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CAMBRIAN – EARLY ORDOVICIAN BRACHIOPODS FROM MALYI KARATAU, THE WESTERN BALKHASH REGION, AND TIEN SHAN, CENTRAL ASIA

BY

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with 51 plates, 27 tables and 19 text-figures

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ABSTRACT. Carbonate platform deposits of the Shabakty Group in the Malyi Karatau Range of southern Kazakhstan contain rich brachiopod faunas of early Cambrian (Botomian)–early Ordovician (Arenig) age. Seven biostratigraphically successive assemblages are defined across this interval. Four further discrete microbrachiopod assemblages occur in Middle–Upper Cambrian sequences of various adjacent Central Asian regions, including the Suukadyr Mountains of the southern Betpak-Dala Desert (Darbaza Formation), the western side of Lake Balkhash (Zhalgyz Formation), north-west Balkhash (Sarykumy Formation), the Kostek Range of North Tien Shan (Karagajly Formation), and the Moldotau Range in Central Tien Shan (Karadzhorga Formation). Linguliformean (organophosphatic-shelled) stocks are dominant, comprising 74 of the 88 described species. In a total of 55 identified genera, 47 are linguliformeans and eight are rhynchonelliformeans. *Diencobolus* is defined as a new linguliformean genus, and there are 11 new species of linguliformeans, referred to the lingulides *Notiobolus indefinitus*, *Canalilatus*? *major*, *Mirilingula postuma*, *Diencobolus simplex*, *Canthylotreta atasuica*, *Dactylotreta septata*, *Picnotreta karakichiensis*, *Stilpnotreta minuta*, *Pomeraniotreta obtusa*, *Kleithriatreta kostekensis*, and *Eoscaphelasma*? *delicata*. Twenty-four taxa are described under open nomenclature.

Brachiopods from different segments of the Central Asian tectonic collage have different biogeographical signatures. In the early Cambrian, Malyi Karatau was probably part of the Yangtse Plate (South China). Middle Cambrian affinities were with East Gondwana (eastern Australia), but by the end of the mid Cambrian westward drift introduced links with Baltica and Laurentia. Balkhash and Tien Shan terranes retained East Gondwanan relationships throughout the Cambrian.

KEY WORDS: Brachiopoda, Linguliformea, Rhynchonelliformea, Cambrian, Ordovician, biostratigraphy, biogeography, Central Asian terranes.

WELL-EXPOSED Cambrian and Lower Ordovician sections (Shabakty Group) in the Malyi Karatau Range of southern Kazakhstan (Text-figs 1–7) form one of the most complete carbonate successions in Central Asia; they contain rich brachiopod faunas, providing excellent opportunities to trace major patterns of change in brachiopod assemblages across the long interval from the early Botomian (early Cambrian) to the Kogashik Regional Stage [Text-fig. 13; corresponding to the upper Hunneberg and Billingen stages of Baltoscandia (early Arenig)]. According to Cook *et al.* (1991), the limestones and dolomites of the Shabakty Group include carbonate platform and slope-rise lithofacies, deposited originally on a submarine sea-mount (named by those authors as the Aish-ibi mound), which was situated a considerable distance away from major continental massifs. However, abundant Lower Cambrian trilobite faunas associated with brachiopods in the Malyi Karatau Range demonstrate close similarity to the *Redlichia* Trilobite Province, which includes faunas that inhabited areas of North and South China as well as the Australian part of Gondwana (Ergaliev and Pokrovskaya 1977). Similar congruence of trilobite assemblages from South Kazakhstan, South China and Australia can also be traced in the late Cambrian and early Ordovician (Shergold 1988). Detailed conodont biozonation and correlation have been established for the late Cambrian and early Ordovician intervals in Malyi Karatau (Dubinina 1991), allowing precise stratigraphical ranges to be plotted for the brachiopod faunas.

The only other evidence of continuous late Precambrian–early Palaeozoic carbonate sedimentation within the Kazakhstanian orogen is from the area north-west of Lake Balkhash (Text-figs 1, 8–9), where severely dislocated sedimentary rocks, comprising mostly limestones and dolomites of the Sarykumy Formation, are exposed in numerous scattered outcrops between the Atasu and Zhamshy rivers. Because of complicated tectonics, the Cambrian–early Ordovician sedimentary history of this area was reconstructed from study of numerous fragments of the sequence preserved in separate tectonic blocks (Zhemchuzhnikov 1990).

Two Middle–early Upper Cambrian lingulate brachiopod assemblages have been recovered from isolated localities in north Kyrgyzstan [Kirgizia] (Kostek Ridge in North Tien Shan, and the Moldotau Range in Central Tien Shan; Text-figs 10–11). This is the first documented record of diverse Cambrian microbrachiopod faunas in these areas.

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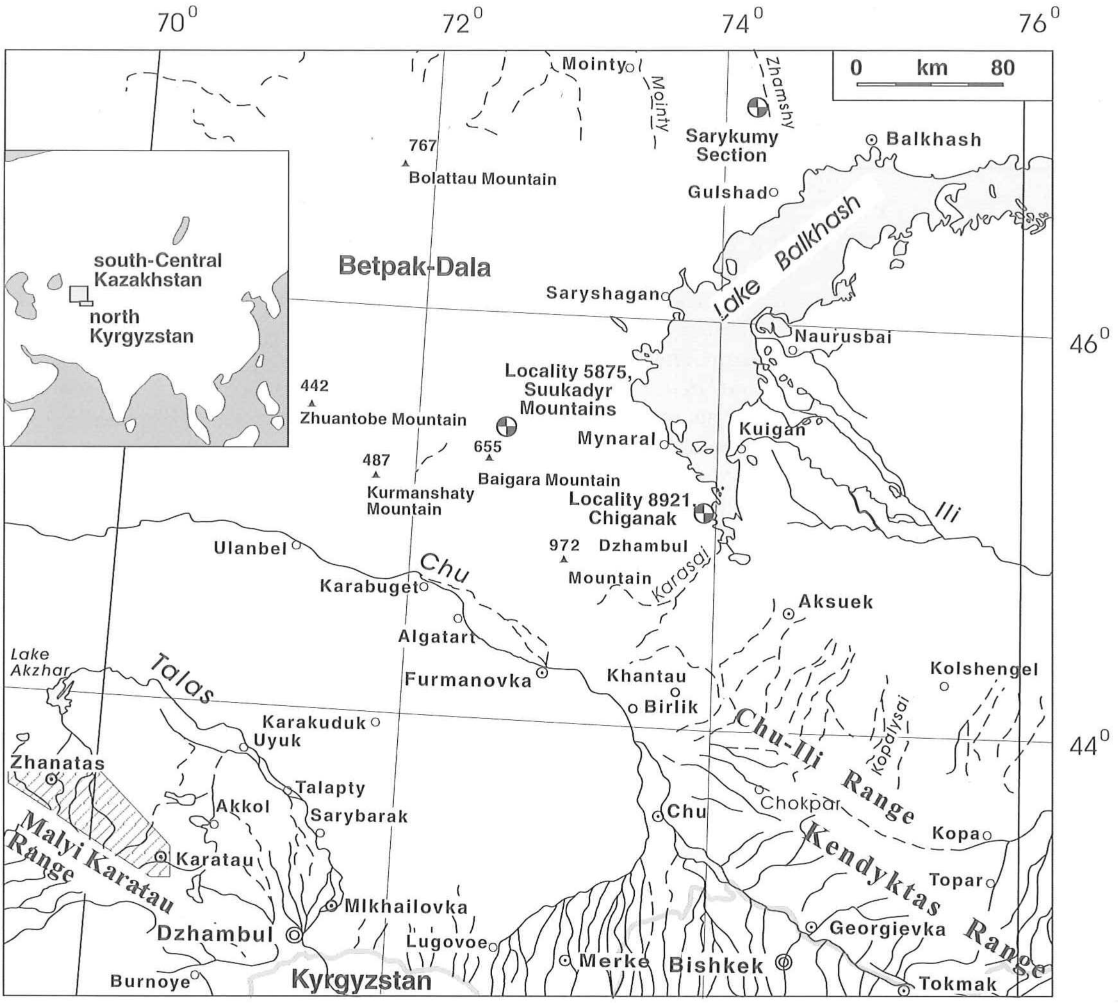
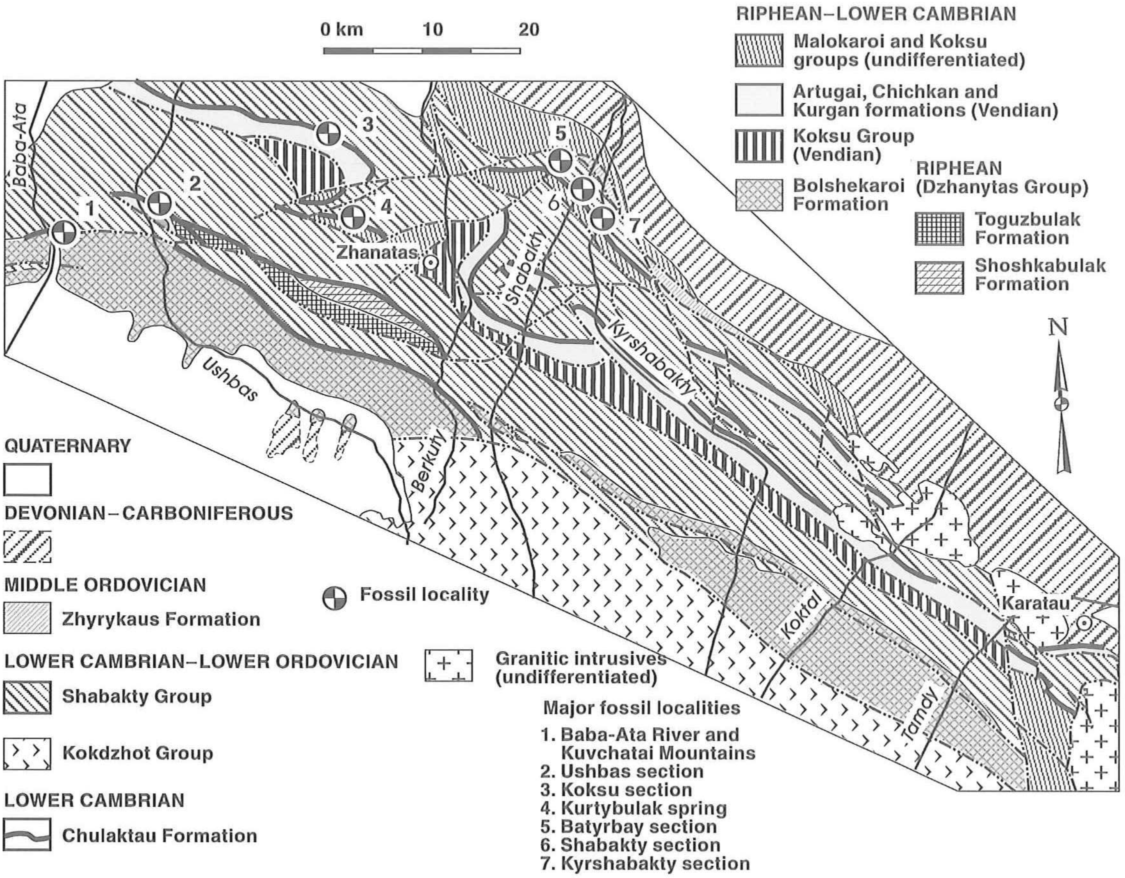


TEXT-FIG. 1. Locality map of south-central Kazakhstan showing the general outcrop area of Cambrian–Ordovician rocks in the Malyi Karatau Range, and Cambrian fossil localities of the Lake Balkhash region.

The Middle and Upper Cambrian sequences of Sarykumy and north Kyrgyzstan do not provide satisfactory information on precise stratigraphical ranges of brachiopod assemblages, but the abundance of lingulate taxa with strong Australian affinities adds important supplementary data to those from Malyi Karatau for analysis of the palaeobiogeography and tectonic history of Kazakhstanian terranes during the Cambrian.

GEOLOGY AND STRATIGRAPHY OF MALYI KARATAU

In the Malyi Karatau Range fossiliferous Cambrian and Lower Ordovician carbonate deposits are exposed continuously in several fault-bounded blocks between the Baba-Ata River in the north-west and the town of Karatau in the south-east (Text-figs 1–2). Details of the late Precambrian and early Palaeozoic geology and stratigraphy of this area, together with interpretations of the depositional environments, have been

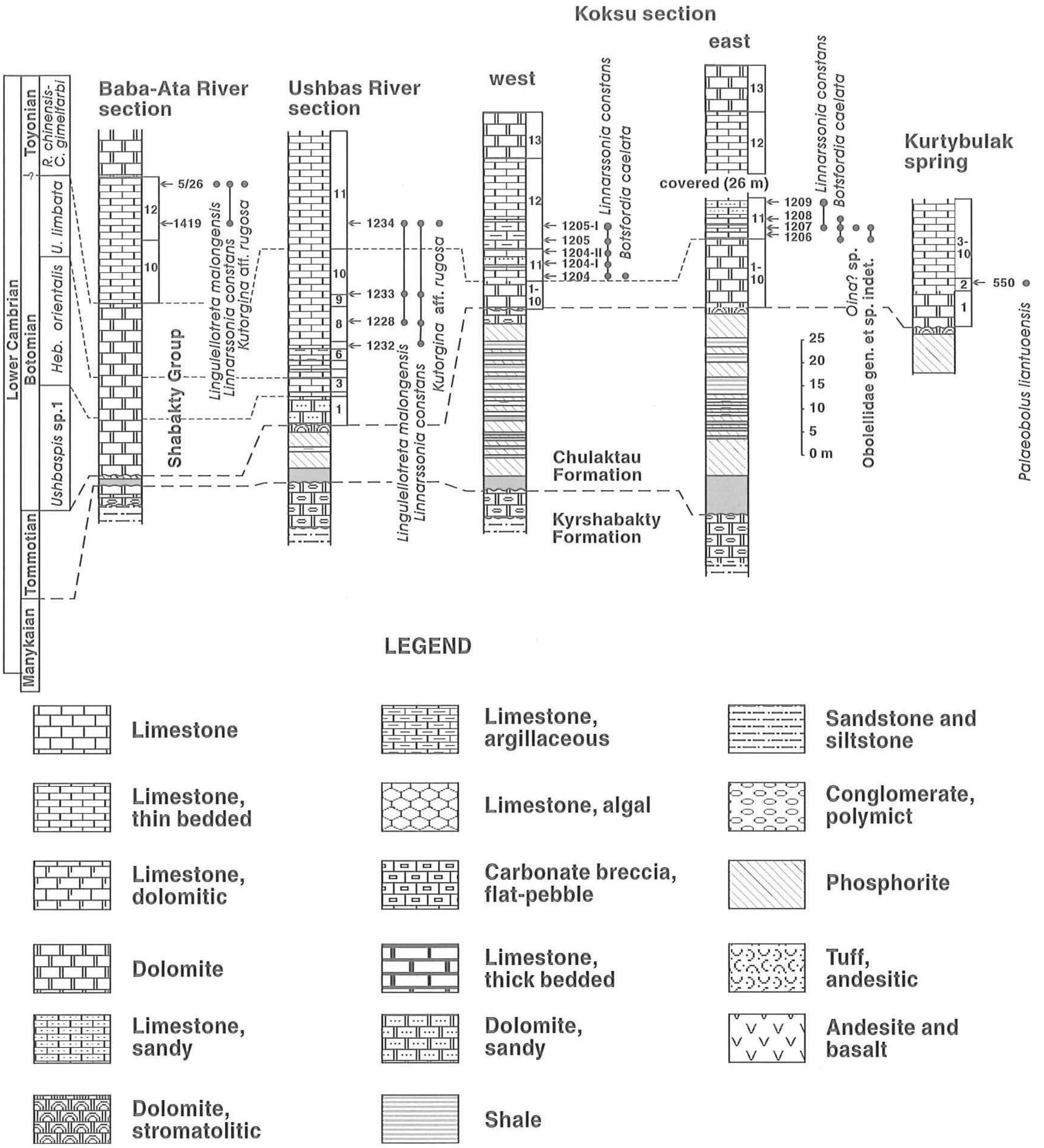


TEXT-FIG. 2. Schematic geological map of the Malyi Karatau Range with location of the major Cambrian and Lower Ordovician sections; mainly after Eganov and Sovetov (1979).

published by Esenov (1971), Eganov and Sovetov (1979), Missarzhevsky and Mambetov (1981), Abdulin *et al.* (1986, 1990), Cook *et al.* (1991), Mambetov (1993), and others.

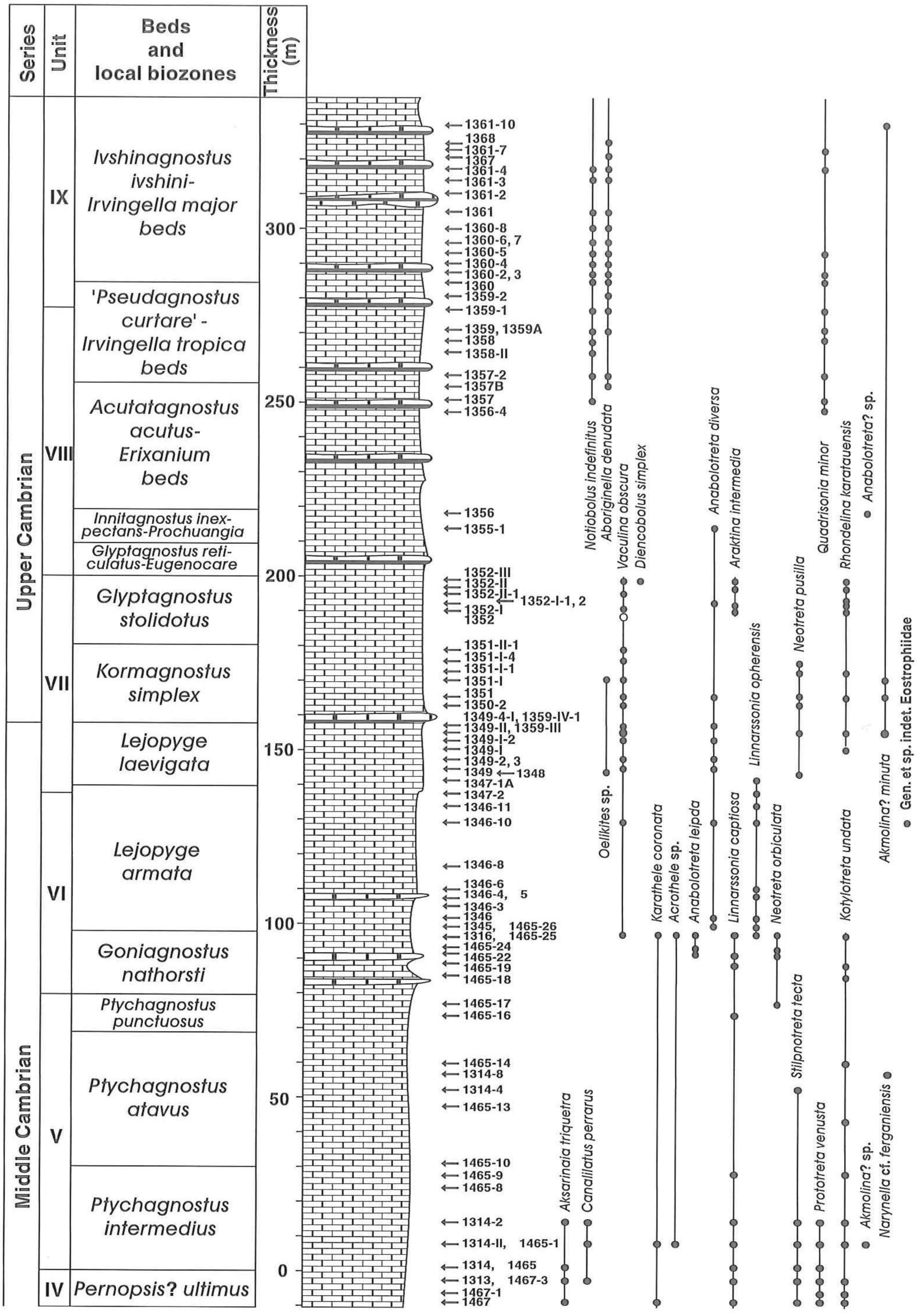
Lower Palaeozoic strata in Malyi Karatau are not strongly dislocated tectonically, so that relationships between major stratigraphical units can be recognised confidently, but the local stratigraphical terminology, as well as ranges and ranks of some lithostratigraphical and biostratigraphical units, vary considerably. To avoid confusion, we here refer to local lithostratigraphical nomenclature somewhat minimally, and instead we use mainly the local biostratigraphical subdivisions (Text-figs 4–6) based on small shelly fossils for the Lower Cambrian (Missarzhevsky and Mambetov 1973; Mambetov 1993), trilobites for the Lower Cambrian–Lower Ordovician interval (Ergaliev and Pokrovskaya 1977; Ergaliev 1980; Apollonov 1988; Abdulin *et al.* 1990), and conodonts for the Upper Cambrian–Lower Ordovician (Dubinina 1991). The major lithostratigraphical subdivisions accepted and discussed here are: (1) Lower Cambrian (Manykaian) Kyrshabakty Formation (=Kengobysai Formation of Abdulin *et al.* 1990); (2) Lower Cambrian (Tommotian) Chulaktau Formation; (3) Lower Cambrian (upper Atdabanian)–Lower Ordovician (Arenig) Shabakty Group (Text-fig. 3).

There are several concurring concepts of the lithostratigraphical subdivision of the Shabakty Group (Eganov and Sovetov 1979; Abdulin *et al.* 1990; Zhemchuzhnikov 1990). As with the lithostratigraphy of the Malyi Karatau Range as a whole we use a Shabatky lithostratigraphical scheme as simply as possible,

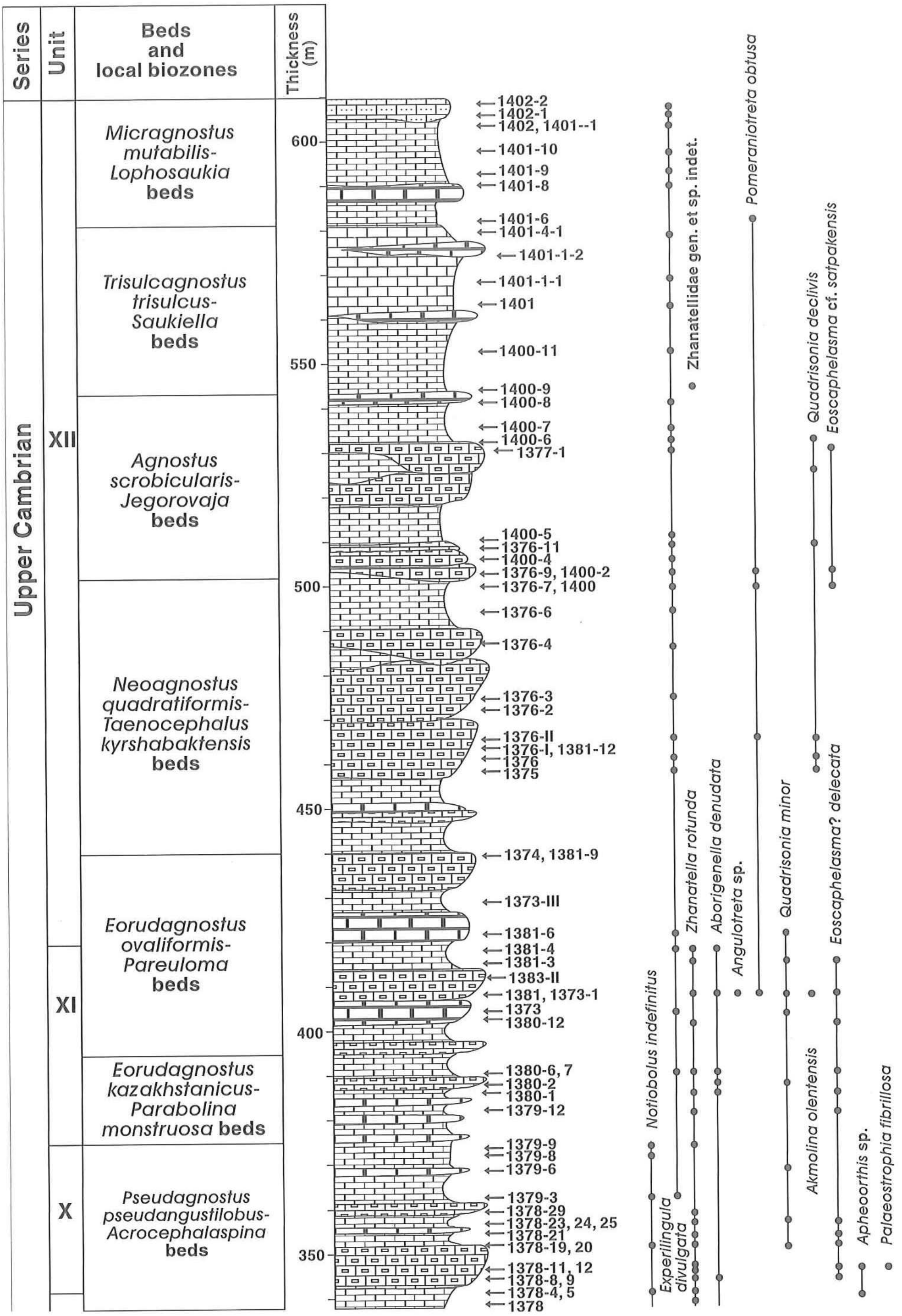


TEXT-FIG. 3. Generalized stratigraphical successions through the main Lower Cambrian sections in the Malyi Karatau Range showing distribution of brachiopods; modified after Gorjansky and Koneva (1983, fig. 2). The lithological key is also applicable to Text-figures 4–6, 9 and 11.

and thus we employ the informal units (and biostratigraphical divisions) established for the Batyrbay and Kyrshabakty sections in the readily available guide book of Abdulin *et al.* (1990). However, biostratigraphical subdivision of the Middle and Upper Cambrian strata based on trilobites is also not very stable and has been amended several times in the last two decades, in parts significantly (Ergaliev 1977, 1980; Abdulin *et al.* 1990). Cambrian biostratigraphy of Malyi Karatau is discussed in more detail below.



TEXT-FIG. 4. Generalized stratigraphical succession through the Middle–lower Upper Cambrian of the Kyrshabakty section, Malyi Karatau, showing sampled levels and distribution of brachiopods; modified after Abdullin *et al.* (1990). Key as in Text-figure 3.



TEXT-FIG. 5. Generalized stratigraphical succession through the upper Upper Cambrian deposits of the Kyrshabakty section, Malyi Karatau, showing sampled levels and distribution of brachiopods; modified after Abdullin *et al.* (1990). Key as in Text-figure 3.

Brachiopods appear in the Malyi Karatau sequence within the lower part of the Shabakty Group (*Microcornus parvulus* Biozone), whereas the underlying Kyrshabakty and Chulaktau formations do not contain brachiopods. However, a brief outline of the stratigraphy and non-brachiopod biostratigraphy of the Lower Cambrian deposits of Malyi Karatau is of relevance for our discussion below of correlation of these sections, as well as for understanding the palaeogeographical position of south Kazakhstanian terranes in the early Palaeozoic.

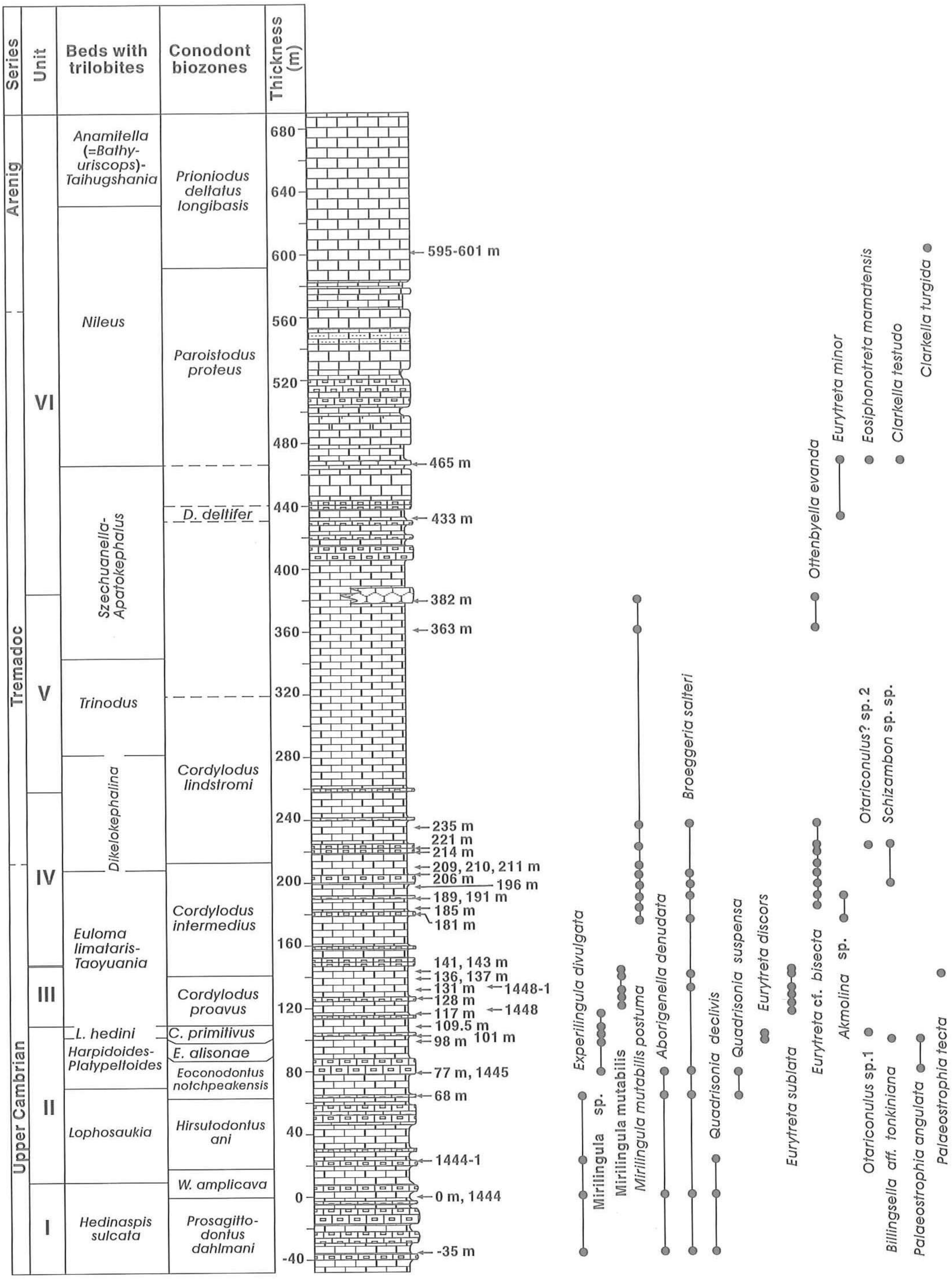
The Kyrshabakty Formation, up to 160 m thick, is the oldest fossiliferous unit in the sequence, comprising mainly fine clastic rocks with up to four beds of glauconitic sandstone and lenses and interlayers of dolomite. It rests discontinuously on Precambrian rocks of the Malakaroi Group (Eganov and Sovetov 1979, pp. 32–58). According to Missarzhevsky (*in* Rozanov and Sokolov 1984) and Mambetov (1993), the Kyrshabakty Formation also includes a bed of stromatolitic dolomite up to 12 m thick, known also as the 'Lower Dolomite' or Berkuty Formation, which was assigned in some publications to the overlying Chulaktau Formation (Eganov and Sovetov 1979; Abdulin *et al.* 1990). The 'Lower Dolomite' contains a diverse assemblage of small shelly fossils interpreted by Missarzhevsky and Mambetov (1981) as diagnostic for the *Protohertzina anabarica* Biozone.

Recent studies by Mambetov (1993) demonstrated the presence of a low diversity assemblage of anabaritids, including *Anabarites trisulcus* Missarzhevsky, *A. signatus* Missarzhevsky, *Cambrotubulus decurvatus* Missarzhevsky and the protoconodonts *Protohertzina anabarica* and *P. unguliformis* Missarzhevsky, in a basal dolomitic conglomerate; this fauna is thus within the *P. anabarica* Biozone, indicative of an early Cambrian (Manykaian) age for the unit. Previously, the Kyrshabakty Formation was regarded as latest Vendian in age (Eganov and Sovetov 1979; Abdulin *et al.* 1990).

The Chulaktau Formation is up to 65 m thick and subdivided into three formal units (Eganov and Sovetov 1979; Mambetov 1993): (1) the *Aksai Member*, a lower unit of bedded chert with thin units of argillite and phosphorite, total up to 20 m thick; (2) the Karatau Member consisting of two ('lower' and 'upper') phosphoritic beds separated by a unit of argillite and chert, total usually about 20 m, but in some sections up to 40 m thick; (3) the upper, *Ushbas Member* containing a lower conglomeratic bed with a ferromanganese dolomitic matrix, and an overlying bed of stromatolitic dolomite, in total 2–5 m thick. The lower boundary of the Chulaktau Formation is a discontinuity surface with traces of erosion of underlying dolomites of the Berkuty Member (Eganov and Sovetov 1979, p. 72). Missarzhevsky (*in* Rozanov and Sokolov 1984) suggested a conformable contact between the Kyrshabakty and Chulaktau formations.

Three local biozones based on small shelly fossils (*Tiksitheca licis* Biozone, *Pseudorthotheca costata* Biozone and *Bercutia cristata* Biozone) are recognised in the Chulaktau Formation (Missarzhevsky and Mambetov 1981; Mambetov 1993). These data suggest a Tommotian age.

The Shabakty Group is a thick, continuous sequence of carbonate rocks. The Lower Cambrian part of the Group (Dzhylandy Formation of Eganov and Sovetov 1979, p. 107), 50–250 m thick, consists mostly of recrystallized, massive dolomites with several interbeds of argillaceous dolomitic limestones and dolomites. Eganov and Sovetov (1979) recorded the presence of stromatolitic structures in the dolomites, suggesting very shallow water depositional environments (mostly tidal flat according to Cook *et al.* 1991). The lower boundary of the Shabakty Group is diachronous. According to Missarzhevsky and Mambetov (1981), Missarzhevsky (*in* Rozanov 1984), and Mambetov (1993), the late Atdabanian *Rhombicorniculum cancellatum* Biozone (Zhaanaryk and Taldybulak members), is recognised as a basal biostratigraphical unit only in north-eastern sections, whereas the overlying Geres Member with small shelly fossils of the *Microcornus parvulus* Biozone, of Botomian age, sits unconformably on the Chulaktau Formation in south-western sections (e.g. Ushbas and Koksu sections, Text-fig. 3). The overlying Lower Cambrian strata are subdivided by Ergaliev and Pokrovskaya (1977) into *Hebidiscus orientalis, Ushbaspis limbata* and *Redlichia chinensis-Kootenia gimmelfarbi* local trilobite biozones (Text-fig. 3). Ergaliev and Pokrovskaya (1977) and Eganov and Sovetov (1979) proposed a somewhat different correlation of the Lower Cambrian deposits within the Malyi Karatau Range, but the biostratigraphical correlation proposed



TEXT-FIG. 6. Generalized stratigraphical succession through the Batyrbay section, Malyi Karatau, showing sampled levels and distribution of brachiopods; modified after Dubinina (1992). Key as in Text-figure 3.

by Missarzhevsky and Mambetov is not in contradiction with data available from the distribution of brachiopods, so we therefore accept it here.

The main Middle Cambrian–Lower Ordovician part of the Shabakty Group comprises deposits of a carbonate platform formed on a microcontinental block (Aisha-Bibi sea-mount of Cook *et al.* 1991) about 40 km across and isolated from siliciclastic source areas. Our brachiopod collections were sampled from two sections in the north-eastern part of the Malyi Karatau Range (Batyrbay and Kyrshabakty sections). They represent shallowing-upward and seaward-prograding sequences of carbonate turbidites, replaced in the upper levels by lagoonal lithofacies of the sea-mount interior; discussion of these depositional environments is given by Cook *et al.* (1991). Detailed local biostratigraphical units based on trilobites were established for the Kyrshabakty section by Ergaliev (*in* Abdulin *et al.* 1990) and for the Batyrbay section by Apollonov and Chugaeva (1982), Chugaeva and Apollonov (1982), and Apollonov (1991) (Text-fig. 6). Detailed information on conodont biozonation of the Batyrbay section is given by Dubinina (1991).

Localities

Baba-Ata River. The western fossiliferous Lower Cambrian section in the Malyi Karatau Range is along the eastern side of the Baba-Ata River about 3 km north of Baba-Ata village (Text-figs 2–3). Here the Lower Cambrian sits discontinuously across the Riphean Bolshekaroi Formation and comprises the 'Lower Dolomite', the Chulaktau Formation (about 3·8 m thick) and the lower Shabakty Group (more than 65 m). The lingulate brachiopods described here are from a unit of bedded, dark grey limestone within an interval of approximately 55–63 m above the base of the Shabakty. In the lower part of this interval (sample 1419) *Linnarssonia constans* Koneva and *Lingulellotreta malongensis* (Rong) occur together with the trilobite *Bonnia septonaria* Ergaliev, suggesting the *Redlichia chinensis-Kootenia gimmelfarbi* Biozone. These two lingulate species were also sampled in abundance by L. N. Kraskov from the upper part of bed 12 in the Shabatky Group (sample 5/26, VSEGEI sample numbers) about 800 m south-west of height 593·2 m in the Kuvchatai mountains (Text-fig. 2).

Ushbas River. On the eastern side of the Ushbas River, Lower Cambrian rocks are exposed for a distance of about 9 km along the ridge and north-eastern slope of the Kengobysai Valley (Text-figs 2–3). These beds here sit unconformably on Riphean and Vendian sedimentary rocks of the Bolshekaroi and Koksu formations, and are represented by the Kyrshabakty Formation including the 'Lower Dolomite', Chulaktau Formation (about 20–35 m thick), and lower units of the Shabakty Group (up to 55 m thick). Detailed descriptions of the geology of this area and information on the location and stratigraphical position of the main fossil samples are given by Ergaliev and Pokrovskaya (1977, p. 18, figs 2–4). The Shabakty Group was subdivided by Ergaliev and Pokrovskaya into 11 informal units. Unit 1 comprises sandy dolomites up to 4·5 m thick and does not contain diagnostic trilobites, with the exception of *Ushbaspis* sp. Units 2 and 3 consist of dark grey to black, bedded limestones up to 5 m thick, referred to the *Hebidiscus orientalis* Biozone. Units 4–10 belong to the *Ushbaspis limbata* Biozone, comprising black and dark grey bedded limestones in the lower part and light grey to pink, massive limestones in the upper units (units 8–10) which total about 21 m thick in western sections. Unit 11 of dark to light grey, massive limestones contains trilobites of the *Redlichia chinensis-Kootenia gimmelfarbi* Biozone.

In the eastern part of the area the lingulate *Linnarssonia constans* occurs in a dolomite unit about 4–4·5 m thick close to the base of the Shabakty Group (sample 1235, section VI of Ergaliev and Pokrovskaya 1977, fig. 4) together with rare trilobites identified as *Ushbaspis* sp.; note that the thickness of the Lower Cambrian interval within the Shabakty Group is reduced significantly in this section, because in western sections this species is recorded first in the older *Hebidiscus orientalis* Biozone (samples 1224, 1227, 1235 of Ergaliev and Pokrovskaya 1977 are from the *Redlichia chinensis-Kootenia gimmelfarbi* Biozone). *L. constans* and *Lingulellotreta malongensis* become abundant in the *Ushbaspis limbata* Biozone (samples 1215, 1225, 1228, 1232, 1233) and also occur in the *R. chinensis-K. gimmelfarbi* Biozone (sample 1234), and *Kutorgina* sp. occurs in sample 1229.

Koksu River. Lower Cambrian strata are exposed on both sides of the Koksu River (Text-fig. 3) and about 10 km west along the southern slope of the unnamed ridge to the south-west of the road connecting Zhanatas and Kumkent. Detailed descriptions of the Lower Cambrian sequence and locations of the major fossil samples are given by Ergaliev and Pokrovskaya (1977, pp. 13–16, figs 4–5). The Lower Cambrian sits discontinuously across the Vendian Malokaroi Formation. The thickness of the Chulaktau Formation increases here up to 60–75 m, whilst the Lower Cambrian part of the Shabakty Group is about 80 m thick. The basal unit of the Shabakty Group is a polymict phosphoritic conglomerate about 0·5–0·7 m thick, overlain by about 10–15 m of dolomites lacking diagnostic fossils. Lingulate brachiopods have been recovered from several levels in the overlying bedded sandy and argillaceous limestone, 9–13 m thick (samples 1204, 1204-I, 1204-II, 1205, 1205-I, 1206, 1207, 1209; Text-fig. 3). *Linnarssonia constans* and *Lingulellotreta malongensis* are the most common. *Palaeobolus liantuoensis*, *Botsfordia* cf. *caelata* and Obolellidae gen. et sp. indet. also occur occasionally in some samples. The associated trilobite assemblage suggests the *R. chinensis*-*K. gimmelfarbi* Biozone (Ergaliev and Pokrovskaya 1977, pp. 14–15).

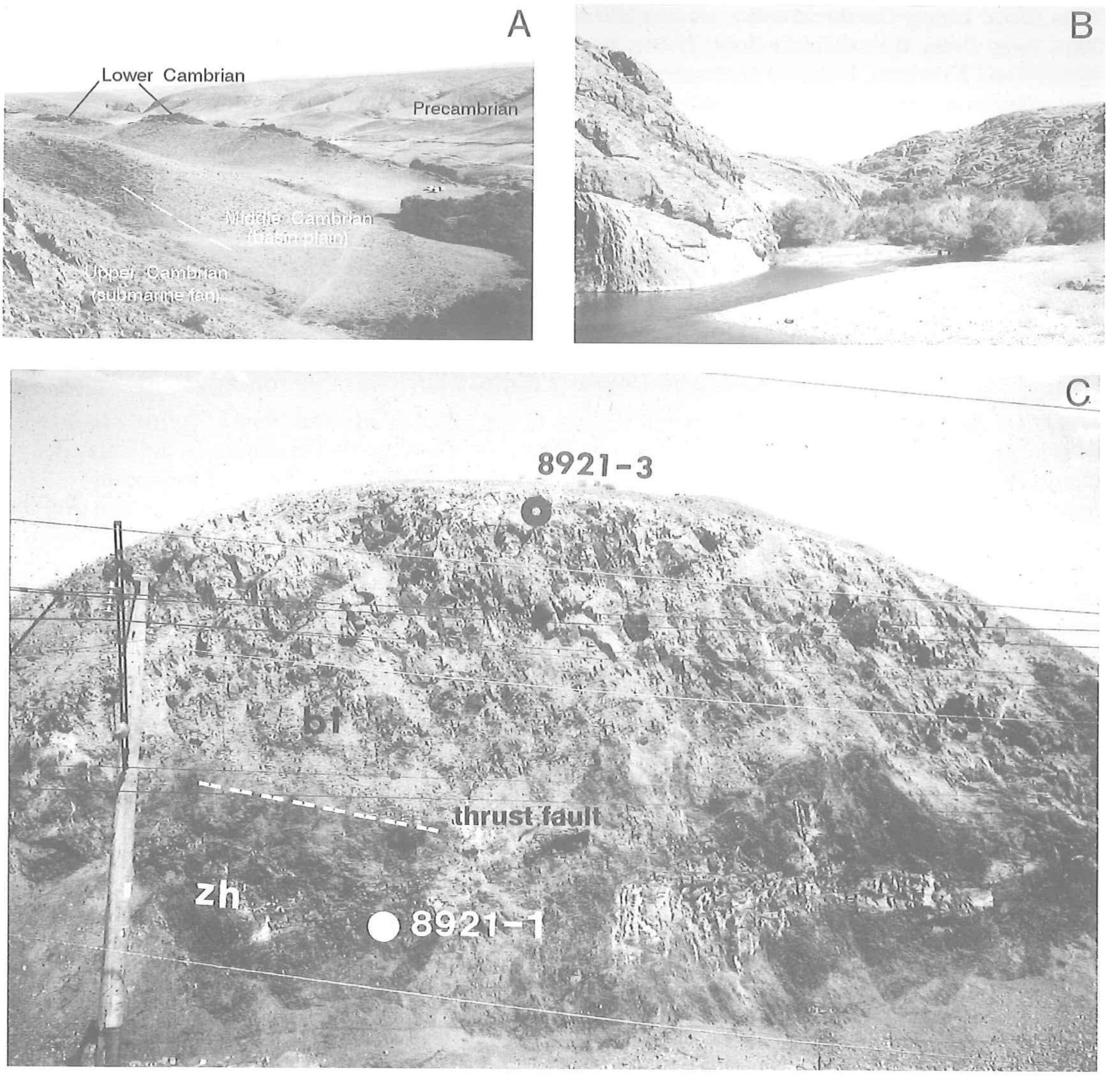
Kurtybulak Spring. In the Lower Cambrian section to the north of the Kurtybulak Spring (Text-fig. 3) *Palaeobolus liantuoensis* occurs in the lower part of a unit of black, bedded limestone in the interval about 8–10 m above the base of the Shabakty Group (samples 12b-I/27, 550; Text-fig. 3); the exposure is about 2 km west of map height 464 m. The associated trilobite assemblage includes *Ushbaspis limbata* (Ergaliev and Pokrovskaya 1977, p. 12).

Kyrshabakty River. The most complete section of the Shabakty Group is some 28 km north-west of the town of Zhanatas along the latitudinally-oriented meander in the middle course of the Kyrshabakty River (Text-fig. 2); the beds dip at 80–90 degrees to the south-west. Lower Palaeozoic deposits exposed here include the Kyrshabakty and Chulaktau formations as well as the main, Cambrian part of the Shabakty Group. The latter division, with a total thickness of 730 m, is divided into 12 informal units (Ergaliev, *in* Abdulin and Chakabaev 1984, pp. 44–51, fig. B10). The lower units (I–III) are unfossiliferous dolomites 127 m thick. Overlying deposits are bedded, black lime mudstones, lime wackestones and argillaceous lime mudstones up to 100 m thick, which represent basin-plain lithofacies (units IV–V of Ergaliev 1980); turbidites of a carbonate submarine fan about 490 m thick (units VI–XI) are succeeded finally by >22 m of laminated, grey to white dolomites, dolomitic flat-pebble breccias and dark brown limestones and dolomitic limestones which characterise shallow-subtidal lagoon and tidal-flat facies (Unit XII). For a detailed description of this section, its trilobite assemblages and biostratigraphy, and for further information on the fossil localities, see Ergaliev (1980), Abdulin and Chakabaev (1984), Abdulin *et al.* (1990), and Koneva (1992).

Shabakty River. Lingulate brachiopods were sampled from several isolated localities on the eastern side of the Shabakty River (samples 1412–1414). Details of their location and stratigraphical position are given by Ergaliev (1980, figs 1–2).

Batyrbay. The Batyrbay [Batyrbaisai] section is situated about 13 km west of the Kyrshabakty River (Text-figs 2, 6). It begins about 100 m north-east of the Ungur cave and is exposed along the eastern side of the Batyrbay ravine. The lithofacies here are closely similar to those of the Kyrshabakty section, occurring on the same, north-eastern (present-day coordinates) slope of the sea-mount. However, in Cambrian–early Ordovician times the submarine margin prograded seaward from the Kyrshabakty to the Batyrbay section, and the age of the sea-mount margin and submarine fan lithofacies at the Batyrbay section is somewhat younger (Cook *et al.* 1991).

Six informal lithostratigraphical units were established by Apollonov and Zhemchuzhnikov (*in* Abdulin *et al.* 1990) in the Batyrbay section (Text-fig. 6). Unit I, >67 m thick, consists of dark grey bedded limestones with several interbeds of flat-pebble breccias, interpreted as deposits of a basin-plain and fan-fringe. Units II–IV, about 190 m thick, represent deposition of turbidites from a carbonate submarine fan. The upper part of the sequence (Unit V–Unit VI, total >325 m thick) represents shallow-subtidal lagoonal and tidal-flat facies. Details of lithologies and faunal assemblages are published in several accounts



TEXT-FIG. 7. A, general view of the lower part of the Kyrshabakty section, Malyi Karatau, looking south-east across the succession through the lower Shabakty Group in shallowing upward facies from basin plain to carbonate submarine fan. B, north-westerly view of the Kyrshabakty river valley showing Upper Cambrian deposits in sea-mount margin facies. C, eastern side of the railway excavation about 1·5 km south of Chiganak showing radiolarian cherts of the Burubaital Formation (bt) thrust on the Cambrian Zhalgyz Formation (zh), and the position of localities containing late Cambrian brachiopods and arthropods (locality 8921-1) and mid Ordovician conodonts (locality 8921-3).

(Apollonov and Chugaeva 1982; Chugaeva and Apollonov 1982; Abdulin and Chakabaev 1984; Abdulin *et al.* 1990, *inter alia*).

GEOLOGY OF SOUTHERN BETPAK-DALA AND THE REGION WEST OF LAKE BALKHASH

In the southern Betpak-Dala desert and the region west of Lake Balkhash (Text-fig. 1), Cambrian sedimentary and volcanic rocks crop out within the Buruntau tectonofacies zone (*sensu* Nikitin *et al.*

1991), which represents a composite subduction complex formed during early–mid Ordovician times along the north-eastern side of the Chu-Ili terrane (Popov and Tolmacheva 1995; Popov *et al.* 1997). This is part of the Stepnyak-Zailiyski Alatau tectonic unit of Nikitin *et al.* (1992; Ye. L. Alperovich, pers. comm. 1993; see also Koren' *et al.* 1993). Cambrian brachiopods have been collected from two localities in this region.

Locality 5875 (A. P. Korobkin 1959, Geological Survey of South Kazakhstan, Almaty), situated in the Suukadyr Mountains (72° 40′ 51″ E, 45° 26′ 32″ N; Text-fig. 1). In this area, fossiliferous early Middle Cambrian deposits, referred provisionally to the Darbaza Formation, are exposed within the isolated block north-west of the Maikul massif of granitic intrusives. Lingulate brachiopods were collected from a bed of argillaceous limestone within a unit consisting of quartzose sandstones and black argillites. The assemblage includes only *Kleithriatreta najmanica* and *Micromitra*? *semicircularis*.

Locality 8921-1 (L. E. Popov and T. Yu. Tolmacheva 1989; VSEGEI locality number) is on the western side of southern Lake Balkhash about 1·5 km south of Chiganak railway station, on the eastern side of a railway excavation (Text-fig. 1). The lingulates *Zhanatella* sp. and Obolidae gen. et sp. indet. were recovered here, together with fragments of arthropods, from a mudstone interbed in graded, fine clastic deposits incorporating several layers of a tuffite, presumably in the upper part of the Zhalgyz Formation. This unit in this outcrop is overthrust by cherts of the Burubaital Formation containing a Llanvirn-age assemblage of conodonts including *Periodon aculeatus* (locality 8921-3, Text-fig. 7).

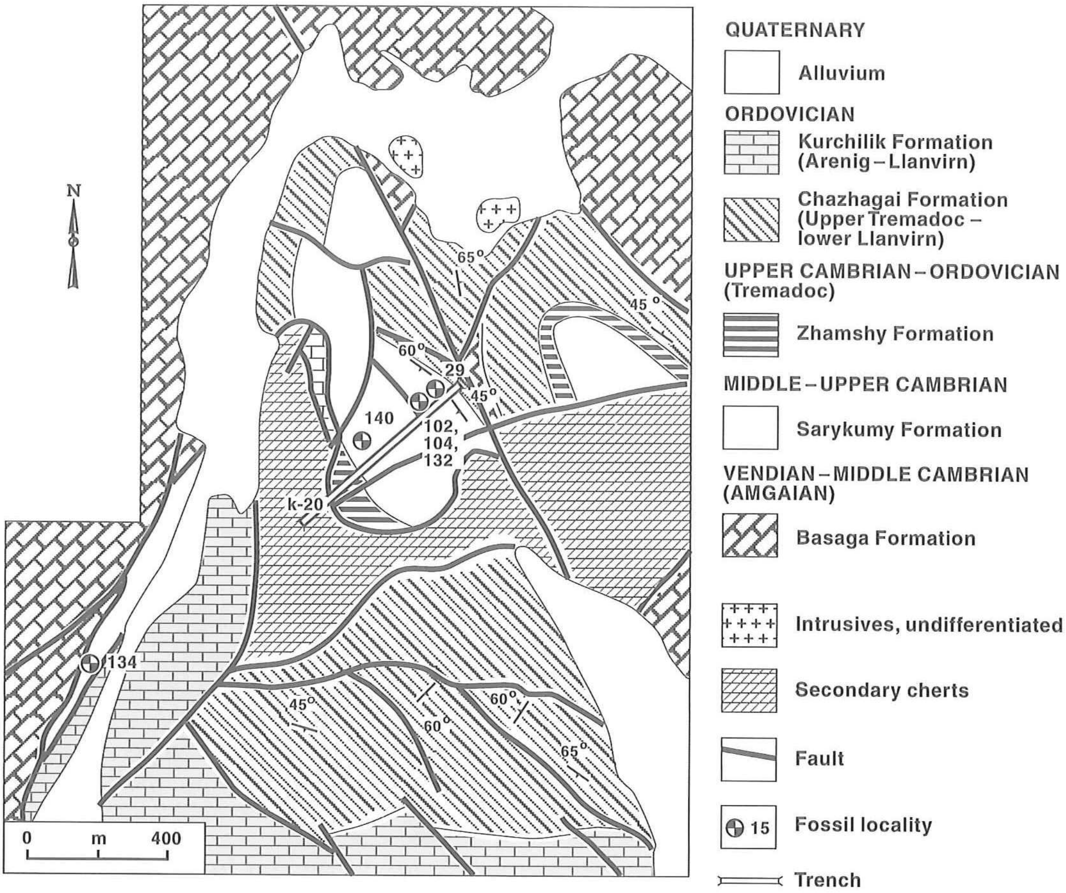
GEOLOGY OF THE ATASU–ZHAMSHY REGION, NORTH-WEST OF LAKE BALKHASH

To the north-west of Lake Balkhash, Proterozoic and Lower Palaeozoic limestones and dolomites are exposed in numerous scattered outcrops within complexes of sedimentary and intrusive rocks preserved between the Atasu River to the west and the Zhamshy River to the east (Text-fig. 1). According to Apollonov and Patalakha (1989), these carbonate sequences formed initially as late Precambrian–mid Ordovician platform and slope-rise marginal deposits on a separate, small crustal terrane (Balkhash Massif). Sengör *et al.* (1993) included this region in the Jungaro-Balkhash tectonofacies unit. Outlines of late Precambrian and early Palaeozoic geology and stratigraphy of the area have been published by Alperovich *et al.* (1971), Pupyshev *et al.* (1974), and Apollonov *et al.* (1990).

The main fossil localities discussed here, containing Middle–early Late Cambrian lingulate brachiopods, are about 4 km north-west of Sarykumy railway station on the western side of the Zhamshy River, about 70 km west of the town of Balkhash (Text-fig. 1). Detailed data on the geology were published by Apollonov *et al.* (1990). The major late Precambrian–early Palaeozoic lithostratigraphical units established in the region are: Basaga Formation (Vendian–?Middle Cambrian); Sarykumy Formation (Middle Cambrian–Upper Cambrian); Zhamshy and Chazhagai formations (upper Tremadoc–Arenig, ?Llanvirn) (Text-figs 8–9).

The Basaga Formation, about 600–700 m thick, consists of dolomites, oncolitic and dolomitic limestones, with abundant stromatolites at some levels. The formation lacks diagnostic fossils and its age is defined mainly by its stratigraphical position below the Sarykumy Formation (Text-fig. 9).

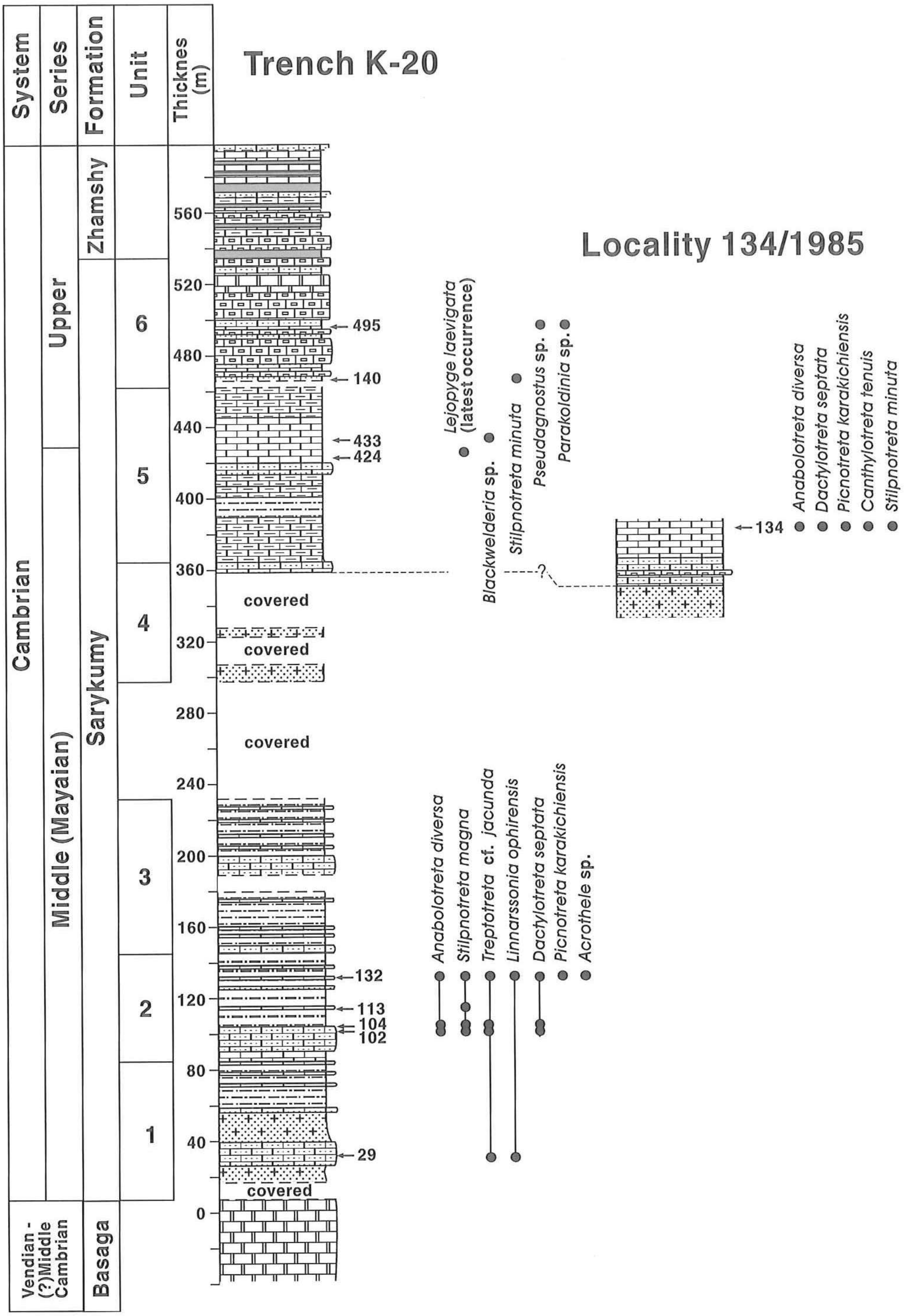
The Sarykumy Formation, about 530 m thick, has been subdivided by Apollonov (pers. comm. 1996) into six informal units (Text-fig. 9): Unit 1 comprises arkosic calcareous sandstones with interlayers of siltstones and sandy limestones, total thickness about 82 m; Unit 2, approximately 63 m of alternating arkosic sandstones, siltstones and sandy limestones; Unit 3, about 135 m of bedded dark grey and black limestones and argillaceous limestones with interbeds of sandy limestones and siltstones in the lower levels; Unit 4, about 83 m of sandy limestones; Unit 5, about 100 m of bedded, dark grey and black limestones, including argillaceous limestones with several interbeds of sandy limestones and siltstones; Unit 6, containing flat-pebble carbonate breccias with interbedded calcarenites and with a bed of dolomite 15–20 m thick in the upper part.



TEXT-FIG. 8. Schematic geological map of the area about 4 km south-east of Sarykumy railway station, north-western Balkhash, showing the position of the main localities containing Cambrian brachiopods; modified after Apollonov *et al.* (1990).

The best section of the Sarykumy Formation in the area north-west of Sarykumy railway station was exposed in a trench (K-20; Text-fig. 9), studied and sampled by M. K. Apollonov and V. Zhemchuzhnicov in 1986–1988, but results of their study remain unpublished; however, abundant trilobite and lingulate brachiopod faunas were collected. The lowermost occurrence of lingulates is about 29 m above the base of this section (Unit 1, sample 29; Text-fig. 9), containing only *Treptotreta* cf. *jucunda* and *Linnarssonia ophirensis*. *Anabolotreta diversa*, *Stilpnotreta magna*, *T.* cf. *jucunda* and *Dactylotreta septata* sp. nov. are the most abundant in Unit 2 (samples 102, 104, 132). The assemblage from the uppermost sample in this unit also includes rare specimens of *L. ophirensis*, *Picnotreta* sp. and *Acrothele* sp. In the Malyi Karatau sequence the range of *Linnarssonia ophirensis* is restricted within the interval of the *Goniagnostus nathorsti* and *Lejopyge armata* local trilobite biozones, whilst *Anabolotreta diversa* appears at the base of the *Lejopyge armata* Biozone. This suggests that Unit 2 of the Sarykumy Formation is most probably a stratigraphical equivalent of the *L. armata* Biozone of Malyi Karatau, and Unit 2 may correspond to the *Goniagnostus nathorsti* Biozone. The Middle/Upper Cambrian boundary in this section is within Unit 5 (Text-fig. 9), between the latest occurrence of *Lejopyge laevigata* (sample 424) and the earliest occurrence of *Blackwelderia* sp. (sample 433).

Stilpnotreta minuta sp. nov. occurs in a bed of a dark grey calcarenite at the base of Unit 6 (sample



TEXT-FIG. 9. Generalized stratigraphical successions through two profiles in the Sarykumy section, north-western Balkhash, showing sampled levels and distribution of brachiopods; mainly from Apollonov (pers. comm. 1996) and Popov (field observations 1985). Key as in Text-figure 3.

140/1985), together with the trilobites *Pseudagnostus* sp. and *Parakoldinia* sp. (sample 495), suggesting a late Cambrian age, as reported by Apollonov (pers. comm. 1996) for the middle part of this unit.

Lingulate brachiopods have also been recovered from the isolated, fault-bounded block of the Sarykumy Formation exposed about 900 m south-west of the south-western end of the trench K-20 on the western side of the unnamed longitudinal valley (Text-fig. 9; locality 134/1985). Here the Sarykumy sequence comprises a unit of about 20 m of pink-grey arkosic sandstones, followed by about 18 m of pink-grey calcareous sandstones, sandy limestones and siltstones with numerous trilobites forming coquinoid lenses and with a carbonate flat-pebble breccia horizon at about 32 m above the base of the section, and then about 22 m of black and dark grey laminated limestones containing numerous lingulate brachiopods within some 5–10 m from the top. The brachiopod assemblage contains *Anabolotreta diversa*, *Stilpnotreta minuta* sp. nov., *Canthylotreta tenuis* sp. nov., *Dactylotreta septata* sp. nov. and *Picnotreta karakichiensis* sp. nov. Lithologies suggest that the lower bed of arkosic sandstone may correspond to Unit 4 of the trench section K-20, with the overlying beds of sandy and laminated limestones equating with Unit 5. The lingulate assemblage in sample 134/1985 contains *Anabolotreta diversa*, which ranges up into the *Glyptagnostus stolidotus* Biozone in Malyi Karatau, whereas *Treptotreta* cf. *jucunda* and *Linnarssonia ophirensis* are missing. *Dactylotreta* appears in Australian sections from the base of the Mindyallian, so that these assemblages are more probably confined within the interval of the uppermost *Lejopyge laevigata–Glyptagnostus stolidotus* biozones.

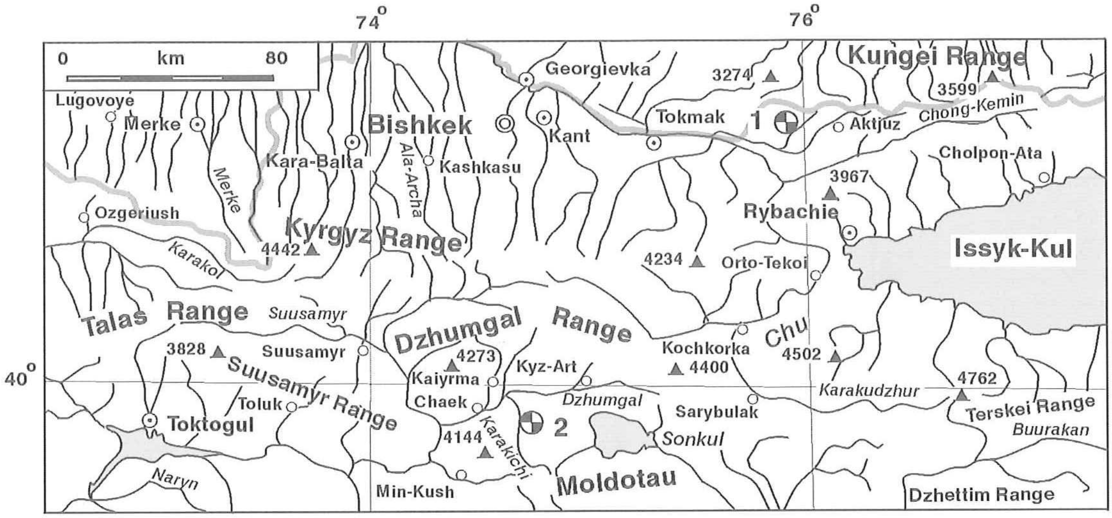
The Zhamshy Formation, about 80 m thick, conformably succeeds the Sarykumy Formation (Text-fig. 9). It consists of black, bedded limestones alternating with cherts and with several beds of a carbonate flat-pebble breccia in the lower levels. Conodonts of the *Eoconodontus notchpeakensis–Cordylodus lindstroemi* biozones occur (Dubinina 1991). Trilobite assemblages in the basal beds include *Lotagnostus hedini*, *L. asiaticus*, *Hedinaspis* sp., *Charchaqia* sp. and others, together with the chitinozoan *Desmochitina antiqua* (Apollonov *et al.* 1990).

The Chazhagai Formation comprises 200–250 m of black and dark grey radiolarian cherts alternating with siliceous argillites. Abundant conodonts provide evidence of the *Drepanoistodus deltifer–Oepikodus evae* biozones, and the graptolites *Phyllograptus* sp., *Isograptus* sp. and *Didymograptus* sp. in the upper part of the formation suggest a probable Arenig or early Llanvirn age (Apollonov *et al.* 1990).

GEOLOGY OF NORTH TIEN SHAN, KOSTEK RANGE

In the Kostek Ridge, North Tien Shan (Kazakhstan–northern Kyrgyzstan; Text-figs 10–11), Cambrian deposits form the Kirtabulga Formation (early Cambrian, Tommotian–Atdabanian) and the Karagajly Formation (early Cambrian, Botomian–early Ordovician, Tremadoc). The best exposures are on the north-western side of the Karagajly River between the Vodopadnyi and Kembrijskii rivulets. Diverse assemblages of lingulate brachiopods were recovered by V. Yu. Gorjansky from a sample of dark grey limestones in the middle part of the Karagajly Formation (sample 1639, Kyrgyzstanian Geological Survey; Text-fig. 11), collected by the Aktjuz-Kuperly geological mapping team in 1959. According to A. Mambetov (pers. comm. 1995), this formation here sits unconformably on basaltic tuffs of the Kirtabulga Formation and can be subdivided into four informal units (Text-fig. 11): (1) 75–95 m of algal limestones with a bed of carbonate breccia about 10–15 m thick at the top; (2) 225 m of laminated cherts with lenses and interbeds of dark grey to black limestones in the upper part, and with a 25-m dark grey bedded limestone at the top; (3) 130 m of alternating argillites, siltstones and fine grained sandstones; (4) 150 m of argillites and siltstones with interlayers of sandstones near the base and the top.

The early Cambrian age of Unit 1 is supported by the occurrence of the brachiopod *Kutorgina* sp. A Middle Cambrian lingulate assemblage was recovered from lenses of a dark grey limestone in the upper part of Unit 2, containing *Kyrshabaktella* cf. *certa*, Zhanatellidae gen. et sp. indet., *Anabolotreta*? sp., *Neotreta karagajlensis*, *Canthylotreta* sp., *Kotylotreta undata*, *Kleithriatreta kostekensis* sp. nov., and *Kleithriatreta najmanica* (Imanaliev and Pelman). *K.* cf. *certa* and *K. undata* are recorded from the



TEXT-FIG. 10. Locality map of north Kyrgyzstan showing Cambrian fossil localities; 1, Kostek Ridge; 2, Moldotau Range.

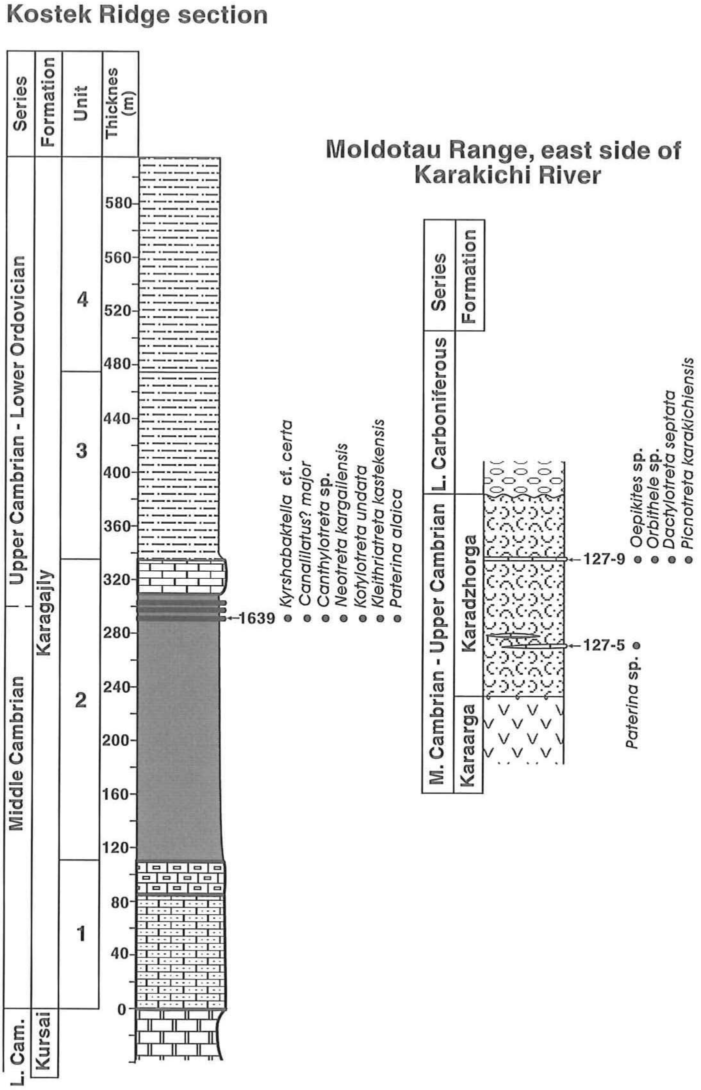
Peronopsis? *ultimus–Ptychagnostus atavus* biozonal interval of the Malyi Karatau Range and are thus evidence of a late Amgaian age for this assemblage. The late Cambrian conodonts *Phakelodus tenuis* and *Westergaardodina amplicava* have also been recorded by Mambetov (*in litt.* 1994) from interlayers and lenses of limestone in the upper part of the chert beds, whilst an overlying limestone bed at the top of Unit 2 contains the conodont *Proconodontus posterocostatus*, suggesting the *Proconodontus* Biozone. The siliciclastic units 3 and 4 of the Karagajly Formation do not contain diagnostic fossils, and their late Cambrian–early Ordovician age is deduced from their stratigraphical position between Unit 2 and the base of the early–middle Ordovician Kirtabulga Formation.

GEOLOGY OF THE MOLDOTAU RANGE

In the Moldotau Range, central Tien Shan (Text-fig. 10), late Middle–early Late Cambrian lingulate brachiopods are known currently only from a single fossil locality (127-9) on the eastern side of the Karakichi River 25 km above its mouth. The Middle–Upper Cambrian deposits here are fine clastic sediments and tuffs of the Karadzhorga Formation, with a total thickness of about 150 m. This formation sits on andesitic volcanic rocks and tuffs of the Karaarcha Formation and is overlain unconformably by Lower Carboniferous strata. A lingulate assemblage was recovered by V. L. Klishevich (VSEGEI, St. Petersburg) in 1983 from a limestone lens in the upper part of the Karadzhorga Formation about 50 m below its upper boundary; it includes *Orbithele* sp., *Dactylotreta septata* sp. nov. and *Picnotreta karakichiensis* sp. nov. This assemblage is comparable with that from locality 135 in the Sarykumy section, but it does not contain *Anabolotreta* and *Canthylotreta*.

SYSTEMATIC PALAEONTOLOGY

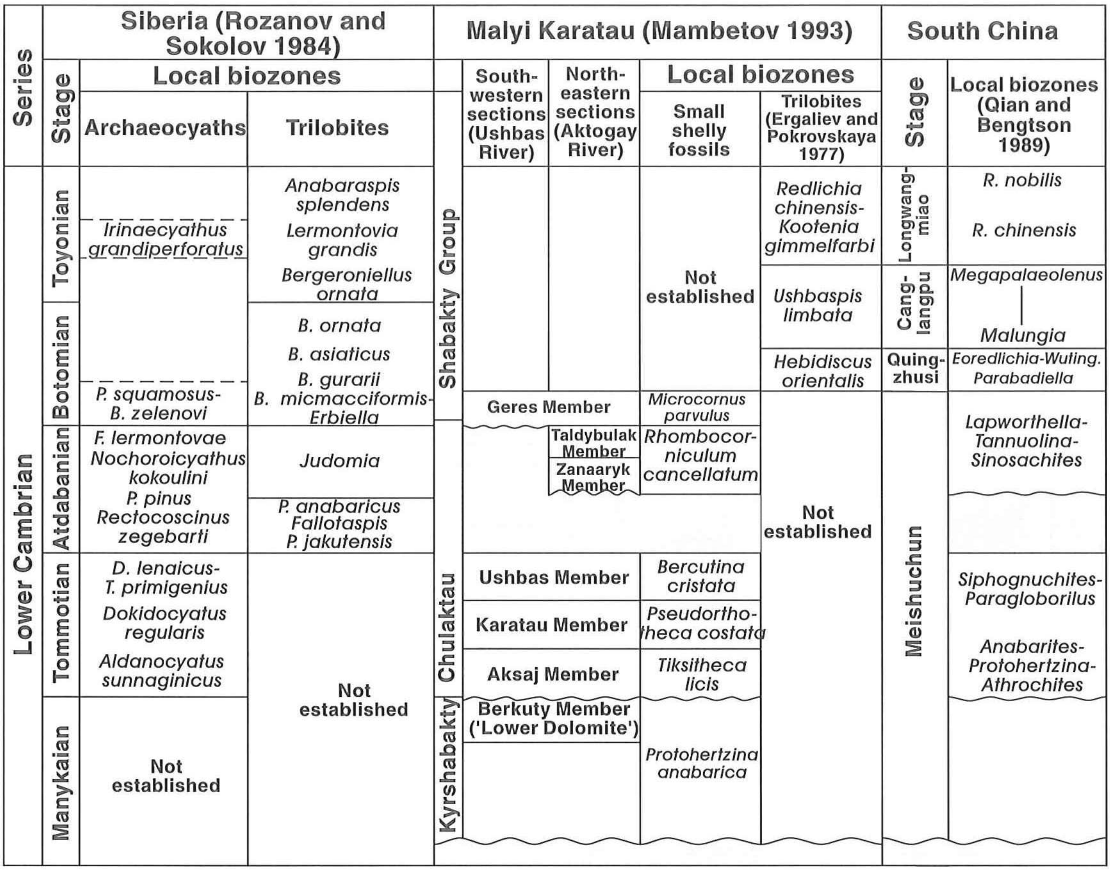
Abbreviations for parameters measured on specimens are (in millimetres; Text-figs 15, 17–18; Tables 1–27): W, L, T, maximum width, length, thickness of the shell; Lv, Ld, maximum length of ventral and dorsal valve; B, distance between the posterior margin and maximum shell width; Iw, Il, maximum width and length of pseudointerarea; Pw, width of median groove or pedicle groove; Pl, median length of pseudointerarea; Aw, Al, width, length of apical process; Cw, Cl, width, length of cardinal muscle field; Vw, Vl, width, length of visceral area; Sa, length of dorsal median septum; Sm, position of maximum



TEXT-FIG. 11. Generalized stratigraphical successions with sampled levels and brachiopod distributions through the Karagajly section, Kostek Range (mainly after A. Mambetov, pers. comm. 1995), and the Karakichi section in the Moldotau Range (after V. L. Klishevich, pers. comm. 1992). Key as in Text-figure 3.

height of dorsal median septum; St, maximum height of dorsal median septum; OR, observed range; X, mean value; S, standard deviation; N, number of measurements; MAX, MIN, maximum value, minimum value.

The morphological terminology for lingulate brachiopods used here mainly follows that of Rowell (1965), Koneva (1986), Holmer (1989), Popov and Holmer (1994), Williams *et al.* (1997) and Holmer and Popov (2000). Illustrated and described material is housed in the following repositories: Geological Museum of the Institute of Geological Sciences, Almaty (IGNA); Geological Institute of the Academy of Sciences of Kyrgyzstan, Bishkek (IGB); Central Scientific Research Geological Exploration Museum, St Petersburg (CNIGR); Naturhistoriska Riksmuseum, Stockholm (RM); National Museum of Wales, Cardiff (NMW); Palaeontological Museum, Uppsala University (PM).



TEXT-FIG. 12. Correlation of Lower Cambrian biostratigraphical divisions between the Malyi Karatau Range, Siberia, and South China.

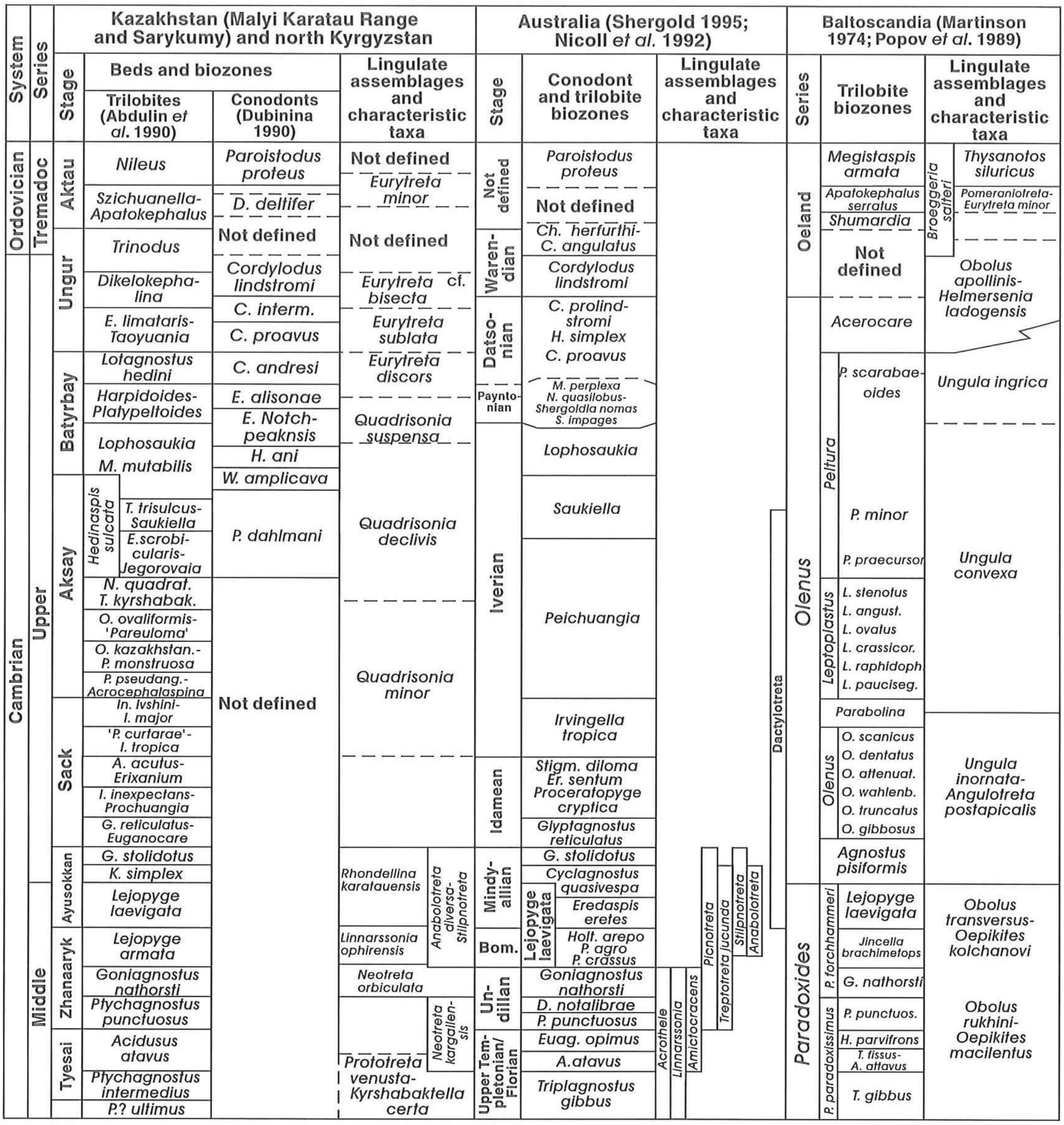
Phylum BRACHIOPODA Dumeril, 1806
Subphylum LINGULIFORMEA Williams, Carlson, Brunton, Holmer and Popov, 1997
Class PATERINATA Williams, Carlson, Brunton, Holmer and Popov, 1996
Order PATERINIDA Rowell, 1965

Remarks. Detailed discussion and revision of the morphology and systematics of paterinides was published recently by Williams *et al.* (1997; see also Laurie 2000). There is thus no reason to repeat diagnoses and characteristics of the three paterinide genera in our assemblages (*Paterina*, *Dictyonina*, *Micromitra*), which form only a minor component of the Middle and early Late Cambrian brachiopod faunas of Kazakhstan and north Kyrgyzstan.

Superfamily PATERINOIDEA Schuchert, 1893
Family PATERINIDAE Schuchert, 1893

Genus PATERINA Beecher, 1891

Type species. Original designation by Beecher (1891); *Obolus labradoricus* Billings, 1861; Lower Cambrian of Labrador, Canada.



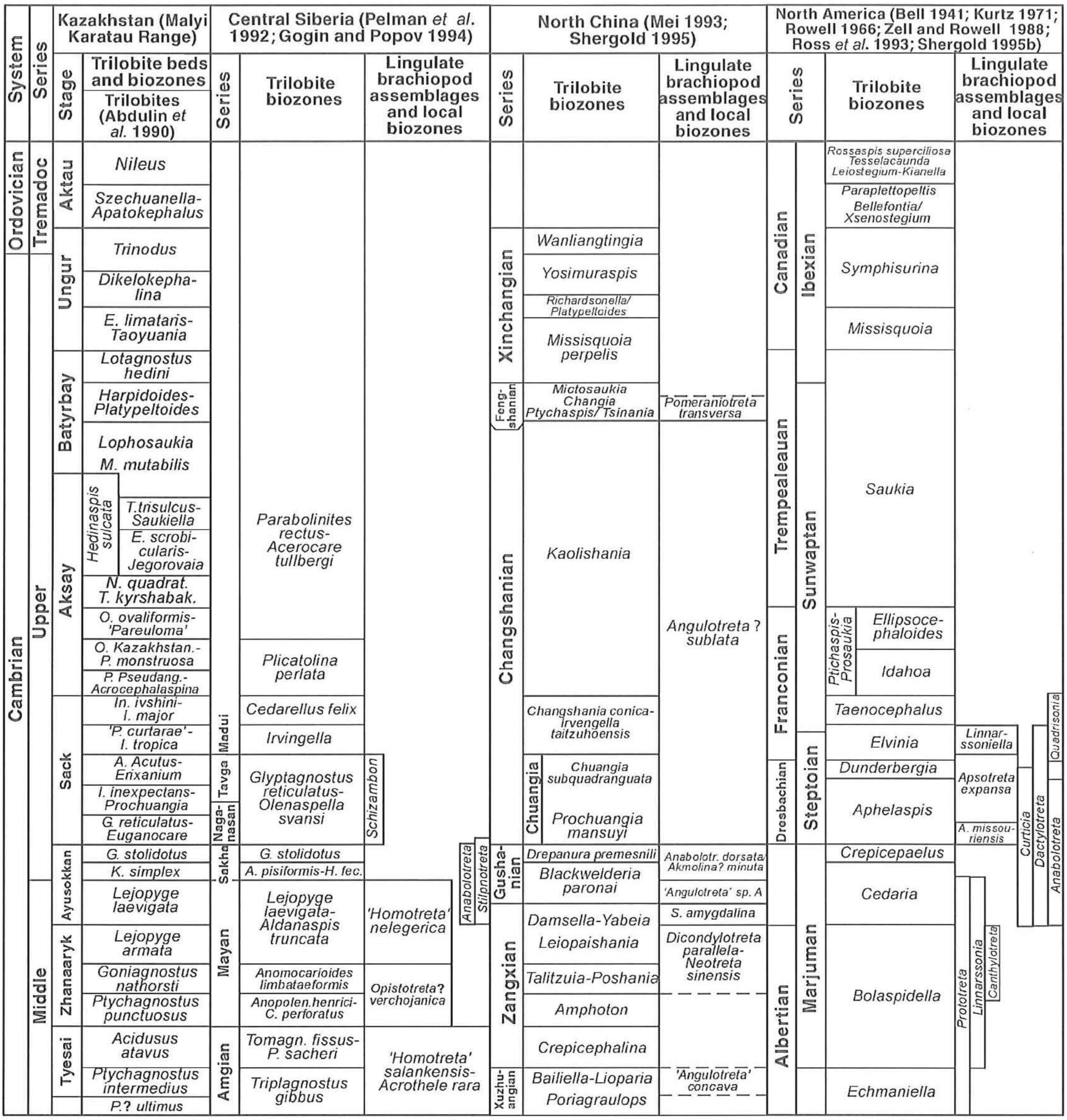
TEXT-FIG. 13. Correlation of Middle Cambrian–Lower Ordovician (Tremadoc) biostratigraphical divisions between the Malyi Karatau Range, Australia, and Baltoscandia.

Paterina alaica Imanaliev and Pelman, 1988

Plate 1, figures 6–13; Plate 2, figures 1–2

1988 *Paterina alaica* Imanaliev and Pelman, p. 166, pl. 20, figs 6–11.
1998 *Paterina alaica* Imanaliev and Pelman; Williams, Popov, Holmer and Cusack, pl. 11, fig. 4; pl. 12, figs 1–3.

Holotype. IGB 110/315, ventral valve; Middle Cambrian, Amgaian, Ulugtau Mountains, south Kyrgyzstan.



TEXT-FIG. 14. Correlation of Middle Cambrian–Lower Ordovician (Tremadoc) biostratigraphical divisions between the Malyi Karatau Range, Central Siberia, North China, and North America.

Material. One complete shell, three ventral and two dorsal valves.

Emended diagnosis. Strongly ventribiconvex, transversely subrounded to subrectangular in outline; ventral valve with maximum thickness slightly anterior to the margin of the larval shell; ventral interarea weakly apsacline with narrow triangular propareas and open, broadly triangular delthyrium; dorsal valve gently convex with maximum thickness in the umbonal area; dorsal interarea anacline, notothyrium broad, triangular with deeply concave median plate. Larval shell lobate, 250–300 μm long and 450 μm wide with fine, pustulose micro-ornament. Post-larval shell with fine, evenly spaced concentric rugellae; ventral valve interior with short, strongly thickened ridges on lateral margins of delthyrium; characters of dorsal internal morphology weakly impressed.

Dimensions. NMW 98.61G.47, ventral valve, L = 0·76, W = 1·08; NMW 98.61G.316, dorsal valve, L = 2·6, W = 3·28.

Remarks. Specimens from the Karagajly Formation of North Tien Shan are closely similar to topotypes of *Paterina alaica* from the lower Middle Cambrian of the Ulugtau Mountains, south Kyrgyzstan in size, general shell shape, ornamentation, and morphology of interareas of both valves. The presence of strong ridges on the lateral margins of the deltidium and a median plate at the base of the notothyrial cavity were not recorded in the original description of this species, but both features are clearly visible on the original illustrations (Imanaliev and Pelman 1988, pl. 20, figs 6, 9).

This species is distinguished from *Paterina labradorica* (Billings) in having a less transverse, subrounded to subrectangular (not suboval) shell outline, a flattened dorsal valve and a longitudinal ventral valve profile with maximum thickness slightly anterior to the margin of the larval shell.

P. alaica differs from *Paterina*? *suspiciosa* Aksarina, 1975, which occurs in the *Pseudoanomocarina* Beds of the Turkestan Range, Uzbekistan, in having a more transverse shell outline, short, fine ridges on the lateral margins of the delthyrium, and in the absence of a homeodeltidium. Our observations suggest that the presence of a homeodeltidium and the absence of strong ridges on the delthyrial margins are not characteristic of typical *Paterina* and, in particular, of the type species *P. labradorica*. The generic assignment of *P.*? *suspiciosa* thus remains provisional.

Occurrence. Middle Cambrian, Amgaian, Ulugtau Mountains, south Kyrgyzstan; Karagajly Formation, Kostek Range, north Kyrgyzstan, sample 1639.

Genus DICTYONINA Cooper, 1942

Type species. Original designation by Cooper (1942, p. 228); *Trematis pannulus* White, 1874; Lower–lower Middle Cambrian Pioche Shale, Nevada, USA.

Diagnosis. See Rowell, 1980, p. 19.

Dictyonina hexagona (Bell, 1941)

Plate 1, figures 1–5; Plate 41, figures 7–11

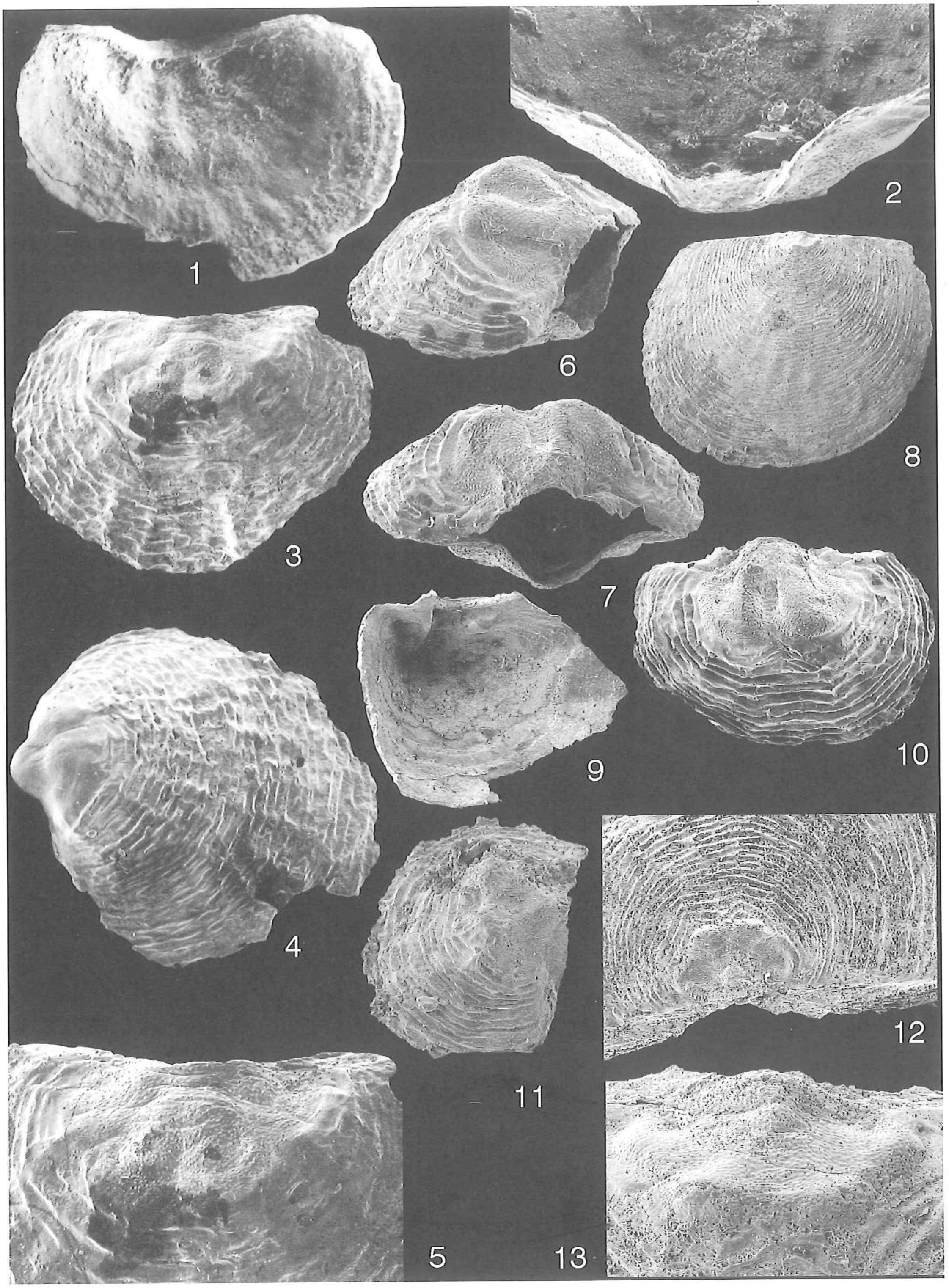
1912	*Iphidella pannula* (White); Walcott, pl. 4, figs 1b, f, t, *non* White 1874.
1941	*Iphidella hexagona* Bell, p. 210, pl. 29, figs 30–35.
1975	*Micromitra iriensis* Sobolev, p. 134, pl. 29, figs 30–35.
1986*b*	*Dictyonina hexagona* (Bell) Koneva, p. 207, pl. 31, figs 1–15.

EXPLANATION OF PLATE 1

Figs 1–5. *Dictyonina hexagona* (Bell); Middle Cambrian, *Ptychagnostus intermedius* Biozone, Malyi Karatau Range, Kyrshabakty section, all from sample 1314. 1, IGNA 427/416, dorsal valve interior; ×33. 2, NMW 98.61G.313, ventral valve, oblique posterior view of delthyrium and interarea; ×125. 3, 5, NMW 98.61G.314, dorsal valve exterior, ×67, and enlargement of larval shell, × 93. 4, NMW 98.61G.315, ventral valve, oblique lateral view; ×48.

Figs 6–13. *Paterina alaica* Imanaliev and Pelman; Middle Cambrian, Amgaian, Karagajly Formation, Kostek Range, sample 1639. 6–7, 10, PM Kg5, conjoined valves in oblique lateral view, posterior view, and ventral view; 6, 7, ×73; 10, ×66. 8, 12–13, NMW 98.61G.316, dorsal valve exterior, oblique posterior view of umbonal area, and enlargement of larval shell; 8, ×16; 12, ×52; 13, ×130. 11, NMW 98.61G.47, ventral valve in oblique lateral view; ×43.

PLATE 1



HOLMER *et al.*, *Dictyonina*, *Paterina*

1992 *Dictyonina hexagona* (Bell); Sobolev, *in* Pelman *et al.* 1992, p. 106, pl. 16, figs 10–14.
1975 *Dictyonina* sp.; Aksarina, p. 96, pl. 5, figs 1–8.

Lectotype. USNM 97078a, ventral valve, Middle Cambrian, *Ehmania* Zone, Michigan, USA.

Material. 20 ventral and 15 dorsal valves.

Diagnosis. See Bell 1941, p. 210.

Description of Kazakhstanian specimens. Shell small, ventribiconvex, outline transversely semioval, 75–85 per cent as long as wide, posterior commissure slightly shorter than maximum shell width, anterior commissure rectimarginate; ventral valve strongly convex to subconical, about 20–30 per cent as thick as long with maximum thickness slightly anterior to the umbo, usually at about the anterior margin of the larval shell. Ventral interarea high with open, broad, subtriangular delthyrium, covered apically by a rudimentary homeodeltidium in adult specimens. Dorsal valve gently convex with maximum thickness close to the anterior margin of the larval shell. Nothyrium open, broadly triangular, flanked by narrow propareas. Surface of the larval shell finely pustulose. Post-larval shell covered by rounded, hexagonal pits forming distinctive rows radiating from the margins of the larval shell; pits small and shallow in the umbonal area, but enlarged and becoming more transverse towards the anterior and lateral margins.

Ventral valve interior with strongly thickened inner margins of the interarea along both sides of the homeodeltidium and with weakly impressed, saccate mantle canals with subparallel *vascula media*. Dorsal interior with a strip-like median plate supported by a pair of short, divergent ridges and with four slightly thickened, radially arranged adductor muscle tracks extending anteriorly to mid-valve. Mantle canals saccate.

Dimensions. NMW 98.61G.313, ventral valve, L = 1·22, W = 1·50; NMW 98.61G.315, ventral valve, L = 1·42, W = 1·80.

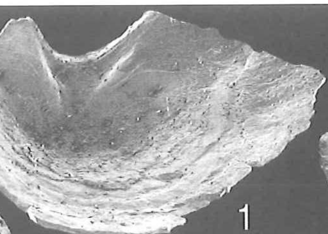
Remarks. In general shell shape and ornament, as well as in characters of the interareas of both valves, our specimens closely resemble those of *D. hexagona* from the Middle Cambrian Pagoda Limestone of Montana. The only difference is the smaller size of the Kazakhstanian specimens, which do not exceeded 3 mm in length and 4 mm in width. Specimens from south-east Siberia described originally under the name *Micromitra iriensis* by Sobolev (1975, p. 134) and later reassigned to *Dictyonina hexagona* (Sobolev, *in* Repina and Rozanov 1992, p. 106) are also closely similar; our study of Siberian specimens kindly provided by V. Yu. Gorjansky confirms their synonymy with *D. hexagona* as proposed by Sobolev.

Occurrence. Middle Cambrian, Shabakty Group, *Ptychagnostus intermedius–Goniagnostus nathorsti* biozones, Malyi Karatau Range, Kyrshabakty section, samples 1313, 1314-1, 1316, 1467, 1467-1, 1465, 1465-2, 1465-8, 1465-9, 1465-19; Dzhavodi Group, south-east Siberia, Dzhagdy Range; Pagoda Limestone, Montana.

EXPLANATION OF PLATE 2

Figs 1–2. *Paterina alaica* Imanaliev and Pelman; Middle Cambrian, Amgaian, Karagajly Formation, Kostek Range, sample 1639. 1, PM Kg6, ventral valve interior, oblique anterior view; ×28. 2, NMW 98.61G.317, dorsal valve interior; ×45.

Figs 3–11. *Micromitra*? *semicircularis* Imanaliev and Pelman; Lower Cambrian, Darbaza Formation, Suukadyr Mountains, locality 5875. 3, 10, NMW 98.61G.318, dorsal valve, oblique lateral and normal views of interior; ×18, ×14. 4, 8, NMW 98.61G.319, dorsal valve exterior in normal and oblique lateral views; ×20, ×14·5. 5, NMW 98.61G.320, ventral valve interior, oblique anterior view; ×40. 6, NMW 98.61G.321, ventral valve exterior; ×24. 7, 11, NMW 98.61G.322, dorsal valve in oblique and posterior views showing pseudointerarea and notothyrium; ×80, ×44. 9, NMW 98.61G.323, ventral valve, oblique lateral view of umbonal area; ×37.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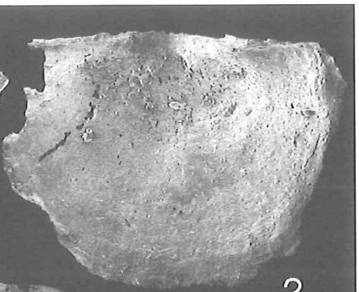
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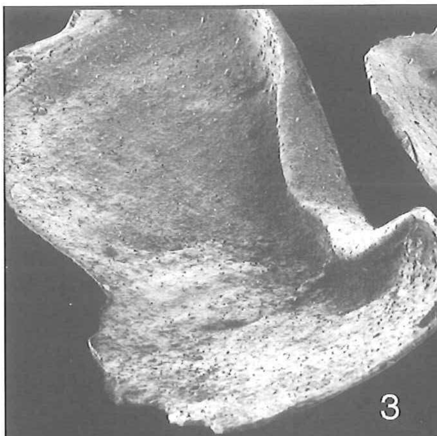
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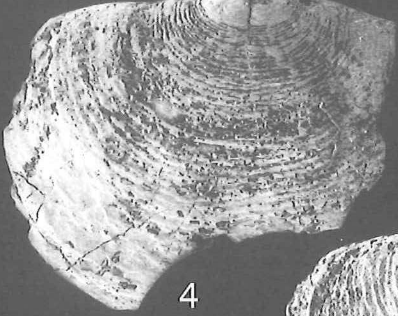
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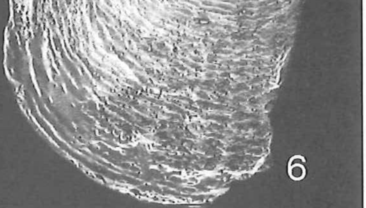
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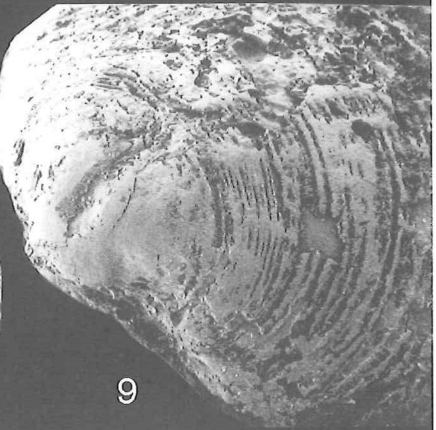
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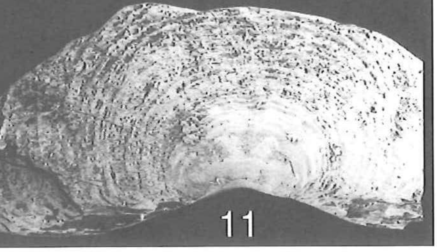
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HOLMER *et al.*, *Micromitra*?, *Paterina*

Genus MICROMITRA Meek, 1873

Type species. Original designation by Meek (1873, p. 479); *Iphidea*? *sculptilis* Meek, 1873, Middle Cambrian, Montana, USA.

Micromitra? *semicircularis* Imanaliev and Pelman, 1988

Plate 2, figures 3–11; Plate 47, figures 1–2

1988 *Micromitra semicircularis* Imanaliev and Pelman, p. 166, pl. 21, figs 1–6.

Holotype. IGB 110/321, ventral valve from the Lower–lower Middle Cambrian, Ulugtau Mountains, south Kyrgyzstan.

Material. 45 ventral and 10 dorsal valves.

Diagnosis. Micromitra with moderately convex ventral valve and apsacline ventral interarea; delthyrium broadly triangular with a vestigial homeodeltidium in the umbonal area; dorsal valve with low, anacline, strongly thickened interarea divided by concave median groove; shell covered by fine, irregular costellae and superimposed, regularly spaced, fine rugellae, lamellose peripherally; ventral interior with strongly thickened inner side of homeodeltidium and marginal parts of propareas surrounding the delthyrium; visceral area bisected by a pair of fine, slightly divergent submedian grooves; dorsal interior with weak median ridge and pair of slightly diverging submedian ridges; mantle canal system pinnate in both valves.

Description of specimens from central Kazakhstan. Ventribiconvex, transverse, semioval to subcircular in outline, about 84 per cent as long as wide. Ventral valve moderately convex with maximum thickness somewhat anterior to the umbo; ventral pseudointerarea slightly apsacline, gently concave in cross section with a broadly triangular open delthyrium covered by a vestigial homeodeltidium in the umbonal area. Dorsal valve weakly convex with a low, planar, anacline, strongly thickened interarea with concave median plate and open, broadly triangular notothyrium. Shell surface with numerous, closely spaced growth lamellae anteriorly and fine, reticulate ornament formed by fine, irregular costellae superimposed on fine, evenly spaced concentric rugellae. Larval shell about 400 μm long and 500–600 μm wide, covered by fine, pustulose micro-ornament.

Ventral interior with strongly thickened inner margins of the homeodeltidium, and propareas surrounding the delthyrial opening, with a pair of slightly divergent submedian furrows in the posterior half of the valve. Dorsal interior with weak median ridge bisecting the slightly thickened visceral area in the posterior part of the valve.

Dimensions. NMW 98.61G.321, ventral valve, L = 1·58; NMW 98.61G.325, ventral valve, L = 2·92, W = 3·38; NMW 98.61G.150, ventral valve, L = 2·22, W = 2·58; NMW 98.61G.319, dorsal valve, L = 2·88.

Remarks. These specimens are identical to topotypes of *Micromitra*? *semicircularis* Imanaliev and Pelman (1988) from the Lower–lower Middle Cambrian of the Ulugtau Mountains of southern Kyrgyzstan in all main aspects of external and internal morphology, and are here regarded as conspecific. Distinctive features of this species are the vestigial homeodeltidium and strongly thickened inner margins of the mainly open delthyrium. A difference from *Paterina* is that distinct ridges flanking the delthyrium are not formed in *Micromitra*? *semicircularis*.

This species differs from the majority of *Micromitra* species (Bell 1941) in having a mainly open delthyrium with a vestigial homeodeltidium in the umbonal part, and pinnate mantle canals in both valves, which makes the generic attribution of our material somewhat provisional. It resembles *Olenkina olenkensis* Ushatinskaya (1997, p. 55) to some extent in its reticulate ornament, low dorsal median ridge, and the absence of a homeodeltidium, but it differs in its much larger size, highly raised dorsal median plate, and in the absence of widely divergent ridges along the posterior margin of the dorsal valve. *O. olenkensis* is known from small paterinide shells (up to 1·5 mm wide), which exceed the size of the larval shell by only two or three times. The homeodeltidium in

Micromitra appears usually in adult, fully grown shells, and it is very likely that the open delthyrium and relatively late appearance of reticulate ornament in *Olenkina* can be explained by the immature nature of specimens in the type series, which places some doubts on the validity of *Olenkina* as a separate taxon of generic rank.

Occurrence. Middle Cambrian, Amgaian, Darbaza Formation of the Suukadyr Mountains, central Kazakhstan, sample 5875; upper Lower Cambrian–lower Middle Cambrian (Amgaian)? olistoliths in the Ulugtau Mountains, south Kyrgyzstan.

Micromitra cf. *modesta* (Lochman, 1940)

Plate 42, figure 10

1992 *Micromitra* cf. *modesta* (Lochman, 1940); Koneva, p. 98, pl. 11, figs 10–11.

Material. Three ventral valves and one dorsal.

Description. Inequivalved, strongly ventribiconvex, transversely suboval in outline. Ventral valve evenly convex with a high, triangular, procline pseudointerarea and wide triangular delthyrium covered apically by a convex homeodeltidium. Dorsal valve moderately and evenly convex with a marginal umbo, about 64 per cent as long as wide. Shell ornamented by fine, evenly spaced, slightly undulose concentric fila and fine, irregular radial ribs originating between umbonal area and mid-valve. Dorsal pseudointerarea and interiors of both valves unknown.

Dimensions. IGNA 427/163, dorsal valve, L = 2·65, W = 4·15.

Remarks. Specimens of *Micromitra* occurring rarely in the upper part of the Middle Cambrian sequence of Malyi Karatau are comparable with *Micromitra modesta* described and illustrated by Bell (1944, p. 144, pl. 18, figs 1–8, 18–19) and Lockman and Hui (1960, p. 820, pl. 95, figs 37–40) in characters of outline, convexity and ornamentation; however, incomplete preservation of the Kazakhstanian shells and the absence of information on the internal morphology of both valves makes precise specific discrimination uncertain.

Occurrence. Middle Cambrian of the Malyi Karatau Range, Kyrshabakty section, *Goniagnostus nathorsti* and *Lejopyge armata* biozones, samples 1465-18, 1465-8a, 1346-10, 1346-11.

Micromitra sp.

Plate 41, figures 12–14

1992 *Micromitra* sp.; Koneva, p. 99, pl. 11, fig. 12.

Material. Two ventral and six dorsal valves.

Remarks. Fragmentary valves of *Micromitra* have been obtained from the lower part of the Upper Cambrian sequence of the Malyi Karatau Range. They are characterised by a typical *Micromitra* surface ornament of fine, undulating concentric fila crossed by irregular fine ribs, but the interareas of both valves are poorly preserved and their internal morphology is unknown.

Occurrence. Upper Cambrian, Malyi Karatau Range, Kyrshabakty section, *Innitagnostus inxpectans* beds, samples 1355, 1355-1, 1355-2, 1357-2, 1357-3, 1361, 1361-9.

Class LINGULATA Gorjansky and Popov, 1985
Order LINGULIDA Waagen, 1885
Superfamily LINGULOIDEA Menke, 1828
Family OBOLIDAE King, 1846
Subfamily OBOLINAE King, 1846

Genus AKSARINAIA Koneva, 1992

Type and only species. Aksarinaia triquetra Koneva, 1992; Middle Cambrian, Amgaian, *Peronopsis ultimus* and *Ptychagnostus intermedius* biozones; Kyrshabakty River, Malyi Karatau, southern Kazakhstan.

Diagnosis. Shell subtriangular, weakly biconvex; pseudointerareas of both valves with flexure lines; ventral pseudointerarea orthocline with a deep, subtriangular pedicle groove and strongly raised, narrow propareas, ventral umbo with small semicircular emarginature; dorsal pseudointerarea moderately high, with broad median groove and narrow, elevated propareas; visceral areas of both valves finely pitted; pedicle nerve impressions well defined; dorsal visceral area slightly thickened, extending anterior to mid-valve; dorsal *vascula media* marginal, arcuate; larval and post-larval shell smooth.

Remarks. *Aksarinaia* was referred originally (Koneva 1992) to the Family Zhanatellidae, mainly because it has a small, semicircular emarginature in the ventral umbo. However, the smooth larval and post-larval shell are features significantly different from all known zhanatellid genera, which invariably have a pitted larval and post-larval shell (Popov and Holmer 1994).

Among genera of the Family Obolidae, *Aksarinaia* is comparable only with *Kyrshabaktella* in the presence of the ventral emarginature. However, *Aksarinaia* is readily differentiated in having an acuminate shell with a relatively high ventral pseudointerarea and narrow pedicle groove; wide, raised ventral propareas, which take the form of long, straight, narrow strips diverging from the apex; weakly impressed visceral areas of both valves; and it lacks a dorsal median ridge.

Aksarinaia triquetra Koneva, 1992

Plate 3, figures 1–14; Plate 4, figure 11; Plate 6, figure 2; Text-figure 15

1992 *Aksarinaia triquetra* Koneva p. 92, pl. 9, figs 15–19; pl. 10, figs 1–5.

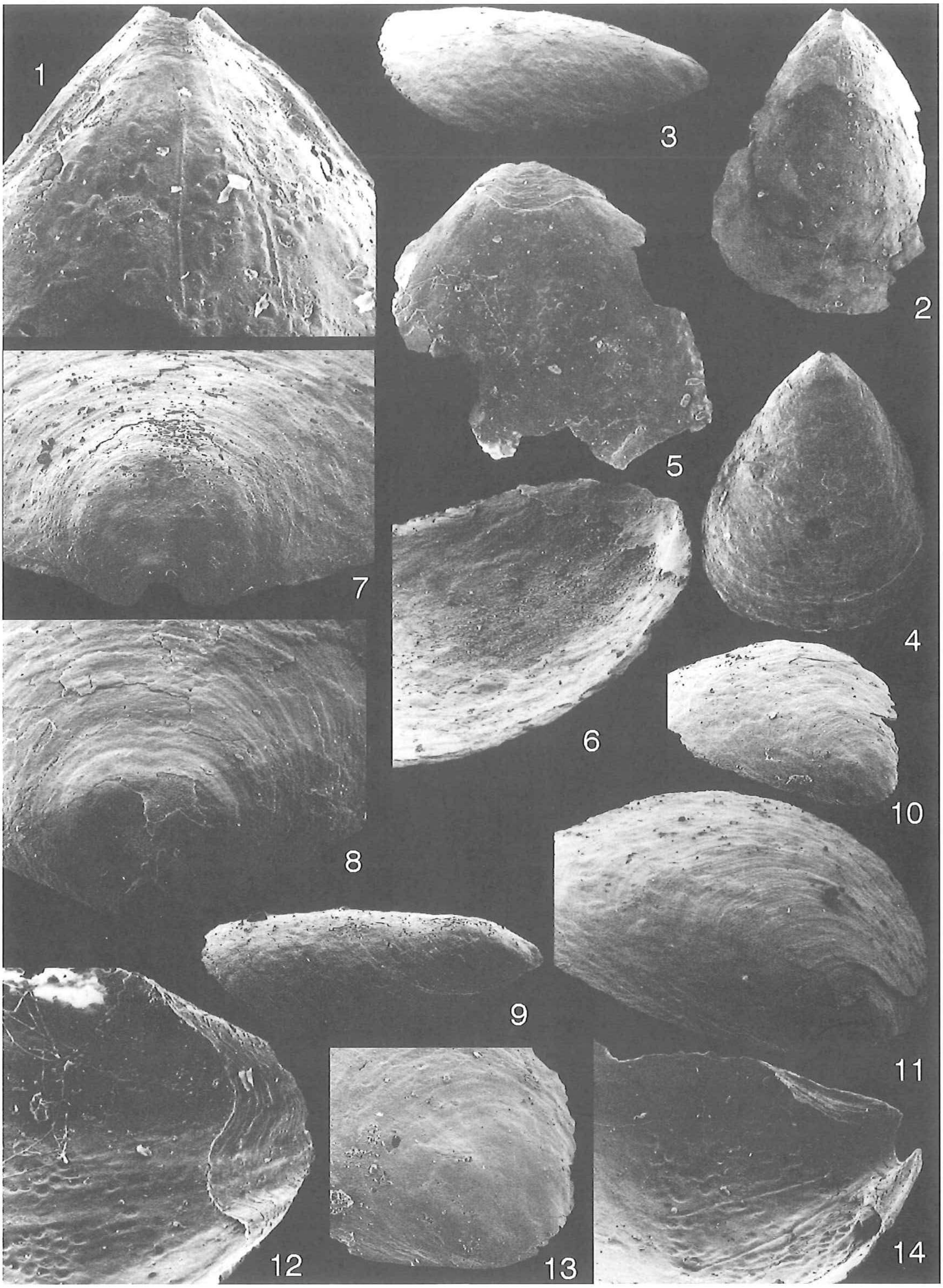
Holotype. IGNA 427/547, ventral valve; Middle Cambrian, Amgaian (*Peronopsis ultimus* beds); Kyrshabakty section, Malyi Karatau.

Material. 76 ventral and 51 dorsal valves.

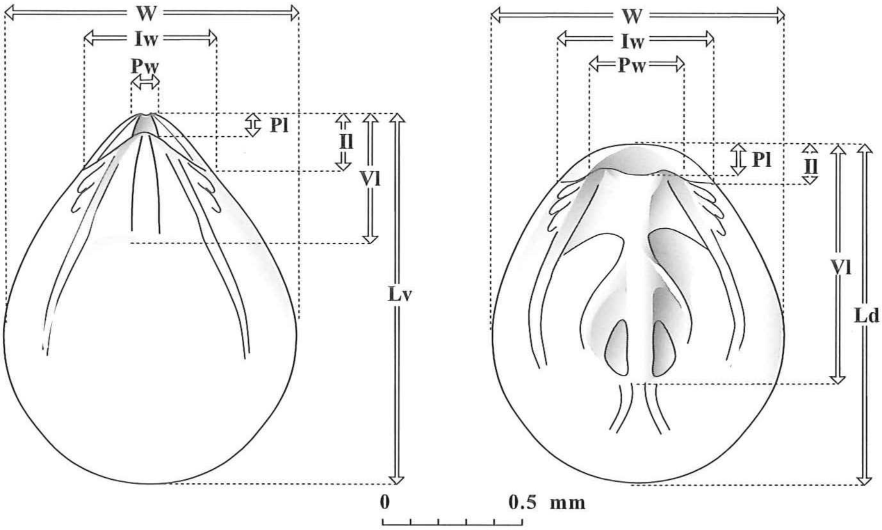
EXPLANATION OF PLATE 3

Figs 1–13. *Aksarinaia triquetra* Koneva; Middle Cambrian, Shabakty Group, Malyi Karatau Range, Kyrshabakty Section. 1–2, RM Br136345, sample 1314-2, ventral valve interior, detail of pseudointerarea and visceral area bisected by pedicle nerve impression, ×135, and view of full internal morphology, ×135. 3–4, 8, RM Br136344, sample 1314-2, ventral valve in lateral view, ×30, exterior, ×25; and posterior view of umbonal area showing emarginature, ×90. 5, 12, RM Br136347, sample 1314-2, dorsal valve interior, ×30 and oblique lateral view of interior posterior region, ×120. 6, NMW 98.61G.1, sample 1314-2, oblique lateral view of dorsal interior; ×135. 7, 9, NMW 98.61G.2, sample 1314-2, ventral valve exterior, posterior view of umbonal area, ×90, and lateral view, ×35. 10, 13, NMW 98.61G.3, sample 1465-1, dorsal valve exterior in oblique lateral view, ×36, and detail of larval shell, ×91. 11, NMW 98.61G.4, sample 1465-1, dorsal valve exterior in oblique posterior view; ×32. 14, RM Br136345a, sample 1314-2, oblique view of ventral interior; ×98.

PLATE 3



HOLMER *et al.*, *Aksarinaia*



TEXT-FIG. 15. *Aksarinaia triquetra* Koneva; reconstruction of the ventral (left) and dorsal (right) interiors showing the disposition of the musculature and vascular system, and the location of measured parameters (see Table 1).

Diagnosis. As for genus.

Description. Shell slightly ventribiconvex, elongate, subtriangular in outline, about 130 per cent as long as wide. Ventral valve gently and evenly convex in sagittal profile, acuminate with a high, triangular pseudointerarea. Pedicle groove deep, subtriangular. Propareas strongly raised, elongate subtriangular, bisected by deep flexure lines. Dorsal valve gently convex with maximum thickness in the posterior third of the valve length, about 120 per cent as long as wide (Table 1). Dorsal pseudointerarea weakly anacline, about 50 per cent as wide as the valve. Median groove gently concave. Dorsal propareas narrow, slightly raised, with flexure lines. Shell surface smooth with fine growth fila.

Ventral interior with poorly defined visceral area bisected medially by two deeply impressed, slightly divergent furrows (pedicle nerve impression) extending anteriorly to mid-valve and crossing weakly impressed umbonal muscle scars. Dorsal interior with weakly impressed visceral area forming a narrow median tongue extending slightly anterior to the mid-valve.

Occurrence. Middle Cambrian, Kyrshabakty section, *Peronopsis ultimus* and *Ptychagnostuss intermedius* biozones, samples 1465/1, 1313, 1314, 1314/2.

TABLE 1. *Aksarinaia triquetra* Koneva, dimensional data for dorsal valves from the Kyrshabakty section (samples 1314-1 and 1314-2, Middle Cambrian, *Ptychagnostus intermedius* Biozone).

	Ld	W	B	Il	Iw	Pl	Ld/W	B/L	Iw/W
N	8	8	8	4	4	4	8	8	4
X	1·31	1·1	0·805	0·24	0·5775	0·24	119%	61%	52%
S	0·279	0·244	0·207	0·067	0·164	0·067	9·17	4·4	15·9
MIN	0·96	0·82	0·52	0·16	0·46	0·16	105%	54%	37%
MAX	1·72	1·42	1·08	0·32	0·82	0·32	138%	66%	69%

Genus EXPERILINGULA Koneva and Popov, 1983

Type and only species. Original designation by Koneva and Popov (1983, p. 113); *Experilingula divulgata* Koneva and Popov, 1983; Upper Cambrian (*Pseudagnostus pseudangustilobus–Micragnostus mutabilis* beds); Malyi Karatau Range, southern Kazakhstan.

Diagnosis. See Popov and Holmer 1994, p. 35.

Remarks. The only genus similar to *Experilingula* is *Chakassilingula* Ushatinskaya, 1992 from the Middle Cambrian (Amgaian) of the Altai Mountains. *Experilingula* is distinguished by the absence of two strong plications on the dorsal pseudointerarea lateral to the median groove.

Ushatinskaya (1992) referred both of these genera to the Family Experilingulidae, mainly on the basis of the presence of the highly raised pseudointerareas in both valves. However, such types of pseudointerareas appear repeatedly in various lingulide lineages. In particular, they are present in the Family Lingulellotretidae and in some obolid genera (e.g. *Fordinia*, *Ungula* and others), as well as in some genera of the families Zhanatellidae and Elkaniidae. Phylogenetic analysis of these stocks (Holmer and Popov 1996) suggests that numerous lingulide features, including the morphology of pseudointerareas, evolved repeatedly in various lineages and the major lingulide clades can be defined only on the basis of a combination of various features, including the micro-ornament of the larval and post-larval shell, the nature of the pedicle opening and pseudointerareas, and the internal morphology of both valves. In main aspects of the morphology of the visceral areas, muscle system, mantle canals in both valves, as well as in having a smooth larval and post-larval shell, both *Experilingula* and *Chakassilingula* are closely similar to genera of the Family Obolidae; the Family Experilingulidae is thus regarded here as junior synonym of the Obolidae.

Experilingula divulgata Koneva and Popov, 1983

Plate 4, figures 1–10, 12–13; Plate 5, figures 1–2

1983 *Experilingula divulgata* Koneva and Popov, p. 115, pl. 26, figs 1–13; pl. 27, figs 1–14.
1994 *Experilingula* cf. *divulgata* Koneva and Popov; Popov and Holmer, p. 35, fig. 41.

Holotype. CNIGR 2/11991, ventral valve; Upper Cambrian, *Trisulcagnostus trisulcus* beds; Batyrbay section, Malyi Karatau.

Material. 15 complete shells and more than 800 disarticulated ventral and dorsal valves.

Diagnosis. As for the genus.

Remarks. A detailed description of this species, and basic statistics, were given by Koneva and Popov (1983). *Experilingula* cf. *divulgata* from the late Cambrian Kujandy Formation of north-eastern Central Kazakhstan (Popov and Holmer, 1994, p. 35) is indistinguishable from topotypes in all main aspects of external and internal shell morphology, but is known mostly only from juvenile shells. It is the only known record of the presence of *Experilingula* outside the Malyi Karatau Range.

Occurrence. Upper Cambrian, Kyrshabakty section, *Eorudagnostus ovaliformis–Trisulcagnostus trisulcus* beds, samples 1360-3, 1373, 1373-II, 1374, 1375, 1375-I, 1376, 1376-1, 1376-3–7, 1376-11, 1377, 1377-1, 1377-2, 1377-6–8, 1377-I, 1378-2, 1379-3, 1379-6, 1380-7, 1381, 1381-1, 1381-4, 1381-6, 1400, 1400-1, 1400-2, 1400-4–6, 1400-8–11, 1401, 1401-2, 1401-4, 1401-8, 1401-9a, 1401-10, 1401-10a, 1401-11, 1401-12, 1402, 1402-1, 1402-2, 1402-4; Batyrbay section, *Hedinaspis sulcata* and *Harpidoides-Platypeltoides* beds, samples 1444-1, 1444-3–5, –35 m, 0 m; east side of Shabakty River, samples 1412–1414.

Genus KYRSHABAKTELLA Koneva, 1986

1977 *Dysoristus* (*pars*), Pelman, p. 34.
1986*a* *Kyrshabaktella* Koneva, p. 52.
1990 *Kyrshabaktella* Koneva; Krause, p. 25.

Type species. Original designation by Koneva (1986*a*, p. 52); *Kyrshabaktella certa* Koneva 1986*a*; Middle Cambrian, *Peronopsis*? *ultimus* Biozone; Malyi Karatau.

Diagnosis. See Krause 1990, p. 35.

Species included. *Kyrshabaktella certa* Koneva, 1986; *Kyrshabaktella mudedirri* Krause, 1990; *Kyrshabaktella rectangulata* Ushatinskaya, 1992; *Kyrshabaktella tatjanae* Ushatinskaya, 1992; *Dysoristus belli* Pelman, 1977.

Remarks. *Kyrshabaktella* was assigned originally to the Family Zhanatellidae, mainly on the basis of having a semicircular emarginature in the ventral umbo; however, it lacks a pitted larval and post-larval shell, which are the most distinctive features of zhanatellids. Therefore it is reassigned here to the Family Obolidae.

Kyrshabaktella certa Koneva, 1986*a*

Plate 5, figures 3–11; Plate 6, figure 1

1986*a* *Kyrshabaktella certa* Koneva, p. 53, pl. 5, figs 13–24.
1996 *Kyrshabaktella certa* Koneva; Engelbretsen, p. 96, figs 13A–J.

Holotype. GA 427/421, ventral valve; Middle Cambrian, Amgaian, *Peronopsis*? *ultimus* Biozone; Kyrshabakty section, Malyi Karatau.

Material. 39 ventral and 41 dorsal valves.

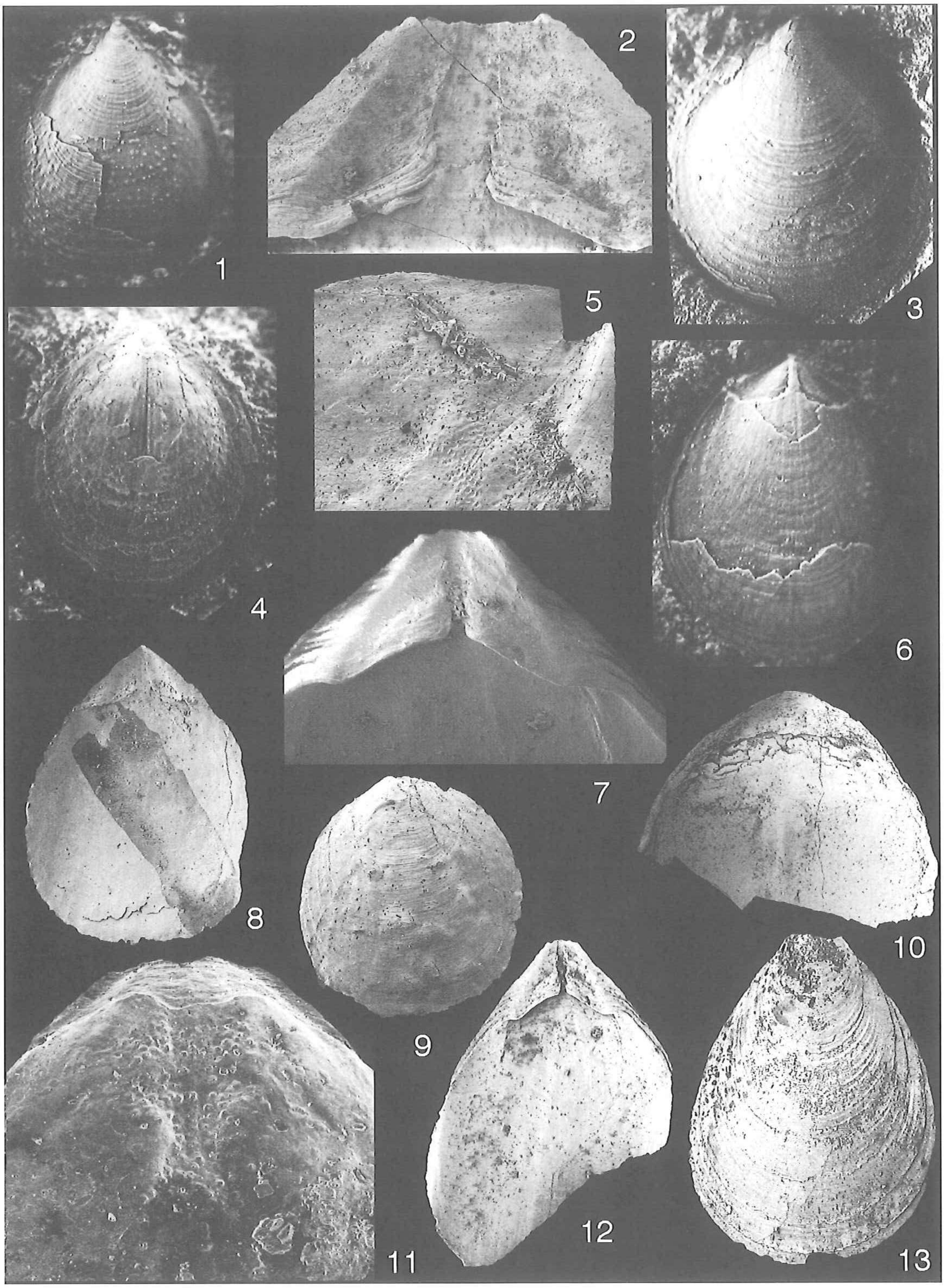
Diagnosis. Shell slightly ventribiconvex, elongate, subtriangular in outline with maximum width at about one-third of the distance from the anterior margin; ventral valve moderately and evenly convex in cross section with a low, orthocline pseudointerarea divided by a deep pedicle groove; ventral propareas narrow, flattened, lacking flexure lines; emarginature broad, semicircular; dorsal valve unevenly convex in sagittal profile, with maximum thickness posterior to the mid-valve; umbo marginal, divided by a shallow groove; dorsal pseudointerarea low, orthocline to slightly apsacline with a broad, concave median groove in the valve floor and slightly raised, narrow propareas divided by flexure lines.

EXPLANATION OF PLATE 4

Figs 1–10, 12–13. *Experilingula divulgata* Koneva and Popov; Upper Cambrian, Shabakty Group, Malyi Karatau. 1, IGNA 427/101, ventral valve exterior, sample 1376-3, *Neorudagnostus quadratiformis-Taenocephalus kyrshabaktensis* beds; ×10. 2, NMW 98.61G.5, ventral valve showing pseudointerarea and pedicle groove, Batyrbay section, *H. sulcata* beds, sample 0 m; ×41. 3, IGNA 427/102, dorsal valve exterior, sample 1376-7, *N. quadratiformis-T. kyrshabaktensis* beds; ×8. 4, IGNA 427/105, dorsal internal mould, sample 1374, *Eorudagnostus ovaliformis-Pareuloma* beds; ×8. Figs 5, 7–13, all from Batyrbay section, *H. sulcata* beds, sample 0 m. 5, NMW 98.61G.6, dorsal valve interior showing oblique lateral view of pseudointerarea and visceral area; ×45. 6, IGNA 427/104, ventral internal mould, sample 1375-I; ×12·5. 7, 12, NMW 98.61G.7, ventral valve showing detail of pseudointerarea, ×24, and interior, ×9. 8, NMW 98.61G.10, ventral valve interior, ×23. 9, NMW 98.61G.8, dorsal valve exterior; ×13·5. 10, NMW 98.61G.9, dorsal valve interior; ×12·5. 13, NMW 98.61G.11, ventral valve exterior; ×22.

Fig. 11. *Aksarinaia triquetra* Koneva; Middle Cambrian, Shabakty Group, Malyi Karatau, Kyrshabakty section, sample 1465-2; NMW 98.61G.5, dorsal valve interior; ×95.

PLATE 4



HOLMER *et al.*, *Aksarinaia, Experilingula*

Remarks. Krause (1990) and Ushatinskaya (*in* Aksarina *et al.* 1992) comprehensively discussed the affinities between all known species of *Kyrshabaktella*. *K.* cf. *certa* is also recorded from the Karagajly Formation in north Kyrgyzstan. In the outline and convexity of both valves, as well as in the morphology of both pseudointerareas, these specimens are closely comparable with the type material, but they differ in their slightly smaller sizes and weakly impressed muscle scars in both valves.

Occurrence. Middle Cambrian, Amgaian Stage; Kyrshabakty section, *Peronopsis ultimus* and *Ptychagnostus intermedius* beds, samples 1467, 1467-1, 1467-3, 1465-1, 1465-10, 1465-13, 1313 (= 1467-3), 1314 (= 1465), 1314-2, 1314-3, 1314-5; Karagajly Formation, Kostek Range, sample 1639. Engelbretsen (1996) also recorded this species from the Murrawong Creek Formation (Florian–Boomerangian stages) of New South Wales, Australia.

Genus NOTIOBOLUS Popov, 1981

Type species. Original designation by Popov (*in* Popov and Solovjev 1981, p. 67); *Notiobolus tenuis* Popov, 1981, Middle Cambrian, Mayaian, West Antarctica Shackleton Range, erratic boulders.

Diagnosis. Subcircular to subtriangular, thin-shelled, slightly inequivalved; pseudointerareas of both valves low, with flexure lines; ventral pseudointerarea with flattened propareas and deep, narrow pedicle groove; ventral visceral area subtriangular, not extending to mid-valve; dorsal visceral area bisected by low median ridge, bounded laterally by two ridges, with anterior tongue extending slightly anterior to mid-valve; mantle canals usually strongly impressed, baculate with *vascula lateralia* of both valves peripheral, arcuate; *vascula media* long, widely divergent.

Species included. *Notiobolus tenuis* Popov, 1981; *Notiobolus indefinitus* sp. nov.

Remarks. *Notiobolus* is most similar to *Palaeobolus* Matthew, 1899, but can be distinguished by having arcuate, submarginal ventral *vascula lateralia* and paired submedian ridges bounding the anterior tongue of the dorsal visceral area.

Notiobolus indefinitus sp. nov.

Plate 6, figures 3–15; Plate 7, figures 1–13; Plate 8, figures 15–16

Derivation of name. Latin *indefinitus*, indeterminate, uncertain.

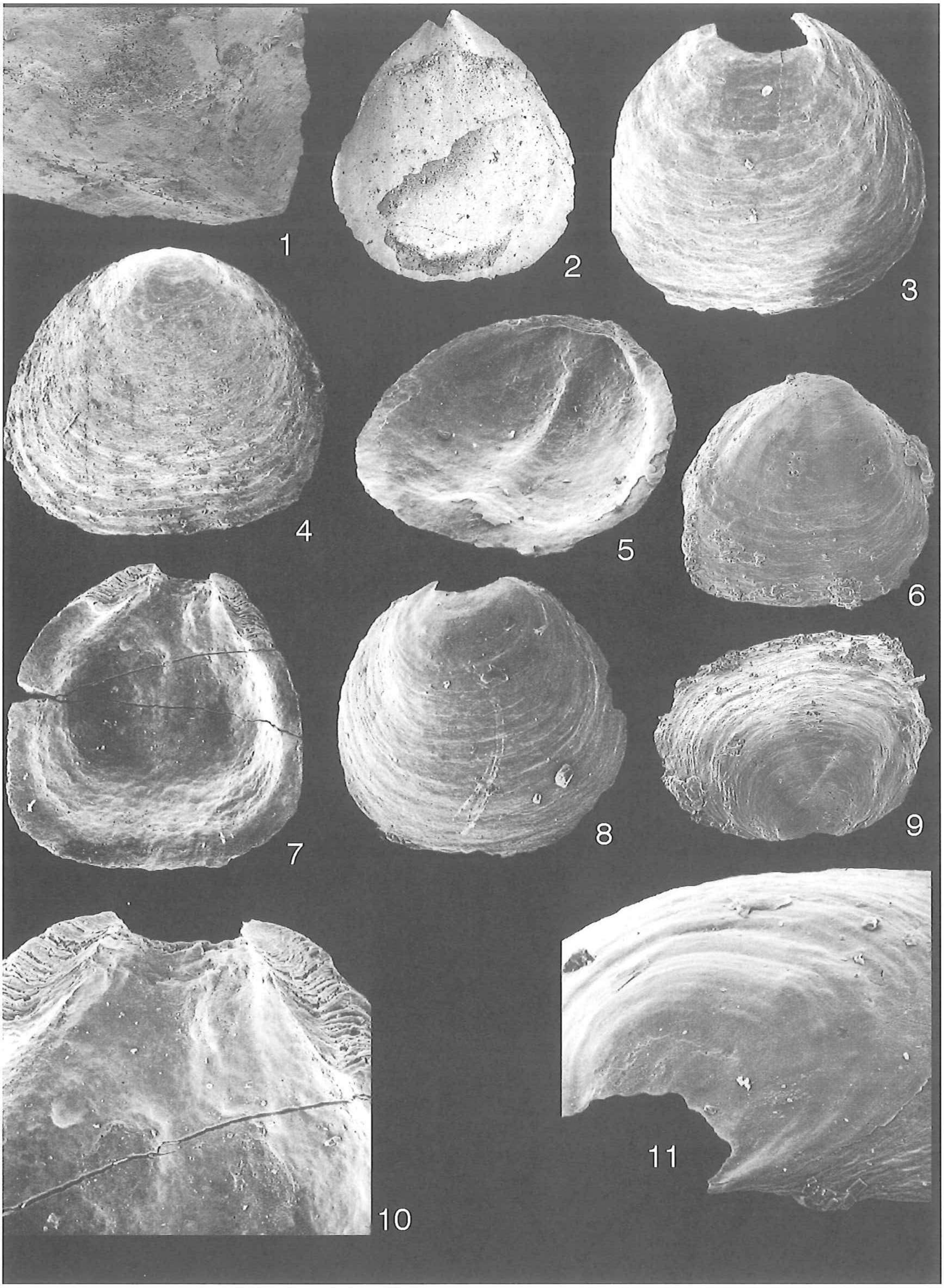
Holotype. IGNA 427/2, ventral valve; Upper Cambrian *Ivshinagnostus ivshini*-*Irvingella major* beds, sample 1360-8, Kyrshabakty section, Malyi Karatau.

EXPLANATION OF PLATE 5

Figs 1–2. *Experilingula divulgata* Koneva and Popov; Upper Cambrian, Shabakty Group, Malyi Karatau, Batyrbay section, *Hedinaspis sulcata* beds, sample 0 m. 1, NMW 98.61G.10, ventral valve interior, oblique posterior view; ×59. 2, NMW 98.61G.6, dorsal valve interior; ×22.

Figs 3–11. *Kyrshabaktella certa* Koneva; Middle Cambrian, all except 6 and 9 from the Kyrshabakty section, *Ptychagnostus intermedius* Biozone. 3, 11, NMW 98.61G.12, sample 1314, ventral valve exterior, ×51, and oblique posterior view of umbonal area, ×125. 4, RM Br136356, dorsal valve exterior, sample 1314; ×51. 5, RM Br136357, sample 1314, dorsal valve interior, oblique anterior view; ×46. 6, 9, NMW 98.61G.14, Karagajly Formation, Kostek Range, sample 1639, dorsal valve exterior, ×42, and oblique posterior view, ×49. 7, 10, NMW 98.61G.13, sample 1314, ventral valve, ×49, and details of umbonal area showing pseudointerarea, emarginature and umbonal muscle scars, ×113. 8, RM Br136354, ventral valve exterior, sample 1314; ×60.

PLATE 5



HOLMER *et al.*, *Experilingula*, *Kyrshabaktella*

Material. Two complete shells, 173 dorsal and ventral valves of mature specimens, and about 200 complete shells, dorsal and ventral valves of juveniles.

Diagnosis. *Notiobolus* with narrow pseudointerareas in both valves about 50 per cent as wide as maximum shell width, deeply impressed flexure lines on ventral propareas; ventral visceral area slightly raised and bounded anteriorly by a distinct rim; dorsal visceral area with a narrow median tongue extending anteriorly for about 66 per cent of maximum valve length.

Description. Shell weakly biconvex, slightly elongate to transversely subcircular or subtriangular in outline. Ventral valve gently convex with maximum thickness about 25 per cent of sagittal valve length from the umbo; ventral pseudointerarea low, triangular, orthocline with deep, subtriangular pedicle groove and slightly raised propareas divided into two approximately equal parts by deep flexure lines. Dorsal valve gently convex with maximum thickness slightly posterior to mid-valve length; dorsal pseudointerarea low, divided by a broad, shallow median groove and with flexure lines on propareas. Shell surface ornamented by fine, closely placed fila. Ventral interior with subtriangular visceral area slightly raised and bounded anteriorly by a low rim. The pedicle nerve impression crosses the whole visceral area. Ventral scars of outside, internal and median lateral muscles clearly separated in mature specimens. Combined ventral scars of transmedian and anterior lateral muscles are short and raised slightly above the valve floor. Ventral *vascula lateralia* submarginal, arcuate with widely divergent proximal parts. Dorsal interior with slightly thickened visceral area occupying the posterior third of the valve, and with a narrow anterior tongue bounded laterally by two fine, slightly divergent submedian ridges and extending slightly anterior to the mid-valve length. Median ridge fine and long, crossing the whole visceral field. Dorsal *vascula lateralia* arcuate, submarginal.

Ontogeny. Samples from the '*Pseudagnostus curtare*'-*Irvingella tropica* to *Pseudagnostus pseudaugustilobus*-*Acrocephalaspina* beds contain a relatively large number of larval and early post-larval obolid shells, which probably belong to *Notiobolus indefinitus* (Pl. 7, figs 5, 7–9; Pl. 8, fig. 15). These specimens are characterised by subcircular shells with a short but well-defined ventral pseudointerarea. A small, strip-like, undivided pseudointerarea is also present in the dorsal valve. A smooth semicircular area, about 300–320 μm wide, bounded by the first strong growth ring, is evident in some shells (Pl. 7, fig. 5; Pl. 8, fig. 15); it possibly represents the embryonic shell.

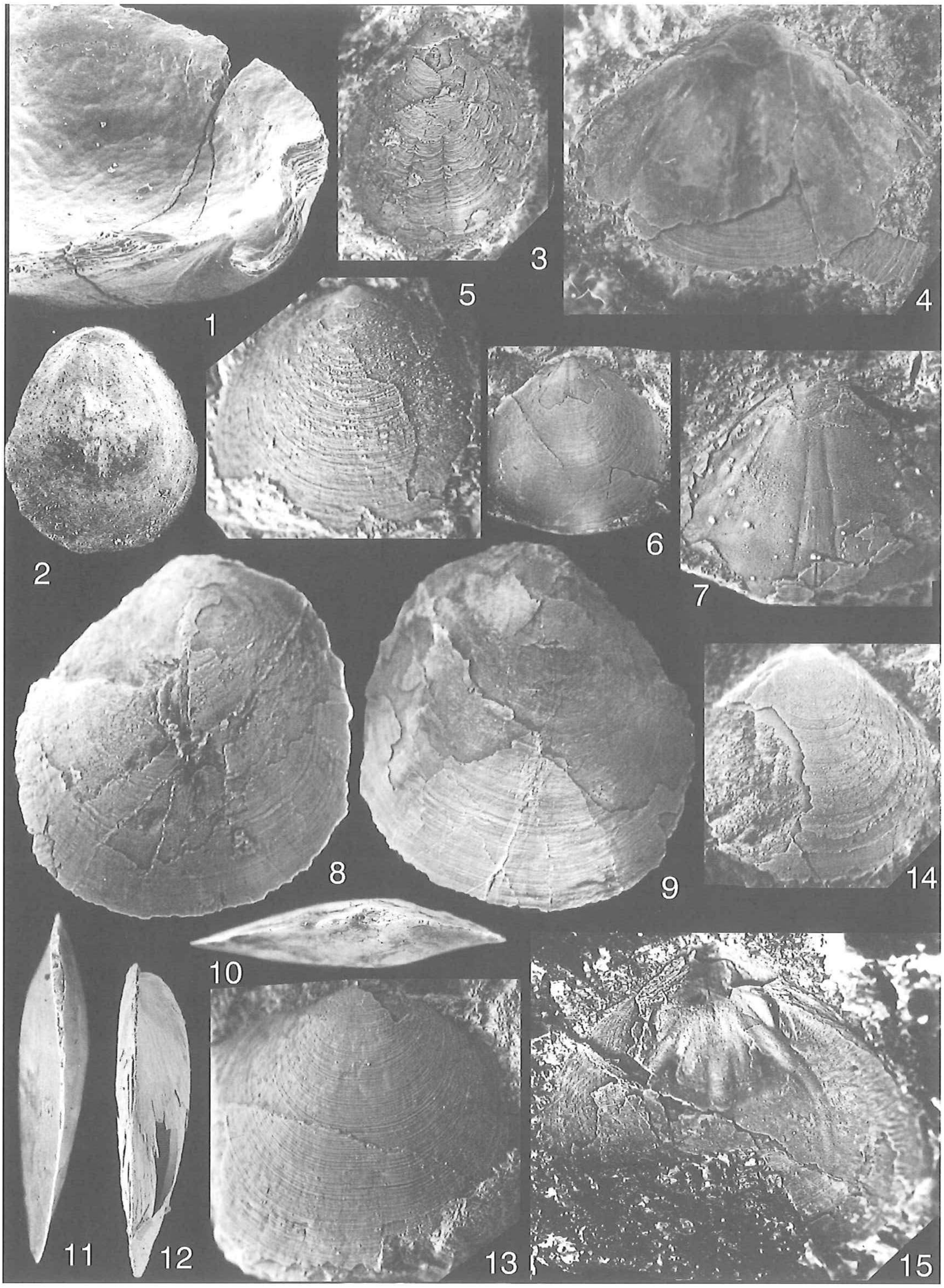
Remarks. *Notiobolus indefinitus* is similar only to *Notiobolus tenuis* Popov (*in* Popov and Solovjev 1981, p. 49; figured here for comparison on Pl. 8, figs 1–3) from the Middle Cambrian, Mayaian Stage of West Antarctica. The Kazakhstanian species differs in having a relatively narrow, triangular ventral pseudointerarea divided by a wide, triangular pedicle groove and deeply impressed flexure lines on the ventral propareas, as well as in having a thickened ventral visceral area.

EXPLANATION OF PLATE 6

Fig. 1. *Kyrshabaktella certa* Koneva; Middle Cambrian Shabakty Group, Kyrshabakty section, Malyi Karatau, *Ptychagnostus intermedius* Biozone; NMW 98.61G.13, sample 1314, ventral valve interior, oblique posterior view; ×75.

Fig. 2. *Aksarinaia triquetra* Koneva; Middle Cambrian, Shabakty Group, Kyrshabakty section, Malyi Karatau; NMW 98.61G.5, dorsal valve interior, sample 1465-2, ×37.

Figs 3–15. *Notiobolus indefinitus* sp. nov.; Upper Cambrian, Malyi Karatau, Kyrshabakty section, all except fig. 13 from the *Ivshinagnostus ivshini*-*Irvingella major* beds. 3, IGNA 427/19, ventral valve exterior showing regeneration of the valve damaged by predator, sample 1360-8; ×6. 4, IGNA 427/5, dorsal valve interior, sample 1360-8; ×8. 5, IGNA 427/26, dorsal valve exterior, sample 1360-8; ×5. 6, IGNA 427/6, dorsal valve exterior, sample 1360-5; ×3. 7, IGNA 427/21, ventral valve interior, sample 1360-8; ×5. 8–11, conjoined valves in ventral, dorsal, posterior and lateral views, sample 1360-5; ×4. 12, NMW 98.61G.16, lateral view of conjoined valves of juvenile specimen, sample 1361-4; ×35. 13, IGNA 427/48, dorsal valve exterior, '*Pseudagnostus curtare*'-*Irvingella tropica* beds, sample 1359-1; ×4. 14, IGNA 427/24, ventral valve exterior, sample 1360-8; ×6·7. 15, IGNA 427/2, holotype, ventral valve interior, sample 1360-8; ×4.



HOLMER *et al.*, brachiopods

TABLE 2. *Notiobolus indefinitus* sp. nov., dimensions of ventral and dorsal valves from the Kyrshabakty section (Upper Cambrian, '*Pseudagnostus curtare*'-*Irvingella tropica* beds and *Pseudagnostus pseudangustilobus*-*Acrocephalaspina* beds).

	Ventral valves				Dorsal valves	
Museum no.	NMW 98.61G.211	NMW 98.61G.303	NMW 98.61G.342	NMW 98.61G.341	NMW 98.61G.307	NMW 98.61G.193
Sample no.	1357-3	1360-5	1360-5	1360-5	1357-2	1357-3
L	10·3	11·7	11·4	11·4	5·1	12·3
W	10·45	13·0	12·2+	12·6	4·7	11·0
T	0·9	–	–	–	–	–

Occurrence. Kyrshabakty section, '*Pseudagnostus curtare*'-*Irvingella tropica* and *Pseudagnostus pseudangustilobus*-*Acrocephalaspina* beds, samples 1357-2, 1357-3, 1357-I, 1358-II, 1359-1, 1359-2, 1360-1–4, 1360/5, 1360-6–8, 1361, 1361-1, 1361-3, 1361-4, 1370-I, 1378-1, 1378-2, 1378-19, 1379-3, 1379-8.

Genus OEPIKITES Khazanovich and Popov, 1984

Type species. Original designation by Khazanovich and Popov (*in* Khazanovich *et al.* 1984, p. 40); *Oepikites macilentus* Khazanovich and Popov, 1985; Middle Cambrian, Sablinka Formation, north-western Russia (Ingria).

Diagnosis. See Puura and Holmer 1993, p. 220.

Oepikites? sp.

Plate 8, figures 4–10

Material. Three ventral and three dorsal valves.

Remarks. Middle–Upper Cambrian boundary beds in Malyi Karatau and north Kyrgyzstan contain lingulides with a characteristically elongate, suboval, smooth shell. The dorsal interiors of these specimens have a slightly raised visceral area with a long anterior tongue extending well anterior to mid-valve length.

EXPLANATION OF PLATE 7

Figs 1–13. *Notiobolus indefinitus* sp. nov.; Upper Cambrian, Malyi Karatau Range, Kyrshabakty section. 1–4, 6, 9, 10, 13 from *Ivshinagnostus ivshini*-*Irvingella major* beds; 5, 8, 11 from *Pseudagnostus pseudangustilobus*-*Acrocephalaspina* beds. 1, IGNA 427/16, exfoliated dorsal valve interior, sample 1360-5; ×6·7. 2, IGNA 427/11, dorsal valve exterior, sample 1360-5; ×4. 3, IGNA 427/13, dorsal valve exterior, sample 1360-5; ×3. 4, IGNA 427/6, dorsal valve exterior, sample 1360-5; ×3. 5, NMW 98.61G.155, dorsal view of conjoined valves of the larval shell, sample 1378-23; ×79. 6, IGNA 427/15, dorsal valve exterior, sample 1360-5; ×6·7. 7, NMW 98.61G.152, dorsal view of conjoined valves of larval shell, *Eorudagnostus kazakhstanicus*-*Parabolina monstruosa* beds, sample 1380-1; ×66. 8, NMW 98.61G.15, ventral view of conjoined valves of larval shell, sample 1379-8; ×51. 9, NMW 98.61G.17, dorsal view of conjoined valves of larval shell, sample 1361-5; ×42. 10, IGNA 427/8, dorsal valve interior, sample 1360-5; ×4. 11, NMW 98.61G.224, dorsal valve, interior of larval shell, sample 1379-8; ×51. 12, IGNA 427/203, ventral valve interior, '*Pseudagnostus curtare*'-*Irvingella tropica* beds, sample 1359; ×9. 13, IGNA 427/5, ventral valve exterior, sample 1360-5; ×4.

PLATE 7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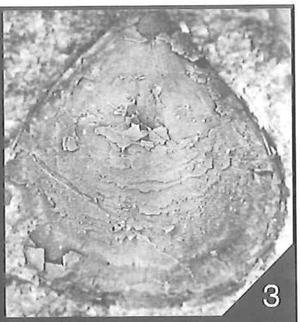
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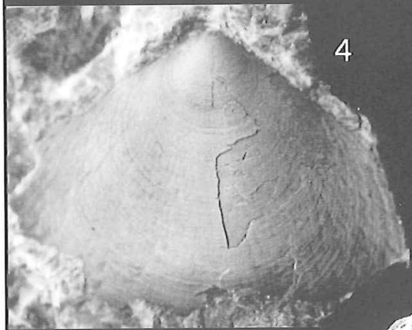
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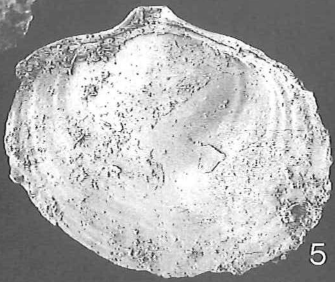
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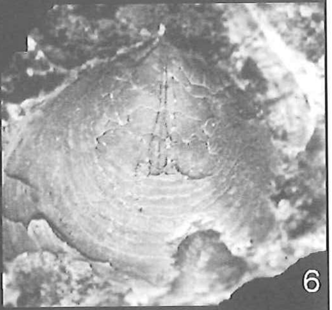
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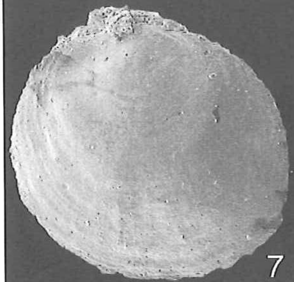
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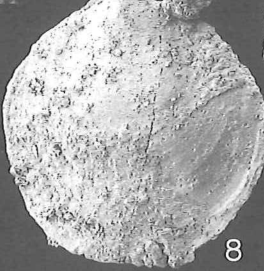
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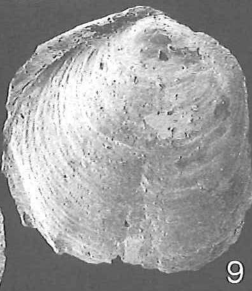
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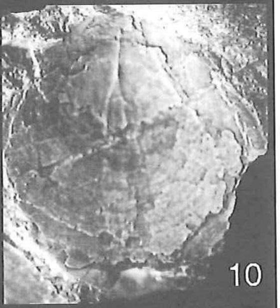
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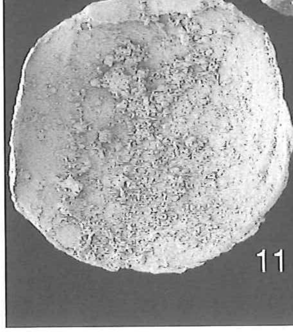
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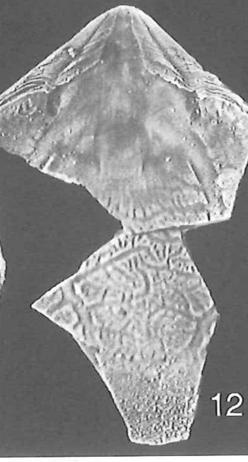
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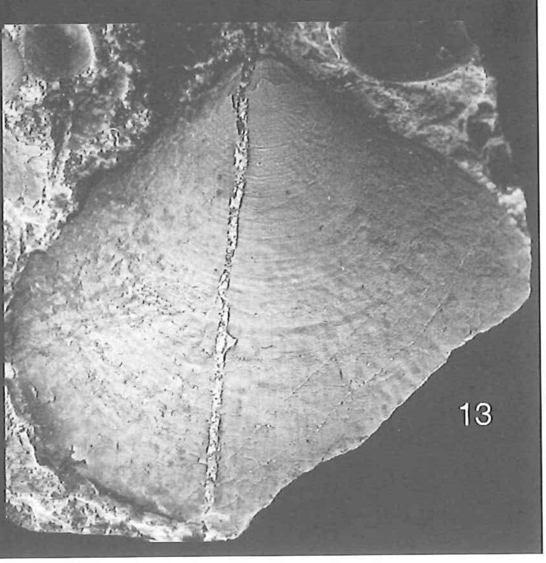
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HOLMER *et al.*, *Notiobolus*

Small, elongate oval, dorsal, outside lateral muscle scars are situated close to the anterior margin of the valve and are separated by a short median ridge. These dorsal features, together with the absence of pitted surface micro-ornament on the larval and post-larval shell, suggest a close affinity with *Oepikites*. Precise taxonomic discrimination is difficult because of the limited number of specimens and their imperfect preservation.

Occurrence. Middle Cambrian, Mayaian–lower Upper Cambrian, Karadzhorga Formation, Moldotau Range, sample 127/9; *Lejopyge laevigata* and *Kormagnostus simplex* biozones, Kyrshabakty section, Malyi Karatau, samples 1348 and 1351-4.

Genus PALAEOBOLUS Matthew, 1899

1899 *Palaeobolus* Matthew, p. 210.
?1936 *Obolopsis* Saito, 1936, p. 349 [type, *O. margaritae*; OD].

Type species. Original designation by Matthew (1899, p. 210); *Palaeobolus bretonensis* Matthew, 1899; Middle Cambrian, Amgaian, Bourinot Group, Cape Breton, Canada.

Diagnosis. Shell slightly elongated, subtriangular to subcircular in outline, slightly dorsibiconvex and inequivalved, ornament of fine concentric rugellae; pseudointerareas in both valves with flexure lines on propareas and raised slightly above the valve floor; ventral interior with slightly raised visceral area not extending anteriorly to mid-valve length, and with submedian, straight, slightly divergent *vascula lateralia*; dorsal interior with fine median ridge and narrow anterior tongue to the visceral field extending slightly anterior to mid-valve length.

Species included. Palaeobolus bretonensis Matthew, 1899; ?*Obolopsis margaritae* Saito, 1936; *Palaeobolus liantuoensis* Zeng, 1987.

Remarks. Obolopsis Saito, 1936, with its type and only known species *O. margaritae* from the upper Upper Cambrian of South Korea, is very similar to *Palaeobolus bretonensis* in shell outline, characters of the

EXPLANATION OF PLATE 8

Figs 1–3, *Notiobolus tenuis* Popov (*in* Popov and Solovijev, 1981); Middle Cambrian, Mayaian, Antarctica, Shackleton Range, erratic boulder. 1, CNIGR 26/11378, ventral internal mould; ×5. 2, CNIGR 25/11378, dorsal internal mould, holotype; ×5. 3, RM Br136360, ventral valve exterior; ×6.

Figs 4–10. *Oepikites*? sp.; 4–5, NMW 98.61G.18, dorsal valve interior in oblique lateral and normal views, Upper Cambrian, *Kormagnostus simplex* Biozone, Malyi Karatau, Kyrshabakty section, sample 1351-I; both ×51. 6, NMW 98.61G.20, ventral valve interior, Middle–Upper Cambrian, Karadzhorga Formation, Moldotau Range, Karakichi River, sample 127/9; ×19. 7, NMW 98.61G.21, dorsal valve interior, age and locality as for 6; ×12·5. 8, NMW 98.61G.22, dorsal valve exterior, age and locality as for 6; ×19. 9, NMW 98.61G.23, ventral valve exterior, age and locality as for 6; ×24. 10, NMW 98.61G.24, ventral valve exterior, Middle Cambrian, *Lejopyge laevigata* Biozone, Malyi Karatau, Kyrshabakty section, sample 1348; ×68.

Figs 11–14. Obolidae gen. et sp. indet.; Ordovician, lower *Paroistodus proteus* Biozone, Malyi Karatau, Batyrbay section, sample 465 m. 11–12, NMW 98.61G.25, dorsal valve of juvenile specimen, exterior, ×34, and detail of larval shell, ×67. 13, NMW 98.61G.26, dorsal valve exterior; ×22. 14, NMW 98.61G.27, ventral valve interior; ×34.

Figs 15–16. *Notiobolus indefinitus* sp. nov.; Upper Cambrian, Malyi Karatau, Kyrshabakty section. 15, NMW 98.61G.28, ventral view of conjoined valves of the larval shell, *Eorudagnostus kazakhstanicus-Parabolina monstruosa* beds, sample 1380-1; ×78. 16, NMW 98.61G.29, external shell surface of mature specimen, *Ivshinagnostus ivshini-Irvingella major* beds, sample 1361-4; ×37.

PLATE 8


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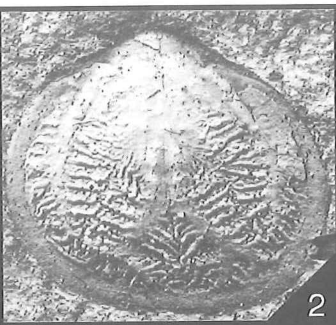
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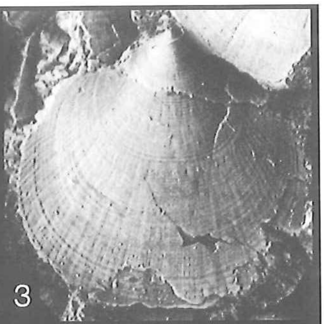
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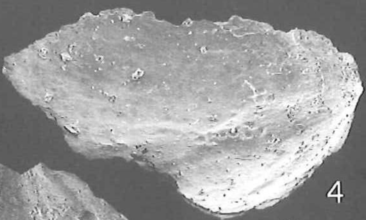
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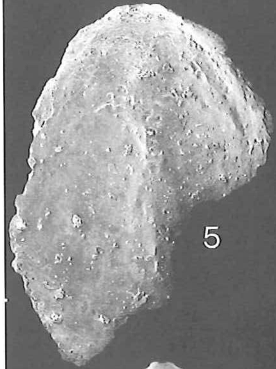
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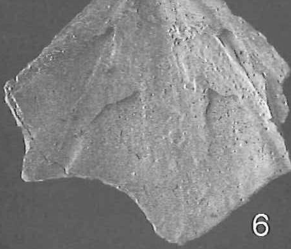
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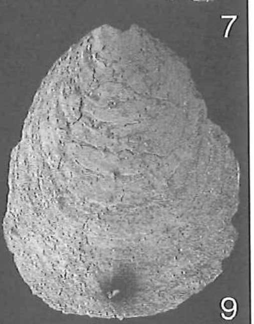
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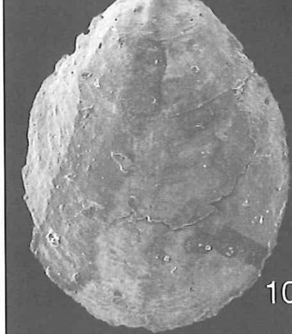
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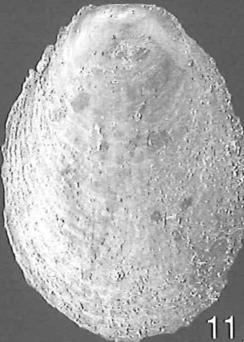
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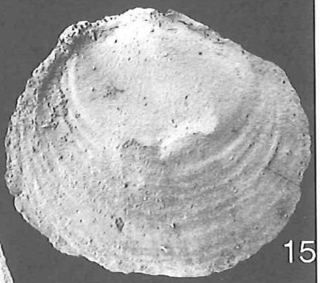
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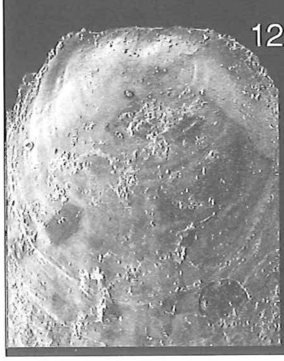
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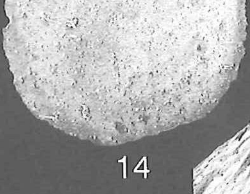
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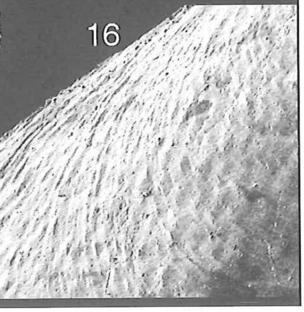
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ventral and dorsal visceral areas, and straight, submedian ventral *vascula lateralia*. According to Saito (1936), the most distinctive features of *Obolopsis* are the vestigial pseudointerareas in both valves; observation of the single dorsal valve preserved in the type collection (PB1429, University of Tokyo, illustrated by Saito, 1936, pl. 1, figs 1, 12; all other type material was lost during the Second World War) gives no new information on internal shell morphology, but Saito's illustrations suggest that the absence of pseudointerareas reported in the original description are more probably a preservational artefact rather than a morphological character. *Obolopsis* is thus regarded here provisionally as a junior subjective synonym of *Palaeobolus*; however, precise generic assignment of *O. margaritae* will be possible only after re-study of new topotype material.

There are several species of *Palaeobolus* described from the Cambrian of China. Among them only *Palaeobolus liantuoensis* Zeng, 1987 definitely belongs in the genus. Original descriptions of *P. discus* Wang, 1956 and *P. rotundus* Wang, 1956 lack satisfactory information on the morphology of pseudointerareas, mantle canals and muscle impressions in both valves, and thus their precise generic assignment within the Lingulida remains uncertain.

Palaeobolus liantuoensis Zeng, 1987

Plate 9, figures 1–13

1983 *Palaeobolus bretonensis* Matthew; Gorjansky and Koneva, p. 130, pl. 27, figs 1–14 (*non* Matthew 1899).

1987 *Palaeobolus liantuoensis* Zeng, p. 209, pl. 8, figs 9–13, text-fig. 5-1.

Material. One complete shell and about 100 disarticulated dorsal and ventral valves.

Diagnosis. Ventral valve with acute, slightly acuminate beak; ventral pseudointerarea high, triangular, bisected by a deep, narrow pedicle groove with steep, slightly diverging lateral margins; propareas flattened, raised above valve floors; dorsal valve almost circular with a low pseudointerarea divided by a broad, shallow median groove; visceral area in both valves slightly thickened anteriorly, with numerous pits; dorsal interior with a long, narrow, median tongue extending anteriorly for about 75 per cent of the sagittal valve length, and with a strong median ridge bisecting the whole visceral area.

Description of specimens from Kazakhstan. Shell weakly biconvex, slightly inequivalved, subcircular in outline, about 105–110 per cent as long as wide. Ventral valve gently convex with a pointed beak and triangular, orthocline pseudointerarea divided by a deep, narrow pedicle groove with subparallel lateral margins; propareas flattened, raised above the valve floor, with flexure lines. Dorsal valve gently convex, almostly circular in outline, with a low, orthocline pseudointerarea divided by a broad, shallow median groove. Exterior covered by fine, regular concentric fila, finely lamellose peripherally.

EXPLANATION OF PLATE 9

Figs 1–13, *Palaeobolus liantuoensis* Zeng. 1–9, Lower Cambrian, *Ushbaspis limbata* Biozone, Ushbas River (1–8) and Koksu River (9), Malyi Karatau. 1, IGNA 2224/2, exfoliated ventral valve exterior, sample 1220; ×4·5. 2, IGNA 2224/1, ventral valve exterior, sample 1220; ×4·5. 3, IGNA 2224/2, ventral internal mould, sample 1220; ×4·5. 4, IGNA 2224/100, ventral valve exterior, sample 5-II/52; ×4·5. 5, IGNA 2224/11, dorsal internal mould, sample 1009; ×4·5. 6, IGNA 2224/103, ventral valve exterior, detail of postlarval shell, sample 5-II/52; ×15. 7, IGNA 2224/101, dorsal valve interior, sample 5-II/52; ×4·5. 8, IGNA 2224/10, dorsal internal mould, sample 1220; ×4·5. 9, IGNA 2224/12, dorsal valve interior, sample 1009; ×4·5. 10–13, Lower Cambrian, South China. 10, YIGM IV45931, dorsal internal mould; ×5·2. 11, YIGM IV45929, ventral internal mould, holotype; ×5·2. 12, YIGM IV45931, exfoliated dorsal valve interior; ×6·5. 13, YIGM IV45930, ventral internal mould; ×5·2.


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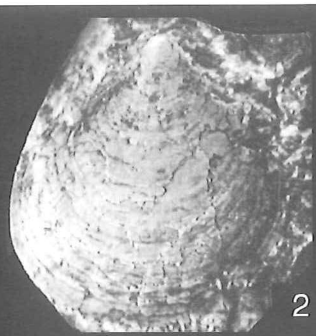
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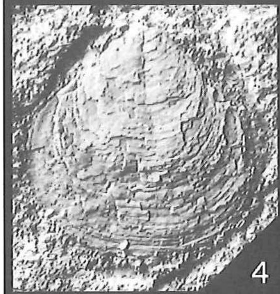
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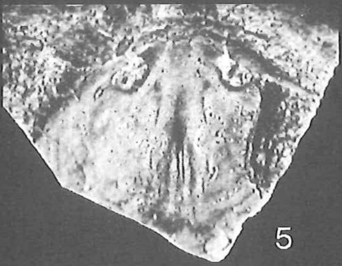
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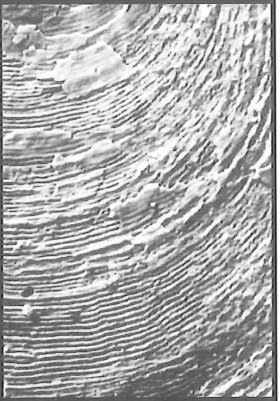
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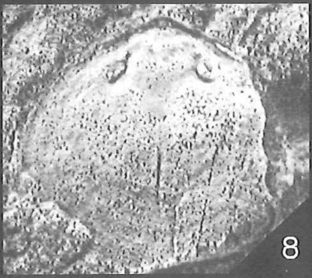
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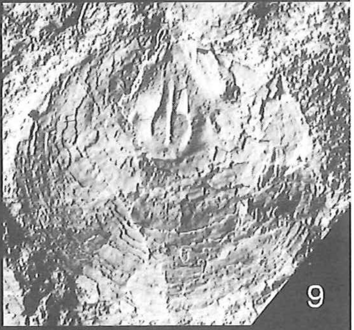
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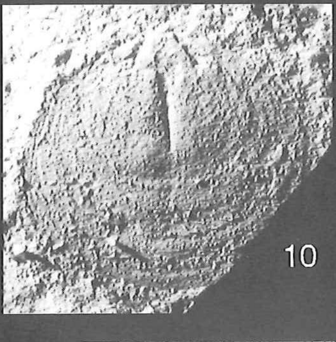
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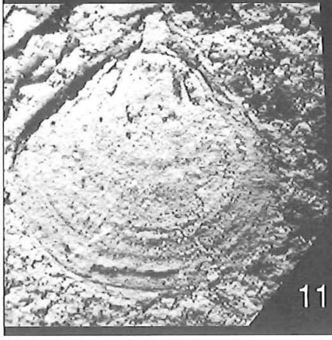
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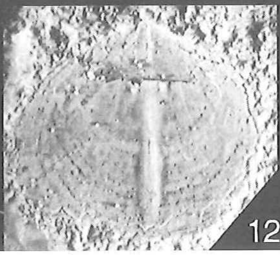
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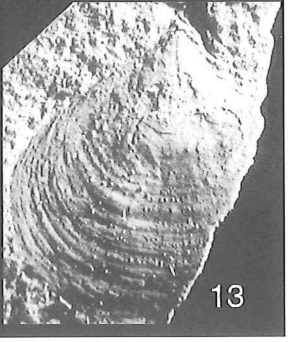
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Ventral interior with thickened visceral area extending to mid-valve length and bounded anteriorly by a low rim; viscera divided medially into three parts by a strongly impressed pedicle nerve impression; paired ventral scars of the internal, external and middle lateral muscles approximately equal in size, elongate, disposed radially; posterolateral muscle fields small, slightly thickened. Ventral *vascula lateralia* submedial with straight, divergent proximal parts. Dorsal interior with strongly impressed, elongate, suboval, posterolateral muscle scars; anterior tongue of the dorsal visceral area long and narrow, extending anteriorly to about 75 per cent of the sagittal valve length and with gently impressed, elongate, suboval, central muscle scars in the proximal part; median ridge strong, bisecting the whole visceral field; dorsal mantle canals weakly impressed.

Dimensions. Ventral valves: GA 2224/1, L = 10·0, W = 9·5, T = 1·0; GA 2224/2, L = 10·0, W = 9·0, T = 0·3; GA 2224/3, L = 9·5, W = 9·0, T = 0·3. Dorsal valves: GA 2224/7, L = 9·5, W = 10, T = 0·5; GA 2224/7-1, L = 10·5, W = 10·5, T = 1·0; GA 2224/25, L = 9·5, W = 10·0, T = 0·94.

Remarks. Specimens of *Palaeobolus* from the Lower Cambrian of Malyi Karatau were referred originally by Koneva (*in* Gorjansky and Koneva 1983) to *P. bretonensis* Matthew. However, our examination of specimens of *P. bretonensis* in the United States National Museum and the Royal Ontario Museum demonstrates that Kazakhstanian specimens differ from the topotypes in having a less acuminate ventral valve, widely divergent proximal parts of the ventral *vascula lateralia*, and a strong dorsal median ridge extending anteriorly for about 75 per cent of the valve length.

The Kazakhstanian shells are most similar to *P. liantuoensis* Zeng, 1987 from the Lower Cambrian of South China in general shell outline, as well as in having a slightly acuminate ventral valve, a relatively high ventral pseudointerarea, and a strong dorsal median ridge. The only difference is the somewhat larger (more than 10 mm length) sizes of the shells from Malyi Karatau, but we do not regard shell size difference to be a sufficient taxonomic character to preclude assignment of our material to *P. liantuoensis*. Some topotypes of *P. bretonensis* (Pl. 14, figs 1–3) and *P. liantuoensis* (Pl. 9, figs 10–13) are re-illustrated here for comparison.

Occurrence. Lower Cambrian, Botomian–Toyonian, *Hebediscus orientalis* and *Ushbaspis limbata* biozones, Malyi Karatau; Ushbas section, samples 1001, 1008, 1220, 1235-a, 5B-52; Kurtybulak spring, sample 550.

EXPLANATION OF PLATE 10

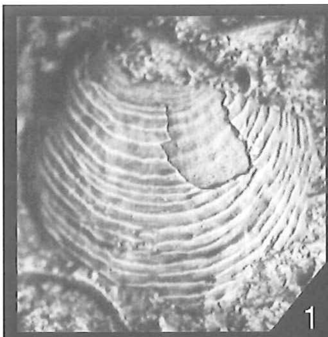
Figs 1–3. Zhanatellidae? gen. et sp. indet.; Upper Cambrian, *Trisulcagnostus trisulcus-Saukiella* beds, Malyi Karatau, Kyrshabakty section. 1, IGNA 427/112, incomplete dorsal(?) valve exterior, sample 1400-9; ×12·5. 2, IGNA 427/113, incomplete ventral(?) valve exterior, sample 1400-9; ×12·5. 3, IGNA 427/223, incomplete dorsal(?) valve exterior, sample 1400-8; ×10.

Figs 4–7. *Broeggeria salteri* (Holl); Upper Cambrian–Ordovician, Malyi Karatau, Batyrbay section. 4–5, NMW 98.61G.41, dorsal valve exterior and interior, *Cordylodus lindstroemi* Biozone, sample 235 m; both ×14. 6, NMW 98.61G.43, ventral valve interior, *Cordylodus intermedius* Biozone, sample 1449-3; ×17. 7, NMW 98.61G.42, dorsal valve exterior, *Cordylodus proavus* Biozone, sample 131 m; ×3.

Figs 8–11. *Zhanatella rotunda* Koneva; Upper Cambrian, *Eorudagnostus ovaliformis-Pareuloma* beds, Malyi Karatau, Kyrshabakty section. 8, NMW 98.61G.44, incomplete dorsal valve exterior, sample 1381; ×17. 9. IGNA 427/699, incomplete ventral valve interior, sample 1381-4; ×23. 10, NMW 98.61G.45, incomplete dorsal valve interior, sample 1381-3; ×25. 11, NMW 98.61G.46, incomplete ventral valve interior, sample 1381; ×17.

Figs 12–14. *Fossuliella*? sp.; Upper Cambrian, Malyi Karatau, Kyrshabakty section. 12, ventral valve interior, *Glyptagnostus stolidotus* Biozone, sample 1352; ×23. 13, NMW 98.69G.2, ventral valve showing detail of pitted micro-ornament on larval shell, *Ivshinagnostus ivshini-Irvingella major* beds, sample 1361-4; ×1014. 14, NMW 98.61G.48, pitted micro-ornament on ventral postlarval shell; ×1014.

Figs 15–16. *Zhanatella* sp.; Upper Cambrian, Zhalgyz Formation, Chaganak, sample 8921-1; NMW 98.61G.49, ventral valve interior, ×15, and detail of visceral area and pseudointerarea, ×48.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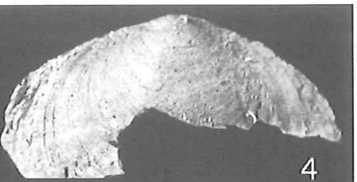
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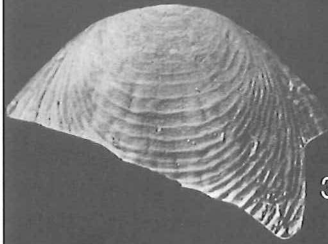
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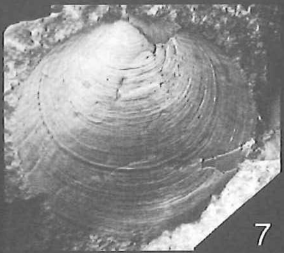
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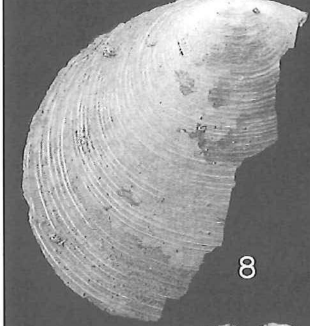
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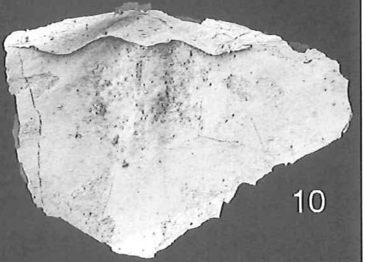
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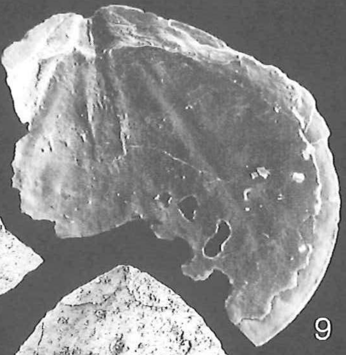
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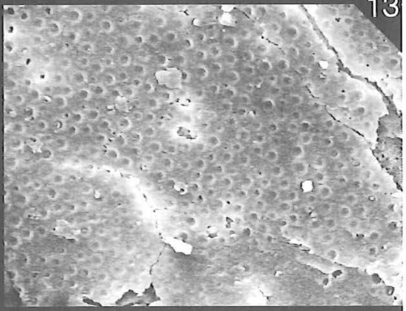
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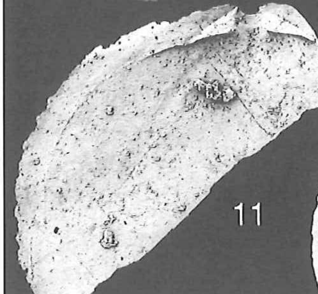
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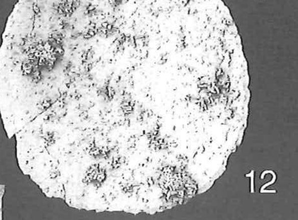
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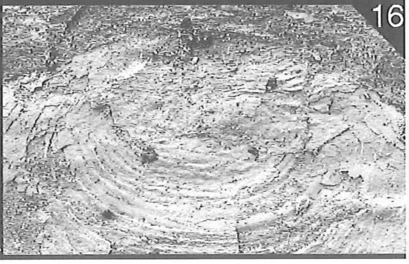
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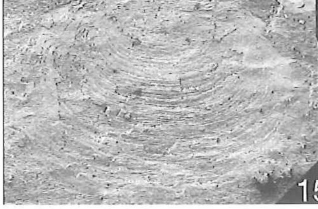
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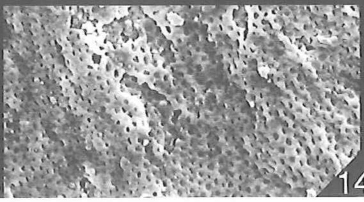
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HOLMER *et al.*, brachiopods

OBOLIDAE gen. et sp. indet.

Plate 8, figures 11–14; Plate 12, figure 1; Plate 23, figure 19

Material. Two complete shells and 156 dorsal and ventral valves.

Description. Shell smooth, slightly dorsibiconvex, elongate subtriangular in outline, about 125 per cent as long as wide and with maximum width at about 50–60 per cent of shell length anterior to the ventral umbo. Ventral valve slightly acuminate, gently and unevenly convex with maximum thickness at about one-third of the shell length anterior to the umbo. Pseudointerarea high, triangular, about 25 per cent as long and 60–65 per cent as wide as the valve. Pedicle groove deep and narrow with subparallel lateral margins. Ventral propareas with deeply impressed flexure lines. Dorsal interarea with narrow, undivided pseudointerarea lying on the valve floor. Ventral interior with visceral area raised slightly, about 40–45 per cent as long as the valve and bounded anteriorly by a low rim. Pedicle nerve impressions as a pair of fine, slightly divergent furrows bisecting the umbonal muscle scar and crossing the whole visceral area. *Vascula lateralia* straight, submedian, slightly divergent in their proximal parts. Dorsal interior with weakly impressed visceral area whose anterior border forms a long tongue extending anteriorly from the mid-valve. *Vascula media* short, divergent. *Vascula lateralia* submarginal, arcuate.

Remarks. These juvenile specimens are comparable with *Lingulella*, *Palaeoglossa* or *Leptembolon* in characters of the pseudointerareas, visceral areas and mantle canals. Their precise generic discrimination is impossible without mature shells.

Occurrence. Lower Ordovician, *Szechuanella-Apatokephalus* and *Nileus* beds, Batyrbay section, samples 382, 383, 396, 465 m.

Family ZHANATELLIDAE Koneva, 1986

Genus ZHANATELLA Koneva, 1986

Type species. Original designation by Koneva (1986*a*, p. 50); *Zhanatella rotunda* Koneva, 1986; Upper Cambrian, Malyi Karatau, southern Kazakhstan.

Diagnosis. See Popov and Holmer 1994, p. 70.

Zhanatella rotunda Koneva, 1986

Plate 10, figures 8–11

1986 *Zhanatella rotunda* Koneva, p. 50, pl. 5, figs 1–12.
1992 *Zhanatella rotunda* Koneva; Popov and Ushatinskaya, pl. 2, figs 5–6; pl. 3, figs 1–3.
1994 *Zhanatella rotunda* Koneva; Popov and Holmer, p. 70, figs 40, 65.

Holotype. IGNA 427/259, ventral valve; Upper Cambrian, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds; Kyrshabakty River, Malyi Karatau.

Material. One complete shell and about 50 dorsal and ventral valves.

Diagnosis. See Popov and Holmer 1994, p. 70.

Remarks. We illustrate here new specimens of *Zhanatella rotunda* from the type locality. Popov and Holmer (1994) gave a detailed description and discussed the affinities of the species based on well-preserved material from the Upper Cambrian Kujandy Formation of north-eastern central Kazakhstan.

Occurrence. Upper Cambrian, Malyi Karatau, Kyrshabakty section, '*Pseudagnostus curtarae*'-*Irvingella tropica* to *Eurudagnostus ovaliformis*-'*Pareuloma*' beds, samples 1357, 1361, 1361-2, 1368, 1373-11, 1378, 1378-5, 1378-7, 1378-9, 1378-12, 1278-20, 1378-21, 1378-23, 1378-29, 1379-9, 1379-12, 1380, 1380-1, 1380-7, 1380-12, 1381, 1381-1–4.

Zhanatella sp.

Plate 10, figures 15–16

Material. Four ventral and three dorsal valves, numerous shell fragments.

Remarks. In the Zhalgyz Formation west of Lake Balkhash, lingulides with a rounded shell typical of *Zhanatella* occur, ornamented by coarse, regularly spaced concentric rugellae, with an emarginature in the umbonal area of the ventral valve, and slightly raised, anteriorly positioned, ventral visceral area bisected by the pedicle nerve impression. Their preservation is not sufficiently good for specific determination, but their occurrence provides the only known evidence for a late Cambrian age of the upper part of this formation.

Occurrence. Upper Cambrian, Zhalgyz Formation, railway cut 1·5 km south of Chaganak railway station, locality 8921-1.

Genus CANALILATUS Pelman, 1983

1983 *Canalilatus* Pelman, p. 126.
1992 *Pelmania* Koneva, p. 89 [type, *P. perrara*; OD].

Type species. Original designation by Pelman (1983, p. 126); *Canalilatus paululus* Pelman, 1983; Middle Cambrian, Amgaian, north-central Siberia.

Diagnosis. Shell small, subcircular; ventral pseudointerarea small; pedicle groove wide, shallow; dorsal pseudointerarea vestigial, undivided; larval and post-larval shell finely pitted with circular pits of about equal size; ventral visceral field slightly thickened posteromedially, not extending to mid-length, bisected by pedicle nerve impression which is accentuated by a pair of divergent submedian ridges; dorsal visceral field slightly thickened posteriorly with broad anterior projection, extending anteriorly beyond mid-length, bounded laterally by ridges and bisected by a fine median ridge.

Species included. *Canalilatus paululus* Pelman, 1983; *Pelmania perrara* Koneva, 1992; *Canalilatus*? *major* sp. nov.

Remarks. *Pelmania perrara* Koneva, 1992 closely resembles *Canalilatus paululus* in having a small, subcircular shell with rudimentary dorsal and ventral pseudointerareas, a finely pitted larval and post-larval shell surface, and in features of the visceral areas in both valves. We take these similarities to indicate that the species are congeneric, with *Pelmania* thus being a subjective junior synonym of *Canalilatus*.

The finely pitted micro-ornament of the larval and post-larval shell suggests affinities of *Canalilatus* with the families Zhanatellidae and Elkaniidae; however, it lacks elevated muscle platforms in both valves, which are diagnostic for the elkaniids, and therefore it is here assigned provisionally to the Zhanatellidae. *Canalilatus* differs from the majority of other genera in the Zhanatellidae in being much smaller and in having poorly developed pseudointerareas in both valves. Both the Siberian and Kazakhstanian material of *Canalilatus* are probably immature specimens of zhanatellids that inhabited nearshore environments. There are no large lingulide shells preserved with *Canalilatus perrarus* through the stratigraphic interval of the *Peronopsis*? *ultimus* and *Ptychagnostus intermedius* biozones in the Kyrshabakty section. However, relatively large zhanatellid shells do occur occasionally in the overlying part of the Middle Cambrian sequence; these larger specimens, referred provisionally to *Canalilatus* and described below as *C.*? *major* sp. nov., are probably mature specimens of the genus.

Canalilatus perrarus (Koneva, 1992)

Plate 11, figures 1–14

1992 *Pelmania perrara* Koneva, p. 89, pl. 9, figs 1–14.

Holotype. GA 427/610, ventral valve; Middle Cambrian, Amgaian Stage, *Peronopsis ultimus* and *Ptychagnostus intermedius* biozones; Kyrshabakty River, Malyi Karatau.

Material. 45 ventral and 74 dorsal valves.

Diagnosis. Shell subcircular, about 90 per cent (S = 6·0, N = 6) as long as wide; ventral pseudointerarea rudimentary with a wide, subtriangular pedicle groove and very narrow, slightly raised pseudointerareas; dorsal valve moderately convex with very short, strip-like undivided pseudointerarea; larval and post-larval shell finely pitted with rounded pits of about equal size; ventral interior with slightly raised, paired umbonal muscle scars and short, slightly divergent, pedicle nerve impression accentuated by ridges; visceral area large, extending anteriorly to mid valve length; dorsal interior with large visceral area on average 77 per cent as long as the valve (S = 2·5, N = 6) forming a large anterior tongue bounded laterally by a low rim.

Remarks. This species closely resembles the type of the genus, *C. paululus*, differing mainly in lacking a median ridge in the anterior part of the visceral area and in having a more rounded shell outline with maximum width at the mid-length. Both species are known from presumed larval and early post-larval shells.

Occurrence. As for the holotype; samples 1465, 1465-1, 1313, 1314, 1314-2.

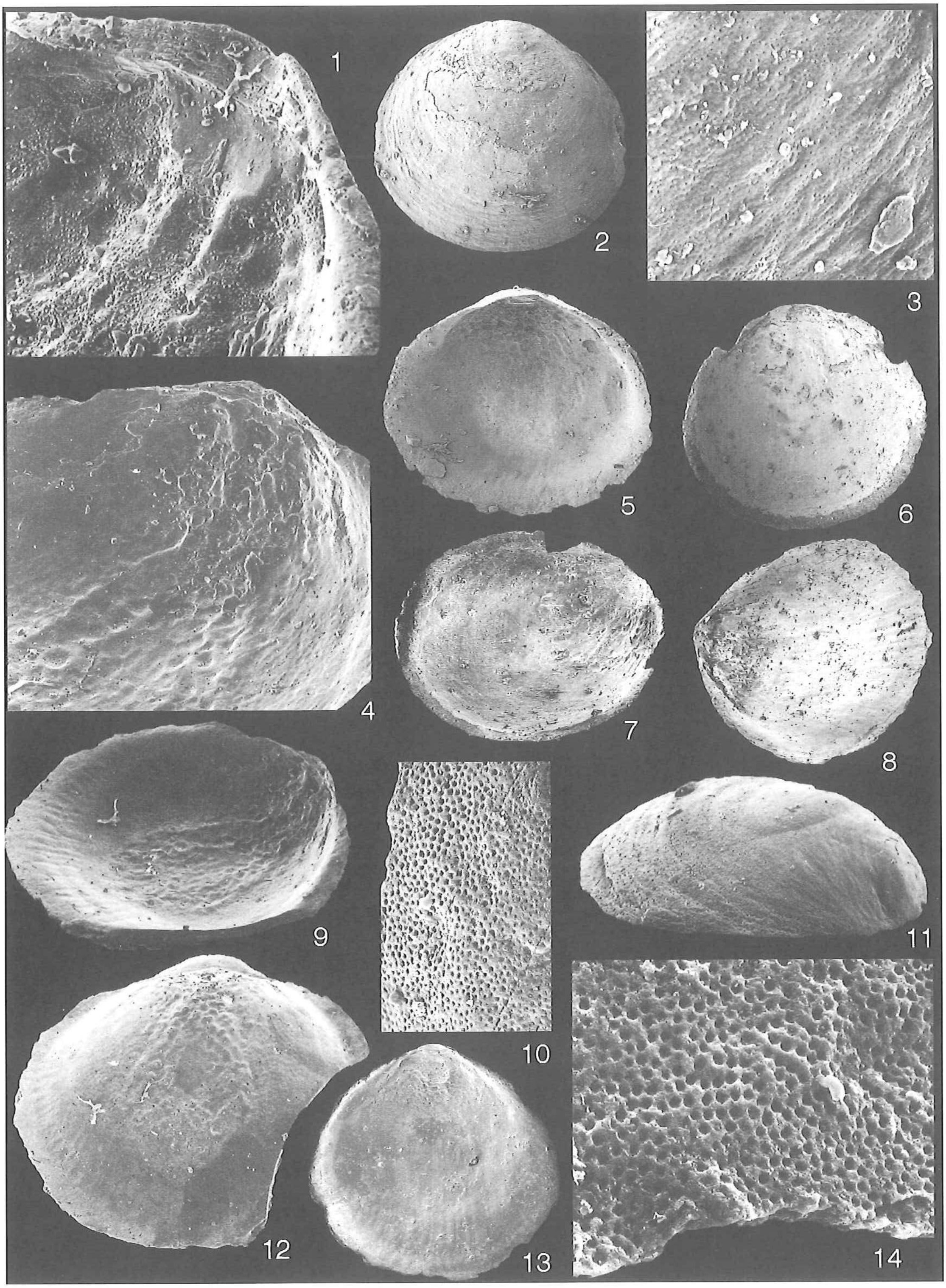
TABLE 3. *Canalilatus perrarus* (Koneva), dimensions of ventral and dorsal valves from the Kyrshabakty section (Middle Cambrian, *Peronopsis*? *ultimus* and *Ptychagnostus intermedius* biozones).

	Ventral valves			Dorsal valves			
Museum no.	NMW 98.61G.52	NMW 98.61G.50	NMW 98.61G.347	RM Br 136367	RM Br 136368	NMW 98.61G.348	NMW 98.61G.54
Sample no.	1314-2	1314	1314	1314	1314	1314	1314-2
L	0·72	0·76	0·72	0·76	0·74	0·70	0·90
W	0·76	0·88	0·76	0·84	0·76	0·86	0·94
Vl	0·40	0·52	–	–	0·58	0·52	0·62

EXPLANATION OF PLATE 11

Figs 1–14. *Canalilatus perrarus* (Koneva); Middle Cambrian, *Peronopsis*? *ultimus-Ptychagnostus intermedius* biozones; Malyi Karatau, Kyrshabakty section. 1, NMW 98.61G.50, ventral valve interior, sample 1314; ×293. 2–3, 11, RM Br136367, sample 1314, ventral valve exterior, ×60; pitted micro-ornament of post-larval shell, ×325; and lateral view, ×98. 4, 9, 12, RM Br136368, dorsal valve interior in oblique lateral view showing rudimentary pseudointerarea and visceral area, ×117; oblique lateral view of complete valve, and normal view, sample 1314; both ×50. 5, 8, NMW 98.61G.51, dorsal valve interior in normal and oblique lateral views, sample 1314; ×60, ×40. 6–7, NMW 98.61G.52, ventral valve interior in normal and oblique views, sample 1314-2; both ×56. 10, 14, NMW 98.61G.53, micro-ornament of larval shell, sample 1314; ×820, ×1350. 13, NMW 98.61G.54, dorsal valve interior, sample 1314-2; ×47.

PLATE 11



HOLMER *et al.*, *Canalilatus*

Canalilatus? *major* sp. nov.

Plate 12, figures 4–13

1992 *Lingulella* sp. 1, Koneva, p. 96, pl. 12, figs 9–11; pl. 13, figs 1–3.

Derivation of name. Referring to the relatively large size of the species.

Holotype. GA 427/611, dorsal valve; Middle Cambrian, Mayaian, *Goniagnostus nathorsti* Biozone; sample 1465-20, Kyrshabakty River, Malyi Karatau.

Material. 26 ventral and 43 dorsal valves.

Diagnosis. Shell slightly transversely suboval to subcircular, well-developed dorsal pseudointerarea occupied mostly by the median groove; pedicle nerve impression accentuated by a pair of fine, divergent, submedian ridges; dorsal interior with small visceral area bisected by fine median ridge and with narrow median tongue ending slightly anterior to mid-valve length.

Description. Shell dorsibiconvex, outline subcircular, up to 5–7 mm long. Ventral valve weakly convex with a wide, triangular, orthocline pseudointerarea. Pedicle groove deep, narrow, triangular. Propareas raised above the valve floor, with strongly impressed flexure lines. Inner sides of propareas inclined slightly towards the pedicle groove. Dorsal valve moderately convex with a slightly swollen umbonal region. Dorsal pseudointerarea moderately high, orthocline with very narrow propareas and a deep, broad, median groove in the valve floor.

Ventral valve interior with a visceral area bisected by divergent submedian ridges following the pedicle nerve impressions; median part of the visceral field between the impression of the pedicle nerve slightly depressed. Umbonal muscle scars paired, situated on low platforms raised slightly above the valve floor. Dorsal valve with a small visceral area located in the posterior third of the valve and with a narrow median tongue extending slightly anterior to mid-valve length, and bounded laterally by two fine, slightly divergent ridges. An indistinct median ridge bisects the whole dorsal visceral area. Umbonal muscle scars paired, raised slightly above the valve floor.

Remarks. This species is assigned provisionally to *Canalilatus* based mainly on the presence of a finely pitted larval and post-larval shell, and its occurrence in deposits of similar age in the same section as

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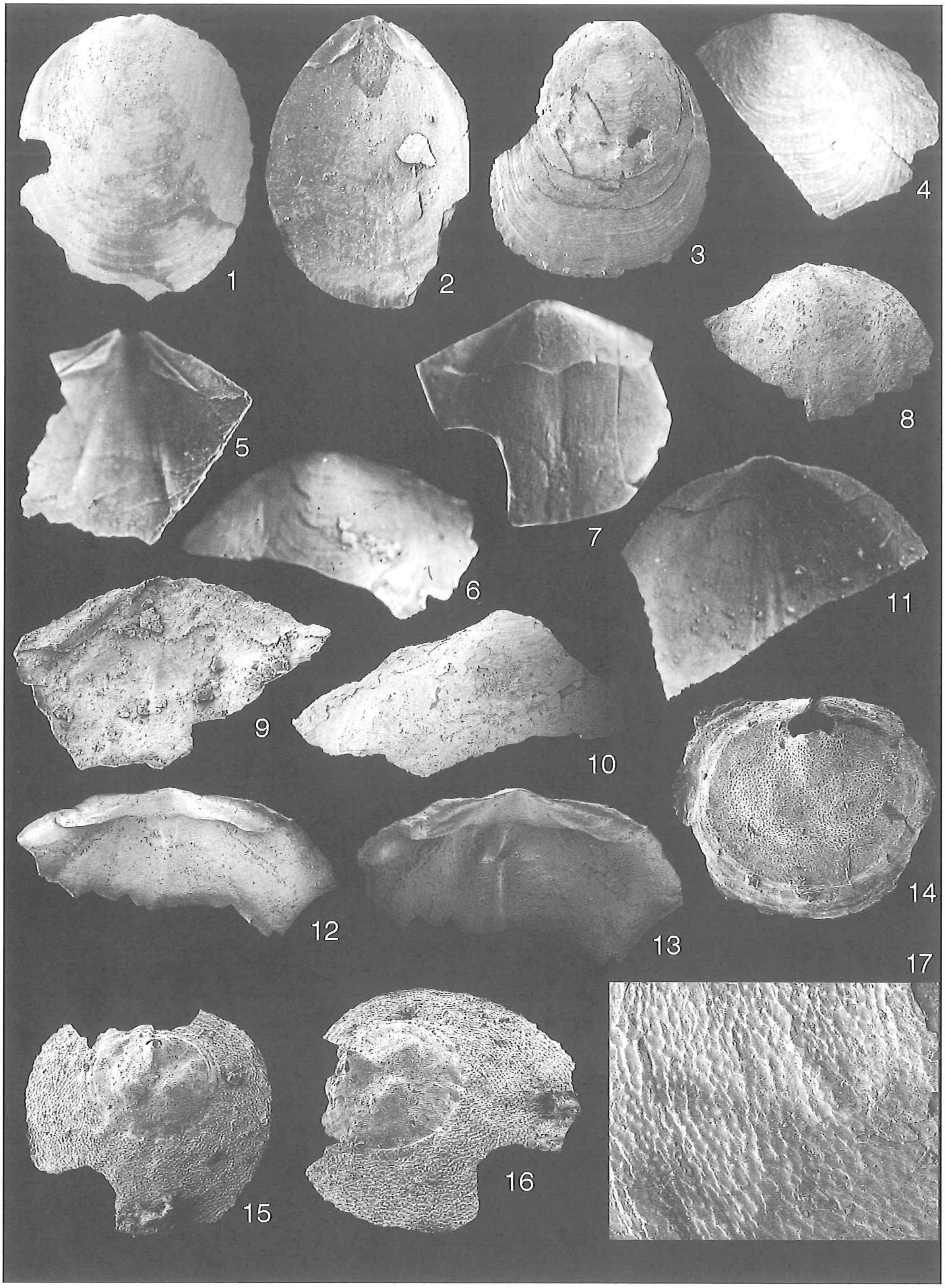
EXPLANATION OF PLATE 12

Fig. 1. Obolinae gen. et sp. indet.; Ordovician, Kogashik Regional Stage, lower *Paroistodus proteus* Biozone, Malyi Karatau Range, Batyrbay section, sample 465 m; NMW 98.61G.30, dorsal valve exterior of juvenile specimen; ×25.

Figs 2–3. *Fossuliella*? sp.; Upper Cambrian, Malyi Karatau Range, Kyrshabakty section, *Ivshinagnostus ivshini*-*Irvingella major* beds, sample 1361-4. 2, NMW 98.61G.31, ventral valve interior; ×32. 3, NMW 98.61G.32, ventral valve exterior; ×15·5.

Figs 4–13. *Canalilatus*? *major* sp. nov.; Middle Cambrian. 4, IGNA 427/619, incomplete dorsal valve exterior, Malyi Karatau Range, *Goniagnostus nathorsti* Biozone, sample 1465-20; ×15. 5, IGNA 427/611, incomplete ventral valve interior, same age and locality as 4; ×22. 6, IGNA 427/624, incomplete dorsal valve exterior, same age and locality as 4; ×11; 7, IGNA 427/611, holotype, incomplete dorsal valve interior, same age and locality as 4; ×20. 8, NMW 98.61G.34, ventral valve exterior, Karagajly Formation, Kostek Range, sample 1639; ×15. 9, NMW 98.61G.33, incomplete dorsal valve interior, Sarykumy Formation, Sarykumy section, sample 134; ×40. 10, NMW 98.61G.35, incomplete dorsal valve exterior, Karagajly Formation, Kostek Range, sample 1639; ×18. 11, IGNA 427/617, dorsal valve interior, Malyi Karatau Range, *Goniagnostus nathorsti* Biozone, sample 1346-2; ×18. 12, NMW 98.61G.36, incomplete dorsal valve interior, Karagajly Formation, Kostek Range, sample 1639; ×15. 13, NMW 98.61G.37, incomplete dorsal valve interior, Karagajly Formation, Kostek Range, sample 1639; ×21.

Figs 14–17. *Acrothele* sp.; Middle Cambrian, Malyi Karatau, Kyrshabakty section, *Ptychagnostus intermedius* Biozone, sample 1314-2. 14, NMW 98.61G.38, ventral valve, larval shell; ×75. 15–16, NMW 98.61G.39, ventral valve; exterior, ×37; oblique lateral view, ×43. 17, NMW 98.61G.40, finely pustulose surface of the post-larval shell; ×107.



HOLMER *et al.*, brachiopods

Canalilatus perrarus (Koneva). Such distinctive characters of the latter species as poorly developed pseudointerareas in both valves and a relatively large dorsal visceral area are typical for shells of juvenile obolides and probably do not represent morphological characters of mature specimens. *C. perrarus* is otherwise similar to *C.*? *major* in having a pair of submedian ridges following the pedicle nerve impression as well as slightly raised, paired, ventral umbonal muscles (Pl. 11, fig. 1).

Occurrence. Middle Cambrian, Mayaian Stage, Kyrshabakty section, *Goniagnostus nathorsti–Lejopyge laevigata* biozones, samples 1314-5, 1465-20, 1346-6, 1246-10, 1346-11, 1358; Kostek Range, Karagajly section, Karagajly Formation, sample 1639; Sarykumy section, trench K-20, sample F-132.

Genus FOSSULIELLA Popov and Ushatinskaya, 1992

Type species. Original designation by Popov and Ushatinskaya (1992, p. 66); *Lingulella linguata* Pelman, 1977; Middle Cambrian, Mayaian, north-central Siberia.

Fossuliella? sp.

Plate 10, figures 12–14; Plate 12, figures 2–3

Material. One dorsal and four ventral valves.

Remarks. Several samples from the Upper Cambrian and Lower Ordovician successions of Malyi Karatau contain significant numbers of larval and juvenile lingulid shells approximately 0·5–2·0 mm long. Some can be attributed fairly confidently to genera and species identified from mature individuals in the same samples (e.g. *Experilingula*, *Mirilingula*, *Notobolus*), but there are a number of taxa represented apparently only by juveniles. In most cases the simple shell morphology, weakly impressed internal characters, and rudimentary pseudointerareas make precise taxonomic discrimination of these specimens impossible, but we have identified a small number whose finely pitted larval and post-larval shell is closely reminiscent of *Fossuliella*, and we illustrate a few examples here as a record of the probable occurrence of this genus.

Occurrence. Upper Cambrian, Malyi Karatau, Kyrshabakty section; *Glyptagnostus stolidotus* Biozone, sample 1352; *Ivshinagnostus-Irvingella major* beds, sample 1361-4.

ZHANATELLIDAE gen. et sp. indet.

Plate 10, figures 1–3

Material. One ventral and two dorsal valves.

Remarks. Both valves of this un-named taxon are elongated suboval and convex with a distinctive ornament of highly raised concentric rugellae. Pitted micro-ornament, pseudointerareas, and interiors of both valves are not preserved in the sample, but the strong concentric ornament is relatively common in the Family Zhanatellidae (e.g. *Zhanatella, Rowellella, Paldiskia, Thysanotos*). In size, shell outline and ornament the specimens are perhaps most comparable with *Rowellella*, but the unsatisfactory preservation makes precise generic discrimination impossible.

Occurrence. Upper Cambrian, Malyi Karatau, Kyrshabakty section; *Agnostus scrobicularis–Trisulcagnostus trisulcus* beds, samples 1400-8, 1400-9.

Family ELKANIIDAE Walcott and Schuchert, 1908

Genus BROEGGERIA Walcott, 1902

Type species. Original designation by Walcott (1902, p. 605); *Obolella salteri* Holl, 1885; Upper Cambrian (Merioneth Series); Malvern Hills, Herefordshire, England.

Diagnosis. See Popov and Holmer 1994, p. 59.

Broeggeria salteri (Holl, 1865)

Plate 10, figures 4–7

1982	*Broeggeria salteri* (Holl); Rushton and Bassett, *in* Owens *et al.* p. 23, pl. 7, figs a–g, i (see for earlier synonymy).
1994	*Broeggeria salteri* (Holl); Holmer and Popov, p. 59, figs 45N–O, 55C–Q, 56–61A–D.

Lectotype. Selected by Cocks (1978, p. 18); The Natural History Museum, London B4044, external mould of dorsal or ventral valve from the Upper Cambrian White-Leaved-Oak Shales; Malvern Hills, Herefordshire, England.

Material. Eight ventral and three dorsal valves.

Diagnosis. See Popov and Holmer 1994, p. 59.

Remarks. This species is described and illustrated in detail by Popov and Holmer (1994). A few specimens from Cambrian/Ordovician boundary beds of Malyi Karatau are illustrated here in order to document its presence in the region.

Occurrence. Upper Cambrian–Lower Ordovician; Batyrbay section, *Hedinaspis sulcata–Dikelokephalina* beds, samples 0, 77, 141, 181, 191, 196, 235 m.

Family LINGULELLOTRETIDAE Koneva and Popov, 1983

Diagnosis. See Holmer *et al.* 1997.

Genera assigned. *Lingulellotreta* Koneva, 1983; *Aboriginella* Koneva, 1983; *Mirilingula* Popov, 1983; *Vaculina* Koneva, 1992.

Remarks. The Family Lingulellitretidae is unique among lingulids in having the pedicle foramen perforating the ventral pseudointerarea, and a pedicle groove transformed into an internal pedicle tube.

Genus LINGULELLOTRETA Koneva, 1983

Type and only species. Original designation by Koneva (*in* Gorjansky and Koneva 1983, p. 132); *Lingulellotreta ergalievi* Koneva, 1983, a subjective junior synonym of *Lingulepis malongensis* Rong, 1974.

Diagnosis. See Holmer *et al.* 1997, p. 581.

Lingulellotreta malongensis (Rong, 1974)

Plate 13, figures 11, 13–15

1974 *Lingulepis malongensis* Rong, p. 114, pl. 44, figs 27, 32.
1997 *Lingulepis malongensis* Rong; Holmer *et al.*, p. 581, figs 4·1–4·15 (full synonymy).

Holotype. Whereabouts uncertain, formerly in Nanjing Institute of Geology and Palaeontology, No. 22154, ventral valve; Tsanglangpu Formation, Lower Cambrian, Malong, Yunnan, China.

Diagnosis. As for genus.

Remarks. A detailed morphological description and discussion of the synonymy and affinities of this species are given by Holmer *et al.* (1996). Here we illustrate some specimens of *L. malongensis* from the Malyi Karatau Range to record the presence of this distinctive taxon in the region.

Occurrence. Lower Cambrian, Botomian–Toyonian, *Ushbaspis limbata* and *Redlichia chinensis–Kootenia gimmelfarbi* biozones; Baba-Ata section, sample 5/26b; Ushbas section, samples 1224, 1228, 1233, 1234.

Genus ABORIGINELLA Koneva, 1983

Type and only species. Original designation by Koneva (*in* Koneva and Popov 1983, p. 116); *Aboriginella denudata* Koneva, 1983; Upper Cambrian, *Pseudagnostus curtarae* beds–*Lophosaukia* beds, Malyi Karatau.

Diagnosis. Shell smooth, outline elongate oval, moderately to strongly biconvex; ventral pseudointerarea flattened, lacking flexure lines; pedicle foramen elongate suboval, originating at the post-larval growth stage; dorsal pseudointerarea flat, undivided, highly elevated; ventral visceral field raised, forming a pair of posterolateral muscle platforms and an anterior muscle platform extending to the mid-valve length; dorsal visceral field strongly thickened posteriorly, with a low, narrow anterior projection, extending to mid-valve length; dorsal central and anterior lateral muscle scars small, situated close to one another.

Remarks. *Aboriginella* is comparable with *Lingulellotreta* in having an elongate, dorsibiconvex, inequivalved shell and a pedicle foramen on the ventral pseudointerarea. However, it differs in having a high visceral platform in both valves, an undivided dorsal pseudointerarea raised high above the valve floor, and lacks flexure lines on the propareas of both valves.

EXPLANATION OF PLATE 13

Figs 1–10, 12. *Diencobolus simplex* sp. nov.; Upper Cambrian, *Glyptagnostus stolidotus* Biozone, Malyi Karatau, Kyrshabakty section, sample 1352-III. 1, 3–6, NMW 98.61G.55, dorsal valve. 1, micro-ornament of larval shell; ×650. 3, micro-ornament of post-larval shell; ×1088. 4, larval shell; ×136. 5, exterior of complete valve; ×40. 6, oblique lateral view of exterior; ×43. 2, IGNA 427/86, ventral valve exterior; ×13. 7, NMW 98.61G.57, dorsal valve exterior; ×21. 8, NMW 98.61G.58, dorsal? valve exterior; ×65. 9, IGNA 427/729, ventral valve interior; ×23. 10, IGNA 427/730, dorsal valve interior; ×32. 12, IGNA 427/87, holotype, dorsal valve interior; ×13.

Figs 11, 13–15. *Lingulellotreta malongensis* (Rong); Lower Cambrian, Malyi Karatau. 11, IGNA 2224/36, dorsal valve interior, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, Baba-Ata River, sample 1420; ×20. 13, IGNA 2224/40 ventral valve exterior, *Ushbaspis limbata* Biozone, Ushbas River, sample 1228; ×15. 14, NMW 98.61G.59, ventral valve exterior, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, Baba-Ata River, sample 5/26; ×14. 15, NMW 98.61G.58, ventral valve interior, *Ushbaspis limbata* Biozone, Ushbas River, sample 1233; ×20.

Aboriginella denudata Koneva, 1983

Plate 14, figures 4–13; Plate 15, figures 1–2

1983 *Aboriginella denudata* Koneva, *in* Koneva and Popov, p. 122, pl. 30, figs 1–13; pl. 31, figs 1–18.

Holotype. IGNA 427/117, ventral valve; Upper Cambrian, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds; Malyi Karatau, Kyrshabakty section, sample 1379-2.

Material. One complete shell and about 250 disarticulated ventral and dorsal valves.

Diagnosis. As for genus.

Remarks. The original description of *Aboriginella denudata* incorporated numerous illustrations, as well as detailed information on shell morphology and ontogeny. The species is relatively abundant in the mid Upper Cambrian of Malyi Karatau, but it remains unknown elsewhere outside the type area. Numerous additional small, elongate suboval, lingulide larval shells, about 0·5–1·5 mm long, and with a smooth external surface (Pl. 14, figs 11–12) occur within the interval of the '*Pseudagnostus curtarae*'-*Irvingella tropica–Eurudagnostus ovaliormis*-'*Pareuloma*' beds. They usually lack some typical characters of *Aborigenalla*, including the strongly raised ventral pseudointerarea with a pedicle foramen and high visceral platform in both valves, but they are otherwise distinctive and it is probable that they are immature and belong mostly to *A. denudata*.

Occurrence. Upper Cambrian; Kyrshabakty section, '*Pseudagnostus curtarae*'-*Irvingella tropica–Eurudagnostus ovaliorms*-'*Pareuloma*' beds, samples 1357-b, 1357/3, 1359, 1359-a, 1360, 1361-3, 1361-4, 1362, 1367, 1368, 1373, 1373-III, 1374, 1376, 1376-I, 1376-II, 1377-1, 1377-2, 1378-2, 1378-3, 1378-8, 1380-1, 1381, 1381-1, 1381-2, 1381-4; Batyrbay section, *Hedinaspis sulcata–Lophosaukia* beds, samples −35 m, 0 m, 68 m; east side of Shabakty river, *Agnostus scrobicularis* beds, sample 1413, *Trisulcagnostus trisulcus* beds, sample 1414.

Genus MIRILINGULA Popov, 1983

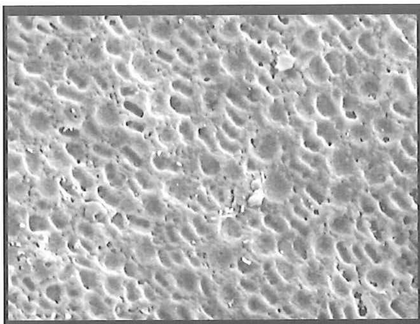
Type species. Original designation by Popov (*in* Koneva and Popov 1983, p. 119); *Mirilingula mutabilis* Popov, 1983; Lower Ordovician, *Euloma limataris–Taoyuania* beds; Malyi Karatau.

Diagnosis. See Popov and Holmer 1994, p. 68.

EXPLANATION OF PLATE 14

Figs 1–3. *Palaeobolus bretonensis* Matthew; Middle Cambrian, Amgaian, Bourinot Group, Cape Breton, Canada. 1, ROM CM (A), partly exfoliated ventral valve; ×3. 2, USNM 51664a, ventral valve exterior; ×3. 3, USNM 51664b, partly exfoliated dorsal valve; ×2·5.

Figs 4–13, *Aboriginella denudata* Koneva; Upper Cambrian, Malyi Karatau, Kyrshabakty section. 4, NMW 98.61G.63, dorsal valve interior in oblique lateral view, *Neorudagnostus quadratiformis-Taenocephalus kyrshabaktensis* beds, sample 1376; ×75. 5, 13, NMW 98.61G.64, dorsal valve exterior in oblique lateral view, and detail of umbonal area, horizon and sample as for 4; ×40, ×135. 6, IGNA 427/248, incomplete dorsal valve interior, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds, sample 1379-3; ×26. 7, NMW 98.61G.65, incomplete juvenile ventral valve interior, *Ivshinagnostus ivshini-Irvingella major* Biozone, sample 1360; ×29. 8, IGNA 427/169, incomplete ventral valve interior, horizon as for 7, sample 1360-5; ×6. 9, IGNA 427/169, incomplete ventral valve interior, horizon as for 6, sample 1379-2; ×12. 10, IGNA 427/328, incomplete ventral valve, pseudointerarea, horizon as for 7, sample 1381; ×24. 11, IGNA 427/732, ventral? valve exterior of juvenile specimen; ×20. 12, IGNA 427/733, dorsal valve exterior of juvenile specimen; ×20.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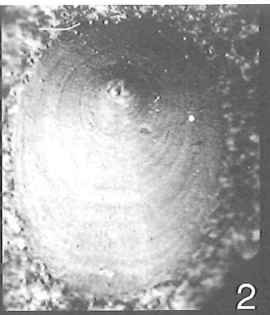
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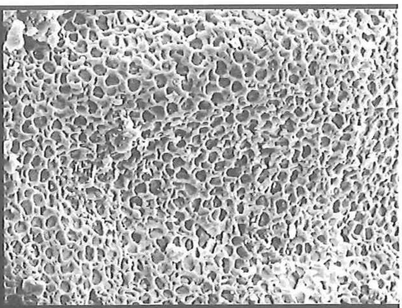
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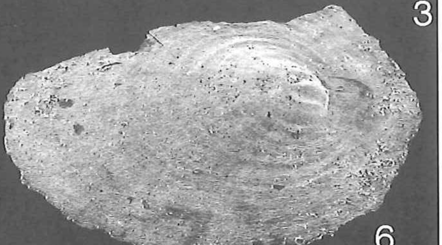
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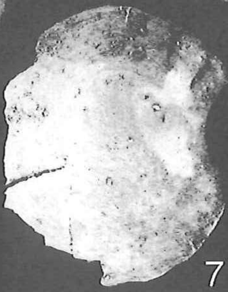
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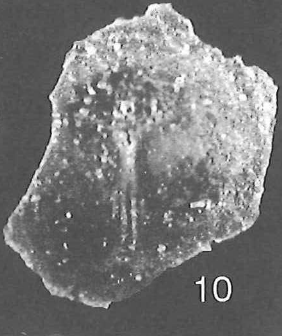
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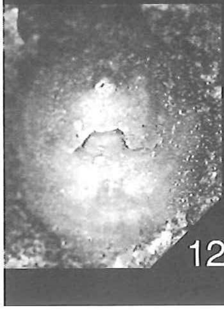
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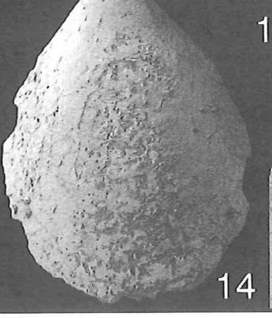
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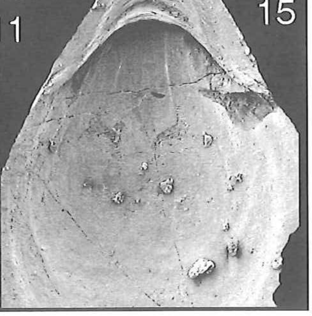
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HOLMER *et al.*, *Diencobolus*, *Lingulellotreta*

Species assigned. *Mirilingula mutabilis* Popov, 1983; *Mirilingula postuma* sp. nov.; *Mirilingula* sp. (Popov and Holmer 1994).

Mirilingula mutabilis Popov, 1983

Plate 15, figures 3–9

1983 *Miriligula mutabilis* Popov, *in* Koneva and Popov, p. 119, pl. 28, figs 4–8, 10–15; pl. 29, fig. 11, text-figs 3–7.

Holotype. CNIGR 11991/26, ventral valve, figured by Koneva and Popov (1983, pl. 28, fig. 10); Upper Cambrian, *Euloma limitaris-Taoyuania* beds; Batyrbay Section, 127 m, Malyi Karatau.

Material. 14 complete shells and 186 ventral and dorsal valves.

Diagnosis. Slightly dorsibiconvex, elongate oval shell, on average 150 per cent as long as wide with maximum width at about 60 per cent of sagittal length from the ventral beak; ventral valve gently and evenly convex, about 10 per cent as thick as long; ventral pseudointerarea high, subtriangular, apsacline, bisected by the strongly elongated pedicle foramen; dorsal valve with a highly raised, flat, anacline, undivided pseudointerarea; a shallow sulcus originates near the umbo in both valves; ventral interior with visceral area slightly raised posteriorly and bisected by a pair of slightly divergent submedian ridges (pedicle nerve impression); ventral umbonal muscle scars clearly impressed, elongate suboval, situated beneath the pseudointerarea; dorsal interior weakly impressed, with a fine median ridge extending anteriorly for about 66 per cent of the sagittal valve length and bisecting the visceral area.

Remarks. The smallest specimens of *Mirilingula mutabilis* obtained from the Batyrbay section are about 0·5 mm long. They are characterized by having very thin, plate-like valves lacking distinctive pseudointerareas, with the exception of the strongly incurved posterolateral margins of the ventral valve, which mark a vestigial pseudointerarea.

Occurrence. Upper Cambrian, Malyi Karatau, Batyrbay section, *Euloma limitaris-Taoyunia* beds, samples 117 m, 128 m, 131 m, 137 m, 141 m, 1448, 1448-3.

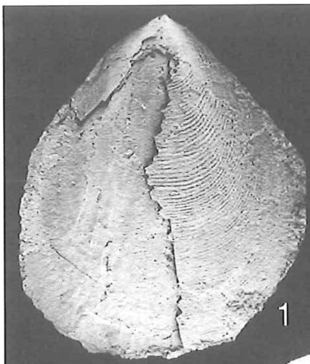
EXPLANATION OF PLATE 15

Figs 1–2. *Aboriginella denudata* Koneva; Upper Cambrian, *Agnostus scrobicularis-Jegorovaja* beds, Malyi Karatau, east side of Shabakty River, sample 1413; NMW 98.61G.66, incomplete ventral valve. 1, lateral view of interior; ×19. 2, interior; ×19.

Figs 3–9. *Mirilingula mutabilis* Popov; Upper Cambrian, *Cordylodus proavus* Biozone, Malyi Karatau, Batyrbay section. 3, CNIGR 27/12991, ventral valve exterior, sample 127 m; ×6. 4–5, NMW 98.61G.67, ventral valve interior, and detail of pseudointerarea and pedicle foramen, sample 1448; ×6·5, ×15·5. 6, NMW 98.61G.70, dorsal valve interior showing pseudointerarea, sample 1448; ×9. 7, CNIGR 28/12991, dorsal valve exterior, sample 143 m; ×10. 8, NMW 98.61G.68, ventral valve interior, sample 1448; ×6. 9, NMW 98.61G.69, ventral valve exterior, sample 1448; ×6.

Fig. 10. *Mirilingula postuma* sp. nov.; Ordovician, *Szechuanella-Apatocephalus* beds, Malyi Karatau, Batyrbay section, sample 382 m. CNIGR 12/12991, ventral valve exterior; ×7·5.

Figs 11–13. *Mirilingula* sp.; Upper Cambrian, *Eoconodontus notchpeakensis* Biozone, Malyi Karatau, Batyrbay section, sample 77 m. 11–12, NMW 98.61G.71, juvenile ventral valve interior in normal and oblique lateral views; both ×42. 13, NMW 98.61G.72, juvenile dorsal valve interior; ×27.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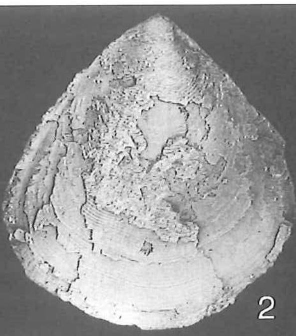
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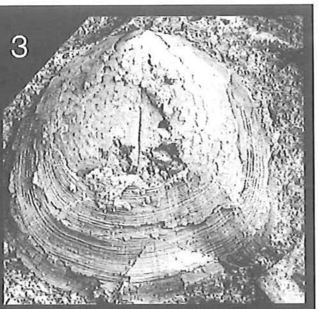
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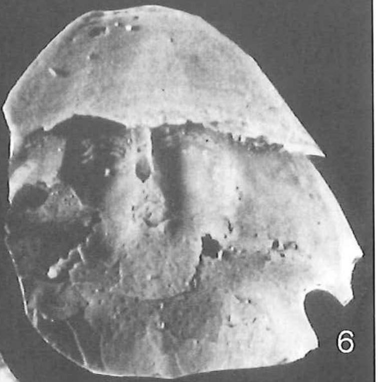
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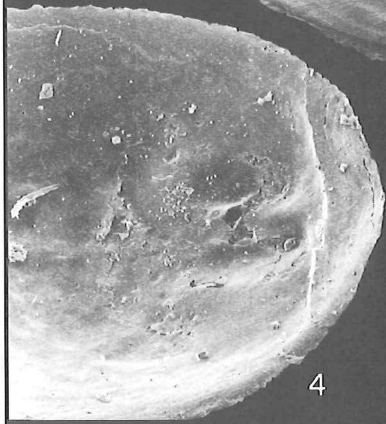
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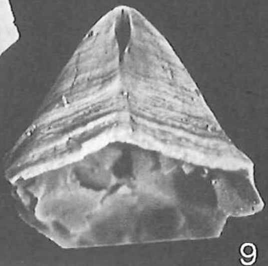
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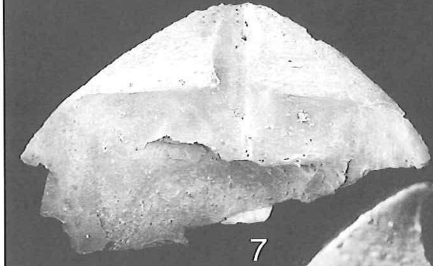
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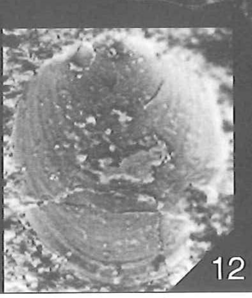
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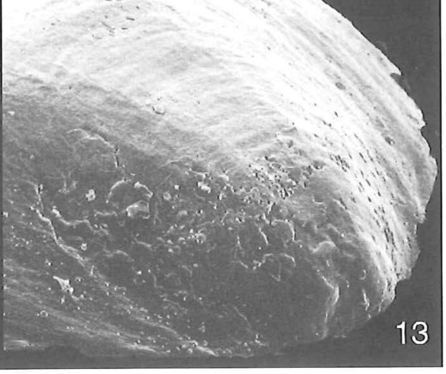
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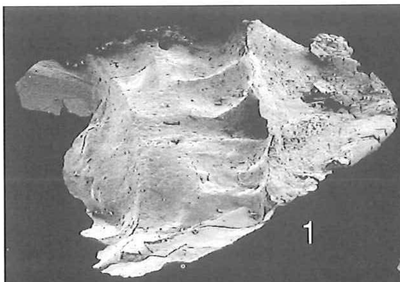
HOLMER *et al.*, *Aboriginella*, *Palaeobolus*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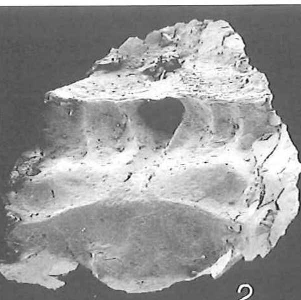
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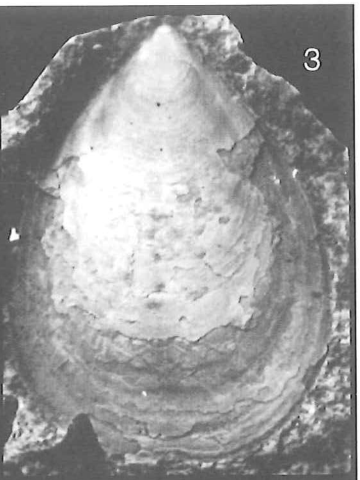
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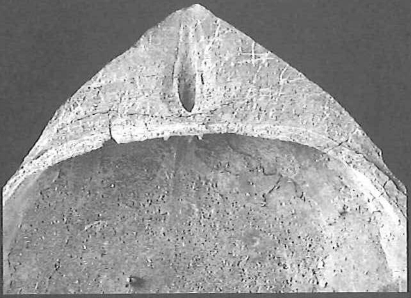
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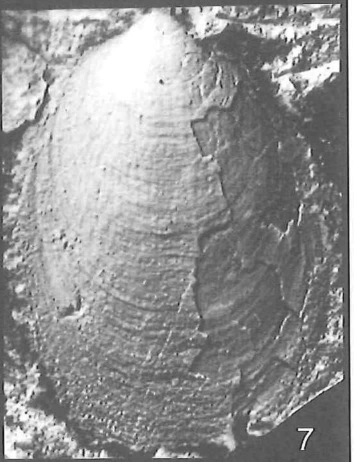
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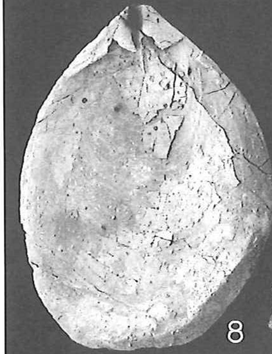
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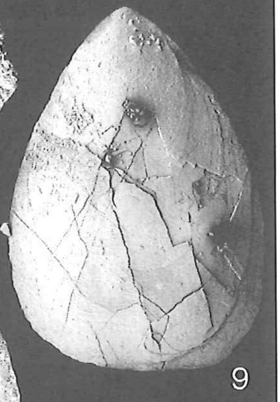
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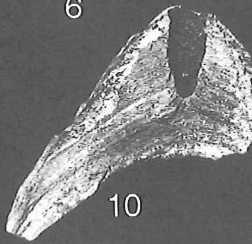
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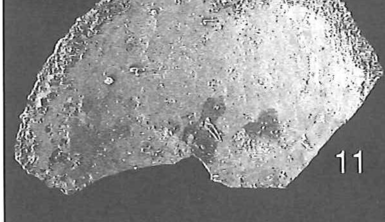
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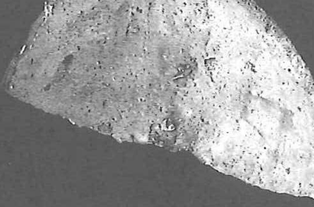
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HOLMER *et al.*, *Aboriginella*, *Mirilingula*

Mirilingula postuma sp. nov.

Plate 15, figure 10; Plate 16, figures 1–6

1983 *Mirilingula* aff. *mutabilis* Koneva and Popov 1983, p. 120, pl. 28, figs 9, 16, 17; pl. 29, figs 1–6.

Derivation of name. Latin *postumus*, last.

Holotype. CNIGR 12/11991, incomplete ventral valve; Lower Ordovician, *Szechuanella-Apatokephalus* beds; sample 382 m, Batyrbay section, Malyi Karatau.

Material. 62 dorsal and ventral valves.

Diagnosis. Shell slightly dorsibiconvex, elongate oval with subparallel lateral margins, about 120 per cent as long as wide with maximum width at about mid-length; ventral valve about 15 per cent as thick as long; ventral pseudointerarea high and flat, apsacline with elongate suboval pedicle foramen; dorsal valve about 20 per cent as high as long with highly raised, flat, anacline, undivided pseudointerarea occupying on average about half of the maximum valve width; an indistinct, shallow sulcus is usually present in both valves, but the ventral sulcus is poorly defined; ventral interior with visceral area slightly raised posteriorly and bisected by a pair of slightly divergent submedian ridges (pedicle nerve impression); ventral umbonal muscle scars clearly impressed, elongate suboval in outline, situated closely beneath the pseudointerarea; dorsal interior weakly impressed, with a fine median ridge bisecting the visceral area; submedian ridges underlying the pedicle nerve impression poorly developed or absent.

Dimensions. CNIGR 17/11991, ventral valve, L = 4·2, W = 2·7, T = 2·2; CNIGR 18/11991, ventral valve, L = 3·7, W = 2·9, T = 1·5.

Remarks. *M. postuma* occurs in the Batyrbay section mainly as numerous juvenile and larval shells, but mature specimens are relatively rare. This species is not as elongate on average as *M. mutabilis*, but the difference probably reflects a predominance of immature valves in the samples within the 206–382 m interval. By comparison with *M. mutabilis*, adult shells of the new species have a generally more regular elongate oval outline and subparallel lateral shell margins; they also develop a larger suboval pedicle foramen with sharp lateral margins, and the ventral submedian ridges are weakly developed.

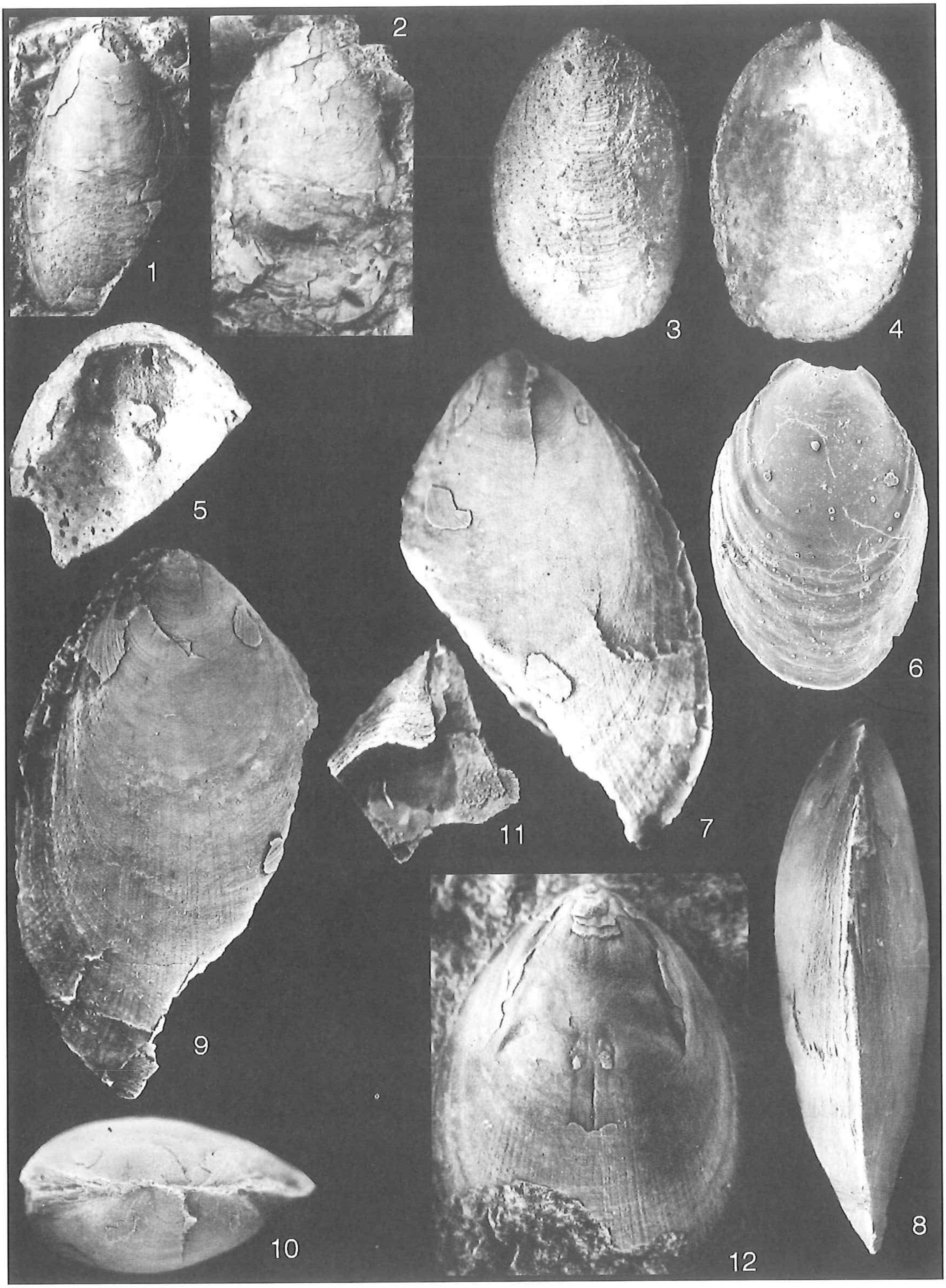
Occurrence. Lower Ordovician of Malyi Karatau, Batyrbay section, *Dikelokephalina* and *Szechuanella-Apatokephalus* beds, samples 206, 209, 210, 235, 382 m.

EXPLANATION OF PLATE 16

Figs 1–6. *Mirilingula postuma* sp. nov.; Ordovician, Malyi Karatau, Batyrbay section. 1, CNIGR 14/12991, ventral valve exterior, *Szichuanella-Apatocephalus* beds, sample 382 m. 2, CNIGR 15/12991, dorsal valve exterior, horizon and sample as 1; ×3. 3–4, CNIGR 17/12991, exterior and interior of juvenile ventral valve, uppermost *Cordylodus intermedius* Biozone, sample 206 m; both ×15. 5, CNIGR 13/12991, holotype, dorsal valve interior, horizon and sample as 1; ×15. 6, NMW 98.61G.73, dorsal valve of larval shell exterior, uppermost *Cordylodus intermedius* Biozone, sample 191 m; ×79.

Figs 7–12. *Vaculina obscura* Koneva; Upper Cambrian, Malyi Karatau, Kyrshabakty section. 7–10, IGNA 427/583, exfoliated conjoined valves, holotype, dorsal, lateral, ventral and posterior views, *Glyptagnostus stolidotus* Biozone, sample 1352-III; ×4. 11, IGNA 427/589, incomplete ventral valve, pseudointerarea and pedicle opening, *Kormagnostus simplex* Biozone, sample 1351; ×13. 12, IGNA 427/584, dorsal valve internal mould, horizon and sample as 7; ×4.

PLATE 16



HOLMER *et al. Mirilingula*, *Vaculina*

Mirilingula sp.

Plate 15, figures 11–13

1956 *Lingulella* aff. *mosia* (Hall); Nikitin, p. 11, pl. 1, figs 2–4.
1983 *Mirilingula* sp.; Koneva and Popov 1983, p. 121, pl. 28, figs 1–3; pl. 29, figs 7–10.
1994 *Miriligula* sp.; Popov and Holmer, p. 69, fig. 64.

Material. Two complete shells, 60 dorsal and ventral valves.

Remarks. Specimens of *Mirilingula* are fairly common in the *Lophosaukia* and *Harpidoides-Platypeltoides* beds of the Batyrbay section, but only as juvenile specimens with vestigal pseudointerareas in both valves. These specimens are very similar to, and probably conspecific with, *Mirilingula* sp., described by Popov and Holmer (1994, p. 69) from the Upper Cambrian Selety Formation of north-eastern central Kazakhstan; however, their relationship to *M. mutabilis* is somewhat uncertain because there are no mature shells preserved below the *Cordylodus proavus* Biozone interval.

Occurrence. Upper Cambrian of Malyi Karatau; Batyrbay section, *Lophosaukia-Ivshinaspis* beds, 68 m; *Harpidoides-Platypeltoides* beds, 77 m, 98 m.

Genus VACULINA Koneva, 1992

1992 *Vaculina* Koneva, p. 90.

Type and only species. Original designation by Koneva (1992, p. 90); *Vaculina obscura* Koneva, 1992; Middle Cambrian, Mayaian, *Lejopyge armata* and *Lejopyge laevigata* biozones, Malyi Karatau.

Diagnosis. Shell elongate oval, subequally biconvex to somewhat dorsibiconvex; ventral propareas highly elevated, with flexure lines; dorsal pseudointerarea with shallow median groove; ventral visceral area forming low rhomboidal platform, slightly raised anteriorly, extending to mid-valve length; ventral *vascula lateralia* straight, slightly divergent, submarginal; dorsal visceral area forming low, subtriangular platform with narrow anterior projection, extending anteriorly beyond mid-valve length and bisected by median ridge; dorsal *vascula lateralia* marginal, weakly arcuate.

Remarks. Vaculina is comparable with *Lingulellotreta* in having flexure lines and a shallow median groove on the dorsal pseudointerarea. However, it differs in having a raised visceral area in both valves.

Vaculina obscura Koneva, 1992

Plate 16, figures 7–12; Plate 18, figures 1–2

1992 *Vaculina obscura* Koneva, p. 91, pl. 10, figs 6–13.

Holotype. IGNA 427/583, conjoined valves; Upper Cambrian, *Glyptagnostus stolidotus* beds; sample 1352-III, Kyrshabakty River, Malyi Karatau.

Material. One complete shell, 80 ventral and 111 dorsal valves.

Diagnosis. As for genus.

Remarks. Koneva (1992, p. 91) gave a detailed description of this species; the holotype and some specimens with well-preserved internal characters are re-illustrated here.

Occurrence. Middle Cambrian (*Lejopyge armata* Biozone)–Upper Cambrian (*Glyptagnostus stolidotus* Biozone) of Malyi Karatau, Kyrshabakty section, samples 1316-a, 1346-10, 1349, 1349-I-1, 1349-I-2, 1349-3, 1349-II-1, 1349-III, 1349-IV, 1350-II, 1351, 1351-1, 1351-2, 1351-I, 1351-I-4, 1351-II-1, 1352-III.

Family PATERULIDAE Cooper, 1956

Genus DIENCOBOLUS gen. nov.

Derivation of name. Greek, *dienco-*, continuous or unbroken, and *obolus*, a small Greek coin, alluding to the absence of a pedicle opening or notch.

Type species. Diencobolus simplex sp. nov.; Upper Cambrian, *Glyptagnostus stolidotus* Biozone, Malyi Karatau.

Diagnosis. Shell weakly biconvex, equivalved, elongate oval to subcircular in outline; both valves with holoperipheral growth and excentric to submarginal umbo, lacking pseudointerareas and pedicle notch; larval and post-larval shell finely pitted with subcircular to subelliptical pits of varying sizes; ventral valve with weakly impressed visceral area occupying the median part of the valve posterior to the mid-length; dorsal interior with a low median ridge widening anteriorly and bearing small, elongate suboval, anterior lateral muscle scars at the posterior end; central muscle scars large, suboval, situated in the mid-valve lateral to the median ridge.

Species included. Orbiculoidea? *subovalis* Biernat, 1973; *Paterula*? *naukatensis* Holmer, Popov and Bassett, 2000.

Remarks. Diencobolus is generally comparable only with *Paterula* in having a small, elongate-oval shell lacking pseudointerareas and with a finely pitted larval and post-larval shell. However, it is easily distinguished by the position of its excentric, not submarginal, ventral umbo, the dorsal median ridge, and rounded, not rhomboidal, pits covering the post-larval shell, as well as in the absence of an emarginature or notch in the posterior margin of the ventral valve.

In a recent paper (Holmer *et al.* 2000, caption to fig. 4) we inadvertently introduced the generic name *Diencobolus* for a species that we described in the text as *Paterula*? *naukatensis* sp. nov., although we then made it quite clear that this species was congeneric with more abundant specimens from Malyi Karatau. This latter statement referred to our material described here as *Diencobolus simplex* and defined as the type of the genus. Our previous use of the name was as a *nomen nudum* in the figure caption, and the legal definition of the genus *Diencobolus* is as in this present publication.

Diencobolus simplex sp. nov.

Plate 13, figures 1–10, 12

Derviation of name. Latin *simplex*, simple.

Holotype. IGNA 427/87, dorsal valve; Upper Cambrian, *Glyptagnostus stolidotus* Biozone; sample 1352-III, Kyrshabakty River, Malyi Karatau.

Material. 31 ventral and dorsal valves.

Diagnosis. As for genus.

Description. Shell biconvex, equivalved, elongately suboval in outline, about 115 per cent as long as wide; both valves externally very similar, with maximum height at the excentric umbo situated about mid way between the posterior margin and the mid-valve length; shell surface with micro-ornament of fine, circular pits; interior of both valves as for genus.

Dimensions. IGNA 427/729, ventral valve, L = 1·87, W = 1·60; IGNA 427/730, dorsal valve, L = 1·30; IGNA 427/737, dorsal valve, L = 1·77, W = 1·62; IGNA 427/87, dorsal valve, L = 3·1, W = 2·4.

Remarks. D. simplex is characterised by its very simple morphology, but it is easily distinguished from other known Cambrian lingulides in having excentric apices in both valves and in the absence of pseudointerareas and a pedicle opening. The dorsal and ventral valves are almost indistinguishable externally, but the dorsal valve is distinctive internally because it has a median ridge dividing the large central muscle scars.

The species described by Holmer *et al.* (2000, p. 372) as *Paterula*? *naukatensis*, from an early Ordovician (Arenig) olistolith in the Silurian Pulgon Formation of southern Kyrgyzstan, also belongs to *Diencobolus*; it differs from *D. simplex* in having a more convex dorsal valve with a submarginal umbo (rather than excentric), and finer, more regularly rounded micro-ornament pitting. Specimens described originally by Biernat (1973, p. 103) as the possible discinid *Orbiculoidea*? *subovalis*, from lower Ordovician (Tremadoc) chalcedonites of the Holy Cross Mountains, Poland, is also re-assigned by Biernat and Holmer (in press) to *Diencobolus*. *D. subovalis* differs from *D. simplex* and *D. naukatensis* in being more strongly biconvex, with a submarginal umbo in both valves, lamellose ornamentation, and an elevated ventral visceral area.

Occurrence. As for holotype.

Superfamily ACROTHELOIDEA Walcott and Schuchert, 1908
Family BOTSFORDIIDAE Schindewolf, 1955
Subfamily BOTSFORDIINAE Schindewolf, 1955

Genus BOTSFORDIA Matthew, 1891

Type species. Original designation by Matthew (1891, p. 148); *Obolus pulcher* Matthew, 1889; upper Lower Cambrian, Hanford Brook Formation, New Brunswick, Canada.

Diagnosis. Shell subcircular; ventral pseudointerarea catacline; ventral interior with small, slightly thickened visceral field, with three anterior lobe-like projections, not extending to mid-valve length; dorsal interior with narrow anterior projection extending to mid-valve, bisected by median ridge; ventral larval shell with single median tubercle.

Botsfordia caelata (Hall, 1847)

Plate 17, figures 4–9

1847	*Orbicula caelata* Hall, p. 290, pl. 69, figs 9a–c.
1977	*Botsfordia caelata* (Hall); Pelman, p. 30, pl. 10, figs 1–7 (full synonymy).
1983	*Botsfordia caelata* (Hall); Gorjansky and Koneva, p. 135, pl. 29, figs 11–13.

EXPLANATION OF PLATE 17

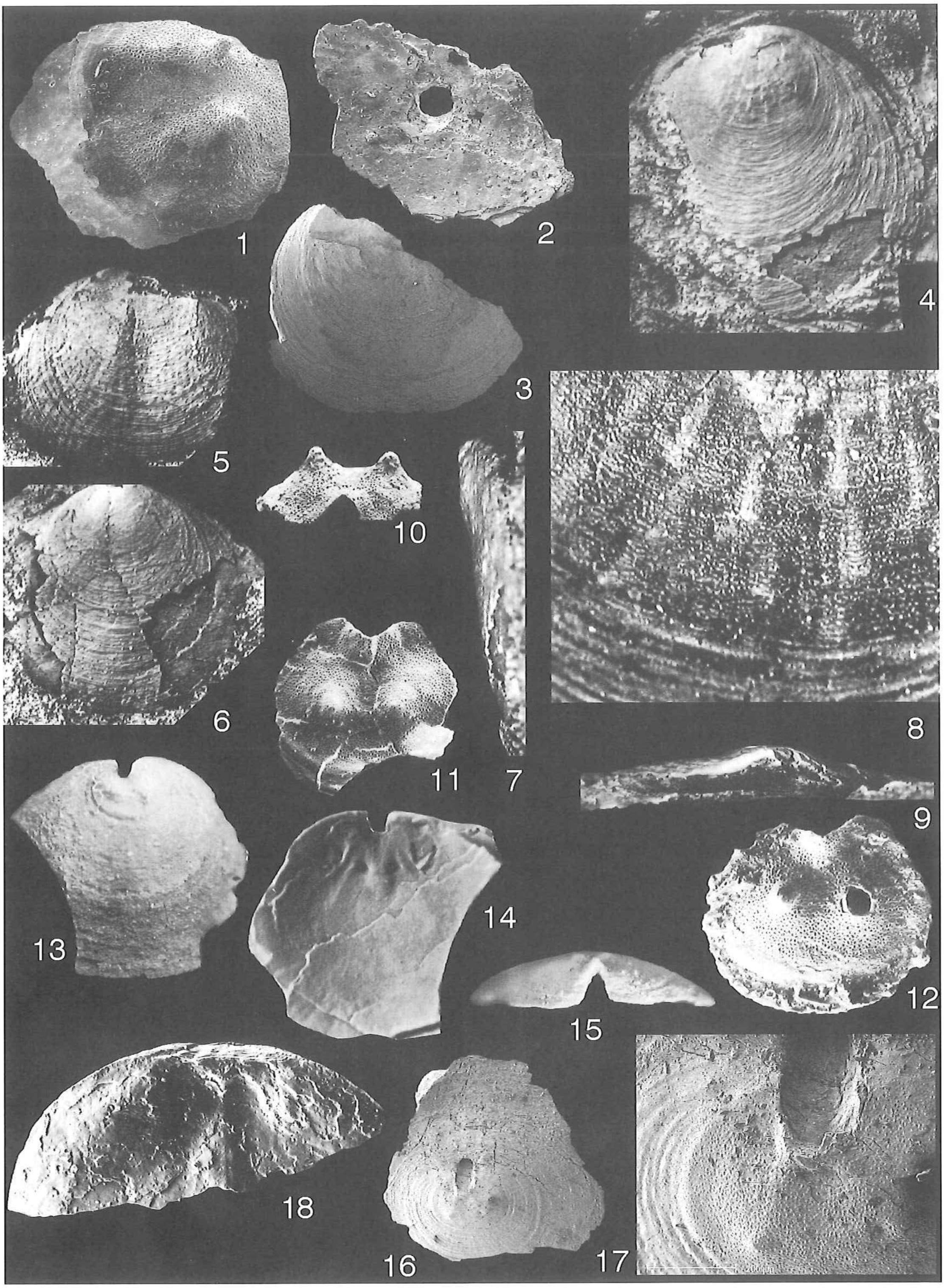
Figs 1–3, 18. *Acrothele* sp., Middle Cambrian, Malyi Karatau Range, Kyrshabakty section, *Ptychagnostus intermedius* Biozone. 1, NMW 98.61G.60, dorsal larval shell, lateral view, sample 1314-2; ×84. 2, NMW 98.61G.61, incomplete ventral valve interior showing internal foramen, sample 1314; ×32. 3, NMW 98.61G.40, incomplete dorsal valve exterior, sample 1314-2; ×13. 18, IGNA 427/670, incomplete dorsal valve interior, sample 1314-2; ×21.

Figs 4–9. *Botsfordia coelata* (Hall); Lower Cambrian, Toyonian, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, Koksu River. 4, 7–9, IGNA 2224/71, sample 1204, ventral valve exterior, ×4·5; lateral view, ×4·5; ornament of the post-larval shell, ×30; posterior view, ×4·5. 5, IGNA 2224/73, dorsal valve exterior, sample 1208; ×4·5. 6, IGNA 2224//72, ventral valve exterior, sample 1208; ×4·5.

Figs 10–15. *Karathele coronata* Koneva; Middle Cambrian, Malyi Karatau Range, Kyrshabakty section. 10, IGNA 427/374, ventral valve of larval shell, posterior view, *Goniagnostus nathorsti* Biozone, sample 1316; ×41. 11, IGNA 427/369, ventral valve of larval shell exterior, *Ptychagnostus intermedius* Biozone, sample 1467; ×55. 12 IGNA 427/375, ventral valve of larval shell exterior, *Goniagnostus nathorsti* Biozone, sample 1316; ×50. 13–15, IGNA 427/365, ventral valve, holotype, exterior, interior, posterior view, *Ptychagnostus intermedius* Biozone, sample 1465-1; ×21.

Figs 16–17. *Orbithele* sp.; Upper Cambrian, Karadzhorga Formation, Moldotau Range, Karakichi River, sample 127/9; NMW 98.61G.62, incomplete ventral valve exterior, ×16; detail of larval shell and pedicle foramen, ×61.

PLATE 17



HOLMER *et al.*, brachiopods

Material. 12 dorsal and ventral valves.

Remarks. Specimens of *Botsfordia caelata* from Malyi Karatau illustrated here were described fully by Gorjansky and Koneva (1983).

Occurrence. Lower Cambrian, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone; Malyi Karatau, Koksu section, samples 1204, 1206-1208.

Genus KARATHELE Koneva, 1986

Type species. Original designation by Koneva (1986, p. 206); *Karathele coronata* Koneva, 1986; Middle Cambrian, Amgaian, *Peronopsis*? *ultimus* and *Ptychagnostus atavus* biozones; Malyi Karatau.

Diagnosis. See Holmer *et al.* 1996, p. 8.

Remarks. Karathele was assigned originally to the Family Acrothelidae mainly on the basis of similarities in the morphology of the larval shell (Koneva 1986*b*). However, *Karathele* has an open delthyrium and rudimentary ventral pseudointerareas, which are characters of the Botsfordiidae, and it was thus reassigned by Holmer *et al.* (1996), who also gave a detailed discussion of the affinities and evolutionary significance of the genus. In all main aspects of shell morphology, development, and nature of the pedicle opening, *Karathele* occupies an intermediate position between early Cambrian Botsfordiidae and the early acrothelide genus *Eothele* Rowell, 1980.

Karathele coronata Koneva, 1986

Plate 17, figures 10–15

Holotype. GA 427/365, ventral valve; Middle Cambrian, Amgaian, *Peronopsis*? *ultimus* Biozone, sample 1467, Kyrshabakty section, Malyi Karatau.

Material. Three complete shells, four ventral valves and one dorsal.

Diagnosis. Shell small, flattened, slightly ventribiconvex, outline subcircular to slightly transversely suboval; ventral valve with narrow, triangular, catacline pseudointerarea and deep, short pedicle groove; ventral larval shell with median tubercle and one pair of lateral tubercules; dorsal valve flattened, with vestigial pseudointerarea; dorsal larval shell with posterior and anterior pairs of tubercles; post-larval shell finely pustulose; larval shell with micro-ornament of fine circular pits of varying sizes; ventral interior with slightly thickened visceral area not extending anteriorly to the mid-valve; posterolateral and anterior muscle fields clearly impressed, approximately equal sized; ventral *vascula lateralia* with straight, widely divergent proximal parts; dorsal interior with slender median ridge.

Remarks. K. coronata is rare in the Middle Cambrian of the Malyi Karatau sequences, with only a few specimens from the type collection available for this study. By comparison with *Karathele napuru* (Krause, 1990), it is distinguished in having two pairs of tubercules on the dorsal larval shell, a shallower ventral pedicle groove, and straight, widely divergent proximal parts of the ventral *vascula lateralia.*

Occurrence. Middle Cambrian, Amgaian, *Peronopsis*? *ultimus* and *Ptychagnostus atavus* biozones; Kyrshabakty section, Malyi Karatau, samples 1467, 1465-I, 1316.

Family ACROTHELIDAE Walcott and Schuchert, 1908
Subfamily ACROTHELINAE Walcott and Schucher, 1908

Genus ACROTHELE Linnarsson, 1876

Type species. By subsequent designation of Oehlert (1887, p. 1279); *Acrothele coriacea* Linnarsson, 1876; from the Middle Cambrian (*P. forchammeri* Biozone) of Sweden.

Acrothele sp.

Plate 12, figures 14–17; Plate 17, figures 1–3, 18.

1986 *Acrothele* sp.; Koneva, p. 205, pl. 30, figs 1–3.

Material. Six ventral and two dorsal valves.

Remarks. Juvenile and fragmentary adult specimens of *Acrothele* occur occasionally in the lower part of the Middle Cambrian sequence of the Kyrshabakty section. Detailed descriptions and illustrations were given by Koneva (1986).

Occurrence. Middle Cambrian, *Ptychagnostus atavus* and *Goniagnostus nathorsti* biozones, samples 1465-I and 1316; Kyrshabakty section, Malyi Karatau.

Order SIPHONOTRETIDA Kuhn, 1949
Superfamily SIPHONOTRETOIDEA Kutorga, 1848
Family SIPHONOTRETIDAE Kutorga, 1848

Genus SCHIZAMBON Walcott, 1884

Type species. By subsequent designation of Oehlert (1887, p. 1266); *Schizambon typicalis* Walcott, 1884 from the Lower Ordovician Pogonip Limestone of Hamburg Ridge, Eureka district, Nevada, USA.

Diagnosis. See Popov and Holmer 1994, p. 86.

Schizambon sp.

Plate 18, figures 4–5

Remarks. Schizambon is present in our samples only as two incomplete, exfoliated ventral valves, which have an elongate triangular pedicle track anterior to the apex, and a weakly concave, orthocline, undivided ventral pseudointerarea. These valves are somewhat similar to the specimens of *Schizambon* sp. described by Popov and Holmer (1994, p. 87) from the upper part of the Agalatas Formation of the Kendyktas Range in Kazakhstan. Precise specific attribution remains uncertain because of their imperfect preservation and the absence of information on dorsal valve morphology.

Occurrence. Lower Ordovician, Batyrbay section, *Dikelokephalina* beds, Malyi Karatau; samples 196 and 221 m.

Genus EOSIPHONOTRETA Havlíček, 1982

Type species. Original designation by Havlíček (1982, p. 57); *Terebratula verrucosa* Eichwald, 1840; Lower Ordovician, Volkhovian, Baltoscandia.

Diagnosis. See Havlíček 1982, p. 57.

Species included. *Terebratula verrucosa* Eichwald, 1840; *Siphonotreta krafti* Rúzicka, 1927; *Siphonotreta mamatensis* Popov, 1980.

Remarks. Havlíček (1982) discussed the affinities of *Eosiphonotreta* and also listed the species that he assigned to the genus. We regard only one of his listed species as congeneric with the type species *E. verrucosa*. Among the other taxa listed by Havlíček, *Siphonotreta uralensis* Lermontova, 1933 was re-assigned by Popov and Holmer (1994) to *Siphonobolus*. *Siphonotreta acrotretomorpha* Gorjansky, 1969 is more probably a separate, new genus because it has a relatively high, conical ventral valve with a catacline to procline ventral pseudointerarea divided by a median plication, as well as a high, conical internal pedicle tube; all of these features are substantially different from features of *Eosiphonotreta*. *Siphonotreta circularis* Sdzuy, 1955 remains inadequately known and its generic assignment is uncertain. Re-study of the types of *Siphonotreta intermedia* Gorjansky, 1969 from the Uhaku and Kukruse regional stages of Baltoscandia deposited in the Tschernyshev Museum, St Petersburg suggests that this species differs from *Siphonotreta unguiculata* Eichwald, 1840, the originals of which were from the Kundan Regional Stage, and thus occupies a different stratigraphical position; we consider *S. intermedia* to be congeneric with the type species of *Siphonotreta*.

Occurrence. Lower Ordovician, Volkhov Regional Stage of Baltoscandia; Trenice and Klabova formations of Bohemia; Mamat Formation of the Chingiz Range and *Nileus* beds of Malyi Karatau.

Eosiphonotreta mamatensis (Popov, 1980)

Plate 18, figures 3, 6–12

1980 *Siphonotreta mamatensis* Popov, *in* Nazarov and Popov, p. 116, pl. 29, figs 11–14.

Holotype. CNIGR 235/11352, dorsal valve; Lower Ordovician, Mamat Formation, Mamat Mountain, Chingiz Range.

Material. Three ventral and two dorsal valves.

Diagnosis. Shell ventribiconvex, outline subcircular; ventral valve subconical with procline to weakly apsacline pseudointerarea poorly defined laterally; pedicle foramen large, subcircular, situated anterior to the umbo; dorsal valve with rudimentary pseudointerarea with lensoid median groove and reduced propareas; shell ornament of regular concentric rugellae and growth lamellae, with hollow spines of two different sizes; ventral interior with short, free, subconical internal pedicle tube; dorsal interior with short median ridge.

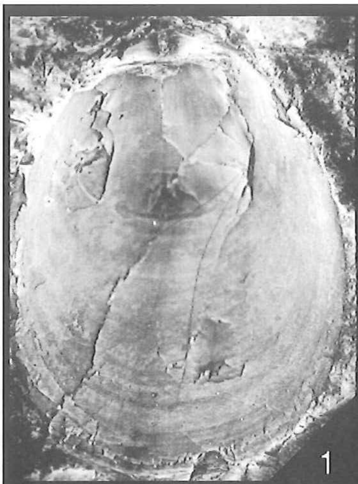
EXPLANATION OF PLATE 18

Figs 1–2. *Vaculina obscura* Koneva; Upper Cambrian, Malyi Karatau, Kyrshabakty section. 1, IGNA 427/581, dorsal valve interior, *Kormagnostus simplex* Biozone, sample 1351; ×4. 2, IGNA 427/585, dorsal valve exterior, *Glyptagnostus stolidotus* Biozone, sample 1352-III; ×5.

Figs 3, 6–12. *Eosiphonotreta mamatensis* (Popov); Ordovician, Kogashik Regional Stage, Malyi Karatau, Batyrbay section, *Paroistodus proteus* Biozone, sample 465 m. 3, NMW 98.61G.74, incomplete ventral valve interior showing internal pedicle tube; ×42. 6–9, NMW 98.61G.75, ventral valve, exterior, ×27; posterior view, ×32; detail of umbonal area and pedicle foramen, ×76; and lateral view, ×29. 10, NMW 98.61G.76, shell fragment showing concentric ornament and hollow spines; ×38. 11–12, NMW 98.61G.77, dorsal valve exterior in lateral and normal views; ×76, ×60.

Figs 4–5, *Schizambon* sp.; Ordovician, Malyi Karatau, Batyrbay section. 4, NMW 98.61G.78, incomplete ventral valve exterior showing umbonal area and pedicle track, *Cordylodus lindstroemi* Biozone, sample 221 m; ×69. 5, NMW 98.61G.79, incomplete ventral valve interior, *Cordylodus intermedius* Biozone, sample 198 m; ×64.

PLATE 18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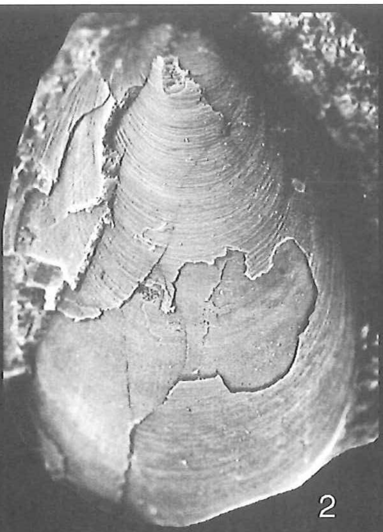
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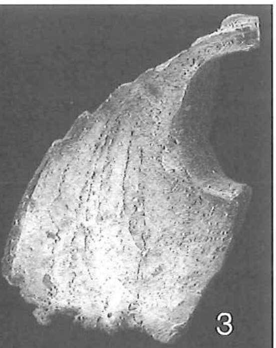
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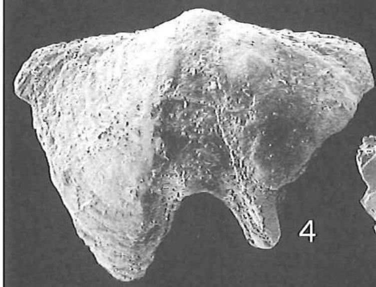
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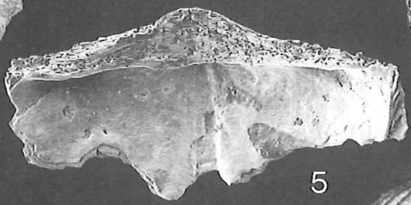
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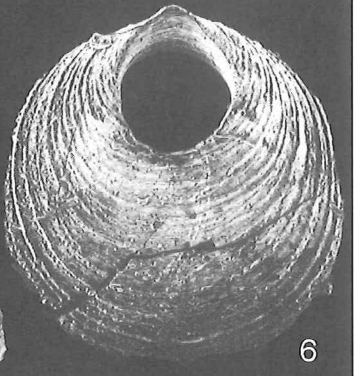
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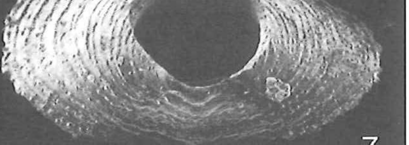
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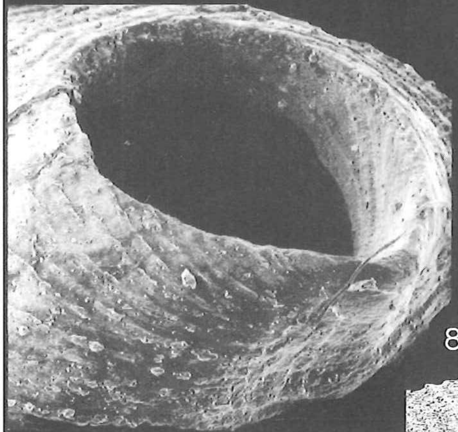
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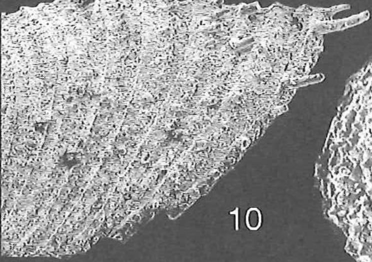
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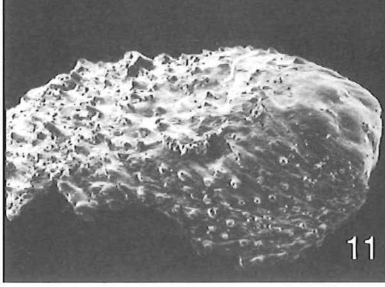
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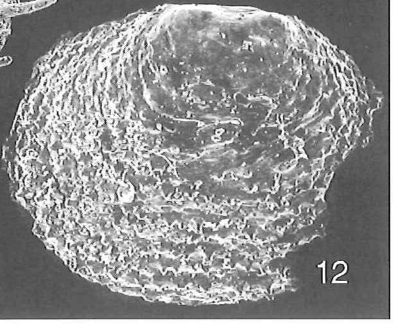
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HOLMER *et al.*, brachiopods

Remarks. Eosiphonotreta mamatensis differs from *E. verrucosa* (Eichwald, 1840) and *E. krafti* (Rúzicka, 1927) in having a relatively small shell with a large pedicle foramen and strong concentric rugellae covering the surface. The type horizon of *E. mamatensis* in the Mamat Formation has been regarded generally as contemporaneous with uppermost Tremadoc strata of Baltoscandia (Nikitin 1972; Nazarov and Popov 1980). However, the co-occurrence of *E. mamatensis* in the Chingiz Range with such brachiopod species as *Mamatia retracta* (Popov, 1980) and *Clarkella supina* Nikitin, 1956, which are also known from the Olenty Formation of north-eastern Central Kazakhstan and coeval beds in the South Urals, more probably suggests a younger (Hunnebergian or Billingenian) age for the Mamat Formation. In Malyi Karatau, *E. mamatensis* occurs together with conodonts of the *Paroistodus proteus* Biozone.

Occurrence. Lower Ordovician; Malyi Karatau, *Nileus* beds, sample 465 m; Mamat Formation, Chingiz Range.

Order ACROTRETIDA Kuhn, 1949
Superfamily ACROTRETOIDEA Schuchert, 1893
Family ACROTRETIDAE Schuchert, 1893

Genus ANABOLOTRETA Rowell and Henderson, 1978

Type species. Original designation by Rowell and Henderson (1978, p. 8); *Anabolotreta tegula* Rowell and Henderson, 1978; Middle Cambrian (Mindyallian Stage), Georgina Basin, Queensland, Australia.

Diagnosis. See Rowell and Henderson 1978, p. 8.

Species included. Anabolotreta tegula Rowell and Henderson, 1978; *Anabolotreta diversa* Koneva, 1986; *Anabolotreta dorsata* Mei, 1993; *Anabolotreta groenlandica* Zell and Rowell, 1988; *Anabolotreta lepida* Koneva, 1986; *Anabolotreta parva* Ushatinskaya, 1994; ?*Linnarssonia vitalis* Sobolev, 1975; *Anabolotreta* sp. (Popov 1985); *Anabolotreta* sp. (Popov *et al.* 1996).

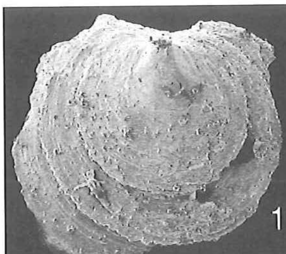
Remarks. The late Middle Cambrian *Linnarssonia vitalis* Sobolev, 1975 was re-assigned to *Anabolotreta* by Sobolev (1992, p. 102). However, this species differs from the type species, and from all other known species of *Anabolotreta*, in having a slightly dorsibiconvex shell, with flattened peripheral areas in the ventral valve, a relatively high dorsal pseudointerarea, and a high apical process which is connected posteriorly with a low, internal pedicle tube; its generic assignment therefore remains tentative.

Occurrence. Middle–Upper Cambrian; Australia, New South Wales and western Queensland (Boomerangian and Mindyallian), New Zealand (Tasman Formation); north-central Siberia (Ejrina and Tjuessala formations, *Lejopyge laevigata–Glyptagnostus stolidotus* biozones); south-eastern Siberia (Dzhavody beds); Novaya Zemlya (*Lejopyge*

EXPLANATION OF PLATE 19

Figs 1–2, 4–5. *Anabolotreta lepida* Koneva; Middle Cambrian, *Goniagnostus nathorsti* Biozone, Malyi Karatau, Kyrshabakty section, sample 1316. 1–2, NMW 98.61G.88, ventral valve exterior in normal and oblique lateral views; ×57, ×64. 4–5, NMW 98.61G.89, dorsal valve exterior in normal and oblique lateral views; both ×59.

Figs 3, 6–17. *Anabolotreta diversa* Koneva; Middle Cambrian; 3, 7, 10–15, Sarykumy Formation, Sarykumy section; 6, 8–9, 11, 16–17, Maly Karatau, Kyrshabakty section, *Lejopyge armata* Biozone. 3, NMW 98.61G.90, ventral valve exterior, oblique lateral view, sample 134; ×60. 6, NMW 98.61G.91, dorsal valve interior, sample 1345; ×51. 7, NMW 98.61G.226, ventral valve exterior, sample K-20/29; ×19·5. 8, 11, NMW 98.61G.92, dorsal valve exterior in normal and oblique lateral views, sample 1348; ×57, ×62. 9, NMW 98.61G.93, ventral valve interior, sample 1345; ×42. 10, NMW 98.61G.94, ventral valve interior, sample 134; ×45. 12, NMW 98.61G.95, dorsal valve exterior, sample 134; ×38. 13–14, NMW 98.61G.96, dorsal valve exterior in oblique lateral and normal views, sample 134; ×30, ×28. 15, NMW 98.61G.97, dorsal valve interior, sample 134; ×32. 16, NMW 98.61G.99, dorsal valve interior, sample 1345; ×35. 17, NMW 98.61G.100, dorsal valve exterior, sample 1345; ×61.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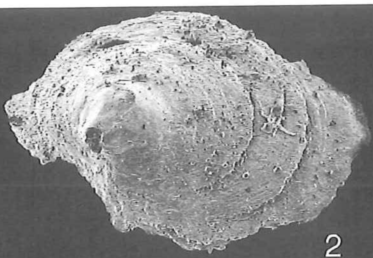
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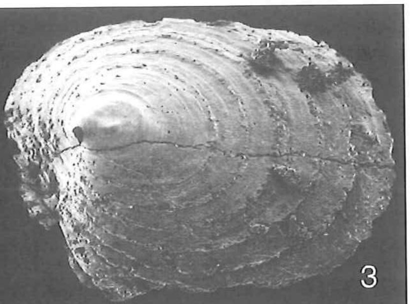
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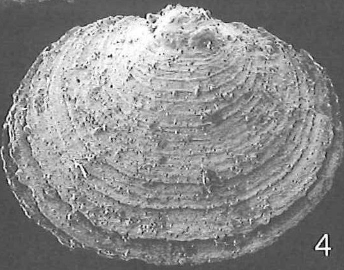
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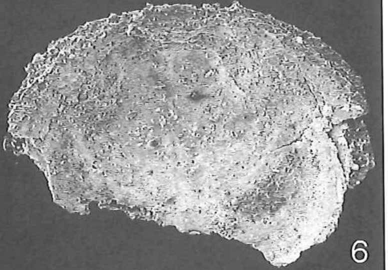
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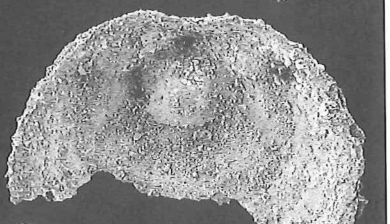
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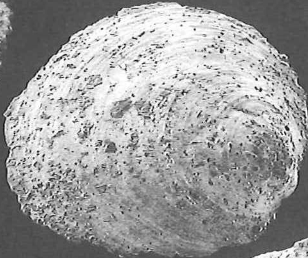
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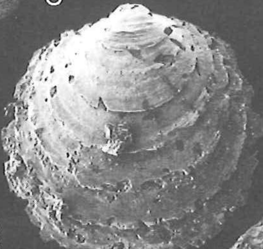
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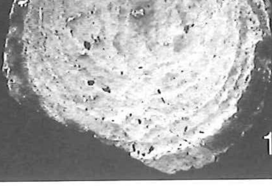
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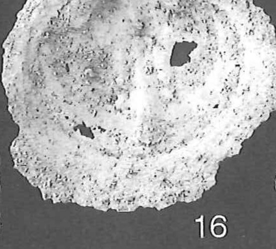
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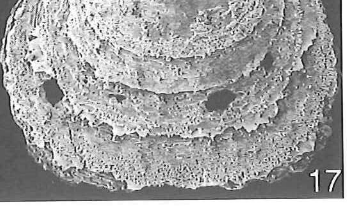
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HOLMER *et al.*, *Anabolotreta*

laevigata Biozone); North Greenland (Holm Dal Formation); Kazakhstan, Malyi Karatau, (*Lejopyge armata–Glyptagnostus reticulatus-Euganocare* biozones, *Innitagnostus inexpectans-Prochuangia* beds); Kazakhstan, Atasu–Zhamshy area (Sarykumy Formation) and Tarbagatay Range (Mayaian Stage); North China (*Blackwelderia orygma–Drepanura–Liostracina* biozones); western USA (*Crepicephalus* and *Aphelaspis* biozones).

Anabolotreta diversa Koneva, 1986

Plate 19, figures 3, 6–17

1986*b* *Anabolotreta diversa* Koneva, p. 204, pl. 19, figs 13–18.

Holotype. IGNA 427/359, ventral valve (Koneva 1986*b*, pl. 29, fig. 13); Upper Cambrian (*Glyptagnostus stolidotus* Biozone); Kyrshabakty section (sample 1352), Malyi Karatau. Koneva (1986*b*, p. 204) erroneously referred to specimen IGNA 427/349 (sample 1316) as the holotype, but this is obviously a mistake, and in the plate and its explanation (Koneva 1986*b*, p. 222, pl. 29), specimen IGNA 427/359 (sample 1352) is illustrated and recorded as the holotype of this species. IGNA 427/349 is instead the holotype of *Anabolotreta lepida* (see below).

Material. Six complete shells, 39 ventral and 37 dorsal valves.

Emended diagnosis. Shell large, slightly ventribiconvex, transversely suboval to subcircular with maximum width at about the mid-length; ventral interior with boss-like, subtriangular apical process and arcuate, widely divergent *vascula lateralia*; dorsal interior with raised cardinal muscle scars, bounded by a low rim; median ridge poorly defined to incipient.

Description. Slightly ventribiconvex, transversely suboval to subcircular shells, on average 85 per cent as long as wide, with maximum width slightly anterior to mid-valve length. Ventral valve low subconical, about one-third as high as long (Table 4). Anterior slope of valve straight in sagittal section, lateral slopes gently convex in transverse profile. Ventral pseudointerarea procline with intertrough. Pedicle foramen apical, not enclosed within the larval shell. Dorsal

TABLE 4. *Anabolotreta diversa* Koneva, dimensional data for ventral valves from the Sarykumy section (sample 102, Middle Cambrian, Sarykumy Formation).

	Lv	W	T	Al	Aw	Lv/W	T/Lv	Vl/Lv
N	5	4	5	4	4	4	5	4
X	1·13	1·235	0·37	0·38	0·295	88%	33%	40%
S	0·331	0·393	0·113	0·088	0·057	5·3	1·7	4·4
MIN	0·72	0·78	0·24	0·28	0·22	81%	31%	32%
MAX	1·48	1·62	0·52	0·48	0·34	92%	35%	40%

TABLE 5. *Anabolotreta diversa* Koneva, dimensional data for dorsal valves from the Sarykumy section (sample 102, Middle Cambrian, Sarykumy Formation).

	Ld	W	T	Il	Iw	Cl	Sa	Ld/W	Iw/W	Cl/Ld	T/Ld
N	5	5	5	4	4	5	3	5	4	3	5
X	1·22	1·39	0·34	0·13	0·34	0·45	0·75	88%	27%	36%	29%
S	0·315	0·341	0·073	0·042	0·075	0·101	0·180	9·3	74	41	63
MIN	0·80	0·90	0·24	0·08	0·26	0·34	0·56	76%	19%	31%	24%
MAX	1·64	1·74	0·42	0·18	0·44	0·54	0·92	100%	36%	39%	39%

valve moderately convex, about 30 per cent as thick as long, with maximum thickness slightly posterior to mid-length (Table 5). Dorsal pseudointerarea vestigial with wide median groove and minute propareas, occupying about 25–30 per cent of valve width. Ornamentation of variably developed growth lamellae.

Ventral interior with boss-like apical process extending anterior to the internal foramen. Ventral *vascula lateralia* widely divergent, arcuate. Dorsal interior with median ridge incipient to weakly developed, extending forward about two-thirds of the valve length. Dorsal cardinal muscle scars slightly raised, bounded by a low rim and extending forward for about one-third of the valve length. Dorsal anterocentral muscle scars at about mid-valve length and bounded laterally by very fine, straight, slightly divergent ridges.

Remarks. A. diversa differs from the type species mainly in having a larger, more transversely suboval outline, with the maximum width at mid-length, and in having dorsal cardinal muscle scars raised above the valve floor. Koneva (1986) considered the absence of a dorsal median ridge as a distinctive feature of *A. diversa*, but our study of specimens from Malyi Karatau and Sarykumy shows that a fine to vestigial median ridge is present in the majority of valves. Rowell and Henderson (1978) noted the considerable variation in shape and number of growth lamellae in *Anabolotreta*, and this is also apparent in our material.

Occurrence in Central Asia. Middle Cambrian (Mayaian)–Upper Cambrian (*Lejopyge armata–Glyptagnostus reticulatus–Euganocare* local biozones, *Innitagnostus inexpectans–Prochuangia* beds), Kyrshabakty section, samples 1345, 1346, 1346-4, 1346-6, 1346-10, 1346-11, 1348, 1349, 1349-2, 1349-I-1,1349-I-2, 1349-III-2, 1349-IV-1, 1351, 1352, 1352-1, 1352-I-1; 1355-1; Middle Cambrian (Mayaian)–Upper Cambrian, area about 4 km south-east of Sarykumy railway station, Kazakhstan, Sarykumy Formation, samples F-102, F-104, F-132, F-135; Moldotau Range, eastern side of Karakichi River, Kyrgyzstan, Karadzhorga Formation, sample 127/9.

Anabolotreta lepida Koneva, 1986

Plate 19, figures 1–2, 4–5; Plate 20, figures 10–13; Plate 21, figures 8, 10–13

1986*b* *Anabolotreta lepida* Koneva, p. 203, pl. 19, figs 6–12.

Holotype. IGNA 427/349, ventral valve; Middle Cambrian (*Glyptagnostus nathorsti* Biozone); Kyrshabakty section, sample 1316, Malyi Karatau.

Material. Two complete shells, 19 ventral and 12 dorsal valves.

Emended diagnosis. Shell slightly ventribiconvex, transversely oval with maximum width at mid-length; ventral interior with high, narrow, subtriangular, boss-like apical process; ventral *vascula lateralia* strongly impressed, with straight, subparallel or only slightly divergent proximal parts; dorsal median ridge well developed for genus, with maximum height near the anterior extremity; dorsal cardinal muscle scars weakly impressed.

Description. Slightly ventribiconvex, transversely oval, about 80–90 per cent as long as wide (Table 6) with maximum width at the mid-length. Ventral valve low, subconical with procline pseudointerarea divided by a shallow intertrough.

TABLE 6. *Anabolotreta lepida* Koneva, dimensional data for ventral valves from the Kyrshabakty section (sample 1345, Middle Cambrian, *Lejopyge armata* Biozone).

	Lv	W	T	Vl	Vw	Lv/W	Vl/Lv
N	4	5	3	5	5	4	4
X	0·90	1·12	0·33	0·33	0·136	81%	33·5%
S	0·186	0·216	0·108	0·076	0·18	9·6	4·5%
MIN	0·72	0·88	0·21	0·24	0·16	74%	28·6%
MAX	1·16	1·38	0·42	0·42	0·24	91%	38·3%

TABLE 7. *Anabolotreta lepida* Koneva, dimensional data for dorsal valves from the Kyrshabakty section (sample 1345, Middle Cambrian, *Lejopyge armata* Biozone).

	Ld	W	T	Il	Iw	Cl	Cw	Sa	Ld/W	Iw/W	Cl/Ld	Cw/W	T/Ld	Sa/Ld
N	4	4	4	4	4	4	4	4	4	4	4	4	4	4
X	0·965	1·11	0·285	0·1	0·28	0.29	0·575	0·63	86%	9%	3%	53%	30%	65%
S	0·218	0·211	0·055	0·028	0·049	0.042	0·068	0·146	6·2	2·0	9·7	6·1	4·3	3·3
MIN	0·64	0·8	0·22	0·08	0·22	0.24	0·48	0·42	80%	7%	26%	47·5%	24%	61%
MAX	1·1	1·26	0·34	0·14	0·32	0·34	0·64	0·76	93%	11%	47%	60%	34%	69%

Dorsal valve moderately and evenly convex. Dorsal pseudointerarea vestigial, undivided, occupying about 25 per cent of the valve width (Table 7). Ornament of variably developed concentric growth lamellae.

Ventral interior with narrow, subtriangular, boss-like apical process anterior to the internal pedicle foramen, flanked laterally by small apical pits. Ventral *vascula lateralia* strongly impressed with straight, subparallel or only slightly anteriorly divergent proximal parts; dorsal median ridge fine with maximum height near the anterior extremity; cardinal muscle scars weakly impressed.

Remarks. *A. lepida* is distinguished from both *A. tegula* and *A. diversa* in having a high, narrow, triangular apical process and strongly impressed ventral *vascula lateralia* with straight, subparallel proximal parts. It also differs from *A. diversa* in having weakly impressed dorsal cardinal muscle fields.

A. lepida is older than *A. diversa*, and in the Kyrshabakty section the latter replaces the former in the *Lejopyge laevigata* Biozone. In the uppermost Middle Cambrian of the Kyrshabakty section, however, specimens of *Anabolotreta* are rare and are difficult to differentiate. Therefore the assignment of material from this interval (samples 1345, 1346, 1346-10, 1349) to *A. diversa* is somewhat provisional.

Occurrence in Central Asia. Middle Cambrian (*Goniagnostus nathorsti* Biozone), Kyrshabakty section, samples 1465-18, 1465-22, 1465-24, 1465-25, 1316.

Anabolotreta? sp.

Plate 20, figures 6–9; Plate 44, figure 16

Material. Four dorsal valves.

Description. Dorsal valve moderately convex with the maximum height near the anterior margin of the larval shell. Outline transversely oval, about 80 per cent as long as wide, with strongly swollen umbonal area. Dorsal

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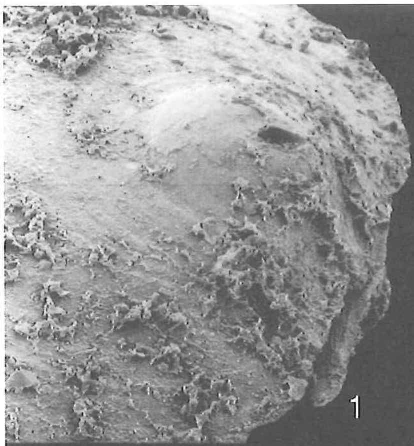
EXPLANATION OF PLATE 20

Figs 1–4. *Araktina intermedia* Koneva; Upper Cambrian, *Glyptagnostus stolidotus* Biozone, Malyi Karatau, Kyrshabakty section. 1, RM Br136398, oblique lateral view of conjoined valves, sample 1352; ×98. 2, NMW 98.61G.80, ventral valve interior, oblique view showing apical process, sample 1352-III; ×75. 3, IGNA 427/479, ventral valve, umbonal area, sample 1352; ×84. 4, RM Br136399, incomplete ventral valve, umbonal area, sample 1352; ×76.

Figs 6–9. *Anabolotreta*? sp. 6–7, NMW 98.61G.81, dorsal valve exterior in oblique lateral and normal views, Upper Cambrian, *Innitagnostus inexpectans*-*Prochuangia* beds, Malyi Karatau, Kyrshabakty section, sample 1356; both ×74. 8–9, NMW 98.61G.82, dorsal valve interior in oblique lateral and normal views, Middle Cambrian, Amgaian, Karagajly Formation, Kostek Range, sample 1639; ×29·9, ×26.

Figs 5, 10–13. *Anabolotreta lepida* Koneva; Middle Cambrian, *Goniagnostus nathorsti* Biozone, Malyi Karatau, Kyrshabakty section, sample 1316. 10–11, NMW 98.61G.83, dorsal valve interior in oblique lateral and normal views; ×34, ×30. 5, 12–13, NMW 98.61G.84, ventral valve interior showing umbonal area with ridge-like apical process and internal foramen, and oblique lateral and normal views; ×100, ×46.

PLATE 20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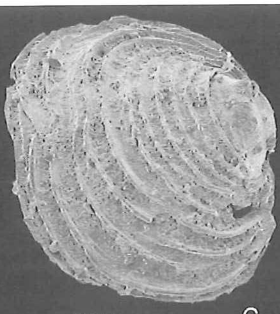
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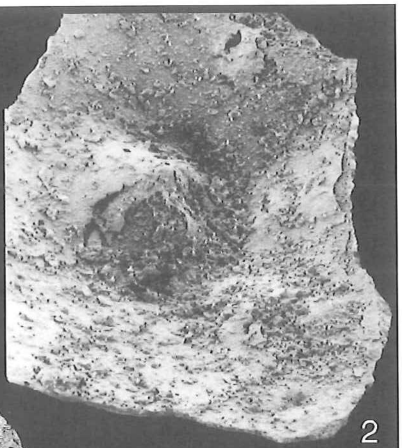
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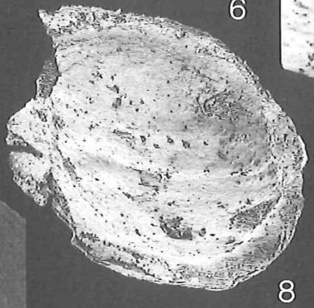
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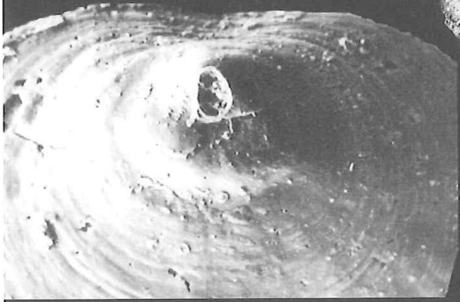
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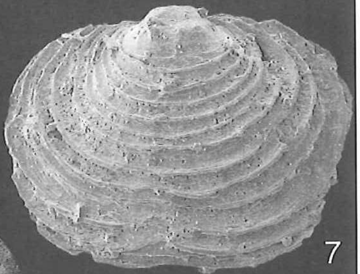
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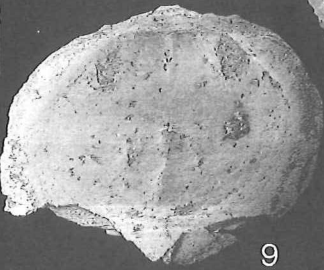
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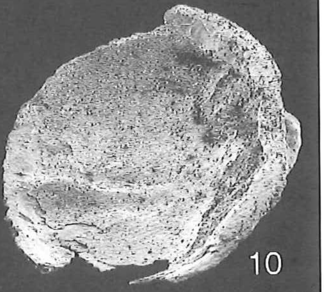
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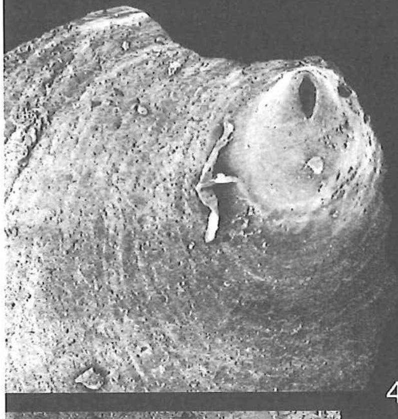
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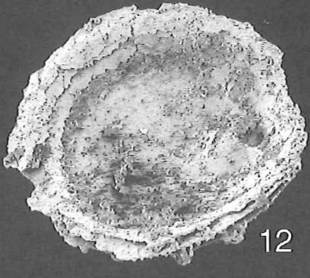
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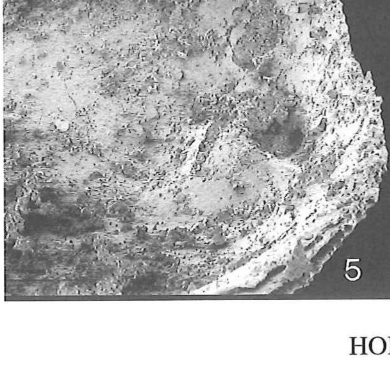
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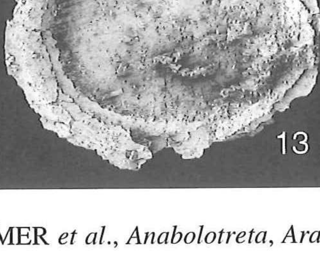
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HOLMER *et al.*, *Anabolotreta*, *Araktina* pseudointerarea low, occupying slightly over one-half of the total valve width, occupied mainly by a lens-like median groove. Ornament of up to 11 evenly spaced, high, ridge-like growth lamellae.

Dorsal interior with very faint median ridge, flanked by slightly raised, elongate suboval anterocentral muscle scars at about mid-valve length. Cardinal muscle fields weakly impressed.

Dimensions. NMW 98.61G.81, dorsal valve, L = 0·52, W = 0·66, T = 0·18, Il = 0·10, Iw = 0·36.

Remarks. This species is known only from dorsal valves, which are generally comparable with those of *Anabolotreta* in outline and overall shape, as well as in having a lamellose concentric ornament. However, the ornament of our specimens differs in detail in comprising distinctive high, ridge-like, rugellae. A similar type of ornament is known otherwise mainly in the Ordovician Scaphelasmatidae (e.g. *Rhysotreta*), but has not been observed in Cambrian genera of this family (e.g. *Eoscaphelasma*). Because the ventral valve of this species remains unknown, precise taxonomic discrimination is impossible.

Occurrence in Central Asia. Upper Cambrian (*Acutagnostus acutus-Erixanium* beds), Kyrshabakty section, sample 1356; Middle Cambrian (Amgaian, Karagajly Formation), Kostek Range, sample 1639.

Genus ANGULOTRETA Palmer, 1954

Type species. Original designation by Palmer (1954, p. 769); *Angulotreta triangularis* Palmer, 1954; Upper Cambrian, Dresbachian (*Aphelaspis* Biozone), central Texas, USA.

Emended diagnosis. Shell with weakly incurved posterior margin; ventral pseudointerarea procline to weakly apsacline with intertrough; foramen enclosed within larval shell; dorsal pseudointerarea with wide median groove; apical process well developed, long, forming broad ridge along posterior slope, partly enclosing internal pedicle tube anteriorly; apical pits well developed, deep, set posterior to internal foramen; dorsal triangular median septum high, may be digitate; dorsal median buttress and antero-central muscle scars present.

Species assigned. Angulotreta triangularis Palmer, 1954; *Angulotreta postapicalis* Palmer, 1954; *Angulotreta*? *sublata* Mei, 1993; *Angulotreta*? sp.

Remarks. Among four species of *Angulotreta* described from China by Mei (1993), three Middle Cambrian taxa (*Angulotreta concava* Mei, *A. flata* Mei and *A. retrideclivata* Mei) do not appear to be comparable with the type species of the genus; most importantly, the Chinese species have a pedicle foramen that is not enclosed within the larval shell, and they differ also in the morphology of the apical process. *Angulotreta sublata* Mei, 1993, from the Upper Cambrian *Kaolishania* Biozone of North China, is more comparable with *Angulotreta* in having a foramen within the larval shell, but it differs in having a small, narrow, ridge-like apical process situated anterior to the internal foramen; we thus regard the generic assignment of this species as provisional.

Occurrence. ?Middle Cambrian–Upper Cambrian; USA (Texas, Montana, Wyoming, Missouri); Estonia (Upper Cambrian, Uglase Formation); Russia (Ingria, lower Upper Cambrian, Lower Ladoga Formation); ?Siberia, Novaya Zemlya (Karpinskaya Formation); West Antarctica (Idamean); ?North China (Hebei, Zhangxian–Kushanian).

Angulotreta? sp.

Plate 22, figures 1–3

Material. Four dorsal valves and one questionable ventral valve.

Description. Dorsal valve gently convex, about 80 per cent as long as wide. Dorsal pseudointerarea moderately high, weakly apsacline, occupying slightly more than 50 per cent of the maximum valve width. Median groove broadly triangular, poorly defined, with anterior margin incurved to form a low, thin rim.

Dorsal cardinal muscle fields slightly thickened, extending forward for slightly less than 50 per cent of the total valve length and bounded by an elevated rim. Dorsal median septum high, triangular, occupying about 90 per cent of total valve length, with a thickened, triangular surmounting platform incorporating up to five folds on the ventral side. Proximal parts of *vascula lateralia* deeply impressed, straight, widely divergent.

Dimensions. NMW 98.61G.102, dorsal valve, L = 1·22, W = 1·50, Il = 0·20, Iw = 0·82, Pw = 0·58, Cw = 0·96, Sa = 1·12, St = 0·40

Remarks. The four available dorsal valves of *Angulotreta* sp. are similar to *A. triangularis* Palmer, 1954 in having a high, triangular median septum with a thickened platform and large, strongly impressed cardinal muscle scars.

The single incomplete ventral valve, only questionably identified as conspecific with the dorsal valves, is from a different sample (1378); it has a high, apsacline, poorly defined pseudointerarea, and a small circular pedicle foramen enclosed within the larval shell.

Occurrence in Kazakhstan. Upper Cambrian (*Eorudagnostus ovaliformis*-'*Pareuloma*' beds), Kyrshabakty section, sample 1381.

Genus ARAKTINA Koneva, 1992

Type species. By monotypy (Koneva, *in* Repina and Rozanov 1992, p. 94); *Araktina intermedia* Koneva, 1992 (*in* Repina and Rozanov); Upper Cambrian (*Glyptagnostus stolidotus* Biozone), Kyrshabakty section, Malyi Karatau.

Emended diagnosis. Shell subcircular to transversely oval with short posterior margin; ventral valve convex to low subconical; ventral pseudointerarea catacline to procline, rarely apsacline, with intertrough; foramen small, elongate suboval, enclosed within larval shell; dorsal valve gently convex with vestigial pseudointerarea; apical process high, boss-like, anterior to foramen, grooved posteriorly; apical pits shallow, situated immediately lateral to internal foramen; dorsal interior with high median ridge extending slightly anterior to mid-valve length and buttressed posteriorly; dorsal cardinal muscle scars small, rounded, bounded by elevated rim, dorsal anterocentral muscle scars well defined, at about mid-valve length.

Remarks. *Araktina* is most similar to *Linnarssonia* in external shell morphology, as well as in having a boss-like apical process, a buttressed dorsal median ridge, and an undivided dorsal pseudointerarea. The main differences between these two genera are the elongate suboval pedicle foramen within the larval shell in *Araktina*, and the dorsal cardinal muscle fields which in *Araktina* are smaller and not so strongly impressed as in *Linnarssonia*.

Araktina is also comparable with *Amictocracens* Henderson and MacKinnon, 1981 in both the external and internal morphology of the ventral valve, including the pedicle foramen within the larval shell and the rudimentary dorsal pseudointerarea. However, *Amictocracens* differs in having a blade-like, triangular median septum.

Occurrence. As for the type species, which remains the only species assigned to the genus.

Araktina intermedia Koneva, 1992

Plate 20, figures 1–4; Plate 21, figures 7, 9

1992 *Araktina intermedia* Koneva, p. 95, pl. 12, figs 1–8.

Holotype. IGNA 427/481, ventral valve; Upper Cambrian, *Glyptagnostus stolidotus* Biozone; Kyrshabakty section, sample 1352/III, Malyi Karatau.

Material. Four complete shells, 44 ventral and five dorsal valves.

Diagnosis. As for genus.

Remarks. Koneva (1992) gave a detailed description of this species; the holotype and some topotypes are re-illustrated here.

Occurrence in Kazakhstan. Kyrshabakty section, Upper Cambrian, *Glyptagnostus stolidotus* Biozone; samples 1352, 1352/I-1, 1352/II, 1352/III.

Genus CANTHYLOTRETA Rowell, 1966

Type species. Original designation by Rowell (1966, p. 5); *Acrotreta marjumensis* Walcott, 1905; Middle Cambrian, House Range, Utah, USA.

Diagnosis. See Rowell 1966, p. 5.

Species included. Acrotreta marjumensis Walcott, 1905; *Canthylotreta grada* Zell and Rowell, 1988; *Canthylotreta atasuica* sp. nov.; *Canthylotreta* sp.

Species rejected. Canthylotreta flexa Mei, 1993; *Canthylotreta cornuta* Mei, 1993; *Canthylotreta rhynchophora* Mei, 1993.

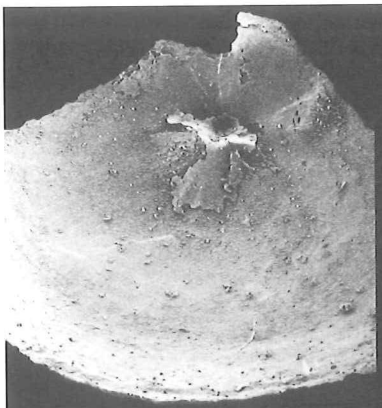
Remarks. Canthylotreta flexa and *C. cornuta*, both described by Mei (1993) from the Middle Cambrian of North China, differ from the type species of this genus in the shape, profile and overall morphology of the ventral valve, and in having a poorly defined median ridge rather than a triangular median septum. The morphology of the ventral valve of *C. rhynchophora* Mei, 1993 is poorly known, but again the absence of a triangular median septum makes the generic assignment doubtful. Moreover, all the Chinese species lack a dorsal sulcus, which is present in *C. marjumensis* and all other known species of this genus.

Occurrence. Middle–Upper Cambrian; Utah, USA (upper Middle Cambrian); Greenland (*Lejopyge laevigata* Biozone); north Kyrgyzstan (late Amgaian); Central Kazakhstan [Middle Cambrian (Mayaian)–Upper Cambrian].

EXPLANATION OF PLATE 21

Figs 1–7, 9. *Araktina intermedia* Koneva; Upper Cambrian, *Glyptagnostus stolidotus* Biozone, Malyi Karatau, Kyrshabakty section. 1, 3, RM Br136400, ventral valve interior, and detail of apical process, sample 1352; ×49, ×76. 2, IGNA 427/481, holotype, ventral valve exterior, sample 1352-III; ×36. 4, IGNA 427/486, dorsal valve interior, sample 1352; ×20. 5, IGNA 427/479, ventral valve exterior, sample 1352; ×52. 6, RM Br136399, detail of ventral larval shell, sample 1352; ×1125. 7, 9, RM Br136398, conjoined valves in posterior and ventral views, sample 1352; both ×45.

Figs 8, 10–13. *Anabolotreta lepida* Koneva; Middle Cambrian, *Goniagnostus nathorsti* Biozone, Malyi Karatau Range, Kyrshabakty section, sample 1316. 8, 12, NMW 98.61G.85, dorsal valve exterior in oblique lateral and normal views; ×39, ×53. 10, NMW 98.61G.86, dorsal valve exterior of juvenile specimen; ×119. 11, IGNA, holotype, 427/349, ventral valve interior; ×21. 13, NMW 98.61G.87, dorsal valve exterior; ×43.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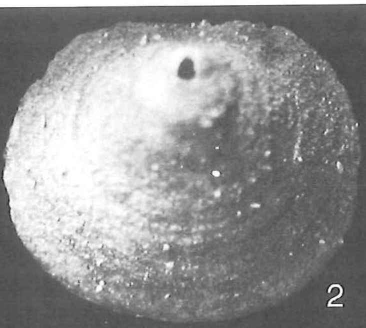
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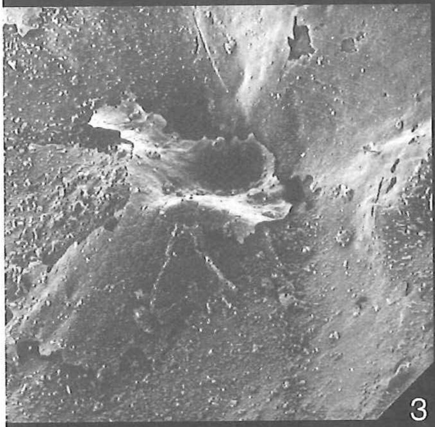
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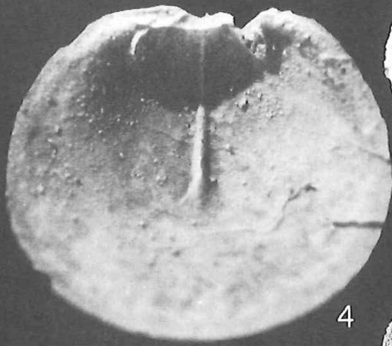
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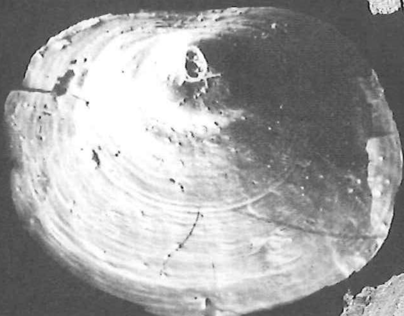
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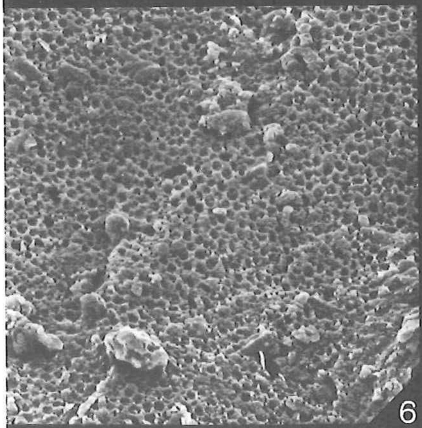
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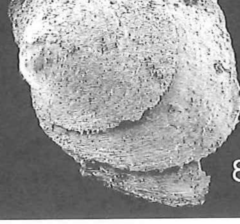
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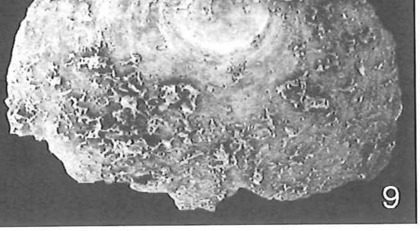
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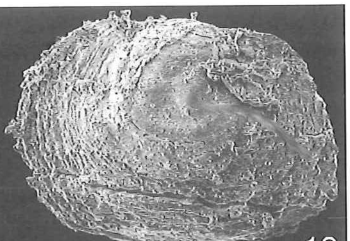
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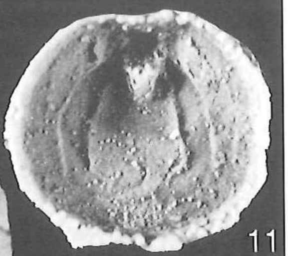
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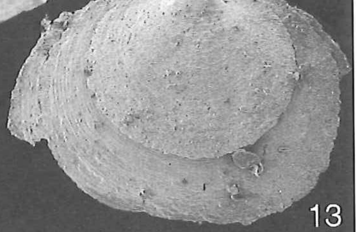
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HOLMER *et al.*, *Anabolotreta*, *Araktina*

Canthylotreta atasuica sp. nov.

Plate 22, figures 4–15

Derivation of name. After the Atasu River, close to the type locality.

Holotype. NMW 98.61G.104, ventral valve; Middle Cambrian (Mayaian)–Upper Cambrian; Sarykumy Formation (sample 135), Sarykumy section, Kazakhstan.

Material. 13 ventral and four dorsal valves.

Diagnosis. Shell slightly ventribiconvex, rounded subtriangular in outline with maximum width anterior to mid-length; ventral valve gently convex; ventral pseudointerarea low and narrow, weakly apsacline, occupying about one-third of valve width; dorsal interior with a moderately high, blade-like, triangular median septum extending forward to about two-thirds of the valve length.

Description. Slightly ventribiconvex. Ventral valve about 90 per cent as long as wide (Table 8) with maximum width between the anterior margin and the mid-valve length. Ventral profile gently convex with maximum thickness at about 33 per cent of length anterior to the umbo. Ventral pseudointerarea very narrow, occupying about 33 per cent of the valve width and divided by a narrow, shallow intertrough. Ventral beak pointed and slightly incurved. Pedicle foramen small, directed posteriorly, almost but not completely enclosed within larval shell. Dorsal valve about 90 per cent as long as wide with a narrow, shallow, dorsal sulcus originating in the umbonal area. Dorsal profile weakly convex with maximum thickness near the anterior boundary of the larval shell. Dorsal pseudointerarea narrow, about 35–45 per cent as wide as the valve, with a deep median groove and well-defined, narrow, flattened, slightly anacline propareas.

Ventral interior with strongly thickened, subtriangular apical process situated anterior to the internal pedicle foramen. Cardinal muscle fields relatively small, lobate, raised slightly above the valve floor and extending to about 35–40 per cent of the sagittal valve length from the umbo. Dorsal median septum triangular, thin, blade-like, occupying about 66 per cent of the valve length, with maximum height at about mid-valve length. Median buttress fine, elongate subtriangular in outline.

Remarks. *Canthylotreta atasuica* differs from the type species and from *C. grada* Zell and Rowell, 1988 in having a gently convex ventral valve with a low, narrow, ventral pseudointerarea, small and weakly impressed cardinal muscle scars in both valves, and in its triangular shell outline. It also differs from *C. marjumensis* (Walcott, 1905) in having a median buttress and in the weakly developed umbonal thickening of the shell inside the ventral valve.

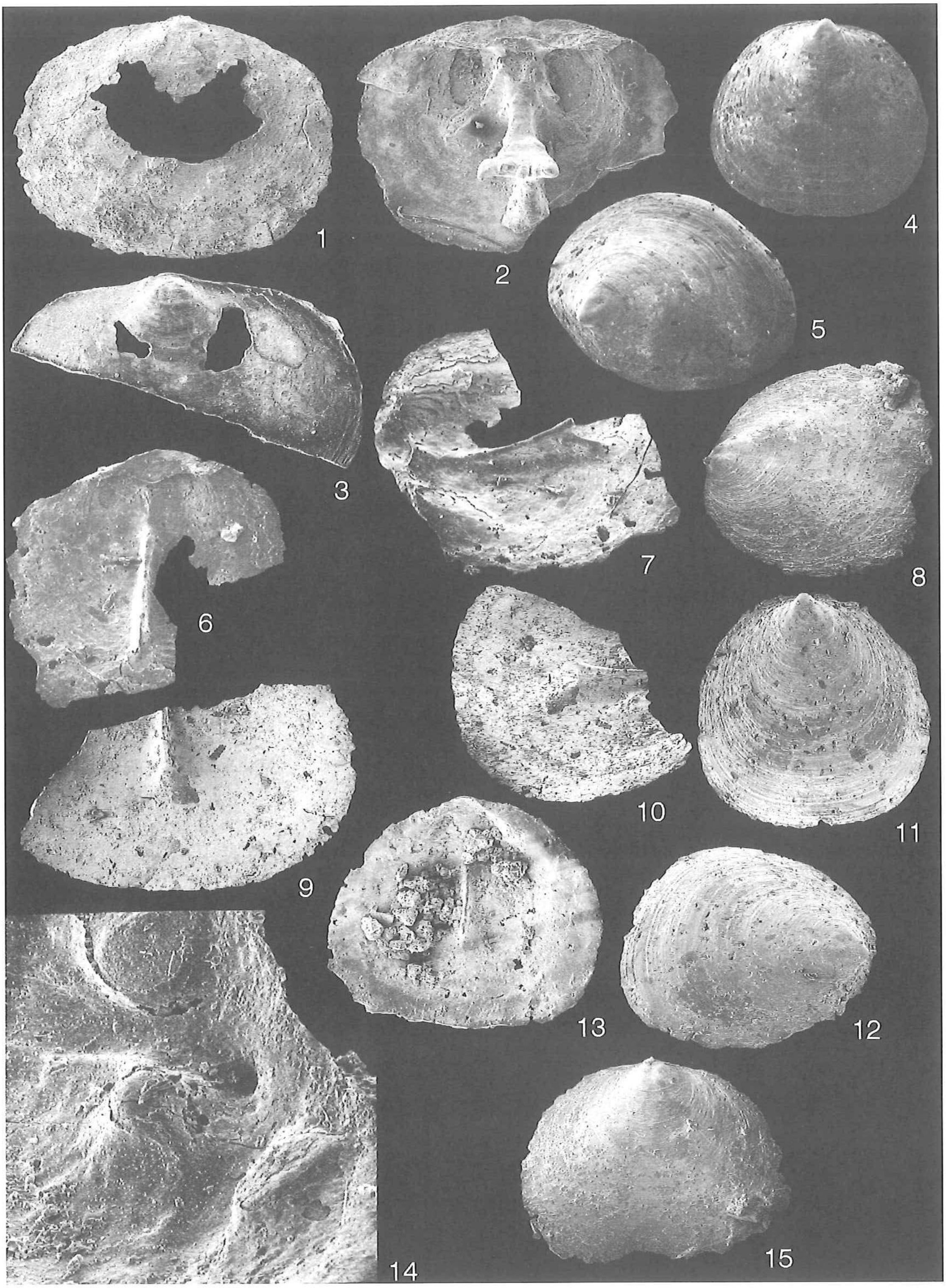
Occurrence. As for holotype.

EXPLANATION OF PLATE 22

Figs 1–3. *Angulotreta*? sp.; Upper Cambrian, *Eorudagnostus ovaliformis*-'*Pareuloma*' beds, Malyi Karatau, Kyrshabakty section, sample 1381. 1, NMW 98.61G.101, dorsal valve exterior; ×32. 2, NMW 98.61G.102, dorsal valve interior; ×25. 3, NMW 98.61G.103, dorsal valve exterior; ×40.

Figs 4–15. *Canthylotreta atasuica* sp. nov.; Middle–Upper Cambrian, Sarykumy Formation, Sarykumy section, sample 134. 4–5, NMW 98.61G.104, holotype, ventral valve exterior, and oblique posterior view; ×30, ×35. 6–7, NMW 98.61G.105, dorsal valve interior, and oblique lateral view; ×35, ×45. 8, 15, NMW 98.61G.106, dorsal valve exterior in oblique lateral and normal views, both ×48. 9–10, NMW 98.61G.107, incomplete dorsal valve interior, and oblique lateral view; ×42, ×40. 11–12, NMW 98.61G.108, ventral valve exterior in normal and oblique lateral views; ×45, ×47. 13, NMW 98.61G.109, dorsal valve interior; ×44. 14, NMW 98.61G.110, ventral valve interior showing apical process and cardinal muscle fields; ×76.

PLATE 22



HOLMER *et al.*, *Angulotreta*?, *Canthylotreta*

TABLE 8. *Canthylotreta atasuica* sp. nov., dimensional data for ventral valves from the Sarykumy section (sample 134, Middle Cambrian, Sarykumy Formation).

	Lv	W	T	Al	Aw	L/vW	T/Lv	Al/Lv
N	6	4	6	5	5	4	6	5
X	0·76	0·84	0·21	0·272	0·22	90%	27%	34%
S	0·185	0·256	0·064	0·07	0·068	6·2	3·7	7
MIN	0·52	0·58	0·16	0·18	0·14	83%	24%	25%
MAX	0·96	1·16	0·32	0·36	0·32	98%	33%	41%

Canthylotreta sp.

Text-figure 16

Material. One complete shell, three ventral and 11 dorsal valves.

Description. Shell ventribiconvex with subcircular to slightly transversely suboval outline, about 80–90 per cent as long as wide. Ventral valve convex with maximum thickness near the anterior margin of the larval shell. Lateral slopes evenly convex in profile. Ventral pseudointerarea procline, slightly incurved near the umbo, divided by deep intertrough. Pedicle foramen small, posteriorly directed, not completely enclosed within larval shell. Dorsal valve gently convex with weakly defined sulcus originating in the umbonal area. Dorsal pseudointerarea narrow, about 66 per cent as wide as the valve, with a broad concave median plate. Ventral interior with a strongly thickened, rounded subtriangular apical process slightly grooved beneath the internal foramen. Ventral cardinal muscle fields small, slightly thickened, situated on the posterolateral sides of the valve. Apical pits small, deeply impressed, situated lateral to the foramen. Dorsal interior with lobate cardinal muscle fields raised slightly above the valve floor, their anterior margins situated about 40 per cent of the sagittal valve length from the umbo. Triangular median septum thin, blade-like, about 75 per cent as long as the valve and 28–30 per cent as high as the maximum valve length, buttressed slightly posteriorly.

Dimensions. NMW 98.61G.333, ventral valve, L = 2·16, W = 2·88, Al = 0·72; NMW 98.61G.337, dorsal valve, L = 0·64, W = 0·82, Sa = 0·44; NMW 98.61G.335, dorsal valve, L = 1·72.

Remarks. This unnamed species is most similar to *Canthylotreta atasuica* sp. nov., but differs in having a higher and more blade-like dorsal median septum. Additionally, the shell outline of *Canthylotreta* sp. is somewhat different, being more subcircular to slightly transversely suboval; the material is, however, somewhat distorted.

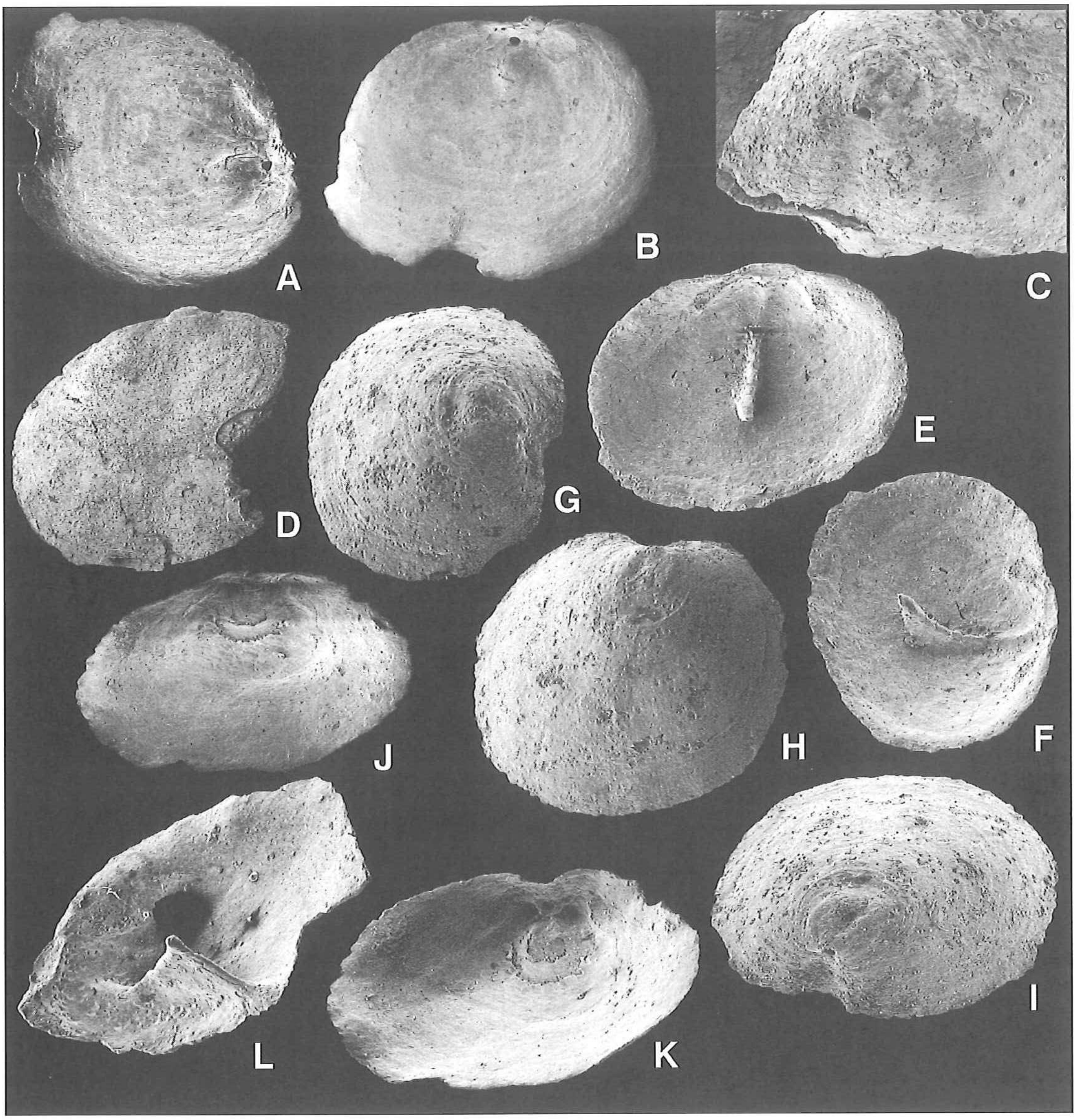
Occurrence. Middle Cambrian, Amgaian; Karagajly Formation of the Kostek Range, north Kyrgyzstan, sample 1639.

Genus DACTYLOTRETA Rowell and Henderson, 1978

Type species. Original designation by Rowell and Henderson (1978, p. 3); *Dactylotreta redunca* Rowell and Henderson, 1978; Upper Cambrian (Idamean Stage), Georgina Limestone; Glenormiston district, western Queensland, Australia.

Diagnosis. See Popov and Holmer 1994, p. 91.

Remarks. This geographically and stratigraphically widely distributed genus has been recorded recently from the upper Middle–lower Upper Cambrian of the San Juan Precordillera, western Argentina (Holmer *et al.* 1999), and from the Upper Cambrian of Kyrgyzstan (herein).



TEXT-FIG. 16. A–L, *Canthylotreta* sp., Middle Cambrian, Karagajly Formation, Kostek Range, sample 1639. A–B, NMW 98.61G.333, ventral valve, oblique lateral and normal views of interior; both ×16. C, NMW 98.61G.334, oblique posterior view of conjoined valves; ×67. D, NMW 98.61G.335, dorsal valve exterior; ×37. E–F, NMW 98.61G.337, dorsal valve, normal and oblique lateral views of interior; ×61. G–I, NMW 98.61G.336, ventral valve, oblique lateral, normal, and oblique posterior views of exterior; G–H, ×60; I, ×65. J–K, NMW 98.61G.339, ventral valve interior, normal view, ×40, and oblique anterior view, ×46. L, NMW 98.61G.338, oblique lateral view of dorsal interior showing triangular median septum; ×40.

Species included. Dactylotreta septata sp. nov., in addition to the species listed by Popov and Holmer 1994.

Occurrence. Upper Middle Cambrian–lower Ordovician (Tremadoc); USA (Great Basin, upper Dresbachian–lower Franconian); Greenland (upper Middle Cambrian); Sweden and Norway (Tremadoc); Kazakhstan and Kyrgyzstan

(Upper Cambrian); Russia (South Urals, Tremadoc); Australia (Queensland, Mindyallian–Iverian); West Antarctica (Idamean); Argentina (San Juan Precordillera, upper Middle–lower Upper Cambrian).

Dactylotreta septata sp. nov.

Plate 23, figures 1–18

Derivation of name. Latin *septatus*, a wall; alluding to the long dorsal median septum.

Holotype. NMW 98.61G.116, dorsal valve; Upper Cambrian, Sarykumy Formation; locality F-134, area about 4 km north-east of Sarykumy railway station, central Kazakhstan.

Material. 28 ventral and 21 dorsal valves.

Diagnosis. Ventral valve high conical, anterior slope gently concave in lateral profile and lateral slopes almost straight in transverse profile; intertrough shallow and narrow; dorsal median septum triangular, moderately high, blade-like, extending forward for about 75 per cent of the valve length.

Description. Ventral valve moderately high conical, about 80 per cent as high as long, with anterior slope gently and evenly concave in profile towards the apex, becoming straight or weakly convex towards the anterior commissure; lateral slopes near straight in transverse section. Ventral pseudointerarea catacline, weakly defined laterally, slightly concave in sagittal profile. Intertrough shallow and narrow. Pedicle foramen small, apical, posteriorly directed, situated within the larval shell. Dorsal valve flattened with gently convex, slightly transverse, umbonal area, subcircular in outline, about 90 per cent as long as wide (Table 9) with shallow dorsal sulcus originating in the umbonal area. Dorsal pseudointerarea low, triangular, occupying more than 50 per cent of the valve width, and with a median groove occupying more than half the width of the area.

Ventral interior dominated by the apical process, occluding the apex and perforated by the internal pedicle tube. Apical pits strongly impressed, directly posterolaterally to the internal foramen. Dorsal interior with moderately high, triangular, blade-like median septum, extending forward to about 75 per cent of the sagittal valve length (Table 9). Cardinal muscle scars weakly impressed, subcircular, bounded by a low rim and extending forward for an average of 40 per cent of the valve length (Table 9). Median buttress elongated subtriangular, narrowing anteriorly.

Remarks. Dactylotreta septata is most similar to *D. solitaria* Popov (*in* Solovjev *et al.* 1984) from the Middle Cambrian Nelson Formation of West Antarctica. Both species have a high, conical ventral valve with a well-defined intertrough; however, *D. septata* differs in its moderately high, blade-like dorsal

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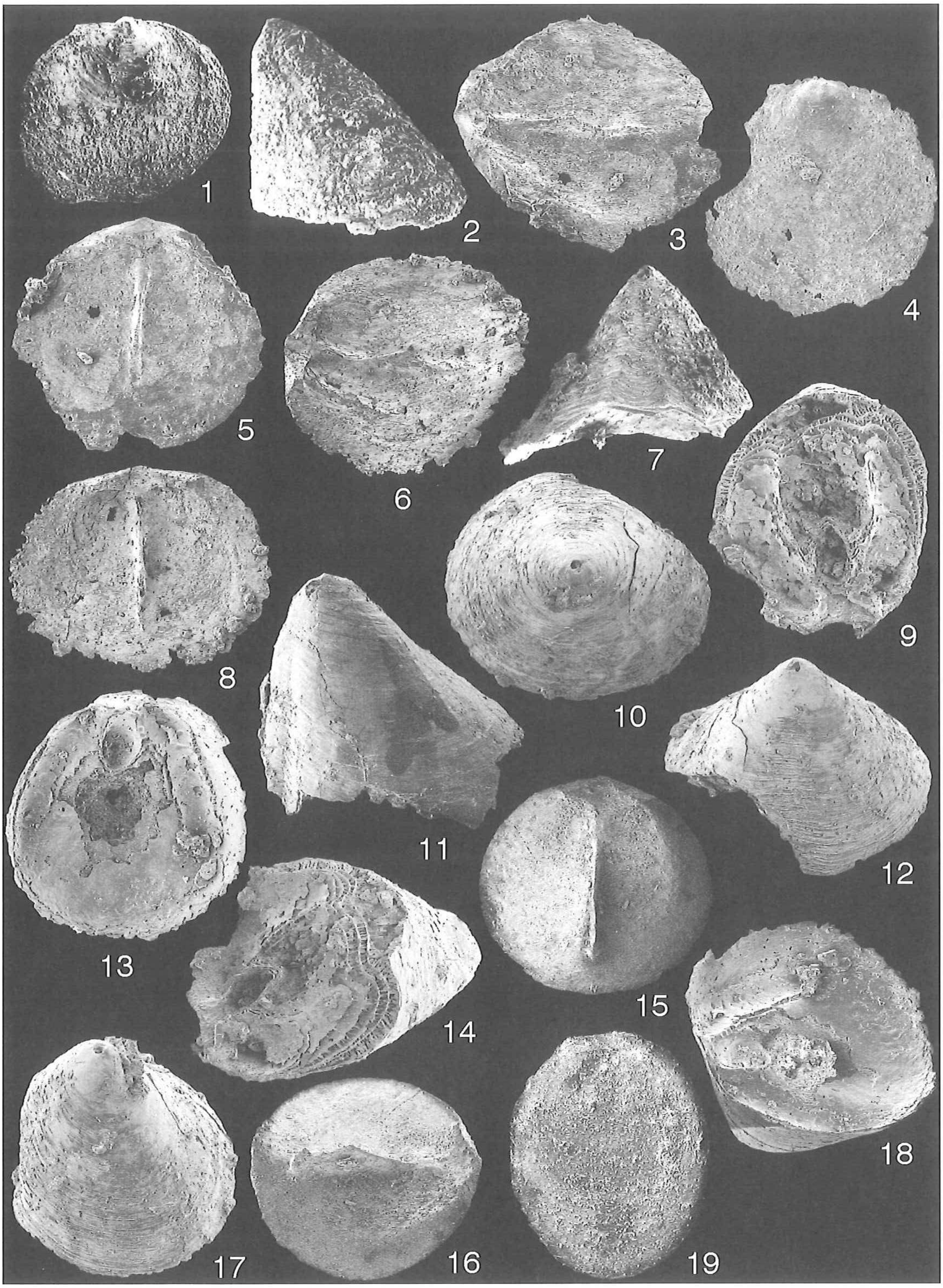
EXPLANATION OF PLATE 23

Figs 1–18. *Dactylotreta septata* sp. nov.; Middle–Upper Cambrian. 1–2, 15–16, Karadzhorga Formation, Moldotau Range, eastern side of Karakichi River, sample 127/9; 3–14, 17–18, Sarykumy Formation, Sarykumy section. 1, NMW 98.61G.112, dorsal valve exterior; ×30. 2. NMW 98.61G.113, ventral valve in lateral view; ×25. 3, 5, NMW 98.61G.114, dorsal valve interior in oblique lateral and normal views, sample 134; ×38, ×33. 4, NMW 98.61G.115, dorsal valve exterior, sample 134; ×40. 6, 8, NMW 98.61G.116, holotype, dorsal valve, oblique lateral and normal views of interior, sample 134; ×39, ×37. 7, NMW 98.61G.117, ventral valve, posterior view, sample 29; ×31. 9, 14, NMW 98.69G.11, incomplete ventral valve, interior showing apical process and internal foramen, and oblique lateral view, sample 134; ×60, ×63. 10, 12, 17, NMW 98.61G.119, ventral valve exterior, in oblique posterior and lateral views, sample 134; ×33. 11, NMW 98.61G.120, ventral valve, lateral view, sample 134; ×66. 13, 18, NMW 98.61G.121, incomplete ventral valve interior in normal and oblique lateral views, sample 134; both ×60. 15–16, NMW 98.61G.122, dorsal valve interior in normal and oblique lateral views; ×32, ×33.

Fig. 19. Obolidae gen. et sp. indet.; Ordovician, Kogashik Regional Stage, lower *Paroistodus proteus* Biozone, Malyi Karatau, Batyrbay section, sample 465 m; NMW 98.61G.123, dorsal valve exterior of juvenile specimen; ×29.

PLATE 23



HOLMER *et al.*, *Dactylotreta*, Obolidae indet.

TABLE 9. *Dactylotreta septata* sp. nov., dimensional data for dorsal valves from the Sarykumy section (sample 134, Middle Cambrian, Sarykumy Formation).

	Ld	W	Il	Iw	Pw	Cl	Cw	Sa	Sm	Ld/W	Iw/W	Pw/Iw	Cl/L	Cw/W	Sa/Ld	Sm/Ld
N	9	9	9	8	9	9	8	8	6	9	8	8	9	8	8	6
X	1·02	1·16	0·12	0·65	0·36	0·40	0·74	0·74	0·75	88%	56%	57%	40%	0·63%	72%	76%
S	0·117	0·163	0·025	0·076	0·053	0·051	0·104	0·139	0·076	5·9	7·0	5·7	4·1	5·4	10·9	6·8
MIN	0·82	0·9	0·08	0·48	0·28	0·34	0·52	0·52	0·64	76%	46%	47%	33%	56%	55%	66%
MAX	1·2	1·38	0·16	0·72	0·44	0·48	0·86	0·94	0·84	96%	64%	67%	46%	73%	87%	86%

median septum and slightly concave anterior ventral profile. *D. septata* is also similar to *D. partiella* Zell and Rowell, 1988, from the Middle Cambrian Holm Dal Formation of Greenland, in the convexity, sagittal profile and internal morphology of the ventral valve, but the ventral anterior slope of *D. septata* is only gently concave in the posterior half of the valve length and becomes gently convex towards the anterior margin. Additionally, the dorsal median septum in *D. septata* is somewhat shorter and higher by comparison with that in *D. partiella* and the maximum height is only slightly anterior to the mid-valve length.

Occurrence in Central Asia. Middle Cambrian (Mayaian)–Upper Cambrian; area about 4 km north-east of Sarykumy railway station, Sarykumy Formation, samples F104, 132, F-134, Moldotau Range, eastern side of Karakichi River, Karadzhorga Formation, sample 127/9, Kyrgyzstan.

Genus EURYTRETA Rowell, 1966

Type species. Original designation by Rowell (1966, p. 9); *Acrotreta curvata* Walcott, 1902; Lower Ordovician Pogonip Limestone; Eureka district (Walcott 1912, locality 203a), Nevada, USA.

Diagnosis. See Popov and Holmer 1994, p. 95, who also summarised current information on species assigned to the genus.

Eurytreta discors Popov, 1988

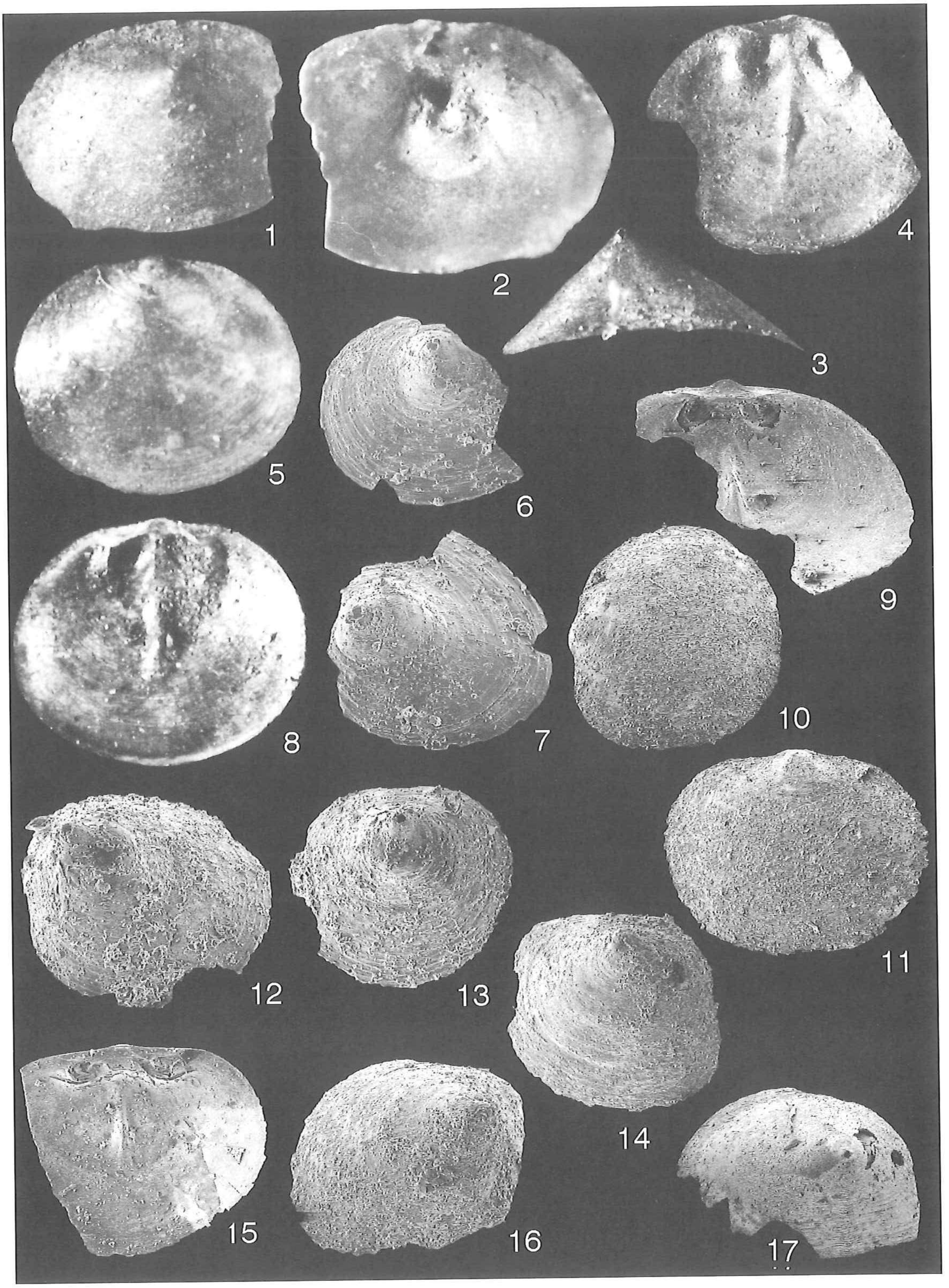
Plate 24, figures 1–8

1988 *Eurytreta discors* Popov, *in* Koneva and Popov, p. 59, pl. 2, figs 1–3.

EXPLANATION OF PLATE 24

Figs 1–8. *Eurytreta discors* Popov; Upper Cambrian, Shabakty Group, *Eoconodontus alisonae* Biozone, Malyi Karatau, Batyrbay section. 1–3, CNIGR 10/12034, holotype, ventral valve, exterior, interior, posterior view, sample 98 m; ×26, ×30, ×30. 4, CNIGR 11/12034, dorsal valve interior, sample 98 m; ×20. 5, 8, CNIGR 12/12034, dorsal valve exterior and interior, sample 98 m; both ×30. 6–7, NMW 98.61G.124, ventral valve exterior in normal and oblique lateral views, sample 101 m; ×49, ×61.

Figs 9–17. *Eurytreta sublata* Popov; Upper Cambrian, *Cordylodus proavus* Biozone, Malyi Karatau, Batyrbay section. 9, NMW 98.61G.125, dorsal valve interior, sample 117 m; ×39. 10–11, NMW 98.61G.126, dorsal valve exterior in oblique lateral and normal views, sample 1448; ×43, ×48. 12–13, NMW 98.61G.127, ventral valve exterior in oblique lateral and normal views, sample 136; ×63, ×53. 14, 16, NMW 98.61G.128, ventral valve exterior in normal and oblique lateral views, sample 1448; ×38, ×43. 15, NMW 98.61G.129, dorsal valve interior, sample 136; ×26. 17, NMW 98.61G.130, ventral valve exterior, oblique posterior view, sample 117 m; ×27.



HOLMER *et al.*, *Eurytreta*

Holotype. CNIGR 10/12034, ventral valve (L 1·06, W 1·39, T 0·56); Upper Cambrian (*Harpidoides-Platypeltoides* beds); Batyrbay section (98 m), Malyi Karatau.

Material. Five ventral and four dorsal valves.

Diagnosis. Ventral valve about half as high as long, with maximum height at umbo; ventral pseudointerarea procline, with interridge; apical process subtriangular, grooved posteriorly, surrounding internal foramen; median buttress elongated subtriangular.

Description. Valves slightly transversely oval in outline, about 85–95 per cent as long as wide. Ventral valve conical, about 50–55 per cent as high as long, with maximum height at the umbo. Ventral pseudointerarea weakly procline, bisected by a low interridge, slightly incurved in sagittal section. Anterior and lateral slopes of ventral valve almost straight in cross section. Dorsal valve gently convex with maximum thickness about mid way between the umbo and mid-valve length. Dorsal sulcus shallow, originating in the umbonal area. Dorsal pseudointerarea low, about half as wide as the valve, divided by a broad, lens-shaped median groove.

Ventral interior with a posteriorly grooved, subtriangular apical process, not enclosing the internal foramen. Dorsal median ridge subtriangular, extending forward for about 60–75 per cent of the maximum valve length. Median buttress elongate subtriangular. Dorsal cardinal muscle scars small, slightly elongate suboval, raised above the valve floor and bounded by a rim, extending forward for about 35 per cent of the valve length from the umbo.

Measurements of specimens from Batyrbay were given by Koneva and Popov (1988).

Remarks. *Eurytreta discors* is the oldest known species of *Eurytreta*, and in the Batyrbay section it is replaced in the overlying *Euloma-Leiostegium* beds by *E. sublata*. Both species are very similar in external morphology and size of the valves, but the former is distinguished by its more procline ventral pseudointerarea, the elongated subtriangular median buttress, and the grooved subtriangular apical process that does not enclose the pedicle foramen.

Occurrence in Kazakhstan. Upper Cambrian (upper *Harpidoides-Platypeltoides* beds), Malyi Karatau, Batyrbay section, sample 98 m.

Eurytreta sublata Popov, 1988

Plate 24, figures 9–17; Plate 25, figures 1–2, 4

1988 *Eurytreta sublata* Popov, *in* Koneva and Popov, p. 60, pl. 2, figs 4–8; pl. 3, fig. 11; text-fig. 3.

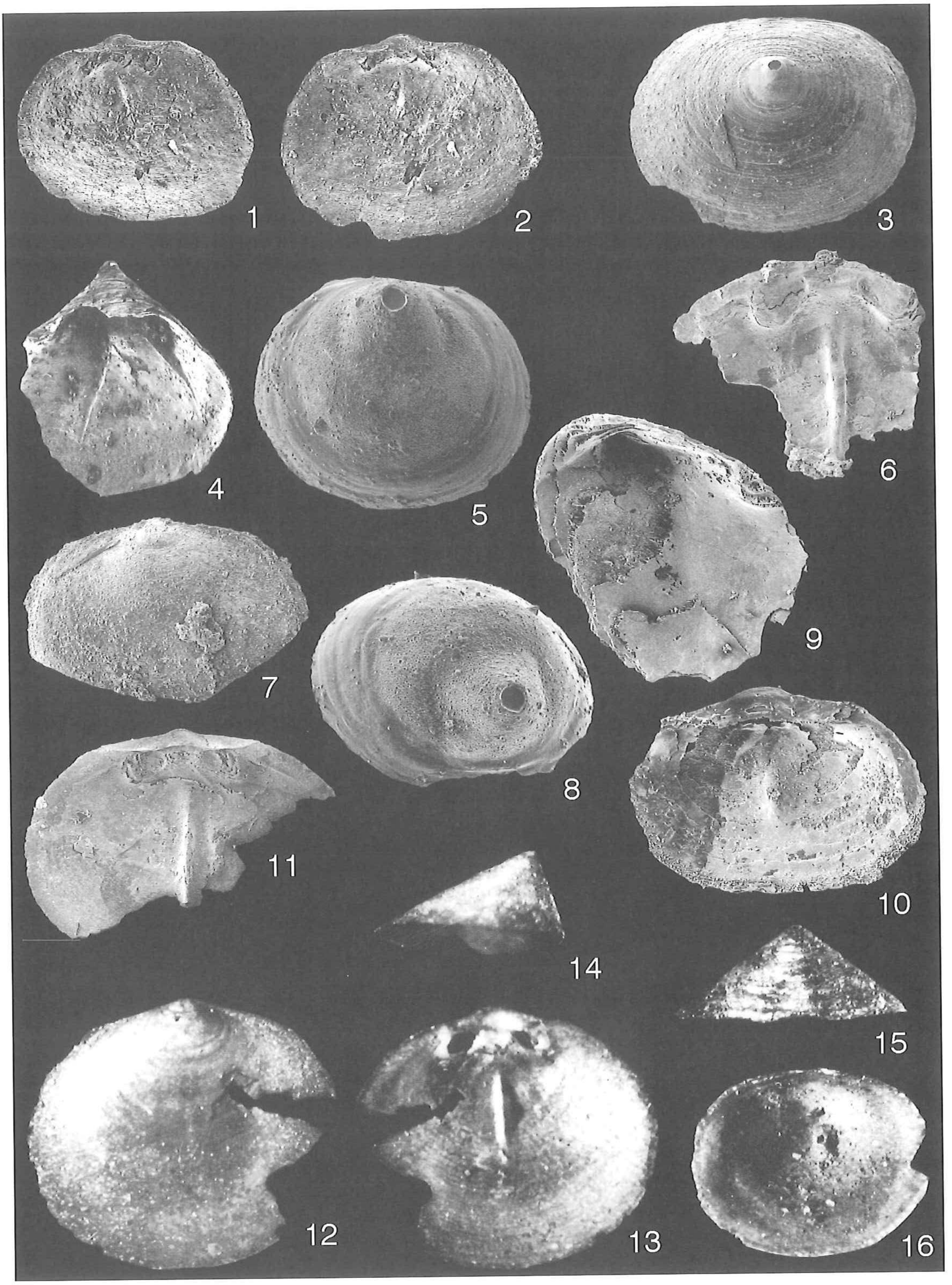
Holotype. CNIGR 13/12034, dorsal valve; figured by Koneva and Popov (1988, pl. 2, fig. 6); Upper Cambrian (*Euloma-Leiostegium* beds); Malyi Karatau, Batyrbay section (131 m).

EXPLANATION OF PLATE 25

Figs 1–2, 4. *Eurytreta sublata* Popov; Upper Cambrian, *Cordylodus proavus* Biozone, Malyi Karatau, Batyrbay section. 1–2, NMW 98.61G.131, dorsal valve interior in oblique lateral and normal views, sample 1448; both ×32. 4, NMW 98.61G.132, ventral valve interior, sample 1441-3; ×24.

Figs 3, 5–11. *Eurytreta* cf. *bisecta* (Matthew); Upper Cambrian–Ordovician, *Cordylodus intermedius–Cordylodus lindstroemi* biozones, Malyi Karatau, Batyrbay section. 3, NMW 98.61G.133, ventral valve exterior, sample 185 m; ×46. 5, 8, NMW 98.61G.134, ventral valve exterior of juvenile specimen in normal and oblique posterior views, sample 198 m; ×162, ×170. 6, NMW 98.61G.135, dorsal valve interior, sample 221 m; ×32. 7, NMW 98.61G.341, dorsal valve exterior, sample 210 m; ×56. 9, NMW 98.61G.136, ventral valve interior; ×56. 10, NMW 98.61G.137, dorsal valve interior of juvenile specimen, sample 198 m; ×86. 11, NMW 98.61G.138, dorsal valve interior, sample 191 m; ×32.

Figs 12–16. *Ottenbyella evanda* (Popov); Ordovician, *Szechuanella-Apatokephalus* beds, Malyi Karatau, Batyrbay section, sample 383 m. 12–13, CNIGR 19/12034, dorsal valve exterior and interior; both ×30. 14–16, CNIGR 20/12034, ventral valve exterior in lateral and posterior views, interior; all ×20.



HOLMER *et al.*, *Eurytreta*, *Ottenbyella*

Material. 26 ventral and 18 dorsal valves.

Diagnosis. Ventral valve about half as thick as long with maximum thickness at umbo; ventral pseudointerarea usually catacline, with interridge; apical process subtriangular, directly anterior to internal foramen; median buttress high, transversely subrectangular.

Description. Shell slightly transversely oval in outline, about 85 per cent as long as wide. Ventral valve conical, about 50–55 per cent as thick as long, with the maximum thickness at about the umbonal area. Ventral pseudointerarea catacline, more rarely weakly procline, divided by an interridge. Ventral anterior and lateral slopes almost straight in cross section. Dorsal valve gently convex with the maximum thickness at about mid way between the umbo and mid-valve length. Dorsal sulcus poorly defined. Dorsal pseudointerarea low, occupying about 50 per cent of the valve width, divided by a median groove.

Ventral interior with a slightly elongate subtriangular apical process, situated anterior to the internal foramen. Dorsal median ridge high, subtriangular, with the highest point near mid-valve, and extending forward for about 66 per cent of the sagittal valve length from the umbo. Median buttress high, transversely subrectangular in outline. Dorsal cardinal muscle scars elongate suboval, slightly raised and bounded by a high rim.

Dimensions of specimens from Batyrbay were given by Koneva and Popov (1988).

Remarks. Eurytreta sublata differs from *E.* cf. *bisecta* (Matthew, 1901), which occurs in the overlying *Dikelokephalina* and *Szechuanella-Apatokephalus* beds, in having a relatively short median ridge and a narrow, triangular apical process. The ventral pseudointerarea of *E. sublata* is invariably bisected by a low, narrow intertrough, whereas in *E.* cf. *bisecta* an interridge is weakly developed or absent. According to Rushton and Bassett (*in* Owens *et al.* 1982) this character of the ventral pseudointerarea is variably developed in British specimens of *bisecta.*

E. sublata is somewhat comparable with *E. sabrinae* (Callaway, 1877), as well as with specimens of *E.* cf. *sabrinae* described and illustrated by Popov and Holmer (1994), in the external morphology of both valves, and in having a relatively short dorsal median ridge. The most distinctive features of *E. sublata* are: its less transverse outline (about 85 per cent as long as wide in *E. sublata* and 75–80 per cent in *E. sabrinae*); the presence of a low, narrow interridge instead of a weak intertrough or undivided ventral pseudointerarea as in *E. sabrinae*; straight ventral lateral slopes; a strong, narrow, subtriangular apical process; and more widely spaced dorsal, cardinal muscle scars.

Occurrence. Upper Cambrian (*Cordylodus proavus* Biozone), Malyi Karatau, Batyrbay section, samples 116, 117 m, 127 m, 131 m, 141 m. Upper Cambrian (*Cordylodus proavus* Biozone), Utah (Lawson Cove), USA.

Eurytreta cf. *bisecta* (Matthew, 1901)

Plate 25, figures 3, 5–11

cf. 1901	*Eurytreta bisecta* Matthew, p. 275, pl. 5, figs 5a–g.
cf. 1982	*Eurytreta bisecta* (Mathew, 1901); Rushton and Bassett, *in* Owens *et al.* p. 24, pl. 7h, j–r; pl. 8i, l–q (with synonymy).
1994	*Eurytreta* cf. *bisecta* (Matthew, 1901); Holmer and Popov, p. 106, figs 86G–H (with synonymy).

Material. 13 ventral and 32 dorsal valves.

Remarks. Rushton and Bassett (*in* Owens *et al.* 1982) gave a detailed description of *Eurytreta bisecta* and re-illustrated the lectotype from the Lower Ordovician McLeod Brook Formation of Cape Breton, Canada. Popov and Holmer (1994) referred to the fact that several acrotretide species described by Walcott (1912), Moberg and Segerberg (1906), and Poulsen (1922) from the 'Dictyonema' Shale of Sweden and Bornholm, Denmark are probably conspecific with *E. bisecta*. The specimens from the *Dikelokephalina* and *Szechuanella-Apatokephalus* beds of the Kyrshabakty section are closely comparable with *E. bisecta* in general shell shape and morphology, as well as in having a strong, broadly triangular apical process anterior to the pedicle foramen. However, as noted by Popov and Holmer (1994), there is a considerable problem in comparing the type material of *E. bisecta*, which is preserved as moulds or distorted shells in shale, with the etched shells from the Batyrbay section.

Dimensions. NMW 98.61G.133, ventral valve, L = 0·82, W = 1·14; NMW 98.61G.341, dorsal valve, W = 1·42.

Occurrence. Lower Ordovician (*Dikelokephalina* and *Szechuanella-Apatokephalus* beds), Batyrbay, Kazakhstan; samples 185, 191, 196, 206, 209–211, 214, 221, 235 m. Cambrian/Ordovician boundary beds, Utah (Lawson Cove), USA.

Eurytreta minor Biernat, 1973

Plate 26, figures 1–10

1973 *Eurytreta minor* Biernat, p. 74, pl. 9, figs 1–6; fig. 26.
1988 *Eurytreta*(?) *exigua* Popov, *in* Koneva and Popov, p. 64, pl. 3, figs 3–10.
1994 *Eurytreta minor* Biernat, 1973; Popov and Holmer, p. 100, fig. 84 (with full synonymy).

Holotype. Bp XV/16n; ventral valve; Lower Ordovician (Tremadoc) chalcedonites; Wysoczki, Holy Cross Mountains, Poland.

Material. 45 ventral and 17 dorsal valves.

Diagnosis. See Popov and Holmer (1994, p. 100).

Description of material from Kazakhstan. Shell transversely oval, about 80 per cent as long as wide. Ventral valve conical, about 66 per cent as thick as long with maximum thickness at the umbo. Anterior and lateral valve slopes gently and evenly convex in profile. Ventral pseudointerarea procline, poorly defined laterally. Pedicle foramen small, rounded, situated at the end of a short external pedicle tube. Dorsal valve gently convex, somewhat less than 20 per cent as thick as long, with maximum thickness between the umbo and mid-valve length. Dorsal pseudointerarea short and narrow, occupying somewhat more than 50 per cent of the maximum valve width. Median groove wide, concave, occupying about 50 per cent of the width of the pseudointerarea. Larval shell finely pitted with subcircular and oval pits of two sizes.

Ventral interior with vestigial apical process, perforated posteriorly by a short internal pedicle tube and extending anteriorly as a short, thickened ridge. Dorsal interior with a very low median ridge, slightly thickened anteriorly and buttressed posteriorly. Dorsal cardinal muscle scars small, subcircular, bounded by a low rim and extending forward for about 40 per cent of the valve length.

For measurements of specimens from Batyrbay, see Koneva and Popov (1988, p. 65).

Remarks. *Eurytreta*? *exigua* Popov, *in* Koneva and Popov, 1988, was referred to *Akmolina* by Popov and Holmer (1994); however, our new Kazakhstanian material is more or less identical with the Polish *E. minor* in all major characters, such as the outline, convexity and morphology of the pseudointerarea of both valves, and the very faint median ridge that originates at a small distance from the pseudointerarea. A more detailed comparative discussion is given by Popov and Holmer (1994).

Occurrence in Kazakhstan. Batyrbay section, *Szechuanella-Apatokephalus* beds (433 m), *Nileus* beds (465 m).

Genus PROTOTRETA Bell, 1938

Type species. Original designation by Bell (1938, p. 405); *Prototreta trapeza* Bell, 1938; Middle Cambrian, Meagher Limestone (*Bathyuriscus* Biozone), Montana, USA.

Remarks. Popov *et al.* (1996) discussed the nature and affinities of *Prototreta*. It is likely that in its present concept the genus is heterogeneous and includes several different groups of species, but precise definition is impossible without a revision of the types of both *Prototreta* and *Homotreta* (see further below) as well as some other American and Siberian Lower–Middle Cambrian species that are usually assigned to these genera (e.g. Bell 1941; Pelman 1977, 1983). We have also noted the presence of *Prototreta* in samples from the Middle Cambrian of the San Juan Precordillera, western Argentina (currently under study).

Occurrence. ?Lower Cambrian–Middle Cambrian; USA (Montana, Utah, upper Middle Cambrian); Greenland (upper Middle Cambrian); ?Germany (Lower Cambrian); Novaya Zemlya, Altai and ?Siberia (Mayaian); Kazakhstan (?Lower–Middle Cambrian); western Argentina (Precordillera, Middle Cambrian); ?China; ?West Antarctica.

Prototreta venusta Koneva, 1990

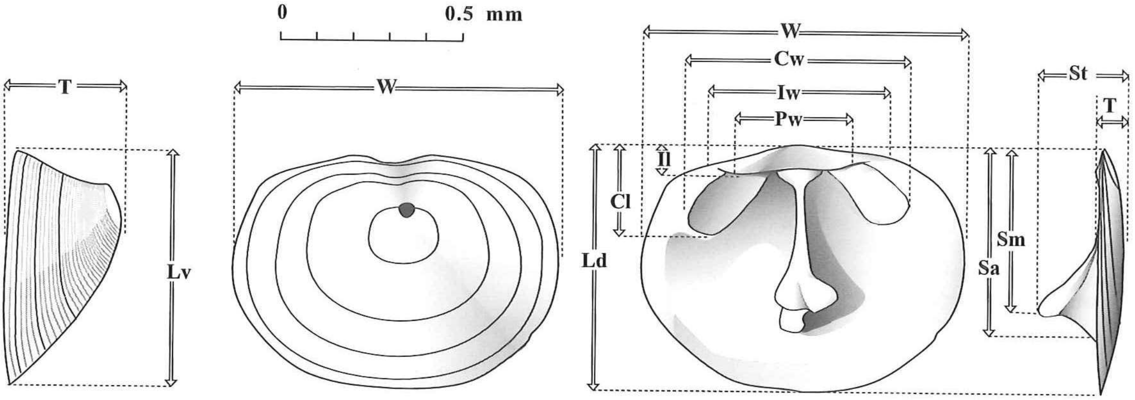
Plate 30, figures 15–17; Plate 32, figures 1–11; Text-figure 17

1990 *Prototreta venusta* Koneva, p. 47, pl. 5, figs 1–8.

Holotype. IGNA 427/187, ventral valve; Middle Cambrian (Amgaian, *Ptychagnostus intermedius* Biozone); Kyrshabakty section, Malyi Karatau.

Material. One complete shell, 120 ventral and 97 dorsal valves.

Diagnosis. Ventral valve low conical, about half as thick as long with maximum thickness at umbo; ventral pseudointerarea procline; dorsal pseudointerarea moderately short, occupying more than one-half of valve width; apical process broad, somewhat ridge-like; dorsal median septum moderately high, sometimes with triangular surmounting plate, or with single upper septal rod; median buttress not well developed; dorsal cardinal muscle poorly defined.



TEXT-FIG. 17. *Prototreta venusta* Koneva. From left to right: lateral profile of ventral valve; ventral exterior; dorsal interior; lateral profile of dorsal interior showing morphology of the septum. Measured parameters as in Tables 16–17.

TABLE 10. *Prototreta venusta* Koneva, dimensional data for ventral valves from the Kyrshabakty section (sample 1314-2, Middle Cambrian, *Ptychagnostus intermedius* Biozone).

	Lv	W	T	Lv/W	T/Lv
N	30	30	30	30	30
X	0·68	0·88	0·35	77%	52%
S	0·091	0·130	0·057	4·7	5·7
MIN	0·52	0·66	0·26	69%	42%
MAX	0·88	1·28	0·48	86%	66%

Table 11. *Prototreta venusta* Koneva, dimensional data for dorsal valves from the Kyrshabakty section (sample 1314-2, Middle Cambrian, *Ptychagnostus intermedius* Biozone).

	Ld	W	T	Il	Iw	Pw	Cl	Cw	Sa	Sm	St	L/W	T/L	Iw/W	Pw/Iw	Cl/L	Cw/W	Sa/L	Sm/L	St/L
N	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	28
X	0·68	0·87	0·15	0·08	0·47	0·23	0·27	0·56	0·53	0·48	0·29	78%	22%	54%	50%	40%	65%	77%	72%	41%
S	0·128	0·156	0·021	0·024	0·095	0·067	0·055	0·088	0·108	0·086	0·081	3·7	2·6	9·3	8·6	4·7	6·9	6	6·7	7·3
MIN	0·48	0·62	0·12	0·04	0·24	0·12	0·14	0·42	0·34	0·32	0·14	72%	16%	39%	29%	27%	51%	64%	58%	29%
MAX	0·97	1·2	0·2	0·16	0·7	0·4	0·38	0·76	0·78	0·66	0·46	85%	27%	77%	62%	49%	83%	88%	84%	53%

Description. Shell ventribiconvex, transversely suboval in outline, about 75–80 per cent as long as wide (Tables 10–11). Ventral valve low conical, about 50 per cent as thick as long (Table 10), maximum thickness at the umbo. Ventral pseudointerarea poorly defined, procline, divided by an intertrough, with incurved posterior margin. Pedicle foramen subcircular, directed posteriorly and not enclosed within the larval shell. Dorsal valve moderately convex, about 20 per cent as thick as long (Table 11). Dorsal pseudointerarea moderately short, somewhat anacline, occupying about 55 per cent of the valve width (Table 11). Median groove poorly defined, shallow, broad, triangular.

Internal pedicle tube along the posterior slope of the valve, supported anteriorly by a broad, somewhat ridge-like apical process. Apical pits posterolateral to foramen. Dorsal median septum moderately high, sometimes with platform, extending forward for an average 70 per cent of the valve length, with a single upper septal rod. Maximum height of septum about 70 per cent of valve length. Median buttress not well developed, narrow, elongate, short. Dorsal cardinal muscle scars poorly defined, extending forward for an average of 40 per cent of valve length, and occupying about 65 per cent of the valve width.

Remarks. The most characteristic feature of *Prototreta venusta* is the dorsal median septum, which in most specimens has a triangular, non-digitate surmounting plate. A similar type of septum occurs also in *P. convexa* Aksarina, *in* Aksarina and Pelman 1978 from the Mayaian of Kuznetskii Alatau, south-western Siberia, and in *P. gribovensis* Popov, 1985 from the Mayaian of Novaya Zemlya. However, by comparison with both of these species, *P. venusta* has a much lower conical ventral valve with a procline pseudointerarea.

Occurrence in Kazakhstan. Middle Cambrian, Amgaian, *Peronopsis ultimus* and *Ptychagnostus intermedius* biozones, samples 1467, 1467-1, 1465, 1465-1, 1313, 1314, 1314-2.

Genus HOMOTRETA Bell, 1941

Type species. Original designation by Bell (1941, p. 230); *Homotreta interrupta* Bell, 1941; Middle Cambrian Pagoda Limestone, Montana, USA.

Remarks. Homotreta has been considered generally to be a junior synonym of *Prototreta* Bell, 1938 (e.g. Rowell 1965; see also above). However, Pelman (1973, 1977) resurrected the genus to include a group of poorly understood *Prototreta*-like species from Lower and Middle Cambrian rocks of Siberia. It is possible that the type species, *H. interrupta*, and the forms assigned by Pelman (1977) to *Homotreta* (e.g. *H. salancaniensis* and *H. gorjanskii*) differ from the type species of *Prototreta* in having a shorter, less well-developed dorsal pseudointerarea and a shorter dorsal median septum, which generally appears to be more simple and blade-like (see also Popov *et al.* 1996).

'Homotreta' sp.

Plate 27, figures 1–12

Material. Two ventral and four dorsal valves.

Description. Shell ventribiconvex, elongate to transversely suboval. Ventral valve low convex to obtusely conical, about 33 per cent as thick as long with maximum thickness at the umbo. Anterior slope of ventral valve flattened, gently convex in profile; ventral posterior slope gently concave. Ventral pseudointerarea narrow, triangular, procline, divided by intertrough. Pedicle foramen small, subcircular, directed posteriorly, not enclosed within larval shell. Dorsal valve flattened. Dorsal pseudointerarea short, weakly anacline, occupying more than 50 per cent of the valve width; median groove broad, triangular.

Internal pedicle tube along posterior slope of valve, supported anteriorly by a high, ridge-like apical process, widening to form muscle platform. Apical pits posterolateral to foramen. Dorsal median septum low, blade-like, triangular, extending forward for about 70 per cent of valve length, with single upper septal rod. Median buttress not well developed, short. Dorsal cardinal muscle scars poorly defined, short, extending forward for about 20 per cent of valve length.

Dimensions. NMW 98.61G.185, ventral valve, L = 2·80, T = 0·90; NMW 98.61G.186, dorsal valve, L = 3·20, W = 2·88, Il = 0·32, Iw = 1·68, Sa = 2·44, Cl = 0·78, Cw = 1·32; NMW 98.61G.188, dorsal valve, L = 1·20, W = 1·50, Il = 0·14, Iw = 0·84, Sa = 0·92, Cl = 0·40, Cw = 0·82.

Remarks. These specimens from Kyrgyzstan (North Tien Shan) are somewhat similar to *'Homotreta' salancaniensis* Pelman, 1977 from the Middle Cambrian of Central Siberia, which is also characterized by a procline, moderately conical ventral valve, a distinctive, transverse apical process with a steep and almost straight posterior slope, as well as a low, ridge-like dorsal median septum, but the Kyrgyzstanian specimens are strongly distorted, which makes precise comparison difficult. In addition *'Homotreta' salancaniensis* itself is poorly understood and has never been revised from well-preserved material, so cannot be compared in any detail.

Occurrence in Kyrgyzstan. Middle Cambrian (Amgaian, Karagajly Formation), Kostek Range, sample 1639.

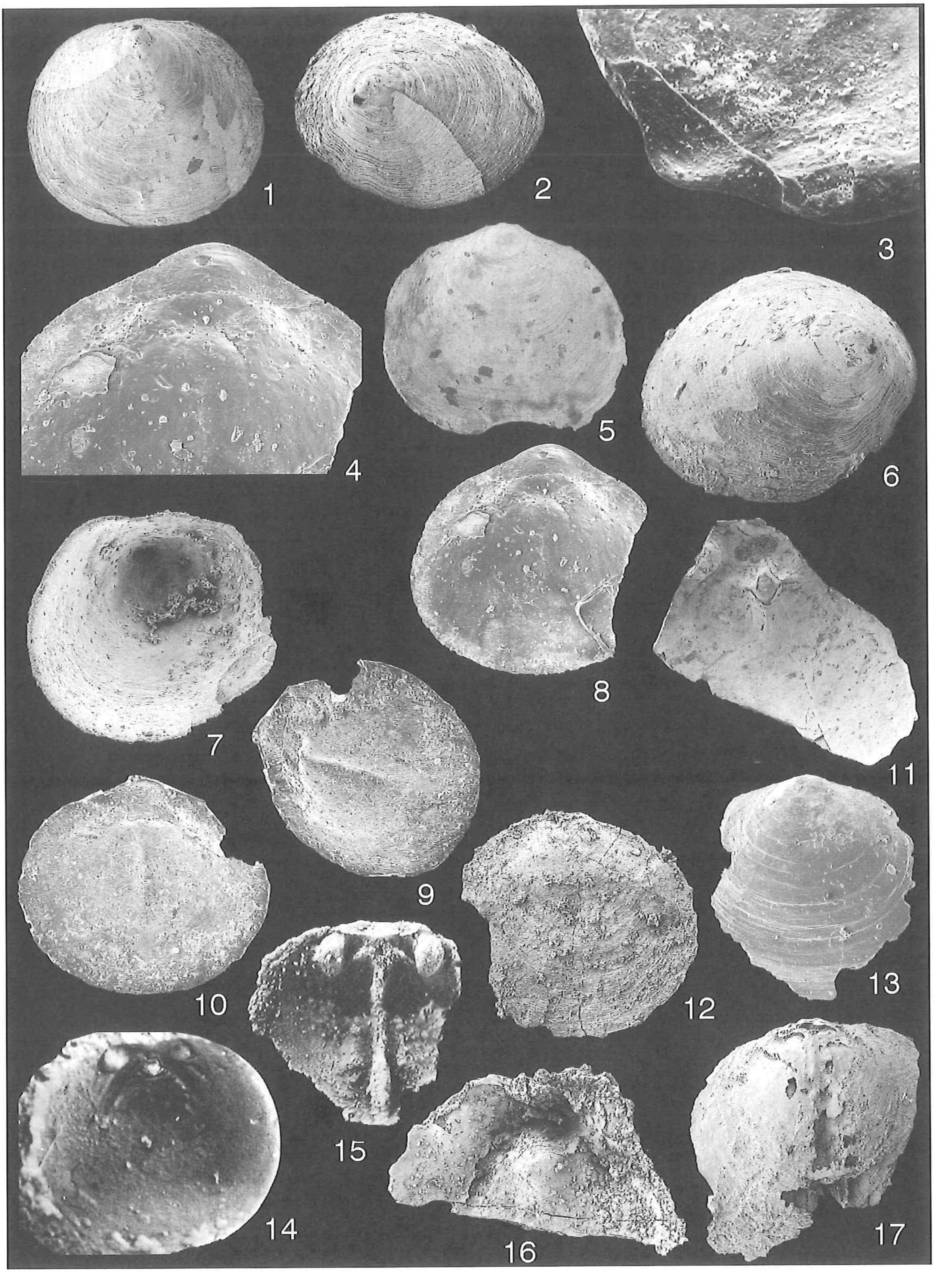
Genus LINNARSSONIA Walcott, 1885

1885	*Linnarssonia* Walcott, p. 115.
?1941	*Pegmatreta* Bell, p. 231.

EXPLANATION OF PLATE 26

Figs 1–10. *Eurytreta minor* Biernat; Ordovician, *Drepanoistodus proteus* Biozone, Batyrbay section, sample 465 m. 1–2, NMW 98.61G.139, ventral valve exterior in normal and oblique posterior views; ×44, ×47. 3, CNIGR 12034, dorsal valve, oblique posterior view of pseudointerarea; ×75. 4, 8, NMW 98.61G.141, dorsal valve, detail of pseudointerarea, and interior; ×96, ×60. 6, NMW 98.61G.142, ventral valve exterior, oblique lateral view; ×54. 9–10, NMW 98.61G.140, dorsal valve interior in oblique lateral and normal views; both ×37.

Figs 11–17. *Linnarssonia ophirensis* (Walcott); Middle Cambrian. 11, 13–15 *Lejopyge armata* Biozone, Malyi Karatau, Kyrshabakty section; 12, 16–17, Sarykumy Formation, Sarykumy section. 11, NMW 98.61G.143, incomplete ventral valve interior showing apical process, sample 1347-II; ×24. 12, NMW 98.61G.144, dorsal valve exterior, sample K-20/29; ×45. 13, NMW 98.61G.145, dorsal valve exterior, sample 1347-6; ×56. 14, IGNA 427/527, ventral valve interior, *Lejopyge armata* Biozone, sample 1346-10; ×13. 15, IGNA 427/526, incomplete dorsal valve interior, *Lejopyge armata* Biozone, sample 1346-6; ×18. 16, NMW 98.61G.146, incomplete ventral valve interior, sample K-20/29; ×40. 17, NMW 98.61G.147, incomplete exfoliated dorsal valve, sample K-20/29; ×39.



HOLMER *et al*., *Eurytreta*, *Linnarssonia*

Type species. Original designation by Walcott (1885, p. 115); *Obolella transversa* Hartt, *in* Dawson, 1868; Middle Cambrian of New Brunswick, Canada.

Diagnosis. Shell subcircular to transversely oval with short, convex posterior margin; ventral valve convex to low subconical; ventral pseudointerarea catacline to procline, rarely apsacline, with intertrough; foramen not enclosed within larval shell; dorsal valve gently convex with vestigial, undivided pseudointerarea; apical process high, boss-like, anterior to foramen; dorsal interior with high median ridge and median buttress; antero-central scars well defined.

Remarks. *Linnarssonia* is a very difficult genus to understand taxonomically, as noted by several previous authors (see summary in Rowell 1966). This is partly because the type species is known only from poorly preserved material (Rowell 1966), but also because the genus appears to incorporate very morphologically variable species. As presently best understood (Rowell and Henderson 1978) it is characterized mainly by its biconvex shell and high, boss-like apical process. Rowell (1966) considered *Pegmatreta* Bell as a junior synonym to *Linnarssonia*, whereas Rowell and Henderson (1978) then proposed that *Pegmatreta* could be used for *Linnarssonia*-like taxa with a comparatively lower apical process and lower cardinal muscle scars. As noted by Rowell and Henderson (1978), both genera are in need of revision based on the type species, which is outside the scope of this work. Here we use *Linnarssonia* provisionally in a wide sense to include also forms with a somewhat lower apical process and cardinal muscle scars.

Occurrence in Central Asia and Siberia. Middle Cambrian, Amgaian, *Pseudoanamocarina* beds of the Fergana Valley, Uzbekistan; Lower Cambrian, *Hebidiscus orientalis–Redlichia chinensis-Kootenia gimmelfarbi* biozones and Middle Cambrian *Peronopsis*? *ultimus–Lejopyge armata* local biozones of Malyi Karatau; Sarykumy Formation of the Atasu–Zhamshy area, Kazakhstan; Lower Cambrian (Atdabanian, upper *Judomia* Biozone) to Middle Cambrian (Amgaian), Central Siberia.

Linnarssonia captiosa Koneva, 1990

Plate 29, figures 1–14; Plate 31, figures 1–3

1990 *Linnarssonia captiosa* Koneva, p. 51, pl. 6, figs 1–5.
1990 *Linnarssonia ventosa* Koneva, p. 52, pl. 6, figs 6–11.

Holotype. IGNA 427/539, ventral valve (Koneva 1990, pl. 6, fig. 1); Middle Cambrian, Amgaian (*Ptychagnostus intermedius* beds), Kyrshabakty section (sample 1465), Malyi Karatau.

Material. One complete shell, 117 ventral and 31 dorsal valves.

Diagnosis. Shell only slightly ventribiconvex; ventral valve about 33 per cent as thick as long, with maximum thickness somewhat anterior to umbo; ventral pseudointerarea poorly defined, procline to

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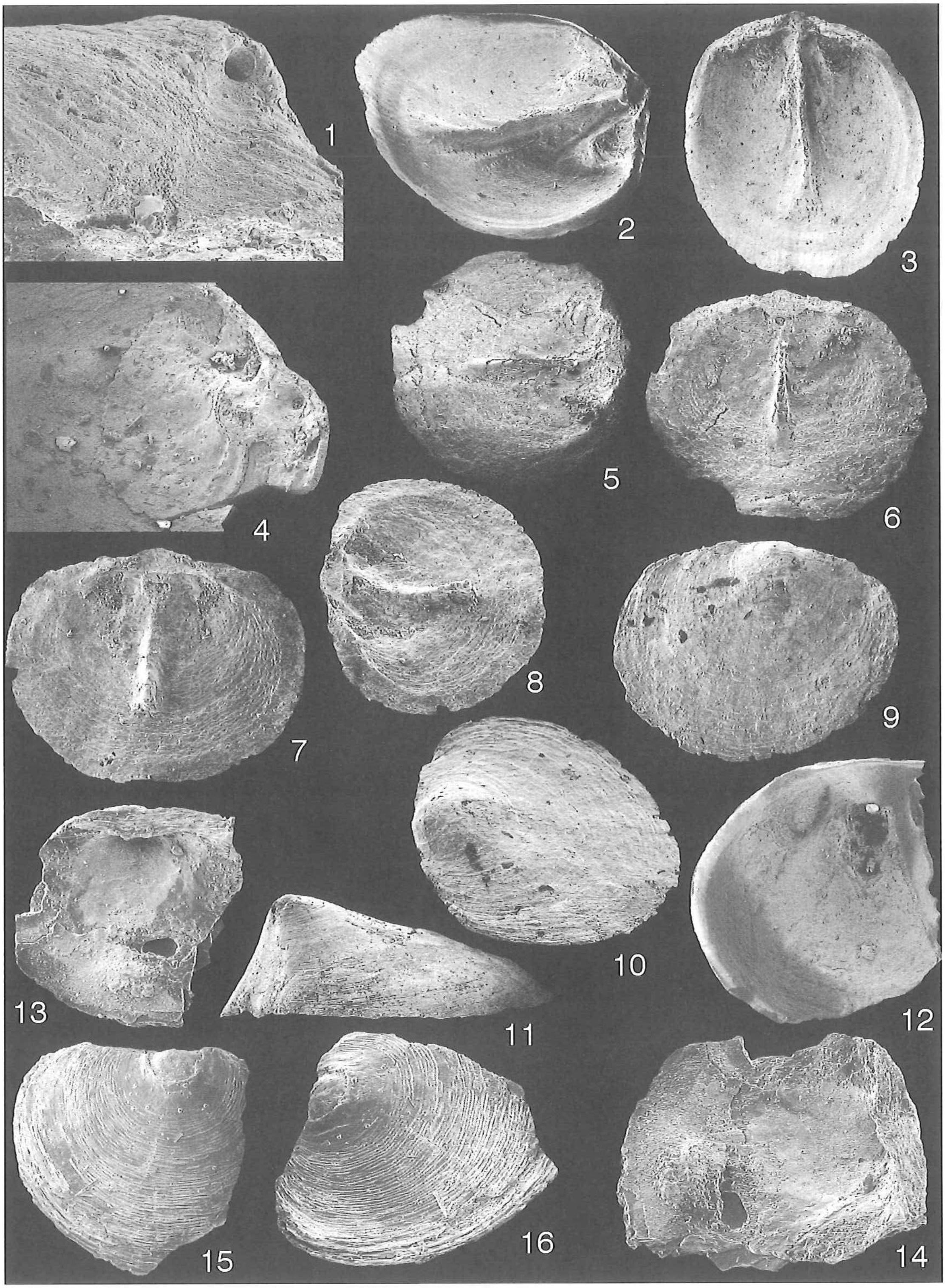
EXPLANATION OF PLATE 27

Figs 1–12. ‘*Homotreta*’ sp.; Middle Cambrian, Amgaian, Karagajly Formation, Kostek Range, sample 1639. 1, 4, NMW 98.61G.187, ventral valve, oblique view of posterior margin and oblique anterior view of interior; ×100, ×52. 2–3, NMW 98.61G.186, oblique lateral and normal views of dorsal valve interior; ×14, ×12·5. 5–6, NMW 98.61G.188, oblique lateral and normal views of dorsal valve interior; ×31, ×29. 7–8, NMW 98.61G.189, dorsal valve interior in normal and oblique lateral views; ×48, ×51. 9–10, NMW 98.61G.190, dorsal valve exterior in normal and oblique lateral views; ×45, ×55. 11–12, NMW 98.61G.185, ventral valve, lateral view and interior; ×21, ×15.

Figs 13–16. *Otariconulus* sp. 1; Upper Cambrian, Shabakty Group, *Harpidoides-Platypeltoides* beds, Malyi Karatau, Batyrbay section, sample 101 m. 13–14, NMW 98.61G.191, dorsal valve interior in normal and oblique lateral views; ×81, ×112. 15–16, NMW 98.61G.192, dorsal valve exterior, in normal and oblique lateral views; ×69, ×81.



HOLMER *et al.*, '*Homotreta*'. *Otariconulus*

TABLE 12. *Linnarssonia captiosa* Koneva, dimensional data for ventral valves from the Kyrshabakty section (sample 1465-1, Middle Cambrian, *Ptychagnostus intermedius* Biozone).

	Lv	W	T	Al	Aw	Sm	Lv/W	T/Lv	A/Lv
N	4	3	4	2	2	6	3	4	2
X	0·73	0·7	0·21	0·24	0·19	0·75	90%	32%	32%
S	0·324	0·347	0·050	0·141	0·071	0·076	1·7	10·8	1·6
MIN	0·44	0·48	0·16	0·14	0·14	0·64	88%	20%	30%
MAX	1·04	1·1	0·28	0·34	0·24	0·84	92%	45%	33%

TABLE 13. *Linnarssonia captiosa Koneva*, dimensional data for dorsal valves from the Kyrshabakty section (samples 1314 and 1465-1, Middle Cambrian, *Ptychagnostus intermedius* Biozone).

	Ld	W	T	Iw	Sa	Ld/W	T/Ld	Iw/W	Sa/Ld
N	4	4	4	4	4	4	4	4	4
X	0·88	1·00	0·225	0·25	0·545	87%	26%	22.7%	63%
S	0·302	0·298	0·05	0·208	0·149	7·6	4·0	11·3	6·0
MIN	0·64	0·8	0·16	0·12	0·42	76%	21%	13%	58%
MAX	1·32	1·44	0·28	0·56	0·76	92·5%	30%	39%	70%

catacline; apical process widely subtriangular; dorsal median ridge very low and long, occupying about 66 per cent of valve length; median buttress poorly defined, subcircular; dorsal cardinal muscle scars short, only slightly raised.

Description. Shell only slightly ventribiconvex, transversely suboval to subcircular, on average 90 per cent as long as wide (Table 12). Ventral valve moderately convex, about 33 per cent as thick as long (Table 12), maximum height slightly anterior to the boundary of the larval shell. Anterior and lateral slopes of the valve evenly convex in profile. Ventral pseudointerarea narrow, procline to catacline, poorly defined laterally, with deep intertrough. Pedicle foramen slightly elongate oval, not enclosed within the larval shell. Dorsal valve gently convex, about 25 per cent as high as long (Table 13). Dorsal pseudointerarea vestigial, consisting of a small concave median groove, occupying just over 20 per cent of the total valve width (Table 13).

Ventral interior with high, boss-like, widely subtriangular apical process, bounded by widely divergent *vascula lateralia*. Internal pedicle foramen directly posterior to apical process. Apical pits small, closely spaced, poorly

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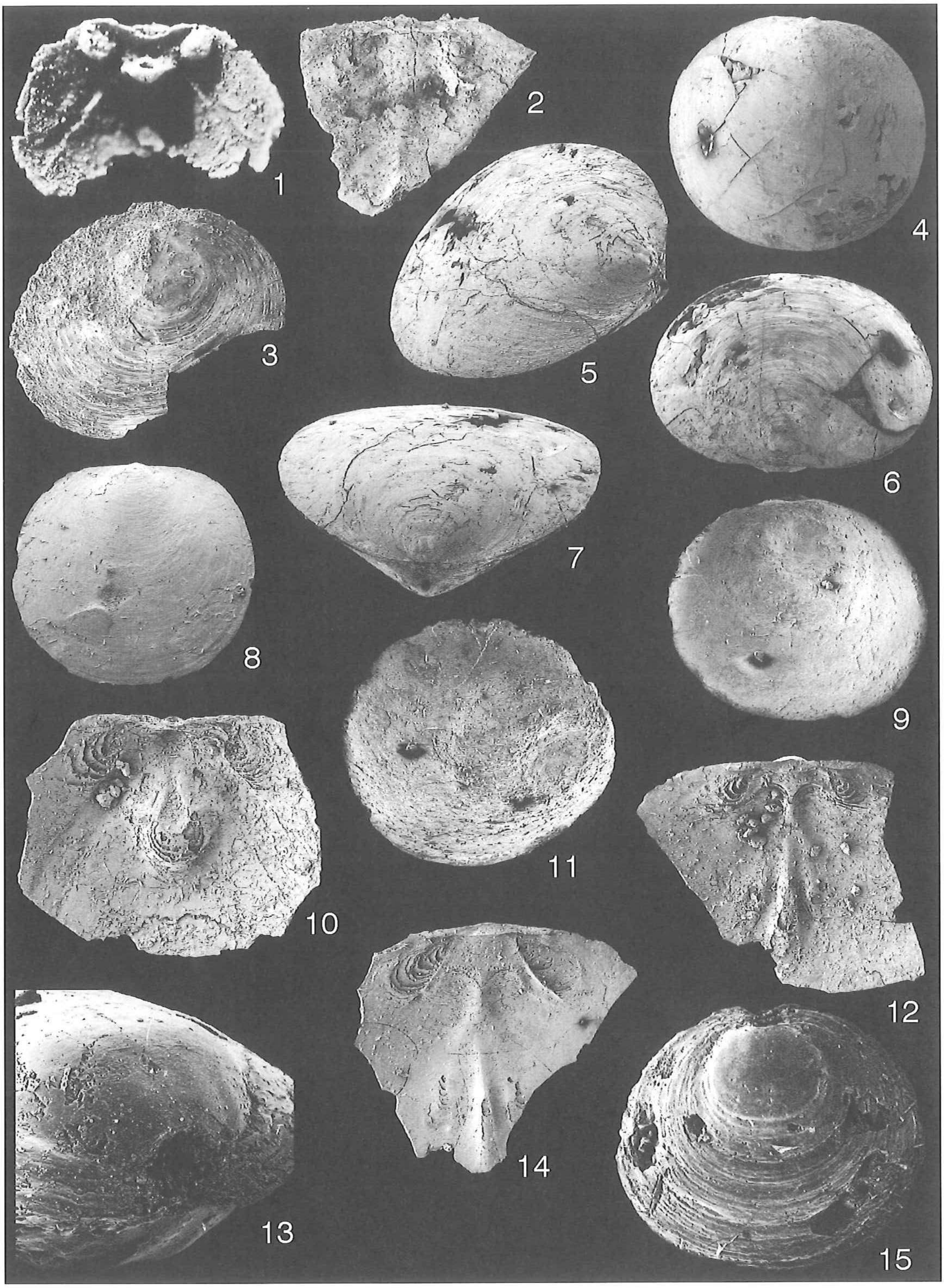
EXPLANATION OF PLATE 28

Figs 1–3. *Linnarssonia ophirensis* (Walcott); Middle Cambrian. 1, IGNA 427/522, incomplete ventral valve interior (holotype of *Linnarssonia rudis* Koneva), *Lejopyge armata* Biozone, Malyi Karatau, Kyrshabakty section, sample 1346-10; ×22. 2, NMW 98.61G.148, incomplete dorsal valve interior, Sarykumy Formation, Sarykumy section, sample K-20/29; ×35. 3, NMW 98.61G.149, incomplete ventral valve exterior of juvenile specimen, *Lejopyge armata* Biozone, Malyi Karatau, Kyrshabakty section, sample 1347-2; ×20.

Figs 4–15. *Linnarssonia constans* Koneva; Lower Cambrian, Shabakty Group, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, Malyi Karatau, Baba-Ata section, sample 5/26b. 4–8, NMW 98.69G.6, conjoined valves in ventral view, ×17; oblique lateral view, ×19; oblique posterior view from the ventral side, ×17; oblique posterior view from the dorsal side, ×21; and dorsal view, ×17. 9, NMW 98.61G.151, dorsal valve exterior; ×17. 10, NMW 98.69G.8, ventral valve interior; ×31. 11, NMW 98.61G.153, ventral valve, oblique lateral view of interior; ×20. 12, NMW 98.61G.154, dorsal valve interior; ×17. 13, 15, NMW 98.69G.7, conjoined valves of juvenile specimen. 13, oblique posterior view of ventral larval shell, and ventral view; ×50, ×75. 14, NMW 98.61G.156, dorsal valve interior; ×17.

PLATE 28



HOLMER *et al.*, *Linnarssonia*

defined, anterolateral to foramen. Ventral cardinal muscle scars strongly raised, bulbous, subcircular. Dorsal median ridge very low and long, extending forward for about 60 per cent of valve length. Median buttress poorly defined, subcircular. Dorsal cardinal muscle scars short, only slightly raised.

Remarks. Linnarssonia captiosa differs from all other species of the genus in having a mainly procline ventral valve and a widely subtriangular apical process, as well as lower cardinal muscle scars in both valves. Also, the dorsal median ridge is relatively longer by comparison with that of, for example, *L. ophirensis* (Walcott; see Rowell 1966). It is most similar to the poorly known *L.*? *perplexa* Bell, 1941 (the type species of *Pegmatreta*), which is apparently also procline, but seems to have a less boss-like apical process.

Occurrence. Kyrshabakty section, *Ptychagnostus punctuosus* and *Goniagnostus nathorsti* biozones, samples 1467, 1467/3, 1465, 1465/1, 1465/9, 1465/16, 1465/19, 1465/22, 1465/24, 1465/25, 1314, 1314/1, 1316.

Linnarssonia constans Koneva, 1983

Plate 28, figures 4–15; Plate 36, figure 15; Plate 51, figures 12–14; Text-figure 18

1983 *Linnarssonia constans* Koneva, *in* Gorjansky and Koneva, p. 34, pl. 29, figs 1–10.

Holotype. IGNA 2224/51, ventral valve (Koneva 1983, pl. 29, fig. 1); Lower Cambrian, Toyonian (*Redlichia chinensis-Kootenia gimmelfarbi* Biozone), Baba-Ata section (sample 1420), Malyi Karatau.

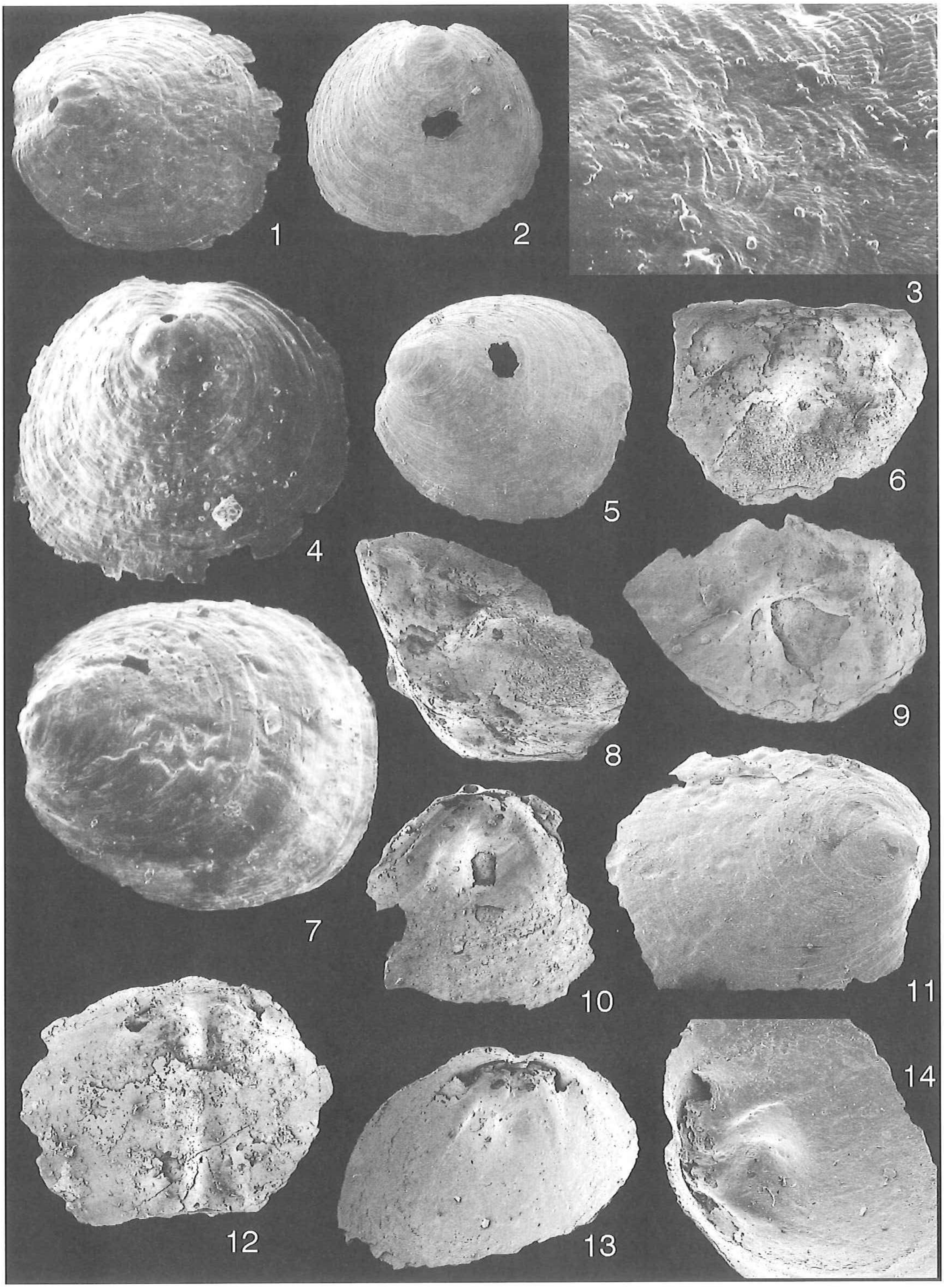
Material. 23 complete shells, 240 ventral and 102 dorsal valves.

Diagnosis. Ventral valve strongly convex, about 20 per cent as thick as wide with maximum thickness slightly anterior to umbo; ventral pseudointerarea low, slightly apsacline to procline; apical process moderately high, subtriangular, anterior to internal foramen, with two pairs of muscle scars; dorsal median ridge low, extending forward to about 66 per cent of valve length; median buttress high, elongate subtriangular; dorsal cardinal muscle fields well defined.

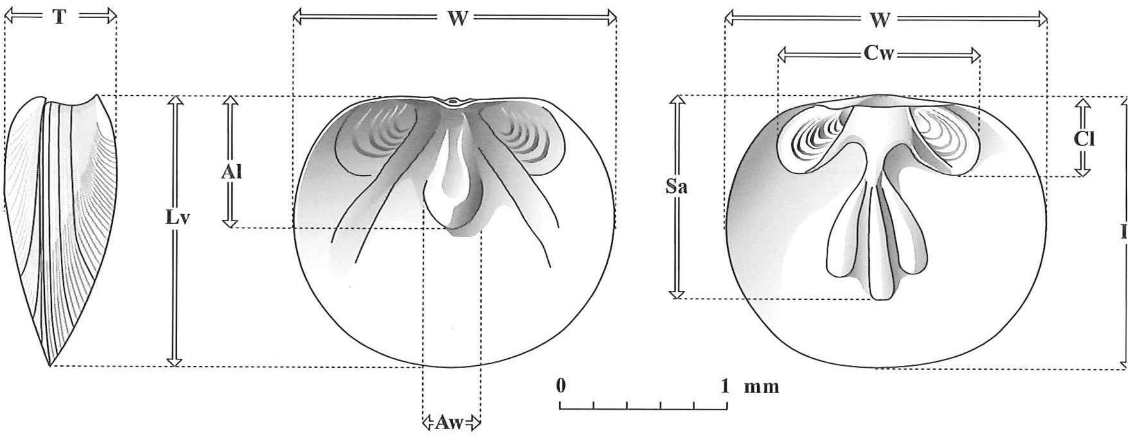
Description. Shell slightly ventribiconvex, transversely suboval to subcircular, about 90 per cent as long as wide and 40 per cent as thick as long (Tables 14–16). Ventral valve strongly and unevenly convex, about 20 per cent as high as wide (Table 14), with the maximum height slightly anterior to the umbo. Ventral pseudointerarea low, weakly apsacline to procline, with shallow intertrough. Propareas poorly differentiated from lateral sides of the valve. Lateral slopes of valve moderately and evenly convex in profile. Pedicle foramen small, subcircular, not enclosed within the larval shell. Dorsal valve gently convex. Dorsal pseudointerarea comparatively narrow, consisting almost entirely of concave, lens-shaped median groove, and occupying about 30 per cent of valve width (Table 15). Larval shell with pits of slightly varying sizes.

EXPLANATION OF PLATE 29

Figs 1–14. *Linnarssonia captiosa* Koneva; Middle Cambrian, Shabakty Group, *Peronopsis*? *ultimus–Goniagnostus nathorsti* biozones, Malyi Karatau, Kyrshabakty section. 1, 3–4, NMW 98.61G.157, sample 1465-1, ventral valve in oblique lateral view; ×35; detail of external shell surface, ×280; and ventral view, ×46. 2, 5, NMW 98.61G.158, ventral valve in normal and oblique lateral views, sample 1465-1; ×44, ×51. 6, 8, NMW 98.61G.159, incomplete ventral valve interior, and oblique lateral view of interior; ×40, ×42. 7, NMW 98.61G.160, dorsal valve exterior in oblique lateral view, sample 1467; ×52. 9, NMW 98.61G.118, incomplete ventral valve interior, oblique anterior view showing apical process, sample 1467; ×35. 10, NMW 98.61G.161, incomplete ventral valve interior, sample 1465-1; ×39. 11, NMW 98.61G.162, ventral valve exterior in oblique lateral view, sample 1467; ×42. 12, NMW 98.61G.163, incomplete dorsal valve interior, sample 1314; ×41. 13–14, NMW 98.61G.164, incomplete ventral valve interior, and oblique anterior view showing apical process, sample 1314; ×42, ×58.



HOLMER *et al.*, *Linnarssonia*



TEXT-FIG. 18. *Linnarssonia constans* Koneva; lateral view (left) and reconstruction of the ventral (centre) and dorsal (right) interiors showing the disposition of the musculature and vascular system and the location of the measured parameters (see Tables 12–14).

TABLE 14. *Linnarssonia constans* Koneva, dimensional data for ventral valves from the Ushbas section (sample 5/26b, Lower Cambrian, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone).

	Lv	W	T	Al	Aw	Lv/W	T/Lv	A/Lv
N	11	10	11	10	10	10	11	10
X	2·21	2·35	0·815	0·9	0·81	99%	29%	32%
S	1·342	0·602	0·241	0·190	0·170	6·7	9·0	8·0
MIN	0·76	0·76	0·26	0·42	0·36	80%	18%	16%
MAX	5·9	2·88	1·04	1·08	0·88	104%	48%	48%

TABLE 15. *Linnarssonia constans* Koneva, dimensional data for dorsal valves from the Ushbas section (sample 5/26b, Lower Cambrian, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone).

	Ld	W	T	Il	Iw	Cl	Cw	Sa	Ld/W	T/W	Iw/W	Cl/Ld	Cw/W	Sa/Ld
N	12	13	13	13	13	13	13	13	12	12	13	12	13	12
X	2·34	2·66	0·492	0·131	0·86	1·24	1·59	1·58	93%	21%	32%	51%	60%	65%
S	0·591	0·778	0·109	0·030	0·318	0·355	0·421	0·415	3·5	3·9	4·3	07·1	8·2	07·2
MIN	1·8	1·9	0·38	0·08	0·46	0·72	1	1	87%	14%	24%	40%	49%	54%
MAX	3·8	4·48	0·72	0·18	1·48	1·88	2·48	2·48	99%	23%	38%	62%	79%	75%

TABLE 16. *Linnarssonia constans* Koneva, dimensional data for complete shells from the Ushbas section (sample 5/26b, Lower Cambrian, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone).

	L	W	T	L/W	T/L
N	17	17	17	17	17
X	1·08	1·17	39%	92%	39%
S	0·593	0·617	16·2	3·6	9·6
MIN	0·48	0·52	16%	86%	18%
MAX	2·88	3·00	54%	96%	55%

Ventral apical process moderately high, subtriangular, anterior to internal foramen and bearing two pairs of muscle scars. Ventral cardinal muscle fields slightly raised, elongate subtriangular, situated posterolaterally. Apical pits deeply impressed, situated lateral to internal foramen. Ventral mantle canals baculate with wide, deeply impressed *vascula lateralia*, slightly divergent in proximal part. Dorsal interior with low median ridge, extending forward on average for 65 per cent of valve length (Table 15). Raised scars of gastroparietal bands well defined, extending to the dorsal anterocentral muscle scars at about mid-valve length. Median buttress high, elongate subtriangular. Dorsal cardinal muscle fields well defined directly on either side of median buttress, extending forward to about mid-valve length, and bounded by an elevated rim.

Remarks. Linnarssonia constans is characterized mainly by its low, weakly apsacline to procline ventral pseudointerarea, its moderately high, subtriangular apical process bearing two pairs of muscle scars, and the very low dorsal median ridge. This combination of characters is not known in any other species of *Linnarssonia*.

Occurrence in Kazakhstan. Lower Cambrian Alazhar Formation of Malyi Karatau; Baba-Ata section, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, samples 5/26b and 1419; Ushbas Section, *Hebidiscus orientalis* Biozone, sample 1227; *Ushbaspis limbata* Biozone, samples 1215, 1224, 1225, 1228, 1232, 1233; *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, samples 1228, 1234; Koksu section, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, samples 1204, 1204-I, 1205-I, 1207, 1209.

Linnarssonia ophirensis (Walcott, 1902)

Plate 26, figures 11–17; Plate 28, figures 1–3

1902 *Acrotreta ophirensis* Walcott, 1902, p. 591.
1966 *Linnarssonia ophirensis* (Walcott) Rowell, p. 24, pl. 4, figs 1–11; table 6; text-figs 24–25.
1990 *Linnarssonia rudis* Koneva, p. 51, pl. 5, figs 18–22.

Holotype. USNM 35281q, ventral valve; Middle Cambrian (lower *Bolaspidella* Biozone or *Bathyuriscus-Elrathia* Biozone), Oquirrh Range, Utah.

Material from Kazakhstan. 33 ventral and 30 dorsal valves.

Diagnosis. See Rowell 1966, p. 24.

Remarks. Linnarssonia rudis Koneva is here considered to be a junior synonym of *L. ophirensis*, which is also characterized by a very high, boss-like apical process, very high, bulbous cardinal muscle fields in both valves, and a moderately high dorsal median ridge. The ridge is somewhat higher in the Kazakhstanian material, but this is a variable character in most *Linnarssonia*.

Occurrence in Kazakhstan. Kyrshabakty section, *Goniagnostus nathorsti* and *Ptychagnostus intermedius* biozones, samples 1465/25, 1465/26, 1346, 1346/4–6, 1346/10, 1346/11, 1347/1a, 1347/2, 1347/2d; area about 4 km south-east of Sarykumy railway station, samples 29, 132.

Genus NEOTRETA Sobolev, 1976

Type species. Original designation by Sobolev (1976, p. 131); *Neotreta tumida* Sobolev, 1976; Middle–lower Upper Cambrian transitional beds, Dzhagdy Range, Uda River Basin, south-eastern Siberia.

Diagnosis. See Popov *et al.* 1994, p. 347.

Remarks. *Neotreta* was discussed in detail by Popov *et al.* (1994). Since that time a new occurrence of the type species has been recorded from Middle/Upper Cambrian boundary beds in the San Juan Precordillera of western Argentina (Holmer *et al.* 1999), and *Neotreta*? sp. has also been reported from the Middle Cambrian of the Tarbagatay Range, Kazakhstan (Popov *et al.* 1996).

Neotreta pusilla Koneva, 1986

Plate 30, figures 8–11

1986 *Neotreta pusilla* Koneva, p. 202, pl. 29, figs 1–5.
1994 *Neotreta pusilla* Koneva; Popov *et al.*, p. 350.
non 1986 *Neotreta*? *pusilla* Ushatinskaya, *in* Ushatinskaya *et al.*, p. 37, pl. 4, figs 1–10.

Holotype. IGNA 427/341, ventral valve (Koneva 1986, pl. 29, fig. 1). Upper Cambrian, *Glyptagnostus stolidotus* Biozone, Kyrshabakty section, Malyi Karatau.

Material. Three complete shells, two ventral and four dorsal valves.

Diagnosis. See Popov *et al.* 1994, p. 350.

Remarks. *Neotreta*? *pusilla* Ushatinskaya, *in* Ushatinskaya *et al.* 1986 is a junior homonym of *Neotreta pusilla* Koneva, 1986. The material described by Ushatinskaya is not conspecific with *N. pusilla* Koneva, and it was assigned to *Stilpnotreta* by Popov *et al.* (1996).

Occurrence. Middle Cambrian, Mayaian–Upper Cambrian, *Lejopyge laevigata–Glyptagnostus stolidotus* biozones; Malyi Karatau, Kyrshabakty section, samples 1348, 1349-III-2, 1350-2, 1351, 1351-I-4, 1352-I-1.

Neotreta orbiculata Koneva, 1990

Plate 30, figures 1–7, 12

1990 *Neotreta orbiculata* Koneva, p. 53, pl. 6, figs 12–17.
1994 *Neotreta orbiculata* Koneva; Popov *et al.*, p. 350, figs 3J–Q, table 2.
1996 *Neotreta orbiculata* Koneva; Engelbretsen, p. 84, figs 7A–I.

Holotype. IGNA 427/155, ventral valve (Koneva 1990, pl. 6, fig. 13); Middle Cambrian, Mayaian (*Goniagnostus nathorsti* beds), Kyrshabakty section, sample 1316, Malyi Karatau.

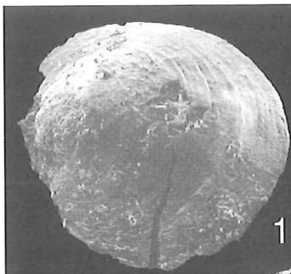
EXPLANATION OF PLATE 30

Figs 1–7, 12. *Neotreta orbiculata* Koneva; Middle Cambrian, Malyi Karatau, Kyrshabakty section, *Goniagnostus nathorsti* Biozone. 1, 6, NMW 98.61G.177, ventral valve exterior in oblique lateral and normal views, sample 1316; ×65, ×56. 2–4, NMW 98.61G.178, ventral valve exterior in oblique posterior, oblique lateral and normal views, sample 1316; ×86, ×80, ×73. 5, NMW 98.61G.179, ventral valve interior, sample 1316; ×81. 7, NMW 98.61G.180, dorsal valve exterior, sample 1316; ×5. 12, NMW 98.61G.181, dorsal valve exterior, sample 1465-22; ×60.

Figs 8–11. *Neotreta pusilla* Koneva; Middle Cambrian, Mayaian–Upper Cambrian, *Lejopyge laevigata–Glyptagnostus stolidotus* biozones, Malyi Karatau, Kyrshabakty section. 8, IGNA 427/341, holotype, ventral valve exterior, sample 1352-I-1; ×44. 9, IGNA 427/345, dorsal valve interior, sample 1350-2; ×45. 10, IGNA 427/345, ventral valve, exterior, sample 1352-I-1; ×45. 11, IGNA 427/343, conjoined valves, posterior view, sample 1349-III-2; ×40.

Figs 13–14. *Satpakella*? sp.; Upper Cambrian, Shabakty Group, *Trisulcagnostus trisulcus-Saukiella* beds, Malyi Karatau, Kyrshabakty section, sample 1401-6; NMW 98.61G.182, dorsal valve interior in normal and oblique lateral views; both ×34.

Figs 15–17. *Prototreta venusta* Koneva; Middle Cambrian, Shabakty Group, *Ptychagnostus intermedius* Biozone, Malyi Karatau, Kyrshabakty section, sample 1314. 15–16, NMW 98.61G.183, ventral valve exterior in oblique lateral and normal views; ×78, ×87. 17, NMW 98.61G.184, ventral valve, oblique posterior view; ×58.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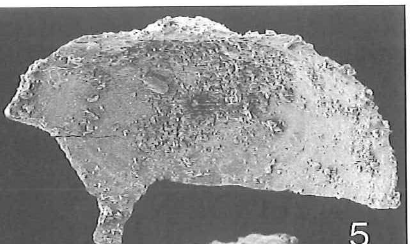
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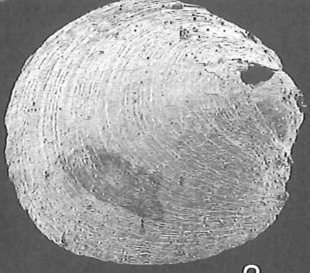
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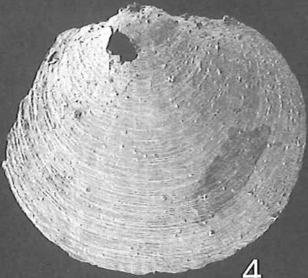
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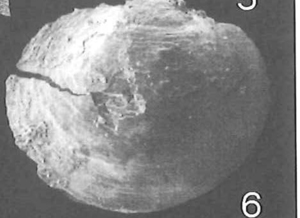
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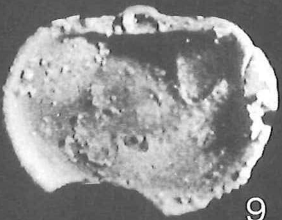
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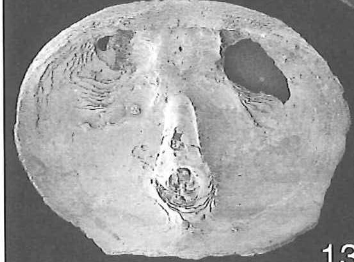
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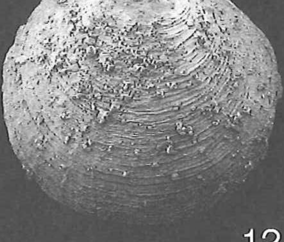
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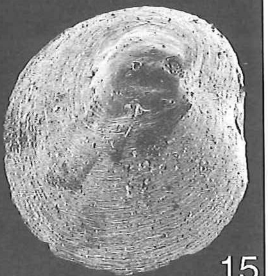
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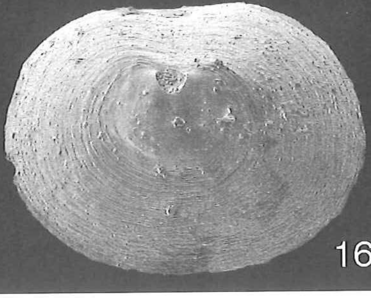
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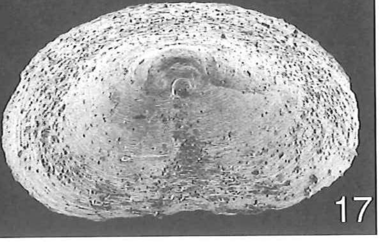
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HOLMER *et al.*, brachiopods

Material. 23 complete shells, 23 ventral and 14 dorsal valves.

Diagnosis. See Popov *et al.* 1994, p. 350.

Remarks. N. orbiculata was also described recently from the Middle Cambrian of north-eastern New South Wales (Engelbretsen 1996). There is also a new occurrence of this species from the Middle Cambrian of Texas, USA (Holmer and Popov, unpublished).

Occurrence in Kazakhstan. Middle Cambrian, Kyrshabakty section, *Goniagnostus nathorsti* Biozone, samples 1465/17, 1465/25, 1316.

Genus OTTENBYELLA Popov and Holmer, 1994

Type species. Original designation by Popov and Holmer (1994, p. 114); *Acrotreta carinata* Moberg and Segerberg, 1906; Lower Ordovician Bjørkåsholmen Limestone, Fågelsång, Scania, Sweden.

Diagnosis. See Holmer and Popov 1994, p. 114.

Species included. Acrotreta carinata Moberg and Segerberg, 1906; *Eurytreta evanda* Popov, 1988.

Occurrence. Lower Ordovician, Bjørkåsholmen Limestone, Scandinavia; *Szechuanella-Apatokephalus* beds, Malyi Karatau.

Ottenbyella evanda (Popov, 1988)

Plate 25, figures 12–16

1988 *Eurytreta evanda* Popov, *in* Koneva and Popov, p. 63, pl. 2, fig. 9; pl. 3, fig. 1 (*non* pl. 3, fig. 2).

Holotype. CNIGR 20/12034, ventral valve (Koneva and Popov 1988, pl. 2, fig. 1), Lower Ordovician, Batyrbay section, *Szechuanella-Apatokephalus* beds, 383 m, Malyi Karatau.

Material. Two ventral and three dorsal valves.

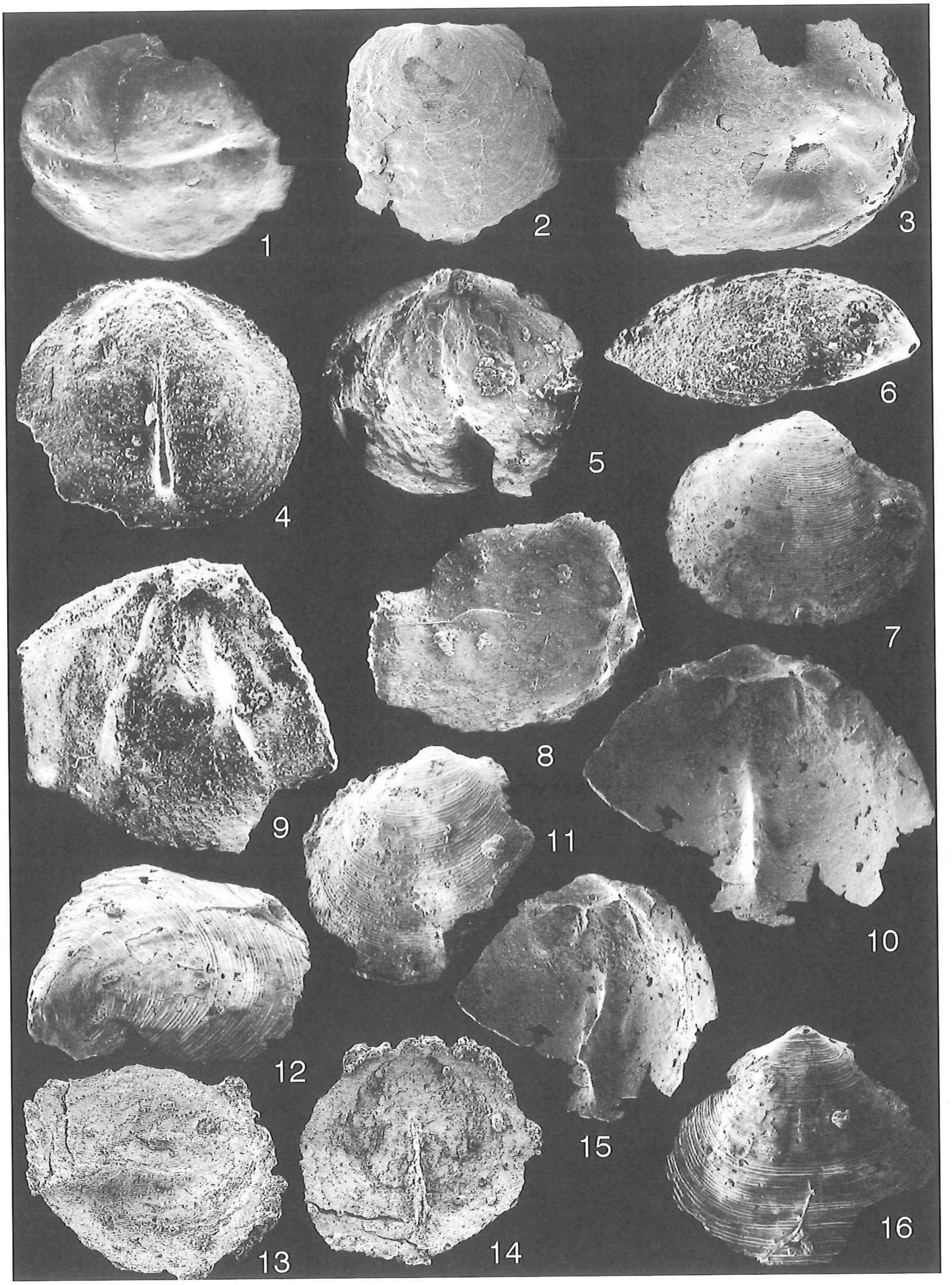
Diagnosis. Ventral valve broadly conical; dorsal pseudointerarea narrow, occupying about one-third of the valve width; dorsal median ridge thin, extending to mid-valve length.

EXPLANATION OF PLATE 31

Figs 1–3. *Linnarssonia captiosa* Koneva; Middle Cambrian, Shabakty Group, *Peronopsis*? *ultimus–Goniagnostus nathorsti* biozones, Malyi Karatau, Kyrshabakty section. 1, NMW 98.61G.165, incomplete dorsal valve interior, oblique lateral view, sample 1314; ×30. 2, NMW 98.61G.167, ventral valve exterior, sample 1467; ×29. 3, NMW 98.61G.166, incomplete ventral valve interior, oblique lateral view showing apical process, sample 1465-1; ×39.

Figs 4–16, *Picnotreta karakichiensis* sp. nov.; Middle–Upper Cambrian. 4, 6, 9, Karadzhorga Formation, Moldotau Range, eastern side of Karakichi River, sample 127/9; 5, 7–8, 10–16, Sarykumy Formation, Sarykumy section. 4, NMW 98.61G.168, dorsal valve interior; ×30. 5, NMW 98.61G.169, dorsal valve interior, sample 134; ×35. 6, NMW 98.61G.170, ventral valve exterior, lateral view; ×90. 7, 11, NMW 98.61G.171, dorsal valve exterior in normal and oblique lateral views, sample 134; ×25, ×27. 8, NMW 98.61G.172, incomplete ventral valve interior, oblique lateral view, sample 134; ×30. 9, NMW 98.61G.173, incomplete ventral valve interior; ×30. 10, 15, NMW 98.61G.174, dorsal valve interior in normal and oblique lateral views, sample 134; ×67, ×47. 12, 16, NMW 98.61G.175, dorsal valve exterior in oblique lateral and normal views, sample 134; ×67, ×55. 13–14, NMW 98.61G.176, incomplete dorsal valve interior in oblique lateral and normal views sample K-20/132; ×50, ×44.

PLATE 31



HOLMER *et al.*, *Linnarssonia*, *Picnotreta*

Description. Shell ventribiconvex, transversely oval, about 75–90 per cent as long as wide. Ventral valve broadly conical with maximum thickness at the umbo. Ventral pseudointerarea weakly procline, poorly defined laterally, bisected by a low, narrow interridge. Ventral anterior and lateral valve slopes straight in profile. Dorsal valve gently convex with shallow sulcus originating in umbonal region. Dorsal pseudointerarea narrow, orthocline, occupying about 35 per cent of valve width, with lens-shaped median groove.

Ventral interior with very short, ridge-like apical process and baculate mantle canals. Dorsal interior with low, thin median ridge, extending forward to about mid-valve length. Median buttress fairly well developed, subtriangular. Dorsal cardinal muscle scars raised but small, rounded, extending forward for about one quarter of the valve length.

Remarks. This rare species is known only from a limited number of valves. It was referred originally to *Eurytreta*, but in having a slightly procline ventral valve, with maximum height at the umbo, a small apical process anterior to the foramen, and a sulcate dorsal valve with a low dorsal median ridge, it is comparable only with the type species of *Ottenbyella*, *O. carinata* (Moberg and Segerberg) from the Bjørkåsholmen Limestone of Scandinavia (Popov and Holmer 1994). *O. evanda* differs, however, in having a narrower dorsal pseudointerarea, occupying about 33 per cent of the valve width, and a thin dorsal median ridge that does not extend anterior to the mid-valve.

The dorsal valve (CNIGR 21/12034) from the *Euloma-Leiostegium* beds of the Batyrbay section (sample 235 m) illustrated by Koneva and Popov (1988, pl. 3, fig. 2) is not conspecific with *Ottenbyella evanda*. Study of new material from these beds suggests that it belongs to *Eurytreta* cf. *bisecta*.

Dimensions. CNIGR 20/12034, ventral valve, holotype, L = 1·06, W = 1·23, T = 0·60; CNIGR 21/12034, dorsal valve, L = 1·33, W = 1·83, Iw = 0·63, Sa = 0·60, Cl = 0·33, Cw = 0·64.

Occurrence in Kazakhstan. Batyrbay section, *Szechuanella-Apatokephalus* beds, samples 363, 383 m.

Genus QUADRISONIA Rowell and Henderson, 1978

Type species. Original designation by Rowell and Henderson (1978, p. 6); *Quadrisonia minor* Rowell and Henderson, 1978; Upper Cambrian Orr Formation (*Taenicephalus* Biozone), Steamboat Pass, Utah, USA; Windfall Formation (*Elvinia* Biozone), Nevada, USA.

Diagnosis and species included. See Popov and Holmer 1994, pp. 119–120.

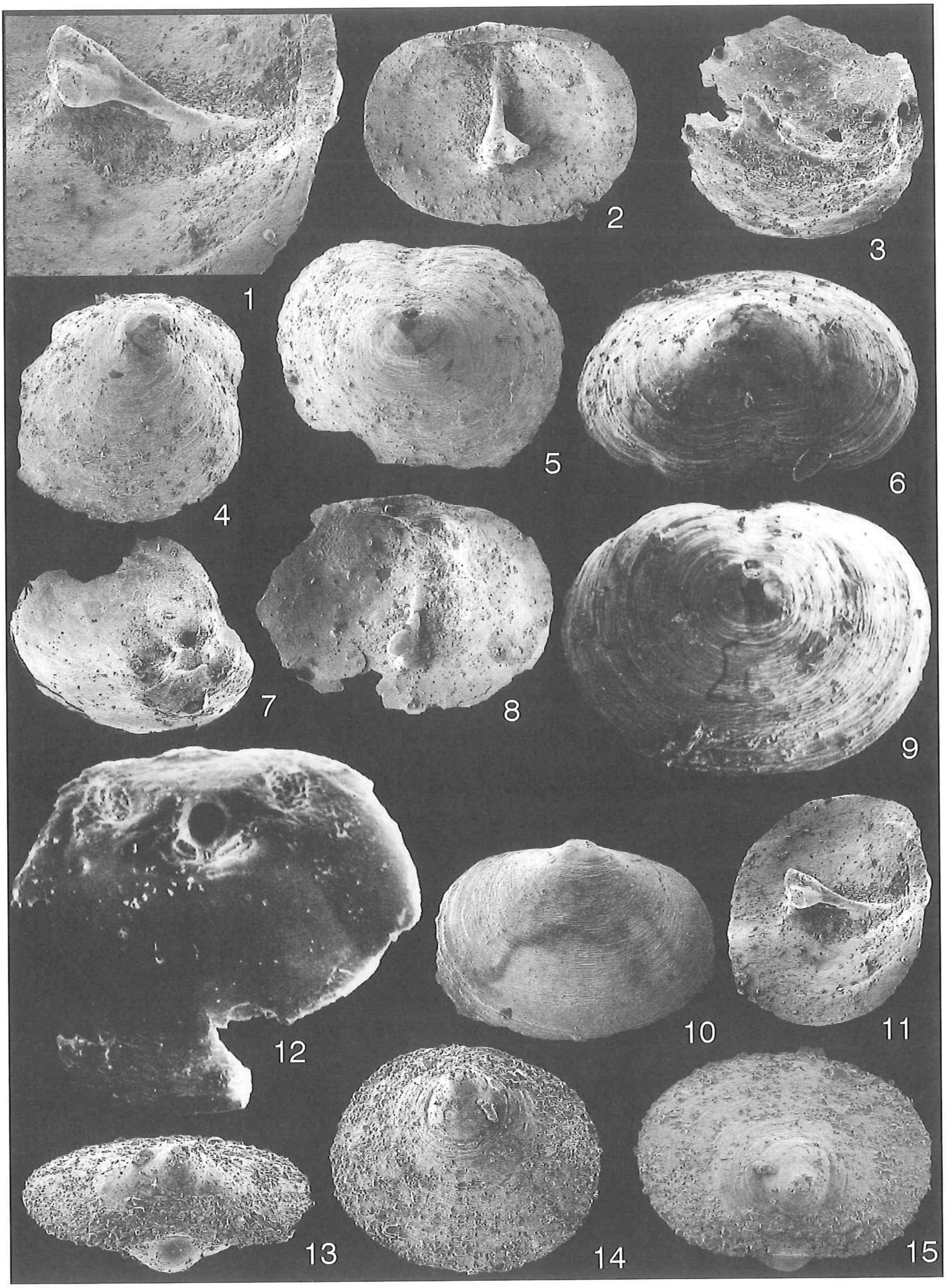
Occurrence. Upper Cambrian; Australia (Idamean–pre Payntonian); West Antarctica (Idamean); USA (Great Basin, Franconian); Kazakhstan (Upper Cambrian); ?Sweden (Upper Cambrian); western Argentina, San Juan Precordillera (Upper Cambrian).

EXPLANATION OF PLATE 32

Figs 1–11. *Prototreta venusta* Koneva; Middle Cambrian, Shabakty Group, *Ptychagnostus intermedius* Biozone, Malyi Karatau, Kyrshabakty section. 1–2, 11, NMW 98.69G.12, sample 1314-2, dorsal valve interior, oblique lateral view of median septum, ×91; dorsal view, ×45; and oblique lateral view of interior, ×45. 3, 8, NMW 98.61G.194, dorsal valve interior of juvenile specimen in oblique lateral and normal views, sample 1314; ×79, ×71. 4–5, NMW 98.61G.195, ventral valve exterior in oblique lateral and ventral views, sample 1314; both ×51. 6, 9, NMW 98.61G.196, ventral valve exterior in oblique posterior and normal views, sample 1314; ×55, ×60. 7, NMW 98.61G.197, ventral valve interior, oblique lateral view, sample 1314-2; ×44. 10, NMW 98.61G.198, dorsal valve exterior, sample 1314; ×53.

Figs 12–15. *Quadrisonia suspensa* Koneva and Popov; Upper Cambrian, *Lophosaukia-Ivshinaspis* to *Harpidoides-Platypeltoides* beds, Malyi Karatau, Batyrbay section. 12, CNIGR 7/12034, ventral valve interior, sample 77 m; ×62. 13–15, NMW 98.61G.199, sample 68, conjoined valves in posterior view, ×59; ventral view, ×57; and oblique posterior view, ×59.

PLATE 32



HOLMER *et al.*, *Prototreta*, *Quadrisonia*

Quadrisonia declivis Koneva and Popov, 1988

Plate 33, figures 1–9

1988 *Quadrisonia declivis* Koneva and Popov, p. 54, pl. 1, figs 1–8.
1994 *Quadrisonia declivis* Koneva and Popov; Popov and Holmer, p. 120, fig. 97.

Holotype. CNIGR 4/12034, ventral valve (Koneva and Popov 1988, pl. 1, fig. 11); Upper Cambrian, Batyrbay section (0 m), Malyi Karatau.

Material. More than 300 ventral and dorsal valves.

Remarks. For a diagnosis and detailed morphological description and discussion of this species, see Popov and Holmer (1994). Here we re-illustrate the holotype and some new material from the Batyrbay and Kyrshabakty sections.

Occurrence in Central Asia. Upper Cambrian, Kyrshabakty section, *Eorudagnostus ovaliformis–Trisulcagnostus trisulcus* beds, samples 1373, 1375, 1376, 1376-11, 1378/19, 1378/24, 1378/25, 1379/2, 1379/6, 1381, 1381/1, 1381/4, 1381/6, 1400/6; Batyrbay section, *Hedinaspis sulcata–Lophosaukia beds,* samples 1444, 1444-1, −35 m, 0 m; east side of Shabakty River, *Neoagnostus quadratiformis* beds, sample 1412, *Agnostus scrobicularis* beds, sample 1413, *Trisulcagnostus trisulcus* beds, sample 1414.

Quadrisonia minor Rowell and Henderson, 1978

Plate 33, figures 10–19

1978 *Quadrisonia minor* Rowell and Henderson, p. 6, pl. 1, fig. 9; pl. 2, figs 1–6; text-figs 4–6.

Holotype. UKMNP 115501, ventral valve; Upper Cambrian Orr Formation (*Taenicephalus* Biozone), Steamboat Pass, Utah, USA.

Material. Six complete shells, 38 ventral and 28 dorsal valves.

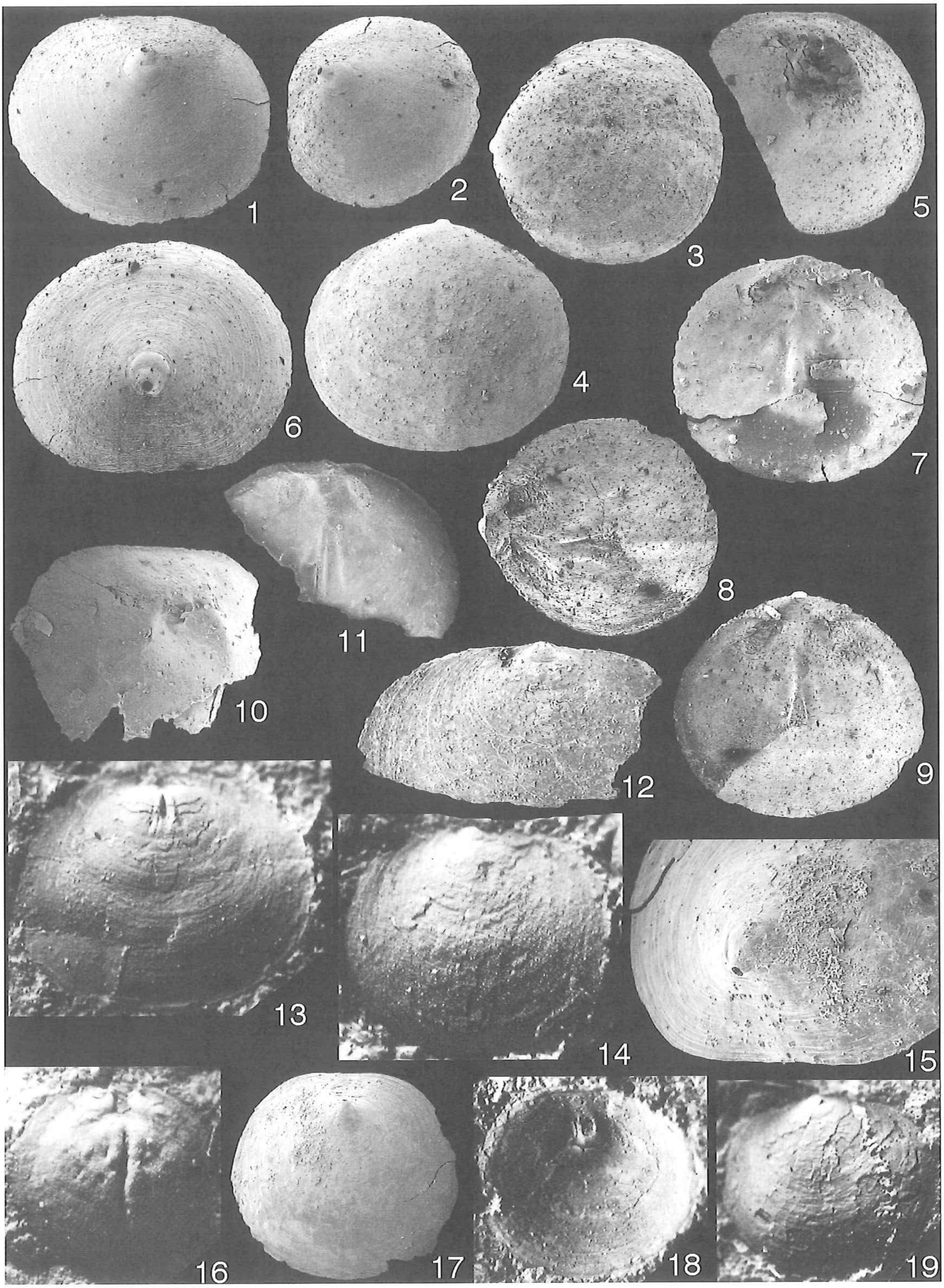
Diagnosis. See Rowell and Henderson (1978, p. 6).

Description of material from Kazakhstan. Valves subcircular to transversely suboval. Ventral valves convex with maximum thickness slightly anterior to the umbo. Lateral slopes of valve straight or very gently convex in profile. Ventral pseudointerarea narrow, weakly procline, poorly defined from lateral margins and bisected by a weak intertrough. Pedicle foramen small, rounded, posteriorly directed, enclosed within larval shell.

EXPLANATION OF PLATE 33

Figs 1–9, *Quadrisonia declivis* Koneva and Popov; Upper Cambrian, Shabakty Group, *Hedinaspis sulcata* beds, Malyi Karatau, Batyrbay section. 1–2, 6, NMW 98.61G.200, ventral valve exterior in normal, oblique lateral and oblique posterior views; ×27, ×25, ×29. 3–4, NMW 98.61G.201, dorsal valve exterior in oblique lateral and normal views; both ×21. 5, NMW 98.61G.202, ventral valve interior, oblique lateral view; ×22. 7, NMW 98.61G.203, dorsal valve interior; ×31. 8–9, NMW 98.61G.204, dorsal valve interior in oblique lateral and normal views; ×25 ×24.

Figs 10–19, *Quadrisonia minor* Rowell and Henderson; Upper Cambrian, *Acutagnostus acutus-Erixanium–Eorudagnostus ovaliformis-Pareuloma* beds, Malyi Karatau, Kyrshabakty section. 10, NMW 98.61G.204, ventral valve interior, sample 1360; ×35. 11, NMW 98.61G.205, incomplete dorsal valve interior, sample 1360; ×28. 12, NMW 98.61G.206, incomplete dorsal valve exterior, sample 1360; ×29. 13, IGNA 427/734, exfoliated dorsal valve, sample 1357-3; ×14. 14, IGNA 427/341, dorsal valve exterior, sample 1360-5; ×18. 15, 17, NMW 98.61G.207, ventral valve exterior in oblique posterior and normal views; ×46, ×24. 16, IGNA 427/735, dorsal internal mould, sample 1357; ×17. 18, IGNA 427/736, ventral valve interior, sample 1358; ×25. 19, IGNA 427/737, dorsal valve exterior, sample 1355-6; ×14.



HOLMER *et al.*, *Quadrisonia*

Dorsal valve gently and evenly convex with narrow, orthocline to weakly anacline pseudointerarea. Median groove deep, lens-shaped.

Ventral interior with rounded subtriangular apical process, mainly on the anterior valve slope and somewhat occluding the apex. Posterior slope of the process grooved below the internal foramen, with two small, strongly impressed apical pits. Cardinal muscle fields slightly raised, situated on the posterolateral slopes of the valve. Dorsal interior with low median ridge extending somewhat anterior to mid-valve length. Dorsal cardinal muscle scars small, rounded, separated by narrow median buttress. Dorsal anterocentral muscle scars forming elevated track terminating slightly posterior to mid-valve length.

Dimensions. NMW 98.61G.342, complete shell, L = 2·48, W = 2·92, T = 1·10; NMW 98.61G.343, complete shell, L = 2·24, W = 2·48, T = 0·98; NMW 98.61G.207, ventral valve, L = 1·50, W = 1·76; NMW 98.61G.344, ventral valve, L = 2·12, W = 2·72, T = 0·58.

Remarks. The specimens from Malyi Karatau are identical with the roughly coeval type material from Utah in their most important characters. However, the Kazakhstanian samples mostly comprise fragmentary specimens, with a greater maximum size than the American material, and the dorsal pseudointerarea is relatively somewhat wider in the Malyi Karatau specimens, but we do not regard these features as being specifically different. *Q.* cf. *minor* is also known from the Upper Cambrian of the San Juan Precordillera, western Argentina (Holmer *et al.* 1999).

Occurrence in Kazakhstan. Upper Cambrian, Kyrshabakty section, *Acutagnostus acutus-Erixanium* beds to *Eorudagnostus ovaliformis-Pareuloma* beds, localities 1356-4, 1357, 1357-1–3, 1358, 1359, 1359-1, 1360, 1360-1, 1360-2, 1360-5, 1361-4, 1360-7, 1373, 1378-20, 1378-23, 1379, 1381, 1381-2, 1381-3.

Quadrisonia suspensa Koneva and Popov, 1988

Plate 32, figures 12–15

1988 *Quadrisonia suspensa* Koneva and Popov, p. 57, pl. 1, figs 9–11.

Holotype. CNIGR 8/12034, dorsal valve (Koneva and Popov 1988, pl. 1, fig. 5); Upper Cambrian, *Lophosaukia–Ivshinaspis* beds, Batyrbay section (68 m), Malyi Karatau.

Material. One complete shell, nine ventral and five dorsal valves.

Emended diagnosis. Ventral valve low conical with maximum height at submarginal umbo; ventral pseudointerarea invariably procline. Well-developed external and internal pedicle tube.

Description. Shell subcircular to transversely suboval, about 80 per cent as long as wide. Ventral valve forming a low cone with maximum height at the submarginal umbo. Ventral pseudointerarea procline, poorly defined laterally and bisected by a weak interridge. Anterior and lateral valve slopes gently and evenly convex in profile. Pedicle foramen enclosed within the larval shell at the end of short external pedicle tube. Dorsal valve moderately convex with the maximum thickness in the posterior third of the valve. Dorsal pseudointerarea low, occupying about 50 per cent of the valve width, divided by a concave, lens-like median groove.

Apical process subtriangular, bridging posterior and anterior slopes of the valve, extending forward for somewhat less than 50 per cent of the valve length and perforated posteriorly by a short, conical internal pedicle tube. Dorsal median ridge low, slightly thickened, extending anteriorly for about 66 per cent of the maximum valve length and buttressed posteriorly. Dorsal anterocentral muscle scars poorly defined, at about mid-valve length. Dorsal cardinal muscle fields strongly impressed, elongate suboval and bounded by an elevated rim.

Dimensions of specimens from Batyrbay were given by Koneva and Popov (1988, p. 57).

Remarks. *Quadrisonia suspensa* differs both from *Q. minor* and *Q. declivis* in having a more procline ventral valve with the maximum height at a relatively long external pedicle tube. The ventral valve of *Q. simplex* Koneva, Popov and Ushatinskaya has a more subcentral apex by comparison with *Q. suspensa*, and the latter also differs from all other species of *Quadrisonia* in having a well-developed internal pedicle tube.

Occurrence in Kazakhstan. Upper Cambrian, Batyrbay section, Malyi Karatau; *Lophosaukia–Ivshinaspis* beds, sample 68 m; *Harpidoides-Platypeltoides* beds, sample 77 m.

Quadrisonia? sp.

Plate 44, figures 14–15

Material. One complete shell (L = 1·34).

Remarks. This single specimen from the *Kormagnostus simplex* Biozone in the Kyrshabakty section (sample 1351-I) of Malyi Karatau is referred only questionably to *Quadrisonia*. It has a subcircular, ventribiconvex shell with a weakly procline ventral pseudointerarea divided by an indistinct intertrough. The small pedicle foramen is confined within the larval shell. The dorsal valve is gently convex and has a narrow pseudointerarea with a broad, lens-like median groove. The interior of both valves is unknown and there are no other comparable acrotretid shells in our samples.

Genus PICNOTRETA Henderson and MacKinnon, 1981

Type species. Original designation by Henderson and MacKinnon (1981, p. 301); *Picnotreta debilis* Henderson and MacKinnon, 1981; Upper Cambrian, Mindyallian, Mungerebar Limestone, western Queensland, Australia.

Diagnosis. See Henderson and MacKinnon 1981, p. 300.

Remarks. Rowell (1988, p. 139) most recently summarised information on this comparatively rare but widely distributed genus. According to Rowell *et al.* (1984) and Rowell and Zell (1988) there are a number of undescribed species from North America and questionably also from Antarctica. Our new species extends its distribution through Central Asia.

Species assigned. *Picnotreta debilis* Henderson and MacKinnon, 1981; *Picnotreta* sp., Zell and Rowell 1988; *Picnotreta karakichiensis* sp. nov.

Occurrence. North America, Middle Cambrian–lower Upper Cambrian; Australia (Queensland), New Zealand and ?Antarctica (northern Victoria Land), Middle Cambrian (Mindyallian); Kyrgyzstan and Kazakhstan, Middle Cambrian (Mayaian)–lower Upper Cambrian; North Greenland, upper Middle Cambrian; western Argentina (Precordillera), upper Middle Cambrian–lower Upper Cambrian.

Picnotreta karakichiensis sp. nov.

Plate 31, figures 4–16

Derivation of name. After the Karakichi River near the type locality in Kyrgyzstan.

Holotype. NMW 98.61G.168, dorsal valve; Upper Cambrian, Karadzhorga Formation, sample 127/9, Moldotau Range, eastern side of Karakichi River, Kyrgyzstan.

Material. 22 ventral and 23 dorsal valves.

Diagnosis. Dorsal valve with shallow sulcus originating somewhat anterior to mid-valve length; dorsal pseudointerarea well defined, narrow, occupied mainly by median groove; apical process low, elongate subtriangular, extending to mid-valve length.

Description. Shell biconvex, subtriangular. Ventral valve moderately convex with maximum thickness between the umbo and mid-valve length. Ventral pseudointerarea strongly apsacline, narrow, occupied mainly by a broad, weakly

TABLE 17. *Picnotreta karakichiensis* sp. nov., dimensional data for dorsal valves from the Moldotau Range, eastern side of Karakichi River (sample 127/9, Middle Cambrian, Karadzhorga Formation).

	Ld	W	Il	Iw	Cl	Cw	Sa	Sm	Ld/W	Iw/W	Cl/L	Cw/W	Sa/Ld	Sm/Ld
N	4	4	4	4	3	3	4	4	4	4	3	3	4	4
X	1·00	1·18	0·135	0·52	0·4	0·64	0·73	0·7725	84%	44%	35%	49%	74%	77%
S	0·278	0·283	0·053	0·158	0·053	0·04	0·336	0·241	7·7	8·1	4·4	2·3	25·3	7·0
MIN	0·58	0·78	0·06	0·3	0·36	0·6	0·4	0·44	74%	36%	33%	46%	36%	68%
MAX	1·16	1·38	0·18	0·64	0·46	0·68	1·02	0·96	93%	54%	40%	51%	89%	84%

concave intertrough. Pedicle foramen small, rounded, within the larval shell. Dorsal valve moderately and evenly convex, just over 80 per cent as long as wide (Table 17) with a variably developed, very shallow median sulcus. Dorsal pseudointerarea narrow, occupied mainly by a concave median groove. Propareas rudimentary, weakly apsacline. Ornament of very fine, regularly spaced rugellae.

Ventral interior with apical process occluding the apex, extending anteriorly as a low, subtriangular, elongated platform with a shallow depression anterior to the internal foramen. Dorsal interior with a blade-like, triangular median septum, originating as low ridge directly beneath the pseudointerarea and extending forward for about three-quarters of valve length. Dorsal cardinal muscle scars usually weakly impressed, but bounded by an elevated rim in gerontic specimens.

Remarks. These specimens from Kazakhstan are comparable with the type species in the size and profile of both valves, as well as in having a low, subtriangular apical process occluding the apex, and a blade-like, triangular dorsal median septum. The main difference between the species is in the narrow, but well-defined dorsal pseudointerarea in *P. karakichiensis*. A well-defined dorsal pseudointerarea is also present in *Picnotreta* sp. (Rowell and Zell 1988) from Greenland, but the apical process in this species is perforated by the internal pedicle foramen. The Kazakhstanian species differs from both these taxa in having a very shallow dorsal sulcus.

Occurrence in Kazakhstan. Middle Cambrian (Mayaian)–Upper Cambrian, area about 4 km south-east of Sarykumy railway station, Sarykumy Formation, samples F-132, F-135; Karadzhorga Formation, eastern side of Karakichi river, sample 129/7.

Genus RHONDELLINA Rowell, 1986

1986 *Rhondellina* Rowell, p. 1059.

Type species. Original designation by Rowell (1986); *Rhondellina dorei* Rowell 1986; Upper Cambrian, *Crepicephalus* Biozone, upper Hamburg Limestone, McGill, Nevada, USA.

Diagnosis. See Rowell 1986, p. 1059.

Species included. Rhondellina dorei Rowell 1986; *Rhondellina karatauensis* Koneva, 1992.

Occurrence. Middle–Upper Cambrian (*Lejopyge laevigata–Glyptagnostus stolidotus* biozones); USA (Nevada), northern Greenland, Kazakhstan (Malyi Karatau Range).

Rhondellina karatauensis Koneva, 1992

Plate 34, figures 1–14

1992 *Rhondellina karatauensis* Koneva, p. 93, pl. 11, figs 1–9.

Holotype. IGNA 427/461, conjoined valves (Koneva 1992, pl. 11, fig. 4); Upper Cambrian, *Glyptagnostus stolidotus* Biozone, Kyrshabakty section, sample 1352-III, Malyi Karatau.

Material. Four complete shells, 41 ventral and 25 dorsal valves.

Diagnosis. Rhondellina with a fine, bifurcating, dorsal median ridge.

Description. Shell slightly dorsibiconvex, transversely oval, about 80–85 per cent as long as wide. Ventral valve gently convex with a marginal umbo. Ventral pseudointerarea vestigial, apsacline, undivided. Pedicle foramen subcircular, situated within a flattened, slightly depressed posterior part of the larval shell. Dorsal valve moderately and evenly convex with a low, orthocline pseudointerarea divided by a narrow, concave median groove.

Ventral interior with a high, ridge-like apical process, extending forward to about mid-valve length. Dorsal cardinal muscle fields slightly raised. Dorsal median ridge faint, extending anterior to mid-valve length, and bifurcating near its anterior extremity.

Dimensions. NMW 98.61G.208, ventral valve, L = 0·94, W = 1·02, Al = 0·38; NMW 98.61G.210, incomplete dorsal valve, L = 0·78, W = 0·84.

Remarks. R. karatauensis is very similar to the type and only other known species *R. dorei* in the external morphology of both valves, as well as in having a vestigial, undivided ventral pseudointerarea and a ridge-like apical process anterior to the internal foramen. The main difference is the presence of the fine bifurcating dorsal median ridge in *R. karatauensis*. Koneva (1992, p. 94) also pointed to some further differences between the two species in the morphology of the umbonal areas of both valves, but our observations suggest that characters of the larval shell are identical for both species.

Occurrence in Kazakhstan. Kyrshabakty section, *Glyptagnostus stolidotus* Biozone, samples 1351, 1351-1-1, 1352, 1352-I-1, 11352-II, 1352-I-III.

Genus SATPAKELLA Koneva, Popov and Ushatinskaya, 1990

Type and only species. Original designation by Koneva *et al.* (1990, p. 162); *Satpakella inconstans* Koneva, Popov and Ushatinskaya, 1990; Upper Cambrian, Kujandy Formation, north-eastern central Kazakhstan.

Diagnosis. Shell transversely oval; ventral valve subcylindrical; pseudointerarea procline to apsacline, poorly defined laterally with weak intertrough; foramen enclosed within larval shell; dorsal pseudointerarea anacline or orthocline with wide median groove; apical process small, perforated by short pedicle tube; dorsal median septum triangular, strongly thickened with bulbous projection at top; median buttress present; dorsal cardinal muscle field forming thickened platform.

Satpakella? sp.

Plate 30, figures 13–14

Material. One dorsal valve (L = 1·21, W = 1·54, Il = 0·16, Iw = 0·98, Pw = 0·48; Cl = 0·56, Cw = 1·04, Sa = 1·08, Sm = 0·96, St = 0·36).

Description. Ventral valve unknown. Dorsal valve moderately convex, transversely oval, about 80 per cent as long as wide. Dorsal pseudointerarea moderately high, subtriangular, raised above the valve floor, occupying about 65 per cent of valve width. Median groove concave, broadly subtriangular, occupying about 30 per cent of width of pseudointerarea.

Dorsal interior with strongly impressed, subcircular cardinal muscle fields bounded by a high rim. Median septum triangular, strongly thickened anteriorly, with bulbous thickening on the top and extending forward for about 90 per cent of the valve length.

Remarks. This single valve is most similar to *Satpakella inconstans* in having strongly impressed dorsal cardinal muscle scars and a strongly thickened, triangular, median septum with a bulbous projection on the top. It differs in having a longer median septum and in the absence of dorsal geniculation, so we refer it only provisionally to *Satpakella*.

Occurrence in Kazakhstan. Kyrshabakty section, *Trisulcagnostus trisulcus-Saukiella* beds, sample 1401-6.

Genus STILPNOTRETA Henderson and MacKinnon, 1981

1981 *Stilpnotreta* Henderson and MacKinnon, p. 297

Type species. Original designation by Henderson and MacKinnon (1981, p. 297); *Stilpnotreta magna* Henderson and MacKinnon, 1981; Upper Cambrian, Mindyallian, Mungerebar Limestone, western Queensland, Australia.

Diagnosis. Shell almost equibiconvex, subcircular to transversely oval with short, convex posterior margin; ventral pseudointerarea vestigial; foramen enclosed within larval shell; dorsal pseudointerarea orthocline with wide median groove and vestigial propareas; apical process subtriangular, occluding apex, extending to mid-valve; dorsal visceral field with narrow anterior projection extending to mid-valve, bisected by low median ridge; median buttress absent.

Species included. *Stilpnotreta magna* Henderson and MacKinnon, 1981; *Stilpnotreta tecta* Koneva, 1990; *Stilpnotreta* sp. (Puura and Holmer 1993); *Stilpnotreta inaequalis* Ushatinskaya, 1994; *Stilpnotreta galinae* Popov, Holmer and Gorjansky, 1996 [=*Neotreta* (?) *pusilla* Ushatinskaya, 1986]; *Stilpnotreta minuta* sp. nov.

Occurrence. Middle–Upper Cambrian; Australia (New South Wales, Queensland) and New Zealand (Boomerangian–Mindyallan), Kazakhstan, Kyrgyzstan, Novaya Zemlya, Siberia (Eirina and Tjuessaly formations), Antarctica, Sweden, Great Britain.

Stilpnotreta magna Henderson and MacKinnon, 1981

Plate 34, figures 15–18; Plate 35, figures 1–11

1981 *Stilpnotreta magna* Henderson and MacKinnon, p. 298, figs 7A–J, 8, table 3.

Holotype. JCF 10720, dorsal valve; Upper Cambrian, Mindyallian, Mungerebar Limestone, western Queensland, Australia.

Material. 14 complete shells, 462 ventral and 313 dorsal valves.

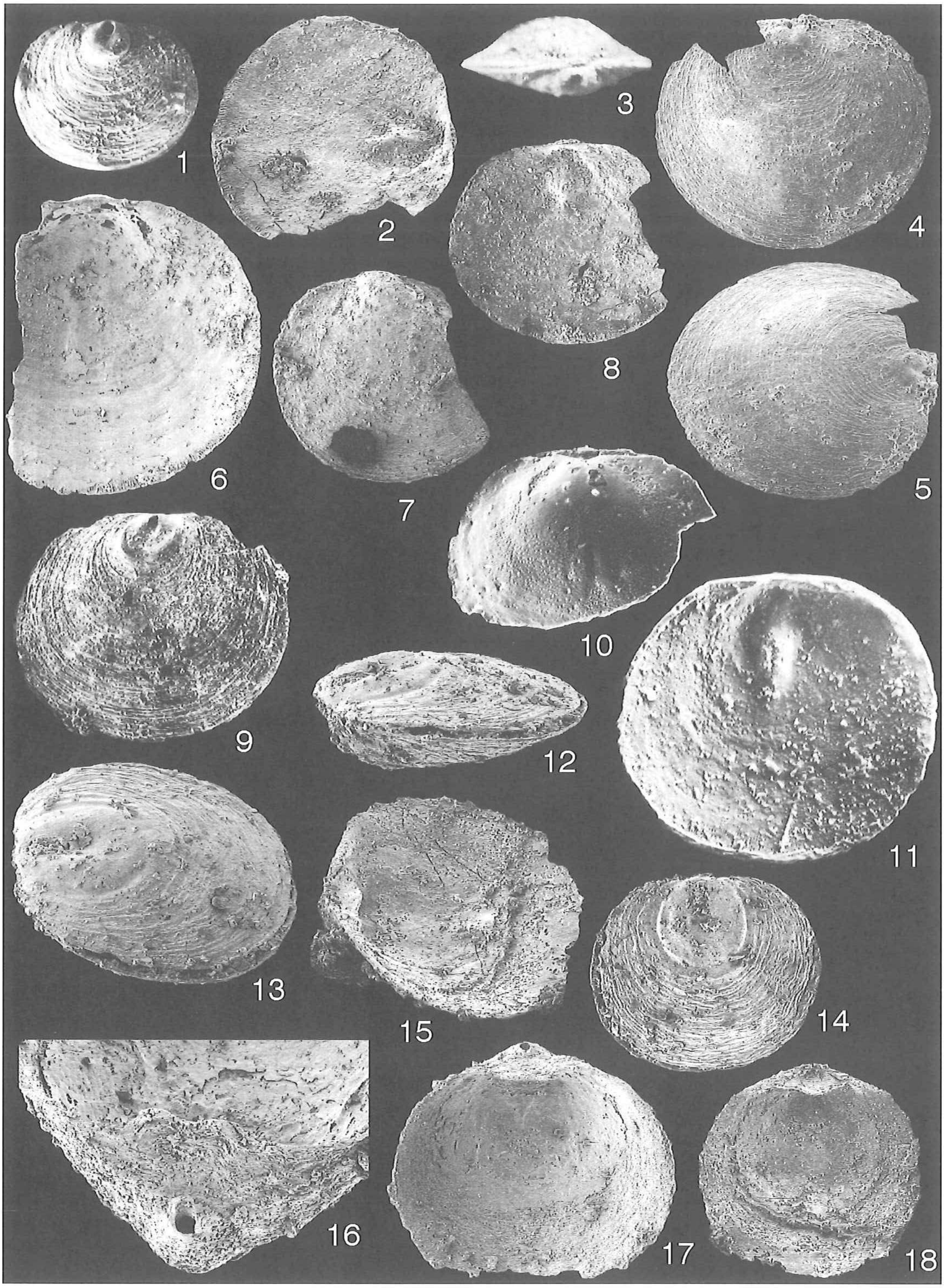
Diagnosis. See Henderson and MacKinnon 1981, p. 298.

Remarks. Our material from Kazakhstan is more or less identical with the Australian type species in the development of the dorsal and ventral pseudointerarea and in the convexity and shape of both valves. However, the apical process is somewhat less well developed and the dorsal median septum is slightly lower and less pronounced than in type *S. magna*, and the cardinal muscle scars are difficult to observe. The Kazakhstan shells are less well preserved, and it is possible that the observed differences are due at least partly to this fact rather than to specific separation.

EXPLANATION OF PLATE 34

Figs 1–14. *Rhondellina karatauensis* Koneva; Upper Cambrian, Shabakty Group, *Glyptagnostus stolidotus* Biozone, Malyi Karatau, Kyrshabakty section. 1, IGNA 427/471, ventral valve exterior, sample 1352-III; ×33. 2, 8, NMW 98.61G.208, ventral valve interior in oblique lateral and normal views, sample 1352-III; ×45, ×53. 3, IGNA 427/461, conjoined valves, posterior view, sample 1352; ×41. 4–5, NMW 98.61G.226, ventral valve exterior in normal and oblique posterior view, sample 1352-II; ×45, ×40. 6, NMW 98.61G.209, incomplete dorsal valve interior, sample 1352-II; ×63. 7, NMW 98.61G.210, incomplete dorsal valve exterior, sample 1352-III; ×48. 9, IGNA 427457, ventral valve exterior, sample 1352; ×30. 10, IGNA 427469, incomplete dorsal valve interior, sample 1352-III; ×40. 11, IGNA 427/463, ventral valve interior, sample 1352-III; ×60. 12–14, NMW 98.69G.16, sample 1352-III, conjoined valves in lateral view, ×89; oblique lateral view, ×96; and ventral view, ×69.

Figs 15–18. *Stilpnotreta magna* Henderson and MacKinnon; Middle Cambrian, Sarykumy Formation, Sarykumy section, sample K-20/132. 15, 18, NMW 98.61G.212, dorsal valve interior in oblique lateral and normal views; ×62, ×53. 16–17, NMW 98.61G.213, ventral valve interior, oblique posterior view showing detail of pseudointerarea with intertrough and paired denticles, and normal view; ×146, ×74.



HOLMER *et al.*, *Rhondellina*, *Stilpnotreta*

Occurrence in Kazakhstan. Middle Cambrian, Sarykumy Formation, samples F-29, F-102, F-104, F-132, F-134.

Stilpnotreta minuta sp. nov.

Plate 35, figures 12–16; Plate 36, figures 1–13

Derivation of name. Latin *minutus*, small; alluding to the small size.

Holotype. NMW 98.61G.227, ventral valve; Upper Cambrian, Sarakumy Formation, area about 4 km north-east of Sarakumy railway station, locality F-134, central Kazakhstan.

Paratypes. Five complete shells, 66 ventral and 53 dorsal valves.

Diagnosis. Shell small for genus, slightly ventribiconvex, subcircular, almost as long as wide; ventral pseudointerarea extremely short and wide, vestigial and almost not visible; dorsal pseudointerarea better developed; pseudointerarea of both valves lacking 'denticles' and 'sockets'; apical process, low, subtriangular, extending forward for about 50 per cent of valve length.

Description. Shell small for genus, slightly ventribiconvex, subcircular, about 95–100 per cent as long as wide (Table 18). Ventral valve moderately convex, close to 40 per cent as high as long, with maximum thickness somewhat anterior to the umbo. Ventral pseudointerarea extremely small to vestigial, consisting only of a narrow and short, concave intertrough, and occupying about 40 per cent of valve width (Table 18). Dorsal valve moderately convex, about 33 per cent as high as long (Table 19). Dorsal pseudointerarea better developed by comparison with ventral areas, consisting almost entirely of a broad, concave, lens-shaped median groove and occupying on average 40 per cent of the valve width (Table 19); pseudointerarea of both valves lacking 'denticles' and 'sockets'.

Apical process poorly visible, low, subtriangular, extending forward to close to 50 per cent of the valve length. Cardinal muscle fields of both valves poorly preserved. Dorsal median ridge very faint, extending anteriorly on average to 65 per cent of valve length (Table 19). Median buttress not developed.

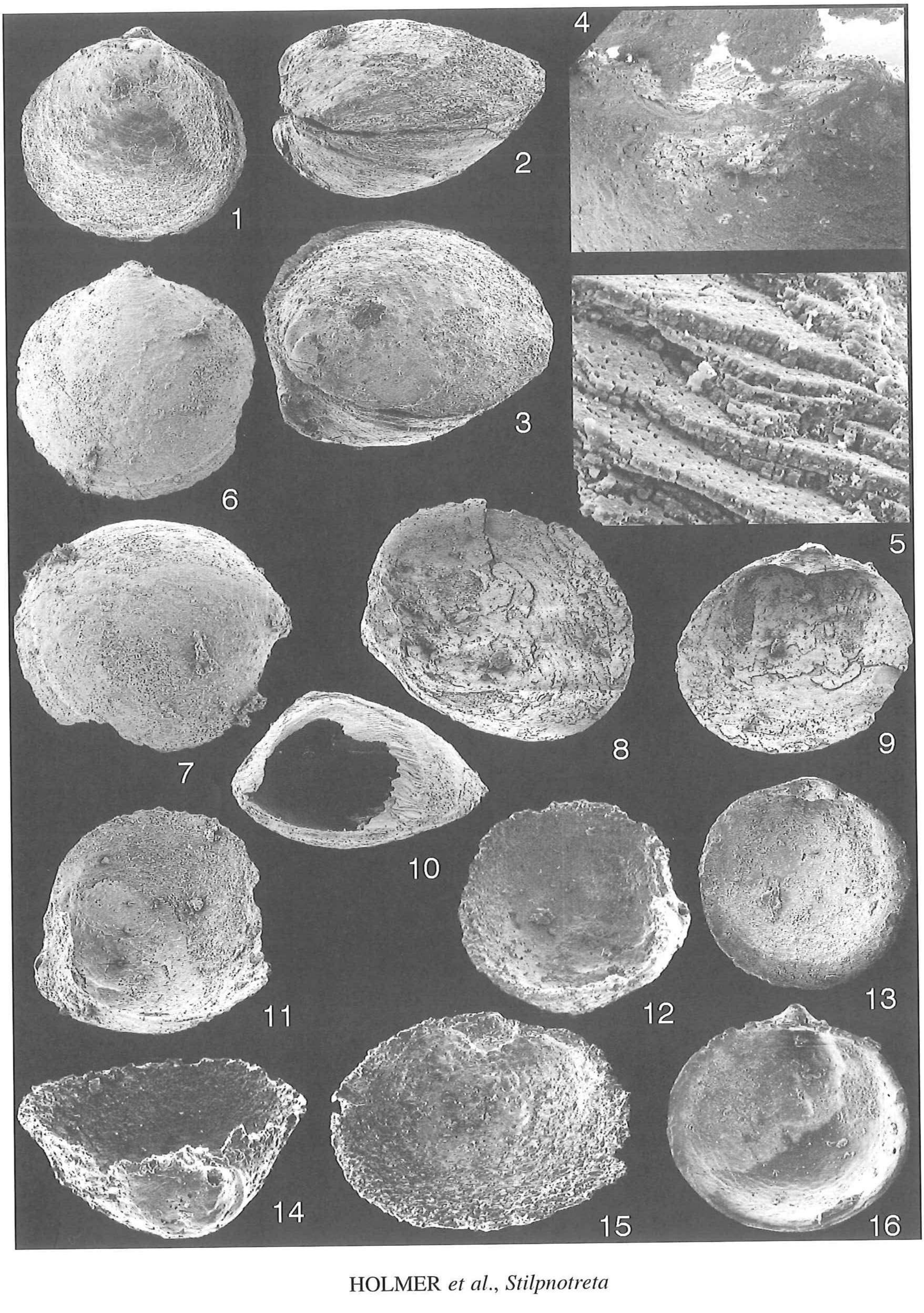
TABLE 18. *Stilpnotreta minuta* sp. nov., dimensional data for ventral valves from the Sarykumy section (sample 134, Middle Cambrian, Sarykumy Formation).

	Lv	W	T	Il	Iw	Al	Lv/W	T/L	A/L	Il/L	Iw/W
N	30	30	29	30	30	20	30	29	20	29	30
X	0·47	0·47	0·18	0·07	0·20	0·22	100%	38%	48%	15%	42%
S	0·037	0·044	0·022	0·011	0·036	0·026	4·7	4·5	5·0	2·0	6·1
MIN	0·42	0·42	0·14	0·06	0·16	0·16	87%	29%	36%	12·5%	32%
MAX	0·58	0·62	0·23	0·10	0·30	0·26	108%	46%	62%	19%	55%

EXPLANATION OF PLATE 35

Figs 1–11. *Stilpnotreta magna* Henderson and MacKinnon; Middle Cambrian, Sarykumy Formation, Sarykumy section, sample K-20/132. 1–3, NMW 98.61G.214, conjoined valves in dorsal view, ×64; lateral view, ×82; and oblique lateral view, ×87. 4–5, 10, NMW 98.61G.215, conjoined valves showing detail of umbonal area and articulation inside the shell, ×300; shell structure, ×1272; and oblique lateral view of the specimen, ×75. 6–7, NMW 98.61G.216, ventral valve exterior in normal and oblique lateral views; ×68, ×79. 8–9, NMW 98.61G.217, dorsal valve interior in oblique lateral and normal views; ×73, ×58. 11, NMW 98.61G.218, ventral valve interior in oblique lateral view; ×75.

Figs 12–16. *Stilpnotreta minuta* sp. nov.; Middle–Upper Cambrian, Sarykumy Formation, Sarykumy section. 12, 14, NMW 98.61G.219, ventral valve interior in oblique lateral and oblique posterior views, sample 140; both ×65. 13, NMW 98.61G.220, dorsal valve interior, sample 134; ×85. 15, NMW 98.61G.221, dorsal valve interior, sample 140; ×65. 16, NMW 98.61G.222, ventral valve interior, sample 134; ×75.



HOLMER *et al.*, *Stilpnotreta*

TABLE 19. *Stilpnotreta minuta* sp. nov., dimensional data for dorsal valves from the Sarykumy section (sample 134, Middle Cambrian, Sarykumy Formation).

	Ld	W	T	Il	Iw	Sa	Ld/W	T/Ld	Sl/Ld	Il/Ld	Iw/W
N	22	22	22	22	22	13	22	21	10	21	22
X	0·45	0·47	0·14	0·06	0·18	0·29	96%	32%	65%	13%	40%
S	0·050	0·044	0·028	0·015	0·024	0·057	5·8	6·5	8·5	2·1	4·9
MIN	0·34	0·38	0·10	0·04	0·14	0·20	88%	22%	57%	9%	33%
MAX	0·54	0·54	0·18	0·10	0·24	0·40	110%	53%	83%	19%	50%

Remarks. This species is smaller than other known species of *Stilpnotreta* (e.g. Tables 19–20). *S. minuta* also differs from most other species in the poorly developed pseudointerareas of both valves, which invariably lack 'denticles' and 'sockets'. In the nature of the pseudointerareas it is most similar to *S. tecta* (see below), but it differs markedly from the latter in the poor development of a dorsal median ridge and apical process, and in the complete absence of a median buttress.

Occurrence in Kazakhstan. Upper Cambrian, Sarykumy Formation, samples F-134, 140.

Stilpnotreta tecta Koneva, 1990

Plate 36, figure 14; Plate 37, figures 1–14

1990 *Stilpnotreta tecta* Koneva, p. 54, pl. 6, figs 18–24.

Holotype. IGNA 427/451, ventral valve (Koneva 1990, pl. 6, fig. 18); Middle Cambrian, Amgaian, *Ptychagnostus intermedius* beds; Kyrshabakty section, 1465/1, Malyi Karatau.

Material. Four complete shells, 41 ventral and 25 dorsal valves.

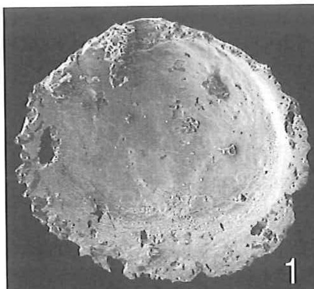
Emended diagnosis. Pseudointerareas of both valves very small to vestigial, lacking 'denticles' and 'sockets'; apical process long, extending almost to mid-valve length; dorsal median ridge low, slightly thickened posteriorly and extending anteriorly to about 66 per cent of valve length; median buttress well developed; cardinal muscle fields of both valves comparatively short, extending to about 33 per cent of valve length.

EXPLANATION OF PLATE 36

Figs 1–13. *Stilpnotreta minuta* sp. nov.; Middle–Upper Cambrian, Sarykumy Formation, Sarykumy section. 1, NMW 98.61G.223, dorsal valve interior, sample 134; ×90. 2, 5, 7, NMW 98.69G.9, sample 134, ventral valve exterior in normal view, ×90; oblique lateral view, ×102; and detail of pitted micro-ornament of the larval shell, ×364. 3, NMW 98.61G.221, dorsal valve interior, oblique posterior view, sample 140; ×111. 4, 11, NMW 98.61G.225, ventral valve in oblique lateral and normal views, sample 134; ×102, ×84. 6, 10, NMW 98.69G.10, dorsal valve exterior, oblique posterior view of larval shell, and normal view, sample 134; ×205, ×84. 8, NMW 98.61G.227, holotype, ventral valve interior, sample 134; ×91. 9, NMW 98.61G.230, dorsal valve exterior sample 134; ×95. 12, NMW 98.61G.229, conjoined valves, lateral view, sample 134; ×99. 13, NMW 98.61G.228, ventral valve interior, oblique lateral view, sample 134; ×82.

Fig. 14. *Stilpnotreta tecta* Koneva; Middle Cambrian, *Ptychagnostus intermedius* Biozone, Kyrshabakty section, sample 1314; NMW 98.61G.231, dorsal valve exterior, oblique lateral view; ×60.

Fig. 15. *Linnarssonia constans* Koneva; Lower Cambrian, Shabakty Group, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, Malyi Karatau, Baba-Ata section, sample 5/26b; NMW 98.69G.8, ventral valve interior, oblique lateral view showing apical process and cardinal muscle fields; ×80.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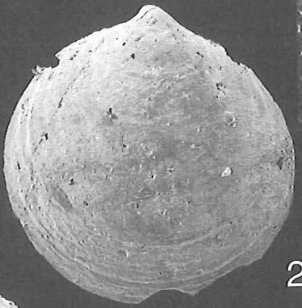
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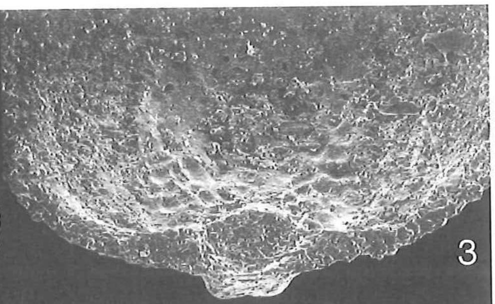
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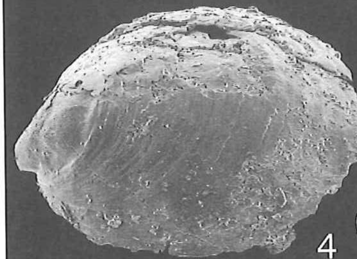
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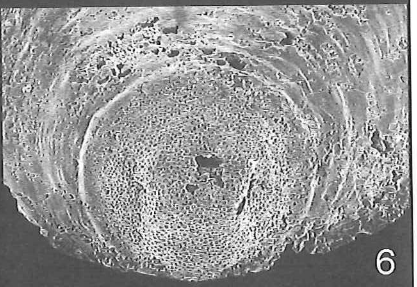
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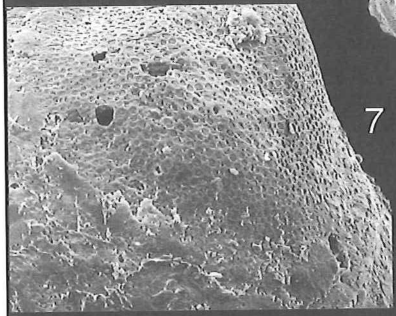
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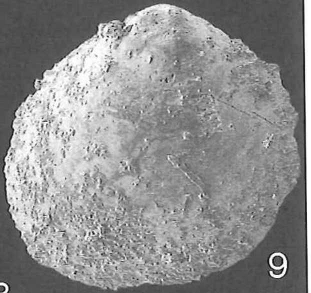
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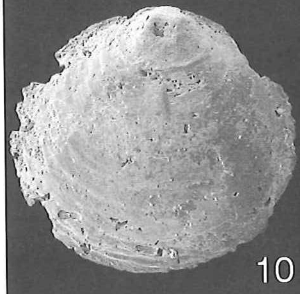
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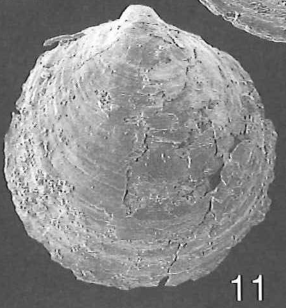
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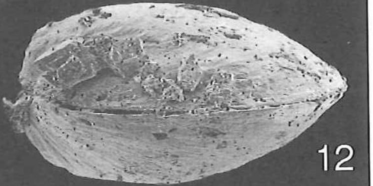
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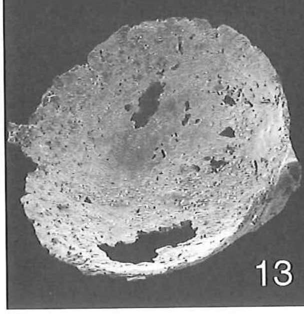
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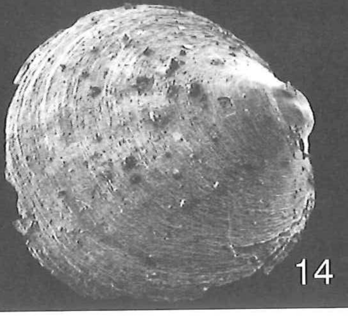
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HOLMER *et al*., *Linnarssonia*, *Stilpnotreta*

Description. Shell equibiconvex, transversely oval, close to 90 per cent as long as wide (Table 20). Ventral valve moderately convex, about 33 per cent as high as long with maximum height somewhat anterior to umbo. Ventral pseudointerarea small, low, strongly apsacline, occupied mainly by a broad, concave intertrough, and occupying 25–30 per cent of valve width (Table 20). Dorsal valve moderately convex, about 30 per cent as high as long (Table 21). Dorsal pseudointerarea vestigial, consisting almost entirely of a broad, concave, lens-shaped median groove, and occupying about 25 per cent of valve width (Table 21).

Apical process low, subtriangular, occluding the umbonal area, with a shallow excavation in the median part and extending forward to about 45 per cent of valve length (Table 20). Ventral cardinal muscle fields large but comparatively short, elongate, suboval, strongly impressed. Dorsal median ridge low, slightly thickened posteriorly and extending anteriorly to just over 60 per cent of valve length (Table 21). Median buttress well developed, subtriangular. Dorsal cardinal muscle fields large but comparatively short, elongated, suboval, extending anteriorly to about 33 per cent of the valve length (Table 21). Anterocentral muscle scars small, elongate suboval, located at about mid-valve, usually weakly impressed.

TABLE 20. *Stilpnotreta tecta* Koneva, dimensional data for ventral valves from the Kyrshabakty section (samples 1314, 1314-2, Middle Cambrian, *Ptychagnostus itermedius* Biozone).

	Lv	W	T	Il	Iw	Al	Aw	Lv/W	T/Lv	Iw/W	A/Lv
N	10	10	10	10	19	9	9	10	10	10	9
X	0·66	0·75	0·22	0·061	0·19	0·30	0·18	89%	34%	27%	44%
S	0·238	0·265	0·082	0·025	0·049	0·069	0·059	5·6	4·9	5·5	5·2
MIN	0·32	0·40	0·12	0·03	0·12	0·22	0·11	80%	26%	21%	35%
MAX	1·16	1·24	0·36	0·10	0·26	0·41	0·28	96%	42%	36%	53%

TABLE 21. *Stilpnotreta tecta* Koneva, dimensional data for dorsal valves from the Kyrshabakty section (samples 1314, 1314-2 m, Middle Cambrian, *Ptychagnostus intermedius* Biozone).

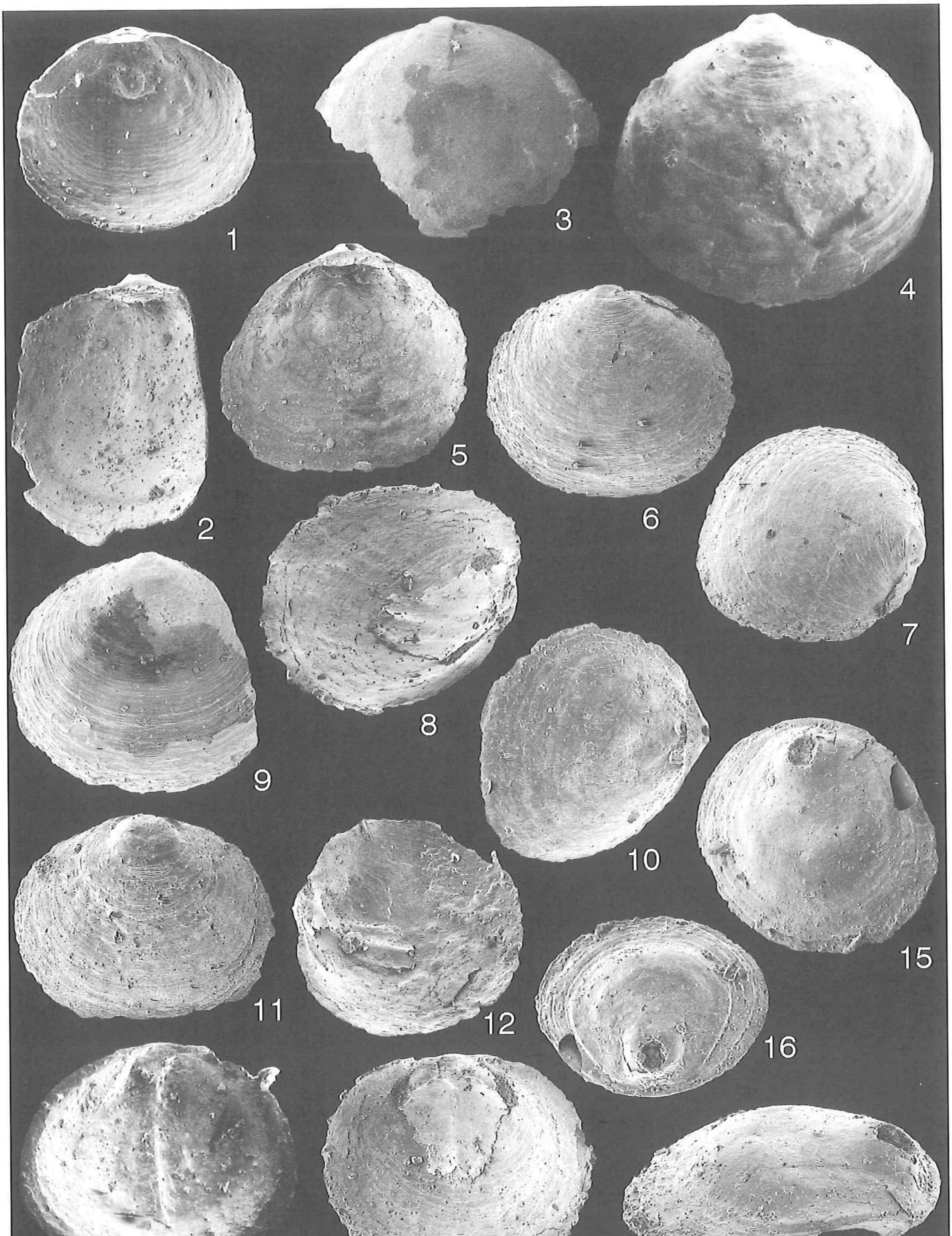
	Ld	W	T	Il	Iw	Cl	Cw	Sa	Ld/W	T/Ld	Iw/W	Cl/Ld	Cw/W	Sa/Ld
N	8	8	8	8	8	8	8	6	8	8	8	8	8	6
X	0·62	0·70	0·18	0·06	0·18	0·20	0·38	0·38	88%	29%	24%	32%	54%	63%
S	0·110	0·126	0·046	0·029	0·073	0·045	0·096	0·087	4·1	4·5	5·4	3·2	5·9	5·6
MIN	0·52	0·58	0·11	0·02	0·12	0·14	0·28	0·28	83%	19%	19%	27%	47%	54%
MAX	0·80	0·92	0·24	0·10	0·30	0·26	0·54	0·54	94%	33%	33%	36%	63%	69%

EXPLANATION OF PLATE 37

Figs 1–14. *Stilpnotreta tecta* Koneva; Middle Cambrian, *Peronopsis*? *ultimus–Ptychagnostus intermedius* biozones, Malyi Karatau, Kyrshabakty section. 1, IGNA 427/451, holotype, ventral valve interior, sample 1465; ×44. 2, NMW 98.61G.232, incomplete ventral valve interior, sample 1314; ×55. 3, NMW 98.61G.232, incomplete dorsal valve exterior, sample 1314-2; ×33. 4, NMW 98.61G.234, ventral valve exterior, sample 1314-2; ×24. 5, 10, NMW 98.61G.235, ventral valve interior in normal and oblique lateral views, sample 1314-2; ×72, ×73. 6–7, NMW 98.61G.236, dorsal valve exterior in normal and oblique lateral views, sample 1314; both ×51. 8, 14, NMW 98.61G.237, dorsal valve interior in oblique lateral and normal views, sample 1314; ×70, ×61. 9, NMW 98.61G.238, dorsal valve exterior, sample 1314-2; ×55. 11, NMW 98.61G.239, dorsal valve exterior, sample 1314; ×61. 12, NMW 98.61G.240, dorsal valve interior, oblique lateral view, sample 1314; ×49. 13, NMW 98.61G.241, dorsal valve interior, sample 1314; ×44.

Figs 15–17. *Akmolina*? aff. *minuta* (Mei); Upper Cambrian, *Ivshinagnostus ivshini-Irvingella major* beds, sample 1361-10, Malyi Karatau, Kyrshabakty section; NMW 98.61G.242, conjoined valves of juvenile specimen in ventral view, ×102; oblique posterior view, ×89; and lateral view, ×136.

PLATE 37



HOLMER *et al.*, *Akmolina*?, *Stilpnotreta*

Remarks. S. tecta differs from the type species and from most other species of the genus mainly in having smaller and less well-developed pseudointerareas in both valves, and in lacking the typical 'denticles' and 'sockets' present on the dorsal and ventral pseudointerareas of typical *Stilpnotreta*; these latter structures are best developed in *S. galinae* (Popov *et al.* 1996). Additionally, the cardinal muscle fields of *S. tecta* are shorter by comparison with those of the type species, which extend almost to mid-valve length.

Occurrence in Kazakhstan. Kyrshabakty section, *Peronopsis ultimus* and *Ptychagnostus intermedius* beds, samples 1467, 1465, 1465-1, 1314, 1314-2, 1314-4.

Genus TREPTOTRETA Henderson and MacKinnon, 1981

Type species. Original designation by Henderson and MacKinnon (1981, p. 293); *Treptotreta jucunda* Henderson and MacKinnon, 1981; Middle Cambrian, *Goniagnostus nathorsti* Biozone, Mailchange Limestone, western Queensland, Australia.

Diagnosis. See Popov and Holmer 1994, p. 123.

Remarks. Ushatinskaya (1994) regarded *Treptotreta* as junior synonym of *Angulotreta* Palmer, 1954. Both genera are closely similar in external shell characters, but *Treptotreta* differs in having a procline ventral pseudointerarea, a low, ridge-like apical process, mostly on the posterior slope of the valve, and a posteriorly located internal foramen. Moreover, the dorsal median septum in the type species of *Angulotreta*, *A. triangularis* Palmer, 1954, has a complex surmounting plate, whereas in *Treptotreta* the septum is invariably moderately high and blade-like. Some species of *Angulotreta* (e.g. *A. postapicalis* Palmer) are somewhat similar to *Treptotreta* in having a simple, triangular median septum, but they otherwise have the typical morphology of *Angulotreta*. As noted by Popov and Holmer (1994), *T. conversa* and *T. mutabilis* described by Mei (1993) from the Middle Cambrian of China (Hebei) differ from all other species in having a pedicle foramen that is not enclosed within the larval shell, and their systematic position is uncertain.

Species included. Angulotreta obliqua Ushatinskaya, 1994 in addition to species listed by Popov and Holmer (1994) and Engelbretsen (1996).

Occurrence. Middle Cambrian (Mayaian)–Upper Cambrian; Australia (Queensland, New South Wales), New Zealand, Novaya Zemlya, north-central Siberia, Kazakhstan, West Antarctica.

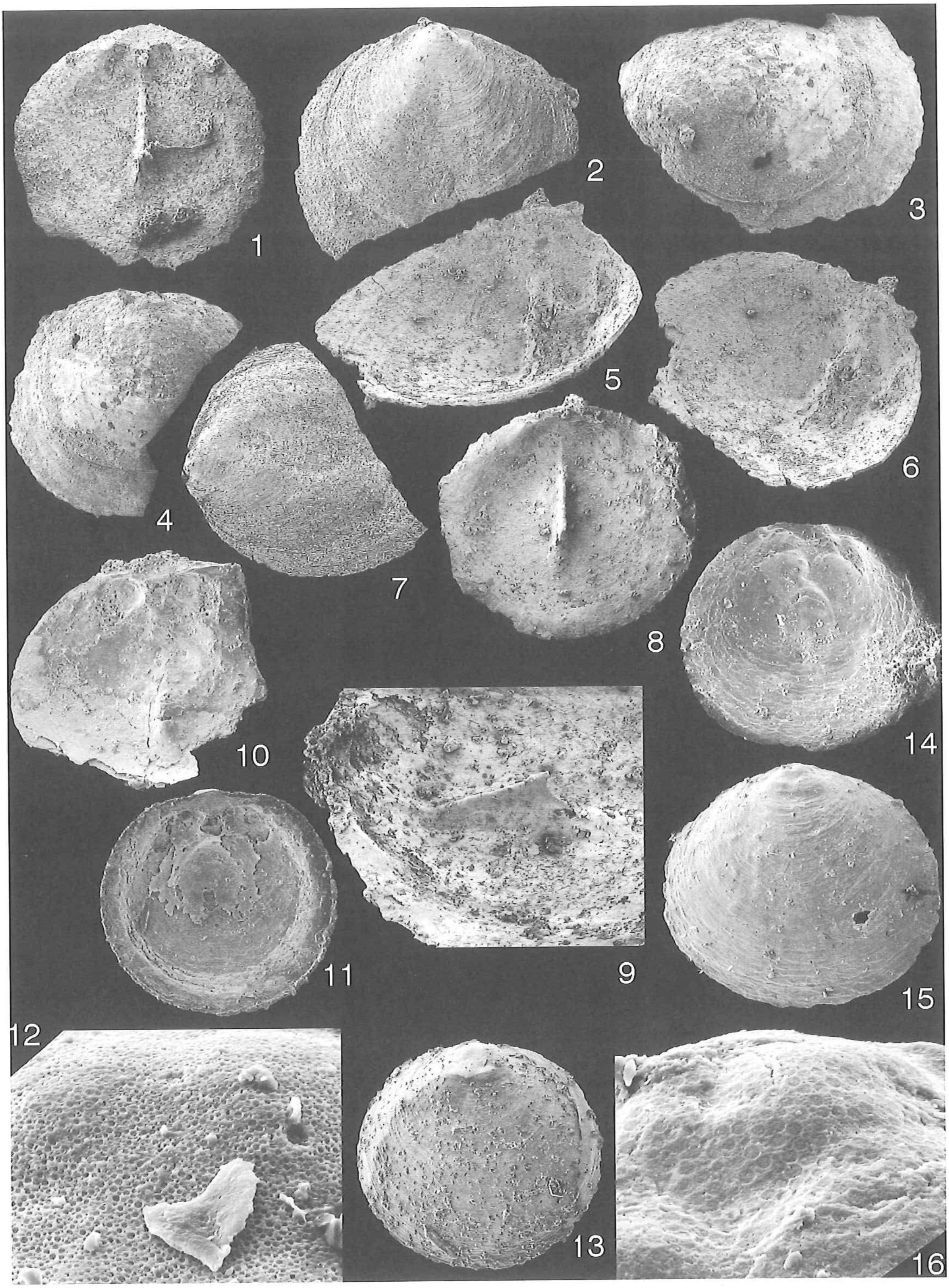
EXPLANATION OF PLATE 38

Figs 1–9. *Treptotreta* cf. *jacunda* Henderson and MacKinnon; Middle Cambrian, Sarykumy Formation, Sarykumy section. 1, NMW 98.61G.343, dorsal valve interior, sample K-20/132; ×44. 2, 7, NMW 98.61G.243, dorsal valve exterior in normal and oblique lateral views, sample K-20/132; both ×37. 3–4, NMW 98.61G.244, ventral valve exterior in oblique lateral and normal views, sample K-20/29; ×28, ×24. 5–6, NMW 98.61G.245, ventral valve interior in oblique anterior and oblique lateral views, sample K-20/132; ×40, ×36. 8–9, NMW 98.61G.246, dorsal valve interior in normal and oblique lateral views, sample K-20/29; ×42, ×77.

Figs 10–13. *Akmolina*? aff. *minuta* (Mei); Middle Cambrian, *Lejopyge laevigata* Biozone–Upper Cambrian, Malyi Karatau, Kyrshabakty section. 10, NMW 98.61G.247, incomplete dorsal valve interior, sample 1349-II; ×50. 11, NMW 98.61G.248, dorsal valve interior, sample 1351-I; ×55. 12–13, NMW 98.61G.249 dorsal valve exterior, detail of pitted micro-ornament of larval shell, and dorsal view, sample 1351; ×719, ×68.

Figs 14–16. *Akmolina*? sp. 2; Middle Cambrian, *Ptychagnostus intermedius* Biozone, Malyi Karatau, Kyrshabakty section, sample 1465-I. 14, NMW 98.61G.251, dorsal valve interior; ×64. 15–16, NMW 98.61G.250, dorsal valve exterior in normal view, and detail of pitted micro-ornament of larval shell; ×70, ×719.

PLATE 38



HOLMER *et al.*, *Akmolina*?, *Treptotreta*

TABLE 22. *Treptotreta* cf. *jucunda* Henderson and MacKinnon, dimensional data for dorsal valves from the Sarykumy Formation (sample 134, Middle Cambrian, Sarykumy Formation).

	Ld	W	Il	Iw	Pw	Cl	Cw	Sa	Ld/W	Iw/W	Cl/Ld	Cw/W	Sa/Ld
N	9	9	9	9	8	9	9	6	9	9	9	9	6
X	1·08	1·14	0·14	0·55	0·315	0·41	0·66	0·81	95%	48%	38%	56%	75%
S	0·319	0·344	0·062	0·218	0·111	0·139	0·244	0·339	7·1	10·1	3·7	6·8	5·6
MIN	0·78	0·76	0·08	0·34	0·22	0·26	0·38	0·54	83%	19%	27%	47%	69%
MAX	1·69	1·78	0·28	1·04	0·54	0·70	1·14	1·32	103%	58%	46%	64%	84%

Treptotreta cf. *jucunda* Henderson and MacKinnon, 1981

Plate 38, figures 1–9

cf. 1981 *Treptotreta jucunda*; Henderson and MacKinnon, p. 295, figs 5J–P, 6.
cf. 1996 *Treptotreta jucunda* Henderson and MacKinnon; Engelbretsen, p. 73, figs 2A–J (with synonymy).

Material. Four complete shells, 41 ventral and 25 dorsal valves.

Description. Shell subcircular. Ventral valve conical with eccentric umbo and maximum thickness in the umbonal area. Anterior and lateral valve slopes straight to gently convex in profile. Ventral pseudointerarea procline, poorly defined laterally and divided by a narrow, shallow intertrough. Pedicle foramen small, rounded, enclosed within the larval shell. Dorsal valve on average about 95 per cent as long as wide (Table 22), weakly convex in profile. Dorsal pseudointerarea low, weakly anacline, occupying close to 50 per cent of the valve width. Median groove concave, broadly subtriangular.

Ventral interior with apical process forming a low, broad ridge widening anteriorly and bridging posterior and anterior valve slopes. Internal pedicle tube short, conical, perforating the apical process near its posterior margin. Apical pits usually weakly impressed. *Vascula lateralia* baculate, poorly impressed proximally. Dorsal median septum moderately high, blade like, triangular, extending forward for about 80 per cent of the valve length. Maximum height of septum slightly anterior to mid-valve. Median buttress low, elongate subtriangular, widening posteriorly. Dorsal cardinal muscle fields poorly impressed, slightly elongate suboval, extending forward to close to 40 per cent of the valve length.

Remarks. Our material is not significantly different from the Australian type species in the convexity and sagittal profile of the ventral valve, inclination of the ventral pseudointerarea, and in characters of the apical process, dorsal cardinal muscle field and median septum. However, the Kazakhstanian valves are smaller on average, and the ventral valves are invariably strongly fragmented, making exact taxonomic discrimination difficult.

Occurrence in Kazakhstan. Middle Cambrian, Sarykumy Formation, Sarykumy section, samples F-29, F-102, F-104, F-132, F-134.

Family EPHIPPELASMATIDAE Rowell, 1965

Genus AKMOLINA Popov and Holmer, 1994

Type species. Original designation by Popov and Holmer (1994, p. 125); *Akmolina olentensis* Popov and Holmer, 1994; Upper Cambrian, Kujandy Formation, north-eastern central Kazakhstan.

Diagnosis. See Holmer and Popov 1994, p. 126.

Species included. Akmolina? *minuta* (Mei, 1993), *Akmolina*? aff. *minuta* (Mei, 1993); *Akmolina*? sp. 1 (herein), *Akmolina* sp. 2 (herein) in addition to species listed by Popov and Holmer (1994).

Occurrence. Upper Cambrian, Kujandy Formation, north-east central Kazakhstan; ?Middle Cambrian–Upper Cambrian (*Eorudagnostus kazakhstanicus-Pareuloma* beds)–Lower Ordovician (*Nileus* beds), Malyi Karatau; ?Upper Cambrian, upper *Blackwelderia paranai–Drepanura premesnili* biozones, North China

Akmolina cf. *olentensis* Popov and Holmer, 1994

Plate 39, figures 4–8, 11–13, 16

cf. 1994 *Akmolina olentensis* Popov and Holmer, p. 126, fig. 101.

Material. Five ventral and two dorsal valves.

Description. Shell ventribiconvex, slightly transversely subcircular. Ventral valve conical, up to almost 80 per cent as long as thick, with the maximum thickness in the umbonal area near the anterior margin of the larval shell. Anterior and lateral slopes of valve convex in profile. Ventral pseudointerarea catacline to weakly procline with a wide, shallow intertrough bisected by a weak median plication. Pedicle foramen small, rounded, within the larval shell at the end of a short external pedicle tube, which is strongly inclined posteriorly. Dorsal valve gently and unevenly convex with maximum thickness in the umbonal area. Dorsal pseudointerarea low and relatively short, occupying slightly more than 50 per cent of maximum valve width and divided by a shallow median groove which occupies up to 50 per cent of the width of the pseudointerarea. Ornament of very fine, evenly spaced rugellae.

Ventral interior with a weakly developed apical process, occluding the umbonal area, slightly ridged anteriorly. Dorsal interior weakly impressed, lacking median septum and buttress.

Dimensions. NMW 98.61G.261, ventral valve, L = 0·60, W = 0·68, T = 0·44; NMW 98.61G.263, ventral valve, L = 0·84, W = 0·89, T = 0·56; NMW 98.61G.264, L = 0·70, W = 0·82, Il = 0·08, Iw = 0·48, Pw = 0·22.

Remarks. Ventral valves from the Kyrshabakty section are indistinguishable from specimens of *Akmolina olentensis* from north-east central Kazakhstan. However, the dorsal valves in our material are somewhat different in having an unevenly and gently convex profile. There are too few specimens to make a more detailed comparison, and they are referred only provisionally to the species.

Occurrence in Kazakhstan. Kyrshabakty section, *Eurudagnostus kazakhstanicus-Pareuloma* beds (sample 1381); Kujandy Formation, north-east central Kazakhstan.

Akmolina? aff. *minuta* (Mei, 1993)

Plate 37, figures 15–17; Plate 38, figures 10–13

aff. 1993 *Opisthotreta minuta* Mei, p. 414, pl. 3, figs 3–10.

Material. One complete shell and four dorsal valves.

Description. Shell ventribiconvex, subcircular, about 90–100 per cent as long as wide. Ventral valve (known only from a single juvenile specimen) moderately convex, with maximum thickness slightly posterior to the mid-valve length. Ventral pseudointerarea low procline, undivided, poorly differentiated. Lateral valve slopes gently convex in profile. Pedicle foramen small, rounded, facing posteroventrally. Dorsal valve gently and evenly convex. Dorsal pseudointerarea narrow, occupying slightly less than half the valve width, occupied mainly by a median groove. Larval shell finely pitted with pits of slightly varying sizes.

Ventral interior unknown. Dorsal median ridge weakly defined to completely absent. Dorsal cardinal muscle scars small, weakly impressed, slightly lobate, extending forward to just over 40 per cent of valve length. Anterocentral muscle scars large, bounded anteriorly and laterally by arcuate ridges and extending slightly anterior to the mid-valve length. Median buttress elongate subtriangular.

Dimensions. NMW 98.61G.242, conjoined valves of juvenile shell, L = 0·40, W = 0·46; NMW 98.61G.248, dorsal valve, L = 0·58, W = 0·60, Il = 0·26, Cl = 0·24, Cw = 0·36; NMW 98.61G.249, dorsal valve, L = 0·62, W = 0·64.

Remarks. The dorsal valve of our Kazakhstanian specimens is closely comparable with those described by Mei (1993) from the Upper Cambrian of North China under the name *Opisthotreta minuta*. The single ventral valve is also similar in having a procline, undivided pseudointerarea, but otherwise the ventral morphology is known inadequately. The main difference between *Akmolina* aff. *minuta* and the Chinese material is the presence of a weak dorsal median ridge in some valves from Kazakhstan.

The dorsal valves of *A.* aff. *minuta* are also somewhat similar to *Pomeraniotreta obtusa* sp. nov. in having a weak median ridge, buttressed posteriorly, and incurved ridges bounding the anterior projection of the dorsal visceral area. However, the ventral external morphology of *A.* aff. *minuta* differs in its moderately convex profile, with a low, apsacline, undivided pseudointerarea.

Occurrence in Kazakhstan. Kyrshabakty section; Middle Cambrian, *Lejopyge laevigata* Biozone, sample 1349-II; Upper Cambrian, *Kormagnostus simplex* Biozone, samples 1351, 1351-I; *Ivshinagnostus ivshini-Irvingella major* beds, sample 1361-10.

Akmolina sp. 1

Plate 39, figures 9–10, 14–15

Material. One ventral and six dorsal valves.

Remarks. This unnamed species is similar to *Akmolina olentensis* in having a flattened to weakly convex dorsal valve with a narrow, triangular pseudointerarea, an indistinct dorsal median ridge, and a vestigial apical process which occludes the apex and extends anteriorly as a short, thick ridge. The dorsal cardinal muscle fields are weakly impressed. A single incomplete ventral valve is moderately high conical, and has a convex, incurved profile of the anterior valve slope. Precise specific discrimination of these shells remains unclear in the absence of further material.

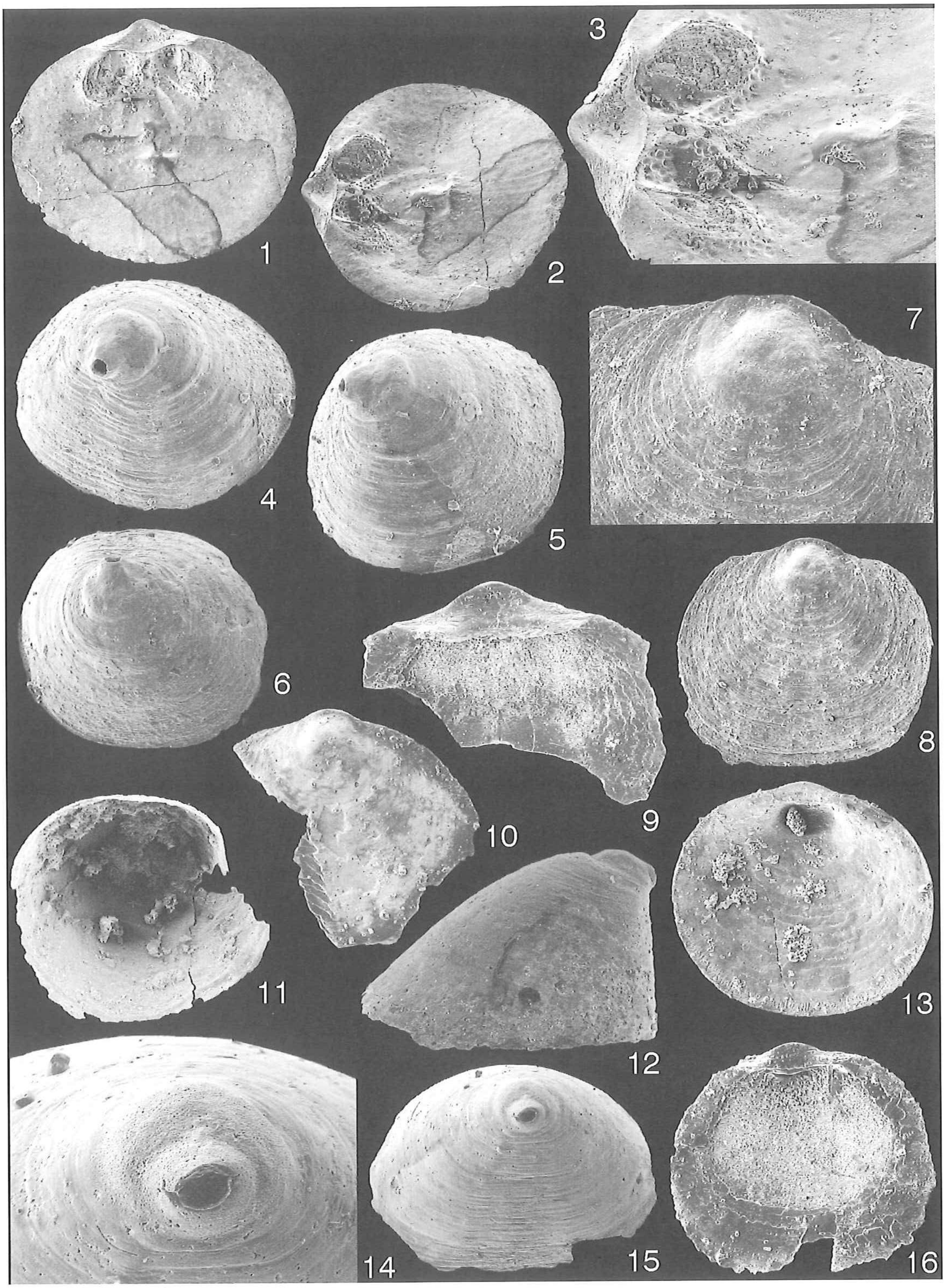
Occurrence in Kazakhstan. Batyrbay section, *Euloma limataris-Tauyuania* beds, samples from 181 m and 196 m.

EXPLANATION OF PLATE 39

Figs 1–3. *Pomeraniotreta obtusa* sp. nov.; Upper Cambrian, *Trisulcagnostus trisulcus* beds, Malyi Karatau, east side of Shabakty river, sample 1414; NMW 98.61G.347, dorsal valve interior in normal view, ×33; oblique lateral view ×36; and detail of cardinal muscle fields and pseudointerarea, ×73.

Figs 4–8, 11–13, 16. *Akmolina* cf. *olentensis* Popov and Holmer; Upper Cambrian, Shabakty Group, *Neoagnostus ovaliformis-Pareuloma–Neorudagnostus quadratiformis-Taenocephalus kyrshabaktensis* beds, Malyi Karatau, Kyrshabakty section. 4–6, NMW 98.61G.260, sample 1381, ventral valve exterior in oblique posterior view, ×74, oblique lateral view, ×74; and ventral view, ×64. 7–8, NMW 98.61G.261, dorsal valve exterior, larval shell and normal view, sample 1400; ×125, ×56. 11, NMW 98.61G.262, ventral valve interior, sample 1381; ×46. 12, NMW 98.61G.263, ventral valve, lateral view, sample 1381; ×64. 13; NMW 98.61G.264, dorsal valve interior, sample 1400; ×84. 16, NMW 98.61G.265, dorsal valve interior, sample 1381; ×55.

Figs 9–10, 14–15. *Akmolina* sp. 1; Upper Cambrian, *Cordylodus intermedius* Biozone, Malyi Karatau, Batyrbay section. 9, NMW 98.61G.266, incomplete dorsal valve interior, sample 196 m; ×71. 10, NMW 98.61G.267, incomplete dorsal valve exterior, sample 181 m; ×66. 14–15, NMW 98.61G.268, ventral valve, detail of larval shell in oblique posterior view, and oblique posterior view of complete valve, sample 191 m; ×179, ×61.



HOLMER *et al.*, *Akmolina*, *Pomeraniotreta*

Akmolina? sp. 2

Plate 38, figures 14–16

Material. Two dorsal valves.

Remarks. This species is also somewhat similar to *Akmolina olentensis* and to *A*. sp. 1 in its flattened dorsal valve, narrow pseudointerarea consisting mainly of a lens-shaped median groove, and its weak, posteriorly buttressed median ridge; it also has an incurved ridge bounding the anterior projection of the dorsal visceral area. The dorsal cardinal muscle fields are weakly impressed. Apart from these comments, the material may represent the oldest known ephippelasmatid; at the same time however, the larval pitting is more comparable with that of scaphelasmatids.

Dimensions. Dorsal valves; NMW 98.61G.251, L = 0·66, W = 0·68, Il = 0·06, Iw = 0·32, Cl = 0·24, Cw = 0·44; NMW 98.61G.250, L = 0·68, W = 0·66.

Occurrence in Kazakhstan. Batyrbay section, Middle Cambrian, *Ptychagnostus intermedius* beds, sample 1465/1.

Genus POMERANIOTRETA Bednarczyk, 1986

Type species. Original designation by Bednarczyk (1986, p. 415); *Pomeraniotreta biernatae* Bednarczyk, 1986; Lower Ordovician, *Paroistodus proteus* Biozone, northern Poland.

Diagnosis. See Popov and Holmer 1994, p. 130; also for a re-description of the type species and discussion of generic relationships.

Species included. *Pomeraniotreta obtusa* sp. nov. in addition to species listed by Popov and Holmer (1994).

Occurrence. Upper Cambrian–Lower Ordovician (Arenig); Bohemia (Arenig); Poland (Tremadoc–Arenig); Norway and Sweden (Tremadoc–Arenig); Kazakhstan (Upper Cambrian); North China (Hebei, Fengshanian).

Pomeraniotreta obtusa sp. nov.

Plate 39, figures 1–3; Plate 40, figures 1–14

Derivation of name. Latin, *obtusus*, obscure; referring to the rather rare occurrence of the species.

Holotype. NMW 98.61G.253, ventral valve; Upper Cambrian, *Hedinaspis sulcata* beds, sample 1444, Batyrbay section, Malyi Karatau.

Material. 27 ventral and 20 dorsal valves.

Diagnosis. Ventral valve moderately thick, generally procline; dorsal pseudointerarea well developed with widely subtriangular median groove; dorsal median ridge low, thickened, buttressed; dorsal cardinal and anterocentral muscle scars well developed.

Description. Shell strongly ventribiconvex subcircular to slightly transversely ovate, about 85 per cent as long as wide (Tables 23–24). Ventral valve subconical with maximum thickness slightly anterior to the umbo. Ventral pseudointerarea procline to slightly apsacline, poorly defined laterally, with poorly defined intertrough. Pedicle foramen within the larval shell at the end of a short external pedicle tube. Dorsal valve flattened, with convex umbonal area. Dorsal pseudointerarea well developed, low, divided by widely subtriangular median groove.

Ventral interior with thick apical process, occluding the umbonal area, and perforated posteriorly by conical internal

TABLE 23. *Pomeraniotreta obtusa* sp. nov., dimensional data for ventral valves from the Batyrbay section (sample 1444, Upper Cambrian, *Hedinaspis sulcata* beds).

	Lv	W	T	Lv/W	T/Lv
N	11	11	11	11	11
X	0·77	0·91	0·64	85%	85%
S	0·165	0·208	0·129	5·5	10·1
MIN	0·52	0·58	0·42	76%	67%
MAX	1·08	1·24	0·84	92%	102%

TABLE 24. *Pomeraniotreta obtusa* sp. nov., dimensional data for dorsal valves from the Shabakty section (sample 1413, 1414, Upper Cambrian, *Eorudagnostus ovaliformis-Paraeuloma* beds and *Micragnostus mutabilis* beds).

	Ld	W	Il	Iw	Pw	Cl	Cw	Sa	Ld/W	Iw/W	Cl/Lv	Cw/W	Sa/Ld
N	8	8	6	6	6	6	6	5	9	9	9	9	6
X	0·88	0·96	0·12	0·44	0·28	0·36	0·58	0·57	95%	48%	38%	56%	75%
S	0·196	0·209	0·027	0·095	0·070	0·092	0·103	0·142	7·1	10·1	3·7	6·8	5·6
MIN	0·64	0·78	0·10	0·34	0·22	0·22	0·46	0·40	83%	19%	27%	47%	69%
MAX	1·30	1·42	0·16	0·60	0·38	0·46	0·72	0·72	103%	58%	46%	64%	84%

pedicle tube. Ventral mantle canals baculate with widely diverging *vascula lateralia*. Dorsal interior with low median ridge, strongly thickened anteriorly and buttressed posteriorly. Dorsal cardinal muscle fields subcircular, deeply impressed and surrounded by elevated rim. Dorsal anterocentral muscle scars large, forming low platform bounded laterally by distinctive ridges that converge anteriorly.

Remarks. In external morphology *Pomeraniotreta obtusa* is somewhat comparable with *Akmolina olentensis* Popov and Holmer (1994), but it is distinguished in having a thick apical process that occludes the umbo, a well-developed buttressed dorsal median ridge, and distinctive anterocentral muscle scars on a low platform. It also differs from *P. biernatae* in having a much lower, procline ventral valve, a well-developed divided dorsal pseudointerarea, and strong development of the buttressed dorsal median septum and dorsal cardinal and anterocentral muscle scars.

Occurrence in Kazakhstan. Batyrbay section, *Hedinaspis sulcata* beds, samples −35 m, 0 m, 1444, 1444-1; Kyrshabakty section, *Eorudagnostus ovaliformis-Paraeuloma* beds and *Micragnostus mutabilis* beds, localities 1376, 1376-7, 1376-II, 1381, 1400-2, 1401-6; eastern side of Shabakty River, *Micragnostus mutabilis* beds, samples 1412–1414.

Family CERATRETIDAE Rowell, 1965

Genus KLEITHRIATRETA Roberts, 1990

Type species. Original designation by Roberts (*in* Roberts and Jell 1990, p. 289); *Kleithriatreta lamellosa* Roberts, 1990 from the Middle Cambrian (Ordian), Coonigan Formation, New South Wales, Australia.

Diagnosis. See Roberts and Jell 1990, p. 291.

Remarks. Holmer and Ushatinskaya (1994) published new information on early and mid Cambrian genera of the Family Ceratretidae from Baltoscandia, north-central Kazakhstan, and south-western Siberia. They also discussed the affinities of the early ceratretides with other acrotretide families. Popov *et al.* (1996) described *K.* cf. *lamellosa* from the Middle Cambrian of the Tarbagatay Range, Kazakhstan.

Species included. Kleithriatreta lamellosa Roberts, *in* Roberts and Jell 1990; *Kleithriatreta* cf. *lamellosa* Roberts (Popov *et al.* 1996); *Kleithriatreta najmanica* (Imanaliev, *in* Imanaliev and Pelman 1988); *Kleithriatreta kostekensis* sp. nov.

Occurrence. Lower Cambrian (?Toyonian)–Middle Cambrian; Australia (New South Wales, Ordian), Kyrgyzstan (North Tien-Shan), Kazakhstan.

Kleithriatreta najmanica (Imanaliev, 1988)

Plate 41, figures 1–6; Plate 42, figures 4–8

1988 *Linnarssonia najmanica* Imanaliev, *in* Imanaliev and Pelman, p. 162, pl. 19, figs 1–4.
1988 *Linnarssonia tchonkojensis* Imanaliev, *in* Imanaliev and Pelman, p. 163, pl. 19, figs 5–9.
1988 *Linnarssonia digitalis* Imanaliev, *in* Imanaliev and Pelman, p. 164, pl. 19, fig. 9 (*non* pl. 20, figs 1–2).

Holotype. IGB 110/301, ventral valve; Lower–lower Middle Cambrian, Ulugtau Mountains, south Kyrgyzstan.

Material. 23 ventral and 6 dorsal valves.

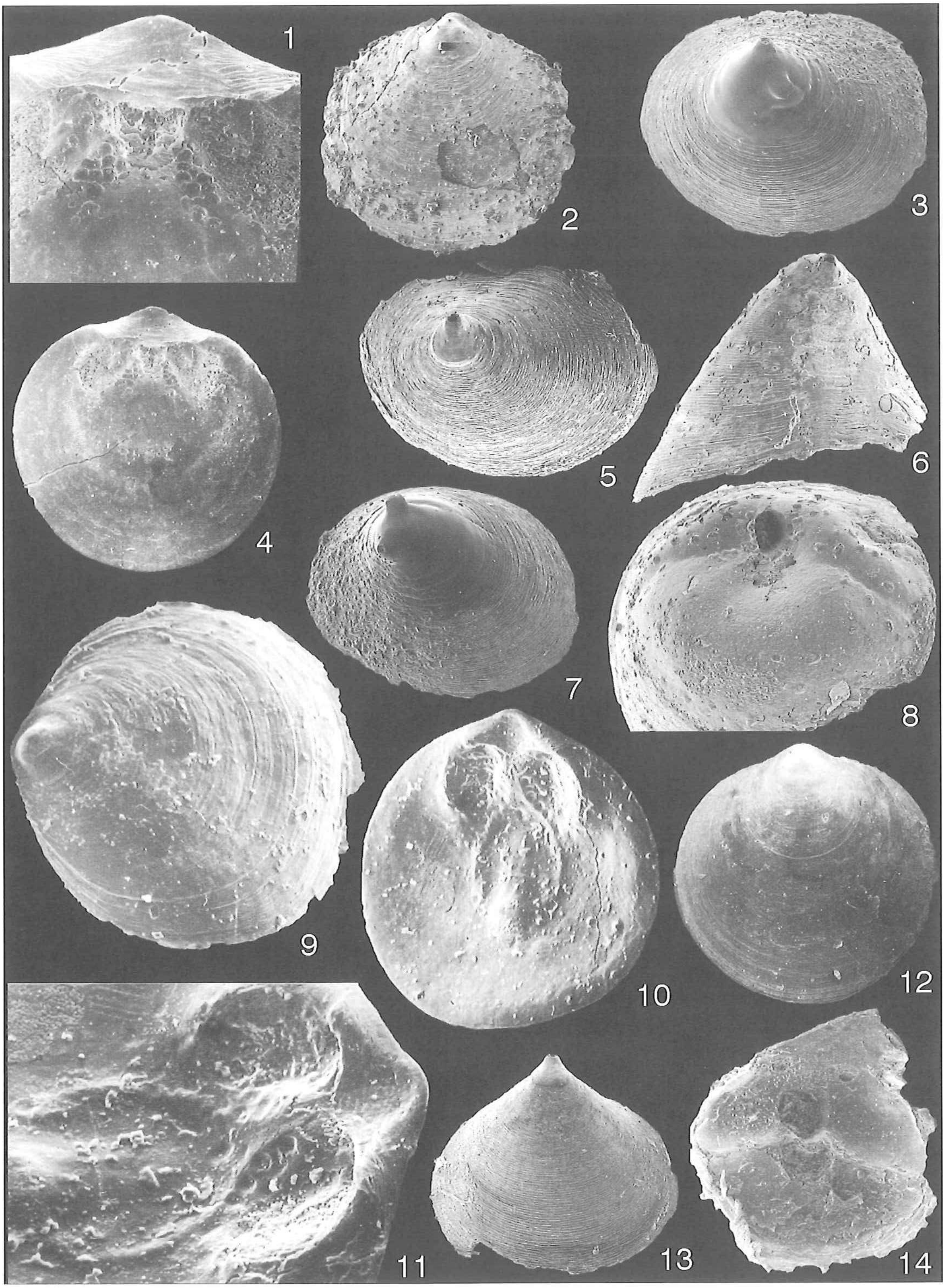
Emended diagnosis. Shell transversely oval, about 75 per cent as long as wide; ventral valve obtusely conical, about 50 per cent as thick as long; dorsal valve lacking sulcus; dorsal pseudointerarea occupying somewhat more than 50 per cent of valve width; dorsal medium septum low triangular, without upper septal spine.

Description of specimens from central Kazakhstan. Shell strongly ventribiconvex, transversely oval in outline, about 75 per cent as long as wide. Ventral valve strongly convex to obtusely conical, about 50 per cent as thick as long with maximum thickness in the umbonal area. Ventral pseudointerarea procline to slightly catacline, well-defined laterally and bisected by a deep intertrough. Lateral slopes of valve evenly convex in profile. Pedicle foramen elongate, elliptical, about 60 μm wide, situated posterior to the umbo. Dorsal valve flatly convex with maximum thickness slightly anterior to the umbo. Dorsal pseudointerarea low, slightly anacline, occupying somewhat more than 50 per cent of the valve width. Median groove deep, lens-shaped, well-defined from propareas, occupying about 25 per cent of width of dorsal pseudointerarea. Ornamentation with up to seven growth lamellae.

Ventral interior with high, ridge-like apical process, thickened anteriorly and penetrated posteriorly by internal pedicle tube. Ventral cardinal muscle fields on low platforms, posterolateral to apical process. Ventral mantle canal system baculate. Dorsal interior with low triangular median septum, buttressed posteriorly, with maximum height at about 75 per cent of valve length, and extending forward for about 80 per cent of valve length. Dorsal cardinal muscle fields strongly thickened, elongate suboval in outline and extending forward for about 40 per cent of valve length.

EXPLANATION OF PLATE 40

Figs 1–14. *Pomeraniotreta obtusa* sp. nov.; Upper Cambrian, Malyi Karatau. 1, 4, IGNA 427/729, *Agnostus scrobicularis-Jegorovaja* beds, east side of Shabakty River, dorsal valve interior, detail of cardinal muscle fields and pseudointerarea, and normal view of valve, sample 1414-b; ×112, ×43. 2, NMW 98.61G.252, *Hedinaspis sulcata* beds, Batyrbay section, dorsal valve exterior, sample 1444; ×53. 3, 7, NMW 98.61G.253, horizon and section as 2, ventral valve exterior in normal and oblique posterior views, sample 1444; ×37, ×38. 5–6, NMW 98.61G.254, horizon and section as 2, ventral valve exterior in ventral and posterior views, sample 1444; ×46, ×54. 8, NMW 98.61G.255, horizon and section as 2, ventral valve interior, sample 1444; ×68. 9, NMW 98.61G.256, horizon and section as 2, dorsal valve exterior, oblique lateral view, sample 0 m; ×85. 10, IGNA 427/730, horizon, locality and sample as 1, dorsal valve interior; ×77. 11, NMW 98.61G.257, horizon and section as 2, dorsal valve interior, oblique lateral view, sample 0 m; ×128. 12, NMW 98.61G.259, horizon, locality and sample as 1, dorsal valve exterior; ×40. 13, NMW 98.61G.260, horizon and section as 2, ventral valve exterior, sample 0 m; ×37. 14, IGNA 427/731, horizon, locality and sample as 1, incomplete ventral valve interior; ×62.



HOLMER *et al.*, *Pomeraniotreta*

Dimensions. NMW 98.61G.309, ventral valve, L = 1·06, W = 1·40; NMW 98.61G.308, dorsal valve, L = 1·14, W = 1·54; NMW 98.69G.345, L = 1·22, W = 1·78, Il = 0·16, Iw = 1·06, Pw = 0·50, Cl = 0·54, Cw = 1·24, Sa = 0·98; NMW 98.69G.346, L = 1·08, W = 1.62, Il = 0·10, Iw = 1·02, Pw = 0·36, Cl = 0·50, Cw = 1·14, Sa = 0·90.

Remarks. The Kazakhstanian specimens are most similar to three species (*Linnarssonia najmanica, L. tchonkojensis, L. digitalis*) assigned to *Linnarssonia* by Imanaliev (*in* Imanaliev and Pelman 1988) from the Lower–lower Middle Cambrian of south Kyrgyzstan. All these taxa have strongly raised ventral cardinal muscle fields, a high apical process bridging the anterior and posterior valve slopes, with a boss-like muscle platform on the process anterior to the internal pedicle tube, as well as a dorsal pseudointerarea with a broad median groove, strongly raised dorsal cardinal muscle scars, and a blade-like median septum; all three species are here referred to *Kleithriatreta. K. tchonkojensis* and *K. digitalis* are from the same locality, and differ from *K. najmanica* only in minor details of the apical process; the former two species are regarded here as junior synonyms of the latter (which has page priority), and our new Kazakhstanian material is conspecific. The dorsal valves illustrated by Imanaliev (*in* Imanaliev and Pelman 1988, pl. 20, figs 1–2) under the name *Linnarssonia digitalis* have a vestigial dorsal pseudointerarea and minute median ridge, very unlike *Kleithriatreta*, and most likely belong to a different acrotretide genus (maybe *Linnarssonia* itself). However, the illustrated ventral valve (the holotype, IGB 110/309) undoubtedly belongs to *Kleithriatreta.*

K. najmanica is similar to the Australian type species, but the Asian species is distinguished in having a low, triangular, dorsal median septum lacking an upper septal spine, and a relatively narrow median groove, and also lacks a dorsal sulcus.

Occurrence in Central Asia. Upper Lower Cambrian–lower Middle Cambrian (Amgaian)? olistoliths in the Cambrian Zhalgyz Formation of the Suuk-Adver Mountains, central Kazakhstan; upper Lower Cambrian–lower Middle Cambrian (Amgaian?) olistoliths, Ulugtau Mountains, south Kyrgyzstan.

Kleithriatreta kostekensis sp. nov.

Plate 42, figures 1–3; Plate 43, figures 1–11; Plate 44, figures 9–13

Derivation of name. After the Kostek Ridge in north Kyrgyzstan.

Holotype. NMW 98.61G.304, ventral valve; Middle Cambrian, Amgaian, Karagajly Formation, sample 1639, Kostek Range, Kyrgyzstan.

EXPLANATION OF PLATE 41

Figs 1–6. *Kleithriatreta najmanica* (Imanaliev); Lower Cambrian, Darbaza Formation, Suukadyr Mountains, locality 5875. 1, NMW 98.61G.305, ventral valve interior showing internal foramen, apical pits, and apical process and cardinal muscle fields; ×40. 2, NMW 98.61G.306, ventral valve interior; ×60. 3, NMW 98.69G.346, dorsal valve interior; ×29. 4, NMW 98.69G.345, oblique lateral view of dorsal interior; ×40. 5, NMW 98.61G.308, dorsal valve exterior; ×33. 6, NMW 98.69G.347, ventral valve, detail of pedicle foramen and larval shell; ×120.

Figs 7–11. *Dictyonina hexagona* (Bell); Middle Cambrian, *Ptychagnostus intermedius* Biozone, Malyi Karatau, Kyrshabakty section. 7, IGNA 427/160, incomplete dorsal valve interior; ×31. 8, NMW 98.61G.310, ventral valve exterior, sample 1314; ×29. 9, NMW 98.61G.311, ventral valve interior, sample 1314; ×27. 10, IGNA 427/397, ventral valve interior, sample 1465-1; ×22. 11, IGNA 427/408, dorsal valve interior, sample 1316; ×26.

Figs 12–14. *Micromitra* sp.; Upper Cambrian, *Innitagnostus inexpectans-Prochuangia–'Pseudagnostus curtare'-Irvingella tropica* beds, Malyi Karatau, Kyrshabakty section. 12, IGNA 427/160, dorsal valve exterior, sample 1355; ×20. 13, IGNA 427/161, dorsal valve exterior, sample 1357-3; ×9. 14, IGNA 427/162, incomplete ventral valve exterior, sample 1355; ×11.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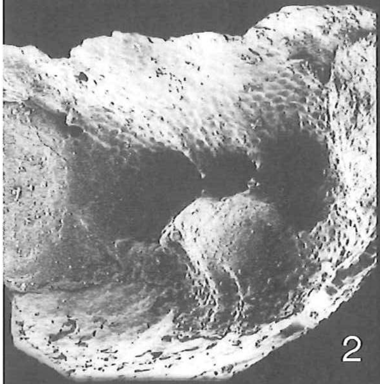
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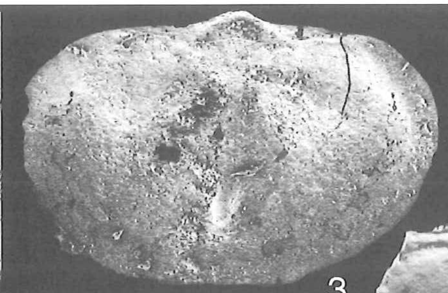
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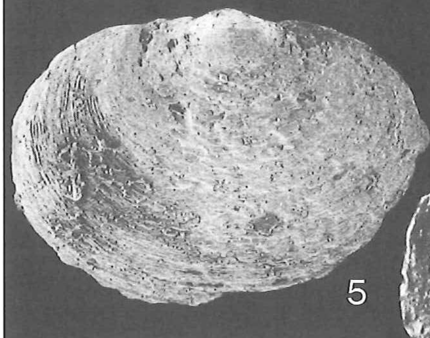
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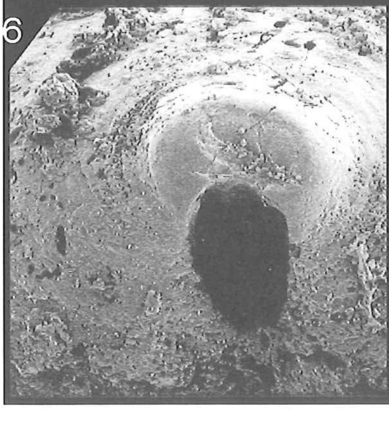
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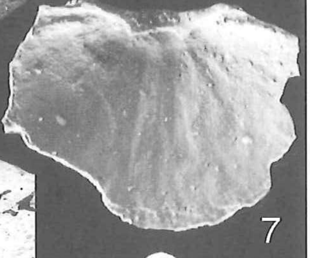
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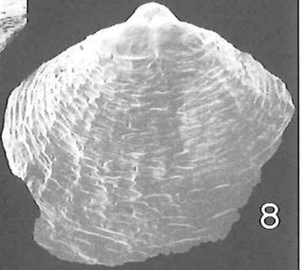
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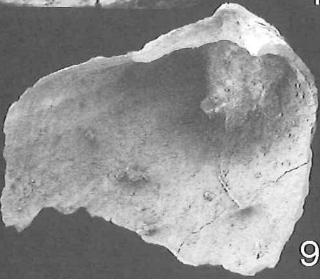
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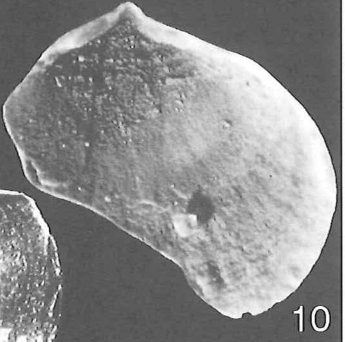
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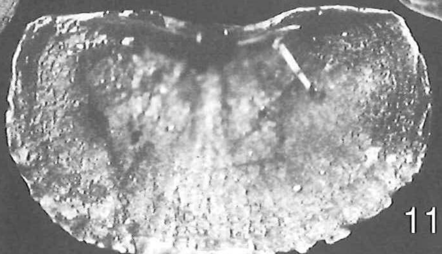
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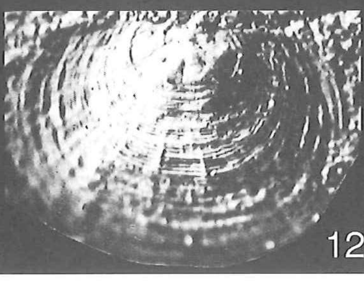
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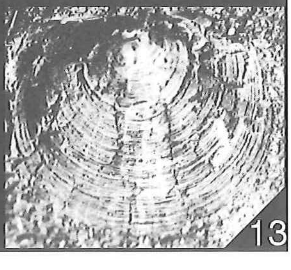
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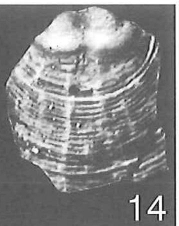
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TABLE 25. *Kleithriatreta kostekensis* sp. nov., dimensional data for ventral valves from the Kostek Range (sample 1639, Middle Cambrian, Karagajly Formation).

	Lv	W	T	Lv/W	T/Lv
N	10	8	10	8	10
X	1·24	1·49	0·78	80%	63%
S	0·328	0·359	0·195	6·6	5·5
MIN	0·66	0·88	0·4	68%	55%
MAX	1·76	2·02	1·04	87%	70%

TABLE 26. *Kleithriatreta kostekensis* sp. nov., dimensional data for dorsal valves from the Kostek Range (sample 1639, Middle Cambrian, Karagajly Formation).

	Ld	W	T	Il	Iw	Pw	Cl	Cw	Sa	Sm	Ld/W	T/Ld	Il/Iw	IW/W	Pw/Iw	Cl/Ld	Cw/W	Sa/Ld	Sm/Ld
N	16	16	16	16	16	16	16	16	16	13	16	16	16	16	16	16	16	16	13
X	1·29	1·50	0·28	0·20	0·96	0·48	0·51	0·93	1·00	0·79	86%	22%	21%	64%	50%	40%	62%	78%	62%
S	0·238	0·263	0·095	0·048	0·167	0·108	0·105	0·163	0·212	0·143	7·3	5·9	3·3	6·5	8·5	3·2	4·9	9·1	7·1
MIN	0·84	1·12	0·18	0·12	0·64	0·28	0·32	0·66	0·68	0·56	74%	13%	14%	53%	33%	33%	56%	59%	48%
MAX	1·72	2·04	0·5	0·3	1·28	0·62	0·68	1·22	1·32	1·04	95%	36%	26%	73%	67%	44%	74%	87%	73%

Material. 19 ventral and 32 dorsal valves.

Diagnosis. Shell transversely oval, about 80 per cent as long as wide; ventral valve obtusely conical, about 66 per cent as high as long; dorsal valve with shallow sulcus; dorsal pseudointerarea moderately high, occupying about 66 per cent of valve width, divided by a broad, triangular median groove; dorsal median septum triangular, high with a single septal rod at the top, which may be strongly thickened in adults.

Description. Shell strongly ventribiconvex, transversely oval, about 80 per cent as long as wide (Table 25). Ventral valve strongly convex to obtusely conical, about 66 per cent as thick as long with maximum thickness at the umbonal area. Ventral pseudointerarea procline to slightly catacline, well defined laterally and bisected by a deep intertrough. Lateral slopes of valve evenly convex in profile. Pedicle foramen elongate elliptical, posterior to the umbo. Dorsal valve moderately convex, about 20 per cent as thick as long (Table 26) with maximum thickness slightly anterior to the umbo. Dorsal sulcus shallow, originating at about mid-way between the umbo and mid-valve. Dorsal pseudointerarea moderately high, occupying about 66 per cent of valve width, slightly anacline. Median groove deep, broadly triangular, well defined from propareas, occupying about 50 per cent of the width of the dorsal pseudointerarea. Ornamentation with fine, evenly spaced concentric fila, lamellose peripherally.

Ventral interior with high, ridge-like apical process, thickened anteriorly and perforated posteriorly by an internal

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EXPLANATION OF PLATE 42

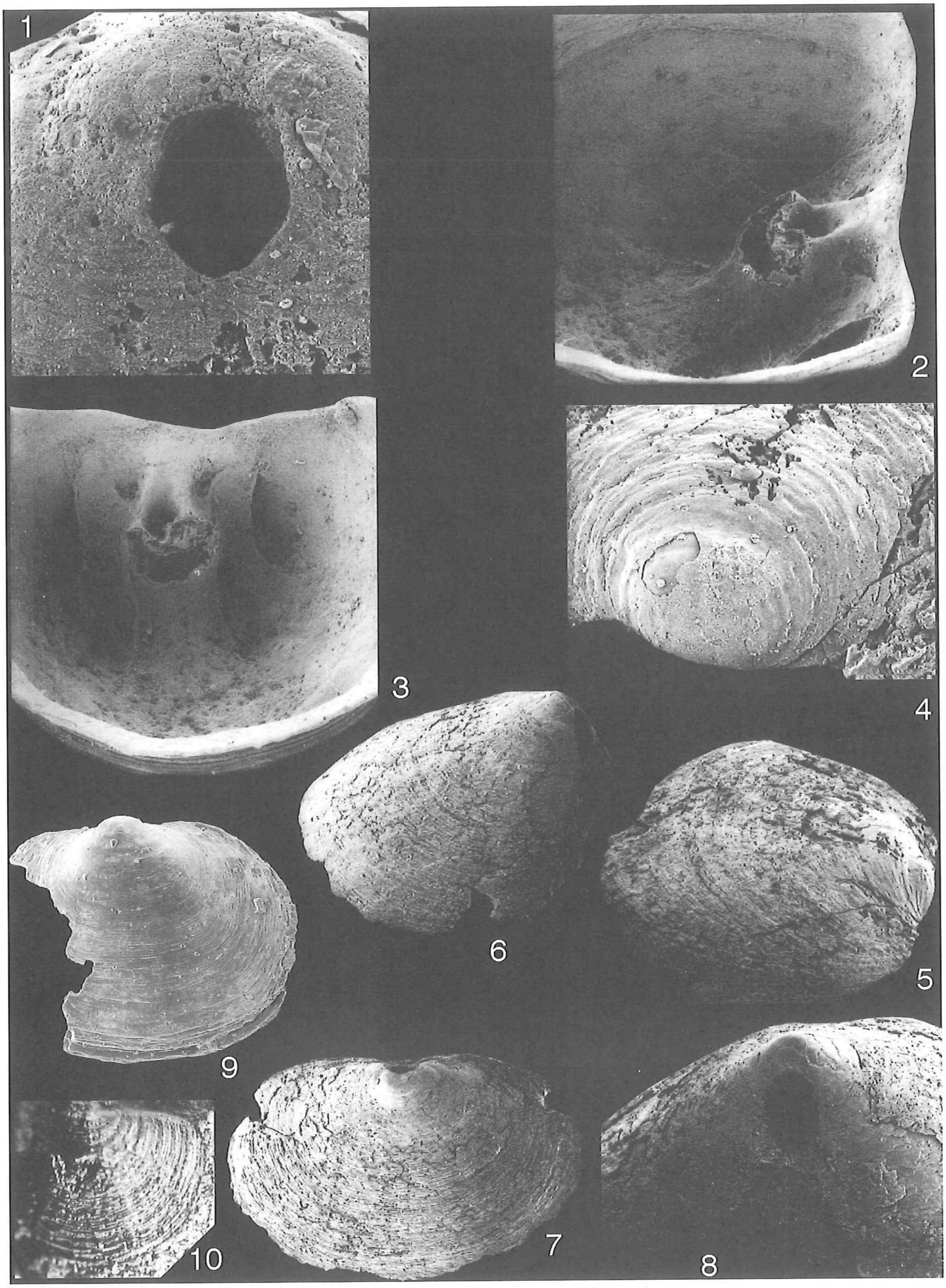
Figs 1–3. *Kleithriatreta kostekensis* sp. nov.; Middle Cambrian, Amgaian, Karagajly Formation, Kostek Range, sample 1639. 1, NMW 98.61G.302, ventral valve, detail of pedicle foramen and larval shell; ×310. 2–3, NMW 98.61G.304, holotype, ventral valve interior, in oblique lateral and oblique anterior views; both ×82.

Figs 4–8. *Kleithriatreta najmanica* (Imanaliev); Lower Cambrian, Darbaza Formation, Suukadyr Mountains, locality 5875. 4–5, NMW 98.61G.308, dorsal valve exterior, detail of larval shell and oblique lateral view; ×120, ×50. 6–8, NMW 98.61G.309, ventral valve exterior in oblique lateral view, dorsal view, and posterior view; ×43, ×33, ×67.

Fig. 9. *Otariconulus*? sp. 2; Ordovician, Shabakty Group, *Cordylodus lindstromi* Biozone, Malyi Karatau, Batyrbay section, sample 221 m; NMW 98.61G.312, dorsal valve exterior; ×72.

Fig. 10. *Micromitra* cf. *modesta* (Lochman); Middle Cambrian, *Goniagnostus nathorsti* Biozone, Malyi Karatau, Kyrshabakty section, sample 1465-18; IGNA 427/164, ventral valve exterior; ×13.

PLATE 42



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pedicle tube, and with a highly raised muscle platform anterior to the internal foramen. Ventral cardinal muscle fields strongly impressed. Apical pits small but strongly impressed posterolateral to the internal foramen. Ventral mantle canal system baculate. Dorsal median septum high triangular, buttressed posteriorly, with maximum height at about 66 per cent of valve length and extending forward for about 80 per cent of valve length. Dorsal cardinal muscle fields elongate suboval, on raised platform, bounded by a thickened rim and extending forward for about 40 per cent of the valve length.

Remarks. *Kleithriatreta kostekensis* differs from the type species and from *K. najmanica* in being larger, having a more convex dorsal valve, a wider dorsal pseudointerarea, and a better developed, thick dorsal median septum with a very strongly developed upper spine.

Occurrence in Kazakhstan. Type locality only.

Family SCAPHELASMATIDAE Rowell, 1965

Genus EOSCAPHELASMA Koneva, Popov and Ushatinskaya, 1990

Type species. Original designation by Koneva, Popov and Ushatinskaya (*in* Koneva *et al.* 1990, p. 165); *Eoscaphelasma satpakensis* Koneva, Popov and Ushatinskaya, 1990; Upper Cambrian, Kujandy Formation, north-eastern central Kazakhstan.

Diagnosis. See Popov and Holmer 1994, p. 137.

Species included. *Eoscaphelasma satpakensis* Koneva, Popov and Ushatinskaya, 1990; *Eoscaphelasma* cf. *satpakensis* Koneva, Popov and Ushatinskaya (herein); *Eoscaphelasma*? *delicata* sp. nov.

Occurrence. Upper Cambrian, Kazakhstan.

Eoscaphelasma cf. *satpakensis* Koneva, Popov and Ushatinskaya, 1990

Plate 44, figures 3–8

cf. 1990	*Eoscaphelasma satpakensis* Koneva, Popov and Ushatinskaya, *in* Koneva, Popov, Ushatinskaya and Esakova, p. 165, pl. 30, figs 1–7.
cf. 1994	*Eoscaphelasma* cf. *satpakensis* Koneva, Popov and Ushatinskaya; Popov and Holmer, p. 137, fig. 109.

Material. Two ventral and five dorsal valves.

Remarks. This scant material of *Eoscaphelasma* is almost indistinguishable from specimens of *E. satpakensis* described from the Upper Cambrian Kujandy Formation of north-eastern central Kazakhstan by Popov and Holmer (1994, p. 137). However, the two incomplete ventral valves from Malyi Karatau

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EXPLANATION OF PLATE 43

Figs 1–11. *Kleithriatreta kostekensis* sp. nov.; Middle Cambrian, Amgaian, Karagajly Formation, Kostek Range, sample 1639. 1–2, NMW 98.61G.297, dorsal valve exterior, oblique lateral view showing weak sulcus, and dorsal view; ×44, ×39. 3–4, NMW 98.61G.298, dorsal valve interior in oblique lateral and dorsal views; ×39, ×32. 5, 7–8, NMW 98.61G.299, ventral valve exterior in oblique lateral view, oblique posterior view and normal view; ×21, ×24, ×21. 6, 11, NMW 98.61G.300, ventral valve in oblique posterior view, and oblique posterior view of larval shell and pedicle foramen; ×31, ×42. 9, NMW 98.69G.14, dorsal valve interior; ×34. 10, NMW 98.61G.301, dorsal valve interior; ×68.

seemingly lack an internal pedicle tube, which is characteristic of the specimens from the Kujandy Formation. We therefore report the material from Malyi Karatau under comparative nomenclature.

Occurrence in Kazakhstan. Kyrshabakty section, *Agnostus scrobicularis-Jegorovaja* beds, sample 1400.

Eoscaphelasma? *delicata* sp. nov.

Plate 44, figures 1–2; Plate 46, figures 6, 8–15

Holotype. NMW 98.61G.286, dorsal valve; Upper Cambrian, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds; Kyrshabakty section, Malyi Karatau, sample 1378-12.

Material. Two complete shells, 23 ventral and 89 dorsal valves.

Diagnosis. Shell transversely oval with weakly concave posterior margin; ornament of fine fila, occasionally weakly wrinkled; ventral valve moderately thick conical; ventral pseudointerarea procline to almost catacline, poorly defined laterally with broad intertrough; pedicle foramen rounded, enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea low, orthocline with poorly defined, widely triangular median groove; apical process extremely poorly developed; dorsal median ridge vestigial to absent.

Description. Shell ventribiconvex, transversely oval, about 75 per cent as long as wide (Table 27). Ventral valve moderately widely conical, about half as thick as long with maximum thickness subcentral to the marginal umbo. Pedicle foramen rounded, enclosed within the larval shell. Ventral pseudointerarea poorly defined, procline to almost catacline with a wide intertrough. Dorsal valve gently convex with maximum thickness somewhat anterior to the umbo. Dorsal pseudointerarea low, orthocline, occupying about 45 per cent of valve width. Median groove wide, occupying more than 50 per cent of the width of the pseudointerarea. Ornamentation of fine fila. Larval pitting with pits of varying size.

Ventral interior with poorly defined characters. Apical process poorly developed to absent. Dorsal cardinal muscle fields weakly impressed, large, elongate oval, about 40 per cent as long as the valve. Anterocentral muscle scars somewhat raised at about mid-valve length. Dorsal median septum poorly developed to absent.

Remarks. Eoscaphelasma? *delicata* is similar to *E. satpakensis* in the general shape of the shell and in the development of the dorsal pseudointerarea and dorsal interior. The most important difference is that the pedicle foramen of *E.*? *delicata* is enclosed within the larval shell, which is unlike the development in any other scaphelasmatid. The new species also differs from the type species in having a thicker conical, less

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EXPLANATION OF PLATE 44

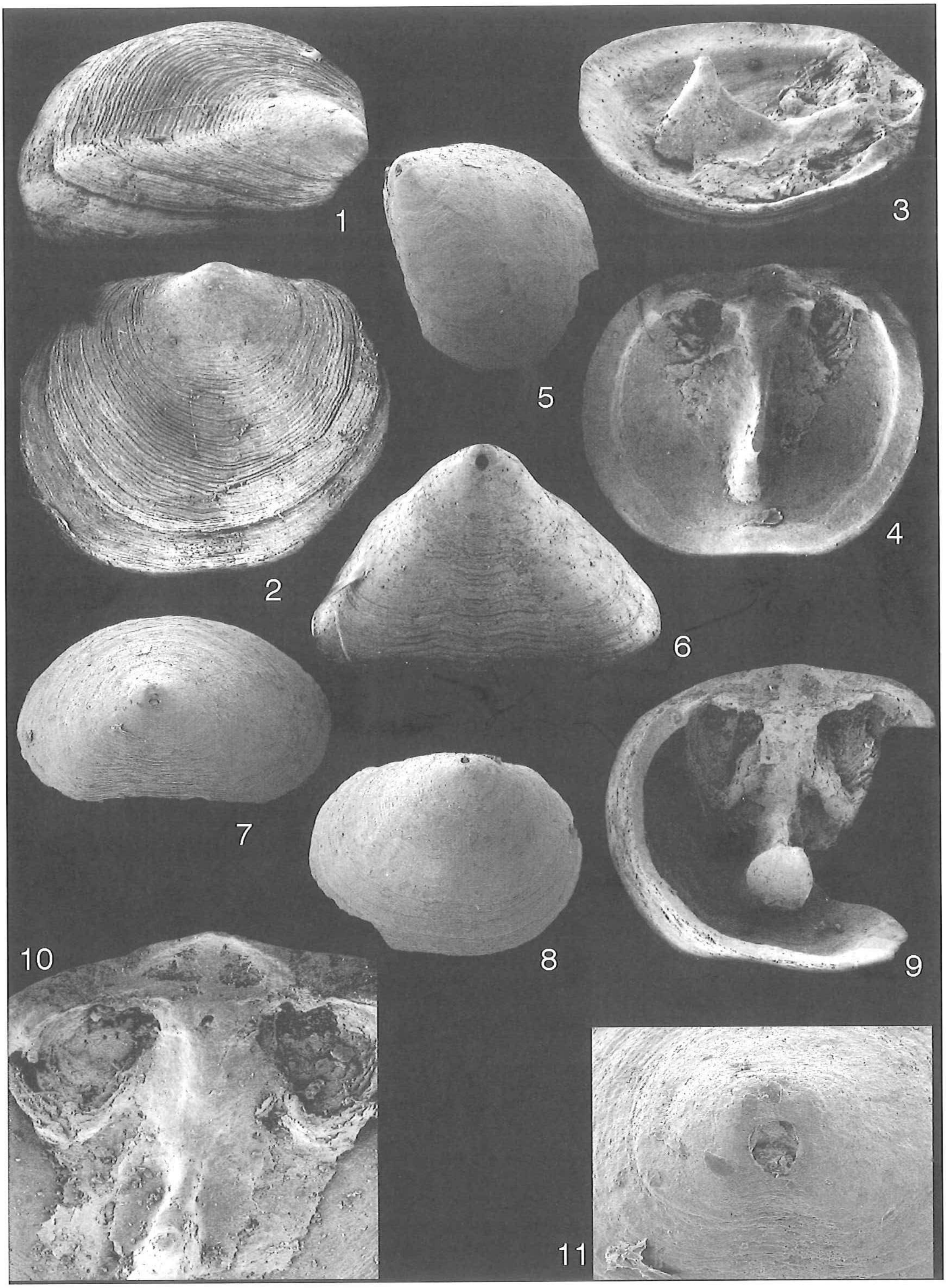
Figs 1–2. *Eoscaphelasma*? *delicata* sp. nov.; Upper Cambrian, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds, Malyi Karatau, Kyrshabakty section. 1, NMW 98.61G.286, dorsal valve interior, sample 1378-12; ×70. 2, NMW 98.61G.287, ventral valve interior, sample 1378-19; ×103.

Figs 3–8. *Eoscaphelasma* cf. *satpakensis* Koneva, Popov and Ushatinskaya; Upper Cambrian, *Agnostus scrobicularis-Jegorovaja* beds, Malyi Karatau, Kyrshabakty section, sample 1400. 3, NMW 98.61G.289, dorsal valve exterior; ×71. 4–5, NMW 98.61G.288, ventral valve exterior, detail of larval shell, and normal view; ×234, ×87. 6, NMW 98.61G.290, dorsal valve exterior; ×71. 7, NMW 98.61G.291, dorsal valve interior; ×56. 8, NMW 98.61G.292, dorsal valve interior; ×71.

Figs 9–13. *Kleithriatreta kostekensis* sp. nov.; Middle Cambrian, Amgaian, Karagajly Formation, Kostek Range, sample 1639. 9–10, NMW 98.61G.293, dorsal valve exterior in normal and oblique lateral views; ×21, ×22. 11, NMW 98.61G.302, ventral valve, oblique posterior view; ×31. 12–13, NMW 98.61G.294, dorsal valve of juvenile interior in normal and oblique lateral views; ×51, ×49.

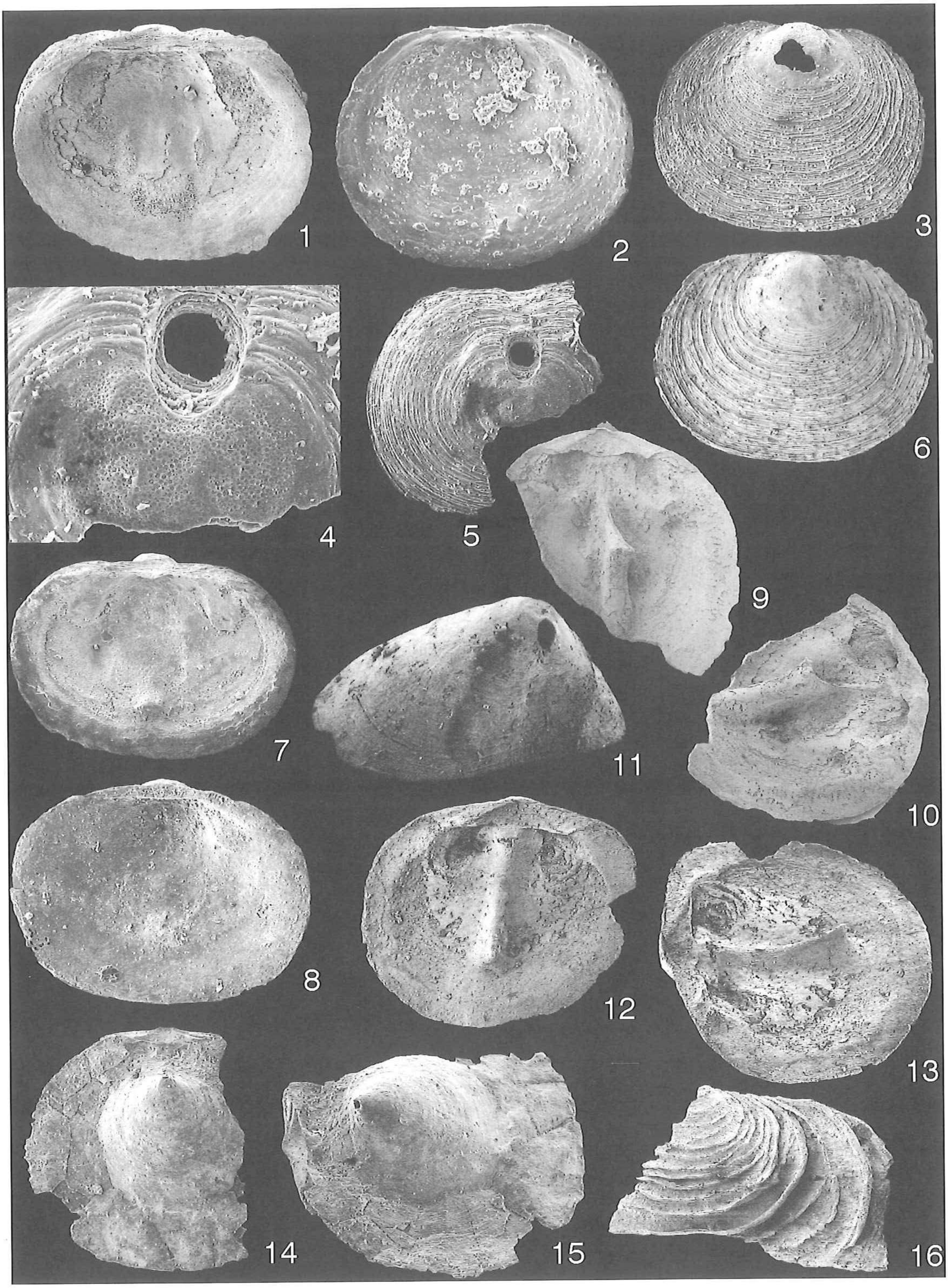
Figs 14–15. *Quadrisonia*? sp.; Upper Cambrian, *Kormagnostus simplex* Biozone, Malyi Karatau, Kyrshabakty section, sample 1351-I; NMW 98.61G.295, conjoined valves in ventral and oblique lateral view; ×32, ×40.

Fig. 16. *Anabolotreta*? sp.; Middle Cambrian, Amgaian, Karagajly Formation, Kostek Range, sample 1639; NMW 98.61G.296, dorsal valve exterior; ×43.



HOLMER *et al.*, *Kleithriatreta*

PLATE 44



HOLMER *et al.*, brachiopods

TABLE 27. *Eoscaphelasma*? *delicata* sp. nov., dimensional data for dorsal valves from the Kyrabakty section (sample 1381-12, Upper Cambrian, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds).

	Ld	W	Il	Iw	Cl	Cw	Sa	Ld/W	Iw/W	Cl/Ld	Cw/W	Sa/Ld
N	10	10	10	10	8	8	8	10	10	8	8	8
X	0·575	0·77	0·06	0·35	0·24	0·54	0·43	74%	44·5%	40%	69%	72%
S	0·103	0·135	0·015	0·077	0·065	0·134	0·101	4·1	5·9	6·0	9·7	4·9
MIN	0·41	0·52	0·04	0·18	0·14	0·34	0·28	66%	35%	34%	58%	68%
MAX	0·70	0·98	0·08	0·42	0·36	0·76	0·56	79%	53%	53%	88%	80%

procline ventral valve, and in the almost complete lack of an apical process, which appears as a fine rim anterior to the foramen in gerontic specimens. It cannot be referred confidently to *Eoscaphelasma*.

Occurrence. Kyrshabakty section; Upper Cambrian, *Pseudagnostus pseudangustilobus-Acrocephalaspina–Eurudagnostus ovaliformis-'Pareuloma'* beds, samples 1378-12, 1378-19, 1378-21–23, 1378-25, 1379-8, 1380-6, 1381, 1381-3, 1376-9, 1377-1, 1377-I.

Genus KOTYLOTRETA Koneva, 1990

1990 *Kotylotreta* Koneva, p. 49.
?1996 *Pegmatreta* Bell, 1941; Engelbretsen, p. 88 (*non* Bell 1941).

Type species. Original designation by Koneva (1990, p. 49); *Kotylotreta undata* Koneva, Middle Cambrian, Mayaian, *Goniagnostus nathorsti* Biozone, Malyi Karatau.

Emended diagnosis. Shell transversely oval with concentric ornament of fine, evenly spaced fila; ventral valve low, conical, pseudointerarea procline, weakly defined laterally, with intertrough; foramen not enclosed within larval shell; dorsal pseudointerarea vestigial with wide, shallow median groove; apical process broad, subtriangular, extending between posterior and anterior slope of the valve and perforated posteriorly by short pedicle tube; apical pits deeply impressed, directly lateral to foramen; ventral mantle canals baculate; cardinal muscle fields transversely oval, weakly thickened; dorsal median ridge low; larval shell covered with circular pits of two sizes.

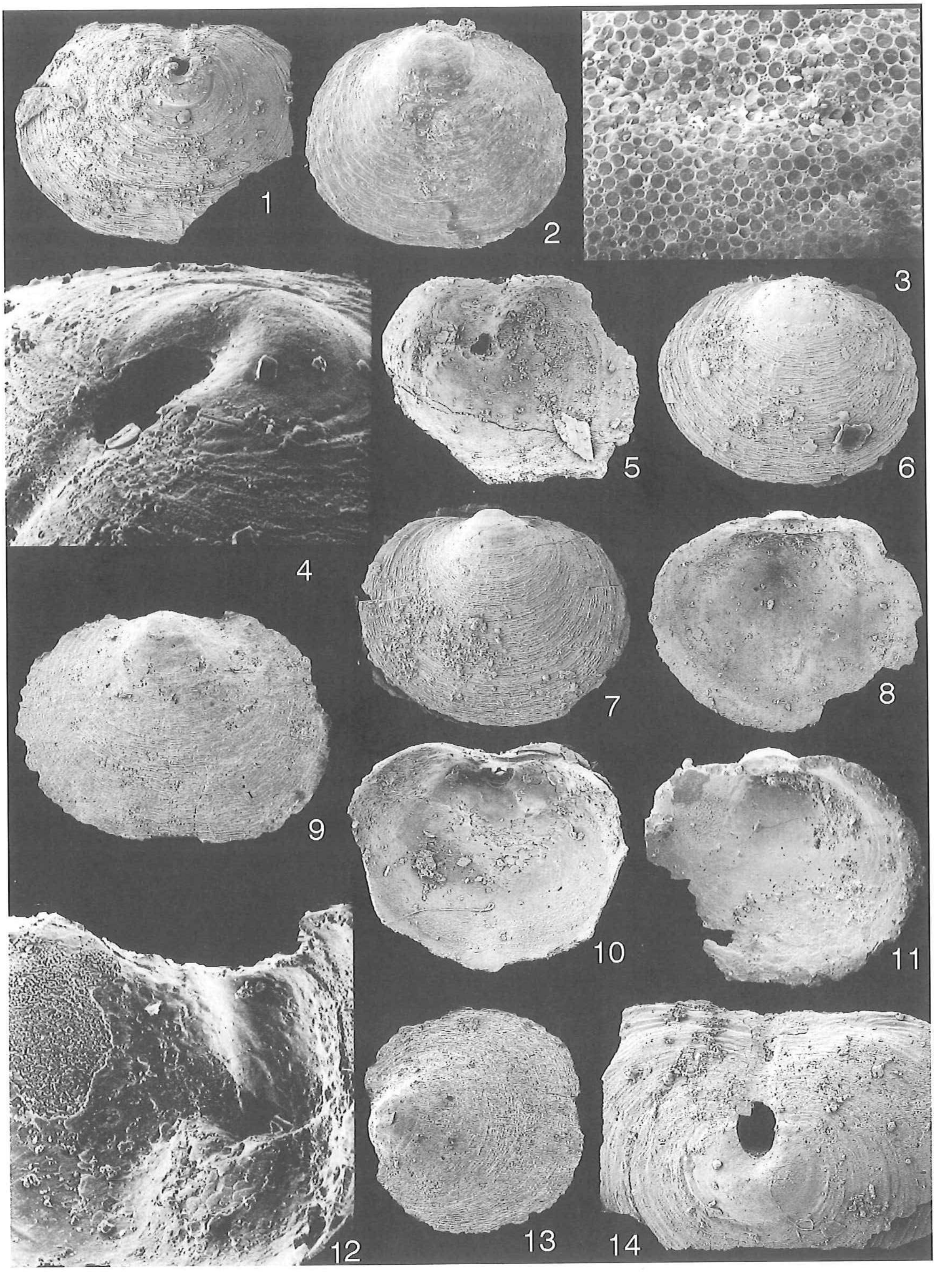
Remarks. *Kotylotreta* is closely similar to *Eoscaphelasma* in external morphology and in the dorsal valve interior. It is distinguished in having the low, broadly triangular apical process perforated posteriorly by the short internal pedicle tube, and in the absence of growth lamellae.

Species included. *Kotylotreta undata* Koneva, 1990; ?*Pegmatreta clavigera* Engelbretsen, 1996.

Occurrence. Middle Cambrian (Amgaian–Mayaian); *Peronopsis ultimus* and *Ptychagnostus intermedius* biozones, Malyi Karatau; Middle Cambrian, Amgaian, Karagajly Formation, Kyrgyzstan; ?Middle Cambrian, Murrawong Creek Formation, New South Wales, Australia.

EXPLANATION OF PLATE 45

Figs 1–14. *Kotylotreta undata* Koneva; Middle Cambrian. 1–8, 10–12, 14 from *Peronopsis*? *ultimus–Ptychagnostus intermedius* biozones, Malyi Karatau, Kyrshabakty section; 2–3 from sample 1465-I; all others from sample 1465-9. 1, NMW 98.61G.269, ventral valve exterior; ×40. 2–3, NMW 98.61G.270, dorsal valve exterior and detail of pitted micro-ornament of larval shell; ×81, ×719. 4, RM Br 135404, ventral valve umbonal area and pedicle foramen; ×100. 5, NMW 98.61G.272, ventral valve interior, ×60. 6, RM Br 135403, dorsal valve exterior; ×60. 7, NMW 98.61G.273, dorsal valve exterior; ×58. 8, NMW 98.61G.271, dorsal valve interior; ×60. 9, 13, NMW 98.61G.274, dorsal valve exterior in normal and oblique lateral views, Karagajly Formation, Kostek Range, sample 1369; ×60, ×55. 10, NMW 98.61G.276, ventral valve interior; ×87. 11, NMW 98.61G.275, dorsal valve exterior; ×81. 12, RM Br136406, ventral valve interior showing apical process and internal foramen; ×120. 14, NMW 98.61G.277, ventral valve umbonal area and pedicle foramen; ×120.



HOLMER *et al.*, *Kotylotreta*

Kotylotreta undata Koneva, 1990

Plate 45, figures 1–15; Plate 46, figures 1–5, 7

1990 *Kotylotreta undata* Koneva, p. 50, pl. 5, figs 9–17.

Holotype. IGNA 427/510, ventral valve (Koneva 1990, pl. 5, fig. 9); Middle Cambrian, Mayaian, *Goniagnostus nathorsti* Biozone, Kyrshabakty section, sample 1465-19, Malyi Karatau.

Material. One complete shell, 60 ventral and 90 dorsal valves.

Diagnosis. Ventral valve low conical; half of pedicle foramen outside larval shell; apical process broad, low, subtriangular, extending between posterior and anterior slope of the valve; dorsal median ridge low to absent.

Description. Shell transversely oval with concentric ornament of fine, evenly spaced rugellae; ventral valve low, conical, pseudointerarea procline, weakly defined laterally, with intertrough; foramen not enclosed within larval shell; dorsal pseudointerarea vestigial with wide, shallow median groove; apical process broad, subtriangular, extending between posterior and anterior slope of the valve and perforated posteriorly by short pedicle tube; apical pits deeply impressed, directly lateral to foramen; ventral mantle canals baculate; cardinal muscle fields transversely oval, weakly thickened; dorsal median ridge low; larval shell covered with circular pits of two sizes.

Remarks. *Kotylotreta undata* is most similar to the Australian *Pegmatreta clavigera* Engelbretsen, 1996, which is here referred questionably to *Kotylotreta*. However, the pedicle foramen in *K.*? *clavigera* is not entirely outside the larval shell as in the type species, and the apical process is higher; also, the dorsal median septum is better developed in the Australian species.

Occurrence in Kazakhstan. Middle Cambrian, Kyrshabakty section, *Peronopsis ultimus* and *Ptychagnostus intermedius* beds, samples 1313, 1316, 1465-1, 1465-8, 1465-9, 1465-14, 1465-17, 1465-19, 1467; Kostek Ridge, Karagajly Formation, locality 1639.

Family EOCONULIDAE Rowell, 1965

Genus OTARICONULUS Holmer and Popov, 2000

[*nom. subst. pro Otariella* Popov and Holmer, 1994, p. 141, *non* Waterhouse, 1978]

Type species. *Otariella prisca* Popov and Holmer, 1994, p. 141; Upper Cambrian–Lower Ordovician Satpak Formation, north-central Kazakhstan.

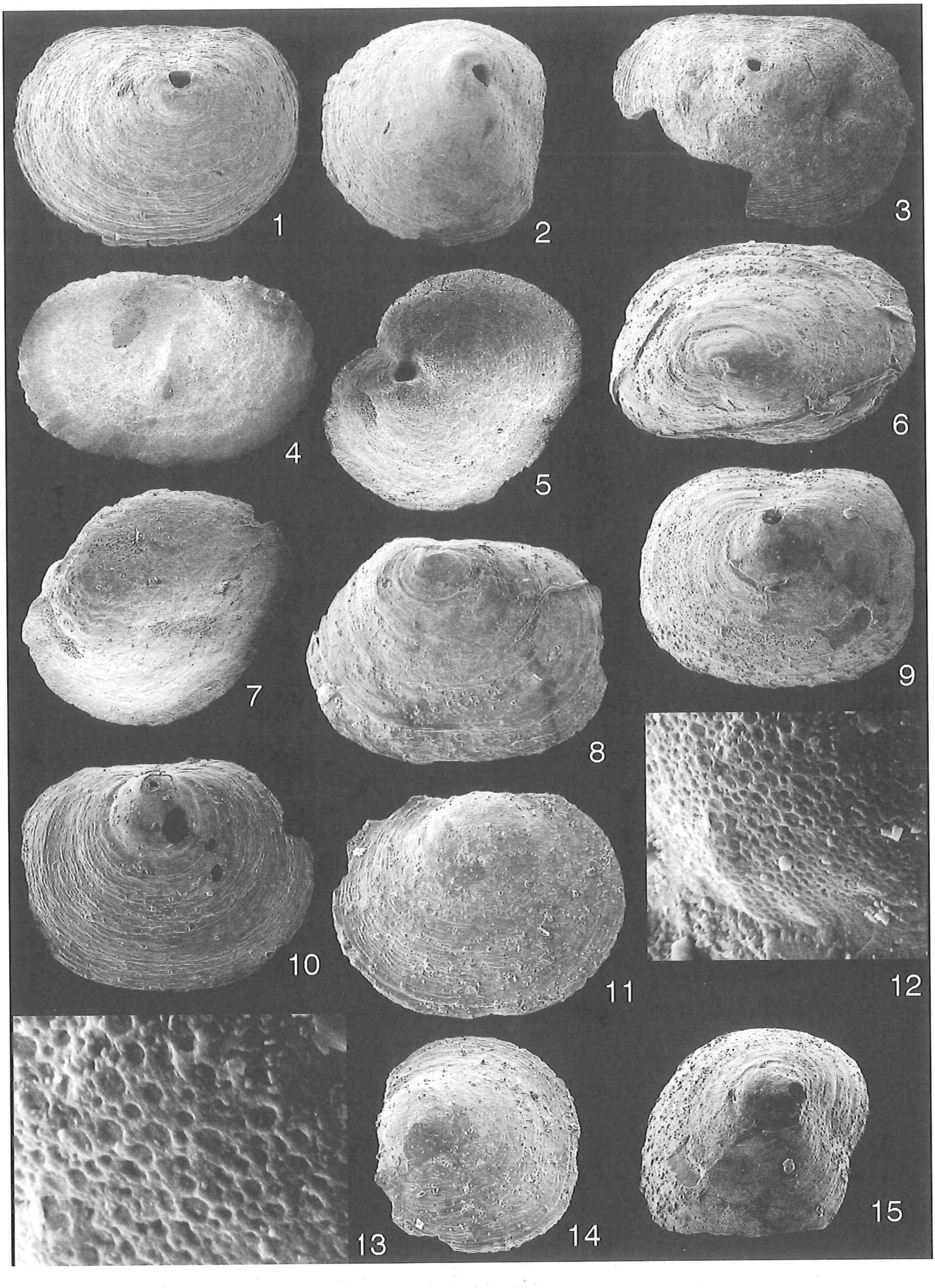
Diagnosis. See Popov and Holmer 1994, p. 141.

EXPLANATION OF PLATE 46

Figs 1–5, 7. *Kotylotreta undata* Koneva; Middle Cambrian, Amgaian, Karagajly Formation, Kostek Range, sample 1639. 1–2, NMW 98.61G.278, ventral valve exterior in normal and oblique lateral views; both ×51. 3, NMW 98.61G.279, ventral valve exterior; ×53. 4, 7, NMW 98.61G.280, dorsal valve interior in normal and oblique lateral views; ×41, ×46. 5, NMW 98.61G.281, ventral valve interior, oblique lateral view; ×43.

Figs 6, 8–15. *Eoscaphelasma*? *delicata* sp. nov.; Upper Cambrian, Malyi Karatau, Kyrshabakty section. 6, 8, NMW 98.61G.282, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds, ventral valve exterior in oblique posterior and normal views, sample 1378-29; ×65, ×60. 9, 12, 15, NMW 98.61G.283, horizon as for 6, ventral valve exterior, detail of pitted micro-ornament of larval shell, and oblique, lateral view, sample 1378-21; ×81, ×740, ×79. 10, NMW 98.61G.284, *Eorudagnostus ovaliformis-Pareuloma* beds, ventral valve exterior, sample 1373; ×64. 11, 13–14, NMW 98.61G.285, horizon as 6, dorsal valve exterior in normal view, detail of pitted microornament of larval shell, oblique lateral view, sample 1378-12; ×95, ×1380, ×84.

PLATE 46



HOLMER *et al.*, *Eoscaphelasma*?, *Kotylotreta*

Species included. Otariconulus sp. 1 and *Otariconulus*? sp. 2, in addition to those listed by Popov and Holmer (1994, p. 141).

Occurrence. Upper Cambrian–Ordovician (Tremadoc–lower Arenig); Kazakhstan, South Urals, Sweden.

Otariconulus sp. 1.

Plate 27, figures 13–16

Material. Two dorsal valves.

Description. Ventral valve unknown. Dorsal valve slightly asymmetrical, gently convex with maximum thickness in the umbonal area, transversely semielliptical in outline with maximum width slightly anterior to the posterior margin. Dorsal umbo marginal, pseudointerarea wide, divided by wide, shallow median groove. Larval shell finely pitted with pits of two slightly varying sizes; postlarval shell with fine, slightly irregular, closely spaced concentric rugellae. Dorsal valve interior with large, elongate, suboval cardinal muscle fields and low, weakly defined median ridge, slightly thickened anteriorly.

Remarks. The asymmetrical outline of these dorsal valves together with the marginal position of the umbo suggest that they are most closely related to *Otariconulus priscus* (Popov and Holmer, 1994) from the Upper Cambrian–Lower Ordovician (Tremadoc) Satpak Formation of south-central Kazakhstan. However, the shells from Malyi Karatau differ in having a relatively wide, straight posterior margin and a gently convex transverse dorsal profile.

Occurrence in Kazakhstan. Batyrbay section, *Harpidoides-Platypeltoides* beds, sample 101 m.

Otariconulus? sp. 2.

Plate 42, figure 9

Material. One dorsal valve (L = 0·58, T = 0·18, Il = 0·08, Iw = 0·32, Pw = 0·16, Cl = 0·26).

Description. Dorsal valve strongly convex with maximum thickness at about mid-way between the posterior margin and mid-length. Umbonal area strongly swollen. Dorsal pseudointerarea low, divided medially by a lens-shaped, gently concave median groove. Ornament comprises fine, evenly spaced, concentric rugellae, and a single growth lamella in the peripheral region. Dorsal interior with large but weakly impressed cardinal muscle scars. Median ridge absent.

Remarks. This single specimen is somewhat comparable with dorsal valves of both *Eoscaphelasma* and *Otariconulus* in its external characters and convexity, as well as in the weakly impressed cardinal muscle scars and the absence of a dorsal median septum.

Occurrence in Kazakhstan. Batyrbay section, *Dikelokephalina* beds, sample from 221 m.

Subphylum RHYNCHONELLIFORMEA Williams, Carlson, Brunton, Holmer and Popov, 1996
Class OBOLELLATA Williams, Carlson, Brunton, Holmer and Popov, 1996
Order OBOLELLIDA Rowell, 1965
Superfamily OBOLELLOIDEA Walcott and Schuchert, 1908
Family OBOLELLIDAE Walcott and Schuchert, 1908

OBOLELLIDAE gen. et sp. indet.

Plate 47, figure 7

1983 *Obolella*? sp., Gorjansky and Koneva, p. 136, pl. 30, fig. 4.

Material. One dorsal internal mould.

Remarks. The single specimen of this unnamed species is characterised by a low, narrow notothyrial platform with a pair of transverse shallow sockets on the lateral margins, deeply impressed, obliquely arranged, elongate suboval posterior adductors, and a fine median ridge extending slightly anterior to the mid-valve. The internal morphology suggests affinity with *Alisina* and *Trematobolus*, but the absence of ventral valves makes it impossible to resolve the generic discrimination of the specimen.

Occurrence. Lower Cambrian, Botomian, *Ushbaspis limbata* Biozone, Ushbas River, sample 1219, Malyi Karatau.

Order NAUKATIDA Popov and Tikhonov, 1990
Superfamily NAUKATOIDEA Popov and Tikhonov, 1990
Family NAUKATIDAE Popov and Tikhonov, 1990

Genus OINA Popov and Tikhonov, 1990

Type species. Original designation by Popov and Tikhonov (1990, p. 42); *Oina rotunda* Popov and Tikhonov, 1990 from the Lower Cambrian (Botomian) of the Alai Range, south Kyrgyzstan.

Diagnosis. See Popov and Tikhonov 1990, p. 42.

Oina? sp.

Plate 47, figures 5–6, 8

1983 *Obolella*? sp., Gorjansky and Koneva, p. 136, pl. 30, figs 1–3.

Material. One exfoliated ventral valve and one dorsal internal mould.

Description. Strongly biconvex, smooth, subcircular in outline with narrow posterior margin and rectimarginate anterior commissure. Lateral profile of the ventral valve strongly and unevenly convex, with maximum thickness in the posterior third. Dorsal valve strongly convex with low, narrow, linear interarea. Ventral valve interior unknown. Dorsal valve interior with transversely suboval posterior adductor muscle scars. Strong median septum and pair of slightly divergent submedian septa extending anteriorly to mid-valve length.

Remarks. The ventral pseudointerarea and interior, as well as characters of the articulation, remain unknown in this species, but the smooth shell surface, strongly biconvex shell, and the presence of a strong median and pair of submedian septa suggest a probable affinity with the Order Naukatida, and in particular with the genera *Oina* and *Bajarinovia* (Aksarina, *in* Aksarina and Pelman 1978, p. 106). However, the internal morphology of the latter genus is known imperfectly. The assignment to *Oina* of these two specimens thus remains provisional.

Occurrence. Lower Cambrian, Toyonian, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, Koksu River, sample 1207, Malyi Karatau.

Class KUTORGINATA Williams, Carlson, Brunton, Holmer and Popov, 1996
Order KUTORGINIDA Kuhn, 1949
Superfamily KUTORGINOIDEA Schuchert, 1893
Family KUTORGINIDAE Schuchert, 1893

Genus KUTORGINA Billings, 1861

Type species. Original designation by Billings (1861, p. 8); *Kutorgina cingulata* Billings, 1861, from the Lower Cambrian of Labrador, Canada.

Diagnosis. See Popov *et al.* 1996, p. 346.

Remarks. Redescription of the type species and detailed discussion of this genus are given by Popov *et al.* (1996).

Kutorgina cf. *rugosa* Gorjansky, 1983

Plate 47, figures 3–4

cf. 1983 *Kutorgina rugosa* Gorjansky, *in* Gorjansky and Koneva, p. 137, pl. 30, figs 5–6.
1983 *Kutorgina* sp., Gorjansky and Koneva, p. 137, pl. 30, figs 7–9.

Material. Three ventral and two dorsal valves.

Remarks. *Kutorgina* was mentioned by Ergaliev and Pokrovskaya (1977) as a relatively common brachiopod in the upper part of the Lower Cambrian sequence in the Malyi Karatau Range. Calcareous brachiopods are invariably poorly preserved in these beds and only five identifiable specimens of *Kutorgina* are available for this study. All are from the *Redlichia chinensis-Kootenia gimmelfarbi* Biozone and some are closely similar to topotypes of *Kutorgina rugosa* from the Lower Cambrian (Toyonian) of the Rassokha River (Gorjansky *et al.* 1964) in having the gently convex ventral valve ornamented by strong, high, concentric ridges. However, specimens with weakly developed concentric ornament also occur in the samples and it is likely that ornamentation is variable within the species. The interiors of both valves from Malyi Karatau remain unknown, so that their specific determination remains somewhat tentative.

Occurrence. Lower Cambrian, Toyonian, Malyi Karatau, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, samples, 1216a, 5-IV-52.

Superfamily NISUSIOIDEA Walcott and Schuchert, 1908
Family NISUSIIDAE Walcott and Schuchert, 1908

Genus NARYNELLA Andreeva, 1987

Type species. Original designation by Andreeva (1987); *Nisusia ferganensis* Andreeva, 1962, p. 89; Middle Cambrian, Amgaian, Fergana valley, Uzbekistan.

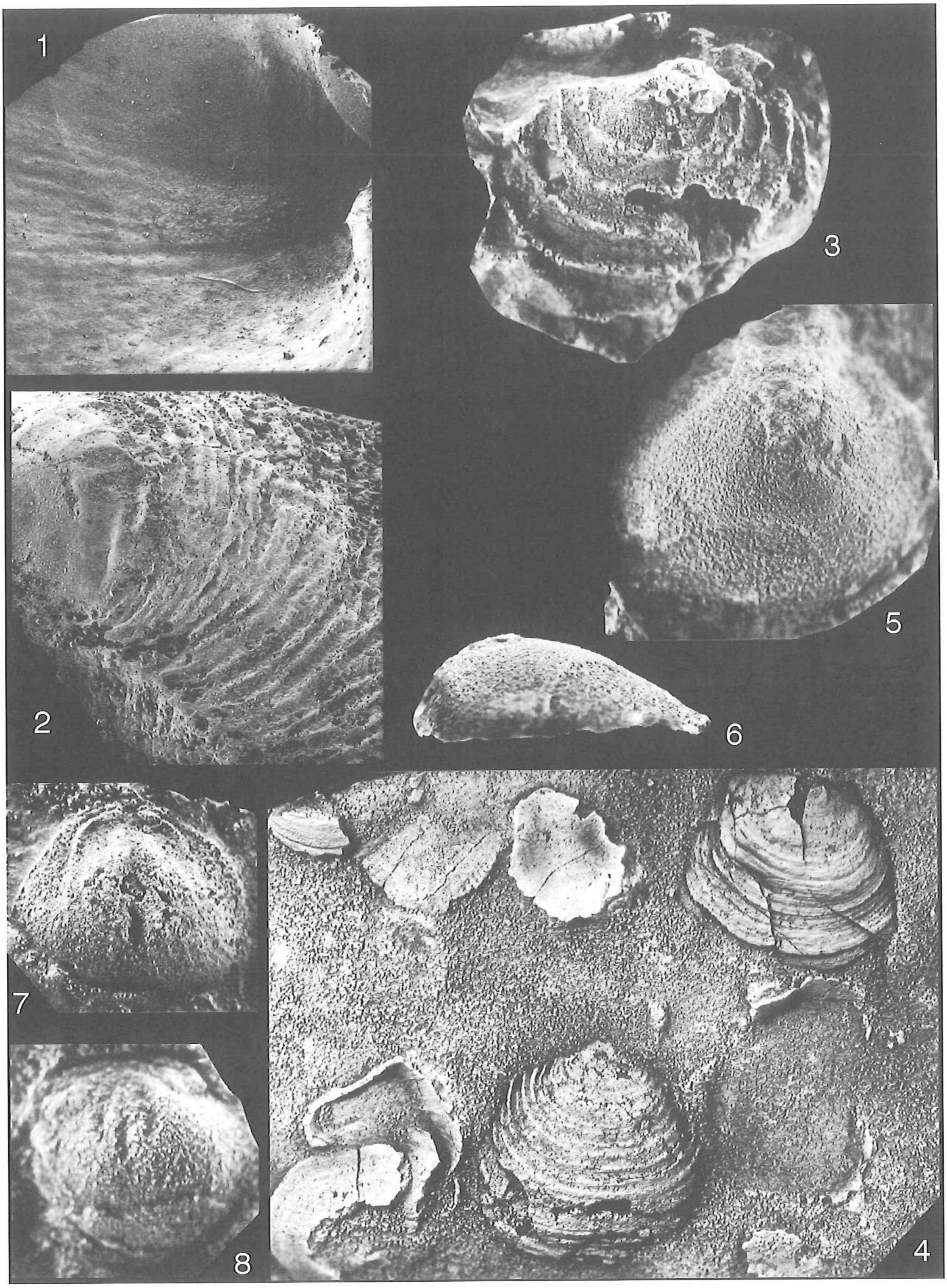
EXPLANATION OF PLATE 47

Figs 1–2. *Micromitra*? *semicircularis* Imanaliev and Pelman; Lower Cambrian, Darbaza Formation, Suukadyr Mountains, locality 5875. 1, NMW 98.61G.324, ventral valve interior, oblique lateral view showing pinnate mantle canals; ×29. 2, NMW 98.61G.325, ventral valve, larval and post larval shell ornament; ×400.

Figs 3–4. *Kutorgina* cf. *rugosa* Gorjansky; Lower Cambrian, Toyonian, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, Malyi Karatau, Ushbas River section. 3, exfoliated ventral valve, sample 1216a; ×3. 4, IGNA 2224/98, group of disarticulated valves on bedding surface, sample 5-IV/52; ×3.

Figs 5–6, 8. *Oina*? sp.; Lower Cambrian, Toyonian, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, Malyi Karatau, Koksu River section, sample 1207. 5–6, IGNA 2224/84, exfoliated ventral valve, exterior and lateral views; both ×6. 8, IGNA 2224/88, dorsal internal mould; ×6.

Fig. 7. Obolellidae gen. et sp. indet.; Lower Cambrian, Botomian, *Ushbaspis limbata* Biozone, Malyi Karatau, Ushbas River section, sample 1219; IGNA 2229/86, dorsal internal mould; ×6.



HOLMER *et al.*, brachiopods

ferganensis in characters of radial ornament, sagittal profile and convexity of both valves, as well as in the inclination of the ventral pseudointerarea and nature of the pseudodeltidium. However, imperfect preservation of the ventral valves in the Kazakhstan specimens and inadequate information on the internal morphology of the types of *N. ferganensis* make specific discrimination of the Malyi Karatau shells slightly tentative.

Specimens described by Aksarina (1975) under the name *Nisusia nasuta* var. *ramosa* Nikitin, 1956 from the Middle Cambrian (Amgaian) *Sdzuyella–Aegunaspis* beds of the Turkestan Range, Uzbekistan, closely resemble *N. ferganensis* in external morphology, including a well-defined ventral sulcus, apsacline ventral pseudointerarea, absence of spines, and radial ornament, and we re-assign this material to *ferganensis*.

Occurrence. Middle Cambrian, Amgaian, Malyi Karatau, Kyrshabakty section, *Ptychagnostus atavus* Biozone, sample 1314-8.

Class RHYNCHONELLATA Williams, Carlson, Brunton, Holmer and Popov, 1996
Order ORTHIDA Schuchert and Cooper, 1932
Superfamily BILLINGSELLOIDEA Schuchert, 1893
Family BILLINGSELLIDAE Schuchert, 1893

Genus BILLINGSELLA Hall and Clarke, 1892

Type species. Original designation by Hall and Clarke (1892); *Orthis pepina* Hall, 1863, Upper Cambrian, Potsdam Sandstone, New York State, USA.

Billingsella aff. *tonkiniana* Mansuy, 1915

Plate 48, figures 8–13

1983 *Billingsella* aff. *tonkiniana* Mansuy; Nikitin and Popov, p. 125, pl. 32, figs 1–10.

Material. 20 ventral and 13 dorsal valves.

Description. Shell flat, dorsibiconvex, slightly transverse, subrectangular to subpentagonal in outline, about 85 per cent as long as wide with the maximum width slightly anterior to or along the posterior commissure. Cardinal extremities slightly obtuse to right-angled. Ventral valve gently convex, about 10–15 per cent as thick as long, subcarinate in the posterior half, with pointed beak perforated by a small, rounded foramen. Ventral interarea flat, high, triangular, strongly apsacline, with a broad, convex triangular pseudodeltidium. Dorsal valve gently convex, about 75 per cent as long as wide and 15 per cent as thick as long, with a shallow sulcus originating in the umbonal area and a low, planar, anacline interarea. Ornament multicostellate with some tendency towards fasciculate ribbing and with about 15 primary costae in the umbonal area. About 5–7 costellae in 5 mm at 10 mm from the beak. Concentric ornament of fine, evenly spaced fila.

Ventral interior with thick, boss-like teeth lacking dental plates, and a rhomboidal muscle field which is slightly raised and rounded anteriorly. Diductor scars clearly impressed, linear, divided completely by the broad, triangular adductor scars. Ventral mantle canals baculate with straight, divergent proximal parts of the *vascula media*. Dorsal interior preserved incompletely, but a wide, slightly raised notothyrial platform, low, widely divergent socket plates, and a short median ridge are present as observed in internal moulds and transverse serial sections.

Remarks. In general shell shape and internal morphology of the ventral valve, the Kazakhstanian specimens are closely comparable with *Billingsella tonkiniana* Mansuy (1915, p. 7, pl. 1, fig. 2a; 1916, pl. 1, figs 11–12) from the Upper Cambrian *Billingsella* beds of north Vietnam, and with specimens described as *B.* aff. *tonkiniana* by King (1930, p. 322, pl. 17, fig. 8, text-fig. 3) from the Upper Cambrian of Iran; however, study of specimens from Iran deposited in The Natural History Museum, London, indicates that the Malyi Karatau specimens differ in being larger and in having slightly coarser radial ornament and a more transverse shell outline. *B.* aff. *tonkiniana* is also comparable with *Billingsella fluctuosa* var. *insignis* Nikitin (1956, p. 37, pl. 7, figs 1–17) from the Upper Cambrian Kujandy Formation of north-eastern central Kazakhstan, but is readily distinguished in having a shorter posterior margin with normal to slightly obtuse cardinal extremities, a gently convex and sulcate dorsal valve, and weakly developed fasciculation of the costellae.

Occurrence. Upper Cambrian of Malyi Karatau, Batyrbay section, *Harpidoides-Platypeltoides* beds, sample 98 m.

Superfamily ORTHOIDEA Woodward, 1852
Family EOORTHIDAE Walcott, 1908

Genus APHEOORTHIS Ulrich and Cooper, 1936

Type species. Original designation by Ulrich and Cooper (1936, p. 62); *Eoorthis linnecocosta* Walcott 1924, lower Ordovician, Colorado, USA.

Apheoorthis sp.

Plate 49, figures 1–4

1983 *Apheoorthis* sp.; Nikitin and Popov, p. 127, pl. 32, figs 11–15.

Material. Three ventral and two dorsal valves.

Remarks. Specimens of *Apheoorthis* in Upper Cambrian rocks of Malyi Karatau are rare and usually poorly preserved. Descriptions and discussion of affinities were given by Nikitin and Popov (1983); some silicified specimens are re-illustrated here.

Occurrence. Upper Cambrian, Malyi Karatau, Kyrshabakty section, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds, samples 1378-4, 1378-12.

Order PENTAMERIDA Schuchert and Cooper, 1931
Suborder SYNTROPHIIDINA Ulrich and Cooper, 1936
Superfamily SYNTROPHIOIDEA Ulrich and Cooper, 1936
Family HUENELLIDAE Schuchert and Cooper, 1931

Genus PALAEOSTROPHIA Ulrich and Cooper, 1936

Type species. Original designation by Ulrich and Cooper (1936, p. 627); *Syntrophia orthia* Walcott, 1905, Upper Cambrian, Chaumitien Limestone, Shantung Province, North China.

Diagnosis. See Ulrich and Cooper 1938, p. 194, and Nikitin 1956, p. 75.

Species included. Palaeostrophia angulata Nikitin and Popov, 1983; *Palaeostrophia fibrillosa* Nikitin and Popov, 1983; *Palaeostrophia tecta* Nikitin and Popov, 1983 in addition to species listed by Nikitin (1956, p. 76).

Remarks. We here give emended diagnoses and illustrate some type material of the three stratigraphically successive species of *Palaeostrophia* from Malyi Karatau described in detail by Nikitin and Popov (1983). The oldest is *P. fibrillosa*, which can be distinguished easily from the two younger species, *P. angulata* and *P. tecta*, in having a relatively wide hinge line and a weak umbonal dorsal sulcus reversed posteriorly into a high median fold which is rounded in cross section. *P. angulata* also has a strong ventral sulcus and dorsal median fold originating in the umbonal area, but is distinguished in having a carinate dorsal valve, and the ventral sulcus is angular in cross section. *P. tecta* differs from the other two Kazakhstanian species in having a relatively weak, gently rounded cross section to the dorsal median fold and a ventral sulcus originating between the umbo and mid-length.

Palaeostrophia fibrillosa Nikitin and Popov, 1983

Plate 50, figures 1–2, 4–8

1983 *Palaeostrophia fibrillosa* Nikitin and Popov, p. 129, pl. 32, figs 18, 21; pl. 34, figs 5–13.

Holotype. CNIGR 27/12068, dorsal valve; Upper Cambrian, Kyrshabakty section, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds, sample 1362, Malyi Karatau, southern Kazakhstan.

Material. 34 ventral and 29 dorsal valves.

Diagnosis. Shell dorsibiconvex, transversely suboval, about 80 per cent as long as wide; posterior margin slightly shorter than maximum width, which is at the mid-length, cardinal extremities obtuse to right-angled; anterior commissure uniplicate; ventral valve moderately convex, close to 30 per cent as thick as long with pointed, slightly erect beak; sulcus originating closely anterior to the umbo, widening anteriorly and evenly curved in cross section; tongue high, suboval, occupying about 50 per cent of maximum valve width; dorsal valve strongly convex, about one-third as thick as long with maximum thickness near the anterior margin; umbonal area with indistinct sulcus reversed into a high median fold at mid-valve length; the fold is bounded laterally by plications which deepen near the anterior margin; shell surface mostly smooth, finely lamellose peripherally; ventral interior with sessile spondylium; dorsal interior with short, discrete brachiophore plates converging anteriorly.

Occurrence. Upper Cambrian of Malyi Karatau, Kyrshabakty section, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds, samples 1362, 1378-11, 1378-12.

Palaeostrophia angulata Nikitin and Popov, 1983

Plate 50, figures 3, 9–18

1983 *Palaeostrophia angulata* Nikitin and Popov, p. 127, pl. 33, figs 1–11, text-fig. 1.

Holotype. CNIGR 38/12068, ventral valve, figured by Nikitin and Popov (1983, pl. 33, fig. 2); Upper Cambrian, Malyi Karatau, Batyrbay section, *Harpidoides-Platypeltoides* beds, sample 98 m.

Material. 11 ventral and 18 dorsal valves.

Diagnosis. Shell smooth, dorsibiconvex, slightly transversely subtriangular to subtriangular in outline, about 80 per cent as long as wide; hinge line short, about 50 per cent as wide as the shell width; anterior

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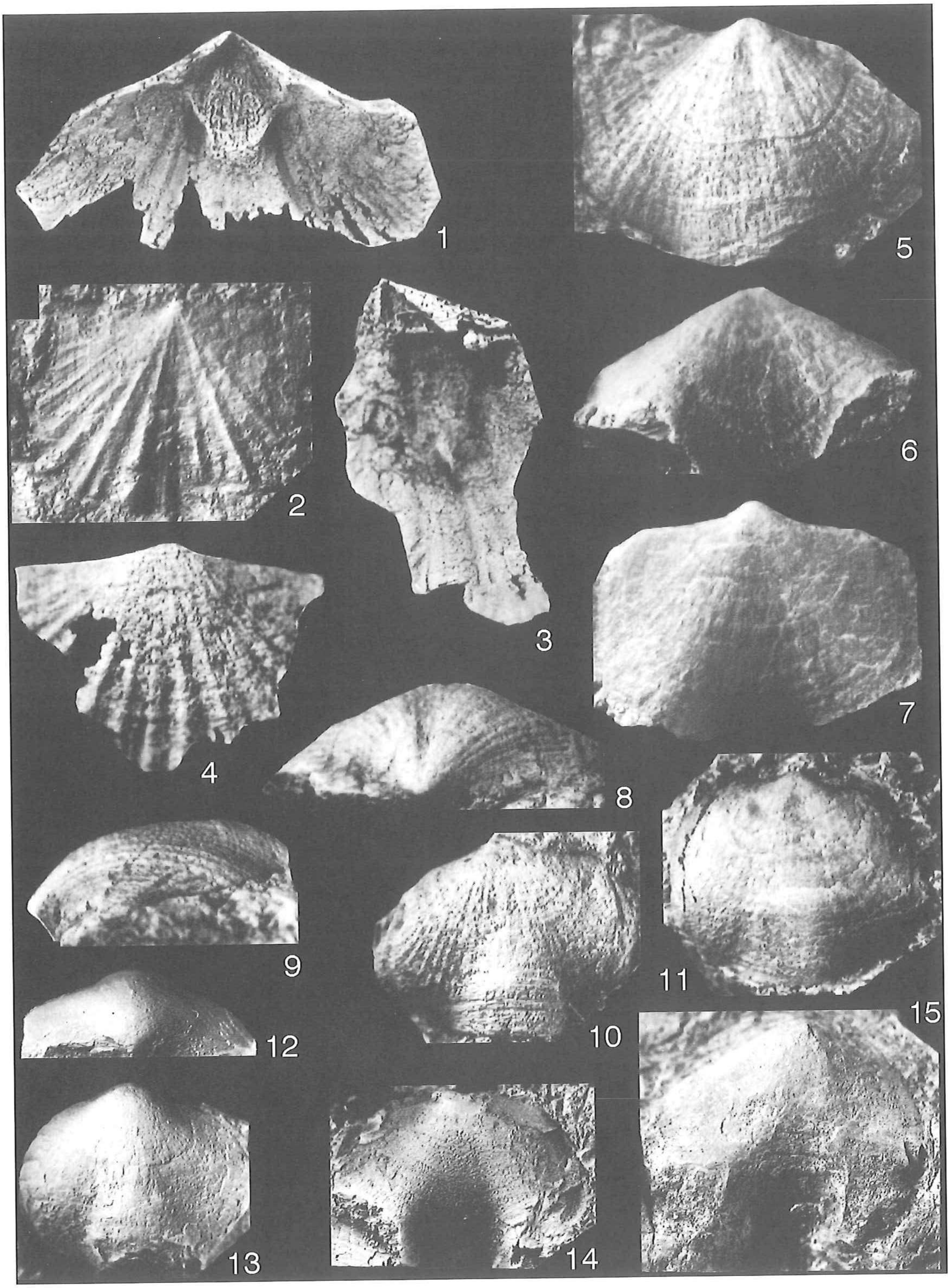
EXPLANATION OF PLATE 49

Figs 1–4. *Apheoorthis* sp.; Upper Cambrian, Shabakty Group, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds, Malyi Karatau, Kyrshabakty section. 1, CNIGR 12/12068, ventral valve interior, sample 1378-12; ×8. 2, CNIGR 11/12068, dorsal valve exterior, sample 1378-4; ×6. 3, CNIGR 15/12068, dorsal valve interior, sample 1378-12; ×6. 4, CNIGR 14/12068, ventral valve exterior, sample 1378-12; ×8.

Figs 5–11. *Mesonomia*? sp.; Upper Cambrian, Shabakty Group, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds, Malyi Karatau, Kyrshabakty section. 5, 8–9, CNIGR 22/12068, dorsal valve exterior in normal view, posterior view, lateral view, sample 1378-12; all ×8. 6–7, CNIGR 24/12068, ventral valve exterior in anterior and normal views, sample 1378-12; both ×8. 10, CNIGR 22/12068, dorsal valve exterior, sample 1378-12; ×8. 11, CNIGR 18/12068, dorsal valve exterior, sample 1362; ×8.

Figs 12–15. *Palaeostrophia tecta* Nikitin and Popov; Upper Cambrian, Shabakty Group, *Euloma limataris-Taoyuania* beds, Malyi Karatau, Batyrbay section, sample 136 m. 12–13, CNIGR 54/12068, dorsal valve exterior in posterior and normal views; ×4. 14, CNIGR 55/12068, ventral valve exterior; ×4·7. 15, CNIGR 56/12068, ventral valve exterior; ×4·7.

PLATE 49



HOLMER *et al.*, brachiopods

commissure deeply uniplicate; ventral valve with maximum thickness posterior to mid-length, deep sulcus with subtriangular cross section originating near the beak, tongue high, subtriangular, occupying close to 50 per cent of maximum valve width; dorsal valve strongly convex, about 40 per cent as thick as long with maximum thickness near the anterior margin; median fold high, carinate, originating slightly anterior to the beak; ventral interior with pseudospondylium and subparallel dental plates; dorsal interior with brachiophore plates joined at the valve floor.

Occurrence. Upper Cambrian, Malyi Karatau, Batyrbay section, *Harpidoides-Platypeltoides* beds, samples from 77–98 m.

Palaeostrophia tecta Nikitin and Popov, 1983

Plate 49, figures 12–15

1983 *Palaeostrophia tecta* Nikitin and Popov, p. 130, pl. 33, figs 13–15, text-fig. 2.

Holotype. CNIGR 54/12068, dorsal valve, figured by Nikitin and Popov (1983, pl. 33, fig. 13); Upper Cambrian, Batyrbay section, *Euloma limataris–Batyraspis* beds, sample from the 136 m interval, Malyi Karatau.

Material. Four ventral and three dorsal valves.

Diagnosis. Shell slightly dorsibiconvex, transversely suboval in outline, posterior margin short, cardinal extremities obtuse, rounded; anterior commissure strongly uniplicate; ventral valve moderately convex with slightly incurved, swollen beak; sulcus originating just posterior to the mid-valve length, deepening anteriorly and forming a high, semioval tongue directed normal to the commissural plane; dorsal valve moderately convex with small, strongly incurved beak, umbonal area swollen; median fold originating close to mid-valve length, semioval in cross section; ventral interior with sessile spondylium raised anteriorly; dorsal interior with short brachiophore plates joined at the valve floor as a sessile septalium.

Occurrence. Upper Cambrian, Malyi Karatau, Batyrbay section, *Euloma limataris-Taoyuania* beds, sample 136 m.

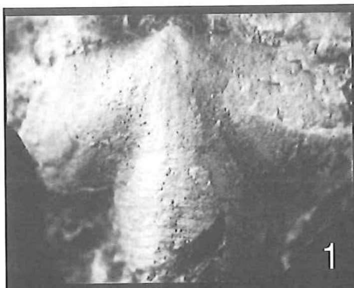
Genus MESONOMIA Ulrich and Cooper, 1936

Type species. Original designation by Ulrich and Cooper (1936, p. 627); *Eoorthis iophon* Walcott, 1924, Upper Cambrian, Lyell Formation, British Columbia, Canada.

EXPLANATION OF PLATE 50

Figs 1–2, 4–8. *Palaeostrophia fibrillosa* Nikitin and Popov; Upper Cambrian, Shabakty Group, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds, Malyi Karatau, Kyrshabakty section. 1, 5, CNIGR 27/12068, dorsal valve exterior in normal and posterior views, sample 1362; both ×4·2. 2, CNIGR 19/12068, ventral valve exterior, sample 1378-12; ×5·6. 4, CNIGR 28/12068, dorsal valve exterior, sample 1378-12; ×5·6. 6, CNIGR 34/12068, dorsal valve interior, sample 1378-12; ×11. 7, CNIGR 35/12068, ventral valve interior, sample 1378-12; ×11·2. 8, CNIGR 32/12068, ventral valve interior, sample 1378-12; ×11·2.

Figs 3, 9–18. *Palaeostrophia angulata* Nikitin and Popov; Upper Cambrian, Shabakty Group, *Lophosaukia* and *Harpidoides-Platypeltoides* beds, Malyi Karatau, Batyrbay section. 3, CNIGR 51/12068, ventral valve exterior, sample 77 m; ×5·2. 9–11, CNIGR 28/12068, dorsal valve exterior in normal, posterior and lateral views, sample 98 m; all ×5·2. 12–16, CNIGR 41/12068, conjoined valves in ventral, anterior, posterior, dorsal, and lateral views, sample 98 m; all ×5·2. 17, CNIGR 52/12068, ventral valve exterior of juvenile specimen, sample 98 m; ×5·2. 18, CNIGR 47/12068, dorsal valve exterior of juvenile specimen, sample 98 m; ×5·2.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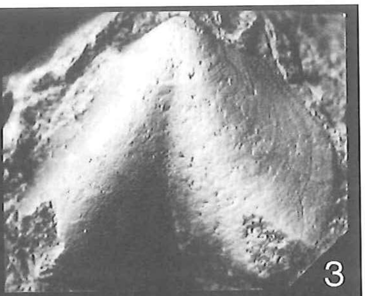
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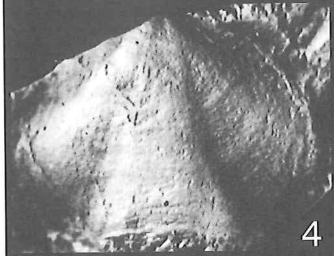
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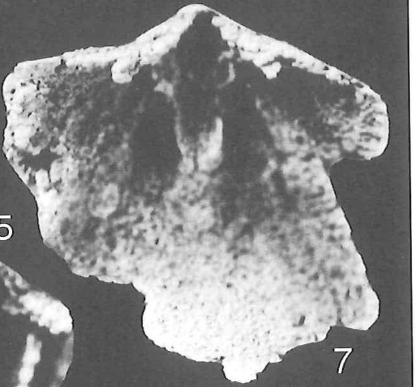
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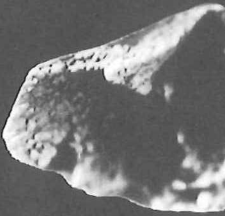
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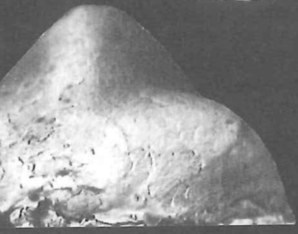
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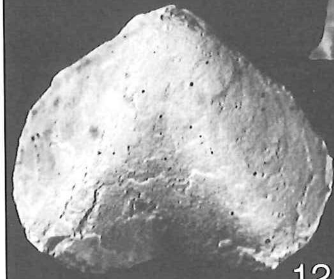
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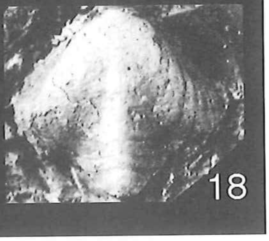
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HOLMER *et al.*, *Palaeostrophia*

Mesonomia? sp.

Plate 49, figures 5–11

1983 *Mesonomia*? sp., Nikitin and Popov, p. 131, pl. 32, figs 16–17, 20, 23–25.

Material. Two ventral and three dorsal valves.

Remarks. Externally these shells are similar to *Palaeostrophia fibrillosa* Nikitin and Popov, 1983 but have finer radial ornament; they are rare in the *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds of the Kyrshabakty section. They were questionably assigned originally to *Mesonomia* (Nikitin and Popov 1983), but there is no additional material available for further analysis and the interiors of both valves remain unknown. Some specimens described by Nikitin and Popov (1983) are re-illustrated here.

Occurrence. Upper Cambrian of Malyi Karatau, Kyrshabakty section, *Pseudagnostus pseudangustilobus-Acrocephalaspina* beds, sample 1362.

Family CLARKELLIDAE Schuchert and Cooper, 1932

Genus CLARKELLA Walcott, 1908

Type species. Original designation by Walcott (1908, p. 110); *Polytoechia*? *montanensis* Walcott, 1905 from the Lower Ordovician of Montana, USA.

Species included. *Clarkella testudo* Nikitin and Popov, 1983, in addition to species listed by Nikitin (1956, p. 88).

Clarkella supina Nikitin, 1956

Plate 51, figures 8–11

1956 *Clarkella supina* Nikitin, p. 91, pl. 11, figs 1–39, text-figs 11, 12B.

Holotype. IGNA 241/601, Ordovician, Kogashik Regional Stage, Olenty Formation, north-central Kazakhstan, Sasyksor Lake, locality 601.

Remarks. Silicified specimens of *Clarkella supina* from the South Urals are illustrated here to compare with two somewhat older species of the same genus from the Malyi Karatau Range.

Occurrence. Ordovician, Kogashik Regional Stage, Olenty Formation, north-central Kazakhstan; Kuagash Formation, *Prioniodus elegans–Oepikodus evae* biozones, South Urals.

Clarkella testudo Nikitin and Popov, 1983

Plate 51, figures 1–4

1961 *Clarkella orientalis* Ulrich and Cooper; Rukavishnikova, p. 44, pl. 1, figs 18–19, text-fig. 3; *non* Ulrich and Cooper 1936

1983 *Clarkella testudo* Nikitin and Popov, p. 132, pl. 34, figs 14–19, text-fig. 3a–b.

Holotype. CNIGR 66/12068, dorsal valve figured by Nikitin and Popov (1983, pl. 34, fig. 14); Lower Ordovician, Batyrbay section, *Nileus* beds, sample 465 m, Malyi Karatau, southern Kazakhstan.

Material. Four ventral and four dorsal valves.

Diagnosis. Shell smooth, slightly dorsibiconvex, transversely suboval in outline, about 80 per cent as long as wide, anterior margin uniplicate; ventral valve moderately and evenly convex, about 25 per cent as thick as long, with shallow sulcus originating close to the mid point between the umbo and mid-valve; tongue low, suboval, oriented almost at right angles to the commissural plane; dorsal valve moderately convex, about 33 per cent as thick as long, with maximum thickness near the anterior margin; dorsal beak strongly swollen; median fold low, suboval in cross section, bounded laterally by weak plications; ventral interior with spondylium supported by median septum and two short lateral septa in umbonal part; dorsal interior with paired brachial plates supported laterally by accessory septa.

Remarks. Nikitin and Popov (1983) gave a detailed description, statistics and discussion of the affinities of this species.

Occurrence. Lower Ordovician, Malyi Karatau Range, Batyrbay section, *Nileus* beds, sample 465 m.

Clarkella turgida Nikitin, 1956

Plate 51, figures 5–7

1956 *Clarkella supina* var. *turgida* Nikitin, p. 95, pl. 10, figs 40–59.
1983 *Clarkella turgida* Nikitin; Nikitin and Popov, p. 134, pl. 32, figs 19–22, text-fig. 3c–d.

Holotype. IGNA 231/B6-49, dorsal valve, figured by Nikitin (1956, pl. 10, figs 44–46); Lower Ordovician, Olenty Formation, Lake Sasyksor, locality 49, north-eastern central Kazakhstan.

Material. Four ventral and four dorsal valves.

Diagnosis. Dorsibiconvex, slightly transversely suboval to subcircular in outline with a strongly uniplicate posterior commissure; ventral valve strongly convex in cross section with maximum thickness between the slightly swollen beak and mid-valve length; ventral sulcus originates near mid-valve; tongue semioval, inclined almost at right-angles to the commissural plane; ventral interarea very narrow, subtriangular, apsacline; dorsal valve hemispherical, with maximum thickness anterior to mid-valve and with a strongly swollen umbonal area; dorsal fold originating close to mid-valve length, with steep lateral slopes poorly defined at the lateral margins of the valve.

Remarks. These shells closely resemble those described by Nikitin (1956) as *Clarkella supina* var. *turgida* in their size, subcircular outline, and transverse profile of the dorsal median fold. Nikitin and Popov (1983) separated *C. turgida* as a distinct species.

Occurrence. Lower Ordovician, Malyi Karatau, Batyrbay section, *Nileus* beds, sample 595–601 m.

Family EOSTROPHIIDAE Ulrich and Cooper, 1936

EOSTROPHIIDAE gen. et sp. indet.

Plate 48, figures 14–15

1983 *Eostrophiidae* gen. et sp. indet.; Nikitin and Popov, p. 134, pl. 32, figs 19, 22.

Material. One ventral and one dorsal valve.

Remarks. Middle Cambrian syntrophiidine brachiopods from Malyi Karatau remain known only from the two valves described and illustrated by Nikitin and Popov (1983, p. 134); they are re-illustrated here.

Occurrence. Middle Cambrian, Mayaian, Malyi Karatau, Kyrshabakty section, *Lejopyge armata* Biozone, sample 1346-10.

FAUNAL ASSEMBLAGES AND BIOSTRATIGRAPHY

Malyi Karatau Range

Seven successive lingulate brachiopod assemblages can be recognised in the Malyi Karatau sequences across the stratigraphical interval spanning the early Cambrian *Microcornus parvulus–Hebidiscus orientalis* local biozones to the late Cambrian *Hedinaspis sulcatus* beds.

1. *Lingulellotreta malongensis-Linnarssonia constans* assemblage. The oldest known lingulate in the Lower Cambrian is *Linnarssonia constans* from the overlapping *parvulus–orientalis* interval. *Palaeobolus liantuoensis* then appears in the *orientalis* Biozone, with *Lingulellotreta malongensis* recorded first in the *Ushbaspis limbata* Biozone. These three taxa range up into the *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, where they occur together with *Botsfordia caelata*, *Kutorgina* cf. *rugosa*, Obolellidae gen. et sp. indet. and *Oina*? sp. *Linnarssonia*, *Botsfordia* and *Kutorgina* are cosmopolitan taxa with wide stratigraphical ranges; however, *K.* cf. *rugosa* is very close to this species from the Toyonian Stage of north-central Siberia (Gorjansky 1964; Gorjansky and Koneva 1983).

P. liantuoensis and *L. malongensis* are confined geographically to the Malyi Karatau Range and to South China. The similarly close affinity of Lower Cambrian trilobite faunas from Malyi Karatau and the Yangtze Platform was recognised by Ergaliev and Pokrovskaya (1978). In particular, *Hebidiscus orientalis* was described originally from the Shypai Shale of western Hubei (Chang 1953), and the first appearance of *Redlichia chinensis* in the upper part of the Lower Cambrian of Malyi Karatau provides good ground for correlation with the base of the Lungwangmiaoan Stage of China and the base of the Ordian in Australia (Shergold 1995). The stratigraphical range of *L. malongensis* in western Yunnan and Malyi Karatau is probably synchronous, being most common in both areas in the lower *R. chinensis* Biozone, but making its first appearance just below the lower boundary of this level. Thus its lowermost occurrence in the upper part of the Chiungchussu Formation (Yuanshan Member) in the Maotianshan section, Chengjiang County, Yunnan suggests close correlation of this interval with the *U. limbata* Biozone of Kazakhstan (see also Holmer *et al.* 1997).

It has long been practice in both China and Kazakhstan to correlate stratigraphical units below the first appearance of *R. chinensis* with the Atdabanian of Central Siberia. Brachiopod-based correlations with Siberian sections are difficult, but the orders Lingulida and Acrotretida, and, in particular, *Linnarsonia* and *Botsfordia*, first appear in Siberia in the latest Atdabanian (upper *Judomia* Biozone). In fact nowhere is there good evidence of the presence of lingulides and acrotretides in the Atdabanian below this level. Thus the occurrence of the relatively derived lingulide *L malongensis* well above the earliest occurrence of

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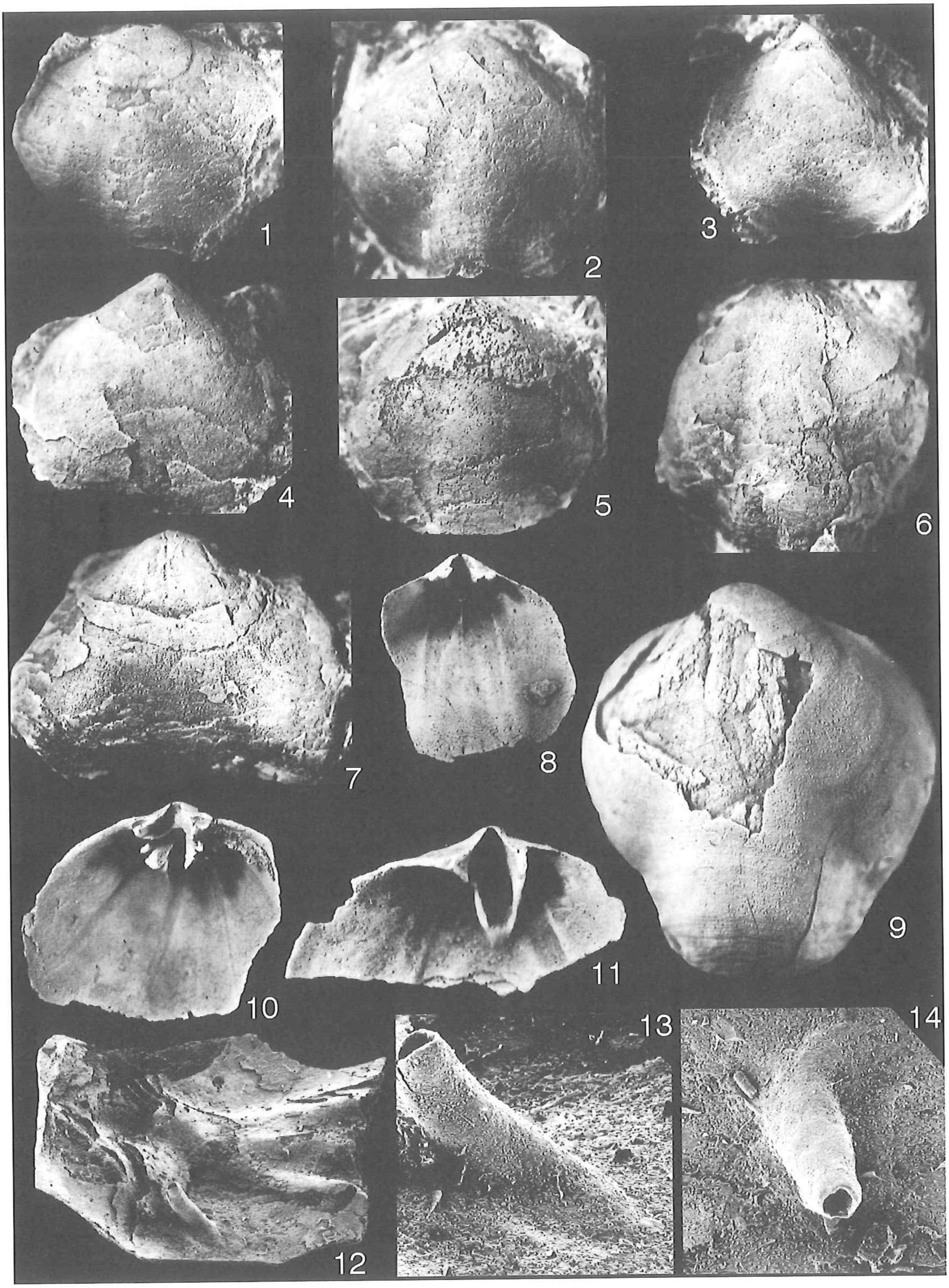
EXPLANATION OF PLATE 51

Figs 1–4. *Clarkella testudo* Nikitin and Popov; Lower Ordovician, Kogoshik Regional Stage, *Drepanoistodus proteus* Biozone, Malyi Karatau, Batyrbay section, sample 465 m. 1, CNIGR 67/12068, dorsal valve exterior. 2, CNIGR 66/12068, holotype, dorsal valve exterior. 3, CNIGR 64/12068, ventral valve exterior. 4, CNIGR 62/12068, ventral valve exterior. All ×5·3.

Figs 5–7. *Clarkella turgida* Nikitin; Lower Ordovician, Kogoshik Regional Stage, *Prioniodus deltatus longibasis* Biozone, Malyi Karatau, Batyrbay section, sample 595–601 m. 5, CNIGR 71/12068, dorsal valve exterior. 6, CNIGR 70/12068, dorsal valve exterior. 7, CNIGR 69/12068, ventral valve exterior. All ×4.

Figs 8–11. *Clarkella supina* Nikitin; Lower Ordovician, Kuagash Formation, *Prioniodus elegans–Oepikodus evae* biozones; South Urals, Kuagash River, locality B-523 of Korinevskii (for reference, see Popov and Holmer 1994, text-fig. 21). 8, NMW 98.61G.330, ventral valve interior. 9, NMW 98.61G.331, dorsal valve exterior. 10, NMW 98.61G.332, dorsal valve interior. 11, NMW 98.61G.327, ventral valve interior. All ×4.

Figs 12–14. *Linnarssonia constans* Koneva; Lower Cambrian, Shabakty Group, *Redlichia chinensis-Kootenia gimmelfarbi* Biozone, Malyi Karatau, Baba-Ata section, sample 5/26b; NMW 98.69G.8, incomplete dorsal valve. 12, oblique lateral view of valve interior showing tubular outgrowth of inner shell formed by secondary secretion around a symbiont; ×47. 13, side view of the tube showing junction with floor of dorsal valve; ×120. 14, anterior view of the tube showing aperture; ×90.



HOLMER *et al.*, *Clarkella*, *Linnarssonia*

Linnarssonia in Malyi Karatau probably suggests a Botomian to younger age for the *U. limbata* Biozone and overlying Lower Cambrian strata. This observation lends support to an alternative interpretation of correlation of basal levels of the Shabakty Group, equating the *Microcornus parvulus* Biozone with the Botomian and Toyonian of Siberia (Missarzhevsky, *in* Rozanov and Sokolov 1984; Mambetov 1993; Text-fig. 12).

2. *Prototreta venusta-Kyrshabaktella certa* assemblage. This unit corresponds with the lower Middle Cambrian *Peronopsis*? *ultimus* and *Ptychagnostus atavus* trilobite biozones of the Kyrshabakty section. The most characteristic species are the lingulides *Aksarinaia triquetra* and *Canalilatus perarus*, together with the acrotretides *Kotylotreta undata*, *Linnarssonia captiosa*, *Prototreta venusta* and *Stilpnotreta tecta*. *Acrothele* sp., *Karathele coronata*, *Dictyonina hexagona* and *Micromitra* cf. *modesta* are also present occasionally. Co-occurrence of such genera as *Acrothele*, *Karathele* and *Stilpnotreta* is most unusual. Recent studies of acrotheloideans (Holmer *et al.* 1996; Korovnikov 1998) clearly suggest direct phylogenetic relationships between *Karathele*, *Eothele* and *Acrothele*, with the latter being the most derived in the lineage. *Acrothele* first appears in the upper part of the *Kounamkites* Biozone in Siberia (Korovnikov 1998), and at the base of the *Paradoxides paradoxissimus* Biozone in Scandinavia (Martinsson 1974), suggesting that there is a considerable hiatus in the Lower–Middle Cambrian sections of Malyi Kartau and that significant parts of Ordian–early Templetonian equivalents of Australian sequences are missing.

Stilpnotreta tecta apparently represents the oldest known species of the genus, which appears in microbrachiopod assemblages of New South Wales, Australia from the Boomerangian *Proampix agra* Biozone (Shergold 1995, fig. 2).

The upper part of the *Ptychagnostus intermedius* Biozone and the *Acidusus atavus* Biozone are poor in lingulates, with only *Linnarssonia captiosa* and *Kotylotreta undata* occurring continuously through these intervals in the Kyrshabakty section. The species of *Kotylotreta* described by Engelbretsen (1996) under the name *Pegmatreta clavigera* is from the Murranwong Creek Formation of New South Wales, Australia, which ranges from the uppermost Florian (*Euagnostus opimus* Biozone) to the lowermost Boomerangian (*Ptychagnostus cassis* Biozone); the appearance of the genus is thus somewhat later in Australia, overlapping only with the upper range in south Kazakhstan. Another species common to the lower Middle Cambrian of Malyi Karatau and the Murranwong Creek Formation is *Kyrshabaktella certa* (Engelbretsen 1996), but it does not extend above the *P. atavus* Biozone in Malyi Karatau so that the known occurrences in Australia are somewhat younger.

Stilpnotreta tecta ranges up to the middle of the *A. atavus* Biozone, with no record of the genus in younger deposits of Malyi Karatau. The kutorginoidean *Narynella* cf. *ferganensis* is also from the *A. atavus* Biozone.

3. *Neotreta orbiculata-Anabolotreta lepida* assemblage. This assemblage corresponds mainly with the *Ptychagnostus punctuosus* and *Goniagnostus nathorsti* biozones. *A. lepida* is diagnostic in being restricted almost entirely to the *G. nathorsti* interval, but all other lingulate taxa are transitional from the underlying beds. They include *Acrothele* sp., *Karathele coronata*, *Linnarssonia captiosa*, *Kotylotreta undata*, *Dictyonina hexagona* and *Micromitra* cf. *modesta*, all of which disappear near the base of the *Lejopyge armata* Biozone.

4. *Linnarssonia ophirensis* assemblage. Only four lingulate taxa make up this low diversity assemblage. Among them, *Linnarssonia ophirensis* is restricted to the *L. armata* Biozone, whereas *Vaculina obscura* and *Anabolotreta diversa* range up into the Upper Cambrian, and *Micromitra* cf. *modesta* is the only species transitional from older Middle Cambrian assemblages.

5. *Rhondellina karatauensis* assemblage. This assemblage spans the *Lejopyge laevigata*, *Kormagnostus simplex* and *Glyptagnostus stolidotus* trilobite biozones. Faunal replacement near the base of the *L. laevigata* Biozone is also accentuated by the appearance of *Neotreta pusilla* and *Pomeraniotreta*? cf. *minuta*, the latter species representing the oldest known Ephippelasmatidae. *V. obscura* and *A. diversa* are

transitional from the underlying assemblage. *Neotreta pusilla* disappears by the end of the *K. simplex* Biozone and is replaced in the *G. stolidotus* Biozone by *Diencobolus simplex* and *Araktina intermedia*. Most of these taxa disappear below the base of the *Glyptagnostus reticulatus-Eugenocare* Biozone, with only *A. diversa* ranging up into the *Innitagnostus inexpectans-Prochuangia* beds.

The appearance of *Rhondellina* in this assemblage is remarkable because outside Kazakhstan it occurs only in North America and Greenland, where it has a restricted stratigraphical range in the *Cedaria–Crepicephalus* biozones. It exists in Malyi Karatau with the endemic lingulotretid *Vaculina*, but outside Kazakhstan no taxa of Lingulotretidae are known from rocks younger than the Middle Cambrian. Excluding the cosmopolitan *Neotreta* and *Anabolotreta*, other components of this assemblage also emphasise endemicity. The lingulides *Diencobolus* and *Vaculina* and the acrotretide *Araktina* are unknown outside of Malyi Karatau, while early ephippelasmatids similar to *Pomeraniotreta*? cf. *minuta* have been reported previously only from North China.

6. *Quadrisonia minor* assemblage. The stratigraphical interval covering the *Glyptagnostus reticulatus-Eugenocare* Biozone, *Innitagnostus inexpectans-Prochuangia* beds and *Acutagnostus acutus-Erixanium* beds lacks diagnostic lingulate brachiopods. They reappear in the Kyrshabakty section just below the overlying '*Pseudagnostus curtare*'-*Irvingella major* beds, where all taxa are genera and species not recorded in underlying assemblages. The newcomers are the lingulides *Notiobolus indefinitus* and *Aborigenella denudata*, and the acrotretide *Quadrisonia minor*. The latter is known also from western North America, also in the *Irvingella* Biozone (Rowell and Henderson 1978). The paterinide *Micromitra* sp. is a rare component of the assemblage at this level.

Diversity increases upwards in the *Pseudagnostus pseudangustilobus* beds, where *Experilingula divulgata*, *Zhanatella rotunda* and *Eoscaphelasma*? *delicata* make their first appearance, and maximum diversity is then reached in the *Eorudagnostus ovaliformis-Pareuloma* beds with the occurrence of *Angulotreta* sp., *Pomeraniotreta*? *obtusa* and *Akmolina olentensis*.

In addition to *Quadrisonia*, the occurrence of *Angulotreta* is another link with contemporaneous faunas of North America, where it is widespread in the *Cedaria* to *Dunderbergia* biozones. Of the other taxa, *Zhanatella*, *Eoscaphelasma* and *Experilingula* are also reported from the Upper Cambrian of north-central Kazakhstanian terranes (Popov and Holmer 1994), and *Zhanatella* is known also from the Upper Cambrian of West Antarctica (Henderson *et al.* 1992).

7. *Quadrisonia declivis* assemblage. The diversity of lingulates again declines significantly towards the top of the *Eorudagnostus ovaliformis-Pareuloma* beds, and only *Aborigenella denudata*, *Experilingula divulgata* and *Pomeraniotreta*? *obtusa* continue into the overlying *Neoagnostus quadratiformis-Taenocephalus kyrshabaktensis* beds, where *Quadrisonia declivis* first appears. These species remain the most characteristic until the level of the *Eoconodontus notchpeakensis* conodont Biozone, with *Broeggeria salteri* and *Eoscaphelasma* cf. *satpakensis* also occurring occasionally through the same stratigraphical interval. The rhynchonelliformean brachiopods *Apheoorthis* sp., *Mesonomia*? sp. and *Palaeostrophia fibrillosa* are also present in the *Ivshinagnostus ivshini-Irvingella major* beds and the *Pseudagnostus pseudangustilobus* beds, but their occurrence is sporadic as they are mostly shallow water faunas transported into the basin by turbidity flows, so that their full stratigraphical range in the sequence remains unknown.

This assemblage has strong affinities with contemporaneous lingulate microbrachiopod assemblages of north-central Kazakhstanian terranes (Popov and Holmer 1994) where most taxa occur in common. Comparison with faunas outside Kazakhstan is difficult because of poor knowledge of contemporary late Cambrian lingulates of North America, Siberia and North Gondwana.

Brachiopods from the Cambrian/Ordovician boundary interval. The diversity and abundance of lingulates declines significantly in Malyi Karatau through the interval from the *Eoconodontus notchpeakensis* to *Cordylodus lindstromi* conodont biozones. A single lingulide (*Mirilingula*) and an acrotretide lineage (*Quadrisonia suspensa–Eurytreta discors–Eurytreta sublata–Eurytreta* cf. *bisecta*) are the main components (Text-fig. 6). Other taxa include *Broeggeria salteri*, which has a wide stratigraphical range from the *Hedinaspis sulcata* beds up to the *C. lindstromi* Biozone, and *Schizambon* sp., which appears near the *Cordylodus intermedius*/*C. lindstromi* boundary (Text-fig. 6). From the *C. lindstromi* Biozone up to the *Prioniodus deltatus lingibasis* Biozone, lingulates are very rare. However, the appearance of *Ottenbyella evanda* together with the latest occurrences of *Mirilingula* in the lower part of the *Szechuanella-Apatokephalus* beds, and the subsequent appearance of *Eurytreta minor* in the upper part of these beds are notable. *Ottenbyella* is known otherwise only from the upper Tremadoc (*Paltodus deltifer* Biozone) of Scandinavia, where *E. minor* is also a characteristic species.

Rhynchonelliformean brachiopods occur sporadically across this same interval. *Billingsella* aff. *tonkiniana* and *Palaeostrophia angulata* occur through the *E. notchpeakensis* and *Eoconodontus alisonae* biozones, and *Palaeostrophia tecta* is rare in the lower *C. intermedius* Biozone. The oldest occurrence of *Clarkella testudo* is recorded near the base of the *Paroistodus proteus* Biozone, with *Clarkella turgida* reported first from the lower *Prioniodus deltatus lingibasis* Biozone.

Lingulate assemblages from other Central Asian terranes

Middle and Upper Cambrian successions of western Balkhash and northern Tien Shan contain somewhat different lingulate faunas from those of Malyi Karatau. Four discrete microbrachiopod assemblages can be recognized in these other regions.

1. *Anabolotreta diversa-Stilpnotreta* assemblage. This is a low diversity assemblage in the lower Sarykumy Formation of north-west Balkhash, characterised by the predominance of *Anabolotreta diversa* and species of *Stilpnotreta*, with relatively rare *Canalilatus*? *major*, *Picnotreta karakichiensis*, *Treptotreta* cf. *jucunda* and *Linnarssonia ophirensis*. *Dactylotreta septata* appears in the uppermost part of the stratigraphical range of this fauna (Text-fig. 9). In the Malyi Karatau sequence the range of *L. ophirensis* is restricted to the *Goniagnostus nathorsti–Lejopyge armata* biozonal interval, while *A. diversa* appears at the base of the *L. armata* beds; this suggests that the lower Sarykumy Formation (Unit 2) also falls within this interval. This assemblage has closest similarity with faunas of the Undillan and Boomerangian regional stages of New South Wales, Australia. In particular, *Stilpnotreta magna*, *Picnotreta* and *Treptotreta* are characteristic of this stratigraphical interval in the Australian sequence (Shergold 1995; Engelbretsen 1996), but they are completely missing in the Malyi Karatau Range.

2. *Dactylotreta septata-Picnotreta karakichiensis* assemblage. The upper part of the Sarykumy Formation in the Sarykumy area is characterised by the increased abundance of *Dactylotreta septata* and *Picnotreta karakichiensis*, and by the appearance of *Canthylotreta atasuica* and *Stilpnotreta minuta*, while *Linnarssonia* and *Treptotreta* disappear completely. Also present is *Anabolotreta diversa*, which is stratigraphically transitional up into the *Glyptagnostus stolidotus* Zone in Malyi Karatau. *Dactylotreta* appears in Australian sections from the base of the Mindyallian. This assemblage is therefore probably confined within the uppermost *L. laevigata–Glyptagnostus stolidotus* interval. The fauna is also comparable with a small lingulate assemblage from the Karadzhorga Formation in the Moldotau Range of northern Kyrgyzstan, although the latter lacks *Canthylotreta* and *Stilpnotreta*.

3. *Kleithriatreta najmanica-Micromitra semicircularis* assemblage. The only components of this assemblage are the acrotretide *Kleithriatreta najmanica* and the paterinide *Micromitra semicircularis*. It occurs in the Vendian–Middle Cambrian Darbaza Formation of southern Betpak-Dala, south-central Kazakhstan (Text-fig. 9) and has nothing in common with the upper Lower–lower Middle Cambrian brachiopod faunas of Malyi Karatau. However, both species are known from upper Lower–lower Middle Cambrian (Amgaian) limestones in the Ulugtau Mountains, southern Fergana Valley, Kyrgyzstan. The associated faunal list from these beds published by Imanaliev and Pelman (1988) is rather contradictory, because it includes late Amgaian trilobites (e.g. *Corynexochus* sp., *Dorypyge* cf. *richthofeniformis*) suggestive of the *Paradoxides hicksi* Biozone, together with archaeocyathans (*Irinaecyathus* sp., *Robustocyathus* sp., *Coninocyathus* ex gr. *elongatus*) diagnostic of an early Cambrian age. The Lower Palaeozoic geology of the area is complex (Holmer and Popov, field observations 1993; V. Lytochkin, pers. comm. 1993,

1994) and it is likely that this list includes a mixture of faunas, with at least one assemblage of early Cambrian age (presumably Botomian or Toyonian) and one of mid Cambrian age (early–mid Amgaian), sampled from olistoliths in a tectonic mélange. Among the lingulate brachiopods listed by Imanaliev and Pelman (1988), *Paterina alaica* occurs also in the Karagajly Formation of the Kostek Range, northern Kyrgyzstan, in association with a diverse lingulate assemblage of late Amgaian age (see discussion below). The occurrence of *Acrothele* sp. suggests a Middle Cambrian correlation (not older than equivalents of the late Templetonian–Florian in the Australian squence); *Botsfordia* sp. more probably suggests late Early Cambrian.

The type species of *Kleithriatreta*, *K. lamellosa* was first described (Roberts 1990) from the Coonigan Formation (Ordian Stage) of New South Wales, Australia. The Ordian is regarded in Australia as basal Middle Cambrian, but in Malyi Karatau the beds with *Redlichia chinensis*, which are approximately contemporaneous with the Ordian, are referred to the Lower Cambrian and correlated with the Toyonian Stage of Siberia (Ergaliev and Pokrovskaya 1977; Rozanov 1984). Outside Australia *Kleithriatreta* is reported from the lower Amgaian Stage of the Tarbagatai Range, east-central Kazakhstan (Popov *et al.* 1996).

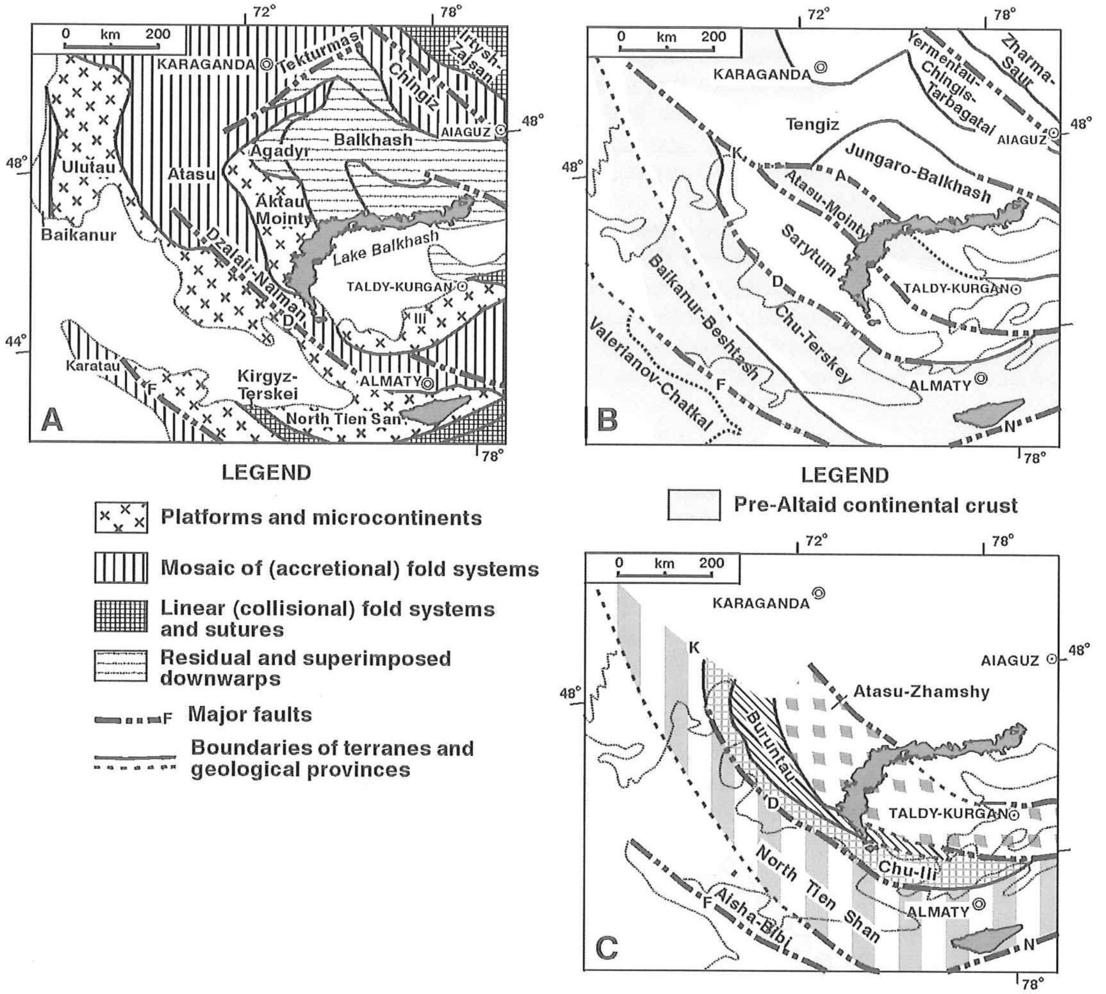
4. *Neotreta kargailensis* assemblage. This assemblage is present only in the Karagajly Formation of the Kostek Range, North Tien-Shan. It includes a total of nine taxa: *Kyrshabaktella certa*, *Canalilatus*? *major*, *Anabolotreta* sp., *Canthylotreta* sp., '*Homotreta*' sp., *Neotreta kargailensis*, *Kotylotreta undata*, *Paterina alaica* and *Kleithriatreta kostekensis*. *K.* cf. *certa* and *K. undata* occur in the interval of the *Peronopsis*? *ultimus–Ptychagnostus atavus* biozones of Malyi Karatau and thus provide evidence for an Amgaian age of this assemblage in Tien Shan. *Kleithriatreta* is known from the late Templetonian–Florian of New South Wales, and is also reported from the Amgaian in a number of Kazakhstanian terranes (Popov *et al.* 1996), but is absent in Malyi Karatau. *Neotreta* appears in the Malyi Karatau sequence from the *Goniagnostus nathorsti* Biozone and ranges up to the Upper Cambrian, while in New South Wales this genus occurs in the Undillan and Boomerangian regional stages (Engelbretsen 1996; Popov *et al.* 1994). Because of the essentially endemic character of this assemblage at the species level, and in the absence of information on associated trilobites, the age can be estimated only roughly as equivalent to the *Acidusus atavus-Goniagnostus nathorsti* biozones of the Malyi Karatau sequence.

BIOGEOGRAPHY

From the seminal work of Zonenshain (Zonenshain *et al.* 1990) there is little doubt that Kazakhstan and adjacent regions of Central Asia represent an amalgam of microplates and ancient volcanic island arcs situated originally somewhere between eastern Gondwana, the Baltica Plate and Siberia, which came together only in middle Palaeozoic times. In the Cambrian and Ordovician these microplates and arcs lay along the migration routes of benthic faunas linking Baltica with East Gondwana and adjacent small plates (e.g. Tarim, North and South China). They were also sites of origin of some biogeographically important taxa (e.g. trimerellide brachiopods) and benthic faunal assemblages (Popov *et al.* 1996, 1997). At the same time, the early Palaeozoic tectonic and accretional histories of these terranes remain very poorly known.

There is still no consensus as to the number, boundaries and possible original source of the first order Palaeozoic lithotectonic units, or suspect terranes incorporated in this tectonic collage. For example, Sengor *et al.* (1993) proposed a model in which early Palaeozoic Kazakhstanian and Central Asian terranes were parts of a single magmatic arc situated between the Siberia and Baltica plates. They also established the presence of a number of major lithotectonic units whose boundaries are mostly major strike-slip faults of mid Palaeozoic age, which do not always follow early Palaeozoic sutures (Popov *et al.* 1996).

In an alternative interpretation Mossakovsky *et al.* (1994) suggested that all major crustal fragments incorporated into the Kazakhstanian and Central Asian orogen were rifted from east Gondwana sometime during the Vendian–early Cambrian, and converged in proximity to the Siberian Plate by the end of the Ordovician. Weak points in all these palaeotectonic reconstructions stem from a lack of palaeomagnetic data, the absence of a comprehensive analysis of early Palaeozoic depositional history and sedimentary



TEXT-FIG. 19. Varying reconstructions of the Palaeozoic composition of terranes in central Kazakhstan–north Kyrgystan. A, after Mosakovsky *et al.* (1994). B, after Sengör *et al.* (1993). C, modifications proposed here incorporating our biogeographical data. In each map the letters D and F denote the Dzalair-Naiman and Talas-Fergana faults, respectively.

linkages between terranes, and almost complete ignorance of biogeographical relationships. Together these factors make existing plate tectonic reconstructions for the region highly speculative and inconclusive.

A detailed review of the early Palaeozoic accretional history of this segment of Central Asia is beyond the scope of this paper, but our faunas allow us to provide valuable data on Cambrian–early Ordovician brachiopod biogeography as a contribution towards the resolution of the location of various terranes in relation to the major palaeocontinental blocks during this interval.

Rhynchonelliformean ('articulated') brachiopods in particular provide some of the best tools for studies of Palaeozoic biogeography. Their lecitotrophic larvae with a very short free-swimming duration, from only several hours to a few days (Williams *et al.* 1997), preclude dispersion across even small oceanic basins. It is generally possible therefore to distinguish well-constrained biogeographical patterns. By contrast, linguliformean (organophosphatic) brachiopods behave differently. All Recent linguliformeans have planktotrophic larvae with a free swimming stage of up to several months, allowing travel for long distances across seaways; there is no reason to doubt that the majority of early Palaeozoic linguliformeans had the same capability. For example, patterns of geographical distribution of Ordovician lingulate microbrachiopod assemblages do not follow those described for rhynchonelliformeans, but they are remarkably similar to the biogeographical distributions of pelagic organisms, e.g. conodonts of the North Atlantic Province. Microbrachiopod assemblages were widespread geographically through most of the Cambrian and some taxa demonstrate almost cosmopolitan distribution. However, climatic and environmental factors, as well as oceanic circulation, set some constraints on the dispersion of these brachiopods and analysis of their geographical distributions can provide important biogeographical data.

General aspects of Cambrian brachiopod biogeography have been discussed by Ushatinskaya (1986, 1995), but the rich faunas from the composite sections of Kazakhstan and Central Asia were not available for that study. Our material is from four separate early Palaeozoic terranes (Text-fig. 19).

Malyi Karatau Range

The affinities of the Cambrian and early Ordovician linguliformean faunas of Malyi Karatau form the main focus of our discussion. This region corresponds mainly to the southern segment of the Baikonur-Bestach tectonofacies unit of Sengör *et al.* (1993). Its south-western boundary now coincides with the Talas-Fergana strike slip fault (Zonenshain *et al.* 1990, fig. 46; Sengör *et al.* 1993, fig. 2), whilst the north-eastern boundary with the Chu-Terskey tectonofacies unit of Sengör *et al.* (1993) or North Tien Shan microcontinent of Mossakovsky *et al.* (1994) is probably concealed below a Carboniferous and Cenozoic cover and has not yet been located with certainty.

The Lower Cambrian sequence of Malyi Karatau is distinctive. Especially close affinities of the trilobite and brachiopod faunas with those of South China (Yangtse Plate) are noted above in discussion of the *Lingulellotreta malongensis-Linnarssonia constans* assemblage. The long Cambrian–early Ordovician evolutionary history of the lingulide family Lingulellotretidae can be traced through the Malyi Karatau sequence, and South China is the only other region where this family occurs in the early Cambrian (Holmer *et al.* 1997). Abundant early Cambrian trilobite faunas associated with brachiopods in Malyi Karatau demonstrate close similarity to those of the *Redlichia* Trilobite Province, which also includes faunas that inhabited areas of North and South China, as well as the Australian part of Gondwana (Ergaliev and Pokrovskaya 1977). Similar relationships of trilobite assemblages from South Kazakhstan, South China and Australia are also evident for the late Cambrian and early Ordovician (Shergold 1988).

Lower Cambrian phosphorite deposits of the Chulaktau Formation in Malyi Karatau and at Meishucun, west Yunnan, are very similar in age, lithology and thickness of units, and display similar patterns of major discontinuities (Rozanov and Sokolov 1984; Holmer *et al.* 1997). In both regions these deposits sit discontinuously on dolomites containing the earliest small shelly fossils (the Kyrshabakty Formation with a *Protohertzina anabarica* Biozone assemblage in Malyi Karatau (Mambetov 1993), and the Baiyanshao Member of the Dengying Formation in Yunnan (Qian and Bengtson 1989). Overlying beds in both regions contain two phosphorite-bearing units separated by a unit of siliceous shells and chert, with an overlying unit of stromatolitic dolomite or conglomerate with a ferromanganese dolomitic matrix. Discontinuities at the base of the phosphorite-bearing units and at the base of overlying dolomites are accentuated in both areas by significant faunal replacements (Qian and Bengtson 1989; Mambetov 1993).

These strong sedimentological and faunal affinities support the view that during the early Cambrian Malyi Karatau was part of the Yangtse Plate. Discontinuity near the Lower/Middle Cambrian boundary and the formation of a deep basin with pelagic carbonate sedimentation within the *Peronopsis*? *ultimus* Biozone gives evidence of the possible time of formation and separation of the Aisha-Bibi sea-mount (Cook *et al.* 1991), which was isolated from major continental blocks. Linguliformean microbrachiopod assemblages characteristic of the Middle Cambrian basin biofacies of this sea-mount, with the exception of *Linnarssonia*, have nothing in common with the early Cambrian *Lingulellotreta malongensis-Linnarssonia constans* assemblage that accumulated in shallow shelf and lagoon environments. This marked contrast between the early and mid Cambrian lingulate faunas was mainly a result of biofacies control. In the basin plain deposits of the Kyrshabakty sequences, latest Middle Cambrian–early Late Cambrian turbidity flows introduced large shells of shallow water lingulids, which now form coquinas at the base of Bouma cycles. These shells belong to the lingulellotretid genera *Vaculina* and *Aborigenella*, and the obolide *Notiobolus*; the latter genus is similar to, and probably a distant relative of the early Cambrian *Palaeobolus*. Larval shells of these lingulids also occur sporadically in the pelagic carbonates of the same sequences.

Comparison between Middle and Upper Cambrian brachiopod assemblages of Malyi Karatau and South China is impossible because of lack of definitive data. However, the microbrachiopod faunas from the basin around the Aisha-Bibi sea-mount have close affinities with those of East Gondwana, and especially with the well-known assemblages that characterise the Florian–Mindyallan of New South Wales, although the stratigraphical ranges of some typical genera are not coeval. *Kotylotreta*, *Neotreta* and *Stilpnotreta* appear in the Aisha-Bibi sea-mount earlier than in East Gondwana, whilst the persistent botsfordiid *Karathele*, which survived at Aisha-Bibi through most of the mid Cambrian, disappeared in New South Wales from the Florian. At the same time, the Middle and early Late Cambrian brachiopod faunas lack such characteristic and widespread acrotretide genera as *Dactylotreta*, *Kleithriatretra*, *Picnotreta* and *Treptotreta*. It seems likely therefore that some taxa evolved originally in the Aisha-Bibi sea-mount region and then migrated to East Gondwana, whereas migration in the opposite direction was very limited.

Faunal turnover rates in the microbrachiopod assemblages of the basinal biofacies around the Aisha-Bibi sea-mount increased by the end of the mid Cambrian, when some more endemic taxa (e.g. *Araktina* and *Diencobolus*) appeared. The appearance of *Rhondellina* and *Quadrisonia minor* suggests links with Laurentian faunas, whereas affinities with East Gondwanan microbrachiopod assemblages weakened. Nearly all mid Cambrian lineages disappeared by the end of the *Glyptagnostus reticulatus-Eugenocare* Biozone. New linguliformean faunas that characterise the *Quadrisonia minor* and *Quadrisonia declivis* assemblages demonstrate close similarity with approximately contemporaneous assemblages of north-east Kazakhstanian terranes (Popov and Holmer 1994). A rapid decline in diversity and abundance of microbrachiopod assemblages occurred from *Eoconodontus notchpeakensis* Biozone times, and from the *Eoconodontus alisonae* Biozone the acrotretide *Eurytreta* remained the only dominant taxon by the end of the Tremadoc. According to Shergold (1988), the latest Cambrian and earliest Ordovician trilobite faunas of Malyi Karatau are transitional between Baltic and south-east China trilobite provinces.

West Balkhash region

The Sarykumy section is within a terrane that corresponds partly with the Aktau-Mointy microcontinent of Mossakovsky *et al.* (1994), or the Atasu-Mointy tectonofacies unit of Sengör *et al.* (1993). However, the most precise definition of the boundaries of this tectonofacies unit was given by Apollonov *et al.* (1990, fig. 1) and therefore the term Atasu-Zhamshy Terrane proposed by those authors is accepted here. In the Early and early Middle Cambrian, deposition of dolomitic sediments with numerous stromatolites was typical across this region. The dolomites are underlain by thick units of quartzose and arkosic sandstones and conglomerates, presumably of late Precambrian–early Cambrian age (Avdeev *et al.* 1974). From the mid Cambrian (early Mayaian), normal marine depositional environments were established in the region and the Sarykumy area was apparently situated on the south-western (present coordinates) slope of a prograding carbonate platform (Apollonov *et al.* 1990; Zhemchuzhnikov 1990).

The late Middle Cambrian microbrachiopods of the Atasu-Zhamshy Terrane have closest faunal similarity with those of East Gondwana. The sedimentology and precise ages of the late Precambrian and early Cambrian sediments are poorly known, but their general characters are comparable with widespread sequences in the Middle East (Iran, Jordan, Israel; our field observations). Across all these regions, deposition of latest Precambrian–early Cambrian fluvial to shallow marine clastic sequences was replaced upwards by extensive early Cambrian accumulation of stromatolitic dolomites and then by shallow marine platform carbonate sedimentation in the mid Cambrian.

The Sarykumy tectonofacies unit of Sengör *et al.* (1993) was not an internally homogeneous geological province during the Cambrian and early Ordovician, but included a small crustal terrane (Chu-Ili Terrane after Popov *et al.* 1997) and an accretionary subduction complex formed along its north-east margin (present coordinates) during the Arenig–early Caradoc (Popov and Tolmacheva 1995), known also as the Burultas Terrane (Popov *et al.* 1997). Its boundary with the Atasu-Zhamshy Terrane is a mid Ordovician (early Caradoc) suture.

There is no record of early–mid Cambrian sedimentation in the Chu-Ili Terrane. The oldest well-documented Palaeozoic rocks are referred to the Arenig Akzhal Formation, which rests on Precambrian basement (Keller 1956). However, olistoliths and large blocks of presumably Cambrian dolomite and quartzose sandstone (Darbaza Formation) are preserved in the subduction-accretion complex of the Burultas [Buruntau] Terrane. It is possible that these blocks and olistoliths represent fragments of the collapsed early–mid Cambrian carbonate platform that slumped into the rift basin. The presence of *Kleithriatreta* in the early Middle Cambrian (Amgaian) *Kleithriatreta najmanica-Micromitra semicircularis* assemblage of the Darbasa Formation in the Suukadyr Mountains within the Burultas Terrane suggests affinity with the early Middle Cambrian of Australia and some Kazakhstanian and Central Asia terranes (Tarbagatai Range, North Tien Shan and Alai Range). This is the only evidence at this level suggestive of affinity to East Gondwanan brachiopod faunas.

North Tien Shan

According both to Sengör *et al.* (1993) and Mossakovsky *et al.* (1994), North Tien Shan together with Ulutau were a separate geological province in the early Palaeozoic, named here as the North Tien Shan Terrane. Its palaeogeographical position and affinities during the Middle and most of the Late Cambrian cannot be resolved with certainty from available data. *Kyrshabaktella*, *Neotreta* and *Anabolotreta* from the Karagajly Formation are cosmopolitan taxa, whilst the latest Middle Cambrian *Dactylotreta* and *Picnotreta* are known outside North Tien Shan from the Atasu-Zhamshy Terrane, Greenland (Zell and Rowell 1988) and Australia (Henderson and MacKinnon 1981).

In summary, of the available biogeographical and lithological evidence we conclude that the Aisha-Bibi sea-mount of Malyi Karatau was part of the Yangtse Plate by the end of the early Cambrian. It separated from this plate during the mid Cambrian and drifted westward within temperate southern latitudes towards the group of north Kazakhstanian terranes located in the proximity of the Uralian margin of the Baltica Plate. The Atasu-Zhamshy Terrane retained East Gondwanan affinities throughout the Cambrian. It was probably originally one of the peri-Gondwanan microplates and island arcs attached to the Middle East part of Gondwana, before breaking away in the late Middle Cambrian.

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