



Early Cambrian bradoriide and phosphatocopide arthropods from King George Island, West Antarctica: Biogeographic implications

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Abstract: Arthropod carapaces have been recovered from the Early Cambrian fossiliferous limestone erratics (dropstones) in the Early Miocene glaciomarine Cape Melville Formation of King George Island (South Shetland Islands), West Antarctica. The arthropod fauna comprises the bradoriide carapaces of *Albrunnicola bengtsoni* Hinz-Schallreuter, *Liangshanella birkenmajeri* sp. nov., *Melvilleella corniculata* gen. et sp. nov., *Mongolitubulus squamifer* Missarzhevsky, *Zepaera* sp., the phosphatocopid *Dabashanella* sp., and one problematic taxon. With the exception of *M. squamifer*, all described species are recorded from Antarctica for the first time. The described Antarctic bradoriide assemblage attests to a close relationship with similar faunas from South Australia and South China, but also includes more widely distributed taxa extending the relationship to the palaeocontinents of Siberia, Baltica and Laurentia.

Key words: Antarctica, King George Island, Cambrian, Arthropoda, Bradoriida, Phosphatocopida.

Introduction

Bradoriide arthropods are an important component of the Cambrian skeletal fauna, with a more or less cosmopolitan distribution in the Cambrian world. However, bradoriides have only been reported from one locality on the Antarctic continent (Rode *et al.* 2003), but are nevertheless quite common in the glacial dropstones studied here.

The total fossil assemblage recovered from the Early Cambrian glacial erratics comprises, in addition to the bradoriides described herein, an abundance of skeletal remains such as calcified cyanobacteria, archaeocyaths and spiculate sponges (Wrona and Zhuravlev 1996), lingulate brachiopods (Holmer *et al.* 1996), small shelly molluscs (Wrona 2003), echinoderm ossicles, and trilobite exoskeletons.

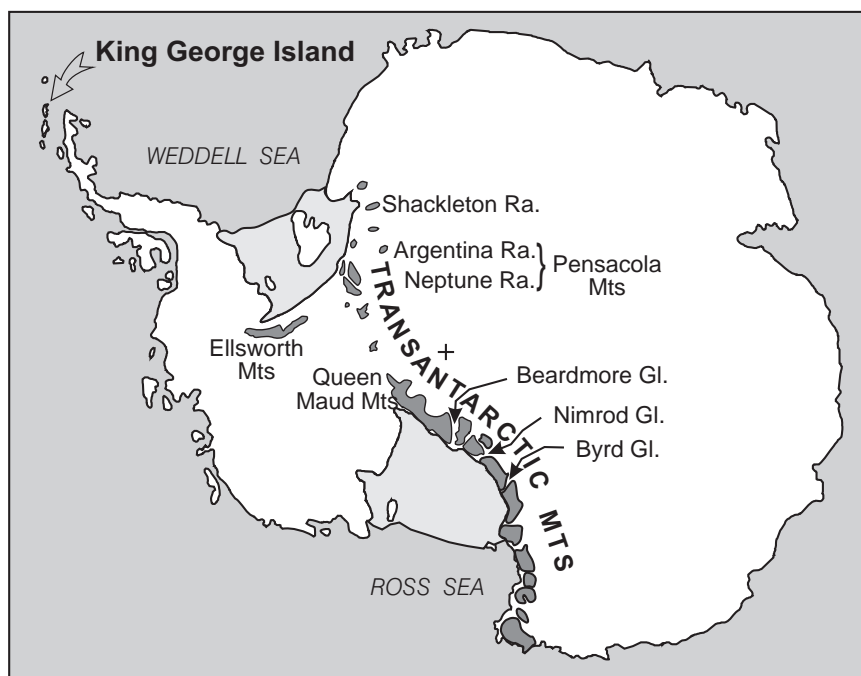


Fig. 1. Location map of King George Island (arrowed) and outcrops of Cambrian rocks (dark shaded) in Antarctica.

These fossils are accompanied by an abundant fauna of phosphatic or phosphatized microfossils representing various shells, exoskeletal sclerites, spines and tubes referred to as small shelly fossils (Wrona 1989, 2004). Cambrian small shelly fossils have been described from many localities around the world: Australia, North Africa, South China, Europe, Kazakhstan, Siberia, eastern Laurentia and Greenland, and bradoriides are common components in many of these (*e.g.* Hinz-Schallreuter 1987, 1993a, b; Siveter *et al.* 1996; Melnikova *et al.* 1997; Siveter and Williams 1997; Hou *et al.* 2002; Skovsted 2006; Skovsted *et al.* 2006). Until recently, Early Cambrian shelly fossil assemblages from Antarctica have mainly been recorded from outcrops of the Shackleton Limestone in the Churchill Mountains (Fig. 1), the Holyoake Range, and from the southeast of Mount Bowers (Rowell *et al.* 1988; Evans and Rowell 1990; Evans 1992), the Pensacola Mountains (Popov and Solovjev 1981; Solovjev *et al.* 1984), the Argentina Range (Solovjev and Grikurov 1979), and Early Cambrian allochthonous boulders at Mount Provender, Shackleton Range (Clarkson *et al.* 1979). However, *in situ* bradoriide arthropods are only known from a single locality in the Transantarctic Mountains (Pensacola Mountains), East Antarctica (Rode *et al.* 2003). Although the material presented here derives from glacial erratics, it is considerably richer and better preserved than any Antarctic Cambrian fauna described thus far. The Antarctic bradoriide assemblage includes similar fauna as that known from South

Australia and South China, but also more widely distributed taxa extending the relationship as far as the Laurentian palaeocontinent.

Geological setting

The Early Miocene glaciomarine Cape Melville Formation (CMF) is restricted to Melville Peninsula on easternmost part of King George Island (Figs 1, 2). The CMF sediments are exposed in northern and southern cliffs of Melville Peninsula (Fig. 3) and on the surface of its flat plateau (Birkenmajer 1982a, b; Gaździcki and Wrona 1982; Birkenmajer *et al.* 1983).

The fossil assemblage of the CMF contains diatoms, chrysomonad (Gaździcki 1989) and dinoflagellate cysts (Troedson and Riding 2002), silicoflagellates, calcareous and arenaceous foraminifers, solitary corals, polychaetes and bryozoans (Hara and Crame 2004), brachiopods (Bitner and Crame 2002), gastropods, bivalves (Anelli *et al.* 2006), decapods (Förster *et al.* 1985; Feldmann and Crame 1998; Feldmann and Gaździcki 1998), echinoids, asteroids and fish remains of Miocene age (for further references see Gaździcki 1987), as well as reworked Cretaceous calcareous nannofossils (Dudziak 1984) and belemnites (Birkenmajer *et al.* 1987). The age of the formation is determined by K-Ar radiometrically dated basalt lavas of the underlying Sherrat Bay Formation and transverse dikes, as well as by biostratigraphic studies, which indicate its deposition during the earliest Miocene glaciation in the Antarctic Peninsula region, the Melville Glaciation (see Birkenmajer *et al.* 1983; Birkenmajer 1987, 1995, 2001; Dingle and Lavelle 1998; Troedson and Riding 2002).

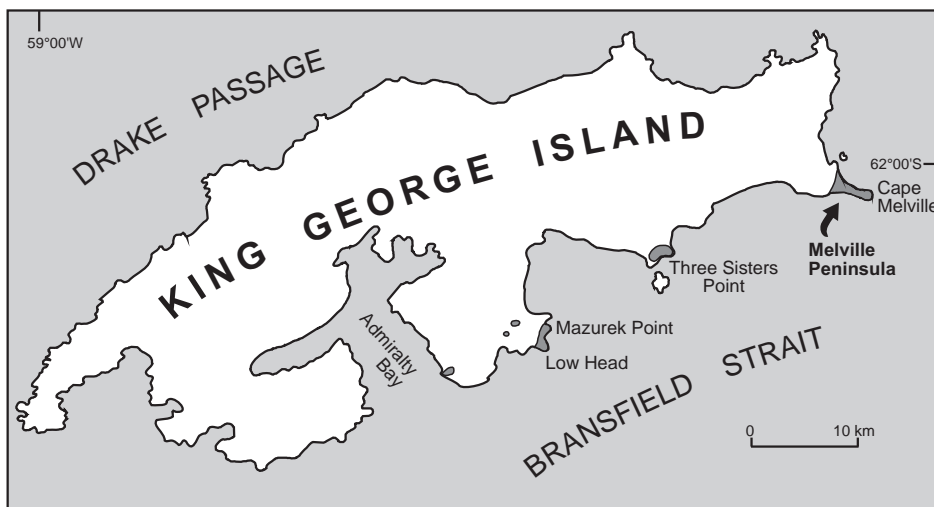


Fig. 2. Occurrence of Oligocene–Miocene glaciomarine strata (shaded) on King George Island and collection site in the Early Miocene Cape Melville Formation (arrowed).

Material

The Early Cambrian arthropod fauna described in this paper comes from the limestone glacial erratics (dropstones) within the Early Miocene Cape Melville Formation.

Originally phosphatic and/or secondary phosphatized arthropod carapaces were recovered from these carbonate rocks using 10% acetic or formic acid. Selected specimens were examined by scanning electron microscope. Most of the figured stereoscan micrographs were taken using a Philips LX-20 scanning electron microscope at the Institute of Paleobiology, Warszawa. The studied collections of Antarctic glacial erratics (labelled as Me) and collection of fossils (labelled as ZPAL V. VI/1S) of King George Island are housed in the Institute of Paleobiology, Polish Academy of Sciences, Warszawa (abbreviated as ZPAL). The thin section (SMNH X 4226) of *Mongolitubulus squamifer* from the Lower Cambrian of River Uchbas, Kazakhstan (sample 264; see Meshkova 1985 for locality data) is housed in the Department of Palaeozoology, Swedish Museum of Natural History.

Glacial erratics: lithology and age

Allochthonous limestone rocks studied for their petrography were classified in three main lithological groups (see Wrona 1989; Wrona and Zhuravlev 1996).

Group 1. — Represented by dark packstone-wackestone and burrowed mudstone, very rich in skeletal fossils. Hollow shells are often filled with phosphatic material which has produced internal moulds. This group yields a very rich and diverse SSF assemblage with sponge spicules. Bivalved arthropods are represented by the bradoriides *Albrunnicola bengtsoni* Hinz-Schallreuter, 1993b (Figs 5A, B, 6A–D, 7A–D, 8A, B, 9A, B), *Liangshanella birkenmajeri* sp. nov. (Fig. 10A–E), *Melvilleella corniculata* gen. et sp. nov. (Fig. 11A, B), ?*Zepaera* sp. (Fig. 12A–G), *Mongolitubulus squamifer* Missarzhevsky, 1977 (Fig. 13A, B), the phosphatocopids ?*Dabashanella* sp. 1 (Fig. 14A–E), ?*Dabashanella* sp. 2 (Fig. 15A–D) and one dabashanella-like problematic taxon (Fig. 16A–C). Molluscs presented previously elsewhere by Wrona (2003) are represented by the helcionellides *Paraconus* cf. *staitorum* Runnegar in Bengtson *et al.*, 1990; *Yochelcionella* sp., *Anabarella* cf. *argus* Runnegar in Bengtson *et al.*, 1990 and *Pelagiella madianensis* (Zhou and Xiao, 1984) and the helically coiled *Beshtashella tortilis* Missarzhevsky, 1981; the hyoliths *Conotheca australensis* Bengtson in Bengtson *et al.*, 1990; *Microcornus petilus* Bengtson in Bengtson *et al.*, 1990; *Parkula bounites* Bengtson in Bengtson *et al.*, 1990; *Hyptiotheca carraculum* Bengtson in Bengtson *et al.*, 1990 and “*Hyolithes*” *conularioides* Tate, 1892 and the hyolith-like fossil *Cupitheca holocyclata* (Bengtson in Bengtson *et al.*, 1990). Tommotiides are rep-



Fig. 3. **A.** View of the north coast of Melville Peninsula with exposure of stratified deposits of the Early Miocene Cape Melville Formation. Dropstones as residual enrichment (author for scale) on top of glaciomarine strata. **B.** Detail of the lowermost part of the CMF showing dropstone distribution in horizontally bedded strata. Photographs by A. Gaździcki, February 1986.

resented by *Dailyatia ajax* Bischoff, 1976; *Lapworthella fasciculata* Conway Morris and Bengtson in Bengtson *et al.*, 1990 and *Shetlandia multiplicata* Wrona, 2004. Coeloscleritophorans include the cancelloriides *Ch. racemifundis* Bengtson in Bengtson *et al.*, 1990; *Allonnia* ex gr. *tripodophora*, A. cf. *tetrathallis* and ?*Archiasterella* sp., and the halkieriide *Halkieria parva* Conway Morris in Bengtson *et al.*, 1990. Tubes are diverse, represented by *Hyolithellus filiformis* Bengtson, 1990 in Bengtson *et al.* 1990; *H. micans* (Billings, 1871), *Torelrella* sp. and ?*Byronia* Wrona, 2004. In addition, trilobite fragments, archaeocyath internal moulds, ?radiocyathian nesasters, palaeoscolecid sclerites and the problematic microfossil *Aetholicopalla adnata* Conway Morris in Bengtson *et al.*, 1990 are present (see Wrona 2004).

The absence of typical late Atdabanian fossils in this group suggests a lower age limit of the fossil assemblage within the *Pararaia tatei* trilobite Zone (Bengtson *et al.* 1990) or *Halkieria parva* SSF “zone” (Gravestock *et al.* 2001); thus a lower Botomian age is the most plausible because many of King George Island Cambrian fossils are not known from later deposits (Bengtson *et al.* 1990; Zhuravlev and Gravestock 1994; Wrona and Zhuravlev 1996; Gravestock *et al.* 2001; Wrona 2003, 2004). This assemblage is closely similar to late Atdabanian–early Botomian Australian assemblages, especially that from the Parara Limestone of

Yorke Peninsula, Stansbury Basin, (Bengtson *et al.* 1990, Gravestock *et al.* 2001, Jago *et al.* 2006, Skovsted *et al.* 2006, Paterson *et al.* 2007).

Group 2. — Represented by calcimicrobial-archaeocyathan reef limestone. An assemblage with reef organisms represented by archaeocyaths, coralomorphs and calcified cyanobacteria described by Wrona and Zhuravlev (1996) contains elements of the *Syringocnema favus* beds assemblage of South Australia which is correlated by Zhuravlev and Gravestock (1994) with the late Botomian (Jago *et al.* 2006, Paterson *et al.* 2007).

Group 3. — Bituminous dark grey limestone with brachiopod shells and trilobite carapaces. This group yield an assemblage with lingulate brachiopod valves (Holmer *et al.* 1996), accompanied by sponge spicules, cancelloriide sclerites, shells of the mollusc *Pelagiella madianensis* (Zhou and Xiao, 1984), hyolith conchs, trilobite exoskeleton fragments and palaeoscolecide sclerites. The brachiopods are similar to those in assemblages described from the Toyonian Wirrealpa Limestone of the Flinders Ranges, Ramsay Limestone of Yorke Peninsula, South Australia, Tindall Limestone of the Daly Basin, Montejinni Limestone of the Wiso Basin and Gum Ridge Formation of the Georgina Basin, Northern Territory (Kruse 1990, 1998; Brock and Cooper 1993; Holmer *et al.* 1996; Gravestock *et al.* 2001). This assemblage in general belongs to the middle Toyonian *Archaeocyathus abacus* beds, correlated with the molluscan *Pelagiella madianensis* and SSF *Kaimenella reticulata* “zones” (Zhuravlev and Gravestock 1994; Gravestock *et al.* 2001; Wrona 2003, 2004).

Provenance of limestone erratics

The erratics of the CMF glaciomarine deposits, interpreted as ice-rafted dropstones, were delivered to the Miocene basin by drifting icebergs derived from the margin of the Antarctic ice shelves and transported by sea surface currents (Birkenmajer 1987, 1995, 2001; Birkenmajer *et al.* 1983; Birkenmajer and Butkiewicz 1988; Wrona 1989; Troedson and Riding 2002). The dropstones are mainly igneous, metamorphic or siliciclastic rocks, whereas limestones account for not more than 5% of the total number of rocks (Wrona 1989; Wrona and Zhuravlev 1996). Petrographic features of these rocks point to source areas on the Antarctic continent (Morycowa *et al.* 1982; Birkenmajer and Butkiewicz 1988; Wrona 1989; Wrona and Zhuravlev 1996). However, only three Antarctic occurrences *in situ* containing small shelly fossils are known. These are the Shackleton Limestone outcrops in the Churchill Mountains between Nimrod and Byrd Glaciers and in the southeast of Mount Bowers (Rowell *et al.* 1988; Evans and Rowell 1990; Evans 1992; Palmer and Rowell 1995), the upper Lower Cambrian (Botomian) of the Pensacola Mountains (Popov and Solovjev 1981; Rode *et al.* 2003),

and Lower Cambrian allochthonous boulders at Mount Provender, Shackleton Range yielding molluscs compared with *Helcionella* and *Mellopegma* by Clarkson *et al.* (1979). These localities have not yielded any species in common with the King George Island erratics. It is likely that strata bearing small shelly fossils are presently covered by the Antarctic continental ice sheet. However, the lithological composition of the whole spectrum of erratics from the Cape Melville Formation clearly suggests that Lower Cambrian bedrock in the northern Transantarctic Mountains acted as parent rocks for the glacial erratic (Fig. 1). Birkenmajer (1982a, b, 1987 2001) and Birkenmajer and Butkiewicz (1988) suggested that the main sources of the igneous erratics of King George Island might be the Antarctic Peninsula and Ellsworth, Pensacola and Theron mountains, which provide the entire diversity of igneous and metamorphic dropstone rock types.

Taphonomy

The small shelly fossils, together with bradoriide valves, were chemically liberated from dark or black, slightly bituminous and bioturbated wackestones and packstones. Both the small shelly fossil and the bradoriide assemblages are rich in juvenile specimens (Holmer *et al.* 1996; Wrona 2004). Energy dispersive spectrometry obtained by microprobe analysis under SEM confirmed the presence of pyrite and calcium phosphate in isolated valves. The bradoriide valve composition is presumed to be primarily phosphatic or calcareous-phosphatic, with some organic (chitin) compounds present (Zhang 2007; Zhang and Pratt 2008). Euhedral pyrite crystals encrusted the external surface of some bradoriide valves (Fig. 15A₂), whereas framboidal pyrite encrusted or filled the valves interiors. The enriched pyrite mineralization on the bradoriide valves indicates sulphate reduction, presumably due to microbial activity in the surrounding sediment. Packstones and wackestones, with variably oriented shells, exhibit a biofabric interpreted as indicative of condensed deposits and reworked taphocenoses. This may be the result of slow sedimentation and prolonged exposure of skeletal remains to destructive processes. Their lithology and palaeontological contents suggest that they represent sediments of a relatively deep marine environment with oscillating anaerobic, dysaerobic and aerobic bottom conditions (Wrona and Zhuravlev 1996; Zhuravlev and Wood 1996).

Palaeobiogeographic distribution

Bradoriide faunas are cosmopolitan and now known from all palaeocontinents of the Early Cambrian world (Fig. 4): Gondwana, South China, Avalonia, Baltica, Laurentia, Siberia and the small terranes of the Siberian Far East, Tuva-Mongolia and Kazakhstan-Kirghizia (*e.g.* Hinz-Schallreuter 1993a,b; Melnikova *et al.* 1997;

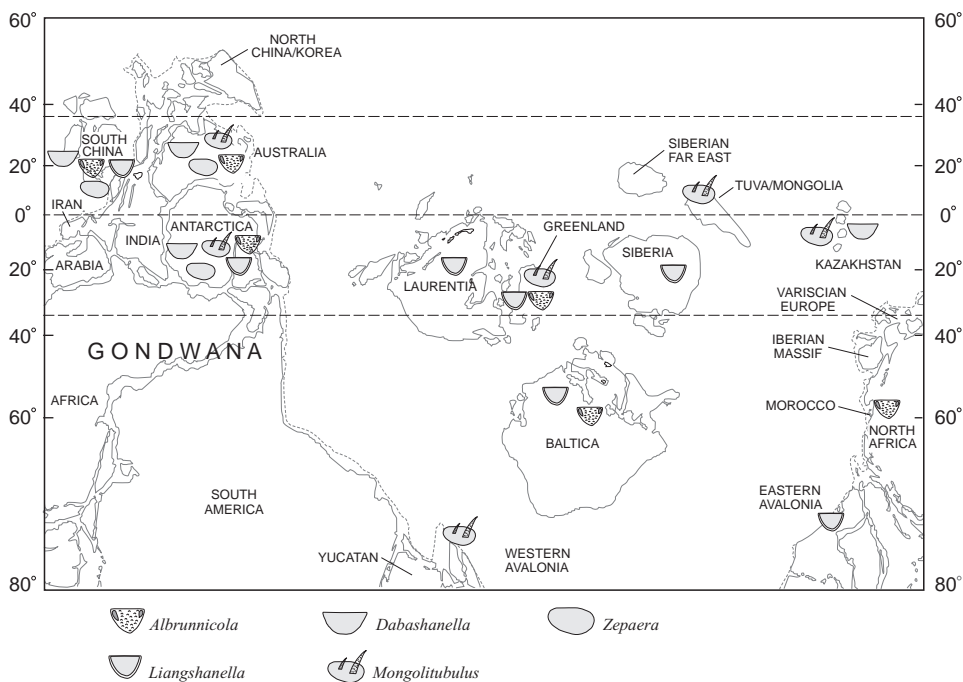


Fig. 4. Early Cambrian palaeogeographic map (modified after Eldridge *et al.* 1997 and Brock *et al.* 2000) showing distribution of most important Antarctic bradoriid and phosphatocopid genera recorded herein.

Williams *et al.* 2007; Zhang 2007). Although the Early Cambrian bradoriides, in general, exhibit distinct biogeographic provinciality (Williams *et al.* 2007), their overall pattern of geographic distribution strongly depends on an insufficient fossil record and their proper taxonomic identification. The bradoriide and phosphatocopid faunas of Antarctica are poorly known since little material has been extracted and described thus far, but at the generic level, they show close relationship with equivalent assemblages from Australia and South China (Topper *et al.* 2007; Williams *et al.* 2007). The Early and Middle Cambrian bradoriide faunas of Australia are abundant, diverse and well documented (*e.g.* Öpik 1968; Bengtson *et al.* 1990; Hinz-Schallreuter 1993a; Jones and Laurie 2006; Skovsted *et al.* 2006; Topper *et al.* 2007). General comparisons of the Australian and Antarctic Early Cambrian fossil assemblages are based on monographic studies of skeletal fossil faunas from Australia (Daily 1956; Öpik 1968; Bengtson *et al.* 1990; Brock and Cooper 1993; Brock *et al.* 2000; Gravestock *et al.* 2001; Skovsted *et al.* 2006) and Antarctica (Wrona 1987, 1989, 2003, 2004; Evans and Rowell 1990; Cooper and Shergold 1991; Holmer *et al.* 1996; Wrona and Zhuravlev 1996; Rode *et al.* 2003). The bradoriide fauna described here from glacial erratics of King George Island attests to a close relationship at the genus level (in particular *Albrunnicola*, *Daba-*

shanella and *Zepaera*) with similar faunas from the Arrowie Basin (Ajax Limestone of Flinders Ranges) and Stansbury Basin (Parara Limestone of Yorke Peninsula) in South Australia (Fig. 4; Bengtson *et al.* 1990; Brock *et al.* 2000; Gravestock *et al.* 2001; Skovsted *et al.* 2006; Brock and Percival 2006; Jago *et al.* 2006; Topper *et al.* 2007). These similarities are consistent with those observed between coeval archaeocyathan and small shelly faunas (Holmer *et al.* 1996; Wrona and Zhuravlev 1996; Wrona 2003, 2004). The most probable explanations are that both basins, particularly the Stansbury Basin, were situated along a continuous East Antarctic-Australian shelf along which the fauna freely migrated (Fig. 4), or that several more or less isolated basins might have existed along Australian and Antarctic parts of the East Gondwana margin (Wrona and Zhuravlev 1996; Wrona 2003, 2004). Transgressive tracts were already suggested for early and late Botomian times based on sedimentological data from South Australian basins (Gravestock and Shergold 2001; Gravestock *et al.* 2001). Many species of small shelly fossils common to Antarctica and Australia are now known from Early Cambrian localities in many parts of the world and may become useful for global biostratigraphic and palaeogeographic correlation (Elicki and Schneider 1992; Elicki 1998; Brock *et al.* 2000). However, poor preservation and limited number of specimens sometimes make species level identification difficult, the biogeographic significance and relationships at the generic or higher taxonomic levels may be more important. In particular because the evolution and extinction of local species is common and typical for faunas in shelf environments. *Mongolitubulus squamifer* recorded here is likely to be a cosmopolitan species (Topper *et al.* 2007). Many genera or even families previously thought to be restricted to certain Asiatic faunal provinces or to Laurentia or Baltica, are described herein for the first time from Antarctica. The palaeogeographical distribution of such genera as *Albrunnicola*, *Liangshanella*, *Dabashanella* and *Zepaera*, and such families as Svealutidae and Comptalutidae is thereby markedly extended to the eastern margin of Gondwana.

Systematic palaeontology

The Cambrian Order Bradoriida as currently defined represents two distinct groups of bivalved arthropods: the Bradoriida Raymond, 1935 *sensu stricto* and the Phosphatocopida Müller, 1964 and the systematic criteria and differences in valve morphology of bradoriides and phosphatocopids have been summarised by Siveter and Williams (1997), Williams and Siveter (1998), Hou *et al.* (2002) and Zhang (2007).

Morphological terms used in the present study generally follow Öpik (1968), Hinz-Schallreuter (1993b), Siveter and Williams (1997), Hou *et al.* (2002) and Zhang (2007).

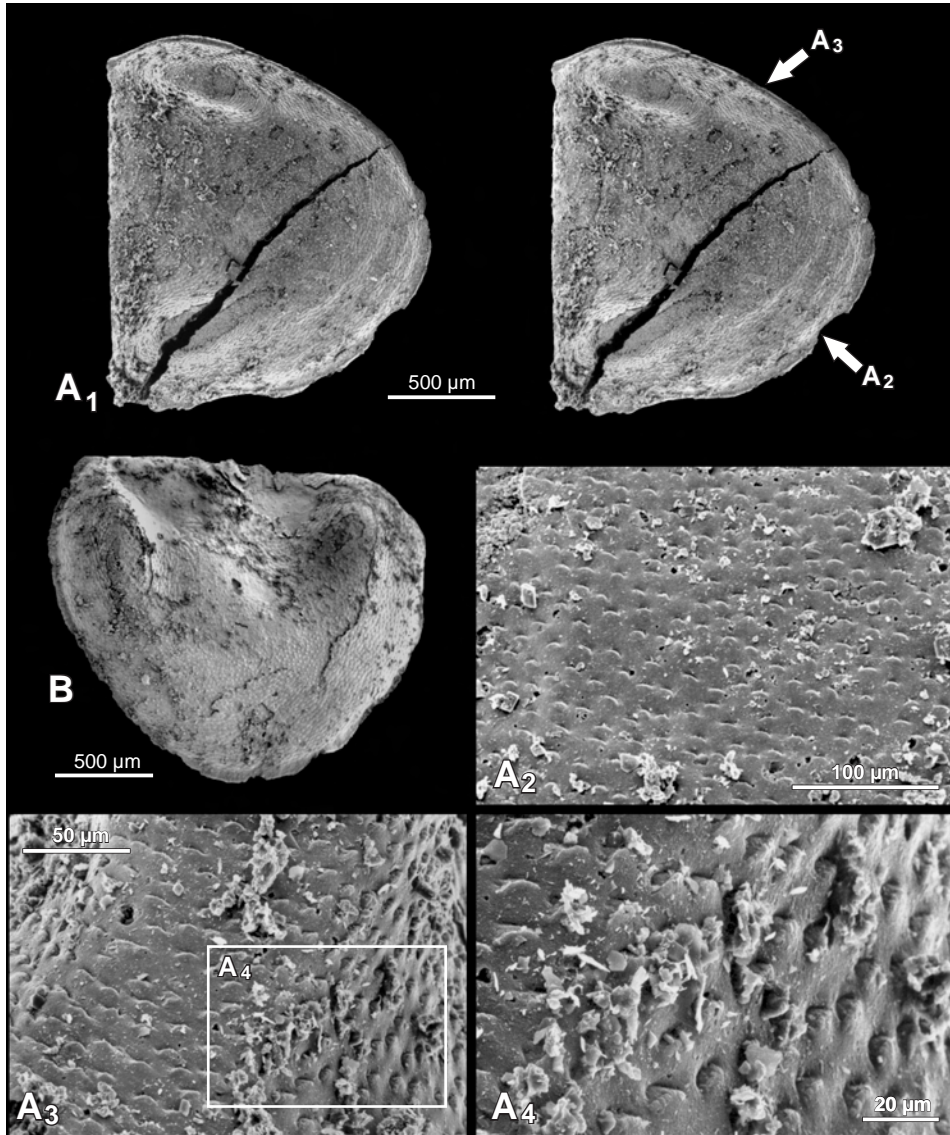


Fig. 5. *Albrunnicola bengtsoni* Hinz-Schallreuter. A. ZPAL V.VI/35S1, erratic Me66. **A₁**. Right valve in lateral view, stereo image. **A₂**. Detail of central part of valve exterior detail showing surface sculpture. **A₃**. Detail of lateral view of anterior lobe showing surface sculpture forming fine crescentic scale pattern. **A₄**. Detail of same surface showing slight imbrications of scale ornament. B. ZPAL V.VI/26S14, erratic Me33. Left valve in lateral view: note partially exfoliated surface layer with ornament; indistinct central node indicated by arrow.

Open nomenclature is used following the recommendations given by P. Bengtson (1988) for situations where full identification is not possible. This is the case with the fragmentary or poorly preserved specimens from the Antarctic glacial erratics of King George Island.

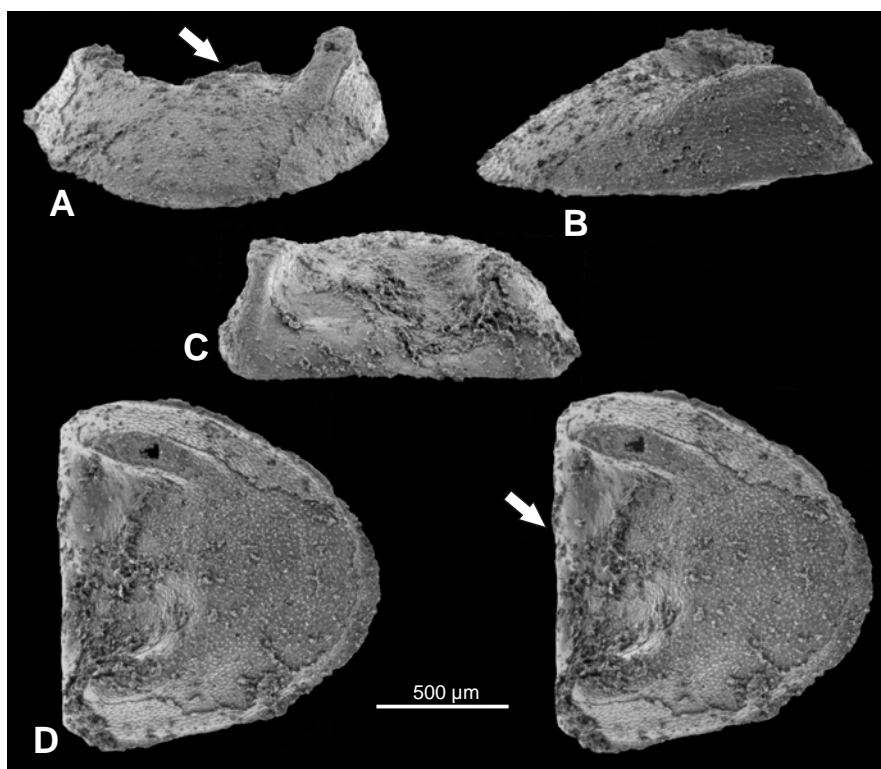


Fig. 6. *Albrunnicola bengtsoni* Hinz-Schallreuter. **A.** Complete right valve in oblique ventral view; indistinct central node indicated by arrow. **B.** Same in oblique posterior view. **C.** Dorsal view. **D.** Lateral view: indistinct centrodorsal node indicated by arrow; note partially exfoliated surface layer showing uncovered pustulose ornamentation of underlying surface, stereo image. ZPAL V.VI/109S3, erratic Me33.

Order Bradoriida Raymond, 1935

Family Hipponicharionidae Sylvester-Bradley, 1961

Genus *Albrunnicola* Martinsson, 1979

Type species: *Longispina oelandica* Andres, 1969,

Species included: Type species and *Albrunnicola bengtsoni* Hinz-Schallreuter, 1993b; *Albrunnicola oelandicus maroccanus* Hinz-Schallreuter, 1993b.

Occurrence. — The type species is known from the Middle Cambrian of Sweden (Andres 1969).

Albrunnicola bengtsoni Hinz-Schallreuter, 1993b

(Figs 5A, B, 6A–D, 7A–D, 8A, B, 9A, B)

2007. *Albrunnicola bengtsoni* Hinz-Schallreuter; Topper *et al.*, p. 85, fig. 10A–K (with synonymy).

Material. — Ten valves studied under SEM are ZPAL V.VI/21S15; 26S14, 15; 32S35; 35S1, 36S5; 39S32; 46U6; 109S3; 114S9 and numerous uncounted specimens, all from glacial erratics Me33 and 66.

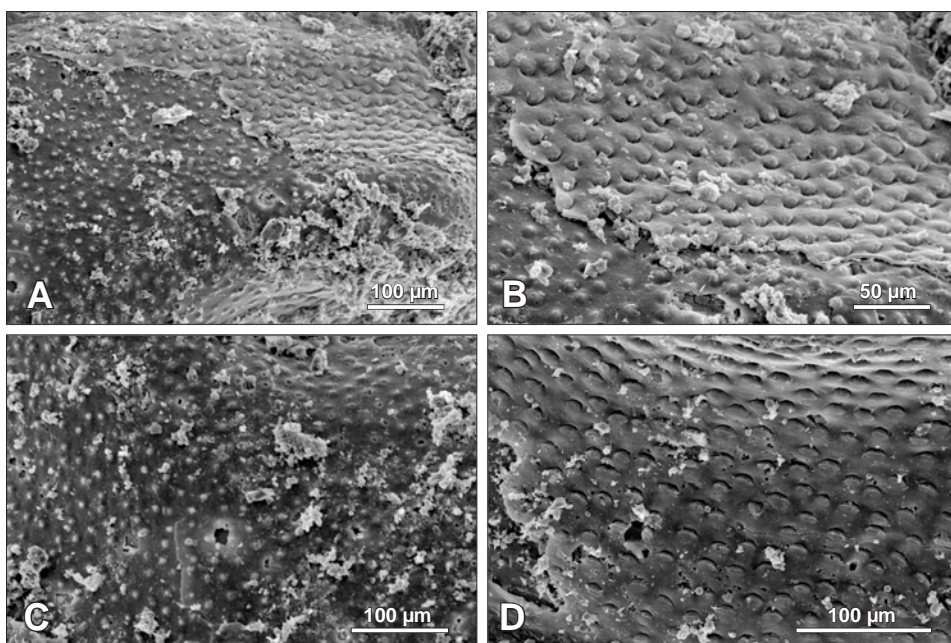


Fig. 7. *Albrunnicola bengtsoni* Hinz-Schallreuter. **A.** External surface of same valve as illustrated in Fig. 4; note partially exfoliated surface layer, showing ornament of tiny crescentic scales on carapace and pustular microstructure (pattern) of underlying layer. **B.** Detail of same, note each pustule corresponds to single crescentic scale. **C.** Detail of pustulose ornament of same inner layer. **D.** Crescentic scaly ornament on same valve external surface. ZPAL V.VI/109S3, erratic Me66.

Measurements. — Nine specimens were measured under SEM, these are 860–1600 μm long and 810–1390 μm high. A single carapace with articulated valves (Fig. 9A, B) is 865 μm long and 812 μm high.

Description. — Valves rounded triangular in outline, slightly postplete to subplete, small, less than 2 mm in length, with straight dorsal margin. Valve shape varies in outline from triangular to almost semicircular. Anterodorsal lobe swings parallel to anterior margin and extends ventrally for about half height of valve (Figs 5A, B; 6A–D, 7A, B, 9A, B). Posterodorsal lobe weaker and often shorter than anterior lobe. Central dorsal node between anterior and posterior lobes, situated close to dorsal margin and somewhat anteriorly, is broad and low with indistinct borders (Figs 5B; 6A, C, D; 8A, B). Posterior and anterior lobes are variously developed, usually well differentiated, in some valves of almost equal size. However, the lobes never extending ventrally more than half of valve height. Central dorsal node absent in some valves. Narrow but distinct marginal rim. Exterior surface of carapace covered with an ornament of crescentic pits extending into tiny scales (Figs 5A, B, 7A–D), scales up to 17 μm wide but averaging 11–15 μm . Scales locally show a slight imbrication with scales inclined outwards from their base (Fig. 5A₄). Sculpture varies with valve size, be-

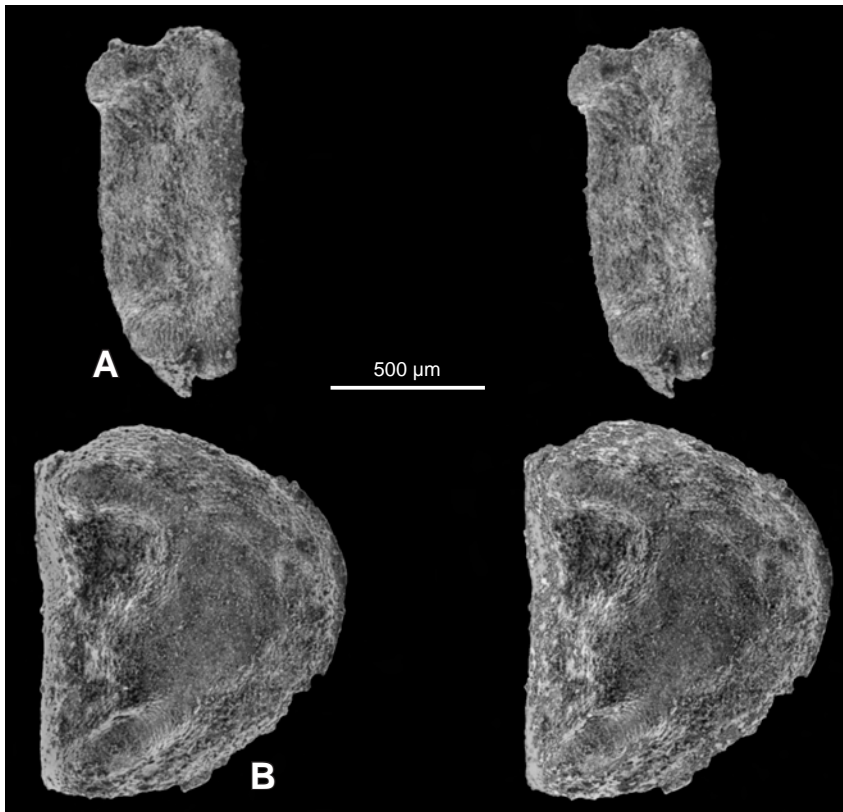


Fig. 8. *Albrunnicola bengtsoni* Hinz-Schallreuter. **A.** Complete left valve in dorsal view, note pronounced anterodorsal lobe, less well developed posterodorsal lobe and weakly developed broad centrodorsal node, stereo image. **B.** Left valve in lateral view: note low, indistinct central node, stereo image. ZPAL V.VI/39S32, erratic Me33.

ing more distinctly developed and with more strongly imbricated scales on convex surface of lobes (Figs 5A₃, A₄).

Remarks. — The crescentic scale ornament is also well visible in valves of *A. bengtsoni* illustrated from the Mernmerna Formation, South Australia (Skovsted *et al.* 2006, fig. 10H; Topper *et al.* 2007, figs 10A–D, G) and described as a pitted ornament of “U- to V-shaped indentations”. This fine ornament can also be barely visible on another South Australian specimen, from the Parara Limestone (Melnikova 2001, fig. 26b) described, as having a “smooth carapace”. In low magnification, the crescentic scale ornament, can indeed be visible as small crescentic pits (Figs 5A₂, B). Valves are often exfoliated without the primary ornamented surface layer, but with exposed under lying pustular microstructure that produces a secondary false ornamentation (Figs 5B, 6D, 7C) and each pustule corresponds to single scale (Fig. 7B). Where this outermost thin layer possessing minute crescentic scale ornament is totally exfoliated or not preserved, the carapace would leave a

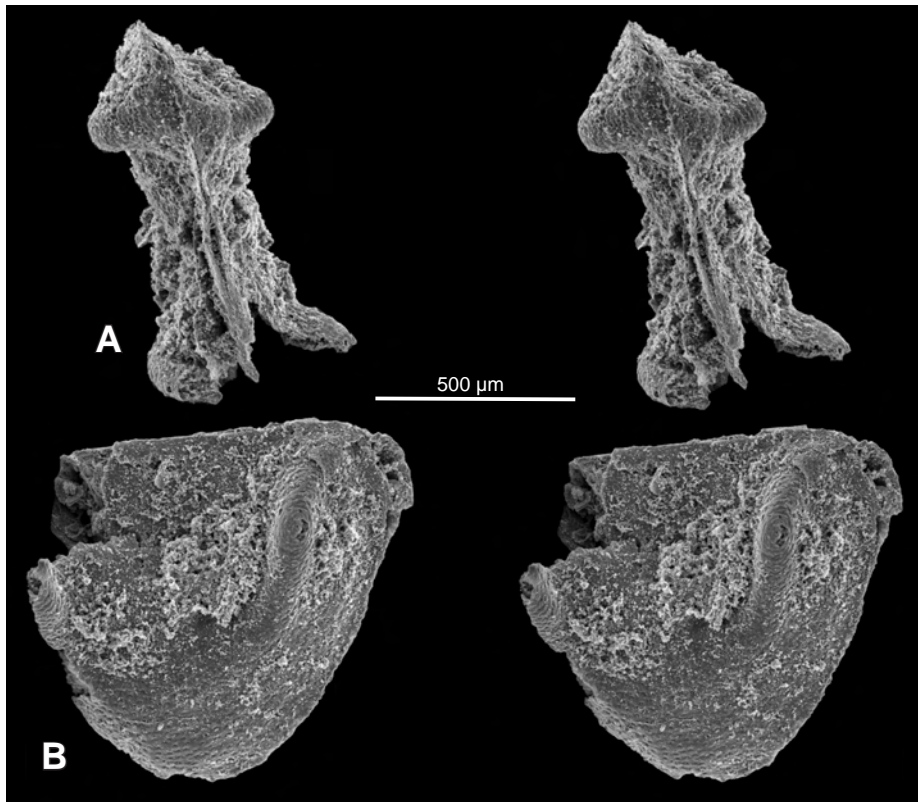


Fig. 9. *Albrunnicola bengtsoni* Hinz-Schallreuter. **A.** Near complete carapace, somewhat deformed, with associated valves in dorsal view: note pronounced anterodorsal lobe and less well developed posterodorsal lobe; note damaged posterodorsal lobe, stereo image. **B.** Right valve of same carapace in lateral view; note flat, indistinct central node, stereo image. ZPAL V.VI/114S9, erratic Me33.

smooth or pustulose outer surface, exactly as in the case of *Bicarinella evansi* Rode *et al.* (2003, fig. 5). It is worth noting, that very similar crescentic tiny scale ornament, also showing slight imbrications of the scale ornament, is often present and distinct in other bradoriide taxa, ex. gr. *Yucola bucerus* (Zhang, 1987) (see Zhang 2007, pl. 19: 6) or *Kumingella typica* Huo and Shu, 1985 (see Zhang 2007, pl. 4: 6). The latter species possesses a carapace surface covered with a reticulated network of fine ridges arranged in minute polygons. Those polygons on the prominent posterior lobe, commonly extended into a spine, are arranged longitudinally into a rhomboid polygonal sculpture. The corners of the rhomboids bear a tiny node and are inclined outwards to form an imbricate surface sculpture (Zhang 2007, pl. 4: 4–6, 15). On the other hand, the scaly ornament is also very similar to the ornament of numerous “ornamented tubes”, in particular is typical of *Mongolitubulus* spines (Fig. 13A, B), which are common components of the Early Cambrian small shelly fossil assemblages (*e.g.* Skovsted and Peel 2001; Wrona 2004;

Skovsted *et al.* 2006; Topper *et al.* 2007). Topper *et al.* (2007) have definitively demonstrated that all morphotypes of *Mongolitubulus* represent broken spines of bradoriide arthropod carapaces.

Occurrence. — Glacial erratics of inferred Early Cambrian age from King George Island, Antarctica, and Ajax Limestone and Mernmerna Formation of Bunkers Range, Flinders Ranges (Arrowie Basin) and Parara, Ramsay and Stansbury limestones of Yorke Peninsula, South Australia.

Family Svealutidae Öpik, 1968

Genus *Liangshanella* Huo, 1956

Type species: *Liangshanella liangshanensis* Huo, 1956.

Species included: Type species and *L. rotundata* (Huo, 1956), *Liangshanella yuannensis* Zhang, 1974; *L. sayutinae* (Melnikova, 1988); *L. burgessensis* Siveter and Williams, 1997; *L. baensis* Zhang, 2007 and *L. birkenmajeri* sp. nov.

Occurrence. — Early Cambrian of South China (Hou *et al.* 2006; Zhang 2007), Siberia (Melnikova *et al.* 1997) and from Antarctica recorded for the first time; Early and Middle Cambrian of North America (Williams *et al.* 2007).

Liangshanella birkenmajeri sp. nov.

(Fig. 10A–E)

Holotype: Specimen ZPAL V.VI/23S12, illustrated in Fig. 10.

Type horizon: Inferred upper of Early Cambrian, Botomian, *Pararaia tatei* trilobite Zone or *Halkieria parva* SSF Zone.

Type locality: Glacial erratic (Me 66) of the Antarctic origin in the glaciomarine Cape Melville Formation (Lower Miocene), Melville Peninsula, King George Island, West Antarctica.

Derivation of name: In honour of Professor Krzysztof Birkenmajer, the prominent geologist of polar regions and leader of several Polish Arctic and Antarctic expeditions.

Diagnosis. — Small, subovate, slightly postplete, svealutid valve, with very weak or absent anterodorsal node. Dorsal margin gently arched upwards. Well developed marginal ridge, extending between cardinal corners and demarcated from lateral surface by a distinct furrow. External surface smooth and evenly convex.

Material and measurements. — One valve: holotype ZPAL V.VI/23S12 from erratic Me66. Figured holotype is 1490 µm long and 1215 µm high, with dorsal margin 1245 µm long.

Description. — Small, subovate, slightly postplete, svealutid valve, evenly convex, but moderately flattened dorsally, with very weakly developed anterodorsal node. Well developed marginal ridge, extending between cardinal corners along free margin and demarcated from lateral surface by a distinct furrow. Valve is black under light microscope, which may suggest that some organic material is present in its phosphatic matrix. External surface smooth, but where partially corroded exhibits a wall microstructure showing an arrangement of phosphate crystallites in medial layer of carapace wall (Fig. 10C–E).

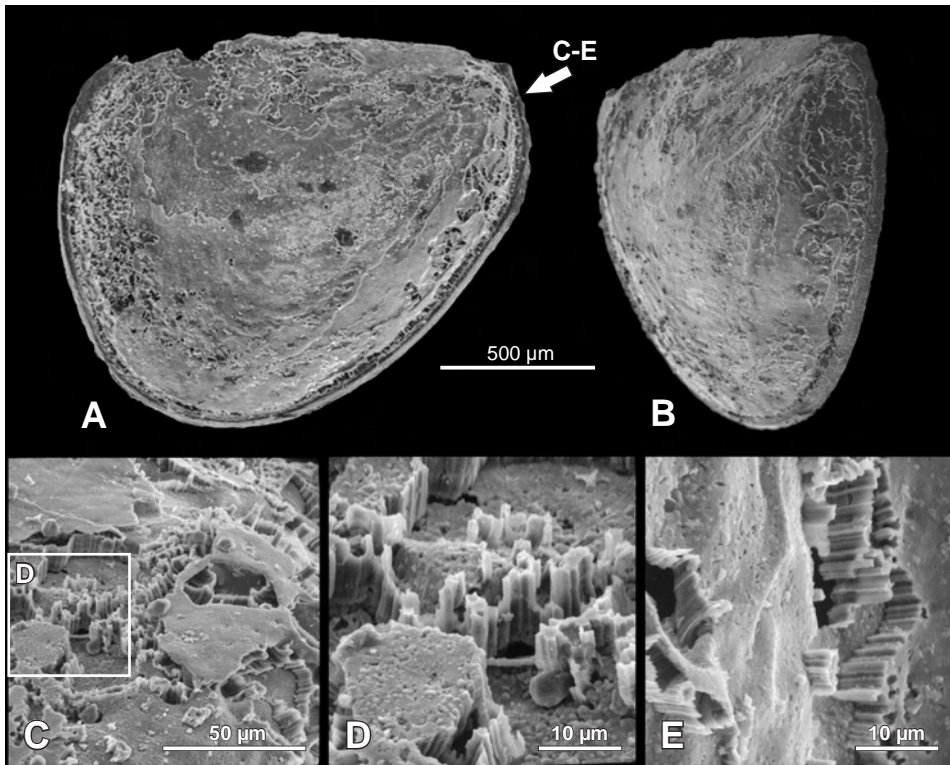


Fig. 10. *Liangshanella birkenmajeri* sp. n., **A**. Right valve in lateral view; note partially corroded surface layer. **B**. Same in oblique anterior view. **C**. Detail of same specimen showing enlarged anterodorsal termination with corroded surface layer. **D**. Detail of phosphatised carapace microstructure. **E**. Detail showing arrangement of phosphate crystallites in external carapace layer. ZPAL V.VI/23S12, erratic Me33.

Remarks. — This species is readily distinguishable from all other species of *Liangshanella* by its overall outline, very weak or virtually absent anterodorsal node, narrow deep furrow and smooth external surface. The new species resembles some valves of *Matthoria* in having a moderately postplete valve with slightly arched dorsal margin, but differs in apparently lacking anterodorsal node. Valves of the new species are somewhat similar in outline to some postplete beyrichonid valves of *Parahoulongdongella*, but differs lacking any distinct lobation, sulcus or rear gape in its valves. Similarities between valves of *Liangshanella* and *Parahoulongdongella* have been also pointed out and discussed by Zhang (2007). The valve wall microstructure may indicate an originally phosphatic and/or secondarily phosphatized carapace. Transversely oriented phosphate crystallites in the middle layer of the valve wall may be interpreted as a result of a secondary phosphatizing process after decomposition of the originally organic or weakly mineralized calcium phosphatic carapace. The internal, originally organic (chitinous or proteinaceous) layer of the valve may acts as the base and framework for

phosphate crystallization (Fig. 10C–E). The SEM observation has often demonstrated a multilayered carapace wall among bradoriides, which might be an effect of early or late diagenetic factors, especially selective phosphatization (e.g. Zhang 2007). There is no doubt then that bradoriide carapace ultrastructure may be more complex than unilayered, and in SEM investigation most often appears three layers: a very thin organic, weakly mineralized inner layer, a thicker, mineralized middle layer with in some cases a crystallite (fibrous) ultrastructure, and an outermost thin layer bearing a varied fine ornament (Figs 5B; 6A, D; 7A–D; 10C–E; 11A₃–A₄; Rode *et al.* 2003, fig. 5.5).

Occurrence. — Glacial erratic of inferred Early Cambrian age from King George Island, Antarctica.

Genus *Melvilleella* gen. nov.

Type species: *Melvilleella corniculata* sp. nov.

Derivation of name: After Melville Peninsula, King George Island.

Diagnosis. — Small svealutid valves, rounded triangular in outline and complete. Dorsal margin, with stout anterocardinal spine directed upward dorsally. Marginal rim extending between cardinal corners demarcated from lateral surface by a distinct furrow. External surface smooth and convex, with moderate centro-dorsal inflation.

Remarks. — The lateroadmarginal rim and anterodorsal node suggest a svealutid affinity. The new genus differs from other svealutids in having a stout anterocardinal spine, directed upward dorsally.

Melvilleella corniculata sp. nov.

(Fig. 11A, B)

Holotype: Specimen ZPAL V.VI/103S1, illustrated in Fig. 11.

Type horizon: Inferred upper part of Early Cambrian, Botomian, *Pararaia tatei* trilobite Zone or *Halkieria parva* SSF Zone.

Type locality: Glacial erratic (Me 66) of Antarctic origin in glacio-marine Cape Melville Formation (Lower Miocene), Melville Peninsula, King George Island, West Antarctica.

Derivation of name: From Latin *corniculatus* – horned, referring to the carapace possessing a cardinal spine.

Diagnosis. — *Melvilleella*-like valves, with entire marginal rim extending between cardinal corners and demarcated from lateral surface by a distinct furrow. External surface smooth and convex, with moderate centrodorsal inflation.

Material and measurements. — Two valves: holotype ZPAL V.VI/103S1 and paratype 37S28. Figured holotype is 968 µm long and 940 µm high, its dorsal margin is 620 µm long with cardinal spine 85 µm long and 71 µm wide.

Description. — Valves small, very high, rounded triangular in outline, complete, with straight dorsal margin, possessing short, stout anterocardinal spine, directed upward dorsally. Entire marginal rim, extending between cardinal corners and demarcated from lateral surface by a distinct furrow. External surface smooth

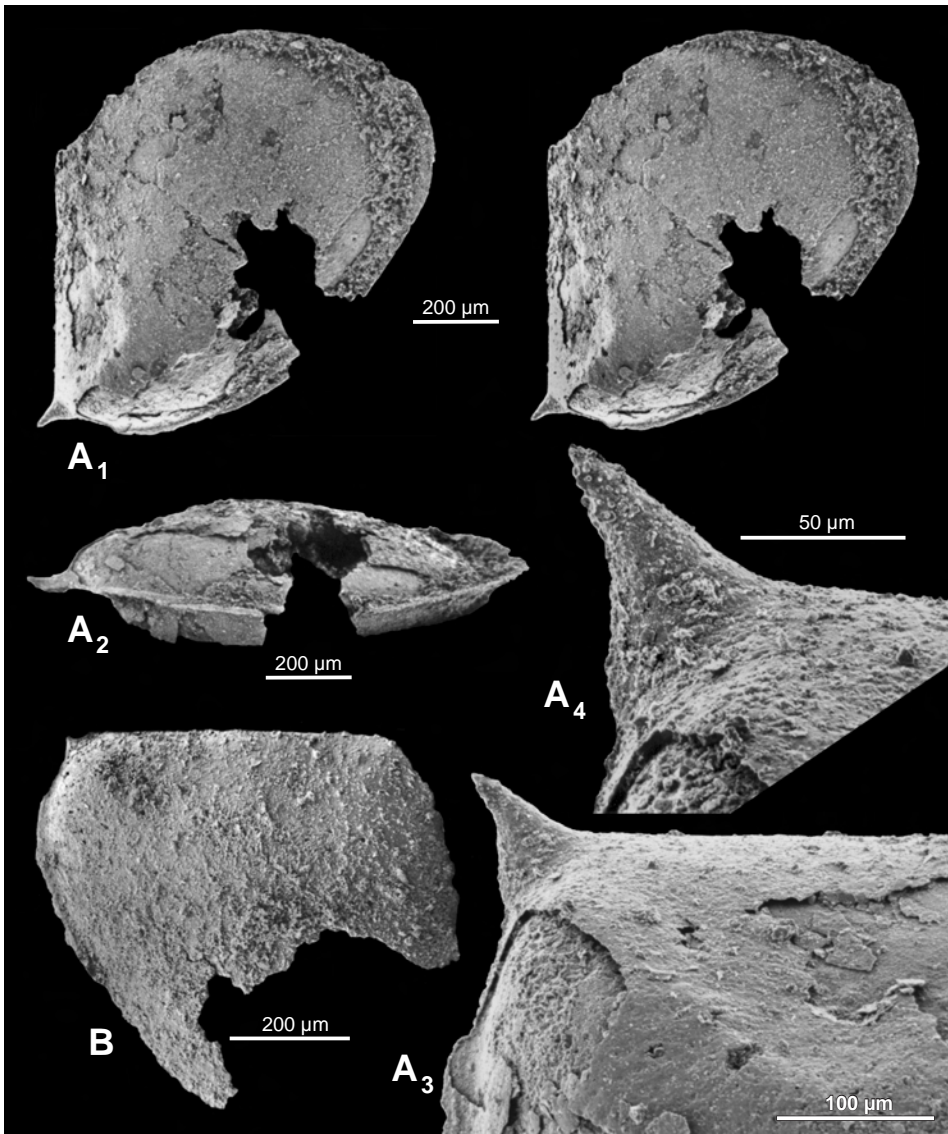


Fig. 11. *Melvillevella corniculata* gen. et sp. n. A. ZPAL V.VI/103S1, erratic Me66. **A₁**. Left valve in lateral view, damaged and partially exfoliated surface layer, stereo image. **A₂**. Oblique anterolateral view showing associated poorly preserved right valve. **A₃**. Detail of anterodorsal corner showing cardinal spine and partially exfoliated surface layer. **A₄**. Detail of anterior cardinal spine. **B**. ZPAL V.VI/37S28, erratic Me66. Poorly preserved left valve in lateral view.

and convex, with moderate centrodorsal inflation. External layer of valves are strongly exfoliated.

Occurrence. — Glacial erratic of inferred Early Cambrian age from King George Island, Antarctica.

Family Comptalutidae Öpik, 1968

Discussion. — See Skovsted *et al.* 2006.

Genus *Zepaera* Fleming, 1973

Type species: *Zepaera rete* Fleming, 1973.

Species included: Type species and *Z. bandeli* Hinz-Schallreuter, 1999.

Occurrence. — The genus is recorded here for the first time from Antarctica and to date has been described only from the Early Cambrian of Australia and South China, and the Middle Cambrian of Australia (Skovsted *et al.* 2006).

?*Zepaera* sp.

(Fig. 12A–G)

Material and measurements. — One carapace (ZPAL V.VI/117S3) from erratic Me66. Figured specimen is 678 µm long, 348 µm wide and 545 µm high, with both associated valves slightly compressed transversely.

Description. — Carapace small, elongate, subcomplete in outline, strongly convex. Dorsal margin straight, shorter than valve length, anterior and posterior margin rounded. Ventral margin gently curved. Two broadly rounded subdorsal nodes, situated close to each other and to border hingeline. Weak depression separates nodes and one (posterior?) node is more prominent than the other. Exterior surface of valve covered with a reticulate network of fine ridges which produce a regular polygonal ornament. Except for subdorsal nodes there is no distinct lobation or marginal structures preserved. External surface toward ventral margin is exfoliated.

Remarks. — Lateral compression of the carapace has deformed the hinge line along its dorsal margin, so that together with compressed subdorsal nodes and transversely convex valve, the carapace somewhat differs from the type species shape. The polygonal surface sculpture is well preserved in the centodorsal parts of the valves and probably reflects the imprints of epidermal cells. The specimen resembles in overall outline some specimens of *Zepaera* from Australia (Jones and McKenzie 1980, fig. 5F; Kruse 1998, fig. 23A; Skovsted *et al.* 2006, fig. 11A), however the lack of distinct lobes as well as the weak V-shaped depression between the subdorsal nodes may be a result of a late growth stage or lateral compression of the valves. The specimen described here bears closer similarity to those comptalutid specimens having a broad mid-dorsal node, assigned to genus et species indeterminate (Topper *et al.* 2007, fig. 14AC–H) from the Early Cambrian Mernmerna Formation of the Flinders Ranges, South Australia.

Occurrence. — Glacial erratic of inferred Early Cambrian age from King George Island, Antarctica.

Family uncertain

Genus *Mongolitubulus* Missarzhevsky, 1977

Type species: *Mongolitubulus squamifer* Missarzhevsky, 1977

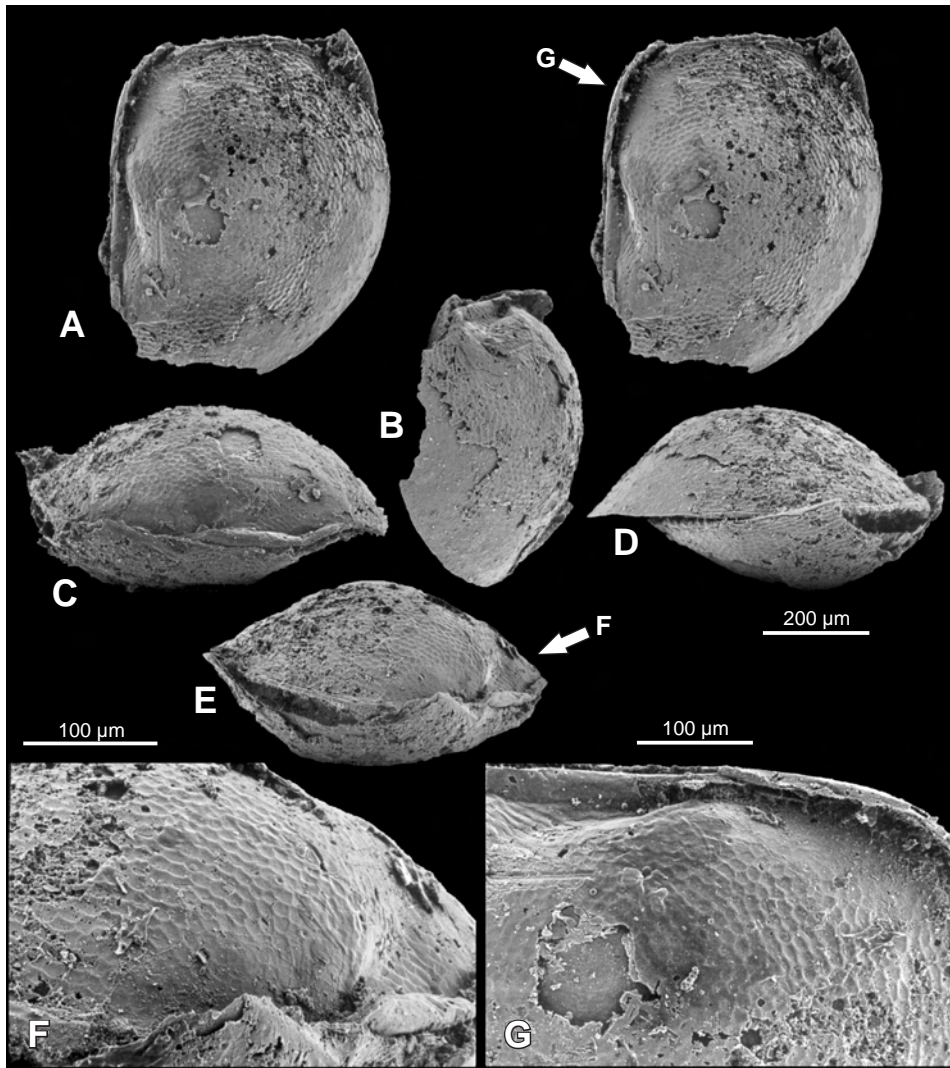


Fig. 12. Comptalutid-like bradoriide ?*Zepaera* sp. **A**. Poorly preserved associated valves in lateral view, incomplete both anteriorly and posteriorly, external surface layer partially exfoliated, stereo image. **B**. Oblique posterior view of broken valve. **C**. Oblique posterodorsal view. **D**. Oblique anteroventral view of associated valves. **E**. Oblique dorsal view. **F**. Detail of E, showing reticulate ornament. **G**. Detail of anterodorsal part of A showing exfoliation and reticulate ornament of external layer. ZPAL V.VI/117S3, erratic Me66.

Species included: Type species and *Mongolitubulus henrikseni* Skovsted and Peel, 2001; *Mongolitubulus unispinosa* Topper *et al.*, 2007.

Discussion. — The systematic position and bradoriide affinity of the genus has been profoundly documented and discussed by Skovsted *et al.* (2006) and Topper *et al.* (2007).

Mongolitubulus squamifer Missarzhevsky, 1977

(Fig. 13A, B)

2007. *Mongolitubulus squamifer*; Missarzhevsky, Topper *et al.*, p. 76, fig. 5A–H (with synonymy).

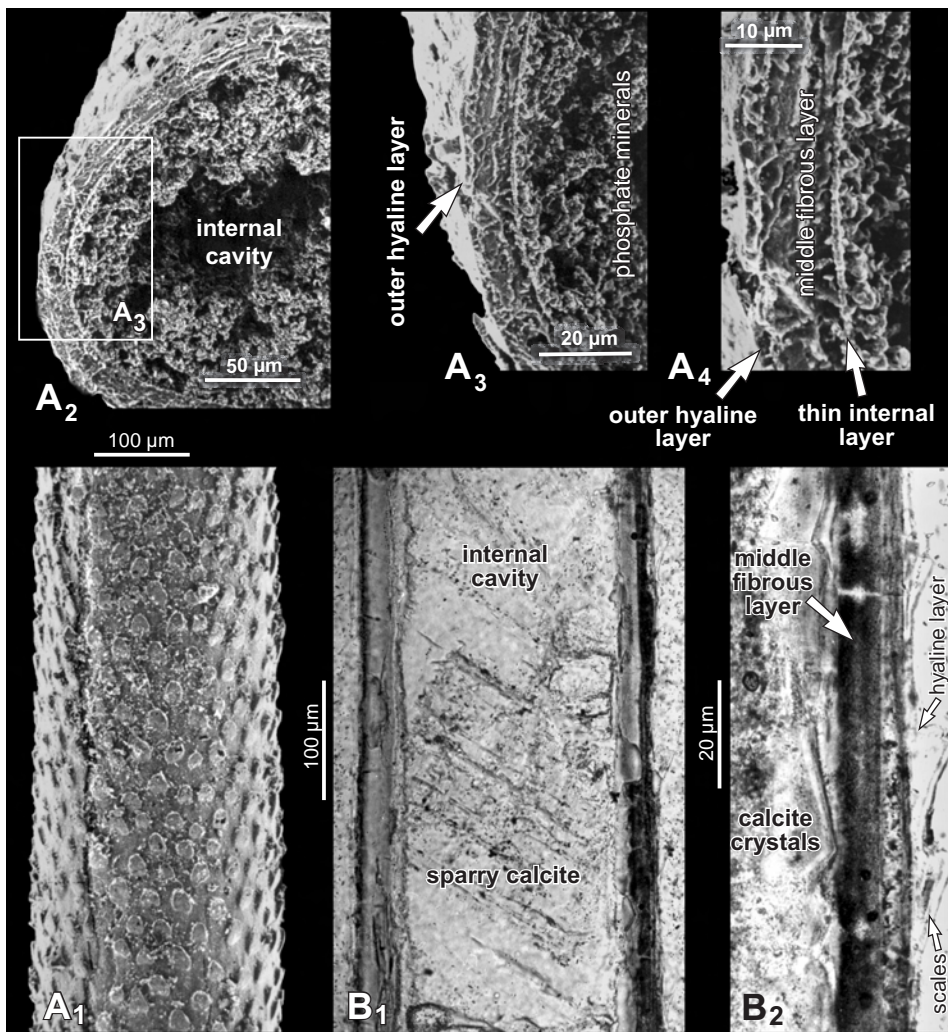


Fig 13. *Mongolitubulus squamifer* Missarzhevsky. **A.** ZPAL V.VI/106S22, erratic M66. **A₁**. Lateral view of central part of spine showing scale pattern. **A₂**. Broken adapical end of spine showing wall structure and internal cavity filled by phosphate minerals. **A₃**. Detail of same spine in cross-fracture showing three-layered wall structure. **A₄**. Detail of **A₃** showing fragment of spine wall. Specimen also figured by Wrona (2004, fig. 23F₁–F₄). **B.** Specimen SMNH X 4226 from Lower Cambrian of Kazakhstan, collected by Meshkova (1985), River Uchbas. **B₁**. Longitudinal thin section of spine embedded in epoxy medium showing layered wall structure and internal cavity filled by sparry calcite. **B₂**. Detail of same spine in cross-section; note totally damaged inner layer and middle fibrous layer partially destroyed by expanded calcite crystals.

Description. — For detailed description and illustration see Wrona 2004, 42, figs 23A–H, 24A–C, as well as Topper *et al.* 2007, 76, fig. 5A–H.

Remarks. — The systematic affinities of various scale-ornamented tubular or spine-shaped fossils common in Early to Middle Cambrian small shelly fossils assemblages, referred to the problematic taxon *Mongolitubulus*, have attracted many palaeontologists and has been extensively studied and discussed during the last decade (Melnikova 2000; Skovsted and Peel 2001; Dzik 2003; Wrona 2004). The origin of *Mongolitubulus* spines have recently been positively documented as broken spines of various bradoriide spiny carapaces (see Melnikova 2000; Skovsted *et al.* 2006; Brock and Percival 2006). Evidence for the bivalve, bradoriide origin of *Mogolitubulus* has been provided by Melnikova (2000); Skovsted and Peel (2001); Skovsted (2005); Skovsted *et al.* (2006) and most recently and definitively by Topper *et al.* (2007), are quite extensive and not only limited to surface microstructures. It is also possible to compare the layered wall structure of *Mongolitubulus* (Figs 13A₂–A₄, 13B₁–B₂, and Wrona 2004, figs 23D₂, F₃, 24) to the another bradoriide carapace structure documented in the present paper (Figs 5–7, 10–12) and elsewhere (see Zhang 2007, 105). The three-layered wall structure of *Mongolitubulus* is clearly visible on a spine cross-sections illustrated here (Fig. 13A₂–A₄) and by Wrona (2004, fig. 23F₃), and thus the diagrammatic cross-section (Wrona 2004, fig. 24) should be reinterpreted accordingly. The details of bradoriide carapace wall microstructure have a long history of investigation (*e.g.* Öpik 1968; Fleming 1975; Huo and Shu 1985; Zhang 2007), but still remain unclear and controversial. It is quite probable that the three-layered carapace structure observed in well preserved specimens is the most common and represent the original, primary structure (Zhang 2007). The delicate, thin innermost layer can be very easily damaged (Fig. 13B₁–B₂) and ultimately not preserved, and the outermost thin layer is in many cases totally exfoliated.

Occurrence. — Early Cambrian glacial erratic from King George Island, Antarctica; as well as Early Cambrian of England, Mongolia, Kazakhstan (Maly Karatau), North America (Labrador, Quebec and New York State), South Australia and western New South Wales.

Order Phosphatocopida Müller, 1964

Family Dabashanellidae Zhao, 1989a

Genus *Dabashanella* Huo, Shu and Fu, 1983 in Huo *et al.* 1983

Type species: *Dabashanella hemicyclica* Huo, Shu and Fu in Huo *et al.* 1983.

Species included: Type species and for further species see Hou *et al.* (2002).

Occurrence. — Early Cambrian of South China, Kazakhstan (Maly Karatau), South Australia and Antarctica; Middle Cambrian of China and Australia.

?*Dabashanella* sp. 1

(Fig. 14A–E)

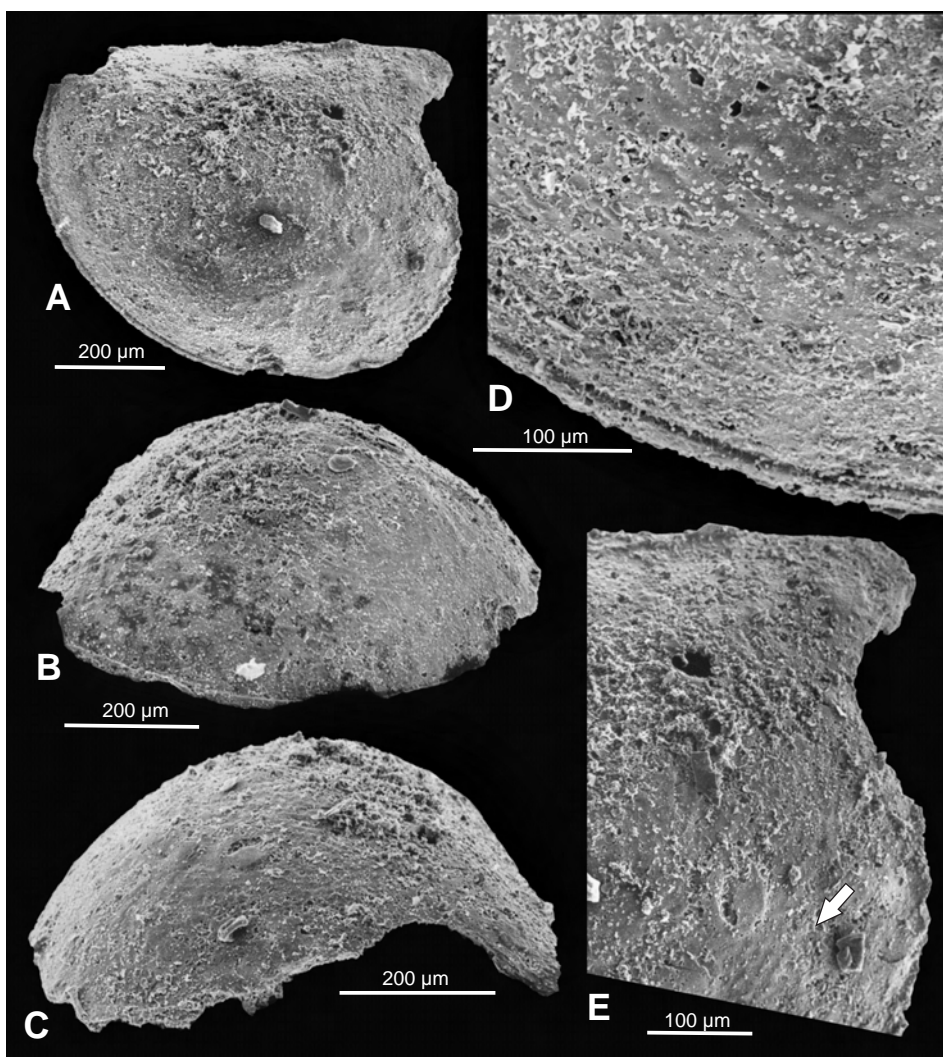


Fig. 14. *?Dabashanella* sp. 1. **A.** Lateral view of anteriorly incomplete right? valve. **B.** Oblique posterior view. **C.** Oblique anterior view of broken valve. **D.** Detail of posteroventral part of valve. **E.** Detail of anterodorsal part with poorly preserved possible reticulate surface sculpture indicated by arrow. ZPAL V.VI/29S4, erratic Me66.

Material and measurements. — One valve ZPAL V.VI/29S4 from erratic Me66. Figured incomplete valve is about 805 µm long and 602 µm high, with dorsal margin about 688 µm long (without cardinal spines).

Description. — Valve small, amplete, strongly elevated. Dorsal margin straight; free margin regularly semicircular with narrow, but well developed marginal rim which is separated from lateral surface by a distinct, small furrow. Cardinal corners broken and cardinal processes not preserved. External surface covered with fine pustules and weakly visible reticulate? ornament (Fig. 14E).

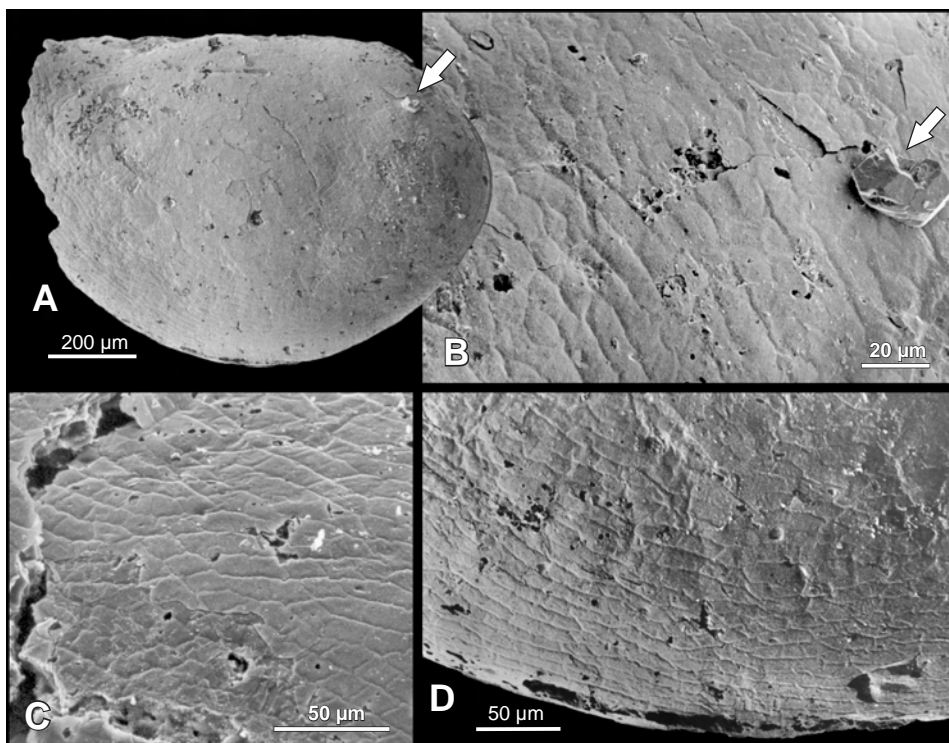


Fig. 15. *?Dabashanella* sp. 2. **A.** Anteriorly incomplete left valve in lateral view. **B.** Detail of posterodorsal part of valve showing reticulate ornament. **C.** Anteroventral part of valve showing reticulate pattern of surface sculpture. **D.** Detail of mid-ventral part of valve. ZPAL V.VI/35S14, erratic Me66.

Remarks. — Unfortunately, the single specimen is incompletely preserved, lacking diagnostic processes at the cardinal corner, and cannot be more precisely identified to species level. The specimen resembles *D. hemicyclica* recorded from South China (Hou *et al.* 2002, fig. 25b) and from Australia (Skovsted *et al.* 2006, fig. 14), but is also somewhat similar to the Indianidae gen. et sp. indet. A recorded from the Lower Cambrian of Australia (Bengtson *et al.* 1990, fig. 207B, C).

Occurrence. — Glacial erratic of inferred Early Cambrian age from King George Island, Antarctica.

?Dabashanella sp. 2

(Fig. 15A–D)

Material and measurements. — One valve ZPAL V.VI/35S14 from erratic Me66. Figured incomplete valve is about 997 µm long and 766 µm high, with dorsal margin about 690 µm long (without cardinal spines).

Description. — Valve small, elongate preplete, gently convex. Dorsal margin straight, shorter than valve length and probably bearing an anterocardinal spine. Cardinal corners broken and anterocardinal process not preserved. Anterior cardi-

nal angle seems to be much greater than posterior cardinal angle. Free margin semicircular, without marginal structures or rim (Fig. 14E). Valve thin and weak. External surface is covered with net of fine furrows that forms polygonal reticulate ornament (Fig. 15B–D).

Remarks. — The single specimen is damaged, without cardinal processes, but the overall shape somewhat resembles *?Dielymella dubia* recorded from the Middle Cambrian of Queensland, Australia by Jones and McKenzie (1980, 217, fig. 8E–I), but recently considered by Skovsted *et al.* (2006) to be synonymous with *Dabashanella*. The polygonal wrinkles on exterior surface might be a result of the taphonomic shrinkage of weakly mineralised valve.

Occurrence. — Glacial erratic of inferred Early Cambrian age from King George Island, Antarctica.

Taxa of uncertain systematic
Phosphatocopida genus et species indeterminate
(Fig. 16A–C).

Material and measurements. — One valve ZPAL V.VI/28S17 from erratic Me66. Figured incomplete valve is about 1985 μm long and 1480 μm high, with dorsal margin about 580 μm long.

Description. — Valve dabashanellid-like, elongate, strongly convex, with rounded lateral outline. Dorsal margin straight, much shorter than valve length, moderately rounded at posterior and anterior margins. Exterior surface covered with a fine irregular granular ornament. There are no lobation or marginal structures. Interior valve shows fragment of a problematic lamella attached to inner valve margin, which can be interpreted as a fragmentary preserved duplicature, a characteristic feature of phosphatocopides (Fig. 16C).

Occurrence. — Glacial erratic of inferred Early Cambrian age from King George Island, Antarctica.

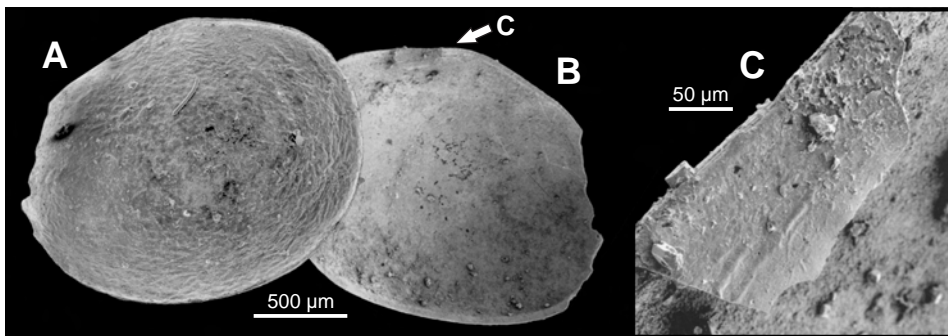


Fig. 16. Problematic phosphatocopide gen. et sp. indet. **A.** Anteriorly incomplete right valve in lateral view, ZPAL V.VI/28S17, erratic Me66. **B.** Internal view of broken valve. **C.** Detail of marginal part with fragment of *?duplicature* attached.

Acknowledgements. — Fieldwork in Antarctica was carried out during the Polish Antarctic expeditions (1981/82 and 1985/86). I wish to acknowledge the extensive editorial efforts of Andrzej Gaździcki (Institute of Paleobiology, Warszawa). I am deeply indebted to Stefan Bengtson (Swedish Museum of Natural History, Stockholm) for offered comparative material and his help during the course of this work at the Department of Palaeozoology. The microfossils were processed with the assistance of Ewa Hara and the figures were enhanced by Aleksandra Holda-Michalska and Andrzej Baliński (all Institute of Paleobiology, Warszawa). I appreciate the valuable suggestions of Brian R. Pratt (University of Saskatchewan), who read an early version of the manuscript. I am very grateful to Christian B. Skovsted (Uppsala University) and one anonymous reviewer for many constructive comments, helpful suggestions and linguistic corrections which greatly improved the manuscript. Many thanks are also extended to Pierre Kruse (Adelaide) for his friendly help, discussion and thoroughgoing language improvement. This research received support from the SYNTHESYS Project which is financed by the European Community-Research Infrastructure Action under the FP6 “Structuring the European Research Area” Programme. SYNTHESYS Contribution number SE-TAF-4785.

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Received July 2009

Accepted 23 November 2009