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LATE ORDOVICIAN BRACHIOPODS FROM THE DULANKARA FORMATION OF THE CHU-ILI RANGE, KAZAKHSTAN: THEIR SYSTEMATICS, PALAEOECOLOGY AND PALAEOBIOGEOGRAPHY

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Abstract: Brachiopods from the late Ordovician (late Caradoc) Dulankara Formation of the Chu-Ili Range, Kazakhstan, are reviewed. Those from the upper two members of the formation, the Degeres and Akkol members, are systematically described. New genera from the Dulankara Formation are *Nikitinamena* (Plectambonitoidea: Leptellinidae), with type species *Nikitinamena bicostata* sp. nov., and *Weberorthis* (Orthoidea: Plectorthidae), with type species *Mimella brevis* Rukavishnikova. Another new genus is *Glyptomenoides* (Strophomenoidea: Glyptomenidae), with type species *Rafinesquina girvanensis* Salmon from the Caradoc of Girvan, Scotland. Other new species from the Dulankara Formation are *Holtedahlina orientalis*, *Platymena tersa*, *Christiania proclivis*, *Leangella* (*Leangella*) *paletsae*, *Metambonites subcarinatus*, *Ogmoplecia nesca* and *Plectorthis licta*. The ecology and assemblages of all three members of the Dulankara Formation are identified or reviewed, and their palaeogeographical significance assessed: the Chu-Ili Terrane (on which the Dulankara Formation was situated during the Ordovician) formed part of the relatively low-latitude peri-Gondwanan complex of terranes, and was probably not far from North and South China. The faunal links suggested between the Dulankara brachiopods and contemporary faunas from Australia are now perceived to be weaker than previously thought.

Key words: Ordovician, Caradoc, Brachiopods, Kazakhstan, Chu-Ili Terrane.

KAZAKHSTAN was divided into a great number of separate terranes in the Early Palaeozoic. Their individual identity, faunal affinities and palaeogeographical positions are a continuing source of controversy. The two principal competing theories are those published by Sengör and Natal'in (1996), who postulated that the terranes were strung out in an enormous island arc, which they termed the Kipchak Arc, stretching in an curve from Baltica to Siberia, and that of Nikitin *et al.* (1991), who postulated a series of generally arcuate and subparallel belts containing the terranes. A preliminary faunal analysis of some of the terranes has been published by Fortey and Cocks (2003), indicating that some of the major terranes were peri-Gondwanan, rather than related to either Baltica or Siberia.

One of the best-known terranes is the Chu-Ili Terrane of southern Kazakhstan, which includes the Chu-Ili Range (Text-fig. 1). Two substantial and important Caradoc formations in the Ordovician of that terrane are the Anderken Formation, whose brachiopod faunas have been published by Popov *et al.* (2002), and the overlying Dulankara Formation. The Dulankara is divided into three members. In ascending order, these are: the Otar Member, whose brachiopods were described by Popov *et al.* (2000); the Degeres Member, whose brachiopods are the focus of this paper; and the Akkol Member, whose rather sparse brachiopod faunas are also mentioned here briefly.

After revision of the systematics of the brachiopod fauna of the Degeres and Akkol members, we are now in a position to define the community associations of the whole Dulankara Formation, and to assess its biogeographical relationships in relation to other brachiopod faunas of similar age from neighbouring terranes, and these are the chief purposes of the present paper.

STRATIGRAPHICAL SETTING

The Late Ordovician brachiopods described herein were sampled from the Degeres and Akkol members, which

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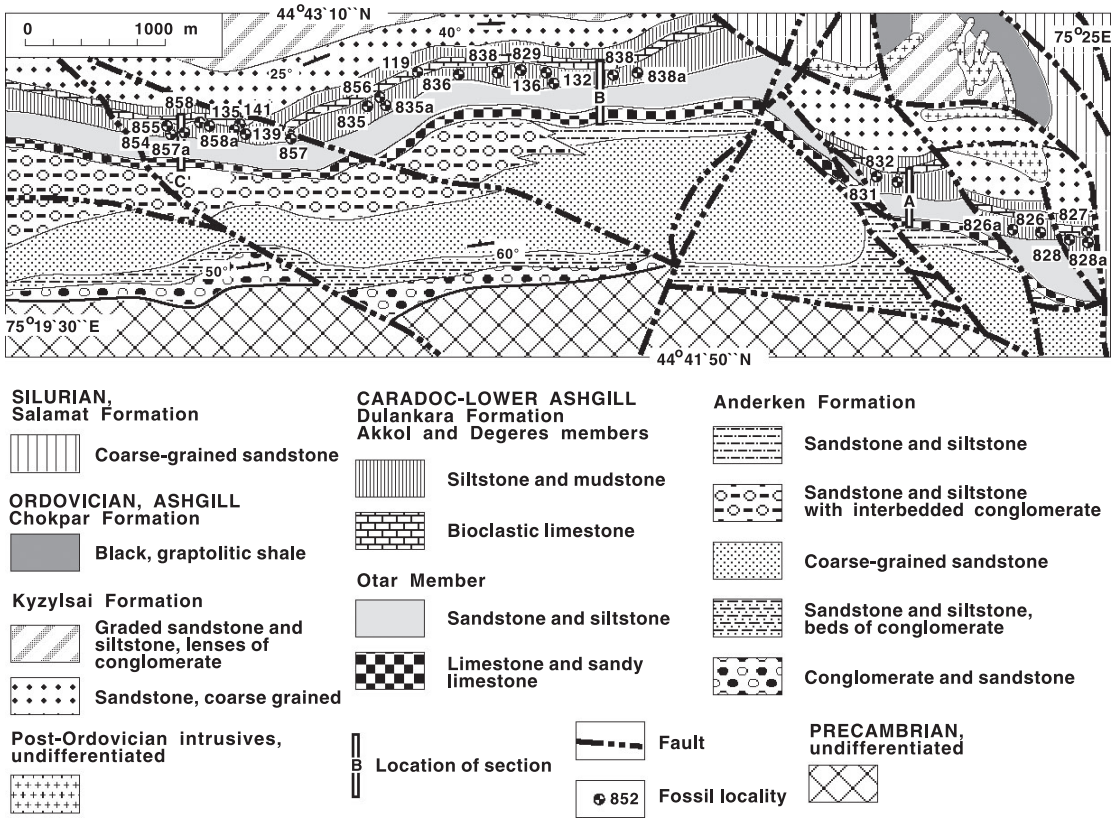
TEXT-FIG. 1. Outline map of central and south-eastern Kazakhstan showing the location of the Dulankara section and major terrane boundaries (mainly after Apollonov 2000 and Holmer *et al.* 2001); 1, North Tien Shan; 2, Chu-Ili; 3, Buruntau (accretion-subduction complex on the active early–mid Ordovician margin of the Chu-Ili Terrane); 4, Atasu-Zhamshi; 5–6, Chingiz-Tarbagatai (mostly assemblage of intraoceanic volcanic arcs with some small crustal fragments); 7, Karaganda; 8, Zaisan-Saur composite terrane to the north-east of the Chinghiz-Tarbagatai: there are a number of Devonian and later accretionary wedges; 9, Bakanas Terrane and Kazyk ophiolitic belt. The Dulankara section marked in the south is the area shown in more detail on Text-figure 2.

constitute the middle and upper part of the Dulankara Formation in its type section in the Dulankara Mountains, southern Chu-Ili Range, Kazakhstan (Text-fig. 1). The brachiopods from the underlying Otar Member of the formation were monographed by Popov *et al.* (2000), and a summary of the Ordovician geology and stratigraphy of the region can be found in the papers by Keller (1956), Nikitin (1972, 1973) and Nikitin *et al.* (1980); the trilobites were described by Chugaeva (1958), and the gastropods by Vostokova (1956). The Chu-Ili Range, which includes the Dulankara Mountains, is situated within the southern segment of the Selety-Shugaty tectonofacies unit of Nikitin *et al.* (1991), which is regarded as a separate early Palaeozoic microplate termed the Chu-Ili Terrane. In the Ordovician, this terrane was situated somewhere between the eastern margin of the old terranes of Baltica and equatorial East Gondwana, and was in relative proximity to both the North and South China Terranes in the late Ordovician (Popov *et al.* 2000, 2002).

The rocks of the Dulankara Formation crop out continuously along the northern slope of the Dulankara Mountains for about 7 km, where they conformably overly the lower–middle Caradoc Anderken Formation (Text-fig. 2). The Otar Member was described by Popov *et al.* (2000), and we therefore concentrate here on the overlying Degeres and Akkol members.

The Degeres Member is a monotonous sequence of intercalated fine-grained sandstones and silstones which vary in thickness from 60 m in the western part of the outcrop area up to 240 m in the eastern part. Two informal lithostratigraphic units can be recognised (Text-fig. 3). The lower unit varies in thickness from 45 m in the west to 150–200 m in the east of the outcrop area, and consists mostly of fine-grained sandstone with characteristic shell pavements on the bedding surfaces that are formed mostly by concentrations of the disarticulated valves of *Strophomena orthonurensis* and *Platymena tersa* (Localities 826, 826a, 857-1). The upper unit is siltstone with a few beds of sandstone and varies in thickness from 20 to 50 m (Text-fig. 3). In the western part of the outcrop area the top 10 m of the upper unit is built up of silty mudstones with nodules of argillaceous limestone about 10–15 cm across. The Akkol Member consists of a lower unit of bedded and nodular limestone from 15 to 25 m thick, which contains calcareous algae and tabulate corals (Bondarenko 1958) and is termed the *Amsassia chaetetoides* Beds. An



TEXT-FIG. 2. Geological map of the northern Dulankara Mountains, showing the lower Palaeozoic geology, the location of samples, and the section lines shown in Text-figure 3.

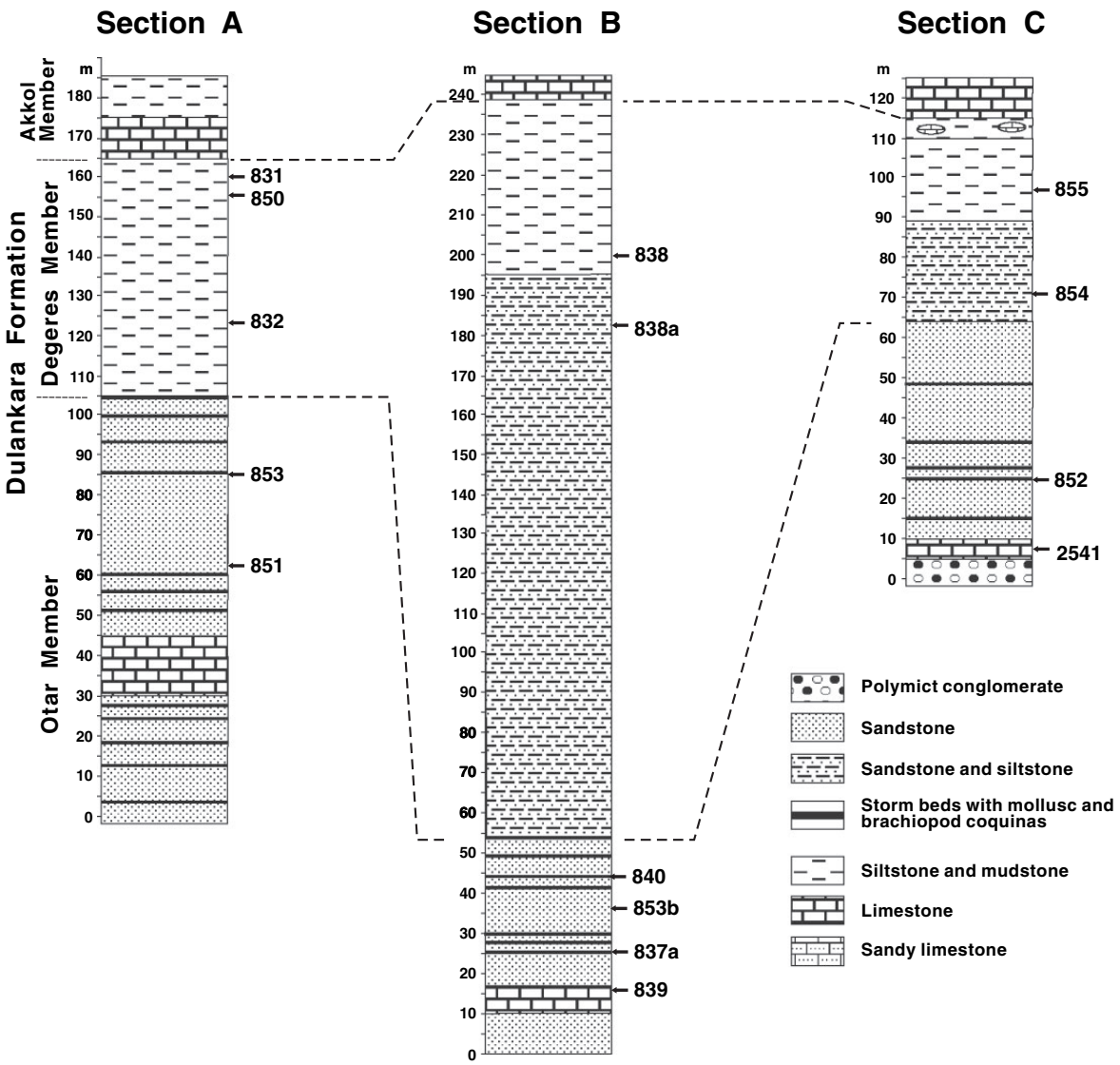
upper unit of argillite with the graptolites *Climacograptus styloides*, *Rectograptus sharenbergi* and *Orthograptus quadrimucronatus*, and trilobites, is about 10 m thick.

The Otar and Degeres members of the Dulankara Formation lack diagnostic conodont or graptolite faunas, and their late Caradoc age is defined by the underlying occurrence of the graptolite *Pseudoclimacograptus scharenbergi* in the uppermost part of the underlying Anderken Formation (Nikitin 1972; Popov *et al.* 1999; Text-fig. 2), which is characteristic of the *Climacograptus caudatus* Biozone, the local equivalent of the *Climacograptus clingani* Biozone. At the top of the Dulankara Formation, in the uppermost Akkol Member, the age is constrained by the graptolites of the *Dicellograptus pumilis* Biozone listed above, which is the local equivalent of the *Pleurograptus linearis* and *Dicellograptus complanatus* biozones (Nikitin 1972; Popov *et al.* 1999; Text-fig. 2). Tabulate corals of the *Amsassia chaetetoides* Beds occur in both the Otar and the Akkol members, and elsewhere in Kazakhstan they are considered to be characteristic of the upper Caradoc–lower Ashgill Dulankara Regional Stage.

Thus the Dulankara Formation is of late Caradoc age, constrained chiefly by the graptolites present below it and within the upper member.

ECOLOGY AND COMMUNITIES OF THE DULANKARA FORMATION

The Degeres Member represents the middle part of a transgressive sequence that started with the shallow marine deposits of the Otar Member and ended with the turbidites of the Kyzylsai Formation and the black graptolitic shales of the Chokpar Formation (Keller 1956; Nikitin 1972; Popov *et al.* 1981, 2002; Text-figs 2–3). The Otar Member was deposited in a rather turbulent inshore environment (Popov *et al.* 2000), which was much affected by seasonal storms and carried a Benthic Assemblage Zone (BA) BA 2 fauna. In contrast, the Degeres Member consists mainly of finer clastics varying from fine sandstones to sandy siltstones in which there are no extensive shell accumulations and coquinas as in the Otar Member, but many shell pavements occur in the Degeres Member, particularly of the *Platymena-Strophomena* Association. The calcareous algae in the Akkol Member and the occasional dasyclad algae in the Degeres Member suggest deposition within the photic zone, but in less turbulent environments than the Otar Member, although the selective orientation of the pelmatozoan stems and brachiopod

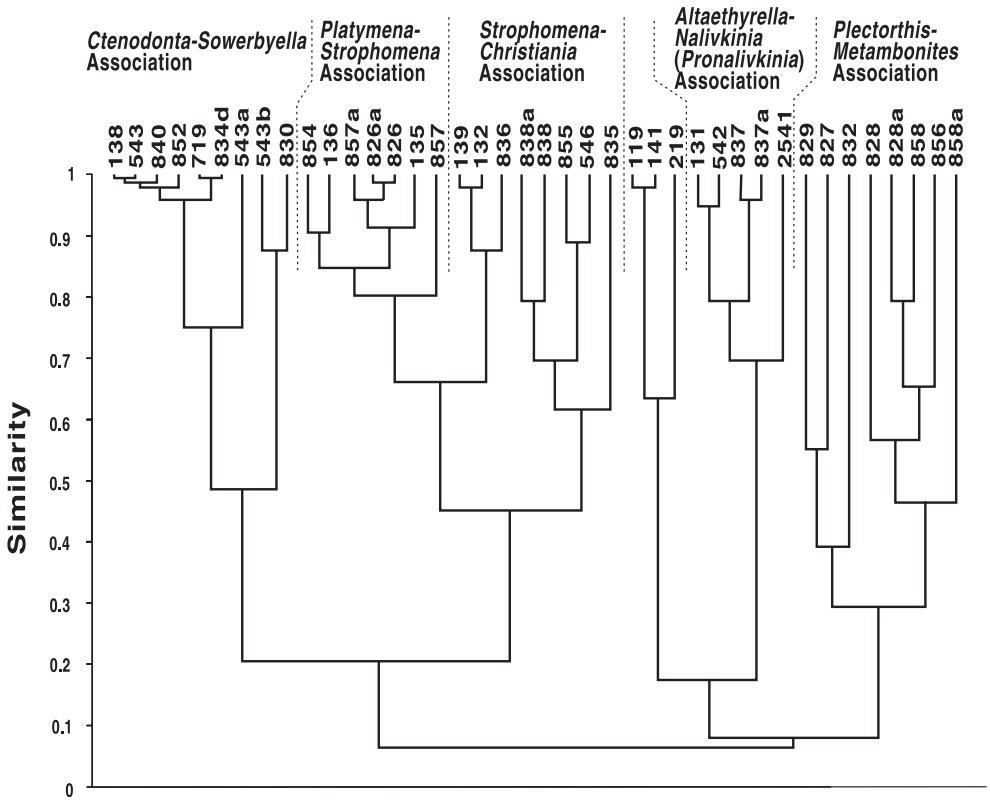


TEXT-FIG. 3. Schematic stratigraphic sections of the Otar, Degeres and Akkol members in the Dulankara Mountains, showing position of selected samples. The section lines are marked in Text-figure 2.

shells suggest that the sediments were occasionally affected by strong storms or tidal currents.

A matrix based on the distribution of 1800 brachiopod specimens from the Otar Member and 1400 from the Degeres and Akkol members was subjected to a cluster analysis (Text-fig. 4) using the statistical package PAST (distributed by Hammer *et al.* 2001). The Morista Index was chosen because it is relatively independent of sample size effects. The analysis resulted in the recognition of four associations with a Similarity Index of less than 0·3. These are in addition to the *Dinorthis* Association described by Popov *et al.* (2000), which is a low-diversity assemblage found at only three localities at the base of the Otar Member. The first two, the *Altaethyrella-Nalivkinia* (*Pronalivkinia*) Association and the *Ctenodonta-Sowerbyella* Association, were described by Popov *et al.* (2000). The second pair, the *Platymena-Strophomena* Association and the *Plectorthis-Metambonites* Association, are described below, as well as what we have termed the *Strophomena-Christiania* Association, which consists of less distinctive assemblages at various Degeres Member localities. The diversity index is calculated from the number of species minus 1 divided by the natural logarithm of the number of individual brachiopods in the sample (for details, see Williams *et al.* 1981).

The *Platymena-Strophomena* Association (average Diversity Index 1·46; observed range 0·34–2·09, N = 10; Table 1). This is a low- to medium-diversity assemblage



TEXT-FIG. 4. Results of the cluster analysis of the relative abundance data (Morista Index) for the brachiopod genera from the Degeres and Otar members of the Dulankara Formation. The Otar data are from Popov *et al.* (2000).

occurring at Localities 132, 135, 136, 139, 826, 826a, 836, 854, 857 and 857a, and is confined to the lower part of the Degeres Member (Text-fig. 2). *Strophomena orthonurensis* and *Platymena tersa* are the dominant taxa, usually together comprising more than half of the brachiopods present. Other common brachiopods are *Shlyginia extraordinaria* (up to 19 per cent), *Qilianotryma suspecta* (up to 21 per cent) and *Weberorthis brevis* (up to 15 per cent). *Christiania proclivis*, *Sowerbyella akdombakensis* and *Altaethyrella otarica* are usually present but only up to 10 per cent and usually less. *Paracraniops* is represented by only a few specimens in a single sample. Some shells were encrusted by bryozoans after death. Among other fossils are gastropods and bivalves and rarely the trilobites *Pliomerina iliensis* (Chugaeva), *Isotelus*? *levis* Chugaeva, *Dulanaspis levis* Chugaeva and *Remopleurides* sp.

The *Plectorthis-Metambonites* Association (average Diversity Index 3·16; observed range 2·33–3·52, N = 7; Table 2). This is a medium-diversity assemblage confined to the sandy siltstones of the upper part of the Degeres Member at Localities 828, 828a, 829, 832, 856, 858 and 858a, as well as a single example from a bioclastic mudstone within the Akkol Member at Locality 827. The assemblage lacks unique dominants, but *Metambonites subcarinatus*, *Plectorthis licta*, *Glyptomenoides* sp. and *Sowerbyella ampla* each often exceed 10 per cent of the population, although not all are present in all the samples. Other brachiopods often present, but not exceeding 5 per cent, are *Holtedahlina orientalis*, *Leangella paletsae*, *Nikitinamena bicostata* and *Ogmoplecia nesca*. Table 2 also shows some rarer forms, including *Anoptambonites kovaleskii* and *Altaethyrella otarica*, which occur only sporadically. However, *Christiania proclivis* and *Qilianotryma suspecta* are present at over 10 per cent in a few localities. Also recorded in low quantities are the trilobites *Pliomerina iliensis* (Chugaeva), *Dulanaspis levis* Chugaeva, *Remopleurides*? sp., *Cybele*? *weberi* Kolova, *Ampyx sergunkovae* Kolova, *Isotelus*? *levis* Chugaeva and *Birmanites kolovae* (Chugaeva), as well as many pelmatozoan columnals.

The *Strophomena-Christiania* Association (average Diversity Index 2·27; observed range 1·62–3·19, N = 5; Table 3). This medium-diversity association is intermediate between the previous two, and occurs at Localities 546, 835, 838, 838a and 855, all in the middle part of the Degeres Member (Text-fig. 2). *Strophomena orthonurensis* at 14–29 per cent is the dominant species, whilst the

TABLE 1. Localities and number of individual specimens of the *Platymena-Strophomena* Association. For each entry, the conjoined, ventral and dorsal valve numbers are shown.

	Platymena-Strophomena Association					
Locality no.	135	136	139	826	826a	836
Number of individuals	28	52	19	80	30	39
Diversity Index	1·50	1·52	0·34	1·37	1·47	1·64
Strophomena orthonurensis	0:2:3	0:3:8	0:13:9	3:11:11	0:7:5	0:0:21
Glyptomenoides? sp.		0:0:3				
Platymena tersa	0:14:11	0:3:11	0:6:1	1:41:52	0:10:18	0:2:1
Christiania proclivis	0:0:1			0:1:3		
Shlyginia extraordinaria	1:3:0	0:2:10		0:6:4	0:1:2	0:0:1
Sowerbyella akdombakensis		0:4:1		0:0:1	0:0:1	0:0:1
Sowerbyella ampla				0:0:1		
Hebertella brevis	0:1:1	0:2:5		0:0:2	0:1:0	1:4:5
Altaethyrella otarica						2:3:2
Qilianotryma suspectum	2:3:1	3:8:4			0:1:1	1:2:2

	Platymena-Strophomena Association			
Locality no.	132	854	857	857a
Number of individuals	79	11	83	65
Diversity Index	1·83	2·09	1·13	1·68
Paracraniops sp.				3
Strophomena orthonurensis	0:37:27	0:2:1	0:26:29	0:14:13
Holtedahlina orientalis				
Platymena tersa	0:15:12	0:2:4	0:19:33	0:17:32
Christiania proclivis	0:1:2			
Shlyginia extraordinaria		0:0:2		0:4:3
Sowerbyella akdombakensis	0:0:2		0:4:1	0:1:7
Sowerbyella ampla	0:1:3			
Phragmorthis sp.	0:0:1			
Hebertella brevis	0:2:1	0:1:1	0:3:1	0:3:2
Altaethyrella otarica	0:1:1	0:1:1	3:3:8	0:2:1
Qilianotryma suspectum	0:0:1	0:1:1	0:1:1	0:0:2

abundance of *Platymena tersa* declines and is recorded from only two of these samples. In contrast, *Christiania proclivis* is an insignificant component of the *Strophomena-Platymena* Association but occurs at between 14 and 29 per cent in the *Strophomena-Christiania* Association. *Shlyginia extraordinaria* and *Weberorthis brevis* are also more abundant. *Sowerbyella akdombakensis* occurs only at Locality 835, whereas *Sowerbyella ampla* occurs at four localities at between 5 and 14 per cent. *Qilianotryma suspecta* is common, and *Metambonites subcarinatus*, *Holtedahlina orientalis*, *Leangella paletsae*, *Nikitinamena bicostata* and *Ogmoplecia nesca* occur sporadically. *Epitomyonia* sp., which has, however, only been found rarely at Localities 828a and 546, appears to be the only brachiopod confined to this association. Thus the mixed nature of this association is also seen in the cluster analysis (Text-fig. 4).

The results of the Principal Components Analysis (PAST package) show two distinct trends, which are different for the associations from the Otar and Degeres members (Text-fig. 5). The pattern is mainly defined by the occurrences and relative abundances of such taxa as *Altaethyrella otarica* (+0·07, −0·18), *Christiania proclivis* (−0·12, −0·13), *Platymena tersa* (−0·26, +0·68), *Sowerbyella akdombakensis* (+0·90, +0·30), *Sowerbyella ampla* (−0·05, −0·085) and *Strophomena orthonurensis* (−0·26, +0·53), which are characterised by high to medium values of Component 1 (first score) and Component 2 (second score), and apparently represent the main sourse of variance. Samples of the *Plectorthis-Metambonites* Association form a compact cluster, with low negative values of components 1 and 2. The negative values for Component 1 persist in two other assemblages from the Degeres Member; however, they acquire positive values for Component 2, which is defined mainly by the abundance of *Strophomena orthonurensis* and *Platymena tersa*, and reach their maximum in the samples of the *Platymena-Strophomena* Association, whereas samples of the *Strophomena-Christiania* Association occupy an intermediate position. In the latter assemblage the abundance of *Platymena tersa* has declined considerably, whereas the taxa with moderately negative scores of Component 2, such as *Christiania proclivis* and *Sowerbyella ampla*, become relatively common. In contrast, nearly all the samples from the Otar Member are characterised by positive values for Component 1. Medium to high positive scores of Component 1, characteristic of the *Ctenodonta-Sowerbyella* Association, are defined chiefly by the abundance of *Sowerbyella akdombakensis*.

The brachiopod fauna from the carbonate unit of the Akkol Member is associated with tabulate corals and is usually of low diversity and dominated by the rhynchonellides *Altaethyrella otarica* and the atrypides *Eospirigerina pennata* and *Schachriomonia parva* (Table 4). The only exception is the bedded algal limestone at Locality 827, which contains a relatively diverse brachiopod assemblage with abundant plectambonitoids that fits well into the *Plectorthis-Metambonites* Association following both cluster analysis and Principal Components Analysis. It differs, however, in the relative abundance of *Dulankarella* cf. *magna*, which is completely absent from the Degeres Member, as well as in the more diverse atrypide component of the assemblage, which consists of *Eospirigerina pennata*, *Qilianotryma suspecta* and *Schachriomonia parva*.

TABLE 2. Localities and number of individual specimens of the *Plectorthis-Metambonites* Association. For each entry, the conjoined, ventral and dorsal valve numbers are shown.

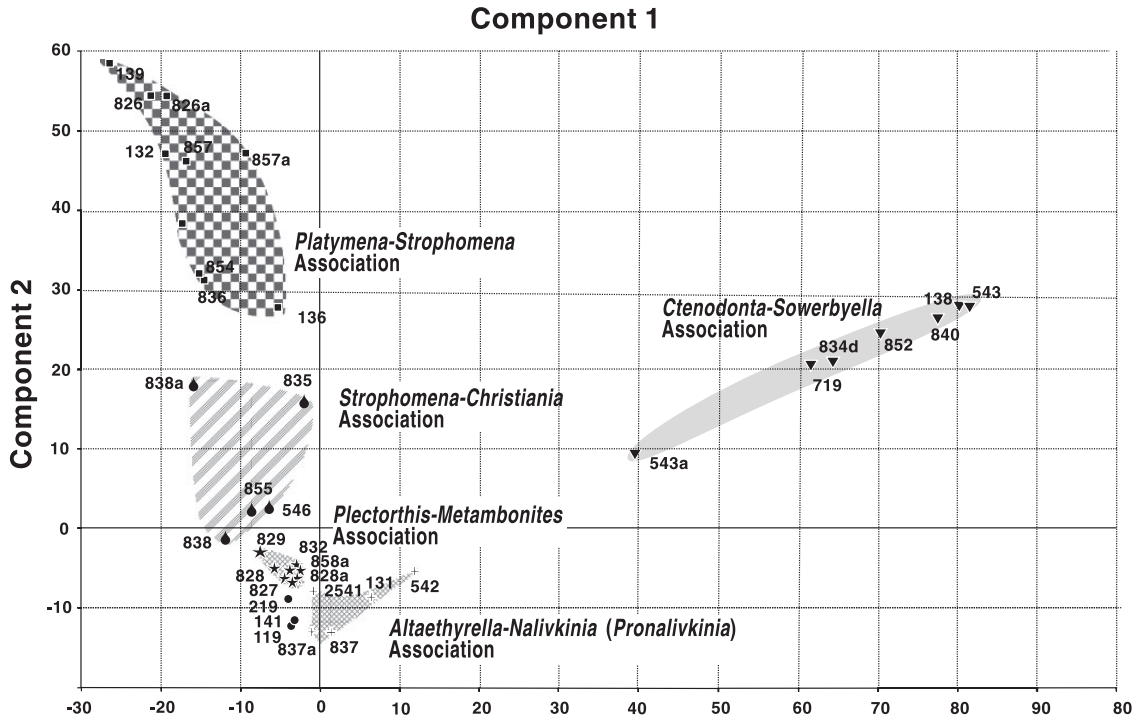
	Plectorthis-Metambonites Association						
Locality	828	828a	829	832	856	858	858a
Number of individuals	40	28	31	10	30	28	13
Diversity index	3·52	3·00	2·33	–	3·23	2·40	3·12
Trematis sp.	0:0:1						0:1:1
Acrosaccus sp.	0:1:1						0:0:1
Strophomena orthonurensis		0:0:1	0:1:2				
Rhipidomena sp.							0:1:1
Holtedahlina orientalis		0:2:1			0:3:1	1:0:2	0:1:0
Glyptomenoides? sp.	0:1:0	0:2:3	0:2:1		0:1:1	0:2:4	0:0:2
Christiania proclivis	1:2:4	1:6:5	0:5:3	0:1:0	0:3:2	2:3:1	
Glyptambonites sp.	0:3:1		0:0:1				
Nikitinamena bicostata	0:1:0	1:0:0	0:0:1	1:1:2	0:0:1		
Leangella paletsae				0:1:1	0:3:0	1:0:0	0:0:1
Anoptambonites kovalevskii	0:2:3				0:0:1		
Metambonites subcarinatus	1:1:1	0:2:3		0:2:1	0:0:1	3:4:3	
Sowerbyella ampla	1:6:5	0:1:2	1:1:9	0:1:0	0:2:0		
Gunningblandella sp.	0:1:0			1:0:0			
Ogmoplecia nesca	0:2:2	0:1:0			1:3:2	1:0:0	
Plectorthis licta	2:9:3	0:1:3	0:1:1		1:3:2	0:2:2	1:1:1
Phragmorthis sp.				0:0:1		0:0:1	
Orthoidea gen. et sp. indet.	0:0:1	0:0:3	0:2:2		0:0:1		
Dalmanelloidea gen. et sp. indet.	1:0:0						
Altaethyrella otarica							0:1:0
Qilianotryma suspectum		0:1:2	1:6:0	0:1:0	3:2:2	2:2:1	0:1:0

TABLE 3. Localities and number of individual specimens of the *Strophomena-Christiania* Association. For each entry, the conjoined, ventral and dorsal valve numbers are shown.

	Strophomena-Christiania Association				
Locality no.	546	835	838	838a	855
Number of individuals	23	35	22	20	–
Diversity Index	3·19	1·97	1·62	2·00	2·57
Strophomena orthonurensis	0:0:3	1:3:6	1:1:2	0:5:2	0:1:1
Holtedahlina orientalis				0:1:2	
Platymena tersa		0:3:4			
Christiania proclivis	0:0:4	0:3:5	0:3:14	0:1:6	1:2:1
Shlyginia extraordinaria	0:1:3	0:6:11	0:0:1	0:0:1	0:0:1
Leangella paletsae	2:0:0				
Metambonites subcarinatus	0:1:0				
Sowerbyella akdombakensis		0:1:3			
Sowerbyella ampla	1:1:1		0:0:1	0:0:2	0:0:1
Ogmoplecia nesca	1:0:0				
Phragmorthis sp.			0:0:1		
Epitomyonia sp.	0:0:1				
Orthoidea gen. et sp. indet.	0:0:1				
Hebertella brevis	0:0:3	0:1:1	0:1:2	0:4:4	0:0:1
Altaethyrella otarica		0:2:0			
Qilianotryma suspectum	0:2:2	0:2:1		0:2:5	1:0:0

BIOGEOGRAPHICAL SIGNIFICANCE

The shallow-shelf Caradoc rocks of the Chu-Ili Terrane, which consists mainly of shallow clastics but includes mud mounds and algal buildups, carries brachiopod faunas of BA 2 and 3 (Nikitin *et al.* 1996; Popov *et al.* 2002), which are generally conservative in nature. By comparison with the underlying Anderken Formation, the Dulankara Formation shows firstly a proliferation of atrypides [*Nalivkinia* (*Pronalivkinia*), *Qilianotryma*, *Schachriomonia*, *Sulcatospira* and *Eospirigerina*], and secondly a development of strophomenoids which, in addition to widespread genera such as *Christiania* and *Strophomena*, are partly endemic (*Karomena*, *Dzebaglina*), but are mostly newcomers from other terranes, including *Glyptomenoides*?, *Holtedahlina*, *Platymena* and *Rhipidomena*. Most plectambonitoids (*Anoptambonites*, *Dulankarella*, *Glyptambonites*, *Shlyginia* and *Sowerbyella*) continued on up from the Anderken Formation, although *Acculina* and *Tesikella* did not. Overall, the proportion of endemic genera increased, principally by the introduction of the plectambonitoids *Nikitinamena* and *Metambonites*, the orthides *Bokotorthis* and *Weberorthis*, and the rhynchonellides *Altaethyrella* and *Paraoligorhyncha*. Some of these



TEXT-FIG. 5. Two-dimensional correspondence analysis plot of scores of sites on first (F1) and second (F2) eigenvectors of selected brachiopod samples from the Otar Member shown on Text-figure 2 and Table 1.

TABLE 4. Localities and number of individual specimens from the Akkol Member. For each entry, the conjoined, ventral and dorsal valve numbers are shown.

Locality no.	119	141	219	827
Number of individuals	44	119	41	52
Glyptomenoides? sp.			0:1:0	
Christiania sp.				0:3:1
Bandaleta sp.			2:1:1	2:1:1
Glyptambonites sp.				0:3:1
Nikitinamena bicostata				0:1:1
Dulankarella cf. *magna*			3:7:0	3:10:7
Leangella paletsae				2:3:2
Anoptambonites kovalevskii		0:0:2	0:0:1	0:7:7
Metambonites subcarinatus			0:1:0	0:6:1
Sowerbyella ampla			0:1:0	2:14:5
Placotriplesia sp.			0:1:0	0:3:0
Ptychopleurella? sp.				1:0:0
Dolerorthis sp.			0:1:1	1:2:1
Bokotorthis kasachstanica				0:1:1
Orthoidea gen. et sp. indet.				1:3:3
Altaethyrella otarica	13:0:0	2:3:0	9:6:6	2:4:5
Eospirigrerina pennata	12:0:0	4:1:0		3:4:1
Qilianotryma suspectum			2:1:1	1:3:1
Schachriomonia parva	19:0:0	7:0:0	0:4:1	0:1:1

Kazakh endemics made a slightly later appearance in North and South China during the early to mid Ashgill (Zhan and Cocks 1998; Popov *et al.* 1999, 2000). The links with the Caradoc of New South Wales, Australia (Percival 1979, 1991), discerned earlier by Popov *et al.* (2000), now appear to be weaker than originally thought, but they are supported by such distinctive genera as *Dulankarella*, *Gunningblandella* and *Phaceloorthis*, which all occur only in New South Wales and Kazakhstan.

Another feature of the Dulankara Formation fauna in the Chu-Ili Range is the appearance of *Glyptomenoides*?, *Platymena* and *Plaesiomys*, which have no apparent roots in the earlier local Kazakh brachiopod assemblages, but which are well known from the early to mid Caradoc rocks of Laurentia. What the migration paths of these genera may have been is unclear. It is also notable that the *Glyptambonites* species occurring in the Dulankara Formation is essentially identical to one from Laurentia.

Thus the brachiopods from the Anderken and Dulankara formations have little in common with those from either Siberia or Baltica and therefore give little support for the Kipchak Arc hypothesis between those two major terranes put forward by Sengör and Natal'in (1996). The data presented here support the probability that the Chu-Ili Terrane was an independent entity in the late Ordovician, but situated not too far from both the North China and the South China terranes in the peri-Gondwanan collage.

SYSTEMATIC PALAEONTOLOGY

Figured and cited specimens are housed in The Natural History Museum, London (B, BB and BC collection numbers) and the Institute of Geological Sciences, Alma-Ata (IGNA). 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 of median sulcus and height of tongue in the ventral valve; BBl, BBw, length and distance between outer margins of brachiophores 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. Bibliographic references to families and above are omitted here since they can be found in the Treatise on Invertebrate Paleontology (Kaesler 2000, 2002).

All the specimens come from the Dulankara Mountains, except where stated.

Order LINGULIDA Waagen, 1885
Superfamily DISCINOIDEA Gray, 1840
Family TREMATIDAE Schuchert, 1893

Genus TREMATIS Sharpe, 1848

Type species. *Orbicula terminalis* Emmons, 1842, from the Caradoc Trenton Group of New York State, USA.

Trematis sp.
Plate 1, figures 1–4

Material. One ventral valve and two dorsal valves from the Degeres Member, Localities 828 (BC 57748), and 858a (BC 57608, 57609).

Description. Shell convexiplane, subcircular; ventral valve with eccentric umbo situated at about one-quarter valve length from the posterior margin; narrow triangular delthyrium covered umbonally by a short, concave listrium. Dorsal valve evenly convex with a weak sulcus. Shell ornamented by rounded, subpentagonal pits about 0·25–0·30 mm across and by fine growth lamellae. Interiors of both valves unknown.

Measurements. BC 57609, ventral valve, L, 9·2; W, 10·6, BC 57608, dorsal valve, L, 15·3; W, 16·0.

Remarks. These specimens can be compared to *Trematis parva* Cooper, 1956, from the Chatham Hill Formaton of Tennessee and Virginia, USA, *T.* aff. *parva* Cooper, from the Baigara Formation of south Betpak-Dala (Nazarov and Popov 1980) and *T. melliflua* Reed, 1917, from the Balclatchie Group of the Girvan District, Scotland (Williams 1962). However, firm specific identification of the Dulankara material is not possible from the limited amount of material available.

Family DISCINIDAE Gray, 1840

Genus ACROSACCUS Willard, 1928

Type species. *Acrosaccus shuleri* Willard, 1928, from the Caradoc Rich Valley Formation of Virginia, USA.

Acrosaccus sp.
Plate 1, figures 5–6

Material. Three ventral valves from Localities 835 (BC 57815), 858 (BC 57610) and 858a, Degeres Member.

Description. Ventral valve high, subconical, slightly elongate, subcircular in outline; about 1·2 times as long as wide and about 65 per cent as high as long, with slightly eccentric, acute umbo. Posterior slope of the valve slightly convex in transverse section, with a pedicle track covered by the long narrow listrium. Lateral profile of the anterior slope of the valve gently concave. Shell surface covered by fine regular concentric rugellae. Dorsal valve and interior of both valves unknown.

Measurements. BC 57610, ventral valve, L, 8·6; W, 8·2; T, 5·3.

Remarks. These specimens are comparable with *Schizotreta microthyris* Cooper, 1956, from the Oranda Formation of Virginia, which we now place in *Acrosaccus*, in the high conical ventral valve, but they differ in having a subcentrally placed umbo and a concave lateral profile of the anterior slope of the ventral valve. Similar, perhaps conspecific, shells to those in the Degeres Member were described by Nikitin *et al.* (1996) as *Acrosaccus* aff. *posteroconvexus* (Cooper, 1956) from the Dulankarian (upper Caradoc) carbonate mud in the north Betpak-Dala desert in central Kazakhstan, but the absence of dorsal valves in our collection makes further comparison difficult.

Superfamily CRANIOPSOIDEA Williams, 1963
Family CRANIOPSIDAE Williams, 1963

Genus PARACRANIOPS Williams, 1963

Type species. *Craniops pararia* Williams, 1962, from the Upper Caradoc Kiln Mudstones, Girvan, Scotland.

Paracraniops sp.
Plate 1, figure 7

2000 *Paracraniops* sp. Popov, Nikitin and Cocks, p. 842, pl. 1, fig. 2.

Material. Three ventral and dorsal valves, including BC 57828 and 57745, from Localities 857a and 826, Degeres Member.

Remarks. These Degeres Member shells appear conspecific with the specimens of *Paracraniops* sp. described by Popov *et al.* (2000) from the underlying Otar Member of the Dulankara Formation.

Superfamily STROPHOMENOIDEA King, 1846
Family STROPHOMENIDAE King, 1846
Subfamily STROPHOMENINAE King, 1846

Genus STROPHOMENA de Blainville, 1824

Type species. *Leptaena planumbona* Hall, 1847, from the Trenton Group of Cincinnati, Ohio, USA. Although Rong and Cocks (1994), when selecting the lectotype, thought that it came from rocks of late Caradoc age, Jin and Zahn (2001), after reviewing possible type localities, thought that the specimen is more likely to be of Ashgill age. Final clarification awaits a detailed review of North American faunas from all of the Upper Ordovician.

Strophomena (*Strophomena*) *orthonurensis* Misius, 1986
Plate 1, figures 8–17

1986 *Strophomena orthonurensis* Misius, p. 163, pl. 17, figs 1–8.

Holotype. Geological Institute, Bishkek, Kyrgistan 931/5, from the Upper Caradoc Ishkebash Formation, *Dinorthis-Nuria* Beds, Kelpe-sai, Dzebagly Mountains, south Kazakhstan.

Material. Degeres Member, Localities 132 (BC 57666–69, 57671–79, 57681), 135 (BC 57620, 57682–83), 136 (BC 57684), 139, 546 (BC 57823), 826 (BC 57699, 57824), 826a (BC 57661), 828a, 829, 835, 836, 838, 838a (BC 57685–87), 854, 855, 857 (BC 57698, 57807–09), 857a (BC 57867).

Description. Shell convexoconcave, transverse, suboval in outline, about 80 per cent as long as wide, with maximum width at the hinge line. Cardinal extremities slightly acute to near right angled. Anterior commissure rectimarginate. Ventral valve evenly concave with slightly raised umbo. Ventral interarea moderately high, triangular, apsacline with a narrow triangular delthyrium covered by a convex pseudodeltidium. Lateral profile of dorsal valve strongly convex, with maximum height at mid length. Dorsal interarea linear, anacline. Radial ornament of fine parvicostellae nearly equal in posterior half and with some accentuated costellae anterior to mid-length in mature specimens, which vary from 4 to 6 per mm along anterior margin.

Ventral interior with large subpentagonal muscle field up to 40 per cent valve length in mature specimens. Teeth large, supported by divergent dental plates continuing as converging muscle-bounding ridges, flanking the ventral muscle field laterally. Ventral adductor muscle scars in central part of muscle field and completely surrounded by diductor muscle scars. Mantle canals saccate with short, widely divergent vascula media and strongly impressed vascula genitalia. Dorsal interior with double cardinal process on low and wide notothyrial platform, wide socket ridges curved distally. Small, subtrapezoidal dorsal adductor muscle field narrowing anteriorly and bisected by a fine median septum.

Variability. The shells of this species underwent significant growth changes. Juvenile shells up to 10–12 mm long are characterised by a small ventral muscle field with the adductor scars not enclosed by the diductors and straight socket plates, and very short median septum in the dorsal valve, whereas the radial ornament is finely and equally parvicostellate. The relative size of the ventral muscle field increases considerably in specimens over about 15 mm long, and the adductor scars become surrounded by the diductors, but the relative length of the dorsal median septum evidently increased considerably with growth.

EXPLANATION OF PLATE 1

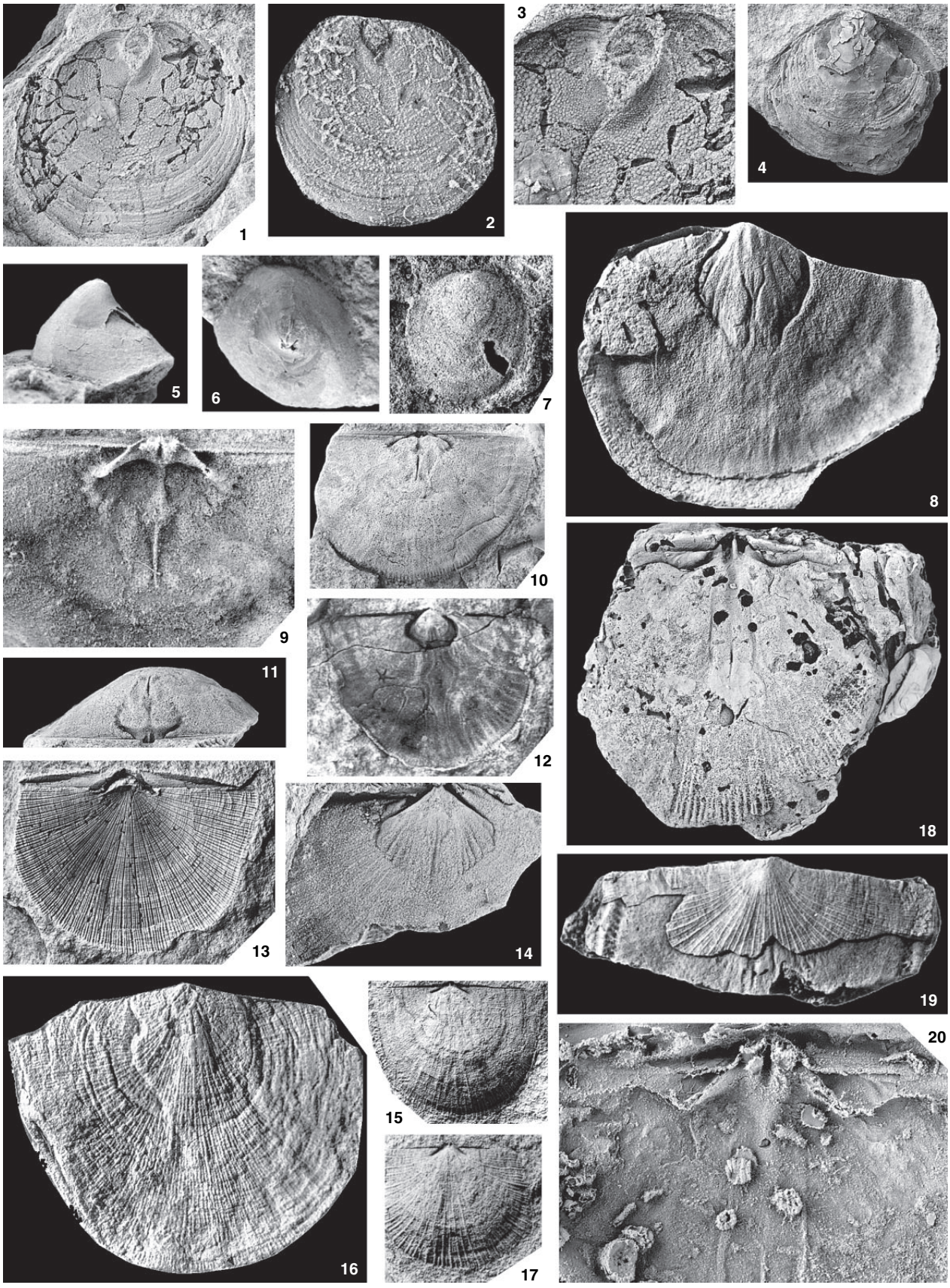
Figs 1–4. *Trematis* sp., Degeres Member. 1–3, BC 57609, Locality 858a, ventral external mould and latex cast, × 3; pedicle opening and pitted ornament, × 6. 4, BC 57608, Locality 858a, dorsal valve exterior; × 2.

Figs 5–6. *Acrosaccus* sp., Degeres Member. BC 57610, Locality 858, ventral exfoliated ventral valve, lateral and ventral views; × 3.

Fig. 7. *Paracraniops* sp., Degeres Member, BC 57745, Locality 826, ventral? internal mould; × 6.

Figs 8–17. *Strophomena* (*Strophomena*) *orthonurensis* Misius, Degeres Member. 8, BC 57675, Locality 132, ventral internal mould; × 3. 9–11, BC 57620, Locality 135, latex cast of interior showing cardinalia, × 4; dorsal and posterior views of dorsal internal mould, × 2. 12, BC 57684, Locality 136, ventral internal mould; × 2. 13, BC 57824, Locality 826, dorsal external mould; × 2. 14, BC 57673, Locality 132, ventral internal mould; × 3. 15, BC 57681, Locality 132, dorsal internal mould; × 2. 16, BC 57667, Locality 132, ventral valve exterior; × 3. 17, BC 57679, Locality 132, dorsal internal mould of a smaller individual; × 2.

Figs 18–20. *Rhipidomena* sp., Degeres Member, Locality 858a. 18, 20, BC57621, internal mould, × 1·5, and latex cast, × 3, of dorsal valve showing cardinalia. 19, BC 57697, ventral exterior; × 2.



POPOV and COCKS, Ordovician brachiopods

Remarks. The generic concept of *Strophomena* was stabilised following revision of the type species by Rong and Cocks (1994). However, there are an enormous number of nominal taxa within the genus; for example, Cooper (1956) listed and described 42 species and subspecies of *Strophomena* from middle and early late Ordovician deposits of North America alone, and there are many others from late Ordovician rocks in many parts of the world. There is also one junior generic synonym (*Rugomena*) and two other subgenera (*Keilamena* and *Tetraphalerella*) recognised in the review of Cocks and Rong (2000). Thus a root and branch revision of the whole generic group is desirable; this is, however, made difficult by the variability often seen within large populations at many localities. For example, in the Kazakhstan material considered here there is remarkable variation within the ventral interior: compare the overall shape of the muscle field and its size relative to its length in the three valves figured in Plate 1, figures 8, 12 and 14. We identify the Kazakh form as *Strophomena orthuronensis*, whose type specimen comes from the adjacent North Tien-Shan Terrane (Misius 1986). It is abundant within the Degeres Member (Tables 1–3). The species differs from *S. planumbona* in the more evenly convex profile of the dorsal valve, but because of the plasticity of the whole generic stock, further work is necessary to characterise all the species satisfactorily.

Subfamily FURCITELLINAE Williams, 1965

Genus HOLTEDAHLINA Foerste, 1924

Type species. *Leptaena sulcata* Verneuil, from the Upper Caradoc Whitewater Formation, Ohio, USA.

Holtedahlina orientalis sp. nov.
Plate 2, figures 1–11

Derivation of name. Latin *orientalis*, eastern.

Holotype. BC 57623, Plate 2, figures 1–2 and 4, internal and external moulds of a dorsal valve from Locality 856, Degeres Member.

Material. Two complete shells, eight ventral and five dorsal valves. Degeres Member, Localities 546 (BC 57624, 57694), 856 (BC 57622–23, 57695–96, 57715), 858, 858a.

Diagnosis. Transverse and strongly sulcate *Holtedahlina* with subcircular ventral muscle field virtually enclosed by muscle-bounding ridges; relatively straight socket plates.

Description. Shell dorsibiconvex, transverse and semioval in outline; about 65 per cent as long as wide, with maximum width at hinge line. Cardinal extremities acute and slightly alate. Anterior commissure gently uniplicate. Ventral valve gently convex with low apsacline interarea. Deltidium narrow, triangular, covered apically by pseudodeltidium. Low ventral median fold originating at umbo and reversing into ventral sulcus at about 3–4 mm anterior of beak. Sulcus terminated by high semioval tongue about 45 per cent as wide as valve. Lateral profile of dorsal valve moderately convex with maximum height at mid-length. Dorsal interarea low, anacline with a small convex chilidium. Shallow dorsal umbonal median sulcus reversed into median fold about 3–4 mm from beak. Radial ornament finely and unequally parvicostellate with 4–5 parvicostellae per mm along anterior margin of mature specimens. Ventral interior with small teeth and thin, divergent dental plates continuing as muscle-bounding ridges. Ventral muscle field small, subpentagonal, about 35 per cent as long as the valve. Ventral adductor scars narrow, triangular, raised, and completely separating strongly impressed diductor scars. Dorsal interior with a double cardinal process with vertical ridges on myophore, which is situated on a low transverse notothyrial platform. Socket ridges low, subparallel to hinge line, about 25 per cent of maximum valve width. Adductor muscle field clearly impressed, rhomboidal in outline, bisected by a fine median septum and two pairs of side septa.

Remarks. Bearing in mind how cosmopolitan the genus *Holtedahlina* is in rocks of both late Caradoc and Ashgill age, it is somewhat surprising that so few nominal species have been erected within it. *Holtedahlina orientalis* differs from the type species, *H. sulcata*, in having fine, strongly differentiated parvicostellate radial ornament, acute and alate cardinal extremities, and a subcircular ventral muscle field bordered by strong muscle-bounding ridges, in contrast to the muscle field of *H. sulcata*, which is open anteriorly (Cocks and Rong 2000, fig. 136:3b). It is also more deeply sulcate. *H. sinica* Zhan and Cocks, 1998, from the mid Ashgill of South China, is rounder and smaller, and has a much reduced fold and sulcus, a more pentagonal ventral muscle field, a larger dorsal myophragm and slightly more curving socket plates. Oraspõld (1956) erected two species, *H. sakuensis* from the Oandu Beds and *H. rakverensis* from the Rakvere Beds, both in the Upper Caradoc of Estonia. The ventral interior of *H. sakuensis* is unknown, but the dorsal myophragm is much more swollen than *H. orientalis* and there is no appreciable sulcus. *H. rakverensis* has a weak sulcus and is poorly characterised internally: again no ventral interior is figured. Both Estonian species are less laterally elongate and alate than *H. orientalis*. The *Holtedahlina* sp. of Nikiforova and Andreeva (1961), from the Early Ashgill of Siberia, has a higher ventral interarea, and apparently bilobed ventral muscle-bounding ridges. The *Holtedah-*

lina sp. of Cocks and Modzalevskaya (1997) from the middle Ashgill of Taimyr, now considered to be part of Siberia rather than Baltica in the Ordovician (Fortey and Cocks 2003), is rather similar to *H. sulcata*.

Family RAFINESQUINIDAE Schuchert, 1893
Subamily RAFINESQUININAE Schuchert, 1893

Genus RHIPIDOMENA Cooper, 1956

Type species. *Strophomena tennessensis* Willard, 1928, from the Upper Llanvirn Benbolt Formation of Virginia, USA.

Rhipidomena sp.
Plate 1, figures 18–20

Material. One ventral and one dorsal valve from Locality 858a.

Description. Shell resupinate, subquadrate in outline with rectimarginate anterior commissure and right-angled cardinal extremities. Ventral valve with lateral profile gently convex in posterior half and concave anteriorly. Interarea apsacline with a narrow convex pseudodeltidium. Dorsal valve gently convex in lateral profile; somewhat flattened anteriorly, with linear, anacline interarea and chilidium. Radial ornament unequally parvicostellate with 5–6 parvicostellae per mm along anterior margin. Each third to sixth rib accentuated. Concentric ornament of regular fine fila, about 6 per mm. Ventral interior unknown. Dorsal interior with a double cardinal process on low and broad notothyrial platform, strong, curved socket plates bounding deep, transverse sockets. Fine dorsal median septum and one pair of side septa about equal in length to median septum.

Measurements. Ventral valve, BC 57697, W, 40·4; dorsal valve, BC 57621, L, 35·7.

Remarks. These specimens differ from other known species of *Rhipidomena* in having only one weakly developed pair of side septa. In addition, the socket plates are longer and curve round more towards the posterolateral extremities than the type species, *R. tennesseensis*, as revised by Cooper (1956). However, since no ventral interiors are known from the Degeres Member, the species is left in open nomenclature, otherwise a new species would probably have been erected here.

Family GLYPTOMENIDAE Williams, 1965

Genus GLYPTOMENOIDES gen. nov.

Type species. *Rafinesquina girvanensis* Salmon, 1942, from the Lower Caradoc Balclatchie Conglomerate of Girvan, Scotland.

Diagnosis. Glyptomenid with characteristic Type C cardinal process of Rong and Cocks (1994) and with geniculation and rugation. Prominent socket plates and dorsal myophragm but the latter extends only a short distance anteriorly.

Remarks. In Cooper's original (1956) erection and diagnosis of *Glyptomena* he attributed only two species to it without query: *G. parvula* from the Effna-Rich Valley Formation of Porterfield Quarry, Virginia, and the type species, *G. sculpturata*, from the Chatham Hill Formation of Sharon Springs, Virginia. Neither species has a hint of rugae, their lateral profile is described as concavo-convex, and there is no mention of geniculation. The profile of *G. parvula* is 'evenly convex' (Cooper 1956, p. 883), although *G. sculpturata* is 'unequally convex in lateral profile, the posterior two-thirds gently convex and the anterior third fairly strongly bent towards the brachial valve' (Cooper 1956, p. 885). No description was given of the ventral interior of *G. sculpturata*, but in the overall generic diagnosis (Cooper 1956, p. 881) it is described as having 'short oblique dental plates with narrow umbonal cavities. Muscle field small, subcircular in outline and with the anterior ends of the adductors separated by a low ridge.' Williams (1963, p. 210) reviewed *Glyptomena* and other genera, and concluded that (1) *Glyptomena* differed in its small subcordate muscle field from *Oepikina*, which has a large flabellate muscle field; (2) *Oslomena* Spjeldnaes, 1957, is a subjective synonym of *Glyptomena*; (3) his two Girvan species, *G. girvanensis* and *G. trippi* 'can on no account be placed in two different genera' because their internal morphology is identical, although they differ specifically in their outline and convexity (with *G. girvanensis* possessing geniculation). Both species have ventral muscle fields of approximately 40 per cent valve length.

Davidson (1883) illustrated the Girvan specimens under the name of *Strophomena deltoidea* Conrad, 1839, a species which was originally described from New York State, USA. Reed (1917) re-illustrated the same specimens and consequently made *S. deltoidea* the type of a new subgenus *Playfairia*; however, the interior of *S. deltoidea* is unknown and its systematic position therefore uncertain (Cocks and Rong 2000, p. 302): its type locality is merely 'Trenton Group, Trenton Falls, New York'. Both *Strophomena deltoidea* and therefore the genus *Playfairia* are considered *nomina dubia* here.

Rong and Cocks (1994) and Cocks and Rong (2000) also revised *Oepikina*, and re-illustrated the type species *O. septata* Salmon, 1942, demonstrating that true *Oepikina* has a substantially different cardinal process and septal arrangement from *Glyptomena*, which places it within the subfamily Furcitellinae of the family Strophomenidae, rather than within the Glyptomenidae. Thus, although *Oepikina* and *Glyptomenoides* have a comparable outline,

sporadic rugation and a ventral valve muscle field, the two genera are placed in different families on the basis of their dorsal valve interiors. Despite Williams' (1962) different opinion cited above, *Oslomena* remains a problem. Spjeldnaes (1957, p. 161) erected the genus, with type species *O. osloensis* from the 4bα Beds, now termed the Arnestad Formation, of Middle Caradoc (Burrelian) age in the Oslo Region, Norway. In his description of that species, Spjeldnaes mentioned two pairs of dorsal lateral septa, although only one pair appears to be present in the only figured dorsal interior (1957, pl. 12, fig. 12). The prominent side septa of *Oepikina* are certainly absent, and the two genera are not synonyms. However, the cardinal process of *Oslomena* is poorly known; hence Cocks and Rong (2000) queried its attribution to the Furcitellinae.

Thus the new genus *Glyptomenoides* is erected here. It differs from *Glyptomena* in the presence of rugae and in its geniculation. In some characters it resembles *Hesperinia*, particularly in the geniculation, although that genus is poorly known; no ventral interiors were illustrated by Cooper (1956), but *Hesperinia* lacks rugae. In addition, *Hesperinia* has more flaring socket plates than the new genus. Otherwise none of the Glyptomenidae is geniculate, as can be seen in the illustrations of all the genera in the family in Cocks and Rong (2000).

Glyptomenoides girvanensis (Salmon, 1942)
Plate 3, figures 11–12, 14–18, 21–22

1883 *Strophomena deltoidea* Conrad; Davidson, p. 197, pl. 15, figs 16–22.
1917 *Rafinesquina* (*Playfairia*) *deltoidea* (Conrad); Reed, p. 866, pl. 11, figs 21–30.
1942 *Rafinesquina girvanensis* Salmon, p. 571.
1957 *Oslomena girvanensis* Spjeldnaes, p. 165.
1962 *Glyptomena girvanensis* (Salmon) Williams, p. 211, pl. 21, figs 5–9, 16.
1978 *Glyptomena girvanensis* (Salmon); Cocks, p.112, p. 216.

Lectotype. B 73286, selected Cocks (1978, p. 112) from the Balclatchie Conglomerate, old quarry at Balclatchie, Girvan, Scotland. This is the specimen in the Gray Collection figured by Davidson (1883, pl. 15, fig. 22) as *Strophomena deltoidea* Conrad, and by Reed (1917, pl. 11, fig. 23) as *Rafinesquina* (*Playfairia*) *deltoidea* (Conrad).

Remarks. This species was erected as *Rafinesquina girvanensis* by Salmon (1942), who simply referred without re-illustration to the specimens figured as *R. deltoidea* by Reed (1917). The species was fully revised and figured, and its distribution listed in the Girvan area, by Williams in 1962 (p. 211, pl. 21, figs 5–9, 16). We illustrate some specimens from Girvan here, including specimens figured by Reed (1917) and Williams (1962). Unfortunately the lectotype, although an original shell, is somewhat broken in the posterocentral area, and does not show the key features as clearly as the specimens figured here.

Glyptomenoides? sp.
Plate 3, figures 5–10, 13

Material. Three articulated specimens, one dorsal and five ventral valves. Degeres Member, Localities 546 (BC 57627, 57688), 828 (BC 57625, 57689), 828a (BC 57690), 829, 832 (BC 57626), 835 (BC 57691), 836a (BC 57628), 856 (BC 57692), 858; Akkol Beds, Locality 119.

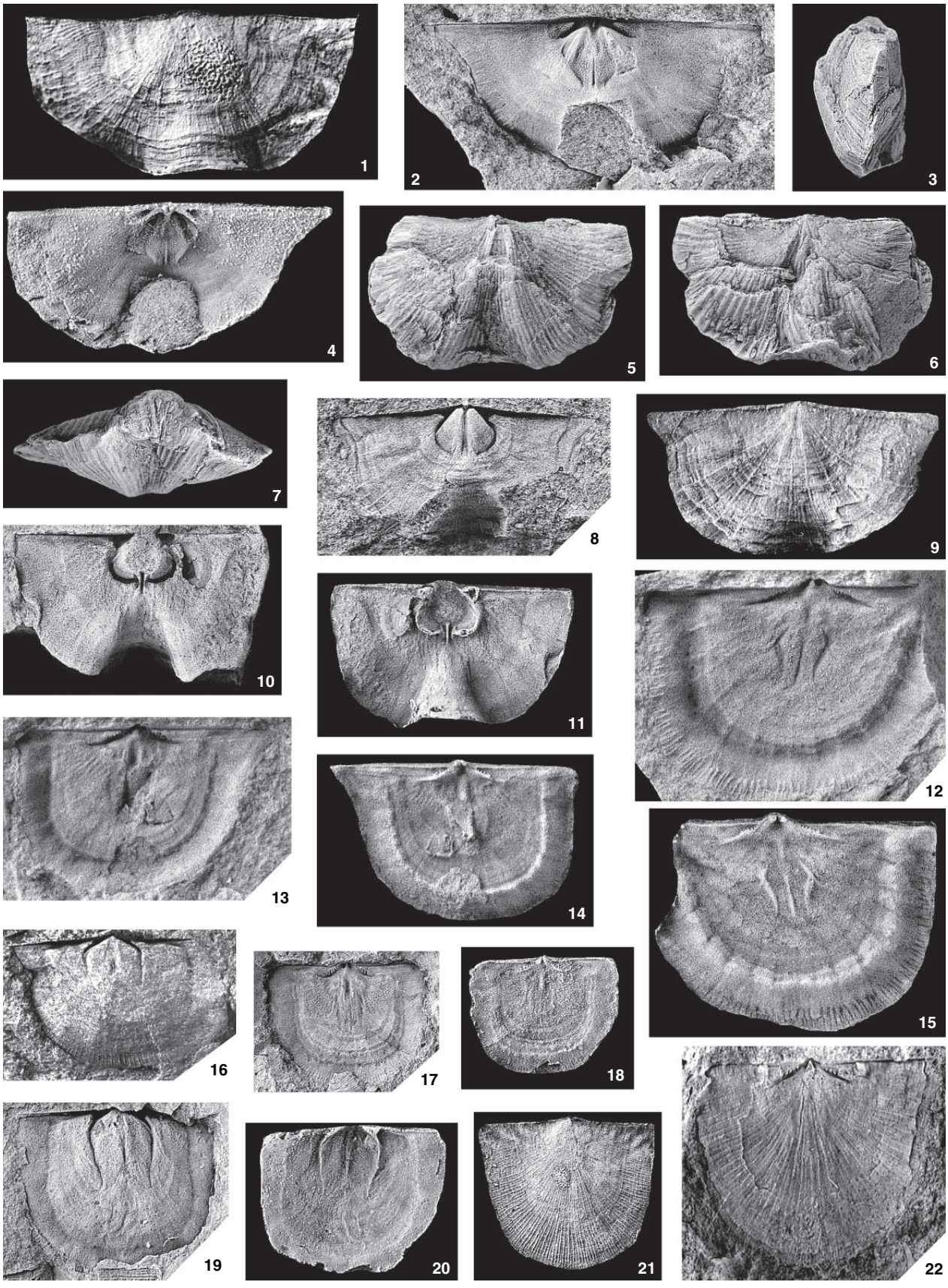
Description. Shell concavoconvex, transverse semi-oval in outline, about 70 per cent as long as wide along hinge line, with acute cardinal extremities and rectimarginate anterior commissure. Ventral valve moderately convex in lateral profile with maximum height at point of geniculation about 11–13 mm from umbo; flattened posteriorly. Ventral interarea low with delthyrium half covered by a convex pseudodeltidium with small apical foramen. Notothyrium completely covered by broad, convex chilidium. Radial ornament unequally parvicostellate with each third to fifth rib accentuated and with 12–13 parvicostellae per 3 mm along the anterior margin. Concentric ornament of 5–8 rounded rugellae in posterior half of shell and fine, evenly spaced concentric fila.

Ventral valve interior with small, vertically striated teeth and divergent dental plates continuous with muscle-bounding ridges that surround a small, heart-shaped muscle field about one-third

EXPLANATION OF PLATE 2

Figs 1–11. *Holtedahlina orientalis* sp. nov., Degeres Member. 1–2, 4, BC 57623, holotype, Locality 856, latex cast of dorsal exterior, dorsal internal mould and latex cast of interior; ×3. 3, 5–7, BC 57694, Locality 546, conjoined valves, lateral, ventral and dorsal views; ×4. 8–9, BC 57622, Locality 856, ventral internal mould and latex cast of ventral exterior; ×4. 10–11, BC 57624, Locality 546, ventral internal mould and latex cast of interior; ×3.

Figs 12–22. *Platymena tersa* sp. nov., Degeres Member. 12, 15, BC 57818, Locality 838, dorsal internal mould, ×4, and latex cast of interior, ×3. 13–14, BC 57819, Locality 838, dorsal internal mould and latex cast of interior; ×3. 16, BC 57691, Locality 83522, ventral internal mould; ×2. 17–18, BC 57619, Locality 857-1a, dorsal internal mould and latex cast of dorsal interior; ×2. 19–20, BC 57657, Locality 826a, ventral internal mould and latex cast of ventral interior; ×2. 21, BC 57638, Locality 135, latex cast of ventral exterior; ×2. 22, BC 57629, Locality 132, dorsal valve exterior with exfoliated umbonal part showing cardinalia; ×3.



POPOV and COCKS, *Holtedahlina*, *Platymena*

as long as valve. Adductor scars on low ridge completely dividing strongly impressed, somewhat longer diductor scars. Mantle canal system saccate with thin, diverging *vascula media*. Dorsal interior unknown.

Remarks. This form appears to be most similar to *Glyptomenoides girvanensis* (Salmon), as revised by Williams (1962) and above here, but the mature shell is one and a half times to twice as large, with more than five concentric rugellae crossing all the posterior surface of the shell and geniculation developed in specimens more than 11 mm long. A new species would be erected from the Degeres Member material if the dorsal interior was known; however, in view of the lack of such specimens, the Kazakh form can only be attributed questionably to *Glyptomenoides*.

Genus PLATYMENA Cooper, 1956

Type species. *Platymena plana* Cooper, 1956, from the Caradoc Arline Formation of Tennessee, USA.

Platymena tersa sp. nov.
Plate 2, figures 12–22; Plate 3, figures 1–4

Derivation of name. Latin *tersus*, clean.

Holotype. BC 57665, the internal mould of a dorsal valve, from the Degeres Member, Locality 857a (Pl. 3, figs 1–2).

Diagnosis. Like *P. plana* except that socket plates diverge at a wider angle and dorsal valve side septa are more pronounced (especially in adults) and variably curved. Dorsal valve median septum variably developed, sometimes almost absent.

Material. Degeres Member, Localities 132 (BC 57629–33, 57640), 135 (BC 57635–40), 136, 139, 546 (BC 57641), 826 (BC 57643–56, 57813), 826a (BC 57657–59, 57662, 57700), 835, 836, 838 (BC 57818–19), 854 (BC 57663), 857 (BC 57664, 57804–06), 857a (BC 57619, 57665, 57814, 57881).

Description. Shall planoconvex, slightly transverse, subrectangular, about 80 per cent as long as wide along hinge line, with slightly acute cardinal extremities. Anterior commissure rectimarginate. Ventral valve gently convex in lateral profile, with maximum height about one-third length from umbo. Ventral interarea low, anacline, and with delthyrium covered apically by a convex pseudodeltidium. Dorsal valve usually almost flat, but may be slightly concave along posterior and lateral margins in largest specimens. Dorsal interarea low, apsacline with convex chilidium. Radial ornament slightly unequally parvicostellate, with 6–8 parvicostellae per mm. Ventral interior with transverse teeth striated posteriorly and low diverging dental plates. Muscle field subcircular, about one-third valve length, bordered by low, muscle-bounding ridges. Ventral adductor ridge-like muscle scars crossing all muscle field. Ventral mantle canal system saccate with vascular media diverging at about 60 degrees. Dorsal valve with double cardinal process on low transverse, subrectangular notothyrial platform, which continues anteriorly as a short, thick, median ridge merging anteriorly with a thin median septum. Socket ridges low, straight and widely divergent, bordering deep, transverse sockets with 5–7 vertical ridges on their anterior slopes. Adductor muscle field weakly impressed, bisected by a pair of side septa fully developed only in gerontic specimens. Inner pairs of side septa usually stronger and curved towards plane of symmetry in their anterior half.

Remarks. Although dominantly with the Type C cardinalia typical of the Glyptomenidae, the cardinal process of *Platymena* has some tendency towards the morphology of the Type A cardinalia typical of the Strophomenidae; however, we feel that the genus is best placed in the Glyptomenidae. *Platymena* is not widespread; for example, it is absent from the Girvan area of Scotland (Williams 1962). This Kazakh species is comparable with the type species, *Platymena plana* Cooper, 1956, from the Arline Formation of the southern Appalachians, in its size and overall shape, but it differs in the absence of a dorsal sulcus and in the variable presence of a pair of dorsal side septa in mature specimens. Neither species has any rugation over most of the valve area, although a few short rugae are weakly developed at the alar extremities in a small minority of specimens. *P. tersa* is a dominant constituent of the brachiopod fauna of the Degeres Member at several localities (Table 1).

Family CHRISTIANIIDAE Williams, 1953

Genus CHRISTIANIA Hall and Clarke, 1892

Type species. *Leptaena subquadrata* Hall, 1883, from the Upper Caradoc of Perry County, Tennessee, USA.

Christiania proclivis sp. nov.
Plate 3, figures 19–20, 23–31

1956 *Christiania tenuicincta*; Rukavishnikova, p. 148, pl. 4, figs 6–9.
1986 *Christiania tenuicincta*; Misius, p. 173, pl. 16, figs 7–18.

Derivation of name. Latin *proclivis*, sloping.

Holotype. BC 57759, a dorsal internal mould, Plate 3, figure 28, from Locality 136, Degeres Member.

Diagnosis. Relatively elongate *Christiania* with dorsal median septum usually less than half valve length. Dorsal transverse septa concave anteriorly.

Material. Five complete shells, 30 ventral and 51 dorsal valves. Degeres Member, Localities 132, 135 (BC 57756), 136 (BC 57758–60), 546 (BC 57761–64), 826, 828, 828a, 829 (BC 57765), 829a (BC 57766–68) 832, 835, 838 (BC 57769–71), 838a (BC 57772–74), 855, 856, 858.

Description. Shell smooth, concavoconvex, elongate and subrectangular in outline, with lateral margins slightly diverging anteriorly; maximum width in anterior third of shell length. Cardinal extremities flattened and slightly alate. Anterior commissure weakly uniplicate. Lateral profile of ventral valve strongly convex, with maximum height at about one-third valve length from beak. Ventral interarea moderately high and anacline, with convex narrow triangular deltidium and small umbonal foramen. Umbonal region swollen and extending slightly beyond hinge line. Lateral sides of ventral valve decline steeply towards commissural plane. A very shallow ventral sulcus originates in umbonal area. Dorsal valve moderately concave with low hypercline interarea and large, convex chilidium. Shell surface covered with strong, slightly irregular fila and several fine growth lamellae in anterior half.

Ventral interior with strong, transverse teeth lacking dental plates and a small, bilobed muscle field divided by low median ridge. *Vascula media* strong, subparallel. Dorsal valve interior with double cardinal process bearing strong vertical ridges on myophore. Socket plates short, widely divergent, bounding deep sockets. Median septum very thin and rarely exceeding one-third valve length. Two pairs of strong, blade-like side septa joined near anterior margin. Pair of variably developed transverse septa diverging posteriorly from inner pair of side septa at an acute angle, which then curve anteriorly and join with outer pair of side septa at about same level as inner pair.

Remarks. *Christiania* is a cosmopolitan genus with a great number of nominal species that badly need overall revision, a task beyond the scope of this paper. However, key specific distinguishing features include the relative length of the dorsal median septum; that in *C. proclivis* is usually less than half valve length (although BC 57773, figured in Pl. 3, fig. 30, is an exception, the septum being just over half valve length). This is in contrast to *C. bilobata* Reed, 1917, *C. perrugata* Reed, 1917 and its subspecies *elongata* Mitchell, 1977, *C. oblonga* (Pander, 1830) (and its synonyms *ovata* and *semiglobosa* as revised by Spjeldnaes 1957) and *C. hastata* Rukavishnikova, 1956. Unfortunately the *elongata* of Mitchell (1977) is a junior homonym of *C. elongata* Spjeldnaes, 1957, and requires a new name. A second distinguishing feature concerns those species that are relatively elongate in overall shape; this distinguishes *C. proclivis* from the more transverse *C. auriculata* Cooper, 1956, *C. platys* Cooper, 1956, *C. sulcata* Williams, 1962, *C. portlocki* Mitchell, 1977, *C. holtedahli* Spjeldnaes, 1957 and *C. elusa* Lockley and Williams, 1981. This is probably also the case with *C. taldyboensis* Klenina, 1984, although no interiors are illustrated for that species. Other species, such as *C. hollii* (Davidson) and *C. tenuicincta* (M'Coy) are too poorly known to enable useful comparison (Cocks 1978). *C. zhitangensis* Liang, *in* Liu *et al.* 1983 has a much stronger ventral median septum.

In addition, numerous authors have described or figured '*Christiania* sp.' or '*Christiania tenuicincta*', but these forms are not revised here. There are other nominal species from rocks of Ashgill age. *C. proclivis* can be distinguished from most of the other species in having a smooth shell, a weak median septum and transverse septa curved posteriorly. It is somewhat similar to *C. egregia* Popov, 1980, from the underlying Anderken Formation (Popov *et al.* 2002) in the characters of the interior of the dorsal valve, including the arrangements of the side and transverse septa, but completely lacks the radial ornament characteristic of the latter species. It is possible that *C. gigantea* Fu, 1982, from China, is a synonym of *C. egregia*. Although Cooper (1956) redescribed the type species, *C. subquadrata* Hall, unfortunately he neither designated a lectotype nor illustrated material from Hall's type locality, thus making true comparison difficult, but, assuming that the material illustrated by Cooper as *C. subquadrata* is correctly identified, then this species differs from *C. proclivis* in the more pronounced convexity of the dorsal valve, the much thicker and incurved dorsal side septa, and the opposite convexity of the dorsal transverse septa; those of *C. proclivis* are concave anteriorly, whilst those of *C. subquadrata* are concave posteriorly (Cooper 1956, pl. 214, fig. 30), as are those of *C. trentonensis* Ruedemann as revised by Cooper (1956); they can also be oblique (Cooper 1956, pl. 214, fig. 33), as are those of *C. skolia* Percival, 1991.

Superfamily PLECTAMBONITOIDEA Jones, 1928
Family PLECTAMBONITIDAE Jones, 1928

Genus BANDALETA Nikitin and Popov, 1996

Type species. *Bandaleta plana* Nikitin and Popov, 1996, from the late Dulankara mud mound, Betpak-Dala Desert, Kazakhstan.

Bandaleta cf. *plana* Nikitin and Popov, 1996
Plate 5, figure 1

cf. 1996 *Bandaleta plana* Nikitin and Popov, p. 5, fig. 3A–I.

Material. Four complete shells, two ventral and two dorsal valves. Akkol Member, Localities 219 and 827 (BC 57859).

Measurements. BC 57859, dorsal valve, L, 10·8; W, 18·7.

Remarks. Specimens from the Akkol Limestone show close similarity in the lateral profile of their planoconvex

shells, unequally parvicostellate radial ornament and shallow dorsal median sulcus to the approximately contemporaneous shells of *Bandaleta plana* Nikitin and Popov, 1996, in the same Chu-Ili Terrane, but the interiors of both valves are unknown. Exfoliated dorsal valves reveal a double septum, which indicates affinities of the shells from the Akkol Limestone to *Bandaleta*, but their specific attribution remains provisional.

Family LEPTELLINIDAE Ulrich and Cooper, 1936
Subfamily PALAEOSTROPHOMENINAE Cocks and Rong, 1989

Genus GLYPTAMBONITES Cooper, 1956

Type species. *Glyptambonites musculosus* Cooper, 1956, from the Lower Caradoc Oranda Formation of Virginia, USA.

Glyptambonites aff. *musculosus* Cooper, 1956
Plate 4, figures 1–6

aff. 1956 *Glyptambonites musculosus* Cooper, p. 715, pl. 171, fig. 15; pl. 175, figs 9–13; pl. 176, figs 1–5.

Material. Four ventral and two dorsal valves. Degeres Member, Locality 828 (BC 57724–25); Akkol Member, Locality 827.

Description. Shell planoconvex, semi-oval in outline, about 60–70 per cent as long as wide, with maximum width at hinge line. Cardinal extremities acute. Anterior commissure rectimarginate. Ventral valve very gently and evenly convex with a low, apsacline interarea. Pseudodeltidium small, apical. Dorsal valve gently concave to almost flat with a linear, anacline interarea and a well-developed convex chilidium. Radial ornament unequally parvicostellate with seven accentuated ribs originating at umbo and 8–10 intervening parvicostellae per mm in interspaces between them. Fine oblique rugellae about 2 per mm developed along posterior margin of both valves. Ventral interior with small teeth and short, slightly diverging dental plates continuing as straight, muscle-bounding ridges flanking a bilobed muscle field with elongate, nearly subparallel diductor scars extending to mid valve and completely separated by short, subtriangular adductor scars slightly raised anteriorly. Mantle canal system saccate with very short, diverging vascula media. Bottom of valve near cardinal extremities somewhat thickened. Dorsal interior with simple, bulbous cardinal process situated on a broad, short notothyrial platform. Socket plates narrow, subparallel to hinge line. Median septum fine, bisecting a subquadrate adductor muscle field bordered laterally by a pair of subparallel muscle-bounding ridges.

Measurements. Ventral valve (BC 57724), L, 15·7; W, 24·2.

Remarks. These specimens resemble the type species *Glyptambonites musculosus* in their general shell shape, surface ornament and in the internal details of both valves. *G. musculosus* is of early Caradoc age, substantially older than the Degeres Member material. Because we have only a few specimens, we are reluctant to attribute firmly the Kazakh material to Cooper's species; however, if confirmed, the presence of the American species in Kazakhstan would be remarkable.

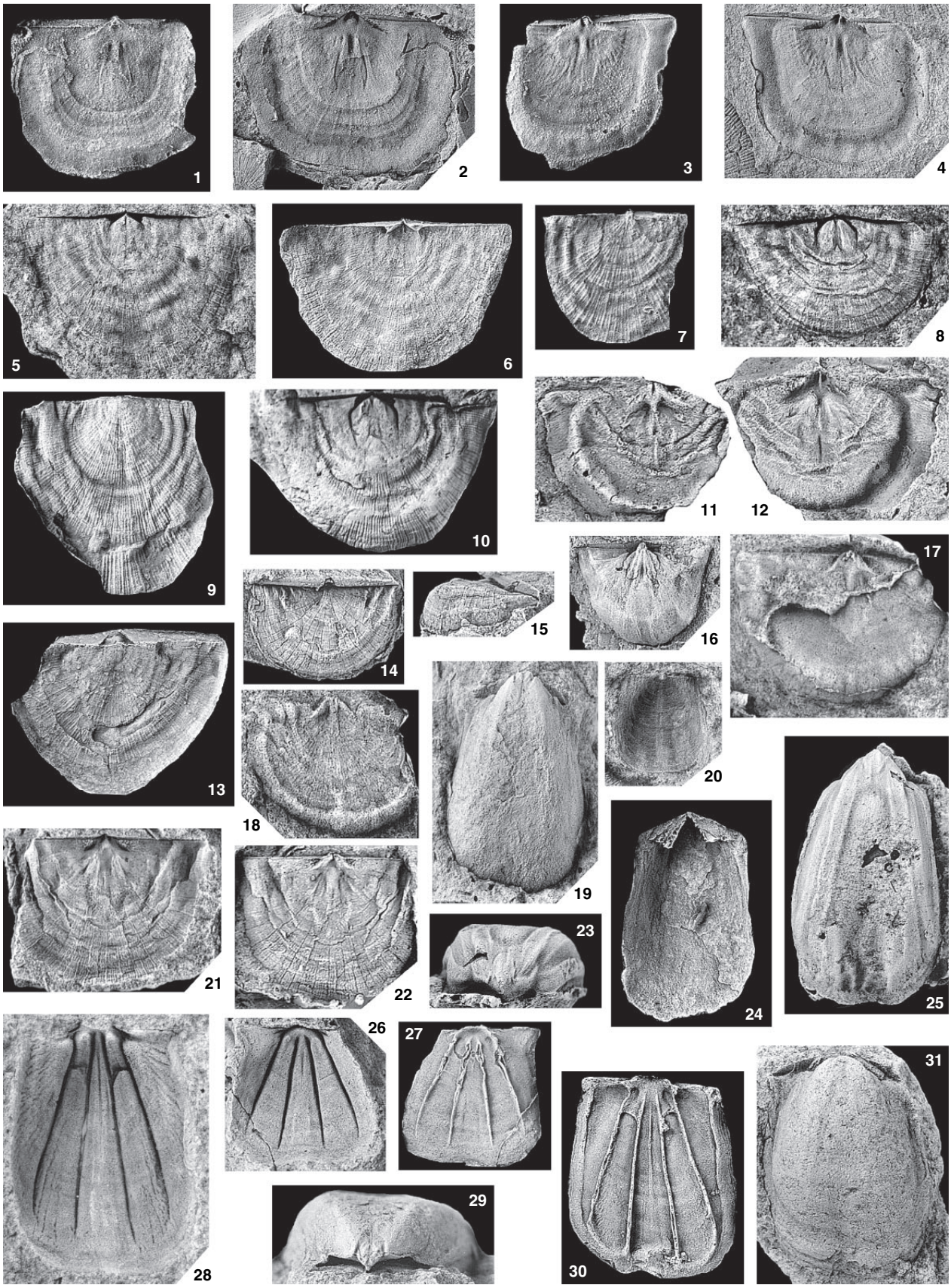
EXPLANATION OF PLATE 3

Figs 1–4. *Platymena tersa* sp. nov., Degeres Member. 1–2, BC 57665, holotype, Locality 857-1a, latex cast of dorsal interior and dorsal internal mould; × 2. 3–4, BC 57658, Locality 826a, latex cast of dorsal interior and dorsal internal mould; × 2.

Figs 5–10, 13. *Glyptomenoides*? sp., Degeres Member. 5–6. BC 57628, Locality 836a, ventral internal mould and latex cast of interior; × 2. 7, BC 57627, Locality 546, latex cast of dorsal exterior; × 3. 8, BC 57688, Locality 546, ventral internal mould; × 2. 9, BC 57625, Locality 828, latex cast of dorsal exterior; × 3. 10, BC 57689, Locality 828, ventral internal mould; × 2. 13, BC 57626, Locality 832, latex cast of dorsal exterior of conjoined valves; × 2.

Figs 11–12, 14–18, 21–22. *Glyptomenoides girvanensis* (Salmon, 1942), Balclatchie Formation, Balclatchie, Girvan, Scotland. 11–12, B 73290, latex cast and internal mould of dorsal interior, figured Reed (1917, pl. 11, fig. 27); × 3. 14–15, BB 15211, dorsal and lateral views of internal moulds of conjoined valves, figured Williams (1962, pl. 21, fig. 9); × 2. 16, B 73288, ventral internal mould, figured Reed (1917, pl. 11, fig. 25); × 2. 17, BC 58252, latex cast of dorsal interior, BC 58252; × 3. 18, B 73274, latex cast of dorsal interior; × 3. 21–22, B 15213, internal mould and latex cast of dorsal valve; × 4.

Figs 19–20, 23–31. *Christiania proclivis* sp. nov., Degeres Member. 19, 24, 29, BC 57769, Locality 838, ventral internal mould, × 2; latex cast of ventral interior, and posterior view of ventral internal mould showing adductor scars, × 3. 20, BC57770, Locality 838, latex cast of dorsal exterior; × 2. 23, 25, BC 57765, Locality 828, ventral internal mould, posterior and ventral views; × 2. 26–27. BC 57774, Locality 838a, dorsal internal mould and latex cast of interior of juvenile specimen; × 3. 28, BC 57759, Locality 136, holotype, dorsal internal mould; × 3. 30, BC 57773, Locality 838a, latex cast of dorsal interior; × 2. 31, BC 57766, Locality 829a, ventral internal mould; × 2.



POPOV and COCKS, Ordovician brachiopods

Genus NIKITINAMENA gen. nov.

Derivation of name. After Igor F. Nikitin, distinguished Kazakhstanian geologist and palaeontologist.

Type species. *Nikitinamena bicostata* sp. nov., Degeres Member.

Diagnosis. Shell concavoconvex, geniculate; rhomboidal outline; anterior commissure weakly uniplicate; ventral valve with two widely diverging, low, angular plications enclosing very shallow sulcus; ventral interarea apsacline with small, apical pseudodeltidium; dorsal valve with low median fold and linear, hypercline interarea. Chilidial plates separate; radial ornament finely and unevenly parvicostellate. Ventral interior with small teeth and small bilobed muscle field; short adductor scar completely separating larger diductor scars; ventral mantle canal system saccate with short, diverging vascula media; dorsal interior with simple, bulbous cardinal process on low notothyrial platform and with small curved socket plates; median septum fine, extending anteriorly to mid length.

Remarks. This genus resembles *Apatomorpha*, *Titanambonites* and *Sowerbyites* in having a simple cardinal process and a bilobed ventral muscle field with short adductor scars completely separating large, diverging diductor scars. However, it differs from these genera in having a geniculate shell and a slightly uniplicate anterior commissure with two angular plications on the ventral valve. The rhomboidal outline, with the central part of the anterior commisure subparallel to the hinge line, is particularly distinctive. The ventral muscle field in *Nikitinamena* is very small by comparison with these three genera and dental plates are completely absent, whereas the dorsal interior has a very fine median septum and weakly impressed adductor scars. It also differs from *Sowerbyites* and the rest of the Syndielasmatidae in the absence of side septa. It differs from *Leptastichidia* Zhan and Jin (2005), from the Arenig–Llanvirn of South China, in its straight central anterior outline, its dorsal median septum separated from the cardinal process area, its bilobed ventral muscle field, and its much finer and less well-differentiated ornament.

Nikitinamena bicostata sp. nov.
Plate 4, figures 13–14, 16–21

Derivation of name. After the two strong accentuated ribs.

Material. Two complete shells, four ventral and five dorsal valves. Degeres Member, Localities 828, 835a (BC 57723), 856 (BC 57716–17), 858 (BC 57718–22).

Holotype. BC 57716, a ventral internal mould, Degeres Member, Locality 856.

Description. Shell concavoconvex, trapezoidal in outline, about 55 per cent as long as wide, with maximum width at hinge line. Cardinal extremities acute and alate. Anterior commissure gently uniplicate. Ventral valve very gently and evenly convex with a low, apsacline interarea; pseudodeltidium small, apical. Dorsal valve gently concave to almost flat, with a linear, anacline interarea and well-developed convex chilidium. Radial ornament unequally parvicostellate with seven accentuated ribs originating at umbo and 8–10 intervening parvicostellae per mm in interspaces between them. Fine oblique rugellae, about 2 per mm, developed along posterior margin of both valves.

Ventral interior with small teeth and short, slightly diverging dental plates continuing as straight, muscle-bounding

EXPLANATION OF PLATE 4

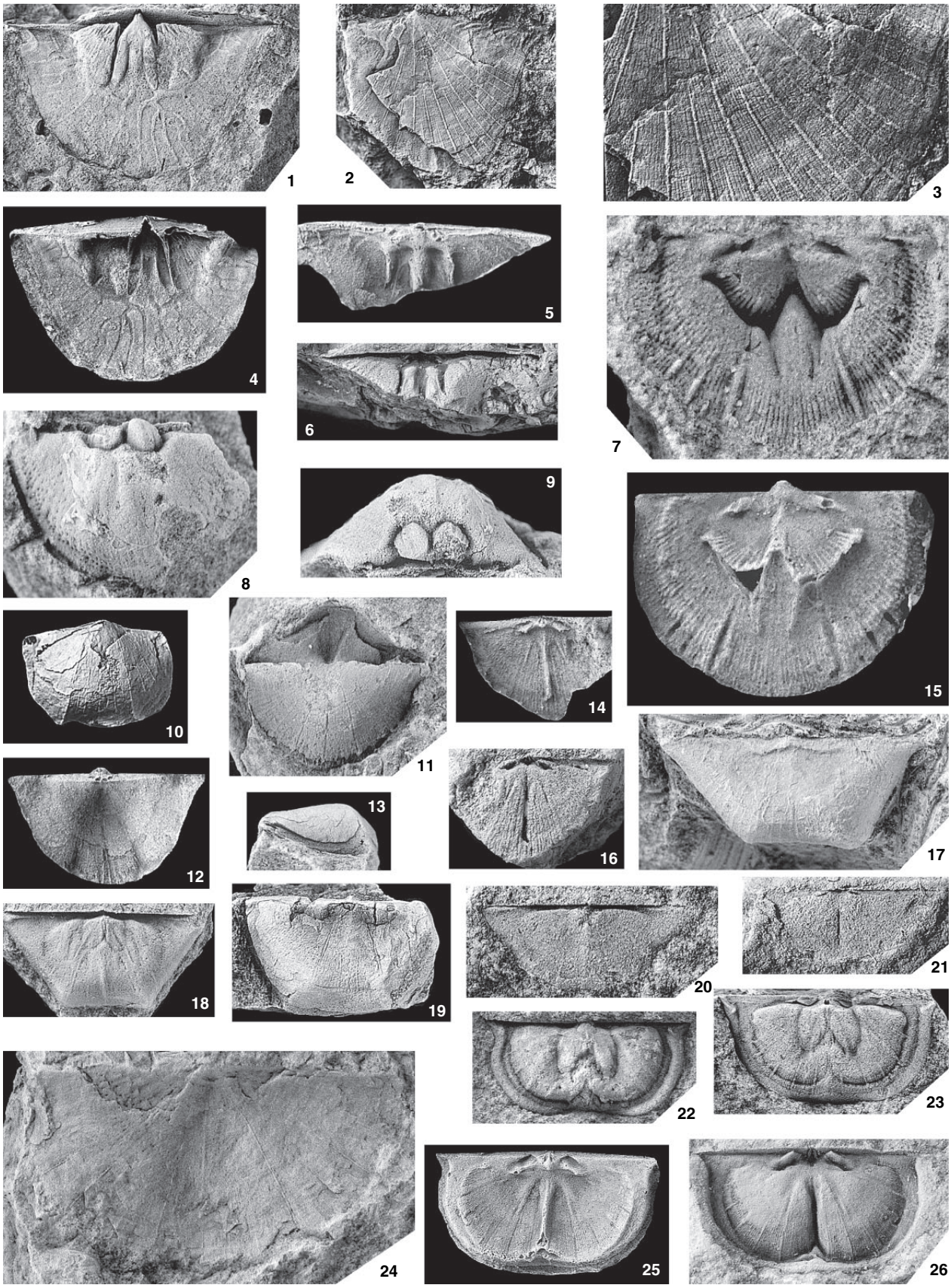
Figs 1–6. *Glyptambonites* aff. *musculosus* Cooper, 1956. 1, 4, Degeres member, Locality 828, BC 57724, dorsal ventral mould and latex cast of ventral interior; × 3. 2–3, Akkol Member, Locality 827, BC 57726, ventral valve exterior, × 2, and external surface showing radial ornament, × 4. 5–6, Degeres Member, Locality 828, BC 57725, latex cast of dorsal interior and dorsal internal mould; × 3.

Figs 7–12, 15. *Leangella* (*Leangella*) *paletsae* sp. nov. 7–9, 11–12, 15, Degeres Member; 10, Akkol Member. 7, 15, BC 57741, Locality 858a, holotype, dorsal internal mould and latex cast of dorsal interior; × 7·7. 8–9, BC 57738, Locality 829, ventral internal mould, ventral and posterior views; × 5. 10, BC 57848, Locality 827, ventral view of conjoined valves; × 4. 11, BC 57737, Locality 829, dorsal view of external mould of conjoined valves; × 4. 12, BC 57740, Locality 832, latex cast of dorsal interior; × 4.

Figs 13–14, 16–21. *Nikitinamena bicostata* sp. nov., Degeres Member. 13, 19, BC 57722, Locality 858, ventral and lateral views of conjoined valves; × 5. 14, 16, BC 57723, Locality 835a, latex cast of dorsal valve interior and dorsal internal mould; × 5. 17, BC 57717, Locality 856, ventral valve exterior; × 5. 18, BC 57716, Locality 856, holotype, ventral internal mould; × 4. 20, BC 57718, Locality 858, ventral internal mould of juvenile specimen; × 4. 21, BC 57720, Locality 858, dorsal internal mould; × 4.

Figs 22–23, 25–26. *Shlyginia extraordinaria* (Rukavishnikova), Degeres Member. 22, BC 57729, Locality 835, ventral internal mould; × 3. 23, BC 57728, Locality 835, ventral internal mould; × 3. 25–26, BC 57727, Locality 826a, latex cast of dorsal interior and dorsal internal mould; × 3.

Fig. 24. *Dulankarella* cf. *magna* Rukavishnikova, Akkol Member, Locality 827, BC 87849, dorsal valve exterior; × 3.



POPOV and COCKS, Ordovician brachiopods

ridges flanking a bilobed muscle field with elongate, nearly subparallel diductor scars extending to mid valve and completely separated by short, subtriangular adductor scars slightly raised anteriorly. Mantle canal system saccate with very short, diverging vascula media. Anterior of valve somewhat thickened near cardinal extremities. Dorsal interior with simple, bulbous cardinal process situated on a broad, short notothyrial platform. Socket plates narrow, subparallel to hinge line. Median septum fine, bisecting a subquadrate adductor muscle field bordered laterally by a pair of subparallel, muscle-bounding ridges.

Remarks. So far, *Nikitinamena bicostata* is the only species within this distinctive genus, and it is apparently restricted to the Degeres Member of the Dulankara Formation.

Subfamily LEPTELLININAE Ulrich and Cooper, 1936

Genus DULANKARELLA Rukavishnikova, 1956

Type species. *Dulankarella magna* Rukavishnikova, 1956, from the Dulankara Formation, Chu-Ili Range, Kazakhstan. The holotype of *D. magna* is IGNA 36/1369, a complete shell from the Zhartas River near the town of Gornoe.

Dulankarella cf. *magna* Rukavishnikova, 1956
Plate 4, figure 24

cf. 1956 *Dulankarella magna* Rukavishnikova, p. 139, pl. 3, figs 4–9.
cf. 2000 *Dulankarella magna* Rukavishnikova; Popov, Nikitin and Cocks, p. 852, pl. 3, figs 9–16.

Material. Six pairs of conjoined valves, 17 ventral and seven dorsal valves from the Akkol Member, Localities 219, 827 (BC 57849), Dulankara Mountains.

Remarks. The type locality of *Dulankarella magna* at the Zhartas River (from which topotypes include BC 57895) is within the middle part of the Dulankara Formation, but the three members described in this paper cannot be distinguished with certainty in that section. Keller (1956, pp. 32–33) referred all the Upper Ordovician section at this locality to the Otar Member. However, the two upper units of the Ordovician deposits of his description, which contain *Dulankarella magna*, may represent the stratigraphic equivalent of the Degeres Member. The specimens from the Akkol Member do not appear to differ significantly from the shells described by Popov *et al.* (2000) from the basal Otar Member, or from the types described and illustrated by Rukavishnikova (1956), but their preservation is poor; hence, the species has not been identified with confidence there.

Genus SHLYGINIA Nikitin and Popov, 1983

Type species. *Shlyginia declivis* Nikitin and Popov, 1983, from the Andriushin Formation (Llanvirn–Caradoc) of north-central Kazakhstan.

Shlyginia extraordinaria (Rukavishnikova, 1956)
Plate 4, figures 22–23, 25–26

1956 *Dulankarella extraordinaria* Rukavishnikova, p. 138, pl. 3, figs 1–3.
1996 *Shlyginia extraordinaria* (Rukavishnikova); Nikitin and Popov, p. 7.
2000 *Shlyginia extraordinaria* (Rukavishnikova); Popov, Nikitin and Cocks, p. 853, pl. 3, figs 17–21; pl. 5, figs 1–3.

Holotype. IGNA 35/1369, ventral internal mould; Dulankara Formation, Degeres Member, Raisai, Chu-Ili Range.

Material. One complete shell, 27 ventral and 42 dorsal valves. Degeres Member, Localities 135, 136 (BC 12897–98), 546 (BC 57726), 826, 826a (B 57727), 829, 835 (BC 57728–29), 836, 838 (BC 57730), 838a, 854, 855, 857a, Dulankara Mountains.

Remarks. This species was described in detail by Popov *et al.* (2000) and the description is not repeated here. The type locality at Raisai is more than 100 km from the Dulankara Mountains. The specimens from the Degeres Member illustrated here are conspecific with the shells from the Otar Member (Popov *et al.* 2000), but are not as common and do not form a core species in any of the benthic associations.

Family LEPTESTIIDAE Öpik, 1933

Genus LEANGELLA (LEANGELLA) Öpik, 1933

Type species. *Leptaena scissa* J. de C. Sowerby, 1839, from the Lower Llandovery of the type area, Wales.

Discussion. Cocks and Rong (1989) differentiated the two subgenera within *Leangella* by the entire platform of *L.* (*Leangella*) in contrast to the discrete septules making up the platform in *L.* (*Leptestiina*). The new species described below does not have an unbroken platform, but it is nevertheless continuous enough for us to apportion it to the former subgenus rather than the latter.

Leangella (*Leangella*) *paletsae* sp. nov.
Plate 4, figures 7–12, 15

Derivation of name. In memory of the late Lydia M. Palets, who provided a significant contribution to knowledge of the Lower Palaeozoic geology of South Kazakhstan.

Material. Five pairs of conjoined valves, six ventral and four dorsal valves. Degeres Member, Localities 546, 829 (BC 57737–39), 832 (BC 57740), 850 (BC 57816), 858, 858a (BC 57741); Akkol Member, Locality 827 (BC 57848).

Holotype. BC 57741, a dorsal internal mould, Degeres Member, Locality 858a.

Description. Shell concavoconvex, semi-oval in outline, about 80 per cent as long as wide. Cardinal extremities right angled to acute and slightly alate. Anterior commissure rectimarginate. Lateral profile of ventral valve strongly convex, with maximum height at mid length. Ventral interarea low, apsacline to near orthocline, with a small, triangular delthyrium partly covered by pseudodeltidium. Dorsal valve moderately concave with linear, procline to hypercline interarea and discrete chilidial plates. Radial ornament finely and unequally parvicostellate with 10–11 parvicostellae per mm and up to six accentuated ribs per 3 mm along anterior margin of mature specimens.

Ventral interior with strong teeth, lacking dental plates. Muscle field transverse, cordate in outline, slightly exceeding one-quarter of sagittal valve length. Adductor scars narrow, ridge-like, separated by strongly impressed diductor scars. Mantle canals saccate with widely divergent vascula media and long, curved vascula arcuata following a weak subperipheral rim. Dorsal valve with trifid cardinal process and widely divergent socket plates occupying about one-third of maximum shell width. Median septum strong, bifurcating at about 20 per cent of sagittal valve length from umbo in mature specimens. Bema bilobed for about half as long as valve, bordered by high diaphragm. A fine subperipheral rim borders valve margins, becoming weaker towards its median part. Mantle canal system lemniscate, with vascula media, vascula myaria and vascula cruralia crossing diaphragm.

Measurements. BC 57816, ventral valve, L, 6·3; W, 7·9; Ml, 2·0; Mw, 2·7. BC 57738, ventral valve, L, 4·5; W, 6·2; Ml, 1·7; Mw, 2·3. BC 57741, holotype, dorsal valve, L, 5·8; W, 7·8; Bel, 2·5; Bew, 4·1.

Remarks. *Leangella* (*Leangella*) *paletsae* differs from the majority of Ordovician species of *Leangella* listed by Cocks and Rong (1989) in having a larger bema of about one-half valve length supported by bifurcating dorsal septa which extend far beyond the anterior boundary of the bema. It also has more dense accentuated ribs (up to 12 in the umbonal area and up to 18–20 in mature shells). It differs from *Leangella hamari* Spjeldnaes, 1957, from the Caradoc *Cyclocrinus* Shale of Furuberget, Norway, in having a semi-oval rather than subtriangular shell outline, and from *Leangella cylindrica* (Reed, 1917), from the Upper Ordovician Mill Formation of Girvan, Scotland, revised by Harper (1989), in having a well-defined dorsal subperipheral rim.

Leangella (*Leangella*) *paletsae* also differs from the group of Ordovician species previously assigned to *Diambonia* [e.g. *L. anatoli* (Spjeldnaes, 1957) from the 4bα Beds (Ashgill) of the Asker district, Norway; *L. septata* (Cooper) (Schuchert and Cooper 1930) from the upper Ashgill of Percé, Canada, and *L. discuneata* Lamont, 1935, from the lower Ashgill Auldthorns Conglomerate of Girvan] in the absence of a ventral median ridge anterior in the ventral muscle field. This ridge was to be considered the diagnostic generic character of *Diambonia*, but Cocks and Rong (1989) demonstrated that some populations had ventral median ridges ranging from strong through weak to absent, thereby invalidating *Diambonia* as an independent genus, although Candela (2003) still separated the two genera on that basis.

Family HESPEROMENIDAE Cooper, 1956

Genus ANOPTAMBONITES Williams, 1962

Type species. *Leptaena grayae* Davidson, 1883, from the Upper Caradoc Craighead Limestone of Girvan, Scotland.

Anoptambonites kovalevskii Popov, Nikitin and Cocks, 2000
Plate 5, figure 27

2000 *Anoptambonites kovalevskii* Popov, Nikitin and Cocks, p. 853, pl. 4, figs 9–18.

Material. Ten ventral and 14 dorsal valves; Degeres Member, Localities 828 (BC 57742), 829 (BC 57743–44), 856; Akkol Member, Localities 141, 219, 827 (BC 57856–58).

Remarks. This species is relatively uncommon but it occurs in all three members of the Dulankara Formation; for the Otar Member occurrences, see Popov *et al.* (2000). The genus is widespread, both in Kazakhstan and in marginal facies elsewhere, such as those associated with the type species in Scotland. In the Caradoc it appears more prevalent in marginal facies, but by the Ashgill *Anoptambonites* is also found in the cratonic deposits; for example, in the Middle Ashgill Boda Limestone of Sweden (Cocks 2005).

Family XENAMBONITIDAE Cooper, 1956

Genus METAMBONITES Zhan and Rong, 1995

Type species. *Metambonites meritus* Zhan and Rong, 1995, from the Ashgill Xiazhen Formation of Zhejiang Province, China.

Metambonites subcarinatus sp. nov.
Plate 5, figures 2–12

Derivation of name. After the characteristic profile of the ventral valve, which is subcarinate posteriorly.

Holotype. BC 57733, mould of conjoined dorsal and ventral valves, Degeres Member, Locality 828.

Material. Four complete shells, 17 ventral and ten dorsal valves; Degeres Member, Localities 546 (BC 57731–32, 57821–22), 828 (BC 57733), 828a (BC 57820), 829 (BC 57734–35), 832, 835a (BC 12908–14), 856 (BC 57736), 858; Akkol Member, Locality 827.

Description. Shell resupinate, transverse, semi-oval in outline, about 70 per cent as long as wide, with maximum width at hinge line; acute cardinal extremities and rectimarginate anterior commissure. Ventral valve subcarinate in umbonal area with flat, apsacline interarea and delthyrium half covered by convex pseudodeltidium. Lateral profile of ventral valve gently convex in umbonal region and concave in anterior half of valve. Lateral profile of dorsal valve gently concave in posterior half and convex anteriorly to mid valve length. Dorsal interarea low, anacline with discrete chilidial plates. Radial ornament finely and inequally parvicostellate, with 5–7 strong accentuated ribs originating at umbo. Parvicostellae usually poorly visible because of dense comae developed at about 3–5 mm anterior to umbones of both valves.

Ventral valve interior with small teeth lacking dental plates. Ventral muscle field small, bilobed, about 25 per cent as long as valve, bisected medially by a low median ridge flanked by narrow lanceolate adductor scars. A strong diaphragm, interrupted by impressions of vascula media developed in ventral valve near mid length of mature specimens. Ventral mantle canals saccate with vascula arcuata following diaphragm until hinge line. Dorsal valve interior with undercut cardinal process and high socket ridges nearly parallel to hinge line; distance between their distal ends at about 25 per cent of maximum valve length. Dorsal median septum high and short, about 40 per cent as long as valve, highly raised anteriorly and joined to high rim bounding bilobed bema. Mantle canals lemniscate, with paired vascula media, vascula myaria and vascula cruralia cutting rim surrounding lophophore platform.

Remarks. This species differs from *Metambonites meritus* Zhan and Rong, 1995, from the Middle Ashgill (Changwu and Xiashen formations) of South China, in having a slightly resupinate shell, rectimarginate anterior commissure and strongly developed comae. So far, the South China and Chu-Ili terranes are the only ones from which *Metambonites* is known.

Family SOWERBYELLIDAE Öpik, 1930

Genus SOWERBYELLA (SOWERBYELLA) Jones, 1928

Type species. *Leptaena sericea* J. de C. Sowerby, 1839, from the Lower Caradoc of Shropshire, England.

Sowerbyella (*Sowerbyella*) *akdombakensis* Klenina, 1984
Plate 5, figures 13–14

1984 *Sowerbyella akdombakensis* Klenina, p. 82, pl. 7, figs 12, 15, 17, 19–20, 22; pl. 9, figs 2–3.
2000 *Sowerbyella akdombakensis* Klenina; Popov, Nikitin and Cocks, p. 855, pl. 4, figs 1–8.

Holotype. IGNA 411/172, ventral valve, Akdombak Formation, Lower Ashgill, Akdombak Mountain, Chingiz Range, Kazakhstan.

Material. One ventral and 16 dorsal valves. Degeres Member, Localities 132 (BC57701, 57702, 57707), 135 (BC 57703–04) 546, 832, 856, 858, 858a, Dulankara Mountains.

Remarks. A detailed description of this species was provided by Popov *et al.* (2000). It is the dominant species of the *Sowerbyella-Ctenodonta* Association in the underlying Otar Member; however, it is less abundant in the Degeres Member.

Sowerbyella (*Sowerbyella*) *ampla* (Nikitin and Popov, 1996)
Plate 5, figures 15–21, 25

1996 *Anisopleurella ampla* Nikitin and Popov, p. 12, pl. 8, fig. 5K–P.

Holotype. CNIGR 21/12877, ventral valve, from the Upper Ordovician (Dulankarinian) carbonate mud mound, Sartan Manai, northern Betpak-Dala desert, Kazakhstan.

Material. Degeres Member, Localities 136 (BC 57708), 546 (BC 57705, 57709), 826, 828 (BC 57706, 57711, 57817), 828a, 829, 832 (BC 57713), 836 (BC 57714), 838, 838a, 856, 857 (BC 57810); Akkol Member, Locality 827 (BC 57850, 57860–64); Dulankara Mountains.

Description. Shell concavoconvex, transverse, semi-oval in outline, about 60 per cent as long as wide, with acute cardinal extremities. Anterior commissure rectimarginate. Ventral valve

evenly convex with a low, apsacline interarea and small delthyrium covered apically by pseudodeltidium. Dorsal valve very gently concave, with a linear, hypercline interarea and discrete chilidial plates. Radial ornament unequally parvicostellate with 7–10 parvicostellae per mm along anterior margin of mature specimens and with 5–7 accentuated ribs at umbo. One or two new generations of accentuated ribs originated between umbonal area and mid-length, increasing in number up to 15 in mature specimens. Oblique rugellae along the posterior margin variably developed; if present they occur at between two and four per mm.

Ventral interior with small teeth and short, widely divergent dental plates. Ventral muscle field cordate, slightly transverse, about one-third as long as valve. Strongly impressed elongate diductor scars completely enclosing small, lanceolate adductor scars. Mantle canals system with pair of straight, divergent vascula media. Dorsal interior with undercut cardinal process with widely divergent socket plates occupying about 25 per cent of maximum valve width. Long median septum and two pairs of side septa on a slightly raised subtriangular bema about 60 per cent as long as valve.

Remarks. These specimens closely resemble the shells described by Nikitin and Popov (1996) as *Anisopleurella ampla* in the outline and lateral profile of the shell, the characters of radial ornament, and the development of strong concentric rugellae along the hinge line, and in having a small ventral muscle field, a raised bema and two pairs of side septa. The undivided (not bilobed) bema and two pairs of prominent side septa in this species prevent its attribution to *Anisopleurella* (for details, see Cocks and Rong 1989) and it is reassigned here to *Sowerbyella*. Similar shells were reported by Popov *et al.* (2002) under the name *Sowerbyella* aff. *ampla* from the lower–middle Caradoc Anderken Formation of the Chu-Ili Range, but their dorsal interiors remain unknown.

This species does not co-occur with *Sowerbyella akdombakensis* and it is characteristic of the *Strophomena-Christiania* Association. It differs from *S.* (*S.*) *akdombakensis* in having a raised bema, two pairs of side septa in the dorsal valve and the strongly convex lateral profile of the ventral valve. Another similar contemporaneous species with two pairs of side septa is *Sowerbylla intricata* Nikiforova, 1978, from the mid Ashgill Archalyk beds of Uzbekistan, but the Uzbek shells lack the dorsal median septum and characteristic 'quinquecostate' pattern of unequally parvicostellate radial ornament.

Another similar species is *Sowerbyella insueta* Klenina, 1984, from the upper Caradoc–lower Ashgill Taldyboi Formation of the Chingiz Range, Kazakhstan, but its ventral interior remains unknown, and information on the dorsal interior is based on a single incomplete dorsal internal mould. According to the original description this species has a single pair of side septa, but a second pair of small side septa can be recognized from the illustrations provided by Klenina (1984, pl. 8, fig. 10). Therefore, the affinities of that species remain uncertain.

Subgenus SOWERBYELLA (RUGOSOWERBYELLA) Mitchell, 1977

Type species. *Plectambonites subcorrugatella* Reed, 1917, from the Lower Ashgill Whitehouse Group of Girvan, Scotland.

Sowerbyella (*Rugosowerbyella*) sp.
Text-figure 6L

Material. One specimen, BC 57865, from the Akkol Member, Locality 827.

Remarks. Only the pedicle exterior can be seen of the solitary specimen, which is in a limestone, and it is not certain whether it is only a ventral valve or a pair of conjoined valves. Regardless, it clearly shows the distinctive ornament of costellae interrupted by rugellae so characteristic of *Rugosowerbyella*, a subgenus that is widespread in the Upper Ordovician. The subgenus also occurs in the uppermost mid Ashgill Chokpar Formation of the Chu-Ili Range (Nikitin *et al.* 1980, p. 49), where it is recorded as *Sowerbyella* (*Rugosowerbyella*) cf. *ambigua* (Reed). Although never common, the subgenus occurs in the Ashgill Boda Limestone of Sweden (Cocks 2005), as well as in the Laurentian margins of Scotland and Ireland (Mitchell 1977) and the deeper-water Ashgill *Foliomena* Fauna of Poland (Mergl 1990), where it is recorded as *R.* cf. *rosettana* (Henningsmoen 1948). Henningsmoen's species, which originally came from the Kullatorp Core in Sweden, requires revision.

Genus GUNNINGBLANDELLA Percival, 1979

Type species. *Gunningblandella resupinata* Percival, 1979, from the Caradoc of New South Wales, Australia.

Gunningblandella sp.
Plate 5, figures 22–23, 26

Material. BC 57710, external mould of conjoined valves, L, 8·6; W, 14·5, Locality 828; and BC 57712, ventral internal mould, L, 8·2; W, 13·1; Ml, 2·6; Mw, 3·1, Locality 832, both Degeres Member.

Remarks. This distinctive sowerbyelline, the only one to show resupination in the subfamily (Cocks and Rong 2000), was previously only known from the type locality of its type species. Although certainly referable to the

genus, the Degeres material appears to represent a species different from that from Australia because of the presence of a distinctive uniplicate anterior commissure. However, the absence of dorsal interiors from our Dulankara collections precludes the erection of a new species.

Suborder TRIPLESIIDINA Moore, 1952
Superfamily TRIPLESIOIDEA Schuchert, 1913
Family TRIPLESIIDAE Schuchert, 1913

Genus PLACOTRIPLESIA Amsden, 1968

Type species. *Triplecia praecipta* Ulrich and Cooper, 1936, from the Wenlock St Clair Limestone of Arkansas, USA.

Placotriplesia sp.
Plate 6, figures 1, 5

Material. Four ventral valves including BC 57832, from the Akkol Member, Localities 219 and 827.

Remarks. The ventral valve has a wide, flat pseudodeltidium lacking a monticulus and with a median sulcus originating at some distance from the umbo. This is the second known record of the genus in the Upper Ordovician. The only other Ordovician species is *Placotriplesia spisa* Popov, Cocks and Nikitin, 2002, from the underlying lower Caradoc Anderken Formation of the Chu-Ili Range. The latter species is considerably smaller and has a posteriorly erect ventral beak, whereas the specimens from the Akkol Member have a relatively low and broad ventral interarea. Similar, but as yet undescribed, shells of *Placotriplesia* are also known from the upper Caradoc–lower Ashgill Angrensor Formation of north-eastern central Kazakhstan.

Genus GRAMMOPLECIA Wright and Jaanusson, 1993

Type species. *Grammoplecia triplesioides* Wright and Jaanusson, 1993, from the Middle Ashgill Boda Limestone of Dalarna, Sweden.

Grammoplecia subcraegensis (Rukavishnikova, 1956)

Material. Otar Member Locality 543a (BC 56762), Degeres Member Locality 125 (BC 56765–66, 57775).

Remarks. Rukavishnikova originally described this species within *Oxoplecia*, but Wright and Jaanusson (1993, p. 104) correctly ascribed the species to their new genus *Grammoplecia*. Rukavishnikova's original type locality (1956) lies in the Degeres Member on the west side of the Kopalysai River. Specimens from both the Otar and Degeres members from the Chu-Ili Range were illustrated by Popov *et al.* (2000, pl. 1, figs 9–11), and thus the species is not refigured here.

Genus OGMOPLECIA Wright and Jaanusson, 1993

Type species. *Triplecia plicata* Wiman, 1907, from the Ashgill of Öland, Sweden.

EXPLANATION OF PLATE 5

Fig. 1. *Bandaleta* cf. *plana* Nikitin and Popov, Akkol Member, Locality 827. BC 57859, dorsal exterior; ×2.

Figs 2–12. *Metambonites subcarinatus* sp. nov., Degeres Member. 2, BC 12909, Locality 829, dorsal internal mould; ×3. 3, 6, BC 57734, Locality 829, dorsal internal mould and latex cast of interior; ×2. 4–5, BC 12914, Locality 835a, dorsal and ventral views of conjoined valves; ×3. 7, BC 57733, Locality 828, holotype, ventral and dorsal internal moulds; ×3. 8–9, BC 57735, Locality 829, dorsal and ventral views of conjoined valves; ×4. 10, BC 57731, Locality 546, ventral internal mould of juvenile specimen; ×4. 10, 12, BC 57732, Locality 546, latex cast of ventral interior, ×3, and ventral internal mould, ×2.

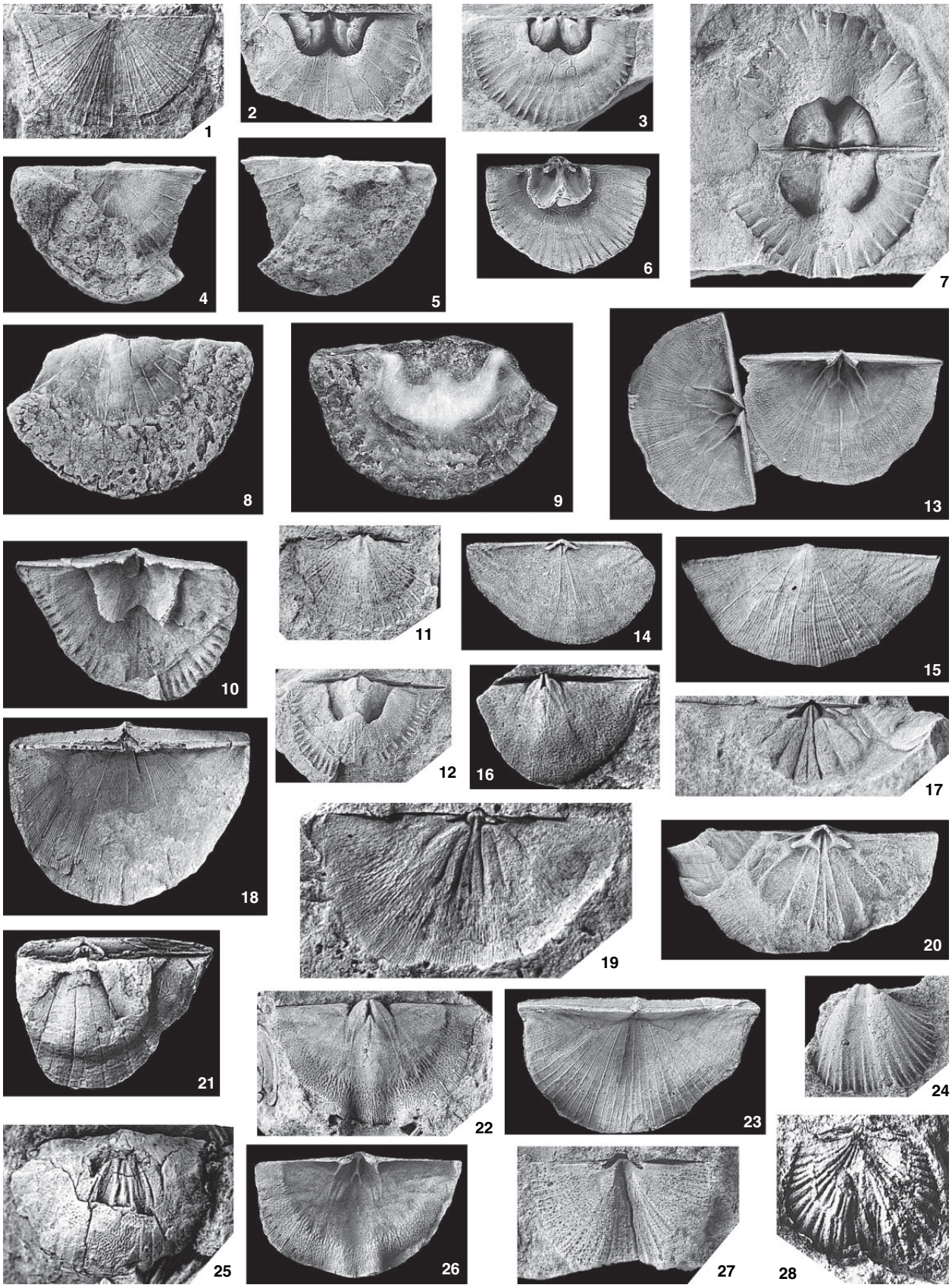
Figs 13–14. *Sowerbyella* (*Sowerbyella*) *akdombakensis* Klenina, Degeres Member, Locality, 132. 13, BC 87701, 87702, latex casts of interiors of ventral valves; ×2. 14, BC 57707, latex cast of dorsal interior; ×2.

Figs 15–21. *Sowerbyella* (*Sowerbyella*) *ampla* (Nikitin and Popov), Degeres Member. 15, BC 57709, Locality 546, latex cast of ventral exterior; ×4. 16, BC 57711, Locality 828, ventral internal mould; ×2. 17, 20, BC 57714, Locality 836, dorsal internal mould and latex cast of dorsal interior; ×3. 18, BC 57713, Locality 832, latex cast of dorsal exterior; ×3. 19, specimen missing, dorsal internal mould; ×3. 21, BC 57706, Locality 828, dorsal external mould of conjoined valves; ×2. 25, BC 57705, Locality 546, ventral view of conjoined valves showing median and side septa inside a broken shell; ×2.

Figs 22–23, 26. *Gunningblandella* sp., Degeres Member. 22, 26, BC 57712, Locality 832, ventral internal mould and latex cast of ventral interior; ×3. 23, BC 57710, Locality 828, latex cast of dorsal internal mould; ×3.

Fig. 27. *Anoptambonites kovalevskii* Popov, Nikitin and Cocks, Degeres Member, Locality 829, BC 57744, dorsal internal mould of juvenile specimen; ×3.

Figs 24, 28. *Epitomyonia* sp., Degeres Member. 24, BC57617, Locality 828a, ventral internal mould; ×5. 28, BC 57826, Locality 546, dorsal external mould; ×6.



POPOV and COCKS, Ordovician brachiopods

Ogmoplecia nesca sp. nov.
Plate 6, figures 2–4, 6–9

Derivation of name. Latin *nescus*, ignorant.

Holotype. BC 57777, Plate 6, figures 2–3, 6, internal moulds of conjoined valves, Degeres Member, Locality 828.

Material. Four complete shells, six ventral and four dorsal valves. Degeres Member, Localities 546, 828 (BC 57618, 57777–78), 828a (BC 57776), 856 (BC 57779), 858.

Diagnosis. Medium size for the genus, with transverse, flattened, dorsibiconvex shell of subpentagonal outline ornamented with three strong, simple angular ribs in the ventral sulcus, four in the dorsal median fold and 6–14 on the flanks of both valves.

Description. Shell dorsibiconvex transverse, subpentagonal in outline, about 60–75 per cent as long as wide, with the maximum width near mid-length, and about 40 per cent as thick as long. Anterior commissure uniplicate. Ventral valve very gently convex with low, apsacline interarea and small apical foramen. Pseudodeltidium flat with monticulus. Ventral sulcus originating in the umbonal area and with steep, smooth lateral slopes terminating in a low nearly rectangular tongue about half maximum shell width. Dorsal valve moderately convex with a low, flat median fold originating at umbo. Radial ornament coarsely costate with three ribs in ventral sulcus, four on dorsal median fold and 6–14 on flanks of both valves. Concentric ornament of fine, regular concentric filae, about 8 per mm.

Ventral interior with small teeth: subpentagonal muscle field slightly transverse and about one-third valve length. Dorsal interior with forked cardinal process on a low massive staff; low, short, blade-like socket ridges and small adductor field bisected by a median ridge about 25 per cent as long as valve.

Remarks. This species differs from *Ogmoplecia plicata* (Wiman, 1907) from the Ashgill of Öland (Wright and Jaanusson 1993) and the Ashgill of Taimyr, Arctic Russia (Cocks and Modzalevskaya 1997), in having a less convex lateral profile in both valves, and a costate (rather than costellate) ornament of simple angular ribs completely lacking bifurcations. There are invariably four ribs on the dorsal median fold and three ribs in the ventral sulcus.

Superfamily ORTHOIDEA Woodward, 1852
Family HESPERORTHIDAE Schuchert and Cooper, 1931

Genus DOLERORTHIS Schuchert and Cooper, 1931

Type species. Orthis interplicata Foerste, 1909, from the Upper Llandovery Osgood Formation of Indiana, USA.

Dolerorthis sp.
Plate 6, figures 11–12

Material. One pair of conjoined valves, three ventral and two dorsal valves, including BC57846, a ventral internal mould and BC 57847, a dorsal exterior, from the Akkol Member, Locality 827.

Remarks. Dolerorthis sp. resembles *Dolerorthis pristina* Popov, Cocks and Nikitin, 2002 from the lower–middle Caradoc Anderken Formation of the Chu-Ili Range and also *Dolerorthis* aff. *hubeiensis* Zeng (Nikitin *et al.* 1996) from the Dulankarinian carbonate mud mound in northern Betpak-Dala, Kazakhstan, in having a weakly ventribiconvex,

EXPLANATION OF PLATE 6

Figs 1, 5. *Placotriplesia* sp., Akkol Member, Locality 827. BC 57832, ventral valve exterior and posterior view showing flat pseudodeltidium lacking a monticulus; ×2.

Figs 2–4, 6–9. *Ogmoplecia nesca* sp. nov., Degeres Member. 2, 3, 6, BC 57777, Locality 828, holotype, internal mould of conjoined valves, lateral, dorsal and anterior views; ×2. 4, BC 57779, Locality 856, ventral valve exterior; ×2. 7–8, BC 57618, Locality 828, internal mould of conjoined valves ventral and dorsal views; ×2. 9, BC 57618, Locality 828, latex cast of ventral exterior; ×2.

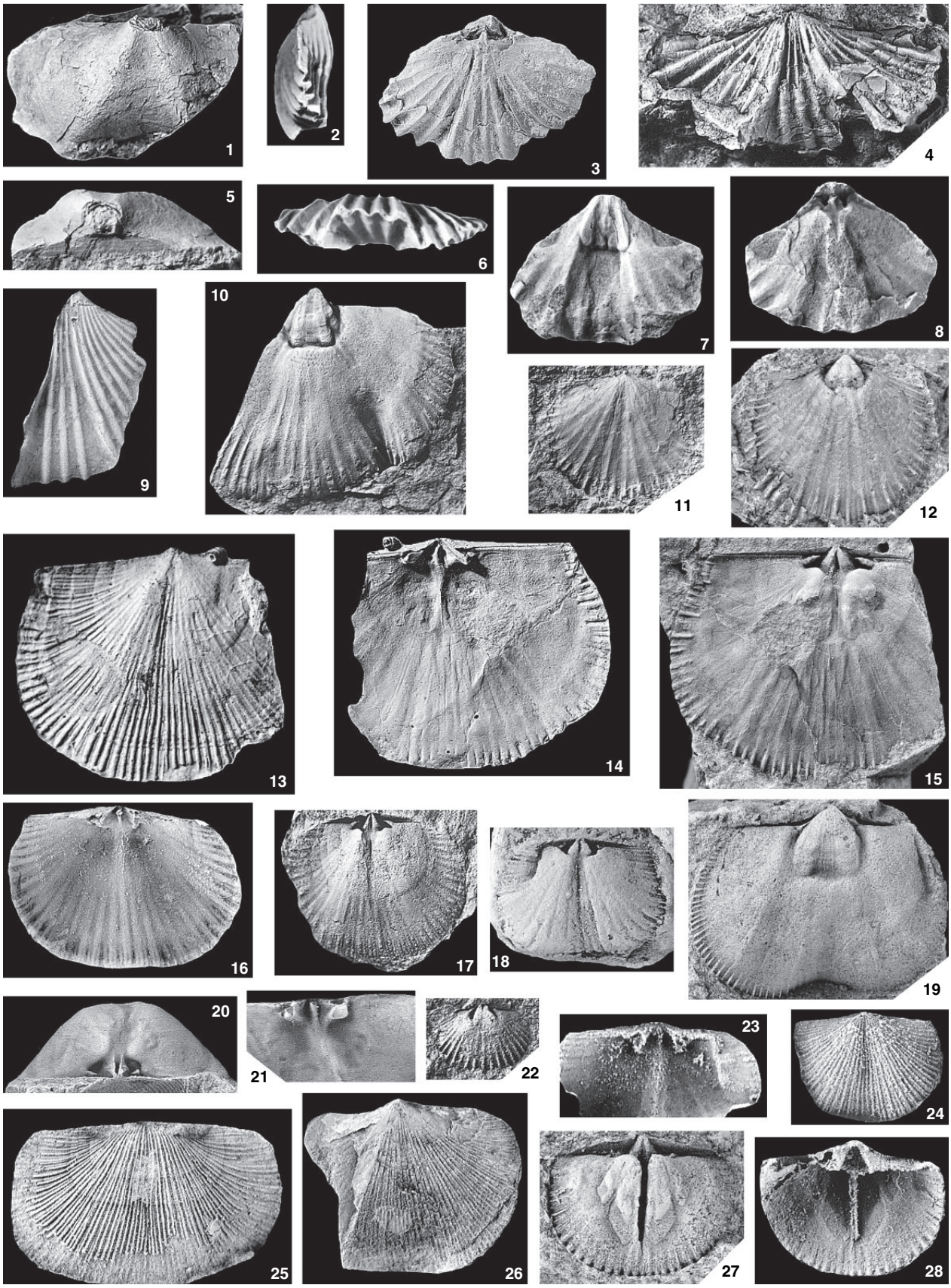
Figs 10, 13–17. *Plectorthis licta* sp. nov., Degeres Member. 10, BC 57830, Locality 828a, ventral internal mould; ×2. 13–15, BC 57753, Locality 828, holotype, latex casts of dorsal exterior and interior, dorsal internal mould; ×2. 16, BC 57611, Locality 828a, latex cast of dorsal interior; ×3. 17, BC 57831, Locality 828, dorsal internal mould; ×2.

Figs 11–12. *Dolerorthis* sp., Akkol Member, Locality 827. 11, BC 57847, exfoliated dorsal valve exterior; ×2. 12, BC 57846, ventral internal mould; ×2·5.

Figs 18, 22–23. Orthoidea family and genus indet., Degeres Member. 18, 23, BC 57616, Locality 546, dorsal internal mould, ×4, and latex cast of dorsal interior, ×6. 22, BC 57825, Locality 828, dorsal internal mould; × 4.

Figs 19–21, 25–26. *Weberorthis brevis* (Rukavishnikova), Degeres Member. 19, BC57749, Locality 135, ventral internal mould; ×2·5. 20–21, BC 57751, Locality 855, latex cast of dorsal interior showing cardinalia, ×3, and posterior view of dorsal internal mould, ×2. 25, BC 57613, Locality 136, latex cast of dorsal exterior; ×3. 26, BC 56774, Locality 855, ventral valve exterior; ×2·5.

Figs 24, 27–28. *Phragmorthis* sp., Degeres Member, Locality 858. 24, BC 57615, latex cast of dorsal exterior; ×4. 27–28, BC57614, latex cast of dorsal interior and dorsal internal mould; ×4.



POPOV and COCKS, Ordovician brachiopods

slightly transverse shell, ramicostellate radial ornament with about 35–40 costellae in mature specimens and a relatively small, elongate, subpentagonal, ventral muscle field. However, these shells differ from typical *Dolerorthis hubeiensis* Zeng, 1987, from the South China Terrane, in the absence of a ventral median ridge anterior of the muscle field. Inadequate preservation of the material and the absence of information on the dorsal interior makes precise taxonomic identification of the shells from the Akkol Member impossible.

Genus PTYCHOPLEURELLA Schuchert and Cooper, 1931

Type species. *Orthis bouchardi* Davidson, 1847, from the Wenlock, Much Wenlock Limestone Formation of Shropshire, England.

Ptychopleurella? sp.
Text-figure 6M–O

Material. BC 57834, conjoined valves, from the Akkol Member, Locality 827.

Remarks. The single specimen consists of biconvex conjoined valves with a procline ventral interarea with a narrow open delthyrium, a shallow, narrow dorsal median sulcus and slightly unequally ramicostellate radial ornament, all features characteristic of *Ptychopleurella*. It is comparable with *Ptychopleurella aleksandrovae* Nikitin and Popov, from the upper Caradoc – lower Ashgill carbonate mud mound in north Betkpak-Dala, central Kazakhstan (Nikitin *et al.* 1996), but differs in having the dorsal median sulcus terminating at the anterior margin and a weakly sulcate anterior commissure. The queried generic identification here is only because no interiors are known. The distinctive shape makes assignment to *Ptychopleurella* probable, even though the Dulankara specimen has a slightly different ornament from the type species.

Orthoidea family and genus indet.
Plate 6, figures 18, 22–23

Material. One pair of conjoined valves, five ventral and 11 dorsal valves from the Degeres Member, Localities 546, 828 (BC 57825, 57827), 828a, 829, 856 (BC 57616), and a dorsal valve from the Akkol Member, Locality 827.

Remarks. A few small impunctate orthoidean shells with fine ramicostellate or multicostellate ornament occur in the uppermost Degeres and Akkol members. Information on the interiors of both valves is inadequate, and the specimens probably belong to two or more separate taxa, but a few dorsal internal moulds show orthoid cardinalia, with diverging brachiophore bases and a simple, ridge-like cardinal process.

Superfamily PLECTORTHOIDEA Schuchert and Cooper, 1931
Family PLECTORTHIDAE Schuchert and Cooper, 1931

Genus PLECTORTHIS Hall and Clarke, 1892

Type species. *Orthis plicatella* Hall, 1847, from the Ashgill of Cincinnati, Ohio, USA.

Plectorthis licta sp. nov.
Plate 6, figures 10, 13–17; Text-figure 6F

Derivation of name. Latin *lictus*, abandoned.

Holotype. BC 57753, Plate 6, figures 13–15, internal and external moulds of dorsal valve, Degeres Member, Locality 828.

Material. Three complete shells, 17 ventral and 12 dorsal valves. Degeres Member, Localities 828 (BC 57753–54), 828a (BC 57611, 57752, 57755, 57829–31), 829, 855 (BC 57612), 858, 858a.

Diagnosis. Ventribiconvex shell about 75 per cent as long as wide, with maximum width at mid length, about 60–70 multicostellate ribs, subcarinate ventral valve and a weak dorsal sulcus fading anteriorly.

Description. Shell subequally biconvex, transverse and subrectangular in outline, about 75 per cent as long as wide. Hinge line slightly shorter than maximum width at mid length. Cardinal extremities rounded. Anterior commissure gently sulcate. Ventral valve subcarinate, gently convex in lateral profile, with maximum height at about one-third valve length from beak. Interarea low, apsacline, with open delthyrium. Dorsal valve gently convex with linear, orthocline interarea and shallow sulcus originating at umbo and fading anteriorly. Radial ornament slightly unequally multicostellate with first generation of ribs bifurcating at about 2–3 mm from umbo and with 4–7 ribs per 3 mm along anterior margin and about 60–70 costellae along anterior margin of mature specimens. Concentric ornament of fine, evenly spaced, elevated fila about 8–10 per mm.

Ventral interior with strong teeth supported by long, diverging, dental plates. Ventral muscle field transverse suboval, about 30 per cent as long as valve. Strongly impressed adductor scars divided by subtriangular diductor scar strongly raised anteriorly. Ventral mantle canals saccate with diverging vascula media. Dorsal interior with low notothyrial platform and subtriangular brachiophores with slightly diverging bases and deep sockets with fulcral plates. Ridge-like cardinal process with

crenulated myophore. Dorsal adductor muscle field small, subquadrate in outline, about 40 per cent as long as valve, divided medially by broad ridge. Mantle canal system lemniscate.

Remarks. This species resembles *Plectorthis equivalvis* Hall, but differs in having fine ribs bifurcating as close as 2–3 mm from the umbo, and a sulcate anterior commissure. *Plectorthis licta* can be distinguished from *Plectorthis scotica* (McCoy), from the Upper Ordovician (middle Caradoc) Craighead Limestone of Girvan, Scotland (Williams 1962), in having about twice as many ribs, which number more than 60 in mature specimens, a distinctly ventribiconvex lateral profile, and a weak dorsal sulcus fading anteriorly. It differs from *P.*? *tanshiensis* (Liang), revised by Zhan and Cocks (1998), in having a ventral valve with a less convex lateral profile, with maximum height posterior to mid length, a coarser radial ornament with only 4–7 ribs per 3 mm in mature specimens, and converging brachiophore bases. *P. licta* differs from *Plectorthis*? *burultasica* Popov, Cocks and Nikitin, 2002, from the underlying Anderken Formation of the Chu-Ili Range, in being twice as large, and in having a gently sulcate anterior commissure and a radial ornament with up to 70 bifurcating ribs, and in the absence of exopunctae.

Genus WEBERORTHIS gen. nov.

Type species. *Mimella brevis* Rukavishnikova, 1956, from the Dulankara Formation, Chu-Ili Range.

Derivation of name. In tribute to the late V. N. Weber, known for his pioneering studies of Ordovician trilobites from Kazakhstan.

Diagnosis. Shell strongly dorsibiconvex with uniplicate anterior commissure and relatively straight anterior margin subparallel to hinge line; ornament finely and evenly multicostellate; short dental plates continuing anteriorly into well-developed muscle-bounding ridges completely enclosing muscle field; bulbous cardinal process on high but narrow notothyrial platform linked to median ridge on which a fine septum is developed centrally; short brachiophores directed ventrolaterally; brachiophore bases convergent on to median ridge.

Remarks. The previously existing genera within the Plectorthidae have been revised by Williams and Harper (2000). None has the same combination of key characteristics as our new genus. *Hebertella* has a comparable external shape and ornament and similar entire ventral muscle-bounding ridges, but the brachiophore bases diverge and do not merge with the median septum, and the cardinal process is ridge-like rather than bulbous. None of the other genera has a strong uniplicate anterior commissure; however, *Doleroides*, although lacking a uniplicate commissure, is similarly ornamented, has entire muscle-bounding ridges and convergent brachiophore bases, but the last of these do not merge with the median septum. *Apollonorthis* has similar cardinalia, but the ornament is ramicostellate, the anterior commissure is weakly sulcate, and the muscle-bounding ridges do not enclose the muscle field. All the other genera in the family, *Plectorthis* itself, *Atlantida*, *Corineorthis*, *Desmorthis*, *Irhirea*, *Mimella*, *Oligorthis*, *Paterorthis*, *Pseudomimella*, *Schizophorella* and *Severginella*, are not nearly so similar to *Weberorthis* as those discussed above.

Weberorthis brevis (Rukavishnikova, 1956)
Plate 6, figures 19–21, 25–26

1956 *Mimella brevis* Rukavishnikova, p. 116, pl. 1, figs 1–2.
non 1984 *Mimella brevis* Rukavishnikova; Klenina, p. 45, pl. 1, fig. 9; pl. 3, figs 5, 8–13; pl. 4, figs 4–5, 9–18.
2000 *Hebertella*? *brevis* (Rukavishnikova); Popov, Nikitin and Cocks, p. 844, pl.1, figs 13–22.

Holotype. IGNA 1369/1, complete shell; Dulankara Formation, Zhartas River, near the town of Gornyi, Chu-Ili Range, Kazakhstan.

Material. One complete shell, 24 ventral and 30 dorsal valves. Degeres Member, Localities 132, 135 (BC 57749), 136 (BC 57613), 546, 826, 826a, 835 (BC 57866), 836, 838, 838a (BC 56763), 854, 855 (BC 56767, 56774, 57751), 857 (BC 57811), 857a (BC 57750). The Otar Member localities are in Popov *et al.* (2000).

Remarks. A revised diagnosis and a description of this species were provided by Popov *et al.* (2000), together with photographs of specimens from both the Otar and Degeres members. The three separate members of the Dulankara Formation cannot be recognised within the section at Rukavishnikova's type locality. Klenina's (1984) specimens, from the Upper Caradoc of the Taldyboi Formation of the Chinghiz Range, Kazakhstan, have a distinct dorsal sulcus and finer radial ornament, and are not congeneric with our Chu-Ili material.

Family CREMNORTHIDAE Williams, 1963

Genus PHRAGMORTHIS Cooper, 1956

Type species. *Pragmorthis buttsi* Cooper, 1956, from the Effna-Rich Valley Formation of Virginia, USA.

Phragmorthis sp.
Plate 6, figures 24, 27–28

Material. Degeres Member, Localities 132 (0:0:1) and 858, including BC 57614–15 (0:0:1).

Description. Shell transverse and suboval, about 75 per cent as long as wide, with maximum width at mid length. Cardinal extremities acute to near right-angled. Anterior commissure weakly sulcate. Dorsal valve gently and evenly convex with linear, orthocline interarea. Shallow dorsal sulcus originating at umbonal area. Radial ornament multicostellate, with 60–70 ribs and with about 5–6 ribs per 1 mm along anterior margin. Dorsal interior with simple, ridge-like cardinal process on low, subtriangular notothyrial platform and high, subtriangular brachiophores.

Remarks. These shells strongly resemble *Phragmorthis conciliata* Popov, 1985, from the underlying lower–middle Caradoc Anderken Formation of the Chu-Ili Range, in the general shape, radial ornament and interior of the dorsal valve, but differ in their weakly developed dorsal sulcus, which fades anteriorly.

Family PLAESIOMYIDAE Schuchert, 1913

Genus BOKOTORTHIS Popov, Nikitin and Cocks, 2000

Type species. *Schizophorella kasachstanica* Rukavishnikova, 1956, from the Dulankara Formation, Chu-Ili Range.

Bokotorthis kasachstanica (Rukavishnikova, 1956)

1956 *Schizophorella kasachstanica* Rukavishnikova, p. 118, pl. 1, figs 3–4.
2000 *Bokotorthis kasachstanica* (Rukavishnikova); Popov *et al.* 2000, p. 848, pl. 2, figs 11–18.

Holotype. IGNA 1369/3, complete shell; Dulankara Formation, from about 3 km south-east of the Bokot Well, southern Chu-Ili Range.

Material. CNIGR 33/12375, ventral valve exterior, and a dorsal valve from Locality 827, Akkol Member, Dulankara Mountains.

Remarks. Description and discussion of this species, including illustrations of a specimen from the Akkol Beds and several from the Otar Member, were provided by Popov *et al.* (2000) and are not repeated here. The detailed position of the Bokot Well is not known precisely: the well does not exist any longer and Rukavishnikova's material was collected over 50 years ago; hence, the member from which the holotype came is unknown.

Superfamily DALMANELLOIDEA Schuchert, 1913
Family DICOELOSIIDAE Cloud, 1948

Genus EPITOMYONIA Wright, 1968

Type species. *Epitomyonia glypha* Wright, 1968, from the Middle Ashgill Boda Limestone of Dalarna, Sweden.

Epitomyonia sp.
Plate 5, figures 24, 28

Material. One ventral internal mould, BC 57617, from Locality 828a, and one dorsal external mould BC 57826, from Locality 546, both Degeres Member.

Remarks. These specimens have the generically characteristic bilobed shell shape and are undoubtedly attributable to *Epitomyonia*. Although this genus is widespread and occurs on many Ordovician terranes, this is the first record of it from the Chu-Ili Terrane.

Dalmanelloidea gen. et sp. indet.
Text-figure 6P–Q

Material. BC 57827, conjoined valves, Locality 828; BC 57826, dorsal internal mould, Locality 546, both Degeres Member.

Remarks. These two specimens are certainly endopunctate, and therefore enteletoids or dalmanelloids; however, their generic position is indeterminate. They, and the two specimens of *Epitomyonia*, are the only dalmanelloids known from the Dulankara Formation; endopunctate orthides are very rare in the Caradoc of the whole of Kazakhstan.

Superfamily ANCISTRORHYNCHOIDEA Cooper, 1956
Family ANCISTRORHYNCHIDAE Cooper, 1956

Genus ALTAETHYRELLA Severgina, 1978

Type species. *Altaethyrella megala* Severgina, 1978, from the Ashgill of north-west Altai, Siberia, Russia.

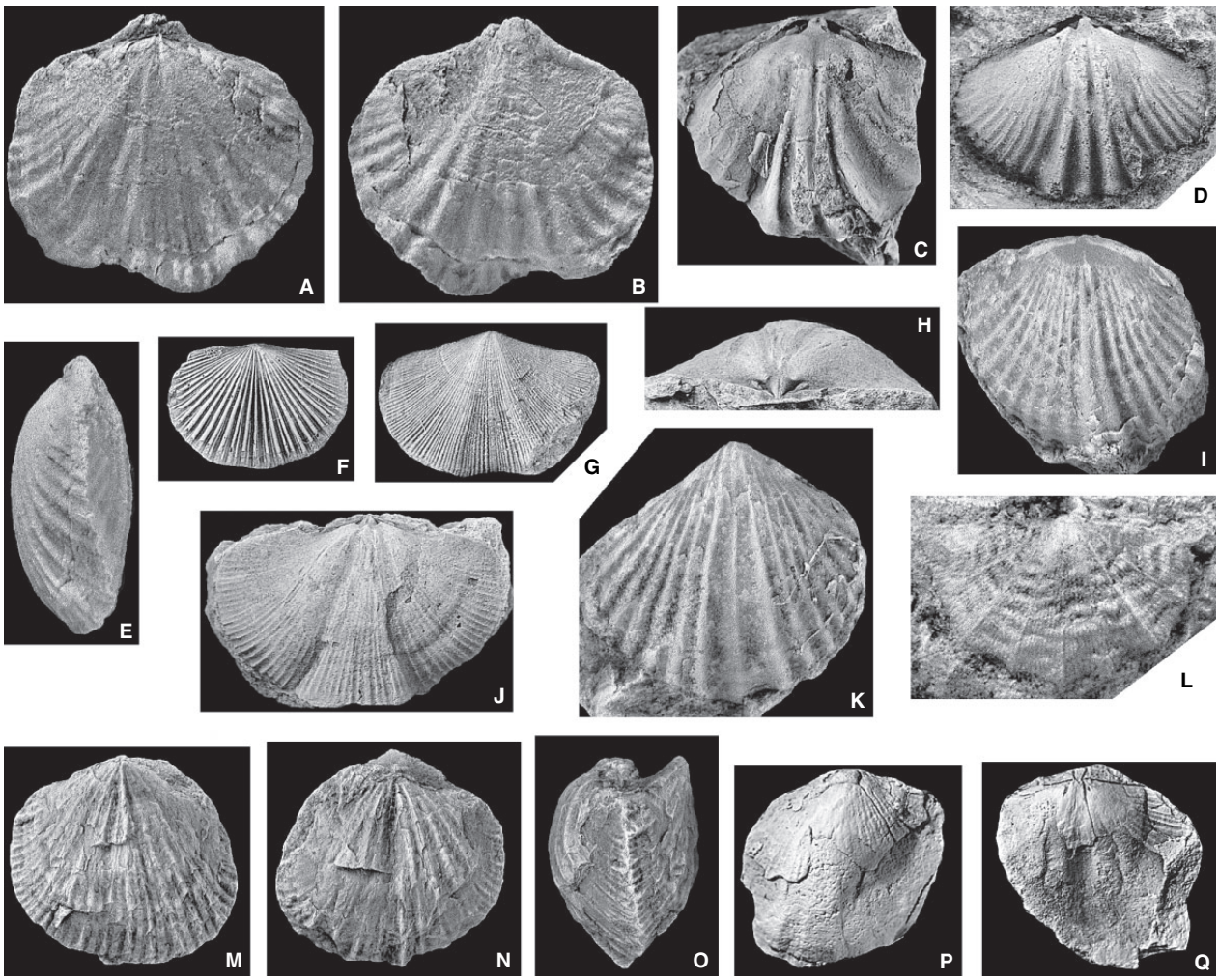
Altaethyrella otarica (Rukavishnikova, 1956)
Text-figure 6C–D

1956 *Rhynchotrema otarica* Rukavishnikova, p. 156, pl. 5, figs 6–10.
2000 *Altaethyrella otarica* (Rukavishnikova); Popov, Nikitin and Cocks, p. 862, pl. 4, figs 19–23.

Holotype. IGNA 1369/56 complete shell; Dulankara Formation, area about 3 km south-east of Bokot Well, southern Chu-Ili Range.

Material. 31 complete shells, 26 ventral and 24 dorsal valves. Degeres Member, Localities 132, 546 (BC 57780), 826a (BC 57781), 835, 836, 854, 857, 857a and 858a, and Akkol Member, Localities 119, 141, 219 and 827; all from the Dulankara Mountains. The material from the Otar Member is listed in Popov *et al.* (2000, p. 863).

Remarks. A synonymy is given in Popov *et al.* (2000) and a full description in Nikiforova and Popov (1981), in which the species was attributed to *Otarorhyncha*, a genus later placed within the synonymy of *Altaethyrella*. In Kazakhstan this species is widespread in the Upper Ordovician, including the Taldyboi Formation of the Chingiz Range (Klenina 1984), the Dulankara Formation of the Chu-Ili Range and the Upper Ashgill Archalyk Beds of Uzbekistan (Nikiforova and



TEXT-FIG. 6. A–B, E, *Eospirigerina pennata* (Rukavishnikova), Akkol Member, Locality 119, BC 57833, dorsal, ventral and lateral views of conjoined valves of juvenile specimen; ×4. C–D, *Altaethyrella otarica* (Rukavishnikova, 1956). C, BC 56777, dorsal internal mould, Otar Member, Locality 131; ×2. D, BC 57780, dorsal internal mould, Degeres Member, Locality 546; ×3. F, *Plectorthis licta* sp. nov., Degeres Member, Locality 855, BC 57612, latex cast of dorsal exterior; ×2. G–H, J, *Qilianotryma suspectum* (Popov), Degeres Member. G, BC 57784, latex cast of ventral exterior, Locality 136; ×2. H, J, BC 57795, dorsal internal mould in posterior and dorsal views, Locality 836; ×2. I, K, *Schachriomonia parva* (Rukavishnikova), Akkol Member, Locality 5 of T. B. Rukavishnikova. I, BC 57845, dorsal valve exterior; ×3. K, BC 57844, ventral valve exterior; ×3. L, *Rugosowerbyella* sp., Akkol Member, Locality 827, BC 57865, ventral valve exterior; ×8. M–O, *Ptychopleurella*? sp., Akkol Member, Locality 827, BC 57834, ventral, dorsal and lateral views of conjoined valves; ×4. P, Q, Dalmanelloidea gen. et sp. indet., Degeres Member, Locality 828, BC 57827, ventral and dorsal view of exfoliated conjoined valves; ×3.

Popov 1981). It also occurs in China (Zhan and Li 1998).

Order ATRYPIDA Rzhonsnitskaya, 1960
Superfamily ATRYPOIDEA Gill, 1877
Family ATRYPINIDAE McEwan, 1939

Genus EOSPIRIGERINA Boucot and Johnson, 1967

Type species. *Zygospira putilla* Hall, *in* Hall and Clarke 1895, from the Ashgill of eastern USA.

Eospirigerina pennata (Rukavishnikova, 1956)
Text-figure 6A–B, E

1956 *Plectatrypa pennata* Rukavishnikova, p. 160, pl. 5, figs 12–13.
1999 *Eospirigerina pennata* (Rukavishnikova, 1956); Popov *et al.*, p. 630, pl. 1, figs 1–6, text-fig. 4.

Holotype. IGNA 1369/52 complete shell; Dulankara Formation, Akkol Member, Akdalasai River, southern Chu-Ili Range, Kazakhstan.

Material. 26 complete shells, five ventral and two dorsal valves from the Akkol Member, Localities 119 (BC 57833, 57800, 58253–4), 141, 219, 827, Dulankara Mountains.

Remarks. This species was re-described and illustrated by Popov *et al.* (1999, p. 630), who listed the other occurrences in Kazakhstan.

Genus QILIANOTRYMA Xu, *in* Jin et al. 1979

Type species. *Qilianotryma mirabile* Xu, *in* Jin et al. 1979, from the Ashgill of Qinghai, China.

Qilianotryma suspectum (Popov, *in* Nikiforova *et al*. 1982)
Text-figure 6G–H, J

1956 *Cliftonia* ex gr. *spirigeroides* (M'Coy); Rukavishnikova, p. 51, pl. 4, figs 14–15.
1982 *Euroatrypa suspecta* Popov, *in* Nikiforova *et al.*, p. 57, pl. 6, figs 9–12.
1999 *Qilianotryma suspectum* (Popov); Popov *et al.*, p. 634, pl. 1, figs 11–15.

Holotype. CNIGR Museum 25/11943, conjoined valves, Locality 827, Akkol Member.

Material. 16 complete shell, 39 ventral and 21 dorsal valves. Degeres Member, Localities 132 (BC 57783), 135, 136 (BC 57782, 57784–88), 546, 826a (BC 57789–90), 828a (BC 57791), 829 (BC 57792–94), 832, 835, 836 (BC 57795), 838, 838a (BC 57796–99), 854–857, 857a, 858, 858a; Akkol Member, Localities 219 and 827.

Remarks. A detailed description of this species was provided by Nikiforova *et al.* (1982) and Popov *et al.* (1999). Some specimens from the type area are illustrated here.

Genus SCHACHRIOMONIA Nikiforova, 1978

Type species. *Schachriomonia schachriomonica* Nikiforova, 1978, from the Ashgill of Uzbekistan.

Schachriomonia parva (Rukavishnikova, 1956)
Text-figure 6I, K

1956 *Zygospira parva* Rukavishnikova, p. 162, pl. 5, figs 14–16.
1999 *Schachriomonia parva* (Rukavishnikova, 1956); Popov, Nikitin and Sokiran, p. 635, pl. 2, figs 1–9.

Holotype. IGNA 1369/64, Akkol Member.

Material. 19 complete shells, one dorsal and five ventral valves from the Akkol Member, Localities 119, 141 (BC 57835–37), 827, and Rukavishnikova Locality 5, the type locality (BC 57838–45). For other occurrences in Kazakhstan, see Popov *et al.* (1999).

Remarks. A detailed description of this species was provided by Popov *et al.* (1999). Our illustrated specimens are topotypes, kindly donated by Dr T. B. Rukavishnikova.

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