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Bradoriid arthropods from the lower–middle Cambrian of Scania, Sweden

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Three species of bradoriid arthropods from the lower to middle Cambrian transitional interval of Scania, southern Sweden, are described and illustrated: *Beyrichona tinea* from the top of the traditional lower Cambrian (Gislöv Formation; *Ornamentaspis*? *linnarssoni* Zone), and *Hipponicharion eos* and *Alutella* sp. from the basal portion of the traditional middle Cambrian (lowermost part of the Alum Shale Formation). The bradoriid fauna compares most closely with others previously described from western and eastern Avalonia (New Brunswick and England). The record of *B. tinea* suggests a correlation between the "*Protolenus* Zone" (*Hupeolenus* Zone) of western Avalonia and the *O.*? *linnarssoni* Zone of Scandinavia. *Hipponicharion eos* appears to be a fairly long-ranging species as it has previously been recorded from upper lower Cambrian or lower middle Cambrian strata in New Brunswick, Poland, and probably Sardinia. The record of *H. eos* from the lowermost part of the Alum Shale Formation suggests that this largely unfossiliferous interval in the Scanian succession is not younger than the *Acadoparadoxides oelandicus* Superzone. The genus *Alutella* has not previously been recorded from the Acado-Baltic Province.

Key words: Arthropoda, Bradoriida, taxonomy, biostratigraphy, Cambrian, Scania, Sweden.

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Introduction

The order Bradoriida sensu stricto, excluding the Phosphatocopina, comprises small (generally less than 10 mm long), bivalved arthropods of uncertain affinity, ranging from the lower Cambrian to the Lower Ordovician (for a general review, see Williams et al. 2007). Their dorsal carapace is weakly mineralised and commonly preserved as disarticulated valves, though conjoined valves, preserved in articulated "butterfly" orientation, are common in some successions, for instance in the lower Cambrian Chengjiang Lagerstätte of South China (e.g., Hou et al. 2004). Bradoriids have traditionally been regarded as ostracod crustaceans. However, evidence from the soft parts of *Kunmingella* from the Chengjiang biota indicate that they do not belong to the crown-group of the Crustacea (Hou et al. 1996; Shu et al. 1999).

Bradoriids are characteristic elements of many Cambrian faunas, and occur in a variety of sedimentary facies. Most genera and species, however, appear to have occupied well-oxygenated marine shelf environments (Williams et al. 2007). Bradoriids had a worldwide distribution and most species appear to be short-ranging (e.g., Hinz-Schallreuter 1993; Melnikova et al. 1997; Siveter and Williams 1997; Williams and Siveter 1998). Thus, they have considerable potential for use in biostratigraphy and correlations (e.g., Williams et al. 1994; Siveter et al. 1996; Gozalo and Hinz-Schallreuter 2002; Hinz-Schallreuter et al. 2008). It must be emphasized, however, that in most cases collections of bradoriids were made on the sideline as a result of targeted collecting for other fossils, and the ranges of most bradoriids are not precisely known. During recent years, bradoriids have also been utilized in palaeobiogeographical analyses (e.g., Shu and Chen 1994; Siveter et al. 1996; Williams and Siveter 1998; Hou et al. 2002; Gozalo et al. 2004; Vannier et al. 2005; Williams et al. 2007; Hinz-Schallreuter et al. 2008).

Bradoriids are generally sparsely represented in the Cambrian of Scandinavia, and most taxa are known only from glacial erratics (e.g., Wiman 1905; Hinz-Schallreuter 1993; for a brief review of Baltic bradoriids, see Streng et al. 2008). Thus, little is known of their stratigraphical ranges and geographical distribution. One notable exception is *Anabarochilina primordialis* (Linnarsson, 1869), a common and well-documented species in the middle Cambrian *Lejopyge laevigata* Zone (Guzhangian Stage) of Scandinavia (e.g., Hinz-Schallreuter 1993; Axheimer et al. 2006). It is one of the most widespread of all bradoriid species, and outside of Scandinavia it has been recorded from coeval strata in England and Siberia (Siveter et al. 1993; Melnikova et al. 1997; Williams and Siveter 1998; Williams et al. 2007).

In this paper, we describe and illustrate three species of bradoriids from the lower–middle Cambrian transitional interval in Scania (Skåne), southern Sweden, and briefly discuss their biostratigraphical and biogeographical significance.

Institutional abbreviation.—LO (for Lund Original) Department of Geology, Lund University, Lund, Sweden.

Geological setting and localities

Epicontinental Cambrian rocks crop out in several areas of Scandinavia, from Finnmark in the north to Scania and the Island of Bornholm in the south (for general reviews, see Martinsson 1974, Bergström and Gee 1985). The traditional lower Cambrian consists predominantly of sandstones, whereas middle Cambrian through Furongian (upper Cambrian) strata are largely represented by the Alum Shale Formation, a highly condensed succession of kerogen-rich, dark grey to black shales with concretionary carbonate lenses and a few primary limestone beds (see, e.g., Andersson et al. 1985 and Buchardt et al. 1997). For a comprehensive review of the lithostratigraphic subdivision of the Cambrian of southern Scandinavia, see Nielsen and Schovsbo (2006).

Cambrian deposits are widely distributed in Scania, southern Sweden (Fig. 1). The greater part of the middle Cambrian through Furongian succession is poorly exposed and best known from boreholes (e.g., Westergård 1944; Axheimer and Ahlberg 2003; Terfelt et al. 2005). Hence, the stratigraphical succession has been pieced together using data from various outcrops combined with information from drill cores. The total thickness of the Cambrian succession of Scania is of the order of 220–230 m (see Nielsen and Schovsbo 2006).

The lower–middle Cambrian transitional interval displays significant biotic turnovers and environmental changes associated with regressive and transgressive events. In Scania, this interval is represented by the Gislöv Formation (top of the traditional lower Cambrian) and the lowermost part of the Alum Shale Formation (base of the traditional middle Cambrian). The Gislöv Formation consists of calcareous siltstones and limestones, and is upwardly truncated by a diachronous erosive unconformity, the Hawke Bay unconformity (Bergström and Ahlberg 1981; Nielsen and Schovsbo 2006). The Gislöv Formation is richly fossiliferous and has yielded a diverse fauna, including, e.g., trilobites, brachiopods, helcionellid molluscs and a few bradoriids (Bergström and Ahlberg 1981). The lowermost part of the Alum Shale Formation, i.e. the succession below the Forsemölla Limestone Bed (i.e., "Fragment Limestone" in older literature) of the *Ptychagnostus gibbus* Zone, predominantly consists of dark grey to almost black shales and mudstones. This part of the succession is barren of trilobites and other calcareous-shelled fossils but has yielded linguliformean brachiopods and bradoriids (Axheimer and Ahlberg 2003). Following Nielsen and Schovsbo (2006), it is tentatively assigned to the *Acadoparadoxides oelandicus* Superzone.

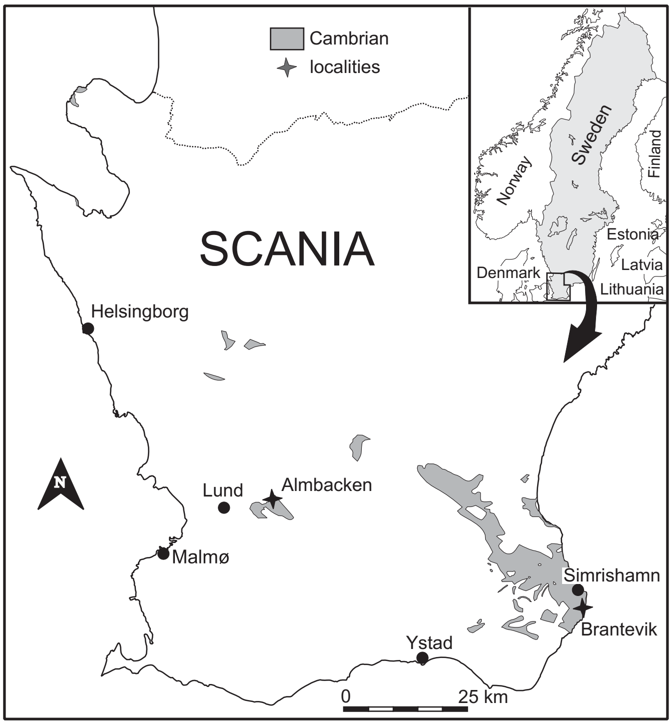


Fig. 1. Map of Scania (Skåne), southern Sweden, showing major outcrop areas of Cambrian strata and the location of the Brantevik section (Bergström and Ahlberg 1981: fig. 5) and the Almbacken borehole (Axheimer and Ahlberg 2003).

Pioneer studies of the fauna and stratigraphy of the lower–middle Cambrian transitional interval of Scania were carried out by, among others, Nathorst (1869, 1877), Tullberg (1880), Linnarsson (1883), Grönwall (1902), and Troedsson (1917). Subsequent faunal and stratigraphical investigations include de Marino (1980), Bergström and Ahlberg (1981), and Axheimer and Ahlberg (2003).

The bradoriids described herein were recovered from the lower–middle Cambrian transitional interval in Scania, both from an outcrop and a drill core (Fig. 2). The outcrop material (three valves assigned to *Beyrichona tinea* Matthew, 1886) was collected by PC from a dark grey limestone (unit F of Bergström and Ahlberg 1981: fig. 5) forming the uppermost part of the Gislöv Formation on the Baltic seashore 1 km SW of Brantevik, southeastern Scania. Associated trilobites include *Ellipsocephalus lunatus* Bergström and Ahlberg, 1981 and *Comluella*? *scanica* Ahlberg and Bergström, 1978, and are indicative of the uppermost trilobite zone in the traditional lower Cambrian of Scandinavia (the *Ornamentaspis*? *linnarssoni* Assemblage Zone). The drill core material is from the lowermost three metres of the Alum Shale Formation in the Almbacken drill core from

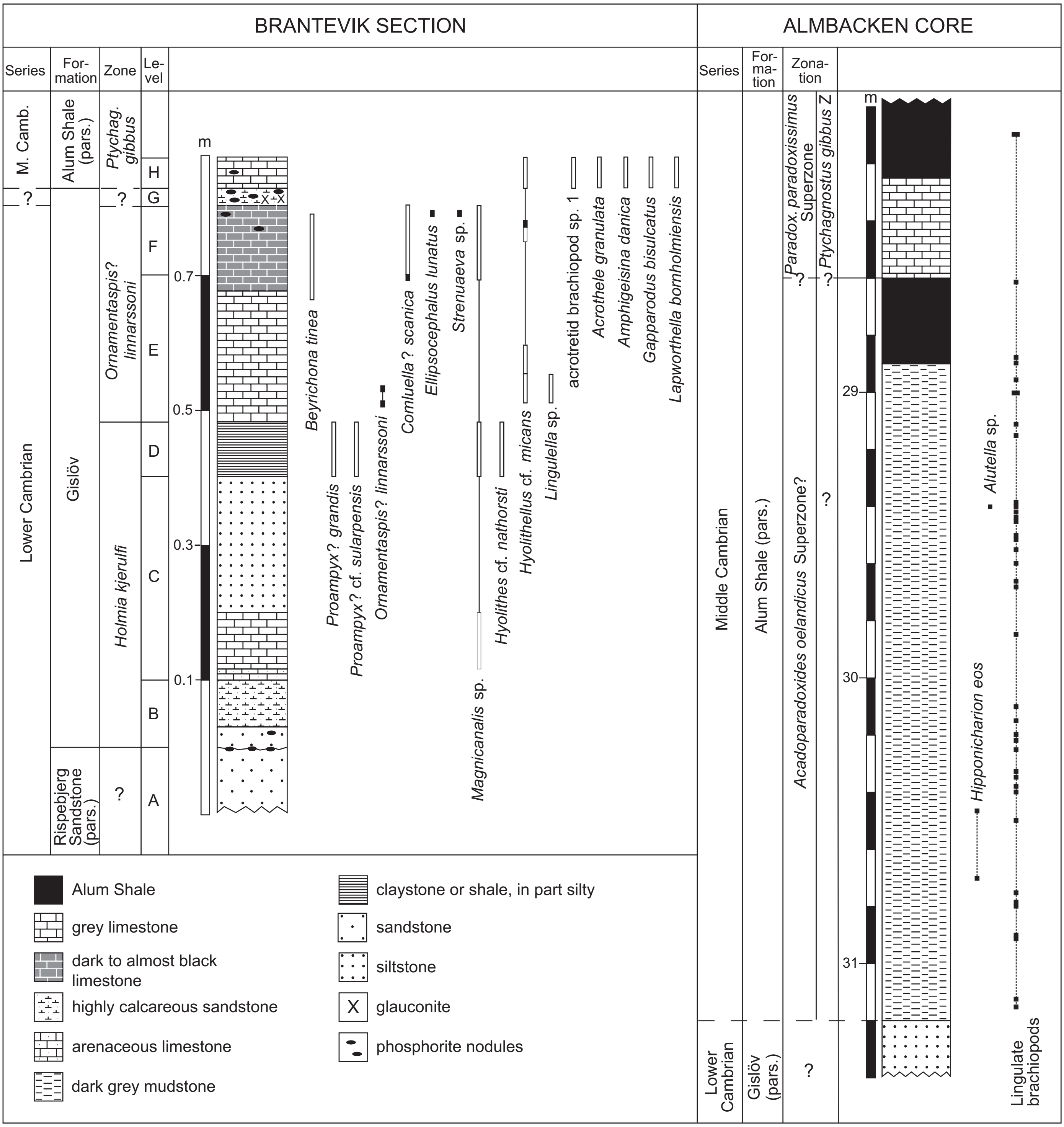


Fig. 2. Lithological succession, stratigraphy and occurrences of fossils in the Brantevik section and the Almbacken drill core. Based on Bergström and Ahlberg (1981: fig. 5) and Axheimer and Ahlberg (2003: fig. 3). For the occurrences of fossils, a black square indicates a precisely localized find of at least one specimen, whereas an open bar indicates the approximate stratigraphical position of at least one specimen. Abbreviations: pars., part of; M., Middle; *Paradox*., *Paradoxides*; *Ptychag*., *Ptychagnostus*; Z, Zone.

Södra Sandby east of Lund. The drill core was described in detail by Axheimer and Ahlberg (2003), and comprises a stratigraphical succession ranging from the middle Cambrian *Lejopyge laevigata* Zone down into the uppermost lower Cambrian (upper Gislöv Formation; probably *Holmia kjerulfi* Assemblage Zone). Two bradoriid species, *Hipponicharion eos* Matthew, 1886 and *Alutella* sp., were recovered from the dark grey to almost black shale-mudstone succession below the Forsemölla Limestone Bed (within the core interval 29.40–30.75 m).

Systematic palaeontology

The morphological terms applied herein are those advocated by Williams and Siveter (1998) and Hou et al. (2002).

Class uncertain

Order Bradoriida Raymond, 1935

(= Archaeocopida Sylvester-Bradley, 1961)

Family Beyrichonidae Ulrich and Bassler, 1931

Genus *Beyrichona* Matthew, 1886

Type species: *Beyrichona papilio* Matthew, 1886, from the lower Cambrian Hanford Brook Formation, *Protolenus elegans* Zone, in New Brunswick, Canada; designated by Ulrich and Bassler (1931: 43).

Remarks.—The concept of *Beyrichona* was discussed by Siveter and Williams (1997) and Williams and Siveter (1998), and their emended diagnosis is followed herein. *Beyrichona gevalensis* Wiman, 1905 and *B*.? *alta* Wiman, 1905, both from erratic sandstone boulders in the southern part of the Gulf of Bothnia, Sweden, were questionably considered as junior synonyms of *B. tinea* by Siveter and Williams (1997). The new record of *B. tinea* in the Gislöv Formation of Scania confirms the presence of the genus in the upper lower Cambrian of Scandinavia.

Stratigraphic and geographic distribution.—Lower Cambrian of New Brunswick and middle Cambrian of Nova Scotia, Canada (Siveter and Williams 1997); middle Cambrian St David's Series and early Ordovician Tremadoc Stage of southern Britain (Williams and Siveter 1998); Furongian Series? of Belarus and middle Cambrian and Furongian Series of Kazakhstan (Melnikova et al. 1997); lower Cambrian of Scandinavia (Scania and possibly the Gulf of Bothnia).

Beyrichona tinea Matthew, 1886

Fig. 3A, B.

1886 *Beyrichona tinea* sp. nov.; Matthew 1886: 66, pl. 6: 21, 21a, b.

1997 *Beyrichona tinea* Matthew, 1886; Siveter and Williams 1997: 42–43, pl. 5: 2–12 [see for complete synonymy].

2007 *Beyrichona tinea* Matthew; Williams et al. 2007: fig. 5.2.

Material.—Three nearly complete left valves of which LO 9347t (Fig. 3A$_1$, A$_2$) is largely exfoliated and LO 9348t (Fig. 3B$_1$, B$_2$) is original carapace.

Diagnosis (after Siveter and Williams 1997).—Species of *Beyrichona* with prominent anterior lobe and sub-circular anterodorsal sulcus. Ventral part of lateral outline gently convex. Valve length subequal to or less than valve height.

Description.—Slightly postplete valves with sub-triangular outline. Dorsal margin straight, 70–75% of valve length. Lateral outline curved anterodorsally and ventrally, and gently convex posteriorly. Trilobate; lobes developed dorsally, confluent ventrally with broadly convex lateral surface. Prominent and sub-conical anterior lobe overreaching dorsal margin. Sub-circular anterodorsal sulcus. Central lobe broad, gently convex. Subdued, gently convex posterior lobe. Posterior sulcus narrow, weakly developed. Marginal ridge entire between cardinal corners, broadest anterodorsally. Valve surface smooth.

Remarks.—The valves agree in all essential respects with those of *B. tinea* from New Brunswick. The main difference is the sub-conical morphology in the anterodorsal lobe in specimens preserved with the original carapace (e.g., Fig. 3B$_1$, B$_2$). In the largely exfoliated specimen (Fig. 3A$_1$, A$_2$), the morphology of this lobe is very similar to the Canadian specimens. Another minor difference is that the central lobe is narrower in the Scanian material and the posterior sulcus is slightly broader than in the Canadian material. These differences are here considered to be of minor taxonomical importance and our material is assigned to *B. tinea*.

Stratigraphic and geographic distribution.—Upper part of the traditional lower Cambrian in New Brunswick, eastern Canada (Hanford Brook Formation, *Protolenus elegans* Zone; Siveter and Williams 1997), and Scania, southern Sweden (upper Gislöv Formation, *Ornamentaspis*? *linnarssoni* Zone). Possibly also from the ?lower Cambrian of the Gulf of Bothnia (Siveter and Williams 1997).

Family Hipponicharionidae Sylvester-Bradley, 1961

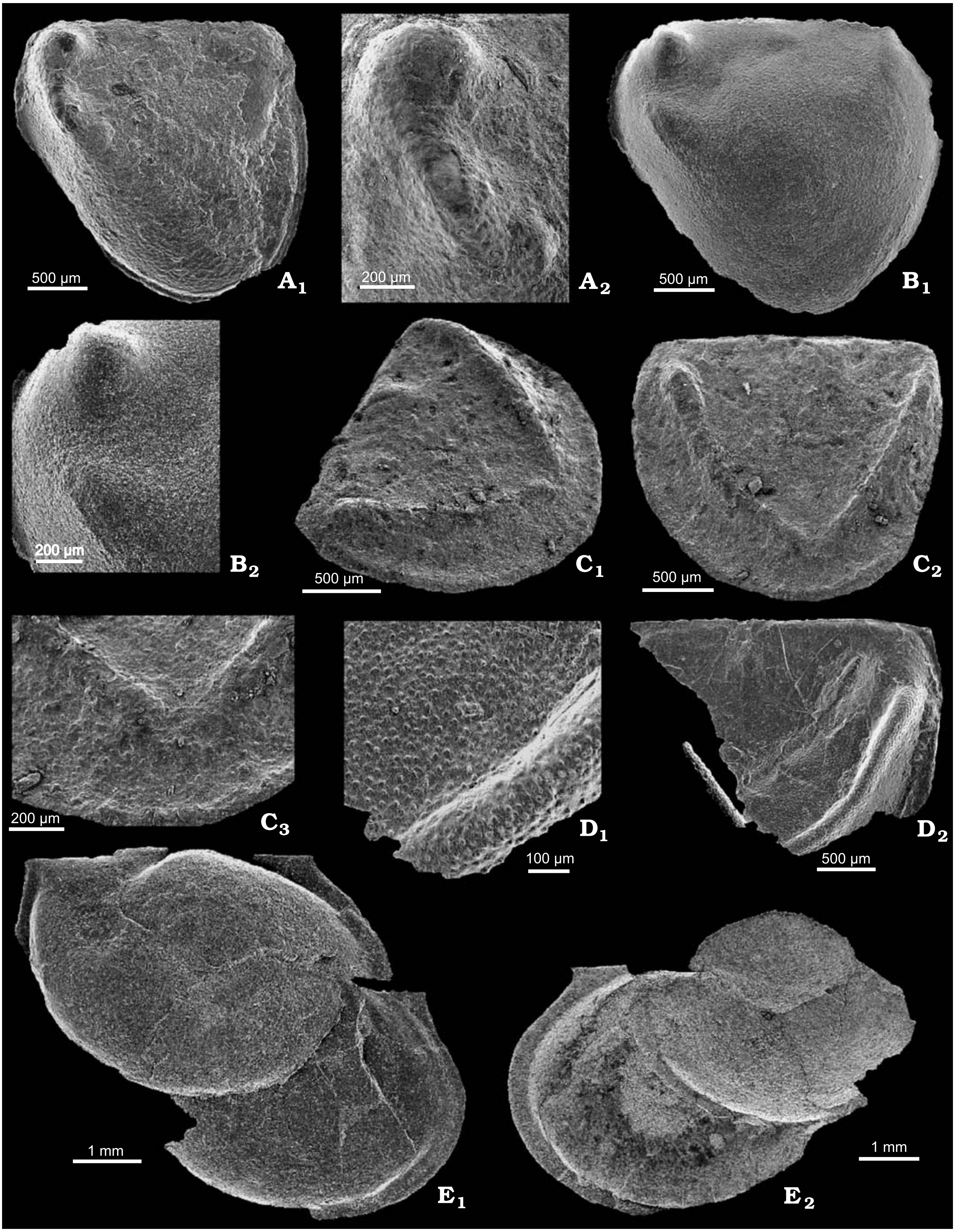
Genus *Hipponicharion* Matthew, 1886

Type species: *Hipponicharion eos* Matthew, 1886 from the lower Cambrian Hanford Brook Formation, *Protolenus elegans* Zone, in New Brunswick, Canada; by monotypy.

Remarks.—The most recent appraisal of the genus is by Siveter and Williams (1997), who also examined the type material of the type species. Their diagnosis of *Hipponicharion* is followed here. We also follow Siveter and Williams (1997) in considering *H. cavatum* Matthew, 1894 and *H. minus* Matthew, 1894 as junior synonyms of *H. eos*.

Hinz-Schallreuter (1993) and Gozalo and Hinz-Schallreuter (2002) described four other species from lower and ?middle Cambrian strata in Morocco, Germany, and Spain. The oldest of them, *H. elicki* Gozalo and Hinz-Schallreuter, 2002 from the upper Zwethau Formation of the Torgau-Doberlug Syncline, Germany, has relatively short anterior

Fig. 3. Bradoriid arthropods from the lower–middle Cambrian of Scania. **A**, **B**. *Beyrichona tinea* Matthew, 1886 from the *Ornamentaspis*? *linnarssoni* Zone at Brantevik. **A**. Left valve largely exfoliated, LO 9347t, in lateral view (A$_1$) and close-up of the anterior lobe (A$_2$). **B**. Left valve, LO 9348t, in lateral view (B$_1$) and close-up of the anterior lobe (B$_2$). **C**, **D**. *Hipponicharion eos* Matthew, 1886 from the ?*Acadoparadoxides oelandicus* Superzone in the Almbacken drill core. **C**. Right valve, LO 9349t, in postero-lateral view (C$_1$), lateral view (C$_2$) and close-up of the ventral region (C$_3$). **D**. Latex cast of incomplete right valve, LO 9350t, in lateral view (D$_2$) and close-up of the ornamentation (D$_1$). **E**. *Alutella* sp. from the ?*Acadoparadoxides oelandicus* Superzone in the Almbacken drill core, LO 9351t. Two partially overlapping valves, belonging to the same specimen, part (E$_1$, epoxy replica) and counterpart (E$_2$) with the right valve partially obscured anterodorsally by the left valve. →


500 µm
A1
200 µm
A2
500 µm
B1
200 µm
B2
500 µm
C1
500 µm
C2
200 µm
C3
100 µm
D1
500 µm
D2
1 mm
E1
1 mm
E2

and posterior lobes and a weak anterodorsal node. In these respects it is similar to the genus *Bicarinella* Rode, Lieberman, and Rowell, 2003 from the lower Cambrian of the Pensacola Mountains, East Antarctica. The general morphology of the lobes is, however, more in accordance with *Hipponicharion*.

The genus *Wimanicharion* Hinz-Schallreuter, 1993 is closely similar to the genus *Hipponicharion* and they differ mainly by the presence or lack of a connection between the anterior and the posterior lobe (see Hinz-Schallreuter 1993; Siveter et al. 1994; Siveter and Williams 1997). The material studied herein has a ventral gap between the two lobes (Fig. 3C$_3$), suggesting that it belongs to *Hipponicharion*.

Neokunmingella Zhang, 1974 is another genus similar to *Hipponicharion*, but it differs from the latter in having confluent anterior and lateral lobes (Williams and Siveter 1998; Hou et al. 2002).

Stratigraphic and geographic distribution.—*Protolenus elegans* Zone (Branchian Series) of New Brunswick, Canada (Siveter and Williams 1997). Protolenid-strenuellid Zone (Comley Series) of England (Williams and Siveter, 1998). ?*Sectigena* Zone (Banian Stage; lower Cambrian) and ?*Ornamentaspis frequens* Zone (middle Agdzian Stage; middle Cambrian) of Morocco (Hinz-Schallreuter 1993; Gozalo and Hinz-Schallreuter 2002). Ovetian Stage (lower Cambrian) of Germany (Elicki 1994; Gozalo and Hinz-Schallreuter 2002). Upper Marianian and lower Bilbilian Stage (lower Cambrian) of Spain (Gozalo and Hinz-Schallreuter 2002; Gozalo et al. 2004). Uppermost Bilbilian Stage of Sardinia (Elicki and Pillola 2004). *Eccaparadoxides insularis* Zone (middle Cambrian) of Poland (Bednarczyk 1984) and *Ptychagnostus praecurrens* Zone (= *Eccaparadoxides pinus* Zone; middle Cambrian) of Närke, south-central Sweden (Streng et al. 2008). ?*Acadoparadoxides oelandicus* Superzone (middle Cambrian) of Scania, southern Sweden (Axheimer and Ahlberg 2003; herein).

Hipponicharion eos Matthew, 1886

Fig. 3C, D.

1886 *Hipponicharion eos* sp. nov.; Matthew 1886: 64, pl. 6: 19, 19a, b.
1984 *Hipponicharion* cf. *eos* Matthew; Bednarczyk 1984: pl. 5: 6.
1997 *Hipponicharion eos* Matthew, 1886; Siveter and Williams 1997: 45–46, pl. 6: 4–8, pl. 7: 1, 2 [see for complete synonymy].
1998 ?*Hipponicharion* sp. cf. *eos* Matthew, 1886; Williams and Siveter 1998: 18, pl. 2: 6, 7.
2002 *Hipponicharion eos* Matthew, 1886; Gozalo and Hinz-Schallreuter 2002: figs. 4A, 5C.
2004 *Hipponicharion ichnusum* sp. nov.; Elicki and Pillola 2004: 392, text-fig. 6, pl. 2: 1, 2.
2007 *Hipponicharion eos* Matthew; Williams et al. 2007: fig. 5.9.

Material.—One nearly complete right valve (LO 9349t; Fig. 3C$_1$–C$_3$) preserved as an internal mould and a fragment of the external mould, one incomplete valve and its external mould (LO 9350t; Fig. 3D$_1$, D$_2$), and one almost complete valve preserved as an external mould with a fragment of the internal mould.

Description.—Carapace sub-semicircular in outline. Dorsal margin straight and slightly shorter than maximum valve length. Lateral outline evenly convex. Free margin evenly developed with narrow admarginal ridge well defined, demarcated from lobal area by deep, narrow groove. Lobation consists of two ridge-like lobes and a smaller sinusoidal central lobe in slightly anterior-median position. Anterior and posterior lobes broadening dorsally, subparallel to adjacent valve outline, separated ventrally by a narrow gap. Anterior lobe shorter than posterior lobe. Anterior sulcus ventrally shallow. Posterior sulcus broad and shallow. Surface distinctly granulose.

Remarks.—The gross morphology of the valves at hand corresponds well to those of *H. eos*, but differs from this species in having a slightly narrower ventral gap between the anterior and the posterior lobe. Modest variation in the length and width of anterior and posterior lobes, as well as the length of the ventral gap between these lobes, can, however, be observed in *H. eos* (see Siveter and Williams 1997: pl. 6: 4–8, pl. 7: 2).

The specimen figured by Bednarczyk (1984) is poorly preserved, but it closely resembles *H. eos*, as described by Siveter and Williams (1997).

Elicki and Pillola (2004) described a new species, *H. ichnusum*, from the uppermost Bilbilian Stage of Sardinia. The holotype (a right valve) is incomplete but clearly exhibits the anterior and posterior lobes. It differs from *H. eos* in having a sub-triangular lateral outline and in the presence of a more prominent central lobe. The central lobe is broken but seems to show a sinusoidal morphology. It has a narrow gap between the anterior and posterior lobes. We find no significant morphological differences between *H. eos* and *H. ichnusum*, and regard *H. ichnusum* as a junior subjective synonym.

Stratigraphic and geographic distribution.—Upper part of the traditional lower Cambrian in New Brunswick, eastern Canada (Hanford Brook Formation, *Protolenus elegans* Zone; Siveter and Williams 1997); lower part of the traditional middle Cambrian (Łeba Formation, *Eccaparadoxides insularis* Zone) in the Łeba area (Białogóra 2 core) of northern Poland (Bednarczyk 1984); lower part of the traditional middle Cambrian (probably *Acadoparadoxides oelandicus* Superzone) in the Almbacken drill core (depth: 30.75 and 30.47 m) of Scania, southern Sweden; probably upper lower Cambrian (uppermost Bilbilian Stage) of Sardinia (Elicki and Pillola 2004).

Family Comptalutidae Öpik, 1968

Genus *Alutella* Kobayashi and Kato, 1951

Type species: *Alutella nakamurai* Kobayashi and Kato, 1951 from the lower Cambrian Mantou Formation of Jinxian County, Liaoning Province, China; by original designation.

Remarks.—The concept of *Alutella* was discussed by Hou et al. (2002), who provided a discussion of the family Comptalutidae and the genus *Alutella* that we follow in this paper. They also noted that the genus *Alutella* can not be readily assigned to any of the four subfamilies of Comptalutidae discussed by Hinz-Schallreuter (1999).

Stratigraphic and geographic distribution.—Tsanglangpuan and Lungwangmiaoan stages (lower Cambrian) and, probably, lowermost middle Cambrian of North China (Huo et al. 1991; Hou et al. 2002). *Yunnanocephalus–Malungia* and *Palaeolenus* zones (lower Cambrian) of South China (Hou et al. 2002). Atdabanian (lower Cambrian) of central Kazakhstan (Melnikova et al. 1997). Botoman (lower Cambrian) of the Eastern Trans-Baikal region (Melnikova et al. 1997). Lower part of the traditional middle Cambrian (probably *Acadoparadoxides oelandicus* Superzone) of Scania (Almbacken drill core), southern Sweden (herein).

Alutella sp.

Fig. 3E.

2003 *Hipponicharion* sp.; Axheimer and Ahlberg 2003: 156.

Material.—Two partially overlapping valves belonging to the same individual (LO 9351t). The left valve is almost complete, whereas the right valve is incomplete, showing only the posterior and ventral areas (the anterior and dorsal areas are obscured by the left valve).

Description.—Valves postplete of medium size (5.5 mm long). Dorsal margin fairly straight, ca. 75% of valve length, with a posterodorsal curve and a more pronounced anterior curve. Lateral outline suboval. Lateroadmarginal ridge entire between cardinal corners, separated from lateral surface by distinct furrow. Anterodorsal node ventrally confluent with inflated lobal area. Anterodorsal sulcus broad and V-shaped. Both node and sulcus weakly developed (although the overlapping between the two valves partly obliterates the relief of this area). Anterior cardinal angle is smaller than posterior cardinal angle. Lateroadmarginal ridge is expanding into a pointing edge at posterior cardinal angle. Outer surface of carapace is punctate.

Remarks.—The outline of the valve, the broad and V-shape anterodorsal sulcus, the single anterodorsal node and the absence of connecting ridges allow us to include this material in the genus *Alutella*. With the limited and poorly preserved material it is left under open nomenclature. It differs from the Chinese species (see Huo et al. 1991; Hou et al. 2002; Peng et al. 2005) and *Alutella* sp. (Melnikova et al. 1997) from Kazakhstan in having a suboval outline. The most similar species is *Alutella usloniensis* (Melnikova, 1988) but the posterior margin of this species is completely different from that of *Alutella* sp. described herein.

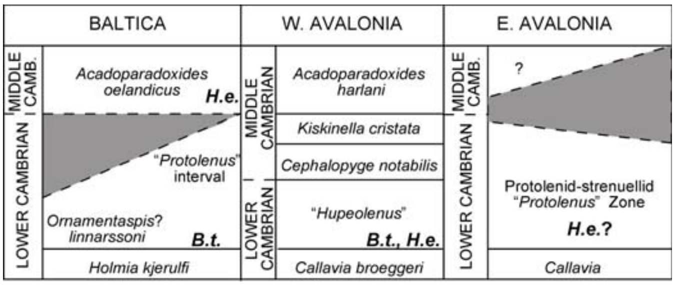


Fig. 4. Correlation chart of the traditional upper lower Cambrian and lower middle Cambrian for Baltica and western and eastern Avalonia. Modified after Geyer (2005) and Axheimer et al. (2007). *B.t.*, *Beyrichona tinea*; *H.e.*, *Hipponicharion eos*.

The genus *Quetopsis* Hinz-Schallreuter, 1999 from lower/middle Cambrian strata of Australia shows a similar morphology; especially the juvenile specimen of *Q. katarcha* Hinz-Schallreuter, 1999 has a very similar outline. However, *Alutella* sp. differs from that specimen by the presence of a V-shaped sulcus and a dorsal node.

Liangshanella nitida (Wiman, 1905) is a poorly known species from glacial erratics in the southern part of the Gulf of Bothnia, Scandinavia. It is closely comparable to the specimen from Scania and appears to have a similar outline and sculpture, but lacks the posterodorsal curve and the V-shaped anterodorsal sulcus.

Stratigraphic and geographic distribution.—Lower part of the traditional middle Cambrian (probably *Acadoparadoxides oelandicus* Superzone) in the Almbacken drill core (depth: 29.40 m) of Scania, southern Sweden.

Biostratigraphical and biogeographical significance

Bradoriids represent significant but generally neglected components in many Cambrian faunas. Most species are short-ranging and hence have considerable potential for biostratigraphy and correlations (Siveter et al. 1996; Melnikova et al. 1997; Siveter and Williams 1997). Three species are known from the lower–middle Cambrian transitional interval of Scania: *Beyrichona tinea* Matthew, 1886, *Hipponicharion eos* Matthew, 1886 and *Alutella* sp. The two first-mentioned species provide additional biostratigraphical data on the age and correlation of this interval.

Beyrichona tinea was originally described from the middle Hanford Brook Formation (*Protolenus elegans* Zone) in New Brunswick, eastern Canada. The record of this species in the upper part of the Gislöv Formation (*Ornamentaspis*? *linnarssoni* Zone) at Brantevik in southeastern Scania suggests a broad correlation between the "*Protolenus* Zone" (*Hupeolenus* Zone) of western Avalonia and the *O*? *linnarssoni* Zone of Scandinavia (Fig. 4). This is in accordance with the recent correlation schemes of Geyer (2005) and Axheimer et al. (2007). *Hipponicharion eos* is also based on material from the Hanford Brook Formation in New Brunswick. It has subsequently been recorded, from the *Eccaparadoxides insularis* Zone of Poland, and hence appears to be a long-ranging species. In Scania, it was recorded from the lowermost part of Alum Shale Formation in the Almbacken drill core (2.15 and 1.87 m below the base of the Forsemölla Limestone Bed), suggesting that this part of the succession is not younger than the *Acadoparadoxides oelandicus* Superzone.

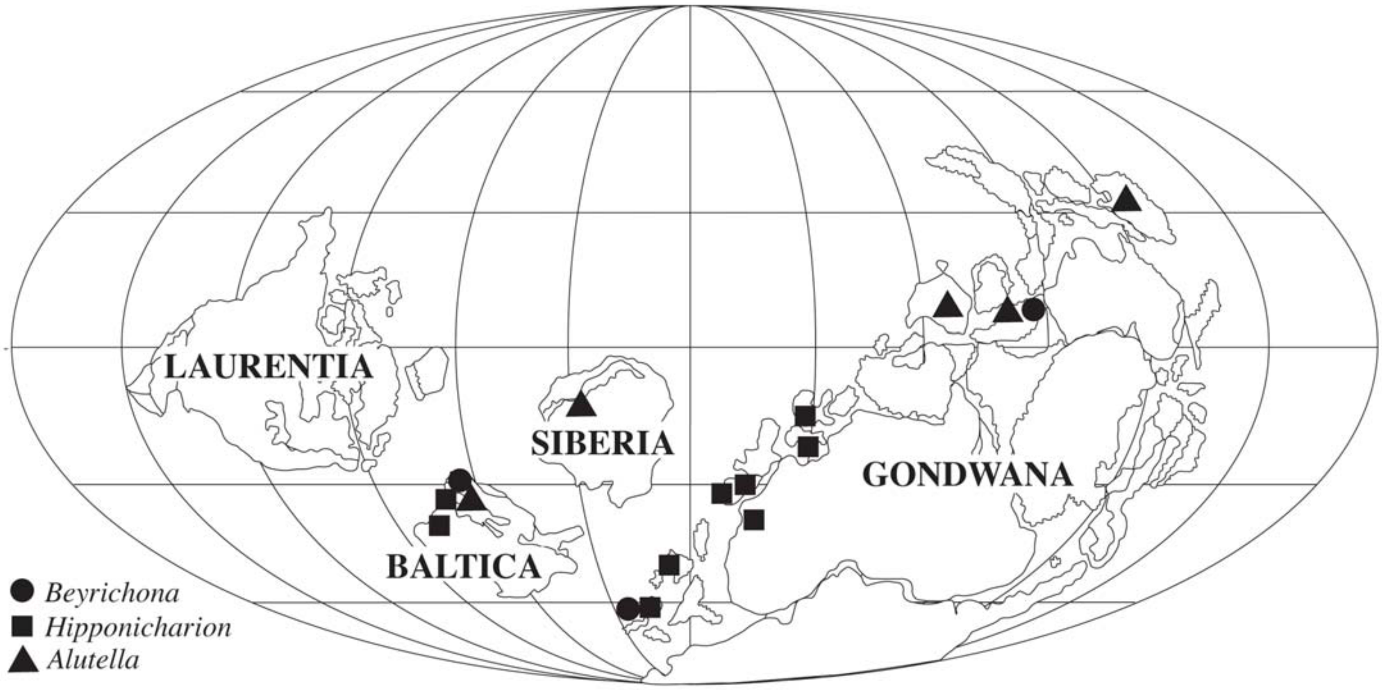


Fig. 5. Distribution of *Beyrichona*, *Hipponicharion*, and *Alutella* plotted on a base map (McKerrow et al. 1992) of reconstructed early–middle Cambrian palaeogeography. Modified after Hou et al. (2002) and Gozalo et al. (2004).

Bradoriids had a global distribution (Fig. 5) and have been recorded from all major Cambrian palaeocontinents (Williams et al. 2007). The distribution of *Alutella* and the comptalutids was discussed by Hou et al. (2002) and Williams et al. (2007), who showed that they appear to have been warm water tropical and sub-tropical bradoriids. The record of *Alutella* from the Alum Shale Formation of southern Scandinavia indicates that at least some comptalutids migrated to mid-latitude sites during early middle Cambrian times.

Hipponicharion is a geographically widely distributed genus that is known from the lower–middle Cambrian of eastern and western Avalonia (New Brunswick and England), western Gondwana (Morocco, Spain, Germany, and Sardinia), and Baltica (Poland and southern Sweden). It was probably a mid- to high latitude genus (Williams et al. 2007), and, as noted by Gozalo and Hinz-Schallreuter (2002), it appears to be restricted to the Acado-Baltic Province sensu Cowie (1971, 1974) and Sdzuy (1972).

Beyrichona has been recorded from the lower–middle Cambrian of New Brunswick, Nova Scotia, England, and Sweden. Thus, it was a characteristic element of many Avalonian and Baltic faunas during early and middle Cambrian times. The genus has, however, also been recorded from the middle Cambrian and Furongian of Maly Karatau, Kazakhstan (Melnikova et al. 1997), suggesting widespread geographical and latitudinal dispersal for this genus (Williams et al. 2007; Fig. 5 herein).

The biogeographical analysis of Williams et al. (2007) shows that Baltic bradoriid faunas most strongly resemble those of western and eastern Avalonia. The faunas in these areas are typified by hipponicharionids and beyrichonids, with cambriids, svealutids, and now comptalutids forming minor elements (Williams et al. 2007). The generic and specific composition of the bradoriid fauna described herein from the lower–middle Cambrian transitional interval of Scania, southern Sweden, support this conclusion.

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