon of *Bristolia bristalensis* (Resser), showing the presence of caecal features at the positions of the parafrontal band, genal ridge, and posterior ocular line (Palmer and Halley, 1979).

only. The principal revisions proposed in this paper and their justifications are summarized below.

Fallotaspidoidea.—The families of early Olenellina, here assigned to the Fallotaspidoidea (Figs. 7–11), were established by Repina (1979) and remain largely unchanged except for the additions of subsequently named Siberian and Laurentian genera (Blaker, 1988; Repina, 1990a; Fritz, 1993, in press). Ahlberg *et al.* (1986) suggested a ranking at the subfamilial level for Fallotaspidae, Daguinaspididae, and Archaeaspididae recognized by Repina but included the Archaeaspidinae in the Callaviidae with very little explanation. *Callavia* has the characteristic genal features of Holmiidae, the modified L3 of Olenelloidea, and also shares a biogeographic region with the Holmiidae. There seems to be little morphologic or biogeographic support for a close phylogenetic relationship between *Callavia* and genera of the Archaeaspididae. The Fallotaspidoidea, as constituted here, share important glabellar features that separate them from all other Olenellina at a high taxonomic level.

Absence of genal spines, which here is a subfamily character (Daguinaspidinae) within the Fallotaspidae, is only of generic importance within the Olenellidae and Nevadiidae. Ahlberg *et al.* (1986) suggest that this character may have been given too much weight in previous family classifications (Table 1). Further reduction in the value of this character within the Fallotaspidae by synonymizing the Daguinaspidinae with the Fallotaspidae, however, produces an awkward taxon. Until more is learned about the early olenellinids, the Daguinaspidinae are retained as a taxon at the subfamily level.

Reexamination of *Bondonella*, which has previously been included most commonly in the Holmiinae following Hupé (1953; Table 1), shows that it has a parallel-sided glabella, an unmodified L3, narrow interocular areas, and a posterior cephalic margin deflected slightly forward distally, all characters shared with *Neltneria*. *Bondonella* is therefore included here in the Neltneriidae.

Olenelloidea.—Substantial elaboration and reorganization within this group has resulted from reexamination of the rich variety of Laurentian Olenellidae. These modifications involve changes in taxonomic rank for previous suprageneric taxa, resurrection of some previously synonymized genera and suprageneric taxa, creation of new genera and new suprageneric combinations, and synonymizing of some previously recognized genera.

A superfamilial taxon Olenelloidea is recognized to include the Olenellidae and Holmiidae, which share such major glabellar features as an expanded L4 and modified L3 glabellar segment, distinguishing them from the Fallotaspidoidea.

The constitution of the Holmiidae (Fig. 6) is changed by removal of *Bondonella* to the Neltneriidae (discussed above). The assignment of *Kjerulfia* to the Callaviinae (Poulsen in Moore, 1959), is followed here, rather than its more recent assignment to the Holmiinae (Suvorova in

Chernysheva, 1960; Repina, 1979; Ahlberg *et al.*, 1986). The similarities in cephalic and thoracic structure between *Kjerulfia* and *Callavia*—an anteriorly pointed L4 that extends onto the border and a wide thorax with falcate pleural spines on each segment—distinguish these two genera from other Holmiidae and are enough to justify their assignment to a separate subfamily.

Changes in the Olenellidae, by far the most diverse family group within the Olenellina, are so extensive that the present classification has little in common with earlier classifications (Table 1). Five subfamilies are recognized. Because of the absence of information about thoracic and pygidial structure of many species, cephalic characters are the primary determinants of subfamily assignment. Several subfamilies, however, seem also to have distinctive thoracic structure.

The core subfamily, the Olenellinae (Fig. 3) contains approximately 35 species, even after some substantial synonymizing begun by Fritz (1972). Except for species of *Mummaspis* and *Fremontella*, whose distinctive characters are clear, all other species are assigned to *Olenellus*. Because almost every character that can be used for taxonomic discrimination in *Olenellus* is part of a continuous variable, there are no sharply defined subdivisions of this genus to justify discrimination of further genera. However, five subtle groupings are assigned a subgeneric status.

The principal character of the subfamily is a glabella that is only slightly to moderately constricted at the S1 level or nearly parallel-sided so that L1 is nearly the same width as the occipital ring. Intergenal spines or intergenal swellings are usually present. Where the thorax is known, the anterior fifteen segments form a prothorax, the third segment is usually slightly to moderately macropleurale, and the fifteenth segment bears a long axial spine. The remainder of the thorax is an opisthothorax that consists of a variable number of segments with markedly reduced (tr.) pleurae.

Subgenera within *Olenellus* are based primarily on combinations of ocular lobe length, intergenal spine or swelling position, and relationships between the border and the preglabellar field.

The Biceratopsinae (Figs. 4, 1, 2) was previously a monotypic subfamily for the unusual genus *Biceratops*, which lacks genal spines and has a greatly enlarged third thoracic segment. Discovery of similar thoracic structure on complete specimens of *Peachella* and a new form still to be described, which differ by having inflated (*Peachella*) or strongly advanced (new genus) genal spines, has expanded understanding of this subfamily. In addition to the shared thoracic structure, all three genera have a distinctly narrow-waisted glabella (narrowest at S1 or L2), poor development of glabellar furrows, and very short ocular lobes situated close to the glabella. Furthermore, all three genera are known only from the upper *Olenellus* Zone in southern Nevada and adjacent parts of California. Genera can be identified easily by using the cephalic outline.

The Bristoliinae (Figs. 4,3,5–7,10) is a new subfamily erected for some genera previously included either in a subfamily Fremontiinae (Repina, 1979; Ahlberg *et al.*, 1986), an undifferentiated Olenellidae (Bergström, 1973b), or Olenellinae (Moore, 1959). Reexamination of the type species of *Fremontia* shows that it has the glabellar outline, short preglabellar field, short ocular lobes, and slightly advanced genal spines characteristic of the resurrected subgenus *Mesonacis*. Thus, *Fremontia* and the Fremontiinae become junior synonyms of *Mesonacis* and the Olenellinae, respectively. *Bristolia*, previously assigned to the Fremontiinae by Repina (1979) and Ahlberg *et al.* (1986), and the new genera *Arcuolenellus*, *Bolbolenellus*, and *Nephrolenellus* are included in this new subfamily. These genera share a generally narrow-waisted glabella with strong development of glabellar furrows and an opisthothorax; their ocular lobes are more prominent and situated farther from the glabella than in the Biceratopsinae. *Bristolia* and *Nephrolenellus*, the only genera in the subfamily known from articulated specimens, also have extreme development of the third thoracic segment that is here inferred also to be a subfamily character. Genera in the Bristoliinae are distinguished primarily by cephalic outline.

Fremontella and *Laudonia*, also previously assigned to the Fremontiinae by Repina (1979) and Ahlberg *et al.* (1986), are reassigned to other subfamilies. *Fremontella*, even though it has strongly advanced genal spines, has a glabella typical of the Olenellinae and is assigned to this subfamily. *Laudonia*, which lacks both an extreme development of the third thoracic segment and a strong axial spine on the fifteenth thoracic segment and has a prominent, reticulate sculpture, is assigned to the new subfamily Laudoniinae.

The Wanneriinae (Fig. 5) includes only *Wanneria*, which is characterized by a strongly laterally expanded L4, a posterior cephalic margin that is nearly straight or curved backward posteriorly, a prominent, reticulate sculpture, and absence of an intergenal spine. The thorax does not have any macropleural modification of the third thoracic segment. In addition, although it has a long axial spine on the 15th thoracic segment, the segments behind the spine are not modified into an opisthothorax. *Wanneria* is found only in the middle third of the *Olenellus* Zone. *Olenellus* (*Olenellus*) *truemani* Walcott, from the earliest beds of the *Olenellus* Zone in Canada, is assigned to the Olenellinae but has a posterior cephalic margin similar to that of *Wanneria*. It is associated with *Mummaspis occidentis* (Walcott), a species with a reticulate sculpture. Both species have a slightly macropleural third thoracic segment typical of the Olenellinae and are approximately coeval with *Olenellus* (*Olenellus*) *muralensis* Fritz, which has the typical posterior cephalic margin for the Olenellinae with the genal spine slightly advanced. Thus, the Olenellinae and Wanneriinae are not well differentiated in the lower *Olenellus* Zone.

The new subfamily Gabriellinae (Fig. 4,9) is named for a single genus, *Gabriellus*, with an anteriorly tapered glabella and a distinctive thorax and pygidium. The thorax

has unusually narrow pleural lobes, an unmodified third segment, and a strong axial spine on the fifteenth segment. Segments behind the fifteenth segment are not differentiated into an opisthothorax. The pygidium is an elongate, subovate plate.

The new subfamily Laudoniinae (Figs. 4,4,8) includes *Laudonia* and perhaps *Olenelloides*. *Laudonia* (Fig. 4,4) has a subrectangular cephalon characterized by prominent, long intergenal spines in the adult and an anteriorly expanded glabella that reaches to the border. The thorax has a weakly macropleural third segment, and it lacks a strong axial spine on the fifteenth segment and a clearly differentiated opisthothorax. Fritz (1992) included *Laudonia* in the Wanneriidae without discussion but both its cephalic and thoracic structure are sufficient reasons for recognizing differences of at least subfamily value. *Olenelloides* (Fig. 4,8) is tentatively included in the subfamily because of the prominent development of all of its marginal cephalic spines in adult forms and similarities with *Laudonia*? *canadiensis* Hu (1971). Its thoracic structure, with both the third and sixth segments macropleural, is unique among Olenellina and suggests that with more knowledge perhaps a separate suprageneric taxon might be justified. If further information supports the subfamilial association of *Olenelloides* and *Laudonia*, then the Laudoniinae will become a junior synonym of the Olenelloidinae (Hupé, 1953).

REVISED CLASSIFICATION OF THE OLENELLINA

Diagnoses for all taxa in this suborder are given below. These include the following new subfamilies, genera, and subgenera: Bristoliinae, Gabriellinae, Laudoniinae, *Olenellus* (*Angustolenellus*), *O.* (*Mesolenellus*), *Arcuolenellus*, *Bolbolenellus*, and *Nephrolenellus* within the Olenellinae; and *Paranevadella* within the Nevadiidae. Resurrected subgenera, previously synonymized with *Olenellus*, are *Olenellus* (*Paedeumias*) and *O.* (*Mesonacis*). Representative specimens of all generic and subgeneric taxa are illustrated in Figures 3 to 11, and their repositories are listed on Table 2. The descriptive nomenclature (Fig. 2) is that worked out by Palmer in correspondence with W. H. Fritz and H. B. Whittington (personal communications, 1991).

SYSTEMATIC PALEONTOLOGY

Order REDLICHIIIDA Richter, 1933

Suborder OLENELLINA Walcott, 1890b

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

Mesonacidae Walcott, 1890b, p. 635; Walcott, 1910, p. 236.
Mesonacida Swinnerton, 1915, p. 538; Poulsen, 1927, p. 315.

Olenellidea Richter and Richter, 1941a, p. 33.

Protoparia Størmer, 1942, p. 59, *non* Swinnerton, 1915.

Olenellacea Henningsmoen, 1951, p. 184; Bergström, 1973a, p. 39; 1973b, p. 284.

Table 2. Repositories containing type material of Olenellina.

AMNH - American Museum of Natural History, New York, USA
BGU - Geological Museum, Buryat Geological Board, Ulan-Ude, Russia
CNIGR - Central Scientific Research Geological Exploration Museum (Chernyshev Museum), St. Petersburg, Russia
GIT - Geological Institute of Tallinn, Estonia
GMU - Geological Museum, Ukrainian Academy of Sciences, Kiev, Russia
GSC - Geological Survey of Canada, Ottawa, Canada
GSE - Institute of Geological Sciences, Edinburgh, Scotland
ICS - Institute for Cambrian Studies, Boulder, Colorado, USA
IGR - Institut of Geology, University of Rennes, France
IGUW - Institute of Geology, University of Warsaw, Poland
KUMIP - University of Kansas Museum of Invertebrate Paleontology, Lawrence, Kansas, USA
LACMIP - Los Angeles County Museum, California, USA
MGUH - Geological Survey of Greenland, Copenhagen, Denmark
MMK - Geological Museum, Copenhagen University, Copenhagen, Denmark
MNN - Museum of Natural History, Paris, France
NYSM - New York State Museum, Albany, New York, USA
PIN - Paleontological Institute, Academy of Sciences USSR, Moscow, Russia
PIW - Institute for Paleontology, University of Würzburg, Germany
PMO - Paleontological Museum, University of Oslo, Norway
SGM - Geological Survey of Morocco, Rabat, Morocco
SGU - Swedish Geological Survey, Uppsala, Sweden
SMF - Senckenberg Museum, Frankfurt-am-Main, Germany
TsGM - Central Scientific and Geological Museum, Novosibirsk, Russia
UBC - Department of Geology, University of British Columbia, Vancouver, Canada
UCR - Department of Earth Sciences, University of California, Riverside, California, USA
UMU - Geological-Paleontological Institute, University of Münster, Germany
USNM - U. S. National Museum, Washington, D.C., USA

Olenelloidea Hupé, 1953, p. 116.

Olenellida Bergström, 1973a, p. 39; Bergström, 1973b, p. 284; Ahlberg *et al.*, 1986, p. 40.

Olenelloidea Repina, 1979, p. 27.

Diagnosis.—Redlichiida lacking dorsal cephalic sutures.

Distribution.—Lower Cambrian. North America (including Greenland), Spitsbergen, Europe, northwestern Africa, northern Asia (Siberia), South America (Argentina).

Superfamily OLENELLOIDEA Walcott, 1890b

Olenellidea Richter and Richter, 1941a, p. 33, *partim*.

Olenellacea Henningsmoen, 1951, p. 184, *partim*; Bergström, 1973b, p. 284, *partim*.

Olenelloidea Hupé, 1953, p. 116, *partim*.

Olenelloidea Suvorova in Chernysheva, 1960, p. 62, *partim*; Repina, 1979, p. 27, *partim*; Whittington, 1989, p. 113, *partim*.

Diagnosis.—Olenellina with L4 usually enlarged and glabella narrowest at L2 or S1. L3 usually modified distally, posterolateral part bending backward at the expense of L2. Ocular lobe connected only to posterolateral part of L4.

Distribution.—Lower Cambrian. North America (including Greenland), Spitsbergen, Europe, northwestern Africa, South America (Argentina), ?Novaya Zemlya.

Family OLENELLIDAE Walcott, 1890b

Olenellidae Walcott, 1890b, p. 635, *sensu* Repina, 1979, p. 20.

Mesonacidae Walcott, 1890b, p. 635, *partim*.

Olenellidae Hupé, 1953, p. 124, *partim*; Poulsen in Moore, 1959, p. O191, *partim*; Suvorova in Chernysheva, 1960, p. 62, *partim*; Bergström, 1973b, p. 40, *partim*; Ahlberg *et al.*, 1986, p. 40.

Diagnosis.—Olenelloidea with width of interocular area generally half or less that of extraocular area. Third thoracic segment slightly to strongly macropleurale.

Distribution.—Lower Cambrian. North America (including Greenland), Spitsbergen, United Kingdom (northwestern Scotland), Argentina (San Juan area), *Olenellus* Zone; ?Novaya Zemlya, zone unknown.

Subfamily OLENELLINAE Walcott, 1890b

Olenellinae Poulsen in Moore, 1959, p. O192, *partim*; Suvorova in Chernysheva, 1960, p. 62, *partim*; Repina, 1979, p. 22, *partim*.

Olenellidae Ahlberg *et al.*, 1986, p. 40, *partim*.

Fremontiinae Repina, 1979, p. 22, *partim*.

Diagnosis.—Olenellidae with glabellar furrows weakly to moderately defined. Transverse width of anterior part of L1 equal to or only slightly less than transverse width of occipital ring. L4 slightly to moderately expanded

anteriorly. Posterior tips of ocular lobes ranging from opposite L2 to opposite posterior part of occipital ring. Posterior margin of cephalon nearly straight or slightly deflected forward distal to intergenal spine or swelling. Intergenal spines or distinct intergenal angle usually present. Prothorax, where known, with axis narrower than inner part of pleurae. Third thoracic segment weakly to moderately macropleural, with pleural spine not greatly elongated. Fifteenth thoracic segment with long axial spine. Opisththorax with variable number of uniformly small segments, each bearing narrow pleurae. Pygidium small, subquadrate, with 1 or 2 pairs of short marginal spines.

Distribution.—Lower Cambrian. North America (including Greenland), Spitsbergen, United Kingdom (northwestern Scotland), Argentina (San Juan area), *Olenellus* Zone; ?Novaya Zemlya, zone unknown.

OLENELLUS Hall, 1861 (1862, p. 114)¹

Type species.—*Olenus thompsoni* Hall, 1859, p. 59; SD Walcott, 1886, p. 163. Holotype (Hall, 1859, p. 59, fig. 1), AMNH 244, New York (lost).

Diagnosis.—Olenellinae with external surface generally smooth or with faint Bertillion markings, rarely granular or reticulate. Occipital ring smooth or with small node near posterior margin; occipital spine rare. Genal spine angle opposite or posterior to L1. Genal spine slender.

Distribution.—Lower Cambrian. North America (including Greenland), United Kingdom (northwestern Scotland), Spitsbergen, ?Argentina (San Juan area), *Olenellus* Zone; ?Novaya Zemlya, zone unknown.

OLENELLUS (OLENELLUS) Hall, 1861 (1862, p. 114)

Figure 3,1

Type species.—Same as for genus.

Diagnosis.—Species of *Olenellus* with genal spines at posterolateral cephalic corners or slightly advanced to position opposite L1. Intergenal spines, if present, small, close to genal spines, and directed slightly posterolaterally. Preglabellar field absent or very short, sagittal length usually less than twice sagittal length of anterior border. Ocular lobes curved; posterior tips convergent toward glabella and situated opposite or posterior to posterior part of L1. S2 isolated from axial furrow, usually present as distinct transverse slits.

Distribution.—Lower Cambrian. North America (including Greenland), *Olenellus* Zone; Spitsbergen, ?*Olenellus* Zone; ?Novaya Zemlya, zone unknown.

OLENELLUS (ANGUSTOLENELLUS) new subgenus

Figure 3,6

Type species.—*Olenellus hamoculus* Cowie and McNamara, 1978. Holotype (Cowie and McNamara, 1978, pl. 70, fig. 3) GSE 13302, Edinburgh.

Diagnosis.—Species of *Olenellus* with posterior margin of

cephalon directed slightly anterolaterally distal to position of intergenal spine. Intergenal spines intermediate between genal spine and axial furrow or closer to axial furrow than to genal spine. Sagittal length of preglabellar field equal to or slightly greater than that of anterior border. Posterior tips of ocular lobes directed nearly straight backward, situated opposite or anterior to midlength of L1.

Distribution.—Lower Cambrian. United Kingdom (northwestern Scotland), ?*Olenellus* Zone.

OLENELLUS (MESOLENELLUS) new subgenus

Figure 3,7

Type species.—*Holmia hyperborea* Poulsen, 1974, p. 84–87. Holotype (Poulsen, 1974, pl. 1, fig. 4) MMK 13008, Copenhagen.

Diagnosis.—Species of *Olenellus* with posterior margin of cephalon directed slightly forward distal to position of intergenal spine or intergenal angle. Sagittal length of preglabellar field equal to or slightly greater than sagittal length of border. Intergenal spine or angle about midway between genal spine and axial furrow or closer to axial furrow. Posterior tips of ocular lobes convergent towards glabella, situated opposite or posterior to occipital furrow.

Distribution.—Lower Cambrian. USA (Nevada), Canada (southern Rocky Mountains, Devon Island), northern Greenland, Argentina (San Juan region), *Olenellus* Zone, ?lower and middle parts only.

OLENELLUS (MESONACIS) Walcott, 1885, p. 328.

Figure 3,2

Fremontia Raw, 1936, p. 243.

Type species.—*Olenus vermontanus* Hall, 1859, p. 60. Holotype (Hall, 1859, p. 60, fig. 2), AMNH 230, New York (lost).

Diagnosis.—Species of *Olenellus* with posterior margin of cephalon angled forward distal to intergenal angle. Preglabellar field absent or very short, with sagittal length generally equal to or less than that of anterior border. Posterior tips of ocular lobes directed nearly straight posteriorly, situated opposite or anterior to medial part of L1. Interocular area may be extended posteriorly as low, broad ridge. Most species with transverse width of inner part of macropleural third segment, exclusive of spine, less than 1.5 times width of axis. Pygidium, known only for type species, has two pairs of short marginal spines.

Distribution.—Lower Cambrian. North America (excluding Greenland), United Kingdom (northwestern Scotland), middle and upper *Olenellus* Zone.

OLENELLUS (PAEDEUMIAS) Walcott, 1910, p. 304

Figure 3,3

Type species.—*Paedeumias transitans* Walcott, 1910, p. 305–310. Lectotype (Walcott, 1910, pl. 34, fig. 1; by subsequent

1. For explanation of the date of 1861 for *Olenellus*, see Whittington, 1989, p. 114.

designation, Resser and Howell, 1938, p. 226), USNM 56808b, Washington, D.C.

Diagnosis.—Species of *Olenellus* with posterior margin of cephalon nearly straight or only slightly angled forward distal to position of intergenal spines. Intergenal spine or swelling generally closer to genal spine than to axial furrow. Sagittal length of preglabellar field characteristically greater than twice sagittal length of anterior border. Posterior tips of palpebral lobes convergent toward glabella, opposite or posterior to posterior part of L1.

Distribution.—Lower Cambrian. North America (all parts), United Kingdom (northwestern Scotland), *Olenellus* Zone.

FREMONTELLA Harrington, 1956, p. 58

Figure 3,4

Type species.—*Wanneria halli* Walcott, 1910, p. 301. Lectotype (Walcott, 1910, pl. 31, fig. 3), USNM 56806c, Washington, D.C.

Diagnosis.—Olenellinae with external surface smooth. Genal spines strongly advanced; genal spine angle anterior to S2. Intergenal angle nearly a right angle. Preglabellar field absent. Posterior tips of ocular lobes opposite anterior part of L1.

Distribution.—Lower Cambrian. USA (Alabama), Argentina (San Juan area), *Olenellus* Zone.

MUMMASPIS Fritz, 1992, p. 17

Figure 3,5

Type species.—*Wanneria occidens* Walcott, 1913, p. 314. Holotype (Walcott, 1913, pl. 53, fig. 2), USNM 60080, Washington, D.C.

Diagnosis.—Olenellinae with posterior margin of cephalon nearly straight. Parts of external surface may be reticulate. Intergenal swelling distal to midlength of posterior margin. Preglabellar field absent or sagittal length less than that of border. S3 deep, continuous across glabella. Occipital spine may be present. Ocular furrow deep; outer band of ocular lobe narrower than inner band. Third thoracic segment generally only weakly macropleural.

Distribution.—Lower Cambrian. Canada (southern Rocky Mountains), lower part of *Olenellus* Zone.

Subfamily BICERATOPSINAE Pack and Gayle, 1971

Olenellidae Bergström, 1973b, p. 312, *partim*; Ahlberg *et al.*, 1986, p. 40, *partim*.

Biceratopsinae Repina, 1979, p. 22.

Diagnosis.—Olenellidae with glabella narrowest at midlength; glabellar furrows very poorly developed; transverse width of L1 less than transverse width of occipital ring. Ocular lobes close to glabella; posterior tips opposite or anterior to L1. Genal spines absent or opposite midlength of ocular lobes. Intergenal spines absent; intergenal angle may be developed. Thorax divided into prothorax and opisththorax; third segment strongly ex-

panded distally and pleural spine extremely long, tips posterior to body; 15th segment with long axial spine.

Distribution.—Lower Cambrian. USA (southern Great Basin), upper *Olenellus* Zone.

BICERATOPS Pack and Gayle, 1971, p. 895–896

Figure 4,1

Type species.—*Biceratops nevadensis* Pack and Gayle, 1971, p. 896–898. Holotype (Pack and Gayle, 1971, pl. 102, figs. 2, 3), USNM 168225, Washington, D.C.

Diagnosis.—Biceratopsinae with posterior margin of cephalon nearly straight. Genal angles broadly rounded; genal and intergenal spines absent. Preglabellar field present; sagittal length equal to or less than that of border. Ocular lobes prominent, close to glabella; posterior tips opposite S1, elevated above top of glabella. Opisththorax of at least 11 segments.

Distribution.—Lower Cambrian. USA (Arizona, Nevada), upper *Olenellus* Zone.

PEACHELLA Walcott, 1910, p. 342

Figure 4,2

Type species.—*Olenellus iddingsi* Walcott, 1884, p. 28. Holotype (Walcott, 1884, pl. 9, fig. 12), USNM 15407a, Washington, D.C.

Diagnosis.—Biceratopsinae with posterior margin of cephalon nearly straight. Glabella extended to or nearly to border furrow. Posterior tips of ocular lobes approximately opposite position of S1. Genal spines at posterolateral corners or slightly advanced, strongly inflated. Opisththorax of at least 10 segments.

Distribution.—Lower Cambrian. USA (California, Nevada), upper *Olenellus* Zone.

Subfamily BRISTOLIINAE new subfamily

Olenellinae Poulsen in Moore, 1959, p. O192, *partim*.

Olenellidae Bergström, 1973b, p. 312, *partim*; Ahlberg *et al.*, 1986, p. 40, *partim*.

Fremontiinae Repina, 1979, p. 22, *partim*.

Diagnosis.—Olenellidae with glabella usually strongly constricted at S1 or L2; transverse width of anterior part of L1 usually distinctly narrower than occipital ring; glabellar furrows generally well developed. Preglabellar field shorter than border or absent. Posterior tips of ocular lobes opposite or anterior to L1. Third thoracic segment with inner part of pleural region strongly expanded distally; pleural spine may be extended posterior to end of thorax. Opisththorax well developed. Pygidium not known.

Distribution.—Lower Cambrian. North America (Appalachian, Cordilleran, and Arctic regions), Greenland (Inglefield Land), ?United Kingdom (northwestern Scotland), Argentina (San Juan area), *Olenellus* Zone.

BRISTOLIA Harrington, 1956, p. 59

Figure 4,5

Type species.—*Mesonacis bristolensis* Resser, 1928, p. 7. Lectotype (Resser, 1928, pl. 2, figs. 5–6; Harrington, 1956, p. 59), USNM 78390, Washington, D.C.

Diagnosis.—Bristoliinae with cephalon subpentagonal to subquadrate in outline. Genal spine originating opposite or anterior to L2. Intergenal spine absent. Preglabellar field absent. Posterior tips of ocular lobes opposite or anterior to L1. Fifteenth thoracic segment with long axial spine. Opisthothorax of at least 17 segments.

Distribution.—Lower Cambrian. USA (California, Nevada), Greenland (Inglefield Land), *Olenellus* Zone.

ARCUOLENELLUS new genus

Figure 4,7

Type species.—*Olenellus arcuatus* Palmer in Palmer and Halley, 1979, p. 67–68. Holotype (Palmer and Halley, 1979, pl. 2, fig. 12), USNM 177200, Washington, D.C.

Diagnosis.—Bristoliinae with posterior margin of cephalon strongly and evenly curved back distally; genal spines short, at posterolateral corners, situated well behind level of occipital ring. Intergenal spine absent. Preglabellar field short. Width of interocular area about half width of glabella at L2. Posterior tips of ocular lobes opposite L1.

Distribution.—Lower Cambrian. U.S.A (California), upper *Olenellus* Zone; Argentina (San Juan area), *Olenellus* Zone.

BOLBOLENELLUS new genus

Figure 4,10

Type species.—*Olenellus euryparia* Palmer in Palmer and Halley, 1979, p. 69–70. Holotype (Palmer and Halley, 1979, pl. 2, fig. 18), USNM 177204, Washington, D.C.

Diagnosis.—Bristoliinae with posterior margin of cephalon nearly straight or deflected anterolaterally distal to intergenal spine or intergenal angle. Genal spine originates opposite or posterior to L1. Intergenal spine present on some species. L4 prominent, subglobular, may overlap border in dorsal view. Preglabellar field absent. Posterior tips of ocular lobes approximately opposite occipital furrow.

Distribution.—Lower Cambrian. USA (California, Nevada), Canada (Cordilleran region, Devon Island), ?northern Greenland, Mexico (Caborca), ?middle and upper *Olenellus* Zone.

NEPHROLENELLUS new genus

Figures 4,3,6

Type species.—*Olenellus multinodus* Palmer in Palmer and Halley, 1979, p. 72–73. Holotype (Palmer and Halley, 1979, pl. 4, fig. 4), USNM 177225, Washington, D.C.

Diagnosis.—Bristoliinae with posterior margin of cephalon directed slightly posterolaterally to intergenal

spine or intergenal swelling that is situated near slightly advanced genal spines. Preglabellar field short. Width of interocular area approximately half or more width of glabella at L2. Posterior tips of ocular lobes opposite L1. Third thoracic segment macropleural, with extremely long pleural spines; tips posterior to end of thorax. Prothorax of 13 segments; opisthothorax of at least 17 segments. Fifteenth segment lacks strong axial spine.

Distribution.—Lower Cambrian. USA (California, Nevada), Canada (southern Rocky Mountains), upper *Olenellus* Zone.

Subfamily GABRIELLINAE new subfamily

Diagnosis.—Olenellidae with posterior margin of cephalon curved forward. Intergenal angle variably developed, situated slightly distal to midlength of posterior margin. Genal spine originating opposite or anterior to S1. Glabella bullet-shaped. Ocular lobes close to glabella, tips opposite or posterior to occipital furrow. Thorax with at least 17 segments; width of thoracic axis greater than width of inner parts of pleural region; third thoracic segment not modified; fifteenth segment with long axial spine. Opisthothorax not clearly differentiated. Pygidium elongate, sides convergent posteriorly, end bluntly pointed.

Distribution.—Lower Cambrian. USA (Nevada), Canada (Cordilleran region), lower *Olenellus* Zone.

GABRIELLUS Fritz, 1992, p. 20

Figure 4,9

Type species.—*Gabriellus lanceatus* Fritz, 1992; OD. Holotype (Fritz, 1992, pl. 17, fig. 6), USNM 443792, Washington, D.C.

Diagnosis.—Characters same as for subfamily.

Distribution.—Lower Cambrian. USA (Nevada), Canada (Cordilleran region), lower *Olenellus* Zone.

Subfamily LAUDONIINAE new subfamily

Diagnosis.—Olenellidae with cephalon subquadrate to subhexagonal in outline. Genal spine strongly advanced, originating anterior to S1. Intergenal spine strongly developed in adult at posterolateral corner of cephalon. Transverse width of anterior part of L1 nearly equal to occipital ring. Thorax has third segment weakly macropleural; fifteenth segment lacks axial spine. Opisthothorax not clearly differentiated. Pygidium small, bilobate.

Distribution.—Lower Cambrian. USA (California, Nevada), Canada (southern Rocky Mountains), Mexico (Caborca area), ?United Kingdom (northwestern Scotland), lower and middle *Olenellus* Zone.

LAUDONIA Harrington, 1956, p. 60

Figure 4,4

Type species.—*Laudonia bispinata* Harrington, 1956, p. 60–61. Holotype (Harrington, 1956, pl. 15, fig. 4), KUMIP 9465T1, Lawrence, Kansas.

Diagnosis.—Laudoniinae with cephalon subquadrate to subpentagonal in outline. Genal spine originating opposite or anterior to L3. Procranial spines not developed in adult. Intergenal ridge distinct. Preglabellar field absent or shorter than border. Posterior tips of ocular lobes opposite or anterior to L1. Thorax of about 20 segments. External sculpture reticulate.

Distribution.—Lower Cambrian. Canada (southern Rocky Mountains), USA (Nevada), Mexico (Caborca), lower *Olenellus* Zone.

?OLENELLOIDES Peach, 1894, p. 668

Figure 4.8

Type species.—*Olenellus (Olenelloides) armatus* Peach, 1894, p. 669–670. Lectotype (Peach, 1894, pl. 32, fig. 4; McNamara, 1978, p. 638) GSE 472, Edinburgh.

Diagnosis.—?Laudoniinae with cephalon subhexagonal in outline; prominent procranial, genal, or intergenal spines at each angle of the hexagon. Intergenal spines close to glabella. L4 subglobular. Preglabellar field absent. Width of narrow interocular area about equal to width of equally narrow extraocular area opposite midlength of ocular lobe. Posterior tips of ocular lobes opposite L2. Thorax of nine segments; axis wider than inner part of pleural region exclusive of spines; third and sixth thoracic segments macropleural.

Distribution.—Lower Cambrian. United Kingdom (north-western Scotland), middle *Olenellus* Zone.

Subfamily WANNERIINAE Hupé, 1953

Olenellinae Suvorova in Chernysheva, 1960, p. 62, *partim*.
Holmiidae Bergström, 1973b, p. 285, *partim*.
Wanneriidae Ahlberg *et al.*, 1986, p. 40, *partim*.

Diagnosis.—*Olenellidae* with L4 enlarged. Posterior margin of cephalon straight or curved backward towards base of genal spine. Intergenal spine absent. Preglabellar field absent. Posterior tips of ocular lobes opposite or anterior to occipital furrow. Thorax of 17 segments, not divided into prothorax and opisththorax; third segment unmodified; fifteenth segment bearing long axial spine. Pygidium small, subquadrate, with prominent median notch. External sculpture reticulate; polygons may have central granule. On well-preserved specimens, boundaries of polygons marked by rows of perforations on underside of exoskeleton.

Distribution.—Lower Cambrian. North America (wide-spread, including Greenland), middle *Olenellus* Zone.

WANNERIA Walcott, 1910, p. 296

Figure 5

Type species.—*Olenellus (Holmia) walcottanus* Wanner, 1910, p. 267. Lectotype (Wanner, 1901, pl. 31, fig. 1; Resser and Howell, 1938, p. 227, pl. 10, fig. 9), USNM 56807e, Washington, D.C.

Diagnosis.—Characters same as for subfamily.

Distribution.—Lower Cambrian. North America (wide-spread, including Greenland), middle *Olenellus* Zone.

Family HOLMIIDAE Hupé, 1953

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

Holmiinae Hupé, 1953, p. 125, *partim*; Poulsen in Moore, 1959, p. O194, *partim*; Suvorova in Chernysheva, 1960, p. 62, *partim*.

Holmiidae Bergström, 1973b, p. 285, *partim*; Repina, 1979, p. 20, *partim*; Ahlberg *et al.*, 1986, p. 43.

Callaviinae Poulsen in Moore, 1959, p. O192, *partim*; Bergström, 1973b, p. 309, *partim*.

Callaviidae Ahlberg *et al.*, 1986, p. 40, *partim*.

Wanneriidae Ahlberg *et al.*, 1986, p. 40, *partim*.

Diagnosis.—*Olenelloidea* with width of interocular area more than half width of extraocular area. Third thoracic segment generally unmodified; prothorax and opisththorax not differentiated.

Distribution.—Lower Cambrian. Europe (Baltic region, *Schmidtiellus mickwitzii*, *Holmia inusitata*, and *Holmia kjerulfi* group zones; United Kingdom, *Callavia* Zone; Spain, *Marianiense* level); North Africa (Morocco, *Sectigena* Zone); North America (Cordilleran region, “*Nevadella*” Zone; Appalachian region, *Olenellus* Zone; Avalonian region, *Callavia* Zone); Russia (Siberian Platform, upper *Pagetiellus anabarus* Zone).

Subfamily HOLMIINAE Hupé, 1953

Holmiinae Poulsen in Moore, 1959, p. O194, *partim*;
Suvorova in Chernysheva, 1960, p. 62, *partim*; Repina, 1979, p. 20, *partim*.

Holmiidae Ahlberg *et al.*, 1986, p. 43, *partim*.

Elliptocephalinae Hupé, 1953, p. 124, *partim*; Poulsen in Moore, 1959, p. O194, *partim*.

Wanneriidae Ahlberg *et al.*, 1986, p. 40, *partim*.

Callaviinae Bergström, 1973b, p. 309, *partim*.

Diagnosis.—*Holmiidae* with glabella expanded forward. Cephalic border generally convex in cross-section. Inner part of pleural region of thorax narrower than axis.

Distribution.—Lower Cambrian. Europe (Baltic region, *Schmidtiellus mickwitzii*, *Holmia inusitata*, and *Holmia kjerulfi* group zones; United Kingdom, *Callavia* Zone; Spain, *Marianiense* level); North Africa (Morocco, *Sectigena* Zone); North America (Cordilleran region, “*Nevadella*” Zone; Appalachian region, *Olenellus* Zone; Avalonian region, *Callavia* Zone); Russia (Siberian Platform, upper *Pagetiellus anabarus* Zone).

HOLMIA Matthew, 1890, p. 160

Figure 6.1

Esmeraldina Resser and Howell, 1938, p. 228.

Type species.—*Paradoxides kjerulfi* Linnarsson, 1871, p. 790. Lectotype, designated herein (Linnarsson, 1871, pl. 16, fig. 1), SGU 5329a,b, Uppsala.

Diagnosis.—Holmiinae with intergenal spine generally well developed at or slightly proximal to midlength of posterior cephalic margin. Glabella expanded anteriorly. Posterior tips of ocular lobes opposite or posterior to L1. Thorax narrow, with 16 or 17 segments; pleural spines thornlike; each segment with axial spines. Pygidium small, subquadrate; posterior margin nearly straight transversely.

Distribution.—Lower Cambrian. Sweden, Norway, Poland, *Schmidtiellus mickwitzi* to *Holmia kjerulfi* group zones; USA (Nevada), lower "Nevadella" Zone; Russia (Siberian Platform), upper *Pagetiellus anabarus* Zone.

ANDALUSIANA Sdzuy, 1961, p. 246

Figure 6,3

Type species.—*Andalusiana cornuta* Sdzuy, 1961, p. 247. Holotype (Sdzuy, 1961, pl. 3, fig. 4), UMU L 3072, Münster.

Diagnosis.—Holmiinae with intergenal spines not apparent. Glabella expanded anteriorly; L4 with distinct lateral projections situated in front of ocular lobe and segregated by longitudinal furrow. Posterior tips of ocular lobes opposite L1. Thorax narrow, with pleural spines short but not constricted at base; each segment with axial nodes; number of segments not known.

Distribution.—Lower Cambrian. Spain (Guadalcanal), Marianiense level; United Kingdom (Comley), *Callavia* Zone; Morocco (Anti-Atlas), *Sectigena* Zone; ?Norway (Oslo Region), *Holmia kjerulfi* group Zone.

ELLIPTOCEPHALA Emmons, 1844, p. 21

Figure 6,7

Type species.—*Elliptocephala asaphoides* Emmons, 1844, p. 21. Lectotype, designated herein (Walcott, 1910, pl. 24, fig. 1), USNM 18350a, Washington, D.C.

Diagnosis.—Holmiinae with posterior margin of cephalon straight or slightly angled forward distal to intergenal swelling. Intergenal spine absent. Posterior tips of ocular lobes opposite or slightly anterior to occipital furrow. Sagittal length of preglabellar field equal to or slightly greater than that of anterior border. Thorax moderately wide, consisting of 18 segments, pleural regions of adults lacking macropleurae. Fifteenth through eighteenth segments with strong axial spines. Pygidium small, subquadrate, with single pair of short anterolateral spines. External surface with some reticulate areas.

Distribution.—Lower Cambrian. USA (New York), Canada (Quebec), *Olenellus* Zone.

HOLMIELLA Fritz, 1972, p. 25

Figures 6,4,6

Type species.—*Holmiella preancora* Fritz, 1972, p. 25. Holotype (Fritz, 1972, pl. 4, figs. 4–6), GSC 27241, Ottawa.

Diagnosis.—Holmiinae with outline of cephalon subpentagonal; genal spine prominent, originating opposite or anterior to S3; short intergenal spine or node located at or on axial side of intergenal angle. Glabella expanded anteriorly. Posterior tips of ocular lobes oppo-

site or posterior to L1. Pygidium large, wider than long, of at least 3 segments; anterior two segments extended into short border spines.

Distribution.—Lower Cambrian. USA (Nevada), Canada (Mackenzie Mountains), "Nevadella" Zone.

SCHMIDTIELLUS Moberg in Moberg and Segerberg, 1906, p. 35 (footnote)

Figure 6,2

Type species.—*Olenellus mickwitzi* Schmidt, 1888, p. 13. Type specimens not designated, original specimens missing. Diagnosis based on *S. mickwitzi torelli* Moberg, 1899; redescribed by Bergström, 1973, p. 296–301.

Diagnosis.—Holmiinae with posterior margin of cephalon nearly straight; intergenal spines not developed. Glabella with prominent axial spine on anterior margin of occipital ring and encroaching on occipital furrow. Posterior tips of ocular lobes opposite or posterior to L1. Thorax narrow; pleural spines short, not constricted at base. Pygidium small, subquadrate.

Distribution.—Lower Cambrian. Sweden (Scania), Estonia, *Schmidtiellus mickwitzi* Zone.

Subfamily CALLAVIINAE Poulsen in Moore, 1959

Callaviinae Poulsen in Moore, 1959, p. 192, *partim*;

Bergström, 1973b, p. 309, *partim*; Repina, 1979, p. 20.

Callaviidae Ahlberg *et al.*, 1986, p. 40, *partim*.

Holmiinae Hupé, 1953, p. 125, *partim*; Suvorova in Chernysheva, 1960, p. 62, *partim*.

Holmiidae Repina, 1979, p. 20, *partim*; Ahlberg *et al.*, 1986, p. 43, *partim*.

Neltneriinae Bergström, 1973, p. 309, *partim*.

Diagnosis.—Holmiidae with glabella subcylindrical in outline or slightly expanded anteriorly; L4 extended onto inner part of border. Preglabellar field absent. Border broad. Posterior tips of ocular lobes opposite or posterior to midlength of L1. Thorax broad, with 16 to 18 segments; not clearly differentiated into prothorax and opisthothorax. Pleural regions lacking macropleurae. Pleural spines elongate. Pygidium small, subquadrate.

Distribution.—Lower Cambrian. Europe (Baltic region, ?*Schmidtiellus mickwitzi*, *Holmia inusitata*, and *Holmia kjerulfi* zones; United Kingdom, *Callavia* Zone); North Africa (Morocco, *Sectigena* Zone); North America (Avalonian sector only, *Callavia* Zone).

CALLAVIA Matthew, 1897, p. 397

Figures 6,5,8

Type species.—*Olenellus (Mesonacis) broeggeri* Walcott, 1890a, p. 41; by subsequent designation, Walcott, 1910, p. 275. Lectotype (Walcott, 1890b, pl. 92, fig. 1; Hutchinson, 1962, p. 119), USNM 18331, Washington, D.C.

Diagnosis.—Callaviinae with intergenal spines well developed, adjacent to genal spines. Intergenal ridge usually present.

Distribution.—Lower Cambrian. United Kingdom (Comley), Canada (Avalon Peninsula), USA (Boston area), *Callavia* Zone.

KJERULFIA Kiaer, 1917, p. 71

Figures 6, 9, 10

Type species.—*Kjerulfia lata* Kiaer, 1917, p. 73. Lectotype (Kiaer, 1917, pl. 10, fig. 1; Nikolaisen and Henningsmoen, 1990, p. 63), PMO 61376, Oslo.

Diagnosis.—Callaviinae with posterior margin of cephalon nearly straight or deflected slightly forward distal to intergenal swellings, which are located closer to genal angle than to axial furrows.

Distribution.—Lower Cambrian. Norway (Oslo region), Denmark (borehole in Sealand), Poland (Holy Cross Mountains), Germany (Görlitz), *Holmia kjerulfi* group Zone; United Kingdom (Comley), *Callavia* Zone; Morocco (Anti-Atlas), *Sectigena* Zone.

Superfamily FALLOTASPIDOIDEA Hupé, 1953

[*nom. transl.* herein, *ex* Fallotaspidae Hupé, 1953, p. 124]

Olenellidae Poulsen in Moore, 1959, p. O191, *partim*.

Daguinaspididae Bergström, 1973b, p. 309, *partim*.

Olenelloidea Suvorova in Chernysheva, 1960, p. 62, *partim*;

Repina, 1979, p. 11, *partim*.

Olenellida Ahlberg *et al.*, 1986, p. 40, *partim*.

Diagnosis.—Olenellina with glabellar outline typically cylindrical or slightly conical in dorsal view. L3 simple, form similar to L2.

Distribution.—Lower Cambrian. North America (Cordilleran region and northern Greenland), Europe (United Kingdom, Comley area; Ukraine), northwestern Africa, northern Asia (Siberia).

Family FALLOTASPIDIDAE Hupé, 1953

[*nom. transl.* Repina, 1979, p. 19, *ex* Fallotaspidae Hupé, 1953, p. 124]

Fallotaspidae Poulsen in Moore, 1959, p. O194.

Holmiinae Suvorova in Chernysheva, 1960, p. 62, *partim*.

Daguinaspididae Bergström, 1973b, p. 309, *partim*; Ahlberg *et al.*, 1986, p. 40, *partim*.

Diagnosis.—Fallotaspidoidea with projection of anterior margin of ocular lobe more or less tangent to anterior end of L4 or continuous as parafrontal band in front of L4. Glabella slightly to moderately tapered forward. Length of L4 less than one-third length of glabella, exclusive of occipital ring. Interocular area ranging from significantly wider to slightly narrower than extraocular area.

Distribution.—Lower Cambrian. North America (Cordilleran region), "*Fallotaspis*" Zone; Europe (United Kingdom, Comley area), sub-*Callavia* Zone; Ukraine, zone unknown; Africa (Morocco, Anti-Atlas), *Fallotaspis tazemmourtensis*, *Choubertella*, *Daguinaspis*, and *Antatlasia hollardi* zones; Asia (Russia, Siberian Platform), *Fallotaspis* Zone.

Subfamily FALLOTASPIDINAE Hupé, 1953

Fallotaspidae Poulsen in Moore, 1959, p. O194; Bergström, 1973b, p. 309, *partim*; Ahlberg *et al.*, 1986, p. 40, *partim*.

Holmiinae Suvorova in Chernysheva, 1960, p. 62, *partim*.

Fallotaspidae Repina, 1979, p. 19, *partim*.

Diagnosis.—Fallotaspidae with genal spines present. Interocular area slightly wider to slightly narrower than extraocular area.

Distribution.—Lower Cambrian. North America (Cordilleran region), "*Fallotaspis*" Zone; Europe (United Kingdom, Comley area), sub-*Callavia* Zone; Africa (Morocco, Anti-Atlas), *Fallotaspis tazemmourtensis*, *Choubertella*, *Daguinaspis*, and *Antatlasia hollardi* zones; Asia (Russia, Siberian Platform), *Fallotaspis* Zone.

FALLOTASPIS Hupé, 1953, p. 125

Figure 7, 2

Type species.—*Fallotaspis typica* Hupé, 1953, p. 131. Holotype (Hupé, 1953, pl. 2, fig. 2), MNN G.26, Paris.

Diagnosis.—Fallotaspidae with posterior margin of cephalon straight or gently curved forward distally. Intergenal spine not developed, but intergenal ridge intersecting posterior border closer to glabella than to genal spine. Glabella slightly tapered forward. Ocular lobes directed posterolaterally from junction with L4. Width of interocular area half or less width of extraocular area. Thorax of 21 segments; 17 in prothorax, 4 in opisthothorax. Opisthothorax not strongly differentiated. Pleural regions, excluding spines, about same width as axis. Third thoracic segment macropleural. Pygidium small, subquadrate.

Distribution.—Lower Cambrian. Morocco (Anti-Atlas), *Fallotaspis tazemmourtensis*, *Choubertella*, *Daguinaspis*, and *Antatlasia hollardi* zones; USA (White-Inyo Mountains), "*Fallotaspis*" Zone; Russia (Siberian Platform), *Fallotaspis* Zone; ?United Kingdom (Comley area), sub-*Callavia* Zone.

EOFALLOTASPIS Sdzuy, 1978, p. 89

Figures 7, 1, 5

Type species.—*Eofallotaspis tioutensis* Sdzuy, 1978, p. 90. Holotype (Sdzuy, 1978, pl. 1, figs. 1–2), SMF 28567, Frankfurt.

Diagnosis.—Fallotaspidae with posterior margin of cephalon nearly straight; small intergenal spine on posterior border approximately midway between axial furrow and genal spine. Glabella slightly tapered forward. Ocular lobes directed posterolaterally from junction with L4. Width of interocular area equal to or greater than width of extraocular area opposite midlength of ocular lobe. Occipital ring simple. Thorax narrow; axis wider than pleural regions; third segment macropleural. External surface strongly pitted.

Distribution.—Lower Cambrian. Morocco (Anti-Atlas), *Eofallotaspis* Zone.

LENALLINA Repina, 1990a, p. 40

Figure 7,7

Type species.—*Lenallina lata* Repina, 1990a, p. 40–41. Holotype (Repina, 1990a, pl. 3, figs. 1–2), TsGM 902/1, Novosibirsk.

Diagnosis.—Fallotaspidae with posterior margin of cephalon directed anterolaterally distal to intergenal angle; intergenal angle closer to axial furrow than to genal spine. Glabella slightly tapered forward. Interocular area narrow; width less than half width of extraocular area. Posterior tips of ocular lobes about opposite occipital furrow. External surface reticulate.

Distribution.—Lower Cambrian. Russia (southeastern Siberian Platform), *Pagetiellus anabarus* Zone.

PARAFALLOTASPIS Fritz, 1972, p. 27

Figure 7,6

Type species.—*Parafallotaspis grata* Fritz, 1972, p. 28. Holotype (Fritz, 1972, pl. 1, figs. 1–2), GSC 27202, Ottawa.

Diagnosis.—Fallotaspidae with posterior margin of cephalon nearly straight or slightly backswept. Glabella moderately tapered forward. Plectrum strongly developed. Ocular lobes directed posterolaterally from junction with L4. Width of interocular area slightly more than half width of extraocular area opposite midlength of ocular lobe. Posterior tips of ocular lobes opposite occipital ring.

Distribution.—Lower Cambrian. Canada (Mackenzie Mountains), "*Fallotaspis*" Zone.

PELMANASPIS Repina, 1990a, p. 41–42

Figure 7,4

Type species.—*Pelmanaspis jurii* Repina, 1990a, p. 42–43. Holotype (Repina, 1990a, pl. 4, figs. 1–2), TsGM 902/15, Novosibirsk.

Diagnosis.—Fallotaspidae with posterior margin of cephalon nearly straight. Glabella gently tapered forward. Occipital ring with prominent axial spine. Sagittal length of preglabellar field greater than length of border. Width of interocular area slightly more than half width of extraocular area. Ocular lobes directed posterolaterally from junction with L4. Posterior tips of ocular lobes about opposite occipital furrow. External surface coarsely pitted, grading to reticulate.

Distribution.—Lower Cambrian. Russia (southeastern Siberian Platform), *Pagetiellus anabarus* Zone.

PROFALLOTASPIS Repina in Khomentovskii and Repina, 1965, p. 110

Figure 7,3

Type species.—*Profallotaspis jakutensis* Repina in Khomentovskii and Repina, 1965, p. 110. Holotype (Khomentovskii and Repina, 1965, pl. 2, fig. 4), TsGM 265/1, Novosibirsk.

Diagnosis.—Fallotaspidae with posterior margin of cephalon straight or slightly backswept. Ocular lobe di-

rected only slightly posterolaterally at junction with L4. Glabella tapered forward, but area opposite L3 and L4 merging laterally with ocular lobes. Interocular area wider than extraocular area opposite midlength of ocular lobe. Posterior tips of ocular lobes opposite L1. Cephalic border concave in sagittal profile. Lateral and posterior border furrows not connected across base of genal spine. External surface coarsely pitted, grading to reticulate.

Distribution.—Lower Cambrian. Russia (southeastern Siberian Platform), *Profallotaspis jakutensis* Zone.

Subfamily DAGUINASPIDINAE Hupé, 1953

Daguinaspidae Poulsen in Moore, 1959, p. O197; Bergström, 1973b, p. 309, *partim*; Repine, 1979, p. 19; Ahlberg *et al.*, 1986, p. 40, *partim*.

Holmiinae Suvorova in Chernysheva, 1960, p. 62, *partim*.

Diagnosis.—Fallotaspidae with interocular area significantly wider than extraocular area. Genal spines absent.

Distribution.—Lower Cambrian. Northwestern Africa, Europe (Ukraine).

DAGUINASPIS Hupé and Abadie, 1950, p. 2112–2113

Figure 8,2

Type species.—*Daguinaspis ambroggii* Hupé and Abadie, 1950, p. 2113. Holotype (Hupé, 1953, pl. 5, fig. 1), MNN G.200, Paris.

Diagnosis.—Daguinaspidae with anterior margin of cephalon bluntly pointed. Width of interocular area less than one-half basal glabellar width; width of extraocular area about equal to width of ocular lobe. Sagittal length of frontal area greater than that of occipital ring. Intergenal ridge well developed. Thorax of 16 (17?) segments; pleura about equal in width to axial lobe, unmodified. Pygidium small, subquadrate.

Hupé (1953) created 3 subgenera for minor morphological variations that seem to have limited merit. These are *Eodaguinaspis* (type species, *D. (E.) abadieii* Hupé, 1953); *Daguinaspis* (type species, *D. (D.) ambroggii* Hupé, 1953); and *Epidaguinaspis* (type species, *D. (E.) angusta* Hupé, 1953).

Distribution.—Lower Cambrian. Morocco (Anti-Atlas, *Daguinaspis* Zone).

CHOUBERTELLA Hupé, 1952, p. 143

Figure 8,1

Type species.—*Choubertella spinosa* Hupé, 1953, p. 144. Holotype (Hupé, 1953, pl. 4, fig. 8), MNN G.230, Paris.

Diagnosis.—Daguinaspidae with anterior margin of cephalon gently curved. Glabella moderately to strongly tapered forward. Width of interocular area opposite tip of ocular lobe nearly equal to basal glabellar width; width of extraocular area about equal to width of ocular lobe. Sagittal length of frontal area greater than that of occipital ring. Intergenal ridge well developed.

Distribution.—Lower Cambrian. Morocco (Anti-Atlas), *Choubertella* Zone.

WOLYNASPIS Chernysheva in Kir'ianov and Chernysheva, 1967, p. 123

Figure 8,3

Type species.—*Wolynaspis unica* Chernysheva in Kir'ianov and Chernysheva, 1967, p. 124. Holotype (Kir'ianov and Chernysheva, 1967, fig. 2), GMU 1731/8, Kiev.

Diagnosis.—Daguinaspidinae with anterior margin of cephalon gently curved. Glabella gently tapered forward. Extraocular area steeply downslipping. Width of interocular area more than half basal glabellar width. Frontal area short; sagittal length about equal to that of occipital ring.

Distribution.—Lower Cambrian. Ukraine, zone unknown.

Family ARCHAEASPIDIDAE Repina, 1979

Archaeaspidinae Ahlberg *et al.*, 1986, p. 40.

Diagnosis.—Fallotaspidoidea with anterior part of L4 anterior to line tangent to anterolateral margin of ocular lobe. Parafrontal band usually present, continuing to or nearly to anterior end of L4. Width of interocular area approximately same as extraocular area. Genal spines usually present.

Distribution.—Lower Cambrian. North America (Canadian Cordilleran region and northern Greenland, "Nevadella" Zone); northern Asia (Russia, Siberian Platform, *Pagetiellus anabarus* Zone; southern Siberian fold belt and Sayan-Altay fold region, *Sajanaspis* Zone; northern Mongolia, *Fallotaspis-Buliaspis* Zone).

ARCHAEASPIS Repina in Khomentovskii and Repina, 1965, p. 116

Figure 9,1

Type species.—*Archaeaspis hupei* Repina in Khomentovskii and Repina, 1965, p. 117. Holotype (Khomentovskii and Repina, 1965, pl. 4, fig.1), TsGM 265/146, Novosibirsk.

Diagnosis.—Archaeaspididae with glabella slightly tapered forward, L4 slightly conical. Interocular area wider than extraocular area opposite midlength of ocular lobe. Posterior tips of ocular lobes approximately opposite occipital furrow. Genal spines short, broad-based. Border broad, convex, well defined; sagittal length greater than length of preglabellar field. Exoskeletal surface strongly reticulate.

Distribution.—Lower Cambrian. Russia (southeastern Siberian Platform), lower *Pagetiellus anabarus* Zone.

BRADYFALLOTASPIS Fritz, 1972, p. 19

Figure 9,2

Type species.—*Bradyfallotaspis fusa* Fritz, 1972, p. 20. Holotype (Fritz, 1972, pl. 3, figs. 1–3), GSC 27226, Ottawa.

Diagnosis.—Archaeaspididae with glabellar outline subcylindrical; anterior end of glabella strongly rounded. Sagittal length of preglabellar field about equal to that of border. Width of interocular area less than width of extraocular area opposite midlength of ocular lobe. Ocular lobes raised above level of glabella.

Distribution.—Lower Cambrian. Canada (northern Rocky Mountains), "Nevadella" Zone.

FALLOTASPIDELLA Repina, 1961, p. 40

Figure 9,4

Type species.—*Fallotaspidella musatovi* Repina, 1961, p. 42. Holotype (Repina, 1961, pl. 1, fig. 1a), TsGM 3556/1001, Novosibirsk.

Diagnosis.—Archaeaspididae with glabella slightly tapered forward; anterior end bluntly rounded. Preglabellar field short, crossed by plectrum. Posterior tips of ocular lobes opposite L1. Width of interocular area about half or less width of extraocular area opposite midlength of ocular lobe. S1 and S2 usually continuous across glabella.

Distribution.—Lower Cambrian. Russia (southern Siberian fold belt and Sayan-Altay fold region), *Sajanaspis* Zone; northern Mongolia, *Fallotaspis-Buliaspis* Zone.

GENUS A Fritz, 1993, in press

Figures 9,3,7

Type species.—*Genus A species A* Fritz, 1993, in press. Holotype (Fritz, 1993, in press), GSC 102363, Ottawa.

Diagnosis.—Archaeaspididae with cephalon strongly arched transversely; anterior and lateral borders about equal in breadth to sagittal length of occipital ring. Intergenal swelling barely apparent; situated nearer to glabella than to genal spine; marked by slight anterior deflection of distal part of posterior margin. Intergenal ridge weak. Glabella slightly constricted at L2; L3 slightly expanded distally. Preglabellar field absent. Width of interocular area less than that of extraocular area. Posterior tips of ocular lobes opposite L1. External sculpture finely reticulate.

Distribution.—Lower Cambrian. Canada (southern Cordillera), "Nevadella" Zone.

SELINDELLA Repina, 1979, p. 27

Figure 9,5

Type species.—*Selindella gigantea* Repina, 1979, p. 28. Holotype (Repina, 1979, pl. 1, fig. 1) TsGM 560/1, Novosibirsk.

Diagnosis.—Archaeaspididae with glabella slightly tapered forward, sides slightly concave; anterior end strongly rounded. Posterior tips of ocular lobes about opposite midlength of L1. Width of interocular area about equal to width of extraocular area. Sagittal length of border about equal to that of preglabellar field.

Distribution.—Lower Cambrian. Russia (southeastern Siberian Platform, lower *Pagetiellus anabarus* Zone; northern Siberian Platform, *Pseudojudomia* Zone).

Family JUDOMIIDAE Repina, 1979

[*nom. transl.*, herein, *ex*] Judomiinae Repina, 1979, p. 20]

Callaviinae Poulsen in Moore, 1959, p. O192, *partim*.
Holmiinae Suvorova in Chernysheva, 1960, p. 62, *partim*.
Nevadiinae Bergström, 1973b, p. 309, *partim*.

Holmiidae Bergström, 1973b, p. 285, *partim*.
Judomiinae Repina, 1979, p. 20; Ahlberg *et al.*, 1986, p. 40.

Diagnosis.—Fallotaspidoidea with posterior margin of cephalon straight or curved backward distally. Glabella typically parallel-sided; glabellar furrows weakly to moderately developed. L4 elongate. Ocular lobe connected only to posterior part of L4. Interocular area very narrow or absent; width equal to or less than width of ocular lobe. Inner margin of ocular lobe typically undifferentiated or only weakly differentiated from interocular area. Posterior tips of ocular lobes posterior to occipital furrow. Intergenital spines not apparent.

Distribution.—Lower Cambrian. Northern Asia (Russia, Siberian Platform), *Judomia* and *Bergeroniellus micmaccaformis-Erbiella* zones.

JUDOMIA Lermontova, 1951, p. 48

Figure 10,7

Type species.—*Judomia dzevanovskii* Lermontova, 1951, p. 48. Lectotype (Lermontova, 1951, pl. 5, fig. 2), CNIGR 53/5156, Leningrad.

Diagnosis.—Judomiidae with glabella barely touching border or with preglabellar field present. Border well defined with sagittal length greater than that of preglabellar field (when present) and about equal to or slightly greater than sagittal length of occipital ring. Posterior tips of ocular lobes opposite occipital ring. Thorax with 15 to 17 thoracic segments; pleural furrows weak or absent. Opisthothorax not developed. Pleural spines long; transverse length of thoracic pleurae more than twice width of axis. Pygidium elongate, with posterior median notch; last two thoracic segments may be fused with pygidium in axial region only.

Distribution.—Lower Cambrian. Russia (southern Siberian Platform, *Judomia* and *Bergeroniellus micmaccaformis-Erbiella* zones; Kharaulakh region, *Judomia* Zone).

JUDOMIELLA Lazarenko, 1962, p. 48

Figure 10,8

Type species.—*Judomiella heba* Lazarenko, 1962, p. 49. Holotype (Lazarenko, 1962, pl. 3, fig. 6), CNIGR 8270-138, 8270-139, Leningrad.

Diagnosis.—Judomiidae with cephalon strongly arched transversely. Glabella reaching nearly to anterior margin. Border poorly differentiated. Ocular lobes adjacent to glabella. Interocular area poorly differentiated from ocular lobe. Posterior tips of ocular lobes reaching to posterior margin of cephalon.

Distribution.—Lower Cambrian. Russia (northern Siberian Platform, *Protolenus borealis* Zone; southeastern Siberian Platform, *Bergeroniellus micmaccaformis-Erbiella* Zone).

PARANEVADELLA new genus

Figure 10,4

Type species.—*Paedeumias? subgroenlandicus* Repina in Khomentovskii and Repina, 1965, p. 121–122. Holotype

(Khomentovskii and Repina, 1965, pl. 3, fig. 8), TsGM 265/174, Novosibirsk.

Diagnosis.—Judomiidae with glabella weakly tapered forward to nearly parallel-sided. Preglabellar field present. Posterior tips of ocular lobes opposite occipital ring. Interocular area distinctly developed.

Distribution.—Lower Cambrian. USA (California), Canada (Mackenzie Mountains), “*Nevadella*” Zone; Russia (Siberian Platform), upper *Pagetiellus anabarus* Zone.

SINSKIA Suvorova, 1960, p. 18

Figure 10,5

Type species.—*Sinskia optabilis* Suvorova, 1960, p. 19–21. Holotype (Suvorova, 1960, pl. 1, fig. 1), PIN 496/121, Moscow.

Diagnosis.—Judomiidae with L4 slightly expanded in front of ocular lobes. Border narrow, its sagittal length less than sagittal length of occipital ring. Sagittal length of preglabellar field approximately equal to that of border. Posterior tip of ocular lobe opposite posterior part of occipital ring.

Distribution.—Lower Cambrian. Russia (Siberian Platform, *Bergeroniellus micmaccaformis-Erbiella* Zone).

Family NELTNERIIDAE Hupé, 1953

[*nom. transl.* herein, *ex* Neltneriinae Hupé, 1953]

Holmiinae Poulsen in Moore, 1959, p. O194, *partim*;
Suvorova in Chernysheva, 1960, p. 62, *partim*; Repina, 1979, p. 20, *partim*; Ahlberg *et al.*, 1986, p. 40, *partim*.
Neltneriinae Poulsen in Moore, 1959, p. O196; Bergström, 1973b, p. 309, *partim*; Repina, 1979, p. 20; Ahlberg *et al.*, 1986, p. 40.

Diagnosis.—Fallotaspidoidea with posterior margin of cephalon deflected slightly forward distally. Glabella parallel-sided, bluntly rounded anteriorly. L4 elongate. Ocular lobe connected only to posterior part of L4. Ocular lobes close to glabella; interocular area poorly differentiated. Thorax has 17 segments.

Distribution.—Lower Cambrian. North Africa (Morocco), *Antatlasia gutta-pluviae* Zone.

NELTNERIA Hupé, 1953, p. 133

Figure 11,1

Type species.—*Wanneria Jacqueti* Neltner and Poctey, 1949, p. 74–75. Holotype (Neltner and Poctey, 1949, pl. 6, fig. 5), SGM Tr711, Rabat.

Diagnosis.—Neltneriidae with preglabellar field absent. Interocular area poorly defined, width less than half that of extraocular area. Posterior tips of ocular lobes opposite L1. Thorax with 17 segments. Pleural spines short; width of pleural regions about same as width of axis; eleventh segment macropleural; twelfth to seventeenth segments decreasing in width rapidly and progressively backward. Pygidium small, subquadrate, possibly of 2 or 3 segments.

Distribution.—Lower Cambrian, Morocco (Anti-Atlas), *Antatlasia gutta-pluviae* Zone.

BONDONELLA Hupé, 1953, p. 135

Figure 11,2

Type species.—*Bondonella typica* Hupé, 1953, p. 136–137. Holotype (Neltner and Poctey, 1949, pl. 6, fig. 1), MNN R50865, Paris.

Diagnosis.—Neltneriidae with preglabellar field present, its sagittal length about equal to length of border. Interocular area poorly defined, width more than half width of extraocular area. Posterior tips of ocular lobes opposite occipital furrow. Thorax with 18 segments; pleural regions of each segment narrower than axis; no macropleural segments.

Distribution.—Lower Cambrian. Morocco (Anti-Atlas), *Antatlasia gutta-pluviae* Zone.

Family NEVADIIDAE Hupé, 1953

[*nom. transl.* Repina, 1979, p. 19, *ex* Nevadiinae Hupé, 1953, p. 124]

Nevadiinae Poulsen in Moore, 1959, p. O196; Suvorova in Chernysheva, 1960, p. 62; Bergström, 1973b, p. 309, *partim*.

Nevadiidae Repina, 1979, p. 19, *partim*; Ahlberg *et al.*, 1986, p. 40, *partim*.

Diagnosis.—Fallotaspidoidea with glabella weakly to strongly tapered forward in dorsal view. L4 elongate. Ocular lobe connected only to posterior part of L4. Interocular area narrow. Posterior tips of ocular lobes opposite or anterior to occipital furrow. Width of interocular area variable. Thorax of 15 to 27 segments, without development of macropleurae.

Distribution.—Lower Cambrian. North America (Cordilleran region and northwestern Greenland), “*Nevadella*” Zone; northern Asia (Russia, Siberian Platform), upper *Pagetiellus anabarus* and *Pseudojudomia* zones.

NEVADIA Walcott, 1910, p. 256

Figure 10,1

Type species.—*Nevadia weeksi* Walcott, 1910, p. 257. Lectotype (Walcott, 1910, pl. 23, fig. 2), USNM 56792b, Washington, D.C.

Diagnosis.—Nevadiidae with width of interocular area less than one-fourth width of extraocular area. Preglabellar field present. Thorax of 27 segments. Pleural spines long. Transverse length of pleurae at least twice width of axis. Transition to opisthothorax between segments 15 and 18. Pygidium small, subquadrate.

Distribution.—Lower Cambrian. USA (White-Inyo region, northeastern Washington), Canada (northern Rocky Mountains), “*Nevadella*” Zone; Russia (northern Siberian Platform), *Nevadella* Zone.

BUENELLUS Blaker, 1988, p. 34

Figure 9,6

Type species.—*Buenellus higginsii* Blaker, 1988, p. 36. Holotype (Blaker, 1988, fig. 3B), MGUH 18.287, Copenhagen.

Diagnosis.—Nevadiidae with glabella slightly tapered forward. Ocular lobes small, posterior tips about opposite

S1 or anterior part of L1. Width of interocular area equal to or greater than that of extraocular area. Thorax of 17 or 18 segments, maintaining width or widening slightly backward to eighth segment, then tapering posteriorly; posterior segment may be fused with anterior part of simple pygidium. Pleural spines short; pleural regions only slightly wider than axis.

Distribution.—Lower Cambrian. Greenland (Peary Land), “*Nevadella*” Zone; Russia (Novaya Zemlya), zone unknown.

GENUS B Fritz, 1993, in press

Figure 10,6

Type species.—*Genus B species A* Fritz, 1993, in press. Holotype (Fritz, 1993, in press), GSC 102330, Ottawa.

Diagnosis.—Nevadiidae with glabella moderately tapered forward; glabellar furrows weakly developed. Posterior tips of ocular lobes opposite L1. Genal spines absent or indicated only by slight angularity of margin opposite L1.

Distribution.—Lower Cambrian. USA (White-Inyo and western Death Valley regions), Canada (southern Rocky Mountains), ?upper “*Fallotaspis*” Zone or ?lower “*Nevadella*” Zone.

NEVADELLA Raw 1936, p. 250

Figure 10,2

Type species.—*Callavia eucharis* Walcott, 1913, p. 315. Holotype (Walcott, 1913, pl. 53, fig. 1), USNM 60079, Washington, D.C.

Diagnosis.—Nevadiidae with glabella distinctly tapered forward, sides slightly concave so that width is narrowest opposite L2 or S2. Preglabellar field short (sag.) or absent. Basal glabellar width about equal to width of extraocular area opposite midlength of ocular lobe. Posterior tips of ocular lobes opposite L1. Width of interocular area more than one-fourth width of extraocular area opposite midlength of ocular lobe. Thorax of 17 to 23 segments. Pleural spines long, falcate. Opisthothorax not clearly differentiated. Pygidium small, subquadrate.

Distribution.—Lower Cambrian. USA (California, Nevada), Canada (Cordilleran region), upper “*Nevadella*” Zone.

PSEUDOJUDOMIA Egorova in Goryanskii *et al.*, 1964, p. 22

Figure 10,3

Type species.—*Pseudojudomia egregia* Egorova in Goryanskii *et al.*, 1964, p. 23. Holotype (Goryanskii *et al.*, 1964, pl. 5, fig. 1a,1b), CNIGR 8363/15, Leningrad.

Diagnosis.—Nevadiidae with border furrows weakly developed. Cephalon strongly convex transversely; posterior margin strongly curved backward. Glabella slightly tapered forward. Basal glabellar width about equal to width of extraocular area. Lateral parts of poorly differentiated border nearly vertical. Ocular lobes poorly differentiated from interocular area; posterior tips about opposite occipital furrow.

Distribution.—Lower Cambrian. Russia (northern Siberian Platform), *Pseudojudomia* Zone.

SUPERFAMILY UNASSIGNED

POLETAEVELLA Dalmatov and Repina, 1971, p. 125

Figure 8, 4

Type species.—*Poletaevella baljutica* Dalmatov and Repina, 1971, p. 125. Holotype (Dalmatov and Repina, 1971, figs. 2b–d, 3), BGU 0213/11, Ulan-Ude, Russia.

Diagnosis.—Olenellinid(?) with posterior margin of cephalon nearly straight. Glabella parallel-sided, bluntly rounded anteriorly; occipital ring unusually short. Palpebral lobes short, prominent, located about midway between axial and lateral border furrows, and connected to posterior part of L4 by narrow ocular ridge; posterior tips of ocular lobes opposite L2. Preglabellar field longer (sag.) than anterior border. Genal spines well developed; intergenal spines not indicated.

The structure of the ocular lobes is unlike that of any other olenellinid trilobite. Assignment of this form even to the *Olenellina* is questionable.

Distribution.—Lower Cambrian. Russia (eastern Sayan region), zone unknown.

POSTFALLOTASPIS Orlowski, 1985, p. 234

Type species.—*Postfallotaspis spinatus* Orlowski, 1985, p. 234–235. Holotype (Orlowski, 1985, pl. 3, figs. 5a–d), IGUW 1.496, Warsaw, Poland.

The type and only specimen of this genus is too incomplete and poorly illustrated for generic or higher level taxonomic evaluation.

Distribution.—Lower Cambrian. Poland (Holy Cross Mountains), *Holmia* Zone.

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Note from A. R. P., 3/93: Because of difficulty of communication with Russia my coauthor has not had an opportunity to approve of changes to the classification brought about by some further evaluation of olenellid morphologies. These involve reduction in the rank of the Daguinaspididae, transfer of *Buenellus* from the Archaeaspididae to the Nevadiidae, transfer of *Paranevadella* from the Nevadiidae to the Judomiidae, and elimination of a superfamily Nevadioidea, which accommodated the Nevadiidae, Judomiidae, and Neltneriidae in our original submittal.

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