

# Cambrian microfossils from glacial erratics of King George Island, Antarctica

RYSZARD WRONA



Wrona, R. 2004. Cambrian microfossils from glacial erratics of King George Island, Antarctica. *Acta Palaeontologica Polonica* 49 (1): 13–56.

Limestone erratics in the Early Miocene glacio-marine Cape Melville Formation of King George Island, West Antarctica, have yielded Early and Middle Cambrian small skeletal fossils (SSF) accompanied by calcified cyanobacteria, archaeocyath and spiculate sponges, trilobites and echinoderms. The SSF assemblage comprises disarticulated sclerites of cancelloriids, halkieriids, tomotiids, lapworthellids, palaeoscolecids, hyolithelminths, lingulate brachiopods, helcionelloid molluscs, hyoliths, and bradoriids. All 24 described species are common to Antarctica and Australia. Most are recorded here from Antarctica for the first time, including *Shetlandia multiplicata* gen. et sp. nov. and two new species *Byronia? bifida* and *Hadimopanella staurata*. The lithological and fossil contents of the boulders are almost identical with autochthonous assemblages from the Shackleton Limestone in the Argentina Range and Transantarctic Mountains. Cambrian outcrops around the Weddell Sea are a plausible source of the erratics. The fauna is closely similar to that from the uppermost Botomian Wilkawillina Limestone in the Flinders Ranges and Parara Limestone on Yorke Peninsula, and Toyonian Wirrealpa and Aroona Creek Limestones in the Flinders Ranges, as well as the Ramsay Limestone on Yorke Peninsula, all in the Arrowie and Stansbury Basins of South Australia. These very similar faunal and facies successions for Antarctica and Australia strongly support their common biotic and sedimentary evolution on the same margin of a greater Gondwana supercontinent throughout the Early Cambrian.

Key words: Problematica, microfossils, Cambrian, Gondwana, Antarctica, King George Island, Australia.

Ryszard Wrona [wrona@twarda.pan.pl], Instytut Paleobiologii, Polska Akademia Nauk, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

## Contents

Introduction . . . . .	14	Family Halkieriidae Poulsen, 1967 . . . . .	28
Geographical and geological setting . . . . .	14	Genus <i>Halkieria</i> Poulsen, 1967 . . . . .	28
Material and methods . . . . .	15	Tomotiids . . . . .	30
Lithology of erratics . . . . .	16	Order Tomotiida Missarzhevsky, 1970 . . . . .	30
Small shelly fauna assemblage . . . . .	18	Family Kennardiidae Laurie, 1986 . . . . .	30
Taphonomy and preservation . . . . .	18	Genus <i>Dailyattia</i> Bischoff, 1976 . . . . .	30
Biostratigraphy and correlations . . . . .	18	Genus <i>Shetlandia</i> nov. . . . .	34
Provenance of limestone erratic boulders . . . . .	19	Family Lapworthellidae Missarzhevsky, 1966 . . . . .	36
Systematic palaeontology . . . . .	20	Genus <i>Lapworthella</i> Cobbold, 1921 . . . . .	36
Domain Eubacteria . . . . .	20	Superphylum Aschelminthes . . . . .	39
Phylum Cyanobacteria Stanier, 1974 . . . . .	20	Order Palaeoscolecida Conway Morris and Robison, 1986 . . . . .	39
Mineralized cyanobacterial filaments . . . . .	20	Family Palaeoscolecidae Whittard, 1953 . . . . .	39
Domain Eukaryota . . . . .	22	Genus <i>Hadimopanella</i> Gedik, 1977. . . . .	40
Phylum Porifera Grant, 1836 . . . . .	22	Ornamented tubes . . . . .	42
Class Calcarea Bowerbank, 1864 . . . . .	22	Genus <i>Mongolitubulus</i> Missarzhevsky, 1977. . . . .	42
Genus <i>Dodecaactinella</i> Reif, 1968 . . . . .	22	Hyolithelminths . . . . .	46
Order Heteractinida Hinde, 1888 . . . . .	22	Order Hyolithelminthida Fisher, 1962. . . . .	46
Family Eiffelidae Rigby, 1986. . . . .	22	Family Hyolithellidae Walcott, 1886 . . . . .	46
Genus <i>Eiffelia</i> Walcott, 1920 . . . . .	22	Genus <i>Hyolithellus</i> Billings, 1871 . . . . .	46
Class Hexactinellida Schmidt, 1870. . . . .	24	Genus <i>Byronia</i> Matthew, 1899 . . . . .	50
Class Radiocyatha Debrenne, Termier and Termier, 1970 . . . . .	24	Family Torellectidae Holm, 1893 . . . . .	50
Family Radiocyathidae Okulich, 1955. . . . .	24	Genus <i>Torellecta</i> Holm, 1893 . . . . .	50
Genus <i>Radiocyathus</i> Okulich, 1937. . . . .	24	Problematica . . . . .	50
Class Coeloscleritophora Bengtson and Missarzhevsky, 1981 . . . . .	24	Genus <i>Aetholicopalla</i> Conway Morris, 1990 . . . . .	50
Order Chancelloriida Walcott, 1920. . . . .	24	in Bengtson et al. 1990 . . . . .	50
Family Chancelloriidae Walcott, 1920 . . . . .	24	Problematic “smooth cones”–?coeloscleritophoran shell . . . . .	51
Genus <i>Chancelloria</i> Walcott, 1920 . . . . .	25	Conclusions . . . . .	52
Genus <i>Archiasterella</i> Sdzuy, 1969 . . . . .	26	Acknowledgements . . . . .	52
Genus <i>Allonnia</i> Doré and Reid, 1965 . . . . .	26	References . . . . .	52
Order Sachtitida He, 1980 in Yin et al. 1980. . . . .	28		

## Introduction

The earliest skeletal fauna emerged abruptly near the Precambrian–Cambrian boundary (~545 Ma) during the so-called “Cambrian explosion” (e.g., Brasier 1979; Conway Morris 1987, 1989; Brasier and Lindsay 2001). Familiar skeletal remains such as sponge spicules, brachiopod valves, ostracode and trilobite carapaces, and echinoderm ossicles are accompanied by extremely abundant microscopic, originally phosphatic or secondarily phosphatized, fossils representing disarticulated exoskeletal sclerites, spines and various shells or tubes colloquially referred to as “small skeletal fossils” or “small shelly fossils” (SSF). This term was introduced by Matthews and Missarzhevsky (1975) for Early Cambrian phosphatic microfossils, and is used for various phosphatic as well as for calcareous or secondarily phosphatized microfossils of the early Palaeozoic (for references see e.g., Bengtson 1994a, b; Dzik 1994). Some of these millimetre-size microfossils have found their place in the classification scheme of metazoans (Bengtson et al. 1990; Peel 1991; Gubanov and Peel 2000), but others, although well-documented in the fossil record, remain enigmatic (Müller and Hinz-Schallreuter 1993; Conway Morris and Peel 1995; Bengtson and Hou 2001). Well-preserved Cambrian shelly fossils have been described from many localities around the world (Fig. 2): Antarctica (Evans and Rowell 1990; Evans 1992), Australia (Bengtson et al. 1990) and Africa (Culver et al. 1988), Canada (Conway Morris 1989; Butterfield and Nicholas 1996), China (Qian and Bengtson 1989; Qian 1990), Europe (Poulsen 1967; Berg-Madsen and Peel 1978; Hinz 1987; Kerber 1988; Elicki 1994, 1998), Greenland (Peel 1991), Kazakhstan (Missarzhevsky and Mambetov 1981), Mongolia (Esakova and Zhegallo 1996), and Siberia (Rozanov et al. 1969; Missarzhevsky 1989). Some of these widespread Early Cambrian SSF assemblages, analysed and compared with similar post-Cambrian small shelly fossils assemblages, in principle might be simply interpreted in such a way, that the “early Cambrian explosion” is of taphonomic nature and concerns an “explosion” of fossils rather than animals (e.g., Runnegar 1982; Dzik 1994). There are still, however, paleontologists, who advocate alternative opinion, that the “Cambrian explosion” is not an artefact of the fossil record, but remains a real event of a significant biotic diversification, at least in a fundamental shift of functional organization, and behavioral and ecological complexity (e.g., Conway Morris 1998).

“Small shelly fossils” from Cambrian deposits of Antarctica are still poorly known; only two occurrences have been found on the continent. To date, a depauperate small shelly fauna, practically restricted to tommotiid sclerites, has been recorded from autochthonous Shackleton Limestone in the Churchill Mountains (Fig. 1B), the Holyoake Range between the Nimrod and Byrd Glaciers, and from the southeast of Mount Bowers (Rowell et al. 1988; Evans and Rowell 1990; Evans 1992), and Early Cambrian boulders at Mount Provender, Shackleton Range (Clarkson et al. 1979). The Early Cambrian small shelly faunas described in this paper have been recovered from erratic boulders of limestone within the

Early Miocene glacio-marine Cape Melville Formation of King George Island (Fig. 1A), South Shetland Islands (Gądzicki and Wrona 1986; Wrona 1987, 1989).

The objective of this paper is the documentation of multiple co-occurring disarticulated skeletal fossils from Cambrian limestone erratics, the interpretation of fossil biota assemblages, and their palaeobiology, affinity and systematic position, as well as the recognition of Antarctic source areas for fossil-bearing erratic boulders. A complementary work concerning the accompanying micromolluscan assemblage, mainly helcionelloids and hyoliths is presented elsewhere (Wrona 2003).

*Abbreviations used.*—The studied collection of fossils is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, abbreviated ZPAL and labelled V.XXVIII. The letters S or U indicate SEM stubs prepared and studied in Warsaw (S) or Uppsala (U) SEM laboratories. The Arabic numerals before the S indicate the number of the SEM stub and after the S, the specimen number on the stub (e.g., 1S25 means specimen no. 25 on the stub no. 1). Collections of the Antarctic erratics of King George Island housed in the Institute of Paleobiology, Warsaw are labelled AE/Me32, M33, T52 etc. 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. SSF, small shelly fossils.

## Geographical and geological setting

Erratic boulders for micropaleontological investigations were sampled from Neogene glacio-marine sediments of King George Island (South Shetlands) in West Antarctica. The position of Tertiary rocks yielding erratic boulders is indicated on the map (Fig. 1A). Abundant and diverse erratics containing Early Cambrian small shelly fossils were collected mainly from the Early Miocene Cape Melville Formation. A limited number (a dozen or so) of light-coloured reef limestone erratics with archaeocyathan cups encrusted by calcimicrobes have also been collected from the Oligocene Polonez Cove Formation (Wrona 1989; Wrona and Zhuravlev 1996). The latter formation is exposed in cliffs between Low Head and Lions Rump on King George Island (Fig. 1A).

The Early Miocene glacio-marine Cape Melville Formation is restricted to the easternmost part of King George Island, on Melville Peninsula (Fig. 1A), which is no more than several dozens of metres across in places. The glacio-marine sediments are exposed in up to 200 m high cliffs besetting the Melville Peninsula and on the ice-free surface of its flat plateau (Wrona 1989). The indigenous fossil assemblage of the Cape Melville Formation contains diatoms, chrysomonad cysts, silicoflagellates, calcareous and arenaceous foraminifers, solitary corals, polychaetes and bryozoans, gastropods, bivalves, decapods, echinoids, asteroids and fish remains of Miocene age (for references see Gądzicki ed. 1987), as well as reworked Cretaceous calcareous nannofossils and belemnites (Dudziak 1984; Birkenmajer et al. 1987). The age of the for-

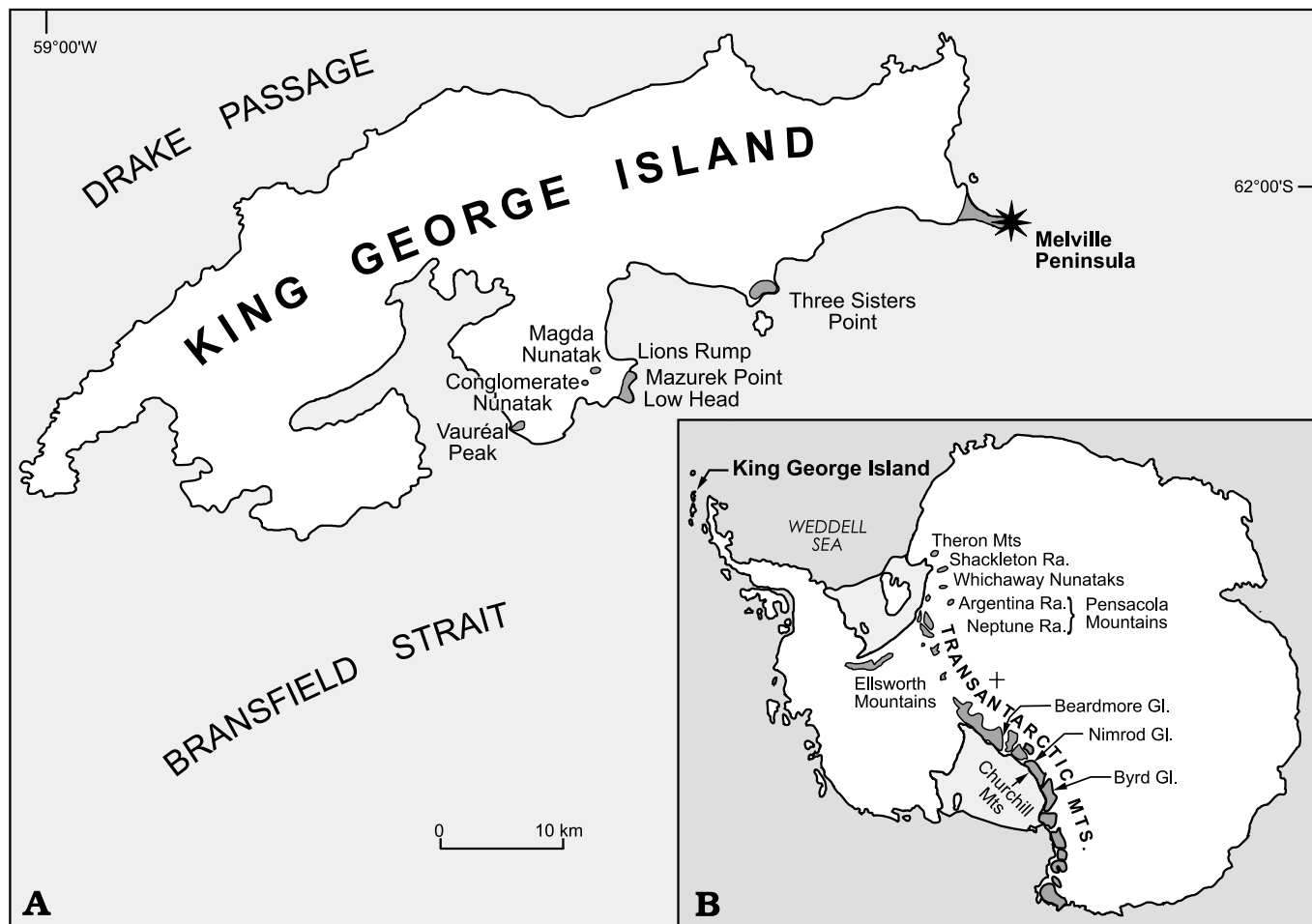


Fig. 1. Location map of King George Island (arrowed) in Antarctica (B) and the outcrops of Cambrian rocks (dark shaded) on the continent referred to in the text. The occurrence of glacio-marine formations (shaded) on the island (A) and the Early Miocene Cape Melville Formation and collection site (asterisk). Abbreviations: Mts., Mountains; Ra., Range; Gl., Glacier.

mation 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 Early Miocene Glaciation of Antarctica (Birkenmajer et al. 1983, 1985; Biernat et al. 1985; Birkenmajer 1987, 1989, 1992, 1995; Gaździcki ed. 1987).

Striated ice-rafted boulders, up to 2 m in size, are scattered randomly within the sediment (Wrona 1989) and have been interpreted as iceberg dropstones delivered during the glacial epoch called the Melville Glaciation of Early Miocene age (for references see Birkenmajer 1995). The erratic boulders are mainly igneous, metamorphic, or siliciclastic rocks, whereas limestones account for some 5% of the total number of boulders (Wrona 1989). Petrographic features of these rocks, in particular the fossiliferous limestones, point to source areas on the Antarctic continent (Morycowa et al. 1982; Wrona 1989). The most common lithologies of limestone erratics reveal a close similarity with the Cambrian rocks that built the mountain ranges and nunataks in the vicinity of the Weddell Sea and are almost identical to the Shackleton Limestone exposed in the central Transantarctic Mountains. At the same time they display some similarities with certain South Australian Cam-

brian successions (Wrona 1989; Holmer et al. 1996; Wrona and Zhuravlev 1996).

## Material and methods

The SSF-bearing limestone boulders, represented by several hundred samples (sample acronym AE/Me), were found in glacio-marine sediments of the Early Miocene Cape Melville Formation of the Melville Peninsula. Limestone dropstones 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 embedded in epoxy medium for sectioning, and their sections were polished and etched in 1% hydrochloric acid for between 10 and 30 seconds, then 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 (SEM). 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,

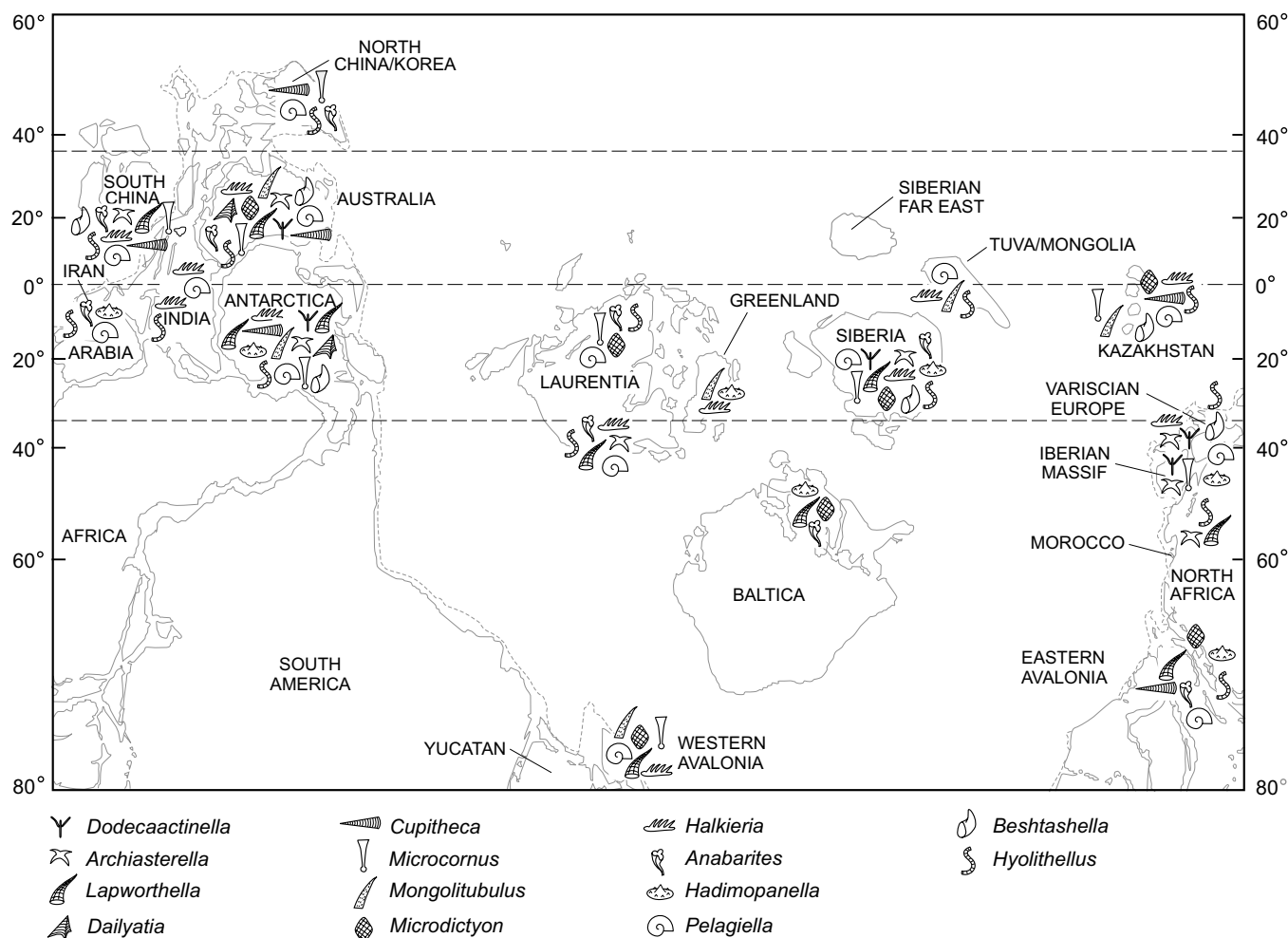


Fig. 2. Early Cambrian palaeogeographic map (modified after Eldridge et al. 1997, Ushatinskaya 1996, and Brock et al. 2000), with the most important localities of small skeletal fossils showing distribution of selected genera. References for distribution data are in the text.

Warsaw. The mineral composition of the skeletal fossils was investigated using energy dispersive spectrometry microprobe (EDS) with a JEOL JSM-840A microscope and a Link Analytical spectrometer AN 1000/85S at the SEM Laboratory of the Institute of Geological Sciences, Polish Academy of Sciences, Warsaw.

## Lithology of erratics

Limestone dropstones studied for their petrography in thin section fall into a limited number of lithological varieties which may originate from one source, and were classified in three main groups (see Wrona 1989; Wrona and Zhuravlev 1996). The richest in small shelly fossils is Group I, represented by dark packstone-wackestone and burrowed mudstone. Among these, erratic boulders AE/Me32, 33, 52, and 66 represent black packstone and wackestone consisting mainly of shelly detritus with interbedded with dark-grey floatstone (Wrona and Zhuravlev 1996: pl. 1: 3, 5). Stacked hyoliths, molluscs, bradoriids, lingulate shells, echinoderm and trilobite fragments, diverse coeloscleritophoran and palaeoscolecid sclerites, as well as

sponge spicules predominate, whereas archaeocyath fragments and *Girvanella* encrustation are rare (Wrona and Zhuravlev 1996: pl. 1: 5). The shells are commonly filled with dark phosphatic material, which has produced internal moulds (steinkerns). Bedding ranges from tabular to nodular and the bedding surfaces are burrowed. Ferroan dolomitization is common, imparting the brown-grey weathering colour. In some floatstone interbeds, the bioclasts have been neomorphosed to ferroan calcite, and ferroan bladed cement diagenetically overgrows hyolith shells. Abundant framboidal pyrite indicates sulphate-reduction, presumably because of the microbial activity in the sediment. Extremely rich and well-preserved fossils, predominantly lingulate brachiopods, originate from erratic boulder AE/Me 52, a brachiopod coquinoid limestone (Holmer et al. 1996). Another representative boulders, in thin sections ZPAL AE/Me1/28, Me60, 106B, show mottling due to slight burrowing of a wackestone with hyolith and trilobite fragments (Wrona and Zhuravlev 1996: pl. 1: 1). Erratic boulder ZPAL AE/Me53 contains non-bedded homogeneous mudstone with few scattered trilobite fragments and silt-size quartz grains, and samples ZPAL AE/Me41, LH2 are a wavy thin-bedded homogeneous and cross-bedded calcimudstone (Wrona 1989: pl. 2: 2, pl. 5: 4).

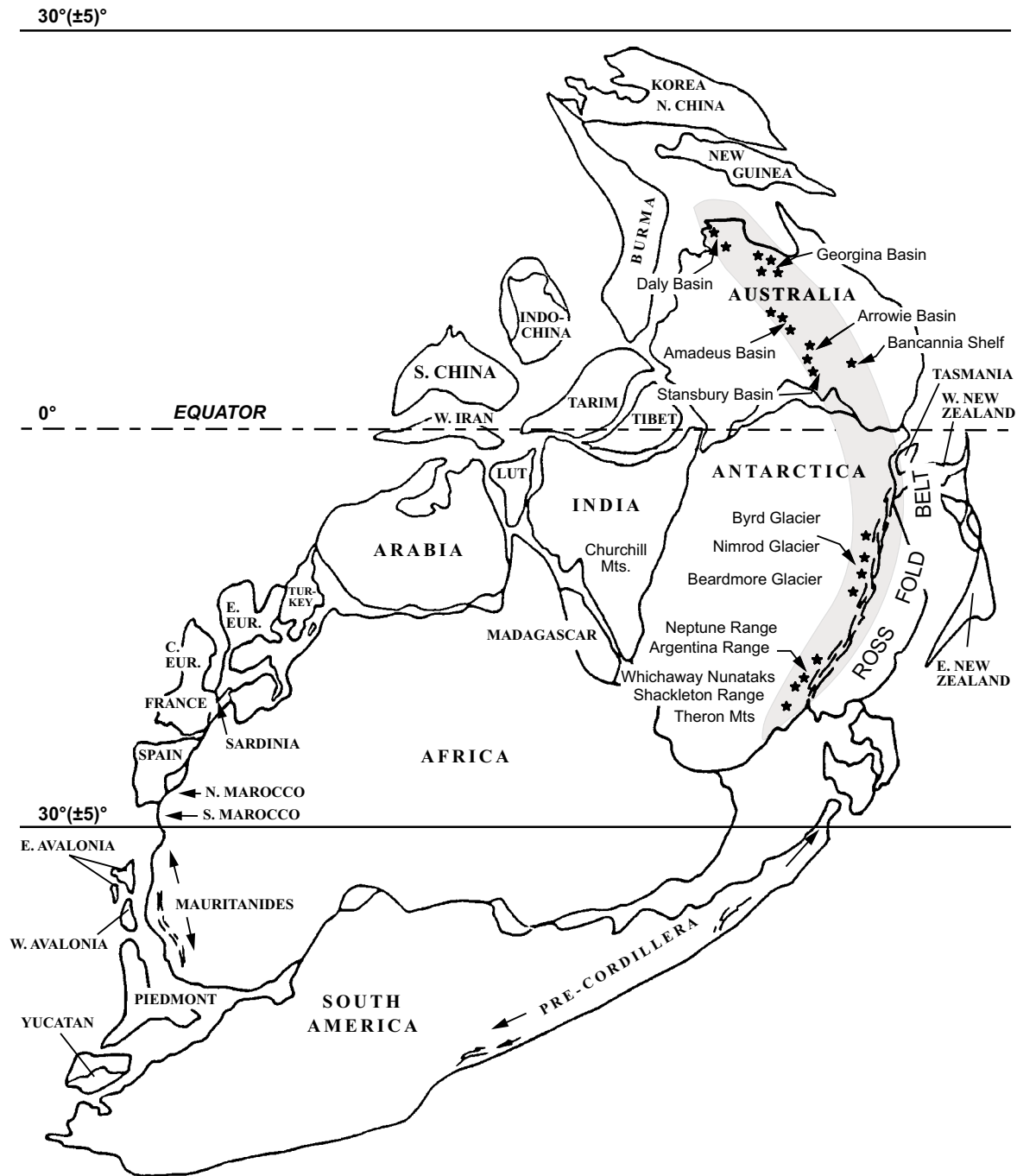


Fig. 3. Paleogeographic map of the major Early Cambrian sedimentary basins of Australia and Antarctica discussed in the text (modified after Courjault-Radé et al. 1992). Asterisks show distribution of archaeocyathan and small shelly fossil occurrences.

Both the lithology and paleontological record of these boulders suggest that they represent sediments of a relatively deep marine environment with oscillating anaerobic (homogeneous mudstone), dysaerobic (burrowed wackestone) and aerobic (graded packstone and wackestone) bottom conditions. Consequently, calm lower slope to moderately active upper slope conditions on the carbonate platform periphery may be implied.

All recognized lithological groups of limestone blocks: black fossiliferous packstone-wackestone (Group I), calci-

microbial-archaeocyathan reef limestone (Group II) and bituminous dark-grey limestone with brachiopod shells and trilobite carapaces (Group III), correspond respectively to those 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 those of the Shackleton Limestone of the central Transantarctic Mountains, Antarctic continent (Rees et al. 1989; Rowell and Rees 1989; Rowell et al. 1992).

## Small shelly fauna assemblage

### Taphonomy and preservation

Phosphatic or phosphatized fossils etched from the limestone erratics are abundant, diverse and include archaeocyathan sponges (Wrona and Zhuravlev 1996), brachiopods (Holmer et al. 1996), molluscs (Wrona 2003), and extremely rich and well-preserved small shelly fossils described in this paper. These latter were preliminarily listed and figured by Gaździcki and Wrona (1986) and Wrona (1987, 1989). The mineral in the shelly fossils was analysed using energy dispersive spectrometry (EDS) microanalysis, and identified as calcium phosphate (Figs. 9, 17, 22, 24). The detailed crystallographic composition was not determined, but most probably it is a granular or microcrystalline phosphate (carbonate fluoroapatite?). The majority of carbonate shelly fossils and archaeocyathan cups (Figs. 25I, 26A) are preserved as phosphatic internal moulds of shells or as selective phosphatic replacements or encrustations (cyanobacteria) (Fig. 4) of the original calcitic or aragonitic skeleton. Lingulate brachiopod shells, as primarily phosphatic, and bradoriid carapaces, as mainly organic-walled (Hinz-Schallreuter 1993a), but completely replaced by phosphate, are as a rule well preserved. Palaeoscolecoid, mongolitulid, and tommotiid sclerites were most probably composed of originally phosphatic minerals. Trilobite carapaces and echinoderm stereoms, which were originally calcareous, are preserved as phosphate replicas (Fig. 25J). The original nature of the calcium carbonate or/and phosphate in Early Cambrian fossils remains poorly known (Brasier 1990). Further detailed petrographic and geochemical investigations are required to elucidate phosphogenic events and taphonomy of the early skeletal fauna. Packstones, wackestones, and especially brachiopod coquinas, consisting of disarticulated, stacked, nested and variably oriented shells, exhibit a biofabric indicative of condensed deposits and reworked taphocenoses. This may be related to prolonged exposure of skeletal remains under conditions of a very slow sedimentation. The studied small shelly fossil assemblage is rich in juvenile benthic as well as nektonic biota (Fig. 8A), and the larval shells of lingulate brachiopods are extremely abundant (Holmer et al. 1996). The Early Cambrian phosphatized SSF assemblages of Antarctica are similar to other small skeletal fossil assemblages that appeared at the beginning of the Cambrian, and are analogous to those occurred throughout the Early Paleozoic (Dzik 1994). It has been argued that the sudden, global appearance of these fossils resulted from an environmental crisis (Dzik 1994; Zhuravlev and Wood 1996), and a vast event of Lower Cambrian phosphogenesis (Cook and Shergold 1984, 1986; Brasier 1990). The fossil assemblages extracted from the Antarctic erratics are less diverse and contain a lower number of specimens than the Australian or Chinese SSF assemblages, probably as consequence of the smaller (limited erratics) sample size. (This could be tested by rarefaction).

### Biostratigraphy and correlations

This study of Early Cambrian fossil assemblages from glacial erratics of Antarctic continental provenance, as well as monographic studies of shelly fossils from Australia and Antarctica (Daily 1956; Gaździcki and Wrona 1986; Wrona 1987, 1989, 2003; Bengtson et al. 1990; Evans and Rowell 1990; Brock and Cooper 1993; Zhuravlev and Gravestock 1994; Yates 1994; Holmer et al. 1996; Wrona and Zhuravlev 1996; Brock et al. 2000; Gravestock et al. 2001) are the basis for correlation of these assemblages. Recently, the rich Cambrian fossil assemblages from Australia, including archaeocyaths, brachiopods, molluscs, trilobites, and accompanying small shelly fossils, have been used for regional biostratigraphic subdivision and worldwide correlation of Australasian and Antarctic Cambrian strata (Brock et al. 2000; Gravestock et al. 2001).

Three distinct faunal assemblages are recognized in the Antarctic derived erratics of King George Island:

(1) A very rich and diverse SSF assemblage with sponge spicules. These include the hexactinellide *Calcihexactina* sp. (Fig. 5C–G), the heteractinide *Eiffelia araniformis* (Missarzhevsky, 1981) (Fig. 5H), and *Dodecaactinella* cf. *cynodontota* Bengtson and Runnegar, 1990 in Bengtson et al. 1990 (Fig. 5A). Molluscs are represented by the univalves *Pararaconus* cf. *staitorum* Runnegar, 1990 in Bengtson et al. 1990, *Yochelcionella* sp., and *Anabarella* cf. *argus* Runnegar, 1990 in Bengtson et al. 1990, *Pelagiella madianensis* (Zhou and Xiao, 1984), and *Beshtashella tortilis* Missarzhevsky, 1981, the hyoliths *Conotheca australensis* Bengtson, 1990 in Bengtson et al. 1990, *Microcornus petilus* Bengtson, 1990 in Bengtson et al. 1990, *Parkula bounites* Bengtson, 1990 in Bengtson et al. 1990, *Hyptiotheca carraculum* Bengtson, 1990 in Bengtson et al. 1990, and “*Hyolithes*” *conularioides* Tate, 1892, and the hyolith-like fossil *Cupithecya holocyclata* (Bengtson, 1990 in Bengtson et al. 1990; for details see Wrona 2003). Arthropods are represented by the bradoriid *Albrunnicola bengtsoni* Hinz-Schallreuter, 1993b (Melnikova 2000), which is conspecific with *Hipponicharion* sp. described by Bengtson (in Bengtson et al. 1990) from the Parara Limestone of Yorke Peninsula, South Australia. The problematic tommotiids are represented by *Dailyatia ajax* Bischoff, 1976 (Figs. 8A, D, E, 11A–D, 12A–D, 15F, K), *Shetlandia multiplicata* gen. et sp. nov. (Figs. 14A–D, 15A–E, G–J), *Camenella* sp. (Fig. 8F), and *Lapworthella fasciculata* Conway Morris and Bengtson, 1990 in Bengtson et al. 1990 (Fig. 12E). The coeloscleritophorans are diverse and include the chancelloriids *Chancelloria* sp. (Fig. 6A–C, G–K, S), *Ch. racemifundis* Bengtson, 1990 in Bengtson et al. 1990 (Fig. 6E, L, T), *Allonnia* ex gr. *A. tripodophora* (Figs. 5J, 6I, F), *A. cf. tetrathallis* (Fig. 5K), and *Archiasterella?* sp. (Fig. 5I), the halkieriid *Halkieria parva* Conway Morris, 1990 in Bengtson et al. 1990 (Fig. 7A–M) and problematic “smooth cones” (Fig. 25N). Tubes represent *Hyolithellus filiformis* Bengtson, 1990 in Bengtson et al. 1990 (Fig. 25A–D), *H. micans* (Billings, 1871) (Fig. 25E), *Torelrella* sp. (Fig. 25F, G) and *?Byronia bifida* sp. nov. (Fig. 25H, L–N), and problematic hyolithelminths. In addition, indistinguishable trilobite fragments, the

archaeocyath *Stapicyathus stapipora* (Taylor) (Fig. 25I) and *S. cera* Debrenne (Fig. 26A), radiocyathid nesasters? *R. minor* Bedford and Bedford, 1934 (Fig. 5L), palaeoscolecid single sclerites, and prominent spines of *Mongolitubulus* Missarzhevsky, 1977 are present (Fig. 23A–H). The problematic spherical microfossil *Aetholicopalla adnata* Conway Morris, 1990 in Bengtson et al. 1990 occurs in the Early Cambrian Antarctic erratics of King George Island (Fig. 26D, E) and the Parara Limestone of Yorke Peninsula, South Australia (Bengtson et al. 1990; Gravestock et al. 2001).

The absence of typical late Atdabanian fossils, namely *Paterimitra*, *Micrina*, *Eccentrotheca* or *Hippopharangites* (Gravestock et al. 2001), 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, lower Botomian age is the most plausible because many King George Island small shelly fossils are not known from later deposits (Bengtson et al. 1990; Zhuravlev and Gravestock 1994; Yates 1994; Gravestock et al. 2001).

The entire assemblage is closely similar to the late Atdabanian–early Botomian Australian assemblages, especially that from the Stansbury Basin, Parara Limestone of Yorke Peninsula.

The small shelly fossil (Rowell et al. 1988; Evans and Rowell 1990; Evans 1992) assemblages from the Shackleton Limestone of the Churchill Mountains, central Transantarctic Mountains (Fig. 3), are restricted in SSF composition to a kennardiid sclerite and shells of the problematic *Marocella* Geyer, 1986 and thus are not very similar either to the King George Island assemblage or to the Australian Yorke Peninsula assemblage. The Antarctic Early Cambrian trilobite fauna also differs conspicuously from the Australian and has only a few elements in common (ichangiid *Hsuaspis* and emuellid ?*Balcoracania*) with the latter (Cooper and Shergold 1991; Palmer and Rowell 1995; Jago in Brock et al. 2000).

(2) An assemblage with diverse archaeocyaths and other reef organisms. These latter are represented by coralomorphs and calcified cyanobacteria, described by Wrona and Zhuravlev (1996). Despite differences in the archaeocyathan composition of the studied erratics, all of them contain common elements with the *Syringocnema favus* beds assemblage of South Australia, which is correlated by Zhuravlev and Gravestock (1994) with the late Botomian. Similar elements have been identified in the King George Island erratics collected from the Polonez Cove Formation by Morycowa et al. (1982), later redescribed and partly refigured by Debrenne and Kruse (1986). Of the total of 52 archaeocyath species known from Antarctica, 31 (60%) are in common with Australia and all of them belong to the Botomian *Syringocnema favus* assemblage (Wrona and Zhuravlev 1996).

(3) An assemblage with brachiopod shells. These are extremely rich and well preserved, though seldom articulated, larval and adult valves (Holmer et al. 1996), accompanied by sponge spicules, cancelloriid sclerites, shells of the mollusc *Pelagiella madianensis* (Zhou and Xiao, 1984), hyolith conchs, trilobite carapaces and palaeoscolecid sclerites. The lingulate brachiopods *Eoobolus* aff. *E. elatus* (Pelman, 1986), *Karathele*

*napuru* (Kruse, 1990), and *Vandalotreta djagoran* (Kruse, 1990) from the sample AE/Me52 are similar to those assemblages described from the Toyonian Wirrealpa Limestone of the Flinders Ranges, and Ramsay Limestone of Yorke Peninsula, South Australia, and the Tindall Limestone of the Daly Basin (Fig. 3), 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. 3). Furthermore, *K. napuru* and *V. djagoran* are also known from the Top Springs Limestone of the northern Georgina Basin, Northern Territory (Kruse 1991). The palaeoscolecid epidermal sclerite *Hadimopanella antarctica* Wrona, 1987, both in morphology and size, closely resembles elements of the tuberculate ornaments on *Chalasiocranos exquisitum* Brock and Cooper, 1993 sclerites from the Ramsay Limestone of Yorke Peninsula, South Australia (Brock and Cooper 1993). It is possible that *H. antarctica* represents intermediate smaller sclerites of the same animal that bears *C. exquisitum* sclerites, similarly to the palaeoscolecid animals possessing sclerites of different kinds (see Kraft and Mergl 1989; Müller and Hinz-Schallreuter 1993). The disarticulated sclerites of *H. staurata* sp. nov. represent an analogous components of this assemblage and are similar to the single plate (*sensu* Conway Morris 1997) of *Kaimenella dailyi* Brock and Cooper (tuberculate unit *sensu* Brock and Cooper 1993: fig. 8: 10–12 and fig. 9: 2). 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), however, some of SSF stratigraphic ranges extend even into the Middle Cambrian.

## Provenance of limestone erratic boulders

The King George Island glacial erratics are believed to have been derived mainly from locations near the Ellsworth Mountains or along the Weddell Sea coast and from the Transantarctic Mountains (Wrona 1989, 2003; Evans and Rowell 1990; Wrona and Zhuravlev 1996). Birkenmajer (1980, 1982a, b), Birkenmajer and Butkiewicz (1988) suggested that the main sources of the igneous erratics of King George Island may be: Antarctic Peninsula, Ellsworth Mountains, Pensacola and Theron Mountains, which provide the entire diversity of igneous and metamorphic dropstone lithologies (Fig. 1). Unfortunately, only the latter two occurrences yield Lower Cambrian rocks. The dropstones occurring in glacio-marine marly shales of the Cape Melville Formation were delivered to the Miocene basin by drifting icebergs derived from the margin of ice shelves. The same icebergs dropped Cambrian fossiliferous limestone erratics, which contain an almost identical shared archaeocyath fauna (Debrenne and Kruse 1986, 1989; Wrona and Zhuravlev 1996) into the Weddell Sea. Of this list, two species are present only in the King George Island and Weddell Sea erratics. The Whichaway Nunataks archaeo-

cyaths contain five species which are common with the King George Island archaeocyath assemblage (Debrenne and Kruse 1989; Wrona and Zhuravlev 1996).

Wrona and Zhuravlev (1996) suggested that archaeocyathan assemblages of these three allochthonous occurrences were derived from the same source. The Carboniferous–Permian conglomerates from the Ellsworth Mountains could not be the source of the erratic blocks, because their archaeocyathan assemblage is very different (Debrenne 1992). The archaeocyath-bearing limestone occurring in the upper part of the Ross Supergroup in the Ross Orogen, at least between Nimrod Glacier and the Theron Mountains, could also be the source area for the archaeocyath-bearing erratics collected from glacial deposits of King George Island (Fig. 1). Taking into account the present and Neogene flow patterns of Antarctic ice-sheets (Drewry 1983; Anderson and Andrews 1999), it seems that the source area of the archaeocyath-bearing erratics was most probably somewhere between the Argentina Range and the Theron Mountains. The Argentina Range (in Pensacola Mountains) is the nearest locality containing *in situ* archaeocyaths (Fig. 1B). Unfortunately, the Argentina Range archaeocyaths were only listed, but never figured (Konyushkov and Shulyatin 1980).

The exact provenance of the King George Island SSF-bearing erratic boulders remains enigmatic since they closely resemble the Early Cambrian rocks of South Australia (Parara and Ramsay Limestones) but lack analogues in Antarctica. Only two 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), and Early Cambrian boulders at Mount Provender, Shackleton Range yielding molluscs compared with *Helcionella* and *Mellopegma* by Clarkson et al. (1979). Neither 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 or have been completely eroded.

## Systematic palaeontology

### Domain Eubacteria

Phylum Cyanobacteria Stanier, 1974

(Cyanophyta Sachs, 1874)

Mineralized cyanobacterial filaments

*Remarks.*—These highly variable mineralized filaments have often been given separate species names. However, wide

stratigraphic range, diversity of habitats, and different manners of preservation led modern researchers to assume that many of these species are “diagenetic taxa” (Pratt 1984, 2001). The most common practice have been to refer them to the genus *Girvanella* Nicholson and Etheridge, 1878 (type species: *G. problematica* Nicholson and Etheridge, 1878) only (e.g., Riding 1991; Pratt 2001). Its morphology and taxonomy was reviewed by Mamet and Roux (1975). For comparison with modern cyanophyte genera and taxonomy see Danielli (1981).

### *Girvanella* sp.

Fig. 4.

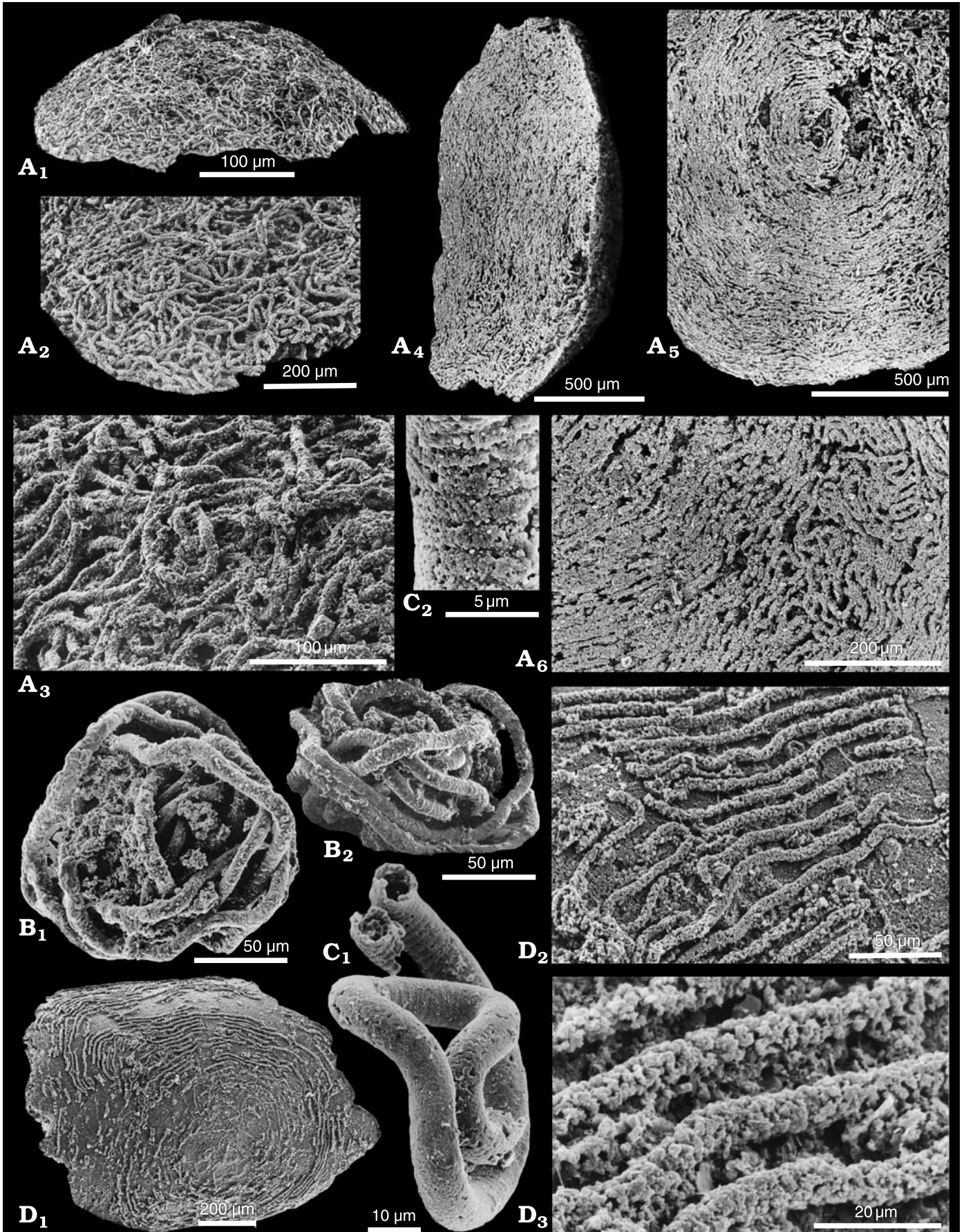
*Material.*—A number of phosphate replacements of filaments or tubes (coats of sheaths) in residuum of erratics Me32, 33, 40, 52, 66. Figured specimens, ZPAL V.VI/25S12, 50; 28S26, 35S4; 37S14; 38S2; 39S29; 103S12; 107S8; 117S1, 2; also see Wrona 1989, pl. 7: 6, and calcified filaments in thin sections, ZPAL Ac.I/M11; see Wrona and Zhuravlev 1996, pl. 8: 7; fig. 3b, c.

*Description.*—Irregularly coiled, unbranched cylindrical tubes or sheath replacements, now phosphatized, but probably originally calcareous, 9.8–12.8  $\mu\text{m}$  in diameter. The tubes are fairly equal in diameter along the entire length of the sheath, and not branched. Tapering has not been observed. The most common types are irregular encrustations on shell or clast surfaces (Fig. 4A, C). They are usually tightly packed, spirally coiled (Fig. 4A) or labyrinthically tangled (Fig. 4C). Somewhat more rare are bundles of irregularly, more or less tightly tangled cylindrical tubes (oncoids?) (Fig. 4B), which may have smooth external surfaces or may possess a sculpture such as annular ribbing (Fig. 4D). This is interpreted as a reflection of the fine, cellular structure of the living cyanobacterial filaments (Danielli 1981; Peel 1988).

*Remarks.*—The described forms are closely similar to the non-reef habits of *Girvanella* distinguished by Pratt (2001: fig. 1). The phosphatized filaments show a most striking similarity to silicified filaments encrusting various hard substrates, such as metazoan skeletons and bioclasts (Pratt 2001: fig. 2D–F). At the same time, however, specimens observed in thin sections of reef limestone erratics show calcified micritic-walled tubes (Wrona and Zhuravlev 1996). Antarctic forms have the same characteristic features as the type material of *G. problematica* (Edhorn 1979) from the Mid-Ordovician of Scotland (Wood 1957), but are about half the diameter. However, they closely match the specimens of *Girvanella* sp. described from the Parara Limestone, Curramulka (Bengtson et al. 1990), and other narrow forms referred to *G. problematica* by Danielli (1981). They also compare well in the external diameter filaments (9–22.5  $\mu\text{m}$ ; mean 15.1  $\mu\text{m}$ ) specimens re-

Fig. 4. Mineralized sheaths of filamentous cyanophyte *Girvanella* sp. **A.** Irregular encrustation on subspherical element, ZPAL V.VI/117S1, erratic Me66; **A**<sub>1</sub>, outer oblique view; **A**<sub>2</sub>, enlargement of densely tangled phosphate filling (replica) of filament; **A**<sub>3</sub>, detail of the same specimen; **A**<sub>4</sub>, the same encrustation on smooth surface of calcareous shell (now dissolved) in other (inner), concave side; **A**<sub>5</sub>, enlargement showing concentrically coiled phosphate filling of filament; **A**<sub>6</sub>, detail showing tightly packed unbranched phosphatized thread. **B.** Specimen ZPAL V.VI/117S2, erratic Me66; **B**<sub>1</sub>, bundle of irregularly tangled tubular phosphate replacements of calcareous sheaths; **B**<sub>2</sub>, the same from the other side. **C.** Specimen ZPAL V.VI/37S14, erratic Me33; **C**<sub>1</sub>, loosely tangled phosphatized tubular sheath, with annulate feature interpreted as a representation of cell structure; **C**<sub>2</sub>, detail of annulation. **D.** Specimen ZPAL V.VI/35S4, erratic Me33; **D**<sub>1</sub>, phosphate filling of calcareous sheaths, now dissolved, as coiled encrustation on bioclast (hyolith conch); **D**<sub>2</sub>, enlargement showing unbranched phosphatized thread labyrinthically tangled; **D**<sub>3</sub>, detail of phosphate filling; showing fine-grained apatite. →





ferred to *G. problematica* from the Ordovician of China (Riding and Fan 2001). This species has been reported from the Cambrian by several authors (e.g., Edhorn 1979; Danielli 1981; Cherchi and Schroeder 1984).

*Occurrence*.—Allochthonous Early Cambrian (Botomian) boulders (Me33, 66), King George Island, Antarctica.

## Domain Eukaryota

Phylum Porifera Grant, 1836

Class Calcarea Bowerbank, 1864

Family uncertain

Genus *Dodecaactinella* Reif, 1968

*Type species*: *Dodecaactinella oncera* Reif, 1968.

*Dodecaactinella* Reif, 1968: 741; Bengtson and Runnegar in Bengtson et al. 1990: 27, fig. 11A–E; Rozanov and Zhuravlev 1992: 227, fig. 14b; Dong and Knoll 1996: 174, fig. 6: 17, 18.

*Polyactinella* Mostler, 1985: 15.

*Sardospongia* Mostler, 1985: 16.

*Demospongia* forma 2, 4; Shabanov et al. 1987: 129; pl. 34: 2–5, 8, 9.

Triactine based spicule Kruse 1990: 49, pl. 24A, B.

*Dodecaactinella* cf. *cynodontota* Bengtson and Runnegar, 1990 in Bengtson et al. 1990

Fig. 5A, B.

*Material*.—Three phosphatic replacements of calcitic spicules from etching residues of limestone erratic boulder Me32. Figured specimens, ZPAL Pf.V/35S23, 26.

*Description*.—Triacts, with rays branching dichotomously (Fig. 5A) or trichotomously (Fig. 5B).

*Remarks*.—These specimens resemble the Early Cambrian type material from the Ajax Limestone at the Mount Scott Range, South Australia (Bengtson et al. 1990), but their subsidiary rays are straight more like the triactine-based spicules from the early Middle Cambrian Tindall Limestone of the Daly Basin, Northern Territory, Australia (Kruse 1990), and their surfaces are corroded and rough as a result of the phosphatic replacement.

*Occurrence*.—Allochthonous Early Cambrian (Botomian) boulders (Me32), King George Island, Antarctica.

Order Heteractinida Hinde, 1888

Family Eiffelidae Rigby, 1986

Genus *Eiffelia* Walcott, 1920

*Type species*: *Eiffelia globosa* Walcott, 1920.

*Eiffelia* Walcott, 1920: 323.

*Lenastella* Missarzhevsky in Missarzhevsky and Mambetov 1981: 75.

*Actinoites* Duan, 1984: 166.

*Niphadus* Duan, 1984: 167.

*Eiffelia araniformis* (Missarzhevsky, 1981)

Fig. 5H.

*Eiffelia araniformis* (Missarzhevsky); Bengtson in Bengtson et al. 1990: 27, figs. 12, 13 [full synonymy].

*Material*.—Eight specimens from etching residues of limestone erratic boulder Me66. Figured specimen, ZPAL Pf.V/38S16.

*Description*.—Spicules with six slender rays, and diverging at 60° in one plane. The spicule surfaces are smooth, and the rays tapering to a point, but usually have broken ends. The rays are set at a low angle to their common plane, and thus form a concave and convex side of the spicule (Fig. 5H). A central ray may occur on the convex side, perpendicularly to the hexiradiate plane.

*Remarks*.—The antarctic forms are most similar to the South Australian ones from Horse Gully and Curramulka, Parara Limestone, and Mount Scott Range, Ajax Limestone discussed and figured by Bengtson (in Bengtson et al. 1990: fig. 13C). Isolated spicules of *Eiffelia* sp. have recently been recorded also in Middle Cambrian phosphatic sediments of the Georgina Basin (Mehl 1998).

*Occurrence*.—Allochthonous Early Cambrian (Botomian) boulders (Me66), King George Island, Antarctica.

?Heteractinida indet.

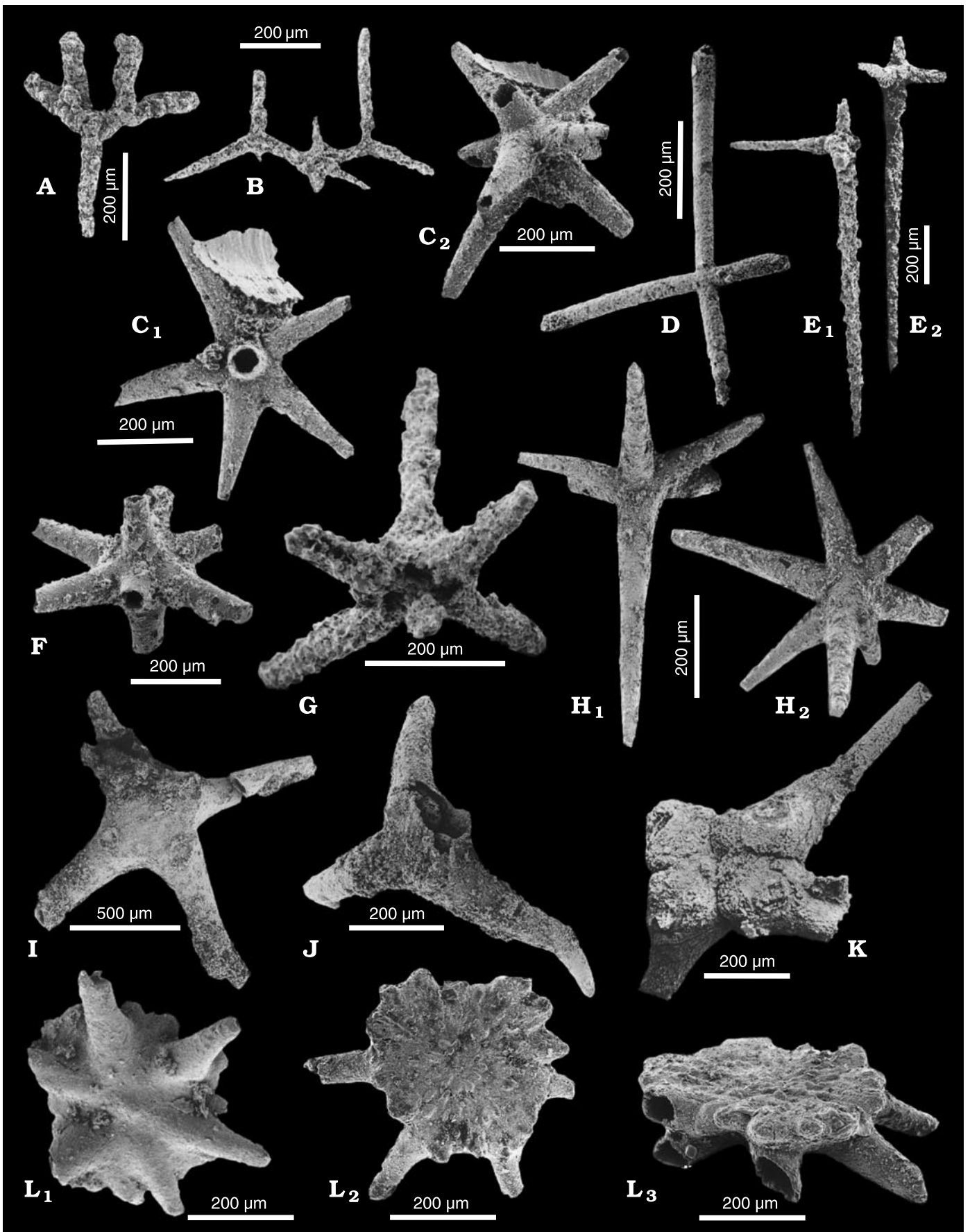
Fig. 5C, F.

*Material*.—A dozen isolated megasclere spicules of polyactine (?octactine) forms, preserved as phosphatic sheaths from etching residues of limestone erratic boulders Me32 and 66. Figured specimens, ZPAL Pf.V/108S16; 29U13.

*Description*.—There are polyaxial spicules, which are usually asymmetric octactines (Fig. 5C) with aberrantly developed rays, and some that are perfectly hexiradially symmetric (Fig. 5F), with six rays in a plane, separated at 60° from each other, and addition of two rays at right angles to the plane (octactine). The spicule surfaces are smooth or coarse, when coated by mineral grains. The spicule rays tapering to a point, but rays usually have broken ends. The spicules were probably initially calcareous, solid rayed, now dissolved and preserved as phosphatic sheaths, with large hollows along ray axes. Such spicules are common in calcareous heteractinid sponges (Rigby 1983; Pickett 2002).

*Remarks*.—The antarctic forms are similar to the South Australian spicules from Horse Gully and Curramulka, Parara Limestone, and Mount Scott Range, Ajax Limestone dis-

Fig. 5. **A, B**. Sponge spicules of *Dodecaactinella* cf. *cynodontota* Bengtson and Runnegar. **A**. Fragment of phosphatized spicule, ZPAL Pf.V/35S23, erratic Me32; **B**. Phosphatized broken triactine spicule, ZPAL Pf.V/35S26, erratic Me32. **C, F**. Heteractinid spicules. **C** Phosphatic sheath of broken polyactine, ZPAL Pf.V/108S16, erratic Me66; **C**<sub>1</sub>, oblique view; **C**<sub>2</sub>, axial view of the same. **D–E, G**. Hexactinellid spicules. **D**. Phosphatized tetractine, ZPAL Pf.V/21S21, erratic Me52. **E**. Phosphatized hexactine in lateral views, ZPAL Pf.V/39S15, erratic Me66. **F**. Phosphatic sheath of broken polyactine, ?oxyaster, ZPAL Pf.V/29U13, erratic Me32. **G**. Phosphatized hexactine, ZPAL Pf.V/25S4, erratic Me33. **H**. *Eiffelia araniformis* (Missarzhevsky) 6-rayed spicule, with 7th central ray, ZPAL Pf.V/38S16, erratic Me66. **I**. Broken cancelloriid sclerite of *Archiasterella?* sp., ZPAL V.VI/37S5, erratic Me32. **J**. *Allonnia* ex gr. *A. tripodophora* Doré and Reid, damaged sclerite, covered with mineral matter, ZPAL V.VI/38S19, erratic Me32. **K**. *Allonnia?* cf. *tetrathallis* (Jiang), broken sclerite ZPAL V.VI/36S7, erratic Me33. **L**. Phosphatic overgrowth of *Radiocyathus?* sp. cf. *R. minor* Bedford and Bedford, ZPAL V.VI/40S9, erratic Me66; **L**<sub>1</sub>, inner surface view; **L**<sub>2</sub>, outer (external) surface of the same rosette; **L**<sub>3</sub>, the same in oblique lateral view. →



cussed by Bengtson (in Bengtson et al. 1990), and to the forms from the early Middle Cambrian Tindall Limestone of the Daly Basin, Northern Territory, Australia (Kruse 1990). These spicules seem to be common isolated sponge spicules in the Cambrian rocks (e.g., Hinz 1987; Kruse 1990; Bengtson et al. 1990; Mehl 1998).

*Occurrence.*—Allochthonous Early Cambrian (Botomian) boulders (Me32, 66), King George Island, Antarctica.

## Class Hexactinellida Schmidt, 1870

### Hexactinellida indet.

Fig. 5D, E, G.

*Material.*—Nine disarticulated spicules of tetractine up to hexactine, preserved as phosphatic replacement from etching residues of limestone erratic boulders Me33, 52, and 66. Figured specimens, ZPAL Pf.V/21S21; 39S15; 25S4.

*Description.*—There are four-rayed spicules (Fig. 5D) oriented in one plane (stauracts) up to six-rayed spicules (hexactines), which are often asymmetric (Fig. 5E, G) with aberrantly developed rays. The spicule surfaces are coarse, when corroded or coated by minearl grains (Fig. 5E, G). The spicule rays tapering to a point, but rays usually have broken ends. They are preserved as recrystallized steinkerns, possibly phosphatized.

*Remarks.*—The antarctic forms are most similar to the South Australian spicules from Horse Gully and Curramulka, Parara Limestone, and Mount Scott Range, Ajax Limestone discussed and figured by Bengtson (in Bengtson et al. 1990: fig. 15). These spicules seem to be the most common disarticulated sponge spicules in the Cambrian rocks from several localities around the world (e.g., Hinz 1987; Kruse 1990; Bengtson et al. 1990; Brock and Cooper 1993; Zhang and Pratt 1996; Dong and Knoll 1996; Mehl 1998; Krautter 2002).

*Occurrence.*—Allochthonous Early Cambrian (Botomian) boulders (Me33, 52 and 66), King George Island, Antarctica.

## Phylum uncertain ?Porifera Grant, 1836

### Class Radiocyatha Debrenne, Termier, and Termier, 1970

#### Family Radiocyathidae Okulich, 1955

#### Genus *Radiocyathus* Okulich, 1937

*Type species:* *Heterocyathus minor* Bedford and Bedford, 1934.

*Remarks.*—Their co-occurrence, together with archaeocyaths, is restricted to the Cambrian, but their close phylogenetic relationship is still doubtful (Zhuravlev 1986).

#### *Radiocyathus?* sp. cf. *R. minor* Bedford and Bedford, 1934

Fig. 5L.

“*Lenastella*”; Wrona 1989: 541, pl. 8: 6.

*Material.*—Two sclerites from erratic boulder Me66. Figured specimen, ZPAL V.VI/40S9.

*Description.*—Simple sclerite consisting of a rounded plate and a six-ribbed stellate rosette. The rays are slightly inclined toward the central perpendicular ray, which is shortened to a

central knob (Fig. 5L<sub>1</sub>). Distally tapering stellate rays are usually broken and hollow. The rounded star-shaped plate, formed by radial rays and numerous small projections in between, has on its external surface a characteristic, radially arranged, granular, starlike sculpture (Fig. 5L<sub>2</sub>, L<sub>3</sub>).

*Remarks.*—The described sclerites represent phosphatic overgrowth (sheaths) of originally calcareous nesasters. This sclerite was described and figured earlier as “*Lenastella*”-type rosettelike spicules (Wrona 1989: 541, pl. 8: 6), and their heteractinid provenance was also considered (Wrona and Zhuravlev 1996: 16). The rosette-like sclerites very much resemble radiocyathan nesasters, and are superficially somewhat similar also to the South Australian ?*Heteractinid* calcareous spicules (Bengtson et al. 1990: fig. 14F–H). The starlike sculpture on the external plate of Antarctic specimens is very similar to the external sculpture of *Radiocyathus minor* nesasters figured by Debrenne et al. (1970: pl. 6: 1). Moreover, the latter species was also recorded in thin sections of Early Cambrian glacial erratics from King George Island, Antarctica (Wrona and Zhuravlev 1996). *R. minor* was originally described from the Ajax Limestone, Flinders Ranges, South Australia (Bedford and Bedford 1934) and Todd River Dolomite (Amadeus Basin), central Australia (Kruse and West 1980). The figured specimen (Fig. 5L) is probably a partial nesaster, because, unlike sclerites, nesasters were interlocked to form a continuous mineralised skeleton. The discussed homology between radiocyathid nesasters and receptaculitid meroms, and the close relationship between both these groups (Nitecki and Debrenne 1979) was finally rejected by Nitecki (1986) as highly speculative.

*Occurrence.*—Allochthonous Early Cambrian (Botomian) boulders (Me66), King George Island, Antarctica.

## Phylum uncertain

### Class Coeloscleritophora Bengtson and Missarzhevsky, 1981

*Remarks.*—This taxon has been established for a group of fossils characterised by an exoskeleton consisting of hollow calcareous (aragonitic) spine-, rosette- or scale-like sclerites with an internal cavity for soft tissues, connected to the animal body through a narrow basal foramen. The principal coeloscleritophorans include cancelloriids, halkieriids, sachtitids, and siphogonuchitids.

#### Order Cancelloriida Walcott, 1920

#### Family Cancelloriidae Walcott, 1920

*Characterization and remarks.*—Exclusively Cambrian, composite, mostly star-shaped sclerites which are very variable in shape, number and arrangement of rays (e.g., Sdzuy 1969; Fernández-Remolar 2001). The rays have their own individual calcareous (possibly aragonitic) wall, which separates the rays from each other, and an inner cavity which is open to the exterior through a basal foramen (Sdzuy 1969; Bengtson et al. 1990; Bengtson and Hou 2001). This sclerite architecture is similar to that found in other sclerites of the Coeloscleritophora (Bengtson and Missarzhevsky 1981;

Bengtson et al. 1990). Extraordinarily preserved specimens of body fossils from the Lower Cambrian Chengjiang biota in China, with articulated sclerites clearly showing details of the flexible integument and scleritome arrangement, indicate that soft skin of the body and sclerites were structurally, functionally and developmentally integrated in the chancelloriid integument (Bengtson and Hou 2001). This as well as many previous records of sclerite arrays on body surfaces (Walcott 1920; Sdzuy 1969; Mostler and Mosleh-Yazdi 1976; Rigby 1978) allow a reconstruction of these enigmatic organisms as having a spherical or saccular body armoured with star-shaped, spiny sclerites (Bengtson and Hou 2001). Their marine, sedentary benthic mode of life as suspension feeding animals has been commonly accepted by most workers (Bengtson et al. 1990; Wood et al. 1993; Mehl 1996; Demidenko 2000; Bengtson and Hou 2001). For detailed taxonomic discussion see Bengtson et al. 1990.

### Genus *Chancelloria* Walcott, 1920

*Type species: Chancelloria eros* Walcott, 1920.

#### *Chancelloria racemifundis* Bengtson, 1990 in Bengtson et al. 1990

Fig. 6E, L, T.

*Chancelloria racemifundis* sp. nov.; Bengtson in Bengtson et al. 1990: 51, figs. 23–25.

*Chancelloria racemifundis* Bengtson; Mehl 1998: 1175, pl. 7: 2, 6, 13.

*Chancelloria racemifundis* Bengtson; Demidenko in Gravestock et al. 2001: 106, pl. 5: 4a, b.

**Material.**—Two articulated sclerites with broken distal ends of lateral rays, and a number of disarticulated central and lateral rays from erratic boulders Me33 and 66. Figured specimens, ZPAL V.VI/36S8, 10; 37S6.

**Description.**—Small sclerites with long, slender lateral rays (formula: 5+1) which slightly diverge from the basal plane. The outer surface of the ray has weak longitudinal striae. The basal facet is encircled by a distinct circular ridge. Protruding ridges well developed, but basal foramina and surrounding spherulitic structures partly covered with minerals.

**Remarks.**—A number of small and slender internal moulds (Fig. 6E, L), which do not express the characteristic feature associated with the basal facet of the ray, may also represent the species *Ch. racemifundis*.

**Occurrence.**—Early Cambrian (Atdabanian–Botomian) of the Kulpara Formation and Parara Limestone, Yorke Peninsula, Stansbury Basin and Ajax Limestone, Flinders Ranges, Arrowie Basin, South Australia; Middle Cambrian (Templetonian) of the Beetle Creek Formation, Georgina Basin, Queensland; allochthonous Early Cambrian (Botomian) boulders (Me33), King George Island, Antarctica.

#### *Chancelloria* sp. A

Fig. 6A, B, G–K, S.

**Material.**—A number of chancelloriid sclerites and their isolated marginal or central rays with broken distal ends from erratic boulders Me32, 33, and 66. Figured specimens, ZPAL V.VI/28S24; 35S18; 103S5; 105S3, 16, 19; 108S12.

**Description.**—Radially symmetric chancelloriid sclerites, which vary in size and number of rays. They seem to be originally composed of 6–8 radial rays and one usually larger central ray (Fig. 6J) or rarely 4–6 radial rays without central element. Radial rays are 0.7–1.6 mm long, and expand slightly from the basal plane. The outer surface of the ray in some cases shows longitudinally oriented needle-like replicas of the originally aragonitic fibres, which composed the sclerite wall (Fig. 6J, S). This pattern corresponds to that observed by Kouchinsky (2000). The basal facet is flat, with radial rays straight, lying in the same plane, or slightly curved and divergent from the basal plane. These articulated sclerites and isolated rays obviously represent phosphatic moulds of their internal cavities.

**Remarks.**—A number of internal moulds of individual disarticulated sclerite rays correspond to the normal sclerite type of *Chancelloria eros* Walcott, 1920 in a broad sense (Bengtson in Bengtson et al. 1990; Mehl 1998). As the figured specimens are very variable in shape and ray composition, some of them may also represent the species *Ch. ex gr. symmetrica* Vasileva recovered from the Stansbury and Arrowie Basins, South Australia (Demidenko in Gravestock et al. 2001). Such specimens were also reported earlier from erratic blocks of Middle Cambrian limestone occurring in moraines of the Argentina Range in Antarctica (Solovjev and Grikurov 1979; Popov and Solovjev 1981). The Antarctic articulated sclerites (Fig. 6J) also resemble closely the articulated specimens of *Ch. lenaica* Zhuravleva and Korde, 1955 from the Lower Cambrian of Comley, Shropshire, England (Hinz 1987: pl. 2: 10, 11).

**Occurrence.**—Allochthonous Early Cambrian (Botomian) boulders (Me33), King George Island, Antarctica.

#### *Chancelloria* sp. B

Fig. 6C.

**Material.**—A dozen isolated marginal rays of chancelloriid sclerites with often broken distal ends from erratic boulders Me33 and 66. Figured specimen, ZPAL V.VI/105S17.

**Description.**—Small sclerites with long slender lateral rays (formula: 4+0) which bend away sharply and may be almost vertical to the basal plane. Outer surfaces of ray steinkerns are provided with minute spines, that may reflect, as counterparts, porosity of the sclerite wall. Basal end of sclerite ray bears the characteristic lateral faces, being a result of their arrangement in the sclerite. Basal foramina and surrounding structures partly covered with mineral grains.

**Remarks.**—A number of these small and slender internal moulds, which do not have the characteristic basal facets and basal foramen of the ray expressed, may also represent species *Ch. racemifundis*. This sclerite composition and arrangement of rays can be compared with those of *Chancelloria* spp. (Bengtson in Bengtson et al. 1990: fig. 26I–K) and a new type *Chancelloria* sp. described from the Middle Cambrian Beetle Creek Formation, Georgina Basin, Queensland (Mehl 1998: 1176, pl. 7: 9).

**Occurrence.**—Allochthonous Early Cambrian (Botomian) boulders (Me32, 33, and 66), King George Island, Antarctica.

## Genus *Archiasterella* Sdzuy, 1969

*Type species: Archiasterella pentactina* Sdzuy, 1969.

### *Archiasterella?* sp.

Fig. 5I.

*Material.*—One sclerite and a number of isolated marginal rays with broken distal ends from erratic boulders Me33 and 66. Figured specimen, ZPAL V.VI/37S5.

*Description.*—Four- or five-rayed bilaterally symmetric sclerites with long lateral rays (formula: 4-5+0), which slightly diverge from the basal plane, but with one of them recurved backwards, to become almost perpendicular to the base. Outer surface of the rays are rough or provided with weak tubercles. Basal facet is relatively large and without visible sutures between sclerite rays. Basal foramina are circular to elliptical in shape and sparsely arranged (displaced distally from the centre of the sclerite) on the basal facet.

*Remarks.*—A number of isolated internal moulds of strongly recurved rays may also represent the median ray of this species.

*Occurrence.*—Allochthonous Early Cambrian (Botomian) boulders (Me33 and 66), King George Island, Antarctica.

## Genus *Allonnia* Doré and Reid, 1965

*Type species: Allonnia tripodophora* Doré and Reid, 1965.

*Remarks.*—Originally this genus was introduced for cancelloriid sclerites having three rays (formula: 3+0), but Qian and Bengtson (1989) also included in this genus sclerites with four (formula: 4+0) and two (formula: 2+0) rays; for synonymy and detailed discussion see Qian and Bengtson (1989) and Bengtson et al. 1990.

### *Allonnia* ex gr. *A. tripodophora* Doré and Reid, 1965

Figs. 5J, 6D, F.

*Material.*—A dozen isolated marginal rays from erratic boulders Me32, 33, and 66. Figured specimens, ZPAL V.VI/385S19; 103S11 and 15.

*Description.*—Small sclerites with 3 equally long, slender tapering lateral rays (formula: 3+0), which strongly diverge from the basal plane. Basal ends of rays have lateral faces diverging at 60° from each other. This reflects the arrangement of articulated marginal rays diverging at 120° from each other. Basal end of rays are somewhat flattened, forming large basal areas without distinct sutures. Basal foramina are small, circular and situated at top of basal end. This morphology indicates

absence of a central ray. Distal ends of lateral rays may be recurved (Fig. 5J). Outer surface of rays and basal facet is partly covered with mineral grains.

*Remarks.*—All specimens are phosphatic internal moulds of isolated slender, recurved rays, with characteristic circular, basal openings and sagittal shape of the ray basal parts, may also represent elements of *A. ex. gr. tripodophora*.

*Occurrence.*—Allochthonous Early Cambrian (Botomian) boulder (Me32, 33 and 66), King George Island, Antarctica.

### *Allonnia* cf. *tetrathallis* (Jiang, 1982 in Luo et al. 1982)

Fig. 5K.

*Material.*—Four internal moulds of sclerites, often with broken-off distal ends from erratic boulders Me33 and 66. Figured specimen, ZPAL V.VI/365S7.

*Description.*—Bilaterally symmetric sclerites with long slender rays (formula: 4+0), which slightly diverge from the basal plane. Outer surface of the ray is provided with weak longitudinal striae, which may reflect originally aragonitic fibres composing the sclerite wall. Basal facet is relatively large with a distinct suture. Basal foramina well developed, but partly covered with mineral grains.

*Remarks.*—Similar cancelloriid sclerites with formula 4+0 were first assigned to the genus *Onychia* by Jiang (in Luo et al. 1982) and included by Qian and Bengtson (1989: see detailed discussion) as a junior homonym in a broadened concept of the genus *Allonnia*. A number of small and slender internal moulds, which have characteristic one large facet and sagittal shape of the base of each ray, may also represent the species *A. cf. tetrathallis*.

*Occurrence.*—Allochthonous Early Cambrian (Botomian) boulders (Me33 and 66), King George Island, Antarctica.

### *Allonnia* sp.

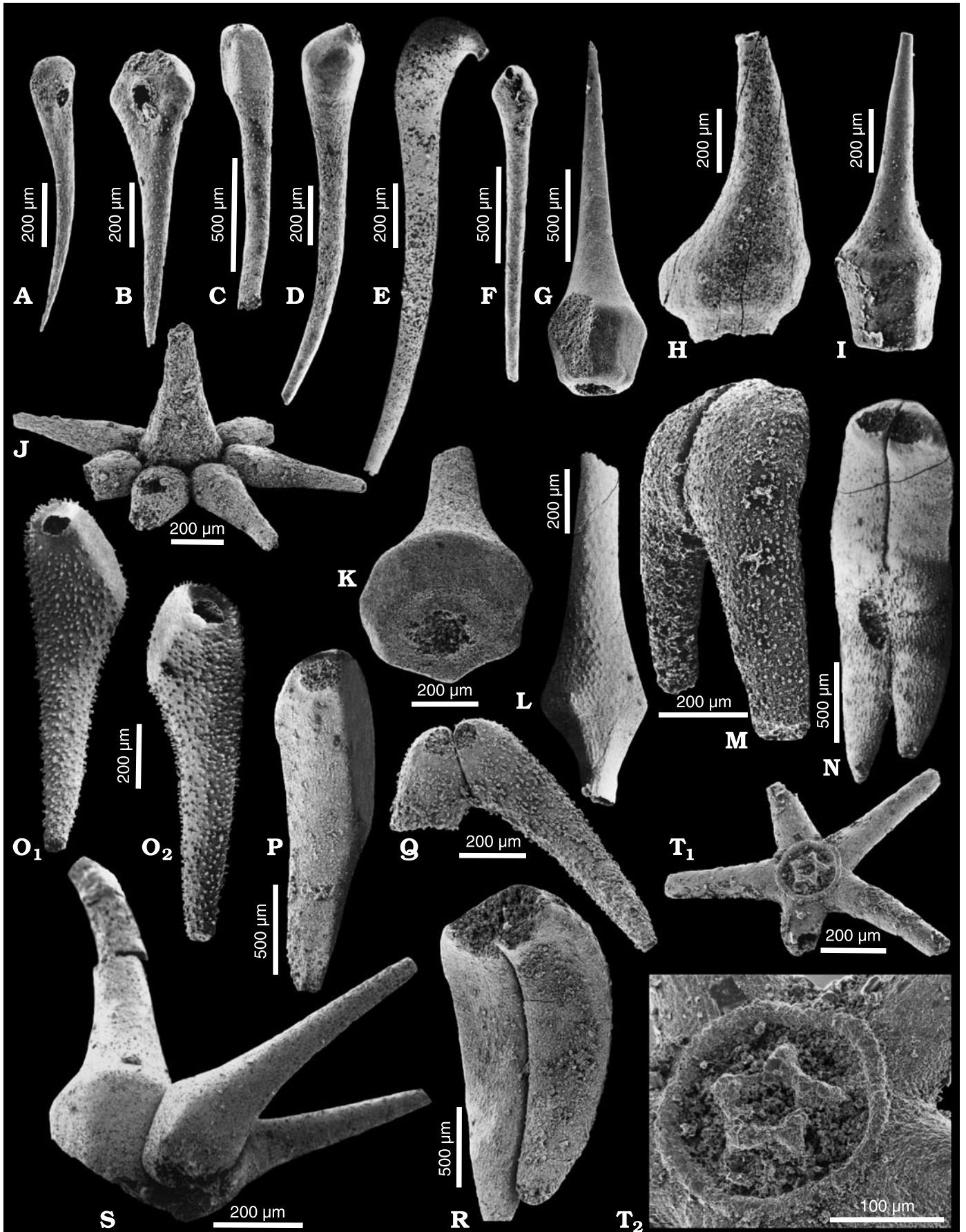
Fig. 6M–R.

*Material.*—A dozen phosphatic steinkerns of isolated sclerite rays, often with broken distal ends from erratic boulders Me33, 66. Figured specimens, ZPAL V.VI/26S18; 37S2; 37S9; 105S7; 107S20; 115S8.

*Description.*—Sclerites distinctly bilaterally symmetric, having two equal rays (formula: 2+0), slightly bent in the basal plane. Distal end tapers to a point. Foramina round and variable in size but relatively small (Fig. 6O, Q). Outer surface of ray steinkerns, except for a small area around the basal pore, is cov-

Fig. 6. **A, B, G–K.** Internal moulds of *Chancelloria* sp. **A.** disarticulated sclerite. **A.** Marginal ray, ZPAL V.VI/105S19, erratic Me66. **B.** Marginal ray, ZPAL V.VI/105S16, erratic Me66. **C.** Broken internal mould of *Chancelloria* sp. **B** marginal ray, ZPAL V.VI/105S17, erratic Me66. **D.** Internal mould of *Allonnia* ex gr. *A. tripodophora* Doré and Reid marginal ray, ZPAL V.VI/103S15, erratic Me33. **E.** Internal mould of *Chancelloria racemifundis* Bengtson marginal ray, ZPAL V.VI/36S10, erratic Me33. **F.** Internal mould of *Allonnia* ex gr. *A. tripodophora* Doré and Reid marginal ray, ZPAL V.VI/103S11, erratic Me66. **G.** Central ray, ZPAL V.VI/35S18, erratic Me33. **H.** Central ray, ZPAL V.VI/108S12, erratic Me66. **I.** Central ray, ZPAL V.VI/103S5, erratic Me33. **J.** Articulated sclerite, ZPAL V.VI/37S15, erratic Me66. **K.** Internal mould of the central ray, ZPAL V.VI/105S3, erratic Me66. **L.** *Chancelloria racemifundis* Bengtson. Internal mould of the central ray, ZPAL V.VI/36S8, erratic Me66. **M–R.** *Allonnia* sp. **M.** Internal mould of the twins articulated sclerite, ZPAL V.VI/105S7, erratic Me66. **N.** Internal mould of the articulated sclerite, ZPAL V.VI/26S18, erratic Me33. **O.** Single sclerite, ZPAL V.VI/37S2, erratic Me66, dissociated on the SEM stub in two rays: left ( $O_1$ ) and right ( $O_2$ ). **P.** One ray of the twins sclerite, ZPAL V.VI/107S20, erratic Me66. **Q.** Partly broken articulated specimen, ZPAL V.VI/115S8, erratic Me66. **R.** Internal mould of the articulated sclerite, ZPAL V.VI/37S9, erratic Me33. **S.** *Chancelloria* sp. **A.**, partly broken articulated sclerite, ZPAL V.VI/28S24, erratic Me33. **T.** *Chancelloria racemifundis* Bengtson, ZPAL V.VI/37S6, erratic Me33; **T<sub>1</sub>**, partly broken articulated sclerite in basal view; **T<sub>2</sub>**, detail of the basal foramina. →





ered with characteristic ornamentation of minute, robust spinules (Fig. 6M), which may reflect porosity of the sclerite wall. Such spiny ornamentation is similar to irregularly spaced pillars on the *Eremactis mawsoni* steinkern surface, interpreted as being originally diagenetic (Bengtson et al. 1990: figs. 35A, B and 36G). These double rays can be fused, with a small attachment surface (Fig. 6O, Q), as is common in this genus, or with a large attachment area (Fig. 6M, P), in nearly parallel position (Fig. 6N, R). The twin rays, fused along their length, resemble certain sclerites of *Eremactis conara* Bengtson and Conway Morris (Bengtson et al. 1990: fig. 32E, F), but their basal foramina remain simple and round, without any pronounced structures like circular ridge, or spherulitic surface. The Antarctic *Allonnia* sp. rays have triangular cross-section in their proximal (fused) part and a more rounded to circular cross-section at the distal end.

*Remarks.*—Similar cancelloriid sclerites with formula 2+0 were first assigned to the genus *Dimidia* by Jiang (in Luo et al. 1982) and synonymized by Qian and Bengtson (1989) with a broad concept of the genus *Allonnia*. A number of internal moulds with large lateral facet on each ray, which reflects a composition of twin rays sclerite, may also represent elements of the Antarctic *Allonnia* sp. Such sclerites with large fusion facet and triangular cross-section are an exclusively abundant and characteristic constituent of the Antarctic Lower Cambrian cancelloriid assemblage.

*Occurrence.*—Allochthonous Early Cambrian (Botomian) boulders (Me33 and 66), King George Island, Antarctica.

## Order Sachitida He, 1980 in Yin et al. 1980

### Family Halkieriidae Poulsen, 1967

*Genera included:* *Halkieria* Poulsen, 1967; *Sinosachites* He, 1980 in Yin et al. 1980.

*Remarks.*—This is a group of bilaterally symmetrical metazoans with a slug-like body, armoured by different types of imbricating sclerites: palmate on the dorsal side, cultrate on the lateral sides and siculate or/and spiniform on the ventrolateral sides. Despite discovery of unique, well-preserved articulated sclerite arrays in compressed complete animals (Conway Morris and Peel 1990, 1995), the precise evolutionary position of the Halkieriidae remains unresolved. For diagnosis see Qian and Bengtson (1989), Conway Morris in Bengtson et al. (1990) and Conway Morris and Peel (1995).

### Genus *Halkieria* Poulsen, 1967

*Type species:* *Halkieria obliqua* Poulsen, 1967.

*Remarks.*—This genus was established on the basis of isolated

sclerites recovered from the Lower Cambrian of Bornholm (Poulsen 1967), and for a long time was known only from a number of disarticulated sclerites, variable in shape but with at least three main types: palmate, cultrate and spiniform (Bengtson and Conway Morris 1984). The discovery of articulated halkieriids confirmed the arrangement of a whole scleritome as the dermal armour of a multisclerite animal (Conway Morris and Peel 1990, 1995). These superbly preserved complete scleritomes in the Lower Cambrian Buen Formation of Peary Land, north Greenland (Conway Morris and Peel 1995) was also of crucial significance for the reconstruction of many Cambrian coeloscleritophoran animals and the interpretation of their taxonomic relationships. The diagnosis has been modified by Conway Morris and Peel (1995).

### *Halkieria parva* Conway Morris, 1990 in Bengtson et al. 1990

Fig. 7.

*Halkieria* sp.; Gaździcki and Wrona 1986: 611, fig. 7h.

*Halkieria parva* Conway Morris in Bengtson et al. 1990; Demidenko in Gravestock et al. 2001: 113, pl. 7: 1–3 [full synonymy].

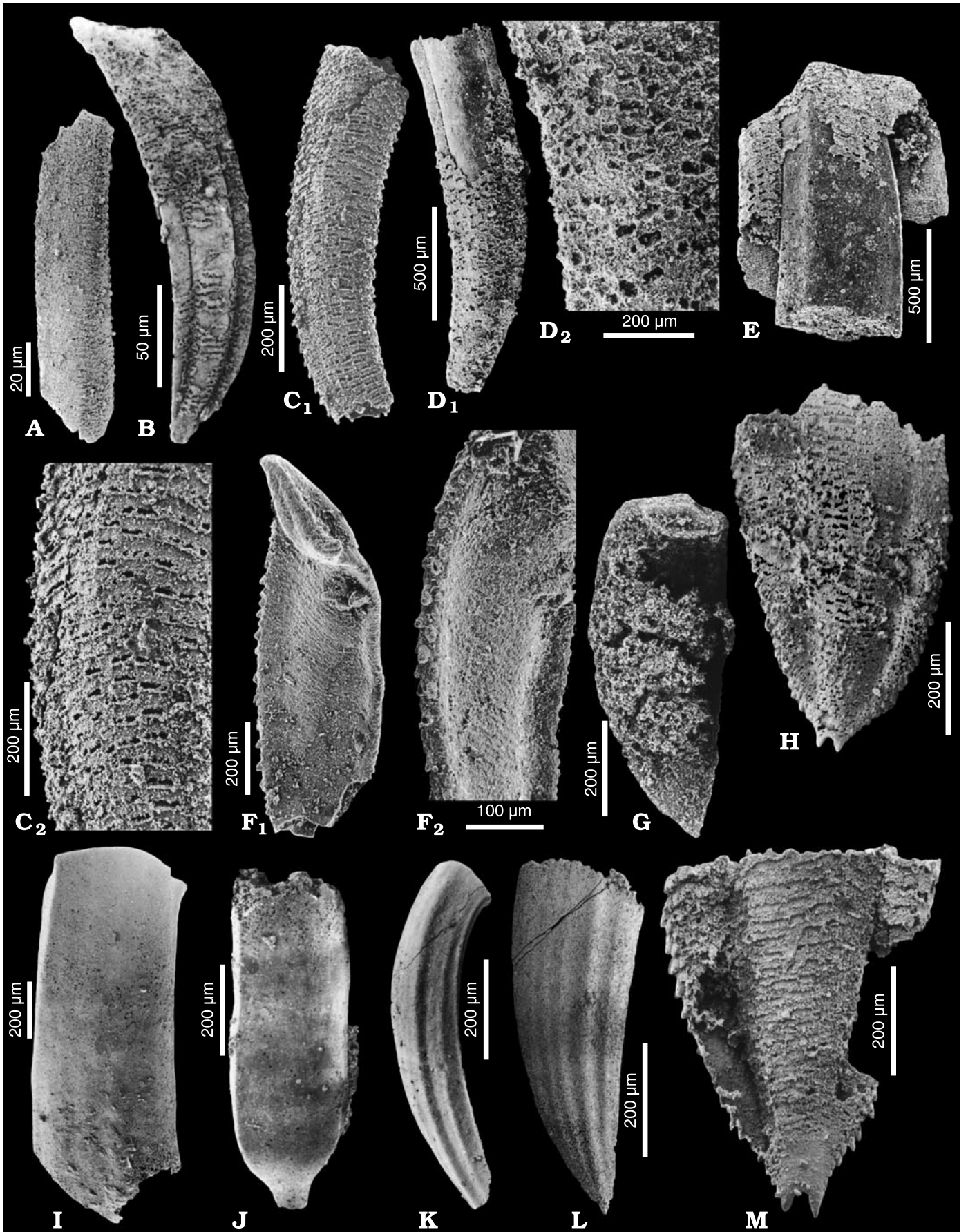
*Material.*—A number of isolated sclerites and phosphatic internal moulds from erratic boulders Me30, 32, 33, and 66. Figured specimens, ZPAL V.VI/25S2; 26S13; 32S5; 35S22; 36S3; 37S2; 39S7; 55S55; 105S7; 106S2; 108S4.

*Description.*—Minute calcareous sclerites of *Halkieria* with left- and right-hand forms representing variable morphotypes: mainly palmate and cultrate. Other known forms (siculate and spiniform) are absent in the present Antarctic collection. Palmate sclerites are elongated triangular, asymmetric, with compressed blade. Their distal end tapers to a point. Base is flattened, with oval foramen in the centre and set at a steep angle to the blade (Fig. 7F, G). Outer surface of the sclerite is covered with longitudinal ridges (Fig. 7A–E) and transverse tuberculation which is more distinct at the lateral edge (Fig. 7F<sub>2</sub>, M). Cultrate sclerites are more symmetric, long, knife-like in shape and strongly bent, tapering distally to a point. Base rhomboid with relatively small circular foramen in the centre. External ornamentation of cultrates is similar to that of palmates. There are a number of internal moulds with external wall partly preserved, which have large central canal and narrow and shorter lateral longitudinal canals (Fig. 7E, I, J) may also represent sclerites of *H. parva*. Steinkerns with a large central canal are abundant and characteristic for the Antarctic assemblage (Fig. 7I–L).

*Remarks.*—The preservation and highly variable sclerite forms make it difficult to classify the three morphocategories

Fig. 7. A–M. *Halkieria parva* Conway Morris. **A.** Broken cultrate sclerite in upper view, ZPAL V.VI/39S7, erratic Me66. **B.** Complete cultrate sclerite in upper view, ZPAL V.VI/26S13, erratic Me30. **C.** Middle part of cultrate sclerite, ZPAL V.VI/108S4, erratic Me66; C<sub>1</sub>, lateral view; C<sub>2</sub>, ornamentation of upper surface. **D.** Broken cultrate sclerite, ZPAL V.VI/29S11, erratic Me66; D<sub>1</sub>, blade preserved as internal mould of central and longitudinal lateral canals, with adhering sclerite wall, in upper view; D<sub>2</sub>, ornamentation of upper surface. **E.** Steinkern of basal part of the sclerite with central and lateral canals, ZPAL V.VI/39S5, erratic Me66. **F.** Palmate sclerite, ZPAL V.VI/106S2, erratic Me66; F<sub>1</sub>, oblique lower view; F<sub>2</sub>, ornament, prominent tubercles at the margin. **G.** Palmate sclerite with basal foramen in lower view, partly obscured by mineral coating, ZPAL V.VI/106S4, erratic Me66. **H.** Distal part of palmate broken sclerite in upper view, ZPAL V.VI/36S3, erratic Me32. **I.** Steinkern of proximal part of the central canal, palmate sclerite, ZPAL V.VI/32S5, erratic Me33. **J.** Steinkern of distal part of the central canal, palmate sclerite, ZPAL V.VI/55S55, erratic Me32. **K.** Steinkern of central blade sclerite, in lateral view, ZPAL V.VI/35S12, erratic Me32. **L.** Steinkern of distal part of cultrate sclerite, in upper view, ZPAL V.VI/37S2, erratic Me32. **M.** Distal part of palmate sclerite, showing broken lateral longitudinal canals, ZPAL V.VI/25S2, erratic Me33. →





in the Antarctic assemblage and to define their position in the halkieriid scleritome. The mollusc-like shells were not identified in Antarctic SSF but it is possible that some enigmatic “smooth cones”, preserved as internal moulds and referred in this paper to problematic molluscs for lack of better diagnostic features (Fig. 25N), may represent poorly preserved internal moulds of coeloscleritophoran halkieriid cap-shaped shells.

**Occurrence.**—This species is restricted to the Early Cambrian (Atdabanian–Botomian) of the Kulpara Formation, Parara Limestone and Koolywurite Limestone Member, Yorke Peninsula, Stansbury Basin and Ajax Limestone, Flinders Ranges, Arrowie Basin, South Australia; allochthonous Early Cambrian (Botomian) boulders (Me30, 32, 33, and 66), King George Island, Antarctica.

## Tommotiids

Order Tommotiida Missarzhevsky, 1970

Family Kennardiidae Laurie, 1986

Genus *Dailyatia* Bischoff, 1976

*Type species: Dailyatia ajax* Bischoff, 1976.

*Dailyatia ajax* Bischoff, 1976

Figs. 8A–E, 9, 11, 12, 15F, K.

*Dailyatia ajax* Bischoff; Demidenko in Gravestock et al. 2001: 114, pl. 8: 4–7 [full synonymy].

**Material.**—A number of isolated, variously shaped sclerites from erratic boulders Me30, 32, 33, and 66. Figured specimens, ZPAL V.VI/25S2; 26S13; 32S5; 35S22; 36S3; 37S2; 39S7; 39S27; 55S55; 105S7; 106S2; 108S4.

**Description.**—Minute sclerites of variable shape, subpyramidal to conical with prominent apex and radial folds and plicae. Sculpture consists of evenly and densely spaced carinate ribs with a distinct cancellate ornament. Sclerites of type A, with rectangular transverse cross-section, are absent in the Antarctic material. Sclerites of type B have subovate transverse cross-section (Figs. 11D, 12D) and prominent radial folds and plicae, and are strongly curved and twisted. Sclerite of type C are triangular (Figs. 8A–E, 11A–C, 12A) or crescentic (Fig. 8C) in transverse cross-section, with moderate curvature and torsion, and without radial folds. Well developed reticulate ornamentation on the juvenile part of the sclerite (Figs. 8A, C, 11D, 12A<sub>4</sub>, B) has been interpreted as representing epithelial cell imprints (e.g., Bengtson et al. 1990; Conway Morris and Chen 1990). The multilamellar wall structure is well visible in the broken and polished cross-sections (Figs. 12C, 15K), and the extension of single laminae can also be easily observed as longitudinal growth lines on the external (Fig. 11A<sub>5</sub>, A<sub>6</sub>) and internal (Fig. 12C<sub>4</sub>) surfaces of the sclerite wall. Transverse sections of wall folds also shows that they were internally overgrown with phos-

phate laminae (Figs. 12C<sub>2</sub>, 15K). However, those laminae neither enclose the entire internal sclerite circumference (see longitudinal growth lines in Fig. 12C<sub>4</sub>), nor extend throughout the entire interior height of the sclerite.

**Remarks.**—The sclerite morphology fits well the description by Bischoff (1976), but only two morphotypes are recognised. They resemble fairly closely *D. ajax* recovered from the Lower Cambrian Ajax and Wilkawillina Limestones, Flinders Ranges (Bischoff 1976) and Kulpara Formation, Parara Limestone, Koolywurite Limestone Member and Ramsay Limestone, Yorke Peninsula (Gravestock et al. 2001), South Australia, and Todd River Dolomite, Amadeus Basin, Northern Territory, central Australia (Laurie and Shergold 1985; Laurie 1986). The excellently preserved Antarctic sclerites of *D. ajax*, with epithelial imprint and multilamellar wall structure, reveal their mode of growth and make possible a modified reconstruction (Fig. 9) of the relationship between sclerite element and secretory tissue earlier proposed by Conway Morris and Chen (1990). The epithelial tissue envelops the whole sclerite in the initial stage of growth (Fig. 9A), as its presence is reflected by cellular imprints; the epithelial tissue enfolds the basal part of the sclerite exterior (reflected by cellular polygonal imprints), and their secretory zone probably lines the interior of the sclerite secreting basal-internal accretion of phosphate laminae (Fig. 9C, E). The sclerite wall has more or less the same thickness over the entire sclerite, since the secretory zone of the soft tissue was restricted to the wide basal part of the interior sclerite.

**Occurrence.**—This species is restricted to the Early Cambrian (Atdabanian–Botomian) of the Kulpara Formation, Parara Limestone, and Koolywurite Limestone Member, Yorke Peninsula, Stansbury Basin and Ajax Limestone, Flinders Ranges, Arrowie Basin, South Australia; allochthonous Early Cambrian (Botomian) boulders (Me30, 32, 33, and 66), King George Island, Antarctica.

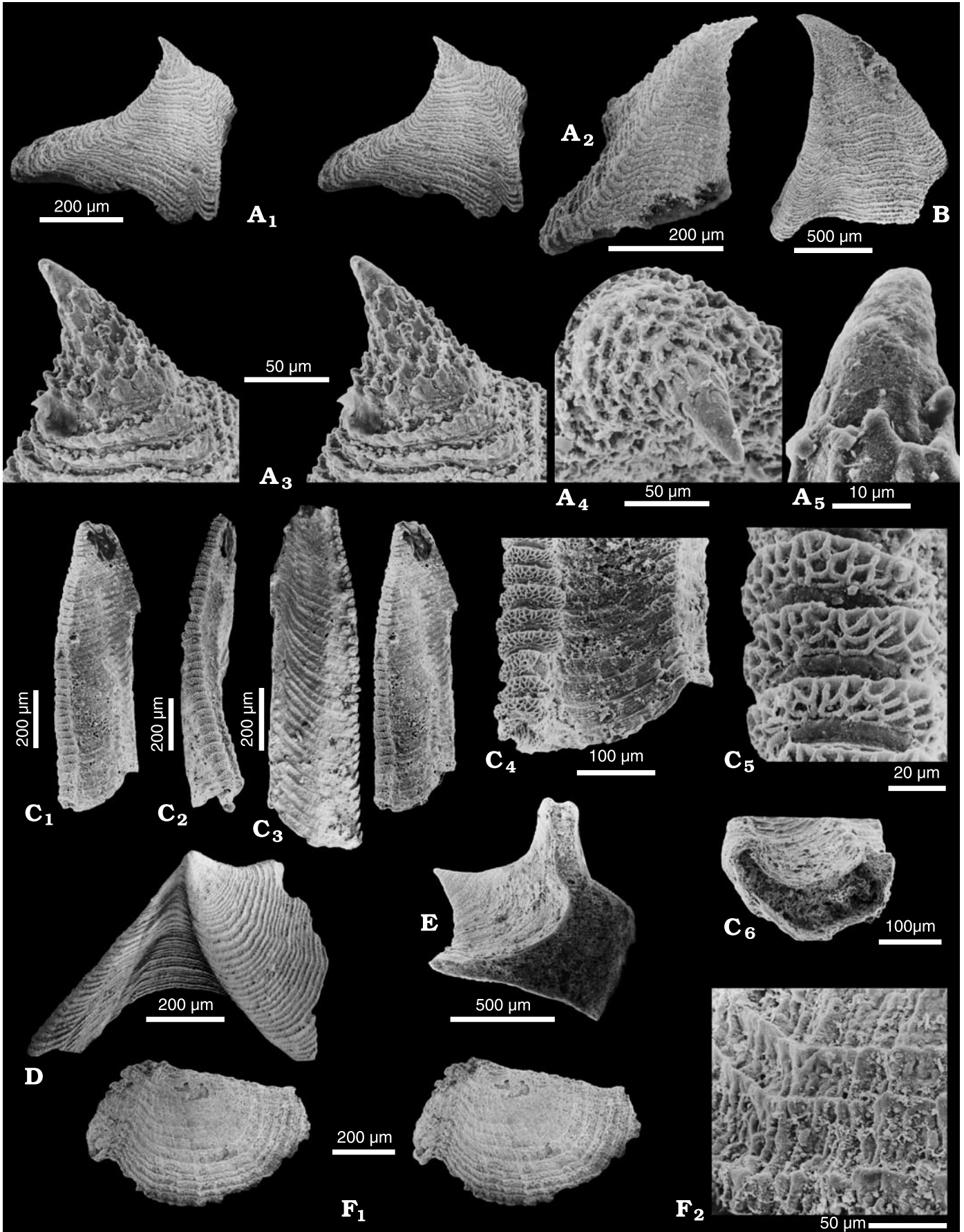
*Dailyatia* sp.

Fig. 10.

**Material.**—Two (one broken) isolated sclerites, ZPAL V.VI/31S2, 8, from erratic boulder Me33.

**Description.**—Gently curved, comparatively large sclerite, with prominent apex and shape ranging from pyramide (Fig. 10) to cornute. The wall is phosphatic, densely lamellar. The external sculpture consists of equally spaced sharp ridges without reticulate micro-ornament between ridges (Fig. 10D). Among the three known *Dailyatia* sclerite forms (e.g., Evans and Rowell 1990), two were recognized in the present collection: type B, subtriangular to subovate in cross-section, pyramidal sellate shape with longitudinal folds and posterior face saddle-like; and type C, triangular to crescentic in cross-section,

Fig. 8. A–E. *Dailyatia ajax* Bischoff. A. Dextral juvenile? sclerite of form C, ZPAL V.VI/15U4, erratic Me66; A<sub>1</sub>, oblique proximal view, stereo-pair; A<sub>2</sub>, lateral inner view; A<sub>3</sub>, detail of epithelial pattern on apex, in oblique lateral view, stereo-pair; A<sub>4</sub>, detail of apex in adapical view; A<sub>5</sub>, detail of apex in oblique lateral view. B. Dextral sclerite, form C, ZPAL V.VI/39S9, erratic Me66, in lateral view. C. Siculate sinistral sclerite, form C, ZPAL V.VI/39S27, erratic Me66; C<sub>1</sub>, inner lateral view, stereo-pair; C<sub>2</sub>, outer lateral edge of sclerite; C<sub>3</sub>, outer lateral view; C<sub>4</sub>, detail of edge at distal part, in lateral view; C<sub>5</sub>, detail showing epithelial polygons; C<sub>6</sub>, distal part, opening cavity. D. Sellate sclerite, form C, ZPAL V.VI/39S26, erratic Me66, in anterior side view. E. Opening cavity of dextral sclerite, form C, ZPAL V.VI/39S34, erratic Me66. F. Isolated sclerite of tommotiide indet., ZPAL V.VI/39S6, erratic Me66; F<sub>1</sub>, proximal outer view, stereo-pair; F<sub>2</sub>, surface ornamentation. →



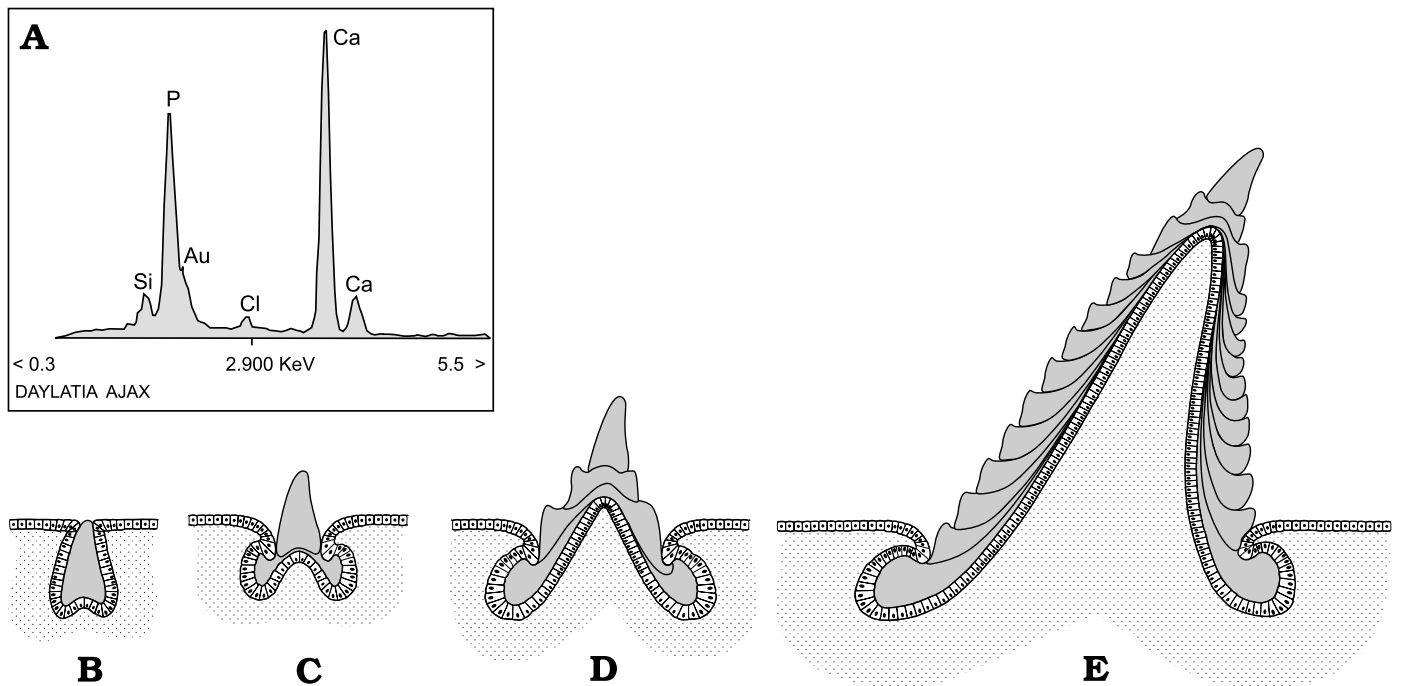


Fig. 9. A. Energy dispersive spectrum (EDS) for *Dailiyatia ajax* Bischoff sclerite. B–E. Diagrammatic reconstruction of the relationship between *Dailiyatia* sclerite element and secretory epithelium during growth, based on the multilamellar wall structure and the polygonal pattern covering the entire sclerite, except for a nipple-like termination of the apex.

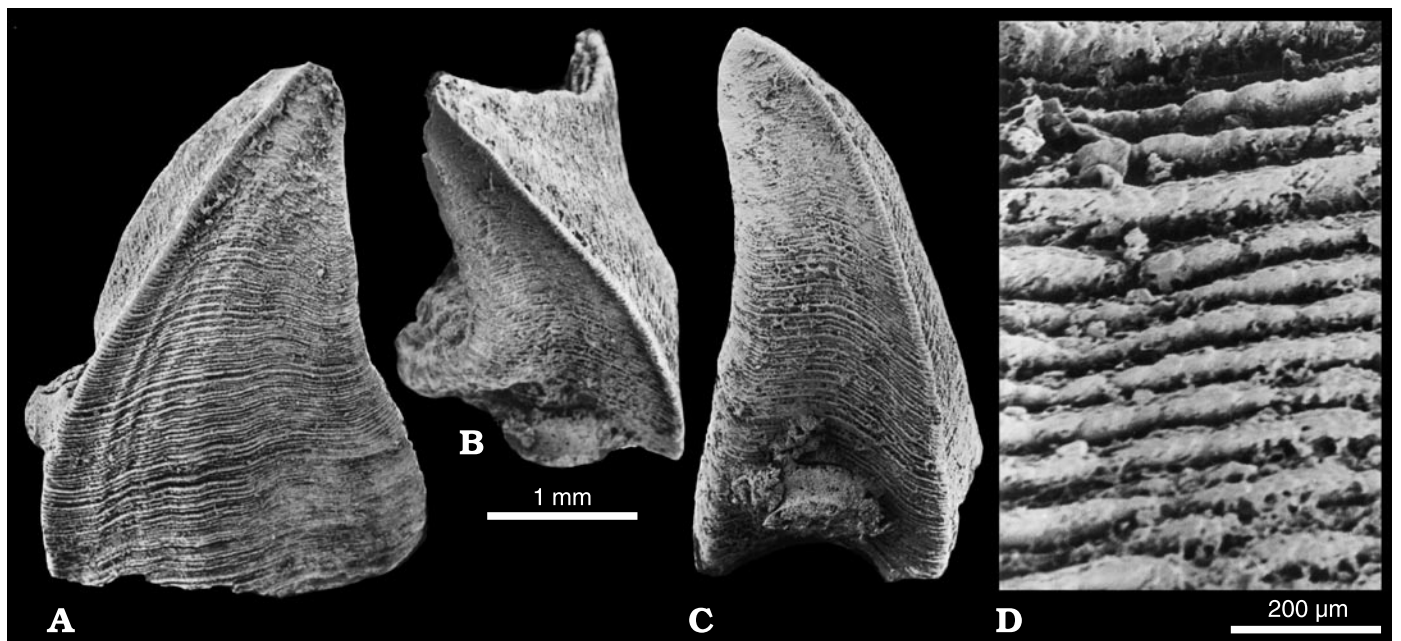
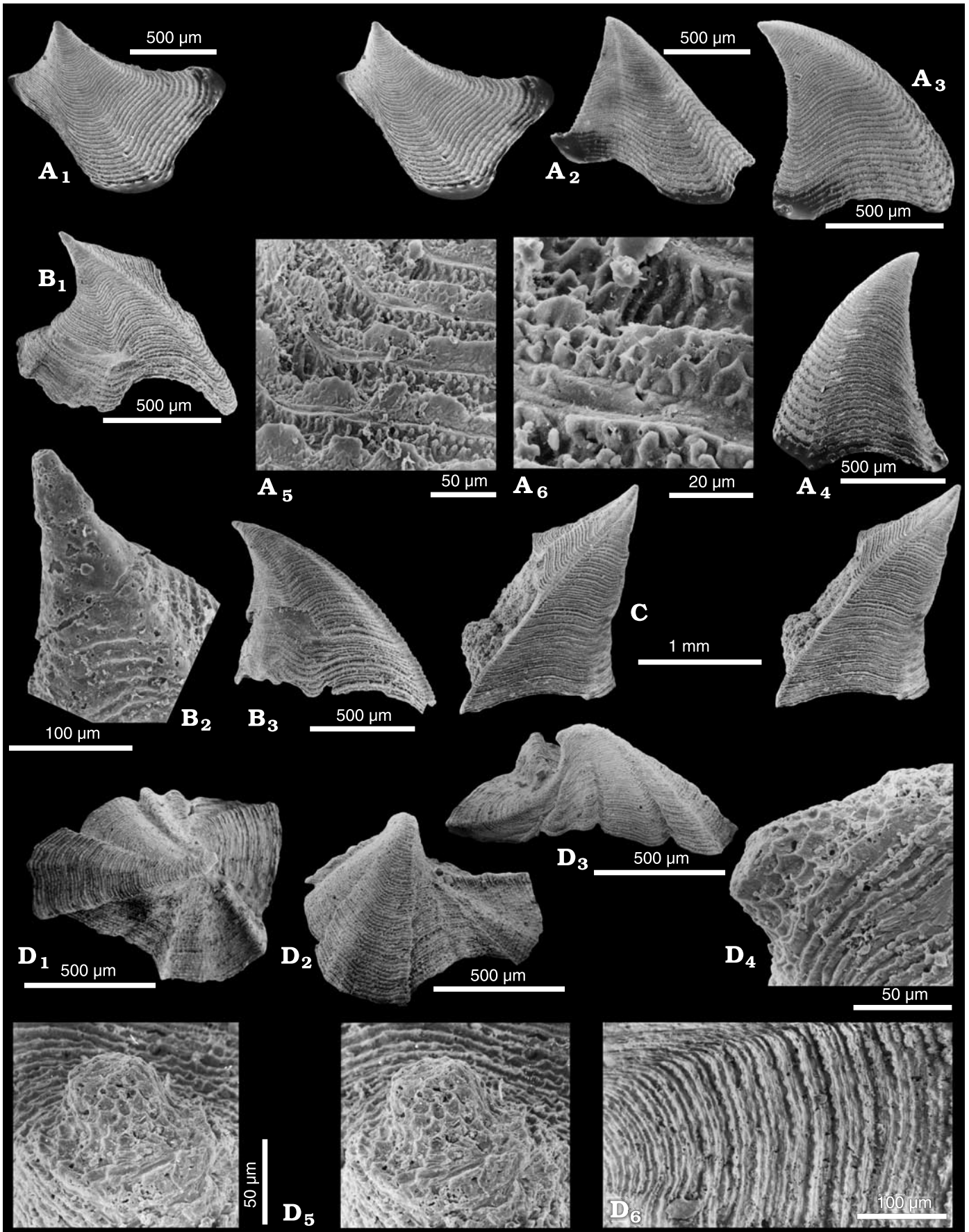


Fig. 10. Sclerite of *Dailiyatia* sp., ZPAL V.VI/31S2, erratic Me33. A. Oblique right lateral (anterior) view of asymmetrical triangular sclerite, type C. B. Oblique apical view. C. Oblique left lateral view. D. Enlargement of ornamentation showing growth ribs.

Fig. 11. *Dailiyatia ajax* Bischoff. A. Sinistral adult? sclerite, form C, ZPAL V.VI/29S7, erratic Me66; A<sub>1</sub>, oblique anterior view, stereo-pair; A<sub>2</sub>, oblique lateral view; A<sub>3</sub>, left lateral view; A<sub>4</sub>, right lateral view; A<sub>5</sub>, detail of growth ribs and inter-rib areas; A<sub>6</sub>, detail of surface, showing ornamentation based on epithelial polygonal pattern. B. Dextral sellate sclerite, form C, ZPAL V.VI/29S3, erratic Me66; B<sub>1</sub>, oblique view; B<sub>2</sub>, detail of apex; B<sub>3</sub>, lateral view, showing distortion of growth ribs. C. Sclerite, form C, ZPAL V.VI/39S19, erratic Me66, in oblique view, stereo-pair. D. Asymmetric sclerite, form B, ZPAL V.VI/32S2, erratic Me33; D<sub>1</sub>, adapical view; D<sub>2</sub>, oblique anterior view; D<sub>3</sub>, outer lateral view; D<sub>4</sub>, apex, in lateral view, showing epithelial polygons; D<sub>5</sub>, the same in oblique anterior view, stereo-pair; D<sub>6</sub>, ornamentation in detail of D<sub>1</sub>.





pyramidal in shape with slight curvature and without longitudinal folds and torsion (Fig. 10).

**Remarks.**—The sculpture, especially the ribbing pattern, seems to change with increase in size, being denser in larger (more adult) specimens (Fig. 10D). The sclerites are somewhat similar to those of *D. bradocki* Evans and Rowell, known only from the Shackleton Limestone, southern Churchill Mountains, Antarctica (Evans and Rowell 1990).

**Occurrence.**—Allochthonous Early Cambrian (Botomian) boulders (Me33), King George Island, Antarctica.

**Tommotiide indet.**

Fig. 8F.

**Material.**—One isolated sclerite, ZPAL V.VI/103S11, from erratic boulder Me33.

**Description.**—Minute sclerite, flattened triangular in shape, with somewhat reduced one side, broad apex, and small radial furrow on the left side. External sculpture consists of growth ridges with superimposed closely spaced longitudinal ribs radially oriented. Sclerite wall has phosphatic composition and lamellar growth. This broadly conical sclerite may represent a sclerite of *Daylatia* in its initial stage of growth. A radial furrow on the sclerite's left side gives the basal margin a sinuous and slightly sellate appearance resembling, in shape and external surface sculpture, the *Camenella* sclerite (Rozanov and Missarzhevsky 1966; Rozanov et al. 1969).

**Occurrence.**—Allochthonous Early Cambrian (Botomian) boulders (Me33), King George Island, Antarctica.

### Genus *Shetlandia* nov.

**Type species:** *Shetlandia multiplicata* sp. nov.

**Derivation of name:** Referring to the occurrence on an island of the South Shetlands archipelago.

**Diagnosis.**—Flat or slightly convex sclerite with left and right hand forms. The wall has lamellar tommotioid-like growth structure. Surface sculpture with distinct continuous growth striae and prominent radial plicae.

### *Shetlandia multiplicata* sp. nov.

Figs. 14, 15A–E, G–J, 16.

**Holotype:** Specimen shown in Fig. 14, ZPAL V.VI/36S3 from erratic boulder Me66.

**Type horizon:** The inferred upper part of the Lower Cambrian.

**Type locality:** Erratic boulders of Antarctic origin. Me33 in glacio-marine Cape Melville Formation (Lower Miocene), King George Island, South Shetland Islands, West Antarctica.

**Derivation of name:** From Latin *multus*, many, numerous; *plicatus*, folded. Referring to the surface sculpture with a number of prominent radial folds, a corrugation of the shell.

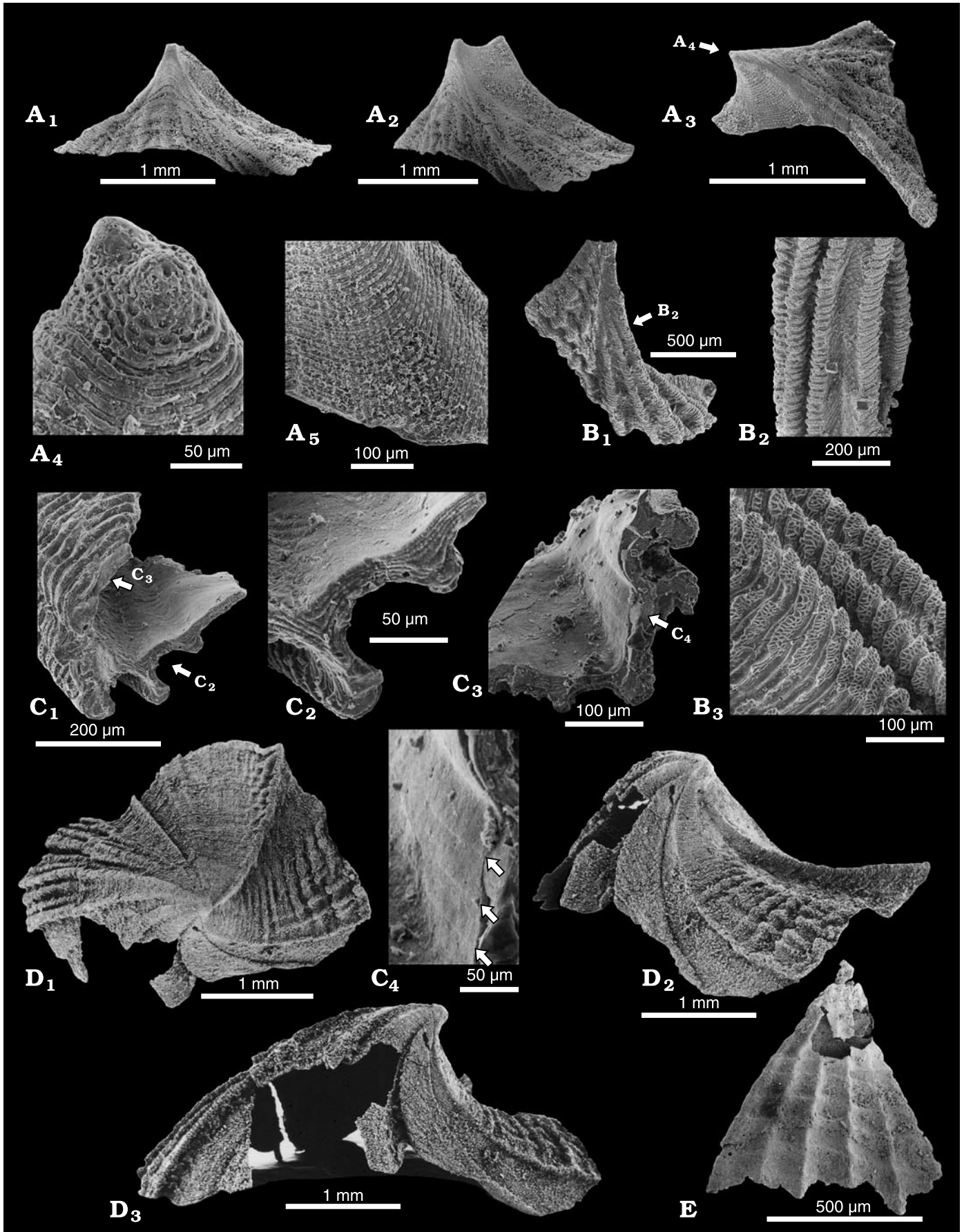
**Diagnosis.**—As for genus.

**Material.**—Four incomplete sclerites and a number of fragments from erratic boulders Me30, 32, 33, and 66. Figured specimens, ZPAL V.VI/25S2; 26S13; 32S5; 35S22; 36S3; 37S2; 39S7; 55S55; 105S7; 106S2; 108S4.

**Description.**—Minute phosphatic elements with left and right hand forms representing a flat sclerite. Their proximal end probably tapers to apices, whereas the wider distal part is almost flat (Figs. 14A–D, 15B–D) or convex externally (Fig. 14A, E). The phosphatic composition of the shells appears to be primary, as it is for all tommotiids (see Bengtson et al. 1990). The outer surface of the sclerite is radially multiplied (densely folded) and covered with evenly spaced carinate growth ribs (Fig. 14I–K), which reflect the lamellar structure of the sclerite wall. The inner surface also shows transverse growth features (Fig. 14G, H, L), and the broken cross-section of the wall (Fig. 14L) shows the lamellar step-like mode of growth, i.e. the last growth layer is added to the underside of the previous one. No muscle scars on the inner side were observed. This arrangement of the lamellar structured wall is consistent with that characteristic for lapworthellids, and certainly other tommotiids too: incremental growth by basal-internal secretion (Bengtson 1983; Landing 1984; Conway Morris and Chen 1990). In addition, the external cancellate sculpture (Fig. 14I–K) could be derived from a modified or distorted polygonal pattern probably representing epithelial imprints on the interior surface. Similar distortion of the external sculpture from regular polygons at the adapical part of the sclerite up to the punctate or denticulate meshwork at the marginal part of the sclerite has been documented in other tommotiids, e.g., *Dailyatia* sclerites (Figs. 11A<sub>5</sub>, A<sub>6</sub>, 12A<sub>5</sub>), and *Lapworthella* (Conway Morris and Chen 1990). The polygonal pattern, possibly representing epithelial cell imprints, indicates also that *S. multiplicata* sclerites were secreted as in many other tommotiids by epithelial tissue partly mantling the basal margin of the sclerite exterior. These characters of the *Shetlandia*-type sclerites show their close relationship with *Dailyatia*-type sclerites, and it cannot be excluded that both sclerite types may belong to the same scleritome. The more complete sclerite assemblage or articulated sclerite arrays may allow a precise reconstruction of the relationship or synonymy of both genera.

**Remarks.**—Although a scleritome interpretation of disarticulated fossils is very difficult, it is not a futile enterprise, because scleritome models have been applied with some success in a number of enigmatic multisclerite-bearing animals (e.g., Bengtson and Conway Morris 1984; Evans and Rowell 1990; Bengtson 1992; Müller and Hinz-Schallreuter 1993; Conway Morris and Peel 1995; Bengtson and Hou 2001). The new

Fig. 12. A–D. *Dailyatia ajax* Bischoff. A. Strongly broken sclerite, form C, ZPAL V.VI/39S33, erratic Me66; A<sub>1</sub>, anterior view; A<sub>2</sub>, oblique view; A<sub>3</sub>, oblique posterior view; A<sub>4</sub>, Detail of A<sub>3</sub>, showing twinned apex with epithelial polygons; A<sub>5</sub>, Ornamentation, detail of A<sub>3</sub>. B. Fragment of plicate wall of the sclerite, ZPAL V.VI/47S1, erratic Me66; B<sub>1</sub>, outer lateral view; B<sub>2</sub>, ornamentation of plicate wall; B<sub>3</sub>, detail of B<sub>2</sub>, showing epithelial pattern. C. Fragment of the sclerite wall, ZPAL V.VI/47S2, erratic Me66; C<sub>1</sub>, broken section of the wall, transverse to the sclerite longitudinal axis; C<sub>2</sub>, detail of multilaminar structure on a slightly etched cross-section; C<sub>3</sub>, the same fragment of the sclerite, showing longitudinal growth lines on the internal surface of wall; C<sub>4</sub>, detail of C<sub>3</sub>, showing longitudinal growth lines (arrowed) of the laminae building the sclerite wall. D. Asymmetric sclerite, form B, ZPAL V.VI/110S1, erratic Me66; D<sub>1</sub>, apical view; D<sub>2</sub>, oblique inner view; D<sub>3</sub>, lateral view. E. *Lapworthella fasciculata* Conway Morris and Bengtson, ZPAL V.VI/39S4, erratic Me33, planiform sclerite in anterior view. →



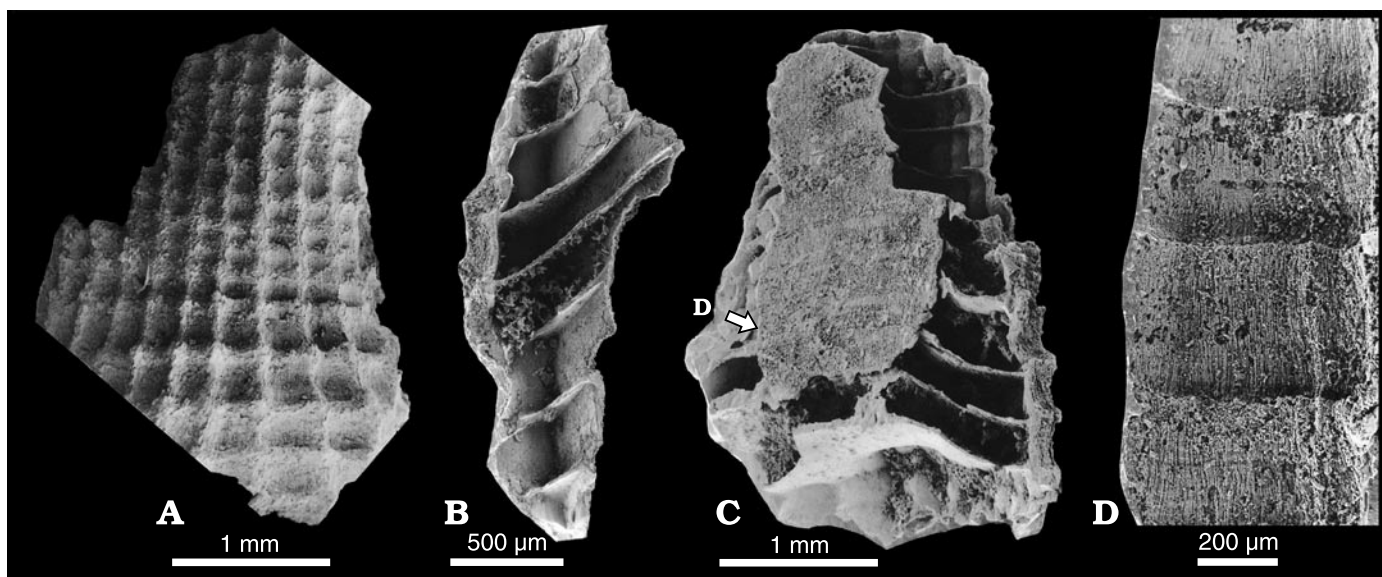


Fig. 13. Broken sclerite of *Lapworthella fasciculata* Conway Morris and Bengtson, ZPAL V.VI/30S1, erratic Me33. **A.** Ornamentation and growth ridges on the dorsal side, anterior view. **B.** Broken longitudinal section showing septa. **C.** The same sclerite, posterior view, showing fragment of flat area resembling duplicature. **D.** Enlargement of posterior side surface, showing growth ribs and interrib areas with longitudinal fluting.

tommotiid type sclerites described herein represent mirror-image pairs (Fig. 16) with two kinds of such paired sclerites in the scleritome: a near planar one (Fig. 14A–D) and an externally more convex (Fig. 15A, E). They are similar in mode of growth and morphology to machaeridian sclerites, especially to terminal (anterior and posterior) sclerites, though differing in their phosphatic composition. A small fragment of tommotiid sclerite densely covered with transverse coarse rugae on the outer surface (Fig. 26B, C) is superficially similar to early Palaeozoic machaeridian sclerites (e.g., Dzik 1986a: 5). The most plausible reconstruction of the tommotiid scleritome proposed earlier by Dzik could be applied also to *S. multiplicata* sclerites, and would be analogous to primitive plumulid machaeridians having a bilaterally symmetric dorsal scleritome composed of two or four longitudinal series of calcitic sclerites (Dzik 1986a, 1994). Those observations support a possible relationship between Tommotiida and Turrilepida within the class Machaeridia, enigmatic Palaeozoic metazoans (Bengtson 1970; Dzik 1986a).

**Occurrence.**—Allochthonous Early Cambrian (Botomian) boulders (Me30, 32, 33, 66), King George Island, Antarctica.

#### Family Lapworthellidae Missarzhevsky, 1966

##### Genus *Lapworthella* Cobbold, 1921

*Type species:* *Lapworthella nigra* Cobbold, 1921.

##### *Lapworthella fasciculata* Conway Morris and Bengtson, 1990 in Bengtson et al. 1990

Figs. 12E, 13.

Mitrosagophoran sclerite; Wrona 1989: 542, pl. 10: 3.

*Lapworthella fasciculata* sp. nov.; Conway Morris and Bengtson in Bengtson et al. 1990: 122, figs. 74–76.

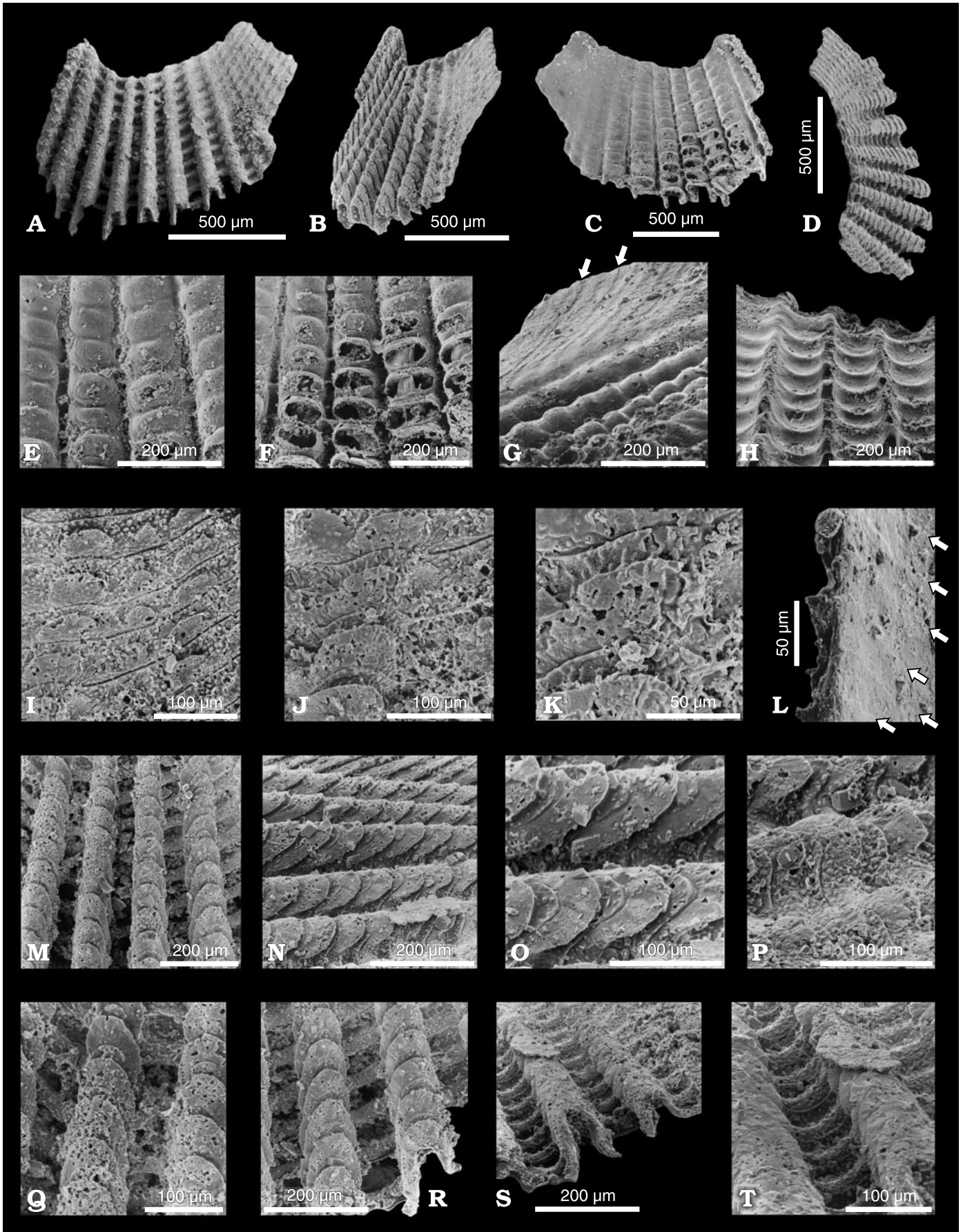
*Lapworthella fasciculata* Conway Morris and Bengtson in Bengtson et al. 1990; Demidenko in Gravestock et al. 2001: 116, pl. 8: 1–3.

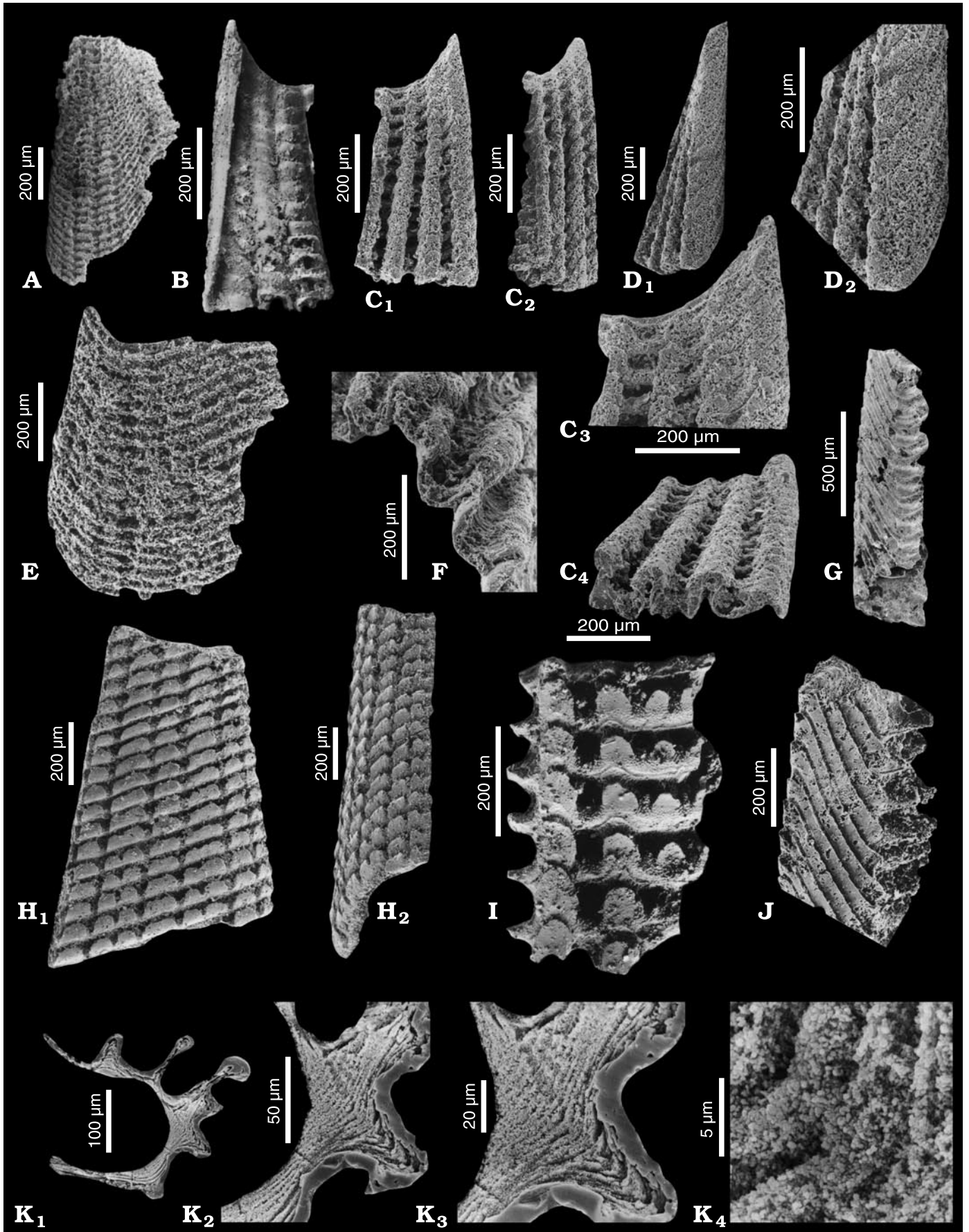
**Material.**—Four isolated sclerites from erratic boulders Me33 and 66. Figured specimens, ZPAL V.VI/103S11 and 15.

**Description.**—Mitral pyramidal sclerites, highly elongate and variable in shape. Anterior side (according to the hypothetical scleritome arrangement; e.g., Evans and Rowell 1990) of the sclerite has external (dorsal) sculpture, which consists of pronounced transverse ridges and longitudinal ribs forming characteristic reticular pattern (Figs. 12E and 13A). Posterior sclerite side (ventral) has flat surface covered with steplike growth ridges with longitudinal fine striae in inter-ridge areas (Fig. 13D). This posterior area resembles the deltoid duplicature extending onto the posterior slope of some other tommotiid sclerites (e.g., *Camenella*, *Micrina*, *Kulparina*). Sclerites cross sections are subcircular apically to triangular in the apertural part. Growth lines, which can be observed on the external and internal sclerite surfaces, reflect lamellar growth of the sclerite wall (Fig. 13B, C) by basal-internal accretion. Multilaminar structure of the sclerite can be often seen in the

Fig. 14. Plate-like sclerite of *Shetlandia multiplicata* gen. et sp. nov., holotype, ZPAL V.VI/36S3, erratic Me66. **A.** Upper (outer) view. **B.** Oblique lateral view. **C.** The same sclerite in internal view. **D.** Upper top (anterior) view. **E.** Detail of plicate internal surface. **F.** Detail of plicate internal surface, showing broken thin wall. **G.** Internal surface of plate, showing growth lines of bands (arrowed). **H.** Proximal part of sclerite, in top view. **I.** Ornamentation in detail, showing band and inter-band growth lines. **J.** Detail of growth band with a weak epithelial pattern. **K.** Detail of J. **L.** Broken section of plate and internal surface of flat part (not plicate) of the sclerite, showing lamellar structure and growth lines (arrowed) on internal surface. **M.** Plicate part of plate in posterior view. **N.** Plicate growth band in lateral view. **O.** Detail of N, showing growth band and inter-band grooves. **P.** Detail of O, showing growth bands with epithelial pattern (similar as in fig. K). **R.** Detail of M, showing epithelial pattern. **S.** Detail of growth band with epithelial pattern. **T.** Detail of plate posterior margin, showing plicate bands. **U.** Detail of plicate surface in posterior view, showing plicae and interplicate bands. →







wall transverse sections (Fig. 13B, C). Internal cavity is separated by septa, which are convex apically.

**Remarks.**—The Antarctic specimens show great similarities to the Australian type material (Bengtson et al. 1990) and additional material newly recovered from the same Australian localities (Gravestock et al. 2001).

**Occurrence.**—Allochthonous Early Cambrian (Botomian) boulders (Me33 and 66), King George Island, Antarctica.

## Superphylum Aschelminthes

### Phylum uncertain (?Nemathomorpha)

#### Order Palaeoscolecida Conway Morris and Robison, 1986

**Remarks.**—These are wormlike metazoans with a papillate epidermis, papillae arranged in transverse rows on narrow annuli. Each annula consists of usually two tubercle rows. This annulation has superficial character and surely not reflect any internal metameric segmentation. The epidermis may form sclerotized cuticular structures—an armour of phosphatic dermal sclerites arranged in array covering the whole integument of animal. The anterior part of the body, if preserved, possesses a usually extended proboscis with rows of spines (scalids) and hooks on the posterior end of the usually coiled trunk. The alimentary canal (gut) is more or less straight with a terminal anus. These characters are diagnostic features for members of the aschelminthes (Hou and Bergström 1994), and in particular show their close relationship with the Priapulida (Conway Morris 1993, 1997; Müller and Hinz-Schallreuter 1993; Hou and Bergström 1994; Zhang and Pratt 1996) or the Nemathomorpha (Hou and Bergström 1994). The precise systematic position of the Palaeoscolecida is not yet resolved (Hou and Bergström 1994; Conway Morris 1997); possibly they represent a link between nematodes and priapulids (Hou and Bergström 1994). The features in common with priapulids (armature, scalids, everted spiny proboscis), also suggest that the Palaeoscolecida can be placed within the newly established Phylum Cephalorhyncha Malakhov, 1980 (Adrianov and Malakhov 1996). The controversy arises also from the differing preservation of compressed specimens and three-dimensional phosphatized cuticle. Both styles of preservation provide somewhat different diagnostic characters of the fossil worms.

Families assigned to this class by Kraft and Mergl (1989) are: Palaeoscolecidae Whittard, 1953 and Plasmuscolecidae Kraft and Mergl, 1989.

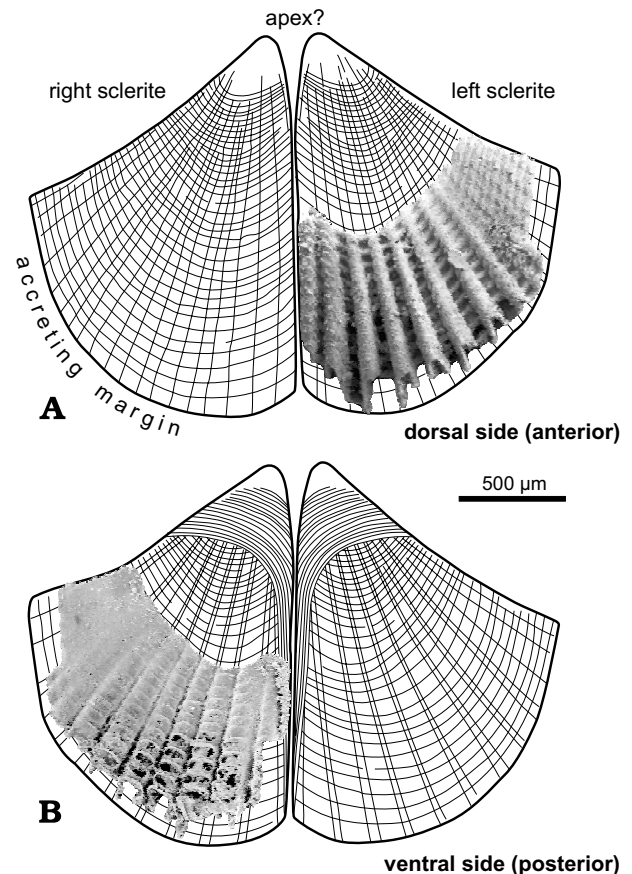


Fig. 16. Hypothetical reconstruction of sclerite of *Shetlandia multiplicata* sp. nov., showing the external (A) and internal (B) views. The reconstruction is more interpretative in the apical portion.

#### Family Palaeoscolecidae Whittard, 1953

**Genera included.**—For list of genera see Wrona and Hamdi (2001). *Hadimopanella* Gedik, 1977 and *Kaimenella* Mars, 1988, known from disarticulated single sclerites, as well as *Milaculum* Müller, 1973 and *Utahphospha* Müller and Miller, 1976, from complex sclerites.

**Brief characterization and remarks.**—The family comprises genera known mainly as external moulds of phosphatized complex cuticular structure. Secondary phosphatization might prevent disintegration of the sclerite array as the three-dimensional structure of the cuticular armour. Detailed studies by Kraft and Mergl (1989), van den Boogaard (1989) as well as by Hinz et al. (1990) and Müller and Hinz-Schallreuter (1993) have documented the congeneric nature of all these isolated sclerites with

← Fig. 15. A–D, G–J. *Shetlandia multiplicata* gen. et sp. nov. A. Slightly convex, partly broken, plate-like sclerite, ZPAL V.VI/39S2, erratic Me66. B. Internal side of sclerite, similar fragment as in C, showing turned down inner edge, ZPAL V.VI/39S30, erratic Me66. C. Fragment of sclerite with natural inner (right) edge, ZPAL V.VI/49S2, erratic Me66; C<sub>1</sub>, upper view; C<sub>2</sub>, upper, more lateral view; C<sub>3</sub>, anterior part of the sclerite, showing suture margin of growth band (top); C<sub>4</sub>, plicate surface, in posterior view, showing tight folds. D. Posterior fragment of sclerite, ZPAL V.VI/49S5, erratic Me66; D<sub>1</sub>, lateral view; D<sub>2</sub>, detail, showing turned down inner edge. E. Posterior part of convex sclerite, ZPAL V.VI/115S13, erratic Me66, similar fragment as in A. F. Plicate fragment of *Dailyatia ajax* Bischoff sclerite wall, in anterior view, showing tight folds, ZPAL V.VI/47S1, erratic Me66. G. One plicate fragment of *Shetlandia multiplicata* gen. et sp. nov. sclerite wall, in lateral view, ZPAL V.VI/49S4, erratic Me66. H. Steinkern of sclerite wall, ZPAL V.VI/115S11, erratic Me66; H<sub>1</sub>, upper (external) view; H<sub>2</sub>, oblique lateral view. I. Steinkern of plicate sclerite wall, ZPAL V.VI/38S17, erratic Me66, in upper view. J. Steinkern of one plicate fragment, ZPAL V.VI/15S2, erratic Me66, in lateral view. K. Polished and etched cross-section of *Dailyatia ajax* Bischoff sclerite, ZPAL V.VI/59S1, erratic Me66; K<sub>1</sub>, fragment of plicate wall embedded in epoxy medium, section oriented oblique transversally to the longitudinal sclerite axis; K<sub>2</sub>, detail of wall structure; K<sub>3</sub>, enlargement, showing non-continuous multilaminar structure; K<sub>4</sub>, detail of K<sub>3</sub> showing granular apatite minerals in structure.

Palaeoscolecida. The morphology and taxonomy of palaeoscolecide worms and their isolated sclerites was reviewed by Müller and Hinz-Schallreuter (1993), Conway Morris (1997), and more recently by Wrona and Hamdi (2001).

### Genus *Hadimopanella* Gedik, 1977

*Type species: Hadimopanella oezgueli* Gedik, 1977.

*Species included.*—For list of species see Wrona and Hamdi (2001); *H. cassiniana* (Repetski, 1981) and the newly described Antarctic species *H. staurata* sp. nov. is also hereby added.

### *Hadimopanella antarctica* Wrona, 1987

Figs. 17, 18A–D.

*Hadimopanella* sp.; Gaździcki and Wrona 1986: 611, fig. 7g.

*Hadimopanella antarctica* Wrona; Wrona 1987: 42, pls. 5–8.

*Hadimopanella antarctica* Wrona; Wrona 1989: 542, pl. 8: 7.

*Holotype:* Specimen ZPAL V.VI/28S3, figured by Wrona (1987: pl. 8: 2).

*Topotype:* Specimen figured (Fig. 18A); ZPAL V.VI/24S9.

*Material.*—Over one hundred isolated sclerites from erratic boulders Me33, 40, and 66. Figured specimens, ZPAL V.VI/103S11, 15; 24S9, 27, 28, 31.

*Description.*—See Wrona 1987: 42.

*Remarks.*—Some unusual sclerites show small circular plate-like nodes in a marginal position (Fig. 18B). Such exceptionally preserved sclerites may document accretional mode of sclerite growth: from very small sclerites, having only a single apex, to much larger sclerite, having numerous apices arranged in a specific pattern (Fig. 18A<sub>2</sub>, B<sub>2</sub>, D<sub>1</sub>). The nodes are equal in size, usually 10 µm in diameter and 15 µm high. They are generally oriented upwards (Figs. 17, 18A<sub>1</sub>, A<sub>3</sub>, D<sub>2</sub>). Some specimens (Fig. 18D) have a fine corrugation on the node surfaces. The crown (cap) sometimes does not cover the base; in such cases the suture between the outer and inner layers is displayed, revealing a striated basal margin in a finer radiating pattern (Fig. 18C). The specimens are assigned to *Hadimopanella* Gedik, 1977 because of their similar morphology and number of nodes, although both characters are variable. The correlation between sclerite size and the number of nodes (Bengtson 1977; Dzik 1986b) suggests that *Milaculum*-type sclerites may also have arisen from an increase in the number and accretion of sclerite nodes. Some sclerites of *Hadimopanella* from Antarctica have one node, as is common in *H. apicata*. These sclerites (with one node) are somewhat like rare forms of *H. apicata* Wrona, 1982 figured by Bendix-Almgreen and Peel (1988: fig. 5). These authors also noted an unusual sclerite of *H. apicata* from Greenland having fewer marginally distributed tubercles (probably about 5), being

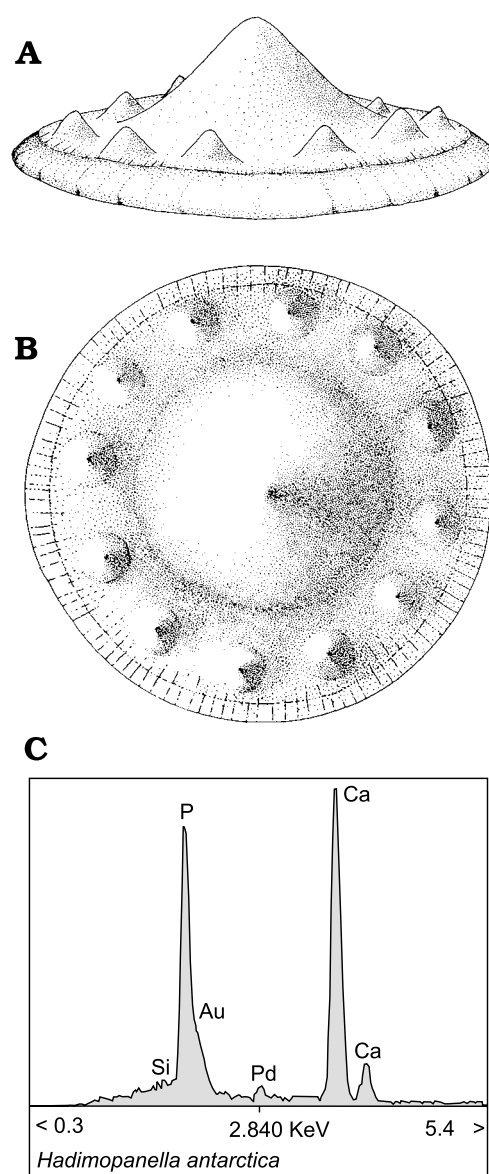
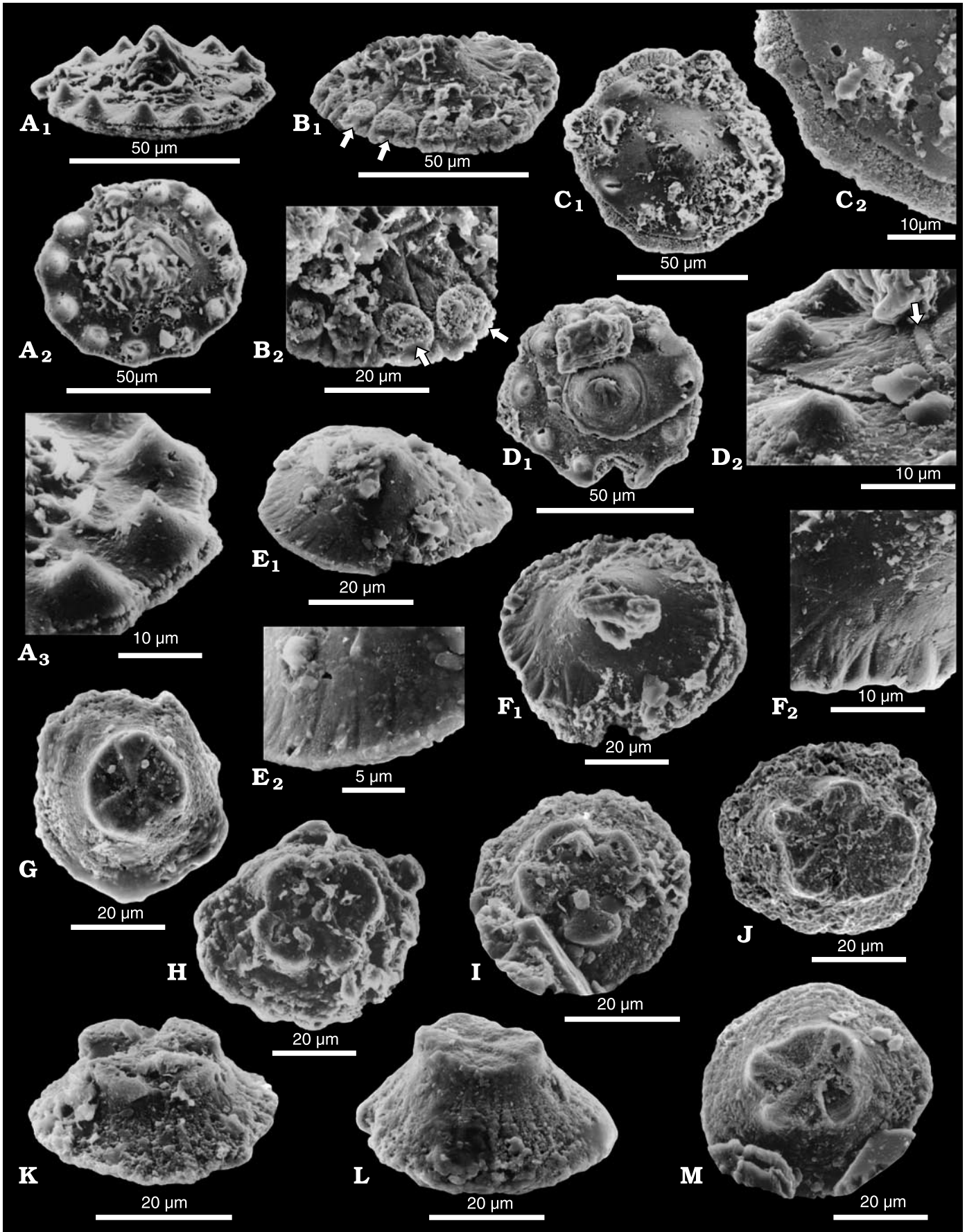


Fig. 17. Diagrammatic reconstruction of the *Hadimopanella antarctica* Wrona sclerite in oblique lateral (A) and dorsal (B) views; see also Wrona (1987). C. Energy dispersive spectrum (EDS) for the *H. antarctica* sclerite.

reminiscent of *H. antarctica* Wrona, 1987. Their ornamentation can also be compared with much smaller platelets occurring in many articulated cuticles of several palaeoscolecoid genera (see Müller and Hinz-Schallreuter 1993). *H. antarctica*, both in morphology and size, closely resembles elements

Fig. 18. A–D. *Hadimopanella antarctica* Wrona. A. Sclerite ZPAL V.VI/24S9, erratic Me66; A<sub>1</sub>, oblique lateral view; A<sub>2</sub>, upper view; A<sub>3</sub>, detail of basal margin in oblique view, with nodes and suture. B. Sclerite ZPAL V.VI/24S28, erratic Me40; B<sub>1</sub>, oblique upper view; B<sub>2</sub>, detail of basal margin, showing marginal nodes (arrowed) fused. C. Sclerite ZPAL V.VI/24S27, erratic Me40; C<sub>1</sub>, upper view; C<sub>2</sub>, detail of wide basal margin showing suture and striae. D. Sclerite ZPAL V.VI/24S31, erratic Me66; D<sub>1</sub>, upper view; D<sub>2</sub>, detail of sclerite in oblique view, showing circular rim (arrowed) surrounding central apex. E, F. *Hadimopanella apicata* Wrona. E. Slightly coated sclerite ZPAL V.VI/24S36, erratic Me66; E<sub>1</sub>, oblique upper view; E<sub>2</sub>, detail of basal margin showing striae. F. Sclerite, slightly coated with mineral grains, ZPAL V.VI/24S20, erratic Me66; F<sub>1</sub>, oblique upper view; F<sub>2</sub>, detail of basal margin and striae. G–M. *Hadimopanella staurata* sp. nov. G. Sclerite in upper view, ZPAL V.VI/24S26, erratic Me40. H. Sclerite, slightly coated with mineral grains, in upper view, ZPAL V.VI/24S18, erratic Me66. I. Sclerite, coated with mineral grains, in upper view, ZPAL V.VI/24S30, erratic Me40. J. Sclerite in upper view, ZPAL V.VI/35S24, erratic Me66. K. Coated sclerite in oblique view, ZPAL V.VI/24S32, erratic Me33. L. Slightly coated sclerite in oblique lateral view, ZPAL V.VI/24S33, erratic Me40. M. Sclerite, coated with mineral grains, in upper view, ZPAL V.VI/24S34, erratic Me40.





of the tuberculate ornament on sclerites of *Chalasiocranos exquisitum* Brock and Cooper, 1993 from the Ramsay Limestone of Yorke Peninsula, South Australia (Brock and Cooper 1993). The latter has nodes arranged in a ring around a central node and resembles also some specimens of *Hdimopanella cassiniana* (Repetski, 1981). It is possible that *H. antarctica* represents intermediate smaller sclerites of the same animal that bears *C. exquisitum* sclerites, similarly to the palaeoscolecoid animals possessing sclerites of different kinds (see Kraft and Mergl 1989; Müller and Hinz-Schallreuter 1993).

### *Hadimopanella apicata* Wrona, 1982

Fig. 18E, F.

cf. *Hadimopanella apicata* Wrona; Müller and Hinz-Schallreuter 1993: 584, fig. 16G, H [full synonymy].

**Material.**—Four isolated sclerites from erratic boulders Me33 and 66. Figured specimens, ZPAL V.VI/24S20, 36.

**Description.**—These small discoidal phosphatic sclerites (diameter 47–84 µm, mode 58 µm) consist of two layers (Fig. 18E, F). The lower layer forms an expanded base, with smooth and flat or slightly convex to concave surface. The upper layer forms the crown (cap), bearing one node. The nodes are usually 10 µm in diameter and 15 µm high. These specimens usually have a fine corrugation on the margin of nodular surfaces. The crown sometimes does not cover the base; in such cases the suture between the outer and inner layers is displayed, revealing a striated basal margin (Fig. 18F<sub>1</sub>) in a characteristic radiating pattern. The elevation of the upper surface ranges from about 25–35 µm.

**Remarks.**—The Antarctic specimens differ slightly in their generally smaller size compared to Spitsbergen type specimens from the Lower Cambrian of the Hornsund region (Wrona 1982). They are reminiscent of *H. apicata* specimens found in the Lower Cambrian of Comley, Shropshire, England (Hinz 1987: pl. 4: 3, 6), as well as of the subcircular plate with a strongly developed, tall central cone identified as Palaeoscolecida genus indeterminate cf. *H. apicata* (Müller and Hinz-Schallreuter 1993). The ornamentation can also be compared with the much smaller platelets occurring in many articulated cuticles of various palaeoscolecoid genera.

**Occurrence.**—Allochthonous Early Cambrian (Botomian) boulders (Me33 and 66), King George Island, Antarctica.

### *Hadimopanella staurata* sp. nov.

Figs. 18G–M, 19–22.

**Holotype:** Specimen shown in Fig. 20; ZPAL V.VI/24S3, from erratic boulder Me66.

**Type horizon:** The inferred upper part of the Lower Cambrian.

**Type locality:** Erratic boulders of Antarctic origin. Me33 in glacio-marine Cape Melville Formation (Lower Miocene), King George Island, South Shetland Islands, West Antarctica.

**Derivation of name:** From Greek *stauratos*, cross-shaped, referring to the cross pattern on the nodular upper face.

**Material.**—Several dozen isolated sclerites from erratic boulders Me33, 40, and 66. Figured specimens, ZPAL V.VI/24S3, 18, 24, 30, 32, 33, 34; 35S24; 103S11, 15.

**Diagnosis.**—*Hadimopanella* species with sclerites having an

upper nodular crown with a flat or shallowly concave crest parallel to the basal side and covered with wedge-shaped nodes or ridges arranged in the form of a Saint George cross.

**Description.**—These small circular phosphatic sclerites (diameter 39–60 µm) consist of two layers (Fig. 18G–M). The lower layer forms an expanded base, with smooth and flat or slightly convex lower surface (Fig. 22). The upper layer forms the crown (diameter about 21–36 µm), bearing three to five wedge-shaped nodes or ridges arranged in the form of a Saint George cross (Figs. 18H, I, 19, 20) or clover-leaf pattern (Fig. 19). Some sclerites with a fractured external layer show the arrangement of phosphate crystallites constituting this hyaline layer (Figs. 20C, 21C, D). The nodes are triangular, usually 10 µm wide and 15 µm high. Some specimens (Fig. 18K, L) have a fine corrugation on the node surfaces. The crown sometimes does not cover the base; in such cases the suture between the outer and inner layers is displayed, revealing a radially striated basal margin typical for *Hadimopanella* sclerite (Figs. 18M, 19) in a finer radiating pattern. The elevation of the upper surface ranges from about 20–25 µm.

**Remarks.**—The sclerites described here differ markedly in their morphology and size from any other known *Hadimopanella* species. They are slightly similar in size, as well as, in their shape and lower number of nodes (elongated as ridges), to some Australian single tubercles (plate *sensu* Conway Morris 1997) of *Kaimenella dailyi* Brock and Cooper found in fragments of palaeoscolecoid cuticle from the Lower Cambrian (Toyonian) Wirrealpa, Aroona Creek and Ramsay Limestones of the Stansbury Basin (tuberculate unit *sensu* Brock and Cooper, 1993: fig. 8: 10–12 and fig. 9: 2). The characteristic striated basal margin (Fig. 18G, K, L) with a finer radiating pattern may reflect radially arranged apatite crystallites, as in the external hyaline layer (Figs. 20C, 21C, D).

**Occurrence.**—Allochthonous Early Cambrian (Botomian) boulders (Me33 and 66), King George Island, Antarctica.

## Ornamented tubes

### Phylum and class uncertain

#### Genus *Mongolitubulus* Missarzhevsky, 1977

*Type species:* *Mongolitubulus squamifer* Missarzhevsky, 1977.

**Emended diagnosis.**—Minute phosphatic spines, straight to slightly arched, covered with distinct rhomboid scale-like ornamentation. Rhomboids are sharp or rounded, inclined away from the spine wall in direction of apex, and arranged in alternating rows. Spine wall bilayered; outer layer is dense or hyaline and structureless, inner layer consists of longitudinal fibres parallel to spine axis. Large internal cavity occupies almost entire length of the spine.

**Species included.**—All species are known as isolated and incomplete spines: *Mongolitubulus squamifer* Missarzhevsky, 1977; *Mongolitubulus ex gr. M. squamifer* Missarzhevsky (Demidenko in Gravestock et al. 2001: 87, pl. 11: 5); *M. henrikseni* Skovsted and Peel, 2001.

**Remarks.**—The problematic microfossil *Mongolitubulus* was first reported and has been known for a long time as incom-

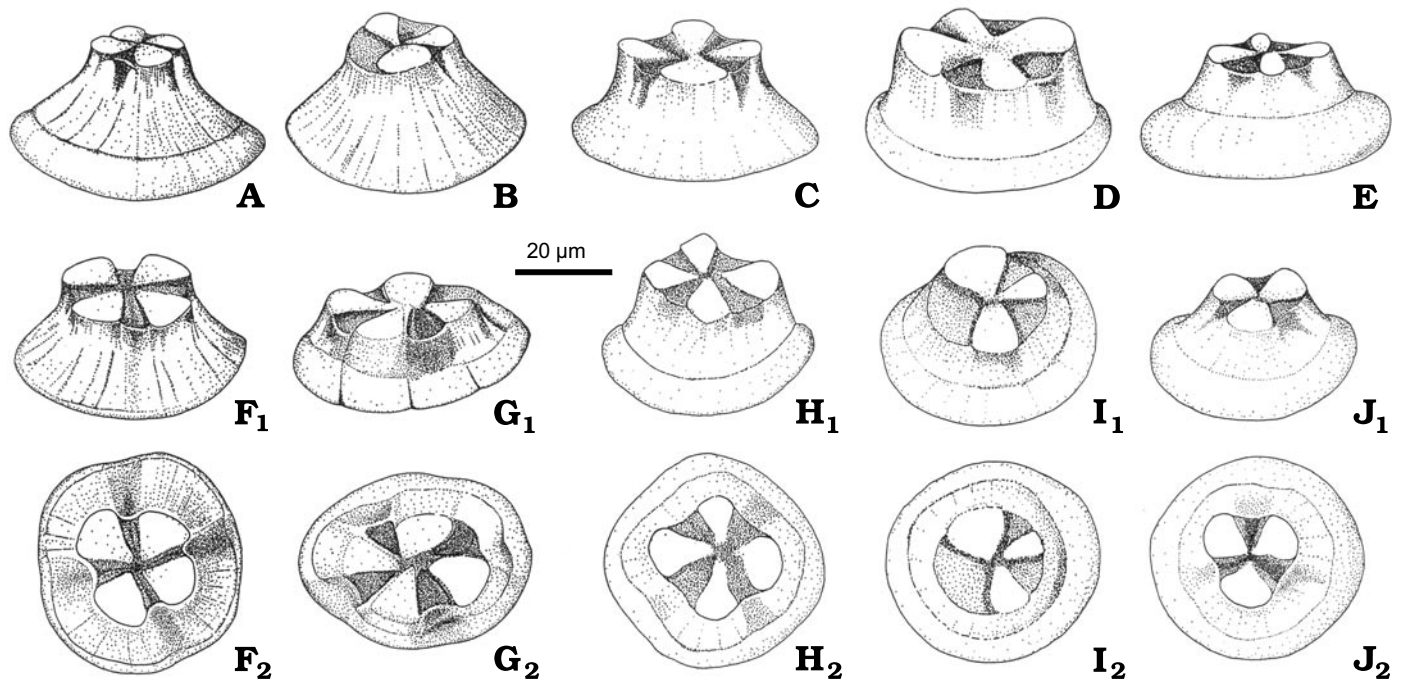


Fig. 19. Representatives of *Hadimopanella staurata* sp. nov. sclerites showing variability in shape and ornamentation. **A.** ZPAL V.VI/24S24. **B.** ZPAL V.VI/24S26. **C.** ZPAL V.VI/24S33. **D.** ZPAL V.VI/19S9. **E.** ZPAL V.VI/24S33. **F.** ZPAL V.VI/24S30, in oblique lateral (F<sub>1</sub>) and upper (F<sub>2</sub>) views. **G.** ZPAL V.VI/24S3, holotype, in oblique lateral (G<sub>1</sub>) and upper (G<sub>2</sub>) views. **H.** ZPAL V.VI/35S24, in oblique lateral (H<sub>1</sub>) and upper (H<sub>2</sub>) views. **I.** ZPAL V.VI/14S9, in oblique lateral (I<sub>1</sub>) and upper (I<sub>2</sub>) views. **J.** ZPAL V.VI/17S8, in oblique lateral (J<sub>1</sub>) and upper (J<sub>2</sub>) views.

plete, 1–2 mm long tubes, later described as hollow spines (Wrona 1989). Recently recovered abundant and more complete specimens from Greenland (Skovsted and Peel 2001) show that they represent only part of a larger skeletal elements or spiny sclerites of the multielement scleritome of a still enigmatic animal. Dzik (2003), analysing *Mongolitubulus* spine morphology and internal structure as well as the whole range of the associated fossil assemblage, in particular the *Microdictyon* component, believed that they protected the body of a lobopodian-like animal similar to *Xenusion*. Some ornamented tubes (Conway Morris and Bengtson in Bengtson et al. 1990: 158, figs. 102 and 103), often referred to the pseudoconodont *Rhombocorniculum* (Brasier 1986: 253; Landing 1988: 687) or *Rushtonites* (Hinz 1987: 74), and having virtually the same distinct internal structure and external morphology, are comparable to *Mongolitubulus*, and judging from the new material described by Skovsted and Peel (2001), they could be certainly referred to this genus.

#### *Mongolitubulus squamifer* Missarzhevsky, 1977

Figs. 23A–H, 24.

*Mongolitubulus squamifer* Missarzhevsky; Missarzhevsky 1977: 13, pl. 1: 1, 2.

*Mongolitubulus squamifer* Missarzhevsky; Missarzhevsky and Mambetov 1981: 79, pl. 14: 1, 2.

*Mongolitubulus squamifer* Missarzhevsky; Meshkova 1985: 127–128, pl. 46: 1–3.

*Mongolitubulus squamifer* Missarzhevsky; Rozanov 1986: 89, fig. 4.

*Mongolitubulus squamifer* Missarzhevsky; Peel and Blaker 1988: 56, fig. 2.

*Mongolitubulus squamifer* Missarzhevsky; Missarzhevsky 1989: 31, figs. 1, 3.

*Mongolitubulus squamifer* Missarzhevsky; Wrona 1989: 543, pl. 8: 5.

*Mongolitubulus squamifer* Missarzhevsky; Esakova and Zhegallo 1996: 103, pl. 4: 9–13.

*Rhombocorniculum* aff. *insolutum* Missarzhevsky and Mambetov; Brasier 1986: 253, fig. 5j, k.

*Rhombocorniculum* n. sp.; Landing 1988: 687, fig. 11.6.

*Mongolitubulus squamifer* Missarzhevsky; Skovsted and Peel 2001: 137, fig. 2.

*Mongolitubulus henrikseni* sp. nov.; Skovsted and Peel 2001: 140, fig. 3.

?*Mongolitubulus* ex gr. *M. squamifer* Missarzhevsky; Demidenko in Gravestock et al. 2001: 87, pl. 11: 5.

*Mongolitubulus squamifer*? Missarzhevsky; Landing et al. 2002: 301, fig. 4: 19.

**Diagnosis.**—As for the genus.

**Material.**—Twelve isolated incomplete spines in different states of preservation from erratic boulders Me33 and 66. Figured specimens, ZPAL V.VI/28S27, 28; 29S16; 39S2; 5106S11, 21; and 22U1, 2.

**Description.**—Slender phosphatic spines, approximately 1–2 mm in length and up to 0.3 mm in diameter, straight to gently curved (Fig. 23A–C). The spines taper to a pointed apex; but the basal margin has not been observed (it is broken off and missing in all specimens). The outer surface bears a distinct scaly sculpture (Fig. 23C–F). The rhomboid scales are arranged in spiral rows that cross each other at about 60° to produce a rhomboidal alternating pattern. The density of the scales varies considerably; the more closely spaced scales have sharp, rhombic outlines (Fig. 23D<sub>4</sub>, E), whereas the sparsely distributed ones are more irregularly placed and rounded or even ovoid in shape (Fig. 23F<sub>4</sub>, D<sub>5</sub>). The scales are inclined outwards about 5–10° from their basal ends, the apical

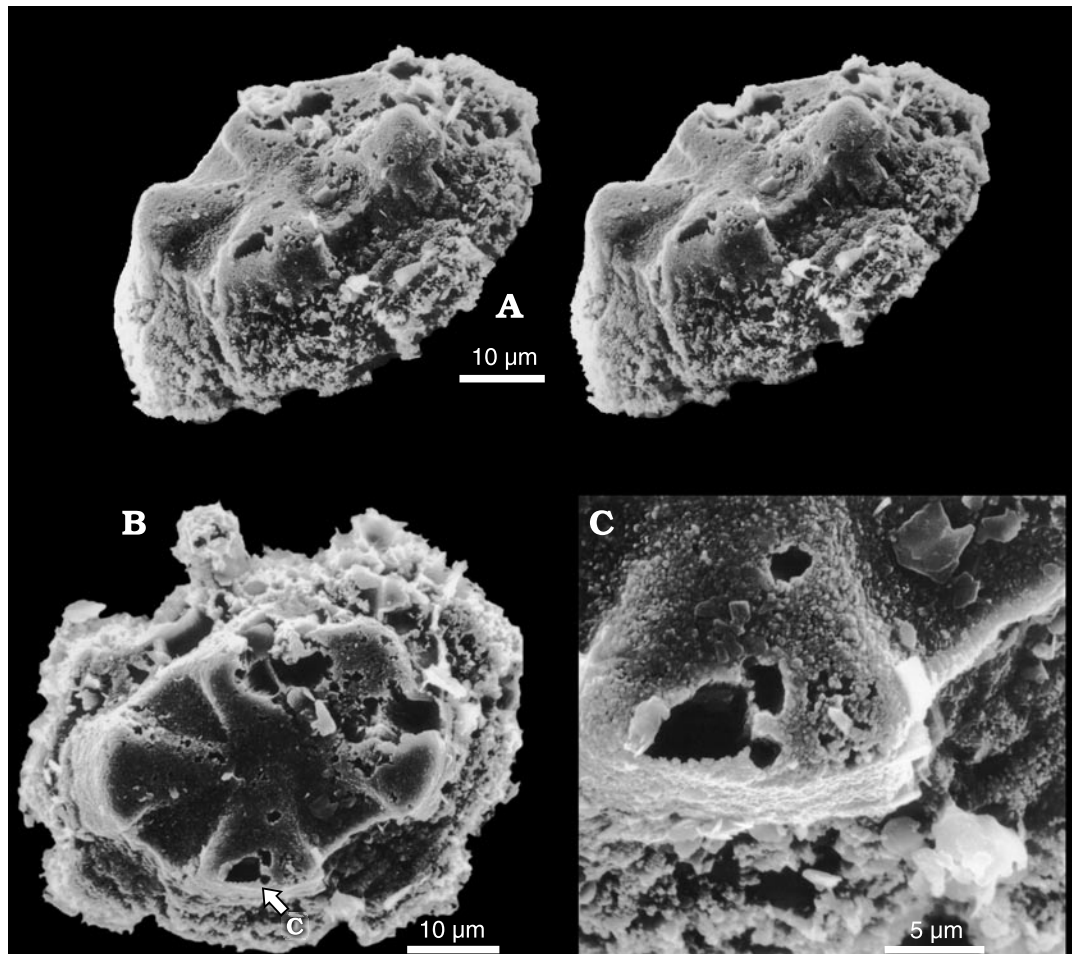


Fig. 20. Holotype of *Hadimopanella staurata* sp. nov., ZPAL V.VI/24S3, erratic boulder Me66. A. Oblique lateral view, stereo-pair. B. Upper view. C. Enlargement showing (in a hole) arrangement of phosphate crystallites in the external sclerite layer.

raised ends pointing towards the tip of the spine (Fig. 23D<sub>3</sub>, D<sub>4</sub>). The spines are circular or suboval in cross-section. The large internal cavity extends into the narrow tip. The wall is thin (about 2–3.5 µm), composed of an outer, dense or hyaline, structureless layer which forms the outer surface and scaly ornament, and a thick (about 10–15 µm) inner layer with a distinctly fibrous structure (Fig. 24). The fibres are straight, less than 1 µm thick, and arranged parallel to the long axis of the spine, on its inner wall (Fig. 23G, H). The spines are black in appearance under the light microscope, which may suggest some organic component in their phosphatic matrix.

*Remarks.*—The spines show distinct morphological variation, especially in their ornamentation, even in this limited assemblage. The spines with sharp, densely packed rhomboid scales have a surface ornament in a clear alternating pattern (Fig. 23D), characteristic also for the type species from Mongolia (Missarzhevsky 1977: pl. 1: 1, 2), and may represent one end of an intraspecific variability series. Spines with rounded, more randomly packed scales (Fig. 23F) are at the opposite end of the series. Such extreme morphotypes have been recently separated as a new species, *M. henrikseni*, by Skovsted and Peel (2001) on the basis of their different morphology and

the preserved basal area. The Antarctic specimens seem to fit very well, in the morphology and wall structure, within the intraspecific variability of the *M. squamifer* morphotype as documented by the abundant Greenland collections (Skovsted and Peel 2001). Spines from Antarctic erratics differ from *M. henrikseni* type specimens from the Upper Bastion Formation of northeastern Greenland, in lacking the flaring base and in having a regular, alternating surface ornament, as well as their thin, hyaline external layer which is not laminated or thicker than the inner layer. The fibrous inner layer, seen as prominent striations on the interior surface (Fig. 23G, H), resembles similar striated structures occurring in coeloscleritophoran sclerites (Qian and Bengtson 1989: fig. 16A<sub>5</sub>, A<sub>6</sub>; Bengtson 1992: fig. 8I–K; Conway Morris and Chapman 1996: fig. 8r), but unlike the latter, which presumably represent phosphatic replacement of an originally calcareous wall (Conway Morris and Chapman 1996), the fibrous structure in the *Mongolitubulus* spine appears to be a primary phosphatic microstructure.

*Discussion.*—*Mongolitubulus* spines certainly do not represent an entire organism, but single elements of a disarticulated scleritome or fragments of exoskeletal elements armouring the body of an enigmatic animal. Their external morphology su-



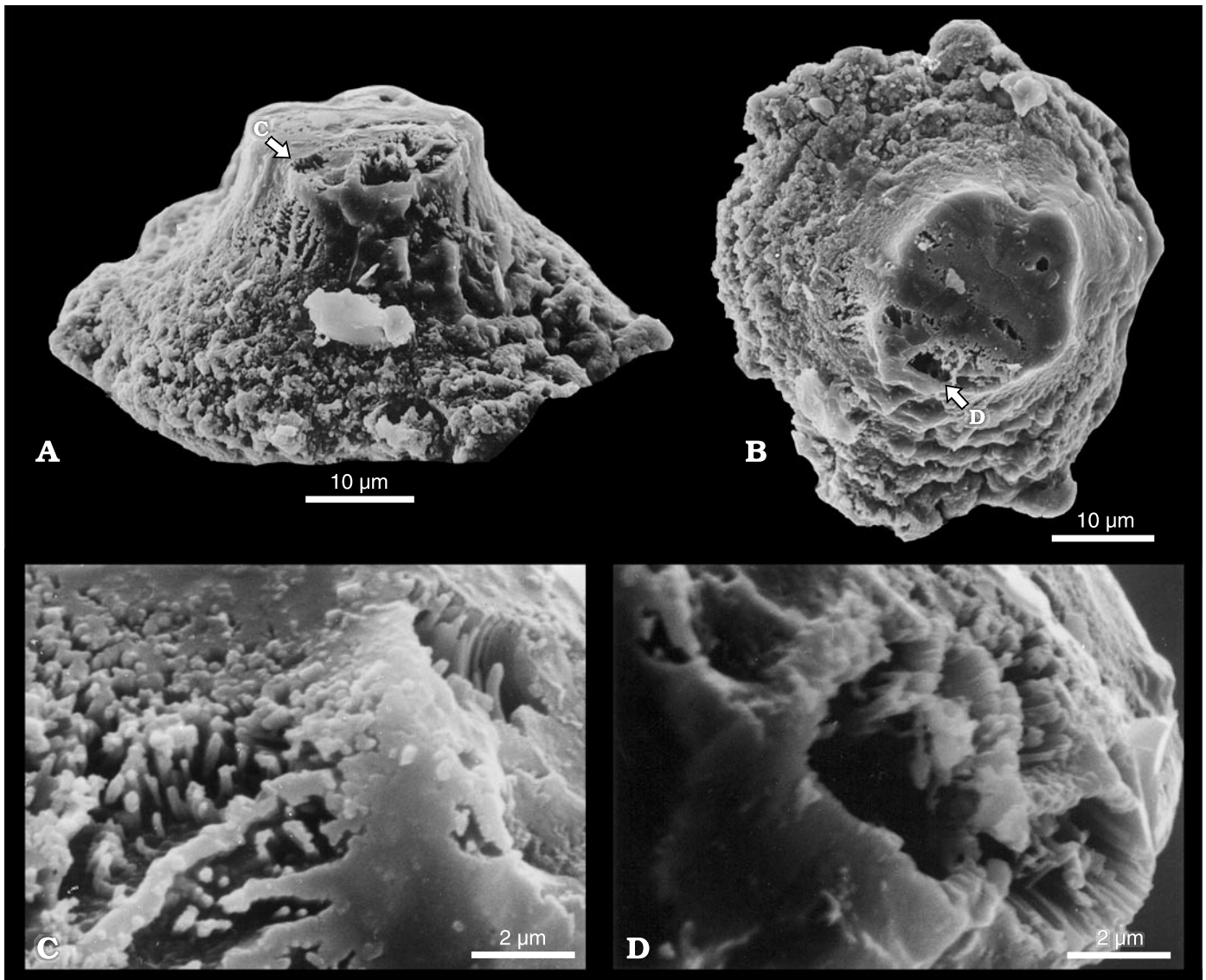


Fig. 21. Sclerite of *Hadimopanella staurata* sp. nov., ZPAL V.VI/24S24, erratic boulder Me40. **A**. Oblique lateral view. **B**. Upper view. **C**, **D**. Enlargements of **B** showing arrangement of phosphate crystallites in the external layer.

perficially resembles scaly ornaments widespread among fossils in the Lower Palaeozoic, particularly trilobite, eurypterid or bradoriid carapaces, remains of the vertebrate *Anatolepis* (Bockelie and Fortey 1976), and problematic ornamented tubes or conodont-like fossils. In particular, enrolled integument fragments from the Upper Cambrian (Trempealeauan–Dreshbachian) Broom Point section in western Newfoundland, show rhomboid surface ornament, and have been assigned to *Anatolepis* sp. by Landing (in Fortey et al. 1982: 115: fig. 9x), but they are clearly similar to *Mongolitubulus* tube fragments. Brasier (1986: fig. 5k) described one specimen from the *Serrodiscus bellimarginatus* Limestone Bed (Ac<sub>3</sub>) at Comley, Shropshire, and referred it tentatively to *Rhombocorniculum* aff. *insolutum* Missarzhevsky and Mambetov, 1981. However, the Comley specimen differs from typical forms and from the rest of Brasier's specimens in having stronger, scale-like sculpture and a trumpet-shaped basal cav-

ity. The same remark concerns Landing's specimens of *Rhombocorniculum* sp. nov. from the Lower Cambrian of eastern Massachusetts, which are straight and slender tubes with wide internal cavity, nearly circular cross-section and characteristic *Mongolitubulus*-type surface ornament (Landing 1988: 687: fig. 11.6). These characters indicate that both the English and American specimens represent a species of *Mongolitubulus*.

*Mongolitubulus* spines also show some similarities with ornamented tubes, form "B", from the Parara Limestone and form "C" from the Ajax Limestone in the Mount Scott Range, South Australia (Bengtson et al. 1990: figs. 102 and 103) and with apical cones of *Lapworthella* (Bengtson et al. 1990: figs. 78F and 80A, B), as well as with *Rushtonites spinosus* Hinz (1987) from the Lower Cambrian of Comley. The latter form was also compared with scale-sculptured organic-walled spines or setae from the Middle Cambrian of the Mackenzie

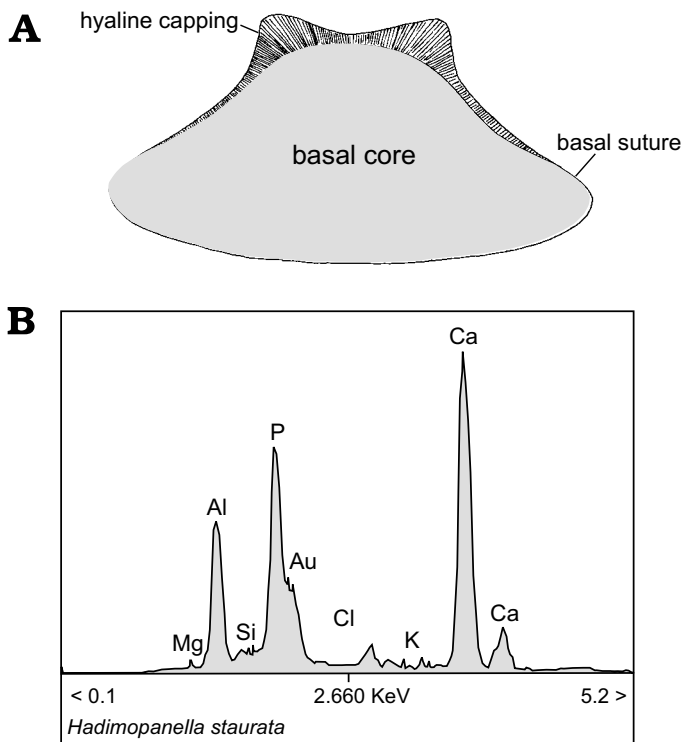


Fig. 22. **A.** Diagrammatic cross section of the sclerite *Hadimopanella staurata* sp. nov. **B.** Energy dispersive spectrum (EDS) for the *H. staurata* sclerite.

Mountains, Canada (Butterfield and Nicholas 1996). Some similarities can be recognized between the *Mongolitubulus* scale ornament and the external tuberculate ornamentation on sclerites of the coleoscleritophoran *Halkieria* (Fig. 7F; also Conway Morris and Chapman 1996: fig. 6: 10 and fig. 8: 2, 3). The most important differences with ornamented tubes are in the composition of the wall and the interior surface of the tube, which shows pits corresponding to the external scale-like ornament (e.g., Bengtson et al. 1990: fig. 101H). Thus, histological investigations of all conodont-like forms and ornamented tubes are crucial. Observations made on the scale ornament of such coniform tubes and lapworthellid apical cones suggests that scales have rather mechanical significance in construction of the spine wall than any functional meaning. The strongly abraded spine fragments from the Lower Cambrian of Ville Guay, Québec very likely represent specimens of *M. squamifer* (Landing et al. 2002). The recently discovered *M. henriksenii* with flaring spine base and co-occurring plate fragments with broken spines from the Lower Cambrian

Bastion Formation of northeastern Greenland may have been an arthropod carapace bearing spines, although possibly this interpretation cannot be extended to the type species (Skovsted and Peel 2001). The alternative interpretation of the *Mongolitubulus* spines as sclerites armouring the body of a lobopodian animal, similar to *Xenusion*, has been suggested by Dzik (2003) on the basis of a low-diversity fossil assemblage dominated by *Mongolitubulus* spines and *Microdictyon* sclerites. Both these interpretations are founded on different incomplete skeletal elements and cannot be extended to all *Mongolitubulus* forms, in particular the type material, until new complete scleritomes or articulated spine arrays of *Mongolitubulus* are discovered.

**Occurrence.**—Mongolia, Sanashhtykgol Horizon, Lower Cambrian (Botomian); Maly Karatau, Koksuu, and Ushbas, from Geress Member of the Shabakty Formation, Lower Cambrian (Botomian or latest Atdabanian, see Missarzhevsky and Mambetov 1981). Turkestan, Middle Cambrian. Central-northern Greenland, Henson Gletscher Formation, Lower Cambrian (Bonnia–Olenellus Zone); Lower Cambrian of eastern Massachusetts and Ville Guay, Québec, North America; Lower Cambrian Comley Limestone (Ac<sub>3</sub>) at Comley, Shropshire, England; allochthonous Early Cambrian (Botomian) boulders (Me32), King George Island, Antarctica.

## Hyolithelminths

### Phylum and class uncertain

#### Order Hyolithelminthida Fisher, 1962

#### Family Hyolithellidae Walcott, 1886

#### Genus *Hyolithellus* Billings, 1871

*Type species: Hyolithes micans* Billings, 1871.

#### *Hyolithellus micans* (Billings, 1871)

Fig. 25E.

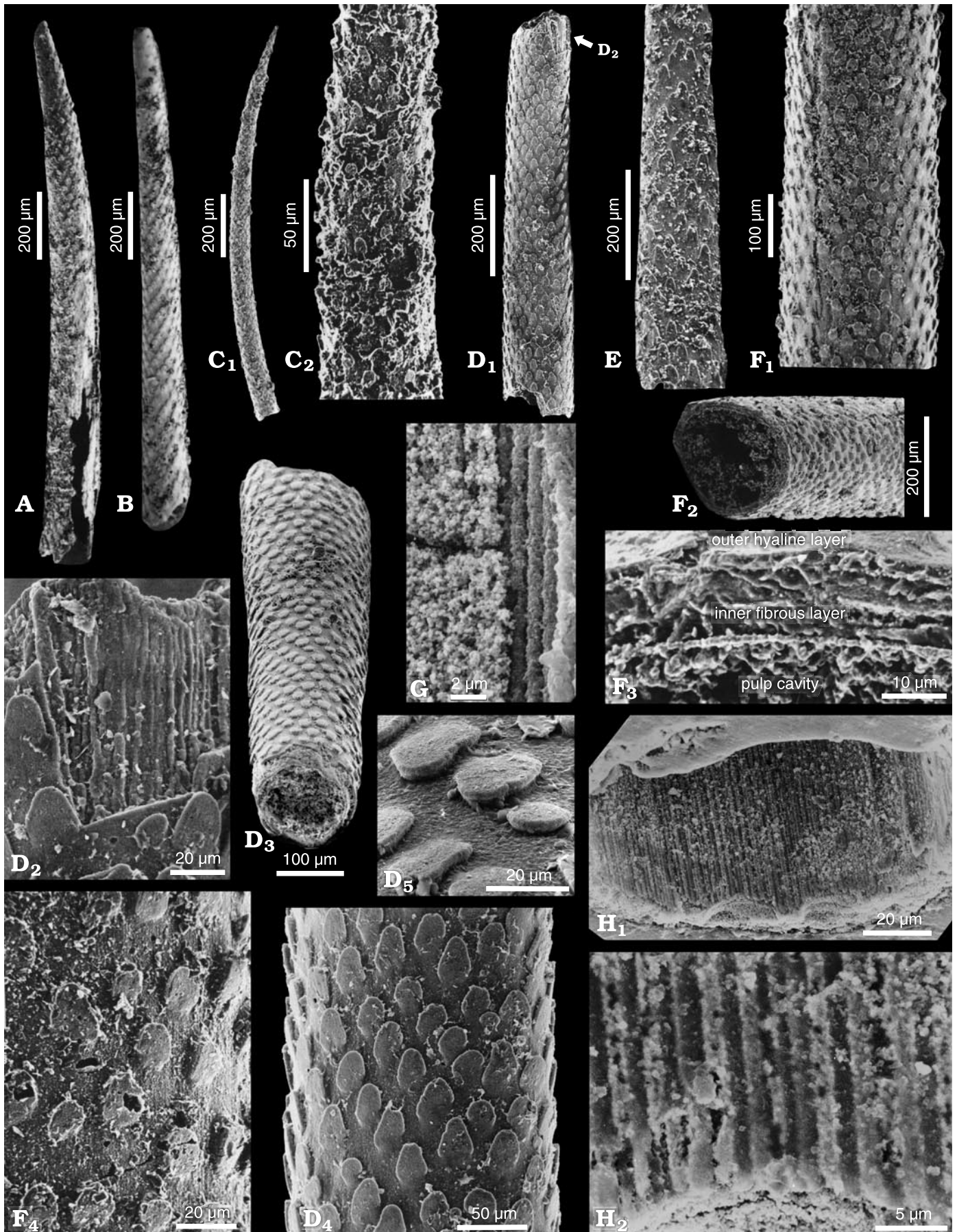
*Hyolithellus* cf. *micans* (Billings) Morphotype C; Brasier 1984: 236, fig. 1v–x.

*Hyolithellus micans* (Billings); Demidenko in Gravestock et al. 2001: 94, pl. 9: 10 [full synonymy].

**Material.**—Six well preserved tube fragments from erratic boulders Me32, 33, 66. Figured specimen, ZPAL V.VI/32S4.

**Description.**—Slightly tapering tubes, with low angle of divergence, up to about 5° (usually less), straight or gently curved and circular in cross-section. Tubes are broken at both ends, in fragments up to 40 μm wide and up to 3 mm long. The wall is phosphatic and up to 30 μm thick. The outer surface is covered with variably spaced (in range 20–80 μm), weakly ex-

Fig. 23. *Mongolitubulus squamifer* Missarzhevsky. **A.** Oblique lateral view, showing almost complete tapering at the top end and damage at the base; ZPAL V.VI/28S28, erratic Me66. **B.** Lateral view showing scale ornamentation arranged clearly in spiral rows, ZPAL V.VI/28S27, erratic Me66. **C.** Spine with corroded surface, ZPAL V.VI/106S11, erratic Me66; C<sub>1</sub>, lateral view; C<sub>2</sub>, detail of surface sculpture. **D.** Middle part of broken spine ZPAL V.VI/29S16, erratic Me66; D<sub>1</sub>, lateral view showing scale pattern and wall structure at the broken ends; D<sub>2</sub>, broken end showing layered wall structure and fibrous inner layer; D<sub>3</sub>, apical oblique view showing imbrication of the scales; D<sub>4</sub>, detail showing surface sculpture. D<sub>5</sub>, detail of imbricated scale ornamentation in apical view. **E.** Middle part of broken spine showing scale pattern, ZPAL V.VI/106S21, erratic Me66. **F.** Middle part of the spine ZPAL V.VI/106S22, erratic Me66; F<sub>1</sub>, lateral view, showing scale pattern; F<sub>2</sub>, adapical end of the spine, in oblique lateral view, showing broken section of the wall; F<sub>3</sub>, detail of the same section, showing outer and inner layer; F<sub>4</sub>, detail showing surface sculpture. **G.** Polished and etched cross-section through the wall, parallel to the spine axis, showing fibrous structure of the inner layer (at right), ZPAL V.VI/22U2, erratic Me66. **H.** Etched inner surface of the internal (pulp) cavity of the spine, ZPAL V.VI/22U1, erratic Me66; H<sub>1</sub>, basal oblique view, showing fibrous inner layer (centre); H<sub>1</sub>, detail of the same.



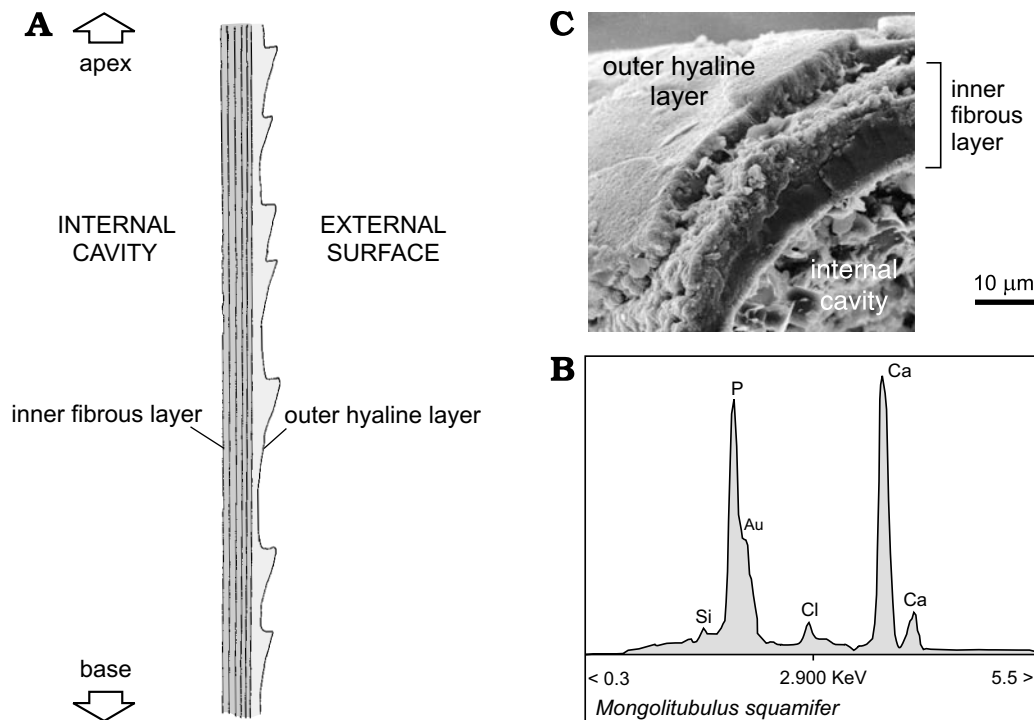


Fig. 24. **A.** Diagrammatic cross-section of the wall of *Mongolitubulus squamifer* Missarzhevsky. **B.** Energy dispersive spectrum (EDS) for the *M. squamifer* sclerite. **C.** Broken end of the specimen figured in Fig. 23D, showing layered wall structure including outer hyaline layer and fibrous inner layer.

pressed transverse ribs (annulae), probably representing growth lines. No opercula closing the aperture and any structure for attachment to the substrate have been observed.

**Remarks.**—The Antarctic specimens demonstrate distinctive characters clearly similar to Australian specimens of *H. cf. micans* (Bengtson et al. 1990) and *H. micans* (Gravestock et al. 2001), and match well *H. micans* in the broad interpretation of many authors (see synonymy in Bengtson et al. 1990). The new Antarctic collection reinforces Bengtson's (in Bengtson et al. 1990) concept of hyolithelmiths as animals with tubes lacking a mineralized operculum.

**Occurrence.**—Cosmopolitan in the Early Cambrian: (Atdabanian/Botomian) Kulpara Formation and Parara Limestone, Horse Gully, Yorke Peninsula, Stansbury Basin, South Australia; Northwest Territories, Canada; Massachusetts and New York, USA; Scania and Bornholm, Sweden; Salaany Gol and Khairkhan Formations, Zavkhan, Salaany Gol, Mongolia; allochthonous Early Cambrian (Botomian) boulders (Me32, 33, 66), King George Island, Antarctica.

*Hyolithellus filiformis* Bengtson, 1990 in Bengtson et al. 1990

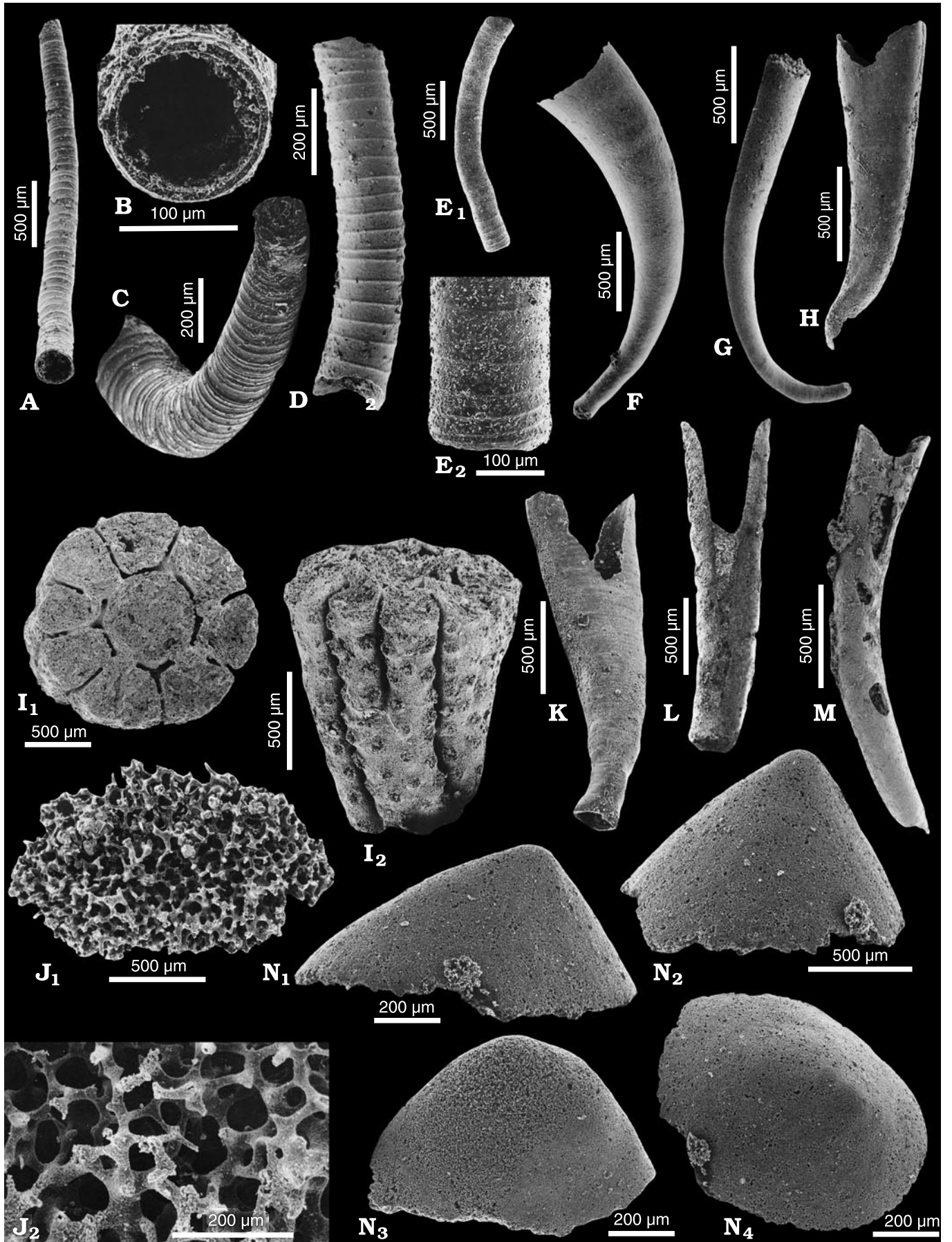
Fig. 25A–D.

*Hyolithellus filiformis* Bengtson in Bengtson et al.; Demidenko in Gravestock et al. 2001: 93, pl. 9: 9, 11 [full synonymy].

**Material.**—Ten fragmented tubes from erratic boulders Me32, 33, 66. Figured specimens, ZPAL V.VI/32S26; 105S2; 106S5; 110S7.

**Description.**—Slightly tapering, almost cylindrical phosphatic tubes, usually variably curved, but short fragments can be straight. They are circular in cross-section with diameter 0.1–0.2 mm. The outer surface is covered with evenly spaced transverse ribs. This regular annulation can be disturbed, especially in curved fragments. Inner surface of tubes is smooth. Broken tubes show wall structure as a system of several thin layers. Some specimens have tube walls with irregular microborings produced by an enigmatic organism. Opercula closing the tube aperture or any structure for attachment to the substrate have been observed.

Fig. 25. **A–D.** *Hyolithellus filiformis* Bengtson. **A.** Fragment of tube in lateral view, ZPAL V.VI/105S2, erratic Me66. **B.** Tube opening, in proximal view, showing thickness of tube wall, ZPAL V.VI/106S5, erratic Me33. **C.** Curved tube, in oblique lateral view, ZPAL V.VI/110S7, erratic Me66. **D.** Tube in lateral view, ZPAL V.VI/32S6, erratic Me32. **E.** Tube of *Hyolithellus micans* (Billings), ZPAL V.VI/32S4, erratic Me66, in lateral view (E<sub>1</sub>), and its enlarged end (E<sub>2</sub>). **F, G.** *Torellella* sp. **F.** Steinkern of slightly curved tube in lateral view, ZPAL V.VI/103S13, erratic Me66. **G.** Steinkern of curved tube in lateral view, ZPAL V.VI/32S11, erratic Me66. **H.** Lateral view of *Byronia? bifida* sp. nov. tube, ZPAL V.VI/115S5, erratic Me66. **I.** Phosphate steinkern of *Stapicyathus stapipora* (Taylor) archaeocyath cup, ZPAL V.VI/37S1, erratic Me33; in transverse upper (I<sub>1</sub>) and oblique longitudinal (I<sub>2</sub>) views. **J.** Echinoderm stereom, ZPAL V.VI/109S10, erratic Me66; J<sub>1</sub>, phosphatized echinoderm plate; J<sub>2</sub>, detail. **K–M.** *Byronia? bifida* sp. nov. **K.** Tube in lateral view, ZPAL V.VI/35S17, erratic Me66. **L.** Distal part of holotype tube in lateral view, ZPAL V.VI/39S8, erratic Me32. **M.** Distal part of tube in lateral view, ZPAL V.VI/33S19, erratic Me33. **N.** Problematic "smooth cone"—steinkern of coeloscleritophoran shell, ZPAL V.VI/35S8, erratics Me33; in lateral (N<sub>1</sub>), anterior (N<sub>2</sub>), oblique upper (N<sub>3</sub>), and oblique apical (N<sub>4</sub>) views. →





**Remarks.**—The Antarctic specimens demonstrate distinctive features closely similar to those of Australian specimens (Bengtson et al. 1990; Gravestock et al. 2001), whose biological function and significance have been broadly discussed by Bengtson (see Bengtson et al. 1990).

**Occurrence.**—Early Cambrian (Atdabanian/Botomian) Kulpara Formation, Parara Limestone, and Koolywurtie Limestone Member, Horse Gully, Yorke Peninsula, Stansbury Basin, and Ajax Limestone, Flinders Ranges, Arrowie Basin, South Australia; allochthonous Early Cambrian (Botomian) boulders (Me32, 33, 66), King George Island, Antarctica.

### Genus *Byronia* Matthew, 1899

*Type species: Byronia annulata* Matthew, 1899.

**Remarks.**—The full synonymy, taxonomy, and biological affinity of byroniids have been broadly discussed by Bischoff (1989). This is a quite cosmopolitan genus, known from North America, Europe, and Australia through a wide stratigraphic range: Early Cambrian up to Early Devonian.

#### *Byronia? bifida* sp. nov.

Fig. 25H, K–M.

*Byronia?* sp. nov. A; Bengtson in Bengtson et al. 1990: 190, fig. 126. *Holotype:* Specimen shown in Fig. 25L, ZPAL V.VI/35S17 from erratic boulder Me66.

*Type horizon:* The inferred upper part of the Lower Cambrian, Botomian Stage, *Syringocnema favus* beds.

*Type locality:* Erratic boulders of Antarctic origin. Me66 in glacio-marine Cape Melville Formation (Lower Miocene), King George Island, South Shetland Islands, West Antarctica.

*Derivation of name:* From Latin *bifidus*, split in two parts, referring to the deep split along the broad, lateral side of the tube.

**Diagnosis.**—Phosphatic tubular fossils, lenticular in transverse section. The conical tube has the proximal end constricted with a distinct margin, slightly deflected upwards. Distally, the tube expands in diameter and is deeply split along the broad lateral side. Apertural margins of both split walls are narrowly rounded and smooth.

**Material.**—Ten well preserved specimens from erratic boulders Me32, 33, 66. Figured specimens, ZPAL V.VI/33S19; 35S17; 39S8; 115S5.

**Description.**—Phosphatic, more or less conical tubes, gently curved and lenticular in cross-section. Proximal (basal) end of the tube is relatively small in diameter and more circular in cross-section than the widened distal end. Basal expanded margin may act as an attachment to the substrate: however, the basal attachment disc has not been recovered. Laterally, the broad sides are split distally to project aperturally as a bifurcating wall. Apertural margins of both split elements are narrowly rounded and smooth. The V-shaped area of slit could represent the proximal end that was covered by a weakly sclerotized, and thus very thin, external layer of the wall, which was incompletely preserved and could have been easily perforated or broken (Fig. 25M). Outer surface is covered with densely spaced, fine, annular growth lines (Fig. 25K). The growth lines are clearly visible in the translucent, thin wall covering the lateral slits. Inner surface of tubes is smooth. Bro-

ken tubes show relatively thick, phosphatic wall structure as a system of several thin layers.

**Remarks.**—These fossils are commonly interpreted as representing sessile tube-dwelling organisms with organic, partly mineralised (phosphatized) tubes (Bischoff 1989; Bengtson in Bengtson et al. 1990). Splitting of the tube wall also occurs in other species of *Byronia* (Bischoff 1989), but the newly assigned species differs distinctly from the most similar Australian species, *B. displosa* Bischoff, 1989 in having a very prominent, long slit with smooth margins and narrowly rounded apertural edge, as well as a thin external layer covering the slit. The Australian specimens described and illustrated by Bengtson (see Bengtson et al. 1990) most probably represent tubes with unpreserved or damaged thin and weak wall in the slits.

**Occurrence.**—Early Cambrian (Atdabanian/Botomian) Kulpara Formation and Parara Limestone, Horse Gully, Yorke Peninsula, Stansbury Basin, South Australia; allochthonous Early Cambrian (Botomian) boulders (Me32, 33, 66), King George Island, Antarctica.

### Family Torellellidae Holm, 1893

#### Genus *Torellella* Holm, 1893

*Type species: Torellella annulata* Holm, 1893.

#### *Torellella* sp.

Fig. 25F, G.

**Material.**—Ten well-preserved specimens from erratic boulders Me32, 33, 52, and 66. Figured specimens, ZPAL V.VI/32S11; 103S13.

**Description.**—Phosphatic steinkerns of slightly tapering tubes, up to 2 mm long, gently curved in initial part but straighter at distal end. Subcircular to oval in cross-section, up to 0.3 mm in diameter. No apical end has been observed, because it is always broken off and missing. The smooth surface does not bear any trace of original shell sculpture. No opercula closing the aperture were observed.

**Remarks.**—These tubes show some resemblance to steinkerns representing diverse species of *Cambrotubulus* Missarzhevsky, 1969 (in Rozanov et al. 1969) or *Circotheca* Syssoiev, 1958 (Hinz 1987; Kerber 1988), but with broken and missing initial end, they are difficult to designate more certainly. Torellellid tubes, similarly as hyolithelminths may be considered as having lacked a mineralized operculum.

**Occurrence.**—Allochthonous Early Cambrian (Botomian) boulders (Me32, 33, 52, 66), King George Island, Antarctica.

### Problematica

#### Phylum, order, and family uncertain

#### Genus *Aetholicopalla* Conway Morris, 1990 in Bengtson et al. 1990

*Type species: Aetholicopalla adnata* Conway Morris, 1990 in Bengtson et al. 1990.

**Remarks.**—These calcareous (secondarily phosphatized) globular fossils with a double wall perforated by tubes that enter its central cavity, appear similar to *Archaeooides* when poorly

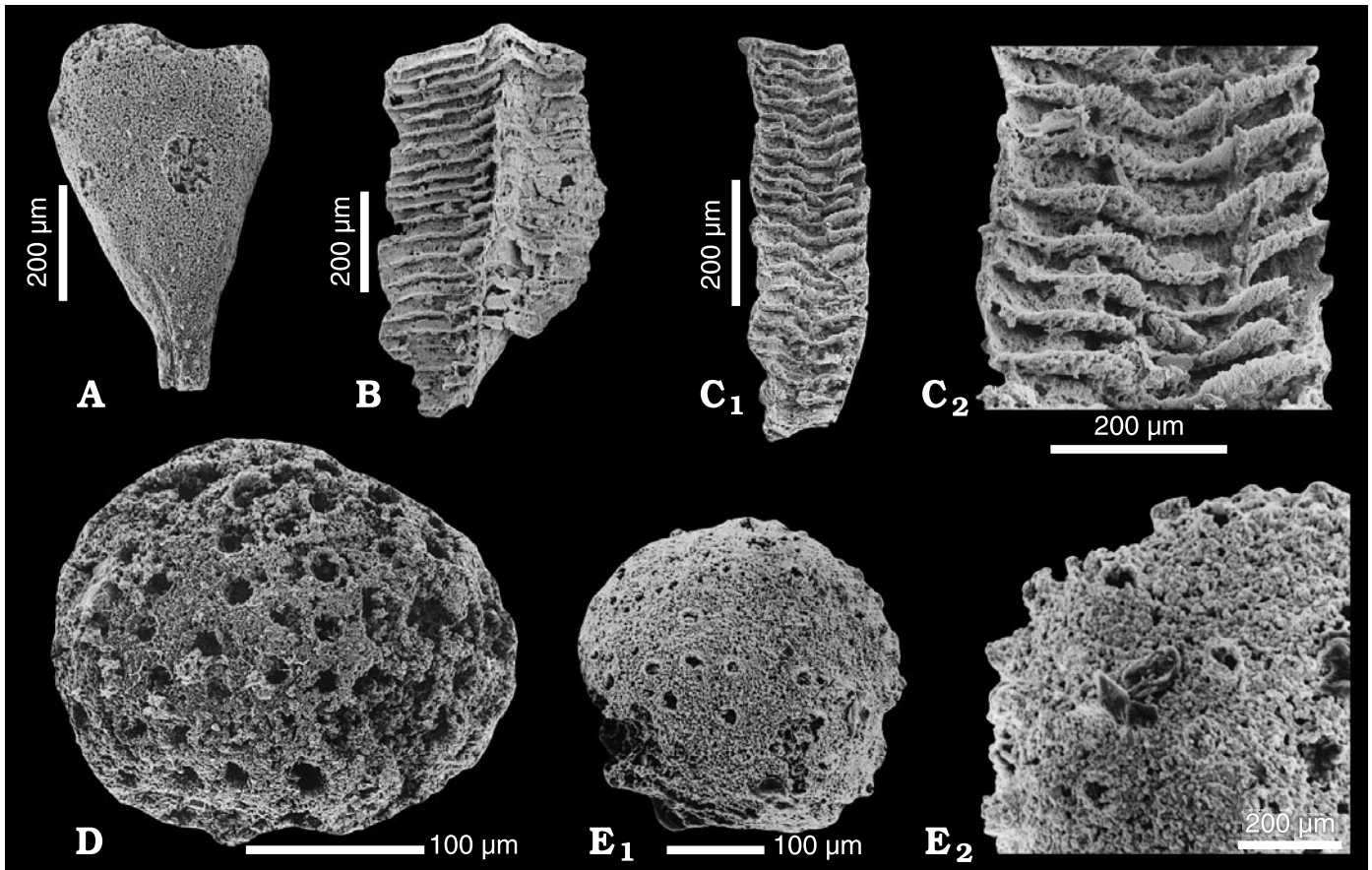


Fig. 26. **A.** Steinkern of initial part of *Stapicyathus cera* Debenne archaeocyath cup, ZPAL Ac.I/53U7, erratic Me33. **B, C.** Problematic ?tommotiid sclerite. **B.** Fragment of sclerite wall, ZPAL V.VI/49U4, erratic Me66. **C.** Fragment of sclerite wall, ZPAL V.VI/49U3, erratic Me66; C<sub>1</sub>, general view; C<sub>2</sub>, detail showing lamellar structure at the edge (arrowed). **D, E.** *Aetholicopalla adnata* Conway Morris. **D.** Specimen with external wall exfoliated, ZPAL V.VI/38S6, erratic Me32. **E.** Specimen ZPAL V.VI/38S1, erratic Me66; E<sub>1</sub>, oblique view, showing inner wall and tubules; E<sub>2</sub>, detail of surface of inner wall.

preserved, with the external wall destroyed. They often occur attached to or encrusting objects.

*Aetholicopalla adnata* Conway Morris, 1990 in Bengtson et al. 1990

Fig. 26D, E.

*Aetholicopalla adnata* Conway Morris; Demidenko in Gravestock et al. 2001: 86, pl. 12: 7, 8 [full synonymy].

**Material.**—Three specimens from erratic boulder Me32. Figured specimens, ZPAL V.VI/38S1, 6.

**Description.**—Spherical to subspherical, phosphatized microfossil about 600 µm in diameter. Normally double-walled globules, with walls connected by hollow pillars. The external wall is usually destroyed, showing height of the pillars (about 30–50 µm), which corresponds to the distance between the inner and outer wall, and remains of the external wall (Fig. 26E). The pillars opened on the outer surface of the globules, and are circular with a constant diameter about 30 µm (Fig. 26D). One specimen shows a flattened area corresponding to a zone of attachment to the substrate (Fig. 26E). The interior of the globules is filled with amorphous phosphates. The ornamentation of the external surface is not visible because of the poor preservation.

**Remarks.**—The vermiform tubules observed in the interior of

the sphere (Conway Morris in Bengtson et al. 1990) may represent diagenetic replacement of a cyanobacterial filaments.

**Occurrence.**—Early Cambrian (Atdabanian/Botomian?), Montagne Noire, southern France; Early Cambrian (Atdabanian/Toyonian), Kulpara Formation, Parara Limestone, Curramulka, Horse Gully, Yorke Peninsula and Ajax Limestone, Flinders Ranges, South Australia; Marianian strata (?uppermost Atdabanian–Botomian), Görlitz Syncline, eastern Germany (Elicki and Schneider 1992; Elicki 1998); allochthonous Early Cambrian (Botomian) boulders (Me32), King George Island, Antarctica.

Problematic “smooth cones”—?coeloscleritophoran shell

Fig. 25N.

**Material.**—Sixteen phosphatic steinkerns from erratic boulder Me33. Figured specimen, ZPAL V.VI/35S8.

**Description.**—Steinkerns of a cap-shaped, low-conical, slightly longitudinally elongate but rather wide shell. The apex is large, blunt, displaced posteriorly. The shell was apparently originally calcitic or aragonitic, with widely elliptical aperture. The surface of the internal mould is smooth without any trace of boundary between protoconch and teleoconch. No texture pattern or muscle scars have been observed on the surface moulds.

*Remarks.*—The shape of the moulds is very similar to that of the “ornamented cone”, Form A from the Parara and Ajax Limestones (Runnegar in Bengtson et al. 1990), which possibly represents some kind of mollusc-like coeloscleritophoran shell closely related to halkieriids (e.g., Qian and Bengtson 1989; Conway Morris and Peel 1990, 1995; Bengtson 1992).

*Occurrence.*—Allochthonous Early Cambrian (Botomian) boulders (Me33), King George Island, Antarctica.

## Conclusions

- The Cambrian Antarctic fossiliferous limestone rocks described in this study exhibit a biofabric indicative of condensed deposits and reworked taphocenoses.
- The studied small shelly fossil assemblage is rich in juvenile benthic and nektonic biota, and larval shells of linguulate brachiopods are extremely abundant (Holmer et al. 1996), possibly a result of increased juvenile biota mortality. The Early Cambrian phosphatized SSF of Antarctica are similar to other small skeletal fossil assemblages that appeared at the beginning of the Cambrian, and are analogous to, those occurred throughout the Early Paleozoic (Dzik 1994). It has been argued that the sudden, global appearance of these fossils resulted from an environmental crisis (Dzik 1994; Zhuravlev and Wood 1996), correlated with the Lower Cambrian phosphogenetic event (Cook and Shergold 1984, 1986; Braiser 1990).
- Both lithologically and palaeontologically, King George Island erratics are closely similar to South Australian Early Cambrian sequences, particularly the Yorke Peninsula succession (Fig. 3). Lithological groups I, II, and III resemble the Parara Limestone, Koolyurt Limestone Member and Ramsay Limestone respectively. Minlaton Formation lithologies are not recorded in the erratics. This may be due to the lack of distinct fossils in the latter formation and to the selective transport of different lithologies in glacial erratic blocks (Wrona 1989). Some similarities also exist between these erratics and the Flinders Ranges (Arrowie Basin) rocks, in particular, the Mernmeria Formation, upper Wilkawillina Limestone and Wirrealpa Limestone, as well as the Tindall Limestone of the Daly Basin, Northern Territory (Fig. 3).
- The Early Cambrian skeletal fauna of King George Island is almost identical to the South Australian one, but the closest similarities are observed between the Stansbury Basin of South Australia and this most remote part of Antarctica (e.g., Dalziel 1992: figs. 2, 3). There are two possible explanations: (1) the Stansbury Basin was an Australian basin proximal to the continuous East Antarctic shelf along which the fauna freely migrated; (2) several more or less isolated basins might have existed along the East Antarctic craton. Those basins might have been connected only during the most prominent transgressions, thus allowing faunal exchange (Fig. 3). In fact, transgressive tracts were suggested for early Botomian, late Botomian and middle Toyonian times based on the sequence stratigraphy of South Australian basins (Gravestock et al. 2001; Gravestock and Hibbert

1991; Gravestock and Shergold 2001). These are the horizons that contain very similar fossil assemblages.

## 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 (Gaździcki and Wrona 1982, 1986). 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. SEM micrographs were taken at the Electron Microscopy Laboratories of the Department of Zoology, Uppsala University and the Institute of Paleobiology, Polish Academy of Sciences, Warsaw. 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 in Uppsala, for the use of the laboratory and SEM facilities at the Department of Palaeontology, Uppsala University. Stefan Bengtson continually supported my work until the final version of the manuscript, and thoroughly reviewed, discussed, criticized, and commented on both the scientific content, and the language of the paper. My sincere warmest thanks are also extended to an anonymous reviewer who provided valuable critical comments and carefully corrected the English. I am grateful to Paweł Zawadzki (SEM Laboratory at the Institute of Geological Sciences, Warsaw) for EDS microanalysis of the phosphate composition of the shelly fossils. Jerzy Dzik (Institute of Paleobiology, Warsaw) kindly corrected an early version of the manuscript. The manuscript has also benefited from linguistic comments by Tomasz K. Baumiller (Museum of Paleontology, University of Michigan).

## References

- Adrianov, A.V. and Malakhov, V.V. [Malakhov, V.V.] 1996. *Priapulidy (Priapulida) stroenie, razvitiie, filogeniia i sistema* [with English summary]. 268 pp. KMK Scientific Press Ltd., Moscow.
- Anderson, J.B. and Andrews, J.T. 1999. Radiocarbon constraints on ice sheet advance and retreat in the Weddell Sea, Antarctica. *Geology* 27: 179–182.
- Bedford, R. and Bedford, W.R. 1934. New species of Archaeocyathinae and other organisms from the Lower Cambrian of Beltana, South Australia. *Memoirs of the Kyancutta Museum* 1: 1–7.
- Bedford, R. and Bedford, J. 1937. Further notes on *Archaeos* (Pleospungia) from the Lower Cambrian of South Australia. *Memoirs of the Kyancutta Museum* 4: 27–38.
- Bendix-Almgreen, S.E. and Peel, J.S. 1988. *Hadimopanella* from the Lower Cambrian of North Greenland: structure and affinities. *Bulletin of the Geological Society of Denmark* 37: 83–103.
- Bengtson, S. 1970. The Lower Cambrian fossil *Tommotia*. *Lethaia* 3: 363–392.
- Bengtson, S. 1977. Early Cambrian button-shaped phosphatic microfossils from the Siberian Platform. *Palaeontology* 20: 751–762.
- Bengtson, S. 1983. The early history of the Conodonts. *Fossil and Strata* 15: 5–19.
- Bengtson, S. 1992. The cap-shaped Cambrian fossil *Maikhanella* and the relationship between coeloscleritophorans and molluscs. *Lethaia* 25: 401–420.
- Bengtson, S. (ed.) 1994a. Early Life on Earth. *Nobel Symposium* 84: 1–630. Columbia University Press, New York.
- Bengtson, S. 1994b. The advent of skeletons. In: S. Bengtson (ed.), Early Life on Earth. *Nobel Symposium* 84: 1–630. Columbia University Press, New York.
- Bengtson, S. and Conway Morris, S. 1984. A comparative study of Lower Cambrian *Halkieria* and Middle Cambrian *Wiwaxia*. *Lethaia* 17: 307–329.
- Bengtson, S. and Hou, X. 2001. The integument of Cambrian chancelloriids. *Acta Palaeontologica Polonica* 46: 1–22.



- Bengtson, S. and Missarzhevsky, V.V. 1981. Coeloscleritophora, a major group of enigmatic Cambrian metazoans. *In*: M.E. Taylor (ed.), Short Papers for the Second International Symposium on the Cambrian System. *U.S. Geological Survey Open-File Report* 81-743: 19–21.
- Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A., and Runnegar, B.N. 1990. Early Cambrian fossils from South Australia. *Memoir of the Association of Australasian Palaeontologists* 9: 1–364.
- Berg-Madsen, V. and Peel, J.S. 1978. Middle Cambrian monoplacophorans from Bornholm and Australia, and the systematic position of the bellerophonitiform molluscs. *Lethaia* 11: 113–125.
- Biernat, G., Birkenmajer, K., and Popiel-Barczyk, E. 1985. Tertiary brachiopods from the Moby Dick Group of King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica* 81: 109–141.
- Billings, E. 1871. On some new species of Palaeozoic fossils. *Canadian Naturalist* 6: 213–223, 240.
- Birkenmajer, K. 1980. Discovery of Pliocene glaciation on King George Island, South Shetland Islands (West Antarctica). *Bulletin de l'Académie Polonaise des Sciences, Série des Sciences de la Terre* 27: 59–67.
- Birkenmajer, K. 1982a. Pliocene tillite-bearing succession of King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica* 74: 7–72.
- Birkenmajer, K. 1982b. Report on geological investigations of King George Island and Nelson Island (South Shetland Islands, West Antarctica). *Studia Geologica Polonica* 74: 175–197.
- Birkenmajer, K. 1987. Oligocene–Miocene glaciomarine sequences of King George Island (South Shetland Islands), Antarctica. *In*: A. Gaździcki (ed.), Paleontological results of the Polish Antarctic Expeditions, Part I. *Palaentologia Polonica* 49: 9–36.
- Birkenmajer, K. 1989. A guide to Tertiary geochronology of King George Island, West Antarctica. *Polish Polar Research* 10: 555–579.
- Birkenmajer, K. 1992. Cenozoic glacial history of the South Shetland Islands and Northern Antarctic Peninsula. *In*: J. López-Martínez (ed.), *Geología de la Antártida Occidental. Simposios T 3*, 251–260. III Congreso Geológico de España y VII Congreso Latinoamericano de Geología. Salamanca, España.
- Birkenmajer, K. 1995. The Cape Melville Formation (Lower Miocene glacio-marine deposits) on King George Island, South Shetland Islands (West Antarctica): its basal and top strata. *Polish Academy of Sciences Bulletin, Earth Sciences* 43: 113–122.
- Birkenmajer, K. and Butkiewicz, T. 1988. Petrography and provenance of magmatic and metamorphic erratic blocks from Lower Miocene glacio-marine deposits of King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica* 95: 23–51.
- Birkenmajer, K., Gaździcki, A., and Wrona, R. 1983. Cretaceous and Tertiary fossils in glacio-marine strata at Cape Melville, Antarctica. *Nature* 303: 56–59.
- Birkenmajer, K., Gaździcki, A., Kreuzer, H., and Müller, P. 1985. K-Ar dating of the Melville Glaciation (Early Miocene) in West Antarctica. *Polish Academy of Sciences Bulletin, Earth Sciences* 33: 15–23.
- Birkenmajer, K., Gaździcki, A., Pugaczewska, H., and Wrona, R. 1987. Recycled Cretaceous belemnites in Lower Miocene glacio-marine sediments (Cape Melville Formation) of King George Island, West Antarctica. *In*: A. Gaździcki (ed.), Paleontological results of the Polish Antarctic Expeditions, Part I. *Palaentologia Polonica* 49: 9–36.
- Bischoff, G.C.O. 1976. *Dailyatia*, a new genus of the Tommotiidae from Cambrian strata of SE Australia (Crustacea, Cirripedia). *Senckenbergiana lethaea* 57: 1–33.
- Bischoff, G.C.O. 1989. Byroniida new order from early Palaeozoic strata of eastern Australia (Cnidaria, thecate scyphopolyps). *Senckenbergiana lethaea* 69: 467–521.
- Bockelie, T. and Fortey, R. A. 1976. An early Ordovician vertebrate. *Nature* 260 (5546): 36–38.
- Boogaard, M. van den 1989. Isolated tubercles of some Palaeoscolecida. *Scripta Geologica* 90: 1–12.
- Bowerbank, J.S. 1864. *A Monograph of the British Spongiade. Vol. 1*. 289 pp. Royal Society, London.
- Brasier, D.M. 1979. The Cambrian radiation event. *In*: M.R. House (ed.), *The Origin of Major Invertebrate Groups. Systematic Association Special Volume 12*: 103–159. Academic Press, London and New York.
- Brasier, D.M. 1984. Microfossils and small shelly fossils from the Lower Cambrian Hyolithes Limestone at Nuneaton, English Midlands. *Geological Magazine* 121: 229–253.
- Brasier, D.M. 1986. The succession of small shelly fossils (especially conoidal microfossils) from English Precambrian–Cambrian boundary beds. *Geological Magazine* 123: 237–256.
- Brasier, D.M. 1990. Phosphogenic events and skeletal preservation across the Precambrian–Cambrian boundary interval. *In*: A.J.G. Notholt and I. Jarvis (eds.) Phosphorite Research and Development. *Geological Society Special Publication* 52: 289–303.
- Brasier, D.M. and Lindsay, F.J. 2001. Did supercontinental amalgamation trigger the “Cambrian explosion”? *In*: A.Yu. Zhuravlev and R. Riding (eds.), *The Ecology of the Cambrian Radiation*, 69–89. Columbia University Press, New York.
- Brock, G.A. and Cooper, B.J. 1993. Shelly fossils from the Early Cambrian (Toyonian) Wirrealpa, Aroona Creek, and Ramsay Limestones of South Australia. *Journal of Paleontology* 67: 758–787.
- Brock, G.A., Engelbretsen, M.J., Jago, J.B., Kruse, P.D., Laurie, J.R., Shergold, J.H., Shi, G.R., and Sorauf, J.E. 2000. Palaeobiogeographic affinities of Australian Cambrian faunas. *In*: A.J. Wright, G.C. Young, J.A. Talent, and J.R. Laurie (eds.), Palaeobiogeography of Australasian faunas and floras. *Memoir of the Association of Australasian Palaeontologists* 23: 1–61.
- Butterfield, N.J. and Nicholas, C.J. 1996. Burgess Shale-type preservation of both non-mineralizing and “shelly” Cambrian organisms from Mackenzie Mountains, northwestern Canada. *Journal of Paleontology* 70: 893–899.
- Cherchi, A. and Schroeder, R. 1984. Middle Cambrian Foraminifera and other microfossils from SW Sardinia. *Bolletino della Società Paleontologica Italiana* 23: 149–160.
- Clarkson, P.D., Hughes, C.P., and Thomson, M.R.A. 1979. The geological significance of a Middle Cambrian fauna from Antarctica. *Nature* 279: 791–792.
- Cobbold, E.S. 1921. The Cambrian horizons of Comley and their Brachiopoda, Pteropoda, Gastropoda, etc. *Quarterly Journal of the Geographical Society of London* 76: 325–386.
- Conway Morris, S. 1987. The search for the Precambrian–Cambrian Boundary. *American Scientist* 75: 157–167.
- Conway Morris, S. 1989. Burgess Shale faunas and the Cambrian explosion. *Science* 246: 339–346.
- Conway Morris, S. 1993. The fossil record and the early evolution of the Metazoa. *Nature* 361: 219–225.
- Conway Morris, S. 1997. The cuticular structure of the 495-Myr-old type species of the fossil worm *Palaeoscolex*, *P. piscatorum* (?Priapulida). *Zoological Journal of the Linnean Society* 119: 69–82.
- Conway Morris, S. 1998. Early metazoan evolution: reconciling paleontology and molecular biology. *American Zoologist* 36(1): 219–225.
- Conway Morris, S. and Chapman, A.J. 1996. Lower Cambrian coeloscleritophorans (*Ninella*, *Siphonochites*) from Xinjiang and Shaanxi, China. *Geological Magazine* 133: 33–51.
- Conway Morris, S. and Chen Menge. 1990. Tommotiids from the Lower Cambrian of South China. *Journal of Paleontology* 64: 169–184.
- Conway Morris, S. and Peel, J.S. 1990. Articulated halkieriids from the Lower Cambrian of North Greenland. *Nature* 345: 802–805.
- Conway Morris, S. and Peel, J.S. 1995. Articulated halkieriids from the Lower Cambrian of North Greenland and their role in early protostome evolution. *Philosophical Transactions of the Royal Society of London B* 347: 305–358.
- Conway Morris, S. and Robison, R.A. 1986. Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. *The University of Kansas Paleontological Contributions* 117: 1–22.
- Cook, P.J. and Shergold, J.H. 1984. Phosphorus, phosphorites and skeletal evolution at the Precambrian–Cambrian boundary. *Nature* 308: 231–236.
- Cook, P.J. and Shergold, J.H. 1986. *Phosphate Deposits of the World. Vol. 1. Proterozoic and Cambrian Phosphorites*. 386 pp. Cambridge University Press, New York.
- Cooper, R.A. and Shergold, J.H. 1991. Palaeozoic invertebrates of Antarctica. *In*: R.J. Tingey (ed.), *The Geology of Antarctica*, 455–486. Clarendon Press, Oxford.
- Culver, J.S., Pojeta, J., Jr., and Repetski, E.J. 1988. First record of Early Cambrian shelly microfossils from West Africa. *Geology* 16: 596–599.
- Courjault-Radé, P., Debrenne, F., and Gandin, A. 1992. Palaeogeographic and geodynamic evolution of the Gondwana continental margins during the Cambrian. *Terra Nova* 4: 657–667.
- Daily, B. 1956. The Cambrian in South Australia. *In*: J. Rodgers (ed.), *El Sistema Cambrico, su paleogeografía y el problema de su base. Report 20<sup>th</sup> International Geological Congress, Mexico* 2: 91–147.
- Daily, B. 1990. Cambrian stratigraphy of Yorke Peninsula. *In*: J.B. Jago and

- P.S. Moore (eds.), The Evolution of a Late Precambrian–Early Palaeozoic Rift Complex: The Adelaide Geosyncline. *Geological Society of Australia, Special Publication* 16: 215–229.
- Danielli, H.M.C. 1981. The fossil alga *Girvanella* Nicholson and Etheridge. *Bulletin of the British Museum (Natural History), Geology series* 35: 79–107.
- Debrenne, F. 1974. Anatomie et systématique des archéocyathes réguliers sans plancher d'Ajax Mine (Cambrian inférieur, Australie du Sud). *Geobios* 7: 91–138.
- Debrenne, F. 1992. The archaeocyathan fauna from the Whiteout Conglomerate, Ellsworth Mountains, West Antarctica. In: G.F. Webers, C. Craddock, and J.F. Spletstoeser (eds.), *Geology and Paleontology of the Ellsworth Mountains, West Antarctica. Geological Society of America Memoir* 170: 279–284.
- Debrenne, F. and Kruse, P.D. 1986. Shackleton Limestone archaeocyaths. *Alcheringa* 10: 235–278.
- Debrenne, F. and Kruse, P.D. 1989. Cambrian Antarctic archaeocyaths. In: J.A. Crame (ed.), *Origins and Evolution of the Antarctic Biota. Geological Society of London, Special Publication* 47: 15–28.
- Debrenne, F., Termier, H., and Termier, G. 1970. Radiocyatha. Une nouvelle classe d'organismes primitifs du Cambrian inférieur. *Bulletin de la Société géologique de France, 7<sup>e</sup> série* 12: 120–125.
- Demidenko, E.Yu. 2000. New Chancelloriid sclerites from the Lower Cambrian of South Australia. *Paleontological Journal* 34 (4): 377–383.
- Ding Wu and Qian Yi 1988. Late Sinian to Early Cambrian small shelly fossils from Yangjiaping, Shimen, Hunan [in Chinese, English summary]. *Acta Micropalaeontologica Sinica* 5: 39–55.
- Dong Xiping and Knoll, A.H. 1996. Middle and Late Cambrian sponge spicules from Hunan, China. *Journal of Paleontology* 70: 173–184.
- Doré, F. and Reid, R.E.H. 1965. *Allonia tripodophora* nov. gen., nov. sp., nouvelle éponge du Cambrien inférieur de Carteret (Manche). *Comptes Rendus Sommaires Séances Société Géologique de la France* 1965: 20–21.
- Drewry, D.J. 1983. The surface of the Antarctic icesheet. In: D.J. Drewry (ed.), *Antarctica: Glaciological and geophysical folio: Sheet 2*. Scott Polar Institute, Cambridge.
- Duan Chenghua. 1984. Small shelly fossils from the Lower Cambrian Xihaoping Formation in the Shennongjia District, Hubei Province—hyoliths and fossil skeletons of unknown affinities. [in Chinese]. *Bulletin of Tianjin Institute of Geological and Mineralogical Research* 7 (1983): 143–188.
- Dudziak, J. 1984. Cretaceous calcareous nannoplankton from glacio-marine deposits of the Cape Melville area, King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica* 79: 37–51.
- Dzik, J. 1994. Evolution of “small shelly fossils” assemblages of the Early Paleozoic. *Acta Palaeontologica Polonica* 39: 247–313.
- Dzik, J. 1986a. *Turrilepadida* and other *Machaeridia*. In: A. Hoffman and M.H. Nitecki (eds.), *Problematic Fossil Taxa*, 116–134 Oxford University Press, Calderon Press, New York, Oxford.
- Dzik, J. 1986b. Chordate affinities of the Conodonts. In: A. Hoffman and M.H. Nitecki (eds.), *Problematic Fossil Taxa*, 240–254. Oxford University Press, Calderon Press, New York, Oxford.
- Dzik, J. 2003. Early Cambrian lobopodian sclerites and associated fossils from Kazakhstan. *Paleontology* 46: 93–112.
- Edhorn, A.-S. 1979. *Girvanella* in the “button algae” horizon of the Fourteau Formation (Lower Cambrian), Western Newfoundland. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* 3: 557–567. Pau.
- Eldridge, J., Walsh, D., and Scotese, C.R. 1997. *Plate Tracker for Windows 95 version 1*. CD-ROM.
- Elicki, O. 1994. Lower Cambrian carbonates from eastern Germany: Palaeontology, stratigraphy and palaeogeography. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 191: 69–93.
- Elicki, O. 1998. First report of *Halkieria* and enigmatic globular fossils from the Central European Marianian (Lower Cambrian, Görlitz Syncline, Germany). *Revista Española de Paleontología* n° extr. Homenaje al Prof. Gonzalo Vidal: 51–64.
- Elicki, O. and Schneider, J. 1992. Lower Cambrian (Atdabanian/Botomian) shallow-marine carbonates of the Görlitz Synclinorium (Saxony/Germany). *Facies* 26: 55–66.
- Esakova, N.V. and Zhegallo, E.A. [Zegallo, E.A.] 1996. Biostratigraphy and fauna of Lower Cambrian of Mongolia [in Russian]. *Sovmestnaâ Rossijsko-Mongol'skaâ Ekspediciâ, Trudy* 46: 1–214. Nauka, Moskva.
- Evans, K.R. 1992. *Marocella*: Antarctic specimen of an enigmatic Cambrian animal. *Journal of Paleontology* 66: 558–562.
- Evans, K.R. and Rowell, A.J. 1990. Small shelly fossils from Antarctica: an Early Cambrian faunal connection with Australia. *Journal of Paleontology* 64: 692–700.
- Fernández-Remolar, D.C. 2001. Chancelloridae del Ovetiense Inferior de la Sierra de Córdoba, España. *Revista Española de Micropaleontología* 16: 39–61.
- Fisher, D.W. 1962. Small conoidal shells of uncertain affinities. In: R.C. Moore (ed.), *Treatise on invertebrate paleontology, Part W, Miscellaneous*. W98–W143. Geological Society of America, Inc. and University of Kansas, Lawrence, Kansas.
- Fortey, R.A., Landing, E., and Skevington, D. 1982. Cambrian–Ordovician boundary sections in the Cow Head Group, western Newfoundland. In: M.G. Basset and W.T. Dean (eds.), *The Cambrian–Ordovician Boundary: Sections, Fossil Distributions, and Correlations. National Museum of Wales, Geological Series* 3: 95–129. Cardiff.
- Gaździcki, A. (ed.), 1987. Palaeontological Results of the Polish Antarctic Expeditions. Part I. *Palaeontologia Polonica* 49: 1–168.
- Gaździcki, A. and Wrona, R. 1982. Paleontological studies carried out during the Vth Antarctic Expedition of the Polish Academy of Sciences (1980–1981) [in Polish, English summary]. *Przegląd Geologiczny* 2: 57–61.
- Gaździcki, A. and Wrona, R. 1986. Polish paleontological studies in West Antarctica (1986) [in Polish, with English summary]. *Przegląd Geologiczny* 11: 609–617.
- Gedik, I. 1977. Conodont stratigraphy in the Middle Taurus. *Bulletin of the Geological Society of Turkey* 20: 35–48.
- Geyer, G. 1986. Mittelkambrische Mollusken aus Marokko und Spanien. *Senckenbergiana Lethaea* 67: 55–118.
- Grant, R.E. 1836. Animal kingdom. In: R.B. Todd (ed.), *The Cyclopaedia of Anatomy and Physiology*, 1, 107–118. Sherwood Gilbert and Piper, London.
- Gravestock, D.I. and Hibbert, J.E. 1991. Sequence stratigraphy of the Eastern Officer and Arrowie basins: a framework for Cambrian oil search. *The APEA Journal* 31: 177–190.
- Gravestock, D.I. and Shergold, J.H. 2001. Australian Early and Middle Cambrian sequence biostratigraphy with implications for species diversity and correlation. In: A. Yu. Zhuravlev and R. Riding (eds.), *Ecology of the Cambrian Radiation*, 107–136. Columbia University Press, New York.
- Gravestock, D.I., Alexander, E.M., Demidenko, Yu.E., Esakova, N.V., Holmer, L.E., Jago, J.B., Lin Tian-rui, Melnikova, L.M., Parkhaev, P.Yu., Rozanov, A.Yu., Ushatinskaya, G.T., Zang Wen-long, Zhegallo, E.A., and Zhuravlev, A.Yu. 2001. The Cambrian biostratigraphy of the Stansbury Basin, South Australia. *Transactions of the Palaeontological Institute* 282: 1–343. Nauka/Interperiodica, Moscow.
- Gubanov, A.P. and Peel, J.S. 2000. Cambrian monoplacophoran molluscs (Class Helcionelloida). *American Malacological Bulletin* 15: 139–145.
- He Tinggui 1981. Lower Cambrian (Meishucunian) sachtitids and their stratigraphic significance [in Chinese, with English summary]. *Chengdu Dizhi Xueyuan Xiebao [Journal of Chengdu College of Geology]* 1981 (2): 84–90.
- Hinde, G.J. 1888. A monograph of the British fossil sponges. *Palaeontographica Part II: Sponges of the Palaeozoic Group* 1887: 93–188.
- Hinz, I. 1987. The Lower Cambrian microfauna of Comley and Rushton, Shropshire/England. *Palaeontographica A* 198: 41–100.
- Hinz-Schallreuter, I. 1993a. Ostracodes from the Middle Cambrian of Australia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*: 188: 305–326.
- Hinz-Schallreuter, I. 1993b. Cambrian ostracodes mainly from Baltoscandia and Morocco. *Archiv für Geschichtekunde* 1 (7): 369–464.
- Hinz, I., Kraft, P., Mergl, M., and Müller, K.J. 1990. The problematic *Hadimopanella*, *Kaimenella*, *Milaculum* and *Utahphospha* identified as sclerites of Palaeoscolecida. *Lethaia* 23: 217–221.
- Holm, G. 1893. Sveriges kambrisk-siluriska Hyolithidae och Conulariidae [with English summary]. *Sveriges Geologiska Undersökning, Ser. C* 112: 1–172.
- Holmer, L.E., Popov, L.E., and Wrona, R. 1996. Early Cambrian lingulate brachiopods from glacial erratics of King George Island (South Shetland Islands), Antarctica. In: A. Gaździcki (ed.), *Palaeontological Results of the Polish Antarctic Expedition, Part II. Palaeontologia Polonica* 55: 37–50.
- Hou Xianguang and Bergström, J. 1994. Palaeoscolecid worms may be nematomorphs rather than annelids. *Lethaia* 27: 11–17.

- Kerber, M. 1988. Mikrofossilien aus unterkambrischen Gesteinen der Montagne Noire, Frankreich. *Palaentographica A* 202: 127–203.
- Konyushkov, K.N. [Konuškov, K.N.] and Shulyatin, O.G. [Šulátin, O.G.] 1980. On the archaeocyaths of Antarctica and their comparison with the archaeocyaths of Siberia [in Russian]. In: I.T. Žuravleva (ed.), *Kembrij Altae-Saïnskoj skládčatoj oblasti*, 143–150. Nauka, Moskva.
- Kouchinsky, A. 2000. Shell microstructures in Early Cambrian molluscs. *Acta Palaeontologica Polonica* 45: 119–150.
- Kraft, P. and Mergl, M. 1989. Worm-like fossils (Palaeoscolecida; ?Chaetognatha) from the Lower Ordovician of Bohemia. *Sbornik geologických věd, Paleontologie* 30: 9–36.
- Krautter, M. 2002. Fossil Hexactinellida: An Overview. In: J.N.A. Hooper and R.W.M. Van Soest (eds.), *Systema Porifera: A Guide to the Classification of Sponges. Vol. 2*, 1211–1223. Kluwer Academic/Plenum Publishers, New York.
- Kruse, P.D. 1990. Cambrian palaeontology of the Daly Basin. *Northern Territory Geological Survey, Report 7*: 1–58.
- Kruse, P.D. 1991. Cambrian fauna of the Top Springs Limestone, Georgina Basin. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 8: 169–188.
- Kruse, P.D. 1998. Cambrian palaeontology of the eastern Wiso and western Georgina Basin. *Northern Territory Geological Survey, Report 9*: 1–68.
- Kruse, P.D. and West, P.W. 1980. Archaeocytha of the Amadeus and Georgina Basins. *BMR Journal of Australian Geology and Geophysics* 5: 165–181.
- Landing, E. 1984. Skeleton of lapworthellids and the suprageneric classification of tommotiids (Early and Middle Cambrian phosphatic problematica). *Journal of Paleontology* 58: 1380–1398.
- Landing, E. 1988. Lower Cambrian of eastern Massachusetts: stratigraphy and small shelly fossils. *Journal of Paleontology* 62: 661–695.
- Landing, E., Geyer, G., and Bartowski, E.K. 2002. Latest Early Cambrian small shelly fossils, trilobites, and Hatch Hill dysaerobic interval on the Québec continental slope. *Journal of Paleontology* 76: 287–305.
- Laurie, J.R. 1986. Phosphatic fauna of the Early Cambrian Todd River Dolomite, Amadeus Basin, central Australia. *Alcheringa* 10: 431–454.
- Laurie, J.R. and Shergold, J.H. 1985. Phosphatic organism and the correlation of Early Cambrian carbonate formations in central Australia. *Bureau of Mineral Resources, Journal of Australian Geology and Geophysics* 9: 83–89.
- Luo Huilin, Jiang Zhiwen, Wu Xiche, Song Xueliang, Ouyang Lin, Xing Yusheng, Lui Guizhi, Zhang Shishan, and Tao Yonghe. 1982. *The Sinian–Cambrian Boundary in Eastern Yunan, China* [in Chinese, English summary]. 265 pp. Peoples Republic of China.
- Malakhov, V.V. [Malahov, V.V.] 1980. Cephalorhyncha—a new phylum of the Animal Kingdom united Priapulida, Kinorhyncha, Gordiacea, and Coelomata [in Russian]. *Zoologičeskij žurnal* 59 (4): 485–499.
- Mamet, B. and Roux, A. 1975. Algues Dévonienues et Carbonifères de la Téthys occidentale. *Revue de Micropaléontologie* 18: 130–187.
- Matthew, G.F. 1899. Studies on Cambrian faunas. No. 3. Upper Cambrian fauna of Mount Stephen, British Columbia. The trilobites and worms. *Transactions of the Royal Society of Canada, Section 4*, 5: 39–66.
- Matthews, S.C. and Missarzhevsky, V.V. 1975. Small shelly fossils of late Precambrian and early Cambrian age: a review of recent work. *Journal of the Geological Society* 131: 289–304.
- Märss, T. 1988. Early Palaeozoic hadimopanellids of Estonia and Kirgizia (USSR). *Proceedings of the Academy of Sciences of the Estonian SSR, Geology* 37: 10–17.
- Mehl, D. 1996. Organization and microstructure of the cancelloriid skeleton: implications for the biomineralization of the Cancelloriidae. *Bulléin de l'Institut Océanographique, Monaco, numéro spécial* 14: 377–385.
- Mehl, D. 1998. Porifera and Cancelloriidae from the Middle Cambrian of the Georgina Basin, Australia. *Palaentologia* 41: 1153–1182.
- Melnikova, L.M. 2000. A new genus of Bradoriidae (Crustacea) from the Cambrian of Northern Eurasia [in Russian]. *Paleontologičeskij žurnal* 2000 (2): 65–68.
- Meshkova, N.P. [Meškova, N.P.] 1985. New tubular problematica of the Middle Cambrian of Siberia and Middle Asia [in Russian]. In: B.S. Skolov and I.T. Žuravleva (eds.), *Problematiki pozdnego dokembrii i paleozoia. Trudy, Institut geologii i geofiziki SO AN SSSR* 632: 127–133. Nauka, Moskva.
- Missarzhevsky, V.V. [Missarževskij, V.V.] 1966. The first finds of *Lapworthella* in the Lower Cambrian of the Siberian platform [in Russian]. *Paleontologičeskij žurnal* 1966 (1): 13–18.
- Missarzhevsky, V.V. [Missarževskij, V.V.] 1970. New generic name *Tommotia* Missarzhevsky, nom. nov. [in Russian]. *Paleontologičeskij žurnal* 1970 (4): 100.
- Missarzhevsky, V.V. [Missarževskij, V.V.] 1977. Conodonts (?) and Cambrian phosphatic problematica from Mongolia and Siberia [in Russian]. In: L.P. Tatarinov (ed.), *Bespozvonočnye paleozoia Mongolii. Sovmestnââ Rossijsko-Mongol'skaâ Ekspediciâ (Trudy)*, 10–19. Nauka, Moskva.
- Missarzhevsky, V.V. [Missarževskij, V.V.] 1981. Early Cambrian hyoliths and gastropods of Mongolia [in Russian]. *Paleontologičeskij žurnal* 1981 (1): 21–28.
- Missarzhevsky, V.V. [Missarževskij, V.V.] 1989. Oldest skeletal fossils and stratigraphy of correlation of the Precambrian and Cambrian boundary beds [in Russian]. *Trudy Geologičeskogo Instituta AN SSSR* 443: 1–238. Nauka, Moskva.
- Missarzhevsky, V.V. [Missarževskij, V.V.] and Mambetov, A.M. 1981. Stratigraphy and fauna of Cambrian and Precambrian boundary beds of Maly Karatau [in Russian]. *Trudy Geologičeskogo Instituta AN SSSR* 326: 1–92. Leningrad.
- Morycowa, E., Rubinowski, Z. and Tokarski, A.K. 1982. Archaeocyathids from a moraine at Three Sisters Point, King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica* 74: 73–80.
- Mostler, H. 1985. Neue heteractinidae Spongien (Calcipongea) aus dem Unter- und Mittel-Kambrium Südwestsardiniens. *Berichte des Naturwissenschaftlich-medizinischen Vereins in Innsbruck* 72: 7–32.
- Mostler, H. and Mosleh-Yazdi, A. 1976. Neue Poriferen aus oberkambrischen Gesteinen der Milafaformation im Elburzgebirge (Iran). *Geologisch-Paläontologische Mitteilungen Innsbruck* 5: 1–36.
- Müller, K.J. 1973. *Milaculum* n. g. ein phosphatisches Mikrofossil aus dem Altpaläozoikum. *Paläontologische Zeitschrift* 47: 217–228.
- Müller, K.J. and Miller, J.F. 1976. The problematic microfossil *Utahphospha* from the Upper Cambrian of the western United States. *Lethaia* 9: 391–395.
- Müller, K.J. and Hinz-Schallreuter, I. 1993. Palaeoscolecoid worms from the Middle Cambrian of Australia. *Palaentologia* 36: 543–592.
- Nicholson, H.A. and Etheridge, R., Jr. 1878. *A monograph of the Silurian fossils of the Girvan District in Ayrshire with special reference to those contained in the "Gray Collection". Vol. I, Fasciculus 1 (Rhizopoda, Actinozoa, Trilobita)*. 135 pp. W. Blackwood and Sons, Edinburgh.
- Nitecki, M.H. 1986. Receptaculitids and their relationship to other problematic fossils. In: A. Hoffman and M. H. Nitecki (eds.), *Problematic Fossil Taxa*, 27–34. Oxford University Press, Calderon Press, New York, Oxford.
- Nitecki, M.H. and Debrenne, F. 1979. The nature of radiocyathids and their relationship to receptaculitids and archaeocyathids. *Geobios* 12: 5–27.
- Okulich, V.I. 1937. Some changes in nomenclature of Archaeocyathi (Cyathospongia). *Journal of Paleontology* 11: 251–252.
- Okulich, V.I. 1955. Archaeocyatha. In: R.C. Moore (ed.), *Treatise on invertebrate paleontology, Part E*, 1–20. Geological Society of America, Inc. and University of Kansas, Lawrence, Kansas.
- Palmer, A.R. and Rowell, A.J. 1995. Early Cambrian trilobites from the Shackleton Limestone of the central Transantarctic Mountains. *The Paleontological Society, Memoir* 45: 1–28.
- Peel, J.S. 1988. *Spirellus* and related helically coiled microfossils (cyanobacteria) from the Lower Cambrian of North Greenland. *Rapport Grønlands Geologiske Undersøgelse* 137: 5–32.
- Peel, J.S. 1991. Functional morphology, evolution and systematics of Early Palaeozoic univalved molluscs. *Rapport Grønlands Geologiske Undersøgelse, Bulletin* 161: 1–116.
- Peel, J.S. and Blaker, M.R. 1988. The small shelly fossils *Mongolitulubus* from the Lower Cambrian of central North Greenland. *Rapport Grønlands Geologiske Undersøgelse* 137: 55–60.
- Pelman, Yu.L. [Pel'man, Ū.L.] and Pereladov, V.S. 1986. Stratigraphy and brachiopods of the Lower–Middle Cambrian of the Arga-Sala River (Southern Anabar area) [in Russian]. In: I.T. Žuravleva (ed.), *Biostratigrafiâ i paleontologijâ kembrii Severnoj Azii. Trudy, Institut geologii i geofiziki SO AN SSSR* 669: 119–133. Nauka, Moskva.
- Pickett, J. 2002. Order Heteractinida Hinde. In: J.N.A. Hooper and R.W.M. Van Soest (eds.), *Systema Porifera: A Guide to the Classification of Sponges. Vol. 2*, 1121–1139. Kluwer Academic/Plenum Publishers, New York.
- Popov, L.E. and Solovjev, I.A. [Sol'ov'ev, I.A.] 1981. Middle Cambrian inarticulate brachiopods, cancelloriids, coniconchiids and trilobites of West Antarctica (Shackleton and Argentina Ranges) [in Russian]. *Antarktika, Doklady Komissii* 20: 64–72. Nauka, Moskva.

- Poulsen, C. 1967. Fossils from the Lower Cambrian of Bornholm. *Danske Videnskaberne Selskab, Matematisk-Fysiske Meddelelser* 36: 1–48.
- Pratt, B.R. 1984. *Epiphyton* and *Renalcis*: Diagenetic microfossils from calcification of coccooid blue-green algae. *Journal of Sedimentary Petrology* 54: 948–971.
- Pratt, B.R. 2001. Calcification of cyanobacterial filaments: *Girvanella* and the origin of lower Paleozoic lime mud. *Geology* 29: 763–766.
- Qian Yi. 1990 [year of imprint 1989]. Early Cambrian small shelly fossils of China with special references to the Precambrian–Cambrian boundary. *Stratigraphy and Palaeontology of Systemic Boundaries in China, Precambrian–Cambrian Boundary* (2) [in Chinese, English summary]. 341 pp. Nanjing University Publishing House, Nanjing.
- Qian Yi and Bengtson, S. 1989. Palaeontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province, South China. *Fossils and Strata* 24: 1–156.
- Rees, M.N., Pratt, B.R., and Rowell, A.J. 1989. Early Cambrian reefs, reef complexes and associated lithofacies of the Shackleton Limestone, Transantarctic Mountains. *Sedimentology* 36: 341–361.
- Reif, W.E. 1968. Schwammreste aus dem oberen Ordovizium von Estland und Schweden. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1968 (12): 733–744.
- Repetski, J.E. 1981. An Ordovician occurrence of *Utahphospha* Müller and Miller. *Journal of Paleontology* 55: 395–400.
- Riding, R. 1991. Calcified Cyanobacteria. In: R. Riding (ed.), *Calcareous algae and stromatolites*, 55–87. Springer-Verlag, Berlin.
- Riding, R. and Fan, J. 2001. Ordovician calcified algae and Cyanobacteria, Northern Tarim Basin subsurface, China. *Palaeontology* 44: 783–810.
- Rigby, J.K. 1978. Porifera of the Middle Cambrian Wheeler Shale, from the Wheeler Amphitheater, House Range, in western Utah. *Journal of Paleontology* 52: 1325–1345.
- Rigby, J.K. 1983. Heteractinida. In: T.W. Broadhead (ed.), *Sponges and spongiomorphs. Paleontological Society Short Courses in Paleontology, 1. University of Tennessee Department of Geological Sciences, Studies in Geology* 7: 70–89.
- Rigby, J.K. 1986. Sponges of the Burgess Shale (Middle Cambrian), British Columbia. *Palaeontographica Canadiana* 2: 1–105.
- Rowell, A.J., Evans, K.R., and Rees, M.N. 1988. Fauna of the Shackleton Limestone. *Antarctic Journal of the United States* 23: 13–14.
- Rowell, A.J. and Rees, M.N. 1989. Early Palaeozoic history of the Beardmore Glacier area: implications for a major Antarctic structural boundary within the Transantarctic Mountains. *Antarctic Science* 1: 249–260.
- Rowell, A.J., Rees, M.N., and Evans, K.R. 1992. Evidence of major Middle Cambrian deformation in the Ross Orogen, Antarctica. *Geology* 20: 31–34.
- Rozanov, A.Yu. 1986. Problematica of the Early Cambrian. In: A. Hoffman and M.H. Nitecki (eds.), *Problematic Fossil Taxa*, 87–96. Oxford University Press, Calderon Press, New York, Oxford.
- Rozanov, A.Yu. [Rozanov, A.Ū.] and Missarzhevsky, V.V. [Missarževskij, V.V.] 1966. Biostratigraphy and fauna of the Cambrian lower horizons [in Russian]. *Trudy Geologičeskogo Instituta Akademii Nauk SSSR* 148: 1–126. Nauka, Moskva.
- Rozanov, A.Yu. and Zhuravlev, A.Yu. 1992. The Lower Cambrian fossil record of the Soviet Union. In: J.H. Lipps and P.W. Signor (eds.), *Origin and Early Evolution of the Metazoa*, 205–282. Plenum Press, New York.
- Rozanov, A.Yu. [Rozanov, A.Ū.], Missarzhevsky, V.V. [Missarževskij, V.V.], Volkova, N.A., Voronova, L.G., Krylov, I.N., Keller, B.M., Korolyuk, I.K. [Korolúk, I.K.], Lenzion, K., Michniak, R., Paychlova, N.G. [Pajchlova, N.G.], and Sidorov, A.D. 1969. Tommotian Stage and the Cambrian lower boundary problem [in Russian]. *Trudy Geologičeskogo Instituta Akademii Nauk SSSR* 206: 1–380. Nauka, Moskva.
- Runnegar, B. 1982. The Cambrian explosion: Animals or fossils? *Journal of the Geological Society* 29: 395–411.
- Schmidt, O. 1870. *Grundzüge einer spongiengfauna des Atlantischen gebietes*. 88 pp. Wilhelm Engelmann, Leipzig.
- Sdzuy, K. 1969. Unter- und mittelkambrische Porifera (Chancelloriidae und Hexactinellida). *Paläontologische Zeitschrift* 43: 115–147.
- Shabanov, Yu.Ya. [Šabanov, Ū.Ā.], Astashkin, V.A. [Astaškin, V.A.], Pegel, T.V., Jegerova, L.I., Zhuravleva, I.T. [Žuravleva, I.T.], Pelman, Yu.I., Sundukov, V.M., Stepanova, M.V., Sukhov, S.S. [Suhov, S.S.], Fedorov, A.B., Shishkin, B.B. [Šiškin, B.B.], Vaganova, N.V., Jermak, V.I., Ryabukha, K.V. [Rābuha, K.V.], Yadrenkina, A.G. [Ādrenkina, A.G.], Abaimova, G.P. Lopushinskaya, T.V. [LopušinskaĀ, T.V.], Sychev, O.V. [Syčev, O.V.], and Moskalenko, T.A. 1987. *Nižnij paleozoj zapadnogo sklona Anabarskoj anteklizy (po materialam bureniĀ)*. 207 pp. Nauka, Novosibirsk.
- Skovsted, C.B., and Peel, J.S. 2001. The problematic fossil *Mongolotubulus* from the Lower Cambrian of Greenland. *Bulletin of the Geological Society of Denmark* 48: 135–147.
- Solovjev, I.A. and Grikurov, G.E. 1979. New evidence on Cambrian trilobites distribution in the Argentina and Shackleton Ranges [in Russian]. *Antarktika, Doklady Komissii* 18: 54–73. Nauka, Moskva.
- Tate, R. 1892. The Cambrian fossils of South Australia. *Transactions of the Royal Society of South Australia* 15: 183–189.
- Ushatinskaya, G.T. 1996. Brachiopod paleozoogeography through the Cambrian. In: P. Cooper and J. Jin (eds.), *Brachiopods, Proceedings of the Third International Brachiopod Congress*, 275–280. Balkema, Rotterdam.
- Walcott, C.D. 1886. Second contribution to the studies on the Cambrian faunas of North America. *U.S. Geological Survey Bulletin* 30: 225.
- Walcott, C.D. 1920. Middle Cambrian Spongiae. *Smithsonian Miscellaneous Collections* 67: 261–364.
- Whittard, W.F. 1953. *Palaeoscolex piscatorum* gen. et sp. nov., a worm from the Tremadocian of Shropshire. *Quarterly Journal of the Geological Society, London* 109: 125–135.
- Wood, A. 1957. The type-species of the genus *Girvanella* (calcareous algae). *Palaeontology* 1: 22–28.
- Wood, A., Zhuravlev, A.Yu., and Chimed Tseren, A. 1993. The ecology of Lower Cambrian buildups from Zuune Arts, Mongolia: implications for early metazoan reef evolution. *Sedimentology* 40: 829–858.
- Wrona, R. 1982. Early Cambrian phosphatic microfossils from southern Spitsbergen (Horsund region). *Palaeontologia Polonica* 43: 9–16.
- Wrona, R. 1987. Cambrian microfossil *Hadimopanella* Gedik from glacial erratics in West Antarctica. In: A. Gaździcki (ed.), *Palaeontological Results of the Polish Antarctic Expeditions, Part I. Palaeontologia Polonica* 49: 37–48.
- Wrona, R. 1989. Cambrian limestone erratics in the Tertiary glacio-marine sediments of King George Island, West Antarctica. *Polish Polar Research* 10: 533–553.
- Wrona, R. 2003. Early Cambrian molluscs from glacial erratics of King George Island, West Antarctica. *Polish Polar Research* 24: 181–216.
- Wrona, R. and Hamdi, B. 2001. Palaeoscolecid sclerites from the Upper Cambrian Mila Formation of the Shahmirzad section, Alborz Mountains, northern Iran. *Acta Geologica Polonica* 51: 101–107.
- Wrona, R. and Zhuravlev, A.Yu. 1996. Early Cambrian archaeocyaths from glacial erratics of King George Island (South Shetland Islands), Antarctica. In: Gaździcki (ed.), *Palaeontological Results of the Polish Antarctic Expedition. Part II. Palaeontologia Polonica* 55: 9–36.
- Xing Yusheng, Ding Qixiu, Luo Huilin, He Tinggui, Wang Yangong, et al. (eds.) 1984 [1983]. The Sinian–Cambrian Boundary of China [in Chinese]. *Bulletin of the Institute of Geology, Chinese Academy of Geological Sciences* 10: 1–262.
- Yates, A.M. 1994. *The Biostratigraphy of the Small Skeletal Fossils of the Early Cambrian, Ajax Limestone*. 38 pp. B.Sc. Honours thesis. Department of Geology and Geophysics, University of Adelaide (unpublished).
- Yin Jicheng, Ding Lianfeng, He Tinggui, Li Shiling, and Shen Lijuan. 1980. *The Palaeontology and Sedimentary Environment of the Sinian System in Emei-Ganuluo Area, Sichuan* [in Chinese]. 231 pp. Geological College of Chengdu, Chengdu.
- Zhang Xiguang and Pratt, B.R. 1996. Early Cambrian palaeoscolecid cuticles from Shaanxi, China. *Journal of Paleontology* 70: 275–279.
- Zhou Benhe and Xiao Ligong. 1984. (Early Cambrian monoplacophorans and gastropods from Huainan and Huoqui counties, Anhui Province) [in Chinese]. *Professional Papers of Stratigraphy and Palaeontology, Chinese Academy of Geological Sciences* 13: 125–140.
- Zhuravlev, A.Yu. 1986. Radiocyathids. In: A. Hoffman and M.H. Nitecki (eds.), *Problematic Fossil Taxa*, 35–44. Oxford University Press, Calderon Press, New York, Oxford.
- Zhuravlev, A.Yu. and Gravesstock, D.I. 1994. Archaeocyatha from Yorke Peninsula, South Australia and archaeocyathan Early Cambrian zonation. *Alcheringa* 18: 1–54.
- Zhuravlev, A.Yu. and Wood, R.A. 1996. Anoxia as the cause of the mid-Early Cambrian (Botomian) extinction event. *Geology* 24: 311–314.
- Zhuravleva, I.T. [Žuravleva, I.T.] and Korde, K.B. 1955. Finds of sponge *Chancelloria* Walcott in the Lower Cambrian deposits of Siberia [in Russian]. *Doklady Akademii Nauk SSSR* 104: 474–477. Nauka, Moskva.