Upper Ordovician brachiopods from the Anderken Formation, Kazakhstan: their ecology and systematics

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SYNOPSIS. The brachiopod fauna from the Anderken Formation (Lower to Middle Caradoc) of the Chu-Ili Range, south-eastern Kazakhstan, is revised and described systematically. It consists of 62 species in 55 genera, of which the genera *Tesikella*, *Olgambonites* and *Zhilgyzambonites* (all Plectambonitoidea) and *Illostrophina* (Camarelloidea) are new, and the species *Bellimurina* (*Bellimurina*) *sarytumensis*, *Teratelmella chugaevae*, *Foliomena prisca*, *Acculina kulanketpesica*, *Dulankarella larga*, *Kajnaria rugosa*, *Anoptambonites convexus*, *Olgambonites insolita*, *Zhilgyzambonites extenuata*, *Gacella institata*, *Placotriplezia spissa*, *Gammoplectia wrighti*, *Dolerorthis pristina*, *Austinella sarybulakensis*, *Plectorthis? burultasica*, *Bowanorthis? devexa*, *Pionodema opima*, *Parastrophina iliana*, *Illostrophina tesikensis*, *Liostrophia pravula*, *Plectosyntrophia unicostata*, *Rhynchotrema akchokense* and *Nikolaispira guttula* are new. Six brachiopod-dominated assemblages are recognised and defined, termed the *Ectenoglossa*, *Tesikella*, *Mabella–Sowerbyella*, *Acculina–Dulankarella*, *Parastrophina–Kellerella* and *Zhilgyzambonites–Foliomena* Associations. The relationships with contemporary faunas are assessed, and the Anderken brachiopods appear to have much in common with those of north-west China.

INTRODUCTION

The global geography of the Lower Palaeozoic has been the subject of widespread international discussion in recent years (references in Cocks 2001), but much is not yet clear. In the Ordovician, the large area of what is today Kazakhstan was then divided into many

separate crustal fragments of variable size. The relative positions of these fragments are contentious; some authors, notably Sengor & Natalin (1996), consider that most of the fragments made up an enormous island arc, termed the Kipchak Arc, which stretched in a long curve all the way from the substantial craton of Baltica to the central Siberian Angaran craton. Others, for example Nikitin, have subdivided Kazakhstan in other ways, with a more conservative

Fig. 1 Generalised map of the Chu-Ili Range and West Balkhash Region (including the southern part of Lake Balkhash), showing the boundaries of the Early Palaeozoic tectonofacies belts, mainly after Nikitin *et al.* (1991), and the position of the brachiopod localities discussed in the text: 1, Anderkenyn-Akchoku; 2, Kujandysai; 3, east side of Kopalysai River; 4, Buldubai-Akchoku Mountain; 5, Tesik River; 6, Burultas Valley; 7, south-east side of Karatal River near Sorbulak spring; 8, 7 km southwest of Karpkuduk Well, Kotnak Mountains.

palaeogeography. Up until now, little assessment of the faunas contained within these tectonic plates has been made, particularly in relationship to contemporary faunas from other areas. One such plate is that forming the Chu-Ili Range, and termed here the Chu-Ili Plate (Fig. 1). Within the Chu-Ili Plate the successions have been known for some time (e.g. Nikitin 1972, 1973). However, although a number of papers have been published on aspects of some of the contained Ordovician faunas, much remains to be done. A central formation within the unit is the Anderken Formation of early Caradoc age. This immediately underlies the Dulankara Formation, whose brachiopods from its lowest Otar Member we have recently revised (Popov *et al.* 2000). Although some pioneering descriptions of some of the Anderken brachiopods were published by Rukavishnikova (1956) and some individual species have been published in a number of publications, e.g. Popov (1980, 1985) and Nikitin & Popov (1983), the whole brachiopod fauna from the formation has never been published, and this is the chief purpose of the present paper. In addition, six brachiopod-dominated associations can be identified from the Anderken Formation. LEP and LRMC are responsible for the whole paper and IFN for input into the systematic palaeontology and biofacies sections.

OUTLINE OF GEOLOGY AND FOSSIL LOCALITIES

The Chu-Ili Plate (Fig. 1), as recognised here, is a small part of Asia today, and is traceable from the Zailiyskiy Alatau Range in the southeast to the northern Betpak-Dala Desert in the northwest, where it disappears under late Palaeozoic and Mezo-Cenozoic deposits. To the southwest it is bordered by the large Dzhalaïr-Najman Fault and northward-dipping homoclinal sequences of Upper Cambrian and Lower to Middle Ordovician age which are mainly siliciclastic slope rise deposits (e.g. the Dzhambul Formation), indicating passive margin development, and several thrust sheets consisting of dismembered ophiolites of the early Palaeozoic Ashchisu Formation (Toporova *et al.* 1971). The Dzhalaïr-Najman Fault mainly follows an early Palaeozoic suture which separates the Lower Palaeozoic Chu-Ili Plate from the Middle to Upper Ordovician volcanic island-arc association traceable along the northeastern margin of the Betpak-Dala-North Tien Shan tectonofacies belt of Nikitin (Nikitin *et al.* 1991), which is the same as the Djezkazaan-Kirgiz (4.1) tectonofacies unit of Sengör & Natalin (1996). To the

Fig. 2 Chart showing the correlation between the Lower Palaeozoic lithostratigraphic units in the Chu-Ili Plate and the Burultas tectonofacies belt.

north-east of the Chu-Ili Plate lies the Burultas tectonofacies belt (Fig. 2), which represents an accretionary wedge suggesting active margin development, island arc volcanism and subduction of the oceanic crust under the Chu-Ili Plate from the early Arenig to the Llandeilo *Pygodus anserinus* Biozone (Koren *et al.* 1993). By the Caradoc, subduction and volcanism had ceased as a result of the docking of a small terrane or island arc, the Mynaral-South Dzhungaria tectonofacies belt of Nikitin *et al.* (1991).

The Ordovician deposits in the central part of the Chu-Ili Plate, the Dzhair-Najman Synclinorium, form a nearly continuous sequence of siliciclastic and carbonate rocks from Arenig to Ashgill in age (Fig. 2), which are relatively unmetamorphosed and chiefly dip gently to the northeast. They are covered conformably by Silurian deposits (Nikitin *et al.* 1980) or unconformably by the Devonian. The Ordovician stratigraphy and major lithostratigraphic units were described by Keller (1956) and Nikitin (1972).

The Lower to Middle Caradoc deposits, which are the main source of the brachiopods described here, are termed the Anderken Formation, which is a transgressive sequence of mainly siliciclastic deposits that contain variably developed lens-like carbonate units in the upper part representing mud mounds or algal build-ups (Nikitin *et al.* 1974; 1996). They are best developed in the following eight general localities (Figs 1, 3):

Localities 1–2. Area between the Ashchisu and Sarybulak rivers.

In the south-eastern part of the Chu-Ili Range the best sections of the Anderken Formation are located in a block with faulted margins between the rivers Ashchisu and Sarybulak (Fig. 1, localities 1–2;

Figs 3, 4). Here the Anderken Formation overlies, with a slight angular unconformity, graded sandstones, siltstones and mudstones of the Beke Formation, which is Llandeilo to early Caradoc in age, dated by numerous graptolites of the *Hustedograptus teretiusculus* and *Nemagraptus gracilis* Biozones (Tsai 1976). The Anderken comprises six lithostratigraphic units traceable up to 40 km along strike, overlain unconformably by Devonian deposits. These units are (in ascending order):

Unit 1. Polymict, pebbly conglomerate, with sandy matrix and with some beds of sandstone and gritstone. Thickness from 45 m to 120 m, with maximum values in the Anderkenyn-Akchoku section.

Unit 2. Coarse- to medium-grained sandstone with subhorizontal stratification alternating with abundant cross-bedded sets. Lenses of polymict, pebbly conglomerate represent shallow channels formed by tidal currents. Thickness varying from 52 m in the Kujandysai section in the west to 180 m in the Anderkenyn-Akchoku section (Figs 3, 5). The upper part contains the lingulide *Ectenoglossa sorbulakensis*, the trilobite "*Isotelus*" *romanovskyi* Weber and gastropods (Samples 8130-1, 7612). The middle part of the unit in the Anderkenyn-Akchoku section contains a carbonate mud-mound up to 16 m thick with a core built of light grey micritic limestone. On the flanks there is bedded biomicrite with the brachiopods *Skenidioides* sp., *Christiania* sp. and *Kellerella misiusi*, the trilobites *Mesotaphraspis spinosus* Lisagor, *Selenoharpes* sp., *Acrolichas* sp., *Eokosovopeltis romanovskyi* and *Sphaerexochus* aff. *hisingeri* Warburg. *Iliaenus* sp. was noted from about 1.0–1.5 m below the top of the mud-mound in the eastern part of its exposure (Sample 8226). Cystoid and crinoid columnals are abundant.

Fig. 3 Columnar sections through the Anderken Formation showing informal units, stratigraphic positions of samples and brachiopod associations: *Ect. A.* - *Ectenoglossa* Association, *T. A.*, *Tesikella* Association, *M.-S. A.*, *Mabella-Sowerbyella* Association, *A.-D. A.*, *Acculina-Dulankarella* Association, *P.-K. A.*, *Parastrophina-Kellerella* Association, *Z.-F. A.*, *Zhilgyzambonites-Foliomena* Association, *G.-B. A.*, *Gastropod-Bivalved Molluscs* Association. The numbers of the sections are the same as those on Fig. 1.

Unit 3. Coarse- to medium- grained sandstone with mostly subhorizontal stratification, about 40–62 m thick in the Anderkenyn-Akchoku section and up to 97 m thick in the Kujandysai section, with some storm beds of coquinas up to 20 cm thick with concentrations of gastropods and the disarticulated bivalved molluscs *Edmondia fecunda* Khalifin, *Ctenodonta* sp. and *Orthonota*? sp. (Sample 8130a). Gastropods, bivalved molluscs and the trilobite *Eokosovopeltis romanovskyi* become increasingly abundant in the flank deposits in the upper 20 m of the unit (Samples 8130, 8134). In the Kujandysai section concentrations of bivalved molluscs occur in the middle part in association with the rare brachiopod *Tesikella necopina* and the pelmatozoan columnals *Clivosocystis clivosus* Stukalina and *Ordinacrinus punctatus* Stukalina (Sample 7611).

Unit 4. Medium- to fine-grained sandstone replaced gradually upwards by siltstone with numerous trace fossils and symmetrical ripple marks. Thickness varies from 22 to 80 m in the Anderkenyn-Akchoku section and is about 28 m in the Kujandysai section. The lower part contains local concentrations of the coalified plant *Akdalaphyton caradoci* Senkevich, and gastropod and bivalved mol-

lucos in association with the brachiopod *Tesikella necopina* (Samples 8127-2b, 8129, 8133, 8138). The upper part contains an abundant brachiopod fauna of the *Sowerbyella-Mabella* Association (Samples 100b, 7613, 8128a, 8128b, 8135, 8137) and the trilobites *Dulanaspis laevis anderkensis* Chugaeva, *Lonchodomas tecturmasi* Weber, *Pliomerina* sp., *Remopleurides* sp., *Styginella macrophthalmia* Pribyl & Vanek, *Bronteopsis extraordinaria* Chugaeva, the cystoid and crinoid columnals *Clivosocystis clivosus*, *Digiticrinus levis* Stukalina, *Ordinacrinus punctatus* Stukalina and *Communicrinus communis* Stukalina and the starfish *Stenaster obtusus* (Forbes).

Unit 5. Limestones varying in thickness from 8 to 98 m forming a chain of carbonate build-ups between the Uzunbulak and the Ashchisu rivers (Fig. 3). The cores of these build-ups rest on a bed of nodular limestone from 2–10 m thick with abundant dasyclad algae *Cyclocrinites nikitini* Gnilovskaya and *Mastopora reticulata* Gnilovskaya (Nikitin *et al.* 1974). A bed of nodular, algal limestone with dasyclad algae is usually present in the interspaces between the carbonate build-ups and contains brachiopods of the *Acculina-Dulankarella* Association (Samples 100, 8251, 85258), the rare

Fig. 4 Geological map showing distribution of the Middle and Upper Ordovician rocks and the positions of measured sections and fossil localities that yielded brachiopods in the area between the Uzunbulak and Ashchisu Rivers, south-eastern Chu-Ili Range (after Nikitin 1972, modified).

tabulate corals *Lichenaria?* sp. and *Amsassia* sp., stromatoporoids, and various trilobites and echinoderms. Locally between the Kujandysai and Sarybulak rivers, and on both sides of the Ashchisu River in the eastern part of outcrop area, carbonate build-ups disappear and the unit comprises bedded limestone varying from biomicrite to biosparite intercalating with siltstone and mudstone, with brachiopods of the *Parastrophina*-*Kellerella* Association (Tables 4–5, Samples 628, 8223, 8223a, 8223b). Brachiopods of this association also occur in pockets of bioclastic limestone in the mud-mound core and the overlying bedded limestone together with large spherical or ellipsoidal ooids of radial calcite up to 1 cm across (Samples 2538, 8217, 8219, 8256).

Unit 6. Siltstone and mudstone with up to 6 interlayers of bentonite up to 0.3 m thick in the lower part, total about 50–60 m thick, containing brachiopods of the *Zhaltyzambonites*-*Foliomena* Association (Samples 8231, 8251, 8255). Abundant trilobites are *Granulatagnostus granulatus* Kolobova, *Sphaeragnostus* sp., *Microparia speciosa* Hawle & Corda, *Hammatocnemis* sp., *Birmanites almatiensis* (Chugaeva), *Cyclopyge* sp., *Cybele weberi* Chugaeva and *Ovalocephalus* sp., and graptolites include *Dicranograptus nicholsoni*, *Diplograptus anderkenensis*, *Glyptograptus trubinensis* and *Pseudoclimacograptus scharenbergi*, suggesting the Lower to Middle Caradoc *Diplograptus multident* Biozone (Keller 1956).

Locality 3. East side of Kopalysai River

On the east side of the Kopalysai River (Fig. 1) the Anderken Formation is about 160 m thick and rests unconformably on the siliciclastic Llandeilo Beke Formation (Fig. 2). Detailed description of this section was provided by Keller (1956: 26), who recognised three units (Fig. 3): (1) bed of intercalating polymict conglomerate

and coarse- to medium-grained sandstone up to 70 m thick with bivalves, rare *Ectenoglossa sorbulakensis* (Sample 8223-1) and numerous plant remains of *Akdalaphyton caradoci*; (2) intercalating fine-grained sandstone and siltstone about 15–20 m thick with brachiopods of the *Tesikella* Association (Sample 127), the trilobites *Dulanaspis levis anderkenensis* and *Lonchodomas tecturmasi*; and (3) mudstones with some siltstones and fine-grained sandstones about 70–80 m thick with abundant brachiopods of the *Mabella*-*Sowerbyella* Association (Sample 8228). The deposits overlying the Anderken Formation are polymict pebbly conglomerates and sandstones of the Dulankara Formation.

Locality 4. Buldukbai-Akchoku Mountain

On the west side of the River Kopalysai, the Anderken Formation includes a large carbonate mud-mound which forms the top of Buldukbai-Akchoku Mountain. The lower part of the formation is exposed on the south-western slope of the mountain, north of an east-west fault (Figs 1, 3, 5–7). It includes, in ascending order:

Unit 1. Medium- to fine-grained sandstone up to 120 m thick with *Ectenoglossa sorbulakensis*.

Unit 2. Dark green, bedded siltstones, about 14 m thick with a few layers of fine grained sandstone 3–10 cm thick, containing *Mabella conferta* and *Shlyginia fragilis* of the *Sowerbyella*-*Mabella* Association.

Unit 3. Siltstones with nodules of algal limestone gradually changing into beds of nodular limestone with dasyclad algae towards the top, 38 m thick in total.

Unit 4. Nodular algal limestone intercalating with siltstone about 0.5–1.5 m thick, up to 22 m thick in total, with brachiopods of the *Acculina*-*Dulankarella* Association (Sample 8231-40).

Fig. 6 A, general view of the Anderken Formation at the Anderkenyn-Akchoku section, showing informal lithostratigraphic units discussed in the text and the position of brachiopod localities. B, view of large complex carbonate buildup at Akchoku Mountain in the upper part of the Kujandysai section. Photographs by Igor Nikitin.

Unit 5. Massive micritic limestone forming the core of the carbonate mud-mound at the top of the mountain, about 30 m thick.

The upper part of the Anderken Formation outcrops along the north-eastern slope of Buldukbai-Akchoku Mountain. It includes:

Unit 6. Laminated, dark green siltstone up to 70 m thick with storm beds of calcareous sandstone rich in brachiopod coquinas about 10–15 cms thick and crinoid columnals. The top is a characteristic bed of laminated brownish-violet siltstone about 0.5 m thick overlain by polymict conglomerate of the Dulankara Formation (Fig. 7B). The

unit contains numerous coalified plant remains of *Akdalaphyton caradoci* concentrated on several bedding surfaces, brachiopods of the *Sowerbyella–Mabella* Association (Samples 8229, 8230) and the echinoderms *Clivosocystis* sp., *Digitocrinus levis* and *Ristnacrinus bifidus* Stukalina.

Locality 5. Tesik River

This locality is on the southern side of the River Tesik about 1.5 km upstream of the bridge crossing the river on the highway from

Fig. 7 The Anderken Formation on the south-western slope of Buldukbaï-Akchoku Mountain. **A**, Units 1 to 5, and Sample localities 8227–80, 110 and 8231–8240; **B**, Unit 6 and the contact with the overlying Dulankara Formation and Sample localities 8229 and 8230. Photographs by Lars Holmer.

Almaty to Balkhash (Fig. 1, locality 5). It is an isolated natural exposure of about 20 m of pink to light red rocks of massive micritic limestone forming the core of a mud-mound with lens-like beds of biosparite at the base of the exposure. Most of the bioclasts are fragmented large cystoid columnals. It contains an

abundant *Parastrophina*–*Kellerella* Association (Sample 948).

Locality 6. Burultas Valley

The Burultas Valley (Fig. 1, locality 6) is about 42–45 km west of Chiganak on the western Balkhash coast (northeastern part of

Quadrangle 73°22'30" to 73°30' E; 45° to 45°05' N). A summary of the Ordovician geology and lithostratigraphy of this locality is in Nikitin *et al.* (1980, text-figs 18, 20). The Anderken Formation consists mainly of siliciclastic rocks with a thick unit of polymict conglomerates at the base and a number of carbonate mud-mounds in the upper part (Fig. 3). The carbonate unit in the top of the sequence is a bed of nodular algal limestone about 6–10 m thick with numerous *Girvanella* sp., *Cyclocrinites nikitini* and *Mastopora reticulata* and brachiopods of the *Acculina*–*Dulankarella* Association (Locality 1041a of Nikitin = Sample 390/76 of Kovalevskii), which underlies a lens of massive, micritic limestone up to 20 m thick which forming the mud-mound core. The unit thins about 200 m westward from Locality 1041a, where it is represented by bedded and nodular limestone with the brachiopods *Pionodema opima*, *Dulankarella larga* and *Mabella conferta* (Sample 818). The uppermost 10 m of the underlying unit, of fine-grained sandstone intercalating with siltstone, contains a different brachiopod assemblage with *Tesikella necopina* (Sample 818a), in association with abundant cystoid columnals.

Locality 7. Sorbulak spring on the east side of the River Karatal

In the south Betpak-Dala Desert, about 20 km west of Baigara Mountain, the Anderken Formation is well exposed on both sides of

the River Karatal (Fig. 1, locality 7). Here it rests on the graded sandstones and siltstones of the Llandeilo to Lower Caradoc upper Baigara Formation (Fig. 2), or is in contact with intrusives. About 2 km south-east of the Karatal river, south of Sorbulak spring, it comprises (1) polymict conglomerates more than 50 m thick, (2) medium- to fine-grained sandstones 169–170 m thick with *Ectenoglossa sorbulakensis* about 10–15 m above the base of the unit (Fig. 3, Sample 1024); and (3) intercalating fine-grained slightly calcareous sandstones and siltstones about 60 m thick with the *Tesikella* Association in the upper 20 m of the unit. The upper part of the section is an unfossiliferous unit of intercalating fine-grained sandstones, lilac and red siltstones and mudstones several hundred metres thick, which is overlain by the basal conglomerate of the Dulankara Formation.

Locality 8. Kotnak Mountains

This incomplete section of the Anderken Formation is situated west of the Kotnak Mountains, about 7 km SW of Karpkuduk Well. There, about 1.5 km north-east of the salt marsh (Figs 1, 3, 8), the formation consists of: (1) siltstone about 70 m thick with some storm beds of calcareous sandstone about 10–20 cm thick with a coquina of the bivalve *Ctenodonta* sp. (Samples 1017, 1019); (2) sandstone intercalating with siltstone in the upper part, total 40 m thick, with brachiopods of the *Tesikella* Association in the lower 10 m of the unit

Fig. 8 Geological map showing the distribution of the Anderken Formation and the position of fossil localities in the area about 7 km south-west of Karpkuduk well, Kotnak Mountains.

Table 1 Composition of *Ectenoglossa* Association from the Anderken Formation showing number of complete shells, ventral and dorsal valves respectively.

Sample number	7612	8130a	8130-1	8223-1	8227-10	8227-40	8227-80	F-1024
Number of specimens	27	1	2	1	6	4	3	12
<i>Ectenoglossa sorbulakensis</i>	24:3:2	0:1:0	0:2:0	0:1:1	6:0:0	0:3:4	0:3:3	0:8:12

(Sample 1018a) below a bed of skeletal calcareous sandstone about 5 m thick with an allochthonous brachiopod fauna with a mixture of taxa of the *Tesikella* and *Mabella-Sowerbyella* Associations (Sample 1018); (3) intercalating beds of sandstone and pebbly polymict conglomerate about 80–90 m thick; and (4) siltstone with a few beds of fine-grained sandstone, total 130 m thick and overlain unconformably by Devonian conglomerate.

FAUNAL ASSOCIATIONS

The Anderken Formation is a transgressive sequence from near shore to outer shelf deposits with predominantly siliciclastic deposition. The lower part of the formation, below the main horizon with carbonate build-ups in the Anderkenyn-Akchoku, Kujandysai, Buldukbaï-Akchoku and Burultas sections, was formed in tide-dominated environments of mostly tidal flat deposits with characteristic sets of pebbly conglomerates, cross-bedded and laminated sands, coquina storm beds and traces of tidal currents. Carbonate build-ups in the upper part of the formation preserve numerous traces of photosynthetic activity and contain a diverse flora of green and red algae (Nikitin *et al.* 1974); suggesting formation in shallow depths within the euphotic zone. The outer shelf deposits are recorded only in the south-eastern Chu-Ili Range and consist of silt and mud containing graptolites. The benthic fauna is dominated by trilobites but includes one of the earliest records of the *Foliomena* brachiopod fauna. Apollonov (1975) has described the trilobite associations of the middle and late Ordovician of the Chu-Ili Plate.

A matrix based on the distribution of about 1800 brachiopod specimens from 33 samples within the Anderken Formation was subjected to Principal Component Analysis (Etter 1999). Plots of

eigenvectors corresponding to three maximum directions of variation (F1–F3) are illustrated on two two-dimensional diagrams (Fig. 9). The Diversity Index is calculated as the number of species minus 1 divided by the natural logarithm of the number of brachiopod individuals in the sample (for details see Williams *et al.* 1981). The analysis of taxonomic composition and relative abundance of brachiopod taxa from numerous localities and samples in the Anderken Formation allows recognition of six brachiopod associations characterised below. They are interpreted within the Benthic Assemblage (BA) scheme of Boucot (1975).

1. The *Ectenoglossa* Association. This is a monospecific lingulide association of BA-1 with *Ectenoglossa sorbulakensis* in the Anderkenyn-Akchoku, Kujandysai and Buldukbaï-Akchoku sections, the east side of the Kopalysai River and on the southern side of the Karatal River south of Sorbulak spring (Table 1). The assemblage shows patchy distribution in lithologies of coarse- to medium-grained sands with subhorizontal and cross-bedded stratification. In most of the localities shells are disarticulated on the bedding surfaces and only in Sample 7612 do conjoined valves predominate (89% of individuals). A cluster of six articulated shells preserved in life position inclined from 62°–80° to the bedding surface was recovered from Sample 8227-40 in the Buldukbaï-Akchoku section, which confirms the infaunal mode of life of this lingulide. The gastropods *Lophospira* sp. and *Latitenia kasachstanica* Vostokova and the bivalved molluscs *Endomionia fecinda*, *Ctenodonta* sp. and *Cyrtodonta? subcentralis* (Khalfin 1958), which are widespread in similar lithologies and form coquina storm beds, do not co-occur together with the lingulides; for example, in Sample 8130 a bedding surface with *Ectenoglossa sorbulakensis* and a storm bed with molluscs and the trilobite *Eokosovopeltis romanovskyi* are separated by an interval only about 2.5 m thick. It is likely that *Ectenoglossa*

Table 2 Composition of *Tesikella* Association from the Anderken Formation showing number of complete shells, ventral and dorsal valves respectively.

Sample numbers	127	818a	F-1018a	7611	8128	F-1018	F-1024b	8127-2b	8138
Number of specimens	18	22	32	7	18	172	20	1	2
Diversity index	0.33	0.65	0.58	0.51	1.38	3.11	2.16		
<i>Trematis</i> sp.	0:0:1								
<i>Tesikella necopina</i>	3:14:12	0:13:12	0:16:7	1:5:5	0:4:2	1:4:3	0:2:2	0:1:0	0:2:0
<i>Longvillia lanx</i>			0:4:5			2:7:3			
<i>Glyptomena onerosa</i>						0:1:5			
<i>Christiania egregia</i>						0:7:18	0:2:7		
<i>Limbimurina</i> sp.						0:1:1			
<i>Isophragma imperator</i>						1:36:34			
<i>Acculina kulanketpesica</i>					0:0:1	0:1:2			
<i>Mabella conferta</i>		1:0:0				0:1:2			
<i>Shlyginia fragilis</i>						0:6:4			
<i>Anaptambonites orientalis</i>						1:4:3			
<i>Sowerbyella rukavishnikovae</i>			0:10:11			0:8:17	0:9:10		
<i>Bicuspina rukavishnikovae</i>						3:1:9			
<i>Plectorthis burultasica</i>					0:0:1	1:6:7			
<i>Dolerorthis expressa</i>						1:12:9			
<i>Phragmorthis conciliata</i>						0:4:4	0:1:0		
<i>Eodalmannella extera</i>		4:4:0		0:0:1		1:28:22			
<i>Pionodema opima</i>					2:8:5				
<i>Rhynchotrema</i> sp. nov.					1:0:0				
<i>Didymelasma</i> cf. <i>transversa</i>						0:0:1

In its pioneer stage, the *Tesikella* Association is characterised by the appearance of *Tesikella necopina* in mollusc-dominated environments, where it is the only brachiopod (Samples 127, 7611, 8127–2b, 8138), or where it comprises more than 50% of the brachiopod fauna together with *Longvillia lanx*, *Sowerbyella rukavishnikovae* (up to 34%) and *Eodalmanella exera* (up to 18%). At its mature stage the association includes four to eight species usually common in the *Sowerbyella*–*Mabella* Association, e.g. *Christiania egregia* (up to 35%), *Sowerbyella rukavishnikovae* (up to 50%) and *Pionodema opima* (56% in one sample). All the other taxa constitute less than 5% of individuals in any particular sample. Among other groups bivalved molluscs, the trilobites "*Isotelus*" *romanovskyi*, *Lonchodomas*

3. *Mabella–Sowerbyella* Association (average Diversity Index 1.30; observed range 0.83–1.86, N=9) is another low diversity association of BA-2 dominated by strophomenides. It is recognised in the Anderkenyn-Akchoku, Kopalysai and Buldukbaï-Akchoku sections by the predominance of *Mabella conferta* and *Sowerbyella rukavishnikovae* which together comprise 40–80% of individuals in the assemblage. *Glyptomena onerosa*, *Shlyginia fragilis* and *Anoptambonites orientalis* mainly occur in this association (Table 3). As in the mature *Tesikella* Association, orthides are represented only by *Eodalmannella exera* and *Pionodema opima*, which do not usually co-occur. This association is confined to a fine clastic substrate of silts and fine-grained sands, usually with traces of bioturbation and locally abundant concentrations of the plant *Akdalaphyton caradoci*. In samples from the Anderkenyn-Akchoku section brachiopods are preserved disarticulated, but in the Kopalysai and Buldukbaï-Akchoku sections the number of articulated specimens increases up to 50 percent, suggesting rapid burial and lack of significant post-mortem displacement of the shells. The most common trilobites in the associated faunal assemblage are *Lonchodomas*

Table 3 Composition of *Mabella*–*Sowerbyella* Association from the Anderken Formation showing number of complete shells, ventral and dorsal valves respectively.

Sample number	100b	7613	8128a	8128b	8137	8257	8228	8229	110	8230	843
Number of individuals	248	50	9	27	10	21	41	5	11	36	75
Diversity index	1.09	1.79	1.82	1.21	1.73	1.31	1.62	1.86	0.83	1.13	1.39
<i>Trematis</i> sp.							0:0:1				
<i>Paracraniops</i> sp.			0:0:1								
<i>Glyptomena onerosa</i>	0:5:9	0:1:2			0:2:2	0:0:2		0:1:0			0:3:4
<i>Christiania egregia</i>		0:0:1									
<i>Foliomena prisca</i>							0:1:0				
<i>Dulankarella larga</i>							0:1:0				
<i>Mabella conferta</i>	0:115:7	1:0:0	0:1:2	0:11:14	0:1:2	6:2:0	13:10:2	1:1:0	7:1:0	1:24:13	0:15:24
<i>Shlyginia fragilis</i>	0:15:10	0:10:16	0:3:1	0:2:0	0:3:2	4:3:1			0:2:0	0:1:2	0:0:1
<i>Anoptambonites orientalis</i>	0:9:20			0:0:2						1:1:1	
<i>Olgambonites insolita</i>					0:0:1						
<i>Sowerbyella rukavishnikovae</i>	0:28:79	0:2:2	0:0:2	0:4:5	0:2:2	0:2:1	0:5:2	0:1:0		0:2:2	
<i>Triplesia</i> sp.							0:2:3				
<i>Phragmorthis conciliata</i>		1:0:0								0:0:1	
<i>Plectorthis burultasica</i>											0:1:2
<i>Eodalmarella externa</i>	0:3:10		0:1:0	0:2:4							0:6:12
<i>Pionodema opima</i>		1:24:24				1:1:0	2:8:5	1:1:1	0:0:1	0:4:4	1:24:24
<i>Rhynchotrema akchokense</i>		0:2:1									2:3:5

Table 4 Composition of *Acculina*–*Dulankarella* and *Parastrophina*–*Kellerella* associations from the Anderken Formation showing number of complete shells, ventral and dorsal valves respectively.

	<i>Acculina</i> – <i>Dulankarella</i> Association					<i>Parastrophina</i> – <i>Kellerella</i> Association	
Sample number	F-100	F-1041a	626	85258	8231–40	628	8219
Number of individuals	168	113	112	32	11	40	2
Diversity index	5.07	1.91	4.87	2.60	1.25	5.42	
<i>Mezotreta</i> ? sp.	0:1:0						
<i>Schizotreta</i> sp.			1:0:0			0:0:1	
<i>Bellimurina sarytumensis</i>		1:4:0				0:0:1	
<i>Teratelmella chugaevae</i>	12:0:0		4:0:2			0:0:1	
<i>Furcitellinae</i> gen. et sp. indet.	1:1:1	2:1:2	1:0:1			0:0:1	
<i>Limbimurina</i> ? sp.	0:0:1					0:1:1	
<i>Christiania</i> aff. <i>sulcata</i>						1:6:4	
<i>Christiania egregia</i>	1:4:1	2:1:3	0:2:0	5:1:0			
<i>Craspedelia tata</i>	7:2:0		6:4:0		0:1:0	1:0:1	
<i>Acculina kulanketpesica</i>	12:1:3	32:3:1	1:1:1	4:2:1	1:5:1		
<i>Dulankarella larga</i>	25:1:0	47:0:0	11:1:0		1:1:1		
<i>Kajnaria rugosa</i>	2:0:0	3:1:0	1:0:0			2:1:0	
<i>Mabella conferta</i>	1:0:0	3:0:0				0:1:0	
<i>Shlyginia fragilis</i>				0:1:0		0:1:0	
<i>Glyptambonites</i> sp.	0:2:0						
<i>Sortanella</i> aff. <i>quinquecostata</i>	1:1:2		2:3:2			0:1:1	
<i>Anoptambonites convexus</i>	12:1:3		13:6:3	1:2:1	1:0:1		
<i>Sowerbyella</i> aff. <i>ampla</i>	0:2:3		2:8:0	0:1:4			
<i>Gacella institata</i>	3:1:4		5:1:3	2:0:0		0:0:1	
<i>Placotriplesia spissa</i>	2:1:0	3:2:1	1:1:3	1:0:0			
<i>Triplesia</i> aff. <i>subcarinata</i>						0:0:2	
<i>Bicuspina rukavishnikovae</i>	1:0:0		1:0:0				
<i>Grammoplectia wrighti</i>			1:0:1			0:0:2	
<i>Skenidioides</i> sp.							
<i>Dolerorthis pristina</i>	1:4:2		0:1:0			0:2:2	
<i>Glyptorthis</i> sp.			1:0:0			0:2:1	
<i>Austinella sarybulakensis</i>				3:1:1			
<i>Plectorthis burultasica</i>		1:1:0				1:0:0	
<i>Phragmorthis conciliata</i>			0:1:0				
<i>Parastrophina iliana</i>	5:1:1	4:0:0	7:0:0	2:0:0		2:0:1	
<i>Parastrophina plena</i>	7:0:0						1:0:0
<i>Liostrophia pravula</i>	3:0:2					1:0:4	
<i>Plectosyntrophia</i> ? <i>unicostata</i>	2:0:0		4:0:0				
<i>Schizostrophina margarita</i>	1:3:0		2:0:0			1:0:0	1:0:0
<i>Rhynchotrema akchokense</i>	2:0:0		1:0:0			1:0:0	
<i>Pectenospira pectenata</i>			1:1:1				
<i>Kellerella misiusi</i>	3:0:0		1:0:0				
<i>Nikolaispira guttula</i>	2:0:0						

tecturmasi, *Dulanaspis levis anderkensis* and *Styginella macrophthalma*, whereas *Bronteopsis extraordinaris*, *Pliomerina* sp. and *Remopleurides* sp. are relatively rare. Bivalved molluscs include *Anderkenia ledomorpha*, *Clionichia crispa*, *Edmondia obliqua* and *Praemyophoris? antiqua* (Khalfin 1958), and gastropods are represented mostly by *Lophospira cribrosa* Vostokova. Other fossils include unidentified fenestrate and ramose bryozoans of at least three different species, cystoid and crinoid columnals identified by Stukalina (1988) as *Clivosisystis clivus*, *Communicystis communis*, *Digiticrinus levis*, *Ordinacrinus punctatus*, *Ristnacrinus bifidus* and *Shizocrinus lentiformis*, the cystoidean *Polycosmites? sp.* and the starfish *Stenaster obtusus*.

4. Acculina–Dulankarella Association (Diversity Index 3.14; observed range 1.25–5.07, N=5) is characteristic of a nodular algal limestone with abundant dasyclad algae which was deposited in the base and flanks of carbonate build-ups in the upper Anderken Formation. It is a medium to high diversity association defined by the occurrence of the plectambonitoideans *Acculina kulanketpesica* and *Dulankarella larga*. Other brachiopods include *Teratelasma chugaevae*, *Kajnaria rugosa*, *Gacella institata* and *Austinella sarybulakensis* which do not exceed 5% in other associations. Other components of the assemblage are taxa common in the *Parastrophina–Kellerella* Association (Tables 4–5), whereas *Christiania egregia* is the only abundant species characteristic also of the *Mabella–Sowerbyella* Association. *Mabella conferta* and *Shlyginia fragilis* occur sporadically and do not exceed 5% in a particular sample. There

are abundant green algae: *Apidium parvulum*, *Cyclocrinites nikitini*, *Mastopora reticulata*, *Mastopora nana* and *Sinuatiopora buccera* and the red alga *Contexta binaria* (Gnilovskaya in Nikitin et al. 1974). Small organic build-ups up to 30 cm across of the algae *Girvanella* and *Renalcis* are also characteristic and encrust brachiopod shells and green algae. The substrate was mainly of silt and lime mud with patches of hardground and numerous bioclasts. The abundance of brachiopods preserved as conjoined valves (45–64%) in combination with the abundant flora of algae suggests quiet environments within the euphotic zone of BA-3. Strophomenides (61–90%) constitute the most diverse and abundant component of the brachiopod fauna. The second most abundant group is the camarelloideans (4–14%), mostly *Parastrophina iliana* and relatively rare *Parastrophina plena*, *Eoanastrophina uncostata*, *Liostrophina pravula* and *Schizotretina margarita*, which do not exceed 5% in a particular sample; and orthides, rhynchonellides and spire-bearing groups form an insignificant part of the association. Among other groups trilobites are the most abundant. These were partly studied by Weber (1948) and Chugaeva (1958), but details remain inadequate. The most characteristic taxa are: *Iliaenus* sp., *Acrolichas punctata*, *Cheirurus* sp., *Eokosovopeltis romanovskyi*, *Mesotaphraspis spinosus*, *Pliomerina sulcifrons* and *Sphaerexochus* sp. A diverse echinoderm fauna was identified mostly from cystoid and crinoid columnals (Stukalina 1988). Among molluscs the most characteristic is the cephalopod *Discoceras kazakhstanensis* Barskov. The rare corals *Amsassia* sp. and *Lichenaria* sp., clathrodictyid stromatoporoids, gastropods and bivalved molluscs are also reported, but remain poorly known.

Table 5 Composition of *Parastrophina–Kellerella* Association from the Anderken Formation showing number of complete shells, ventral and dorsal valves respectively.

Sample number	948	2538	8214	8226	8217	8223	8223a	8223b	8256
Number of individuals	200	200	33	12	13	15	18	9	31
Diversity index	2.64	4.91	2.63	1.61	2.34	2.58	3.11	2.76	2.33
<i>Nushbiella dubia</i>		0:1:1					0:1:0		
<i>Bellimurina</i> sp.	0:2:1	0:1:0	1:2:0						0:1:0
<i>Limbimurina</i> sp.		0:0:1						0:0:2	
<i>Christiania</i> aff. <i>sulcata</i>		0:2:1	1:4:1	0:1:0	0:1:0	0:2:0	0:1:1	0:2:1	
<i>Foliomena prisca</i>						0:0:1			
<i>Craspedelia tata</i>	2:2:1	8:4:3	1:2:0				0:1:0	0:1:0	
<i>Kajnaria rugosa</i>						1:1:0			
<i>Sortanella</i> aff. <i>quinquecostata</i>	3:2:1	4:0:2							
<i>Anoptambonites convexus</i>		9:6:2				0:3:1			1:3:4
<i>Sowerbyella</i> aff. <i>ampla</i>	2:2:1	3:1:1	2:2:2		0:2:0		3:1:0	1:0:0	
<i>Triplesia</i> aff. <i>subcarinata</i>		2:0:0							
<i>Placotriplesia spissa</i>		3:1:7	0:2:1			1:1:0			0:0:1
<i>Grammoplectia wrighti</i>			0:2:1						
<i>Skenidioides</i> sp.			1:0:0	0:1:0				0:1:0	
<i>Dolerorthis pristina</i>	4:5:7	0:1:1	2:1:3		0:0:1	0:0:1		0:1:0	
<i>Glyptorthis</i> sp.	0:2:1	2:2:1	3:1:1				0:1:1		0:0:1
<i>Plectorthis burultasica</i>		3:1:1							
<i>Phaceloorthis</i> sp.		1:0:0							
<i>Bowanorthis? devexa</i>	7:0:0	5:0:0							
<i>Phragmorthis conciliata</i>		2:0:1					0:0:1		
<i>Parastrophina iliana</i>	15:0:0	15:0:1							2:0:0
<i>Parastrophina plena</i>	62:0:0	17:0:1	3:0:0	2:1:1	2:0:0		1:0:0	1:0:0	5:0:0
<i>Liostrophina tesikensis</i>	14:0:0								
<i>Liostrophina pravula</i>	7:0:0	13:0:1				3:0:0			3:0:0
<i>Plectosyntrophia? uncostata</i>		1:0:0			0:0:1				
<i>Schizostrophina margarita</i>		16:0:0			0:0:1	0:0:1			5:3:2
<i>Didymelasma</i> cf. <i>transversa</i>		1:0:0							
<i>Rhynchotrema akchokense</i>	2:0:0	2:0:0							
<i>Pectenospira pectenata</i>	14:1:1	3:0:0	1:0:0				3:0:0		
<i>Kellerella misiusi</i>	15:0:1	39:0:0		2:0:0	5:0:0		2:0:0		5:0:0
<i>Nikolaispira guttula</i>	13:0:0	20:0:0		1:0:0			2:0:0		
<i>Acculina</i> sp.		0:1:1							

5. *Parastrophina*–*Kellerella* Association (Diversity Index 3.17, observed range 1.61–5.42, N=10) is closely associated with carbonate build-ups and also belongs to BA-3. These build-ups were interpreted by Nikitin *et al.* (1974) as a chain of bioherms with a frame built by the cyanobacterians *Girvanella* and *Renalcis*: however, micritic limestone usually comprises the most significant part of the volume of the rock in the core of a build-up. According to Nikitin *et al.* (1974), these build-ups form a low ridge, raised about 1.5–3 m above surrounding areas with fine clastic sedimentation. Fossils are usually concentrated in pockets of bioclastic limestone between individual bioherms and mounds (Samples 948, 2538, 8223a, 8256). Composition of this association is essentially similar to the *Acculina*–*Dulankarella* Association, with more than 80% of recorded species in common. However, the abundance of camarelloideans increases up to 49% (Sample 948) and the archaic spire-bearing brachiopods *Pectenospira pectenata*, *Kellerella misiusi* and *Nikolaishira guttula* constitute a significant part of the association (21–42% in the most representative samples), whereas in the *Acculina*–*Dulankarella* Association they are less than 2% (Table 5). The relative abundance of strophomenides decreases significantly and such genera as *Acculina*, *Dulankarella*, *Mabella* and *Shlyginia* disappear completely. *Christiania* is represented by the species *C. aff. sulcata*, which is closely linked to this association. Diminution in the sizes of the strophomenides might reflect the predominance of hard grounds. Taxonomic composition of the association is modified in the bedded bioclastic limestone which has large ooids (up to 1 cm across) on the top and flanks of the core (Samples 8214, 8217, 8223, 8223b). Brachiopods are relatively rare and dispersed through the rock. Relative abundance of strophomenides, and especially *Christiania aff. sulcata*, increases, whereas spire-bearing brachiopods become rare or completely disappear in some samples (8214, 8223, 9223b). According to the Principal Component Analysis these occupy an intermediate position between the cluster formed by samples of the *Acculina*–*Dulankarella* Association and samples 948, 2538, 8256, which represent the fully developed *Parastrophina*–*Kellerella* Association (Fig. 8B).

The associated trilobite fauna is only partly known and includes such taxa as *Iliaenus* sp., *Acrolichas punctata*, *Amphilichas punctata*, *Eokosovopeltis romanovskyi*, *Glaphurina weberi*, *Mesotaphraspis spinosus*, *Pliomerina sulcifrons*, *Selenoharpes* sp. and *Sphaerexochus aff. hisingeri* (Weber 1948, Chugaeva 1958, Kolobova & Popov, 1986). Crinoid columnals usually represent the most important source of bioclasts in the rock. They mostly belong to *Webericrinus variabilis*, *Ordinacrinus ordinarius*, *Malovicrinus depressus*, *Tatjanicrinus crusciformis*, *Flexicrinus flexus*, *Communicrinus communis* and *Multifidocrinus multrifidus* (Stukalina 1988).

In the eastern part of the Anderkenen–Akchoku section (Sample 8226), isolated carbonate build-ups up to 16 m thick appear within Unit 2, which is mostly cross-bedded sandstone containing lingulide and mollusc associations. It is likely that these build-ups formed almost intertidally, but, except for a much lower diversity, the brachiopod assemblage retains a relative abundance of spire-bearers (*Kellerella misiusi*) and camarelloideans (*Parastrophina plena*) typical of the *Parastrophina*–*Kellerella* Association, whereas trilobites such as *Acrolichas* sp., *Eokosovopeltis romanovskyi*, *Sphaerexochus aff. hisingeri* and *Iliaenus* sp. also show close similarity to the assemblage from the carbonate unit in the upper part of the Anderken Formation.

6. *Zhilgyzambonites*–*Foliomena* Association (Diversity Index 1.21; observed range 1.14–130, N=3) is known from three samples collected from the unit of mudstones and siltstones in the uppermost

Table 6 Composition of *Zhilgyzambonites*–*Foliomena* Association from the Anderken Formation showing number of complete shells, ventral and dorsal valves respectively.

Sample number	2531	8251	8255
Number of specimens	4	4	15
Diversity index	1.44	0.72	1.48
<i>Foliomena prisca</i>	1:0:0	0:1:0	1:3:3
<i>Olgambonites insolita</i>			0:3:2
<i>Zhilgyzambonites extenuata</i>	0:2:1	0:3:3	2:5:5
<i>Kassinella?</i> sp.			0:0:1
<i>Chonetoidea</i> sp.			1:0:0
<i>Anisopleurella</i> sp.	0:1:1		

Anderken Formation in the Anderkenyn–Akchoku section (Figs 3, 5, Unit 6, Table 6). Brachiopods are a minor part of a trilobite-dominated benthic assemblage, which includes *Amphitriton cf. radians*, *Ampixinella* sp., *Birmanites almatiensis*, *Bronteopsis extraordinaris*, *Cheraurus kassini*, *Cybele weberi*, *Dionide kazakhstanica*, *Dindymene* sp., *Hammatocnemis* sp., *Microparia speciosa*, *Ovalocephalus* sp., *Granulatagnostus granulatus* and *Sphaeragnostus* sp. (Chugaeva 1958, Nikitin *et al.* 1974). Co-occurrence of agnostids, cyclopygids and *Ovalocephalus* allows us to refer this assemblage to the *Ovalocephalus* fauna of Fortey (1997) which is characteristic of outer shelf trilobite biofacies corresponding to BA 4–5. Co-occurrence of the *Foliomena* and the *Ovalocephalus* faunas is common in late Caradoc to early Ashgill deep water benthic communities in South China (Rong *et al.* 1994). The *Zhilgyzambonites*–*Foliomena* Association includes only six strophomenide genera. Two of them (*Olgambonites* and *Zhilgyzambonites*) are Kazakhstan endemics, whereas *Anisopleurella* and *Kassinella* are characteristic of early *Foliomena* faunas in the Caradoc of China (Rong *et al.* 1999) and elsewhere.

OVERALL PALAEOECOLOGY

The sequence of brachiopod associations in the Anderken Formation shows an onshore-offshore pattern with a monotaxic lingulide community inhabiting mobile sand nearshore, low diversity mollusc and brachiopod associations of BA-2 on a shallow clastic shelf, medium to high diversity faunas of BA-3 linked with carbonate build-ups, and a deep water *Foliomena* fauna as part of a trilobite-dominated benthic assemblage in BA 4–5. In terms of abundance, diversity and taxonomic composition, the five associations formed by rhynchonelliformean brachiopods can be subdivided into three groups, which show little interaction and apparently evolved independently. They are: 1, low-diversity strophomenide-dominated *Tesikella* and *Mabella*–*Sowerbyella* Associations of shallow clastic shelf corresponding to BA-2; 2, medium to high diversity *Acculina*–*Dulankarella* and *Parastrophina*–*Kellerella* Associations closely linked to carbonate build-ups; and 3, a deeper-shelf *Zhilgyzambonites*–*Foliomena* Association representing an early *Foliomena* Fauna.

The predominance of strophomenides in environments corresponding to BA-2, which is usually dominated by rhynchonellides and spire-bearing taxa in the late Ordovician and Silurian (Boucot 1975; Ziegler *et al.* 1968), is a distinctive feature of the Anderken sequence of communities. The *Tesikella* and *Mabella*–*Sowerbyella* Associations share eight brachiopod species but *Tesikella necopina* (the index species of the former association) does not usually co-occur with *Mabella conferta* and *Shlyginia fragilis*. The *Tesikella necopina* Association also demonstrates significant variations in

Table 7 Additional list of brachiopod taxa from localities in the Anderken Formation not referred to a particular association

Sample number	42	818	1628	8215	620	8251a	8135
Number of specimens	3	4	4	10	13	2	2
<i>Glyptomena onerosa</i>							0:1:0
<i>Christiania</i> aff. <i>sulcata</i>				1:4:1			
<i>Craspedelia tata</i>				0:1:0			
<i>Dulankarella larga</i>		1:0:0					
<i>Mabella conferta</i>					0:1:0		
<i>Shlyginia fragilis</i>	0:1:0	0:0:1			5:7:2		0:1:0
<i>Anaptambonites orientalis</i>							
<i>Sowerbyella</i> ? aff. <i>ampla</i>			1:3:0				
<i>Sowerbyella rukavishnikovae</i>							
<i>Triplasia</i> aff. <i>subcarinata</i>						2:0:0	
<i>Placotriplasia spissa</i>				2:1:0			
<i>Grammoplectia wrighti</i>				1:0:0	2:1:8		
<i>Plectorthis burultasica</i>					1:0:1		
<i>Eodalmannella exera</i>					2:0:1		
<i>Dolerorthis pristina</i>	2:0:0						
<i>Pionodema opima</i>		2:0:0					

relative abundance and taxonomic composition from one sample to another, which may reflect its opportunistic character and higher environmental stress, whereas the *Mabella*–*Sowerbyella* Association, in spite of its low diversity (4 to 8 genera per sample), shows a relatively constant taxonomic composition in most samples (Table 3), and this association forms a compact cluster in the Principal Components Analysis (Fig. 9). Comparison with somewhat younger *Ctenodonta*–*Sowerbyella*, *Altaethyrella*–*Nalivkinia* (*Pronalivkinia*) and *Dinorthis* Associations of the lower Dulankara Formation which inhabited similar environments on the shallow clastic shelf on the Chu-Ili Plate in the late Caradoc–early Ashgill (Popov *et al.* 2000), suggest a rapid faunal turnover. In these younger faunas *Sowerbyella* and *Shlyginia* retained their dominant position and *Anoptambonites* also remained a characteristic minor component, but most of the Anderken genera disappeared (e.g. *Tesikella*, *Eodalmannella* and *Pionodema*) or moved into the middle shelf (*Mabella* and *Glyptomena*) and were replaced by rhynchonellides such as *Altaethyrella* and atrypides such as *Nalivkinia* (*Pronalivkinia*). In contrast, the orthides (e.g. *Plaesiomys*, *Bokorthis* and *Dinorthis*) became increasingly abundant.

The diverse *Acculina*–*Dulankarella* and *Parastrophina*–*Kellerella* Associations, which were closely linked with carbonate build-ups, have little in common with the faunas which inhabited shallow clastic shelves nearby. In the *Acculina*–*Dulankarella* Association strophomenides remain the most abundant brachiopods but they are mostly different genera, such as *Bellimurina*, *Teretelasmella*, *Craspedelia*, *Acculina*, *Dulankarella*, *Kajnaria* and *Sortanella*. *Anoptambonites* occurs in both associations, but as different species. *Mabella* and *Shlyginia* are mostly confined to the *Mabella*–*Sowerbyella* Association, as well as occurring in a few samples of the *Acculina*–*Dulankarella* Association, but as less than 5% of the sample (Table 4). They disappear in the *Parastrophina*–*Kellerella* Association (Table 5), which is possibly the earliest known brachiopod assemblage in which pentamerides together with spire-bearing taxa come to a dominant position. In contrast to the brachiopod fauna of the shallow clastic shelf, assemblages associated with carbonate build-ups did not undergo any significant taxonomic change during the Caradoc. The late Caradoc to early Ashgill brachiopod fauna of the Dulankara carbonate mud-mound in the north Betpak-Dala Desert (Nikitin *et al.* 1996), which was also on the same Chu-Ili Plate, retained a close similarity to the Anderken fauna and contained 14 genera in common including *Parastrophina* and the early athyridides *Kellerella* and *Nikolaispira*. The

strophomenide component was largely unchanged and such genera as *Bellimurina*, *Limbimurina*, *Christiania*, *Craspedelia*, *Sortanella* and *Anoptambonites* are common to both faunas.

The significance of the *Foliomena* fauna was discussed by Cocks & Rong (1988) and Rong *et al.* (1994, 1999). In the Lower to Middle Caradoc it was confined mostly to South China and only in the Ashgill did it become cosmopolitan. In Kazakhstan there are no previous reports of the occurrence of *Foliomena*, but the associated *Ovalocephalus* trilobite fauna occurs in many outer shelf environments from the Middle Caradoc (Apollonov 1975; Nikitin *et al.* 1974). In the Anderken Formation *Foliomena* itself is not restricted to BA 4–5, but occurs occasionally in the *Parastrophina*–*Kellerella* (Sample 8223) and *Mabella*–*Sowerbyella* (Sample 8228) Associations. However, the other taxa, which include the two new genera and species *Olgambonites insolita* and *Zhilgyzambonites extenuata* together with rare *Anisopleurella*, *Chonetoidea* and *Kassinella*, are not present in shallow shelf associations. In addition, there are seven localities (Table 7) whose brachiopods cannot be referred with confidence to any of the six named associations.

Although comprehensive comparisons of the Anderken faunas with other contemporary brachiopods from elsewhere are beyond the scope of this paper, it is worth noting here that the total Anderken assemblage has much in common with that described from north-west China (Fu 1982).

SYSTEMATIC PALAEONTOLOGY

Figured and cited specimens are housed in the Natural History Museum, London (BB and BC collection numbers), Institute of Geological Sciences, Almaty, Kazakhstan (IGNA collection numbers), and in the CNIGR Museum, St. Petersburg, Russia (CNIGR collection numbers). All the quoted sample numbers are from the Anderken Formation except where stated. Bibliographical references to families and above are omitted if they are in the *Treatise on Invertebrate Paleontology* (Kaesler 2000).

Abbreviations given in tables of measurements and in the text are: Lv, Ld – sagittal ventral and dorsal valve length; W – maximum width; T – maximum thickness; Ml, Mw – length and width of the muscle field; Sw, St – width and height of tongue in the ventral valve; BBl, BBw length and distance between outer margins of brachioophores or socket ridges; Sl – length of median ridge; LPl,

LPw length and width of lophophore platform; X – mean; S – standard deviation from the mean; r – coefficient of correlation; OR – observed range; max. – maximum value; min. – minimum value; N – number of measured or counted specimens.

Order **LINGULIDA** Waagen, 1885
 Superfamily **LINGULOIDEA** Menke, 1828
 Family **OBOLIDAE** King, 1846
 Subfamily **GLOSSELLINAE** Cooper, 1956
 Genus **ECTENOGLOSSA** Sinclair, 1945

TYPE SPECIES. *Lingula lesueuri* Rouault, 1850, from the Arenig of Normandy, France.

***Ectenoglossa sorbulakensis* Popov, 1980** Pl. 1, figs 1–4
 1980 *Ectenoglossa sorbulakensis* Popov: 142, pl. 1, figs 1–4.
 1984 *Ectenoglossa sorbulakensis* Popov; Nikitin & Popov in Klenina *et al.*: 142, pl. 1, figs 1–4.

HOLOTYPE. CNIGR 1/11523, ventral internal mould, from the Anderken Formation, locality 1024, east side of Karatal valley.

MATERIAL. Six pairs of conjoined valves, 26 ventral and 31 dorsal valves from Sample 8130a, Anderkenyn-Akchoku; Samples 8227–10, 8227–40 (BC 57370–73), 8227–80, Buldukbai Akchoku; 8228a, east side of Kopalysai; all Chu-Ili Range; Sample 1024, east side of Karatal Valley, south Betpak-Dala.

DESCRIPTION. Shell equivalved, elongate, subrectangular in outline, about 190% as long as wide with maximum width at mid-length, ornamented by fine concentric fila about 13–15 per mm. Ventral valve very gently convex with narrow, triangular pseudointerarea, mainly occupied by deep pedicle groove and small propareas crossed by flexure lines. Dorsal valve gently convex, lacking pseudointerarea. Ventral interior with pair of slightly diverging, elongate, suboval umbonal muscle scars flanked laterally by pair of short diverging ridges; pedicle nerve impression well defined. Dorsal interior with weak median ridge.

DISCUSSION. *Ectenoglossa sorbulakensis* closely resembles *Ectenoglossa minor* Zhan & Cocks (1998: 14) from the Lower Ashgill of South China in having a strongly elongate equivalved shell with subparallel lateral margins, rudimentary ventral pseudointerarea and propareas with well defined flexure lines. However, the interiors of both valves are weakly impressed in the Chinese

species, which makes precise comparison difficult. The main difference of the Kazakh species from the latter is the less elongate shell outline, which is no more than twice as long as wide. A detailed description, discussion and the basic statistics of this species was provided by Popov (1980).

Superfamily **DISCINOIDEA** Gray, 1840
 Family **TREMATIDAE** Schuchert, 1893
 Genus **TREMATIS** Sharpe, 1848

TYPE SPECIES. *Orbicula terminalis* Emmons, from the Trenton Group (Caradoc), New York, U.S.A.

***Trematis?* sp** Pl. 1, figs 5, 6

MATERIAL. Figured dorsal valve, BC 57375 (L=14.8, W=14.4) and another dorsal valve, Samples 127, 8228, Kopalysai.

DESCRIPTION. Shell subcircular, ornamented by radial capillae of about 5 per 1 mm enlarged in number by intercalation and with radially arranged rounded or transversely suboval pits in the interspaces between capillae. Ventral valve unknown. Dorsal valve gently and unevenly convex in transverse profile with maximum height about one-third of the valve length from the marginal umbo. Dorsal interior unknown.

DISCUSSION. These specimens are similar to the shells described by Cooper (1956: 275) as *Trematis* sp. 3 from the *Cyrtototella* Zone of the Edinburg Formation (Caradoc) of Virginia in their pits and radial ornament. The ventral valve in both unnamed species remains unknown, and therefore the generic attribution is provisional.

Family **DISCINIDAE** Gray, 1840
 Subfamily **ORBICULOIDEINAE** Schuchert, 1929
 Genus **SCHIZOTRETA** Kutorga, 1848

TYPE SPECIES. *Orbicula elliptica* Kutorga, presumably Volkhov or Kunda Stage (Upper Arenig-Lower Llanvirn), vicinity of St. Petersburg, Russia.

***Schizotreta* sp.** Pl. 1, figs 7–10

MATERIAL. One pair of conjoined valves, one ventral and two dorsal valves from Samples 100 (BC 57590) and 626, Anderkenyn-Akchoku section; Samples 628 (BC 56825), 2538, Kujandysai section

PLATE 1

Figs 1–4 *Ectenoglossa sorbulakensis* Popov. Sample 8227–40, Buldukbai-Akchoku section, west side of Kopalysai. **1**, BC 57370, ventral exterior, $\times 2$. **2**, BC 57372, dorsal internal mould, $\times 2$. **3**, BC 57371, dorsal exterior, $\times 2$. **4**, BC 57373, ventral internal mould, $\times 2$.

Figs 5, 6 *Trematis?* sp. Sample 8228, east side of Kopalysai, BC 57375, dorsal exterior and surface ornament, $\times 6$, $\times 2$.

Figs 7–10 *Schizotreta* sp. Sample 100, Anderkenyn-Akchoku section, BC 57590, conjoined valves, posterior, dorsal, lateral and ventral views, $\times 2$.

Fig. 11, 12 *Mesotreta?* sp. Sample 100, Akchoku Mountain, Anderkenyn-Akchoku section, CNIGR 1/12361, ventral exterior and lateral view, $\times 8$.

Figs 13, 14 *Nushbiella dubia* Popov. Sample 2538, Akchoku Mountain, Kujandysai section, BC 57591; **13**, dorsal exterior, $\times 8$; **14**, ventral exterior, $\times 8$.

Fig. 15 *Paracraniops* sp. Sample 8128a, Anderkenyn-Akchoku section, BC 57377, dorsal internal mould, $\times 5$.

Figs 16–21 *Longvillia lanx* (Popov), Sample 1018, area 7 km southwest of Karpkuduk well, Kotnak mountains, south Betpak-Dala. **16, 17**, CNIGR 27/11989, latex cast of cardinalia and dorsal interior, $\times 5$, $\times 2$. **18–20**, CNIGR 27/11989, dorsal, ventral and lateral views of conjoined valves, $\times 1$. **21**, CNIGR 30/11989, **holotype**, ventral internal mould, $\times 2$.

Figs 22–28 *Bellimurina* (*Bellimurina*) *sarytumensis* sp. nov. **22, 23**, Sample 8214, BC 57379, **holotype**, Anderkenyn-Akchoku section, ventral exterior and lateral view, $\times 2$. **24, 25**, Sample 2538, Akchoku Mountain, Kujandysai section, BC 57378, conjoined valves, dorsal and ventral views, $\times 3$. **26**, Sample 1041a, Burultas Valley, BC 57364, dorsal internal mould, $\times 2$. **27**, Sample 100, Anderkenyn-Akchoku section, BC 57380, ventral exterior, $\times 3$. **28**, Sample 2538, CNIGR 10/12361, dorsal external mould, $\times 3$.

Fig. 29 *Dolerorthis expressa* Popov. Sample 1018, 7 km southwest of Karpkuduk well, Kotnak Mountains, BC 57368, ventral internal mould, $\times 1.5$.

Figs 30, 31 Furcitellinae gen. et sp. indet. Sample 628, west side of Kujandysai, BC 57381, ventral and dorsal views of conjoined valves, $\times 1.5$.

DESCRIPTION. Shell planoconvex, subcircular, ornamented by strong rounded irregular concentric rugellae of 10–11 per 3 mm. Ventral valve low, subconical with maximum height at the umbo which is situated about 10% of the valve length from the posterior margin. Pedicle foramen small, rounded, located at the end of narrow pedicle track covered by listrium. Dorsal valve flat with submarginal umbo. Interior of both valves not observed.

MEASUREMENTS. BC 57590, conjoined valves, L=14.8, W=14.4, T=4.8.

DISCUSSION. These specimens resemble *Schizotreta triangularis* Popov (Nikitin *et al.* 1996: 85) from the late Caradoc Dulankara Regional Stage of the northern Betpak-Dala Desert, Central Kazakhstan, but differ in their subcircular valve outline, ventral umbo situated close to the posterior margin and strong, irregular concentric rugellae. In concentric ornament they somewhat resemble *Schizotreta corrugata* Cooper (1956: 277) from the Llandeilo Pratt Ferry Formation of Alabama, USA, but can be distinguished in having a larger size, more circular shell outline and more densely spaced concentric rugellae.

Order **SIPHONOTRETIDA** Kuhn, 1949

Superfamily **SIPHONOTRETOIDEA** Kutorga, 1848

Family **SIPHONOTRETIDAE** Kutorga, 1848

Genus **MESOTRETA** Kutorga, 1848

TYPE SPECIES. *Siphonotreta tentorium* Kutorga, 1848: 270, from the Arenig (Volkhov Regional Stage), north-western Russia.

DISCUSSION. The type material of *Mesotreta tentorium* is lost and its taxonomic position within the Siphonotretoidea is unclear. At present, our knowledge of the type species of this genus is based on a single incomplete ventral valve from the Upper Volkhov Stage (Holmer & Popov 2000: Fig. 79,2). *Mesotreta* is unique among the Siphonotretida because of its low conical ventral valve with small, slightly eccentric pedicle foramen, but it possesses the hollow spines characteristic of this order. The ventral interior and dorsal valve of *Mesotreta* remain unknown.

***Mesotreta?* sp.** Pl. 1, figs 11, 12

1986 *Nushbiella dubia* (Popov); Kolobova & Popov: pl. 1, fig. 1, non fig. 2.

MATERIAL. One ventral valve (CNIGR 1/12361) from Sample 100, Anderkenyn-Akchoku section.

DESCRIPTION. Valve slightly transverse, elliptical in outline; low, subconical with eccentric umbo at 20% of valve length from the posterior margin. Foramen small, slightly elongate, suboval. Concentric ornament of up to 16 thin, evenly spaced, crowded growth lamellae and numerous fine hollow spines. Ventral interior and dorsal valve unknown.

DISCUSSION. This unnamed species resembles *Siphonotreta tentorium* in having a low conical ventral valve lacking a well-defined pseudointerarea and small umbonal pedicle foramen, but the Kazakhstani specimen differs in its strongly developed lamellose ornament and more posterior ventral umbo.

Genus **NUSHBIELLA** Popov in Kolobova & Popov, 1986

TYPE SPECIES. *Multispinula? dubia* Popov, 1977; from the Bestamak Formation, Tselinograd Regional Stage (Llandeilo), Chingiz Range, Kazakhstan.

***Nushbiella dubia* (Popov, 1977)** Pl. 1, figs 13, 14

1977 *Multispinula? dubia* Popov: 104, pl. 25, figs 8–11.

1986 *Nushbiella dubia* (Popov) Kolobova & Popov: 251, pl. 1, fig. 2, non fig. 1.

2000 *Nushbiella dubia* (Popov) Holmer & Popov: fig. 79, 6a, b.

HOLOTYPE. CNIGR 1/10847, ventral valve, Bestamak Formation (Llandeilo), locality 553a, east side of Chagan River near Konur-Aulie cave, Chingiz Range, Kazakhstan.

MATERIAL. One ventral and one dorsal valve from Sample 8223a, Anderkenyn-Akchoku section; Sample 2538 (BC 57591), Kujandysai section.

DISCUSSION. The specimens from the Anderken Formation have no significant differences from the rather older topotypes in ornament and external shell morphology.

Order **CRANIOPSIDA** Gorjansky & Popov, 1985

Superfamily **CRANIOPSOIDEA** Williams, 1963

Genus **PARACRANIOPS** Williams, 1963

TYPE SPECIES. *Craniops pararia* Williams, 1962, from the Lower Ardmillan Series (Caradoc), Girvan, Scotland.

***Paracraniops* sp.** Pl. 1, fig. 15

MATERIAL. One dorsal internal mould, BC 57377, from Sample 8128a, Anderkenyn-Akchoku section.

DISCUSSION. A single specimen represents the earliest record of craniopsides from Kazakhstan. There is little doubt of the generic attribution, but there is insufficient material to allow detailed comparison with other named species of the genus.

Order **STROPHOMENIDA** Öpik, 1934

Superfamily **STROPHOMENOIDEA** King, 1846

Family **STROPHOMENIDAE** King, 1846

Subfamily **STROPHOMENINAE** King, 1846

Genus **LONGVILLIA** Bancroft, 1933

TYPE SPECIES. *Orthis grandis* J.de C. Sowerby, 1839, from the Cheney Longville Flags (Lower Caradoc), Shropshire, England.

***Longvillia lanx* (Popov, 1985)** Pl. 1, figs 16–21

1985 *Strophomena lanx* Popov: 58; pl. 1, fig. 13; pl. 2, figs 12, 13; pl. 3, fig. 1.

1985 *Strophomena digna* Popov: 67 *nomen erratum*. pl. 1, fig. 13.

HOLOTYPE. CNIGR 30/11989, ventral internal mould, from the Anderken Formation, Sample 1018a, 7 km south-west of Karpkuduk well, Kotnak Mountains, refigured here (Pl. 1, fig. 21).

MATERIAL. Two pairs of conjoined valves, 11 ventral and 8 dorsal valves from Samples 1018, 1018a, 7 km south-west of Karpkuduk well, Kotnak Mountains.

DESCRIPTION. Shell very gently convexiconcave, slightly transverse, subrectangular in outline with maximum width about one-quarter of the valve length from the hinge line. Anterior commissure rectimarginate. Ventral valve gently and evenly concave in profile with a slightly raised, pointed umbo and steeply apsacline ventral interarea bearing large, convex pseudodeltidium. Dorsal valve evenly convex with flattened umbonal area. Radial ornament

unequally parvicostellate in posterior half of mature valves with 2–4 parvicostellae between accentuated ribs, becoming near equally parvicostellate anteriorly with 5–8 ribs along the anterior margin. Ventral interior with strong teeth and low, diverging dental plates continuing anteriorly as straight muscle bounding ridges bordering posteriorly the open subtriangular muscle field which is about 30% as long as the valve. Adductor scars narrow, weakly impressed, flanked laterally by slightly longer diductor scars. Dorsal interior with cardinal process, low, widely diverging, oblique socket ridges and a short median ridge up to 40% valve length. Adductor field weakly impressed.

MEASUREMENTS. CNIGR 29/11989, conjoined valves, L=22.5, W=26.4, Iw=23.6, T=5.1; CNIGR 30/11989, ventral internal mould, holotype, L=26.8, W=28.3, MI=8.8, Mw=9.6; CNIGR 35/11989, dorsal internal mould, L=16.7, W=18.5, T=3.5, SI=7.8.

DISCUSSION. This species was originally referred to *Strophomena*, but it is characterised by an open ventral muscle field bounded posterolaterally by dental plates and short, diverging bounding ridges, a short dorsal median ridge and the absence of side septa, all suggesting attribution to *Longvillia*. It differs from the type species *Longvillia grandis* in its less transverse outline, with the maximum width slightly anterior to the hinge line, the radial ornament becoming nearly regular in the anterior half of the shell, and in possessing a somewhat stronger median ridge.

Subfamily **FURCITELLINAE** Williams, 1965

Genus **BELLIMURINA** (*BELLIMURINA*) Cooper, 1956

TYPE SPECIES. *Leptaena charlottae* Winchell & Schuchert, from the Caradoc of Minnesota, U.S.A.

Bellimurina (*Bellimurina*) *sarytumensis* sp. nov. Pl. 1, figs. 22–28.

1986 *Bellimurina rudis* [sic] Lu; Kolobova & Popov: pl. 1, fig. 10.

ETYMOLOGY. After Sarytuma Well in the Betpak-Dala Desert.

HOLOTYPE. BC 57379, Pl. 1, figs 22, 23, a ventral valve from Sample 8214, Anderkenyn-Akchoku section.

MATERIAL. Two pairs of conjoined valves, ten ventral and four dorsal valves from Samples 100 (BC 56826, BC 57380), 620 (BC 56827–28) and 626 (BC 56829–31), Anderkenyn-Akchoku section; Sample 8214 (BC 56839–40, BC 57379), west side of Ashchisu River; Samples 628 (BC 56837), 2538 (BC 56838, BC 57378) and 8256 (BC 56841), Kujandysai section; Sample 948 (BC 56832–36), Tesik River; Samples 390 (BC 57365), 1041a (BC 57364), Burultas Valley.

DESCRIPTION. Shell concavoconvex, slightly transverse, subrectangular in outline, about 70% as long as wide with maximum width at mid-length with rounded cardinal extremities and rectimarginate anterior commissure. Ventral valve convex with maximum height at geniculation (about three-quarters valve length). Ventral interarea apsacline with well developed pseudodeltidium perforated apically by a minute foramen. Dorsal valve flattened with geniculation near the anterior margin. Dorsal interarea low, linear, anacline with a well-developed chilidium. Radial ornament unequally parvicostellate with 6–7 accentuated ribs originating at the umbo and up to 7 strong ribs in interspaces. About 4–7 fine parvicostellae per mm along the anterior margin. Concentric ornament

Table 8 Measurements of ventral valves of *Beillimurina sarytumensis* sp. nov. from samples 100, 626 and 8214 from Anderkenyn-Akchoku section, Sample 2538 from Kujandysai section and Sample F-1041a from Burultas valley.

	Lv	W	L/W
N	6	6	6
X	7.8	11.1	69.4%
S	3.62	4.35	6.8
MIN	5.2	8	56.5%
MAX	14.8	19.5	75.9%

of fine, slightly uneven rugellae about 2 per mm, covering all the posterior half of the shell.

Ventral interior with small teeth supported by low, divergent dental plates and small, weakly impressed subtriangular muscle field. Dorsal interior with bilobed cardinal process, widely flaring socket plates, poorly impressed median septum extending about one-third valve length, poorly impressed pair of side septa subparallel to the median septum and not extending beyond it.

MEASUREMENTS. (435/12375) conjoined valves, L=6.4, W=8.3, T=3.0; (436/12375) ventral valve, L=15.4, W=21.3, T=5.4.

DISCUSSION. These shells are most similar to, and possibly conspecific with, the specimens described by Nikitin & Popov (1996: 16, figs 6J–N) as *Bellimurina?* sp. from the Dulankara Regional Stage of north Betpak-Dala in general shell shape and radial ornament with 6–7 accentuated primary ribs, but the dorsal interior in specimens from the Dulankara Stage remains unknown. The Kazakh shells are similar to the specimens described as *Kiaeromena longxianensis* Fu, 1982 from the Pinling Formation of northwest China in size, ornament and weakly geniculated lateral profile, but further comparison is difficult because of poor description and insufficient illustrations of that species, although it is unlikely to belong to *Kiaeromena*, which is known only from the Baltic. Cooper (1956) described eight species of *B. (Bellimurina)* from the Caradoc of Laurentia, of which he named six, but the dorsal interiors do not match *B. (B.) sarytumensis*, nor do those of *B. (B.) rudis* Xu, Rong & Liu (1974) from the early Caradoc Shitzupu Formation of South China. *B. (B.) quadrata* Fu (1982) appears more quadrate in outline and its interior is not illustrated (see also under *Limbimurina?* sp. below).

Genus **TERATELASMELLA** Laurie, 1991

TYPE SPECIES. *Teratelmella plicata* Laurie, 1991, from the Upper Cashions Creek Limestone (Lower Caradoc), Tasmania, Australia.

Teratelmella chugaevae sp. nov. Pl. 2, figs 10–20; Figs 10, 11.

ETYMOLOGY. In memory of the late Marina Chugaeva to honour her outstanding trilobite work.

HOLOTYPE. BC 57392, Pl. 2, figs 14–18, conjoined valves, from the Anderken Formation, Sample 626, Anderkenyn-Akchoku section.

MATERIAL. 16 pairs of conjoined valves and 3 dorsal valves from the Anderkenyn-Akchoku section, Samples 100 (BC 56842–51, BC 57390–91) and 626 (BC 56853–57, 57392); Kujandysai section, Samples 628 (BC 56858) and 85258 (BC 56852).

DESCRIPTION. Shell strongly dorsibiconvex, transverse, suboval, about 70% as long as wide, with maximum width at mid-length, and

Fig. 10 Transverse serial sections of conjoined valves of *Teratelasmella chugaevae* sp. nov. from Sample 100. Distance in mm is measured from the posterior tip of ventral beak. Dorsal valve uppermost. Also lateral view to show section positions and schematic reconstruction.

90% as thick as long. Anterior commissure strongly uniplicate. Ventral valve moderately convex with maximum thickness near quarter valve length. Interarea high, triangular, apsacline with delthyrium completely covered by pseudodeltidium perforated by a small umbonal foramen. Ventral sulcus originating at the umbonal area, strongly deepening anteriorly and ending with prominent, semielliptical tongue inclined at less than a right angle to the commissural plane. Flanks of the valve flattened, slightly inclined to the commissural plane. Dorsal valve very strongly convex, with a low, anacline interarea. Strong median fold, rounded in cross-section, with steep lateral slopes originating near the beak. Very weak and narrow dorsal median sulcus in the umbonal area of some specimens. Radial ornament coarsely parvicostellate with 5 ribs per 3 mm along the posterior margin of mature specimens.

Interiors of both valves were studied in transverse sections (Figs 10, 11). Ventral valve with strong teeth supported by high dental plates continuing anteriorly as muscle bounding ridges. Low median ridge in the anterior half of the ventral muscle field. Dorsal valve interior with bilobed cardinal process and low, curved socket ridges. Median septum high, triangular, blade-like, extending anteriorly to mid-valve, flanked laterally by a pair of short side septa. Adductor field raised anteriorly and bordered by a high rim.

DISCUSSION. This species is similar only to *Teratelasmella plicata*

Laurie, 1991, but it can be distinguished in being larger (up to 25.6 mm wide), with a strongly dorsibiconvex lateral profile, a deep ventral sulcus, a high dorsal median fold originating in the umbonal area rather than at the mid-valve as in the type species, and coarser radial ornament.

Furcitellinae gen. et sp. indet.

Pl. 1, figs 30, 31, Pl. 2, figs 1–4

MATERIAL. Four pairs of conjoined valves, two ventral and six dorsal valves from Samples 100 (BC 56859, 57382, 57384) and 626, Anderkenyn-Akchoku section; Sample 628 (BC 56577, 56863, 57381) and 8220 (BC 56578), Kujandysai section; Sample 1041a (BC 56860–62, 57383), Burultas Valley.

DESCRIPTION. Shell convexoplane, transverse, subrectangular in outline with maximum width near mid-length. Cardinal extremities nearly right angled. Anterior commissure rectimarginate. Ventral valve almost flat with acute and slightly erect beak. Ventral interarea low apsacline with convex pseudodeltidium. Dorsal valve evenly convex with low, orthocline interarea and well-developed chilidium. Radial ornament parvicostellate. Up to 10 mm from the umbo the ribs are nearly equal in size and are 7–9 per 3 mm. In larger specimens 2–5 finer costellae become inserted between the larger

Fig. 11 Transverse serial sections of *Teratelasmella chugaevae* sp. nov. from Sample 100. Distance in mm is measured from the posterior tip of ventral beak. Dorsal valve uppermost. Also lateral view to show section positions and schematic reconstruction.

ribs and ornament becomes unequally parvicostellate, with up to 4 accentuated ribs and 9–15 parvicostellae per 3 mm along the anterior margin.

Ventral interior with delicate teeth and long, divergent dental plates. Ventral muscle field subtriangular, open anteriorly. Dorsal interior with bilobed cardinal process. Other characters of dorsal interior unknown.

DISCUSSION. Within the Furcitellidae as revised by Cocks & Rong (2000) these shells are comparable with *Quondongia* (Percival 1991:151) and *Molongcola* (Percival 1991:153) from the Caradoc of

Australia in their planoconvex lateral shell profile and in the absence of geniculation, but they differ from *Molongcola* in possessing parvicostellate ornament. The absence of information on the dorsal interior makes precise generic attribution impossible.

Family **GLYPTOMENIDAE** Cooper, 1956

Genus **GLYPTOMENA** Cooper, 1956

TYPE SPECIES. *Glyptomena sculpturata* Cooper, 1956, from the Chatham Hill Formation (Llandeilo), Virginia, U.S.A.

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***Glyptomena onerosa* Popov, 1980**

Pl. 2, figs 5–9

1980 *Glyptomena onerosa* Popov: 152, pl. 2, figs 5–7.

HOLOTYPE. CNIGR 50/11523, Anderken Formation, from Sample 100b, Anderkenyn-Akchoku section.

MATERIAL. 14 ventral and 24 dorsal valves from Samples 100b, 843 (BC 57387), 8135, 8137, 8235 (BC 57386), Anderkenyn-Akchoku section; Sample 7613 (BC 57388), Kujandysai section; Samples 8229 (BC 57385), 8257 (BC 56864–65), Buldukbai-Akchoku section; Sample 1018, 7 km SW of Karpkuduk well, Kotnak Mountains.

DESCRIPTION. Shell concavoconvex, semielliptical in outline, about 60% as long as wide, with maximum width at the hinge line. Cardinal extremities slightly acute. Anterior commissure rectimarginate. Ventral valve moderately convex in lateral profile with maximum thickness at about one-third valve length. Ventral interarea low, apsacine, with small apical pseudodeltidium. Dorsal valve flattened with dorsal geniculation at about 75% of valve length from the umbo. Dorsal interarea low, anacine with well developed, broad, convex chilidium. Radial ornament inequally parvicostellate with up to three generations of accentuated ribs separated by 2–5 parvicostellae in the interspaces. Number of ribs along the anterior margin of mature specimens varying from 11 to 15 per 3 mm. Concentric ornament of fine, regularly spaced concentric fila, about 20–25 per mm.

Ventral interior with strong teeth bearing rows of crenulations on the outer side and long, widely divergent dental plates. Ventral muscle field heart-shaped about one-third as long as the valve with strongly impressed diductor scar somewhat longer, but not enclosing slightly raised, narrow triangular adductor track. Dorsal interior with bilobed cardinal process on a low notothyrial platform and widely diverging socket ridges subparallel to the hinge line. Sockets deep, transverse, bearing strong vertical ridges on the anterior slope. Adductor scars weakly impressed, bisected by the fine median septum extending anteriorly about 60% of valve length. Pair of inner side septa about the same length as the median septum, slightly divergent proximally and curved towards the anterior of the median ridge near the mid-valve. Outer side septa very fine or completely absent in some specimens.

DISCUSSION. This species is similar to *Glyptomena sculpturata* Cooper, 1956, but differs in having a geniculated dorsal valve and more densely accentuated ribs.

Family **LEPTAENIDAE** Hall & Clarke, 1894Genus **LIMBIMURINA** Cooper, 1956

TYPE SPECIES. *Limbimurina insueta* Cooper, 1956, from the Nealmont Formation (Caradoc), Pennsylvania, U.S.A.

***Limbimurina?* sp.**

Pl. 3, fig. 1

MATERIAL. One ventral and five dorsal valves from Samples 100, 626 (BC 57395), 8223b (BC 56867–68), Anderkenyn-Akchoku section; Samples 628 and 2538 (BC 56866), Kujandysai section.

DESCRIPTION. Shell flattened, transverse, subrectangular in outline; strongly geniculate ventrally with a trail up to 4 mm long inclined at nearly right angles to the commissural plane. Cardinal extremities nearly right angled. Ventral valve strongly flattened posteriorly to the geniculation, with gently convex umbonal area. Ventral interarea low, planar, apsacine with apical pseudodeltidium. Dorsal valve with strong angular concentric rugae accentuating the geniculation. Dorsal interarea anacine. Radial ornament unequally parvicostellate with 4–5 parvicostellae per mm along the anterior margin. Concentric ornament of oblique rugellae crossing each other at less than 30–40° and covering all the valve surface between hinge line and geniculation. Interior of both valves unknown.

MEASUREMENTS. dorsal valve, L=14.1, W=29.0.

DISCUSSION. Generic assignment of the Kazakh specimens to *Limbimurina* is based mostly on the distinctive shell shape, with strong geniculation enhanced by the characteristic concentric frill and the irregular oblique rugellae forming an interference pattern with concentric rugae in the posterior half of the shell. The specimens from the Anderken Formation differ from *Limbimurina brevilimbata* Cooper, 1956 from the Edinburg Formation of Virginia and *L. insueta* Cooper, 1956 from the Rodman Formation of Pennsylvania in the strongly transverse outline of the shell. The trail in the Kazakh shells is considerably higher than in *L. insueta*, but not as high as in *L. brevilimbata*.

Similar shells were also described as *Limbimurina?* sp. from the Dulankara Regional Stage (Upper Caradoc) of north Betpak-Dala (Nikitin & Popov 1996). They differ from the Anderken specimens in their more densely spaced parvicostellae, which vary from 11 to 14 per mm along the anterior margin.

A similar species is *Bellimurina quadrata* Fu, 1982, from the Pinling Formation of Northwest China, which also possesses a geniculation as well as a characteristic concentric frill, and irregular oblique rugellae forming characteristic interference patterns; but precise comparison is difficult because of the short description and insufficient illustrations. It most likely belongs to *Limbimurina*, but no detailed information was provided on the dorsal interior (Fu 1982:122, pl. 35, figs 20–21).

Family **CHRISTIANIIDAE** Williams, 1952Genus **CHRISTIANIA** Hall & Clarke, 1892

TYPE SPECIES. *Leptaena subquadrata* Hall, 1883, from the Caradoc of the U.S.A.

PLATE 2

Figs 1–4 *Furcitellinae* gen. et sp. indet. **1, 2, 4**, Sample 100, Anderkenyn-Akchoku section; **1, 2**, BC 57382, dorsal radial ornament and exterior, $\times 5$, $\times 2$; **4**, BC 57384, ventral internal mould, $\times 2$. **3**, Sample 1041a, Burultas Valley, BC 57383, ventral exterior, $\times 2.5$.

Figs 5–9 *Glyptomena onerosa* Popov. **5**, Sample 7613, Akchoku Mountain, Kujandysai section, BC 57388, dorsal valve ornament, $\times 3$. **6**, Sample 8229, Buldukbai-Akchoku section, west side of Kopalsai, BC 57385, ventral internal mould, $\times 2$. **7**, Sample 8235, Anderkenyn-Akchoku section, BC 57386, ventral internal mould, $\times 3$. **8**, Sample 100b, Anderkenyn-Akchoku section, CNIGR Museum, dorsal internal mould, $\times 4$. **9**, Sample 843, Anderkenyn-Akchoku section, BC 57387, dorsal exterior, $\times 1.5$.

Figs 10–20 *Teretelasmella chugaevae* sp. nov. Anderkenyn-Akchoku section. **10–13, 19, 20**, Sample 100; **10–13, 19**, BC 57391, conjoined valves, anterior, posterior, dorsal, lateral and ventral views, $\times 1.5$; **20**, BC 57390, conjoined valves, posterior view, $\times 2$. **14–18**, Sample 626, BC 57392, conjoined valves, holotype, dorsal, posterior, lateral, ventral and anterior views, $\times 1.5$.

Cristiania egregia Popov, 1985 Pl. 3, figs 2–6, 8

1985 *Christiania egregia* Popov: 60, pl. 2, figs 7–11.

HOLOTYPE. CNIGR 25/11989, dorsal internal mould from the Anderken Formation, Sample 1018, 7 km south-west of Karpkuduk Well, Kotnak Mountains.

MATERIAL. Eight pairs of conjoined valves, 17 ventral and 30 dorsal valves from Samples 100 (BC 56875–81), 843, 626 (BC 56869–70), 8214 (BC 56871–2), Anderkenyn-Akchoku section; Samples 7613, 628 (BC 56587, 56886–89), Kujandysai section; Sample 1041a (BC 57396–98), Burultas Valley; Sample 1024b, east side of Karatal River near Sorbulak well; Sample 1018 (BC 56873–74), 7 km south-west of Karpkuduk well, Kotnak Mountains.

DESCRIPTION. Shell concavoconvex, strongly elongated, suboval in outline, about 160% as long as wide with maximum width about two-thirds valve length from the hinge line. Cardinal extremities subrectangular, usually slightly alate. Anterior commissure broadly uniplicate. Ventral valve moderately convex in lateral profile with maximum thickness at about one-third valve length, about 20% as thick as long. Ventral interarea strongly apsacline to orthocline with a large convex pseudodeltidium perforated apically by a minute, circular foramen. Very weak ventral sulcus originating at the umbonal area. Dorsal valve gently concave with hypercline interarea and complete, convex chilidium. Radial ornament finely parvicostellate, rarely preserved.

Ventral interior with strong, transverse teeth and low, widely diverging dental plates. Muscle field weakly impressed, bilobate, with short, linear adductor scars bisected by a fine median ridge. Dorsal interior with bilobed cardinal process, low, curved socket ridges subparallel to the hinge line and two pairs of strong side septa. Dorsal median septum very fine, about 61% as long as the valve. Adductor scars bordered anteriorly by strong muscle bounding ridges curved posteriorly.

DISCUSSION. Detailed discussion of this species was provided by Popov (1980: 61). Among the Kazakh species it is most similar to *Christiania tortuosa* Popov, 1980 from the Lidievka Formation (Llandeilo-Lower Caradoc) of north-central Kazakhstan, but differs in having a weak ventral sulcus, very fine radial ornament and a long

dorsal median ridge extending far beyond the mid-valve. There are a large number of nominal *Christiania* species known globally, and the genus as a whole is due for revision.

Christiania aff. *sulcata* Williams, 1962 Pl. 3, figs 7, 9–17

MATERIAL. Three pairs of conjoined valves, 23 ventral and 10 dorsal valves from Samples 8223 (BC 56585–6), 8223a, 8223b (BC 57399, 57401), Anderkenyn-Akchoku section; Sample 8215 (BC 56583–4), west side of Ashchisu River; Samples 628 (=K-107/1970) (BC 56593), 2538 (BC 56579, 81, 89), 8217 (BC 57400), 8220 (BC 56592), Kujandysai section.

DESCRIPTION. Shell concavoconvex, elongate and subtrapezoidal in outline, as long as wide with maximum width at three-quarters valve length. Hinge line about 85% of maximum shell width. Cardinal extremities near right-angled and slightly alate. Lateral commissures near straight, slightly diverging anteriorly. Anterior commissure gently uniplicate. Ventral valve strongly convex in profile with maximum thickness at about one-third valve length. Ventral interarea strongly apsacline to near orthocline with narrow convex pseudodeltidium perforated apically by a minute rounded foramen. Lateral sides of the valve steep inclined near right angle towards the commissural plane. A shallow sulcus v-shaped in cross-section originating near the umbo and flanked by two distinct plications rounded in cross-section. Dorsal valve moderately concave with low and narrow median fold. Dorsal interarea hypercline with a convex chilidium. Shell surface finely and equally parvicostellate with 16 to 18 parvicostellae along the anterior margin of mature specimens.

Ventral interior with small, bilobed muscle field, fine teeth and rudimentary dental plates. Dorsal interior with a double cardinal process, low, curved socket ridges, thin median septum extending somewhat anterior of mid-valve and two pairs of strong side septa.

MEASUREMENTS. (457/12375) ventral valve, L=8.2, Iw=5.7, W=6.8, T=3.8, Sw=3.2; 458/12375), dorsal valve, L=5.6, Iw=5.2, W=5.3, Sw=2.2

DISCUSSION. These specimens resemble *Christiania sulcata* Williams, 1962, from the Stinchar Limestone (Upper Llandeilo-

PLATE 3

Fig. 1 *Limbimurina* sp. Sample 626, Anderkenyn-Akchoku section, BC 57395, ventral exterior, $\times 1.5$.

Figs 2–6, 8 *Christiania egregia* Popov. **2, 3**, Sample 1041a, Burultas Valley, BC 57396, lateral and ventral views of exterior, $\times 2$. **4**, Sample 1018, area 7 km west of Karpkuduk well, Kotnak Mountains, south Betpak-Dala, CNIGR 22/11989, latex cast of dorsal interior, $\times 2$. **5**, Sample 1041a, BC 57397, dorsal valve interior, $\times 2$. **6**, Sample 1018, CNIGR 23/11989, ventral internal mould, $\times 2$. **8**, Sample 1041a, BC 57398, conjoined valves dorsal view showing interareas, $\times 4$.

Figs 7, 9–17 *Christiania* aff. *sulcata* Williams. **7**, Sample 628, west side of Kujandysai, BC 56593, dorsal exterior, $\times 4$. **9**, Sample 8223b, Anderkenyn-Akchoku section, BC 57399, ventral exterior, $\times 3$. **10**, Sample 8217, BC 57400, ventral exterior, $\times 3$. **11–16**, Sample 2538, Akchoku Mountain, Kujandysai section; **11**, BC 56589, dorsal external mould, $\times 3$; **12–14**, BC 56579, conjoined valves, posterior view, $\times 8$, dorsal and ventral views, $\times 6$; **15**, **16**, BC 56581, dorsal internal mould and latex cast, $\times 5$. **17**, Sample 8223b, BC 57401, ventral internal mould, $\times 3$.

Figs 18–23, 25 *Foliomena prisca* sp. nov. **18, 19, 21–23**, Sample 8255, Anderkenyn-Akchoku section; **18**, BC 57402, latex cast of dorsal exterior, $\times 4$; **19**, BC 57403, latex cast of dorsal exterior, $\times 4$; **21**, BC 57404, latex cast of dorsal exterior, $\times 4$; **22, 23**, BC 57405, **holotype**, latex cast and dorsal internal mould, $\times 4$. **20**, Sample 100, Anderkenyn-Akchoku section, BC 57407, dorsal exterior, $\times 4$. **25**, Sample 8217, Kujandysai section, BC 57408, ventral internal mould, $\times 4$.

Fig. 24 *Kassinella* (*Kassinella*)? sp. Sample 2531, Anderkenyn-Akchoku section, BC 56497, dorsal internal mould, $\times 8$.

Figs 26–34 *Craspedelia tata* Popov. **26–28**, Sample 626, Anderkenyn-Akchoku section, BC 57409, conjoined valves, dorsal, lateral and ventral views, $\times 4$. **29–30**, Sample 100, BC 57410, dorsal exterior and anterior views, $\times 3$. **31**, Sample 8238, CNIGR 9/12361, ventral exterior, $\times 2$. **32–34**, Sample 626; **32**, **34**, BC 57411, dorsal anterior and exterior view, $\times 3$; **33**, BC 57412, conjoined valves, dorsal view, $\times 5$.

Fig. 35 *Isophragma imperator* Popov, Sample 1018, 7 km southwest of Karpkuduk well, Kotnak Mountains, south Betpak-Dala, CNIGR 22/11522, latex cast of dorsal interior, $\times 2$.

Figs 36–40 *Acculina kulanketpesica* sp. nov. **36**, Sample 8231–40, Buldukbaï-Akchoku section, BC 57416, ventral exterior, $\times 2$. **37–40**, Sample 1041a, Burultas Valley; **37**, BC 57415, posterior view of ventral and dorsal interareas, $\times 5$; **38**, BC 12903, ventral interior, $\times 2$; **39, 40**, BC 12904, **holotype**, conjoined valves, ventral and dorsal views, $\times 3$.

Table 9 Measurements of ventral valves of *Christiania* aff. *sulcata* Williams, *Parastrophina*–*Kellerella* Association, Anderkenyn-Akchoku and Kujandysai sections.

	Lv	W	Iw	Sw	Lv/W	Iw/W	Sw/W
N	9	9	6	5	9	6	5
X	6.5	5.6	4.8	2.5	115.0%	87.8%	42.9%
S	1.91	1.15	0.85	0.73	16.1	6.4	12.4
MIN	4.0	4.4	3.9	1.7	90.9%	82.8%	23.0%
MAX	9.4	7.4	6.3	3.2	147.5%	100.0%	54.2%

Lower Caradoc) of Girvan, Scotland, but differ in having an elongate subtrapezoidal shell outline and two rounded plications flanking the ventral sulcus. A characteristic feature of the Kazakh specimens is the absence of high ridges bordering the dorsal adductor field anteriorly, which also appear to be absent in *C. sulcata* (Williams 1962: pl. 18, fig. 36). *Christiania* aff. *sulcata* also differs from *C. egregia* in having a stronger ventral median sulcus which is v-shaped in cross-section, a distinctive dorsal median fold and significantly smaller size.

Family **FOLIOMENIDAE** Williams, 1965
Genus **FOLIOMENA** Havlíček, 1952

TYPE SPECIES. *Strophomena folium* Barrande, 1879, from the Králův Dvůr Formation (Ashgill) of Bohemia.

Foliomena prisca sp. nov. Pl. 3, figs 18–23, 25

ETYMOLOGY. After *priscus*, Latin – old.

HOLOTYPE. BC 57405, Pl. 3, figs 22, 23, a dorsal valve, from the Anderken Formation, Sample 8255, Anderkenyn-Akchoku section.

MATERIAL. 2 pairs of conjoined valves, 4 ventral and 3 dorsal valves from Samples 100 (BC 57407), 2531, 8221 (BC 56890), 8223b, 8251, 8255 (BC 57402–06, 08), Anderkenyn-Akchoku section; 628, 2538, 8217, Kujandysai section.

DESCRIPTION. Shell flat and gently resupinate, transverse, subrectangular in outline, about 60% as long as wide, with maximum width at hinge line. Cardinal extremities near right angled. Anterior commissure rectimarginate. Ventral valve gently convex in the posterior half and weakly concave anteriorly. Ventral interarea apsacline with a minute, apical pseudodeltidium. Dorsal valve with lateral profile flat to slightly concave in the posterior half and convex posteriorly, with maximum thickness at about three-quarters valve length in mature specimens. Dorsal interarea linear, anacline, with separate chilidial plates flanking narrow notothyrium. Radial ornament of fine capillae rarely preserved. Concentric ornament of numerous slightly uneven fine rugellae.

Ventral interior with delicate teeth lacking dental plates and an open, weakly impressed muscle field. Dorsal interior with a small bilobed cardinal process in the low notothyrial platform and thin widely diverging socket ridges. Thin median septum, about half the length of the pair of strong curved side septa.

MEASUREMENTS. (463/12375) ventral valve, L=6.0, W=11.7; (464/12375) ventral valve, L=6.4, W=11.4; (466/12375) dorsal valve, L=4.3, W=7.2; (468/12375) dorsal valve, L=4.6, W=8.5; (469/12375) dorsal valve, L=3.6, W=6.3.

DISCUSSION. Cocks & Rong (1988:65) discussed the variation in the ornament of *Foliomena* and noted that, although all the shells from the type locality in Bohemia were devoid of radial ornament,

occasional costae or costellae can be present sporadically in some populations. The presence of fine capillae is a key feature in our new species, as is the resupinate shell shape and the separate chilidial plates, although the features within the interarea are poorly known in *Foliomena folium*. It is difficult to make a precise comparison of our shells with *F. inelegans* Fu, 1982 from the Pingliang Formation (Upper Caradoc) of North China, because of inadequate information on the interior of the latter species. From *F. jieliangensis*, described by Zeng (1987) from the Miapo Formation (Lower Caradoc) of the Yangtze Gorge area, south China, *F. prisca* differs in the presence of the fine ornament, the resupinate shell shape and in the absence of the ventral internal tuberculae seen in *F. jieliangensis*.

Superfamily **PLECTAMBONITOIDEA** Jones, 1928
Family **PLECTAMBONITIDAE** Jones, 1928
Subfamily **TAPHRODONTINAE** Cooper, 1956
Genus **ISOPHRAGMA** Cooper, 1956

TYPE SPECIES. *Isophragma ricevillense* Cooper, 1956, from the Lower Caradoc of Tennessee, U.S.A.

Isophragma imperator Popov, 1980 Pl. 3, fig. 35

1980 *Isophragma imperator* Popov: 147, pl. 2, figs 8–12.

HOLOTYPE. CNIGR 25/11523, from Sample 1018, 7 km south-west of Karpkuduk Well, Kotnak Mountains.

MATERIAL. One pair of conjoined valves, 36 ventral and 34 dorsal valves from Sample 1018.

DISCUSSION. Popov (1980) provided detailed description and discussion of this species.

Family **BIMURIIDAE** Cooper, 1956
Genus **CRASPEDELIA** Cooper, 1956

TYPE SPECIES. *Craspedelia marginata* Cooper, 1956: 773, pl. 213, figs. 1–20, from the Pratt Ferry Formation (Landeilo), Alabama, U.S.A.

Craspedelia tata Popov, 1980 Pl. 3, figs 26–34

1980 *Craspedelia tata* Popov: 55, pl. 17, figs 6–9.

1986 *Craspedelia tata* Popov; Kolobova & Popov: pl. 1, fig. 9.

HOLOTYPE. CNIGR 8/11098, from the Lidievka Formation (Lower Caradoc), Belyi Kardon, north-central Kazakhstan.

MATERIAL. 25 pairs of conjoined valves, 18 ventral and 5 dorsal valves from Samples 100 (BC 56900–03, 57410, 57597) (=K98/1970), 626 (BC 56532, 56907–10, 57409, 57411–12), 8223a (BC 56935), 8223b, Anderkenyn-Akchoku section; Samples 8214 (BC 56925–30, 56932–33, 57598), 8215b (BC 56931), west side of Ashchisu River; Samples 628 (BC 56911), 2538 (BC 56917–24), Kujandysai section; Sample 8231–40, Buldukbai-Akchoku; Sample 948 (BC 56912–16), Tesik River.

DESCRIPTION. Shell smooth, concavoconvex posteriorly, strongly geniculated ventrally with a trail up to 8 mm long which curves back postero-ventrally; semielliptical in outline, about 80% as long as wide, with maximum width slightly anterior to hinge line. Cardinal extremities rounded. Anterior commissure uniplicate. Ventral valve strongly convex posteriorly with maximum thickness about one-third anteriorly. Narrow and shallow sulcus anterior to the

geniculation. Dorsal valve strongly concave with low, planar interarea and notothyrium covered by joined apical chilidial plates. Weak median fold originating anterior to the geniculation. Shell surface smooth with fine growth lines. Ventral interior with strong teeth and *vascula media* subparallel. Dorsal interior with simple, undercut cardinal process, divided bema, low median ridge and a pair of slightly diverging side ridges bisecting the bema.

DISCUSSION. This species differs from *Craspedelia marginata* Cooper (1956) and *C. gabata* Williams (1962: 179), from the Lower Ardwell Formation (Middle Caradoc) of Girvan, in its high (up to 8 mm) ventrally directed trail with a well-defined ventral sulcus and dorsal median fold. It differs from *C. intonsa* Potter, 1991, from Member 1 of the Gregg Ranch Unit (Llandeilo), of California, USA, in having a larger shell, up to 12 mm long, with a less transverse outline and a high trail, which exceeds the thickness of the ventral valve in mature specimens.

Family **LEPTELLINIDAE** Ulrich & Cooper 1936
Subfamily **LEPTELLININAE** Ulrich & Cooper 1936
Genus **ACCULINA** Misius, in Misius & Ushatinskaya, 1977

TYPE SPECIES. *Acculina acculica* Misius in Misius & Ushatinskaya, 1977, from the Tabylgaty Formation (Lower Caradoc: *gracilis* Zone), Moldo-Too Range, North Kirgystan.

Acculina kulanketpesica sp. nov. Pl. 3, figs 36–40, Pl. 4, figs 1–5

ETYMOLOGY. After Kulanketpes (‘donkey cannot escape’ in Kazakh) Valley on the way from Lake Balkhash to the type locality.

HOLOTYPE. BC 12904, Pl. 3, figs 39, 40, conjoined valves, from the Anderken Formation, Sample 1041a, Burultas section.

MATERIAL. 50 pairs of conjoined valves, 13 ventral and 10 dorsal valves from Samples 100 (=K98/1970) (BC 56493–5, 56485–90, BC 57414), 620 (BC 56937–39), 626, 8128, Anderkenyn-Akchoku section; Sample 8231–40 (BC 57416, 18), Buldukbai-Akchoku; Sample 1041a (BC 12900–7, 57413, 15, 19), Burultas Valley; Samples 85258 (BC 56491–2, 56941–6), 2538 (BC 56501–02), Kujandysai.

DESCRIPTION. Shell resupinate, transverse, semielliptical in outline, about 70% as long as wide and 35% as thick as long. Cardinal extremities near right-angled or slightly acute. Anterior commissure rectimarginate. Ventral valve gently to moderately concave in the anterior half and slightly convex posterior to the mid-valve. Ventral interarea apsacline with a narrow, convex pseudodeltidium. Dorsal valve flat and gently sulcate between the umbo and mid-length, becoming moderately convex anteriorly. Interarea anacline with a narrow, convex chilidium completely covering the notothyrium. Radial ornament unequally parvicostellate with 7 accentuated costae in the umbonal area and 27–30 accentuated costellae along the

anterior and lateral margins in full grown specimens. Interspaces between the accentuated costellae occupied by fine parvicostellae about 7–10 per mm along the anterior margin. Fine, closely spaced growth lamellae form comae crossed by accentuated ribs in the anterior half of the shell.

Ventral valve with strong teeth with central grooves; lacking dental plates. Ventral muscle field small, rounded pentagonal with strongly impressed diductor scars completely divided by slightly shorter, narrow, triangular adductor scars. Ventral mantle canals saccate with slightly diverging *vascula media*. Dorsal valve interior with trifid cardinal process situated on the low notothyrial platform. Socket ridges low, widely diverging and slightly incurved posteriorly. Dorsal adductor muscle field subquadrate, bordered laterally by low, subparallel ridges. Median ridge high and strongly thickened, extended anteriorly to the mid-valve, merging with high diaphragm bordering the lophophore platform. Dorsal mantle canals lemniscate.

DISCUSSION. This species also occurs in Betpak Dala, Kazakhstan (the locality in Nikitin & Popov 1996). It differs from *Acculina acculica* Misius (in Misius & Ushatinskaya 1977: 114) in its significantly larger shell, strongly convex anteriorly transverse profile of the dorsal valve and numerous comae (Pl. 3, fig. 39) in the anterior part of full grown specimens. It is also similar to *A. villosa* Nikitina (1985: 24) from the Rgaity Formation (Llandeilo-Lower Caradoc) of the Kandyktas Range, south Kazakhstan, in the development of comae, but can be distinguished in having a well-defined peripheral rim in the ventral valve, a somewhat smaller dorsal lophophore platform, which has a subrectangular, not a flabellate outline, and a pair of fine transmuscle ridges dividing the anterior and posterior adductors. *Acculina* is the only plectambonitoid in the Anderken Formation to possess comae, and its exterior is also normally covered by encrusting girvanellid algae. Two specimens (BC 56502–3, Pl. 4, figs 7, 8) from the Kujandysai section from Sample 2538 differ from other *Acculina* in having a geniculate shell with the lophophore platform less than half the valve length, and probably represent a separate species.

Genus **DULANKARELLA** Rukavishnikova, 1956

TYPE SPECIES. *Dulankarella magna* Rukavishnikova 1956, from the Dulankara Formation (late Caradoc), Kazakhstan, Chu-Ili Range, Kazakhstan.

Dulankarella larga sp. nov. Pl. 4, figs 9–25, Pl. 5, figs 1–3

ETYMOLOGY. After *largus*, Latin – rich.

HOLOTYPE. BC 57421, Pl. 4, figs 9, 10, a dorsal valve interior from Anderken Formation, Sample 8231–40, Buldukbai-Akchoku section.

MATERIAL. 86 pairs of conjoined valves, 3 ventral and 2 dorsal valves, from Samples 100 (=K98/1970) (BC 56514, 16–18, 25–29, 57422, 24, 26), 626 (BC 56522–4), 8223a (BC 56511, 56975), Anderkenyn-Akchoku; Sample 8231–40 (BC 57421, 23), Buldukbai-Akchoku; Sample 8228 (BC 56986), east side of Kopalsai River; Samples 1041a (BC 56512, 19–21, 56947–57), 818a, 1041a (BC 56967, 57425), Burultas Valley.

DESCRIPTION. Shell strongly concavoconvex, transverse and semielliptical in outline, on average 73% as wide as long, with maximum width at the hinge line and 45% as thick as long. Cardinal extremities slightly acute. Anterior commissure weakly sulcate. Ventral valve strongly and evenly convex in lateral profile, subcarinate posteriorly in transverse profile. Ventral interarea low, planar, anacline

Table 10 Basic statistics of complete shells of *Acculina kulanketpesica* sp. nov. from Sample F-1041a, Burultas valley.

	Lv	Ld	W	T	Lv/W	Ld/W	T/Lv
N	6	5	6	5	6	5	5
X	15.5	14.7	22.6	5.4	68.9%	65.6%	34.5%
S	0.89	0.92	0.85	1.13	1.9	2.1	7.0
MIN	14.0	13.5	21.3	3.8	65.7	63.4	24.1
MAX	16.4	16.1	23.5	7.0	71.2%	68.5%	42.9%

Table 11 Basic statistics of complete shells of *Dulankarella larga* sp. nov. from Sample F-1041a, Burultas valley.

	Lv	W	T	Lv/W	T/Lv
N	9	9	7	9	7
X	16.9	24.6	7.7	69.7%	46.1%
S	2.10	3.57	1.19	10.2	3.2
MIN	13.5	19.1	5.7	51.9%	41.5%
MAX	18.8	31.6	9.2	81.3%	50.0%

with delthyrium partly covered by a convex pseudodeltidium. Dorsal valve strongly concave and slightly geniculate anteriorly. Dorsal interarea hypercline with chilidial plates joined apically. Sulcus broad and shallow, originating near mid-valve. Radial ornament unequally parvicostellate with 5–7 accentuated ribs originating at the umbo and two or three generations of accentuated costellae, totaling 31–38 in number in full grown specimens. Parvicostellae between accentuated ribs very fine and closely spaced, about 12–16 per mm along the anterior margin.

Ventral valve interior with strong teeth supported by short dental plates, thickened at the base. Muscle field bilobed with strongly impressed, rounded subrhomboidal diductor scars separated by short, elongate subtriangular adductor scars. Paired nodose swellings anterolateral to the muscle field. Ventral mantle canals saccate with short, divergent *vascula media*. Dorsal interior with trifid cardinal process bearing a strong, ridge-like median lobe and up to 6 fine ridges on the lateral lobes. Socket ridges narrow, widely diverging. Median septum strongly raised and thickened anteriorly with the maximum height at the point of junction with the outer boundary of the lophopore platform accentuated by geniculation of the valve.

DISCUSSION. This species resembles the later *Dulankarella magna* Rukavishnikova (1956:139) in size and transverse profile, but differs in having a finer radial ornament with 5–7 strongly accentuated primary ribs and a characteristic rounded subrhomboidal outline of the ventral diductor scars, which only slightly touch each other anteriorly to the adductor scars. The differences from *Dulankarella? partita* Percival (1979b: 103) are in having a less transverse outline, evenly convex ventral valve, the ventral muscle field lacking a median ridge, and the rhomboidal outline of the ventral diductor scars.

Genus *KAJNARIA* Nikitin & Popov, 1984

TYPE SPECIES. *Kajnaria derupta* Nikitin & Popov in Klenina *et al.* (1984), from the Bestamak Formation (Lower Caradoc), Chingiz Range, Kazakhstan.

Kajnaria rugosa sp. nov.

Pl. 5, figs 6–18

ETYMOLOGY. After *rugosus*, Latin – wrinkled.

HOLOTYPE. BC 56551, Pl. 5, figs 12, 13, a dorsal internal mould from Sample 628, Kujandysai section.

MATERIAL. 9 pairs of conjoined valves and three ventral valves from Samples 100 (BC 56545–47, 57436, 37), 626 (BC 56548), 8223a, Anderkenyn-Akchoku section; Sample 628 (=K107/1970) (BC 56551, 57439), Kujandysai section; Sample 1041a (BC 56543, 44), Burultas Valley; Sample 816 (BC 56549–50, 57438), Alakul lake.

DESCRIPTION. Shell strongly concavoconvex, semielliptical in outline, about 67–82% as long as wide with maximum width at the hinge line. Cardinal extremities acute and slightly alate in adult specimens. Ventral valve strongly convex in lateral profile, weakly geniculate in some specimens, with maximum thickness posterior to mid-length. Relatively weak umbo. Interarea anacline with narrow convex pseudodeltidium. Dorsal valve moderately and evenly convex with hypercline interarea. Notothyrium completely covered by convex chilidium. Radial ornament unequally parvicostellate with 5–7 primary accentuated ribs and two to three generations of accentuated costellae, with the interspaces between them covered by fine closely-spaced parvicostellae, about 7–14 per mm. Concentric ornament of up to 9 undulated rugellae in the posterior half of both valves.

Ventral interior with strong teeth lacking dental plates. Ventral muscle field small, strongly supported by raised muscle bounding ridges which merge centrally and anteriorly. A further pair of strong curved ridges originate posteriorly at one-third of the length of the hinge line on each side of the valve, and curve anterolaterally to form a w-shaped structure which terminates near the end of the bounding ridges at about quarter valve length. Mantle canals saccate with *vascula media* subparallel in the proximal part and diverging anteriorly. Dorsal interior with erect trifid cardinal process fused anteriorly to a strong median ridge. Sockets large. The median ridge merges near the mid-length with a high subperipheral rim bordering the lophopore platform.

DISCUSSION. This species differs from *Kajnaria derupta* in the twice as large shell size and the well defined concentric rugellae in the posterior half of the valves.

Genus *MABELLA* Klenina, 1984

TYPE SPECIES. *Leptellina (Mabella) semiovalis* Klenina in Klenina *et al.* (1984), from the Taldyboy Formation, Dulankara Regional Stage (Upper Caradoc), Chingiz Range, Kazakhstan.

PLATE 4

Figs 1–5 *Acculina kulanketpesica* sp. nov. **1**, Sample 1041a, Burultas Valley, BC 57413, dorsal interior, $\times 2$. **2**, Sample 8137, Anderkenyn-Akchoku section, BC 57417, latex cast of dorsal interior, $\times 3$. **3**, Sample 100, Anderkenyn-Akchoku section, BC 57414, dorsal exterior view of conjoined valves, $\times 2$. **4**, Sample 1018, area 7 km SW of Karpkuduk well, Kotnak Mountains, ventral internal mould, $\times 3$. **5**, Sample 85258, east of Uzunbulak River, BC 56491, ventral internal mould, $\times 2$.

Fig. 6 *Glyptambonites* sp., Sample 628 (=K-107/70), west side of Kujandysai, BC 56510, ventral exterior, $\times 3$.

Figs 7, 8 *Acculina* sp. Sample 2538, Akchoku Mountain, Kujandysai section. **7**, BC 56502, latex cast of dorsal interior, $\times 2$. **8**, BC 56501, ventral internal mould, $\times 1.5$.

Figs 9–25 *Dulankarella larga* sp. nov. **9, 10, 16**, Sample 8231–40, Buldukbaï-Akchoku section, west side of Kopalysai; **9, 10**, BC 57421, **holotype**, dorsal interior, $\times 2.7$; cardinal process and socket plates, $\times 5$; **16**, BC 57423, ventral internal mould, $\times 2$. **11–13, 19–21, 24, 25**, Sample 1041a, Burultas Valley; **11–13**, conjoined valves, lateral, ventral and dorsal views, $\times 2$; **19–21**, BC 57425, conjoined valves, ventral, dorsal and lateral views, $\times 2$; **24**, Sample 1041a, BC 56512, conjoined valves, posterior view showing interareas, $\times 6$; **25**, BC 56967, dorsal view of conjoined valves, $\times 2$. **14, 15, 17, 18, 22, 23**, Sample 100, Anderkenyn-Akchoku section; **14**, BC 56514, incomplete dorsal valve interior, $\times 3$; **15**, BC 57422, ventral internal mould, $\times 2$; **17, 18**, BC 57424, conjoined valves, ventral and dorsal views, $\times 1.5$; **22, 23**, BC 57426, ventral valve exterior, anterior and ventral views, $\times 2$.

SPECIES INCLUDED. *Leptellina (Mabella) semiovalis* Klenina, in Klenina *et al.* 1984: 69, pl. 5, figs. 1, 3, 4; pl. 9, figs 4, 7 (= *Leptellina (Mabella) obtusa* Klenina, in Klenina *et al.* 1984: 71, pl. 5, figs 5, 6; pl. 6, fig. 2; = *Leptellina (Mabella) incurvata* Klenina, in Klenina *et al.* 1984: 72, pl. 5, fig. 2), Upper Caradoc, beds tb_{II-V} of Taldyboi Formation, Chingiz Range, Kazakhstan; *Leptellina? conferta* Popov, 1985: 56, pl. 2, figs 1–6, Lower Caradoc, Anderken Formation, Chulii Range; *Leptelloidea multicostata* Rukavishnikova, 1956: 132; *Wiradjuriella halis* Percival, 1991: 138, fig. 12A–Z, Aa–Al, Upper Caradoc, New South Wales, Australia; *Leptellina* sp., Percival, 1979b, Ordovician, Goonumbla Volcanics, New South Wales, Australia.

DISCUSSION. *Mabella* differs from *Leptellina* in the distinctive median septum which enlarges anteriorly, and is sometimes bifurcating and tubular. However, *Wiradjuriella*, from the Caradoc of Australia (Percival 1991), has this same structure as *Mabella* and can be considered congeneric with it (Cocks & Rong 2000).

***Mabella conferta* (Popov, 1985) Pl. 5, figs 19–29**

1985 *Leptellina? conferta* Popov: 56, pl. 2, figs 1–6, text-figs 1, 2.
1991 *Wiradjuriella conferta* (Popov) Percival: 140.

HOLOTYPE. CNIGR 17/11989, ventral internal mould from the Anderken Formation, Sample 100b, Anderkenyn-Akchoku section.

MATERIAL. 35 pairs of conjoined valves, 183 ventral and 66 dorsal valves from Samples 100, 100b, 843, 8128a, 8128b, 8137 (BC 56982–84), Anderkenyn-Akchoku section; Sample 7613, Kujandysai section; Samples 110, 8229, 8230 (BC 57440), 8257, Buldukbai-Akchoku; Sample 8228 (BC 57441, 43–46), east side of Kopalsai River; Samples 818a (BC 57442), 1041a (BC 56978–81), Burultas Valley; Samples 1018, 1018a, 7 km south-west of Karpkuduk well, Kotnak Mountains.

DESCRIPTION. Shell concavoconvex, transverse, semioval in outline, length about three-quarters of the width, with maximum width at the hinge line. Anterior commissure rectimarginate. Ventral valve strongly convex in transverse and lateral profiles with the maximum thickness slightly posterior to mid-length. Planar strongly apsacline interarea and small, convex pseudodeltidium. Dorsal valve gently concave to almost flat, with a planar, anacline interarea and disjunct chilidial plates. Radial ornament very fine, unequally parvicostellate, with up to five accentuated parvicostellae per 3 mm along the anterior margin of mature specimens.

Ventral interior with strong teeth lacking dental plates. Cordate muscle field with short, ridge-like adductor scars completely separating strongly impressed diductor scars. Strong, slightly divergent, saccate mantle canals. Dorsal interior with low, trifid cardinal process facing posteriorly, short socket ridges subparallel to the hinge line.

Lophophore platform about 90% valve length and 87% as wide as maximum valve width, bordered by a high, ridge-like rim divided medially. High median septum about three-quarters as long as the valve, not joined anteriorly with the subperipheral rim.

DISCUSSION. This species was originally assigned to *Leptellina* and later referred by Percival (1991) to *Wiradjuriella*. Percival also listed and discussed the differences between the various species of the genus, which is so far known only from Australia and Kazakhstan.

Genus *SHLYGINIA* Nikitin & Popov, 1983

TYPE SPECIES. *Shlyginia declivis* Nikitin & Popov, 1983, from the Andriushino Formation, Tselnograd Regional Stage (Llandeilo-Lower Caradoc), north-central Kazakhstan.

DISCUSSION. The affinities of *Shlyginia* and its differences from *Dulankarella* were discussed by Nikitin & Popov (1996).

Table 12 Measurements of complete shells of *Shlyginia fragilis* (Rukavishnikova) Sample 8228 and 8257 from Kopalsai section.

	Lv	W	T	L/W	T/L
N	16	16	16	16	16
X	10.4	16.3	4.2	64.0%	40.4%
S	1.04	1.34	0.54	6.2	4.5
MIN	8.5	13.6	2.9	50.0%	31.2%
MAX	12.2	19	5.1	72.1%	51.8%

Table 13 Measurements of ventral valves of *Shlyginia fragilis* (Rukavishnikova) Sample 8228 from Kopalsai section.

	Lv	W	MI	Mw	Lv/W	MI/L	MI/Mw
N	6	6	6	6	6	6	6
X	9.4	12.8	3.6	4.3	75.2%	37.6%	83.5%
S	2.47	3.61	1.13	1.05	11.2	4.5	16.3
MIN	5.3	5.8	1.8	2.6	60.0%	30.5%	67.9%
MAX	12.8	15.5	5.3	5.6	91.4%	41.4%	110.4%

Table 14 Measurements of dorsal valves of *Shlyginia fragilis* (Rukavishnikova) Sample 8228 from Kopalsai section and sample 8229 from Buldukbai-Akchoku.

	Ld	W	SI	BBI	BBw	Ld/W	SI/L	BBw/W
N	6	6	3	6	6	6	3	6
X	8.1	12.1	5.5	1.2	3.8	67.7%	79.2%	31.7%
S	1.87	2.55	1.25	0.42	0.93	13.2	8.6	8.5
MIN	6.2	7.8	4.3	0.6	2.8	49.7%	69.4%	23.6%
MAX	10.8	14.8	6.8	1.8	5.0	82.1%	84.4%	43.6%

PLATE 5

Figs 1–3 *Dulankarella larga* sp. nov. **1, 2**, Sample 100, Anderkenyn-Akchoku, BC 57427, ventral exterior and lateral views, $\times 2$. **3**, Sample 1041a, Burultas Valley, BC 56513, interareas of conjoined valves, $\times 8$.

Figs 4, 5 *Chonetoidea* sp. Sample 8255, Anderkenyn-Akchoku section, BC 56537, external and internal moulds of conjoined valves, $\times 8$.

Figs 6–18 *Kajnarina rugosa* sp. nov. **6**, unnamed Lower Caradoc formation, about 4 km south-west of Lake Alakul, Sample 816, BC 57438, ventral internal mould, $\times 1.5$. **7–11, 14–16**, Sample 100, Anderkenyn-Akchoku; **7–10**, BC 57436, conjoined valves, lateral, posterior, ventral and dorsal views, $\times 2$; **11, 14–16**, BC 57437, conjoined valves, lateral, posterior, ventral and dorsal views, $\times 2$. **12, 13, 17, 18**, Sample 628, west side of Kujandysai River; **12, 13**, BC 56551, latex cast and dorsal internal mould, **holotype**, $\times 2$; **17, 18**, BC 57439, ventral internal mould, oblique posterior and oblique anterior views, $\times 2$.

Figs 19–29 *Mabella conferta* (Popov). **19, 21, 26, 28, 29**, Sample 8228, east side of Kopalsai; **19**, BC 57445, ventral internal mould, $\times 3$; **21**, BC 57443, ventral internal mould, $\times 4$; **26**, BC 57444, ventral internal mould, $\times 4$; **28**, BC 57446, dorsal exterior, $\times 4$; **29**, BC 57441, internal mould of conjoined valves of juvenile specimen, $\times 4$. **20**, Sample 8230, Buldukbai-Akchoku section, west side of Kopalsai, BC 57440, latex cast of dorsal interior, $\times 3$. **22–25**, Sample 818a, Burultas Valley, BC 57442, conjoined valves, dorsal, posterior, lateral and ventral views, $\times 4$. **27**, Sample 7613, Akchoku Mountain, Kujandysai section, CNIGR 20/11989, latex cast of dorsal interior of juvenile, $\times 3$.

Figs 30, 31 *Tesikella necopina* (Popov, 1980), Kopalsai, Rukavishnikova. **30**, Sample 34, BC 56881, ventral internal mould, $\times 2$. **31**, Sample 818a, Burultas Valley, BC 57435, $\times 2.5$.

Shlyginia fragilis (Rukavishnikova, 1956) Pl. 6, figs 11–25

1956 *Dulankarella fragilis* Rukavishnikova: 136, pl. 2, figs 16–23.

1996 *Shlyginia fragilis* (Rukavishnikova) Nikitin & Popov: 7.

HOLOTYPE. IGNA 28/1369, conjoined valves; Anderken Formation, east side of Kopalysai River.

MATERIAL. Eight pairs of conjoined valves, 57 ventral and 53 dorsal valves from Samples 100b (BC 56989), 620 (BC 56991–99), 843, 8128a, 8128b, 8135, 8137 (BC 57450), Anderkenyn-Akchoku section; Samples 628, 7613, 8258, Kujandysai section; Samples 110, 8230 (BC 57453), 8257, Buldukbaï-Akchoku; Sample 8228 (BC 12881–88, 57447, 48, 52), east side of Kopalysai River; Samples 390, 818 (BC 57451), 1041a, Burultas Valley; Sample 1018, area 7 km south-west from Karpkuduk well, Kotnak Mountains, south Betpak-Dala.

DESCRIPTION. Shell concavoconvex, transverse, semielliptical in outline, length about two-thirds of the width, with maximum width slightly anterior to hinge line or at the hinge line, and 40% as thick as long. Cardinal extremities acute to slightly rounded. Anterior commissure rectimarginate. Ventral valve moderately convex in transverse profile with maximum thickness at about one-third of valve length. Interarea low, planar, apsacline with small triangular delthyrium, covered apically by the minute pseudodeltidium. Dorsal valve moderately convex, slightly geniculate anteriorly with low, planar, hypercline interarea and notothyrium covered laterally by disjunct chilidial plates. Radial ornament finely parvicostellate with 8–11 parvicostellae per mm at the anterior margin and 4–8 parvicostellae between the accentuated costellae which originate in the umbonal area, near the mid-valve and anterior to mid-valve in full grown specimens.

Ventral valve interior with small teeth lacking dental plates. Muscle field flabellate, on average 80% as long as wide and 40% as long as the valve. Diductor scars large, suboval, deeply impressed and completely enclosing small lanceolate adductor scars bisected by a fine median ridge. Ventral mantle canals saccate with short diverging *vascula media*. Dorsal interior with a trifid cardinal process widely diverging, low and short socket ridges and strong median ridge joined anteriorly with the peripheral rim. Dorsal adductor field large, subquadrate.

DISCUSSION. This species differs from the type species *Shlyginia declivis* Nikitin & Popov (1983: 238, pl. 3, figs 1–5) in its larger size and moderately concave lateral profile of the dorsal valve, which is also weakly geniculate anteriorly.

Subfamily **PALAEOSTROPHOMENINAE** Cocks & Rong, 1989

Genus **GLYPTAMBONITES** Cooper, 1956

TYPE SPECIES. *Glyptambonites musculosus* Cooper, 1956, from the Oranda Formation (Caradoc) of Virginia, U.S.A.

Glyptambonites sp.

Pl. 4, fig. 6

MATERIAL. Three ventral valves, from Sample 628 (BC 56510), Kujandysai, Sample 100, Anderkenyn-Akchoku section.

DISCUSSION. *Glyptambonites* is a rare genus in the Anderken Formation and also uncommon in the overlying Dulankara Formation of the Chu-Ili Range. Its internal features are known from specimens from the latter, but not from the Anderken Formation. The exterior of our material appears similar to *Glyptambonites glyptus* Cooper, 1956 from the Llandeilo to early Caradoc of Virginia and Alabama.

Genus **TESIKELLA** gen. nov.

ETYMOLOGY. After the River Tesik.

TYPE SPECIES. *Palaeostrophomena necopina* Popov, 1980, from the Anderken Formation, Chu-Ili Range.

DIAGNOSIS. Shell profile resupinate, ventral valve with low interarea; chilidial plates disjunct; radial ornament unequally parvicostellate; ventral interior with double teeth lacking dental plates; ventral muscle field enclosed by bilobed bounding ridges; adductor scars short; ventral subperipheral rim variably developed; dorsal interior with strong median septum coalescing anteriorly with platform.

DISCUSSION. The subfamily Palaeostrophomeninae has the genera *Palaeostrophomena*, *Apatomorpha*, *Glyptambonites*, *Ishimia*, *Lepidomena*, *Titanambonites* and *Toquimia* definitely attributed to it, and *Goniotrema* is possibly a member (Cocks & Rong 2000). Of these, all are of normal convexity apart from *Palaeostrophomena* which is generally resupinate and *Toquimia*, in which resupination develops anteriorly in larger specimens. *Tesikella* is also resupinate and in external features resembles *Palaeostrophomena* apart from the irregular rugae, which are variable in the latter. However, internally *Tesikella* has a dorsal platform which is absent in *Palaeostrophomena*, and also has a variably developed subperipheral rim in the ventral valve which in some specimens is fully developed but in others consists only of semi-continuous papillae. The ventral muscle field is enclosed by bilobed bounding ridges, which are not present in other members of the subfamily, but are developed in other Leptellinidae.

PLATE 6

Figs 1–6 *Tesikella necopina* (Popov, 1980), Sample 8129, Anderkenyn-Akchoku section. **1**, BC 57433, ventral internal mould, $\times 2$. **2**, BC 57434, ventral exterior, $\times 2$. **3, 4**, BC 57604, latex cast, $\times 3$, and dorsal internal mould, $\times 2$. **5, 6**, BC 57432, latex cast, $\times 3$, and ventral internal mould, $\times 2$.

Figs 7–10 *Sowerbyella* (*Sowerbyella*) *rukavishnikovae* Popov. **7**, Sample 100b, Anderkenyn-Akchoku section, CNIGR 41/11522, latex cast of dorsal exterior, $\times 5$. **8**, Sample 110, Buldukbaï-Akchoku section, BC 57801, ventral internal mould, $\times 4$. **9**, Sample 1018a, 7 km southwest of Karpkuduk well, Kotnak Mountains, south Betpak-Dala, CNIGR 44/11522, dorsal interior, $\times 2.5$. **10**, Sample 100b, CNIGR 38/11989, dorsal interior, $\times 2.5$.

Figs 11–25 *Shlyginia fragilis* (Rukavishnikova). **11, 12, 17–19, 21, 23, 24**, Sample 8228, east side of Kopalysai; **11**, BC 57448, ventral internal mould, $\times 2$; **12**, BC 12882, ventral internal mould, $\times 3$; **17–19**, BC 57447, ventral, dorsal and lateral views of conjoined valves, $\times 2$; **21, 23, 24**, BC 57452, conjoined valves, lateral, dorsal and ventral views, $\times 2$. **13–16**, Sample 818, Burultas Valley, BC 57451, conjoined valves, ventral, dorsal and lateral views, $\times 4$; posterior view of interareas, $\times 6$. **20**, Sample 8230, BC 57453, dorsal internal mould, $\times 3$. **22**, Sample 8137, Anderkenyn-Akchoku section, BC 57450, ventral internal mould, $\times 3$. **25**, Sample 620, Anderkenyn-Akchoku section, BC 57449, ventral internal mould, $\times 3$.

Figs 26–33 *Sortanella* aff. *quinquecostata* Nikitin & Popov. **26–30**, Sample 2538, Akchoku Mountain, Kujandysai section; **26**, BC 57488, ventral internal mould, $\times 2$; **27–29**, BC 56771, conjoined valves, dorsal, ventral and lateral views, $\times 4$; **30**, BC 57460, ventral internal mould, $\times 4$. **31**, Sample 626, Anderkenyn-Akchoku section, BC 57458, dorsal exterior, $\times 2$. **32, 33**, Sample 100, Anderkenyn-Akchoku section, BC 57459, conjoined valves, dorsal and ventral views, $\times 2$.

Tesikella necopina (Popov, 1980)

Pl. 5, figs 30, 31, Pl. 6, figs 1–6

1980 *Palaeostrophomena necopina* Popov: 145, pl. 1, figs 8–11.

HOLOTYPE. CNIGR 15/11523 (L=11.4, W=16.8), dorsal internal mould, Anderken Formation, east side of Kopalysai, Sample 127/K-1970.

MATERIAL. Five pairs of conjoined valves, 60 ventral and 43 dorsal valves from Samples 8128, 8129 (BC 57432–34, 57604), 8138, Anderkenyn-Akchoku section; Sample 7613, Kujandysai section; Sample 127/K-1970 and Rukavishnikova (1956) Sample 34 (BC 56881), east side of Kopalysai; Sample 818a (BC 57435), Burultas Valley; Sample 1024b, east side of Karatal near Sorbulak well; Samples 1018, 1018a, area 7 km south-west of Karpkuduk well, Kotnak Mountains.

DESCRIPTION. Shell profile resupinate, transversely subrectangular outline, about 55–60% as long as wide with maximum width at the hinge line. Cardinal extremities slightly acute to near right angled. Anterior commissure rectimarginate, broadly rounded. Ventral valve with lateral profile slightly convex in the umbonal area, gently concave anteriorly. Ventral interarea low, planar, catacline with a well developed, narrow pseudodeltidium. Dorsal valve with moderately convex lateral profile, flattened posteriorly with low anacline interarea and separate chilidial plates. Radial ornament parvicostellate with 10–12 parvicostellae per mm in mature specimens and accentuated costellae of two-three generations.

Ventral interior with strong, double teeth lacking dental plates and large divided muscle field with strong diductor scars and muscle bounding ridges extending anteriorly to the mid-valve. Adductor scars small, strip-like, divided by a fine median ridge, about half the length of the diductor scars. Subperipheral rim variably developed, posterior to which is a weak median ridge. Mantle canals saccate with very short *vascula media* branching just beneath the anterior margin of the diductor scars. Dorsal interior with trifold cardinal process on a low notothyrial platform and low, widely diverging socket ridges. Median septum strong and narrow, about 75% as long as the valve and joined anteriorly to a low subperipheral rim. Adductor scars radially arranged with smaller anterior pair extending anteriorly to mid-valve.

DISCUSSION. Popov (1980) originally attributed the species to *Palaeostrophomena*, but since then the internal characteristics, particularly of the ventral valve, have become known, and it is clear that this species cannot properly be attributed to that genus.

Family XENAMBONITIDAE Cooper, 1956
Subfamily XENAMBONITINAE Cooper, 1956
Genus SORTANELLA Nikitin & Popov, 1996

TYPE SPECIES. *Sortanella quinquecostata* Nikitin & Popov, 1996, from the Dulankara Regional Stage (Upper Caradoc), north Betpak-Dala, Kazakhstan.

Sortanella aff. *quinquecostata* Nikitin & Popov, 1996
Pl. 6, figs 26–33

MATERIAL. Ten pairs of conjoined valves, 7 ventral and 8 dorsal valves from Samples 100 (=K98/1970) (BC 57459), 626 (BC 57000, 57006–9, 57458), Anderkenyn-Akchoku section; Samples 628, 2538 (BC 56771, 56810, 57010–03, 57460, 88), Kujandysai section; Tesik River, Sample 948 (BC 57002–5).

DISCUSSION. These specimens closely resemble *Sortanella quinquecostata* Nikitin & Popov (1996: 9) in radial ornament, posteriorly subcarinate ventral valve and gently uniplicate anterior commissure. The type locality is about 400 km to the north-west of our localities, and occurs in the overlying Dulankara Regional Stage which is late Caradoc rather than early to middle Caradoc. Because no dorsal interiors are known, the species cannot yet be identified from the Anderken Formation with certainty.

Subfamily AEGIROMENINAE Havlíček, 1961
Genus CHONETOIDEA Jones, 1928

Chonetoidea sp.

Pl. 5, figs 4, 5

TYPE SPECIES. *Plectambonites papillosa* Reed, 1905, from the Slade and Redhill Mudstone Formation (Middle Ashgill), Pembrokeshire, Wales.

MATERIAL. One internal and one external mould of a pair of conjoined valves, BC 56537 (L=3.2, W=5.1) from Sample 8255, Anderkenyn-Akchoku section.

DESCRIPTION. Shell planoconvex, transverse, semielliptical in outline with maximum width at the hinge line. Cardinal extremities acute. Anterior commissure rectimarginate. Ventral valve gently convex in lateral profile with maximum thickness slightly anterior to the apex. Interarea low, planar, anacline with minute apical pseudodeltidium. Dorsal valve flat with a low, anacline interarea. Chilidial plates separate. Radial ornament finely and unequally parvicostellate with five accentuated primary ribs and four secondary costellae originating at about mid valve length.

Ventral interior with small, bilobate muscle field bisected posteriorly by low median ridge. Dorsal interior with simple undercut cardinal process joined to minute socket ridges subparallel to the hinge line. Median ridge originating anterior to the deep alveolus and extending to mid-valve. Six septulae lateral to the anterior part of the median ridge near the mid-valve.

DISCUSSION. These specimens resemble *Chonetoidea virginica* Cooper (1956: 805), from the Edinburg Formation of Virginia, in the size and outline of the planoconvex shell, unequally parvicostellate radial ornament, and number and arrangement of septulae in the dorsal valve.

Family HESPERONOMIIDAE Cooper, 1956
Genus ANOPTAMBONITES Williams, 1962

TYPE SPECIES. *Leptaena grayae* Davidson, 1883, from the Craighead Limestone (Upper Caradoc) of Girvan, Scotland.

Anoptambonites convexus sp. nov.

Pl. 7, figs 5–26; Figs 12.1–12.6

1986 *Anoptambonites* sp.; Kolobova & Popov, pl. 1, figs 7, 8.

ETYMOLOGY. After *convexus*, Latin – convex.

HOLOTYPE. BC 57462, Pl. 7, figs 5, 6, a dorsal interior from Sample 100, Akchoku Mountain.

MATERIAL. 36 pairs of conjoined valves, 21 ventral and 14 dorsal valves from Samples 100 (=K98/1970) (BC 56540, 57014–32, 57462, 64, 69, 71), 626 (BC 57466, 68), 8214 (BC 57480), 8223 (BC 57063–68), 8223b (BC 57467), Anderkenyn-Akchoku section; Samples 628 (BC 56530, 42, 57043–51), 2538 (BC 56531, 57052–61),

Table 15 Measurements of complete shells and ventral valves of *Anoptambonites convexa* sp. nov., *Acculina–Dulankarella* Association, samples 100 and 626 from Anderkenyn-Akchoku section.

	Lv	W	T	Lv/W	T/Lv
N	18	17	8	17	8
X	12.1	16.5	6.9	71.6%	47.1%
S	4.24	5.26	1.86	7.5	6.3
MIN	5.8	8.2	3.5	57.8%	39.4%
MAX	18.0	23.9	9.6	86.5%	58.9%

Table 16 Measurements of complete shells and ventral valves of *Anoptambonites convexa* sp. nov., *Parastrophina–Kellerella* Association, samples 2538, 8217 and 8256 from Kujandysai section.

	Lv	W	T	Lv/W	T/Lv
N	11	11	4	11	4
X	6.4	9.9	2.8	65.5%	44.8%
S	1.13	2.33	0.57	7.6	6.1
MIN	5.2	6.6	2.0	57.0%	38.5%
MAX	9.0	15.3	3.2	79.3%	51.6%

57461, 63, 65), 8217, 8256 (BC 57070–73), Kujandysai section; Samples 8230 (BC 57069), 8231–40, Buldukbai-Akchoku.

DESCRIPTION. Shell concavoconvex, transverse, semielliptical in outline, about 72% as long as wide with maximum width at hinge line and thickness 47% of valve length. Cardinal extremities slightly acute to rectangular. Anterior commissure rectimarginate. Ventral valve carinate posteriorly, strongly convex in lateral profile with the maximum thickness at the point of geniculation somewhat anterior to mid-length. Beak pointed and slightly erect posterior to the hinge

line. Ventral interarea steeply apsacline to procline with mainly open delthyrium covered apically by the minute pseudodeltidium. Dorsal valve gently and unevenly concave in lateral profile, flat to mid-length. A shallow sulcus originates at the umbo and fades towards the anterior margin. Dorsal interarea anacline with convex chilidium. Radial ornament finely and near equally multicostellate with 28–43 primary ribs originating near the umbo and 4–6 ribs per mm at the anterior margin. Concentric ornament of fine, evenly spaced fila.

Ventral valve with teeth lacking dental plates. Muscle field small, cordate, bisected by fine median ridge separating small, lanceolate adductor scars. *Vascula media* short, widely diverging. Dorsal interior with undercut cardinal process bearing up to 8 ridges on both sides of strong central lobe. Lophophore platform semielliptical, bordered by a high rim joined to the median septum. Dorsal adductor muscle field subrectangular, about one-third as long as the valve.

VARIABILITY. The average size of *Anoptambonites convexus* from the *Acculina–Dulankarella* Association, which typically occurs within the nodular limestone deposited on the flanks of carbonate mud mounds (Sample 100), is one and half to two times larger than the average size of the shells from the pockets in the mud mound core (Samples 2538 and 8231–40) and the overlying bedded limestone (Samples 628, 8217, 8223, 8256) in which the *Parastrophina–Kellerella* Association characteristically occurs. However, the specimens from the *Parastrophina–Kellerella* Association retain a similar outline, transverse and lateral profile of the shells from the *Acculina–Dulankarella* Association and are also characterized by their multicostellate ornament which consists of 26 to 36 primary ribs and 4 to 6 ribs along the anterior margin of full grown specimens.

DISCUSSION. This species differs from *Anoptambonites grayae* (Davidson), as revised by Williams (1962: 171) from the Craighead

Fig. 12 1–6. *Anoptambonites convexus* sp. nov. 1, 4, 5, Anderkenyn-Akchoku section, 1, Sample 8223b, BC 57467, ventral exterior, $\times 3$; 4, 5, Sample 100, 4, BC 57470, ventral internal mould, $\times 2$; 5, BC 57472, ventral exterior, $\times 2$. 3, 6, Buldukbai section, 3, Sample 8230, BC 57069, ventral internal mould, $\times 3$; 6, Sample 8231, BC 57473, ventral internal mould, $\times 1.5$. 2, Kujandysai section, Sample 8256, ventral exterior, $\times 2$. 7–14, *Sowerbyella* (*Sowerbyella*) aff. *ampla* (Nikitin & Popov), 7–13, Kujandysai section, Sample 2538, 7, BC 57082, ventral exterior, $\times 3$; 8, 9, BC 57482, lateral and ventral views of ventral exterior, $\times 4$; 10, BC 57081, ventral internal mould, $\times 3$; 11, 12, BC 57479, anterior and ventral views of ventral exterior, $\times 3$; 13, BC 57481, ventral exterior, $\times 3$. 14, Anderkenyn-Akchoku section, Sample 8214, BC 57480, dorsal exterior, $\times 2.5$.

Limestone (Upper Caradoc) of Girvan, in having a strongly concavo-convex lateral profile, a cardinal process with up to 8 vertical ridges on the lateral lobes, a shorter median septum and a relatively small lophophore platform extending anteriorly only to the mid-valve. *Anoptambonites convexus* differs from two somewhat younger Kazakh species, *A. subcarinatus* Nikitin & Popov (1996:10) from the north Betpak-Dala and *A. kovalevskii* Popov, Nikitin & Cocks (2000), from the Dulankara Mountains, both from the Dulankara Regional Stage (Upper Caradoc to lowermost Ashgill), in having equally multicostellate radial ornament and a weakly geniculate ventral valve profile, with the maximum height anterior to the mid-valve and near the point of geniculation. It also differs from the former species in having a rectimarginate anterior commissure.

***Anoptambonites orientalis* Popov, 1980** Pl. 7, figs 1–4, 27
1980 *Anoptambonites orientalis* Popov:149; pl. 2, figs 12–17.

HOLOTYPE. CNIGR 30/11523, dorsal internal mould, from the Anderken Formation, Anderkenyn-Akchoku section, Sample 100b.

MATERIAL. Two pairs of conjoined valves, 14 ventral and 26 dorsal valves from Samples 100b, 8128a (BC 56533, 57476), 8128b, 8137 (BC 57478), Anderkenyn-Akchoku section; Sample 8230, Buldukbaï-Akchoku section, and Sample 1018, about 7 km south-west of Karpkuduk well, Kotnak Mountains.

DISCUSSION. Detailed description of this species was provided by Popov (1980). It differs from the contemporaneous *Anoptambonites convexus* sp. nov. as well as from the somewhat younger *A. subcarinatus* Nikitin & Popov, 1996 and *A. kovalevskii* Popov, Nikitin & Cocks, 2000 in having a flattened shell, a carinate ventral valve with gently and evenly convex lateral profile lacking geniculation, a very weakly concave dorsal valve, and in the presence of a small but well-defined pseudodeltidium. The platform in mature specimens of *A. orientalis* reaches up to 75% of the valve length, whereas in *A. convexus* and *A. kovalevskii* it barely exceeds half the valve length.

Genus **KASSINELLA (KASSINELLA)** Borissiak, 1956

TYPE SPECIES. *Kassinella globosa* Borissiak, 1956, from the Lower Ashgill Kulunbulak Formation, Tarbagatai Range, Kazakhstan.

***Kassinella (Kassinella)?* sp.** Pl. 3, fig. 24

MATERIAL. One dorsal internal mould, BC 56497, from Sample 2531, Anderkenyn-Akchoku section.

DISCUSSION. A single dorsal valve shows the undercut cardinal process and lack of both bema and side septa characteristic of the Hesperomenidae. It possesses an evenly semicircular platform and a median septum not extending anterior of the platform. This evenly

semicircular platform is unlike most species of *Hesperomena*, *Anoptambonites*, *Aulie* and *Chaganella*: within the family only *Kassinella (Kassinella)* has such a platform. However, without knowledge of the ventral interior and the exterior of both valves, generic assignment can only be provisional. *Kassinella (Kassinella)* is known from the late Caradoc and Ashgill of Kazakhstan, South China, Australia, Scotland, Bohemia and Sweden (Zhan & Cocks 1998:36), but if the record from the Anderken Formation is confirmed then this may be its earliest occurrence.

Family **SOWERBYELLIDAE** Öpik, 1930
Subfamily **SOWERBYELLINAE** Öpik, 1930
Genus **SOWERBYELLA (SOWERBYELLA)** Jones, 1928

TYPE SPECIES. *Leptaena sericea* J. de C. Sowerby, 1839, from the Horderley Sandstone (Lower Caradoc) of Shropshire, England.

***Sowerbyella (Sowerbyella) rukavishnikovae* Popov, 1980**
Pl. 6, figs 7–10

1980 *Sowerbyella rukavishnikovae* Popov: 151, pl. 2, figs 1–4.
1984 *Sowerbyella rukavishnikovae* Popov; Nikitin & Popov in Klenina *et al.*:150, pl. 16, figs 17–22.

HOLOTYPE. CNIGR 40/11523, a dorsal internal mould from the Anderken Formation, Anderkenyn-Akchoku section, Sample 100b.

MATERIAL. 70 ventral and 133 dorsal valves. Samples 100b (BC 56554–5), 848, 8128a, 8128b, 8137, Anderkenyn-Akchoku section; Sample 7613, Kujandysai section; Samples 110 (BC 57801), 8229, 8230, 8257, Buldukbaï-Akchoku; Sample 8228, east side of the Kopalysai River; Sample 1024b, east side of Karatal Valley, near Sorbulak well; Samples 1018, 1018a, 7 km south-west of Karpkuduk well, Kotnak Mountains.

DISCUSSION. Description, discussion and basic statistics of this species were provided by Popov (1980). Some further specimens from the Anderken Formation are illustrated here. This species is also reported from the upper Bestamak and lower Sargaldak Formations of the Chingiz Range (Nikitin & Popov in Klenina *et al.* 1984).

***Sowerbyella (Sowerbyella)* aff. *ampla* (Nikitin & Popov, 1996)** Figs 12.7–12.14

1986 *Anisopleurella* sp. Kolobova & Popov: pl. 1, fig. 6.
aff.1996 *Anisopleurella ampla* Nikitin & Popov: 12, figs 5K–R.

MATERIAL. 14 pairs of conjoined valves, 25 ventral and 8 dorsal valves from Samples 100 (=K98/70), 626, 2531, 8214 (BC 57480), 8215, 8223a, 8223b, Anderkenyn-Akchoku section; Samples 628, 2538 (BC 57081, 82, 57479, 81, 82), Kujandysai section; Sample 948 (BC 57084–85), Tesik River.

PLATE 7

Figs 1–4, 27 *Anoptambonites orientalis* Popov. **1–3**, Sample 8128a, Anderkenyn-Akchoku section; **1**, BC 56533, latex cast of dorsal interior, $\times 4$; **2, 3**, BC 57476, ventral internal mould and latex cast, $\times 2$. **4, 27**, Sample 8137, Anderkenyn-Akchoku section, BC 57478, latex cast and dorsal internal mould of immature specimen, $\times 4$.

Figs 5–26 *Anoptambonites convexus* sp. nov. **5, 6, 9, 10, 18, 20–22**, Sample 100, Anderkenyn-Akchoku section; **5, 6**, BC 57462, **holotype**, dorsal internal mould and latex cast, $\times 2$; **9, 10**, BC 57464, posterior view of conjoined valves showing interareas, $\times 1.5$ and $\times 5$; **18**, BC 57469, ventral exterior, $\times 2$; **20–22**, BC 57471, conjoined valves, ventral, lateral and dorsal views, $\times 2$. **7, 8, 11–16**, Sample 2538, Akchoku Mountain, Kujandysai section; **7**, BC 57461, ventral internal mould, $\times 3$; **8**, CNIGR 7/12361, ventral exterior, $\times 3$; **11, 12**, BC 57465, latex cast and dorsal internal mould, $\times 3$; **13–16**, BC 57463, conjoined valves, dorsal, lateral, ventral and posterior views, $\times 3$. **17, 23–26**, Sample 626, Anderkenyn-Akchoku section; **17**, BC 57466, ventral internal mould, $\times 1.5$; **23–26**, BC 57468, conjoined valves, dorsal, posterior, lateral and ventral views, $\times 2$. **19**, Sample 628 (=K-107/70), west side of Kujandysai, BC 56542, ventral internal mould, $\times 2$.

DESCRIPTION. Shell concavoconvex, transverse, semielliptical in outline, about 56% as long as wide, with maximum width at hinge line. Cardinal extremities acute and slightly alate. Anterior commissure broadly rounded and rectimarginate. Ventral valve moderately and unevenly convex in profile with the maximum thickness at about quarter valve length. Ventral interarea strongly apsacline and slightly curved in cross-section, with small triangular delthyrium covered apically by pseudodeltidium. Dorsal valve moderately concave, with hypercline interarea; notothyrium covered laterally by chilidial plates. Radial ornament unequally and finely parvicostellate with closely-spaced parvicostellae varying from 9 to 12 per mm. Five accentuated ribs originating at the umbo and four accentuated costellae inclined between them in the mid-valve. Indistinct radial plications developed sometimes along the accentuated ribs. About 6–9 strong concentric rugellae inclined below 30–40° towards the hinge line.

Ventral interior with small teeth lacking dental plates and small bilobate muscle field with flabellate diductor scars completely surrounding small lanceolate adductor scars. Dorsal interior with undercut cardinal process, small curved socket ridges, bilobed bema, short median ridge and two widely divergent side septa.

DISCUSSION. The Anderken specimens strongly resemble *Anisopleurella ampla* Nikitin & Popov (1996) from the slightly younger Dulankara Regional Stage of north Betpak-Dala, Central Kazakhstan, in size and general shell shape, but differ slightly in having a finer radial ornament with 9–12 parvicostellae per mm instead of 7–10 in the Dulankara specimens, and an uneven ventral valve lateral profile. *Anisopleurella ampla* is reassigned here to *Sowerbyella* (*Sowerbyella*) mainly because it has two pairs of side septa including a closely-spaced more prominent pair. In the variable development of strong concentric ornament it is similar to the subgenus *S.* (*Rugosowerbyella*), but differs in having a median septum and the two pairs of side septa, and in the small, weakly impressed ventral muscle field.

Genus *ANISOPLEURELLA* Cooper, 1956

TYPE SPECIES. *Anisopleurella tricostellata* Cooper, 1956, from the Pratt Ferry Formation (Llandeilo) of Alabama, U.S.A.

DISCUSSION. The relationships of *Anisopleurella* and other genera are unresolved. The Ordovician genera within the subfamily are *Sowerbyella*, *Anisopleurella*, *Eochonetes*, *Eoplectodonta*, *Gunningblandella* and our new genera *Olgambonites* and *Zhilgyzambonites*. *Eochonetes* and *Eoplectodonta* may be interpreted as *Sowerbyella* with hinge lines modified to form denticles (which resulted in the subsequent loss of dental plates), and

Gunningblandella and *Olgambonites* are resupinate modifications of *Sowerbyella*, which was a very plastic stock. *Anisopleurella* has a much more distinctive and erect dorsal median septum and side septa than *Sowerbyella*, with the side septa bisecting the divided bema but not reaching to the anterior edge of it. Both genera occur in rocks of Llandeilo age, but which of the two was ancestral is not known.

Anisopleurella sp.

Pl. 8, figs 1, 2, 5

MATERIAL. One ventral and one dorsal internal mould from Samples 2531 (BC 57489), 8255 (BC 56539), Anderkenyn-Akchoku section.

DISCUSSION. These specimens can be firmly assigned to *Anisopleurella* because they have the characteristic parvicostellate ornament with three accentuated ribs, a dorsal median ridge and a pair of widely diverging prominent side septa bisecting a bilobed bema. They are somewhat comparable to, and may be conspecific with, *Anisopleurella yichangensis* Zeng, 1987 from the early Caradoc Miaopo Formation of Hubei, South China, but the absence of well-preserved exteriors of the Chinese species makes detailed comparison impossible.

Genus *OLGAMBONITES* gen. nov.

ETYMOLOGY. After the late Olga Ivanova Nikiforova, a pioneer in brachiopod studies.

TYPE SPECIES. *Olgambonites insolita* sp. nov. from the Anderken Formation, Chu-Ili Range.

DIAGNOSIS. Shell convexiconcave; anterior commissure rectimarginate to weakly uniplicate; ventral interarea procline to slightly apsacline with apical pseudodeltidium; dorsal interarea anacline with separate chilidial plates; radial ornament unequally parvicostellate; ventral interior with small teeth lacking dental plates and small bilobed muscle field with short adductor scars completely separating larger diductor scars; ventral mantle canals lemniscate; dorsal interior with simple undercut cardinal process joined to narrow socket ridges; fine median ridge and bilobed bema bordered by rim and crossed by up to 8 side septa.

DISCUSSION. *Olgambonites* possesses an undercut cardinal process, divided bema and side septa in the dorsal valve; all characteristic of the Sowerbyellidae, but it differs from most genera in the family in having a convexiconcave shell. The only other resupinate genus is *Gunningblandella* (Percival 1979b) from the Caradoc of Australia, but *Olgambonites* differs from that genus in having a dorsal median septum and numerous side septa.

PLATE 8

- Figs 1, 2, 5** *Anisopleurella* sp. **1, 2**, Sample 8255, Anderkenyn-Akchoku section, BC 56539, dorsal internal mould and latex cast, $\times 12$. **5**, Sample 2531, Anderkenyn-Akchoku section, BC 57489, ventral internal mould, $\times 7$.
- Figs 3, 4, 6–10, 12, 13** *Zhilgyzambonites extenuata* gen. et sp. nov. Anderkenyn-Akchoku section. **3, 9, 10, 12, 13**, Sample 8255; **3**, BC 57493, ventral internal mould, $\times 6$; **9**, BC 56538, latex cast of conjoined ventral and dorsal interiors, $\times 4$; **10**, BC 57494, ventral internal mould, $\times 6$; **12, 13**, BC 12915, **holotype**, latex cast and internal mould of dorsal interior, $\times 5.5$. **4, 7, 8**, Sample 2531; **4**, BC 57490, latex cast of ventral exterior, $\times 6$; **7, 8**, BC 57492, dorsal internal mould and latex cast, $\times 5$. **6**, Sample 8215, BC 57491, latex cast of dorsal exterior, $\times 6$.
- Figs 11, 14–20** *Olgambonites insolita* gen. et sp. nov. Sample 8255, Anderkenyn-Akchoku section. **11**, BC 56535, dorsal external mould, $\times 4$. **14, 15**, BC 56534, latex cast and ventral internal mould, $\times 4$. **16, 17**, BC 56664, latex cast and ventral internal mould, $\times 4$. **18**, BC 57592, ventral exterior, $\times 4$. **19, 20**, BC 56663, **holotype**, internal mould and latex cast of dorsal valve, $\times 4$.
- Figs 21–33** *Gacella institata* sp. nov. **21–25, 32, 33**, Sample 100, Anderkenyn-Akchoku section; **21–25**, BC 57496, conjoined valves, posterior, anterior, dorsal, ventral and lateral views, $\times 2$; **32, 33**, BC 57500, conjoined valves, **holotype**, dorsal and ventral internal moulds, $\times 2$. **26, 27**, Sample 85258, Kujandysai section, BC 56576, latex cast and dorsal internal mould, $\times 3$. **28–31**, Sample 626, Anderkenyn-Akchoku section, BC 57497, conjoined valves, anterior, ventral, lateral and dorsal views, $\times 2$.

Olgambonites insolita sp. nov. Pl. 8, figs 11, 14–20

ETYMOLOGY. After *insolitus*, Latin –extraordinary.

HOLOTYPE. BC 56663, a dorsal valve (Pl. 8, figs 19, 20) from the Anderken Formation, Sample 8255, Anderkenyn-Akchoku section.

MATERIAL. 3 ventral (BC 56534–36, BC 56664) and 2 dorsal valves (BC 56538, BC 56663) from the type locality.

DESCRIPTION. Shell convexoconcave, semielliptical in outline, about half as long as wide, with maximum width at the hinge line, and acute cardinal extremities. Ventral valve gently concave in lateral profile with apsacline interarea and narrow convex pseudodeltidium. Dorsal valve gently convex with anacline pseudointerarea. Radial ornament inequally parvicostellate with 7–9 primary accentuated ribs and two generations of accentuated costellae. Very fine parvicostellae, about 10–11 per mm. Concentric ornament of fine evenly spaced rugellae and very fine crowded growth lamellae in the anterior half of the shell.

Ventral interior with small teeth and highly raised, rounded, subrectangular muscle field bordered anteriorly by the steep rim. Dorsal interior with simple undercut cardinal process joined to the socket ridges and small alveolus. Bema entire, highly raised anteriorly and bordered by a steep rim. Short median ridge originating anterior to bema and joined to the subperipheral rim.

DISCUSSION. The new species is known only from the type locality.

Genus *ZHILGYZAMBONITES* gen. nov.

ETYMOLOGY. After Zhilgyz well, Betpak-Dala Desert.

TYPE SPECIES. *Zhilgyzambonites extenuata* sp. nov. from the Anderken Formation, Chu-Ili Range.

DIAGNOSIS. Shell concavoconvex, with rectimarginate posterior commissure, ventral interarea apsacline with delthyrium completely covered by pseudodeltidium; dorsal interarea anacline with complete chilidium; radial ornament finely and unequally parvicostellate; ventral valve with small teeth lacking dental plates; ventral muscle field small, highly raised anteriorly; dorsal interior with undercut cardinal process joined to socket ridges, deep alveolus and strongly elevated, entire bema; median ridge fine, originating anteriorly to bema and joined anteriorly to the subperipheral rim.

DISCUSSION. *Zhilgyzambonites* is somewhat similar to *Aulie* (Nikitin & Popov in Klenina *et al.* 1984), which is within the Hesperomenidae, in the characteristic pseudodeltidium and chilidium, the ventral valve, which lacks dental plates and has a small muscle field which is strongly raised anteriorly, and the dorsal interior with the deep alveolus and an undercut cardinal process; but it differs in having an elevated bema and a short median ridge between the anterior margin of the bema and the subperipheral rim. However, the presence of a bema in *Zhilgyzambonites* places it within the

Table 17 Measurements of ventral valves of *Zhilgyzambonites extenuata* sp. nov., Samples 2531, 8251, 8255, from Anderkenyn-Akchoku section.

	Lv	W	Lv/W
N	7	7	7
X	3.7	5.2	70.9%
S	0.78	0.97	5.4
MIN	2.2	3.2	61.1%
MAX	4.4	6.2	78.6%

Sowerbyellidae on the criteria established by Cocks & Rong (1989). The dorsal interior of the new genus somewhat resembles *Diambonioidea* (Zeng 1987), but the Kazakh genus differs from the latter in having a strongly raised ventral muscle field, a ventral median ridge anterior to the muscle field, and an undercut cardinal process; the simple, not undercut, cardinal process of *Diambonioidea* places it within the Grorudiidae (Cocks & Rong 2000).

Zhilgyzambonites extenuata sp. nov.

Pl. 8, figs 3, 4, 6–10, 12, 13

ETYMOLOGY. After *extenuatus*, Latin – little, weak.

HOLOTYPE. BC 12915, a dorsal valve (Pl. 8, figs 12, 13) from the Anderken Formation, Sample 8255, Anderkenyn-Akchoku section.

MATERIAL. 2 pairs of conjoined valves, 10 ventral and 10 dorsal valves from Samples 2531 (BC 57490, 92), 8255 (BC 12915–21, 57493, 94) and possibly 8215 (BC 57089, 91, 57491), Anderkenyn-Akchoku section.

DESCRIPTION. Shell concavoconvex, semielliptical in outline, on average 70% as long as wide with maximum width at the hinge line. Cardinal extremities nearly right angled. Ventral valve moderately and evenly convex in lateral profile with apsacline interarea and narrow convex pseudodeltidium completely covering the delthyrium. Dorsal valve moderately concave with linear, anacline interarea and convex chilidium. Radial ornament unequally parvicostellate with 7–9 accentuated primary ribs and two generations of accentuated costellae. Parvicostellae very fine, about 10–11 per mm. Concentric ornament of fine evenly spaced rugellae and very fine crowded growth lamellae in the anterior half of the shell.

Ventral valve interior with small teeth and highly raised, rounded, subrectangular muscle field about 20% valve length and bordered anteriorly by a steep rim. Dorsal interior with simple undercut cardinal process joined to narrow, strongly curved socket ridges; small alveolus. Dorsal adductor scars with anterior pair slightly larger than posterior, strongly impressed, divided by a pair of transmuscle septa. Bema entire, strongly raised anteriorly and bordered by a steep rim. Short median ridge originating anteriorly to bema and joined to the subperipheral rim.

DISCUSSION. As far as is yet known, this is the only species within the new genus. The material from Sample 8215 does not include valve internals and is thus only doubtfully referred to the species.

Table 18 Measurements of dorsal valves of *Zhilgyzambonites extenuata* sp. nov., Samples 2531, 8251, 8255, from Anderkenyn-Akchoku section.

	Ld	W	MI	Mw	LPI	LPw	BBI	BBw	Ld/W	MI/Ld	MI/Mw	PLI/Ld	LPw/W	BBw/W
N	8	8	3	3	3	3	3	3	8	3	3	3	3	3
X	3.8	6.1	1.5	2.6	2.9	4.8	0.3	2.3	62.5%	35.1%	58.6%	67.4%	73.9%	35.7%
S	0.53	0.67	0.17	0.40	0.21	0.20	0.06	0.72	6.0	2.4	10.3	7.2	0.3	12.6
MIN	3	5.2	1.4	2.2	2.7	4.6	0.3	1.7	54.0%	33.3%	46.7%	62.2%	73.5%	26.2%
MAX	4.5	6.8	1.7	3	3.1	5	0.4	3.1	71.7%	37.8%	65.4%	75.6%	74.2%	50.0%

Order

ORTHOTETIDA Waagen, 1884Suborder **ORTHOTETIDINA** Waagen, 1884Superfamily **CHILIDIOPSOIDEA** Boucot, 1959Family **CHILIDIOPSIDAE** Boucot, 1959Subfamily **GACELLINAE** Williams & Brunton, 2000Genus **GACELLA** Williams, 1962

TYPE SPECIES. *Gacella insolita* Williams, 1962, from the Stinchar Limestone (Lower Caradoc), Girvan, Scotland.

Gacella institata sp. nov. Pl. 8, figs 21–33, Pl. 9, figs 1–4

ETYMOLOGY. After *instita*, Latin – a swathe.

HOLOTYPE. BC 57500, Pl. 8, figs 32, 33, from the Anderken Formation, Sample 100, Anderkenyn-Akchoku section.

MATERIAL. 10 pairs of conjoined valves, 2 ventral and 8 dorsal valves, from Samples 100 (=K-98/1970) (BC 57496, 98, 99, 57500), 626 (BC 57497), Anderkenyn-Akchoku section; Samples 628, 85258 (BC 57092–3, 56576), Kujandysai Section..

DESCRIPTION. Shell subequally biconvex, transverse, semielliptical in outline about 80% as long as wide, with maximum width at hinge line. Cardinal extremities acute to rectangular. Anterior commissure gently uniplicate. Ventral valve convex in lateral profile with maximum thickness slightly anterior to the umbo and with flattened sides. Sulcus shallow, originating about 2–3 mm from the umbo. Ventral interarea planar, apsacine with a broad, convex pseudodeltidium perforated apically by a minute foramen. Lateral profile of the dorsal valve gently convex with maximum thickness near the anterior margin. Dorsal median fold low, rounded in cross-section, originating in the umbonal area but very weakly defined until the mid-valve. Dorsal interarea planar, anacline, with convex chilidium. Radial ornament unequally parvicostellate with two to three generations of accentuated ribs, about 4–5 per 3 mm along the anterior margin of mature specimens. Concentric ornament of numerous fine growth lamellae anteriorly.

Ventral interior with teeth supported by long subparallel but slightly divergent dental plates and narrow, elongate subtriangular muscle field divided by median ridge. Numerous fine crenulations on the outer surface of the teeth. Dorsal interior with bilobed cardinal process on a high notothyrial platform: adductor scars elongated slightly, shorter than half valve length, crossed by two pairs of short transmuscle septa. Median ridge fine and faint, originating some distance from the notothyrial platform.

MEASUREMENTS. (471/12375) conjoined valves, L=14.0, W=16.9, T=6.3, Sw=8.9; (474/12375) conjoined valves, L=20.4, W=21.0, T=11.2, Sw=8.7; (475/12375) conjoined valves, L=22.9, W=24.5, T=10.2, Sw=12.8; (476/12375) conjoined valves, L=16.5, W=19.8, T=6.5, Sw=11.2; (479/12375) conjoined valves, L=10.5, T=6.7, Sw=6.7.

DISCUSSION. This species differs from others of the genus in having a concentric ornament of strong growth lamellae and coarser accentuated ribs. It can be compared to *Gacella ponderosa* Williams, 1962, from the Confinis Formation (Llandeilo) of Girvan, south Scotland, in the general shape and size of the shell, but differs in having a less convex lateral profile in both valves in addition to the patterns of radial and concentric ornament.

Gacella institata differs from *G. sulcata* Misius (in Misius & Ushatinskaya 1977), from the Tabylgaty Formation (Upper Caradoc) of the Moldo-Too Range, Kyrgyzstan, in having a shallow ventral median sulcus and low dorsal median fold usually originating in the umbonal region; the convex, not flat, lateral profile of the ventral valve, and in the absence of geniculation in the dorsal valve.

Suborder **TRIPLESIIDINA** Moore, 1952Superfamily **TRIPLESIOIDEA** Schuchert, 1913Family **TRIPLESIIDAE** Schuchert, 1913Genus **TRIPLESIA** Hall, 1859

TYPE SPECIES. *Atrypa extans* Emmons, from the Trenton Group (Caradoc), New York, U.S.A.

Triplesia sp.

Pl. 9, figs 22–26

MATERIAL. Two ventral and three dorsal valves (BC 57512) from Sample 8228, Kopalysai.

DESCRIPTION. Shell dorsibiconvex, transverse suboval in outline, about 80% as long as wide with uniplicate anterior commissure. Ventral valve moderately convex, with maximum thickness at about one-third valve length. Ventral interarea anacline. Sulcus originating near mid-valve, strongly deepening anteriorly, flanked laterally by angular plications. Dorsal valve moderately convex with swollen umbo. Strong median fold with steep sides, originating anteriorly of mid-valve, bisected medianly by fine groove. Shell surface smooth with rare, slightly irregular growth lamellae anteriorly. Ventral interior with teeth supported by short subparallel dental plates. Dorsal interior with forked cardinal process on a short shaft.

MEASUREMENTS. (488/12375) dorsal valve, L=16.2, W=16.9, T=4.5.

DISCUSSION. These shells are comparable with large specimens of *Triplesia* aff. *subcarinata*, but differ in having a narrow groove bisecting the dorsal median fold and a ventral sulcus which is more rounded in cross-section and a dorsal median fold. However, the shape of the dorsal fold and ventral sulcus varies significantly and it is difficult to evaluate observed morphological differences in this species because of the small number of shells available.

Triplesia aff. *subcarinata* Cooper, 1956

Pl. 10, figs 1–8, 19

MATERIAL. 6 conjoined valves, 2 ventral and 3 dorsal valves from Samples 100 (=K-98/1970), 626 (BC 57515), 8251a (BC 57514), Anderkenyn-Akchoku section; Samples 85258 (BC 57094–5), Kujandysai section; Sample 1041a, Burultas Valley.

DISCUSSION. This species resembles *Triplesia carinata* Cooper, 1956, from the Pratt Ferry Formation of Alabama and *T. subcarinata* Cooper, 1956, from the Lebanon Formation of Tennessee, as well as specimens of that species from the Bestamak Formation (Llandeilo-Lower Caradoc) of the Chingiz range, Kazakhstan (Nikitin & Popov in Klenina *et al.* 1984), in having a well-developed sulcus and a carinate dorsal median fold originating near the mid length, but it differs from both in having a larger shell, a strongly convex lateral profile in the dorsal valve with maximum height near the anterior margin, and a variable transverse profile of the dorsal median fold which has a tendency to be rounded in most specimens. *Triplesia* aff. *subcarinata* differs from *T. ainca* Severygina, 1978, from the Lower Ashgill Gurianovka Formation and Marinikha Limestone of the Sayano-Altai Mountain Region in having a strongly dorsibiconvex lateral profile with a slightly accentuated ventral beak erect posteriorly, a narrow ventral sulcus and a dorsal median fold usually rounded in cross-section.

Genus **BICUSPINA** Havlíček, 1950

TYPE SPECIES. *Orthis cava* Barrande, 1848, from the Lower Caradoc of Bohemia.

***Bicuspina rukavishnikovae* Klenina, 1984 Pl. 9, figs 5–13**

1984 *Bicuspina rukavishnikovae* Klenina in Klenina *et al.*: 62, pl. 5, figs 7, 8.

1985 *Bicuspina attrita* Popov: 61, pl. 3, figs 2–4.

HOLOTYPE. IGNA 411/89, conjoined valves, from the Abai Formation (Lower Caradoc), Ordota Mountains, Chingiz Range, Kazakhstan.

MATERIAL. Five conjoined valves, one ventral and 9 dorsal valves from Samples 100 (=K-98/1970) (BC 57505), 626, Anderkenyn-Akchoku section; Sample 1018 (including the holotype of *B. attrita* CNIGR 32/11989), area 7 km southwest of Karpkuduk well, Kotnak Mountains.

DESCRIPTION. Shell dorsibiconvex, about half as thick as long and about 90% as long as wide. Hinge line short, about two-thirds maximum width. Ventral valve gently convex in lateral profile with maximum thickness at about one-third valve length. Beak small, slightly curved. Ventral interarea low, planar, apsacline with small pseudodeltidium bisected by monticulum. Ventral median sulcus originating in umbonal area with flattened bottom and steep lateral sides about 60% valve width. Well-developed semioval tongue. Dorsal valve strongly convex with maximum thickness at mid-length and flattened umbonal area. Median fold high, originating near umbo, with steep lateral slopes. Radial ornament costellate with 6–11 ribs in the fold and sulcus and 13–21 ribs on the lateral sides of mature shells.

Ventral interior with small teeth supported by short diverging dental plates. Ventral muscle field open anteriorly, weakly impressed. Umbonal area with a short internal pedicle tube (Pl. 9, fig. 10). Dorsal interior with forked cardinal process on a short, thickened shaft, and small curved socket ridges.

MEASUREMENTS. (471/12375) conjoined valves, L=14.0, W=16.9, T=6.3, Sw=8.9; (474/12375) conjoined valves, L=20.4, W=21.0, T=11.2, Sw=8.7; (475/12375) conjoined valves, L=22.9, W=24.5, T=10.2, Sw=12.8; (476/12375) conjoined valves, L=16.5, W=19.8, T=6.5, Sw=11.2; (479/12375) conjoined valves, L=10.5, T=6.7, Sw=6.7.

DISCUSSION. Coarsely ribbed triplesiids are characteristic of the Caradoc of West Gondwana (Havlíček 1950; Melou 1990) and Avalonia (Williams 1963; 1974), but they are apparently absent from China and Australia and very rare in Kazakhstan. Specimens from the Chu-Ili Range were previously known as *Bicuspina attrita* Popov (1985). They differ from *Bicuspina rukavishnikovae*, described by Klenina (in Klenina *et al.* 1984) from the Abai Formation of the Chingiz Range, only in having a slightly uneven lateral profile of the ventral valve with maximum height posterior to mid-length, and in a more apsacline ventral interarea. These differences

are regarded here as intraspecific, and specimens of *Bicuspina* from the Chu-Ili and Chingiz ranges are therefore conspecific. Klenina mentioned the presence of a forked cardinal process and internal pedicle tube in the original description of the species, but the interiors of both valves were not illustrated.

The published Llanvirn age of *B. rukavishnikovae* in the Ordota Mountains of the Chingiz Range, which is the type locality, is not supported by analysis of the associated brachiopod assemblage. It co-occurs with *Hesperorthis karaadirensis* Klenina, which is probably synonymous with *Paralenorthis numerosa* (Nikitin & Popov) and rhynchonellids, suggesting that the age of the assemblage is not older than Llandeilo to early Caradoc.

Genus **GRAMMOPLECIA** Wright & Jaanusson, 1993

TYPE SPECIES. *Grammoplecia triplesioides* Wright & Jaanusson, 1993, from the Boda Limestone (Ashgill) of Dalarna, Sweden.

***Grammoplecia wrighti* sp. nov.**

Pl. 9, figs 14–21

ETYMOLOGY. After A.D. Wright, to honour his triplesioid studies.

HOLOTYPE. BC 57509, Pl. 9, figs 17, 18, a dorsal valve from the Anderken Formation, Sample 8214, Anderkenyn-Akchoku section.

MATERIAL. Three pairs of conjoined valves, three ventral and 9 dorsal valves, from Samples 620 (BC 57100–04, 57506, 07, 10, 11), 626 (BC 57105–6), Anderkenyn-Akchoku section; Samples 8214 (BC 57099, 57508–11), 8215b (BC 57107), west side of Ashchisu River; Sample 628, Kujandysai Section.

DESCRIPTION. Shell dorsibiconvex, slightly transverse, subrectangular to suboval in outline, about 83% as long as wide. Hinge line straight, not exceeding two-thirds shell width. Anterior commissure uniplicate. Ventral valve moderately convex with low, apsacline interarea and flat pseudodeltidium bisected by monticulum. Ventral sulcus originating about 3–5 mm from the umbo, ending in wide, trapezoidal tongue about 83% as wide as the valve. Dorsal valve strongly convex with maximum thickness at about one-third valve length. Strong dorsal median fold, flat centrally with steep lateral slopes. Lateral slopes convex in cross-section, strongly inclined to the commissural plane. Radial ornament of fine capillae about 5–7 per mm crossed by fine, closely-spaced concentric fila.

Ventral interior with strong teeth and long, diverging, widely spaced dental plates. Ventral muscle field large, about two-fifths valve length, slightly raised anteriorly with wide, subtriangular adductor track dividing narrow, strip-like diductor scars. Dorsal interior with forked cardinal process on strong short shaft joined to low and short socket plates. Adductor field quadripartite with anterior and posterior pairs separated by strong, transverse ridges. Low

PLATE 9

Figs 1–4 *Gacella institata* sp. nov., Sample 100, Anderkenyn-Akchoku section. **1**, BC 57498, ventral valve, umbonal area, $\times 5$. **2**, Sample 100, BC 57502, enlargement of interarea of conjoined valves, $\times 3$. **3, 4**, BC 57499, dorsal valve exterior, $\times 2$, and umbonal area showing radial ornament, $\times 6$.

Figs 5–13 *Bicuspina rukavishnikovae* Klenina, 1984. **5–9**, Sample 100, Anderkenyn-Akchoku section, BC 57505, conjoined valves, dorsal, lateral, ventral anterior and posterior views, $\times 2$. **10–13**, Sample 1018, area 7 km southwest of Karpkuduk well, Kotnak Mountains; **10**, CNIGR 31/11989, ventral internal mould showing internal pedicle tube, $\times 5$; **11**, CNIGR 32/11989, dorsal exterior, $\times 2$; **12, 13**, CNIGR 33/11989, conjoined valves, ventral view, $\times 2$, posterior view, $\times 5$.

Figs 14–21 *Grammoplecia wrighti* sp. nov. Anderkenyn-Akchoku section. **14, 15, 19–21**, Sample 620; **14**, BC 57506, ventral internal mould, $\times 2$; **15**, BC 57507, conjoined valves, oblique posterior view of internal mould showing cardinal process, $\times 2$; **19, 20**, BC 57510, dorsal and lateral views of exterior, $\times 2$; **21**, BC 57511, dorsal internal mould, $\times 2$. **16–18**, Sample 8214; **16**, BC 57508, dorsal exterior, $\times 2$; **17, 18**, BC 57509, **holotype**, dorsal exterior and lateral views, $\times 2$.

Figs 22–26 *Triplesia* sp. Sample 8228, east side of Kopalysai. **22, 23, 25**, dorsal internal mould, lateral and dorsal views, $\times 2$, posterior view showing cardinal process, $\times 3$. **24**, BC 57512, latex cast of dorsal exterior, $\times 2$. **26**, ventral internal mould, $\times 2$.

Fig. 13 Transverse serial sections of *Placotriplesia spissa* sp. nov., BC 57605 from Sample 628. Distance in mm is measured from the posterior tip of ventral beak. Dorsal valve uppermost.

and narrow median ridge extending to anterior border of the muscle field.

MEASUREMENTS. (490/12375) dorsal valve, L=17.2, W=19.2, T=8.2, Sw=9.6; (491/12375) dorsal valve, L=17.2, W=21.0, T=8.6, Sw=8.2; (495/12375) dorsal valve, L=10.2, W=15.3, T=7.8, Sw=4.6.

DISCUSSION. This species differs from *Grammoplecia triplesioides* Wright & Jaanusson, 1993, *G. globosa* (Nikitin & Popov, 1985), from the Andryushinka Formation (Llandeilo-Lower Caradoc) of north-central Kazakhstan, *G. krotovi* (Chernyshev, 1887) from the Upper Caradoc to Lower Ashgill of Novaya Zemlya, Vaigach and the Urals (Bondarev 1968) and *G. sibirica* (Nikiforova, 1955) from the Upper Caradoc of Siberia, in having a more transverse shell outline, a ventral sulcus and dorsal median fold with steep lateral sides and flat centrally, a strongly and evenly convex dorsal profile with maximum height at mid-length and a broader hinge line.

Genus *PLACOTRIPLESIA* Amsden, 1968

TYPE SPECIES. *Triplesia praecipua* Ulrich & Cooper, 1936a, from the Wenlock of Arkansas, U.S.A.

Placotriplesia spissa sp. nov.

Pl. 10, figs 9–18; Figs 13, 15

HOLOTYPE. BC 57517, Pl. 10, figs 9–13, from Sample 2538, Anderken Formation, Akchoku Mountain, Kujandysai section.

MATERIAL. 9 pairs of conjoined valves, 6 ventral and 12 dorsal valves from Samples 8214, 8215, 8223, Anderkenyn-Akchoku section; Samples 628, 2538 (BC 57517), 8219, 8256, Kujandysai section.

DESCRIPTION. Shell smooth, dorsibiconvex profile, about 80% as thick as long and 75% as long as wide, transverse and suboval in outline, with maximum width at mid-length. Hinge-line short, less than half valve width. Anterior commissure strongly uniplicate. Ventral valve moderately convex, with an erect beak and minute apical foramen. Ventral interarea high, planar, apsacline with flat pseudodeltidium. Ventral sulcus originating from quarter to half valve length, strongly deepening anteriorly, with strong geniculated tongue about 75% valve width, and inclined at less than a right angle towards commissural plane. Lateral sides of sulcus accentuated by angular plications. Dorsal valve strongly convex, with swollen incurved beak; dorsal median fold strong and rounded in cross-section. Ventral interior with delicate teeth and short divergent dental plates. Dorsal interior with grooved forked cardinal process with strongly curved prongs posteriorly with distal parts subparallel to commissural plane, separated proximally and fused with narrow curved socket ridges.

DISCUSSION. This species represents the earliest record of

PLATE 10

- Figs 1–8, 19 *Triplesia* aff. *subcarinata* Cooper. Anderkenyn-Akchoku section. 1–4, 19, Sample 8251a, BC 57514, conjoined valves, ventral, dorsal, posterior and anterior views, $\times 2$, dorsal view of the umbonal area showing pseudodeltidium with monticulus, $\times 4$. 5–8, Sample 100, BC 57515, conjoined valves, $\times 2$. Figs 9–18 *Placotriplesia spissa* sp. nov. 9–14, Sample 2538, Akchoku Mountain, Kujandysai section. 9–13, BC 57517, holotype, conjoined valves, ventral, dorsal, anterior, posterior and lateral views, $\times 2$. 14, CNIGR 3/12361, conjoined valves showing ventral interarea with pseudodeltidium lacking monticulus, $\times 5$. 15–18, Sample 8214, Anderkenyn-Akchoku section, CNIGR 3/12361, conjoined valves, ventral, dorsal, anterior and lateral views, $\times 2$. Figs 20–22 *Skenidioides* sp. Sample 8214, west side of Ashchisu River, BC 57518, conjoined valves, ventral, dorsal and posterior views, $\times 6$. Figs 23–29, 31–36 *Dolerorthis pristina* sp. nov. 23–25, 32, 34, Sample 626, Anderkenyn-Akchoku section. 23–25, 32, BC 57519, conjoined valves, ventral, lateral and dorsal views, $\times 2$, detail of the shell surface, $\times 8$; 34, BC 57522, ventral internal mould, $\times 2$. 26–29, 31, Sample 620, Anderkenyn-Akchoku section, BC 57520, holotype, conjoined valves, dorsal, ventral, lateral, posterior and anterior views, $\times 2$. 33, 35, Sample 2538, Akchoku Mountain, Kujandysai section; 33, BC 57521, ventral exterior, $\times 2$; 35, BC 56768, dorsal interior, $\times 3$. 36, Sample 8214, Anderkenyn-Akchoku section, BC 57523, dorsal internal mould, $\times 2$. Figs 37–42 *Glyptorthis* sp., Kujandysai section. 37, Sample 2538, BC 57524, ventral internal mould, $\times 3$. 38–42, Sample 628 (=K-107/70), west side of Kujandysai, BC 57525, conjoined valves, anterior, dorsal, lateral and ventral views, $\times 3$, dorsal view, $\times 6$. Fig. 43 *Plectrothis? burultasica* sp. nov. Sample 1018, area 7 km SW of Kotnak mountains, south Betpak-Dala, CNIGR 2/11989, latex cast of ventral interior, $\times 2$.

Table 19 Measurements of complete shells of *Placotriplezia spissa* sp. nov., Sample 2538. Kujandysai section, 8221 from Anderkenyn-Akchoku section and Sample F-1041a from Burultas valley.

	L	W	T	Sw	St	L/W	T/L	Sw/W	St/Sw
N	7	7	7	7	3	7	7	7	3
X	13.9	19.0	11.5	10.4	7.7	73.9%	81.6%	75.5%	73.2%
S	2.61	4.27	3.13	1.43	3.04	7.9	12.7	6.1	22.3
MIN	10.5	13.6	6.8	8.2	3.3	60.4%	61.7%	67.9%	37.5%
MAX	16.3	24.5	14.7	11.5	7.6	83.9%	90.2%	83.0%	69.1%

Placotriplezia, which is otherwise known only from the Silurian. It differs from *P. praecipta*, *P. juvenis* Ulrich & Cooper (1936a), *P. waldronensis* (Miller & Dyer), and *P. rostellata* (Ulrich & Cooper 1936a) in having a strongly dorsibiconvex shell, high dorsal median fold and deep ventral median sulcus originating at some distance from the umbo. It also differs from *P. praecipta*, as redefined by Amsden (1968), in having a strongly curved cardinal process with posteriorly-directed prongs.

Order **PROTORTHIDA** Schuchert & Cooper, 1931

Superfamily **PROTORTHOIDEA** Schuchert & Cooper, 1931

Family **SKENIDIIDAE** Kozłowski, 1929

Genus **SKENIDIOIDES** Schuchert & Cooper, 1931

TYPE SPECIES. *Skenidioides billingsi* Schuchert & Cooper, 1931, from the Caradoc of Ontario, Canada.

Skenidioides sp. Pl. 10, figs 20–22

MATERIAL. One pair of conjoined valves (L=2.7, W=5.4, T=1.7), one ventral and one dorsal valves from Samples 8223b and 8226, Anderkenyn-Akchoku section; Sample 8214 (BC 57518), west side of Ashchisu River.

DISCUSSION. The shells from the Anderken Formation closely resemble *Skenidioides anthonensis* (Sardeson), as redescribed and illustrated by Cooper (1956: 491), in the general shape of the shell, narrow median sulcus in the dorsal valve, carinate ventral valve and characters of radial ornament, but differ somewhat in having a more flattened dorsal valve. Although the exterior is characteristic of *Skenidioides*, the absence of known interiors in the specimens from the Anderken Formation precludes specific identification.

Order **ORTHIDA** Schuchert & Cooper, 1932

Suborder **ORTHIDINA** Schuchert & Cooper, 1932

Superfamily **ORTHOIDEA** Woodward, 1852

Family **HESPERORTHIDAE** Schuchert & Cooper, 1931

Genus **DOLERORTHIS** Schuchert & Cooper, 1931

TYPE SPECIES. *Orthis interplicata* Foerste, from the Niagara Group (Silurian) of Indiana, U.S.A.

Dolerorthis expressa Popov, 1980

Pl. 1, fig. 29, Pl. 11, figs 1, 2

1980 *Dolerorthis expressa* Popov: 144, pl. 1, figs 5–7.

HOLOTYPE. CNIGR 11/11523, ventral internal and external moulds (L=18.4, W=24.7), from the Anderken Formation, Sample 1018, 7 km southwest of Karpkuduk well, Kotnak Mountains.

MATERIAL. One pair of conjoined valves, 12 ventral and 11 dorsal valves, internal and external moulds, from Sample 8137 (BC 57526),

Anderkenyn-Akchoku; Sample 817, about 4 km south-west of Alakul Lake; Sample 1018 (BC 57368), 7 km southwest of Karpkuduk well, Kotnak Mountains, south Betpak-Dala.

DESCRIPTION. Shell subequally biconvex, transverse, subrectangular in outline, about 75% as long as wide with maximum width anterior to hinge line. Cardinal extremities slightly rounded; anterior commissure weakly unisulcate; ventral valve gently convex in lateral profile with maximum thickness at about one-third from anterior margin; ventral interarea apsacline, slightly curved in cross-section with open triangular delthyrium. Dorsal valve moderately convex with shallow sulcus originating at the umbo. Interarea low, planar, anacline. Radial ornament variably multicostellate with costellae of two to three generations. 4–6 ribs per 3 mm along the posterior margin of adult specimens. Concentric ornament of fine, ridge-like, evenly spaced fila, 3–4 per mm.

Ventral interior with strong teeth supported by diverging dental plates continuing anteriorly as elevated muscle bounding ridges enclosing an elongate, subrhomboidal muscle field about two-fifths as long as the valve. Adductor scars narrow, strip-like, completely separating large, deeply impressed diductor scars of about equal length. Mantle canals saccate with subparallel to slightly converging *vascula media*. Dorsal interior with simple, ridge-like cardinal process on the high notothyrial platform slightly inclined posteriorly. Brachioophores high, triangular with slightly diverging bases. Weakly impressed dorsal adductor scars divided posteriorly by a very short median ridge.

DISCUSSION. This species is somewhat similar to *Dolerorthis tenuicostata* Williams (in Whittington & Williams 1955: 406) from the Lower Caradoc of Wales, but differs in having a more transverse shell outline, lateral profile of the ventral valve with maximum thickness anterior to the mid-length in full grown specimens and a weak dorsal sulcus continuing towards the anterior margin. It differs from *Dolerorthis* aff. *hubeiensis* Zeng, which occurs in the Dulankara Regional Stage of north Betpak-Dala, Kazakhstan (Nikitin *et al.* 1996), in having a subequally biconvex transverse shell, finer radial ornament and more widely spaced concentric fila.

Dolerorthis pristina sp. nov. Pl. 10, figs 23–29, 31–36

ETYMOLOGY. After *pristinus*, Latin – former.

HOLOTYPE. BC 57520, Pl. 10, figs 26–29, 31, conjoined valves (L=9.7, W=12.6, T=4.2) from the Anderken Formation, Sample 620, Anderkenyn-Akchoku section.

MATERIAL. 8 pairs of conjoined valves, 15 ventral and 18 dorsal valves from Samples 100 (=K-98/1970) (BC 57110–7), 620 (BC 57520), 626 (BC 57130–32, 57519), 8223a (BC 57158, 59), 8223b, Anderkenyn-Akchoku; Sample 8214 (BC 57150–54, 57523), Ashchisu River; Samples 628 (BC 57133–5), 2538 (BC 56768, 57141–45, 57521, 22), 8217 (BC 57156–7), Kujandysai near Akchoku Mountain; Sample 948 (BC 57136–40), Tesik River.

Table 20 Measurements of complete shells of *Dolerorthis pristina* sp. nov., Samples 100 and 626 from Anderkenyn-Akchoku section.

	Lv	W	T	Iw	Lv/W	T/L	Iw/W
N	10	10	6	10	10	6	9
X	10.0	11.8	4.2	10.3	85.2%	47.6%	87.9%
S	3.04	3.36	1.11	2.63	10.0	6.5	9.5
MIN	5.9	7.5	2.8	6.5	70.2%	40.0%	75.0%
MAX	14.2	18.2	5.5	13.7	103.6%	56.3%	100.0%

DESCRIPTION. Shell weakly ventribiconvex, slightly transverse, suboval in outline, on average 82% ($S=7.0$, $N=10$) as long as wide and 48% ($S=6.0$, $N=6$) as high as long. Anterior commissure slightly shorter than maximum shell width at mid-length. Cardinal extremities obtuse. Anterior commissure rectimarginate or weakly sulcate. Radial ornament costellate with up to 17 primary costae and costellae branching near the mid-length and near the anterior and lateral margins. 6–8 costellae per 3 mm along the anterior margin and varying from 31 to 54 in full-grown specimens.

Ventral valve moderately and unevenly convex with maximum thickness at about one-third valve length from the small, pointed beak. Ventral interarea apsacline, slightly curved in cross-section with open, narrow delthyrium. Dorsal valve weakly convex with maximum thickness slightly anterior from the beak. Interarea low, planar, linear. Shallow sulcus usually well defined in the posterior half of the dorsal valve, but fading anteriorly.

Ventral interior with small teeth and low, divergent dental plates. Muscle field small, slightly elongate, subpentagonal in outline. Adductor scars narrow, completely separating diductor scars of about equal length. Mantle canals saccate with slightly divergent proximal parts of *vascula media*. Dorsal valve interior with high, subtriangular brachiophores diverging anteriorly. Cardinal process ridge-like with crenulated myophore, situated on a low subtriangular notothyrial platform. Adductor muscle field subrectangular with anterior adductor scars slightly larger than posterior. Median ridge low and broad, bisecting the entire adductor muscle field.

DISCUSSION. *Dolerorthis pristina* differs from *D. expressa* (Popov 1980) in its less convex dorsal valve, much smaller size (less than half *D. expressa*), and in its evenly convex ventral profile, in contrast to *D. expressa* in which the ventral profile is relatively flat near the umbo, but increases greatly anteriorly. In addition, *D. pristina* has finer radial ornament.

Zeng (1987) erected *Paradolerorthis* as a subgenus within *Dolerorthis*. However, his quoted distinctions and equivocal illustrations do not allow us to recognize his subgenus as useful, but the type species *D. (Paradolerorthis) calla* appears similar to *D. pristina*.

Family **GLYPTORTHIDAE** Schuchert & Cooper, 1931
Genus **GLYPTORTHIS** Foerste, 1914

TYPE SPECIES. *Orthis insculpta* Hall, 1847, from the Richmondian (Ashgill), New York, U.S.A.

Glyptorthis sp. Pl. 10, figs 37–42

MATERIAL. Five pairs of conjoined valves, 7 ventral and 6 dorsal valves from Samples 620 (BC 57163, 64), 8223a, Anderkenyn-Akchoku; Sample 8214, Ashchisu River; Samples 2538 (BC 57166–69, 57524), 8256, Kujandysai near Akchoku Mountain; Sample 628 (BC 57165, 57525), east side of Kujandysai; Sample 948, Tesik River.

DESCRIPTION. Shell slightly ventribiconvex, transverse, rounded

subrectangular in outline, about 80% as long as wide. Hinge line slightly narrower than maximum shell width at mid-length. Cardinal extremities slightly obtuse. Anterior commissure varying from slightly sulcate to rectimarginate. Ventral valve moderately convex with maximum thickness at umbo. Interarea moderately high, triangular, planar, catacline, divided by narrow triangular, open delthyrium. Dorsal valve gently convex with maximum thickness at about one-quarter valve length from the beak. Dorsal sulcus shallow and narrow, originating at umbo and fading anteriorly. Dorsal interarea low, linear, orthocline. Radial ornament coarsely costellate with up to 16 primary ribs and 25–30 costellae (up to 5 costellae per 3 mm) in adult specimens. Secondary costellae in the median part of the dorsal valve bifurcate internally. Concentric ornament of crowded, evenly spaced growth lamellae.

Ventral interior with teeth supported by short and high dental plates. Muscle field small, situated entirely within delthyrial chamber. Mantle canals saccate with straight, slightly diverging anteriorly *vascula media*. Dorsal interior not observed.

DISCUSSION. These specimens closely resemble *Glyptorthis balcletchiensis* (Davidson, 1883) from the Upper Caradoc of the Girvan District, Scotland (Williams 1962) in the size, general outline and convexity of the shell, as well as in the number and bifurcation of the costellae. It differs from another coarsely ribbed Kazakh species *Glyptorthis? bestamaki* Nikitin & Popov (in Klenina *et al.* 1984) from the lower Bestamak Formation (*Nemagraptus gracilis* Zone) of the Chingiz Range in having a rectimarginate or slightly sulcate anterior commissure and a dorsal sulcus not reversed anteriorly into the median fold.

Family **PLAESIOMYIDAE** Schuchert, 1913
Genus **AUSTINELLA** Foerste, 1909

TYPE SPECIES. *Orthis kankakensis* McChesney, from the Maquoketa Formation (Ashgill) of Iowa, U.S.A.

Austinella sarybulakensis sp. nov. Pl. 11, figs 15–22

ETYMOLOGY. After Sarybulak River, 10 km west of the type locality.

HOLOTYPE. BC 56507, Pl. 11, figs 15–18, conjoined valves; Anderken Formation, Sample 85258, east side of Uzunbulak River.

MATERIAL. Three conjoined valves, one ventral and one dorsal valve from Sample 85258 (BC 56505–8), east side of Uzunbulak River; Sample 818a, Burultas Valley.

DESCRIPTION. Shell subequally biconvex, transverse, subrectangular in outline about 93–97% as long as wide and 54–60% as thick as long. Hinge line somewhat shorter than maximum shell width at the mid-length. Anterior commissure uniplicate. Ornament costellate with 8–9 costellae per 5 mm along the anterior margin and 25–28 primary ribs near the umbo. Ventral valve moderately convex with maximum thickness slightly anterior to the umbo. Ventral pseudointerarea high, triangular with open, triangular delthyrium. Shallow sulcus originating at about 7 to 9 mm anterior to the beak, widening and deepening anteriorly. Lateral sides of the valve gently and evenly convex in transverse section. Dorsal valve moderately and unevenly convex. Dorsal interarea low, planar, orthocline. Shallow dorsal sulcus in the umbonal area reverses into a median fold at 5–7 mm from the umbo.

Ventral interior with strong teeth and short, slightly divergent dental plates. Muscle field strongly raised anteriorly in a form of pseudospondylium, rounded subtriangular in outline, about two-

fifths as long as the valve. Mantle canal system saccate with short, diverging *vascula media*. Dorsal interior with blade-like cardinal process situated on a high subtriangular notothyrial platform. Brachioophores high, subtriangular with strongly thickened, slightly divergent bases. Adductor field weakly impressed, quadripartite, bisected by a low median ridge. Anterior adductors larger than posterior ones.

MEASUREMENTS. Conjoined valves; [BC 56507, L=22.2, W=24.0, T=12.2, Sw=14.4, St=6.4; BC 56508, L=25.1, W=26.3, T=14.8, Sw=14.6, St=6.8].

DISCUSSION. This species can be distinguished from other species of the genus such as *Austinella whitfieldi* (Winchell & Schuchert) and *A. kankakensis* (McChesney), re-described by Wang (1949) from the Ashgill Maquoketa Formation of Iowa, by its uniplicate anterior commissure with the dorsal sulcus reversed into the median fold posterior to the mid-valve.

Superfamily **PLECTORTHOIDEA** Schuchert, 1929

Family **PLECTORTHIDAE** Schuchert, 1929

Subfamily **PLECTORTHINAE** Schuchert, 1929

Genus **PLECTORTHIS** Hall & Clarke, 1892

TYPE SPECIES. *Orthis plicatella* Hall, from the Cincinnati (Lower Ashgill), of the U.S.A.

***Plectorthis? burultasica* sp. nov.** Pl. 10, fig. 43, Pl. 11, figs 3–12

1985 *Plectorthis* aff. *altaica* Severgina; Popov: 51, pl. 1, figs 1, 2.

ETYMOLOGY. After the type locality in the Burultas Valley.

HOLOTYPE. BC 57528, Pl. 11, figs 3–4, dorsal valve, Anderken Formation, Sample 7613, Akchoku Mountain, Kujandysai section.

MATERIAL. Five conjoined valves, 8 ventral and 9 dorsal valves from Samples 2538, 7613 (BC 57528), Kujandysai near Akchoku Mountain; Sample 626 (BC 57170, 71), 843, 8128 (BC 57530), Anderkenyn-Akchoku; all Chu-Ili Range; Sample 1041a (BC 57529), Burultas Valley; Sample 1018 (BC 57367), 7 km southwest of Karpkuduk well, Kotnak mountains, south Betpak-Dala.

DESCRIPTION. Shell subequally biconvex, transversely subrectangular in outline, about 60% as thick as long and three-quarters as

long as wide, with maximum width at mid-length. Cardinal extremities obtuse to slightly rounded. Anterior commissure rectimarginate. Ventral valve moderately and gently convex in lateral profile with low, strongly apsacline interarea slightly curved in cross-section. Dorsal valve moderately and evenly convex in lateral profile with low, linear, orthocline interarea and shallow umbonal sulcus fading at mid-length. Radial ornament of 28–32 rounded costellae bifurcating at the posterior half of the shell and separated by interspaces of about equal width as ribs. Radial rows of fine rounded exopunctae on both sides of each rib.

Ventral valve with teeth supported by thin diverging dental plates about one-third shorter than length of the elongate subpentagonal muscle field. Adductor scar narrow triangular, slightly raised anteriorly, about the same length as strongly impressed diductor scars. Dorsal valve interior with high, triangular brachioophores with bases converging anteriorly. Notothyrial platform high and narrow, crossed by ridge-like cardinal process with crenulated myophore. Median ridge strong, extending anteriorly to mid-valve. Dorsal anterior and posterior adductor scars about equal size, separated by fine, slightly oblique, transverse ridges.

DISCUSSION. Criteria for generic separation amongst the Plectorthisidae require revision. The type species of *Plectorthis*, *P. plicatella*, has never been fully revised, although Schuchert & Cooper (1932, pl. 11, figs 4, 9) illustrated ventral and dorsal interiors from the Maysville Formation of Cincinnati, Ohio. Material labelled as *P. plicatella* in the Natural History Museum (eg. BB 14835) from Cincinnati includes well preserved exteriors with no trace of exopunctae. However, our new species has well-developed rows of exopunctae on both sides of each costa, as have other species attributed to *Plectorthis*, e.g. *Plectorthis? punctata* illustrated by Cooper (1956), *P. obesa*, mentioned but not illustrated by Cooper (1956), and the *Plectorthis* sp. of Neuman (1971:21). Thus, until comparable exopunctae have been found in true *P. plicatella*, we attribute the exopunctate species to *Plectorthis* with a query.

Plectorthis? burultasica resembles *Plectorthis altaica* Severgina, 1967 from the Khankhara Formation (Caradoc) of Gornyi Altai in radial ornament, size and outline, but differs in having a weak umbonal dorsal sulcus fading to the mid-valve and a more ventribiconvex profile. *Plectorthis? punctata* has a slightly sulcate dorsal valve by comparison with *P.? burultasica* as well as fewer rib bifurcations. It is also considerably smaller. In addition, *P.? obesa* has a more strongly convex dorsal valve and fewer bifurcations in the ribbing.

PLATE 11

Figs 1, 2 *Dolerorthis expressa* Popov, Sample 8137, Anderkenyn-Akchoku section, BC 57526, dorsal internal mould, $\times 2$, and latex of external mould, $\times 6$.

Figs 3–12 *Plectorthis? burultasica* sp. nov. **3, 4**, Sample 7613, Akchoku Mountain, Kujandysai section. BC 57528, **holotype**, dorsal latex cast and internal mould, $\times 2$. **5–8**, Sample 1041a, Burultas, BC 57529, conjoined valves, lateral, posterior, ventral and dorsal views, $\times 2$. **9–11**, Sample 1018, area 7 km SW of Kotnak mountains, south Betpak-Dala, CNIGR 1/11989, conjoined valves, dorsal, ventral and lateral views, $\times 2$. **12**, Sample 8128, Anderkenyn-Akchoku section, BC 57530, ventral exterior, latex cast, $\times 2$.

Figs 13, 14 *Phaceloorthis? sp.* Sample 2538, Akchoku Mountain, Kujandysai section, BC 57531, conjoined valves, ventral and dorsal views, $\times 1.5$.

Figs 15–22 *Austinella sarybulakensis* sp. nov. Sample 85258, east side of Kujandysai. **15–18**, BC 56507, conjoined valves, **holotype**, ventral, lateral, anterior and dorsal views, $\times 1.5$. **19**, BC 56508, conjoined valves, posterior view, $\times 1.5$. **20**, BC 56505, ventral interior, $\times 2$. **21, 22**, BC 56506, dorsal internal mould and latex cast, $\times 2$.

Fig. 23–37 *Bowanorthis? devexa* sp. nov. Sample 2538, Akchoku Mountain, Kujandysai section. **23–27**, BC 57532, conjoined valves, **holotype**, ventral, lateral, anterior, dorsal and posterior views, $\times 3$. **28–32**, BC 57533, conjoined valves, lateral, dorsal anterior, posterior, and ventral views, $\times 3$. **33–37**, BC 57534, conjoined valves, lateral, posterior, ventral, dorsal and anterior views, $\times 3$.

Figs 38–44 *Phragmorthis conciliata* Popov. **38**, Sample 1018, area 7 km SW of Kotnak mountains, south Betpak-Dala, CNIGR 1/11989, ventral internal mould, $\times 4$. **39**, Sample 7613, Akchoku Mountain, Kujandysai section. BC 57535, ventral internal mould, $\times 5$. **40–42**, Sample 2538, Akchoku Mountain, Kujandysai section, BC 57536, conjoined valves, lateral, dorsal and ventral views, $\times 4$. **43, 44**, Sample 626, Anderkenyn-Akchoku section, BC 57537, ventral exterior and lateral view, $\times 4$.

Genus *PHACELOORTHIS* Percival, 1991

TYPE SPECIES. *P. decoris* Percival, 1991, from the Quondong Limestone (Caradoc) of New South Wales, Australia.

Phaceloorthis? sp. Pl. 11, figs 13, 14

MATERIAL. One pair of conjoined valves (BC 57531) (L=20.8, W=25.6, T=9.8) from Sample 2538, Kujandysai, near Akchoku Mountain.

DESCRIPTION. Shell subequally biconvex, transversely subrectangular in outline with hinge line somewhat shorter than maximum shell width at mid-length. Anterior margin rectimarginate. Ventral valve moderately convex in lateral profile with maximum thickness at one-third valve length. Ventral interarea almost orthocline, slightly curved in cross-section with open, narrow triangular delthyrium. Dorsal valve moderately convex with maximum thickness near the mid-valve. Umbonal area with shallow sulcus fading towards mid-valve. Dorsal interarea anacline, planar, linear. Shell surface with 9 low, angular radial plications and superimposed finely fascicostellate ribs 7–9 per 3 mm along the anterior margin. Interior of both valves unknown.

DISCUSSION. The interior of this species remains unknown, which makes its generic attribution highly provisional, but there are only a few impunctate mid and late Ordovician orthide genera with fascicostellate ornament and they are mostly related to the family Giraldiellidae. Otherwise fascicostellate ribbing is characteristic of the plectorthid genus *Phaceloorthis*. This single specimen somewhat resembles *Phaceloorthis recondita* Popov, Nikitin & Cocks, 2000 from the Otter Member (Upper Caradoc) of the Dulankara Mountains in its general shell shape and size and fascicostellate ornament, but differs in having an orthocline ventral interarea and weak radial plications.

Family **WANGYUIIDAE** Zeng, 1989
Genus **BOWANORTHIS** Percival, 1991

TYPE SPECIES. *Bowanorthis fragilis* Percival, 1991, from the Caradoc of New South Wales, Australia.

Bowanorthis? *devexa* sp. nov. Pl. 11, figs 23–37; Fig. 14

ETYMOLOGY. After *devexus*, Latin – hollow.

HOLOTYPE. BC 57532, Pl. 11, figs 23–27, conjoined valves, from the Anderken Formation, Sample 2538, Kujandysai, near Akchoku Mountain.

MATERIAL. Twelve conjoined valves from Samples 2538 (BC 57178, 57532–34), 8217 (BC 57179) Kujandysai, near Akchoku Mountain; Sample 948 (BC 57172–77), Tesik River.

DESCRIPTION. Shell ventribiconvex, slightly transverse and semioval, about 85–98% as long as wide with hinge line slightly shorter than maximum width at one-quarter shell length. Anterior commissure sulcate. Ventral valve carinate posteriorly, strongly convex in lateral profile with maximum thickness at about one-third valve length. Beak small, erect. Ventral interarea apsacline, incurved in cross-section, with small subtriangular delthyrium. Ventral median fold originating at the umbonal area with steep lateral slopes flanked by folds. Lateral sides of the valves less convex. Dorsal valve evenly convex with linear, anacline interarea and deep, V-shaped median sulcus originating at the beak and ending in a low semioval tongue occupying slightly less than half of the valve length. Radial ornament fascicostellate with three strong angular ribs and 4–5 costellae per mm along the anterior margin of mature specimens. Interior of both valves unknown.

MEASUREMENTS. Conjoined valves; (58/12375) L=6.4, W=6.7, T=3.8, Sw=3.3; (59/12375), L=4.5, W=4.6, T=2.7, Sw=2.6; (60/12375), L=4.8, W=5.6, T=3.1, Sw=2.4.

DISCUSSION. This species is provisionally included within *Bowanorthis* because of the small ventribiconvex shell with strongly sulcate anterior commissure, carinate ventral valve, fascicostellate ornament and receding dental plates, all resembling *B. fragilis* from the Caradoc of New South Wales (Percival 1991); however, it differs in having a strongly apsacline ventral interarea and a less transverse shell outline. The general morphology of the cardinal process and brachioophores in the Kazakh species looks similar to *B. fragilis*, but the presence of the characteristic sigmoidal plates is impossible to

Fig. 14 Transverse serial sections of *Bowanorthis*? *devexa* sp. nov. from Sample 2538, Kujandysai section. Distance in mm is measured from the posterior tip of ventral beak. Dorsal valve uppermost. Also reconstructions of the ventral and dorsal interiors.

confirm from our sections (Fig. 14). In general shell shape and fascicostellate radial ornament the Anderken material is similar to *Ranorthis* Öpik (1939) from the Volkhov and Kunda Stages of Baltica. However, the generic attribution of *devexa* is tentative and it may represent an undescribed genus.

Family **RANORTHIDAE** Havlíček, 1949
Genus **EODALMANELLA** Havlíček, 1950

TYPE SPECIES. *Orthis socialis* Barrande, 1879; from the Sarká Formation (Llanvirn) of Bohemia.

Eodalmanella extera Popov, 1985 Pl. 12, figs 10–12, 15
1985 *Eodalmanella extera* Popov: 54, pl. 1, figs 3–8.

HOLOTYPE. CNIGR 4/11989, ventral internal mould (L=4.1, W=6.1), from the Anderken Formation, Anderkenyn-Akchoku section, Sample 843.

MATERIAL. Five pairs of conjoined valves, 42 ventral and 48 dorsal valves, internal and external moulds, from Samples 100b, 620 (BC 57189), 843, Anderkenyn-Akchoku section; Sample 1018, 7 km southwest of Karpkuduk well, Kotnak Mountains.

DESCRIPTION. Shell ventribiconvex, transverse, subrectangular in outline, about 85% as wide as long with maximum width at mid-length. Anterior commissure gently sulcate. Ventral profile moderately convex, about one-third as thick as long, with maximum thickness at about one-quarter valve length. Dorsal valve gently convex in transverse profile with maximum thickness slightly anterior to the umbo and with shallow median sulcus originating in the umbonal area. Dorsal interarea linear, strongly anacline. Radial ornament multicostellate with 3–6 ribs per mm along the anterior margin of mature specimens. Concentric ornament of very fine ridge-like, evenly spaced fila, often branching anteriorly.

Ventral interior with teeth supported by short, divergent dental plates and rounded subtriangular, slightly elongate muscle field about 37% as long as the valve. Ventral adductor scars narrow, subtriangular, slightly shorter than diductor scars. Cardinal process ridge-like with bilobed, crenulated miophore. Brachioophores high, triangular, with widely diverging bases. Fulcral plates well developed. Dorsal adductor scars quadripartite, extending anteriorly to mid-valve, bordered laterally by low ridges.

DISCUSSION. This species strongly resembles *Scaphorthis? aulacis* Percival (1979a) from the Caradoc Goonumbla Volcanics of New South Wales in the impunctate shell, radial ornament and internal morphology of both valves. The Kazakh species differs in having longer dental plates, a cardinal process with a long shaft crossing all the bottom of the notothyrial cavity and well defined lateral ridges bordering the dorsal adductor field. A detailed discussion and basic statistics of this species were provided by Popov (in Nikitin & Popov 1985).

Table 22 Measurements of dorsal valves of *Pionodema opima* sp. nov., Sample 8228 from Kopalysai Section, sample 8229 from Buldukbai-Akchoku and Sample 7613 from Kujandysai section.

	Ld	W	BBi	BBw	Mi	Mw	Lv/W	Mi/L	BBw/W
N	7	7	5	5	3	3	4	3	5
X	7.6	9.5	1.6	2.6	3.4	3.1	82.8%	41.2%	60.4%
S	2.36	2.86	0.15	0.34	0.32	0.10	10.7	2.9	9.9
MIN	3.2	4.0	1.4	2.3	3.2	3.0	70.1%	38.8%	50.0%
MAX	10.5	12.9	1.7	3.1	3.8	3.2	96.1%	44.4%	73.9%

Family **CREMNORTHIDAE** Williams, 1963
Genus **PHRAGMORTHIS** Cooper, 1956

TYPE SPECIES. *Phragmorthis buttsi* Cooper, 1956, from the Effna-Rich Valley Formations (Llandeilo-Lower Caradoc) of Virginia, U.S.A.

Phragmorthis conciliata Popov, 1985
Pl. 11, figs 38–44; Pl. 12, figs 1–9

1985 *Phragmorthis conciliata* Popov: 52, pl. 1, figs 9–12.
HOLOTYPE. CNIGR 10/11989 (Pl. 12, figs 1, 2), dorsal valve internal mould (L=4.5, W=7.2), from the Anderken Formation, 7 km south-west of Karpkuduk well, Kotnak Mountains, Sample 1018.

MATERIAL. Two pairs of conjoined valves, 6 ventral and 8 dorsal valves, internal and external moulds, from Samples 626 (BC 57537), 8223a, Anderkenyn-Akchoku section; Samples 2538 (BC 57536), 7613 (BC 57535), Kujandysai section; Sample 8230, Buldukbai-Akchoku section; Sample 1018, 7 km southwest of Karpkuduk well Kotnak Mountains; Sample 1024b, south side of Karatal River, south of Sorbulak spring.

DIAGNOSIS. Shell ventribiconvex, transverse, subrectangular outline about 77% as wide as long with maximum width at mid-length, anterior commissure gently unisulcate; ventral valve strongly convex with maximum thickness between the umbo and mid-valve; ventral interarea high triangular, apsacine with narrow open delthyrium; dorsal valve moderately and evenly convex with narrow and shallow sulcus originating at the umbo; radial ornament finely and equally multicostellate with 5 ribs per mm along the anterior margin of mature specimens. Ventral interior with elongate subtriangular muscle field on pseudospondylium 21–26% as long as the valve. Dorsal interior with simple, ridge-like cardinal process on the high notothyrial platform which is strongly raised anteriorly; high, blade-like median septum 88% valve length; large, deeply impressed adductor scars, radially arranged, about 66% valve length.

DISCUSSION. This species differs from *Phragmorthis buttsi* Cooper (1956: 510) in its transverse subrectangular outline and lesser convexity of both valves. It is on average about half the size of *Phragmorthis crassa* Cooper (1956: 511) and has finer radial ornament. Both *P. buttsi* and *P. crassa* have a subcarinate ventral valve, which is another difference from the Kazakh species.

Table 21 Measurements of ventral valves of *Pionodema opima* sp. nov., Sample 8228 from Kopalysai Section, sample 8230 from Buldukbai-Akchoku and Sample 7613 from Kujandysai section.

	Lv	W	Mi	Mw	Lv/W	Mi/L	Iw/W
N	9	9	5	6	9	5	5
X	7.6	9.4	3.2	3.5	81.2%	38.5%	90.5%
S	1.38	2.16	0.63	1.26	8.6	4.9	14.9
MIN	5.0	7.3	2.6	2.3	68.5%	34.2%	64.9%
MAX	9.8	13.8	4.1	5.7	93.2%	46.6%	103.6%

Suborder **DALMANELLIDINA** Moore, 1952
 Superfamily **ENTELETOIDEA** Waagen, 1884
 Family **DRABOVIIDAE** Havlíček, 1950
 Subfamily **DRABOVIINAE** Havlíček, 1950
 Genus **PIONODEMA** Foerste, 1912

TYPE SPECIES. *Orthis subaequata* Conrad, from the Caradoc of Missouri, U.S.A.

Pionodema opima sp. nov. Pl. 12, figs 13, 14, 16–27

ETYMOLOGY. After *opimus*, Latin – fat.

HOLOTYPE. BC 57545, Pl 12, figs 17–18, internal mould of conjoined valves, from the Anderken Formation, Sample 7613, Kujandysai section.

MATERIAL. Nine pairs of conjoined valves, 70 ventral and 64 dorsal valves from Sample 7613 (BC 57545), Kujandysai section; Sample 8128, Anderkenyn-Akchoku; Sample 8228 (BC 57185, 57547, 48), east side of Kopalsai; Samples 110, 8229 (BC 57546), 8230 (BC 57803), 8257 (BC 57544), Buldukbaï-Akchoku section; Sample 818a (BC 57802), Burultas Valley.

DESCRIPTION. Shell slightly dorsibiconvex, transverse, suboval in outline, about 84% as long as wide and 53% as thick as long. Hinge line slightly shorter than the maximum shell width at mid-length. Anterior commissure uniplicate. Ventral valve gently convex with maximum thickness at the umbonal area. Beak curved, pointed and slightly erect posterior to hinge line. Ventral interarea subtriangular, apsacline, weakly curved in cross-section, with open triangular delthyrium. Shallow sulcus originating near mid-valve. Dorsal valve moderately convex with maximum thickness at quarter valve length. Umbonal area with shallow V-shaped sulcus reversed into a low and narrow median fold flanked laterally by weak plications. Radial ornament multicostellate with 28–30 primary ribs and about 3–5 costellae per mm along the anterior margin of full grown specimens. Growth lines fine, ridge-like, crowded, evenly spaced.

Ventral interior with teeth and long, diverging dental plates continuing into ridges bordering laterally slightly elongate suboval muscle field. Ventral adductor scars narrow and subtriangular, raised anteriorly and somewhat shorter than the strongly impressed elongate suboval diductor scars. Ventral mantle canals lemniscate, straight, widely diverging. Dorsal interior with high, triangular brachiophores with slightly diverging bases. Fulcral plates variably developed. Cardinal process ridge-like with crenulated myophore. Dorsal adductor scars bisected by fine median ridge and bordered laterally by subparallel ridges starting from the ends of the brachiophore bases.

DISCUSSION. This species is characterised by a uniplicate anterior commissure with low dorsal median fold and shallow ventral sulcus, which is unusual for *Pionodema* (Cooper 1956), and can be compared only with *P. uniplicata* Cooper, but differs from that species in its more transverse outline and the weak umbonal dorsal sulcus reversing into a median fold at about mid-length. The Anderken specimens also lack the prominent ridge anterior to the ventral muscle field of *P. uniplicata* (Cooper 1956: pl. 154, figs 31–32).

Order **PENTAMERIDA** Schuchert & Cooper, 1931
 Suborder **SYNTROPHIIDINA** Ulrich & Cooper, 1936
 Superfamily **CAMARELLOIDEA** Hall & Clarke, 1894
 Family **CAMARELLIDAE** Hall & Clarke, 1894
 Genus **PARASTROPHINA** Schuchert & LeVene, 1929

TYPE SPECIES. *Atrypa haemiplicata* Hall, 1847, from the Trenton Limestone (Caradoc), New York, U.S.A.

Parastrophina iliana sp. nov.

Pl. 13, figs 30–50; Figs 15, 16

1956 *Camerella haemiplicata* (Hall) var. *rotunda* (Winchell & Schuchert); Rukavishnikova: 129, pl. 2, figs 1, 3 (*non* fig. 2).

1975 *Parastrophina haemiplicata* (Hall); Sapelnikov & Rukavishnikova: 25, pl. 1, figs 1–8.

1986 *Parastrophina haemiplicata* (Hall); Kolobova & Popov; pl. 1, fig. 4.

HOLOTYPE. BC 57557, Pl. 13, figs 38–42, conjoined valves from Sample 100, Anderkenyn-Akchoku section.

MATERIAL. 52 pairs of conjoined valves, one ventral and 3 dorsal valves from Samples 100 (=K-98/1970) (BC 56643–46, 57557), 626 (BC 56634–6), Anderkenyn-Akchoku section; Samples, 628 (BC 56633, 56642, 57559), 2538 (BC 56637–41), 8217 (BC 57556), 8256 (BC 57558), 85258, Kujandysai Section; Sample 948 (BC 57192–99), Tesik River; Sample 1041a, Burultas Valley.

DESCRIPTION. Shell dorsibiconvex to biconvex, transverse, semielliptical in outline, about 90% as long as wide and 75% as thick as long. Anterior commissure uniplicate. Ventral valve gently convex with maximum thickness somewhat posterior to mid-valve. Sulcus originating about 5–6 mm from the umbo, deepening anteriorly and terminating in broad, semioval tongue

PLATE 12

Figs 1–9 *Phragmorthis conciliata* Popov. 1, 2, Sample 1018, area 7 km SW of Karpkuduk well, Kotnak Mountains, CNIGR 10/11989, **holotype**, latex cast and dorsal internal mould, $\times 4$. 3, 5–9, Sample 2538, Akchoku Mountain, Kujandysai section; 3, BC 57538, dorsal exterior, $\times 4$; 5–8, BC 57539, conjoined valves lateral, dorsal, posterior and ventral views, $\times 4$; 9, CNIGR 12/11989, latex cast of dorsal exterior, $\times 4$. 4, Sample, 8230, Buldukbaï-Akchoku section, west side of Kopalsai, BC 57603, dorsal internal mould, $\times 5$.

Figs 10–12, 15 *Eodalmarella exera* Popov. 10, Sample 1018, area 7 km SW of Karpkuduk well, Kotnak Mountains, CNIGR 9/11989, ventral exterior, $\times 4$. 11, Sample 620, Anderkenyn-Akchoku section, BC 57189, dorsal exterior latex cast, $\times 5$. 12, 15, Sample 843, Anderkenyn-Akchoku section; 12, CNIGR 5/11989, dorsal internal mould, $\times 4$; 15, CNIGR 3/11989, ventral internal mould, $\times 4$.

Figs 13, 14, 16–27 *Pionodema opima* sp. nov. 13, 14, Sample 8257, Buldukbaï-Akchoku section, west side of Kopalsai, BC 57544, internal mould, dorsal and ventral views, $\times 3$. 16, Sample 8230, east side of Kopalsai, BC 57803, latex cast of dorsal external mould, $\times 2.7$. 17, 18, Sample 7613, Akchoku Mountain, Kujandysai section, BC 57545, **holotype**, internal mould of conjoined valves, dorsal and ventral views, $\times 3$. 19–24, Sample 818a, Burultas valley, BC 57802, conjoined valves, detail of radial ornament, $\times 8$, and lateral, ventral, dorsal, posterior and anterior views, $\times 4$. 25, Sample, 8229, Buldukbaï-Akchoku section, west side of Kopalsai, BC 57546, dorsal internal mould, $\times 3$. 26, 27, Sample 8228, east side of Kopalsai; 26, BC 57548, ventral internal mould, $\times 3$; 27, BC 57547, ventral internal mould, $\times 2$.

Figs 28–35 *Illostrophina tesikensis* gen. et sp. nov., Sample 948, Tesik River. 28–31, BC 56824, conjoined valves, lateral, anterior, ventral and dorsal views, $\times 4$. 32–35, BC 56823, conjoined valves, **holotype**, dorsal, ventral, lateral and anterior views, $\times 4$.

Fig. 15 Photographs of transverse serial sections, $\times 12$. Distance in mm is measured from the posterior tip of ventral beak. Dorsal valve uppermost. **1–2**, *Placotriplezia spissa* sp. nov., BC 57605, Sample 628, Kujandysai section; **1**, 1.5 mm; **2**, 1.8 mm. **3, 4, 9–14**, *Ilistrophina tesikensis* gen. et sp. nov., Sample 948, Tesik River, **3, 4**, BC 57606, 0.3 and 0.4 mm; **9–14**, BC 57607, 0.4, 0.6, 0.8, 1.0 and 1.4 mm; **5–7**, *Parastrophina iliana* sp. nov., BC 56560, Sample 948, Tesik River; 0.6, 0.8 and 1.2 mm; **8**, *Parastrophina plena* Sapelnikov & Rukavishnikova, BC 57564, Sample 948, Tesik River, 1.0 mm.

about 66% valve width. Dorsal valve strongly convex with maximum thickness at mid-valve or slightly anteriorly. Umbonal area strongly swollen. Broad median fold originating near mid-valve. Radial ornament of coarse rounded-angular ribs originating anterior to mid-valve in mature specimens with 1–3 ribs in the sulcus, 2–4 on the median fold and up to 6 on the flanks of both valves.

Ventral interior with small teeth and narrow spondylium on a low median septum extending anteriorly to mid-valve. Dorsal interior with narrow cruralium on the low median septum. Alate plates small, projecting anteriorly as short brachial processes. Inner plates narrow, gently curved. Outer plates nearly straight in cross-section, converging towards a thin median septum.

MEASUREMENTS. (471/12375) conjoined valves, $L=14.0$, $W=16.9$,

$T=6.3$, $Sw=8.9$; (474/12375) conjoined valves, $L=20.4$, $W=21.0$, $T=11.2$, $Sw=8.7$; (475/12375) conjoined valves, $L=22.9$, $W=24.5$, $T=10.2$, $Sw=12.8$; (476/12375) conjoined valves, $L=16.5$, $W=19.8$, $T=6.5$, $Sw=11.2$; (479/12375) conjoined valves, $L=10.5$, $T=6.7$, $Sw=6.7$.

DISCUSSION. The Kazakh shells are comparable to *Parastrophina haemiplicata* (Hall), and in particular with specimens described and illustrated by Cooper (1956: 606, pl. 106, figs 33–44; pl. 117, figs 19–27) from the lower Martinsburg Formation of Virginia, in outline and profile of both valves, as well as in the characters of the radial ornament, dorsal median fold and ventral sulcus, but they differ in having more conspicuous ribbing on the flanks of mature shells, which may possess up to 7 ribs; however, the number of ribs is

Table 23 Measurements of complete shells of *Parastrophina iliana* sp. nov., Sample 948, Tesik river.

	L	W	T	Ld	Sw	St	L/W	T/L	Ld/W	Sw/W
N	11	10	10	11	10	10	10	10	10	9
X	8.2	9.1	5.8	8.1	6.1	3.6	89.2%	74.0%	87.7%	65.6%
S	2.05	2.87	1.16	2.10	1.65	1.52	6.3	10.4	5.2	6.5
MIN	5.5	5.6	4.2	5.3	3.2	1.6	80%	62%	79%	57%
MAX	11.9	14.8	7.4	11.7	8.5	6.6	98%	95%	95%	78%

Fig. 16 Transverse serial sections from Sample 948, Tesik River. **A**, *Parastrophina iliana* sp. nov., BC 57560; **B**, *Parastrophina plena* Sapelnikov & Rukavishnikova, BC 57564. Distance in mm is measured from the posterior tip of ventral beak. Dorsal valve uppermost.

variable in the studied samples. There is also a strong tendency to asymmetry in the anterior commissure of the Kazakh shells. However, as mentioned by Cooper, his specimens were somewhat different from Hall's types and the species needs more substantial revision. Specimens from the Anderken Formation described by Rukavishnikova (1956) as *Camerella haemplicata* (Hall) var. *rotunda* seem likely to represent a mixture of several taxa. In particular, the specimens illustrated on her pl. 2, fig. 2 may belong to *Liostrophina*, but others appear to be conspecific with ours. It is possible that the Kazakh shells are conspecific with the specimens described as *Parastrophina haemplicata* by Fu (1982: 129, pl. 36, fig. 16) from the Jinhe Formation (Caradoc) of northwest China. The only illustrated specimen is similar to some of the juvenile Kazakh shells in ribbing and in the lateral profile of both valves, but it is impossible to estimate the limits of morphological variation in the Chinese population of *Parastrophina* from the published illustrations and description. There is remarkable general similarity between the brachiopod assemblage from the Jinhe Formation and the fauna from the carbonate mud-mounds in the upper Anderken Formation. In particular, both assemblages contain distinctive genera such as

Schizostrophina and *Pectenospira* (Popov *et al.* 1999) which are otherwise unknown elsewhere.

Parastrophina plena Sapelnikov & Rukavishnikova, 1975
Pl. 13, figs 51–58; Figs 15, 16

1975 *Parastrophina plena* Sapelnikov & Rukavishnikova: 27, pl. 1, figs 12–14.

1982 *Parastrophina uniplicata* Fu:130, pl. 36, fig. 17.

HOLOTYPE. IGNA 436/1861, conjoined valves, from the Anderken Formation, Sample 302 of Keller (1956), Anderkenyn-Akchoku section.

MATERIAL. 102 pairs of conjoined valves, 1 ventral and 2 dorsal valves from Samples 100 (=K-98/1970), 8223a (BC 56595), 8223b (BC 57248–52), 8226, Anderkenyn-Akchoku section; Samples 8214 (BC 57216–37, 57563), 8215 (BC 57238–47), west side of Ashchisu River; Samples 628 (BC 56598–600), 2536 (BC 56605–10), 2538 (BC 57562), 8217, 8219, 8256 (BC 56603–4), Kujandysai Section; Sample 948 (BC 57200–15), Tesik River.

Table 24 Measurements of ventral valves of *Parastrophina plena* Sapelnikov and Rukavishnikova, Sample 948, Tesik river.

	L	W	T	Ld	Sw	St	L/W	T/L	Ld/W	Sw/W
N	34	34	34	34	31	33	34	34	34	31
X	6.6	7.1	4.8	6.7	4.3	3.1	93.6%	72.7%	94.3%	60.7%
S	0.74	0.95	0.91	0.75	0.55	0.82	5.7	8.7	5.5	5.3
MIN	5.5	5.8	3	5.5	3.4	1.4	83.0%	52.6%	83.6%	52.9%
MAX	9	9.7	7.5	9	5.4	4.8	107.5%	87.7%	107.5%	76.8%

DESCRIPTION. Shell smooth, dorsibiconvex, subpentagonal in outline, about 70% as thick as long and 95% as long as wide. Anterior commissure sulciphate. Ventral valve gently convex in lateral profile with maximum thickness about one-third valve length from the small, slightly erect pointed beak posterior to the hinge line. Sulcus about 60% as wide as the valve, originating in the umbonal area at about 4–5 mm from the beak, strongly deepening anteriorly and divided medianly by high angular costa originating near mid-valve. Dorsal valve strongly and evenly convex with maximum thickness at mid-valve with median fold originating slightly anterior to mid-valve and bearing two strong angular ribs.

Ventral interior with small teeth and deep, narrow spondylium on the low median septum. Dorsal interior with narrow cruralium raised anteriorly on a low median septum extending anteriorly not more than 1.5 mm in adults. Inner plates small, thickened, slightly curved in cross-section. Brachial processes short.

MEASUREMENTS. (471/12375) conjoined valves, L=14.0, W=16.9, T=6.3, Sw=8.9; (474/12375) conjoined valves, L=20.4, W=21.0, T=11.2, Sw=8.7; (475/12375) conjoined valves, L=22.9, W=24.5, T=10.2, Sw=12.8; (476/12375) conjoined valves, L=16.5, W=19.8, T=6.5, Sw=11.2; (479/12375) conjoined valves, L=10.5, T=6.7, Sw=6.7.

DISCUSSION. This species usually occurs in the upper Anderken Formation together with *Parastrophina iliana*, but can be easily distinguished in being half the size, in the smooth shell with a single costa in the sulcus and two in the fold of mature specimens, and in the sulciphate anterior commissure.

Parastrophina plena closely resembles *Parastrophina uniplicata* Fu, 1982 from the Jinhe Formation (Caradoc) of northwest China in its smooth shell, sulciphate anterior commissure, and in the characters of the dorsal fold and ventral sulcus. They may be conspecific.

Genus *ILISTROPHINA* Gen.nov.

TYPE SPECIES. *Ilistrophina tesikensis* sp.nov.

DIAGNOSIS. Shell smooth, ventribiconvex with well-developed dorsal median fold and ventral sulcus; ventral interior with spondylium sessile posteriorly, raised anteriorly on low median septum; dorsal interior with cruralium supported by high median septum; well defined alate plates and long brachial processes.

DISCUSSION. Externally *Ilistrophina* is most similar to *Eostrophina* (Zhan & Rong 1995) but differs in having a narrow spondylium sessile posteriorly, raised anteriorly on a low median septum and well developed alate plates. It differs from *Liostrophina* in having strongly raised cruralium supported by a median septum instead of a sessile cruralium or separated outer plates; however, present knowledge of the interior of type species of the former remains inadequate. *Ilistrophina* resembles *Parastrophina* and *Parastrophinella* in the interior morphology of both valves, but differs in having a smooth shell and a sessile spondylium posteriorly. Jin and Copper (1997) demonstrated that in *Parastrophinella* the cruralium is supported by the median septum along its entire length, but, in contrast to *Ilistrophina*, the dorsal median septum in *Parastrophinella* is very low and buried within secondary shell in the apical area.

Ilistrophina tesikensis sp. nov.

Pl. 12, figs 28–35; Figs 15, 17

ETYMOLOGY. After the type locality.

HOLOTYPE. BC 56823, Pl. 12, figs 32–35, conjoined valves, from Sample 948, Tesik River.

MATERIAL. 14 pairs of conjoined valves (including BC 56823–24) and one dorsal valve, all from Sample 948, Tesik River.

DESCRIPTION. Shell smooth, dorsibiconvex, subcircular in outline,

Table 25 Measurements of ventral valves of *Ilistrophina tesikensis* sp. nov., Sample 948, Tesik river.

	L	W	T	Ld	Sw	St	L/W	T/L	Ld/W	Sw/W
N	9	9	9	9	9	8	9	9	9	9
X	7.5	8.2	5.1	7.5	5.7	3.9	92.3%	68.2%	92.2%	70.2%
S	1.01	1.46	0.82	0.98	0.96	0.94	4.7	6.6	4.9	5.4
MIN	6.2	6.4	4.2	6.2	4.6	2.4	83.8%	58.3%	82.9%	63.9%
MAX	9.8	11.7	6.8	9.7	7.8	5	97.5%	79.4%	97.5%	80.7%

PLATE 13

- Figs 1–29** *Liostrophina pravula* sp. nov., Akchoku Mountain, Kujandysai section. **1–15**, Sample 8256; **1–5**, BC 57550, conjoined valves, ventral, dorsal, anterior, posterior and lateral views, $\times 2$; **6–10**, BC 57551, conjoined valves, dorsal, ventral, anterior, posterior and lateral views, $\times 2$; **11–15**, BC 57552, conjoined valves, dorsal, ventral, lateral, posterior and anterior views, $\times 2$. **16–29**, Sample 2538; **16–20**, BC 57553, **holotype**, conjoined valves, dorsal, ventral, lateral, anterior and posterior views, $\times 2$; **21–24**, BC 57554, conjoined valves, ventral, dorsal, anterior and lateral views, $\times 2$; **25–29**, BC 57555, conjoined valves, ventral, dorsal, posterior, lateral and anterior views, $\times 2$.
- Figs 30–50** *Parastrophina iliana* sp.nov. **30–33**, Sample 8217, Kujandysai section, BC 57556, conjoined valves, dorsal, anterior, lateral and ventral views, $\times 2$. **34–37**, Sample 2538, Kujandysai section, CNIGR 4/12361, conjoined valves, lateral, dorsal, ventral and posterior views, $\times 2$. **38–42**, Sample 100, Anderkenyn-Akchoku section, BC 57557, **holotype**, conjoined valves, dorsal, ventral, posterior, anterior and lateral views, $\times 2$. **43–46**, Sample 8256, Kujandysai section, BC 57558, conjoined valves, dorsal, lateral, ventral and posterior views, $\times 2$. **47–50**, Sample 628, Kujandysai section, BC 57559, conjoined valves, dorsal, lateral, ventral and anterior views, $\times 2$.
- Figs 51–58** *Parastrophina plena* Sapelnikov & Rukavishnikova, 1975. **51–54**, Sample 2538, Kujandysai section, BC 57562, conjoined valves, lateral, dorsal, ventral and anterior views, $\times 2$. **55–58**, Sample 8214, Anderkenyn-Akchoku section, BC 57563, conjoined valves, anterior, lateral, ventral and dorsal views, $\times 2$.
- Figs 59–74** *Plectrosyntrophina unicostata* sp. nov., Anderkenyn-Akchoku section. **59–62**, **67–70**, Sample 626; **59–62**, BC 57568, conjoined valves, dorsal, posterior, lateral, and ventral views, $\times 2$; **67–70**, BC 57570, conjoined valves, **holotype**, lateral, ventral, dorsal and posterior views, $\times 2$. **63–66**, **71–74**, Sample 100; **63–66**, BC 57569, conjoined valves, lateral, anterior, dorsal and posterior views, $\times 2$; **71–74**, BC 57571, conjoined valves, lateral, dorsal ventral and anterior views, $\times 2$.
- Figs 75–77** *Didymelasma* cf. *transversa* Fu, Sample 2538, Kujandysai section, BC 57573, conjoined valves, dorsal, lateral and ventral views, $\times 2$.

Fig. 17 Transverse serial sections of *Ilistrophina tesikensis* gen. et sp. nov., BC 57606, Sample 948, Tesik River. Distance in mm is measured from the posterior tip of ventral beak (dorsal valve uppermost), also an axial diagram showing the plates.

about 65% as high as long and 90% as long as wide with maximum width at mid-length. Anterior commissure strongly uniplicate. Ventral valve gently convex in lateral profile with maximum thickness somewhat posterior to mid-length. Beak small, curved towards the hinge line. Sulcus originating about 4–5 mm from the umbo, strongly deepening anteriorly and terminating with a high semioval tongue about 70% valve width. Dorsal valve with moderately convex lateral profile. Beak slightly swollen, curved. Dorsal median fold originating anterior to mid-length, semioval in cross-section.

Ventral interior with small teeth and narrow spondylium, bell-shaped in cross-section, sessile posteriorly and raised anteriorly on a low, thick median septum extending to mid-valve length. Dorsal interior with cruralium supported by high median septum along its entire length. Inner plates present.

MEASUREMENTS. conjoined valves, $L_v=9.8$, $W=11.7$, $T=6.8$, $Sw=7.8$, $St=4.0$; conjoined valves, $L_v=7.8$, $W=8.2$, $T=5.7$; $Sw=5.5$, $St=4.7$.

DISCUSSION. This species is externally comparable to *Eostrophina uniplicata* from the Middle Ashgill Xiazhen Formation of South China, but can be easily distinguished in its smaller size, which does not exceed 10 mm in length in the largest specimens, and in having a dorsal median fold evenly rounded in cross-section and originating anteriorly to the mid-valve.

Genus *LIOSTROPHIA* Cooper & Kindle, 1936

TYPE SPECIES. *Liostrophia glabra* Cooper & Kindle, 1936, from the Ashgill of Canada.

Liostrophia pravula sp. nov. Pl. 13, figs 1–29; Fig. 18

ETYMOLOGY. After *pravus*, Latin – bowed.

HOLOTYPE. BC 57553, pl. 13, figs 16–20, conjoined valves, from the Anderken Formation, Sample 2538, Akchoku Mountain, Kuyandysai section.

MATERIAL. 30 pairs of conjoined valves, one ventral and 7 dorsal valves, from Samples 100 (=K-98/1970) (BC 57253–56), 626 (BC 57263–65), 8223, Anderkenyn-Akchoku section; Samples 2538 (BC 57266–69, 57553–55), 8256 (BC 57550–52), Kuyandysai section; Sample 948 (BC 57257–62), Tesik River.

DESCRIPTION. Shell slightly dorsibiconvex, transverse, subcircular in outline, about 51% as thick as long and 90% as long as wide, with maximum width at mid-length. Anterior commissure gently uniplicate. Ventral valve gently convex in lateral profile, with maximum thickness somewhat posterior to mid-length. Small, pointed beak, slightly erect and posterior to hinge line. Broad shallow sulcus, originating near the anterior margin, usually asymmetrical in cross-section. Dorsal valve moderately and evenly convex in profile with slightly swollen, curved beak. Dorsal median fold usually absent but weakly developed anteriorly in mature specimens. Shell surface smooth with one or two ribs in the fold and sulcus near the anterior margin of the largest specimens.

Ventral interior with teeth and spondylium supported anteriorly by very low septum enclosed posteriorly by a secondary shell thickening (Fig. 18). Dorsal interior with sessile cruralium formed by high outer plates joined at the valve floor. Alate plates small, appearing at some distance from the umbo. Inner plates small, slightly thickened, strongly curved in cross-section with the outer parts located almost within commissural plane. Brachial processes thin and relatively long.

MEASUREMENTS. (518/12375) conjoined valves, $L=7.6$, $W=7.9$,

Table 26 Measurements of ventral valves of *Liostrophia pravula* sp. nov., Sample 2538, Kujandysai section.

	L	W	T	Sw	St	L/W	T/L	Sw/W
N	11	11	11	10	10	9	9	9
X	5.7	6.3	2.9	4.1	1.5	89.7%	50.9%	61.8%
S	1.45	1.56	1.05	0.75	0.18	7.6	6.3	3.7
MIN	3.3	3.5	1.3	3.2	1.2	81.5%	42.6%	57.1%
MAX	8.2	9.2	5.1	5.7	1.8	103.8%	62.2%	70.2%

Fig. 18 Transverse serial sections of *Liostrophia pravula* sp. nov., Sample 2538, Kujandysai section. Distance in mm is measured from the posterior tip of ventral beak. Dorsal valve uppermost. Also lateral view to show section positions and schematic reconstruction.

T=3.4; (519/12375) conjoined valves, L=5.2, W=5.7, T=2.0; (520/12375) conjoined valves, L=7.9, W=7.9, T=3.2; (521/12375) conjoined valves, L=8.7, W=8.2, T=4.1; (522/12375) conjoined valves, L=5.8, T=6.3, Sw=3.7.1; (523/12375) conjoined valves, L=10.6, T=10.5, Sw=4.7.

DISCUSSION. This species differs from *Liostrophia glabra* Cooper & Kindle in having a subcircular outline, weak ventral sulcus and in the absence of a dorsal median fold. The characters of the dorsal interior in the type species remain inadequately known. In particular it is unclear from the existing illustrations whether or not it has a sessile cruralium or if it is supported anteriorly by a very short septum. In external morphology, particularly in the smooth, rounded shell with an uniplicate anterior commissure but without a distinct dorsal median fold, *Liostrophia pravula* resembles *Psilocamera planisulcata* Fu, 1982 from the the Jinhe Formation (Caradoc) of north-west China. However, in the single transverse section provided by Fu (1982, text-fig. 18A) the outer plates appear to be completely separate and there are no alate plates or inner plates illustrated.

Liostrophia pravula differs from juvenile specimens of *Illostrophina*

tesikensis not only in its larger size and sessile cruralium (which hardly exceeds half the maximum length), but also in the absence of a dorsal median fold. A ventral sulcus is present in *Illostrophina tesikensis* when specimens are 4–5 mm long, whereas in *Liostrophia pravula* it is visible only in mature specimens which exceed the average shell size of about 6 mm.

Subfamily ANASTROPHIINAE Nikiforova, 1960
Genus PLECTOSYNTROPHIA Fu, 1982

TYPE SPECIES. *Plectosyntrophia qilianshanensis* Fu, 1982, from the Yingou Group (Middle Ordovician) of North China.

Plectosyntrophia unicostata sp. nov.
Pl. 13, figs 59–74; Fig. 19

HOLOTYPE. BC 57570, Pl. 13, figs 67–70, conjoined valves from Sample 626, Anderkenyn-Akchoku section.

MATERIAL. Seven pairs of conjoined valves and one dorsal valve from Samples 100 (=K-98/1970) (BC 57569, 71), 620 (BC57360), 626 (BC 57271–73, 57568, 70, 72), 8214 (BC 57361), Anderkenyn-Akchoku section; Samples 2538, 8217 (BC 57362), Kujandysai Section.

DESCRIPTION. Shell subequally biconvex, transverse, subpentagonal in outline, about 75% as thick as long and about 89% as long as wide with maximum width slightly anterior to mid-length. Anterior commissure uniplicate. Ventral valve moderately convex with curved beak slightly raised above a narrow triangular, apsacline interarea. Ventral sulcus narrow and shallow, but with steep lateral

Table 27 Measurements of ventral valves of *Plectosyntrophia unicostata* sp. nov., samples 100 and 626 from Anderkenyn-Akchoku section.

	L	W	T	St	Sw	L/W	T/L	Sw/W
N	6	6	6	6	6	6	6	6
X	9.5	10.7	7.2	4.0	5.8	89.4%	74.1%	156.2%
S	1.37	2.10	2.77	1.87	1.82	4.6	18.3	28.4
MIN	7.8	8.4	4.6	2.2	3.5	82.9%	59.0%	119.6%
MAX	11	13.2	11.2	6.5	7.9	92.9%	101.8%	177.1%

Fig. 19 Photographs of transverse serial sections of *Plectosyntrophia unicostata* sp. nov., BC 57572, from Sample 626, Anderkenyn-Akchoku section; $\times$ 12. Distance in mm is measured from the posterior tip of ventral beak. Dorsal valve uppermost.

slopes, originating slightly posteriorly to mid-valve, and ending with a shallow, narrow, trapezoidal tongue about 40% valve width. Dorsal valve strongly convex in lateral profile with maximum thickness near mid-length. Beak slightly swollen and strongly curved towards the hinge line. A low, flattened median fold originates from the umbo. Radial ornament mainly costate, with occasional bifurcating ribs and with 1 primary rib in the sulcus, 2 primary ribs in the median fold and 6–9 on the lateral slopes of the valves. In some specimens one or two small secondary costellae originate in the median fold and dorsal sulcus between the umbo and mid-length. Ventral interior with strong teeth; bell-shaped spondylium in transverse section, sessile posteriorly and raised anteriorly on a low median septum partly covered by secondary shell (Fig. 19). Dorsal interior with narrow cruralium on a high median septum extending anteriorly up to 3 mm in adults. Inner plates narrow, curved; alate plates narrow, bordered laterally by a pair of high subparallel muscle bounding ridges.

MEASUREMENTS. (CNIGR 471/12375) conjoined valves, $L=14.0$, $W=16.9$, $T=6.3$, $Sw=8.9$; (474/12375) conjoined valves, $L=20.4$, $W=21.0$, $T=11.2$, $Sw=8.7$; (475/12375) conjoined valves, $L=22.9$, $W=24.5$, $T=10.2$, $Sw=12.8$; (476/12375) conjoined valves, $L=16.5$,

$W=19.8$, $T=6.5$, $Sw=11.2$; (479/12375) conjoined valves, $L=10.5$, $T=6.7$, $Sw=6.7$.

DISCUSSION. The generic attribution of *unicostata* is tentative because the interior of *Plectosyntrophia qilianshanensis* is inadequately known. In particular, there is no record of the presence of alate plates in the type species, but some illustrations provided in the original description (Fu 1982, text-fig. 17) suggest their presence. The characters of the ventral interior, in particular the presence of a sessile spondylium slightly raised near its anterior margin on a short septum, also needs confirmation, because Fu's illustrations are schematic and it could be a preservational pattern. In the Kazakh species alate plates are well defined, whereas the sessile spondylium is present only in the earliest ontogenetic stages and is characterised by a spondylium supported by a low median septum partly covered by secondary shell. *Plectosyntrophia qilianshanensis* has 3 ribs in the ventral sulcus and 4 in the dorsal fold, which makes it more similar to *Eoanastrophia kurdaica* than to our species.

P. unicostata differs from *Eoanastrophia kurdaica* Sapelnikov & Rukavishnikova (1975) from the Keskentas Formation (Caradoc), of the Kendyktas Range, south Kazakhstan, in having a more pronounced dorsal median fold with two primary ribs and a ventral

sulcus with a single accentuated primary rib originating in the umbonal area. The coarsely ribbed radial ornament, well defined dorsal median fold and ventral sulcus resembles numerous species of *Plectocamara* described by Cooper (1956) from the Caradoc of North America, but there is no evidence of the presence of alate plates in the former genus.

Family **PARALLELLELASMATIDAE** Cooper, 1956
Genus **SCHIZOSTROPHINA** Fu, 1982

TYPE SPECIES. *Schizostrophia margarita* Fu, 1982, from the Jinhe Formation (Caradoc), northwest China.

DIAGNOSIS (emended). Shell equally biconvex with parasulcate anterior commissure; shallow ventral median sulcus and dorsal median fold originating in umbonal area; radial ornament of variably developed coarse angular ribs in posterior half of the shell; ventral interior with delicate teeth and spondylium supported posteriorly and free anteriorly; dorsal interior with separated outer plates, slightly diverging distally, and well-defined brachial processes.

DISCUSSION. *Schizostrophia* was erected originally by Fu (1982) without proper illustrations and detailed description of the interior in the type species. However, the very distinctive exterior morphology

of the shell, which is unique in late Ordovician syntrophiidines, leaves no doubt that the Kazakh shells from the Anderken Formation belong to the same genus and species. Their internal morphology confirms the original assignment of the genus to the *Parallelelasmata* and suggests a close affinity to *Parallelelasma*, but *Schizostrophia* lacks the radial capillae and the characteristic truncated margins of the ribs along the commissure of the former genus. Another difference is the parasulcate anterior commissure.

Schizostrophia margarita Fu, 1982
Pl. 14, figs 2–27; Fig. 20

- 1982 *Schizostrophia margarita* Fu: 132, pl. 37, fig. 5.
- 1982 *Schizostrophia shaanxiensis* Fu: 133, pl. 37, fig. 6.

MATERIAL. 26 pairs of conjoined valves, 6 ventral and 4 dorsal valves from Samples 100 (=K-98/1970) (BC 57275–7), 626 (BC 57279–81), 8223, Anderkenyn-Akchoku section; Samples 628, 2538 (BC 57282–92, 57574–78), 8219 (BC 57294), 8220 (BC 57295), 8256 (BC 57296–9), Kujandysai Section.

DESCRIPTION. Shell equally biconvex, subpentagonal to subtriangular in outline; about as long as wide, with maximum width anterior to mid-valve. Anterior commissure parasulcate. Beaks of both valves swollen and strongly curved. Ventral valve moderately

Table 28 Measurements of ventral valves of *Schizostrophia margarita* Fu, Samples 626, 2538, 8256 from Anderkenyn-Akchoku and Kujandysai sections.

	L	W	T	Sw	St	L/W	T/L	Sw/W	Ld/W	Sw/W
N	18	18	18	17	3	18	18	17	9	9
X	5.8	6.2	4.2	4.3	4.3	94.8%	71.4%	71.7%	92.2%	70.2%
S	1.24	1.68	1.25	1.55	0.92	6.0	9.3%	14.5	4.9	5.4
MIN	3.6	3.7	2.1	2.6	3.2	79.6%	54.5%	45.2%	82.9%	63.9%
MAX	8.0	9.8	6.2	7.8	4.8	102.2%	90.4%	100.0%	97.5%	80.7%

Fig. 20 Transverse serial sections of *Schizostrophia margarita* Fu, Sample 2538, Kujandysai section. Distance in mm is measured from the posterior tip of ventral beak. Dorsal valve uppermost. Also lateral view to show section positions and schematic reconstruction.

convex in lateral profile with maximum thickness slightly posterior to mid-valve. Ventral sulcus originating near the umbo, broad and shallow with low trapezoidal tongue slightly inclined anteriorly. Lateral slopes steep, slightly convex in cross-section. Dorsal valve with moderately convex lateral profile strongly curved posteriorly. Median fold shallow, slightly rounded in transverse section, originating near the beak, flanked by two strong plications. Radial ornament with angular ribs originating near mid-length, 1–3 ribs in the sulcus and 2–4 in the median fold. Pair of ribs occasionally on the lateral slopes of both valves. Ventral interior with deep, narrow spondylium about one-sixth valve length, supported posteriorly by high median septum, free anteriorly. Dorsal interior with separated outer plates, slightly diverging distally, short subtriangular brachial plates and well-defined brachial processes.

MEASUREMENTS. conjoined valves, $L=7.9$, $W=8.6$, $T=5.9$, $Sw=6.9$; conjoined valves, $L=9.8$, $W=11.2$, $T=6.7$, $Sw=8.2$; conjoined valves, $L=7.8$, $W=8.2$, $T=6.2$, $Sw=6.8$; conjoined valves, $L=6.8$, $W=7.2$, $T=6.2$, $Sw=5.4$; conjoined valves, $L=5.7$, $W=5.8$, $T=3.4$, $Sw=4.6$.

DISCUSSION. *Schizostrophina margarita*, the type species of the genus, came from the same unit and locality, the Jinhe Formation (Lower Caradoc) of north-west China, as *S. shaanxiensis* and differs from the latter in having a single poorly defined rib in the ventral sulcus and smooth lateral sides of the valve. The Kazakh shells demonstrate a strong variability in the number and characters of radial ornament with growth. The small shells (about 5–6 mm long) usually lack ribs on the lateral sides of the shell, and the radial ornament in the ventral sulcus and dorsal fold is poorly developed or absent (Pl. 14, figs 22–24), whereas mature specimens possess a radial ornament closely comparable to one of the specimens referred by Fu (1982) to *S. shaanxiensis*. This suggests that all the shells described by Fu represent a single species, which should be termed *S. margarita*. Since there appear to be no constant morphological differences between the Kazakh and Chinese specimens of *Schizostrophina*, they are regarded here as conspecific.

Genus *DIDYMELASMA* Cooper, 1956

TYPE SPECIES. *Didymelasma longicrurum* Cooper, 1956 from the Lebanon Formation (Caradoc), Tennessee, U.S.A.

Didymelasma cf. *transversa* Fu, 1982

Pl. 13, figs 75–77, Pl. 14, fig. 1

MATERIAL. One pair of conjoined valves, BC 57573, from Sample

2538, Kujandysai Section; one dorsal internal mould (BC 57366) from Sample 1018, 7 km southwest of Karpkuduk well, Kotnak Mountains.

DESCRIPTION. Shell smooth, subequally biconvex, transverse to suboval in outline with uniplicate posterior commissure. Ventral valve lateral profile moderately convex with maximum thickness about one-third valve length. Ventral beak swollen and slightly curved. Sulcus originating near mid-length, strongly deepening towards the anterior margin, with low median rib. Tongue semielliptical. Dorsal valve moderately convex in lateral profile with maximum thickness at about two-thirds valve length. Median fold originating somewhat posteriorly to mid-valve, clearly separated from the slightly convex lateral sides of the valve. Ventral interior unknown, except for median septum, possibly supporting spondylium. Dorsal interior with separated, long, subparallel outer plates.

MEASUREMENTS. conjoined valves, $L=13.4$, $T=8.2$.

DISCUSSION. The Kazakh specimens closely resemble *Didymelasma transversa* Fu, 1982, from the Caradoc Jinhe Formation of northwest China, in the external features of their smooth shells, including the shape of the dorsal median fold and ventral sulcus, but our material is insufficient to make a precise attribution to this species. Fu (1982, text-fig. 23) also demonstrated the presence of separated, subparallel outer plates in the Chinese shells, which supports their assignment to *Didymelasma*.

Order **RHYNCHONELLIDA** Kuhn, 1949

Superfamily **RHYNCHOTREMATOIDEA** Schuchert, 1913

Family **RHYNCHOTREMATIDAE** Schuchert, 1913

Genus **RHYNCHOTREMA** Hall, 1860

TYPE SPECIES. *Atrypa increbescens* Hall, 1847, from the Trenton Formation (Caradoc), New York, U.S.A.

Rhynchotrema akchokense sp. nov. Pl. 14, figs 28–42

ETYMOLOGY. After Akchoku Mountain on the east side of Kopalysai.

HOLOTYPE. BC 57579, Pl. 14, figs 28–32, conjoined valves, from the Anderken Formation, Sample 626, Anderkenyn-Akchoku section.

MATERIAL. 11 conjoined valves, five ventral and six dorsal valves

PLATE 14

Fig. 1 *Didymelasma* cf. *transversa* Fu, Sample 1018, area 7 km SW of Karpkuduk well, Kotnak Mountains, BC 57366, dorsal internal mould, $\times 2$.

Figs 2–27 *Schizostrophina margarita* Fu, Sample 2538, Kujandysai section. **2–6**, BC 57574, conjoined valves, dorsal, ventral, posterior, lateral and anterior views, $\times 3$. **7–9**, **11**, **14**, BC 57575, conjoined valves, anterior, dorsal, ventral, lateral and posterior views, $\times 3$. **10**, **12**, **15–17**, BC 57576, conjoined valves, anterior, posterior, dorsal, lateral and ventral views, $\times 3$. **13**, CNIGR 5/12361, dorsal exterior, $\times 3$. **18–22**, BC 57577, conjoined valves, lateral, dorsal, ventral, anterior and posterior views, $\times 3$. **23–27**, BC 57578, conjoined valves, ventral, dorsal, lateral, posterior and anterior views, $\times 3$.

Figs 28–42 *Rhynchotrema akchokense* sp. nov. **28–32**, **38–41**, Sample 626, Anderkenyn-Akchoku section; **28–32**, BC 57579, conjoined valves, **holotype**, ventral, lateral, dorsal, posterior and anterior views, $\times 2$; **38–41**, BC 57582, conjoined valves, dorsal, ventral, anterior and lateral views, $\times 3$. **33–36**, Sample 2538, Kujandysai section, BC 57580, conjoined valves, anterior, dorsal, ventral and lateral views, $\times 2$. **37**, **42**, Sample 843, Anderkenyn-Akchoku section; **37**, BC 57581, ventral internal mould, $\times 3$; **42**, BC 57583, dorsal internal mould, $\times 5$.

Figs 43–46 *Pectenospira pectenata* Popov, Nikitin & Sokiran, Sample 948, Tesik River, BC 57320, dorsal, anterior, ventral and lateral views of conjoined valves, $\times 5.5$.

Figs 47–57 *Nikolaispira guttula* sp. nov. **47–53**, Sample 2538, Kujandysai section; **47–49**, BC 57584, conjoined valves, anterior, dorsal and ventral views, $\times 3$; **50–53**, BC 57585, conjoined valves, **holotype**, ventral, anterior, lateral and dorsal views, $\times 3$. **54–57**, Sample 8221, Anderkenyn-Akchoku section, BC 56770, conjoined valves, anterior, ventral, dorsal and lateral views, $\times 4$.

Figs 58–61 *Kellerella misiusi* Popov, Nikitin & Sokiran, Sample 8214, Anderkenyn-Akchoku section. BC 56773, conjoined valves, anterior, ventral, lateral and dorsal views, $\times 3$.

from Samples 100 (=K-98/1970) (BC 56656–9), 626, 843 (BC 57581–83), Anderkenyn-Akchoku section; Samples 628 (BC 56661), 2538 (BC 57580), 7613 (BC 56649–55), Kujandysai Section; Sample 948 (BC 57311–2), Tesik River.

DESCRIPTION. Shell dorsibiconvex to biconvex, slightly transverse, about 73% as thick as long and about 75% as long as wide with maximum width at mid-length. Anterior commissure uniplicate. Ventral valve moderately convex in lateral profile with maximum thickness at quarter valve length from the slightly curved, pointed beak. Delthyrium open, narrow triangular. Ventral sulcus originating 2–3 mm from the umbo, very shallow posterior to mid-valve, but deepening anteriorly and terminating in low, trapezoidal tongue about 79% valve width. Dorsal valve moderately and evenly convex in lateral profile with shallow umbonal sulcus inverting into a low flattened median fold with steep lateral slopes. Radial ornament of coarse angular ribs, usually with 4 ribs in the dorsal median fold, 3 ribs in the sulcus and 6–8 on flanks of both valves.

Ventral interior with cyrtomatodont teeth and short, thin dental plates flaring close to the sides of the valve. A pedicle base impression occupies the floor of the delthyrial cavity; large, weakly impressed ventral muscle field with small, lanceolate adductor scars completely surrounded by diductor scars anteriorly. Dorsal interior with disjunct hinge plate and narrow cruralium bearing a simple, ridge-like cardinal process and long, high median ridge extending anteriorly to mid-valve. Adjustor scars weakly impressed with posterior and anterior pair of about equal size, separated by fine, oblique transmuscle ridges.

MEASUREMENTS. (471/12375) conjoined valves, L=14.0, W=16.9, T=6.3, Sw=8.9; (474/12375) conjoined valves, L=20.4, W=21.0, T=11.2, Sw=8.7; (475/12375) conjoined valves, L=22.9, W=24.5, T=10.2, Sw=12.8; (476/12375) conjoined valves, L=16.5, W=19.8, T=6.5, Sw=11.2; (479/12375) conjoined valves, L=10.5, T=6.7, Sw=6.7.

DISCUSSION. Rhynchonellides are widespread in the mid and late Ordovician shallow-water benthic assemblages of Kazakhstan, but with few exceptions are represented exclusively by ancystrorhynchids and oligorhynchids (Nikiforova & Popov 1981; Nikitin & Popov in Klenina *et al.* 1984). All other Kazakh rhynchonellide species previously described as *Rhynchotrema* by Rukavishnikova (1956) and Klenina (in Klenina *et al.* 1984) belong in reality to the ancystrorhynchid *Altaethyrella* or atrypides related to *Nalivkinia* (Popov *et al.* 2000). This species represents the earliest known record of rhynchonellides with the cruralium supported by the dorsal median septum in Kazakhstan. Externally it is similar to *Rostricellula sarysuica* Nikitin & Popov (Nikitin *et al.* 1996) from the Upper Caradoc to Lower Ashgill Dulankara Regional Stage of the northern Betpak-Dala Desert, Kazakhstan, but differs in the less convex lateral profile of the dorsal valve, with maximum height at mid-length, the relatively shallow ventral sulcus, and in the presence of a ridge-like cardinal process.

Rhynchotrema akchokense is similar in radial ornament to two Australian species of the genus, *R. oepiki* Percival, 1991, from the

Upper Caradoc of New South Wales, and *R. bailliei* Laurie, 1991, from the Caradoc of Tasmania, in having a more transverse shell outline, a less convex dorsal valve profile, with maximum height near the mid-length, a relatively shallow ventral sulcus and a low dorsal median fold. *R. bailliei* is also characterized by its poorly developed cardinal process, which makes its generic assignment somewhat questionable, although we refer it to *Rhynchotrema*.

Order **ATRYPIDA** Rzhonsnitskaya, 1960

Superfamily **LISSATRYPOIDEA** Twenhofel, 1914

Family **PROTOZYGIDAE** Copper, 1986

Genus **PECTENOSPIRA** Popov, Nikitin & Sokiran, 1999

TYPE SPECIES. *Pectenospira pectenata* Popov, Nikitin & Sokiran, 1999, from the Anderken Formation, Chu-Ili Range.

Pectenospira pectenata Popov, Nikitin & Sokiran, 1999

Pl. 14, figs 43–46

1999 *Pectenospira pectenata* Popov, Nikitin & Sokiran: 648, pl. 4, figs 21–32, text-fig. 10.

HOLOTYPE. CNIGR 23/12986, conjoined valves, from the Anderken Formation, Sample 2538, Kujandysai section.

MATERIAL. 23 conjoined valves, two ventral and one dorsal valve, from Samples 100 (=K-98/1970), 626 Anderkenyn-Akchoku section; Samples 628, 2538 (BC57363), 8257, Kujandysai Section; Sample 948 (BC 57314–20), Tesik River.

DISCUSSION. This species was described and discussed in detail by Popov *et al.* (1999).

Order **ATHYRIDIDA** Boucot, Johnson & Staton, 1964

Suborder **ATHYRIDIDINA** Boucot, Johnson & Staton, 1964

Superfamily **MERISTELLOIDEA** Waagen, 1883

Family **MERISTELLIDAE** Waagen, 1883

Genus **KELLERELLA** Nikitin & Popov in Nikitin, Popov & Holmer, 1996

TYPE SPECIES. *Kellerella ditissima* Nikitin & Popov in Nikitin *et al.* (1996), from the Dulankara Regional Stage (Upper Caradoc), north Betpak-Dala, Kazakhstan.

Kellerella misiusi Popov, Nikitin & Sokiran, 1999

Pl. 14, figs 58–61

HOLOTYPE. CNIGR 26/12986, conjoined valves from the Anderken Formation, Sample 2538, Kujandysai section.

MATERIAL. 72 pairs of conjoined valves and one dorsal valve, from Samples 100 (=K-98/1970), 626, Anderkenyn-Akchoku section; Sample 8214 (BC56773, 57334–9), west side of Aschisu River; Samples 628, 2538, Kujandysai Section.

Table 29 Measurements of ventral valves of *Nikolaia spira guttula* sp. nov., Sample 948, Tesik river.

	L	W	T	Ld	Sw	St	L/W	T/L	Sw/W
N	13	13	13	13	13	13	13	13	13
X	6.5	5.6	4.2	6.0	2.9	1.2	117%	64%	52%
S	0.72	0.57	0.66	0.70	0.45	0.29	5.2	5.1	5.8
MIN	5.6	4.9	2.8	5.0	2.2	0.5	110%	50%	42%
MAX	7.6	6.7	5.3	7.2	3.6	1.6	127%	70%	62%

Fig. 21 Transverse serial sections of *Nikolaispira guttula* sp. nov., 1–3, BC 57588; 4–5, BC 57589, Sample 948, Tesik River. Distance in mm is measured from the posterior tip of ventral beak. Dorsal valve uppermost.

DISCUSSION. This species was described and discussed in detail by Popov *et al.* (1999).

Genus *NIKOLAISPIRA* Nikitin & Popov in Nikitin, Popov & Holmer, 1996

TYPE SPECIES. *Nikolaispira rasilis* Nikitin & Popov in Nikitin *et al.*, 1996, from the Dulankara Regional Stage (Upper Caradoc), north Betpak-Dala, Kazakhstan.

Nikolaispira guttula sp. nov. Pl. 14, figs 47–57; Fig. 21

ETYMOLOGY. After guttula, Latin – small drop.

HOLOTYPE. BC 57585, Pl. 14, figs 50–53, conjoined valves, from the Anderken Formation, Sample 2538, Kujandysai section.

MATERIAL. 38 conjoined valves from Samples 100 (=K-98/1970), 626, 8221 (BC 56770, 37857–58), Anderkenyn-Akchoku section; Samples 628, 2538 (BC 57584, 85), 8257, Kujandysai Section; Sample 948 (BC 57588, 89), Tesik River.

DESCRIPTION. Shell smooth, ventribiconvex, slightly elongate, subpentagonal in outline, about 64% as thick as long and 117% as long as wide. Anterior commissure parasulcate. Ventral valve profile strongly and evenly convex with maximum thickness near the mid-valve. Delthyrium small, open, narrow triangular. Beak slightly acuminate, erect posteriorly. Shallow ventral sulcus originating slightly posterior of the mid-valve, flanked by two low, rounded plications and terminating in a narrow, semicircular tongue. Dorsal valve gently convex with maximum thickness slightly posterior to mid-length. Median fold low and narrow, originating near mid-valve. Ventral interior with delicate teeth and short, thin dental plates placed closely to the lateral sides of the valve. Dorsal interior with small cruralium on a thin, long median septum extending anteriorly to mid-valve (Fig. 21). Spiralia laterally directed comprising up to three whorls. Jugal processes short, situated near the base of spiralia.

DISCUSSION. This species differs from *Nikolaispira rasilis* Nikitin & Popov (in Nikitin, Popov & Holmer 1996), which occurs in the Dulankara Stage (Upper Caradoc to Lower Ashgill) of north Betpak-Dala, Kazakhstan, in having a more elongate outline, like the most elongate specimens of the latter species, and smaller number of whorls of the spiralia.

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