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THE FAMILY OLENIDAE (TRILOBITA, ARTHROPODA): A SYNOPSIS OF ITS TAXONOMIC COMPOSITION, STRATIGRAPHIC AND PALEOGEOGRAPHIC DISTRIBUTION

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Abstract. This paper provides a list of all named species in the family Olenidae, along with their geographic and stratigraphic records. It also discusses each of the valid genera in the family and describes the composition of the entire group and its subfamilies in terms of species and generic richness across different periods and geographical areas. The family encompasses 64 genera and 394 species, primarily concentrated in the subfamilies Oleninae and Pelturinae (65.63% of the genera and 58.12% of the species). The Olenidae was first documented during the Guzhangian in Baltica, and subsequently, its range expanded globally to Eastern Gondwana (Australia), South China, and Siberia. The Furongian saw a peak in species diversity (61.88% of the total) and widespread distribution. During the Tremadocian, the number of species declined, yet the geographic range persisted, and this decrease continued for the rest of the Ordovician. Although the family is cosmopolitan, Baltica and Avalonia host almost half of the records (46.71%). Challenges in olenid systematics include species lacking proper illustrations and/or lost type materials, poorly diagnosed genera, and potential polyphyletic larger families. The study emphasizes the importance of precise species and genus delimitation. The dataset presented serves as an initial step in achieving a clearer phylogenetic classification of the family Olenidae.

Key words. Olenidae. Descriptive statistics. Stratigraphic distribution. Paleogeographic distribution. Cambrian. Ordovician.

Resumen. LA FAMILIA OLENIDAE (TRILOBITA, ARTHROPODA): SINOPSIS DE SU COMPOSICIÓN TAXONÓMICA, DISTRIBUCIÓN ESTRATIGRÁFICA Y PALEOGEOGRÁFICA. Este trabajo presenta una lista de las especies nombradas pertenecientes a la familia Olenidae, detallando su registro estratigráfico y geográfico. Se discuten brevemente los géneros reconocidos como válidos y se describe la composición de la familia y de cada subfamilia en términos de riqueza específica y genérica, considerando su distribución estratigráfica y paleogeográfica. Olenidae abarca 64 géneros y 394 especies, en su mayoría pertenecientes a Oleninae y Pelturinae (65,63% de los géneros y 58,12% de las especies). El grupo se registra por primera vez en el Guzhangiano de Báltica y se expande rápidamente hacia el este de Gondwana (Australia), China Sur y Siberia. En el Furongiano se reconoce su pico de diversidad (61,88% del total) y su mayor expansión paleogeográfica. En el Tremadociano el número de especies disminuye, manteniendo el rango geográfico. Dicha disminución continúa durante el resto del Ordovícico. Aunque la familia presenta una distribución cosmopolita, casi la mitad de los registros se concentran en Báltica y Avalonia (46,71%). Entre las dificultades que presenta la sistemática de los olénidos se incluyen la falta de ilustraciones adecuadas de varias especies, así como la pérdida de materiales tipo y la diagnosis vaga de algunos géneros y subfamilias, especialmente las de mayor número de especies que probablemente sean polifiléticas. Este estudio enfatiza la importancia de una precisa delimitación de las especies y los géneros. Asimismo, los datos provistos sirven de punto de partida para alcanzar una clasificación filogenética para la familia.

Palabras clave. Olenidae. Estadística descriptiva. Distribución estratigráfica. Distribución paleogeográfica. Cámbrico. Ordovícico.

Olenidae is a well-represented and cosmopolitan family known from the Miaolingian (middle Cambrian) to the Ordovician. Its wide geographical distribution and usefulness in solving stratigraphic problems have led to an intense study of the group. The family was erected by Burmeister (1843) to accommodate the genera *Paradoxides* Brongniart, 1822 and *Olenus* Dalman, 1827. Since then, many new species were described belonging to this group. At the present time, in Olenidae were included about 70 genera and more than 400 species distributed in seven subfamilies (Jell & Adrain, 2003; Adrain, 2013), with a stratigraphic record ranging from the Guzhangian (Miaolingian) to the end of the Ordovician. However, its greatest abundance is recorded towards the Cambro/Ordovician boundary (Adrain, 2013).

Olenids were recorded in all the paleocontinents and many terranes. They were very common along the Acado-Baltic province in Baltica (Westergård, 1922; Henningsmoen,

1957), Avalonia (Great Britain, Eastern Canada) and western margin of Gondwana (Argentina, Bolivia, and Colombia) (Harrington & Leanza, 1943, 1957; Přibyl & Vaněk, 1980). They were also known from Laurentia, South and North China, Siberia, and other parts of Eastern Gondwana (*e.g.*, Australia, India, and Iran).

Since their abundance in black shale facies, olenids have traditionally been considered exclusive of disoxic environments (*e.g.*, Henningsmoen, 1957; Fortey, 1975, 1989, 1999, 2000) and have even been proposed a chemoautotrophic symbiotic relationship for them (Fortey, 2000). However, they were capable of living in a great variety of environments; they were found in oxygenated waters (Balseiro *et al.*, 2011) and could even tolerate brackish waters (Mángano *et al.*, 2021; Serra *et al.*, 2021).

The intense study of this family in early works led to propose relationship among different genera based on their stratigraphic record (*e.g.*, Westergård, 1922; Kaufmann, 1935; Henningsmoen, 1957). More recently, phylogenetic relations within the family were explored at different taxonomic levels (Karim, 2008; Monti & Confalonieri, 2013, 2019; Hopkins, 2019; Monti *et al.*, 2022).

Despite the profound knowledge of this group, many aspects remain uncertain. The monophyly of several groups has never been tested, and the geographic affinities of each group are inconclusive. To achieve a complete comprehension of the group, it is necessary first to conduct an updated global synthesis of the family, along with quantifying the geographical distribution of each subgroup within olenids. The main goal of this paper is to present a list of all the named olenids in the scientific literature, and a discussion regarding the genera included within the group. With this information, the composition of the entire group and its subfamilies were described in terms of species and generic richness across different periods and paleogeographical areas.

MATERIALS AND METHODS

A survey of all named olenid species in the scientific literature has been conducted using various paleontological and biological databases (*e.g.*, The Paleobiology Database) and supplemented with available literature. The resulting list of valid olenid species includes considerations of proposed synonyms and detailed stratigraphic and geographic records for each species. Supplementary Information 1 (SI1) summarizes this information. The Appendix provides a discussion of each olenid genus, highlighting key details and pertinent issues. Information for each genus covers encompassed species, subgenera, and subspecies (if applicable), distribution, and key literature references, which are listed in Supplementary Information 2 (SI2).

To quantify the family, stratigraphic and geographic ranges were determined based on the reported records. Each species was assigned to one or more biozones according to presence data. Then, biozonation schemes, specific to taxa and different regions worldwide, were integrated into the global chronostratigraphic chart, assigning each species to one or more stages. Regarding the geographic ranges, all the recorded localities for each species were taken into consideration. Terranes were assigned to each species based on documented records, considering the Cambro–Ordovician basins. Twenty-five areas were defined: Scandinavia, the Holy Cross Mountains, Erratic Boulders, Digermul, Uralian margin, Avalonia, South America (Central Andean Basin, Famatina, Colombia and Venezuela), Oaxaca, Armorica, Precordillera, South China (Yangtze, Cathaysia and Jiangnan), Kazakhstania (Tianshan belt and central Kazakhstan), North China (Nangrim and Qaidam-Qilian), Australia, Tarim, India, Higgan, Iran, Northern Xinjiang Region, Western Laurentia, Eastern Laurentia, Spitsbergen, Central Laurentia, Altai-Sayan, Verkhoyansk margin, and Gorny Altai. These areas were grouped into six major regions, considering paleogeographic reconstructions for the studied period: Baltica, Siberia, Western Gondwana, Eastern Gondwana, Eastern Peri-Gondwana Terranes, and Laurentia (*e.g.*, Cocks & Torsvik, 2002, 2021 and references therein; Torsvik & Cocks, 2016).

The subfamilies were described by examining species and generic richness across various periods and geographical areas. Within olenids, seven subfamilies were considered, according to Adrain (2013) and excluding hypermecaspids in consistence with a recent phylogenetic analysis (Monti *et al.*, 2022): Oleninae, Pelturinae, Leptoplastinae, Plicatolininae, Triarthrinae, Balnibarbiinae, and Hunanoleninae.

All the statistics, tables, and graphics were made with R (R Core team, 2022) and ggplot2 package (Wickham, 2016).

RESULTS

The survey revealed that the family Olenidae comprises 64 genera and 394 species (Tab. 1; SI1). Most olenid species belong to Oleninae and Pelturinae, accounting for 58.12% of the genera and 65.63% of the species. The remaining subfamilies comprise only a few genera (two to seven), each with a variable number of species (Fig. 1; Tab. 1). Specifically, Triarthrinae includes six genera with 70 species and Leptoplastinae seven genera with 55 species. The other subfamilies are smaller, comprising only a few species (ranging from 24 to five) (Fig. 1; Tab. 1).

The oldest recorded species assigned to Olenidae dates to the Miaolingian (Guzhangian) (Fig. 2; Tab. 2). In the early Guzhangian, the Oleninae species *Ullaspis conifrons* Westergård, 1948 was recorded from the *Lejopyge laevigata* zone of Baltica (Appendix; SI1). Towards the end of this stage, additional Oleninae species were documented in Eastern Gondwana (Australia), South China, and Baltica, along with two species of Leptoplastinae from South China and Siberia. The number of described olenid species increased during the Paibian, reaching its peak at the end of the Furongian, with 35.89% of the species occurring in Stage 10. The Furongian accounted for 61.88% of the total olenid species (Fig. 2; Tab. 2). The Tremadocian stands as the second most species-rich stage, with 24.1%. However, towards the end of the Lower Ordovician, the number of species experienced a sharp decline, persisting throughout the rest of the Ordovician (Fig. 2; Tab. 2). The stratigraphic record of 20 species is unknown (SI1).

As mentioned earlier, the family displays a cosmopolitan distribution. However, almost half of the species (46.71%) are concentrated in Baltica and Avalonia. Two other areas present a great number of species: South America (excluding Precordillera) and South China (7.59% each; Fig. 3; Tab. 3). The paleogeographic distribution of the species changes over time and varies among the different subfamilies. During the Furongian, more than half of the species were accumulated in Baltica and Avalonia, while Siberia and South China also exhibited a substantial number of species. However, in the Lower Ordovician, the species count decreased in Baltica and Avalonia, while it increased in South America.

The subfamilies within Olenidae have varying temporal and spatial distributions. Oleninae and Pelturinae exhibit a cosmopolitan distribution with a temporal range limited between the Miaolingian and the Early Ordovician (Fig. 4.1–2; SI3). Triarthrinae is also found all over the world, but with the widest temporal distribution within the family (Furongian to Upper Ordovician) (Fig. 4.3; SI3). Plicatolininae has a cosmopolitan distribution during the Furongian, and in the Tremadocian they present only a few records (Fig. 4.4; SI3). The remaining three groups have more restricted records. Leptoplastinae is known from the Furongian of Baltica and Avalonia (Fig. 4.5; SI3), Hunanoleninae is found in the Furongian of South China (Fig. 4.6; SI3) and Balnibarbiinae is found in the Floian and Dapingian of Laurentia (Fig. 4.7; SI3).

Olenids were traditionally considered restricted to black shale facies; however, almost all the genera reviewed here were found in a variety of lithologies and environments beyond black shales. While all the genera in which lithology was reported were discovered in slope and/or outer platform environments, at least fourteen were also found in inner platform or shallow water environments, with only a few occurring in shallow water settings with restricted circulation. The more diverse and widespread genera, such as *Angelina* Salter in Murchison, 1859, *Parabolina* Salter, 1849, *Parabolinella* Brøgger, 1882, *Jujuyaspis* Kobayashi, 1936, *Bienvillia* Clark, 1924, *Porterfieldia* Cooper, 1953, and *Triarthrus*, Green, 1832, were present across all environments. So, at a generic level, it is hard to tell if an environmental restriction exists (see SI4).

Subfamily Oleninae

The subfamily Oleninae stands out as one of the larger groups within olenids. The survey in this study reveals a total of 22 genera and 135 species belonging to this subfamily (Fig. 1; Tab. 1; SI1; Appendix). Notably, three genera — *Olenus*, *Parabolina*, and *Parabolinella* — exhibit the highest diversity, accounting for 65.19% of the species within the subfamily. They are followed by *Parabolinites* Henningsmoen, 1957, *Angelina*, and *Chekiangaspis* Lu in Qian, 1961, each with ten, seven, and five species, respectively. The remaining genera encompass one to three species (Fig. 5.1).

Throughout the Furongian and Early Ordovician, Oleninae species exhibit a widespread distribution—twenty from the twenty-five areas defined here—across all the paleocontinents, including Gondwana and Peri-Gondwana terranes, Laurentia, Baltica, South and North China, and Siberia (Fig. 6.1; SI3). The group was most abundant in the Acado-Baltic province, which accumulates more than half of the records, with similar proportion of species recorded in both Baltica and Western Gondwana (26.77% and 27.71%, respectively; Fig. 6.1; SI3). Its presence is also notable in the Eastern Peri-Gondwana terranes, especially in South and North China and Kazakhstania (18.8%) and in Laurentia (15.97%) (Fig. 6.1; SI3).

Oleninae was considered an evolutionary branch within olenids that would have originated in *Olenus* (Westergård, 1922; Kaufmann, 1935; Harrington & Leanza, 1952; Henningsmoen, 1957). The diagnosis in the treatise (Moore, 1959, p. O262) was rather vague, defining Oleninae based on a combination of characters rather than clear synapomorphies. Oleninids were described as possessing features commonly associated with the entire family. Henningsmoen (1957) highlighted the presence of genal

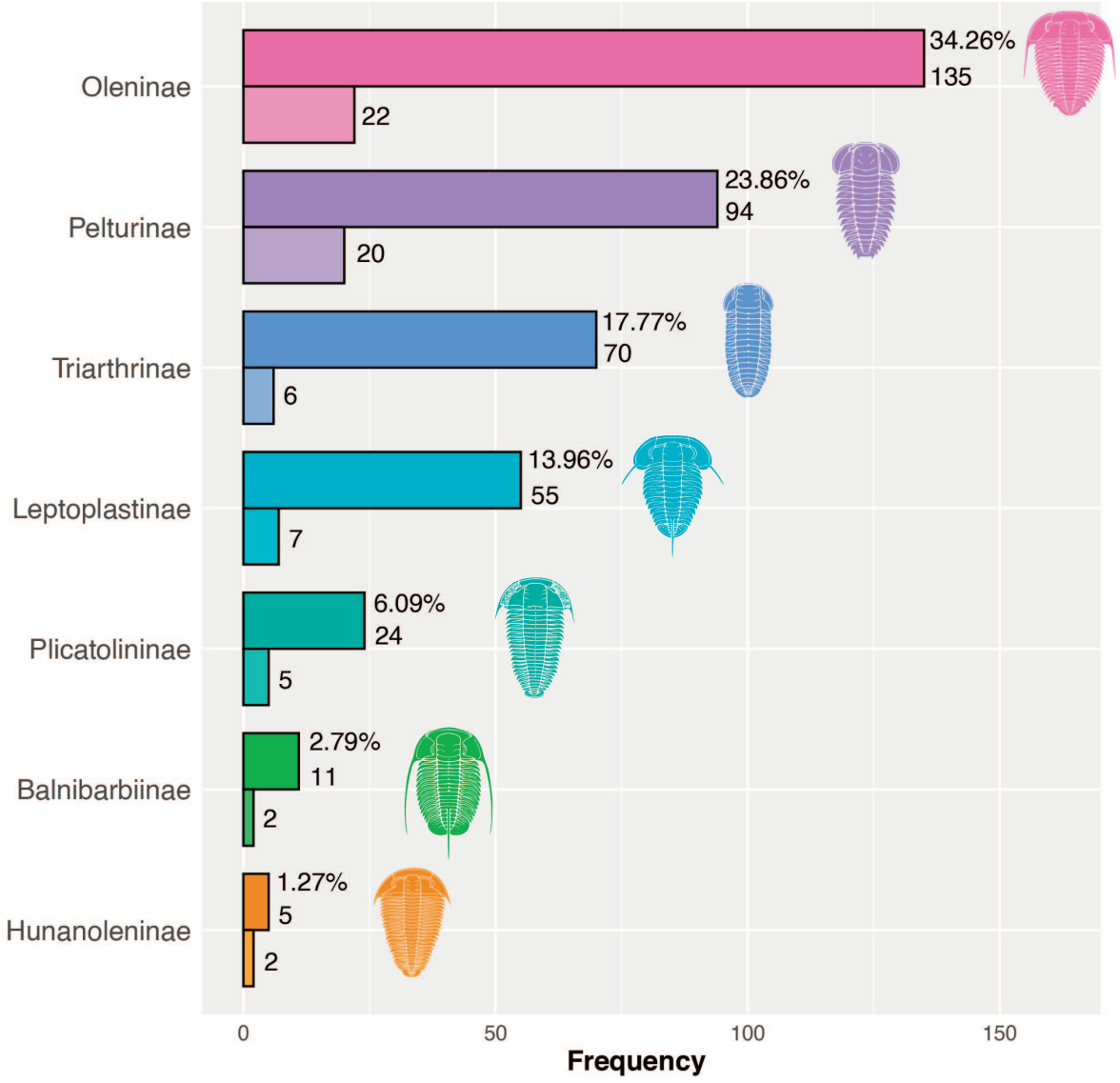

Figure 1. Frequency and percentage of species and genera assigned to each subfamily. See also Table 1.

TABLE 1 – Number of species and genera within each subfamily.

Subfamilies	Species			Genera		
	Frequency	Percentage (%)	Cumulative percentage (%)	Frequency	Percentage (%)	Cumulative percentage (%)
Oleninae	135	34.26	34.26	22	34.38	34.38
Pelturinae	94	23.86	58.12	20	31.25	65.63
Triarthrinae	70	17.77	75.89	6	9.38	75.01
Leptoplastinae	55	13.96	89.85	7	10.94	85.95
Plicatolininae	24	6.09	95.94	5	7.81	93.76
Balnibarbiinae	11	2.79	98.73	2	3.12	96.88
Hunanoleninae	5	1.27	100	2	3.12	100
Total	394	100		64	100	

spines extending along the lateral margin of the librigenae as an exclusive characteristic of this group. Compounding the challenge of defining olenines is the disagreement regarding the included species in this group. Many species originally described as Oleninae are now included in other (new) subfamilies (*e.g.*, Triarthrinae, Plicatolininae). We lack a modern comprehensive review of this group and it is likely to be polyphyletic, as indicated by the results of the phylogenetic analysis conducted on olenids, where the subfamily does not appear monophyletic (Monti & Confalonieri, 2019).

Subfamily Pelturinae

The subfamily Pelturinae represents a significant group within olenids; it includes several iconic species. The group encompasses 20 genera and 94 species (Fig. 1; Tab. 1; SI1; Appendix). In contrast to the Oleninae, the distribution of species among genera within this subfamily is more balanced. *Leptoplastides* Raw, 1908 and *Protopeltura* Brøgger, 1882 stand out with fourteen and thirteen species each, while the species count gradually diminishes across other genera in a relatively uniform manner (Fig. 5.2).

Despite their cosmopolitan presence, their diversity (in terms of species number) is notably prominent in Baltica, which accounts for half of the recorded occurrences (50.66%). The Acado-Baltic province contributes to a significant 73.99% of the species within the group (Fig. 6.2; SI3). However, comparing with olenines, they are less abundant in the other regions, such as Eastern Peri-Gondwana terranes and Laurentia (Fig. 6.2).

Pelturinae was considered a separate evolutionary branch from other olenids, which would have originated in *Protopeltura* (Westergård, 1922; Kaufmann, 1935; Harrington & Leanza, 1952; Henningsmoen, 1957). However, we lack a formal phylogenetic analysis including all the species of pelturines to prove the monophyly of this group. Currently, there is a phylogenetic analysis that tested the relationships between some genera within this group (Karim, 2008) and another in which several pelturines were tested alongside other olenid species (Monti & Confalonieri, 2019). This latter analysis, while recovering typical pelturine species as monophyletic, suggested that the group, as currently defined, may not be monophyletic since it includes the genus *Angelina* within the pelturines. Pelturinae were traditionally grouped by the morphology of the librigenae and a well-developed glabella related to other structures of the cranidium (*e.g.*, Henningsmoen, 1957; Nikolaisen & Henningsmoen, 1985; Żylińska, 2001).

Subfamily Triarthrinae

The Triarthrinae is a well-known group within olenids, largely due to the remarkable preservation of the genus *Triarthrus*. Despite its fame, this subfamily comprises a relatively small number of genera. According to the survey, it encompasses only six genera and 70 species (Fig. 1; Tab. 1; SI1; Appendix). Notably, the diversity of this group is primarily driven by three genera: *Bienvillia*, *Porterfieldia*, and *Triarthrus*. Together, these genera contribute significantly to the diversity of the group, accounting for a total of 63 species, which is equivalent to 90% of the total species (Fig. 5.3).

Their temporal distribution is the widest of the family. They are known from the Furongian and they were the only group that reach the end of the Ordovician with their last record in the early Hirnantian. They were found in all paleocontinents, except for Siberia, being more common in Laurentia, where 30.94% of the species are found. They also were diverse in Western Gondwana (especially in South America and Precordillera) and in the Eastern Peri-Gondwanan terranes (especially in South China and Kazakhstania), with 29.75% and 27.37% of the recorded species, respectively (Fig. 4.3; SI3).

Traditionally, Triarthrinae has been considered an evolutionary branch along with the Oleninae and Plicatolininae, believed to have originated from *Parabolina* (Westergård, 1922; Kaufmann, 1935; Harrington & Leanza, 1952; Henningsmoen, 1957). However, the status of the

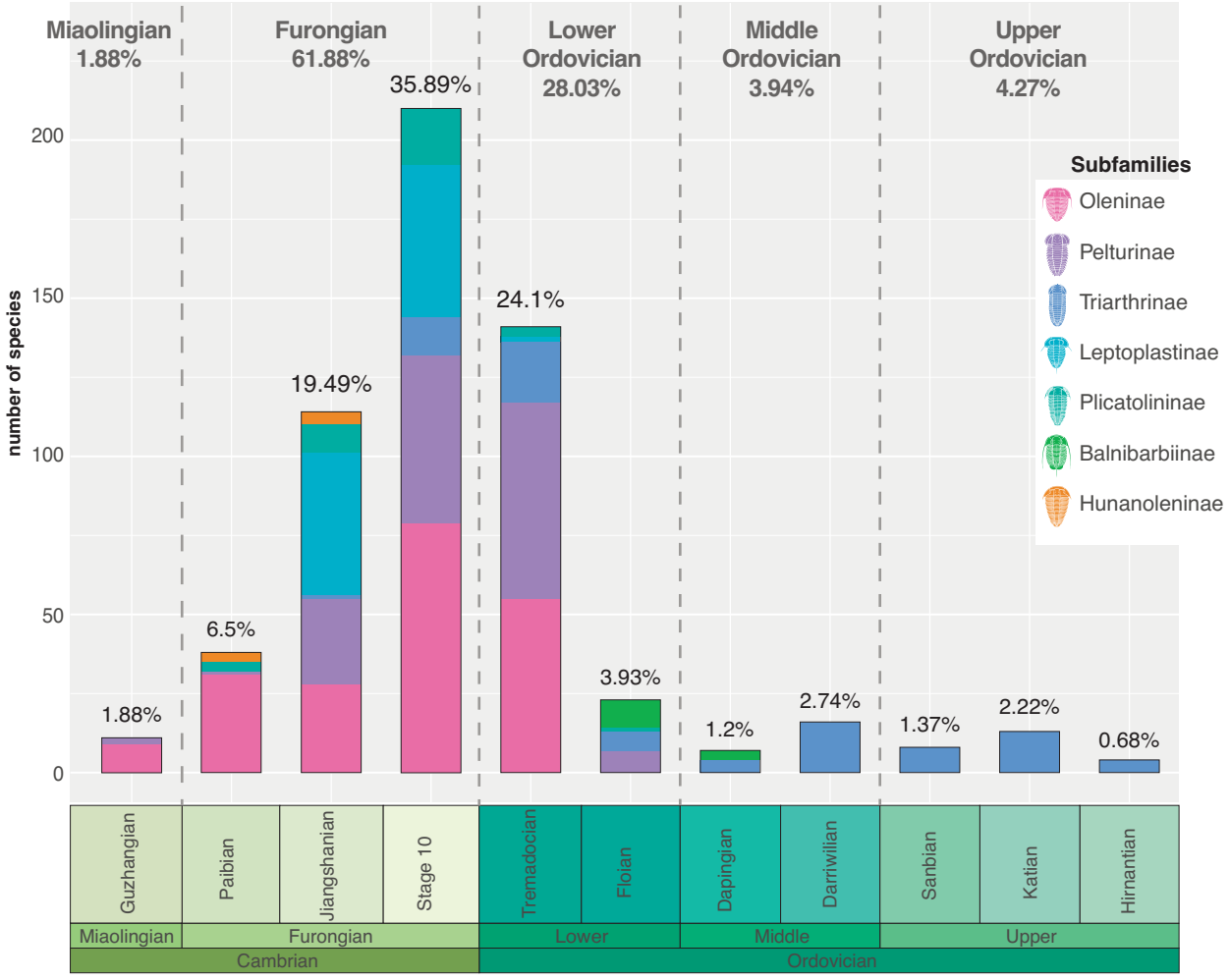

Figure 2. Frequency and percentage of records of olenids species across stages during the Cambro–Ordovician. Colors on each bar show the proportion of the subfamilies. Colors as in Figure 1. Total percentage of records for each period are indicated above. See also Table 2.

TABLE 2 – Number of genera and species for subfamily recorded in each stage. From the total of named species 14 were excluded given its stratigraphic record is unknown.

Stage	Subfamily	Species		Genera	
		Frequency	Percentage (%)	Frequency	Percentage (%)
Guzhangian	Oleninae	9	1.54	3	2.63
	Pelturinae	2	0.36	2	1.75
	Total	**11**	**1.88**	**5**	**4.38**
Paibian	Oleninae	31	5.30	3	2.63
	Pelturinae	1	0.17	1	0.88
	Plicatolininae	3	0.51	2	1.75
	Hunanoleninae	3	0.51	1	0.88
	Total	**38**	**6.50**	**7**	**6.14**
Jiangshanian	Oleninae	28	4.79	8	7.02
	Pelturinae	27	4.62	4	3.51
	Triarthrinae	1	0.17	1	0.88
	Leptoplastinae	45	7.69	5	4.39
	Plicatolininae	9	1.54	2	1.75
	Hunanoleninae	4	0.68	1	0.88
	Total	**114**	**19.49**	**21**	**18.43**
Stage 10	Oleninae	79	13.50	12	10.53
	Pelturinae	53	9.06	10	8.77
	Triarthrinae	12	2.05	4	3.51
	Leptoplastinae	47	8.03	5	4.39
	Plicatolininae	19	3.25	4	3.51
	Total	**210**	**35.89**	**35**	**30.71**
Tremadocian	Oleninae	55	9.40	9	7.89
	Pelturinae	62	10.60	12	10.53
	Triarthrinae	19	3.25	3	2.63
	Leptoplastinae	2	0.34	1	0.88
	Plicatolininae	3	0.51	1	0.88
	Total	**141**	**24.10**	**26**	**22.81**
Floian	Pelturinae	7	1.2	5	4.39
	Triarthrinae	6	1.03	2	1.75
	Plicatolininae	1	0.17	1	0.88
	Balnibarbiinae	9	1.54	2	1.75
	Total	**23**	**3.93**	**10**	**8.77**
Dapingian	Triarthrinae	4	0.68	2	1.75
	Balnibarbiinae	3	0.51	1	0.88
	Total	**7**	**1.20**	**3**	**2.63**
Darriwilian	Triarthrinae	16	2.74	2	1.75
	Total	**16**	**2.74**	**2**	**1.75**
Sandbian	Triarthrinae	8	1.37	2	1.75
	Total	**8**	**1.37**	**2**	**1.75**
Katian	Triarthrinae	13	2.22	2	1.75
	Total	**13**	**2.22**	**2**	**1.75**
Hirnantian	Triarthrinae	4	0.68	1	0.88
	Total	**4**	**0.68**	**1**	**0.88**

Triarthrinae as a separate subfamily has prompted debate. While certain authors consider it part of Oleninae (*e.g.*, Henningsmoen, 1957; Ludvigsen, 1982; Ludvigsen & Tuffnell, 1983), others acknowledge it as a distinct valid group (*e.g.*, Harrington & Leanza, 1952; Moore, 1959; Fortey, 1974; Ludvigsen & Tuffnell, 1994). In either case, the close relationships between the genera *Triarthrus*, *Porterfieldia*, and *Bienvillia* have always been emphasized and they have been regarded as a monophyletic group (*e.g.*, Henningsmoen, 1957; Ludvigsen & Tuffnell, 1983, 1994). Triarthrinae is a cohesive group and is probably a monophyletic lineage. It is characterized by a square-shaped glabella with four pairs of lateral furrows, palpebral lobes close to the glabella, and the presence of two pleural furrows (Ludvigsen & Tuffnell, 1994). A phylogenetic analysis encompassing species of Triarthrinae and other olenids agrees with the monophyly of the group. However, the level of support for this grouping was relatively weak and the synapomorphies were different from previously suggested traits (Monti & Confalonieri, 2019).

Subfamily Leptoplastinae

Leptoplastinae is a small but iconic group within Olenidae. Most of the species included in this subfamily are stratigraphic markers for the Furongian from Baltica and Avalonia. It is also thanks to members of this group that early ontogenetic stages of olenids are well-known. According to the results, the group includes seven genera and 55 species (Fig. 1; Tab. 1; SI1; Appendix). More than half of the counted species (35 species equivalent to 63.63% of the total) correspond to *Ctenopyge* Linnarsson, 1880 and *Leptoplastus* Angelin, 1854. The rest of the genera included one to seven species (Fig. 5.5).

Leptoplastinae is well known from the Furongian of Baltica and Avalonia, with 91% of the species (Fig. 4.5; SI3). The genus *Eurycarina* Ivshin in Petrunina, 2002, including three new species was added to the subfamily (Petrunina, 2002). These three species, coming from the upper Furongian and Lower Tremadocian from Siberia, not only extend the geographic range of the group, but also its stratigraphic range (SI1; Appendix).

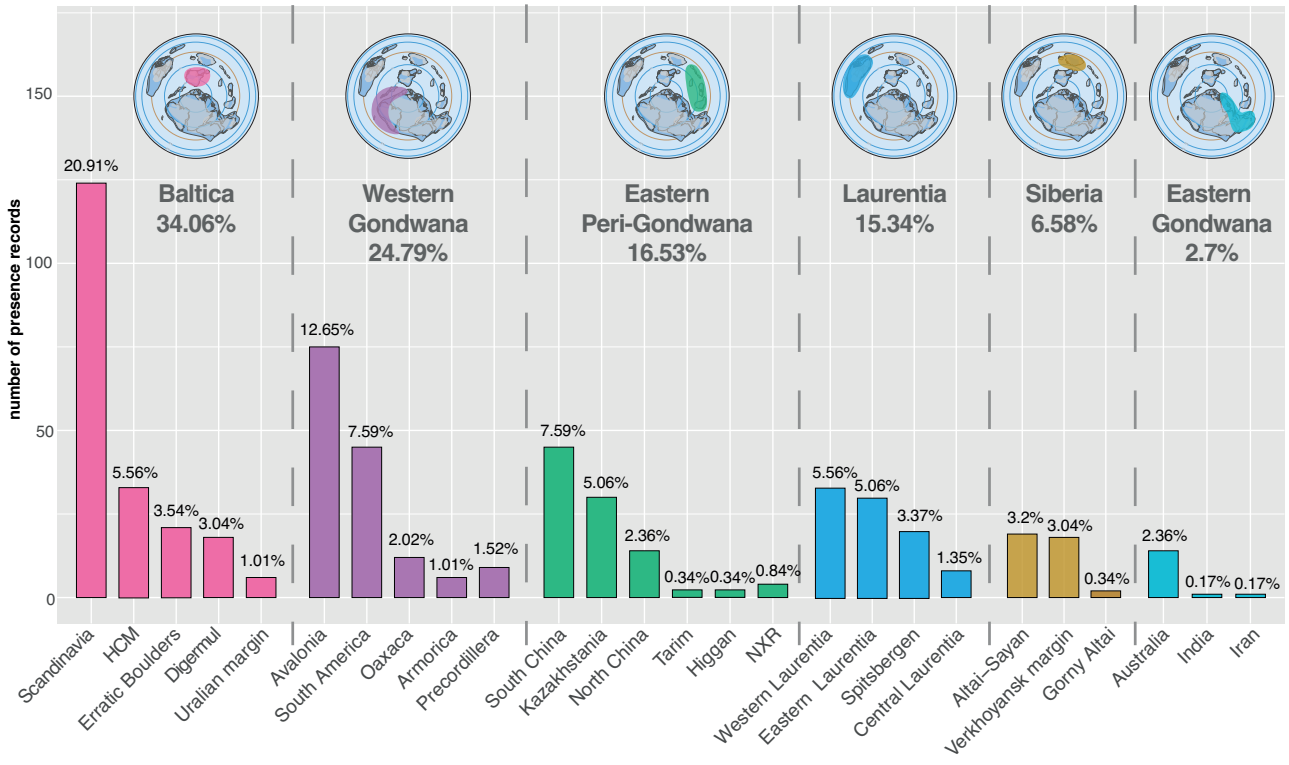

Figure 3. Records of species and their percentages by area**.** Major regions and the corresponding proportions are indicated, along with a schematic paleoreconstruction of the Lower Ordovician (map modified from Cocks & Torsvik, 2021) showing the extension of each region. Abbreviations: **HCM,** Holy Cross Mountains; **NXR,** Northern Xinjiang Region. See also Table 3.

TABLE 3 – **Number of genera and species recorded in each area and region. Dubious records were excluded.**

Region	Area	Species		Genera	
		Frequency	Percentage (%)	Frequency	Percentage (%)
Baltica	Scandinavia	124	20.91	25	10.73
	Holy Cross Mountains	33	5.56	15	6.44
	Erratic Boulders	21	3.54	10	4.29
	Digermul	18	3.04	9	3.86
	Uralian margin	6	1.01	5	2.15
	Total	**202**	**34.06**	**64**	**27.47**
Western Gondwana	Avalonia	75	12.65	19	8.15
	South America	45	7.59	16	6.87
	Oaxaca	12	2.02	7	3
	Armorica	6	1.01	4	1.72
	Precordillera	9	1.52	4	1.72
	Total	**147**	**24.79**	**50**	**21.46**
Peri-Eastern Gondwana	South China	45	7.59	15	6.44
	Kazakhstania	30	5.06	18	7.73
	North China	14	2.36	9	3.86
	Tarim	2	0.34	1	0.43
	Higgan	2	0.34	1	0.43
	Northern Xinjiang Region	5	0.84	2	0.86
	Total	**93**	**16.53**	**46**	**19.75**
Laurentia	Western Laurentia	33	5.56	15	6.44
	Eastern Laurentia	30	5.06	13	5.58
	Spitsbergen	20	3.37	8	3.43
	Central Laurentia	8	1.35	5	2.15
	Total	**91**	**15.34**	**41**	**17.6**
Siberia	Altai-Sayan	19	3.2	10	4.29
	Verkhoyansk margin	18	3.04	8	3.43
	Gorny Altai	2	0.34	1	0.43
	Total	**39**	**6.58**	**19**	**8.15**
Eastern Gondwana	Australia	14	2.36	11	4.72
	India	1	0.17	1	0.43
	Iran	1	0.17	1	0.43
	Total	**16**	**2.7**	**13**	**5.58**

Leptoplastinae was considered the third evolutionary branch within the Olenidae, which would have originated in *Leptoplastus* (Westergård, 1922; Harrington & Leanza, 1952; Henningsmoen, 1957). This group shows cohesive morphological treats and it was stratigraphically and geographically restricted, therefore, it was probably monophyletic. However, we lack a formal phylogenetic analysis including leptoplastines to prove this affirmation.

Subfamily Plicatolininae

The subfamily Plicatolininae was established by Robison and Pantoja-Alor (1968) to encompass olenids characterized by four pairs of transverse glabellar furrows, thorax with numerous segments (21), and a small and wide pygidium that is two to three times its length. They identified three generic lineages within this family: *Plicatolina* Shaw, 1951, *Plicatolinella* Robison and Pantoja-

Alor, 1968, and an as-yet-undescribed genus from the Furongian of Nevada. Today, Plicatolininae includes five genera and 24 species (Fig. 1; Tab. 1; SI1; Appendix). From the five genera, only two account for the diversity of the group, *Plicatolina* and *Wujiajiania* add up twenty of the twenty-four described species for the group (Fig. 5.4). The other three genera are only known from one or two species.

This group is mostly known from the Furongian, only two records of *Plicatolina* species come from the Tremadocian of South China (Fig. 4.4; SI3). Despite being represented by a small number of species, they were more geographically extended than the Leptoplastinae and had a slightly narrower distribution than the cosmopolitan subfamilies. Plicatolines were well-known from Gondwana, South China, Laurentia, and Siberia. However, it is worth noting the scarce presence of plicatolines in Baltica and

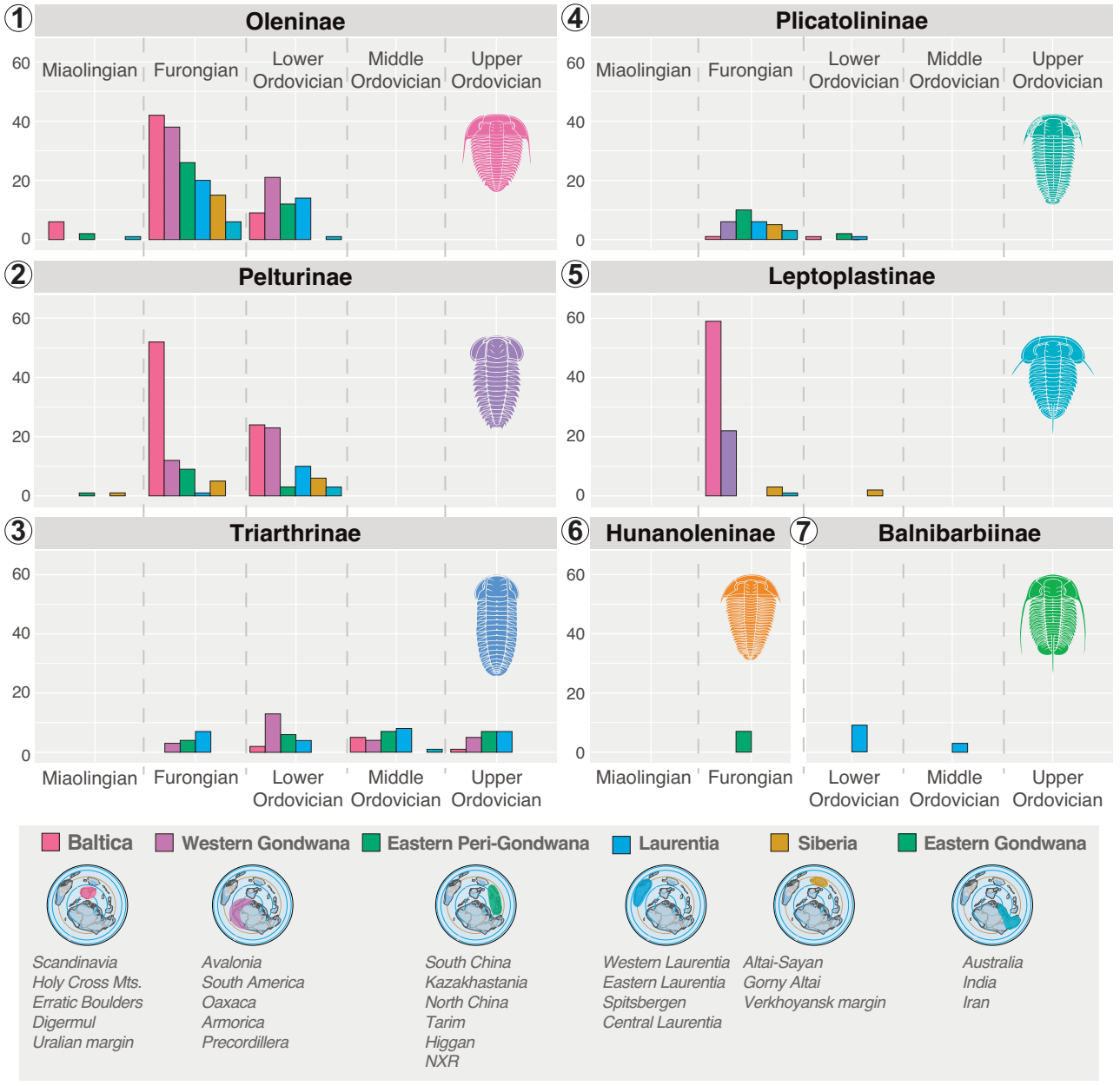

Figure 4. Stratigraphic and geographic distribution of subfamilies within Olenidae. For each subfamily, the graph shows the numbers of recorded species by area and period. **1,** Oleninae; **2,** Pelturinae; **3,** Triarthrinae; **4,** Plicatolininae; **5,** Leptoplastinae; **6,** Hunanoleninae; **7,** Balnibarbiinae. The extension of each region is indicated over a schematic paleoreconstruction of the Lower Ordovician. Colors as in Figure 3.

Avalonia, two regions where other groups were common (Fig. 4.4; SI3).

Plicatolininae has been considered as part of the evolutionary branch developed from Oleninae *sensu lato* (Westergård, 1922; Kaufmann, 1935; Harrington & Leanza, 1952; Henningsmoen, 1957). However, we lack a formal phylogenetic analysis including several plicatolinines to prove its monophyly. So far, the only partial phylogeny where members of the group were included was the previously presented by Monti and Confalonieri (2019), and only representatives of one genus were included.

Subfamily Hunanoleninae

The subfamily Hunanoleninae consists of only two genera and five species (Figs. 1, 5.6; Tab. 1; SI1; Appendix). This group is confined to the mid–late Furongian (Fig. 4.6; SI3) and documented in various locations in China (Anhua, Cili, Taoyuan, and Hunan).

The subfamily was created by Liu (1977) to include olenids with many thoracic segments (23 segments), a small pygidium, and a wide fixigena. Initially, the genus *Hedinaspis* Troedsson, 1951 was also included in this group but was later reassigned to Ceratopygidae (Bao & Jago, 2000; Jell & Adrain, 2003). This small group is probably monophyletic, but its affinities with other olenids are unknown. They share characteristics with several members of the Oleninae, such as *Olenus* and *Parabolinella*. According to Zhou and Zhen (2008), Hunanoleninae is not a valid subfamily, as they consider the two genera included in it to be junior subjective synonyms of *Olenus*. Determining their affinities with the rest of the olenids through a formal phylogenetic analysis is crucial, especially considering their stratigraphic and geographic distribution.

Subfamily Balnibarbiinae

The subfamily Balnibarbiinae comprises only two genera with a total of eleven species (Fig. 1; Tab. 1; SI1; Appendix). The distribution of species is relatively even between the

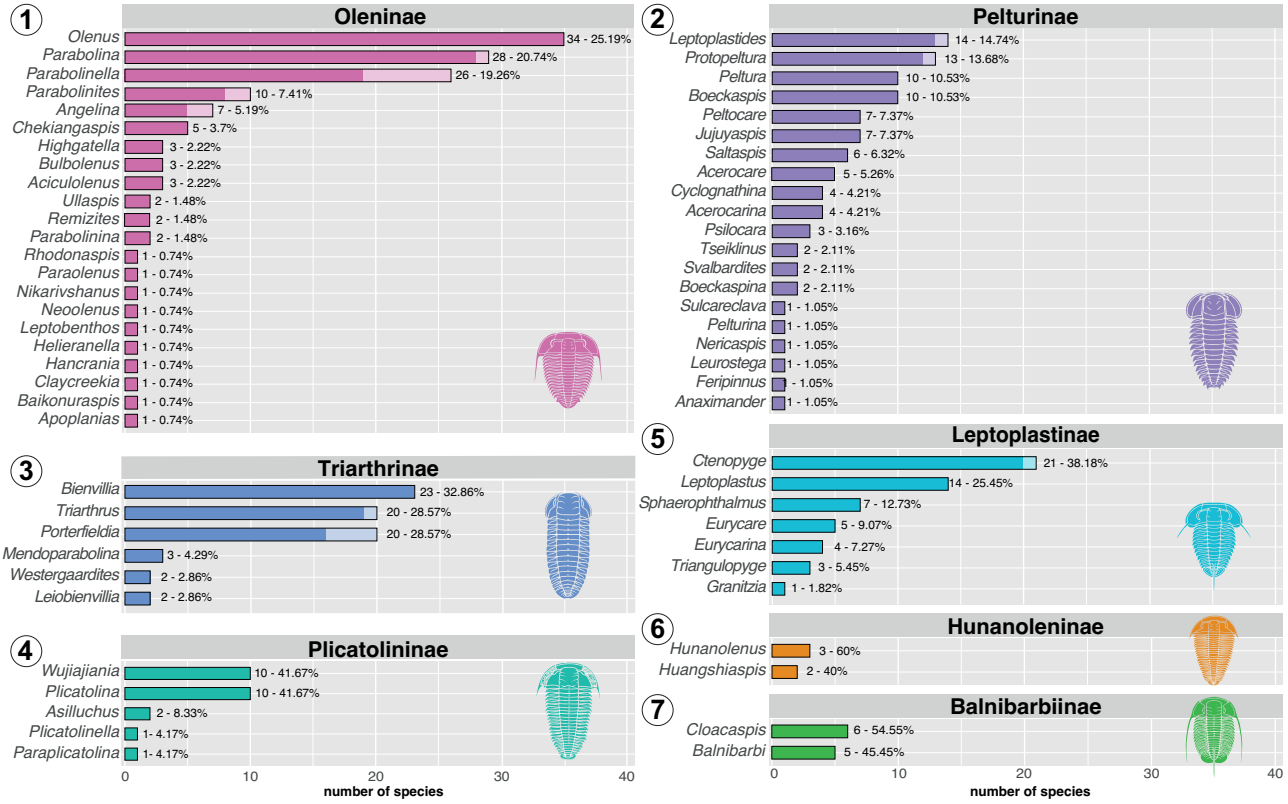

Figure 5. Number of species with their corresponding percentage by genera for each subfamily. **1,** Oleninae; **2,** Pelturinae; **3,** Triarthrinae; **4,** Plicatolininae; **5,** Leptoplastinae; **6,** Hunanoleninae; **7,** Balnibarbiinae. Lighter color in the bars indicates the proportion species with uncertain assignment to the genus. Colors as in Figure 1.

two genera (Fig. 5.7). Its presence is noted in Laurentia, exhibiting greater diversity in Spitsbergen during the Floian. In the Dapingian, its range expands to include Western Laurentia (Fig. 4.7; SI3).

Balnibarbiinae was established by Fortey (1974) for triarthrinae-like olenids characterized by a distinctive triangular ''pleural node'' formed by the forked pleural furrow and the axial furrow. This family represents a homogeneous group, constituting a monophyletic clade that is both stratigraphically and geographically restricted. Fortey (1974) inferred its evolutionary history based on phyletic similarity and stratigraphic range, proposing three distinct evolutionary lineages. In a recent study, Hopkins (2019) reviewed the species within this group and conducted a formal phylogenetic analysis, confirming the proposal of Fortey (1974).

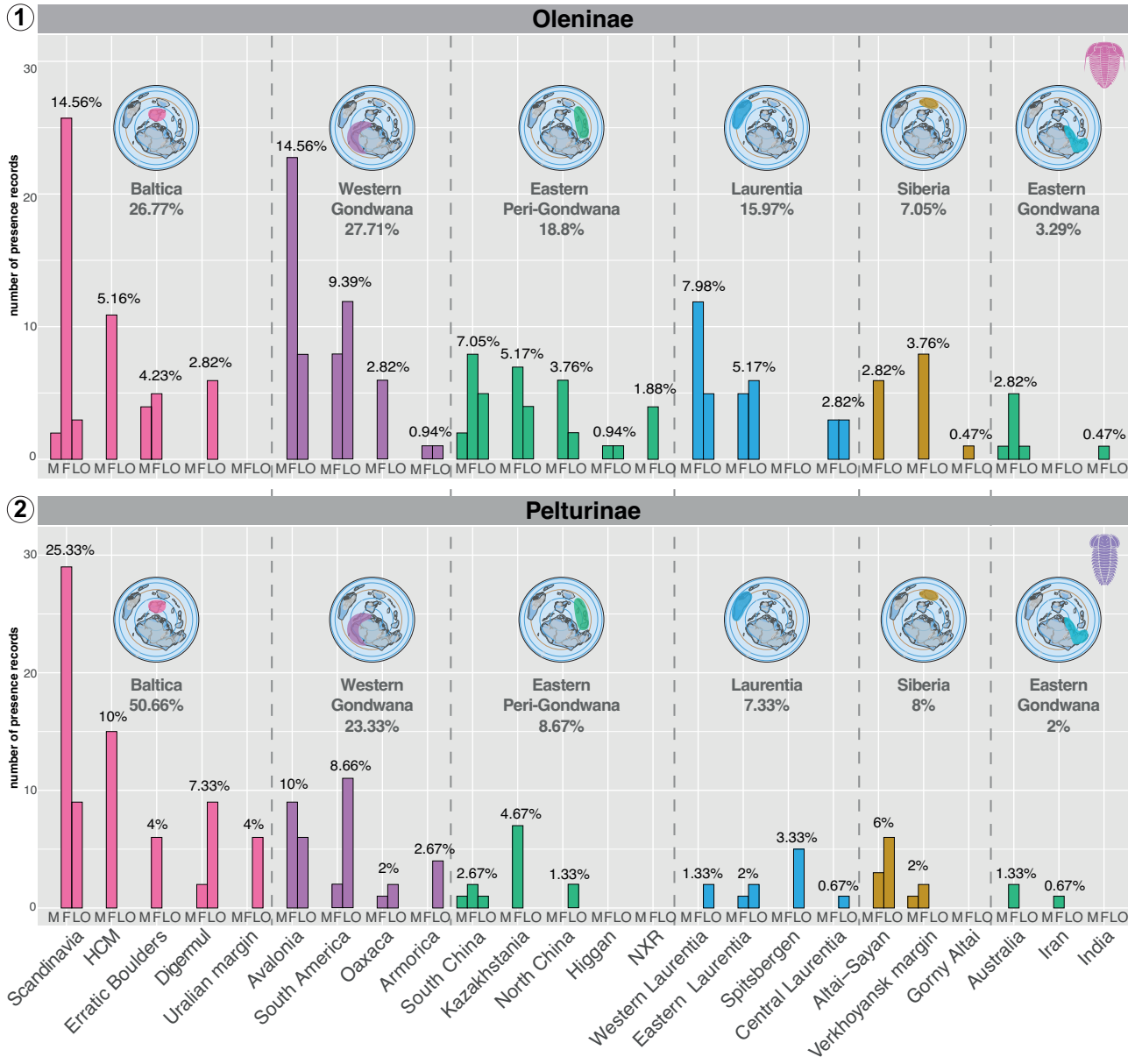

Figure 6. Records of species and percentage by area. For each one, records by period are indicated. **1,** Oleninae; **2,** Pelturinae. Major regions and corresponding proportions are indicated, along with a schematic paleoreconstruction of the Lower Ordovician (map modified from Cocks & Torsvik, 2021) showing the extension of each region. Abbreviations: **M,** Miaolingian; **F,** Furongian; **LO,** Lower Ordovician; **HCM**, Holy Cross Mountains; **NXR**, Northern Xinjiang Region. Colors as in Figure 3.

DISCUSSION

Jell and Adrain (2003) listed 67 valid genera (and four subgenera) belonging to olenids, whereas this study reports 64 genera. There are some differences between the two lists (see SI5). Ten genera were added as valid here, nine of them were described after the list was published: *Nikarivshanus* Petrunina, 2002; *Boekaspina* Petrunina, 2002; *Feripinnus* Petrunina, 2002; *Tseiklinus* Petrunina, 2002; *Eurycarina* Petrunina, 2002; *Leptobenthos* Tortello and Esteban, 2003; *Triangulopyge* Høyberget and Bruton, 2012; *Claycreekia* Chatterton and Gibb, 2016; and *Sulcareclava* Peng *et al.*, 2004. The other one, *Mendoparabolina* Rusconi, 1951, was previously considered a junior synonym of *Bienvillia* (see SI1; SI5 and the Appendix for details). On the other hand, eight genera were excluded from the list since they were transferred to other groups: *Desmetia* Walcott, 1925 (junior synonym of *Clelandia* Cossman, 1902 by Ng and Adrain, 2018; Ng, 2019, family Kingstoniidae); *Euonchonotina* Lu *et al.*, 1986 (junior synonym of *Huzhuia* Zhu, 1965 by Zhou and Zhen, 2008, family Catillicephalidae); *Hypermecaspis* Harrington and Leanza, 1957 (family Hypermecaspididae *sensu* Monti *et al.*, 2022); *Isidrella* Rusconi, 1955 and *Orkekeia* Rusconi, 1955 (excluded from Olenidae by Henningsmoen, 1957); *Magnomma* Lu and Qian, 1983 (family Papyriaspididae *sensu* Lu and Qian, 1983); *Talbotinella* Poulsen, 1960 (family Marjumidae *sensu* Tortello, 2017); *Shihuigouia* Zhu, 1960 (family Richardsonellidae *sensu* Zhou and Zhen, 2008) (see SI1; SI5 and the Appendix for details). *Bondarevites* Lazarenko, 1989 and *Prohedinella* Sivov in Egorova *et al.*, 1955 were also excluded from the family. *Bondarevites* possesses a cranidium resembling that of remopleurids, along with a thorax comprising twelve segments and a spine on the eighth segment (Lazarenko, 1989, pl. 1, figs. 1–7). Therefore, it is considered here as belonging to the family Remopleuridae. *Prohedinella* was established based on a small cranidium from the Wuliuan (Miaolingian) of Kuznetsk Alatau, Russia. The author included this genus in Olenidae, noting its resemblance to *Prohedinia* Lermontova and Chernysheva in Chernysheva, 1950, a genus now placed in Papyriaspididae. The illustration of the type material, which consists of a small photograph (Egorova *et al.*, 1955, pl. 11, fig. 6), complicates the assignment of *Prohedinella* to any specific group. Given its stratigraphic position and the uncertainty regarding its affinities, it is preferred here to exclude *Prohedinella* from Olenidae until new illustrations or additional material become available. Finally, three genera were synonymized with other genera belonging to olenids: *Inkouia* Zhang and Fan, 1960 (junior synonym of *Bienvillia* by Zhou and Zhen, 2008); *Moxomia* Walcott, 1924 (junior synonym of *Parabolinella* by Harrington and Leanza, 1957), and *Westergaardia* Raymond, 1924 (junior synonym of *Boeckaspis* by Karim, 2008) (see SI1; SI5 and the Appendix for details).

Adrain (2013) reported 70 genera and 400 species within Olenidae. In general, a similar number of genera and their distribution across subfamilies is recognized in this work. The differences between these numbers and those presented here may stem from the exclusion of certain genera, such as *Hypermecaspis*, *Bondarevites*, and *Magnomma*. Additionally, the assignment of genera to subfamilies may vary between the two studies. As mentioned throughout the text, the subfamilies within Olenidae are often poorly supported, making the assignment of genera to specific subfamilies tentative until a well-supported phylogenetic analysis is conducted. Furthermore, the definition of species and their assignment to a particular genus is even more complex. Supplementary Information 6 (SI6) provides a list of all species synonyms considered in this study, along with a list of proposed synonyms deemed dubious due to the lack of sufficient material.

This paper highlights that despite the extensive research on olenids, several taxonomic questions remain unanswered. For over a century, researchers have delved into several aspects of olenids, gaining insight into their ontogeny, soft body anatomy, and ecology (*e.g.*, Beecher, 1896; Cisne, 1975, 1981; Clarkson *et al.*, 1997, 2004; Fortey, 1999, 2000; Clarkson & Ahlberg 2002; Bird & Clarkson, 2003; Månsson & Clarkson, 2012, 2016, 2018; Hegna *et al.*, 2017, among many others). However, phylogenetic aspects have received relatively less attention, despite the growing prevalence of such studies in recent decades. As shown in the Appendix, ongoing discussions persist regarding the delimitation of numerous genera, including well-known ones, as well as the determination of the number of species they encompass. Hence, there arises the necessity to organize

the systematics of the group to make further progress in its study.

Several challenges arise when attempting to clarify taxonomic issues within olenids. Many species were described over a century ago, and in numerous cases, the type materials have been lost, leaving only the original drawings or, in the best scenarios, photographs. This situation complicates the diagnosis and the extension of each genus. Recent studies reviewing type materials were published, clarifying the systematics of several genera (*e.g.*, Terfelt, 2006; Terfelt *et al.*, 2008; Rasmussen *et al.*, 2017; Nielsen *et al.*, 2020; Nielsen & Andersen, 2021, among others). Nevertheless, much work remains to be done in this regard.

Another complicating factor in the study of olenids is their widespread global distribution. While olenids were cosmopolitan, the distribution of species was uneven among the regions. A higher concentration of species was discovered in Baltica and Avalonia, accounting for nearly half of the records. Siberia, South China, and South America exhibit significant diversity, though less than in the previous areas, while the remaining regions show even lower diversity. These differences in diversity could be attributed to disparities in study effort or attention given to English publications from the western world.

Addressing the definition of subfamilies poses another challenge. In this study, the traditional classification scheme was followed. However, several genera were tentatively assigned to specific groups. This results from the combination of two factors: not all named species exhibit diagnostic characters and the definition of the subfamilies is not consistently clear. Several subfamilies were non-monophyletic or their presumed monophyly was never challenged. In this context, the dataset generated in this paper could aid in selecting representative taxa for establishing a phylogenetic classification of the group.

CONCLUSIONS

The family Olenidae comprises 64 genera and 394 species, for now distributed in seven subfamilies. Subfamilies Oleninae and Pelturinae accumulate most of the species.

Several challenges arise in clarifying the systematics of olenids. Many species were described over a century ago and lack proper illustrations and/or type materials have been lost. In consequence, several genera are poorly diagnosed, obscuring its assignation to a given subfamily. The vague definition of the subfamilies and the little phylogenetic approach within the group complicates, also, the assignment of the genera to monophyletic groups. The worldwide distribution hinders a global view of the group and different study effort by area may introduce a bias in the diversity of each area.

The work remarks the necessity to delimit the group and all the species included. The dataset generated in this paper could aid in selecting representative taxa for establishing a phylogenetic classification of the group.

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REFERENCES

Adrain, J. M. (2013). A synopsis of Ordovician trilobite distribution and diversity. *Geological Society Memoir*, *38*(1), 297–336. https://doi.org/10.1144/M38.20

Angelin, N. P. (1854). *Palaeontologica scandinavica, Crustacea Formationis Transitionis pars II*. Academiae Regiae Scientarium Sueccanae (Holmiae).

Balseiro, D., Waisfeld, B. G., & Vaccari, N. E. (2011). Paleoecological dynamics of Furongian (late Cambrian) trilobite-dominated communities from northwestern Argentina. *Palaios*, *26*(8), 484–499. https://doi.org/10.2110/palo.2010.p10-152r

Bao, J. -S. & Jago, J. B. (2000). Late Late Cambrian trilobites from near Birch Inlet, south-western Tasmania. *Palaeontology*, *43*(5), 881–917. https://doi.org/10.1111/1475-4983.00154

Beecher, C. E. (1896). The morphology of *Triarthrus*. *Geological Magazine*, *3*(5), 193–197. https://doi.org/10.1017/S001675680013081X

Bird, C. & Clarkson, E. (2003). Observations on the ontogeny of the upper Cambrian trilobite *Peltura scarabaeoides westergaardi* Henningsmoen, 1957. *GFF*, *125*(4), 177–190. https://doi.org/10.1080/11035890301254177

Brongniart, A. (1822). *Histoire naturelle des crustaces fossiles sous les rapports zoologique et geologique, savoir les trilobites*. Chez F.-G. Levrault, Libraire.

Brøgger, W. C. (1882). *Die Silurisćhen Etagen 2 und 3 im Kristianiagebiet und auf Eker, ihre Gliederung, Fossilien, Schichtenstörungen und Contactmetamorphosen*. A. W. Brøgger.

Burmeister, H. (1843). *Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt: nebst einer systematischen Übersicht aller zeither beschriebenen Arten*. De Gruyter, Incorporated.

Chatterton, B. D. E. & Gibb, S. (2016). Furongian (upper Cambrian) trilobites of the McKay Group, Bull River Valley, Near Cranbrook, Southeastern British Columbia, Canada. *Palaeontographica Canadiana*, *35*, 1–275.

Chernysheva, N. E. (1950). [New Middle Cambrian trilobites from eastern Siberia]. *Trudy Vsesoyuznogo Nauchno-Issledovatel'skogo Geologicheskogo Instituta (VSEGEI), palaeontology series*, *1*, 67–77, pl. 1. [in Russian]

Cisne, J. L. (1975). Anatomy of *Triarthrus* and the relationships of the Trilobita. *Fossils and Strata*, *4*, 45–63.

Cisne, J. L. (1981). *Triarthrus eatoni* (Trilobita); anatomy of its exoskeletal, skeletomuscular, and digestive systems. *Palaeontographica Americana*, *9*, 95–142.

Clark, T. H. (1924). The paleontology of the Beekmantown Series at Levis, Quebec. *Bulletins of American Paleontology*, *10*(41), 1–134.

Clarkson, E. N. K. & Ahlberg, P. (2002). Ontogeny and structure of a new, miniaturised and spiny olenid trilobite from southern Sweden. *Palaeontology*, *45*(1), 1–22. https://doi.org/10.1111/1475-4983.00224

Clarkson, E. N. K., Ahlgren, J., & Taylor, C. M. (2004). Ontogeny, structure and functional morphology of some spiny *Ctenopyge* species (Trilobita) from the upper Cambrian of Vätergötland, Sweden. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, *94*(2), 115–143. https://doi.org/10.1017/s0263593300000559

Clarkson, E. N. K., Taylor, C. M., & Ahlberg, P. (1997). Ontogeny of the trilobite *Parabolina spinulosa* (Wahlenberg, 1818) from the upper Cambrian Alum Shales of Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, *88*, 69–89. https://doi:10.1017/S0263593300006842

Cocks, L. R. M. & Torsvik, T. H. (2002). Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society*, *159*(6), 631–644. https://doi.org/10.1144/0016-764901-118

Cocks, L. R. M. & Torsvik, T. H. (2021). Ordovician palaeogeography and climate change. *Gondwana Research*, *100*, 53–72. https://doi.org/10.1016/j.gr.2020.09.008

Cooper, B. N. (1953). Trilobites from the lower Champlainian formations of the Appalachian Valley. *Memoire of the Geological Society of America*, *55*, 1–69.

Cossman, M. (1902). Rectification de nomenclature. *Revue Critique de Paléozoologie*, *6*, 52.

Dalman, J. W. (1827). Om Palaeaderna eller de så kallade Trilobiterna. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, *1826*(2), 113–294.

Egorova, L. I., Lomovitskaya, M. P., Poletaeva, O. K., & Sivov, A. G. (1955). Klass Trilobita, Trilobites. In L. L. Khalfin (Ed.), *Atlas of Index Forms of the Fossil Fauna and Flora of Western Siberia, Vol. 1*. (pp. 102–179). Gosgeoltexizdat.

Fortey, R. A. (1974). The Ordovician Trilobites of Spitsbergen I. Olenidae. *Norsk Polarinstitutt Skrifter*, *160*, 1–129.

Fortey, R. A. (1975). Early Ordovician trilobite communities. *Fossils and Strata*, *41*(1), 339–360.

Fortey, R. A. (1989). There are extinctions and extinctions: examples from the Lower Palaeozoic. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *325*(1228), 327–355. https://doi.org/10.1098/rstb.1989.0092

Fortey, R. A. (1999). Olenid trilobites as chemoautotrophic symbionts. *Acta Universitatis Carolinae, Geologica*, *43*, 355–356.

Fortey, R. A. (2000). Olenid trilobites: The oldest known chemoautotrophic symbionts? *Proceedings of the National Academy of Sciences*, *97*, 6574–6578. https://doi.org/10.1073/pnas.97.12.6574

Green, J. (1832). *A monograph of the trilobites of North America: with coloured models of the species*. J. Brano.

Harrington, H. J. & Leanza, A. F. (1943). La fáunula del Tremadociano inferior de Salitre (Bolivia). *Revista Del Museo de La Plata (Nueva Serie)*, *2*, 343–356.

Harrington, H. J. & Leanza, A. F. (1952). La clasificación de los "Olenidae" y de los "Ceratopygidae" (Trilobita). *Revista de La Asociación Geológica Argentina*, *7*(3), 190–206.

Harrington, H. J. & Leanza, A. F. (1957). Ordovician trilobites of Argentina. *Department of Geology, University of Kansas, Special Publication*, *1*, 1–276.

Hegna, T. A., Martin, M. J., & Darroch, S. A. (2017). Pyritized *in situ* trilobite eggs from the Ordovician of New York (Lorraine Group): implications for trilobite reproductive biology. *Geology*, *45*(3), 199–202. https://doi.org/10.1130/G38773.1

Henningsmoen, G. (1957). The trilobite family Olenidae, with description of Norwegian material and remarks on the Olenid and Tremadocian series. *Skrifter Utgitt av det Norske Videnskaps-Akademi i Oslo, I, Matematisk-naturvidenskapelig Klasse*, *1957*(1), 1–303.

Hopkins, M. J. (2019). Phylogenetic analysis and revision of the trilobite subfamily Balnibarbiinae (Olenidae). *American Museum Novitates*, *3928*, 1–20. https://doi.org/10.1206/3928.1

Høyberget, M. & Bruton, D. L. (2012). Revision of the trilobite genus *Sphaerophthalmus* and relatives from the Furongian (Cambrian) Alum Shale Formation, Oslo Region, Norway. *Norwegian Journal of Geology*, *92*, 433–450.

Jell, P. A. & Adrain, J. M. (2003). Available generic names for trilobites. *Memoirs of the Queensland Museum*, *48*(2), 331–553.

Karim, T. S. (2008). Olenid-dominated trilobite fauna from the Shallow Bay Formation (Cow Head Group), Cambrian-Ordovician boundary interval, western Newfoundland. *Canadian Journal of Earth Sciences*, *45*(4), 407–425. https://doi.org/10.1139/E08-008

Kaufmann, H. P. (1935). *Studien auf dem Fettgebeit*. Verlag Chemie.

Lazarenko, N. P. (1989). A new olenid trilobite from Novaya Zemlya. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchectva*, *32*, 288–293.

Linnarsson, G. (1880). Om försteningarne i de svenska lagren med *Peltura* och *Sphaerophthalmus*. *Geologiska Föreningens i Stockholm Förhandlingar*, *5*(4), 132–161.

Liu, Y. (1977). [A study of two genera of the late Cambrian Olenidae (Trilobita) from Taoyuan, Hunan]. *Acta Palaeontologica Sinica*, *16*(1), 120–126. [in Chinese].

Lu, Y. & Qian, Y. (1983). Cambro-Ordovician trilobites from Eastern Guizhou. *Palaeontologia Cathayana*, *1*, 1–105.

Lu, Y., Zhou, Z., & Zhou, Z. (1986). [New materials of *Onychopyge* faunas, with a discussion on the evolution of *Onychopyge* (Trilobita)]. *Bulletin of the Nanjing Institute of Geology and Palaeontology, Academia Sinica*, *7*, 69–126. [in Chinese]

Ludvigsen, R. (1982). The Cambrian-Ordovician boundary in the western District of Mackenzie, Canada. In M. G. Bassett & W. T. Dean (Eds.), *The Cambrian-Ordovician boundary: sections, fossil distributions, and correlations* (pp. 141–153). National Museum of Wales, Geological Series Nº3.

Ludvigsen, R. & Tuffnell, P. A. (1983). A revision of the Ordovician olenid trilobite *Triarthrus* Green. *Geological Magazine*, *120*, 567–577.

Ludvigsen, R. & Tuffnell, P. A. (1994). The last olenacean trilobite: *Triarthrus* in the Whitby Formation (Upper Ordovician) of southern Ontario. *New York State Museum Bulletin*, *481*, 183–212.

Mángano, M. G., Buatois, L. A., Waisfeld, B. G., Muñoz, D. F., Vaccari, N. E., & Astini, R. A. (2021). Were all trilobites fully marine? Trilobite expansion into brackish water during the early Palaeozoic. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1944), 20202263. https://doi.org/10.1098/rspb.2020.2263

Månsson, K. & Clarkson, E. N. K. (2012). Ontogeny of the Upper Cambrian (Furongian) Olenid trilobite *Protopeltura aciculate* (Angelin, 1854) from Skåne and Västergötland, Sweden. *Palaeontology*, *55*(4), 887–901. https://doi.org/10.1111/j.1475-4983.2012.01162.x

Månsson, K. & Clarkson, E. N. K. (2016). Early ontogeny of the Furongian (Cambrian) olenid trilobites *Sphaerophthalmus alatus* (Boeck, 1838) and *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922 from Bornholm, Denmark. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, *106*(3), 171–183. https://doi.org/10.1017/S1755691016000086

Månsson, K. & Clarkson, E. N. K. (2018). A revised ontogeny of the early Ordovician trilobite *Leptoplastides salteri* (Callaway, 1877). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, *111*(1), 1–16. https://doi.org/10.1017/S1755691018000841

Monti, D. S. & Confalonieri, V. A. (2013). Phylogenetic analysis of the late Cambrian-early Ordovician genus *Parabolinella* Brøgger (Trilobita, Olenidae). *Geological Journal*, *48*(2-3), 156–169. https://doi.org/10.1002/gj.1343

Monti, D. S. & Confalonieri, V. A. (2019). First cladistic analysis of the trilobite family Olenidae from the Furongian and Ordovician. *Lethaia*, *52*(3), 304–322. https://doi.org/10.1111/let.12313

Monti, D. S., Tortello, M. F., & Confalonieri, V. A. (2022). A phylogenetic approach to the study of the evolution of Hypermecaspididae (Olenida, Trilobita). *Papers in Palaeontology*, *8*(3), e1433. https://doi.org/10.1002/spp2.1433

Moore, R. C. (1959). *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1.* Geological Society of America and University of Chicago Press.

Murchison, R. I. (1859). *Siluria: A history of the oldest fossiliferous rocks and their foundations; with a brief sketch of the distribution of gold over the earth.* J. Murray.

Nielsen, A. T. & Andersen, L. F. (2021). Furongian (upper Cambrian) trilobites and agnostoids from the Alum Shale Formation of Bornholm, Denmark: revised taxonomy and biostratigraphy. *Bulletin of the Geological Society of Denmark*, *69*, 123–213. https://doi.org/10.37570/bgsd-2021-69-08

Nielsen, A. T., Høyberget, M., & Ahlberg, P. (2020). The Furongian (upper Cambrian) alum shale of Scandinavia: Revision of zonation. *Lethaia*, *53*(4), 462–485. https://doi.org/10.1111/let.12370

Ng, R. Y. (2019). *The Cambrian-Ordovician trilobite genus* Clelandia*, with phylogeny and morphology of new and revised species* [Unpublished Ms. Thesis] University of Iowa. Retrieved from https://doi.org/10.17077/etd.5fda-79p2

Ng, R. Y. & Adrain, J. M. (2018). Phylogeny and morphology of the Cambrian-Ordovician trilobite genus *Clelandia* with new and revised species. *Abstracts with programs of the Geological Society of America 2018 annual meeting & exposition, Geological Society of America*, *50*(6), EID: 324590.

Nikolaisen, F. & Henningsmoen, G. (1985). Upper Cambrian and lower Tremadoc olenid trilobites form the Digermul peninsula, Finnmark, northern Norway. *Norges Geologiske Undersokelse*, *Bulletin*, *400*, 1–49.

Peng, S., Babcock, L. E., & Lin, H. (2004). *Polymerid trilobites from the Cambrian of northwestern Hunan, China (Vol. 1).* Science Press.

Petrunina, Z. E. (2002). New trilobite taxa of the family Olenidae Burmeister 1843 from the Cambrian-Ordovician boundary beds of the west Siberia. *News of Paleontology and Stratigraphy, Supplement Geology and Geophysics*, *43*(5), 81–111.

Poulsen, C. (1960). Fossils from the late Middle Cambrian *Bolaspidella* Zone of Mendoza, Argentina. *Matematisk-fysiske Meddelelser, Det Kongelige Danske Videnskabernes Selskab*, *32*(11), 1–42.

Přibyl, A. & Vaněk, J. (1980). Ordovician trilobites of Bolivia. *Rozpravy Ceskoslovenské Akademie*, 90, 1–90.

Qian, Y. (1961). [Cambrian trilobites from Sandu and Duyun, southern Kweichow]. *Acta Palaeontologica Sinica*, *9*, 91–129, pls. 1–5. [in Chinese]

R Core Team. (2022). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rasmussen, B. W., Rasmussen, J. A., & Nielsen, A. T. (2017). Biostratigraphy of the Furongian (upper Cambrian) Alum Shale Formation at Degerhamn, Öland, Sweden. *GFF*, *139*(2), 92–118. https://doi.org/10.1080/11035897.2016.1276099

Raw, F. (1908) The trilobite fauna of the Shineton Shales. *Reports of the British Association for the advancement of Science*, *1907*, 511–513.

Raymond, P. E. (1924). No. 4.-New Upper Cambrian and Lower Ordovician trilobites from Vermont. *Proceedings of the Boston Society of Natural History*, *37*, 1–389.

Robison, R. A. & Pantoja-Alor, J. (1968). Tremadocian trilobites from the Nochixtlán region, Oaxaca, Mexico. *Journal of Paleontology*, *42*(3), 767–800.

Rusconi, C. (1951). Trilobitas cámbricos del Cerro Pelado (Mendoza). *Boletín Paleontológico de Buenos Aires*, *24*, 1–4.

Rusconi, C. (1955). Más fósiles cámbricos y ordovícicos de San Isidro, Mendoza. *Boletín Paleontológico de Buenos Aires*, *31*, 1–4.

Salter, J. W. (1849). *Figures and descriptions illustrative of British organic remains, decade 2.* Green and Longmans.

Serra, F., Balseiro, D., Vaucher, R., & Waisfeld, B. G. (2021). Structure of trilobite communities along a delta-marine gradient (lower Ordovician; Northwestern Argentina). *Palaios*, *36*(2), 39–52. https://doi.org/10.2110/palo.2020.013

Shaw, A. B. (1951). The paleontology of northwestern Vermont. I. New late Cambrian trilobites. *Journal of Paleontology*, *25*(1), 97–114. http://www.jstor.org/stable/1299834

Terfelt, F. (2006). Review of uppermost Furongian trilobites from Scania, southern Sweden, based on type material. *Palaeontology*, *49*(6), 1339–1355. https://doi.org/10.1111/j.1475-4983.2006.00600.x

Terfelt, F., Eriksson, M. E., Ahlberg, P., & Babcock, L. E. (2008). Furongian Series (Cambrian) biostratigraphy of Scandinavia–a revision. *Norwegian Journal of Geology/Norsk Geologisk Forening*, *88*(1), 73–87.

The Paleobiology Database. Ocurrence data, Olenidae. Retrieved July 10, 2024 from www.paleobiodb.org

Torsvik, T. H. & Cocks, L. R. M. (2016). Cambrian. In T. H. Torsvik & L. R. M. Cocks (Eds), *Earth History and Palaeogeography* (pp. 85–100). Cambridge University Press. https://doi.org/10.1017/9781316225523.006

Tortello, M. F. (2017). Trilobites from the *Lejopyge laevigata* Zone (Guzhangian; upper middle Cambrian) of the San Isidro area, Mendoza, Argentina. *Ameghiniana*, *54*(4), 465–474. https://doi.org/10.5710/AMGH.16.01.2017.3060

Tortello, M. F. & Esteban, S. B. (2003). Lower Ordovician stratigraphy and trilobite faunas from the southern Famatina Range, La Rioja, Argentina. *Special Papers in Palaeontology*, *70*, 213–240.

Troedsson, G. T. (1951). *Hedinaspis*, new name for *Hedinia* Troedsson non Navás. *Geologiska Föreningens i Stockholm Förhandlingar*, *73*, 1–695.

Walcott, C. D. (1924). Cambrian geology and paleontology. Cambrian and Lower Ozarkian trilobites. *Smithsonian Miscellaneous Collections*, *75*, 53–60.

Walcott, C. D. (1925). Cambrian geology and paleontology. Cambrian and Ozarkian trilobites. *Smithsonian Miscellaneous Colletions*, *75*, 61–146.

Westergård, A. H. (1922). Sveriges Olenidskiffer. *Sveriges Geologiska Undersokning. Serie Ca.*, *18*, 1–205.

Westergård, A. H. (1948). Non-agnostidean Trilobites of the Middle Cambrian of Sweden. *Sveriges Geologiska Undersökning Series C*, *498*, 1–32.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org

Zhang, W. & Fan, J. (1960). Ordovician and Silurian trilobites of the Chilian Mountains. In T. Yin (Ed.), *Geological Gazetter of the Chilian Mountains* (pp. 83–148). Science Press.

Zhou, Z. & Zhen, Y. (2008). *Trilobite record of China*. Science Press.

Zhu, Z. (1960). [Cambrian trilobites from the southern slopes of the Chilian Mountains]. *Geological Gazetteer of Chilian Mountains, 4*(1), 53–68. [in Chinese]

Zhu, Z. (1965). [Some Middle Cambrian trilobites from Huzhu, Tsinghai (=Qinghai)]. *Acta Palaentologica Sinica*, *13*(1), 133–149. [in Chinese]

Żylińska, A. (2001). Late Cambrian trilobites from the Holy Cross Mountains, central Poland. *Acta Geologica Polonica*, *51*(4), 333–383.

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APPENDIX. List of genera with relevant information, species, distribution, and scientific literature. References in SI2. See also SI1 and SI6.

Family OLENIDAE Burmeister, 1843
Subfamily OLENINAE Burmeister, 1843

Genus ***Aciculolenus*** Palmer, 1965

Type species. *Aciculolenus peculiaris* Palmer, 1965, upper part of *Elvinia* zone, Jiangshanian, Great Basin, Nevada.

Remarks. *Aciculolenus* is a small, spiny olenid, characterized by the presence of intergenal and genal spines. Palmer (1965) established the genus and tentatively included it in Olenidae, noting some resemblance to *Acerocare* Angelin, 1854. Later, Chatterton and Ludvigsen (1998) described more specimens and provided a new diagnosis for *Aciculolenus*. Finally, Chatterton and Gibb (2016) provided an amended diagnosis for the genus and discussed its geographic distribution and biogeographical importance (see also Chatterton, 2020).

The morphology of *Aciculolenus* has prompted some discussion. For instance, the presence of two pairs of cephalic marginal spines has generated some doubt about the correct homologies of these spines and the nature of the facial suture. Chatterton and Ludvigsen (1998) and Chatterton and Gibb (2016) interpreted *Aciculolenus* as having intergenal and genal spines and an opisthoparian suture, like most olenids. Additionally, their small size, combined with their spiny morphology, the presence of an intergenal spine, and the relatively low number of thoracic segments have led to the suggestion of a progenetic origin for the genus (Chatterton & Ludvigsen, 1998). The peculiar morphology of *Aciculolenus* also makes it difficult to assign it to any subfamily within olenids. The most similar olenid is *Claycreekia* Chatterton and Gibb, 2016, and therefore this genus is tentative included in Oleninae (see *Claycreekia* below). *Aciculolenus* includes three species: *A. peculiaris*, *A. palmeri* Chatterton and Ludvigsen, 1998, and *A. askewi* Chatterton, 2020.

Geographic and Stratigraphic Occurrence. Furongian from Nevada, USA, and Southeastern British Columbia, Canada.

Genus ***Angelina*** Salter in Murchison, 1859

1938. *Keidelaspis* Harrington, 1937 — Harrington, p. 199 (based on synonymy of the type species with *Angelina steinmanni* Salter in Murchison, 1859).

Type species. (Designated by Vogdes, 1890) *Angelina sedgwickii* Salter in Murchison, 1859, *Angelina sedgwicki* Zone, Tremadocian, North Wales.

Remarks. A diagnosis for *Angelina* was provided by Henningsmoen (1957). Then Robison and Pantoja-Alor (1968) modified it to include both species without pygidial border spines and those with spines. The genus includes five species: *An. sedgwickii* (see synonymy in SI6); *An. hyeronimi* (Kayser, 1876) (see synonymy in SI6); *An. kayseri* Harrington and Leanza, 1957; *An. punctolineata* Kobayashi, 1937; and *An. spinosa* Robison and Pantoja-Alor, 1968. Additionally, two other species were tentatively assigned to *Angelina*: *An.*? *latifrons* (Wilson, 1954) and *An.*? *vexata* (Salter, 1866).

Geographic and Stratigraphic Occurrence. *Angelina* is a Furongian and Lower Ordovician (Tremadocian) genus, mainly distributed in South America. The genus was reported from the Furongian of Famatina, Argentina (Harrington & Leanza, 1957; Tortello & Esteban, 2007); Oaxaca, Mexico (Robison & Pantoja-Alor, 1968); and the Holy Cross Mountains, Poland (Żylińska, 2001, 2002). It was recorded from the Furongian and Early Tremadocian of Northwestern Argentina and Bolivia (*e.g.*, Harrington & Leanza, 1957; Vaccari *et al.*, 2018). Additionally, *Angelina* is known from the Tremadocian of North Wales (Lake, 1919; Fortey & Owens, 1992a), Northwestern Canada (Pratt, 1988), and probably from Texas, USA (Wilson, 1954).

Genus ***Apoplanias*** Lochman, 1964

Type species. *Apoplanias rejectus* Lochman, 1964, Furongian/Tremadocian transition, Williston Basin, Montana.

Remarks. Lochman (1964) described the only species included in the genus, *Apoplanias rejectus* (see synonymy in SI6), and assigned it to Olenidae. Then, Ludvigsen (1982) discussed and illustrated the genus, providing a diagnosis. Ludvigsen also assigned it to Oleninae, noting its similarity to *Parabolinella* Brøgger, 1882 and *Highgatella* Shaw, 1955.

Geographic and Stratigraphic Occurrence. *Apoplanias* is a Furongian and Lower Ordovician (Tremadocian) genus, recorded from the homonymous Zone in North America (Miller *et al.*, 2012). It was recorded from Alberta (Derby *et al.*, 1972; Dean, 1978; Loch *et al.*, 1993) and British Columbia (Ludvigsen, 1982), Canada; and from Montana, Virginia, Oklahoma (Stitt, 1971, 1977), and Wyoming (Lochman, 1964; Hu, 1971, 1973), USA.

Genus ***Baikonuraspis*** Ergaliev, 1983

Type species. *Baikonuraspis multisegmentatus* Ergaliev, 1983, Tremadocian, Karasuir Formation, Kazakhstan.

Remarks. Ergaliev (1983) provided a diagnosis for *Baikonuraspis* and described the only species included in it, *Baikonuraspis multisegmentatus*. Originally, Ergaliev assigned the genus to the family Papyriaspididae. However, Jell and Adrain (2003) transferred it to Olenidae, based on the morphological features observed in the illustration of *B. multisegmentatus* (Ergaliev, 1983, pl. 6, figs. 3–4). This criterion is followed here.

Geographic and Stratigraphic Occurrence. Lower Ordovician (Tremadocian) from Karasuir Formation, Ulytau region, Kazakhstan.

Genus ***Bulbolenus*** Xiang and Zhang, 1985

Type species. *Bulbolenus bellus* Xiang and Zhang, 1985, *Bulbolenus* Zone, Stage 10, Western Tianshan, Northwestern Xinjiang, China.

Remarks. The genus is characterized by the presence of a boss in front of the cranidial border. Fortey and Owens (1997) reconstructed the cranidium of *Bu. bellus* based on the illustration of Xiang and Zhang (1985, pl. 33, figs. 1, 3, 5). Xiang and Zhang (1985) described some trends in the ontogeny from the meraspid to the holaspid stage. Late-stage specimens have a more developed boss in the cranidial border, a shorter cranidium and a narrower or absent anterior cranidial border. The genus is used as a marker for the late Furongian, defining the *Bulbolenus* Zone in the North Tianshan region of Northwestern Xinjiang (Xiang & Zhang, 1985; Zhan, 2003). The genus includes three species: *Bu. bellus*; *Bu. opimus* Xiang and Zhang, 1985; and *Bu. microbulbus* Xiang and Zhang, 1985.

Geographic and Stratigraphic Occurrence. *Bulbolenus* is a late Furongian genus, recorded in the homonymous Zone in Western Tianshan, Northwestern Xinjiang, China.

Genus ***Chekiangaspis*** Lu in Qian, 1961

Type species. *Chekiangaspis chekiangensis* Lu in Qian, 1961, *Eolotagnostus scrobicularis-Jegorovaia* Zone, Stage 10, Sandu Formation, Guizhou, China.

Remarks. *Chekiangaspis* was assigned to Olenidae by Lu and Lin (1989). The genus includes five species: *C. chekiangensis*;

C. sanduensis Li in Yin and Li, 1978; *C. karatauensis* Ergaliev, 1980*; C. concavus* Jell *et al.*, 1991 and *C. subcuadrata* Peng, 1992.

Geographic and Stratigraphic Occurrence. Furongian from Guizhou (Qian, 1961; Yin & Li, 1978), Zhejiang (Lu & Lin, 1989), and Northwestern Hunan (Peng, 1992; Peng & Babcock, 2001), China; the Karatau Range, Kazakhstan (Ergaliev, 1980; Ergaliev & Ergaliev, 2008); and Tasmania, Australia (Jell *et al.*, 1991).

Genus ***Claycreekia*** Chatterton and Gibb, 2016

Type species. *Claycreekia chrisorum* Chatterton and Gibb, 2016, *Taenicephalus* Zone, Jiangshanian, British Columbia, Canada.

Remarks. Chatterton and Gibb (2016) created the new genus *Claycreekia* to include only one species. This tiny spinous olenid is very similar to *Aciculolenus* and they were probably sister taxa. However, they differ in several characters, the most obvious being the absence of integral spines in *Claycreekia*. Chatterton and Gibb (2016) highlighted the resemblance between this new genus and *Parabolina* Salter, 1849 and *Ctenopyge* Linnarsson, 1880 but they did not assign it to any subfamily within Olenidae. Here, due to the general resemblance, especially to the early ontogenetic stages of *Parabolina* (see Clarkson *et al.*, 1997), it is tentatively placed in the Oleninae subfamily.

Geographic and Stratigraphic Occurrence. Furongian of Southeastern British Columbia, Canada.

Genus ***Hancrania*** Kobayashi, 1962

Type species. *Hancrania brevilimbata* Kobayashi, 1962, *Hancrania brevilimbata* Zone, Paibian, Black Shales of Suang-dong, South Korea.

Remarks. A description of *Ha. brevilimbata* and its geographic and stratigraphic distribution can be found in Lee and Choi (1994, 1995). Hwang *et al.* (2000) discuss the morphology and the ontogeny of this species.

Geographic and Stratigraphic Occurrence. Furongian of Suang-dong, South Korea.

Genus ***Helieranella*** Baldis and Gonzáles in Baldis *et al.*, 1984

Type species. *Helieranella negritoensis* Baldis and Gonzáles in Baldis *et al.*, 1984, Tremadocian, Llanos Orientales Basin, Colombia.

Remarks. Baldis *et al.* (1984) described the only species of *Helieranella* obtained from a drilling in Colombia. The authors provided a diagnosis and brief comparison with other olenids such as *Parabolinella*, *Bienvillia* Clark, 1924, and *Leiobienvillia* Rasetti, 1954. The authors initially placed this genus in the subfamily Triarthrinae *sensu* Poulsen (in Moore, 1959). However, subsequent reviews of the diagnostic characters of the subfamily Triarthrinae (Fortey, 1974; Ludvigsen & Tuffnell, 1994) revealed that *Helieranella* lacks specific diagnostic features. As a result, it was assigned to Oleninae due to its overall resemblance to other genera within that group.

Geographic and Stratigraphic Occurrence. Lower Ordovician (Tremadocian) of Negritos Formation, Llanos Orientales Basin, Colombia.

Genus ***Highgatella*** Shaw, 1955

Type species. *Terranovella gelasinata* Shaw, 1951, Tremadocian, Northwestern Vermont, USA.

Remarks. *Highgatella* was first described by Shaw (1955) to include one species he had previously described (*Terranovella gelasinata*). The genus was included in the family Ptychopariidae (Shaw, 1955; Stitt, 1977; Loch *et al.*, 1993). However, Jell and Adrain (2003) listed it as an Olenidae. The similarity between *Highgatella* and *Apoplanias* pointed out by Ludvigsen (1982) suggests that this genus may belong to Oleninae. *Highgatella* includes two other species beyond the type: *Hi. cordilleri* (Lochman, 1964) and *Hi. wilsoni* Derby in Loch *et al.* 1993.

Geographic and Stratigraphic Occurrence. Furongian and Lower Ordovician (Tremadocian) of North America. The genus was recorded from the Furongian of Utah (Miller *et al.*, 2003; Adrain & Westrop, 2006) and Texas (Barnes & Bell, 1977), USA. *Highgatella* is also known from the latest Furongian and Tremadocian of Newfoundland (Whittington, 1968; Fortey & Skevington, 1980) and Alberta (Aitken & Norford, 1967; Dean, 1989; Loch *et al.*, 1993), Canada. Finally, species of this genus were found in the Tremadocian of Vermont (Shaw, 1951, 1958), Montana (Lochman, 1964), New Mexico (Taylor & Repetski, 1995), and Nevada (Cook *et al.*, 1989), USA.

Genus ***Leptobenthos*** Tortello and Esteban, 2003b

Type species. *Leptobenthos roartei* Tortello and Esteban, 2003b, Tremadocian, La Rioja, Argentina.

Remarks. *Leptobenthos* was named by Tortello and Esteban (2003b), and assigned to the subfamily Oleninae.

Geographic and Stratigraphic Occurrence. Lower Ordovician of Famatina, Argentina.

Genus ***Neoolenus*** Liu, 1982

Type species. *Neoolenus minor* Liu, 1982, Lower Ordovician, Hunan, China.

Remarks. The genus *Neoolenus* was established by Liu (1982) based on specimens from Hunan, China. The general morphology of the cranidium, selected as holotype by Liu (1982, pl. 236, fig. 7), aligns with certain olenines, such as *Olenus* and *Parabolinella*. However, the genus was poorly illustrated, and the morphology of the thorax and pygidium remained unknown, making it difficult to assign it to a specific group. For the time being, this genus is tentatively placed within Oleninae, pending further information.

Geographic and Stratigraphic Occurrence. Lower Ordovician from Hunan, China.

Genus ***Nikarivshanus*** Petrunina, 2002

Type species. *Nikarivshanus miraculus* Petrunina, 2002, Zolotokitatsky horizon, Furongian, Kuznetsk Alatau Russia.

Remarks. Petrunina (2002) created the genus *Nikarivshanus* for the species *N. miraculus*. This species was included in the subfamily Oleninae, due to its similarities with *Plicatolina* Shaw, 1951 and *Wujiajiania* Lu and Lin, 1980, which were also considered Oleninae. However, the author also pointed out the morphological similarities with the pygidium of the pelturinid *Acerocare*.

Geographic and Stratigraphic Occurrence. Furongian (Zolotokitatsky horizon) of Northwest of Kuznetsk Alatau, Russia.

Genus ***Olenus*** Dalman, 1827

1992. *Simulolenus* Palmer, 1965 — Pratt.

Type species. *Entomostracites gibbosus* Wahlenberg, 1818.

Remarks. The name *Olenus* was proposed by Dalman (1827) to replace *Paradoxides* Brongniart, 1822. Henningsmoen (1957) provided a detailed taxonomic history of the name *Olenus*, and the list of synonyms. Henningsmoen's work also included a diagnosis of the genus, a list of included species, comments, and occurrence up to that time. Since then, new species of *Olenus* have been documented from Australia (*e.g.*, Whitehouse, 1939; Öpik, 1963; Jago, 1978; Jell *et al.*, 1991) and China (Lu & Qian, 1983; Lu & Lin, 1989; Peng, 1992). Additionally, the description of *Olenus gibbosus* Zone in England (Rushton, 1983), and the re-evaluation of the types of several species of *Olenus* and its stratigraphical significance in Baltica (*e.g.,* Żylińska, 2001; Lauridsen & Nielsen, 2005; Terfelt *et al.*, 2008; Rasmussen *et al.*, 2017; Nielsen *et al.*, 2020; Nielsen & Andersen, 2021) have completed the description and extension of *Olenus*. On the other hand, some species, which were named based on poor materials, have no further mentions in the scientific literature.

Currently, *Olenus* includes 34 species: *O. gibbosus*; *O. alpha* Henningsmoen, 1957; *O. solitarius* (Westergård, 1922) (see synonymy in SI6); *O. cataractes* Salter, 1864; *O. dentatus* Westergård, 1922; *O. scanius* Westergård, 1922; *O. henningsmoeni* Ahlgren and Ahlberg, 1996; *O. micrurus* Salter, 1849; *O. mundus* Lake, 1908; *O. rotundatus* Westergård, 1922; *O. transversus* Westergård, 1922; *O. truncatus* (Brünnich, 1781); *O. wahlenbergi* Westergård, 1922; *O. veles* Rushton, 1983; *O. austriacus* Yang in Zhou *et al.,* 1977; *O. attenuatus* (Boeck, 1838); *O. ogilviei* Öpik, 1963; *O. delicatus* Öpik, 1963; *O. asiaticus* Kobayashi, 1944; *O. altaicus* Ivshin in Khalfin, 1960; *O. apoxysomatus* Jell *et al.*, 1991; *O. guizhouensis* Lu and Qian in Yin and Li, 1978; *O. proximus* Lazarenko, 1966; *O. sinensis* Lu, 1964; *O. haimantensis* Reed, 1910; *O. wilsoni* Henningsmoen, 1957; *O. granulatus* Palmer, 1960; *O. quadrisulcatus* (Palmer, 1965); *O. amplus* Buchholz, 2003; *O. erraticus* Buchholz, 1991; *O. intermedius* Lin and Zhang in Zhu *et al.*, 1979; *O. matures* Buchholz, 2003; *O. punctatus* Peng *et al.*, 2004; and *O. sibiricus* Ivshin in Khalfin, 1960.

Geographic and Stratigraphic Occurrence. *Olenus* is a cosmopolitan Furongian genus. It is well known in several localities from Norway, Sweden, and Bornholm, Denmark (Westergård, 1922; Henningsmoen, 1957; Lauridsen & Nielsen, 2005; Terfelt *et al.*, 2008; Rasmussen *et al.*, 2017; Nielsen *et al.*, 2020; Nielsen & Andersen, 2021), and from North Wales and Central England (Lake, 1908; Rushton,

1983). It also been reported from Glacial Erratic Boulders (Geschiebes) in the coast of Mecklenburg and western Pomerania, Northern Germany (Buchholz, 1991, 2003, 2008); and from the Holy Cross Mountains, Poland (Żylińska, 2001). In Asia, *Olenus* is known from South Korea (Kobayashi, 1944; Lee & Choi, 1994; Choi & Lee, 1995); Kyrshabakty River, Kazakhstan (Ergaliev & Ergaliev, 2008); Hunan, Guizhou, Zhejiang, and Minle County, Gansu Province, China (Lu, 1964; Lu *et al.*, 1974; Yin & Li, 1978; Zhou *et al.*, 1977; Zhu *et al.*, 1979; Yang, 1978; Lu & Qian, 1983; Lu & Lin, 1989; Peng, 1992; Peng *et al.*, 2004); Himalaya, India (Reed, 1910; Shah *et al.*, 1991); and Altai Mountains, Kaliningrad region, and Kharaulakh Range, Sakha Republic, Russia (Khalfin, 1960; Lazarenko, 1966; Karpuzova & Tokareva, 2014). Finally, this genus was found in Tasmania and Northwestern Queensland, Australia (Öpik, 1963; Jell *et al.*, 1991); and in Texas and Nevada, USA (Palmer, 1960, 1965; Cook *et al.*, 1989; Pratt, 1992).

Genus ***Parabolina*** Salter, 1849

1957. *Odontopyge* Corda in Hawle and Corda, 1847 — Henningsmoen, p. 8 (homonym of *Odontopyge* Brandt, 1841).

Type species. *Entomostracites spinulosus* Wahlenberg, 1818, *Leptoplastus paucisegmentatus* Zone, Jiangshanian, Alum Shale, Sweden.

Remarks. *Parabolina* comprises several species which serve as markers for different Furongian biozones worldwide. Diagnosing this genus has been challenging due to the significant morphological variation among its species. Henningsmoen (1957) was the first to provide a diagnosis and a list of species with synonymy for *Parabolina*. However, subsequent adjustments were made to account for the morphological variation and the inclusion of new species (see Rushton, 1982; Nikolaisen & Henningsmoen, 1985).

Nikolaisen and Henningsmoen (1985) introduced the subgenus *Neoparabolina* Nikolaisen and Henningsmoen, 1985, with *P. frequens* (Barrande, 1868) as the type species and provided diagnoses for both the new and nominate subgenera. However, distinguishing between subgenera is possible only when complete specimens are available, and therefore, many species lack subgeneric assignment. Given the significant morphological variation, three species assigned to *Parabolina* (*P. heres* Brøgger, 1882, *P. lobata* [Brøgger, 1882] and *P. frequens*) were subdivided into subspecies. Rushton (1982) reviews the *P. heres* group, providing diagnostic characters and discussing the three subspecies belonging to it. The *P. lobata* group includes two subspecies (Henningsmoen, 1957), distributed in Norway, Sweden, and Germany (Terfelt *et al.,* 2005). The *P. frequens* group was divided into three subspecies (*P. frequens frequens* [Barrande, 1868], *P. frequens argentina* [Kayser, 1876] and *P. frequens finnmarchica* Nikolaisen and Henningsmoen, 1985), but there is some disagreement regarding their validity. Żylińska (2001) compared the morphological variation of these subspecies and considered them within the range of variation of *P. frequens*, making the subspecies division unnecessary. Other authors considered *P. frequens argentina* as a valid taxon (Přibyl & Vaněk, 1980; Waisfeld & Vaccari, 2003; Tortello & Clarkson, 2008). Given these discrepancies and the fact that several species have been described from fragmentary material or lack adequate illustrations, a comprehensive revision of all taxa included in this genus is needed.

This work provides a summary of the genus *Parabolina*, which includes eight species divided into two subgenera. The subgenus *Parabolina* includes six species, one with two subspecies and one with three subspecies: *P.* (*P.*) *acanthura* Angelin, 1854; *P.* (*P.*) *spinulosa spinulosa* (see synonymy in Sl6); *P.* (*P.*) *spinulosa spinulosaformis* Ivshin, 1962; *P.* (*P.*) *heres heres*; *P.* (*P.*) *heres lata* Matthew, 1892 (see synonymy in Sl6); *P.* (*P.*) *heres megalops* Moberg and Möller, 1898; *P.* (*P.*) *kinnekullensis* Henningsmoen, 1957; *P.* (*P.*) *kobayashii* Harrington and Leanza, 1957; and *P.* (*P.*) *laciniata* Nikolaisen and Henningsmoen, 1985. The subgenus *Neoparabolina* includes two species, one comprises three subspecies and the other two subspecies: *P.* (*N.*) *frequens frequens* (see synonymy in Sl6); *P.* (*N.*) *frequens argentina* (see synonymy in Sl6); *P.* (*N.*) *frequens finnmarchica*; *P.* (*N.*) *lobata lobata* (see synonymy in Sl6); and *P.* (*N.*) *lobata praecurrens* Westergård, 1944. The remaining thirteen species were either not assigned to any subgenus or were tentatively assigned to one: *P.* (*P.*?) *jemtlandica* Westergård, 1922; *P.* (*N.*?) *dawsoni* Matthew, 1901 (see synonymy in Sl6); *P.* (*N.*?) *lapponica* Westergård, 1947 (see synonymy in Sl6); *P. brevispina* Westergård, 1922; *P. cylindrica* Lin and Zhang in Zhu *et al.*,

1979; *P. discreta* Buchholz, 1997; *P. laticauda* Buchholz, 2004; *P. mobergi* Westergård, 1922; *P. magna* Pokrovskaya, 1967; *P. monstruosa* Pokrovskaya, 1967; *P. angusta* Pokrovskaya, 1967; *P. sinuata* Petrunina, 2002; and *P. tetracanthura* (Matthew, 1892). Additionally, one species has been assigned with doubt to the genus: *P.? quadrisulcata* Henningsmoen, 1957.

Geographic and Stratigraphic Occurrence. *Parabolina* is a cosmopolitan mostly Furongian genus. It has been recorded from the Furongian in different localities in Norway and Sweden, and from Bornholm, Denmark (*e.g.*, Westergård, 1922, 1944; Henningsmoen, 1957; Terfelt *et al.*, 2005; Terfelt, 2006); North Wales (Rushton, 1982); the Holy Cross Mountains, Poland (Żylińska, 2001, 2002); Glacial Erratic Boulders (Geschiebes) in Western Pomerania, Northern Germany (Buchholz, 1997, 2004). Additional records come from Nova Scotia, Newfoundland, and New Brunswick, Canada (Matthew, 1892); South America (Harrington & Leanza, 1957; Přibyl & Vaněk, 1980; Esteban & Tortello, 2007; Waisfeld & Vaccari, 2008); Oaxaca, Mexico (Robison & Pantoja-Alor, 1968); and from the northern section of Verkhoyansk, Yakutia (Pokrovskaya, 1967; Lazarenko *et al.*, 2011), the Northwest of the Kuznetsk Alatau (Petrunina, 2002), and Yaroslavl Oblast (Karpuzova & Tokareva, 2014), Russia. *Parabolina* is also known from the Furongian of the Karatau range and Central Kazakhstan, Kazakhstan (Ivshin, 1962); Minle County, Gansu Province, China (Zhu *et al.*, 1979); and Spain (Aceñolaza *et al.*, 2014). Finally, species of *Parabolina* have been reported from the lower Tremadocian of the Digermul Peninsula, Finnmark, Norway (Nikolaisen & Henningsmoen, 1985); the Leimitz Shales, Germany (Sdzuy, 1955); the Prague Basin, Czech Republic (Havlicek & Vanek, 1966); and Venezuela (Frederickson, 1958).

Genus ***Parabolinella*** Brøgger, 1882

1957. *Moxomia* Walcott, 1924 — Harrington and Leanza, 1957, p. 105–106.

Type species. *Parabolinella limitis* Brøgger, 1882, *Ceratopyge* shales, Tremadocian, Oslo, Norway.

Remarks. *Parabolinella* has been extensively discussed by Henningsmoen (1957), Harrington and Leanza (1957), and Rushton (1988). More recently, Monti and Confalonieri (2013, 2017) explored the phylogenetic relationships within the genus, provided a comprehensive list of included species, and emended the diagnosis considering synapomorphic characters. The list presented in this paper includes minor updates, with a total of nineteen species assigned to the genus and seven doubtful assignations: *Pa. limitis*; *Pa. argentinensis* Kobayashi, 1936; *Pa. triarthroides* Harrington, 1938; *Pa. coelatifrons* Harrington and Leanza, 1957; *Pa. boliviana* Juarez Huarachi, 2010 (see synonymy in Sl6); *Pa. clarisae* Monti *et al.*, 2016; *Pa. triarthra* (Callaway, 1877) (see synonymy in Sl6); *Pa. prolata* Robison and Pantoja-Alor, 1968 (see synonymy in Sl6); *Pa. tumifrons* Robison and Pantoja-Alor, 1968; *Pa. variabilis* Robison and Pantoja-Alor, 1968; *Pa. hunanensis* Peng, 1991; *Pa. jiangnanensis* Lu and Lin, 1984; *Pa. lata* Henningsmoen, 1957; *Pa. contracta* Lu and Zhou in Lu *et al.*, 1981 (see synonymy in Sl6); *Pa. bolbifrons* Fortey and Owens, 1997; *Pa. hecuba* (Walcott, 1924); *Pa. tarijensis* Juarez Huarachi, 2010; *Pa. edaochuanensis* Lu *et al.*, 1986; *Pa. paijiensis* Liu, 1982; *Pa.? caesa* Lake, 1913; *Pa.? incerta* (Rasetti, 1945) (see synonymy in Sl6); *Pa.? punctolineata* Kobayashi, 1936; *Pa.? simplex* (Salter, 1866); *Pa.? latilimbata* Lu and Chen in Yin and Li, 1978; *Pa.? belli* Matthew, 1902; and *Pa.? posthuma* Matthew, 1892.

Geographic and Stratigraphic Occurrence. *Parabolinella* is a cosmopolitan genus recorded from the Furongian and Lower Ordovician (Tremadocian). It has been described from the Furongian of Famatina, Argentina (Harrington & Leanza, 1957; Tortello & Esteban, 1999); Oaxaca, Mexico (Robison & Pantoja-Alor, 1968); the Holy Cross Mountains, Poland (Żylińska, 2001, 2002); Northwestern Canada (Kobayashi, 1936; Lee & Chatterton, 2007), Quebec (Rasetti, 1945), Canada; and Nevada, USA (Ross, 1970; Cook *et al.*, 1989; Lee & Chatterton, 2007). Species of *Parabolinella* were also described from the Furongian and Tremadocian of Sweden (*e.g.*, Westergård, 1922; Henningsmoen, 1957; Terfelt & Alhgren, 2009); South Wales (Owens *et al.*, 1982); the Lake District (Rushton, 1988) and Breadstone, Gloucestershire (Fortey & Owens, 1997), England; Northwestern Argentina and Bolivia (*e.g.*, Kobayashi, 1936, 1937; Harrington, 1938; Harrington & Leanza, 1957; Přibyl & Vaněk, 1980; Juarez Huarachi, 2010); Vermont and Texas, USA (Shaw, 1951, 1958; Wilson, 1954); and Yumen, Western Gansu, and West of Nei Mongol, China (Lu *et al.*, 1986; Rushton, 1988).

In addition, the genus has been cited from the Tremadocian of Norway (Owen *et al.*, 1990; Henningsmoen, 1957, 1959); West of Hunan, Xiangshan, Jiangshan, Changshan, Northwestern Xinjiang, Western Gansu, and Guangxi, China (*e.g.*, Zhang & Fan, 1960; Lu *et al.*, 1981; Liu, 1982; Lu & Lin, 1984; Xiang & Zhang, 1984; Peng, 1991; Zhou & Zhen, 2008); Nova Scotia, Western Newfoundland, British Columbia, and West of Mackenzie District, Canada (Walcott, 1924; Henningsmoen, 1957; Fortey in Fortey *et al.*, 1982; Ludvigsen, 1982); Southern Tasmania, Australia (Bao & Jago, 2000); Kazakhstan; and probably Russia (Henningsmoen, 1957).

Genus ***Parabolinina*** Lazarenko, 1966

Type species. *Parabolinina edita* Lazarenko, 1966, *Irvingella* Zone, Jiangshanian, Northern Siberia, Russia.

Remarks. Lazarenko (1966) established the genus *Parabolinina* to include the species *Parabolinina edita*. Varlamov *et al.* (2006) transferred the species *Parabolinella*? *fortunata* Lazarenko, 1966 to this genus due to several characteristics of the pygidium. Therefore, the genus includes two species: *Parabolinina edita* and *Parabolinina fortunata*.

Geographic and Stratigraphic Occurrence. Furongian of Khos-Nelege and Olenek sections, Verkhoyansk Range (Kharaulakh Range), Yakutia, Russia.

Genus ***Parabolinites*** Henningsmoen, 1957

Type species. *Parabolinella laticauda* Westergård, 1922, *Peltura* Zone, Stage 10, Alum Shale, Sweden.

Remarks. The genus *Parabolinites* was first described by Henningsmoen (1957). However, many of the species listed at that time were uncertain due to the poor quality of the specimens. Later, additional well-known species from Russia, China, and Kazakhstan were assigned to *Parabolinites* (*e.g.*, Pokrovskaya, 1967; Lazarenko, 1966; Ergaliev, 1980; Xiang & Zhang, 1985), which extend the description and representation of the genus. A total of eight species were included with certainty in the genus *Parabolinites*: *Par. laticaudus*; *Par. rectus* Pokrovskaya, 1967; *Par. levis* Lazarenko, 1966; *Par. bisulcatus* Ergaliev, 1980; *Par. borohoroensis* (Xiang and Zhang, 1985); *Par. henningsmoeni* Petrunina, 2002; *Par. qilianensis* Lin and Zhang in Zhu *et al.*, 1979; *Par. williamsoni* (Belt, 1868) (see synonymy in SI6). Also, two species were assigned with doubt to the genus: *Par.*? *longispinus* (Belt, 1868) and *Par.*? *leptoplastorum* (Westergård, 1947).

Geographic and Stratigraphic Occurrence. Furongian of Sweden (Westergård, 1922; Henningsmoen, 1957); Wales (Henningsmoen, 1957); Northwest of the Kuznetsk Alatau (Petrunina, 2002) and the Verkhoyansk Range (Kharaulakh Range), Yakutia, Russia (Lazarenko, 1966; Pokrovskaya, 1967; Lazarenko *et al.*, 2011); Kyrshabakty River and the Karatau Range, Kazakhstan (Ergaliev, 1980; Ergaliev & Ergaliev, 2008); Western part of Northern Tianshan, Xinjiang (Xiang & Zhang, 1985; Rushton, 1988), and Minle County, Gansu Province (Zhu *et al.*, 1979), China. *Parabolinites* was also mentioned with doubt from the Furongian of the Holy Cross Mountains, Poland (Żylińska, 2001, 2002).

Genus ***Paraolenus*** Lermontova, 1951

Type species. *Paraolenus papilionaceus* Lermontova, 1951, Bala-Shiderta horizon, Stage 10, Bosche-Kul, Northeastern Kazakhstan.

Remarks. There is limited information available on *Paraolenus*, beyond Lermontova's original description. Lermontova (1951) tentatively assigned this genus to the Oleninae but noted that the combination of characters might suggest its inclusion into another subfamily.

Geographic and Stratigraphic Occurrence. Furongian of Bosche-Kul, Northeastern Kazakhstan.

Genus ***Remizites*** Ivshin and Ergaliev in Ergaliev, 1983

Type species. *Remizites anni* Ivshin in Ergaliev, 1983, Zolotokitatsky Horizon, Stage 10, Kuznetsk Alatau, Russia.

Remarks. Ergaliev (1983) provided a diagnosis for *Remizites* and assigned it to the subfamily Oleninae, including two species: *Remizites anni* and *Remizites bolati* Ergaliev, 1983.

Geographic and Stratigraphic Occurrence. Furongian and Lower Ordovician of the Kuznetsk Alatau, Russia; and the Bolshoi Karatau and South Ulutau, Kazakhstan.

Genus ***Rhodonaspis*** Whitehouse, 1939

Type species. *Rhodonaspis longula* Whitehouse, 1939, Mindyallan, Guzhangian, Queensland, Australia.

Remarks. Öpik (1963) provided the diagnosis of *Rhodonaspis*. While the author noted its morphological similarities with *Parabolina* and *Olenus*, they placed this genus within the new olenid subfamily Rhodonaspidinae. However, the validity of this subfamily was not recognized later (Adrain, 2011), and no other genera have been assigned to it. Therefore, based on the similarities mentioned with members of the Oleninae, *Rhodonaspis* is tentatively assigned to Oleninae. The genus is monospecific, including only *Rhodonaspis longula* (see synonymy in SI6).

Geographic and Stratigraphic Occurrence. *Rhodonaspis* was recorded from the Miaolingian (upper Guzhangian), in Queensland, Australia; and in Northwestern Fenghuang, Hunan, China.

Genus ***Ullaspis*** Westergård, 1948

Type species. *Ullaspis conifrons* Westergård, 1948, *Lejopyge laevigata* Zone, Guzhangian, Sweden.

Remarks. Westergård (1948) described the species *Ullaspis conifrons* and erected a new genus to accommodate it. Although he noted some similarities with the family Olenidae, he decided to leave it as an uncertain family. Later, Jell and Adrain (2003) listed *Ullaspis* as part of the Olenidae. Based on its morphological characteristics (Westergård, 1948, pl. 4, figs. 14–15), *Ullaspis,* which includes two species (*U. conifrons* and *U. granifer* Buchholz, 1997), is tentatively assigned to the subfamily Oleninae.

Geographic and Stratigraphic Occurrence. Upper Miaolingian (Early Guzhangian), from Sweden (Westergård, 1948); and the Miaolingian in Glacial Erratic Boulder (Geschiebes) from Northern Germany (Buchholz, 1997, 2010).

Subfamily PELTURINAE Hawle and Corda, 1847

Genus ***Acerocare*** Angelin, 1854

Type species. *Acerocare ecorne* Angelin, 1854, *Acerocare* Zone, Stage 10, Sandby, Sweden.

Remarks. Henningsmoen (1957) provided a diagnosis for this genus and included two Swedish species. Lermontova (1951) assigned one fragmentary specimen to *Acerocare* based on characters found on a fragmentary cranidium. More recently, Petrunina (2002) created the subgenus *Sibacerocare* Petrunina, 2002 based on pygidial characters. This subgenus includes two new Siberian species described by Petrunina along with Lermontova's species. Although several specimens from different parts of the world were assigned to *Acerocare*, they were not given a species designation. Currently, *Acerocare* includes: *Ac. ecorne*; *Ac. tulbergi* Moberg and Möller, 1898; *Ac. optandum* Petrunina, 2002; *Ac. donatum* Petrunina, 2002; and *Ac. angustifrons* Lermontova, 1951.

Geographic and Stratigraphic Occurrence. *Acerocare* is a Furongian genus, recorded in the *Acerocare* Zone from Sweden (*e.g.*, Westergård, 1922, 1944; Moberg & Möller, 1898) and Norway (*e.g.*, Henningsmoen, 1957; Bruton *et al.*, 1982, 1988); from the northwest of the Kuznetsk Alatau and Northeastern Salair, Siberia, Russia (Petrunina, 2002); and from Bosche-Kul, Northern Kazakhstan (Lermontova, 1951). *Acerocare* was also mentioned with doubt from New Brunswick, Canada (Landing *et al.*, 1978); and the Holy Cross Mountains, Poland (Żylińska, 2001).

Genus ***Acerocarina*** Poulsen, 1952

1952. *Cyclognathus* Linnarsson, 1875a — Poulsen (homonym of *Cyclognathus* Saint-Hillaire, 1833).

Type species. *Cyclognathus micropygus* Linnarsson, 1875a, *Acerocare* Zone, Stage 10, Sweden.

Remarks. Henningsmoen (1957) provided a diagnosis of *Acerocarina*, along with a comprehensive summary of its taxonomic history and the description of two Baltic species. Later, additional species from Poland (Żylińska, 2001) and Russia (Antsygin, 2001) were included in the genus. In total, *Acerocarina* includes four species: *Acerocarina micropyga*; *Acerocarina granulata* (Moberg and Möller, 1898); *Acerocarina klonowkae* (Orłowski, 1968); and *Acerocarina keisaranica* (Antsygin, 2001).

Geographic and Stratigraphic Occurrence. *Acerocarina* is a Furongian genus, recorded from the *Acerocare* Zone of Sweden (Moberg & Möller, 1898; Westergård, 1922; Terfelt *et al.*, 2005); Norway (Henningsmoen, 1957); and the Holy Cross Mountains, Poland (Żylińska, 2001, 2002). Also, the genus was mentioned from the Tremadocian of the South Urals Mountains, Russia (Antsygin, 2001; Bergström *et al.*, 2013); and with doubt from Germany.

Genus ***Anaximander*** Fortey, 1974

Type species. *Anaximander clavatus* Fortey, 1974, *protobifidus* subzone, Floian, Valhallfonna Formation, Spitsbergen, Norway.

Remarks. Fortey (1974) provided an extensive discussion on *Anaximander*, which included its diagnosis and potential relationships with other pelturinids. However, Nikolaisen and Henningsmoen (1985) considered *Anaximander* as related to *Bienvillia*, from which it is derived. Consequently, they excluded this genus from Pelturinae and placed it within the Triarthrinae.

Geographic and Stratigraphic Occurrence. Lower Ordovician (Floian), on the type locality, Blackhillsian (Ibexian), Valhallfonna Formation, Spitsbergen, Norway. One specimen possibly assignable to *Anaximander* was also reported from the Tremadocian of Shallow Bay Formation, in the Cow Head Peninsula, Canada (Karim, 2009).

Genus ***Boeckaspis*** Henningsmoen, 1955

1955. *Boeckia* Brøgger 1882 — Henningsmoen (homonym of *Boeckia* Malm, 1870).
1957. *Sphaerophthalmoides* Hutchinson, 1952 — Henningsmoen, p. 253.
2008. *Westergaardia* Raymond, 1924 — Karim, p. 409.

Type species. *Boeckia hirsuta* Brøgger, 1882, Tremadoc Series, Naersnes, Norway.

Remarks. Henningsmoen (1955) provided the first diagnosis of *Boeckaspis* and discussed its relationship with other pelturinids (see also Henningsmoen, 1957). Later, Karim (2008) emended the original diagnosis and provided a more extensive, updated discussion. The author also included a list of species and a formal phylogenetic analysis of *Boeckaspis*. Henningsmoen (1957) explored the potential relationship between *Sphaerophthalmella* Kobayashi, 1955 and *Boeckaspis*, suggesting that they might be congeneric. *Sphaerophthalmella* is only known by two cranidia illustrated by Kobayashi (1955, pl. VII, figs. 10–11). These illustrations lack clarity, which prevents the assignment of this material to *Boeckaspis*.

The genus currently comprises nine species and one tentatively assigned: *Bo. hirsuta*; *Bo. mobergi* (Wiman, 1905) (see synonymy in SI6); *Bo. astricta* Nikolaisen and Henningsmoen, 1985 (elevated to species by Karim [2008]); *Bo. geordii* Karim, 2008; *Bo. ornata* (Hutchinson, 1952); *Bo. scania* (Westergård, 1909); *Bo. lata* (Matthew, 1892) (see synonymy in SI6); *Bo. intermedia* (Westergård, 1944); *Bo. kasachstanicus* Balashova, 1961; and *Bo.*? *inornata* Harrington and Kay, 1951.

Geographic and Stratigraphic Occurrence. *Boeckaspis* is a Furongian and Lower Ordovician (Tremadocian) genus. Species were reported from the Furongian of Norway; Sweden (Henningsmoen, 1957; Terfelt, 2006); Western Newfoundland, Nova Scotia, and New Brunswick, Canada (Matthew, 1892; Westergård, 1944; Hutchinson, 1952; Terfelt, 2006); and from the Tremadocian of Norway; Sweden (Henningsmoen, 1957; Bruton *et al.,* 1982; Nikolaisen & Henningsmoen, 1985); Wales (Allen *et al.*, 1981; Rushton, 1982); and Nova Scotia and Western Newfoundland, Canada (Karim, 2008). *Boeckaspis* was also reported from the Tremadocian of Aktobe region, Kazakhstan (Balashova, 1961); and probably Eastern Colombia (Harrington & Kay, 1951).

Genus ***Boeckaspina*** Petrunina, 2002

Type species. *Boeckaspina compressa* Petrunina, 2002, Tayazinsky horizon, Tremadocian, Gornaya Shoria, Russia.

Remarks. Petrunina (2002) established *Boeckaspina* to classify specimens from Siberia and included two species: *Boeckaspina compressa* and *Boeckaspina shorica* Petrunina, 2002. The author noted the strong resemblance between this new genus and *Boeckaspis*. This genus has a thin spine emerging from the posterior part of the fixigena (Petrunina, 2002, pl. 3, figs. 5, 7, 8), which could be interpreted as indicative of a proparian suture, as in *Saltaspis* Harrington and Leanza, 1952. However, all the specimens described and illustrated are small and deformed to varying degrees and directions. There is no additional information available on *Boeckaspina* and its species beyond the original description.

Geographic and Stratigraphic Occurrence. *Boeckaspina* was reported from the Lower Ordovician (Tremadocian), Tayazinsky horizon of Gornaya Shoria, south of Siberia, Russia.

Genus ***Cyclognathina*** Lermontova, 1951

Type species. *Cyclognathina microps* Lermontova, 1951, Lermontov horizon, Jiangshanian, Boshche-Kulya, Northeastern Kazakhstan.

Remarks. Lermontova (1951) created the genus *Cyclognathina* and assigned it to the subfamily Triarthrinae. Lermontova also provided a diagnosis and discussed the type species, which shares morphological features with other pelturinids like *Jujuyaspis* Kobayashi, 1936 and *Cyclognathus* (now *Acerocarina*). Later, Ivshin (1962) emended the diagnosis of *Cyclognathina*, emphasized its similarities with *Protopeltura* Brøgger, 1882, and moved it to Pelturinae. Ivshin also described new material, increasing the diversity of the group. *Cyclognathina* includes three species, one of them with two subspecies: *Cy. microps microps*; *Cy. microps elevalis* Ivshin, 1962; *Cy. truncata* Ivshin, 1962; and *Cy. sibirica* Gogin, 1990.

Geographic and Stratigraphic Occurrence. Furongian of Southern Verkhoyansk, Siberia (Gogin, 1990; Pegel, 2000, 2014); and Central Kazakhstan and Bosche-Kul, Kazakhstan (Lermontova, 1951; Ivshin, 1962).

Genus ***Feripinnus*** Petrunina, 2002

Type species. *Feripinnus magnialiger* Petrunina, 2002, Zolotokitatsky horizon, Stage 10, Orlinaya mountains, Russia.

Remarks. *Feripinnus* was established by Petrunina (2002) to include specimens from Siberia. No additional information is available beyond the original description.

Geographic and Stratigraphic Occurrence. Furongian of Northeastern Salair, Russia.

Genus ***Jujuyaspis*** Kobayashi, 1936

1985. *Alimbetaspis* Balashova, 1961 — Nikolaisen and Henningsmoen, p. 26.

Type species. *Jujuyaspis keideli* Kobayashi, 1936, Tremadocian, Purmamarca Shales, Jujuy, Argentina.

Remarks. *Jujuyaspis* is an emblematic pelturinid genus due to its biostratigraphic importance. The original description of *Jujuyaspis* was provided by Kobayashi (1936). Harrington and Leanza (1952) discussed the condition of the facial suture in the type materials and later provided a diagnosis for the genus (Harrington & Leanza, 1957). On the other hand, Petrunina (2002) created the subgenus *Nitayanzaspis* Petrunina, 2002 to include species described from Siberia. This subgenus differs from the nominative form in the presence of lateral glabellar furrows and eye ridges, a large width of the anterior parts of the fixigenae, a lower degree of divergence of the posterior branches of the facial sutures, the presence of only nine segments in the thorax and the presence of only two rings on the pygidial rachis and almost smooth pleural parts. Several species were described as belonging to *Jujuyaspis* (*e.g.*, Přibyl & Vaněk, 1980; Baldis *et al.*, 1984; Juarez Huarachi, 2010), but most of them were later synonymized (*e.g.*, Aceñolaza & Aceñolaza, 1992; Tortello & Clarkson, 2003; Vaccari *et al.*, 2018).

Currently, the genus includes six valid species, one of which has two subspecies: *J. keideli keideli* Kobayashi, 1936 (see synonymy in SI6); *J. keideli norvegica* Henningsmoen, 1957; *J. borealis* Kobayashi, 1955; *J. angusta* Henningsmoen, 1957; *J. sinensis* Zhou in Chen *et al.*, 1980; *J. kelleri* (Balashova, 1961); and *J. sibirica* Petrunina, 2002.

Geographic and Stratigraphic Occurrence. *Jujuyaspis* is a widely distributed Tremadocian genus. It was recorded from New Mexico, Utah, and Texas, USA; British Columbia and Alberta, Canada (Kobayashi, 1955; Winston & Nicholls, 1967; Norford, 1969; Westrop, 1986; Stitt & Miller, 1987; Dean, 1989; Miller & Stitt, 1995; Miller & Taylor, 1995; Taylor & Repetski, 1995; Loch *et al.*, 1999; Miller *et al.*, 2003); Northwestern Argentina, Bolivia, and Colombia (Kobayashi, 1936; Harrington, 1938; Harrington & Leanza, 1957; Přibyl & Vaněk, 1980; Baldis *et al.*, 1984; Aceñolaza & Aceñolaza, 1992); Norway (Henningsmoen, 1957; Bruton *et al.*, 1982; Nikolaisen & Henningsmoen, 1985); Hebei Province, China (Chen *et al.*, 1980; Zhou & Zhang, 1985); Aktobe, Kazakhstan (Balashova, 1961; Nikolaisen & Henningsmoen, 1985); Korea (Kim & Choi, 2000); and Gornaya Shoria, Southern Siberia (Petrunina, 2002). *Jujuyaspis* was also mentioned from Spain (Shergold & Sdzuy, 1991) and Australia (Shergold, 2000).

Genus ***Leptoplastides*** Raw, 1908

1957. *Parabolinopsis* Hoek in Steinmann and Hoek, 1912 — Henningsmoen, p. 264.
1957. *Andesaspis* Kobayashi, 1935 — Harrington and Leanza, p. 89 (synonym of *Parabolinopsis*).
1985. *Beltella* Lake, 1919 — Nikolaisen and Henningsmoen, p. 19 (and Żylińska, 2001, p. 359–360).
1989. *Chungkingaspis* Lu in Lu *et al.*, 1962 — Fortey and Owens, p. 71 (synonym of *Parabolinopsis*).
2003. *Rampartaspis* Loch in Loch *et al.*, 1993 — Adrain in Jell and Adrain, p. 438.

Type species. *Conocoryphe salteri* Callaway, 1877, Tremadocian, Shineton Shales, England.

Remarks. *Leptoplastides* was created by Raw (1908) as a subgenus of *Leptoplastus*, but later it was considered a separate genus belonging to Pelturinae (Henningsmoen, 1957). Henningsmoen (1957) provided a diagnosis for *Leptoplastides* and discussed its affinities with other related genera, considering the possibility that *Leptoplastides* and *Beltella* are synonyms. Nikolaisen and Henningsmoen (1985) confirmed that they were indeed synonyms. Consequently, they proposed an emended diagnosis for *Leptoplastides*, including the range of variation of *Beltella*. Morris (1988) followed this criterion, but Fortey and Owens (1989, 1991) rejected it. More recently, Żylińska (2001) provided an extensive discussion on that matter and concluded that *Beltella* should be referred to as junior synonym of *Leptoplastides*, following the emended diagnosis of Nikolaisen and Henningsmoen (1985). Additionally, *Chungkingaspis* was considered a junior synonym of *Leptoplastides*, as revised by Fortey and Owens (1989), according to Jell and Adrain (2003). However, Ghobadi Pour (2019) recognized it as a distinct taxon based on the absence of an anterior cranidial border, a convergent anterior branch of facial sutures, and the absence of axial spines on the occipital ring and the thoracic segments. In the view of this author, *Leptoplastides marianus sensu lato* from Northwestern Argentina constitutes an intermediate form between the two genera. I do not consider the differences mentioned by Ghobadi Pour (2019) to be generic-level differences and they do not justify the inclusion of *Ch. sinensis* in a different genus. Therefore, I agree with Jell and Adrain (2003) in considering *Chungkingaspis* as junior subjective synonym of *Leptoplastides*.

There has been some disagreement among researchers regarding the subfamily placement of *Leptoplastides*. As mentioned above, Henningsmoen (1957) placed it in Pelturinae, a criterion followed by Robison and Pantoja-Alor (1968). However, Nikolaisen and Henningsmoen (1985) placed it in Oleninae. Fortey and Owens (1989, 1991) argued for its placement in Pelturinae, a view supported by Żylińska (2001), who provided a list of characters to justify its inclusion within pelturinines. In this work, *Leptoplastides sensu* Nikolaisen and Henningsmoen (1985) was considered a pelturinine, and thirteen species, as well as one with doubt, were included in it. So, *Leptoplastides* includes: *L. salteri* (see synonymy in SI6); *L. marianus* (Hoek in Steinmann and Hoek, 1912); *L. granulosus* (Harrington, 1938); *L. argentinensis* (Kobayashi, 1935); *L. coniunctus* (Tomczykowa, 1968); *L. irae* (Orłowski, 1968); *L. latus* (Tomczykowa, 1968) (see synonymy in SI6); *L. depressus* (Salter in Murchison, 1859); *L. ulrichi* (Kayser, 1897) (see synonymy in SI6); *L. nodifer* (Rushton, 1982); *L. dissimulosulcus* (Loch in Loch *et al.*, 1993); *L. grindleyi* Wright *et al.*, 1994; *L. sinensis* (Sheng, 1958) (see synonymy in SI6); and *L.*? *versimilis* (Salter, 1866).

Geographic and Stratigraphic Occurrence. *Leptoplastides* is a Furongian and Lower Ordovician (Tremadocian) genus reported from different parts of the world. It was recorded from the Furongian of the Holy Cross Mountains, Poland (Żylińska, 2001, 2002); and Newfoundland and Labrador, Canada (Fortey *et al.*, 1982). Also, *Leptoplastides* is known from the Furongian and Tremadocian of North Wales and from Northwestern Argentina and Bolivia (*e.g.*, Harrington & Leanza, 1957; Tortello & Aceñolaza, 2010; Rao & Tortello, 1998; Tortello & Rao, 2000; Balseiro *et al.*, 2011). Species of *Leptoplastides* were recorded from the Tremadocian of Shropshire, England (Rushton, 1982); Morocco (Hopkins *et al.*, 2024); Oaxaca, Mexico (Robison & Pantoja-Alor, 1968); Alberta and Newfoundland, Canada (Fortey & Owens, 1991); Texas, USA (Wilson, 1954); Mt Patriarch, New Zealand (Wright *et al.*, 1994); Sichuan, South China (Lu in Lu *et al.*, 1962; Zhou & Zhen, 2008); and Eastern Alborz, Iran (Ghobadi Pour *et al.*, 2015; Ghobadi Pour, 2019). This genus was mentioned from Norway (Henningsmoen, 1957; Nikolaisen & Henningsmoen, 1985; Terfelt *et al.*, 2011). Species in open nomenclature were described from Colombia (Harrington & Kay, 1951), and France (Cápera *et al.*, 1975; Babin *et al.*, 1982).

Genus ***Leurostega*** Robison and Pantoja-Alor, 1968

Type species. *Leurostega aphelix* Robison and Pantoja-Alor, 1968, Tiñu Formation, Oaxaca, Mexico.

Remarks. Robison and Pantoja-Alor (1968) provided a diagnosis and discussed its affinities. However, no further mentions of this genus were found in the scientific literature. *Leurostega* was originally assigned to the Tremadocian, but a late Cambrian age has been suggested

instead based on correlation with the Tiñu Formation by Landing *et al.* (2007).

Geographic and Stratigraphic Occurrence. Furongian of Oaxaca, Mexico.

Genus ***Nericiaspis*** Tjernvik, 1955

Type species. *Jujuyaspis? robusta* Tjernvik, 1953, *Peltura* Zone, Stage 10, Sweden.

Remarks. Tjernvik (1955) established the genus *Nericiaspis* based on two cranidia and a pygidium and suggested a relationship with *Peltura* Milne-Edwards, 1840. Henningsmoen (1957) later provided a revised diagnosis for the genus. Żylińska (2001) described another cranidium from Poland.

Geographic and Stratigraphic Occurrence. Furongian from Sweden (Henningsmoen, 1957) and the Holy Cross Mountains, Poland (Żylińska, 2001).

Genus ***Peltocare*** Henningsmoen, 1957

Type species. *Acerocare norvegicum* Moberg and Möller, 1898, Tremadocian, Oslo, Norway.

Remarks. Henningsmoen (1957) provided a diagnosis for *Peltocare* and discussed its affinities. Then, Rushton (1988) expanded the discussion by incorporating new species and materials. There is ongoing disagreement regarding the delimitation of several species included in *Peltocare*. For instance, Robison and Pantoja-Alor (1968) included specimens from Oaxaca in *Pe. norvegicum*, while Nikolaisen and Henningsmoen (1985) considered them as a separate species within *Peltocare*. Additionally, some authors believe that Argentinian specimens originally described as *Cyclognathus glaber* Harrington, 1938 and later transferred to *Acerocarina glaber* by Harrington and Leanza (1957) are synonymous with *P. norvegicum* (Henningsmoen, 1957; Robison & Pantoja-Alor, 1968; Nikolaisen & Henningsmoen, 1985; Waisfeld & Vaccari, 2003; Zeballo & Tortello, 2005). However, alternative views have been presented by other authors who consider Argentinian specimens to be synonymous with *Peltocare olenoides*. Rushton (1988) described additional specimens of *P. olenoides* and provided an emended diagnosis. According to Rushton, the specimens from Argentina were encompassed within the observed variation of *P. olenoides*, leading him to consider *A. glaber* (erroneously referred to as *P. glabrum*) as a synonym of *P. olenoides*. This interpretation was subsequently supported by Landing and Fortey (2011), who referred to the Argentinian species as *P. glabra*. Until new data were available to solve these disagreements, both Argentinian and Mexican specimens were treated as *P. norvegicum*. A total of seven species were included here in the *Peltocare*: *Pe. norvegicum* (see synonymy in Sl6); *Pe. rotundifrons* (Matthew, 1893); *Pe. modestum* Henningsmoen, 1959; *Pe. olenoides* (Salter, 1866); *Pe. compactum* Nikolaisen and Henningsmoen, 1985; *Pe. recta* Antsygin, 2001; and *Pe. inconspica* Antsygin, 2001.

Geographic and Stratigraphic Occurrence. *Peltocare* is a Tremadocian genus from Norway and Sweden (Tjernvik, 1956; Henningsmoen, 1957, 1959; Owen *et al.*, 1990); Welsh Borderlands and the Lake District, England; Cape Breton Island and Southern New Brunswick, Canada (Rushton, 1988; Fortey & Owens, 1992b; Landing & Fortey, 2011); Northwestern Argentina (*e.g.*, Harrington, 1938; Harrington & Leanza, 1957; Zeballo & Tortello, 2005; Balseiro *et al.*, 2011); Oaxaca, Mexico (Robison & Pantoja Alor, 1968); and south Urals Mountains, Russia (Antsygin, 2001; Bergström *et al.*, 2013).

Genus ***Peltura*** Milne-Edwards, 1840

1922. *Anopocare* Angelin, 1854 — Westergård.
1957. *Anthes* Goldfuss, 1843 — Henningsmoen, p. 231 (objective synonym).

Type species. *Entomostracites scarabaeoides* Wahlenberg, 1821, *Peltura* Zone, Stage 10, Alum Shales, Sweden.

Remarks. Henningsmoen (1957) provided a diagnosis for *Peltura*, discussing the included species and their phylogenetic affinities. In more recent studies, Rasmussen *et al.* (2016, 2017) presented a new set of characters for the genus. The species within *Peltura* are of significance in biostratigraphic zonation in Baltica. The genus *Peltura* includes: *Peltura scarabaeoides* (see synonymy in Sl6); *Peltura westergaardi* Henningsmoen, 1957; *Peltura paradoxa* (Moberg and Möller, 1898); *Peltura transiens* (Brøgger, 1882) (see synonymy in Sl6); *Peltura acutidens* Brøgger, 1882; *Peltura costata* (Brøgger, 1882); *Peltura minor* (Brøgger, 1882); *Peltura protopeltorum* Orłowski, 1968; *Peltura hutchinsoni* Nguyen *et al.*, 2022; and *Peltura undulata* Nielsen *et al.*, 2022.

Geographic and Stratigraphic Occurrence. *Peltura* is a Furongian genus that occurs in Sweden, Norway, and Denmark (*e.g.*, Westergård, 1922, 1944; Henningsmoen, 1957; Moberg & Möller, 1898; Ahlberg *et al.*, 2005; Bird & Clarkson, 2003; Nikolaisen & Henningsmoen, 1985; Høyberget & Bruton, 2012); England (McKerrow, 1979); Glacial Erratic Boulders (Geschiebes) in Germany (Henningsmoen, 1957); the Holy Cross Mountains, Poland (Żylińska, 2001, 2002); and New Brunswick and Cape Breton Island, Canada (Nguyen *et al.*, 2022). Also, specimens were reported from the Tremadocian of Montagne Noire, France (Cápera *et al.*, 1975).

Genus ***Pelturina*** Henningsmoen, 1957

Type species. *Pelturina punctifera* Henningsmoen, 1957, *Acerocare* Zone, Stage 10, Alum Shale, Norway.

Remarks. Henningsmoen (1957) established the genus *Pelturina*, comprising a single species, and provided a diagnosis along with a brief discussion of its affinities. No additional species were subsequently included in *Pelturina*.

Geographic and Stratigraphic Occurrence. Furongian from Brummunddalen, Norway (Henningsmoen, 1957); Sweden (Weidner & Nielsen, 2013); and Glacial Erratic Boulders (Geschiebes) in Northern Germany (Buchholz, 2003).

Genus ***Protopeltura*** Brøgger, 1882

Type species. *Peltura praecursor* Westergård, 1909 designed by ICZN Opinion 499 (ICZN & Hemming 1958), Jiangshanian, Alum Shale, Norway.

Remarks. Henningsmoen (1957) discussed *Protopeltura*, providing insights into its history and synonymies. Ivshin (1962) also contributed to the understanding of the genus by presenting a diagnosis, a list of species, and an extensive exploration of its affinities with *Peltura*. Additionally, Ivshin (1962) introduced two new Kazakhstan species, expanding the geographic distribution of the genus. More recently, Rasmussen *et al.* (2015, 2017) proposed a set of characteristics for *Protopeltura*, while maintaining the diagnosis established by Henningsmoen (1957). Rasmussen *et al.* (2015) described species from Norway, providing the most recent revision of the genus in that region. Two additional *Protopeltura* species from the western margin of Gondwana, namely *Pr. mesembria* Harrington and Leanza, 1957 and *Pr.*? *vizcachensis* Benedetto, 1977, have been described. However, their generic assignment remains uncertain. Until new specimens of these two species are discovered, both are tentatively classified within the genus. So, *Protopeltura* includes ten species and three assigned with doubt: *Pr. praecursor* (see synonymy in SI6); *Pr. aciculata* (Angelin, 1854) (see synonymy in SI6); *Pr. pusilla* Westergård, 1922; *Pr. broeggeri* (Holtedahl, 1910); *Pr. holtedahli* Henningsmoen, 1957 (see synonymy in SI6); *Pr. intermedia* Westergård, 1922; *Pr. planicauda* (Brøgger, 1882); *Pr. bidentata* (Brøgger, 1882); *Pr. kasakhstanica* Ivshin, 1962; *Pr. simplicata* Ivshin, 1962; *Pr.*? *mesembria*; *Pr.*? *sinensis* Lu and Qian in Yin and Li, 1978; and *Pr.*? *vizcachensis*.

Geographic and Stratigraphic Occurrence. *Protopeltura* is well-known in the Furongian of Norway, Sweden, Denmark, the Holy Cross Mountains of Poland, and Glacial Erratic Boulders (Geschiebes) in Northern Germany (*e.g.*, Henningsmoen, 1957; Żylińska, 2001; Rasmussen *et al.*, 2015, 2017; Terfelt *et al.*, 2008). It also was recorded from the Furongian of England; Western of Sakha Republic, Northern Siberia (Rushton *et al.*, 2002; Lazarenko *et al.*, 2011); Central Kazakhstan (Ivshin, 1962); and southeast Guizhou, China (Yin & Li, 1978; Lu & Qian, 1983). Species of this genus were also described from the latest Furongian (Benedetto, 1977) and Tremadocian (Harrington & Leanza, 1957) from Northwestern Argentina.

Genus ***Psilocara*** Fortey, 1974

Type species. *Psilocara comma* Fortey, 1974, *Pendeograptus fructicosus* Zone, Floian, Valhallfona Formation, Spitsbergen, Norway.

Remarks. Fortey (1974) introduced the new genus *Psilocara* to accommodate two species from the Floian of Spitsbergen (*Psilocara comma* and *Psilocara patagium* Fortey, 1974). In addition, Fortey provided a diagnosis for *Psilocara* and discussed its affinities. Later, Tortello (1999) described a new species, *Psilocara liliae* Tortello, 1999, that belongs to this genus, expanding its distribution to Northwestern Argentina.

Geographic and Stratigraphic Occurrence. *Psilocara* is known from the Floian of Spitsbergen and Northern Ny Friesland, Norway (Fortey, 1974), and from the Tremadocian of Northwestern Argentina (Tortello, 1999).

Genus ***Saltaspis*** Harrington and Leanza, 1952

Type species. *Jujuyaspis steinmanni* Kobayashi, 1937, *Jujuyaspis keideli* Zone, Tremadocian, Tarija, Bolivia.

Remarks. Kobayashi (1937) described *Jujuyaspis steinmanni*, which is characterized by a distinct long genal spine on the fixigena. Later, Harrington and Leanza (1952) designated *J. steinmanni* as the type species of the newly established genus *Saltaspis*. The defining feature of this new genus is the proparian facial suture. Several specimens from Northwestern Argentina were included in the type species of *Saltaspis* (Harrington & Leanza, 1957). However, the assignation of these Argentinean specimens has been a topic of discussion, with some authors suggesting that they represent a separate species (Nikolaisen & Henningsmoen, 1985; Waisfeld, 2001; Vaccari *et al.*, 2008). The list of species of *Saltaspis* was completed with the description of two additional species by Ebbestad (1999) and Antsygin (2001). *Saltaspis* includes five species: *S. steinmanni* (see synonymy in SI6); *S. viator* Tjernvik, 1956; *S. readingi* Nikolaisen and Henningsmoen, 1985; *S. stenolimbatus* Ebbestad, 1999; and *S. koktugaensis* (Antsygin, 2001).

Geographic and Stratigraphic Occurrence. *Saltaspis* has been recorded from the Tremadocian of Norway (Henningsmoen, 1957; Nikolaisen & Henningsmoen, 1985); south Urals Mountains, Russia (Antsygin, 2001; Bergström *et al.*, 2013); and Northwestern Argentina and Bolivia (Kobayashi, 1937; Harrington & Leanza, 1952, 1957; Juarez Huarachi, 2010; Waisfeld, 2001; Vaccari *et al.*, 2018). Also, *Saltaspis* is known from the Tremadocian and Floian of Sweden (Tjernvik, 1956; Ebbestad, 1999).

Genus ***Sulcareclava*** Peng *et al.*, 2004

Type species. *Sulcareclava sagitta* Peng *et al.*, 2004, Paibian, Hunan, China.

Remarks. The genus was established by Peng *et al.* (2004) to include three cranidia from China. The authors highlighted the similarity of these materials with both *Peltura* and *Protopeltura*.

Geographic and Stratigraphic Occurrence. Miaolingian (Guzhangian) and Furongian (Paibian) of Hunan, China.

Genus ***Svalbardites*** Fortey, 1974

Type species. *Svalbardites hamus* Fortey, 1974, *fruticosus* to *bifidus* zones, Floian, Valhallfona Formation, Spitsbergen, Norway.

Remarks. Fortey (1974) established *Svalbardites*, including two species from Spitsbergen: *Sv. hamus* and *Sv. hebaxis* Fortey, 1974. He provided a diagnosis and discussed its potential relationships with other pelturinids. Nikolaisen and Henningsmoen (1985) considered *Svalbardites* to be a derived form of *Bienvillia*, excluding this genus from Pelturinae and placing it within Triarthrinae.

Geographic and Stratigraphic Occurrence. Floian of Spitsbergen and Northern Ny Friesland, Norway (Fortey, 1974).

Genus ***Tseiklinus*** Petrunina, 2002

Type species. *Tseiklinus orliniensis* Petrunina, 2002, Dobrinsky horizon, Tremadocian, Mountain Shoria, Russia.

Remarks. Petrunina (2002) established *Tseiklinus* to include two species from Siberia: *Ts. orliniensis* and *Ts. alter* Petrunina, 2002. The author's work provided a detailed description of the genus and emphasized its resemblance to the Siberian forms of *Acerocare*. No additional information beyond the original description is currently available for this genus and its species.

Geographic and Stratigraphic Occurrence. Tremadocian of Salair, Siberia, Russia.

Subfamily TRIARTHRINAE Ulrich, 1930

Genus ***Bienvillia*** Clark, 1924

1944. *Diatemnus* Raymond, 1937 — Rasetti, p. 240.
1985. *Agalatus* Lisogor, 1961 — Zhang (synonym of *Inkouia*).
2008. *Inkouia* Zhang and Fan, 1960 — Zhou and Zhen, p. 215.

Type species. *Bienvillia corax* Clark, 1924, Stage 10, Levis Formation, Quebec, Canada.

Remarks. Henningsmoen (1957) provided a diagnosis for *Bienvillia* and discussed its relationship with other olenids, particularly *Parabolinella*. Later, Fortey (1974) discussed the difficulties in distinguishing *Bienvillia* from *Triarthrus* Green, 1832, questioning the current arbitrary differentiation between the two genera. Fortey and Owens (1978) also proposed a diagnosis for *Bienvillia*. Ludvigsen and Tuffnell (1983) reviewed triarthrinid species and introduced a new

diagnostic character involving the border furrows on the librigena and cranidium to differentiate between *Triarthrus*, *Bienvillia*, and *Porterfieldia* Cooper, 1953. According to this criterion, *Bienvillia* is characterized by a well-defined cranidial border furrow, separated from the preglabellar furrow by a noticeable, inflated preglabellar field.

Additionally, the genus *Inkuoia* was established by Zhang and Fan (1960) to include one species from the Lower Ordovician of China. In a separate study, Lisogor (1961) created the genus *Agalatus* and described two species from the Lower Ordovician of Kazakhstan. Lisogor (1961) emphasized the resemblance between *Agalatus* and *Parabolinella triarthroides* and considered *Agalatus* to be closest to *Parabolinella*. Zhang (1985) proposed that *Agalatus* should be considered a junior synonym of *Inkouia*, a criterion followed by Jell and Adrain (2003). Zhou and Zhen (2008) considered *Inkuoia* as a junior subjective synonym of *Bienvillia*.

As a result, *Bienvillia* encompasses twenty-three species, including one with uncertain assignment: *Bi. corax*; *Bi. stikta* Fortey, 1974; *Bi. shinetonensis* (Raw, 1908); *Bi. tetragonalis* (Harrington, 1938) with two subspecies: *Bi. tetragonalis tetragonalis* (Harrington, 1938) (see synonymy in SI6) and *Bi. tetragonalis broeggeri* Henningsmoen, 1957; *Bi. grandis* Robison and Pantoja-Alor, 1968; *Bi. angelini* (Linnarsson, 1869); *Bi. parchaensis* (Harrington and Leanza, 1957); *Bi. rectifrons* (Harrington, 1938); *Bi. jana* Waisfeld and Vaccari, 2006; *Bi. kichka* Waisfeld and Vaccari, 2006; *Bi. caya* Waisfeld and Vaccari, 2009; *Bi. papulosa* (Fortey, 1974); *Bi. praeclava* Fortey and Owens, 1978; *Bi. inkouensis* (Zhang and Fan, 1960); *Bi. lata* (Zhu and Zhang in Zhu *et al.*, 1979); *Bi. cavernosa* (Lisogor, 1961); *Bi. ornata* (Lisogor, 1961); *Bi. jiangshanensis* (Han, 1983); *Bi. brevica* (Xiang and Zhang, 1984); *Bi. eurekensis* Loch and Taylor in Taylor *et al.*, 2024; *Bi. inkouensis* Zhang and Fan in Zhou *et al.*, 1982; *Bi. micula* (Raymond, 1937); and *Bi.*? *australis* (Rusconi, 1951).

Geographic and Stratigraphic Occurrence. *Bienvillia* is a widespread genus, known from the Furongian to the Dapingian in different parts of the world. Species belonging to *Bienvillia* were reported from the Furongian of Quebec, Western Newfoundland, Canada; Vermont and Nevada, USA (Billings, 1865; Rasetti, 1944, 1954; Fortey *et al.*, 1982; Cook *et al.*, 1989; Ludvigsen *et al.*, 1989; Taylor *et al.*, 2024); and probably Mendoza, Argentina (Rusconi, 1951). During the Tremadocian the genus is more diverse and was recorded from Shropshire, England (Lake, 1913); Norway; Sweden (Henningsmoen, 1957); different localities from Northwestern Argentina (*e.g.*, Harrington, 1938; Harrington & Leanza, 1957; Waisfeld & Vaccari, 2003, 2006; Tortello & Esteban, 2014, 2016); Bolivia (Přibyl & Vaněk, 1980; Branisa, 1965); Oaxaca, Mexico (Robison & Pantoja-Alor, 1968); Northeastern Qinghai, Northwestern Xinjiang, and Western Zhejiang, China (Zhu *et al.*, 1979; Han, 1983; Lu & Lin, 1984; Xiang & Zhang, 1984); Keskentas (Kenyitkas), Kazakhstan (Lisogor, 1961; Zhang, 1985); and Vermont, USA (Raymond, 1937). In the Floian, species of *Bienvillia* were known from Spitsbergen, Norway (Fortey, 1974); southwest of Wales (Fortey & Owens, 1978); Famatina, Argentina (Waisfeld & Vaccari, 2009). Finally, in the Dapingian one species of *Bienvillia* was reported from Spitsbergen, Norway; Nevada, USA (Fortey, 1974; Fortey & Droser, 1999); and Gansu, China (Zhang & Fan, 1960; Zhou *et al.*, 1982).

Genus ***Leiobienvillia*** Rasetti, 1954

Type species. *Leiobienvillia laevigata* Rasetti, 1954, Tremadocian, Shallow Bay Formation, Newfoundland, Canada.

Remarks. *Leiobienvillia* was established by Rasetti (1954) to include only the type species. Rasetti also described *Bienvillia terranovica* Rasetti, 1954, which was subsequently transferred to *Leiobienvillia* by Fortey *et al.* (1982). They also provided a discussion on the defining characteristics of *Leiobienvillia*. Karim (2008) later summarized the status of the genus.

Geographic and Stratigraphic Occurrence. Tremadocian from Western Newfoundland and Labrador, Canada.

Genus ***Mendoparabolina*** Rusconi, 1951

Type species. *Mendoparabolina pirquinensis* Rusconi, 1951, Stage 10, Mendoza, Argentina.

Remarks. There has been a debate about the validity of the genus *Mendoparabolina* due to disagreements about the classification of its type species, *M. pirquinensis*. Shergold *et al.* (1995) suggested that *M. pirquinensis* could be considered a species of *Bienvillia*, closely related to the type, *Bi. corax*.

This proposal has been followed by Jell and Adrain (2003) and Cerdeño (2005). However, Tortello (2014) reviewed specimens of *M. pirquinensis* and confirmed the validity of the genus *Mendoparabolina*, providing an emended diagnosis. In a later study, Tortello (2018) further explored the distinctive characters of *Mendoparabolina* and its similarities with other olenids. More recently, Taylor *et al.* (2024) recognized the validity of this genus and proposed another amended diagnosis. They also reassigned the species *Plicatolina nyensis* Taylor, 1976 to this genus, further discussing the affinities of *Mendoparabolina* and including it in the subfamily Plicatolininae. So, three species were included in *Mendoparabolina*: *M. pirquinensis*, *M. brevicauda*, and *M. nyensis*.

Geographic and Stratigraphic Occurrence. Furongian from Mendoza, Argentina (Tortello, 2014, 2018), and Nevada, USA (Taylor, 1976; Taylor *et al.*, 2024).

Genus ***Porterfieldia*** Cooper, 1953

Type species. *Triarthrus caecigenus* Raymond, 1920, Sandbian, Athens Formation, Virginia, USA.

Remarks. Cooper (1953) initially diagnosed the genus *Porterfieldia* as blind, with narrow cheeks and possible ventral facial sutures. However, Whittard (1961) restudied the types and suggested that *Porterfieldia* might be synonymous with *Triarthrus,* a hypothesis that had also been proposed by Whittington (1957). Fortey (1974) suggested that the alleged lateral cephalic border, initially thought by Cooper (1953) to indicate blindness, was actually a well-developed sutural ridge on the cranidium. Fortey and Owens (1978) considered the presence of this well-defined sutural ridge in the adult cranidium as the defining characteristic of *Porterfieldia*. Ludvigsen and Tuffnell (1983) adopted a broader concept of *Porterfieldia*, proposing that a very short (sagittal) or absent preglabellar field distinguishes the genus from *Triarthrus* and *Bienvillia*. They included in the genus a group of species in which the furrow is either present or absent. In contrast, Edgecombe *et al.* (2005) emphasized the presence of a furrow along the facial suture as an apomorphic feature linking species of *Porterfieldia*, considering the presence of a *Bienvillia*-like preglabellar field as a plesiomorphic character. *Porterfieldia* includes twenty species: *Po. caecigena* (see synonymy in SI6); *Po. parapunctata* (Fortey, 1974); *Po. thor* (Fortey, 1974); *Po. turneri* (Baldis and Pöthe, 1995); *Po. cuadrata* Waisfeld, 2001; *Po. acava* Edgecombe *et al.*, 2005; *Po. maanssonae* Edgecombe *et al.*, 2005; *Po. convergens* (Whittard, 1961); *Po. humilis* (Hadding, 1913); *Po. fischeri* (Billings, 1865); *Po. sinensis* (Zhang and Fan in Zhou *et al.*, 1982); *Po. contayaensis* Hughes in Hughes *et al.*, 1980; *Po. delicata* Kolobova in Klishevich and Kolobova, 1990; *Po. turkestanicus* (Weber, 1948); *Po. sponisa* Kolobova in Klishevich and Kolobova, 1990; *Po. goldwyerensis* (Legg, 1976); *Po. punctata* (Crosfield and Skeat, 1896); *Po. pacifica* (Kobayashi, 1955); *Po. altunensis* (Zhang, 1990); and *Po. elantagensis* (Zhang, 1990).

Geographic and Stratigraphic Occurrence. *Porterfieldia* is an Ordovician genus. It occurs in the Floian from the Cordillera Oriental and Precordillera, Argentina (Waisfeld, 2001; Edgecombe *et al.*, 2005); and in the Floian from South Wales (Fortey & Owens, 1978). Also, the genus was recorded during the Darriwilian from Eastern Peru (Hughes *et al.*, 1980); Ny Friesland and Spitsbergen, Norway (Fortey, 1974); Wales (Whittard, 1961); Western Newfoundland, Canada (Billings, 1865); Sweden; Oslo, Norway (Nikolaisen, 1965; Månsson, 1998; Hansen, 2009); Western Australia (Legg, 1976); Gansu and Eastern Xinjiang, China (Lu *et al.*, 1965; Zhou *et al.*, 1982; Zhang, 1990; Zhou & Zhen, 2008); North Tien Shan, Northern Kyrgyzstan (Weber, 1948; Klishevich & Kolobova, 1990); and Kazakhstan (Pouille *et al.*, 2013). One species is known from the Upper Ordovician, Sandbian from Virginia, USA; and Scotland and Ireland (Raymond, 1920; Cooper, 1953; Tripp, 1980; Ingham & Tripp, 1991; Owen & Parkes, 2000). Finally, one record was informed from the Sandbian of Venezuela (Arnold & Smith, 1964).

Genus ***Triarthrus*** Green, 1832

1893. *Brongniartia* Eaton, 1832 — Vogdes (based on synonymy of the type species with *Triarthrus beckii* Green, 1832).

Type species. *Triarthrus beckii* Green, 1832, Katian, Snake Hill Formation, New York, USA.

Remarks. The genus *Triarthrus* is renowned for its remarkably well-preserved pyritized specimens, *T. eatoni*, from the Utica Shale, making it one of the most famous

trilobite species. Previous studies have primarily focused on describing the internal anatomy of *Triarthrus* species (Raymond, 1920; Størmer, 1939, 1951; Cisne, 1975, 1981), with less emphasis on systematic discussions. Henningsmoen (1957) provided a diagnosis for *Triarthrus* and discussed the affinities of Tremadocian species, leaving the post-Tremadocian species unaddressed. Fortey (1974) emphasized the need for a comprehensive revision of the known species. Ludvigsen and Tuffnell (1983) offered a diagnosis for *Triarthrus* and discussed its relationship with *Bienvillia* and *Porterfieldia*. They proposed that *Triarthrus* originated from a species of *Bienvillia* through the backward migration of the transverse portion of the facial suture from the anterior border to the "preglabellar field". Subsequently, Ludvigsen and Tuffnell (1994) further investigated *Triarthrus*, presenting a new diagnosis and discussing the internal relationships within the genus. According to the definition of Ludvigsen and Tuffnell (1983, 1994), *Triarthrus* is characterized by a short and convex frontal area of the cranidium, with the palpebral lobes located anteriorly of the glabellar midlength. Månsson (1998) later expanded the concept of *Triarthrus* to include species with a long (sagittal) frontal area of the cranidium and palpebral lobes positioned opposite the glabellar midlength. Ludvigsen and Tuffnell (1994) introduced the subgenus *Danarcus* Ludvigsen and Tuffnell, 1994, encompassing two species from Eastern North America. However, Månsson (1998) dismissed this classification due to the lack of fitting species from Sweden. Additionally, she described material from Jämtland, extending the stratigraphic range of the genus into the lower Caradoc. Regarding the included species, Ludvigsen and Tuffnell (1983) initially provided a list of ten species, which was later updated by Ludvigsen and Tuffnell (1994). The updated list excluded *T. huguesensis* Foerste, 1924 and raised doubts about the assignment of *T.*? *billingsi* Barrande, 1872. Subsequently, four species were transferred to *Triarthrus* (Månsson, 1998; Edgecombe *et al.*, 2005).

In summary, the genus now comprises at least sixteen confirmed species, with an additional four species assigned with uncertainty: *T. beckii* (see synonymy in Sl6); *T. eatoni* (Hall, 1838) (see synonymy in Sl6); *T. rougensis* Parks, 1921 (see synonymy in Sl6); *T. spinosus* Billings, 1857; *T. glaber* Billings, 1859; *T. canadensis* Smith, 1861; *T. linnearssoni* Thorslund, 1940 (see synonymy in Sl6); *T. freji* Thorslund, 1940; *T. jemtlandicus* Linnarsson, 1875b; *T. latissimus* Månsson, 1998 (see synonymy in Sl6); *T. jachalensis* (Harrington and Leanza, 1957); *T. sichuansis* Lu and Zhang, 1974; *T. pygmaeus* Törnquist, 1884; *T. akkermensis* Ghobadi Pour, 2022; *T. szechuanensis* Lu in Lu and Zhang, 1974; *T. dawanensis* Sheng, 1974; *T.*? *descensus* (Clark, 1924); *T.*? *butuonsis* Li, 1978; *T.*? *similis* Li, 1978; and *T.*? *billingsi*.

Geographic and Stratigraphic Occurrence. *Triarthrus* has been recorded in several parts of the world from the Middle to Upper Ordovician strata. The genus has been recorded from the Sandbian of several localities in Sweden and Norway (Thorslund, 1940; Månsson, 1998); and from Southern Ontario, Canada (Smith, 1861; Thorslund, 1940; Ludvigsen & Tuffnell, 1994; Månsson, 1998). It is also known from the Katian of Dalarna, Sweden (Tornquist, 1884; Henningsmoen, 1957; Ludvigsen & Tuffnell, 1983), and from west Balkhash region and Betpak-Dala, Central Kazakhstan (Ghobadi Pour, 2022). This genus was especially diverse in the Upper Ordovician from North America. It was recorded from the Katian in New York, Kentucky, Cincinnati, Pennsylvania, and Ohio, USA; and in Vermont, Ottawa, Southern Ontario, Quebec, Anticosti Island, and St. Lawrence Valley, Canada (*e.g.*, Billings, 1857, 1859; Smith, 1861; Desbiens & Lespérance, 1989; Briggs *et al.*, 1991; Briggs & Edgecombe, 1993; Ludvigsen & Tuffnell, 1994). Also, *Triarthrus* is known from the Katian/Hirnantian transition in the Precordillera, Argentina (Harrington & Leanza, 1957; Edgecombe *et al.*, 2005); and Sichuan and Northern Guizhou, China (Lu & Zhang, 1974; Sheng, 1974; Nairen & Jialing, 2000). Finally, one dubious record was reported from the Dapingian to Darriwilian in Quebec, Canada (Clark, 1924; Whittington, 1965).

Genus ***Westergaardites*** Troedsson, 1937

Type species. *Westergaardites pelturaeformis* Troedsson, 1937, Furongian, Torsuqtagh Formation, Xinjiang, China.

Remarks. Troedsson (1937) established the genus *Westergaardites* to include a single species from Central Asia. Troedsson provided a diagnosis for *Westergaardites* and discussed its affinities with *Peltura* and *Triarthrus*, identifying thoracic features, such as a high number of segments and an exceptionally wide axis, as the distinguishing features of

the genus. *Westergaardites* is closely related to *Wujiajiania* Lu and Lin, 1980 (Lu & Lin, 1989; Jell *et al.*, 1991; Chatterton & Ludvigsen, 1998), and according to Taylor (1960) the genus might be included into Plicatolininae. Beyond the type species, *W. pelturaeformis*, one more species was doubtfully assigned to the genus, *W.*? *qinghaiensis* Lin and Zhang in Zhu *et al.*, 1979.

Geographic and Stratigraphic Occurrence. Furongian of Eastern Tianshan, Western Xinjiang, Hunan and Minle County, Gansu, China (Troedsson, 1937; Zhu *et al.*, 1979; Peng, 1992); and Kyrshabakty River, the Karatau Range, Kazakhstan (Ergaliev & Ergaliev, 2008). Also, some specimens were assigned to *Westergaardites* from the Furongian of Nevada, USA (Cook & Taylor, 1975; Cook *et al.*, 1989).

Subfamily LEPTOPLASTINAE Angelin, 1854

Genus ***Ctenopyge*** Linnarsson, 1880

Type species. (Designated by Vogdes, 1890) *Olenus* (*Sphaerophthalmus*) *pecten* Salter, 1864, *Peltura* Zone, Stage 10, Dolgellau Member, North Wales.

Remarks. *Ctenopyge* encompasses numerous species that are useful for defining biozones in Scandinavia and Avalonia during the Furongian (*e.g.*, Henningsmoen, 1957; Terfelt *et al.*, 2008; Nielsen & Andersen, 2021). Henningsmoen (1957) was the first to provide a diagnosis and list of species with synonymy for *Ctenopyge*. He distinguished three subgenera based on distinct hypostome features: *Eoctenopyge* Henningsmoen, 1957, *Mesoctenopyge* Henningsmoen, 1957 and *Ctenopyge*, which occur stratigraphically in that order. Since then, new species have been described that belong to *Ctenopyge* (see Clarkson *et al.*, 2003a; Clarkson & Ahlberg, 2002; Nielsen & Andersen, 2021). More recently, Høyberget and Bruton (2012) considered the subgenus *Ctenopyge* (*Eoctenopyge*) to be a junior synonym of *Sphaerophthalmus* Angelin, 1854, an interpretation that was followed by other authors (Rasmussen *et al.*, 2016, 2017; Nielsen & Andersen, 2021). The similarities between *Eoctenopyge* and *Sphaerophthalmus* have been noted before, and even species of *Eoctenopyge* were considered as intermediate forms between the two genera (Henningsmoen, 1957; Clarkson *et al.*, 2003a). Rasmussen *et al.* (2016, 2017) provided a list of characteristics for *Ctenopyge*. Clarkson *et al.* (2003a, 2003b) provided detailed ontogenetic descriptions for several species.

This work includes a summary of twenty species belonging to *Ctenopyge*, and one assigned with doubt. Of these, fourteen species belong to the subgenus *Ctenopyge* (one with dubious assignation): *Ct.* (*Ct.*) *pecten* (see synonymy in Sl6); *Ct.* (*Ct.*) *fletcheri* (Matthew, 1901) (see synonymy in Sl6); *Ct.* (*Ct.*) *linnarssoni* Westergård, 1922; *Ct.* (*Ct.*) *bisulcata* (Phillips, 1848) (see synonymy in Sl6); *Ct.* (*Ct.*) *directa* Lake, 1919; *Ct.* (*Ct.*) *teretifrons* (Angelin, 1854); *Ct.* (*Ct.*) *affinis* Westergård, 1922; *Ct.* (*Ct.*) *gracilis* Henningsmoen, 1957; *Ct.* (*Ct.*) *ahlbergi* Clarkson *et al.*, 2003a; *Ct.* (*Ct.*) *rushtoni* Clarkson *et al.*, 2003a; *Ct.* (*Ct.*) *falcifera* Lake, 1913; *Ct.* (*Ct.*) *tenuis* Poulsen, 1963; *Ct.* (*Ct.*) *magna* Nielsen and Andersen, 2021; and *Ct.* (*Ct.*?) *oelandica* Westergård, 1922. Five species belong to the subgenus *Mesoctenopyge*: *Ct.* (*M.*) *spectabilis* Brøgger, 1882; *Ct.* (*M.*) *tumida* Westergård, 1922; *Ct.* (*M.*) *erecta* Westergård, 1922; *Ct.* (*M.*) *similis* Henningsmoen, 1957; and *Ct.* (*M.*) *tuminoides* Henningsmoen, 1957. Finally, one was not assigned to any subgenus, *Ct. ceciliae* Clarkson and Ahlberg, 2002, and one is assigned with doubt to the genus, *Ct.*? *expansa* (Salter, 1873).

Geographic and Stratigraphic Occurrence. *Ctenopyge* is a Furongian genus, widely distributed in Baltica and Avalonia. Species of this genus were recorded from different localities from Norway, Sweden, and Denmark. Also, species of *Ctenopyge* are known from the Holy Cross Mountains, Poland; Glacial Erratic Boulders (Geschiebes), Germany; England and Wales; and Eastern Canada.

Genus ***Eurycare*** Angelin, 1854

Type species. (Designated by Vogdes, 1925) *Eurycare brevicauda* Angelin, 1854, *Leptoplastus* Zone, Jiangshanian, Andrarum, Sweden.

Remarks. Henningsmoen (1957) provided a diagnosis for *Eurycare* along with a list of included species. Rasmussen *et al.* (2015, 2016, 2017) reviewed the genus and provided a list of diagnostic characteristics. The species list was updated with the addition of *E. bornholmensis* (Poulsen, 1923), previously classified as *Leptoplastus* by Nielsen and Andersen (2021). Therefore, *Eurycare* now consists of five species: *E. brevicauda*; *E. bornholmensis*; *E. latum* (Boeck,

1838) (see synonymy in SI6); *E. explanatum* (Holtedahl, 1910); and *E. spinigerum* (Westergård, 1922).

Geographic and Stratigraphic Occurrence. Furongian (Jiangshanian) from different localities in Norway and Sweden; Bornholm, Denmark; and England. It may also have been recorded from Glacial Erratic Boulders (Geschiebes) in Germany.

Genus ***Eurycarina*** Ivshin in Petrunina, 2002

Type species. *Eurycarina speranskyi* Ivshin in Petrunina, 2002, Zolotokitatsky horizon, Stage 10, Mountain Shoria, Russia.

Remarks. Petrunina (2002) erected the genus *Eurycarina* to include specimens previously studied by Ivshin, who had named the type species (unpublished name cited as *nomen in collection*) and new materials from Siberia. In this work, she assigned the genus to Leptoplastinae due to its resemblance to other members of the group, particularly *Eurycare*. It is worth noting that the inclusion of this genus in Leptoplastinae extended not only the geographic distribution of the subfamily but also its stratigraphic record to the Tremadocian. The inclusion of *Eurycarina* in Leptoplastinae is tentative and requires further examination. *Eurycarina* encompasses four species*: Eu. speranskyi*; *Eu. oblonga* Petrunina, 2002; *Eu. obesa* Petrunina, 2002; and *Eu. triangula* Lazarenko and Pegel in Lazarenko *et al.*, 2011.

Geographic and Stratigraphic Occurrence. Furongian and Lower Tremadocian from Northwest of Kuznetsk Alatau, Mountain Shoria (Petrunina, 2002); and Khos-Nelege section, Western Sakha Republic (Yakutia), Russia (Lazarenko *et al.*, 2011).

Genus ***Granitzia*** Buchholz, 1999

Type species. *Granitzia rugiana* Buchholz, 1999, *Peltura*-Stufe, Stage 10, Pomerania, Germany.

Remarks. *Granitzia* was established by Buchholz (1999) to include a few specimens found in Glacial Erratic Boulders in Northern Germany. It is known only from three cranidia, two of which are considered earlier holaspid developmental stages (Buchholz & Mischnik, 2004). The holotype (Buchholz & Mischnik, 2004, pl. 2, fig. 6) shows morphological similarity with other members of the Leptoplastinae, particularly with *Triangulopyge*. For this reason, the genus was placed within this subfamily.

Geographic and Stratigraphic Occurrence. Furongian in Glacial Erratic Boulders (Geschiebes) from Western Pomerania, Northern Germany.

Genus ***Leptoplastus*** Angelin, 1854

Type species. *Leptoplastus stenotus* Angelin, 1854, *Leptoplastus* Zone, Jiangshanian, Alum Shale, Sweden.

Remarks. *Leptoplastus* included numerous index fossils, which defined different late Cambrian biozones in Baltica and Avalonia (*e.g.*, Henningsmoen, 1957; Terfelt *et al.*, 2008; Nielsen & Andersen, 2021). A comprehensive review of *Leptoplastus* was provided by Henningsmoen (1957) along with a list of species, which almost remains the same. A few species were excluded from *Leptoplastus* and only one was added (Nikolaisen & Henningsmoen, 1985). Given the biostratigraphic importance of several species, they were recently reviewed in this context (*e.g.*, Rasmussen *et al.*, 2015, 2016, 2017, Nielsen *et al.*, 2020; Nielsen & Andersen, 2021). Rasmussen *et al.* (2015, 2016, 2017) redescribed several species of *Leptoplastus* and provided a detailed list of diagnostic characteristics while discussing their precise stratigraphic biozonation. *Leptoplastus* encompasses fourteen species: *Le. stenotus*; *Le. abnormis* Westergård, 1944 (see synonymy in SI6); *Le. crassicornis* (Westergård, 1944); *Le. norvegicus* (Holtedahl, 1910) (see synonymy in SI6); *Le. ovatus* (Angelin, 1854); *Le. angustatus* (Angelin, 1854); *Le. neglectus* (Westergård, 1922); *Le. paucisegmentatus* Westergård, 1922; *Le. raphidophorus* Angelin, 1854; *Le. intermedius* (Westergård, 1944); *Le. deses* Nikolaisen and Henningsmoen, 1985; *Le. minor* Westergård, 1922; *Le. ostrogothicus* Westergård, 1940; and *Le. spinosus* Matthew, 1894.

Geographic and Stratigraphic Occurrence. *Leptoplastus* is a Furongian (Jiangshanian) genus. Species of this genus are common in the *Leptoplastus* superzone from different localities of Norway, Sweden, and Denmark. *Leptoplastus* was also recorded in England, Nova Scotia, and Eastern Canada. A record of *Leptoplastus* was reported from Queensland, Australia (Shergold, 1980).

Genus ***Sphaerophthalmus*** Angelin, 1854

2012. *Eoctenopyge* Henningsmoen, 1957, Høyberget and Bruton, p. 436.

Type species. (Designated by Linnarsson, 1880) *Trilobites alatus* Boeck, 1838, *Ctenopyge* Zone, Stage 10, Alum Shale, Norway.

Remarks. *Sphaerophthalmus* encompasses several species of biostratigraphic significance. The first diagnosis of the genus was provided by Henningsmoen (1957). Later, the diagnosis was emended by Høyberget and Bruton (2012) to include species previously assigned to *Ctenopyge* (*Eoctenopyge*). These authors extensively discussed the genus and completed the description of the species included in it, providing more detailed illustrations. Rassmusen *et al.* (2016, 2017) provided a list of characteristics for *Sphaerophthalmus* and reported its presence in different localities of Scandinavia and refined the biostratigraphic scheme. To date, the genus includes the following seven species: *Sp. alatus* (see synonymy in SI6); *Sp. angustus* (Westergård, 1922); *Sp. arcus* Høyberget and Bruton, 2012; *Sp. drytonensis* (Cobbold in Cobbold and Pocock, 1934) (see synonymy in SI6); *Sp. flagellifer* Angelin, 1854; *Sp. modestus* (Henningsmoen, 1957); and *Sp. postcurrens* (Westergård, 1944).

Geographic and Stratigraphic Occurrence. *Sphaerophthalmus* is a Furongian (Jiangshanian and Stage 10) genus. Species of this genus are known from different localities from the upper part of the *Protopeltura praecursor* Zone and *Peltura minor* Zone from Norway, Sweden, and Denmark. Other species were recorded from the *Peltura minor* Zone from the Holy Cross Mountains, Poland; England; and New Brunswick and St. John, Eastern Canada. *Sphaerophthalmus* was also mentioned with doubt from Glacial Erratic Boulders (Geschiebes) in Germany.

Genus ***Triangulopyge*** Høyberget and Bruton, 2012

Type species. *Olenus humilis* Phillips, 1848, *Peltura scarabaeoides* Zone, Raggedstone Hill, Herefordshire, England.

Remarks. The genus was created by Høyberget and Bruton (2012) to include species previously assigned to other genera. These authors provided a comprehensive description of *Triangulopyge* and the species included within it. Rasmussen *et al.* (2016, 2017) completed the notion of this genus providing a list of characteristics and reporting their presence in different localities of Scandinavia. The genus comprises three species: *Tr. humilis* (see synonymy in SI6); *Tr. majusculus* (Linnarsson, 1880); and *Tr. major* (Lake, 1913).

Geographic and Stratigraphic Occurrence. *Triangulopyge* is an upper Furongian genus recorded in different localities from the *Ctenopyge bisulcata* and *Ct. linnarssoni* zones in Norway, Sweden, and Denmark. Also, species of this genus were known from the *Peltura scarabaeoides* Zone of the Holy Cross Mountains, Poland, and the *Peltura* Zone in Eastern Canada.

Subfamily PLICATOLININAE
Robison and Pantoja-Alor, 1968

Genus ***Asilluchus*** Öpik, 1963

Type species. *Asilluchus nanus* Öpik, 1963, *Erixanium senttum* Zone, Paibian, Pomegranate Lst, Queensland, Australia.

Remarks. *Asilluchus* was established by Öpik (1963), who provided its diagnosis and compared it with other genera within the family. Although Öpik (1963) initially included *Asilluchus* in Oleninae *sensu* Henningsmoen (1957), a comparison with other genera suggests a closer relationship to *Plicatolina*. Therefore, *Asilluchus* was tentatively assigned to the subfamily Plicatolininae. In addition to the type species, *As. nanus*, one other species was included in the genus: *As. curdaicus* Kraskov in Chernysheva and Romanenko, 1977.

Geographic and Stratigraphic Occurrence. Furongian from Queensland, Australia, and Kendyktas Mountains, South Kazakhstan.

Genus ***Paraplicatolina*** Benedetto, 1977

Type species. *Paraplicatolina acantha* Benedetto, 1977, Stage 10, Santa Rosita Formation, Argentina.

Remarks. Benedetto (1977) described a new species, *Paraplicatolina acantha*, based on five cranidia. The species was compared with the genera *Plicatolina* and *Plicatolinella*, showing several similarities. However, *P. acantha* exhibits distinct features, including a long occipital spine and differences in glabellar segmentation, notable for lacking the typical four pairs of glabellar furrows and less incised transglabellar segmentation. Despite these differences, Benedetto assigned the new species to the subfamily

Plicatolininae due to its overall resemblance with the two genera. The precise position of *Paraplicatolina* within the subfamily remains unclear.

Geographic and Stratigraphic Occurrence. Furongian form Northwestern Argentina.

Genus ***Plicatolina*** Shaw, 1951

Type species. *Plicatolina kindlei* Shaw, 1951, *Lotagnostus hedini* Zone, Stage 10, Gorge Formation, Vermont, USA.

Remarks. Shaw (1951) established the genus *Plicatolina* and described a new species from Vermont. Subsequently, Harrington and Leanza (1957) discussed the synonymies and affinities of the species described by Shaw and a new species from Argentina. Robison and Pantoja-Alor (1968) listed the defining characters of *Plicatolina* and included the four species known at that time. In a recent study, Korovnikov (2014) conducted a review of *Plicatolina* species from the Siberian Platform and discussed possible synonyms. Overall, ten species have been documented for *Plicatolina* in the scientific literature: *Pl. kindlei*; *Pl. scalpta* Harrington and Leanza, 1957; *Pl. changshanensis* Lu and Lin, 1980; *Pl. lucida* Lazarenko, 1966; *Pl. perlata* Lazarenko, 1966; *Pl. quadrata* Pokrovskaya, 1967 (see synonymy in Sl6); *Pl. yakutica* Pokrovskaya, 1967 (see synonymy in Sl6); *Pl. xiyangshanensis* Lu and Lin, 1984; *Pl. dunbari* Ludvigsen and Westrop in Ludvigsen *et al.*, 1989; and *Pl. jiangjungouensis* Xiang and Zhang, 1985.

Geographic and Stratigraphic Occurrence. *Plicatolina* is predominantly a Furongian genus. It was recorded from Nevada, USA (Shaw, 1951); the Verkhoyansk Range, Western Sakha Republic (Yakutia), Russia (Pokrovskaya, 1967; Lazarenko, 1966; Korovnikov, 2014); Queensland, Australia (Shergold, 1980); Bolivia, Northwestern Argentina, and Famatina (Harrington & Leanza, 1957; Tortello & Esteban, 2003a, 2007; Esteban & Tortello, 2007); Western Newfoundland, Canada (Ludvigsen *et al.*, 1989); and Western Xinjiang, China (Xiang & Zhang, 1985). *Plicatolina* was also known from the latest Cambrian and Lower Tremadocian in Jiangshan, Zhejiang, China (Lu & Lin, 1984). *Plicatolina* was described in the Furongian of the Holy Cross Mountains, Poland (Żylińska, 2001); in the Tremadocian of Oslo, Norway (Henningsmoen, 1959); and in the Floian of Spitsbergen, Norway (Fortey, 1974).

Genus ***Plicatolinella*** Robison and Pantoja-Alor, 1968

Type species. *Plicatolinella ocula* Robison and Pantoja-Alor, 1968, Stage 10, Tiñu Formation, Oaxaca, Mexico.

Remarks. When Robison and Pantoja-Alor (1968) described *Plicatolinella*, they created the subfamily Plicatolininae, which encompassed this new genus, *Plicatolina*, and an undescribed group from the late Cambrian of Nevada. The authors provided a diagnosis for *Plicatolinella* and discussed its affinities. However, to date, only one species has been included in the genus and no other reports of *Plicatolinella* have been found. *Plicatolinella* was originally assigned to the Tremadocian but based on correlation with the Tiñu Formation by Landing *et al.* (2007), a late Cambrian age has been suggested instead.

Geographic and Stratigraphic Occurrence. Furongian from Oaxaca, Mexico.

Genus ***Wujiajiania*** Lu and Lin, 1980

Type species. *Wujiajiania expansa* Lu and Lin, 1980, Stage 10, Siyangshan Formation, Zhejiang, China.

Remarks. Lu and Lin (1980) established the genus *Wujiajiania*, providing a diagnosis and discussing its affinities. They also transferred to this genus two species previously assigned to *Westergaardites*. Lu and Lin (1984, 1989) further expanded the concept of the genus. Then, Chatterton and Ludvigsen (1998) discussed the characteristics of *Wujiajiania*, the included species, and compared it with other Cambrian olenids. They provisionally assigned this genus to the subfamily Oleninae, although the original description of *Wujiajiania* placed it in the subfamily Plicatolininae. Jell *et al.* (1991) speculated that Chinese and Australian species of *Wujiajiania* form a graded series with increasing numbers of thoracic segments. However, subsequent descriptions of new species from Laurentia challenged this hypothesis. Chatterton and Gibb (2016) also contributed to the discussion surrounding *Wujiajiania.* They not only provided further insights into its characteristics and affinities but also described additional species, completing the species list. Currently, the genus includes the following ten species: *Wu. expansa* (see synonymy in Sl6); *Wu limites* (Qian, 1961); *Wu. tachensis* (Lu, 1964); *Wu. partita* (Lisogor, 1970); *Wu. distorta* Jell *et al.*,

1991; *Wu. quadrisulcata* (Palmer, 1965) (see synonymy in Sl6); *Wu. naomi* (Pratt, 1992); *Wu. sutherlandi* Chatterton and Ludvigsen, 1998; *Wu. lyndasmithae* Chatterton and Gibb, 2016; and *Wu. ricksmithi* Chatterton and Gibb, 2016.

Geographic and Stratigraphic Occurrence. *Wujiajiania* is a Furongian genus recorded from Zhejiang, Guizhou, and Xinjiang, South China (Qian, 1961; Lu & Lin, 1980, 1984; Xiang & Zhang, 1985); and the Karatau Range, Southern Kazakhstan (Apollonov *et al.*, 1984). It was also reported from Tasmania, Australia (Jell *et al.*, 1991); Nevada, USA; and British Columbia, Canada (Chatterton & Ludvigsen, 1998; Sundberg *et al.*, 2007; Chatterton & Gibb, 2016; Chatterton 2020).

Subfamily BALNIBARBIINAE Fortey, 1974

Genus ***Balnibarbi*** Fortey, 1974

Type species. *Balnibarbi pulverea* Fortey, 1974, Floian, Valhallfonna Formation, Spitsbergen, Norway.

Remarks. Fortey (1974) introduced the subfamily Balnibarbiinae and defined the two genera that were included in this group: *Balnibarbi* and *Cloacaspis* Fortey, 1974. Fortey also provided a diagnosis for each genus and discussed the relationship and evolution of the group in detail. Later, Hopkins (2019) further contributed to the discussion on the Balnibarbiinae, by conducting a formal phylogenetic analysis of the clade. To date, *Balnibarbi* encompasses four species, one with two subspecies: *Ba. pulvurea*; *Ba. erugata erugata* Fortey, 1974, and *Ba. erugata sombrero* (Fortey, 1974); *Ba. scimitar* Fortey, 1974; and *Ba. tholia* Fortey, 1974.

Geographic and Stratigraphic Occurrence. Floian from Spitsbergen, Norway (Fortey, 1974).

Genus ***Cloacaspis*** Fortey, 1974

Type species. *Cloacaspis senilis* Fortey, 1974, Dapingian, Valhallfonna Formation, Spitsbergen, Norway.

Remarks. As mentioned above, Fortey (1974) diagnosed the genus and discussed its relationship. Hopkins (2019) later proposed a revised diagnosis based on a comprehensive revision and phylogenetic analysis. *Cloacaspis* includes five species, one of them with two subspecies: *Cl. senilis*; *Cl. dejecta* Fortey, 1974; *Cl. ekphymosa* Fortey, 1974; *Cl. tesselata* Fortey and Droser, 1999; *Cl. ceryx ceryx* (Fortey, 1974); and *Cl. ceryx anataphra* (Fortey, 1974).

Occurrence. *Cloacaspis* has been documented in the Upper Floian and Lower Dapingian from Spitsbergen, Norway (Fortey, 1974); in the Upper Floian from California (Fortey *et al.*, 2024); and in the Lower Dapingian from Nevada, USA (Fortey & Droser, 1999).

Subfamily HUNANOLENINAE Liu, 1977

Genus ***Huangshiaspis*** Liu, 1977

Type species. *Huangshiaspis taoyuanensis* Liu, 1977, Jiangshanian, Hunan, China.

Remarks. *Huangshiaspis* was established by Liu (1977). In the study, Liu provided a diagnosis and illustrations of the species that belong to it. Two new species were described by the author (the type, *H. taoyuanensis* and *H. transversus* Liu, 1977), while two others were left in open nomenclature. Zhou and Zhen (2008) considered this genus synonymous with *Olenus*.

Geographic and Stratigraphic Occurrence. Furongian from Huangshi, Taoyuan County (Liu, 1977), and Fenghuang area (Duan *et al.*, 1999), Hunan Province, China.

Genus ***Hunanolenus*** Liu, 1977

Type species. *Hunanolenus aglaos* Liu, 1977, Paibian, Huaqiao Formation, Hunan, China.

Remarks. *Hunanolenus* was established by Liu (1977), who provided a diagnosis and illustrations of the three species assigned to it: *Hu. aglaos*; *Hu. fengzidongensis* Liu, 1977; and *Hu. genalatus* Liu, 1977. The genus shares morphological similarities with *Olenus* and *Parabolinella*, but it differs from them by having more thoracic segments and distinct cephalon characteristics (Liu, 1977). According to Zhou and Zhen (2008), this genus could be considered synonym of *Olenus*.

Geographic and Stratigraphic Occurrence. Middle Furongian from Huangshi and Taoyuan, Hunan Province, China (Liu, 1977).