ABSTRACT: Molluscan fossils accompanied by familiar SSF have been recovered from Early Cambrian limestone erratics in the Early Miocene glaciomarine Cape Melville Formation of King George Island, West Antarctica. The molluscan fauna comprises the hyoliths *Conotheca*, *Microcornus*, *Parkula*, *Hyptiotheca*, “*Hyolithes*”, the helcionelloids *Pararacornus*, *Yochelcionella*, *Anabarella*, the low dextrally coiled *Pelagiella* and the high helically coiled *Beshtashella*, as well as the problematic mollusc *Cupitheca*. Most of described species are recorded here for the first time from Antarctica. The lithological and fossil contents of the erratics are almost the same as from autochthonous successions the Shackleton Limestone in the Argentina Range and Transantarctic Mountains. Early Cambrian outcrops around the Weddell Sea are a probable source of the erratic boulders. The Antarctic fauna is very similar to that from uppermost Botomian and Toyonian carbonate deposits in the Cambrian Basins of South Australia. These faunal and facies similarities between Antarctica and Australia confirm their neighbouring position and common biotic and basin evolution on the Cambrian Gondwana margin.

Key words: Antarctica, King George Island, Cambrian, Hyolitha, Helcionelloida, Gondwana.

Introduction

The fossil assemblage recovered from Early Cambrian erratics derived from the Antarctica comprises abundant skeletal remains such as calcified cyanobacteria, archaeocyath and heteractinid sponges, lingulate brachiopods, ostracode and trilobite carapaces, and echinoderm ossicles, in addition to the molluscan fauna described herein. These are accompanied also by extremely abundant microscopic, originally phosphatic or secondarily phosphatized, small (usually less than 1–2 mm) fossils representing disarticulated exoskeletal sclerites, spines and various shells or tubes referred to as small skeletal fossils, abbreviated as SSF (Wrona 1989, 2004; Wrona and Zhuravlev 1996). Well-documented Cambrian shelly fossils have been described from many localities around the world (Fig. 4): Antarct-
Shackleton Range (Clarkson et al. 1979). The Early Cambrian molluscan fauna described in this paper has been recovered from erratic boulders of limestone within the Early Miocene glaciomarine Cape Melville Formation of King George Island (Gaździcki and Wrona 1986; Wrona 1987, 1989, 2004).

This paper documents the micromolluscan fauna occurring in the Cambrian limestone erratics from King George Island. A complementary work concerning the accompanied small skeletal fossil assemblage is presented elsewhere (Wrona 2004).

Geographical and geological setting

Erratic boulders were sampled from Tertiary glaciomarine sediments of King George Island (South Shetlands) in West Antarctica (Fig. 1). The position of Tertiary rocks yielding erratic boulders is indicated on the map (Fig. 2). Erratics containing abundant Early Cambrian fossils were collected mainly from the Early Miocene Cape Melville Formation.

The Early Miocene glaciomarine Cape Melville Formation (CMF) is restricted to the easternmost part of King George Island, on Melville Peninsula (Fig. 2). The CMF sediments are exposed in northern and southern cliffs of the Melville Peninsula and on the ice-free surface of its flat plateau (Fig. 3). The local fossil assemblage of the CMF contains diatoms, chrysomonad (Gaździcki and Wrona 1986, Gaździcki 1989) and dinoflagellate cysts (Troedson and Riding 2002), silicoflagellates, calcareous and arenaceous foraminifers (Birkenmajer and Łuczkow-
ska 1987), solitary corals (Roniewicz and Morycowa 1987), polychaetes (Szaniewski and Wrona 1987), bryozoans (Hara 1994), brachiopods (Bitner and Crame 2002), gastropods (Karczewski 1987), bivalves, decapods (Förster et al. 1985, 1987; Feldmann and Crame 1998), echinoids (Jesionek-Szamańska 1987), asteroids and fish remains of Miocene age, as well as reworked Cretaceous calcareous nannofossils and belemnites (Dudziak 1984, Birkenmajer et al. 1987). The age of the formation is determined by radiometrically (K-Ar) dated basalt lavas of the underlying Sherrat Bay Formation and transverse dikes, as well as by biostratigraphic studies, which indicate its deposition during the extensive earliest Miocene Glaciation in the Antarctic Peninsula region, the Melville Glaciation (Birkenmajer et al. 1983, 1984, 1985, 1987, 1989, 1992, 1995; Biernat et al. 1985, Dingle and Lavelle 1998, Gaździcki (ed.) 1987, Troedson and Riding 2002). The formation may represent glaciomarine deposits of regional marine-based grounded ice on the continental shelf and relatively ice-proximal up to ice-distal marine environment, with irregular input of coarse glacigenic debris from ice rafting (Troedson and Riding 2002).

Material and methods

The several hundred samples of fossil-bearing boulders were collected from glaciomarine sediments of the Early Miocene Cape Melville Formation of the

Fig. 3. View of the Melville Peninsula plateau with erratic boulders as residual enrichment on the top of glaciomarine sediments of the Cape Melville Formation; Mount Melville, an extinct volcano, in background. Photographed in February 1981.
Melville Peninsula. Erratic boulders were at first studied for their petrography in thin sections and subsequently digested in acid. Phosphatic or phosphatized fossils were liberated using 10% acetic or formic acid. Selected fossils were prepared for scanning electron microscope examination. The sclerite wall microstructure was studied in broken or polished sections under transmitted light microscopy and scanning electron microscopy. Most of the figured stereoscan micrographs were taken using the Philips LX−20 scanning electron microscope at the SEM Laboratory of the Institute of Paleobiology, Warszawa. The studied collection of fossils is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warszawa (abbreviated as ZPAL), and the collection is labelled as ZPAL V. XXVIII/1S10. The Arabic numerals immediately before the S indicate the number of the SEM stub and after the S, the specimen number on the stub (e.g. 1S10 means specimen no. 10 on the stub no. 1). The collection of the Antarctic erraticsof King George Island housed in the Institute of Paleobiology, Warszawa is labelled: ZPAL AE/Me32, M33, and T52. The Arabic numerals indicate the number of the erratic sample (boulder) and the letters Me, M and T indicate their provenance of the Melville Peninsula, Mazurek Point and Three Sisters Point, respectively.

**Lithology of erratic boulders**

Allochthonous limestone boulders 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 (for detail see Wrona and Zhuravlev 1996). Stacked hyoliths, molluscs, bradoriids, lingulate shells (Holmer et al. 1996), echinoderm and trilobite fragments, coeloscleritophoran and palaeoscolecid sclerites, as well as sponge spicules are characteristic (Wrona and Zhuravlev 1996: pl. 1: 5, Wrona 2004). The shells are often filled with phosphatic material, which has produced internal moulds. Framboidal pyrite indicates sulphate-reduction, presumably because of the microbial activity in the sediment.

**Group 2**: represented by calcimicrobial-archaeocyathan reef limestone.

**Group 3**: bituminous dark-grey limestone with brachiopod shells and trilobite carapaces.

The black fossiliferous packstone-wackestones (Group I), calcimicrobial-archaeocyathan reef limestones (Group II) and bituminous dark-grey limestones with brachiopod shells and trilobite carapaces (Group III), correspond respectively to these of the Parara Limestone, Koolywurtie Limestone Member and Ramsay Limestone of the Yorke Peninsula (South Australia) succession (see Daily 1990, Zhuravlev and Gravestock 1994, Wrona and Zhuravlev 1996, Gravestock et al. 2001), as well as lithologies of the Shackleton Limestone of the central Trans-
antarctic Mountains, Antarctic continent (Rees et al. 1989, Rowell and Rees 1989, Rowell et al. 1992). Some similarities also exist between these erratics and rocks from the Flinders Range (Arrowie Basin), in particular, the Mernmerna Formation, upper Wilkawillina Limestone and Wirrealpa Limestone, as well as the Tindall Limestone of the Daly Basin, Northern Territory (Fig. 4).

Fossil assemblage and the age of erratic boulders

The fossil assemblage from the limestone erratics includes archaeocyathan sponges (Wrona and Zhuravlev 1996), brachiopods (Holmer et al. 1996) and very rich small shelly fossils (Gaździcki and Wrona 1986; Wrona 1987, 1989, 2004). This assemblage is rich in juvenile biota (Holmer et al. 1996, Wrona 2004). The majority of skeletal fossils are preserved as phosphatic internal moulds of shells or as selective phosphatic replacements of the original CaCO₃ skeleton. Stacked, nested and variably oriented shells, especially brachiopod valves in coquoid limestones, packstones and wackestones, exhibit a biofabric indicative of condensed deposits and reworked taphocenoses. This may be a result of very slow sedimentation and prolonged exposure of skeletal remains for destructive process. 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). The Early Cambrian phosphatized SSF assemblages of Antarctica are similar to other small shelly fossil assemblages that appeared at the beginning of the Cambrian, and re-occurred several times throughout the Early Paleozoic (Dzik 1994a, b). It has been argued that the repeated global appearance of these fossils resulted from an extinguishing of benthic environments (Dzik 1994a, Zhuravlev and Wood 1996), and probably a vast event of Early Cambrian phosphogenesis (Cook and Shergold 1984, 1986; Brasier 1990).

Three distinct faunal assemblages are recognized in the Early Cambrian fossils from the King George Island (Wrona and Zhuravlev 1996, Wrona 2004): (1) A very rich and diverse SSF assemblage with sponge spicules. Molluscs are represented by the helcionellids *?Pararaconus* cf. *staitorum* Runnegar in Bengtson et al., 1990 (Fig. 12A–C), *Yocheleonella* sp. (Fig. 13A), *Anabarella* cf. *argus* Runnegar in Bengtson et al., 1990 (Fig. 13B), and *Pelagiella madianensis* (Zhou and Xiao, 1984) (Fig. 13C–E), and the helically coiled *Beshtashella tortilis* Missarzhevsky, 1981 (Fig. 14A–E), the hyoliths *Conotheca australensis* Bengtson in Bengtson et al., 1990 (Fig. 5A–E), *Microcornus petilus* Bengtson in Bengtson et al., 1990 (Fig. 8A–H), *Parkula bounites* Bengtson in Bengtson et al., 1990 (Fig. 5F), *Hyptiotheca carraculum* Bengtson in Bengtson et al., 1990 (Figs 9A–B, 10A–E), and “*Hyolithes* conularioides” Tate, 1892 (Fig. 11G), and the hyolith-like fossil *Cupitheca holocyclata* (Bengtson in Bengtson et al., 1990) (Figs

The absence of typical late Attabanian fossils 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); a lower Botomian age is the most plausible because many King George Island fossils are not known from later deposits (Bengtson et al. 1990, Zhuravlev and Gravestock 1994, Wrona and Zhuravlev 1996, Gravestock et al. 2001, Wrona 2004). This assemblage is closely similar to late Attabanian–early Botomian Australian assemblages, especially that from the Stansbury Basin, Parara Limestone of Yorke Peninsula.

(2) An assemblage with reef organisms represented by archaeocyaths, corallomorphs and calcified cyanobacteria described by Wrona and Zhuravlev (1996). All studied erratics contain common elements with the *Syringocnemafavus* beds assemblage of South Australia which is correlated by Zhuravlev and Gravestock (1994) with the late Botomian. Moreover, similar elements have been identified in the King George Island erratics from the Polonez Cove Formation (Morycowa et al. 1982, Debrenne and Kruse 1986). Of the total of 52 archaeocyath species known from Antarctica, 60% are in common with Australia (Wrona and Zhuravlev 1996).

(3) An assemblage with lingulate brachiopod shells (Holmer et al. 1996), accompanied by sponge spicules, chancelloriid sclerites, shells of the mollusc *Pelagiella madianensis* (Zhou and Xiao, 1984) (Fig. 13C–E), hyolith conchs, trilobite carapaces and palaeoscolecid sclerites. The brachiopods *Eoobolus aff. E. elatus* (Pelman, 1986), *Karathele napuru* (Kruse, 1990), and *Vandalotretadjago−ran* (Kruse, 1990) are similar to assemblages described from the Toyonian Wirre-
Limestone of the Flinders Ranges, and Ramsay Limestone of Yorke Penin-
sula, South Australia, and the Tindall Limestone of the Daly Basin (Fig. 4),
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, see also Fig. 4). Moreover, K. napuru
and V. djagoran are also known from the Top Springs Limestone of the northern
Georgina Basin, Northern Territory (Kruse 1991). The palaeoscolecid sclerite
Hadimopanella antarctica Wrona, 1987 resembles, in size and ornamentation, the
Australian coniform sclerite of Chalasiocranos exquisitum Brock and Cooper,
1993 from the Ramsay Limestone of Yorke Peninsula (Brock and Cooper 1993,
Wrona 2004). The disarticulated sclerites of Hadimopanella sp. nov. (Wrona
2004) represent other components of this assemblage and are similar to the
microplate of Kaimenella dailyi Brock and Cooper, 1993.

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).

Comparison

The comparisons of the Australian and Antarctic Early Cambrian fossil assem-
bilages are based on the monographic studies of skeletal fossils from Australia
(Daily 1956, Bengtson et al. 1990, Brock and Cooper 1993, Brock et al. 2000,
Gravestock et al. 2001) and from Antarctica (Wrona 1987, 1989, 2004; Evans and
Rowell 1990, Cooper and Shergold 1991, Holmer et al. 1996, Rode et al. 2003,
Wrona and Zhuravlev 1996). The present molluscan fauna from allochthonous
blocks of King George Island attests to a close relationship at the species level with
molluscan fauna from the Arrowie Basin, Ajax Limestone of Flinders Ranges and
Stansbury Basin, Parara Limestone of Yorke Peninsula in South Australia (Daily
1990, Runnegar 1983, Runnegar in Bengtson et al. 1990, Brock and Copper 1993,
Brock et al. 2000, Gravestock et al. 2001). The closest similarities occur with the
remote Arrowie and Stansbury Basins of South Australia (Figs 1, 4), and are con-
sistent with the similarities observed between analogous archaeocyatan faunas
(Wrona and Zhuravlev 1996). The most possible explanations are, that both bas-
ins, especially the Stansbury Basin, were Australian basins proximal to the contin-
uous East Antarctic shelf along which the fauna freely migrated (Fig. 4), or that the
several more or less isolated basins might have existed along Australian and Ant-
arctic parts of the East Gondwana margin (Wrona and Zhuravlev 1996). Those
basins might have been connected only during the most prominent transgressions,
thus allowing faunal exchange. In fact, transgressive tracts were suggested for
early Botomian, late Botomian and middle Toyonian times based on the sequence
Early Cambrian molluscs

stratigraphy of South Australian basins (Gravestock et al. 2001, Gravestock and Hibburt 1991, Gravestock and Shergold 2001). Many species common for Antarctica and Australia, but originally documented only from Australia, now known from Early Cambrian localities in many parts of the world and become useful for

Fig. 4. Early Cambrian palaeogeographic map with the major sedimentary basins of Australia and Antarctica discussed in the text (modified after Courjault-Radé et al. 1992). Asterisks show distribution of the most important small skeletal fossil occurrences, and distribution of selected genera are marked with icons. References for distribution data are in the text and are modified partly after Brock et al. 2000.
global biostratigraphic and palaeogeographic correlation (Brock et al. 2000). At the generic level (Conotheca, Microcornus, “Hyolithes”, ?Pararacornus, Yochelcionella, Anabarella, Pelagiella, and Beshtashella), the Antarctic Early Cambrian molluscs show close relationships with equivalent assemblages from Australia, North America, South and North China, Europe, Greenland, Iran, Kazakhstan, Mongolia, Tien Shan, Siberia, eastern Laurentia, and Avalonia.

Provenance of limestone erratic boulders

The erratics in shales of the Cape Melville Formation, interpreted as ice-rafted dropstones, were delivered to the Early Miocene basin by drifting icebergs derived from the margin of Antarctic ice shelves, and transported by sea surface currents (Wrona 1989, Troedson and Riding 2002). The erratic boulders are mainly igneous, metamorphic, or siliciclastic rocks, whereas limestones account for some 5% of the total number of boulders (Wrona 1989, Wrona and Zhuravlev 1996). Petrographic features of these rocks point to source areas on the Antarctic continent (Morycowa et al. 1982, Wrona 1989, Wrona and Zhuravlev 1996). However, only three Antarctic occurrences containing small shelly fossils are known. These are the autochthonous Shackleton Limestone 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 Pansacola 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). No one contains 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 entire lithological composition of a whole spectrum of erratics from the CMF clearly suggest that Lower Cambrian bedrocks around the Weddell Sea (in particular the Argentina Range in Pensacola Mts) and northern Transantarctic Mts acted as parent rocks for the glacial boulders. Namely, Birkenmajer (1980; 1982a, b) and Birkenmajer and Butkiewicz (1988) suggested that the main sources of the igneous erratics of King George Island might be: Antarctic Peninsula, Ellsworth Mountains, Pensacola and Theron Mountains, which provide the entire diversity of igneous and metamorphic dropstone lithologies. Wrona and Zhuravlev (1996) suggested that the archaeocyath-bearing erratics collected, together with SSF-bearing erratics, from glaciogenic deposits of King George Island have been derived mainly from locations along the Weddell Sea coast and from the Transantarctic Mts. The archaeocyath-bearing limestone occurring in the Ross Orogen, at least between Nimrod Glacier and the Theron Mountains (Debrenne and Kruse 1986, 1989), could be the source area for erratics of this lithologic group. The Ar-
gentina Range (in Pensacola Mts) is the locality (Fig. 1) nearest to King George Island with in situ archaeocyaths (Konyushkov and Shulyatin 1980).

Systematic palaeontology

Phylum Mollusca Cuvier, 1797
Class Hyolitha Marek, 1963


Order Orthothecida Marek, 1966
Family Circothecidae Missarzhevsky in Rozanov et al., 1969
Genus Conotheca Missarzhevsky in Rozanov et al., 1969

Type species: Conotheca mammilata Missarzhevsky in Rozanov et al., 1969.

Conotheca cf. C. australiensis Bengtson in Bengtson et al., 1990
(Fig. 5A–E)

Material. — Four phosphatized opercula and seven conch internal moulds with the operculum in place, ZPAL V.VI/52U1, 19U8 from erratic boulders Me32, 33 and 66.

Description. — Circular, phosphatized operculum. The external side is convex and covered with concentric growth lines. The external surface is partly exfoliated, and exhibits internal growth structure and prominent growth centre. The internal side has a characteristic marginal zone in the form of a regular brim. Two cardinal processes are partly broken and diverge at about 30°. Conch internal moulds are not complete, about 2.5 mm long, gently curved, with smooth surface, and circular cross-section.

Remarks. — Internal moulds resemble Conotheca australiensis Bengtson, 1990 (in Bengtson et al. 1990) internal moulds, but are more gently curved; they lack the initial (the proximal?) end. The operculum has cardinal processes which are less closely spaced than in the Australian type material. Lateral pairs of clavicle-like tubules on the internal margin, distinctive for the species, have not been observed because of the missing lower-central portion of the operculum. Conch and operculum were primarily calcitic and in acid residues usually occur as deeply
phosphatized shell or internal moulds. Consequently, a more precise designation of the Antarctic specimens is not possible at present.
Conotheca sp. A  
(Fig. 5G–H)

**Material.** — Seven internal moulds of conchs, often with operculum in place or internal mould of a loose operculum, ZPAL V.VI/106S7l; 115S2; from erratic boulders Me32, 66.

**Description.** — Moderately tapering conch, with slightly bulbous apex. Conch gently curved aperturally. The internal mould is circular to subcircular in cross-section. The surface is smooth, indicating that the conch inner surface is also smooth. Conch primarily calcitic and in acid residues usually occurring as a phosphatic internal mould (Fig. 5G–H).

Conotheca sp. B  
(Fig. 6A–F)

**Material.** — Twelve internal moulds of conchs, often with operculum preserved in situ or internal mould of a loose operculum, ZPAL V.VI/52S4, 103S6, 7, 8; 109S1, 2; 112S1; from erratic boulders Me32, 33, 66.

**Description.** — Moderately tapering conch, with slightly bulbous apex. Conch curved in the initial part and straight or less curved aperturally. The internal mould is subcircular in cross-section, with ventral side flattened. Its surface is smooth, as was the conch inner surface. Conch primarily calcitic and in acid residues usually occurring as a phosphatic internal mould.

**Remarks.** — The incomplete conch and poorly preserved internal moulds, often with the operculum in place, are insufficient for a complete description. The internal moulds are partly etched, but even loose opercula with characteristic shape and sculpture (Fig. 6C–D), possibly belongs to the conch of *Conotheca* sp. B.

Order Hyolithida Matthew, 1899  
Genus Microcornus Mambetov, 1972

Type species: *Microcornus parvulus* Mambetov, 1972.

*?Microcornus ex gr. M. eximius* Duan, 1984  
(Fig. 7A–C)

**Material.** — A dozen internal moulds, ZPAL V.VI/112S2, 3, 9, from erratic boulders Me33, 66.

**Description.** — Conch strongly tapering, straight, with angle of divergence 25° increasing to 30° towards the flared aperture. The apex was not observed. Transverse section of conch is rounded-triangular. Ventral side flat to gently convex, lateral sides rounded, and dorsal side has a distinct rounded median ridge. Internal moulds have a smooth surface, reflecting the smooth inner surface of the conch. Conch primarily calcitic and in acid residues usually occurring as a phosphatic internal mould.
Remarks. — The poorly preserved internal moulds with the missing initial ends are insufficient for a complete description. Some more completely preserved internal moulds of simple morphology can be compared to the conchs of the indeterminate hyolithid recorded by Kruse (1990: fig. 22), from the Middle Cambrian of the Daly Basin, Northern Territory, Australia.

Microcornus petilus Bengtson in Bengtson et al., 1990
(Fig. 8A–H)


Material. — A number of internal moulds, ZPAL V.VI/34S22, 35S9; 106S6; 108S8; 110S4; 5; 114S4; 115S6; from erratic boulders Me32, 33, 66.
Description. — Straight conch up to 3 mm long, usually less, rounded-triangular in cross-section, with dorsal median ridge, and dorsal side more convex than ventral (Fig. 8B, H). Conch slender conoidal, with angle of divergence about 15° to 20°. Ligula not observed. Outer surface of internal moulds smooth, reflecting the smooth inner surface of the conch. Initial part of conch bulbous. Conch primarily calcitic; in acid residues usually occurring only when phosphatized and as a phosphatic internal mould. Operculum not observed.

Occurrence. — Early Cambrian (Atdabanian/Botomian) Kulpara Formation and Parara Limestone, Horse Gully, Yorke Peninsula, Stansbury Basin, South Australia; King George Island, Antarctica.

Microcornus cf. M. petilus Bengtson in Bengtson et al., 1990
(Fig. 8I–J)

Material. — Ten internal moulds, ZPAL V.VI/27S4, 34S17 from erratic boulders Me33, 66, 110.

Description. — Slender conch up to 2 mm long, straight or gently curved and rounded-triangular to subelliptical in cross-section. Outer surface without trace
surface sculpture. Longitudinal ribs at dorsoventral margins and longitudinal keels at the dorsum were not observed. Inner surface of conch is therefore smooth. Conch usually gently tapering apically. Conch primarily calcitic and in acid residues usually occurring as a more or less complete phosphatic internal mould. Operculum not observed.

Remarks. — All available specimens are internal moulds which are too poorly preserved for a more complete description, however they differ from the *M. petilus* type species (Bengtson in Bengtson *et al.* 1990), and from the somewhat similar internal moulds of linevitide conchs (for example *Linevitus* Sysoev, 1958) in lacking longitudinal keels on the dorsum.

Genus *Parkula* Bengtson in Bengtson *et al.*, 1990
Type species: *Parkula bounites* Bengtson in Bengtson *et al.*, 1990.

*Parkula bounites* Bengtson in Bengtson *et al.*, 1990
(Fig. 5F)

*Parkula bounites* sp. nov.; Bengtson in Bengtson *et al.* 1990: 223, figs 149–151.


Material. — One phosphatized operculum, ZPAL V.VI/103S3, from erratic boulder Me66.

Description. — Semicircular, phosphatized operculum with a crescentic cardinal shield. The external side is convex and covered with concentric growth lines and fine radial striae at the ventral margin. The internal side has a distinct marginal brim. Two cardinal processes are closely spaced. These observations confirm the features previously recorded in the Australian specimens (see Bengtson *et al.* 1990).

Remarks. — Wall was primarily calcitic and in acid residues the operculum may occur phosphatized or as internal mould, but the latter is difficult to identify, unless bears distinctive features.

Occurrence. — Early Cambrian (Atdabanian/Botomian) Kulpara Formation and Parara Limestone, Horse Gully, Yorke Peninsula, Stansbury Basin, South Australia; King George Island, Antarctica.

Genus *Hyptiotheca* Bengtson in Bengtson *et al.*, 1990
Type species: *Hyptiotheca karraculum* Bengtson in Bengtson *et al.*, 1990.

*Hyptiotheca karraculum* Bengtson in Bengtson *et al.*, 1990
(Figs 9A–B, and 10A–E)

*Hyptiotheca karraculum* Bengtson; Bengtson et al. 1990: 228–229, figs 152–155.


*Hyptiotheca karraculum* Bengtson; Demidenko in Gravestock *et al.* 2001: 102, pl. 10: 3–6.

Description. — Small conch up to 3 mm long, ovoid in cross-section, with dorsum more convex than venter (Fig. 10C, D). Conch conoidal with angle of divergence 15° in juvenile (Fig. 9A) up to 25° in the adult (Fig. 10A–E). Ligula short, about 0.5 or less of the apertural width and semi-elliptical in outline (Fig. 9A, B; Fig. 10C–D). The dorsal apertural margin is a little thicker, as in the Australian type specimens (Bengtson et al. 1990: fig. 154B), and meets with the ligula at an angle of 120°. Outer conch surface covered with densely spaced growth lines, developed as asymmetric, more steep toward the apex, transverse ribs. Ribs are parallel to apertural margin, with slight median sinus on dorsum (Figs. 8A, B and 9B, E) and parallel to ligula edge on venter. Inner surface of conch smooth. Initial part of conch bulbous (Fig. 10A–D), usually slightly convex apically, and with a wall that is thinner than the rest of the conch wall. Conch primarily calcitic, and in acid residues usually occurring as a more or less deeply phosphatized shell wall (Fig. 9A) and as phosphatic internal moulds (Fig. 9A, Fig. 10E). Operculum not observed.

Remarks. — The Antarctic specimens demonstrate the distinctive features of shape and ribbed sculpture (Figs 9A, 10A–E), seen in the Australian ones (Bengtson et al. 1990).

Occurrence. — Early Cambrian (Atdabanian/Botoman) Kulpara Formation and Parara Limestone, Horse Gully, Yorke Peninsula, Stansbury Basin, South Australia; and King George Island, Antarctica.
"Hyolithes" conularioides Tate, 1892
(Fig. 11G₁–G₂)

"Hyolithes" conularioides sp. n.; Tate, 1892: 186, pl. 2: 1.
"Hyolithes" conularioides Tate; Bengtson in Bengtson et al. 1990: 231, fig. 156.
"Hyolithes" conularioides Tate; Demidenko in Gravestock et al. 2001: 103, pl. 10: 9.

Material. — Three internal moulds of poorly preserved specimens, ZPAL V.VI/112S8; from erratic boulder Me66.

Description. — Strongly tapering conch, with angle of divergence mainly about 30° and trapezoidal in cross-section. The venter is flat, the lateral sides are rounded, and the dorsum is convex with a pair of distinct longitudinal folds bounding a deep median sulcus (Fig. 11G₁–G₂). The inner surface of the conch is smooth. The juvenile part seems to be separated from the rest of the conch by a transverse, septum-like wall.

Remarks. — Incomplete internal moulds with partly adhered badly-preserved phosphatized conchs were recovered from one erratic boulder. Conchs with very distinctive dorsal furrow, size and shell shape are most similar to the specimens described from Early Cambrian, (Atdabanian–Botomian) Horse Gully, Curramulka and Mount Scott Range localities in South Australia (Bengtson et al. 1990, Gravestock et al. 2001).

Phylum, Class and Order uncertain
Family Cupithecidae Duan, 1984
Genus Cupitheca Duan in Xing et al., 1984

Type species: Paragloborilus mirus He in Qian, 1977.

Remarks. — For concept of the genus, its full synonymy and species included see Bengtson in Bengtson et al. (1990: 203). Previous generic name Actinotheca Xiao et Zhou, 1984 has been preoccupied by tabulate coral genus Actinotheca French, 1889, and the next junior synonym is Cupitheca [sic] Duan (in Xing et al. 1984) which is apparently an inadvertent error (lapsus calami) of Cupitheca Duan (1984), which is hereby selected as the correct original spelling in the sense of the ICZN: Article 32.5.1 of the current fourth edition (International Commission on Zoological Nomenclature 1999). For detailed discussion and farther synonymy see Demidenko in Gravestock et al. (2001: 96–97).

Cupitheca holocyclus (Bengtson in Bengtson et al., 1990)
(Fig. 11A–F, G₃)

Actinotheca holocyclus; Bengtson in Bengtson et al. 1990: 204, figs 134–136.
Cupitheca holocyclus (Bengtson in Bengtson et al. 1990); Demidenko in Gravestock et al. 2001: 97, pl. 9: 1.
Early Cambrian molluscs

Material. — Ten well preserved specimens, ZPAL V.VI/15U7, 29S10, 39S22, 36S14, 58S4, 105S15; from erratic boulders Me32, 33, 66.

Description. — Cylindrical to slightly tapering tube, straight or gently curved and circular to oval in cross-section. The outer surface is covered with densely and evenly spaced, symmetric transverse ribs, usually straight to weakly undulating sinuously. The inner surface is smooth. Conch closed apically by a septum-like transverse wall (Fig. 11A2, C2–C3, G3), usually slightly convex apically and thinner than the rest of the conch wall. Conch primarily calcitic, and in acid residues occurring as a more or less phosphatized shell wall (Fig. 12E) or as a phosphatic internal mould (Fig. 11A–C, G3). Broken conchs show phosphatized wall structure as a system of radial rods, apparently representing tubules (Fig. 11E2). Operculum not observed.

Remarks. — Preservation is very similar to the Australian material (Bengtson et al. 1990: figs 134F–L, N, O, 136G), as well as to that of phosphatized tubes from the Lower Cambrian of the Montagne Noire, France (Kerber 1988: text-fig. 10). The Antarctic specimens demonstrate characteristic features, such as the distinctive termination (Fig. 11A2, C2–C3) associated with the zone of decollation of the earlier formed shell, which is analogous to the repeated shedding of earlier ontogenic portions of the shell among Recent prosobranchs, e.g. Caecidae (Bandel 1996); for a detailed discussion of the biological implication see Bengtson et al. (1990).

Occurrence. — Early Cambrian (Attabanian/Botomian) Kulpara Formation and Parara Limestone, Horse Gully, Yorke Peninsula, Stansbury Basin, South Australia; China; King George Island, Antarctica.

Class Helcionelloida Peel, 1991b

Remarks. — The explosive development of the Early Cambrian monoplacophoran molluscan fauna have currently attracted great interest of palaeontologists, because of the find of abundant and well-preserved fossil assemblages and because of their potential for biostratigraphic subdivisions of the Lower Cambrian (Missarzhevsky and Mambetov 1981, He et al. 1984, Hinz 1987, Kerber 1988, Qian and Bengtson 1989, Bengtson et al. 1990, Brock and Cooper 1993, Elicki 1994, Esakova and Zhegallo 1996, Runnegar and Jell 1976, Runnegar 1996, Gravestock et al. 2001). However, their taxonomy and relationships are still in a state of flux (e.g. Runnegar 1983, 1996; Runnegar and Pojeta 1985; Peel 1991a, b; Geyer 1994, Gravestock et al. 2001, Parkhaev 2002a). Most of them are placed in the Class Helcionelloida (Peel 1991a, b; Geyer 1994, Gubanov 1998, Gubanov and Peel 2000, 2001). It is, however, controversial to keep in this class the genera with whorled anisostrophic shells (Pelagiella, Beshtashella and relatives), which are also placed within gastropods (e.g. Landing et al. 2002; Parkhaev 2002a, b). No impressions of the soft-part anatomy are preserved on the helcionelloid internal moulds described from Antarctica, and in general, their fossils do not provide enough information to permit reliable evaluation and discussion of their supra-
generic taxonomy. This is now clearly too much speculative. The univalved molluscan systematic accepted herein follows that of Peel (1991a, b) and Gubanov and Peel (2000, 2001).

Order Helcionellida Geyer, 1994  
Family Helcionellidae Wenz, 1938  
Genus Pararaconus Runnegar in Bengtson et al., 1990  
Type species: Pararaconus staitorum Runnegar in Bengtson et al., 1990.

?Pararaconus cf. P. staitorum Runnegar in Bengtson et al., 1990  
(Fig. 12A–C)

Material. — Three phosphatic internal moulds, ZPAL V.VI/32S3, 112S4, 5, from erratic boulders Me33, 66.

Description. — Shell cap-shaped, highly conical, slightly laterally compressed. The apex is gently rounded, and slightly displaced posteriorly. The aperture has an elliptical outline and a slightly flaring margin. The surface of the internal mould is smooth. No texture pattern or muscle scars have been observed on the surface moulds.

Remarks. — The shell was apparently originally calcitic or aragonitic. The shape of the moulds represents shells very similar to the phosphatized conchs identified as *P. staitorum* Runnegar from the Parara Limestone (Runnegar in Bengtson *et al.* 1990). Internal moulds differ from the originally described Australian material in lacking paired lateral ridges owing to incompleteness of their moulding. In-
ternal moulds probably represent more of the apical part of the shell, since apertural margin and lateral ridges are rarely preserved.

Traces of weakly preserved lateral ridges are visible on one specimen (Fig. 12A).

**Occurrence.** — Early Cambrian, Atdabanian–Botmian stages of the Parara Limestone, Horse Gully, South Australia; King George Island, Antarctica.

**Family Yochelcionellidae Runnegar and Jell, 1976**

**Genus Yochelcionella** Runnegar and Pojeta, 1974

Type species: *Yochelcionella cyrano* Runnegar and Pojeta, 1974.

**?Yochelcionella** sp.  
(Fig. 13A)

**Material.** — One phosphatic internal mould, ZPAL V.VI/32S1, from erratic boulder Me33.

**Description.** — Microscopic cyrtoconic shell, laterally compressed, with trace of a broken-off tube or snorkel on concave side.

**Remarks.** — A single badly preserved, incomplete phosphatic internal mould was recovered from one erratic boulder. The shape and size of the internal mould fragment are most similar to the examples of *Y. chinensis* Pei, 1985, however, the latter has a much more strongly differentiated apex.

**Family Stenothecidae Runnegar and Jell, 1980**

**Genus Anabarella** Vostokova, 1962

Type species: *Anabarella plana* Vostokova, 1962.


(Fig. 13B)

**Material.** — One phosphatic internal mould, ZPAL V.VI/109S2, from erratic boulder Me66.

**Description.** — Laterally compressed cap-shaped shell with distinct notch between apertural margin and umbonal part of the conch. No microsculpture has been observed on the internal mould surface.

**Remarks.** — This single badly preserved specimen recovered from one erratic boulder shows the notch, which is similar in *P. argus* described by Runnegar in Bengtson *et al.* (1990: fig. 164L).

**Order Pelagiellida Runnegar and Pojeta, 1985**

**Family Pelagiellidae Knight, 1952**

**Genus Pelagiella** Matthew, 1895

Type species: *Cyrtolites atlantoides* Matthew, 1894.
**Pelagiella madianensis** (Zhou and Xiao, 1984)
(Fig. 13C–E)

**Pelagiella** sp.; Gaździcki and Wrona 1986: 611, fig. 7d.


**Pelagiella adunca** (He et Pei in He et al., 1984); Runnegar in Bengtson et al. 1990: 254; figs 168E–K.

**Pelagiella** cf. **P. adunca** (He et Pei in He et al., 1984); Brock and Cooper 1993: 780; figs 13: 11–18.

**Pelagiella madianensis** (Zhou and Xiao); Parkhaev in Gravestock et al. 2001: 195, pl. 46: 1–12, pl. 47: 1–8. [full synonymy]

**Material.** — Numerous phosphatic internal moulds, ZPAL V.VI/21S15, 32S35, 36S5, from erratic boulder Me33.

**Description.** — Microscopic to tiny shell, dextrally coiled with an incipient and rapidly expanding open whorl, and with a narrow, laterally flaring, asymmetric aperture. Apical region of coil is very variable, bulbous or hook-shaped. Shell apparently originally aragonitic. The surface of the internal mould is smooth, except for rare traces of fine growth lines (Fig. 13C–D). No texture patterns nor muscle scars.

**Remarks.** — The shape of the internal moulds is similar to examples from the Parara and Ajax Limestones (Runnegar in Bengtson et al. 1990), and Wirrealpa Limestone of southern Australia (Brock and Cooper 1993).

**Occurrence.** — Early to Middle Cambrian, Xinji Formation, Henan Province, Sichuan Province, Yutaishan Formation, Anhui Province (China); Ajax and Wirrealpa Limestones and Mernmerna Formation, Flinders Ranges and Parara, Ramsay, Stansbury and Coobowie limestones, Yorke Peninsula (South Australia); King George Island, Antarctica.

**Order Macluritida Cox and Knight, 1960**
**Family Onychochilidae Koken, 1925**

**Genus Beshtashella** Missarzhevsky in Missarzhevsky and Mambetov, 1981

**Type species:** **Beshtashella tortilis** Missarzhevsky in Missarzhevsky and Mambetov, 1981.

**Remarks.** — The genus is grouped in the Onychochilidae together with **Yuwenia** Runnegar, 1981 (junior synonym **Kistasella** Missarzhevsky, 1989) as was suggested by Parkhaev (in Gravestock et al. 2001) on the basis of their similar shell shape; for detailed discussion see Missarzhevsky (1989), Runnegar (in Bengtson et al. 1990) and Parkhaev (in Gravestock et al. 2001), Parkhaev 2002a.

**Beshtashella tortilis** Missarzhevsky, 1981
(Fig. 14A–E)

**Beshtashella tortilis** Missarzhevsky; Parkhaev in Gravestock et al. 2001: 198, pl. 43: 10–16. [full synonymy]
Material. — Fourteen phosphatic internal moulds, ZPAL V.VI/32S24, 35S5, 13, 36S9, 103S9, from erratic boulders Me32, 33 and 66.

Description. — Minute (up to 1.5 mm), sinistrally coiled univalve shells, with a high helical spire and an oval, asymmetrically flared aperture. Apical region (protoconch) clearly separated from adult part (Fig. 14B). The surface of the internal mould is smooth, with occasionally visible traces of comarginal, fine growth lines (Fig. 14A–C, E). No texture patterns nor muscle scars.

Remarks. — The shells was probably calcitic or aragonitic. The variable shape of the shell possibly is the result of its un-coiled or loose-coiled whorls. This, as well as the co-occurrence of the most tightly coiled forms, even in the same sam-

bles, led Parkhaev (in Gravestock et al. 2001) to suggest that *Yuwenia bentleyi* Runnegar, 1981, *Y. juliana* Elicki, 1994 and *Kistasella spiralis* Missarzhevsky, 1989 are junior synonyms of *B. tortilis*. The polygonal microstructure recently discovered on internal phosphatic shell moulds of *B. tortilis* has been interpreted as a replica of single columnar muscle (Parkhaev 2002b). The latter, however, could be a pair of muscles coalesced during shell evolutionary transformation from cap-shaped, cyrtoconic to helically coiled morphologies, and therefore does not allow for unequivocal higher-level systematic assignation (Parkhaev 2002b).

**Occurrence.** — Early Cambrian, upper Atdabanian, Beshtash Member, Beshtash section, Talassky Alatau, Kirgizstan; Maly Karatau, Kazakhstan; Kharaulakh, Yakutia, Siberian Platform; Early Cambrian, Xiaoping Member, Tongying (Dengying) Formation, Tanabao, Xihaoping, Fangxian, Hubei (China); Early Cambrian, Parara Limestone, Horse Gully (Stansbury Basin), Yorke Peninsula (South Australia); Marianian strata (?uppermost Atdabanian–Botomian), Görlitz Syncline (eastern Germany); King George Island, Antarctica.

**Acknowledgements.** — The fieldwork in Antarctica was carried out during the Fifth and Tenth Polish Antarctic Expeditions organised and financed by the Polish Academy of Sciences. The laboratory studies were supported by the Research Project MR.I.29. from the Polish Academy of Sciences and by the exchange program of the Polish and the Royal Swedish Academies of Sciences. Stereoscan micrographs were taken at the Electron Microscopy Laboratories of the Evolutionary Biology Centre, Uppsala University and the Institute of Paleobiology, Polish Academy of Sciences, Warszawa. I am deeply indebted to Stefan Bengtson (Swedish Museum of Natural History, Stockholm) for arranging the visiting grant from the Royal Swedish Academy of Sciences, and for his invaluable help during the course of this work at the of Institute of Earth Sciences, Department of Historical Geology and Palaeontology, University of Uppsala. Stefan Bengtson and an anonymous reviewer are also thanked for their critical reading and improving the earlier version of this paper, which, at first, was a part of small skeletal fossils elaboration published elsewhere. I thank Jerzy Dzik (Institute of Paleobiology, Warszawa) for discussion of the hyoliths palaeobiology and taxonomy. I am indebted to another anonymous reviewer for his helpful constructive critical comments and linguistic improvements of the submitted final manuscript. My thanks are also extended to Karol Sabath (Institute of Paleobiology, Warszawa) for all his friendly help and discussion.

**References**


Early Cambrian molluscs


Received September 2, 2003
Accepted October 22, 2003