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SYSTEMATIC DESCRIPTIONS OF THE CLASS TRILOBITA

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[Diagnoses of ordinal and higher taxa by R. A. FORTEY and H. B. WHITTINGTON; authorship of other diagnoses indicated within.]

Class TRILOBITA Walch, 1771

[*nom. correct. ex* Trilobiten WALCH, 1771, p. 120] [This name, as "Trilobiten," was published by WALCH (1771, p. 120) in his volume III of KNORR and WALCH (1768-1774). WALCH's work was rejected for nomenclatorial purposes by the International Commission on Zoological Nomenclature (Opinion 529, 1958). However, the Commission's remit extends only to the family-group level (Article 1b(4), *International Code of Zoological Nomenclature*, 1985), hence the name, emended to "Trilobita," remains available. The designation of the genus *Dalmanites* BARRANDE as type (HENNINGSMOEN & MOORE in MOORE, 1959, p. 172) is invalid.]

Extinct marine arthropods, body divided by furrows longitudinally into median (axial) and lateral (pleural) regions, transversely into cephalon of fused segments, thorax of articulated segments, and pygidium of few to many fused segments. Length of mature individuals ranges from a little over 1 mm to about 700 mm.

Dorsal exoskeleton and periphery of venter (doublure) calcified (but see comments on Naraoiidae); calcified plate (hypostome) anterior to mouth and below anterior axial region. Anterior wing of hypostome extending dorsally to a fossula in the axial furrow. Facial suture characteristic, absent in Olenellina, but may be secondarily lost or modified. Rostral plate or median suture present, or cheeks conjoined. Cephalon with one pair of eyes (which may be lost), each eye lobe connected to axial region by raised ridge; eye lenses of crystalline calcite. Slightly oblique-transverse pleural furrows at posterior of cephalon, on each thoracic segment, and on pygidial segments. Growth of exoskeleton proceeded by molting from calcified protaspis about 1 mm long to adult, and by sequential release of segments into thorax. Protaspides of Olenellina and Agnostina not known. Limbs (where known) include one pair of antennae, followed posteriorly by series of generally similar biramous limbs, of which three (possibly four in one species) are

cephalic. *Lower Cambrian (Atdabanian)-Upper Permian.*

Order AGNOSTIDA Salter, 1864

[*nom. correct.* SHERGOLD, LAURIE, & SUN, 1990, p. 32, *pro* Agnostini SALTER, 1864a, p. 2] [=Miomera JAEKEL, 1909, p. 394; Agnostida KOBAYASHI, 1935, p. 81; see discussion in ROBISON & CAMPBELL, 1974, p. 281]

Diminutive, isopygous, 2 or 3 fulcrate thoracic segments. Cephalic shield with deeply parabolic outline and maximum width (tr.) usually anterior to genal angle; border convex; glabella commonly fusiform, widest at base (except in Condylropygidae). Hypostome natant; rostral plate lacking or uncalcified. Outline of pygidium closely matching that of cephalon. *Lower Cambrian-Upper Ordovician.*

Suborder AGNOSTINA Salter, 1864

[*nom. correct.* SHERGOLD, LAURIE, & SUN, 1990, p. 32, *pro* Agnostini SALTER, 1864a, p. 2]

No eye or facial suture; 2 thoracic segments; cephalothoracic aperture present; pygidium generally with wide axis, margin commonly bearing posterolateral spine. Cuticle thin. Calcified protaspis not known. *Lower Cambrian-Upper Ordovician.*

INTRODUCTION TO THE SUBORDER AGNOSTINA

JOHN H. SHERGOLD and JOHN R. LAURIE

The historical background to the classification of this suborder has recently been discussed in detail (SHERGOLD, LAURIE, & SUN, 1990, p. 1-3). The classification presented here is as developed in that paper and essentially follows ideas on relationships that have

short (sag.) or absent (Fig. 30.1). Thorax nonfulcrate. Pygidium narrow (tr.), with few segments. Calcified protaspis unknown; earliest meraspis with segmented interocular area. *Lower Cambrian*.

INTRODUCTION TO SUBORDER OLENELLINA

A. R. PALMER and L. N. REPINA

Olenellina are a morphologically varied and highly diverse group of generally micropygous trilobites that share a primary absence of facial sutures, the presence of a well-developed ocular lobe at all developmental stages, and an ontogeny in which the first mineralized stages are already early meraspids (PALMER, 1957). They are restricted to and characteristic of rocks of later Early Cambrian age and constitute a major suborder within the order Redlichiida (MOORE, 1959). More than 50 genera or subgenera and their associated higher taxa are recognizable (PALMER & REPINA, 1993). These taxa form the principal basis for biostratigraphic subdivisions (Fig. 254) of the later Lower Cambrian rocks of Laurentia (North America exclusive of the eastern seaboard from Newfoundland to Florida and including Spitsbergen and northwestern Scotland) and are major indices for the later Lower Cambrian biostratigraphy of Baltica (northern Europe exclusive of the British Isles), Avalonia (England, Wales, eastern Newfoundland, Nova Scotia, eastern New England, USA), Siberia, and the Moroccan sector of Gondwana (including Spain).

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. The principal phylogenetic trend within the Olenellina involves the relationship between the ocular lobe and the frontal (anterior) lobe (LA) of the glabella (REPINA, 1990a). In all of the earliest Olenellina, which include forms from Siberia, Laurentia, and the Moroccan sector of Gondwana, the

glabella has parallel sides or tapers forward, LA is short, and the ocular lobe is attached along the entire margin of LA (Fallotaspidoidea, Daguinaspidinae). In later genera, LA first becomes elongate, so that the ocular lobes connect only to its posterior part (Judomiidae, Nevadiidae), and then generally expands laterally, and the glabella as a whole expands anteriorly from the level of S1 (Olenellidae, Holmiidae). LA in these genera is also commonly inflated. Accompanying this modification, the distal parts of L3 extend laterally and posterolaterally and encroach on L2, often isolating the S2 furrows (Fig. 255), and L3 takes on a broad M-shape.

This phylogenetic trend underlies the proposed classification of the superfamilies. Within the Fallotaspidoidea, all Fallotaspidoidea, the earliest family of the Olenellina, have the ocular lobe attached along the entire margin of LA and an unmodified L3, and the anterior end of LA 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 (Archaeaspididae, Judomiidae, Neltneriidae, Nevadiidae), the anterior end of LA projects forward of the junction with the anterior margin of the ocular lobe, but L3 remains unmodified. All Olenelloidea, which includes the youngest Olenellina, have the ocular lobe attached to the posterior part of LA 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 the two families in the Olenelloidea is the relationship between the extraocular area and the interocular area. The Holmiidae 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 have a wide extraocular area that is more than twice the width of the interocular area. In the Fallotaspidoidea, the relationship between the ocular lobe and LA, the shape of the glabella (parallel sided versus tapered),

Mummaspis FRITZ, 1992, p. 17 [**Wanneria occidens* WALCOTT, 1913b, p. 314; OD; holotype (WALCOTT, 1913b, pl. 53, fig. 2), 60080, USNM, Washington, D.C.]. Parts of external surface reticulate. Posterior margin of cephalon nearly straight; intergenal swelling slightly distal to midlength of posterior margin. Preglabellar field absent or length (sag.) 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 macropleurale. *Lower Cambrian*: Canada (southern Rocky Mountains), lower *Olenellus* Zone.—FIG. 256, 1a, b. **M. occidens* (WALCOTT); a, complete individual, topotype, USNM 443745, X4 (Fritz, 1992, pl. 9, fig. 2); b, cephalon and partial thorax, topotype, USNM 433750, X1.7 (Fritz, 1992, pl. 10, fig. 2).

Subfamily BICERATOPSINAE Pack & Gayle, 1971

[Biceratopsinae PACK & GAYLE, 1971, p. 895] [=Olenellidae BERGSTROM, 1973b, p. 312, *partim*; AHLBERG, BERGSTROM, & JOHANSSON, 1986, p. 40, *partim*; Biceratopsinae REPINA, 1979, p. 22; PALMER & REPINA, 1993, p. 23]

Glabella narrowest at midlength; glabellar furrows very poorly developed; width (tr.) of L1 less than width (tr.) of occipital ring; ocular lobe close to glabella, its posterior tip opposite or anterior to L1. Genal spine absent or opposite midlength of ocular lobe; intergenal spine absent; intergenal angle may be developed. Thorax divided into prothorax and opisthothorax; third segment strongly expanded distally; pleural spine extremely long, with tips posterior to body; fifteenth segment with long axial spine. *Lower Cambrian*.

Biceratops PACK & GAYLE, 1971, p. 895 [**B. nevadensis*; OD; holotype (PACK & GAYLE, 1971, pl. 102, fig. 2-3), 168225, USNM, Washington, D.C.]. Posterior margin of cephalon nearly straight; genal angle broadly rounded; genal and intergenal spines absent. Length (sag.) of prelabellar field equal to or less than that of anterior border; ocular lobe prominent, close to glabella, with posterior tip opposite S1 and elevated above top of glabella. Opisthothorax of at least 11 segments. *Lower Cambrian*: USA (Arizona, Nevada), upper *Olenellus* Zone.—FIG. 257, 1. **B. nevadensis*, Nevada; complete individual, holotype, USNM 168225, X3 (Pack & Gayle, 1971, pl. 102, fig. 2).

Peachella WALCOTT, 1910, p. 342 [**Olenellus iddingsi* WALCOTT, 1884b, p. 28; OD; holotype (WALCOTT, 1884b, pl. 9, fig. 12), 15407a, USNM, Washington, D.C.]. Posterior margin of cephalon nearly straight. Glabella extended to or nearly to border furrow; posterior tip of ocular lobe approximately

opposite S1; genal spine at posterolateral corner or slightly advanced, strongly inflated. Opisthothorax of at least 10 segments. *Lower Cambrian*: USA (California, Nevada), upper *Olenellus* Zone.—FIG. 257, 2. **P. iddingsi* (WALCOTT), California; nearly complete individual, LACMIP 1162X, X2 (Palmer & Repina, 1993, fig. 4.2). 2

Subfamily BRISTOLIINAE Palmer & Repina, 1993

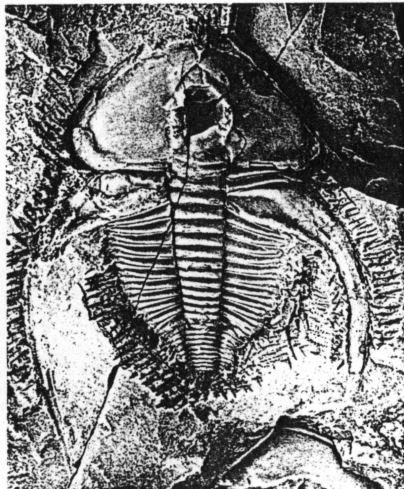
[Bristoliinae PALMER & REPINA, 1993, p. 23] [=Olenellinae POULSEN in MOORE, 1959, p. 162, *partim*; Olenellidae BERGSTROM, 1973b, p. 312, *partim*; AHLBERG, BERGSTROM, & JOHANSSON, 1986, p. 40, *partim*; Fremontiinae REPINA, 1979, p. 22, *partim*]

Glabella usually strongly constricted at S1 or L2; width (tr.) of anterior part of L1 usually distinctly narrower than occipital ring; glabellar furrows generally well developed. Preglabellar field shorter (sag.) than anterior border or absent. Posterior tip of ocular lobe 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. Opisthothorax well developed. Pygidium not known. *Lower Cambrian*.

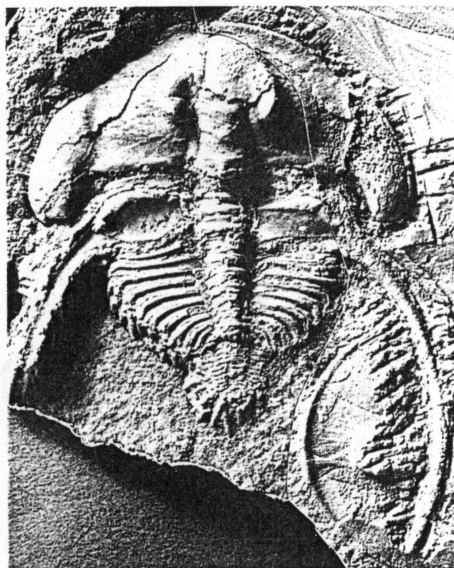
Bristolia HARRINGTON, 1956, p. 59 [**Mesonacis bristolensis* RESSER, 1928, p. 7; OD; lectotype (RESSER, 1928, pl. 2, fig. 5-6; SD HARRINGTON, 1956, p. 59), 78390, USNM, Washington, D.C.]. Cephalon subpentagonal to subquadrate in outline; genal spine originating opposite or anterior to L2; intergenal spine absent. Preglabellar field absent; posterior tip of ocular lobe opposite or anterior to L1. Fifteenth thoracic segment with long axial spine; opisthothorax of at least 17 segments. *Lower Cambrian*: USA (California, Nevada), Greenland (Inglefield Land), *Olenellus* Zone.—FIG. 258, 1. **B. bristolensis*, California; nearly complete individual, UCR 10/7, X1 (Palmer & Repina, 1993, fig. 4.5).

Arcuolenellus PALMER & REPINA, 1993, p. 24 [**Olenellus arcuatus* PALMER in PALMER & HALLEY, 1979, p. 67; OD; holotype (PALMER & HALLEY, 1979, pl. 2, fig. 12), 177200, USNM, Washington, D.C.]. Posterior margin of cephalon strongly and evenly curved back distally; genal spine short, situated at posterolateral corner well behind level of occipital ring; intergenal spine absent. Preglabellar field short (sag.); width of interocular area about half width of glabella at L2; posterior tip of ocular lobe opposite L1. *Lower Cambrian*: USA (California), upper *Olenellus* Zone; Argentina (San Juan area), *Olenellus* Zone.—FIG. 258, 2. **A. arcuatus* (PALMER), California; cephalon, holotype, USNM 177200, X6 (Palmer & Halley, 1979, pl. 2, fig. 12).

Bolbolenellus PALMER & REPINA, 1993, p. 24 [**Olenellus euryparia* PALMER in PALMER & HALLEY,



1 Biceratops



2 Peachella

FIG. 257. Olenellidae (p. 409)

posterior margin. Genal spine originating opposite or anterior to S1. Glabella bullet shaped. Ocular lobe close to glabella, its tip opposite or posterior to occipital furrow. Thorax with at least 17 segments; each segment with width (tr.) 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. *Lower Cambrian*.

Gabriellus FRITZ, 1992, p. 20 [**G. lanceatus*; OD; holotype (FRITZ, 1992, pl. 17, fig. 6), 443792, USNM, Washington, D.C.] Characters as for subfamily. *Lower Cambrian*: USA (Nevada), Canada (Cordilleran region), lower *Olenellus* Zone.—FIG. 259.3. *Gabriellus* sp.; complete individual, Canada, GSC 104195, X1.7 (Palmer & Repina, 1993, fig. 4.9).

Subfamily LAUDONIINAE Palmer & Repina, 1993

[Laudoniinae PALMER & REPINA, 1993, p. 24]

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. Width (tr.) of anterior part of L1 nearly equal to that of occipital ring. Thorax with third segment weakly macropleural; 15th segment lacking axial spine. Opisthothorax not clearly differentiated. Pygidium small, bilobate. *Lower Cambrian*.

Laudonia HARRINGTON, 1956, p. 60 [**L. bispinata*; OD; holotype (HARRINGTON, 1956, pl. 15, fig. 4), 9465T1, KUMIP, Lawrence]. Cephalon subquadrate to subpentagonal in outline; genal spine originating opposite or anterior to L3; procranial spine not developed in adult; intergenal ridge distinct. Preglabellar field absent or shorter (sag.) than border; posterior tip of ocular lobe opposite or anterior to L1. Thorax of about 20 segments. External surface reticulate. *Lower Cambrian*: Canada (southern Rocky Mountains), USA (Nevada), Mexico (Caborca), lower *Olenellus* Zone.—FIG. 259.2. *L. amputata* FRITZ; cephalon and partial thorax, Canada, USNM 443754, X2 (Fritz, 1992, pl. 11, fig. 4).

?**Olenelloides** PEACH, 1894, p. 668 [**Olenellus (Olenelloides) armatus* PEACH, 1894, p. 669; OD; lectotype (PEACH, 1894, pl. 32, fig. 4; SD McNAMARA, 1978, p. 637), 472, GSE, Edinburgh]. Cephalon subhexagonal in outline; prominent procranial, genal, or intergenal spine at each angle of the hexagon; intergenal spine close to glabella; LA subglobular. Preglabellar field absent; width (tr.) of narrow interocular area about equal to width of equally narrow extraocular area opposite midlength of ocular lobe; posterior tip of ocular lobe opposite L2. Thorax with 9 segments; axis wider than inner part of pleural region exclusive of spines; third and sixth thoracic segments macropleural. *Lower Cambrian*: northwestern Scotland, middle *Olenellus* Zone.—FIG. 259.1a,b. **O. armatus* (PEACH); a.

LACMIP
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(not
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