THE EARLIEST ATRYPIDES AND ATHYRIDIDES (BRACHIOPODA) FROM THE ORDOVICIAN OF KAZAKHSTAN

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ABSTRACT. The middle Ordovician brachiopod faunas of Kazakhstan provide one of the most complete records of the evolution and radiation of some of the oldest known spire-bearing brachiopods. By contrast with North American faunas, Kazakhstanian atrypide taxa mostly belong to the suborders Atrypidina and Lissatrypidina, whereas the suborder Anazygidina is completely absent. Kazakhstanian species referred previously to *Zygospira* and *Kuzgunia* are reassigned to *Sulcatospira*, which appeared in the Caradoc *Diplograptus multidens* and *Climacograptus clingani* biozones (*Sulcatospira*? *praecursor* and *Sulcatospira prima* sp. nov.). Primitive, and possibly the oldest known Athyridida also appeared in Kazakhstan sometime during the Caradoc (*Kellerella misiusi* sp. nov.) and became widespread in brachiopod assemblages developed in carbonate mud mounds. Phylogenetic analysis suggests the early divergence of the Anazygidina, Atrypidina and Athyridida, which probably evolved independently from various primitive smooth Lissatrypidina. The new atrypide subfamily Pectenospirinae and two new atrypide genera (*Rozmanospira* gen. nov. and *Pectenospira* gen. nov. with *P. pectenata* sp. nov. as type species) are erected.

THE most complete record of the earliest Ordovician history of the brachiopod order Atrypida is known currently from North America (Copper 1977, 1986; Copper and Gourvennec 1996), where it is represented mostly by the families Cyclospiridae, Protozygidae and Anazygidae. During the late Ashgill the fauna of archaic spire-bearing taxa dominated by anazygidines was replaced rapidly by atrypidines (e.g. *Eospirigerina*) and early athyridides (e.g. *Hindella*). This replacement may suggest immigration (Jaanusson 1979; Copper 1986, p. 830). Indeed, early representatives of the family Atrypinidae (e.g. *Eospirigerina pennata* (Rukavishnikova) and *Qilianotryma suspecta* (Popov)) have been recorded in Kazakhstan from the Dulankara Stage (Rukavishnikova 1956), which corresponds to the upper *Dicellograptus complanatus* and lower *Pleurograptus linearis* graptolite biozones. Athyridides are known from Kazakhstan and South China (Fu 1982; Nikitin *et al*. 1996) in the upper Caradoc. The earliest spiriferide, *Eospirifer*, is known from the middle Ashgill of South China and the Rhuddanian of North China and Kazakhstan (Modzalevskaya and Popov 1995; Rong and Zhan 1996). It is becoming clear that North and South China together with Kazakhstanian terranes are very important for tracing the early phylogeny of spire-bearing brachiopods in the mid and late Ordovician.

These early Atrypida and Athyridida together represent one of the most characteristic elements of the middle Ordovician (Caradoc) brachiopod assemblages in Kazakhstan, associated especially with carbonate mud mounds. However, the internal shell morphology and characters of the lophophore supports in the majority of taxa remain very poorly known. The main object of this paper is the re-examination of types and topotypes of the middle Ordovician atrypides and athyridides from Kazakhstan, as well as description of some new taxa.

Reconstructions of the internal morphology have been made from serial parallel sectioning of the specimens with an accuracy to 0·05-0·1 mm, and subsequent preparation of acetobutyratfolie peels. Three-dimensional reconstructions of the brachidia were made electronically by tracking points from the section plane to the plane of bilateral symmetry and to the commissural plane.

The studied specimens are from collections deposited in the Geological Museum, Institute Geological Sciences of Kazakhstan, Almaty (IGN numbers); Central Scientific-Research and Geological Exploration Museum, St Petersburg (CNIGR numbers) and Geological Institute of the Academy of Sciences of Kirgizstan, Bishkek (GIK numbers).

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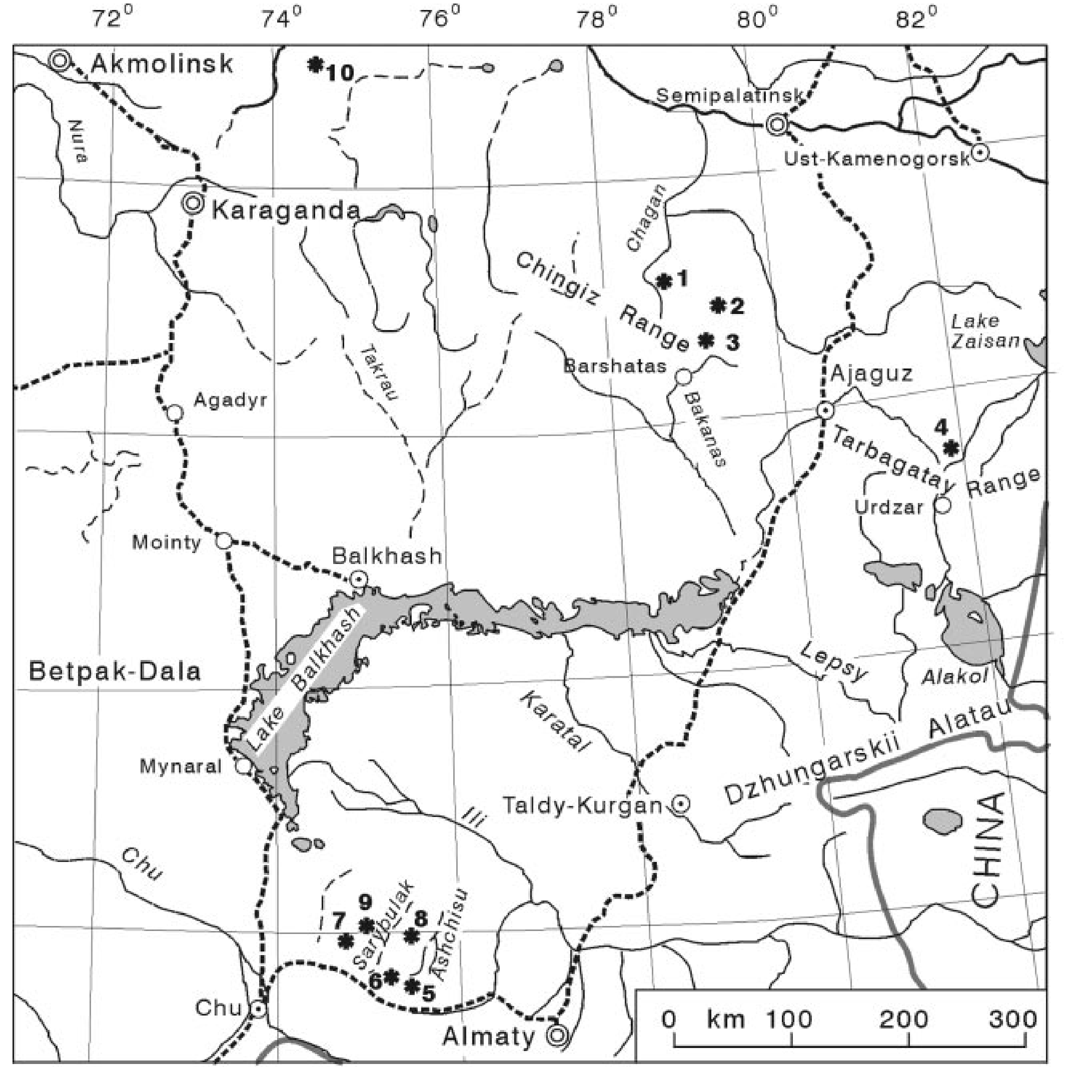
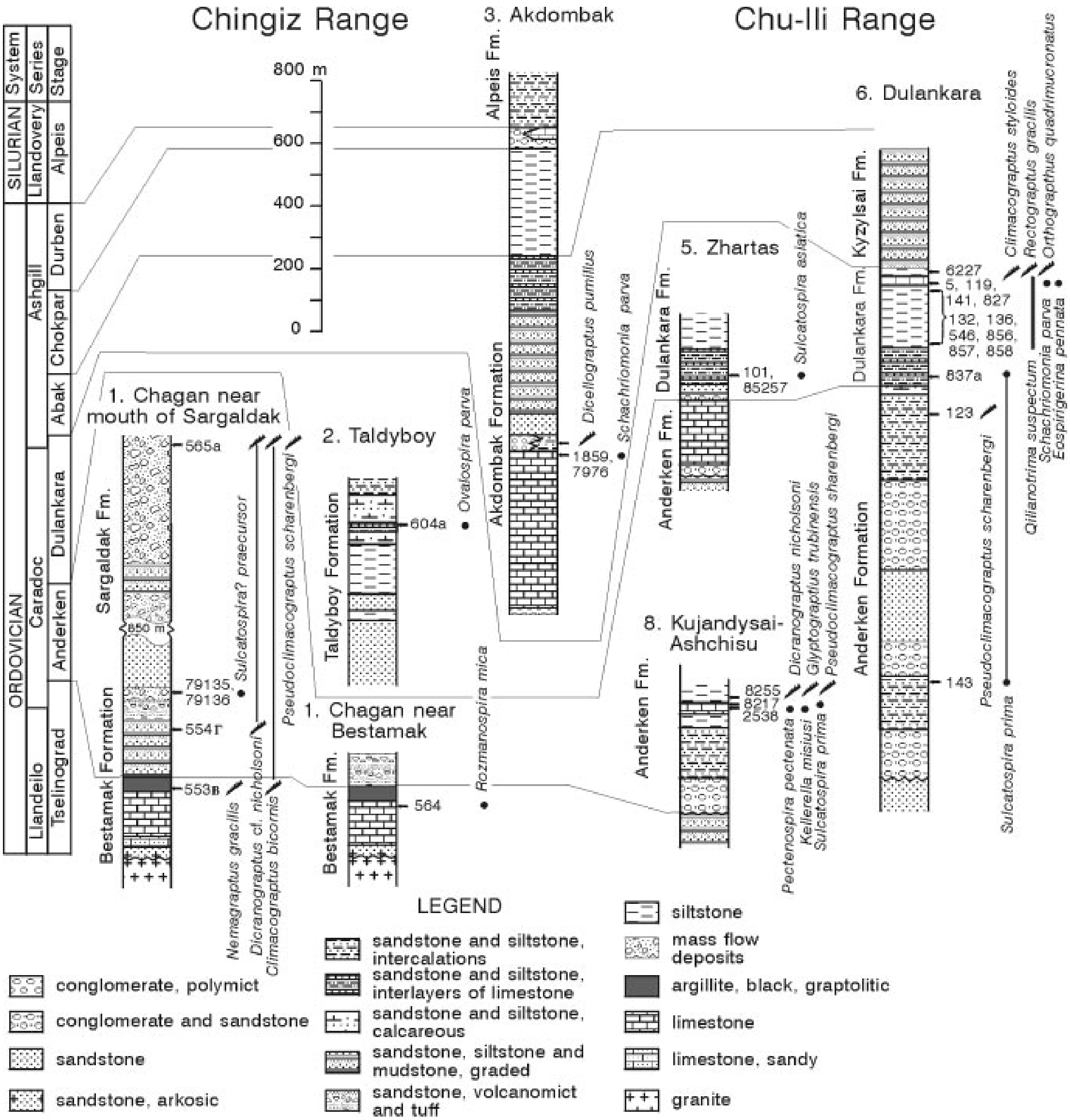


TEXT-FIG. 1. Outline map of eastern Kazakhstan showing localities of the middle Ordovician (Llandeilo–Caradoc) atrypides and athyridides discussed in this paper. **1–3**, Chingiz Range; 1, River Chagan near Bestamak and opposite mouth of river Sargaldak; 2, River Taldyboi and area between rivers Taldyboi and Namas; 3, Akdombak Mountain. **4**, Tarbagatai Range, River Kulunbulak. **5–9**, Chu-Ili Range; 5, River Zhartas near town of Gornoe; 6, Dulankara Mountains; 7, River Adensu; 8, Andyrkenyn-Akchoku valley and River Kujandysai; 9, Buldubai Akchoku mountain and left side of river Kopalysai. **10**, right side of River Shiderty near Odak.

STRATIGRAPHICAL RECORD OF THE EARLIEST SPIRE-BEARING BRACHIOPODS IN KAZAKHSTAN

The oldest known spire-bearing brachiopod species in Kazakhstan is the lissatrypide *Rozmanospira mica* (Nikitin and Popov, 1984), which occurs in the upper part of the Bestamak Limestone (locality 564 of Nikitin 1960) exposed on the east side of the river Chagan near the village of Bestamak in the Chingiz Range (Text-figs 1–2). The overlying unit of graptolitic black shale contains graptolites diagnostic for the



TEXT-FIG. 2. Schematic stratigraphical columns of Ordovician beds in Kazakhstan, showing distribution of atrypides and selected graptolite species. The numbers of the localities are the same as on Text-figure 1.

Nemagraptus gracilis Biozone (Unit 5 of Tsai 1976, p. 10, text-fig. 2), suggesting a mid Llandeilo to earliest Caradoc age for this species and associated fauna of articulated brachiopods, ostracodes and rare tabulate corals. The earliest trimerellides occur in the Bestamak Limestone at about the same stratigraphical level, but form a separate assemblage (Nikitin and Popov 1984; Popov *et al*. 1997).

The Bestamak Formation also contains the earliest known representatives of the suborder Atrypidina, *Sulcatospira*? *praecursor* (Nikitin and Popov, 1984) from the upper part of the formation exposed on the east side of the river Chagan opposite the mouth of the river Sargaldak (localities 79135, 79136 of Nikitin and Popov 1984, text-fig. 26; Unit 8 of Tsai 1976, p. 10, text-fig. 2). Both underlying and overlying units of the Bestamak Formation in this section contain graptolites of the *Diplograptus multidens* Biozone suggesting the lower to middle Caradoc (Anderken Regional Stage). Other brachiopods at this locality are *Eodalmanella subita* Nikitin and Popov, *Shlyginia solida* Nikitin and Popov and *Sowerbyella rukavishnikovae* Nikitin and Popov. All of these taxa are probably from a shallow water benthic assemblage (equivalents of Benthic Assemblage Zone 2 or 3 of Boucot 1975) and were engulfed in mass flow deposits. Lophophore supports are not preserved in *Sulcatospira*? *praecursor*, but it demonstrates features typical of Atrypoidea in characters of the cardinalia and external morphology.

The Chu-Ili Range is another region in Kazakhstan that provides important information on early spire-bearing brachiopod taxa. In particular, they are abundant locally in carbonate mud mounds within the Anderken Formation exposed in the south-east part of the range between the rivers Sarybulak and Ashchisu (Text-figs 1–2). This formation contains the oldest known athyridide, described here as *Kellerella misiusi* sp. nov., and a new lissatrypidine genus and species, *Pectenospira pectenata*. Previously, carbonate mud mounds in the upper part of the Anderken Formation were correlated usually with the uppermost Caradoc or lower Ashgill of the British Standard. However, a graptolite assemblage from the overlying unit of mudstone in the upper part of this Formation (Unit 5 of Nikitin 1972, pp. 75–76) contains the graptolites *Dicranograptus nicholsoni*, *Diplograptus anderkenensis*, *Glyptograptus trubinensis*, and *Pseudoclimacograptus scharenbergi* among others, suggesting a position within the lower Caradoc (*Diplograptus multidens* Biozone).

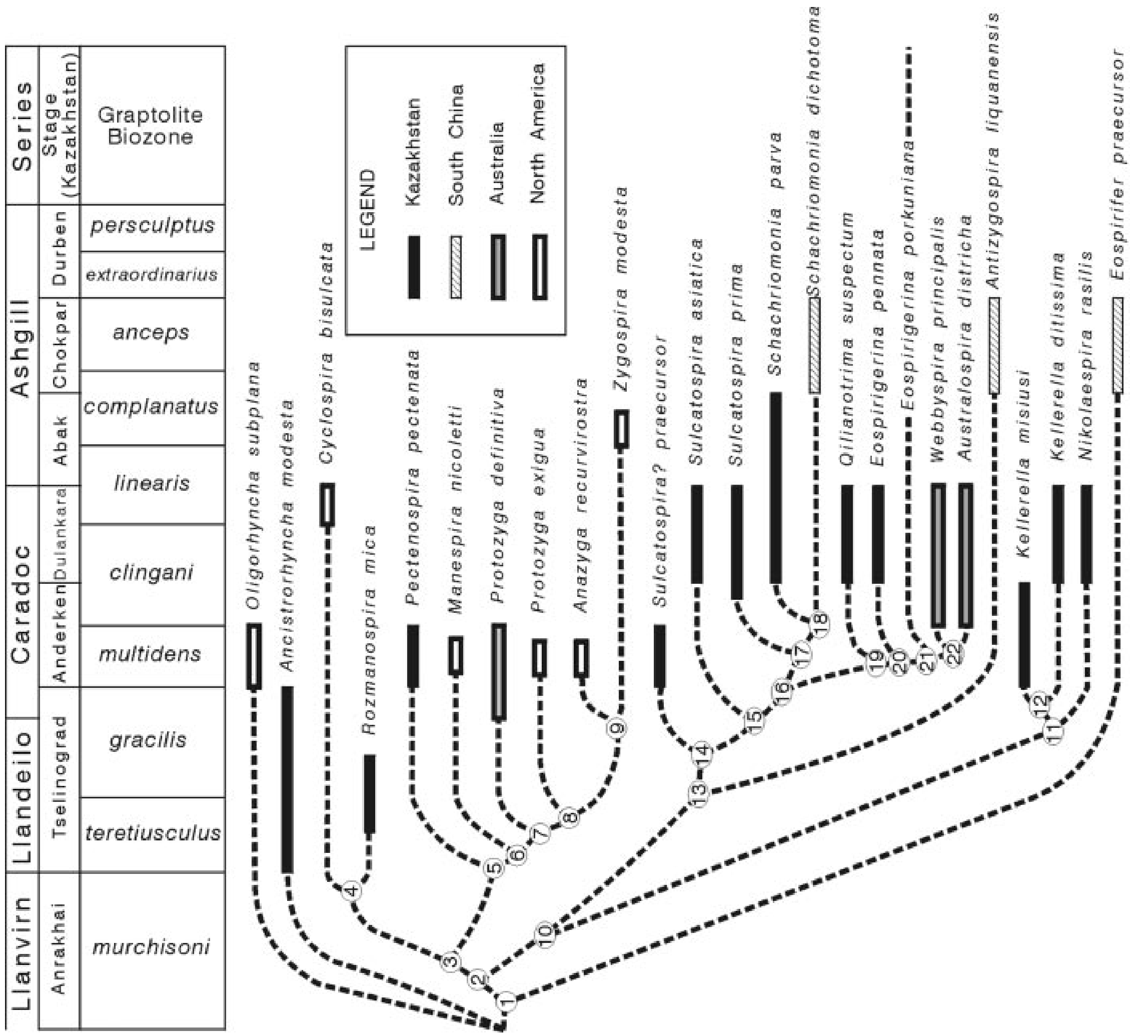
In the upper Anderken Formation of the Dulankara Mountains (locality 143 of Nikitin 1972, pp. 76–78, text-fig. 20) *Sulcatospira prima* sp. nov. makes its earliest appearance in association with numerous gastropods and the trilobite *Pliomerina illiensis*. The overlying unit of fine clastic rocks contains a graptolite assemblage of the *Climacograptus caudatus* Biozone (local equivalent of the *Dicranograptus clingani* Biozone) suggesting a mid or late Caradoc age. *S. prima* occurs in the lower part of the Dulankara Formation in the Chu-Ili Range and is also widespread in the Koskarasu Beds of north-east central Kazakhstan (Text-fig. 1).

Early atrypides and athyridides diversified rapidly during the late Caradoc in Kazakhstan, becoming one of the important components of shallow water brachiopod assemblages of the Dulankara Regional Stage. This unit is a stratigraphical equivalent of the upper Caradoc. In the type section in the Dulankara Mountains, the graptolites *Rectograptus almatiensis* and *Dicellograptus* sp. occur in strata just below its lower boundary. Graptolites of the *Dicellograptus pumilus* Biozone, which is regarded as the Kazakhstanian equivalent of the *Pleurograptus linearis* and *Dicellograptus complanatus* biozones, make their first appearance near the top of the Akkol Beds, the uppermost unit within the Stage (Keller 1956*a*, 1956*b*; Nikitin 1972). In the Chu-Ili Range, atrypidine brachiopods are most abundant in the upper part of the Dulankara Stage, represented by *Sulcatospira asiatica* (Misius, 1986), *Schachriomonia parva* (Rukavishnikova, 1956), *Qilianotryma suspecta* (Popov, *in* Nikiforova *et al*., 1982) and *Eospirigerina pennata* (Rukavishnikova, 1956). Carbonate mud mounds of this age are known in the Betpak-Dala desert (Nikitin *et al*. 1996). The brachiopod fauna associated with these build-ups is characterized by a predominance of the early athyridids *Kellerella ditissima* Nikitin and Popov, 1996, *in* Nikitin *et al*., 1996 and *Nikolaespira rasilis* Nikitin and Popov, *in* Nikitin *et al*., 1996.

Early atrypidines were also widespread in Dulankaranian deposits of other parts of Kazakhstan. In particular, *Sulcatospira parva* is one of the most common taxa in the middle part of the Taldyboi Formation of the Chingiz Range, whilst *Eospirigerina pennata* occurs in the lower Kulunbulak Formation of the Tarbagatai Range (Text-fig. 1).

The Ashgill heralded a further burst of diversification of early spire-bearing brachiopods in Kazakhstan, but this later phase is outside the scope of this review.

There is a remarkable difference between middle Ordovician spire-bearing brachiopod faunas from North America and those from Kazakhstan. It is well known (Copper 1986; Copper and Gourvennec 1996) that in North America the middle Ordovician Atrypida are represented mostly by lissatrypidines of the family Protozygidae and by anazygidines. The oldest and most primitive North American atrypides (e.g. *Manespira* and *Protozyga*) are characterized by smooth or indistinctly ribbed shells with simple, planispiral lophophore supports. With the exception of *Manespira*, a majority of the middle Ordovician



TEXT-FIG. 3. Stratigraphical ranges and inferred phylogenetic relationships of the earliest Ordovician spire-bearing brachiopods from Kazakhstan and North America. Numbered nodes are supported by character states listed in the Appendix.

atrypide genera in North America is characterized by the presence of a complete jugum, located mediodorsally in early taxa but which migrated posteroventrally in the derived anazygidines. Such features as a unisulcate anterior commissure and a dorsal median sulcus predominate among the middle Ordovician genera, whereas taxa with uniplicate and parasulcate anterior commissures became widespread only in the Ashgill. True Cyclospirinae appeared in North America only in the late Caradoc (Copper 1986, p. 829, text-fig. 1) and the earliest athyridides with laterally directed spiralial cones (e.g. *Hindella*) are recorded for the first time in the middle Ashgill.

In Kazakhstan the earliest known atrypides are also lissatrypidines within the subfamily Cyclospirinae (*Rozmanospira*). Unlike the earliest North American taxa they completely lack a jugum. The only known genus of the family Protozygidae in Kazakhstan is *Pectenospira*, which appeared at about the same time as *Manespira* and *Protozyga* in North America and is also characterized by planispiral lophophore supports with only two whorls and an incomplete jugum located mediodorsally. There is no record of anazygidine genera in the middle and upper Ordovician of Kazakhstan, and all previous records of *Zygospira* in that region are related to *Schachriomonia* and *Sulcatospira*, which are regarded here as primitive atrypidines (Text-fig. 3). All of the middle Ordovician spire-bearing taxa in Kazakhstan are characterized by the presence of vestigial, posteriorly placed, separated jugal processes and a parasulcate anterior commissure. Taxa with a uniplicate anterior commissure appeared only in the late Caradoc, whereas forms with a unisulcate anterior commissure typical of early anazygidines and lissatrypidines in North America are completely unknown in Kazakhstan.

The early appearance of taxa with laterally directed spiral cones, which are the earliest known athyridides, is also remarkable (Text-fig. 3). For instance, *Kellerella* appears in the *Diplograptus multidens* Biozone (lower to middle Caradoc) and the closely related *Nikolaespira* is recorded from the upper Caradoc (Nikitin *et al*. 1996). This suggests that Kazakhstanian terranes together with North-west and South China (Xu 1979, 1997; Fu 1982; Zhan and Cocks 1998) represent areas where early atrypidines and athyridides originated and first diversified.

SYSTEMATIC PALAEONTOLOGY

In subdivision of the order Atrypida into suborders, superfamilies and families we follow Copper and Gourvenenc (1996). Modified terminology of shape of the anterior commissure is adopted from Williams and Rowell (1965, fig. 65).

Abbreviations given in tables of measurements and in the text are as follows: Lv, Ld – sagittal ventral and dorsal valve length; W – maximum width; T – maximum thickness; Sw, St – width and height of tongue in the ventral valve; X – mean; S – standard deviation from the mean; OR – observed range; max. – maximum value; min. – minimum value, N – number of specimens measured. Measurements are in mm.

Order ATRYPIDA Rzhonsnitskaya, 1960
Suborder ATRYPIDINA Rzhonsnitskaya, 1960 (emended Copper, *in* Copper and Gourvennec 1996)
Superfamily ATRYPOIDEA Gill, 1871
Family ATRYPINIDAE McEwan, 1939
Subfamily SPIRIGERINIDAE Rzhonsnitskaya, 1974

Genus EOSPIRIGERINA Boucot and Johnson, 1967

Type species. *Zygospira putilla* Hall and Clarke, 1894, p. 365, pl. 54, figs 35–37, Hudson River Group, near Edgewood, Pike County, Missouri, USA. According to Amsden (1974), *Atrypa praemarginalis* Savage, designated by Boucot and Johnson as the type species of *Eospirigerina*, is a junior subjective synonym of *Zygospira putilla*.

Diagnosis. See Copper (1982, p. 687).

Eospirigerina pennata (Rukavishnikova, 1956)

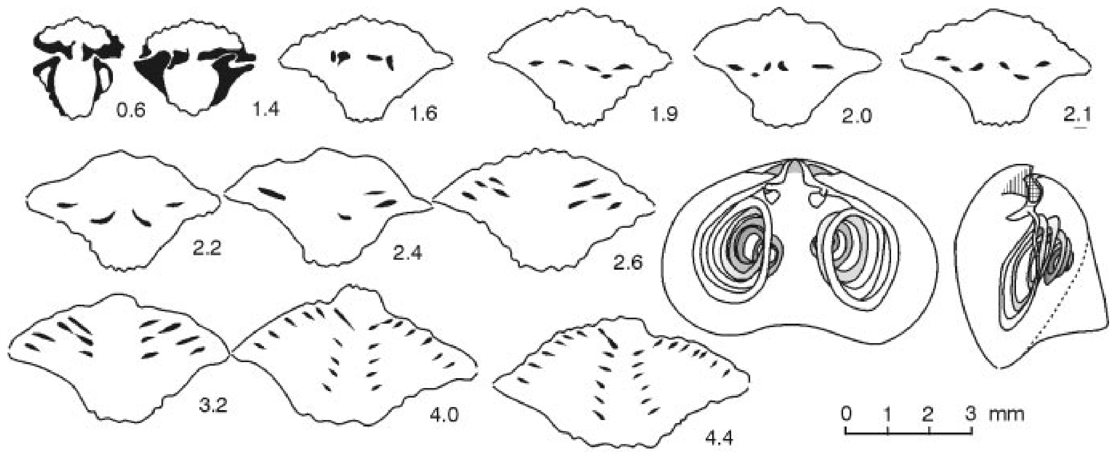
Plate 1, figures 1–6; Text-figure 4

1956 *Plectatrypa pennata* Rukavishnikova, p. 160, pl. 5, figs 12–13.

Holotype. IGN 62/1360, complete shell.

Type locality. Akkol Beds, upper Dulankara Formation, east side of the River Akdalasai, southern Chu-Ili Range. Details of the Ordovician geology and stratigraphy of this area are given by Keller (1956*a*, p. 28, fig. 1).

Material and stratigraphical range. Figured: complete shells, CNIGR 21/12986 and 22/12986 (Lv = 10·5, Ld = 10·0,



TEXT-FIG. 4. Serial sections and reconstruction of spiralia and jugum in *Eospirigerina pennata* (Rukavishnikova, 1956) from a specimen from locality 85203, left side of River Kulunbulak, Tarbagatai Range, lower Kulunbulak Formation, Dulankara Stage (upper Caradoc). Sections with dorsal valve uppermost. Numbers are distances in mm from the ventral beak (also in Text-figs 5–11).

W = 13·1, Sw = 6·9, St = 4·1); total of 33 complete shells, 18 ventral and 18 dorsal valves. In the Chu-Ili Range *E. pennata* is characteristic of the Akkol Beds. It occurs in samples 119, 141, 219 in Unit 10 of Nikitin (1972, p. 76, text-fig. 20) from the Dulankara Mountains, and sample 42/10 of T. Rukavishnikova from the section along the River Babasai (Unit 7 of Keller 1956*a*, p. 40). In the Tarbagatai Range it has been sampled from locality 85203 in the lower Kulunbulak Formation (Dulankara Stage) on the left side of the River Kulunbulak.

Diagnosis. *Eospirigerina* with strongly dorsibiconvex, transversely sub-oval shell about 70–90 per cent. as long as wide; anterior margin strongly uniplicate; ventral valve moderately convex with a posteriorly directed, slightly curved beak; delthyrium with vestigial deltidial plates; sulcus originates at the umbo, deepening markedly anterior to mid-valve and ending as a geniculated, high, trapezoidal tongue aligned almost at right angles to the commissural plane; dorsal valve strongly convex with maximum height anterior to mid-valve, umbonal area with a shallow sulcus reversed into a high median fold between the umbo and mid-valve; dorsal median fold with steep lateral slopes well defined from the valve flanks; radial ornament costellate on the fold and in the sulcus, costate with up to 15 ribs on flanks; spiralia with up to eight whorls and with high, anteroventrally directed jugal processes.

Remarks. *Eospirigerina pennata* is possibly the earliest species of the genus. It differs from late Ordovician (e.g. *E. putilla*) and early Silurian species (e.g. *E. porkuniana*) in having costate radial ornament on the flanks of the valves with bifurcating ribs developed only on the dorsal fold and ventral sulcus. Another characteristic of this species is the strong ventral curvature and distal thickening of the jugal processes.

E. pennata closely resembles *E. yulangensis* (Liang, *in* Liu *et al.*, 1983) as revised by Zhan and Cocks (1998, p. 56) in its external shell morphology and especially in having a strong dorsal median fold and ventral sulcus with a high, trapezoidal tongue. However, the Kazakhstanian species differs in having a mainly open delthyrium with only small, separated deltidial plates and mainly costate radial ornament on the flanks of the shell.

Genus QILIANOTRYMA Xu, 1979

Type species. By original designation, *Qilianotryma mirabile* Xu, 1979; upper Ordovician, Koumenzi Formation, Qinghai region, South-west China.

Diagnosis (emended). Atrypinidae with dorsibiconvex, transverse shell; ventral beak strongly curved dorsally; posterior commissure wide, broadly rounded, anterior commissure parasulcate; ventral sulcus and dorsal median fold originating at the umbonal area and sharpened by low, angular plications on flanks; radial ornament fine, equally multicostellate with accentuated median rib in ventral valve; ventral interior with hinge teeth strong; dental plates rudimentary or absent; dorsal interior with very fine median ridge and pair of oblique submedian ridges; spiralia with up to six whorls and with apices directed dorso-medially, jugum incomplete, located posteriorly.

Species assigned. Qilianotryma mirabile Xu, 1979; *Qilianotryma*? *striatum* Xu, 1979; *Euroatrypa suspecta* Popov, *in* Nikiforova *et al.*, 1982.

Species rejected. Qilianotryma praecursor Nikitin and Popov, 1984 (reassigned here to *Sulcatospira*).

Distribution and stratigraphical range. Upper Ordovician, Koumenzi Formation of the Qinghai region, South-west China; upper Caradoc (Dulankara Stage, upper *Dicranograptus clingani–Pleurograptus linearis* biozones), Chu-Ili Range, Kazakhstan.

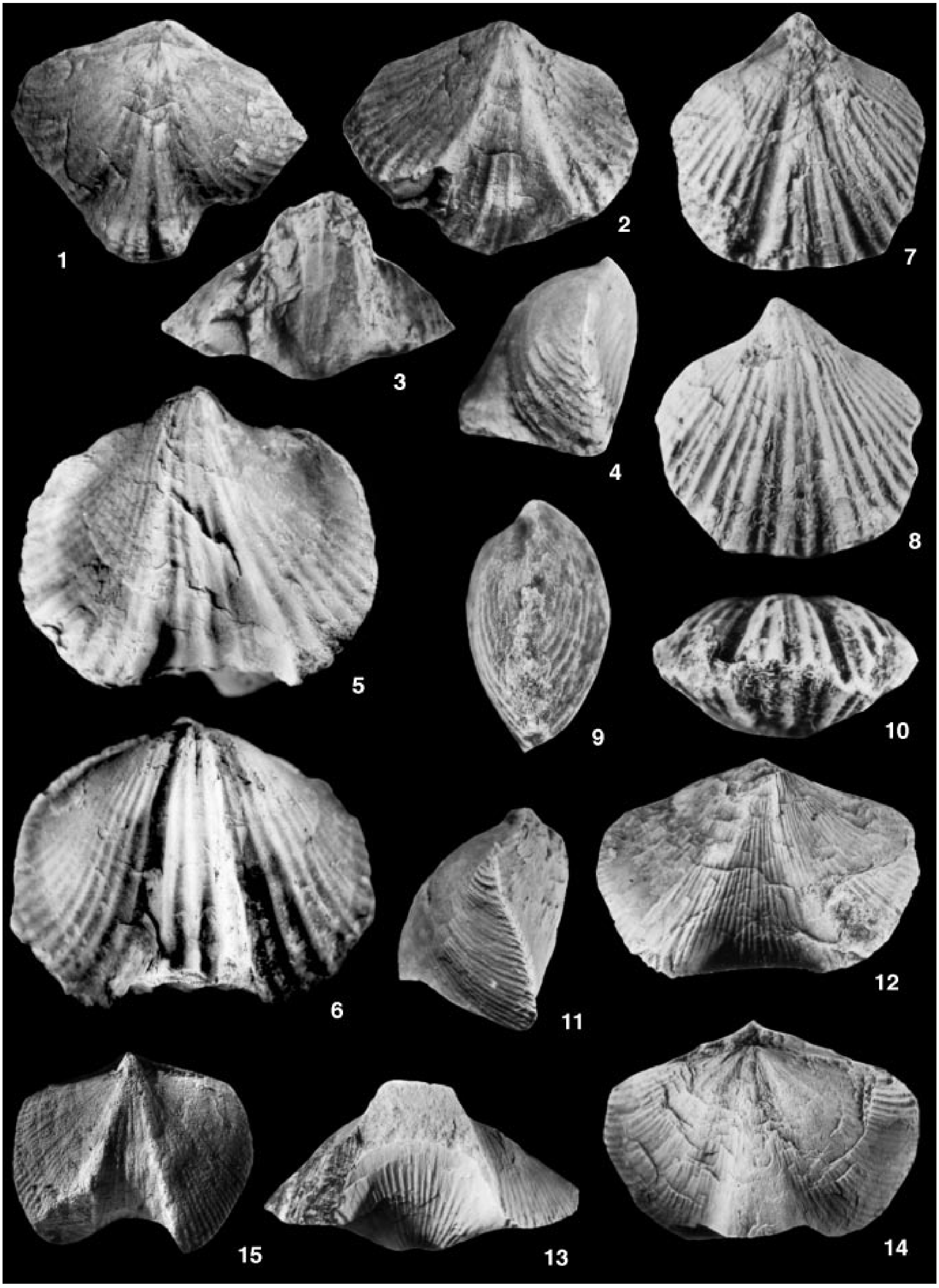
Remarks. In the original description *Qilianotryma* was assigned to the rhynchonellide family Ancistrorhynchidae, but jugal processes and the beginnings of spiralia are clearly visible on the schematic drawings of cross sections made by Xu (1979, fig. 40). Spiralia are known only for *Qilianotryma suspecta* and remain undescribed for the type species. In its spiralia (e.g. mediodorsally directed apices and separated jugal processes) *Qilianotryma* resembles *Eospirigerina*, but differs in its smaller number of whorls and having fine, evenly multicostellate radial ornament. The transverse shell with a wide, broadly rounded posterior margin, strong dorsal median fold and ventral sulcus sharpened laterally by deep plications are among the distinctive features of *Qilianotryma*, but they also occur in some species of *Eospirigerina* (e.g. *E. yulangensis* (Liang)). The radial ornament of *Qilianotryma* is comparable to that of *Euroatrypa* (Nikiforova *et al.* 1982), but the dorsal fold and ventral sulcus in *Euroatrypa* originate near the mid-length and lack lateral plications. It is possible that *Euroatrypa* may be a junior synonym of *Qilianotryma* (Cocks and Modzalevskaya 1997).

EXPLANATION OF PLATE 1

Figs 1–6. *Eospirigerina pennata* (Rukavishnikova, 1956); Dulankara Regional Stage (upper Caradoc) Kazakhstan. 1–4, CNIGR 21/12986; Akkol Beds, locality 42/10 of T. B. Rukavishnikova, River Babasai, southern Chu-Ili Range; dorsal, ventral, anterior and lateral views of conjoined valves; ×4. 5–6, CNIGR 22/12986; lower Kulunbulak Formation, locality 85203, River Kulunbulak, Tarbagatai Range; ventral and dorsal views of conjoined valves; ×4·3.

Figs 7–10. *Sulcatospira*? *praecursor* (Nikitin and Popov, 1984); CNIGR 295/12095; Anderken Stage, *Diplograptus multidens* Biozone (lower–middle Caradoc), upper Bestamak Formation, locality 79136, east side of River Chagan, Chingiz Range, Kazakhstan; dorsal, ventral, lateral and anterior views of conjoined valves; ×6·5.

Figs 11–15. *Qilianotryma suspecta* (Popov, 1982); Dulankara Regional Stage (upper Caradoc), Dulankara Mountains, Chu-Ili Range, Kazakhstan. 11–14, CNIGR 25/11943, holotype; Akkol Beds, locality 827; lateral, ventral, anterior and dorsal views of conjoined valves; ×2·8. 15, CNIGR 2/12986; Degeres Beds, locality 135; ventral internal mould; ×2.



POPOV *et al.*, Ordovician brachiopods

Qilianoatryma suspectum (Popov, *in* Nikiforova *et al.*, 1982)

Plate 1, figures 11–15

1956 *Cliftonia* ex gr. *spiriferoides* (McCoy); Rukavishnikova, p. 51, pl. 4, figs 14–15; *non* M'Coy, 1851, p. 402.
1982 *Euroatrypa suspecta* Popov, *in* Nikiforova *et al.*, p. 57, pl. 6, figs 9–12.

Holotype. CNIGR 25/11943, complete shell (Lv = 12·8, W = 18·2, T = 8·7).

Type locality. Akkol Beds (locality 827, for details see Nikiforova and Popov 1981, pp. 58–59, text-fig. 4), upper Dulankara Formation of the Dulankara Mountains, southern Chu-Ili Range. Details of the Ordovician section in this area are given by Keller (1956*a*) and Nikitin (1972).

Material and stratigraphical range. Total of nine complete shells, 36 ventral and 30 dorsal valves. *Q. suspectum* occurs in Unit 10 of the Akkol Beds (Nikitin 1972, p. 78, text-fig. 20). It is also relatively abundant in the Degeres Beds of the upper Dulankara Formation (Unit 9 of Nikitin 1972). In our collections this species comes from samples 132, 136, 546, 826-a, 827, 829, 835, 836, 854, 857, 858 (for details see Nikiforova and Popov 1981).

Diagnosis. *Qilianotryma* with dorsibiconvex, transverse, sub-oval shell about 76 per cent. as long as wide and 66 per cent as thick as long; radial ornament of fine, closely spaced, costellae about ten to 18 per 5 mm along anterior margin; total of 16–20 costellae on the fold and sulcus and up to 40 on flanks; median rib in sulcus accentuated; concentric ornament of fine, regular, elevated concentric fila about ten to 12 per 1 mm; dental plates rudimentary; dorsal adductor scars arranged radially, separated by pair of fine submedian ridges; median ridge fine and faint, bisecting all the adductor muscle field; spiralia with up to six whorls.

Remarks. Qilianotryma suspectum closely resembles the type species *Q. mirabile* (Xu 1979, p. 97, pl. 20, figs 23–24) in its characteristic radial ornamentation, strong ventral sulcus and dorsal median fold, sharpened laterally by plications, but it is distinguished by its strongly dorsibiconvex shell and in having rudimentary dental plates. Nikiforova *et al.* (1982) gave a detailed description and discussion of this species.

Genus SCHACHRIOMONIA Nikiforova, 1978

1978 *Schachriomonia* Nikiforova, p. 118
1982 *Ovalispira* Fu, p. 157.
1982 *Taoquopospira* Fu, p. 159.
1984 *Zygospira* (*Kuzgunia*) Klenina, p. 113.
1998 *Ovalospira* Zhan and Cocks, p. 60.

Type species. By original designation, *Schachriomonia shacriomonica* Nikiforova, 1978; upper Ordovician, Archalyk beds of south Uzbekistan.

Diagnosis (emended). Spirigerininae with slightly ventribiconvex to biconvex, coarsely costate shell; one or two costellae branching in the fold and sulcus in some species; weakly developed ventral sulcus with single primary rib concentric ornament of fine, elevated, evenly spaced fila; deltidial plates small, separated in early species but uniting medially in derived taxa; dorsal valve with shallow sulcus in the umbonal area reversed anteriorly into indistinct dorsal fold formed by two primary ribs; dental plates short; crura diverging anteroventrally; spiralia with apices directed dorsomedially and with up to eight whorls; jugal processes short, connected to strongly thickened bases of the first spiral whorl.

Species assigned. *Schachriomonia schachriomonica* Nikiforova, 1978; *Taoqupospira dichtoma* Fu, 1982; *Ovalospira ovalis* Fu, 1982; *Zygospira parva* Rukavishnikova, 1956; *Ovalospira yaoxianensis* Fu, 1982.

Species questionably assigned. Zygospira qinghaiensis Xu, 1979 (externally this species is somewhat similar to *Sulcatospira parva*, but its interior morphology is inadequately known).

Distribution and stratigraphical range. Ordovician; upper Caradoc–middle Ashgill, Shaanxi, north China; middle Ashgill, Koumenzi Formation, Qinghai region, Shiyanhe Formation of eastern Qinling, south China; upper Caradoc–middle Ashgill (Dulankara, Abak and Chokpar regional stages, upper *Climacograptus clingani*–lower *Climacograptus supernus* biozones) of Kazakhstan.

Remarks. Schachriomonia closely resembles *Ovalospira* and *Taoquopospira* (Fu 1982) in the main characters of shell morphology, including costate radial ornament, weakly uniplicate anterior commissure with a very shallow ventral sulcus originated in the anterior part of the shell and weak dorsal median fold reversed from the shallow umbonal sulcus and formed by two slightly accentuated ribs. There is no satisfactory information on the characters of brachial supports in the type species of all three genera, but strong affinities in the external shell morphology and characters of cardinala suggest that they are all congeneric and *Schachriomonia* is regarded here as senior synonym.

Zhan and Cocks (1998, pp. 61–62) gave a detailed discussion of the affinities and possible synonymy of *Ovalospira* and *Taoquopospira*. They also mentioned the close similarity of '*Zygospira* (*Kuzgunia*)' *parva* Rukavishnikova, 1956, as revised by Klenina (1984), to *Ovalospira*.

The subgenus *Zygospira* (*Kuzgunia*), with *Zygospira parva* Rukavishnikova, 1956 as type species, was not established in 1969 as mentioned by Klenina (1984). Klenina is responsible for the authorship of this taxon, because the paper of Misius (1969) listed by Klenina is actually an abstract of a doctoral thesis printed in a limited number of copies and does not qualify as a publication under the terms of the International Code of Zoological Nomenclature. A diagnosis of *Kuzgunia* was published by Misius only in 1986 and based on a different type species, *Kuzgunia asiatica* Misius, 1986, which is referred here to *Sulcatospira*.

Schachriomonia differs from *Sulcatospira* in having a relatively poorly developed dorsal median fold and ventral sulcus, which originate near mid-valve. But, in the presence of spiralia with dorsomedially directed apices and short jugal processes connected to thickened proximal parts of the first spiral whorls, these genera are remarkably similar and, possibly, closely related phylogenetically.

Characters of the brachidium in *Schachriomonia* remain unknown in the type species and data provided in the emended diagnosis are based on the study of *Schachriomonia parva.*

Schachriomonia parva (Rukavishnikova, 1956)

Plate 2, figures 1–9, Text-figures 5–6; Table 1

1956 *Zygospira parva* sp. nov. Rukavishnikova, 1956, p. 162, pl. 5, figs 14–16.
1984 *Zygospira* (*Kuzgunia*) *parva* Klenina, p. 114, pl. 11, figs 6–12.
1984 *Zygospira* (*Kuzgunia*) *bakanasensis* Klenina, 1984, p. 115, pl. 5, fig. 15.

Holotype. IGN 64/1369, complete shell.

Type locality. Akkol Beds, upper Dulankara Formation, Dulankara Mountains, southern Chu-Ili Range. This species occurs in bedded and nodular limestone in association with various tabulate corals (Bondarenko 1958), together with the brachiopods *Otarorhyncha otarica* (Rukavishnikova, 1956) and *Eospirigerina pennata* (Rukavishnikova, 1956). Details of the Ordovician section in this area were given by Keller (1956*a*) and Nikitin (1972).

Material and stratigraphical range. Figured; complete shells, CNIGR Museum 2/12986 (Lv = 11·5, Ld = 10·8, W = 12·2, T = 6·45); 3/12986 (Lv = 11·5, Ld = 10·8, W = 12·2, T = 6·45), 4/12986, 5/12986; dorsal valve 6/128896; total of 47 complete shells, 15 ventral and 19 dorsal valves.

According to Klenina (1984) this species is abundant in the Chingiz Range in beds tbII-tbV of the Taldyboi Formation (Dulankara Regional Stage). In our collection, numerous well preserved specimens were sampled from locality 604 of Nikitin (1972, 1973, pl. 4) in the middle part of the Taldyboi Formation on the west side of the River Taldyboi. It occurs in argillaceous limestones together with numerous gastropods and the brachiopods *Otarorhyncha otarica, Plaesiomys* (*Dinorthis*) *abayi* Klenina, 1984, etc. Some additional specimens were found in siltstones of the middle part of the Taldyboi Formation exposed between the rivers Taldyboi and Namas (sample 285/1975 of O. P. Kovalevskii).

S. parva also occurs abundantly in the lower part of the Akdombak Formation near Akdombak mountain (the type locality of *Zygospira* (*Kuzgunia*) *bakanasensis* (Klenina, 1984)). All specimens were sampled from localities 1859 of Kovalevskii and 7976 of Popov, which correspond to Bed akI (Unit 6) of Klenina (1984, pp. 15–16). Atrypides at this locality are part of a low diversity assemblage together with the brachiopod *Sowerbyella akdombakensis* Klenina, 1984 and the tabulate corals *Agetolites mirabilis* Sokolov, *Palaeofavosites acerbus* Kovalevskii, *Sarcinula tarbagataica* Kovalevskii and others.

In the Chu-Ili Range *S. parva* occurs in the Akkol Beds, upper Dulankara Regional Stage. All specimens in our collection are from localities 119 and 141 of Nikitin (1972, fig. 20) and locality 5 of T. Rukavishnikova in the Dulankara Mountains.

Diagnosis. *Schachriomonia* with slightly ventribiconvex, sub-circular to slightly transverse sub-oval shell, about 97 per cent. as long as wide and 55 per cent. as thick as long; anterior commissure weakly uniplicate to near rectimarginate; ventral valve moderately and evenly convex; sulcus very narrow and shallow, originating anterior to mid-valve; dorsal valve moderately and evenly convex with a shallow V-shaped sulcus in the umbonal area and a low, inconspicuous median fold originating between the anterior margin and mid-valve; radial ornament of 14–21 costae with one rib in the sulcus and two in the median fold; spiralia with short jugal process and five to seven whorls.

TABLE 1. Measurements of 30 shells of *Schachriomonia parva* (Rukavishnikova, 1956) from locality 604, Taldyboi Formation, River Taldyboi, Chingiz Range.

	Lv	W	T	Lv/W	T/Lv
N	30	30	30	30	30
X	12·6	13·1	7·0	97%	55%
S	2·14	2·14	2·38	8·0	6·8
min.	8·0	8·1	4·2	84%	42%
max.	18·1	17·9	11·1	121%	74%

Remarks. *Zygospira* (*Kuzgunia*) *bakanasensis* (Klenina 1984, p. 116) was established on the basis of minor differences from *S. parva* in the lateral profile of the ventral valve. Specimens from the type locality of the former species are not different from *S. parva* in size, external shell shape and character of the radial ornament. Therefore, *Z. bakanasesnis* is regarded here as a junior subjective synonym of *S. parva.*

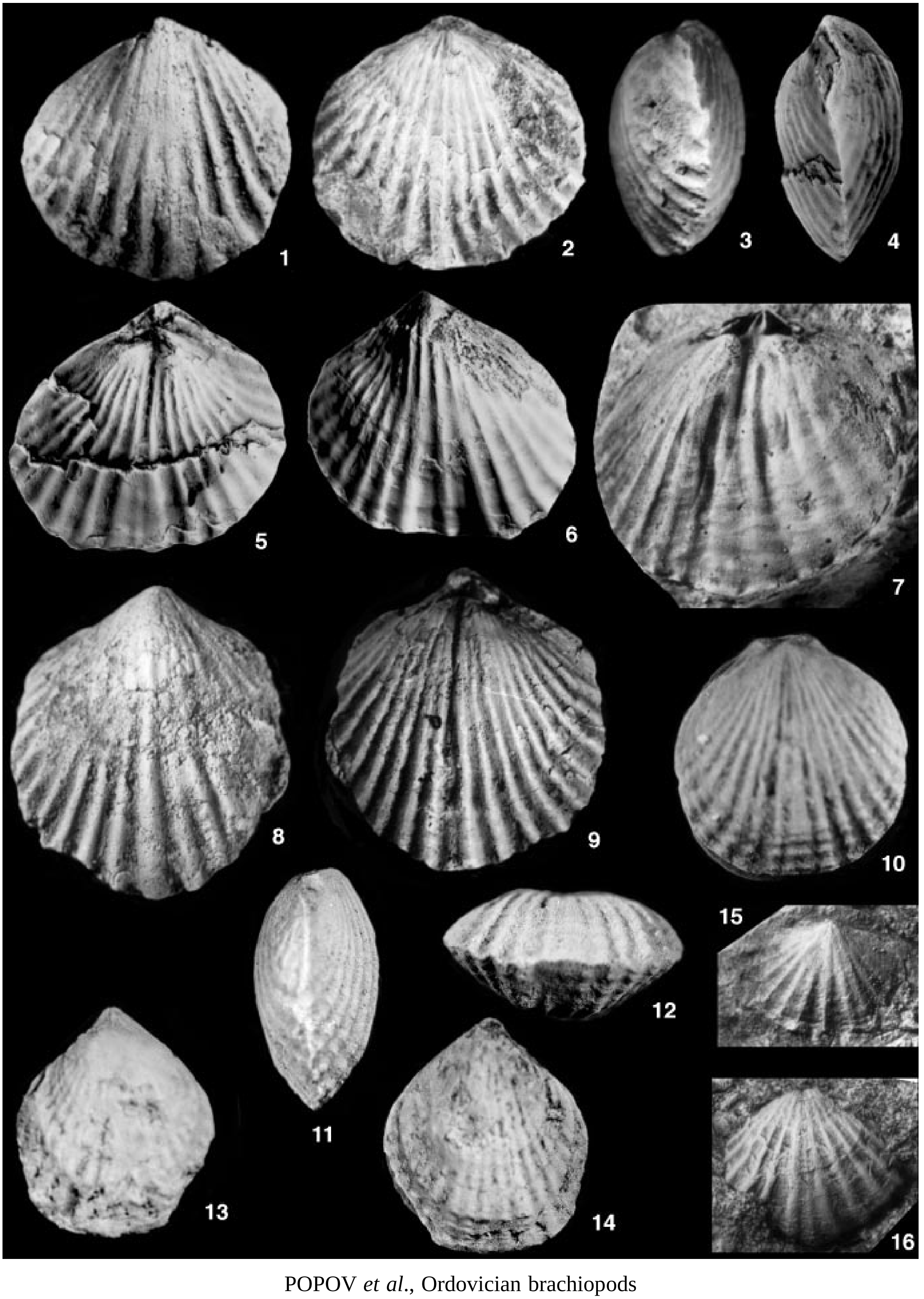
Zygospira qinghaiensis (Xu 1979, p. 108, pl. 21, figs 10–15, 19–21, text-fig. 51) from the Koumenzi Formation of the Qinghai region is another species that strongly resembles *S. parva* in general shell shape and radial ornamentation, as well as in characters of the dorsal median fold and ventral sulcus. Xu did not

EXPLANATION OF PLATE 2

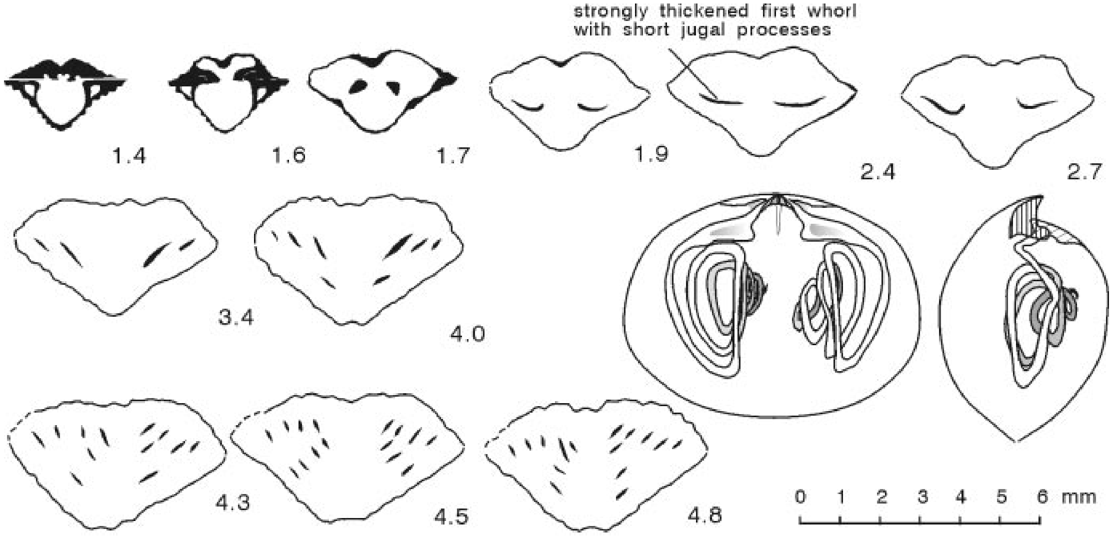
Figs 1–9. *Schachriomonia parva* (Rukavishnikova, 1956); Dulankara and Abak regional stages (upper Caradoc–lower Ashgill), Chingiz Range, Kazakhstan. 1–3, CNIGR 2/12986; lower Akdombak Formation, Bed akI, locality 7976 (type locality and horizon of *Zygospira* (*Kuzgunia*) *bakanasensis* Klenina, 1984), area of Akdombak Mountain, Chingiz Range; ventral, dorsal and lateral views of conjoined valves. 4–6, CNIGR 3/12986; middle Taldyboi Formation, locality 285, area between Taldyboi and Namas rivers, Chingiz Range; lateral, dorsal and ventral views of conjoined valves. 7, CNIGR 4/12986; locality as for figs 4–6; dorsal internal mould showing median ridge and cardinal process. 8–9, CNIGR 5/12986; locality as for figs 1–3; ventral and dorsal views of conjoined valves. All ×4.

Figs 10–14. *Sulcatospira*? *dominanta* (Rukavishnikova, 1956); Chokpar Regional Stage (middle Ashgill), upper *Climacograptus supernus* Biozone, locality 287, River Oisu, southern Chu-Ili Range, Kazakhstan. 10–12, CNIGR 15/12986; dorsal, lateral and anterior views of conjoined valves. 13–14, CNIGR 16/12986; ventral and dorsal views of conjoined valves. All ×5.

Figs 15–16. *Sulcatospira prima* sp. nov.; Chu-Ili Range, Kazakhstan. 15, CNIGR 19/12986; Anderken Stage (Caradoc), Kujandysai, locality 8220; ventral valve exterior. 16, CNIGR 20/12986; Dulankara Stage (upper Caradoc), Otar Beds, Dulankara Mountains, locality 837; dorsal valve exterior. Both ×3.



POPOV *et al*., Ordovician brachiopods

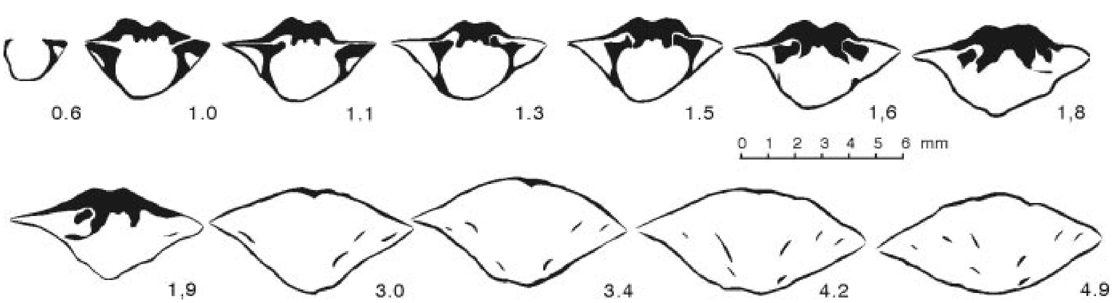


TEXT-FIG. 5. Serial sections and reconstruction of spiralia and jugal processes in *Schachriomonia parva* (Rukavishnikova, 1956) from a specimen from locality 7967, Akdombak section, Chingiz Range, lower Akdombak Formation, Abak Regional Stage (lower Ashgill). Sections with dorsal valve uppermost.

provide information on the spiralia of *Z. qinghaiensis*, but its assignment to *Zygospira* is somewhat doubtful and it more probably belongs to *Sulcatospira*; it may even be conspecific with *S. parva*. Specimens of *Z. qinghaiensis* illustrated by Xu (1997, pl. 5, figs 1–4) from the upper Ordovician, Shiyanhe Formation of eastern Qinling, South China, differ from both *S. parva* and topotypes of *Z. qinghaiensis* in having a vestigial dorsal median fold with three ribs and a dorsal sulcus with two ribs. These specimens are more probably a separate new species; however, their precise generic assignment remains unclear in view of the absence of information on internal shell morphology.

The similarity of *S. parva* to *Schachriomonia* (= *Taoquopospira*) *dichtoma* (Fu, 1982) was discussed by Zhan and Cocks (1998, p. 62). The main differences between these two species are the presence in *S. parva* of an open delthyrium with small separated deltidial plates and a stronger dorsal median ridge.

S. parva differs from *S. schachriomonica* Nikifirova (1978, p. 119, pl. 22, figs 8–13; pl. 23, figs 1–7) in having a coarser radial ornament with no more then 21 ribs and a somewhat more pronounced ventral sulcus and dorsal fold, which are very weakly developed in the former species.



TEXT-FIG. 6. Serial sections of *Schachriomonia parva* (Rukavishnikova, 1956) from a specimen from locality 604a, left side of the River Taldyboi, Chingiz Range, lower Akdombak Formation, Dulankara Stage (upper Caradoc). Sections with dorsal valve uppermost.

Genus SULCATOSPIRA Xu, 1979

1979 *Zygospira* (*Sulcatospira*) Xu, p. 109.
1984 *Zygospira* (*Kuzgunia*) Klenina, p. 113.
1986 *Kuzgunia* Misius, p. 186.

Type species. By original designation, *Zygospira* (*Sulcatospira*) *plicata* Xu, 1984, upper Ordovician, Koumenzi Formation of the Qinghai region South-west China.

Diagnosis (emended). Spirigerininae with slightly ventribivonvex to biconvex, coarsely costate shell; ventral sulcus well developed, with single primary rib and dorsal fold reversed from the shallow umbonal sulcus, formed by two ribs; one or two additional costellae originate in posterior part of fold and sulcus in some species; concentric ornament of fine, elevated, evenly spaced fila; deltidial plates small, separated; dental plates short; crura diverging anteroventrally; spiralia with apices directed dorsomedially and with four to seven whorls; jugal processes short, converging, connected to strongly thickened bases of the first spiral whorl.

Species assigned. *Zygospira* (*Sulcatospira*) *plicata* Xu, 1979; *Zygospira* (*Kuzgunia*) *asiatica* Misius, 1986; *Sulcatospira prima* sp. nov

Species questionably assigned. Qilianotryma? *praecursor* Nikitin and Popov, 1984 (parasulcate anterior commissure, spiralia and jugum unknown); *Zygospira shaanxiensis* Fu, 1982 (somewhat similar to *Sulcatospira asiatica* in the characters of the radial ornament, ventral sulcus and dorsal median fold, but interior of both valves and spiralia unknown); *Zygospiraella dominanta* Rukavishnikova, *in* Nikitin *et al.*, 1980 (externally this species is similar to juvenile *Sulcatospira*, but the brachidium is unknown).

Species rejected. *Zygospira* (*Sulcatospira*) *minor* Xu, 1979 (small shells with three to five indistinct ribs on flanks of both valves, internal characters unknown, reassigned to *Antizygospira* by Zhan and Cocks 1998).

Distribution and stratigraphical range. Ordovician; upper Caradoc–middle Ashgill, South China; middle Caradoc–middle Ashgill (Anderken, Dulankara, and Chokpar regional stages, upper *Diplograptus multidens*–lower *Climacograptus supernus* biozones) of Kazakhstan and north Kirgizia.

Remarks. *Sulcatospira* was defined originally as a subgenus of *Zygospira*, but it differs from the latter in having coarser radial ornament, a uniplicate anterior commissure, and a variably developed dorsal median fold and ventral sulcus. Thickened proximal parts of the spiralia and short jugal processes were not mentioned in the original diagnosis of *Sulcatospira*, but these features can be observed in schematic drawings of cross sections accompanying the description of the type species (Xu 1979, text-fig. 110). Similar morphology of the spiralia and jugal processes can be observed in the Kazakhstanian *S. asiatica*. These data suggest that *Sulcatospira* cannot be retained as a taxon within the suborder Anazygidina and belongs instead to the early Atrypidina. *Sulcatospira* is somewhat comparable to juvenile specimens of some early species of *Eospirigerina* (e.g. *E. pennata*), but differs from mature specimens of the latter genus in having a ventribiconvex shell with a narrow dorsal median fold formed usually by only two ribs, and very short jugal processes.

Sulcatospira asiatica (Misius, 1986)

Plate 3, figures 1–10; Text-figure 7

1986 *Kuzgunia asiatica* sp. nov. Misius, p. 187, pl. 22, figs 6–9; pl. 23, figs 1–5.
1986 *Kuzgunia asiatica longula* subsp. nov. Misius p. 190, pl. 23, figs 10–13; pl. 24, figs 1–4.
1986 *Kuzgunia asiatica parva* (Rukavishnikova); Misius p. 191, pl. 24, figs 5–11.
1986 *Kuzgunia asiatica lata* subsp. nov. Misius p. 193, pl. 23, figs 5–9.

Holotype. GIK 1292/5, complete shell (Lv = 15·1, W = 16·6, T = 11·0).

Type locality. Locality 0123-1 (Misius 1986, pp. 54–57, figs 1, 4) *Kuzgunia* Beds, Tez Formation, middle Ordovician (upper Caradoc), upper reaches of Kashkator river, northern slope of Sary-Dzhaz Range, north Tien-Shan.

Material and stratigraphical range. Figured: CNIGR 10/12986 (Lv = 8·1, Ld = 7·6, T = 4·6), CNIGR 11/12986 (Lv = 10·5, Ld = 9·5, W = 11·5, T = 6·75, Sw = 6·7, St = 2·9), 12/12986 (Lv = 8·25, Ld = 7·8, W = 8·5, T = 4·55, Sw = 4·1, St = 2·35), 13/12986 (Lv = 11·2, Ld = 9·4, W = 11·1, T = 8·1, Sw = 5·8, St = 6·2), 14/12986 (Lv = 7·3, Ld = 6·5, W = 7·5, T = 3·5, Sw = 3·7, St = 2·1); total of 64 complete shells, 20 ventral and 11 dorsal valves. In Kazakhstan this species is known from the Dulankara Regional Stage of the Chu-Ili Range. Most specimens in our collection are from localities 101 and 85257 north-west of the town of Gornoe (for details see Popov *et al.* 1997, p. 586, fig. 3). The species also occurs in the section along the river Akdalasay (locality 145/1970 of O. P. Kovalevskii).

Diagnosis. *Sulcatospira* with slightly dorsibiconvex shell; outline rounded pentagonal, about 91 per cent. as long as wide and 64 per cent. as thick as long; anterior commissure uniplicate; ventral valve moderately convex with posteriorly directed, slightly curved beak and open delthyrium; sulcus originates at the umbonal area, sharpened laterally by strong, angular costae and deepened anterior to mid-length; tongue trapezoidal, strongly inclined to commissural plane and about 64 per cent. as wide as maximum shell width; dorsal valve moderately convex with shallow sulcus in the umbonal area, reversed as a high median fold with steep slopes anterior to mid-valve; radial ornament costate with up to ten ribs on flanks; costellate in the fold and sulcus with one primary rib in fold, two ribs in sulcus, and normally one or two secondary ribs bifurcating anterior to mid-length; accentuated median rib usually present in the ventral valve; crura subparallel, anteriorly directed; jugal process long, strongly thickened near the junction with spiralial base; spiralia with up to seven whorls.

Remarks. *Kuzgunia asiatica longula* Misius, 1986 and *Kuzgunia asiatica lata* Misius, 1986 occur in the same lithostratigraphical unit and localities as topotypes of *Kuzgunia asiatica s.s.* and cannot be regarded as separate taxa; they do not differ markedly in characters of radial ornament or the strongly developed ventral sulcus and dorsal median fold. Some differences in size, transverse profile and outline listed by Misius are regarded here as insignificant. Specimens described by Misius (1986, p. 191) as *Kuzgunia asiatica parva* (Rukavishnikova) are not conspecific with *Sulcatospira parva* as defined originally by Rukavishnikova (1956), because they have a deep ventral sulcus originating in the umbonal area and a well defined dorsal median fold.

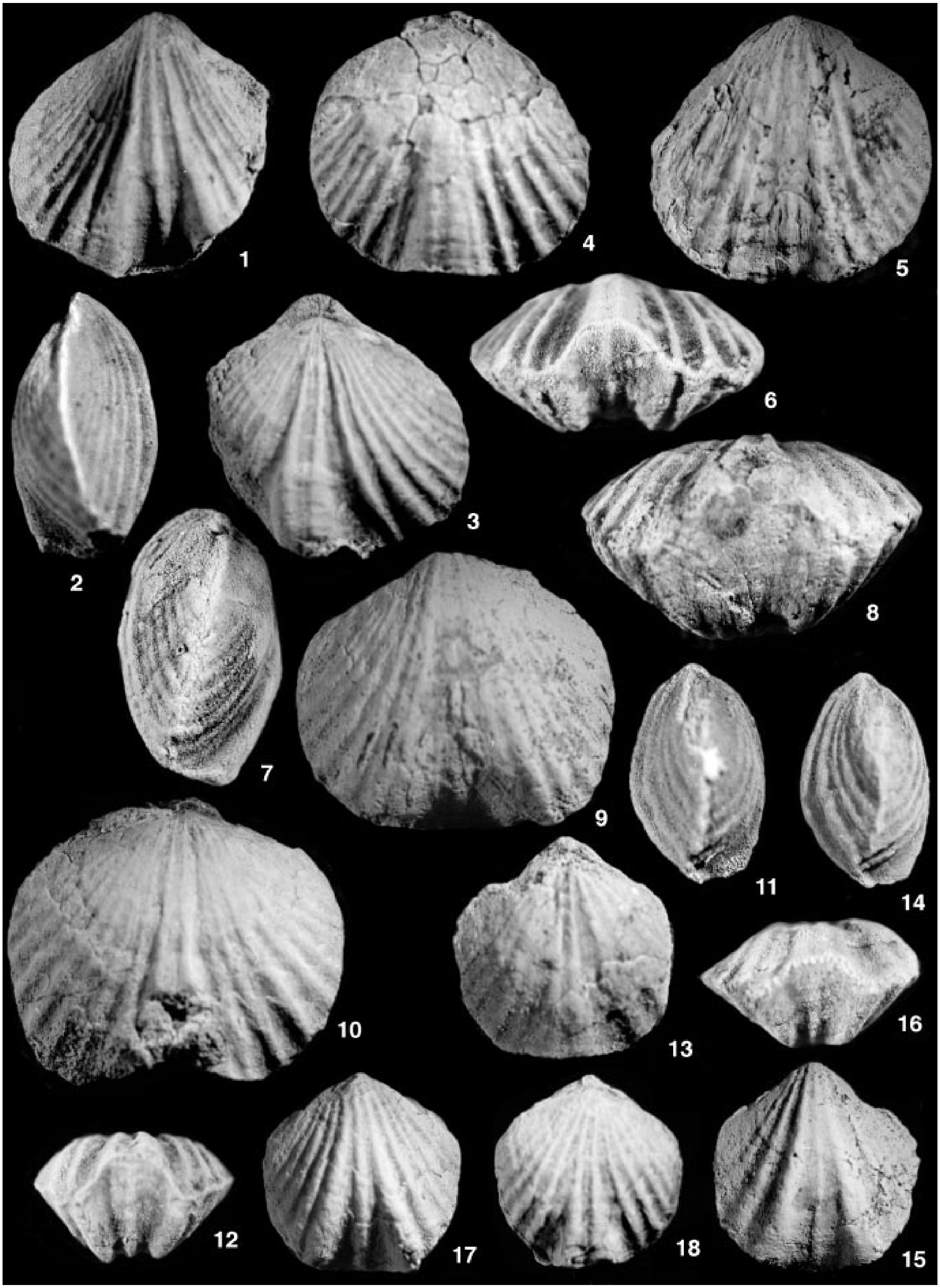
Juvenile specimens of *S. asiatica* resemble the type species *Sulcatospira plicata* (Xu, 1979) in having a well defined ventral sulcus with a single strong rib and a dorsal median fold with two ribs, as well as a ventribiconvex shell and strong angular costae on the flanks, but mature specimens of the Kazakhstanian species differ from the latter in their slightly dorsibiconvex shell, a deep ventral sulcus with a high, trapezoidal tongue, and in the presence of one or two secondary costellae in the anterior part of the fold and sulcus.

Subparallel or slightly diverging crura located close to the commissural plane in *S. asiatica* probably represent a primitive feature, which is recorded also in *Sulcatospira*? *praecursor* but is lost in *Schachriomonia*.

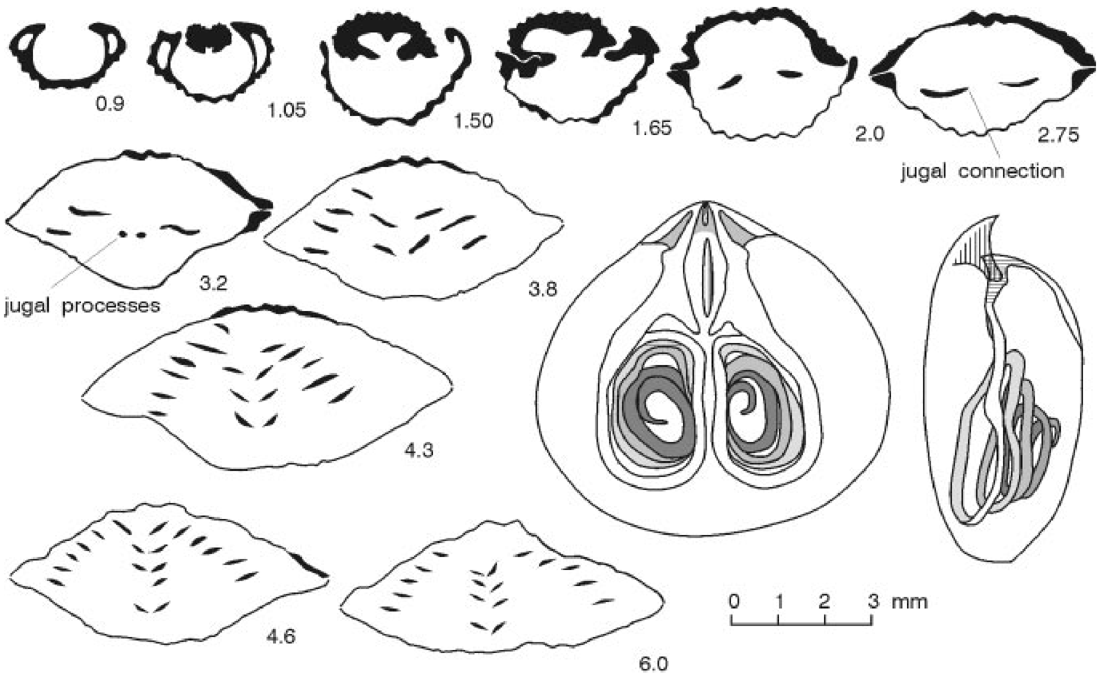
EXPLANATION OF PLATE 3

Figs 1–10. *Sulcatospira asiatica* (Misius, 1986); Dulankara Regional Stage (upper Caradoc), Chu-Ili Range, Kazakhstan. 1–3, CNIGR 11/12986; locality 101, Zhartas River near town of Gornoe; ventral, lateral and dorsal views of conjoined valves; ×4. 4–7, CNIGR 12/12986; locality 145, River Akdalasai; dorsal, ventral, anterior and lateral views of conjoined valves; ×5·2. 8–10, CNIGR 13/12986; locality 145, River Akdalasai; anterior, ventral and dorsal views of conjoined valves; ×4·9.

Figs 11–18. *Sulcatospira prima* sp. nov.; Dulankara Regional Stage (upper Caradoc), Koskarasu Beds, locality 539, River Koskarasu, north-eastern central Kazakhstan. 11, 13, 15–16, CNIGR 17/12986; lateral, dorsal, ventral and anterior views of conjoined valves. 12, 14, 17–18, CNIGR 18/12986; anterior, lateral, ventral and dorsal views of conjoined valves. All ×6.



POPOV *et al.*, *Sulcatospira*



TEXT-FIG. 7. Serial sections and reconstruction of spiralia of *Sulcatospira asiatica* (Misius, 1986) from a specimen from locality 101, Zhartas river near town of Gornoe, southern Chu-Ili Range, Dulankara Formation, Dulankara Regional Stage (upper Caradoc). Sections with dorsal valve uppermost.

Sulcatospira? *dominanta* (Rukavishnikova, *in* Nikitin *et al.*, 1980)

Plate 2, figures 10–14

Remarks. This species was referred originally to *Zygospiraella*, but in its external characters, including its costate radial ornament with bifurcating median costa on the low, narrow dorsal fold and its shallow ventral sulcus (Nikitin *et al.* 1980, text-fig. 9), it closely resembles juvenile *Sulcatospira.* The nature of the spiralia and jugum remain unknown. Two topotypes of *S.*? *dominanta* are illustrated here.

Sulcatospira prima sp. nov.

Plate 2, figures 15–16; Plate 3, figures 11–18; Text-figure 8; Table 2

Derivation of name. Latin *primus*, first.

Holotype. CNIGR 17/12986, complete shell (Lv = 4·9, Ld = 4·6, W = 4·7, T = 3·1, Sw = 2·5, St = 1·6).

Type locality. Koskarasu valley in north-central Kazakhstan (for details see Nikitin 1972, pp. 187–188, text-fig. 57, locality 539); Ordovician, Dulankara Regional Stage, Angrensor Formation, Koskarasu beds.

Paratypes. Figured; CNIGR 18/12986, complete shell (Lv = 5·55, Ld = 5·05, W = 5·6, T = 3·2, Sw = 2·5, St = 1·2); 19/12986, ventral valve; 20/12986, dorsal valve; total of 93 complete shells and six dorsal valves. This species is fairly abundant in a bed of sandy limestone referred to the Anderken Formation in the Dulankara Mountains (Unit 2, locality 143 of Nikitin 1972, text-fig. 20), and occurs also in the uppermost Anderken Limestone at Kujandysai (locality 8220). In the Dulankara Mountains it occurs in the lowermost part of the Dulankara Formation, samples 131 and 837; for details see Popov *et al*. (1980, text-figs 1–2).

Diagnosis. *Sulcatospira* with slightly ventribiconvex shell and uniplicate anterior commissure; ventral valve carinate posteriorly, with sulcus originating near the umbo and sharpened laterally by accentuated ribs; dorsal valve with shallow sulcus in the umbonal area reversed anteriorly into a low fold, sharpened laterally by plications; radial ornament costate with one rib in sulcus, two in fold and four to eight on flanks; spiralia with up to five whorls.

Description. Shell slightly ventribiconvex, sub-circular to rounded sub-pentagonal in outline, about 100 per cent. as long as wide with maximum width at mid-length and 58 per cent. as thick as long. Anterior commissure uniplicate. Ventral valve moderately and evenly convex, carinate posteriorly, with open delthyrium. Beak slightly acuminate, posteriorly directed. Sulcus originates at the umbo, widening and deepening anterior to mid-valve, semi-oval in cross section, sharpened laterally by strong angular costae. Tongue low, sub-oval, inclined anteriorly to the commissural plane, about 51 per cent. as wide as the valve. Dorsal valve gently and evenly convex, about 92 per cent. as long as wide. Umbonal area with a narrow, shallow sulcus, reversed into a sharp median fold near mid-valve. Radial ornament costate with one accentuated rib in sulcus, two in fold and four to eight on flanks; total up to 17 or 18 costae.

Ventral interior with teeth and short divergent dental plates situated close to the valve margin. Dorsal interior with disjunct hinge plates and thin, anteriorly directed crura. Spiralia with up to five whorls and with apices directed dorsomedially. Jugal processes short, disjunct, directed ventrally.

TABLE 2. Measurements of 37 shells of *Sulcatospira prima* sp. nov. from locality 539, Angrensor Formation, Koskarasu valley, north-central Kazakhstan.

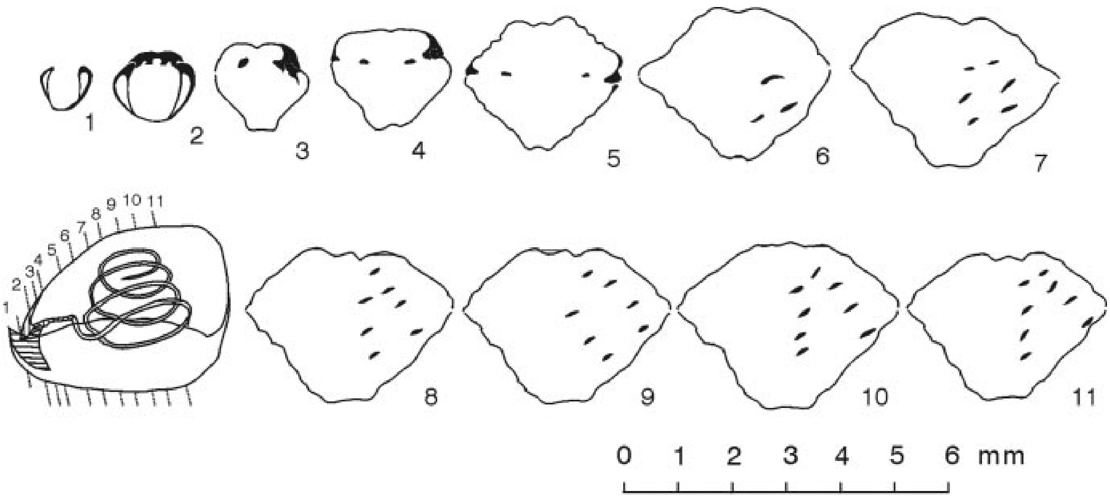
	Lv	Ld	W	T	Sw	St
N	37	37	37	37	37	37
X	5·5	5·0	5·5	3·2	2·8	0·8
S	0·913	0·903	1·14	0·839	0·805	0·493
min.	3·4	3	3·5	1·6	1·3	0·2
max.	7	6·5	8·7	5	5·2	2

	Lv/W	Ld/W	T/Lw	Sw/W
N	37	37	37	37
X	100%	92%	58%	51%
S	10·1	9·8	9·1	7·5
min.	78%	71%	40%	37%
max.	119%	114%	79%	71%

Variation. Specimens with five ribs on the flanks predominate in our collections (about 70 per cent.), whereas specimens with six ribs comprise about 20 per cent. and with four ribs not more then 10 per cent. The number of ribs in the fold and sulcus remains fairly constant, but about 1 per cent. of the total specimens have a smooth fold and about 1 per cent. have two ribs in the sulcus and three in the fold.

Remarks. This species closely resembles juvenile specimens of *Sulcatospira plicata* (Xu 1979, p. 170, pl. 21, figs 6–9) in characters of the radial ornament and development of the ventral sulcus and dorsal median fold. However, *S. prima* differs from mature specimens of the Chinese species in being smaller, as well as in having the dorsal fold and ventral sulcus bordered laterally by very strong, accentuated ribs.

S. prima differs from *Sulcatospira asiatica* (Misius, 1986) in having a ventribiconvex shell, a single rib in the sulcus and two on the fold not bifurcating anteriorly, and not more than six ribs on the flanks.



TEXT-FIG. 8. Serial sections and reconstruction of spiralia in *Sulcatospira prima* sp. nov. from a specimen from locality 539, right side of River Koskarasu, north-eastern central Kazakhstan, lower Koskarasu Beds, Dulankara Regional Stage (upper Caradoc). Sections with dorsal valve uppermost.

Sulcatospira? *praecursor* (Nikitin and Popov, 1984)

Plate 1, figures 7–10

1984 *Qilianotryma*? *praecursor* sp. nov.; Nikitin and Popov, p. 159, pl. 20, figs 15–16, text-fig. 49.

Holotype. CNIGR 204/12095, complete shell (Lv = 8·0, W = 8·3, T = 4·8).

Type locality. Upper Bestamak Formation, lower Anderken Regional Stage (lower to middle Caradoc), locality 79136, east side of the River Chagan opposite the mouth of the River Sargaldak, Chingiz Range, Kazakhstan.

Material and stratigraphical range. Nine complete shells and two ventral valves. All material in the type area is from localities 79135, 79136 (Nikitin and Popov 1984, text-fig. 26; Unit 8 of Tsai 1976, p. 10, text-fig. 2). Both underlying and overlying units of the Bestamak Formation in this section contain graptolites of the *Diplograptus multidens* Biozone suggesting the lower Caradoc (Anderken Regional Stage).

Diagnosis. *Sulcatospira*? with slightly ventribiconvex, rounded pentagonal shell, about 107 per cent. as long as wide and 55 per cent. as thick as long; anterior commissure parasulcate; ventral beak slightly acuminate, posteriorly directed; delthyrium open; ventral sulcus sharpened laterally by accentuated, angular costae originating at the umbo; dorsal valve with shallow sulcus divided medially by low plication, reversed at mid-valve into a low median fold bordered laterally by low angular plications; radial ornament costate with two or three ribs in sulcus, three or four on fold and seven to 13 on flanks; one or two secondary costellae bifurcating in the median part of the fold and sulcus near the anterior margin; accentuated median costa usually developed in the ventral valve.

Remarks. This species is assigned only questionably to *Sulcatospira* because it differs from other known species of the genus in having a parasulcate anterior margin with two or three ribs in the ventral sulcus and three or four on the dorsal median fold, and in lacking a dorsal median ridge.

Sulcatospira? *praecursor* somewhat resembles early species of *Eospirigerina* (e.g. *E. pennata* (Rukavishnikova, 1956)), in its general shell shape, costate radial ornament on the flanks of both valves, and its dorsal sulcus and ventral median fold sharpened laterally by plications; however, it is distinguished by having a parasulcate anterior commissure and mainly costate radial ornament, with only one or two costellae bifurcating from the median ribs in the fold and sulcus.

Suborder LISSATRYPIDINA Copper, *in* Copper and Gourvennec, 1996
Superfamily LISSATRYPOIDEA Twenhofel, 1914
Family LISSATRYPIDAE Twenhofel, 1914
Subfamily CYCLOSPIRINAE Schuchert, 1913

Genus ROZMANOSPIRA gen. nov.

Derivation of name. In recognition of the late Dr Kh. S. Rozman.

Type and only species. Oligorhyncha? *mica* Nikitin and Popov, 1984; upper Bestamak Formation, Anderken Regional Stage (lower to middle Caradoc), Chingiz Range, Kazakhstan.

Diagnosis. Cyclospirine with smooth, ventribiconvex, transverse shell; anterior commissure parasulcate; ventral sulcus originates near the umbo, sharpened by angular plications; dorsal valve with a shallow umbonal sulcus reversed into a narrow, rounded median fold posterior to mid-valve; ventral interior with small teeth and short dental plates; dorsal interior with disjunct hinge plates and anteriorly directed diverging crura; median septum absent; spiralia comprising a single incomplete whorl without jugum.

Remarks. Originally, the rudimentary lophophore supports of *Rozmanospira* were interpreted as long radulifer crura of an early rhynchonellide (Nikitin and Popov 1984), and this species was assigned to *Oligorhyncha* Cooper, 1956. However, simple spiralia consisting of a single, incomplete first whorl can now be recognized from reconstructions based on cross sections (Text-fig. 8). In its general shell shape and in the absence of a jugum this genus closely resembles a small *Cyclospira* (Copper 1986); however, it differs from the latter in having dental plates and very simple spiralia consisting of a single incomplete whorl, as well as in the absence of a median septum. *Rozmanospira* is comparable to *Manespira* (Copper 1986, p. 839) in having simple spiralia and rudimentary dental plates, as well as in characters of the median fold and sulcus; however, it differs from the latter in its smooth shell and absence of a jugum.

Rozmanospira mica (Nikitin and Popov, 1984)

Plate 4, figures 1–8; Text-figure 9

1984 *Oligorhyncha mica*? sp. nov. Nikitin and Popov, p. 156, figs 4–5; text-figs 38–39.

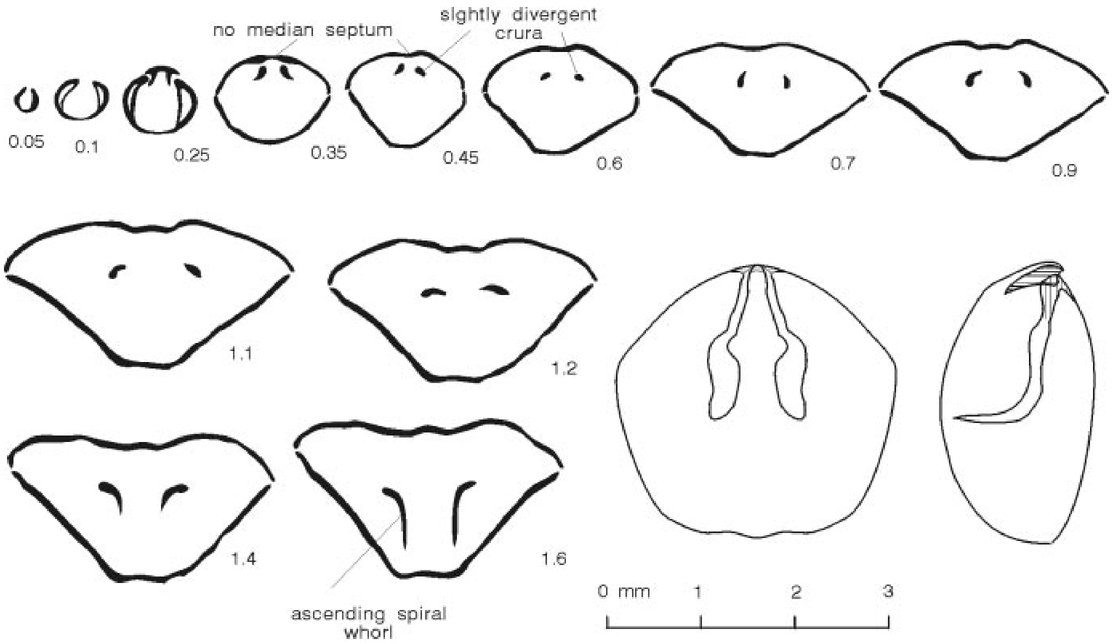
Holotype. CNIGR 197/12095, complete shell.

Type locality. Upper part of Bestamak Limestone (locality 564 of Nikitin 1960), east side of the River Chagan near the village of Bestamak, Chingiz Range. The overlying black shale unit contains graptolites diagnostic of the *Nemagraptus gracilis* Biozone (Unit 5 of Tsai 1976, p. 10, text-fig. 2) suggesting a late Llandeilo or early Caradoc (Costonian) age for this fauna, corresponding with the Tselinograd Regional Stage of the Regional Standard of Kazakhstan.

Material and stratigraphical range. 144 complete shells from the type locality.

Diagnosis. As for genus; see also Nikitin and Popov (1984, p. 156).

Remarks. One of the features of this species is the occasional presence of a median rib in the ventral sulcus (Pl. 4, figs 2–3). A similar rib is also present in the sulcus of the early athyridide *Nikolaespira rasilis* (Nikitin *et al*. 1996, fig. 8F, I). It is also probable that the accentuated median rib occurring in costate



TEXT-FIG. 9. Serial sections and reconstruction of spiralia in *Rozmanospira mica* (Nikitin and Popov, 1984) from a specimen from locality 564, east side of River Chagan, Chingiz Range, lower Bestamak Formation, Tselinograd Regional Stage (Llandeilo–Costonian). Sections with dorsal valve uppermost.

Ordovician atrypoid taxa from Kazakhstan (e.g. *Sulcatospira*, *Eospirigerina praecursor* and *Qilianotryma*) is a homologous character.

Family PROTOZYGIDAE Copper, 1986
Subfamily PECTENOSPIRINAE subfam. nov.

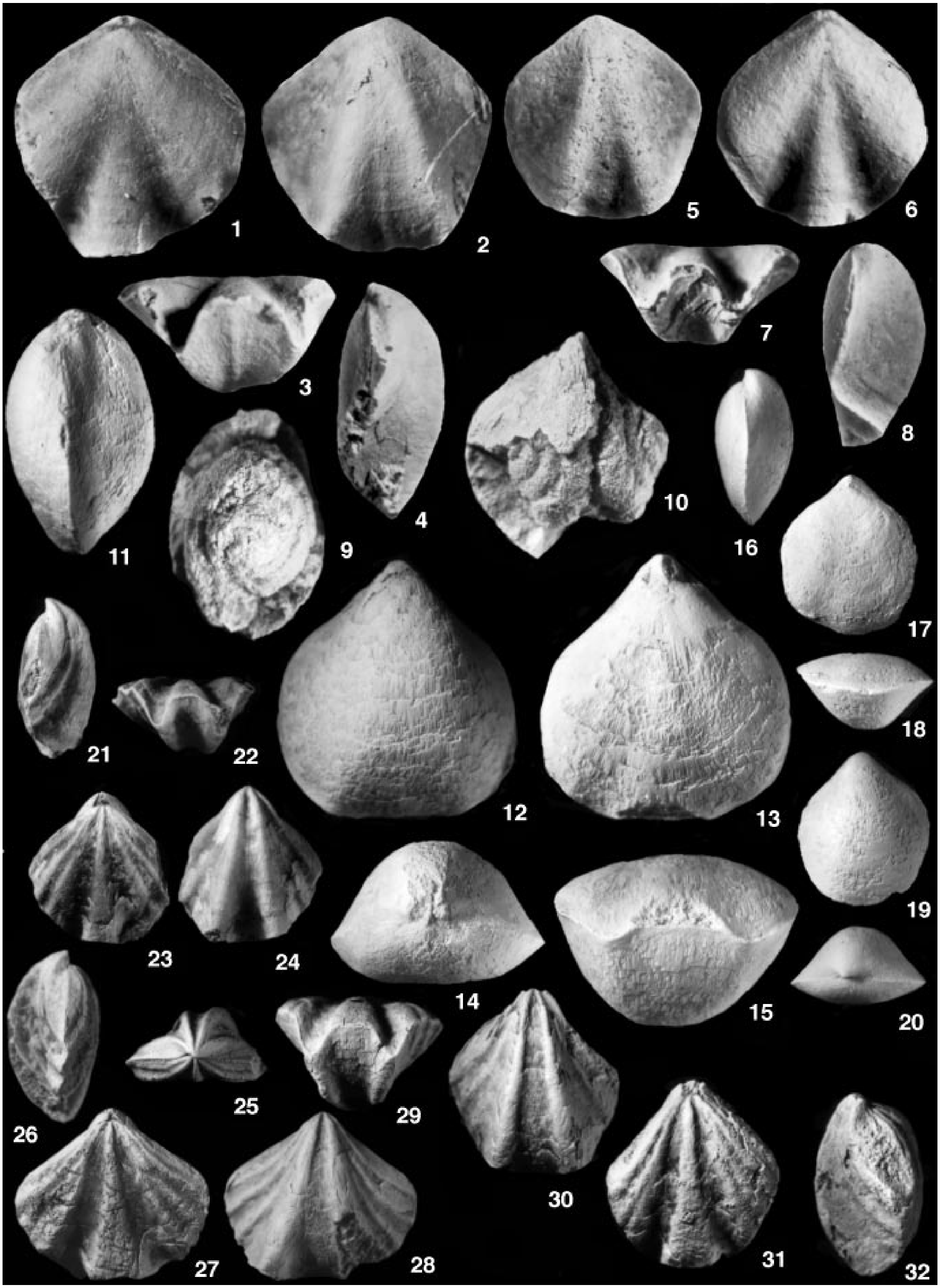
Diagnosis. Coarsely costate Protozygidae with a sharp ventral sulcus and dorsal median fold; anterior commissure parasulcate; spiralia planispiral with incomplete jugum located mediodorsally.

EXPLANATION OF PLATE 4

Figs 1–8. *Rozmanospira mica* (Nikitin and Popov, 1984); Tselinograd Regional Stage (Llandeilo–lower Caradoc), lower Bestamak Formation, locality 564, east side of River Chagan near Bestamak, Chingiz Range, Kazakhstan. 1–4, CNIGR 198/12095, holotype; dorsal, ventral, anterior and lateral views of conjoined valves. 5–8, CNIGR 197/12095; ventral, dorsal, anterior and lateral views of conjoined valves. All ×10.

Figs 9–20. *Kellerella misiusi* sp. nov.; Anderken Regional Stage (lower–middle Caradoc), Anderken Formation, locality 2538, Anderkenyn-Akchoku valley, Chu-Ili Range, south Central Kazakhstan. 9–10, CNIGR 28/12986; lateral and ventral views of incomplete shell showing spiralia. 11–15, CNIGR 26/12986, holotype; lateral, ventral, dorsal, posterior and anterior views of conjoined valves. 16–20, CNIGR 27/12986; lateral, dorsal, anterior, ventral and posterior views of conjoined valves. All ×4.

Figs 21–32. *Pectenospira pectenata* gen. et sp. nov.; locality as for figs 9–20. 21–25, CNIGR 23/12986, holotype; lateral, anterior, dorsal, ventral, and posterior views of conjoined valves. 26–28, CNIGR 24/12986; lateral, dorsal and ventral views of conjoined valves. 29–32, CNIGR 25/12986; anterior, ventral, dorsal and, lateral views of conjoined valves. All ×4.



POPOV *et al*., Ordovician brachiopods

Remarks. This group resembles other Protozygidae mainly in characters of internal morphology, including the simple, medially oriented spiralia of two whorls and a centrodorsal incomplete jugum. However, the new subfamily is unique within the superfamily Lissatrypoidea in having radial ornament of coarse, angular ribs on the shell flanks. There is also some similarity to the external morphology of juvenile shells of some primitive atrypidines of the subfamily Spirigerininae. The main difference of this new subfamily is that the planispiral brachial supports with mediodorsal location of the jugum persisted in mature stages of growth, and the absence of radial ornament in the ventral sulcus and on the dorsal median fold.

Genus PECTENOSPIRA gen. nov.

Derivation of name. Latin, *pecten* (comb) and *spira*, (spire or coil).

Type species. *Pectenospira pectenata* sp. nov., lower Caradoc, Anderken Formation, Chu-Ili Range, south Kazakhstan.

Diagnosis. Protozygide with ventribiconvex, acuminate shell and parasulcate anterior commissure; ventral valve moderately convex with an acute, posteriorly directed beak; sharp ventral sulcus originating near the umbo and bounded by strong, angular ribs; dorsal valve gently convex with narrow, rounded median fold originating at the umbo and bounded by sharp angular plications; sulcus and fold smooth, flanks coarsely costate; ventral interior with teeth and fine dental plates; dorsal interior with disjunct hinge plates and short, subparallel, anterodorsally directed crura; spiralia with two whorls and with apices directed internally to the plane of symmetry; jugal processes thick, disjunct, situated centrodorsally.

Species assigned. Type species only.

Species questionably assigned. *Spirigerina minima* Severgina, 1972; *Cyclospira tetraplicata* Fu, 1982.

Remarks. The simple brachidium of *Pectenospira* suggests an affinity with *Manespira* (Copper 1986, p. 839); however, *Pectenospira* is unique in having coarsely costate valve flanks, a parasulcate anterior commissure, and a mediodorsally placed, disjunct jugum.

There is some similarity in external morphology between *Pectenospira* and *Antizygospira* (Fu 1982), but mature specimens of *Antizygospira liquanensis* Fu, 1982, the type species of the genus (as revised by Zhan and Cocks 1998, p. 58), differs in having a larger number of ribs (up to 14) branching at about mid-length, and well developed deltidial plates. The taxonomic position of *Antizygospira* remains uncertain because of the absence of information on the morphology of the brachial supports. Zhan and Cocks (1998) assigned it to Zygospiridae (= Anazygidae after Copper 1986). Our observations suggest that a parasulcate anterior commissure, dorsal median fold, and ventral sulcus are characteristics of the Ordovician atrypidines but not of the anazygidines. The small size and co-occurrence of *Antizygospira* and *Eospirigerina* is also remarkable; there is a possibility that *Antizygospira* is based on immature specimens of the former genus.

Pectenospira pectenata gen. et sp. nov.

Plate 4, figures 21–32, Text-figure 10; Table 3

Derivation of name. Latin, *pectenatus* (comb-like).

Holotype. CNIGR 23/12986, complete shell (Lv = 6·9, W = 5·3, T = 4·3).

Type locality. Upper Anderken Formation (lower to middle Caradoc), sample 2538, Kujandysai section, southern Chu-Ili Range (for details see Kolobova and Popov 1986).

Material and stratigraphical range. Figured: complete shells, CNIGR 24/12986 (Lv = 5·8, W = 5·2, T = 3·7), 25/12986; total of seven complete shells, two ventral and one dorsal valves.

This is a relatively rare species, occurring in pockets of bioclastic limestone within the core of carbonate mud mounds in the upper part of the Anderken Formation and usually associated with a diverse assemblage of trilobites, brachiopods and echinoderms (Kolobova and Popov 1986, table 1). In the southern Chu-Ili Range outside of the type locality it is also recorded from the Anderken Formation of the Anderkenyn-Akchoku section (localities 626 and 628 in Unit 4 of Nikitin 1972, p. 75, fig. 13).

Diagnosis. *Pectenospira* with strongly ventribiconvex, slightly elongate shell about two-thirds as thick as long, with three or four strong angular ribs on the shell flanks; dorsal median fold rounded in cross section, higher than coarse inner ribs of valve flanks.

Description. Ventribiconvex, acuminate, slightly elongated, rounded sub-pentagonal in outline, about 106 per cent. as long as wide and 64 per cent. as high as long. Anterior commissure parasulcate. Ventral valve moderately and evenly convex with a small acute beak slightly curved dorsally and a small, triangular open delthyrium. Sulcus narrow, originating at the umbo, bounded laterally by high, angular plications and ending in a low, semi-oval tongue. Dorsal valve gently convex with a sharp median fold, rounded in cross section and originating at the umbo. Sulcus and fold smooth, flanks with three or four strong, angular costae. Interior of both valves and spiralia as for genus.

TABLE 3. Measurements of six shells of *Pectenospira pectenata* gen. et sp. nov. from the Anderken Formation, Anderkenyn-Akchku valley, Chu-Ili Range.

	Lv	W	T	Lv/W	T/Lv
N	6	6	6	6	6
X	6·0	5·8	3·8	106%	64%
S	1·13	1·49	0·65	15	6
min.	3·9	3·4	2·8	92%	54%
max.	6·9	7·3	4·7	130%	72%

Remarks. This species closely resembles *Cyclospira tetraplicata* Fu, 1982 (p. 165, pl. 5, fig. 7), from the middle Caradoc of North China, but differs in having a rounded dorsal fold and ventral tongue which only exceeds the level of the coarse ribs flanking the fold in mature specimens, whereas in the Chinese species the dorsal fold and ventral tongue are angular and somewhat higher.

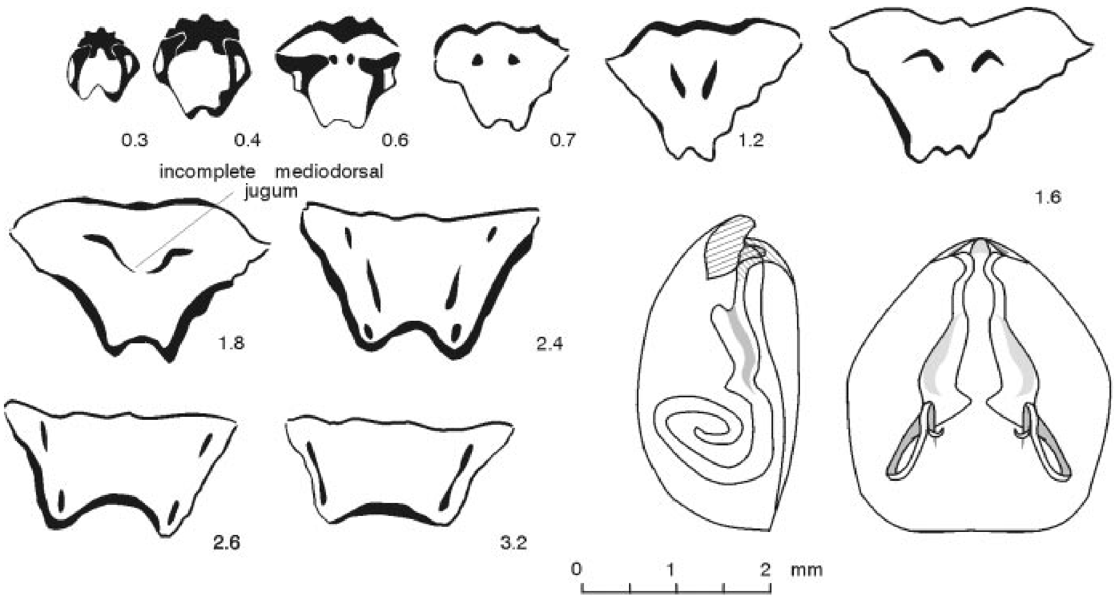
Another similar species is *Spirigerina*? *minima* (Severgina, 1972) from the Orlov Formation of Altai, but its brachidium remains unknown and available data on its morphology are not satisfactory for precise comparison. The Kazakhstanian species differs in having a strongly ventribiconvex shell and only a slightly convex dorsal valve lateral profile with maximum height about mid-way between the umbo and mid-valve length.

Order ATHYRIDIDA Boucot, Johnson and Staton, 1964
Suborder ATHYRIDIDINA Boucot, Johnson and Staton, 1964
Superfamily MERISTELLOIDEA Waagen, 1883
Family MERISTELLIDAE Waagen, 1883

Genus KELLERELLA Nikitin and Popov, *in* Nikitin *et al.*, 1996

Type species. *Kellerella ditissima* Nikitin and Popov, 1996, p. 94, figs 8K–W, 9; Dulankara Regional Stage (upper Caradoc), northern Bandpak-Dala desert, central Kazakhstan.

Diagnosis. See Nikitin *et al.* (1996, p. 93).



TEXT-FIG. 10. Serial sections and reconstruction of spiralia and jugum in *Pectenospira pectenata* gen. et sp. nov. from a specimen from locality 2538, Kujandysai section, Chu-Ili Range, upper Anderken Formation, Anderken Regional Stage (lower–middle Caradoc). Sections with dorsal valve uppermost.

Species assigned. *Kellerella misiusi* sp. nov.; *Kellerella ditissima* Nikitin, *in* Nikitin *et al*., 1996.

Remarks. Fu (1982) suggested that *Apheathyris* and *Weibiella* from the upper Caradoc of China may represent one of the oldest known athyridides. However, interiors and characters of the brachidium remain inadequately known in these taxa and in the latest revision of the classification of the order Athyridida by Alvarez *et al.* (1998, p. 829) they were regarded as spire-bearing brachiopods of uncertain affinity. *Kellerella* differs from *Apheathyris* and *Weibiella* in having a strongly ventribiconvex elongated shell and weakly parasulcate anterior commissure. *Kellerella* possesses well developed dental plates which are completely absent in *Weibiella* (Fu 1982, text-fig. 84).

Kellerella misiusi sp. nov.

Plate 4, figures 9–20, Text-figure 10; Table 4

Derivation of name. After P. P. Misius.

Holotype. CNIGR 26/12986, complete shell (Lv = 10·3, W = 9·4, T = 6·7, Sw = 4·6).

Type locality. Upper Anderken Formation (lower to middle Caradoc), sample 2538, Kujandysai section, southern Chu-Ili Range (for details see Kolobova and Popov 1986).

Material and stratigraphical range. Figured; complete shells, CNIGR 27/12986 (Lv = 5·3, W = 4·6, T = 2·6, Sw = 2·5), 28/12986; total of 76 complete shells. This is one of the most common fossils in pockets of bioclastic limestone within the core of carbonate mud mounds in the upper part of the Anderken Formation (Kolobova and Popov

1986, table 1). In the southern Chu-Ili Range outside the type locality it is also recorded from the Anderken Formation of the Anderkenyn-Akchoku section (locality 626 in Unit 4 of Nikitin 1972, p. 75, text-fig. 13).

Diagnosis. Small *Kellerella* with very short jugal processes and spiralia with up to three whorls.

Description. Shell strongly ventribiconvex, slightly elongated, rounded sub-triangular to sub-pentagonal in outline, about 114 per cent. as long as wide and 61 per cent. as thick as long. Anterior commissure weakly parasulcate. Ventral valve subcarinate posteriorly, strongly and evenly convex in lateral profile. Ventral beak slightly acute, pointed, strongly curved dorsally. Delthyrium narrow, lacking deltidial plates. Shallow sulcus originates near the mid valve. Tongue low, trapezoidal, about 52 per cent. as wide as the valve. Dorsal valve evenly and gently convex, somewhat flattened anteriorly with a low, flattened median fold anterior to mid-length. Ventral interior with delicate teeth and small dental plates situated close to the lateral margins of the valve. Dorsal interior with small, disjunct hinge plate, delicate, anteriorly directed, slightly divergent crura and a fine, faint median ridge bisecting the adductor muscle field. Spiralia of three whorls with laterally directed apices and vestigial jugal processes near the base of the first spiralial whorls.

TABLE 4. Measurements of five shells of *Kellerella misiusi* sp. nov. from locality 2538, Anderken Formation, Kujandysai, Chu-Ili Range.

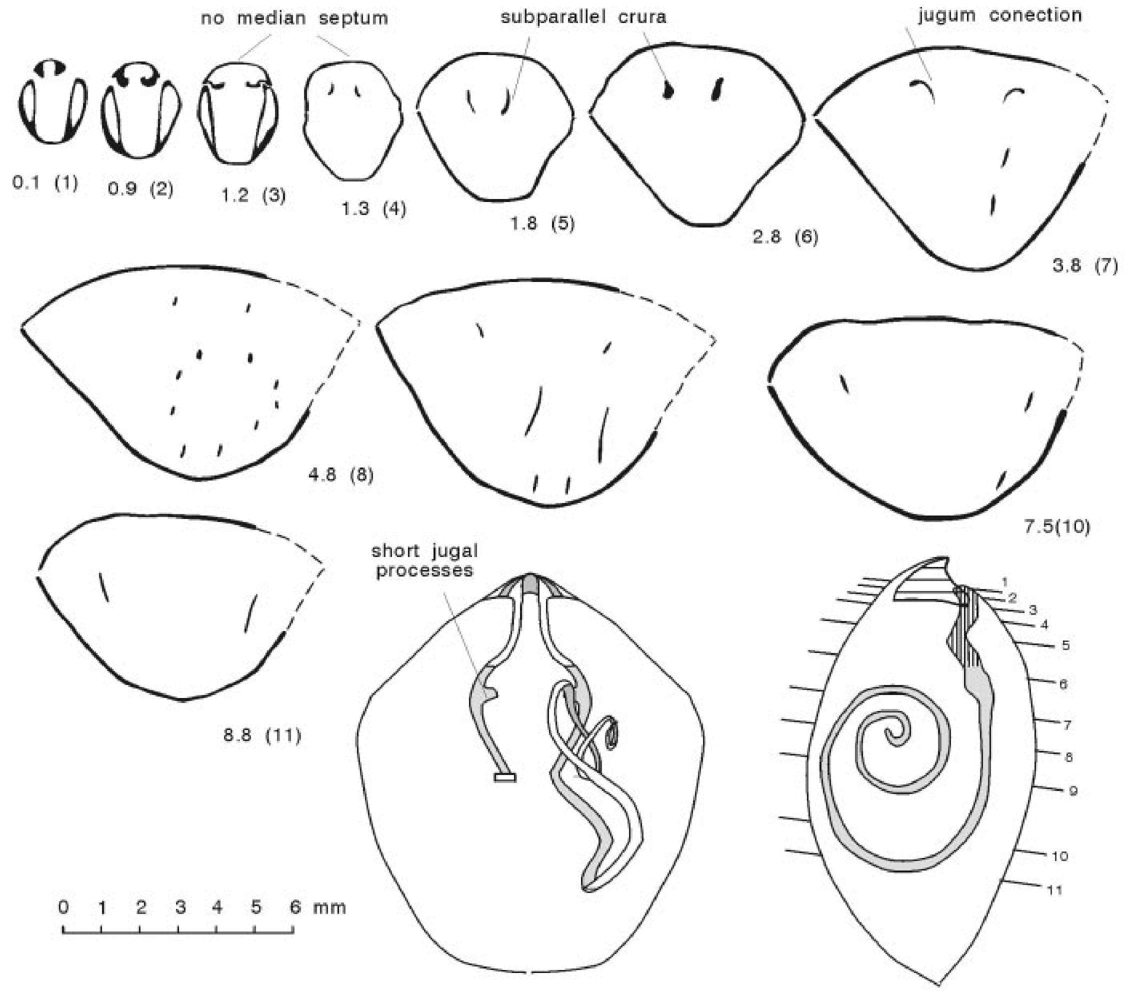
	L	W	T	Sw	L/W	T/L	W/Sw
N	5	5	5	5	5	5	5
X	8·04	7·06	5·12	3·72	114%	61%	52%
S	2·27	2·27	2·04	2·264	1·30	4·3	13·2
min.	5·3	4·6	2·6	2·2	110%	49%	42%
max.	10·3	9·4	7·6	4·8	121%	81%	60%

Remarks. This species differs from *Kellerella ditissima* Nikitin and Popov, *in* Nikitin *et al.,* 1996 (Text-fig. 12) in its somewhat smaller size which does not usually exceed 10 mm, in having a slightly more elongated shell, spiralia with only three whorls, and very short jugal processes.

PHYLOGENETIC ANALYSIS

Outgroup selection. It is generally agreed that rhynchonellides formed the ancestral stock for early spire-bearing brachiopods (Copper 1986; Copper and Gourvenenc 1996). The oldest known astrophic rhynchonelliformean stock with cyrtomatodont teeth and disjunct hinge plates is from the Llanvirn (Jin 1996). The earliest known atrypides (e.g. *Manespira* and *Rozmanospira*) are characterized by a smooth shell with an open, narrow, triangular delthyrium, disjunct hinge plates, and they also lack a median septum and cruralium. They share these features with smooth rhynchonellides of the family Oligorhynchidae, known in North America from the Caradoc (Cooper 1956; Jin 1996). Undescribed oligorhynchids are also present in the Tselinograd Regional Stage (Llandeilo–lower Caradoc) of Kazakhstan. Therefore, early rhynchonellides of the families Ancistrorhynchidae (*Ancistrorhyncha modesta* Popov, *in* Nikiforova and Popov, 1981) and Oligorhynchidae (*Oligorhyncha subplana* Cooper, 1956) are selected here as outgroup stocks. *Eospirifer praecursor* Rong, Zhan and Han, 1994 from the middle Ashgill of South China was also included in order to evaluate affinities with the earliest eospiriferides.

Methods. Data were analysed for all 11 species of athyridides and atrypides recorded in the Llandeilo–Caradoc (Tselinograd, Anderken and Dulankara regional stages) of Kazakhstan, together with the Rhuddanian *Eospirigerina porkuniana* (Jaanusson, *in* Rubel, 1970) from the Porkuni Regional Stage of Estonia). Two atrypide species from the middle Ashgill of South China, three atrypide species from the upper Ordovician of Australia, and five species of early atrypides from North America were also included: they are *Anazyga recurvirostra, Antizygospira liquanensi, Australospira districha*, *Cyclospira bisulcata*,



TEXT-FIG. 11. Serial sections and reconstruction of spiralia and jugum in *Kellerella misiusi* sp. nov. from a specimen from locality 2538, Kujandysai section, Chu-Ili Range, upper Anderken Formation, Anderken Regional Stage (lower–middle Caradoc). Sections with dorsal valve uppermost.

Manespira nicoletti, *Protozyga exigua*, *Protozyga definitiva*, *Sulcatospira dichotoma*, *Webbyspira principalis* and *Zygospira modesta*. Detailed morphological descriptions and illustrations of the listed North American species were published by Cooper (1956) and Copper (1977, 1986), whilst Australian and Chinese species were described by Percival (1991), and by Zhan and Cocks (1998), respectively. These publications provide the main source of information used in the phylogenetic analysis.

The data matrix (Table 5) derived from our selection of what we take to be taxonomically significant characters (Appendices 1 and 2) has been analysed cladistically using the PAUP programme (Phylogenetic Analysis Using Parsimony; Swofford 1993). A total of 99 character states was determined for 27 unordered and unweighted characters. For these data, a heuristic search was performed using global swapping with the MULPARS option.

Results. A single shortest tree was generated, 137 steps long and with a consistency index of 0·537,

TABLE 5. Character state matrix for analysis of taxa, as discussed in the text.

	1 prs	2 anc	3 out	4 rom	5 cor	6 vbk	7 vsc	8 vfd	9 pvl	10 ars	11 dsc	12 dfd	13 pdl	14 vtg	15 dtg	16 pop	17 msz	18 dms	19 csp	20 bsp	21 nrw	22 jug	23 jpr	24 scj	25 psl	26 cpr	27 pmg
Ancistrorhyncha modesta	2	4	1	1	0	1	1	0	1	0	1	2	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0
Oligorhyncha subplana	2	3	3	0	0	0	1	0	2	0	2	2	2	3	2	0	0	0	0	0	0	0	0	0	0	0	0
Rozmanospira mica	1	3	0	0	0	1	2	0	2	1	1	2	2	3	2	0	0	0	1	1	1	1	1	1	1	0	0
Cyclospira bisulcata	1	2	0	0	0	2	2	0	2	0	1	2	2	3	2	2	1	1	1	1	2	1	1	1	1	0	0
Pectenospira pectenata	1	3	0	5	0	0	2	0	2	0	1	2	2	3	2	1	0	0	1	1	2	2	4	5	1	0	0
Protozyga exigua	1	1	1	6	0	1	0	1	0	0	3	0	0	0	1	1	0	0	1	1	2	3	5	3	2	0	0
Manespira nicoletti	1	3	1	6	0	1	2	3	1	0	2	2	1	3	2	1	0	0	1	1	1	2	4	5	1	0	0
Anazyga recurvirostra	1	1	0	1	0	1	0	2	0	1	2	0	0	0	1	0	1	0	1	4	3	3	5	2	3	0	0
Zygospira modesta	1	1	0	1	0	1	0	1	0	0	2	0	0	0	1	0	1	0	1	3	2	3	5	4	3	0	0
Kellerella ditissima	1	3	0	0	0	1	2	0	1	0	0	1	1	2	0	0	2	0	1	2	3	2	3	5	1	0	0
Kellerella misiusi	1	3	0	0	0	1	2	0	1	0	0	1	1	2	0	0	1	0	1	2	2	2	3	5	1	0	0
Nikolaespira rasilis	1	3	0	0	0	1	2	0	2	1	0	1	2	2	0	0	1	1	1	2	3	2	3	5	1	0	0
Sulcatospira? praecursor	1	3	0	2	?	1	2	0	2	2	1	2	2	1	0	0	1	0	1	?	?	?	?	?	?	0	0
Sulcatospira asiatica	1	4	1	2	1	1	2	0	2	2	1	2	2	2	0	0	2	0	1	3	4	2	3	5	2	0	0
Schachriomonia parva	1	4	1	1	1	1	2	0	1	2	1	2	1	2	0	0	2	0	1	3	4	2	2	5	3	0	0
Sulcatospira prima	1	4	1	1	1	1	2	0	2	2	1	2	2	2	0	0	2	0	1	3	3	2	2	5	3	0	0
Eospirigerina pennata	0	4	2	2	1	1	2	0	2	0	1	3	1	2	0	0	2	0	1	3	4	2	3	5	3	0	0
Qilianotryma suspectum	0	4	2	4	1	1	1	0	2	2	1	2	1	1	0	0	3	0	1	3	4	2	3	5	3	0	0
Eospirigerina porkuniana	0	4	2	3	1	2	1	0	2	0	1	3	1	2	0	1	3	0	1	3	4	2	3	5	3	0	0
Antizygospira liquanensis	1	3	0	3	1	0	2	0	2	0	1	2	2	3	0	2	1	0	1	?	?	?	?	?	2	0	0
Schachriomonia dichotoma	1	4	1	1	1	1	2	0	1	2	1	2	1	2	0	2	2	0	1	?	?	?	?	?	3	0	0
Australospira districha	2	3	1	3	?	1	1	0	1	1	0	3	1	2	0	1	3	1	1	3	4	2	3	5	3	0	0
Webbispira principalis	0	4	2	3	?	2	1	0	2	1	0	1	2	1	0	0	3	0	1	3	4	2	3	5	3	0	0
Protozyga definitiva	1	1	0	0	0	1	0	1	0	0	2	0	0	0	2	1	0	0	1	1	1	?	?	?	?	0	0
Eospirifer praecursor	1	4	0	7	0	2	1	0	2	0	0	3	2	2	0	1	0	0	1	2	2	2	3	5	1	1	1

homoplasy index of 0·463, and rescaled consistency index 0·362. The resulting cladogram contains four groups of taxa: (1) the outgroup represented by the rhynchonellides *Ancistrorhyncha modesta* and *Oligorhyncha subplana*; (2) taxa of the atrypide suborders Lissatrypidina and Anazygidina; (3) the atrypide suborder Atrypidina together with earliest Athyridida; and (4) the earliest spiriferide *Eospirifer praecursor*, which is recognized as a sister stock of all other spire-bearing brachiopods.

All brachiopods with calcified brachial supports are recognized in the analysis as a monophyletic group. The validity of the Spiriferida is supported in Text-figure 2 by Node 1. The ancestral stock is recognized as a small (< 5 mm long), smooth, ventribiconvex spire-bearer with a parasulcate anterior commissure, a ventral sulcus originating in the umbonal area, a dorsal median fold reverted from an umbonal dorsal sulcus, an open delthyrium lacking deltidial plates, and a pointed beak erected slightly posteriorly. Calcified brachial supports of two or three whorls with subparallel, slightly divergent primary lamellae, and short, posteroventrally located jugal processes can also represent synapomorphies for all spire-bearing brachiopods. These features characterize the earliest Lissatrypidina (e.g. family Protozygidae and subfamily Cyclospirinae), which can be regarded as a possible stem group for all early Palaeozoic brachiopods with calcified brachial supports.

Monophyly of all other Ordovician atrypide suborders and early athyridides finds relatively weak support in the analysis (Node 2, Text-fig. 3) from a single symplesiomorphy, a ventral sulcus originating anterior to the umbo (character 7, state 2; see Appendix). Subsequent radiation included separation of two major subclades. One includes the lissatrypide families Cyclospiridae, Protozygidae and the suborder Anazygidina (Node 3, Text-fig. 3), which are characterized by such synapomorphies as a complicated fold-sulcus (14:3) and planospiral brachial supports lacking jugal processes (20:1, 23:1). All of these features are retained in early Cyclospirinae which are characterized by the absence of a jugum (Node 4, Text-fig. 3).

All North American middle Ordovician atrypides of the family Protozygidae and superfamily Anazygoidea also form a monophyletic clade according to the analysis (Node 6, Text-fig. 3). Such features as a smooth shell with faint trace of ribs (4:6), a ventral median fold originating anterior to the umbo (8:1, 9:0), a dorsal sulcus originating near the umbo and extending to the anterior margin (11:2, 13:0), and spiralia with a single whorl (21:1) represent symplesiomorphies of this subclade. Subsequent divergence and changes in shell morphology of American protozyginidines and anazygidines derived from the analysis (nodes 7–9) fit very well into the phylogenetic model proposed by Copper (1977, 1986), and his proposal that mid Ordovician lissatrypoids represent the ancestral stock of all early North American spire-bearers also finds very good support in the combined analysis with Kazakhstanian taxa.

The earliest known Kazakhstanian Atrypidina and Athyridida form the second major subclade (Node 10, Text-fig. 3); however their divergence from a common ancestor is only very weakly supported by such features as a medium size of 5–10 mm (17:1) and spiralia with four to five whorls (21:3).

The only recognized symplesiomorphies of early athyridides (Node 11, Text-fig. 3) are: complete absence of a dorsal sulcus (11:0) and the origination of a dorsal median fold anterior to the umbo (12:1). Ventrolaterally directed spiralia may also be a morphological innovation that evolved independently from the early spiriferides and therefore represent a homoplasy which remains unrecognized in the present analysis.

With the exclusion of *Eospirifer praecursor* from the matrix, the number of shortest trees is increased up to eight, but athyridides appear as a sister stock of atrypidines in 75 per cent. of the trees.

The earliest atrypoids (Node 13, Text-fig. 3) are defined by such synapomorphies as: radial ornament costate on flanks and costellate on fold and sulcus (4:2); concentric ornament of evenly spaced, elevated fila (5:1); spiralial cones with five to eight whorls and with apices directed dorsomedially (20:3; 21:4); and primary lamellae of spiralia strongly divergent laterally (27:3).

The relatively high homoplasy index of 0·463 suggests that some important features of shell morphology and the brachidium evolved independently in various lineages of early spire-bearing brachiopods. In particular, the different kinds of radial ornament characteristic of the suborders Anazygidina, Atrypidina and the aberrant lissatrypidine *Pectenospira* evolved independently from the smooth prototype. Spiralia with widely divergent primary lamellae and dorso-medianly directed apices in the Anazygidina and Atrypidina probably also originated independently from primitive spire-bears with a planispiral brachidium.

DISCUSSION AND CONCLUSIONS

The above review and cladistic analysis of data indicate considerable revision of relationships between middle Ordovician members of the spire-bearing suborders Lissatrypidina, Anazygidina and Atrypidina, as well as with the earliest Athyridida. In particular, new material from Kazakhstan provides evidence that Athyridida (e.g. *Kellerella* and *Nikolaespira*) and Atrypidina (e.g. *Sulcatospira*? *praecursor* and *Sulcatospira prima*) appeared by the mid Caradoc and, therefore, do not represent direct descendants of the North American atrypide lineages, but more probably evolved independently from early lissatrypidines.

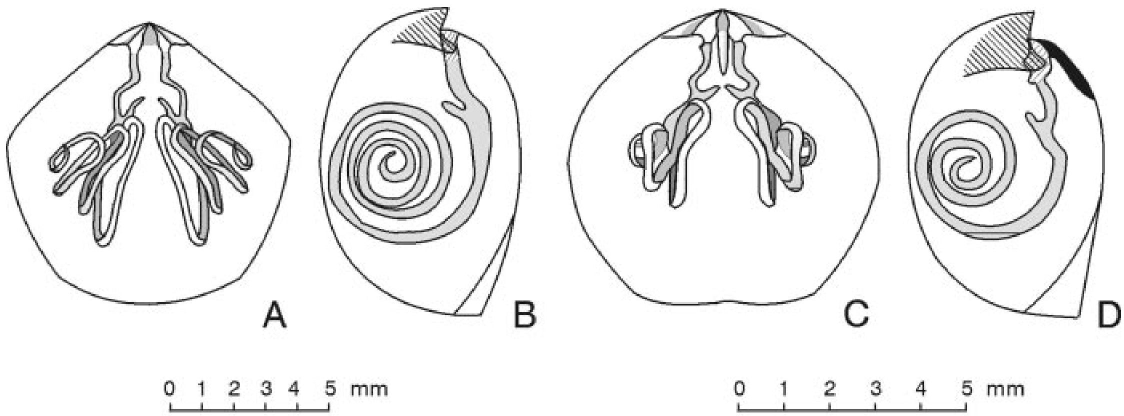
Such a feature of the early atrypidines and athyridides as a parasulcate anterior commissure does not represent a derived state, but can be symplesiomorphic, also recorded in early lissatrypidines (e.g. *Manespira* and *Rozmanospira*) and the rhynchonellide *Oligorhyncha*, but lost in the majority of North American Protozygidae and Anazygidina. A medio-dorsally located complete jugum in middle Ordovician spire-bearing groups from North America obviously represents a derived state in relation to *Cyclospira* and *Rozmanospira*, which lack a jugum or jugal processes. The occurrence of an incomplete medio-dorsal jugum in some of the earliest species of protozygidines, such as the North American *Manespira* and the Kazakhstanian *Pectenospira*, suggests that this feature probably evolved before migration of the ancestral lissatrypidine stock in North America (Node 5, Text-fig. 3).

The recent discovery of spiralia in late Ordovician Eospiriferinae by Rong and Zhan (1996) is important in helping to evaluate the relationships of the earliest spiriferides with other groups of Ordovician spire-bearers. There is no need here to discuss existing models for the origin and early evolution of spiriferides, as they have been covered in some detail in recent publications by Copper and Gourvennec (1996) and Rong and Zhan (1996). Presently available data provided in these publications strongly support the monophyletic nature of all early Palaeozoic spire-beraing brachiopods and disprove the earlier suggestion by Wright (1979), that spiriferides evolved independently from some orthides.

The most remarkable feature is the existence of two athyridide genera (*Kellerella* and *Nikolaespira*) in the middle and upper Caradoc of Kazakhstan. These demonstrate many similarities with *Eospirifer praecursor* in characters of the lophophore supports, which include ventrolaterally directed spiralia of three to five whorls and vestigial posteroventral jugal processes. All of these taxa also share such features as well developed dental plates and crura lacking brachial plates. Juvenile shells of *E. praecursor* (Rong and Zhan 1996, text-fig. 27A–C) closely resemble *Kellerella* and *Nikolaespira* in having a slightly elongated astrophic shell with a parasulcate anterior commissure and a low, flattened dorsal median fold originating near mid-valve. However, adult *E. praecursor* has a strophic shell and fine radial ornament, which are significant differences from primitive Kazakhstanian athyridides. *Nikolaespira* is characterized by the acquisition of a dorsal median septum and cruralium, which are characters of the derived Ordovician athyridides. By contrast, *Kelerella* and *Eospirifer praecursor* lack a dorsal median septum and cruralium. It is very likely that *Kellerella* and *Nikolaespira* are phylogenetically close to the point of divergence of major athyridide and spiriferide lineages; however, both genera remain very close morphologically to the lissatrypidines and can be classified as primitive athyridides because they have a smooth, astrophic shell and a brachidium with ventrolaterally directed spiralia (Text-fig. 12).

The observed affinities in the shell morphology, as well as in characters of brachidium and jugal processess discussed below, provide the evidence that both athyridides and sperifirides evolved from some early smooth lyssatrypidine characterized by planospiral brachidium with short, separated jugal processes located dorsomedially. The spiralial cones with apices directed laterally can be potentially a synapomorphy which unites these two orders, but it is equally possible that this feature had evolved independently in both lineages.

The rudimentary jugal processes of juvenile *E. praecursor* (Rong and Zhan 1996, text-fig. 5A) tend to occupy a medio-dorsal position, which demonstrates a distinctive affinity with the separated jugal processes of the primitive protozygids *Manespira* and *Pectenospira*. Data from Copper (1986) clearly suggest that the complete jugum of more derived Protozygidae (e.g. *Protozyga*) and all Anazygidina evolved directly from this pattern. The jugal processes of adult *E. praecursor* migrated posteriorly (Rong and Zhan 1996, text-fig. 5B) and are located at about the same level as the posterior parts of the second



TEXT-FIG. 12. Reconstruction of spiralia and jugum in some early athyridids from the Dulankara Regional Stage of northern Bandpak-Dala, central Kazakhstan. A–B, *Kellerella ditissima* Nikitin and Popov, 1996, ventral view, lateral view; C–D, *Nikolaespira rasilis* Nikitin and Popov, 1996, ventral view, lateral view.

spiral whorls. This species is closely comparable to *Kelerella misiusi* in the position and rudimentary character of the jugal processes (Text-fig. 11).

The jugal processes in the early atrypoids *Sulcatospira* and *Qilianotryma* are also situated near the proximal ends of the first spiralial lamellae, which may suggest that the complicated jugum of derived athyridides and the disjunct jugal processes of atrypoids are homologous. However, similarities in characters of the complete jugum of *Protozyga* and some late Ordovician athyridides (e.g. *Hindella*) may suggest that the order Athyridida is paraphyletic and unites descendants of different lineages of lissatrypidines.

It is remarkable that the earliest occurrences of all major stocks of Ordovician spire-bearing brachiopods, including the atrypide suborders Lissatrypidina and Atrypidina as well as the orders Athyridida and Spiriferida, have been reported from Kazakhstanian terranes and South and North China. It is most probable that all these regions, which were located somewhere between equatorial Gondwana and the Baltic Plate in the Caradoc (Jaanusson 1979; Popov *et al*. 1997), represent the locus for the origin and initial radiation of the earliest spire-bearing brachiopods. The middle Ordovician (Caradoc) atrypide fauna of North America is unique in its abundance of early protozygides and anazygidines and evolved in geographical isolation. The diachronous appearance of cyclospirines (late Caradoc) and atrypidines (mid Ashgill) in North America clearly suggests subsequent immigration from peri-Gondwanan island arcs and microplates, where these taxa originally evolved.

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APPENDIX 1

Characters and character states in phylogenetic analysis

1. prs - profile (sagittal): dorsibiconvex (0), ventribiconvex (1), biconvex (2)
2. anc - anterior commissure (in adults): rectimarginate (0), unisulcate (1), parasulcate (2), paraplicate (3), uniplicate (4).
3. out - outline: slightly elongate (0), isometric (1), slightly transverse (2), elongate, acuminate (3).
4. rom - radial ornament: smooth (0), costate (1), costate on flanks, costellate on fold and sulcus (2), costellate (3), finely and equally multicostellate (4), smooth on fold and sulcus, costate on flanks (5), smooth with faint trace of ribs at commissure (6).
5. cor - concentric ornament: growth lines only (0), evenly spaced elevated fila (1), lamellose (2).
6. vbk - ventral beak: acuminate, erect posteriorly (0), pointed, slightly extended posteriorly (1), curved dorsally, swollen (2).
7. vsc - ventral sulcus: not developed (0), originating near umbo and extended to anterior margin (1), originating anterior to umbo (2)
8. vfd - ventral median fold: not developed (0), originating anterior to umbo (1), carinate posteriorly (2).
9. pv1 - plications, laterally bounding ventral sulcus: no ventral sulcus (0), absent (1), present (2).
10. ars - accentuated ventral median costa: absent (0), occasionally present (1), present (2).
11. dsc - dorsal sulcus: not developed (0), present in umbonal region only (1), originating near umbo and extending to the anterior margin (2), originating anterior to umbo (3).
12. dfd - dorsal median fold: not developed (0), originating anterior to umbo (1), reversed from umbonal sulcus (2), originating from umbo (3).
13. pd1 - plications, laterally bounding dorsal median fold: no dorsal median fold (0), absent (1), present (2).
14. vtg - ventral tongue: not developed (0), trapezoidal (1), rounded (2), other (3).
15. dtg - dorsal tongue: not developed (0), rounded (1), other (2).
16. pop - pedicle opening: delthyrial (0), bounded laterally by deltidial plates (1), foramen (2).
17. msz - medium size: less than 5 mm (0), 5–10 mm (1), 10–15 mm (2), 15–20 mm (3).
18. dms - dorsal median septum supporting cruralium: absent (0), present (1).
19. csp - calcified brachial supports: absent (0), present (1).

20. bsp - spiralia: absent (0), planispiral (1), cones with apices directed laterally (2), cones with apices directed dorsomedially (3), cones with apices directed medially (4).
21. nrw - number of whorls: no skeletal supports (0), one (1), two or three (2), four or five (3), six to eight (4).
22. jug - jugum: no skeletal supports (0), not developed (1), separated jugal processes (2), complete jugum (3).
23. jpr - jugal processes (if present): no skeletal supports (0), absent (1), short, connected with strongly thickened proximal parts of primary lamellae (2), disjunct, located posteroventrally (3), disjunct, located medio-dorsally (4), other (5).
24. scj - single complete jugum (if present): no skeletal supports (0), absent (1), located posterodorsally (2), located dorso-medially, ventrally directed (3), located dorso-medially, incurved, posteroventrally directed (4), not developed (5).
25. psl - primary spiralial lamellae: no skeletal supports (0), located dorsomedially, subparallel or slightly divergent (1), divergent, submedian in proximal parts, widely divergent distally (2), strongly divergent laterally (3).
26. cpr - cardinal process: absent (0), present, striated (1).
27. pmg - posterior margin: astrophic (0), strophic (1).

APPENDIX 2

List of synapomorphies supporting the numbered nodes in Text-figure 2. Characters and character states are marked as in Appendix 1 and Table 1.

Node 1. Ventribiconvex shell (1:1); calcified lophophore supports (19:1); brachial supports two or three whorls (21:2); separated jugal processes located posteroventrally (22:2, 23:3, 24:5); primary lamellae of spiralia subparallel or slightly divergent (25:1).
Eospirifer praecursor. Uniplicate anterior commissure (2:4); radial ornament of fine capillae (4:7); ventral beak curved dorsally, swollen (6:2); dorsal sulcus not developed (11:0); dorsal median fold originating from umbo (12 :3); delthyrium with separated deltidial plates (16:1); strophic posterior margin (26:1); striated cardinal process (27:1).
Node 2. Ventral sulcus originating anterior to umbo (7:2);
Node 3. (Suborders Lissatrypidina and Anazygidina). Variably developed ventral or dorsal tongue (14:3), (15:2), planospiral brachial supports (20:1); jugal processes absent (23:1)
Node 4. (Family Cyclospiridae). Jugum not developed (22:1; 24:1).
Cyclospira bisulcata. Anterior commissure (in adults) plicosulcate (2:2); ventral beak curved dorsally, swollen (6:2); pedicle foramen (16:2); medium size 5–10 mm (17:1); dorsal median septum supporting cruralium present (18:1).
Rozmanispira mica. Accentuated ventral median costa occasionally present (10:1); spiralia with a single whorl (21:1).
Node 5. Families Anazygidae and Protozygidae. Shell smooth in fold and sulcus, costate on flanks (4:5); delthyrium with separated deltidial plates (16:1); disjunct jugal processes located mediodorsally (23:4).
Pectenospira pectenata. Ventral beak acuminate, erect posteriorly (6:0).
Node 6. Smooth with faint trace of ribs at commissure (4:6); ventral median fold originating anterior to umbo (8:1, 9:0); dorsal sulcus originating near umbo and extending to anterior margin (11:2, 13:0); spiralia with single whorl (21:1).
Node 7. Unisulcate anterior commissure (2:1); ventral sulcus not developed (7:0); dorsal median fold absent (12:0); ventral tongue not developed (14:0); complete jugum located posterodorsally (22:3, 23:5, 24:2).
Node 8. Dorsal tongue rounded (15:1); number of whorls two or three (21:2).
Node 9. Family Anazygidae. Costate radial ornament (4:1); delthyrium without deltidial plates (16:0); medium size 5–10 mm (17:1); cones of spiralia with apices directed dorsomedianly (20:3); primary lamellae of spiralia strongly divergent laterally (25:3).
Node 10. Medium size 5–10 mm (17:1); number of whorls four or five (21:3).
Node 11. Order Athyridida. Dorsal sulcus not developed (11:0); dorsal median fold not developed (12:1).
Nikolaespira rasilis. Accentuated ventral median costa occasionally present (10:1); dorsal median septum supporting cruralium (18:1).
Node 12. (*Kellerella*). Plications bounding ventral sulcus and dorsal median fold absent (9:1, 13:1).
Kellerella ditissima. Medium size 10–15 mm (17:2).
Kellerella misiusi. Number of whorls two or three (21:2).
Node 13. Suborder Atrypidina. Costate on flanks, costellate in fold and sulcus (4:2); concentric ornament of evenly spaced elevated fila (5:1); spiralial cones with apices directed dorsomedially (20:3); number of whorls six to eight (21:4); primary lamellae submedial in proximal parts, widely divergent laterally (25:2).
Antizygospira liquanensis. Radial ornament costellate (4:3); ventral beak acuminate, erect posteriorly (6:0); variably developed ventral tongue (14:3); pedicle foramen (16:2).

Node 14. Accentuated ventral median costa present (10:2).
Sulcatospira praecursor. Ventral tongue trapezoidal (14:1).
Node 15. Anterior commissure uniplicate (2:4); isometric shell outline (3:1); medium size 10–15 mm (17:3).
Sulcatospira asiatica. No apomorphic characters recognized.
Node 16. Plications, laterally bounding the dorsal median fold absent (13:1); primary lamellae of spiralia strongly divergent laterally (25:3).
Node 17. Radial ornament costate (4:1), jugal processes vestigial, developed as strong thickening of the base of spiralia (23:2).
Sulcatospira prima. Plications, laterally bounding the dorsal median fold present (13:2); number of whorls four or five (21:3).
Node 18. *Schachriomonia*. Plications, laterally bounding ventral sulcus, absent (9:1).
Schachriomonia parva. No apomorphic characters recognized.
Schachriomonia dichtoma. Pedicle foramen (16:2).
Node 19. Shell dorsibiconvex (1:0); slightly transverse shell outline (3:2); ventral sulcus originating near umbo and extending to anterior margin (7:1); medium size > 15 mm (17:3).
Qilianotryma suspecta. Radial ornament finely and equally multicostellate (4:4); ventral tongue not developed (5:0), ventral tongue trapezoidal (14:1).
Node 20. Accentuated ventral median costa absent (10:0); dorsal median fold originating from umbo (12:3).
Eospirigerina pennata. Medium size 10–15 mm (17:2).
Node 21. Radial ornament costellate (4:3); ventral beak curved dorsally, swollen (6:2); (6:2); delthyrium with separated deltidial plates (16:1).
Eospirigerina porkuniana. No apomorphic characters recognized
Node 22. Accentuated ventral median costa occasionally present (10:1); dorsal sulcus not developed (11:0).
Australospira districha. Shell subequally biconvex (1:2); anterior commissure parasulcate (2:3); shell outline isometric (3:1); ventral beak pointed, slightly erect posteriorly (6:1); plications laterally bounding ventral sulcus absent (9:1).
Webbyspira principalis. Dorsal median fold originating anterior to umbo (12:1); plications laterally bounding dorsal median fold present (13:2); trapezoidal ventral tongue (14:1); open delthyrium (16:0).