

A low diversity shallow water lingulid brachiopod-gastropod association from the Upper Ordovician of Kyrgyz Range

LEONID E. POPOV, JAN OVE R. EBBESTAD, AMANBEK MAMBETOV,
and FARID KH. APAYAROV



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A low diversity association made up of the lingulid *Tunisiglossa almalensis* Popov and Mambetov, sp. nov. and the gastropod *Ptychonema agyris* Ebbestad, sp. nov. is described from the Upper Member of the Almaly Formation at Kyrgyz Range, North Tien Shan, Kyrgyzstan/Kazakhstan. The specimens co-occur in dense coquinas, made up of different sized individuals, deposited in a shallow water, intertidal, and storm driven depositional environment. The lingulid shells display a completely reduced dorsal pseudointerarea typical of Glossellinae, and the smooth shell lacking fine external granulation, radial or pitted ornament, a small ventral pseudointerarea, and no dorsal median ridge place it in the hitherto monotypic *Tunisiglossa* known previously only from the Lower Ordovician (Tremadocian) Sanhar Formation of Libya. It compares with *Ectenoglossa sorbulakensis* that is widespread in the lower to middle Caradocian Anderken Formation of Chu-Ili Range in southern Kazakhstan. Gastropods of this age have not been reported earlier in Kyrgyzstan; neither can *Ptychonema* be compared with any taxon in the gastropod association earlier described from the contemporary Anderken Formation in Kazakhstan. *Ptychonema* is otherwise commonly associated with peri-Gondwana terranes, but the Late Ordovician dispersal pattern of the genus is unknown. Overall, however, the Upper Ordovician faunas of North Tien Shan show close similarities to contemporaneous faunas of the Chu-Ili terrane, which have strong biogeographic signatures linking them to the faunas of South and North China.

Key words: Brachiopoda, Gastropoda, Lingulida, Ordovician, Kazakhstan, Kyrgyzstan, Almaly Formation, palaeobiogeography, North Tien Shan.

Leonid E. Popov [Leonid.Popov@museumwales.ac.uk], Department of Geology, National Museum of Wales, Cathays Park, CF10 3NP, Cardiff, UK;

Jan Ove R. Ebbestad [jan-ove.ebbestad@pal.uu.se], Department of Earth Sciences, Program of Palaeobiology, Norbyvägen 22, S 752 36 Uppsala, Sweden;

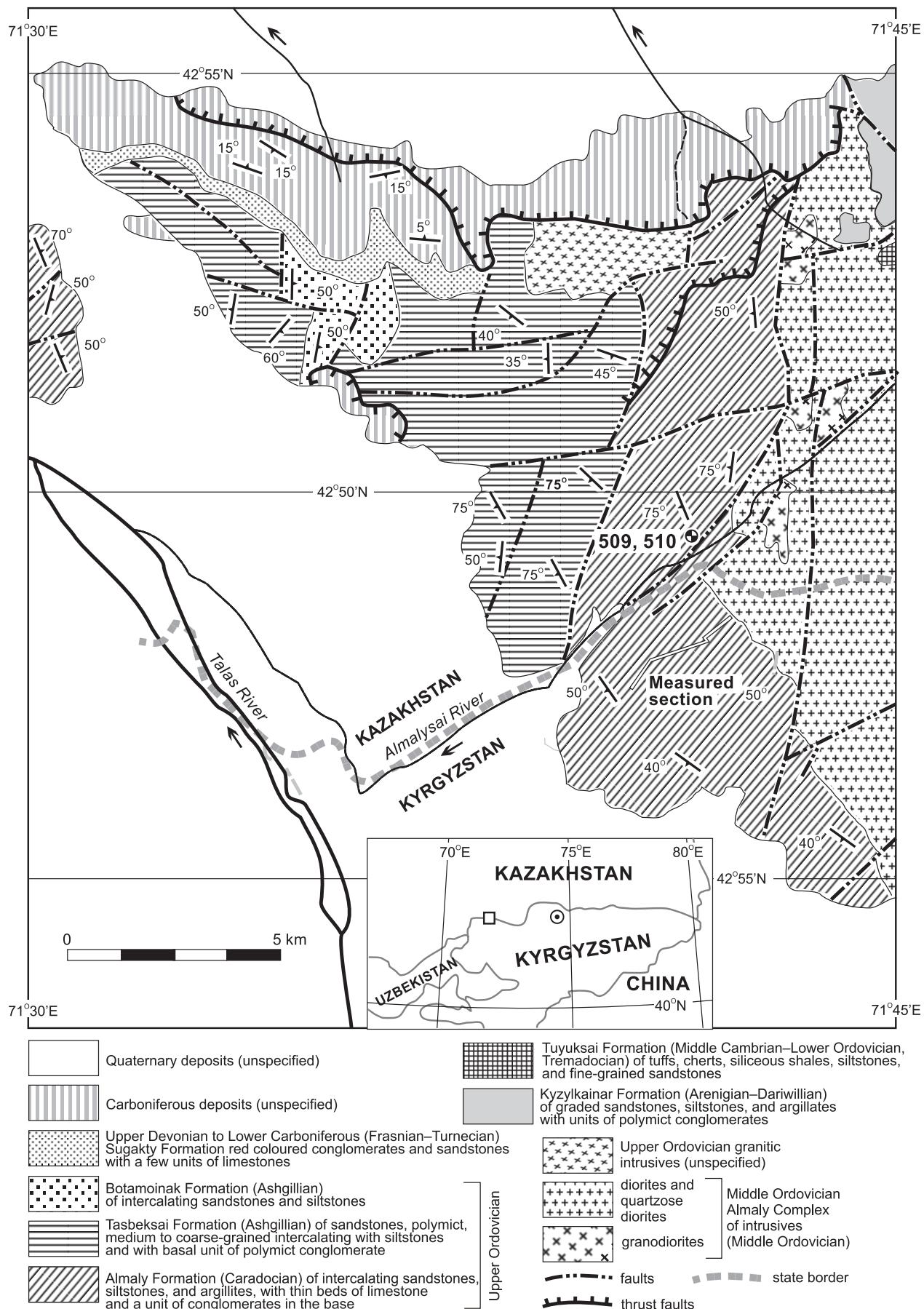
Amanbek Mambetov, and Farid Kh. Apayarov [apayarov@mail.ru] North Kyrgyzian Geological Survey, the State Agency of Geology and Mineral Resources, Ivanovka, 722221, Kyrgyzstan.

Introduction

Central Asia is an amalgamation of accreted terranes (Şengör and Natal' in 1996), the juxtaposition of which during the Palaeozoic is a matter of dispute. Critical faunal evidence is still in much demand to resolve original positions, a need to which this report of a Late Ordovician low diversity lingulid brachiopod-gastropod association from Kyrgyzstan contributes. The Upper Ordovician brachiopod fauna of Kyrgyz Range, North Tien Shan is known mainly from a single publication by Misius (1986) but there are no previous reports of gastropods. The present study describes a low diversity faunal association from the Upper Member of the Almaly Formation, including a lingulid *Tunisiglossa almalensis* Popov and Mambetov, sp. nov. and a gastropod *Ptychonema agyris* Ebbestad, sp. nov.

The Upper Ordovician (lower to middle Caradocian) Almaly Formation is exposed in the Almalsai basin, the eastern tributary of the Talas River, on the southern slope of Kyrgyz Range on both sides of the border between Kyrgyzstan and Kazakhstan (Fig. 1). Here it rests unconformably on granodiorites of the Almaly Complex intrusives, that have a U-Pb zircon date of 464 Ma (Kiselev 1999). The best section of the Almaly Formation is exposed between the Tuleusai and Almalsai rivers southwest of the height 1194.4 m on the Kyrgyz side of the border where it can be subdivided into two members (Fig. 2).

The basal 510 m of the Lower Member is made up of intercalating lilac and brownish-red sandstones with some units of conglomerates, while alternating lilac and green siltstones and argillites with some units of fine-grained sandstones are found in the upper 480 m. The Upper Member of



← Fig. 1. Geological map of the western part of Kyrgyz Range (after Farid Kh. Apayarov and Matevi M. Gutermakher, unpublished) showing position of the measured sections and fossil localities. This mountainous area is a central part of the North Tien Shan mountain system, which is a series of parallel south-southwest to east-northeast ranges stretching for about 2500 km from Turkestan in the west to northern China in the east. Black arrows indicate direction of water flow in tributaries and rivers; 509 and 510 are fossil localities.

the Almaly Formation is about 795 m thick, and consists of intercalating greenish-grey siltstones and argillites with some units of fine grained sandstone and argillaceous limestone. The uppermost unit of the Lower Member and the Upper Member contain several fossiliferous horizons with low diversity benthic fauna represented mainly by lingulids and gastropods (Fig. 2).

The uppermost part of the Amaly Formation is well exposed on the Kazakh side of the border on the east side of the Nogaisai Rivulet, about 5.25 km north-east (azimuth 15°NE) of the zero point of the measured section, where Olga I. Nikitina (personal communication 2003) identified the brachiopods *Eodalmanella extra* Popov, 1985 and *Mabellia conferta* (Popov, 1985), as well as the trilobite *Lonchodus tecturmasi* Weber, 1948, characteristic also of the lower to middle Caradocian Anderken Formation of the Chu-Ili Range in southern Kazakhstan (Popov et al. 2002).

The best fossiliferous exposures of the Upper Member of the Almaly Formation on the northern side of Almalsay about 2 km south of the measured section (localities 509 with geographical coordinates 42°49'19"N, 71°41'27"E and 510 with geographical coordinates 42°49'20"N, 71°41'26"E, WGS 84) contain abundant, low diversity faunal assemblage represented by a single lingulid species *Tunisiglossa almalensis* and the gastropod *Ptychonema agyris*.

Institutional abbreviations.—BMNH, Natural History Museum, London, UK; NMW (accession number 98.66G), National Museum of Wales, Cardiff, UK.

Other abbreviations.—Abbreviations in tables of measurements and in the text are: Lv, Ld, maximum sagittal ventral and dorsal valve length; W, maximum width; Iw, width of pseudointerarea; VI, length of visceral area; X, mean; S, standard deviation from the mean; min, minimum value; max, maximum value; N, number of measured or counted specimens. Measurements of whorl expansion rate (W) are based on Raup (1966). Inclination (E) of the whole apertural plane refers to elevation angle of Vermeij (1971).

Systematic palaeontology

Morphological terminology and taxonomic classification of the lingulid brachiopod follow Holmer and Popov (2000) in the revised volumes of the *Treatise on Invertebrate Paleontology*. Terminology and classification of the gastropod follows mainly that of Wagner (2002).

Formation	Member	Unit	Subunit	Thickness (m)	Lithology
Almaly Formation (Upper Ordovician, Caradoc)					
Upper Member (795 m)					
Unit 2 (300 m)					
1–5	6–7	8–9	10	11	12–14
Unit 1 (510 m)					
Unit 2 (480 m)					
1–5	6–7	8–9	10	11	12–14
Lower Member (990 m)					
Unit 2 (480 m)					
1–5	6–7	8–9	10	11	12–14
Unit 1 (510 m)					
1–5	6–7	8–9	10	11	12–14
Almaly Formation (Upper Ordovician, Caradoc)					
Upper Member (795 m)					
Unit 2 (495 m)					
1–5	6–7	8–9	10	11	12–14
Unit 1 (510 m)					
1–5	6–7	8–9	10	11	12–14
Lower Member (990 m)					
Unit 2 (480 m)					
1–5	6–7	8–9	10	11	12–14
Unit 1 (510 m)					
1–5	6–7	8–9	10	11	12–14
Almaly Formation (Upper Ordovician, Caradoc)					
Upper Member (795 m)					
Unit 2 (495 m)					
1–5	6–7	8–9	10	11	12–14
Unit 1 (510 m)					
1–5	6–7	8–9	10	11	12–14
Lower Member (990 m)					
Unit 2 (480 m)					
1–5	6–7	8–9	10	11	12–14
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1–5	6–7	8–9	10	11	12–14
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Unit 2 (495 m)					
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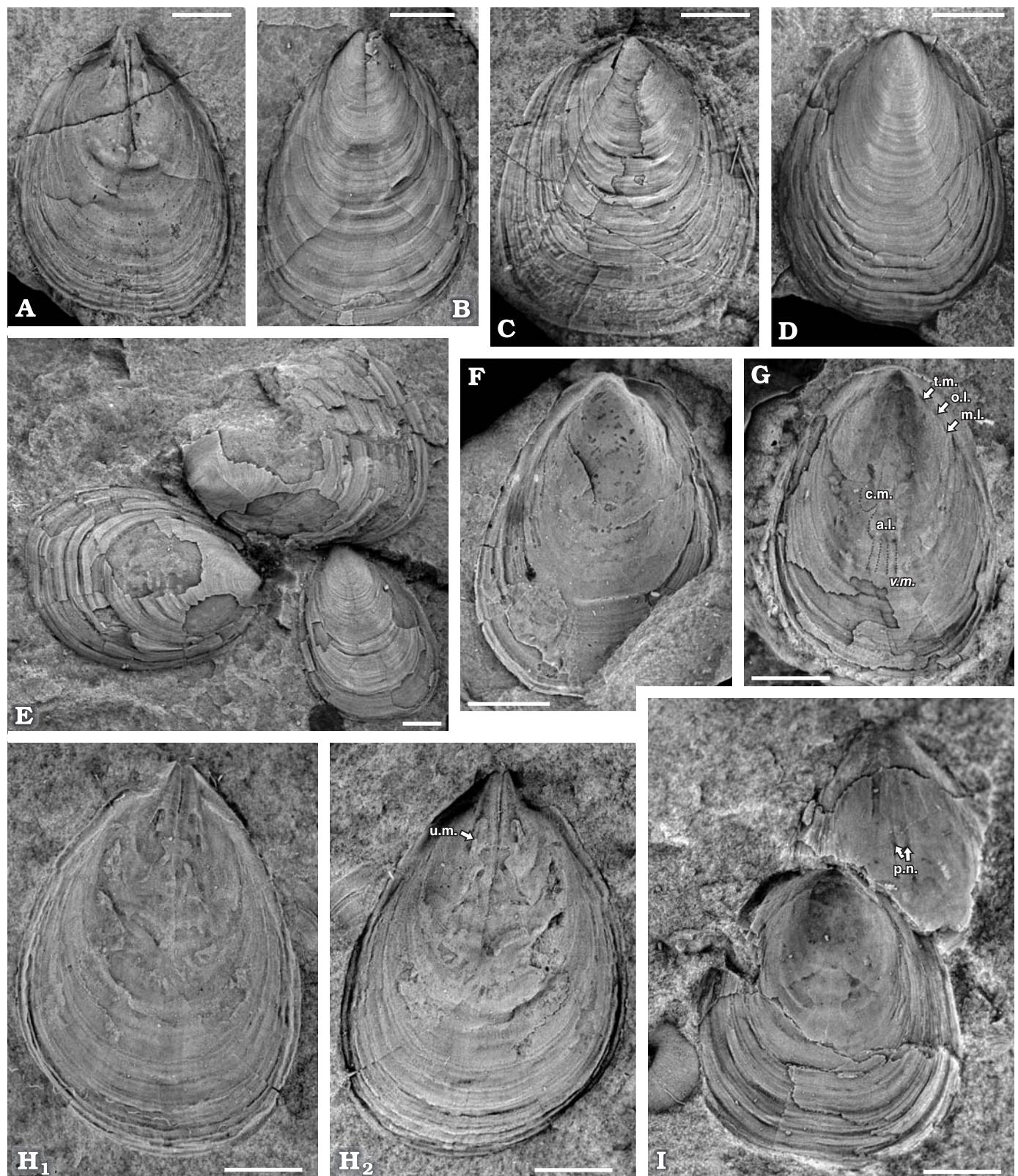


Fig. 3. The lingulid brachiopod *Tunisiglossa almalensis* Popov and Mambetov, sp. nov. from the Almaly Formation, Caradocian (Upper Ordovician) of Kyrgyz Range. **A.** NMW 98.66G.869, ventral internal mould. **B.** NMW 98.66G.871, ventral valve, exterior. **C.** NMW 98.66G.865, dorsal valve exterior. **D.** NMW 98.66G.866, dorsal valve, exterior. **E.** NMW 98.66G.860–862, cluster of three disarticulated valves on a bedding surface. **F.** NMW 98.66G.872, dorsal valve, interior, latex cast. **G.** NMW 98.66G.870, holotype, dorsal valve, interior, latex cast showing position of muscle scars (tm., transmedian; o.l., outside lateral; a.l., middle lateral; c.m., central; anterior lateral) and proximal parts of dorsal vascular media (v.m.). **H.** NMW 98.66G.873, ventral valve, exterior, latex cast (**H**₁) and ventral internal mould showing umbonal muscle scars (u.m.) (**H**₂). **I.** NMW 98.66G.867, ventral valve, interior showing position of pedicle nerve impression (p.n.) and NMW 98.66G.868, dorsal valve interior. Scale bars 2.5 mm.

Class Lingulata Gorjansky and Popov, 1985

Order Lingulida Waagen, 1885

Superfamily Linguloidea Menke, 1828

Family Obolidae King, 1846

Subfamily Glossellinae Cooper, 1956

Genus *Tunisiglossa* Massa, Havlíček, and Bonnefous, 1977

Type species: *Tunisiglossa tripolitanea* Massa, Havlíček, and Bonnefous, 1977; by original designation; Lower Ordovician, Tremadocian, Libya.

Tunisiglossa almalensis Popov and Mambetov, sp. nov.

Figs. 3, 4.

Derivation of the name: After the type locality near the Almalsai River.

Holotype: NMW 98.66G.870, Fig. 3G, dorsal internal mould ($L = 9.8$ mm; $W = 8.4$ mm; $VI = 6.2$ mm).

Type locality: Locality 509, northern side of Almalsai River, Kyrgyz Range, Kazakhstan.

Type horizon: Upper Member of Almaly Formation, Caradocian (Upper Ordovician).

Material.—The holotype and paratypes: 36 ventral and 42 dorsal valves from sample 509 (specimens NMW 98.66G.860–869; 871–945); 6 ventral and 4 dorsal valves from sample 510 (specimens NMW 98.66G.960–969).

Diagnosis.—A species of *Tunisiglossa* with a shell elongate oval in outline, about 140% as long as wide and a small ventral interarea less than half as wide as the valve; ventral interior with visceral area about half valve length bordered anteriorly by a low rim; ventral umbonal muscle scars paired, situated on the ends of slightly raised muscle scars; dorsal interior with long, slightly divergent *vascula media*; differs from *Tunisiglossa tripolitanea* Massa, Havlíček, and Bonnefous, 1977 in having a less elongated oval, not rectangular shell outline, well defined and slightly raised ventral umbonal muscle scars and a low rim bounding anteriorly a ventral visceral area.

Description.—Shell elongate oval to sub-rectangular, about 140% as long as wide with maximum width about mid-length. Ventral valve gently and evenly convex with the apical angle about 90–100°. Ventral pseudointerarea narrow, triangular, slightly less than half as wide as the valve, bisected by a narrow, deep pedicle groove. Ventral proparaeas raised above the valve floor, bearing well defined flexure lines. Dorsal valve evenly convex with a thickened posterior margin lacking pseudointerarea, slightly shorter than ventral valve, about 130% as long as wide. Larval and postlarval shell smooth, ornamented with fine growth lines.

Ventral valve interior with subtriangular visceral area about half valve length, bounded anteriorly by indistinct rim slightly raised above the valve floor and bisected by a pair of slightly divergent furrows representing a pedicle nerve impression (Fig. 3I). Umbonal muscle scars paired, forming elongate, slightly divergent muscle trucks on both sides of the pedicle nerve impression (Fig. 3H₁, H₂). Other muscle scars and mantle canals not impressed. Dorsal valve interior

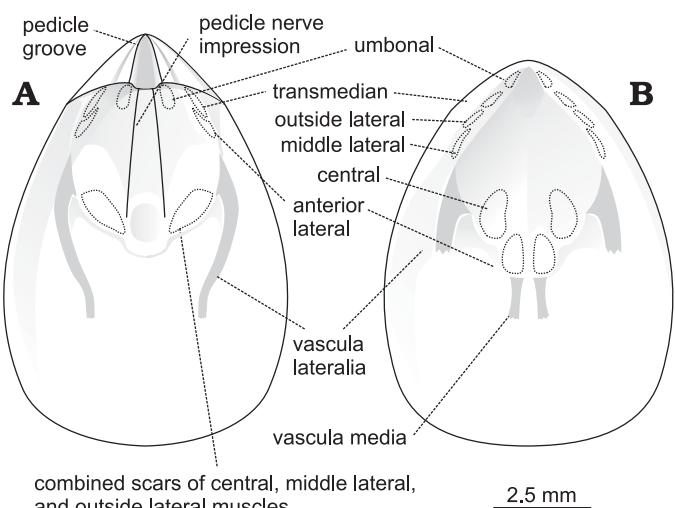


Fig. 4. The lingulid brachiopod *Tunisiglossa almalensis* Popov and Mambetov, sp. nov. from the Almaly Formation, Caradocian (Upper Ordovician) of Kyrgyzstan. Schematic representation of ventral (A) and dorsal (B) valve interior showing position of muscle scars, mantle canals and a pedicle nerve impression.

with visceral area about 55% as long as the valve. Scars of outside lateral, anterior lateral and middle lateral muscles situated on bands of slightly thickened shell along postero-lateral margins of the valve (Fig. 3G). Central muscle scars elongate suboval, situated on anterior terminations of fine, elongate subtriangular muscle tracks divergent from the apex. Small paired scars of anterior lateral muscles occupying a short anterior projection of dorsal visceral area. *Vascula media* long, slightly divergent.

Measurements (in mm).—Ventral valves: $Lv = 11.3$; $S = 1.42$; $\min = 8.5$; $\max = 13.4$; $N = 32$; $W = 8.3$; $S = 1.5$; $\min = 6.2$; $\max = 10.2$; $N = 32$; $Lv/W = 140\%$; $S = 15.2$; $\min = 115\%$; $\max = 181\%$. Dorsal valves: $Ld = 10.1$; $S = 1.25$; $\min = 8.4$; $\max = 13.8$; $N = 38$; $W = 8.5$; $S = 0.87$; $\min = 6.7$; $\max = 10.8$; $N = 38$; $Ld/W = 127\%$; $S = 9.0$; $\min = 112\%$; $\max = 148\%$; $VI/L = 54\%$; $S = 8.1$; $\min = 43.5\%$; $\max = 62\%$, $N = 5$.

Remarks.—The lingulid shells from the Almaly Formation have paired umbonal muscle scars, symmetrically arranged muscle scars in both valves and paired dorsal *vascula media* proving their assignation to the family Obolidae (Fig. 4). They are also characterised by the completely reduced dorsal pseudointerarea typical of Glossellinae. Among genera presently assigned to that subfamily only *Tunisiglossa* Massa, Havlíček, and Bonnefous, 1977 is characterised by a smooth shell lacking fine granulation on the shell surface, radial or pitted ornament, has very small ventral pseudointerarea and no dorsal median ridge (for details, see Holmer and Popov 2000). The only other known species of the genus is its type species *Tunisiglossa tripolitanea* Massa, Havlíček, and Bonnefous, 1977 from the Lower Ordovician, Tremadoc Sanhar Formation of Libya. *Tunisiglossa almalensis* differs from it in having a less elongated oval, rather than rectangular shell

outline, well defined and slightly raised ventral umbonal muscle scars and a low rim bounding anteriorly a ventral visceral area. It is likely that a simple shell morphology that characterises *Tunisiglossa* is more widely spread among the Ordovician obolides, and some poorly known taxa usually referred to *Ectenoglossa*, *Lingulella*, or *Pseudolingula* may belong to *Tunisiglossa*.

Tunisiglossa almalensis has some external similarity to *Ectenoglossa sorbulakensis* Popov, 1980 (see also Popov et al. 2002), that is widespread in the lower to middle Caradocian Anderken Formation of Chu-Ili Range in Southern Kazakhstan, however, the later species has more elongated shell and a fine dorsal median ridge.

Class Gastropoda Cuvier, 1797

Order Archaeogastroda Thiele, 1925

Family Holopeidae Wenz, 1938

Remarks.—Wagner (2002) emphasised a primitively expressed U-shaped sinus and simple growth lines for his “Holopeines” subclade within a “Raphistomatid” clade (informal notation, as indicated by the quotes; see Wagner 2002: 16). Traditionally, a number of Palaeozoic anisostrophically coiled gastropods showing these characters would be classified within the Late Cambrian to Early Ordovician Sinuopeidae Wenz, 1938. Many of these genera are now placed in the family Holopeidae Wenz, 1938 (e.g., *Raphistomina* Ulrich and Scofield, 1897; *Pachystrophia* Perner, 1903; *Sinutropis* Perner, 1903; *Umbospira* Perner, 1903; *Holopea* Hall, 1847), and all are younger than the late Arenigian (Wagner 2002). The genus discussed here, *Ptychonema* Perner, 1903, is placed in Holopeidae by association with morphologically similar mid Ordovician to Silurian genera with a U-shaped sinus; Horný (1997) placed it within Eotomariidae Wenz, 1938.

Genus *Ptychonema* Perner, 1903

Type species: *Ptychonema nigrum* Barrande in Perner, 1903: pl. 57: 16–19 and their figure caption; by monotypy. Middle Ordovician (Beroun) Zahorany Formation at Praha-Strašnice, Barrandian Area, Bohemia, Czech Republic.

Remarks.—Knight (1941) placed *Ptychonema* with some doubt in the synonymy of *Lophospira* Whitfield, 1886. The circumstances surrounding this decision are well explained by Knight (1941) and Horný (1997), and will not be repeated here. However, following studies of topotype material and similar specimens from the Anti-Atlas of Morocco, Horný (1997) was able to confidently re-establish the genus. Species of the genus are typically widely spread in the Early Palaeozoic Mediterranean Province, mainly from the Bohemian part of the Czech Republic, Armorica (Spain, Portugal, and France), and Anti-Atlas, Morocco (see Horný 1997 for

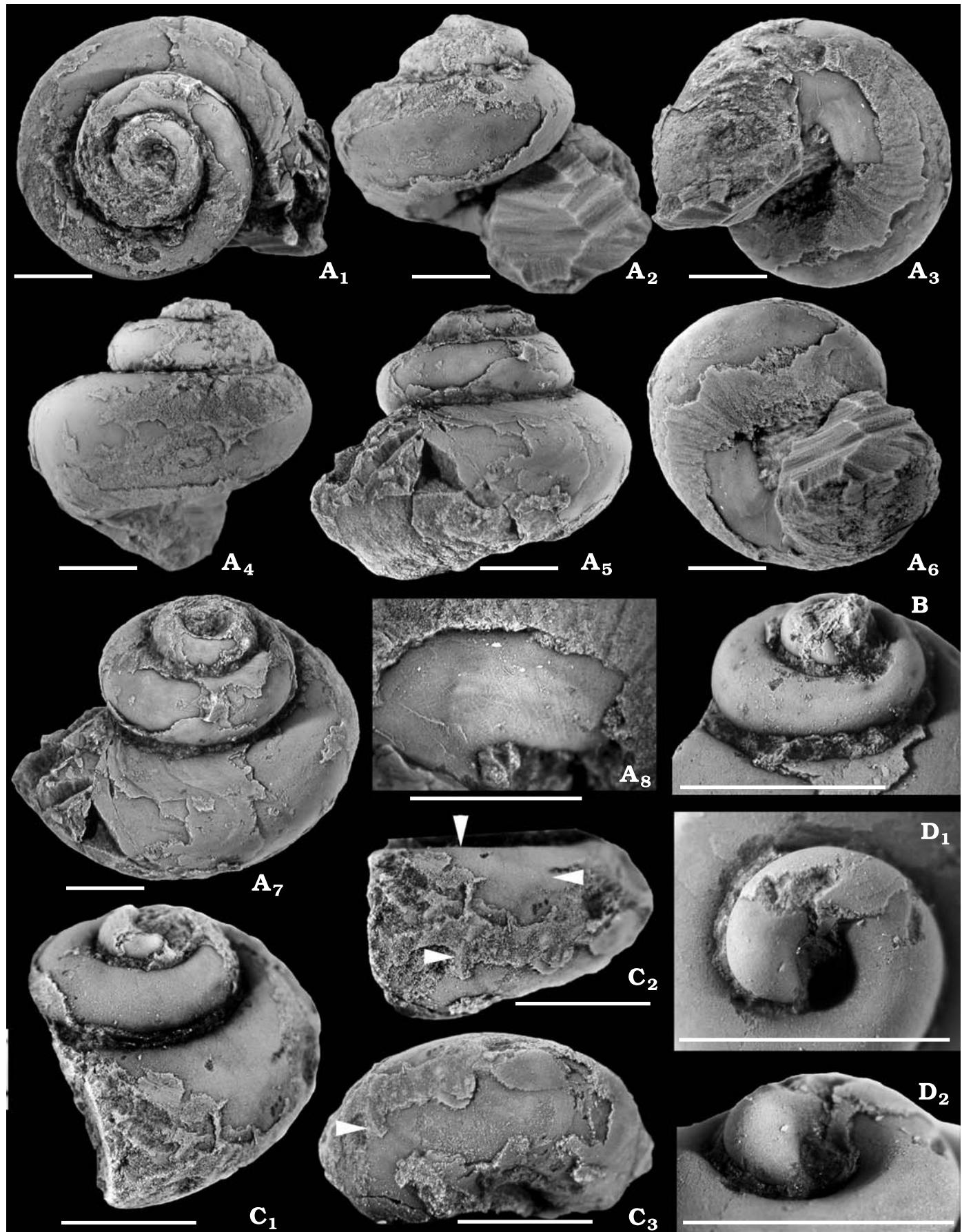
references). Commonly, several tens to hundreds of specimens may occur on bedding planes or in nodules, though preservation is highly variable (Radvan J. Horný, personal communication 2005).

Four species are known from the Mediterranean Province: *Ptychonema nigrum* from the Zahorany Formation (Caradocian) in the Barrandian area, Czech Republic; *P. bussacense* (Sharpe, 1853) from the Llanvirnian to Dobrotivá (Darriwilian) of Portugal, Spain, and France (see Horný 1997: 55 and references); *P. desideratum* (Barrande in Perner, 1903) from the Llanvirnian Šárka Formation and the Dobrotivá Formation (Dobrotivá) in the Barrandian area, Czech Republic; *P. marocanum* Horný, 1997, from the Tachilla Formation (Llanvirnian), Anti-Atlas, Morocco. Horný (1997) considered that *P. desideratum* may be a junior synonym of *P. bussacense*, but lacked access to type and comparative material for a detailed study.

Abundant specimens of *Sinuopea?* sp. were recorded from the shallow water deposits of the Reedsville Formation (Cincinnatian), central Appalachians (Bretsky 1970). The species is large, 35 mm high, with at least five whorls of uniform expansion rate. A distinct U-shaped sinus is developed with its deepest part (ab-aperturally) at the periphery of the evenly rounded whorl. These features seem to place the taxon with *Ptychonema* as currently understood, to which it is here transferred. Museum material of this species at the Yale Peabody Museum has not been studied, so details of the aperture morphology and early whorls are unknown. Both in size and morphology the species is comparable to the type species *P. nigrum*, though the American form is much younger. Inclusion of the species from Kyrgyz Range, described here from the Almaly Formation (Caradocian) in the western Kyrgyz Range, provides the second occurrence of *Ptychonema* outside the Mediterranean Province.

Perner (1903) described several Silurian Gondwana genera (i.e., *Horistostomella*, *Sellinema*, *Turbomaria*) with shallow U-shaped sinuses. These were considered junior synonyms of *Umbospira* Perner, 1903 by Wagner (2002) and placed in the Holopeidae. The affinity of these dominantly Silurian forms with *Ptychonema* is unclear and remains to be studied (Radvan J. Horný, personal communication 2005), and any Ordovician occurrences should be scrutinized in the light of the resurrection of *Ptychonema*. For instance, a common, minute species of *Turbomaria* was reported from the Late Ordovician Boda Limestone of Sweden (Gubanov et al. 1999). This has an anomphalous shell of four whorls, steep and weakly convex whorl profile with the periphery positioned low on the whorl, and a shallowly convex base. A shallow U-shaped sinus is placed somewhat above the periphery of the whorl. Other Ordovician occurrences of *Tur-*

Fig. 5. The holopeid gastropod *Ptychonema agyrus* Ebbestad, sp. nov. from the Almaly Formation, Caradocian (Upper Ordovician) of Kyrgyz Range. →
A. NMW 98.66G.946, holotype, general views dorsally (A_1), aperturally (A_2), ventrally (A_3), laterally (A_4 ; A_5), ventral oblique (A_6), and dorsal oblique (A_7); A_8 shows detail of the pedal muscle scar. **B.** A small specimen (NMW 98.66G.947) with initial bulbous part of infilling. **C.** NMW 98.66G.948 nearly complete specimens with outline of the outer lip preserved (indicated by white arrows). **D.** NMW 98.66G.949, a partial spire with initial bulbous part of infilling (D_1 , D_2). This may represent a heterostrophic protoconch. Scale bars 2.5 mm.



bomaria have not been reported, but *Sellinema?* sp. was identified from the Late Ordovician on Read Island, Canadian Arctic (Miller and Youngquist 1947). This species is comparable in size and age with the Cincinnati *Ptychonema* sp., and was described as having a rounded sinus. Type material in the Yale Peabody Museum has not been investigated, so affinities with respect to *Ptychonema* or the predominantly Silurian *Umbospira* (synonym *Sellinema*) remain open. Furthermore, Horný (1997) predicted that several Ordovician species allied with *Mourlonia* de Koninck, 1883 may belong to *Ptychonema*. However, as presently understood, *Ptychonema* is restricted to the six Ordovician species noted above.

Ptychonema agyris Ebbestad, sp. nov.

Figs. 5, 6, 7.

Derivation of the name: From Greek *agyris*, meaning gathering, pertaining to the occurrence in coquinas, whether fortuitous or not.

Holotype: A near complete specimen with patches of shell preserved (NMW 98.66G.946; Fig. 5A–H). Preserved height and maximum width of the specimen are both 9.0 mm.

Type locality: Locality 510, northern bank of the Almaly Gorge, western Kyrgyz Range, Kazakhstan.

Type horizon: Upper Member of Almaly Formation, Caradocian (Upper Ordovician).

Paratypes: A small specimen (NMW 98.66G.947, Fig. 5I) with nearly complete spire; a nearly complete specimens where the outline of the outer lip is preserved (NMW 98.66G.948, Fig. 5J–L), a partial spire with initial bulbous part of infilling preserved (NMW 98.66G.949, Fig. 5M, N), a specimen with partially preserved aperture (NMW 98.66G.950, Fig. 6A), base of a specimen (NMW 98.66G.951, Fig. 6B) with shell preserved; a partial last whorl with shell intact (NMW 98.66G.952, Fig. 6C); two cross sections (NMW 98.66G.953, Fig. 6D; NMW 98.66G.954, Fig. 6E). All specimens were prepared out of the slab from where the holotype came.

Other material.—The shell is extremely common in the type area and forms coquinas of different sized specimens, together with the *Tunisiglossa almalensis* (see Fig. 2 for distribution).

Diagnosis.—A species of *Ptychonema* with four whorls that differs from other species of the genus by having a strongly rounded, parabolic whorl profile. It shares a small size and deep sinus placed mostly above the periphery with *P. maroccanum* Horný, 1997, but differs from other species of the genus in this respect. It differs from *P. maroccanum* in having more strongly curved growth lines on the upper whorl surface, and by having a less inclined and thicker inner lip. The nature of the inner lip also differ from that of the other species of the genus.

Description.—Shell turbiniform with 4 whorls of moderate whorl translation ($W = 0.5$). The earliest whorl(s) are abandoned and the apex is filled, giving a sunken and tapering infilling of the first open part of the conch. The conch is slightly wider than it is high, with an apical angle of about 90° . Whorls are evenly and strongly rounded, parabolic in profile, nearly flat at the incised sutures and with a corresponding low profile

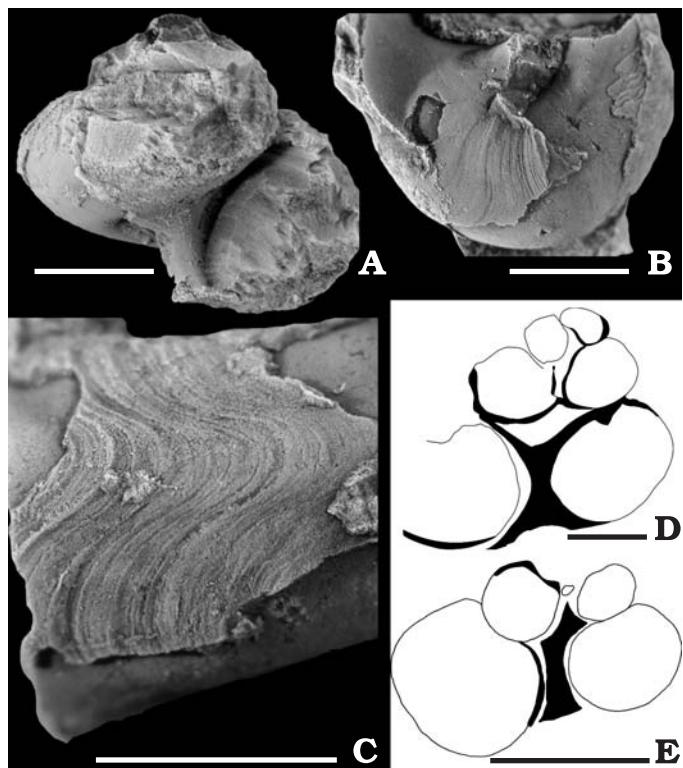


Fig. 6. The holopeid gastropod *Ptychonema agyris* Ebbestad, sp. nov. from the Almaly Formation, Caradocian (Upper Ordovician) of Kyrgyz Range. A. NMW 98.66G.950, specimen with partially preserved aperture. B. NMW 98.66G.951, base of a specimen with shell preserved. C. NMW 98.66G.952, partial last whorl with shell intact. D. NMW 98.66G.953, cross section of large specimen. E. NMW 98.66G.954, cross section of initial whorls of small specimen. Scale bars 2.5 mm.

of the evenly rounded base. Successive whorls overlap at lower 1/3 of whorl height. The shell is anomphalous. Ornamentation consists of fine growth lines only; they are prosocline on the upper whorl surface, sweeping strongly back abaperturally into a wide, symmetrical, or nearly symmetrical, U-shaped sinus. Most of the sinus is placed slightly above the periphery, and is about as wide (axial direction) as it is deep (abaperturally). In some specimens a slightly raised zone (spirally) is associated with the position of sinus. On the lower whorl surface the growth lines sweep strongly forward, with the most anterior point (adaperturally) of the projection at lower 2/3 of whorl height. The growth lines turn more orthocline toward the base, but they are slightly excavated (curved) at the inner-margin base (viewed ventrally). The aperture is tangential, with a low apertural angle ($E \approx 10^\circ$). The outer apertural lip is thin with only slight thickening at the basal part, and a thicker inner margin. Inner margin slightly curved, but essentially parallel to axis of coiling. A single pedal muscle scar is found at the base of the whorl at the umbilical margin, about half a whorl back (the abapertural boundary of the scar is concealed by preserved shell), and curving adaperturally for a short distance. The scar is elongated, widening adaperturally where the margin forms a weak asymmetric arch projecting

furthest adaperturally closest to the aperture. Four marginal lobes are developed at the adapertural part, the broadest near the umbilicus with three lobes of about equal width away from the umbilicus.

Remarks.—With its rounded, tangential aperture *Ptychonema agyris* should in life position have had the apertural plane parallel to the substrate, accompanied by a high degree of inclination of the axis of coiling (Vermeij 1971; Linsley 1977). However, the inclination of the axis of coiling in *P. agyris* is very low, as indicated by the low angle (E) of the apertural plane, and this is contrary to geometric expectations (Fig. 7A, B). This arrangement requires some amount of regulatory detorsion to achieve balance of the shell. Regulatory detorsion effectively ensures that the centre of gravity of the shell is over the mid-line of the foot by reducing the angle between the mid-axis of the foot and the axis of coiling (Linsley 1977; law of shell balance). Inevitably, with such a configuration, the emargination (i.e., the sinus) will not have an anterior position since it is positioned largely above the periphery of the whorl (Fig. 7C, D). This is as well contrary to geometric expectations for emarginations in shells of anisostrophic coiled gastropods (Linsley 1977; law of re-entrants). A steep apertural angle in Palaeozoic gastropods is usually associated with a radial aperture, held normal to the substrate (Linsley 1977). However, Isakar et al. (1991) recognized a pseudo-tangential aperture in the large Silurian gastropod *Horologium*, essentially giving the same morphological arrangement as in a shell with a radial aperture.

The abandoned apex is characteristic of *Ptychonema agyris*, but also seems to be present in *P. marocanum* (personal observation by JORE, November 2005); the character may be shared among all species of the genus (see discussion of *P. bussacense* below). Filled apices are as well seen in other distantly related genera such as *Palliseria*, *Lytospira*, and *Hormotoma*, but these differ in that the infilling (internal mould) of the initial open shell area is bulbous. In *Ptychonema agyris* this part is depressed and tapering (Fig. 5I, M, N). Given that the shell in this species is thin, the internal mould may reflect the original shape of the initial whorl thus indicating the presence of a heterostrophic submerged protoconch. Heterostrophy is characterized by a change from hyperstrophic growth of the protoconch to orthostrophic growth at the onset of the teleoconch, typical for members of the subclass Heterostropha (see Bandel 1994). The oldest undoubtedly heterostrophic gastropod is known from the Lower Ordovician (Frýda and Rohr 2006). Previously, the oldest form was described from the Devonian (Frýda and Blodgett 2001; Bandel and Heidelberger 2002), but an unnamed specimen was also depicted from the Late Ordovician Boda Limestone of Sweden by Gubanov et al. (1999). Without the actual protoconch preserved in *P. agyris* a heterotrophic affiliation is not unequivocal, but because of the suggestive direction of the initial coiling the protoconch is unlikely to compare to a large bulbous archaeogastropod-type. It is, however, prudent to keep in mind that variation of protoconch morphology is evident within the Archaeogastropoda,

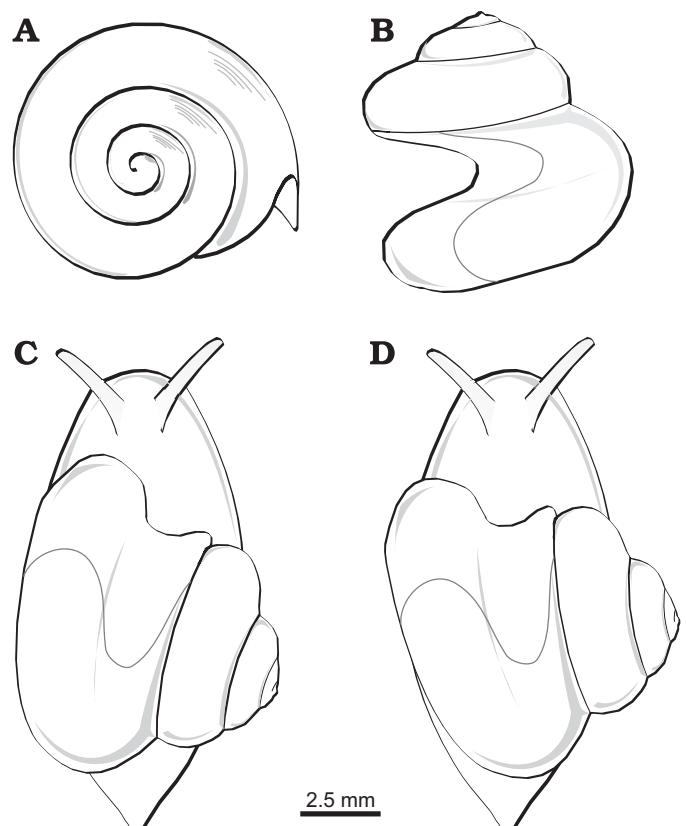


Fig. 7. The holopeiid gastropod *Ptychonema agyris* Ebbestad, sp. nov. from the Almaly Formation, Caradocian (Upper Ordovician) of Kyrgyzstan. **A.** Reconstruction of the shell in dorsal view. **B.** Reconstruction of the shell in lateral view. **C.** Reconstruction of the shell in presumed life position with the apertural plane horizontal and with slight regulatory detorsion to balance the shell. Note how the emargination is not in an anterior position. **D.** Reconstruction of the shell in presumed life position with the apertural plane horizontal, but without regulatory detorsion, so that the emargination is in an anterior position.

for instance exemplified by the Cirroidea, and that the range and variation of assorted open coiled protoconch morphologies are still largely unexplored (see Frýda 1999; Frýda and Rohr 2004).

The species from Kyrgyz Range is similar to *Ptychonema marocanum* Horný, 1997, from Morocco in the small size of the shell, though maximum size is about 30% larger (height about 9 mm vs. 6 mm in the Moroccan species). Other similarities are in number of whorls, the anomphalous shell, and the conch being wider than high. *Ptychonema agyris* differs noticeably in the more strongly rounded whorls, the growth lines that sweep more strongly back on the upper whorl face, a less inclined and thicker inner lip. The sinus may also be deeper in the species from Kyrgyz Range. Horný (1997), on the other hand, described considerable variability of this character in *Ptychonema*, ranging from a short slit making a bordered selenizone, a sinus with a weakly defined pseudo-selenizone, or a simple, sometimes raised, band-like spiral zone. In *Ptychonema marocanum* the variation is manifested by a weakly defined pseudo-selenizone that may be associ-

ated with a raised zone that is rarely bounded by spiral lines and with highly irregular lunulae where such can be distinguished. Even with the limited material prepared for description of the species from Kyrgyz Range, a raised zone associated with the sinus is sometimes evident (Fig. 6C), and there is also variability in the strength of the growth lines (for example Fig. 5G). Anything approaching a pseudo-selenizone, however, is not recognised in *Ptychonema agyris*.

Differences in width and depth of the sinuses and size differences set both *Ptychonema agyris* and *P. marocanum* apart from the other recognised species of *Ptychonema*. Similarities exist between the species from Kyrgyz Range and the Cincinnati *Ptychonema* sp. in the whorl profile, but with a more pronounced shoulder-like upper whorl surface in the American species. Some of the variation though may be owing to larger size, continuous ontogenetic change, and taphonomy. The sinuses in both species are placed high on the whorl, though it is narrower and less deep in the American *Ptychonema* sp. In this it compares to the type species *Ptychonema nigrum* Barrande in Perner, 1903, as well as *P. bussacense* (Sharpe, 1853) and *P. desideratum* (Barrande in Perner, 1903). These three species are all considerably larger than both *Ptychonema agyris* and *P. marocanum*, and seem to develop a better defined pseudo-selenizone, with a less deep sinus.

Similarities among the three large species are many, and Horný (1997) considered that *P. desideratum* may be a junior synonym of *P. bussacense*. In the Natural History Museum, London, three specimens (BMNH Pg3983, Pg3985, Pg3987) labelled *Pleurotomaria bussacensis* Sharpe from Portelo de Leredo in the Serra de Bussaco were studied, which lend support to this suggestion (assessment of the type material is still needed to judge this matter). These partially preserved specimens are from the type area of the species and seem to conform to the description of the species by Sharpe (1853), as well as the description and figure of *P. desideratum* given by Horný (1997). All specimens are large (between 20 and 40 mm across), with five(?) whorls, a wide and not very deep sinus that is raised on a spiral zone in one specimen (BMNH Pg3983). The shells seem to be narrowly phaneromphalous or even anomphalous. In BMNH Pg3985 the apex was clearly abandoned, with preservation similar to that seen in *Ptychonema agyris* (Fig. 5M, N).

Vostokova (1956) described gastropods from the comparable Anderken Formation and the Otar "Horizon" of the Chu-Ili Range in Kazakhstan. Most diverse where a lopho-spirid assemblage preserved in sandstones and siltstones, and a *Maclurina* assemblage found in limestone. In the argillaceous sediments *Latitaenia kasachstanica* Vostokova, 1956 dominates numerically, but neither this nor any of the other species described by Vostokova (1956) can be compared to *Ptychonema*. Part of the reason may be heterogeneous dispersal of the assemblages, and the more shallow nature of the deposits containing *Ptychonema*.

Discussion and results

Ecology and deposition.—In the Almaly Formation brachiopods are usually preserved as accumulations of disarticulated valves on the bedding surfaces of greenish-grey, fine-grained sandstones and siltstones whereas gastropods occur mainly in thin shell beds about 10–30 mm thick. Sedimentological features such as wave ripple marks, bidirectional cross-bedding and tidal channels preserved in the fossiliferous units suggest shallow marine deposition nearshore. Sporadic occurrences of mud cracks suggest that in part sediments were deposited intertidally.

None of the lingulid specimens were preserved in life position. Their infaunal mode of life, however, can be inferred from observations on other Ordovician taxa of the subfamily *Glossleinae* (see Pickerill 1984) and have also been inferred for species of that subfamily from the Ordovician of Bohemia (Mergl 2002). The specimens of *Tunisiglossa almalensis* are preserved in fine grained sands that are considered as a perfect substrate for infaunal burrowing by recent lingulids (Emig 1997).

Observations on taphonomy of recent lingulid shells also suggest that if exposed, they have a low fossilization potential and their deterioration on a sea bed surface requires only a matter of a few weeks. Therefore accumulations of disarticulated lingulid shells on bedding surfaces can be attributed to desalination of nearshore waters, significant increase of sedimentation rate and influx of coarse-grained sediments generated by strong seasonal storms and rains (Emig 1986) that cause exposure, then a catastrophic death and rapid burial of the animals. In the studied localities sandstone beds rich in disarticulated lingulid shells are associated with 10 to 30 mm thick shell beds formed by accumulation of the gastropod *Ptychonema*. It is likely that deposition of gastropod coquinas occurred during the same storm event that caused the mortality of *Tunisiglossa almalensis* and rapid burial of their disarticulated valves. Very similar patterns were recently described by Popov et al. (2002) for the *Ectenoglossa* Association from the lower to middle Caradocian Anderken Formation of the Chu-Ili Range in South Kazakhstan, a low diversity association dominated by the lingulid *Ectenoglossa sorbulakensis* Popov, 1980. It occurs in medium- to coarse-grained sandstones with sub-horizontal and cross-bedded stratification, where brachiopods are often preserved as accumulations of disarticulated valves on the bedding surfaces. However, on a few occasions, occurrences of the conjoined valves in burrows were also observed. The units with lingulids also contain coquinas storm beds formed by the shells of gastropod and bivalved molluscs, but they usually do not co-occur together with lingulids. Coquinas of the gastropod *Latitaenia kasachstanica* Vostokova, 1956 are especially prominent in the siliciclastic sediments, but are replaced by a different gastropod fauna in the limestone facies (Vostokova 1956). It is therefore likely that the lingulide-gastropod association from the Almaly Formation and the *Ectenoglossa* As-

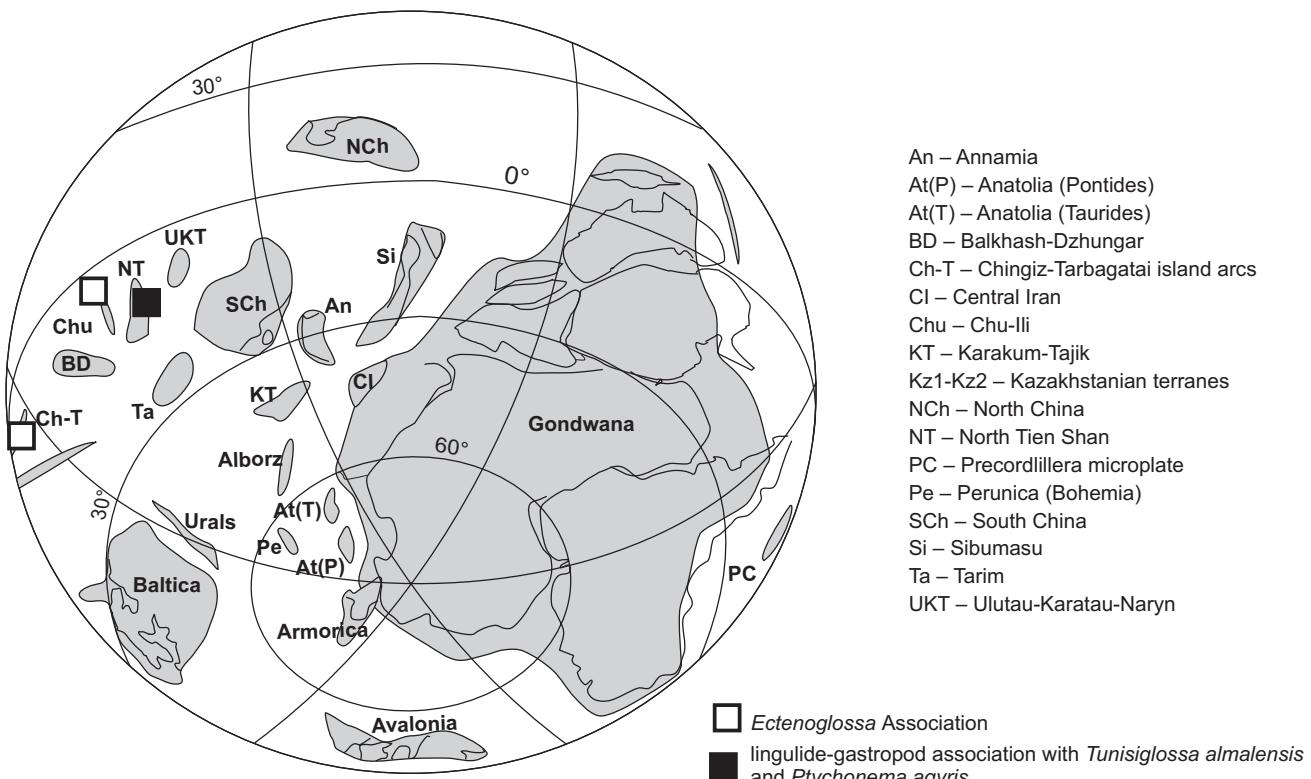


Fig. 8. Palaeogeographic reconstruction for the Late Ordovician (early Caradocian) showing geographical distribution of shallow water (BA1) lingulid-mollusc associations on Kazakh terranes. The reversed position of the North China plate in low northern latitudes and position of Tarim plate at 36.5°S are mainly after Zhao et al. (1996). Relative positions of Gondwana, Armorica, Baltica, Avalonia, and Laurentia are mainly after Torsvik (1998). Kazakhstan in the Ordovician was not a single plate but an assemblage of island arcs and microplates (Apollonov 2000; Webby et al. 2000). Some Kazakh terranes (Chingiz-Tarbagatai) are remnants of several Early Palaeozoic intra-oceanic island arcs, in a part possibly representing the Cambrian eastern active margin of Baltica detached sometime within the Late Cambrian–Early Ordovician. Another group of Kazakh terranes (North Tien Shan, Chu-Ili, Balkhash-Dzhungaria, Ulutau-Karatau-Naryn) are microplates presumably of a peri-Gondwanan origin. Position of North Tien-Shan at low southern latitudes after Bazhenov et al. (2003).

sociation from the Anderken Formation inhabited an environment of mobile sands deposited on a tidal flat nearshore, partly intertidally that was affected by seasonal storms possibly accompanied by strong rains.

Communities with similar depositional and faunal composition found in the Silurian were referred to as the *Turbocheilus* community by Boucot (1975, 1999) and Rohr (1999), and considered indicative of a brackish to estuarine, or possibly lagoonal conditions (Bradfield 1999). Other species of the gastropod *Ptychonema* are as well frequently found in coquinas or abundantly occurring on bedding planes (Horný 1997; Bretsky 1970; this paper), but though the taphonomic preservation of these species may seem to be similar the depositional settings seems to vary. The Cincinnati *Ptychonema* sp. is common in a restricted belt in the Central Appalachians, associated with the gastropod *Lophospira* and a *Sowerbyella-Onniella* brachiopod community (Bretsky 1970). It is only occasionally found in the more shallow community (BA1–2) typified by the trilobed planispiral gastropod *Tritonophon* sp. and lingulid brachiopods (the Plectonotid community of Rohr 1999). Both the Moroccan and Bohemian species occur in transgressive, deepening facies, associated with rich benthic communities (Horný 1997).

Palaeobiogeography.—In spite of several conflicting views in recent publications (Apollonov 2000; Mossakovskiy et al. 1993; Scotese and McKerrow 1991; Şengör and Natal'ın 1996), North Tien Shan region appears to have been a small, separate crustal terrane in the early Palaeozoic. Palaeomagnetic data presented recently by Bazhenov et al. (2003: 139) suggest that during the Late Ordovician North Tien Shan maintained a subequatorial southern position without any significant latitudinal displacement (Fig. 8). In particular, data provided for the Almaly Formation suggest 9°S for the early to middle Caradocian. Bazhenov et al. (2003) favoured the palaeogeographic model of Şengör and Natal'ın (1996) that joined North Tien Shan with other Kazakh terranes as parts of the enormous “Kipchak island arc” that linked Baltica and Siberia. However, it is completely unsupported by existing data on the trilobite and brachiopod biogeography that are critical for evaluation of the relative longitudinal position of ancient plates and associated terranes through the Ordovician–Silurian (Fortey and Cocks 2003).

Two studied taxa are inadequate to prove or disprove these models, but existing information on the Middle and Late Ordovician brachiopods of North Tien Shan (Misius 1986) is strongly in favour of its position in relative proximity to small

plates clustering around equatorial East Gondwana. In particular, *Ishimia* Nikitin, 1974 is known only elsewhere from Chu-Ili, Chingiz, New South Wales, and Sibumasu (Fortey and Cocks 2003; Percival et al. 2001), *Mabella* Misius, 1986 [= *Leptellina multicostata* (Rukavishnikova, 1956)] and *Shlyginia* (= *Leptellina tabylgatensis* Misius, 1986) are known from Chu-Ili, Chingiz and New South Wales, Australia (Popov et al. 2000; Percival et al. 2001), *Sulcospira* Xu, 1979 (= *Kuzgunia* Klenina, 1984) is confined to Chu-Ili, Chingiz, South and North China (Popov et al. 1999), whereas *Acculina* and *Dzebaglina* are endemic for North Tien Shan, Chu-Ili, and Chingiz (Popov et al. 2000; 2002).

The gastropod *Ptychonema* is typically found in terranes of high latitude peri-Gondwana (i.e., Bohemia, France, Portugal, Morocco), in the Middle to early Late Ordovician, but with a disparate distribution in later Ordovician sediments. Though the lineage seems to have its origin in this part of peri-Gondwana, its record of dispersal to Avalonian and North Tien Shan in the Late Ordovician is obscure. Finds of *Ptychonema* in Kyrgyzstan do not therefore necessarily indicate a strong affinity to high latitude peri-Gondwana. Neither does the gastropod fauna of the Anderken Formation and the Otar "Horizon" of the Chu-Ili Range in Kazakhstan (Vostokova 1956). Coquinas of *Latitaenia* are here typical, although the genus is traditionally found in Baltica and Siberia (Koken and Perner 1925; Vostokova 1955, 1962; Yochelson 1963; Bjaly 1974; Zernetskaya 1976; Wagner 2002). Other gastropods are fairly abundant and diverse in the Chu-Ili deposits. However, Vostokova (1956) warned that the identification of taxa in her material was difficult, and therefore comparison with contemporaneous deposits of other regions should proceed only with great caution. In conclusion, therefore, overall the Upper Ordovician faunas of North Tien Shan show close similarities to contemporaneous faunas of the Chu-Ili terrane that have strong biogeographic signatures linking them to the faunas of South and North China (Fortey and Cocks 2003; Popov et al. 2002).

As was recognised by Wilde (1991), due to the presence of large land masses in the Southern Hemisphere during the Ordovician, monsoonal conditions with seasonal stormy weather and strong rain falls can be expected for the north-western peri-Gondwana situated in low latitudes. The inferred geographical position of North Tien Shan and Chu-Ili plates (Fig. 8) suggests that both the lingulid-gastropod association from North Tien Shan and the *Ectenoglossa* Association from Chu-Ili inhabited a sandy bottom within the tidal flat in tropics affected by monsoonal conditions. Remarkably Recent lingulids are still abundant along the coasts of southern and south-east Asia precisely in the same environment (Emig 1986, 1997). However, analysis of the environmental expansion of lingulids during the Ordovician suggests, that in the Early to Middle Ordovician the nearshore lingulid-dominated communities were mostly typical of temperate and high latitudes and usually included a significant number of epibenthic taxa (Havlíček 1982, 1989; Mergl 2002). Significant proliferation of the infaunal lingulid communities occurred mainly in

the Darriwilian when they replaced completely epibenthic obolides in sandy bottom nearshore environment (Bassett et al. 1999). Since that time, associations of large epibenthic lingulids and acrotretids have moved offshore and are preserved exclusively as relicts in deep basinal environments (Holmer et al. 1996). Diversity of nearshore lingulid communities decreased and they often became almost monospecific. Their association with gastropod and bivalve molluscs was relatively common (Bassett et al. 1999) and they become increasingly common at low latitudes.

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References

- Apollonov, M.K. 2000. Geodynamic evolution of Kazakhstan in the Early Palaeozoic (from classic plate tectonic positions) [in Russian]. In: H.A. Bespaev (ed.), *Geidinamika i minerageniya Kazahstana*, 46–63. VAC Publishing House, Almaty.
- Bassett, M.G., Popov, L.E., and Holmer, L.E. 1999. Organophosphatic brachiopods: patterns of biodiversification and extinction in the early Palaeozoic. *Geobios* 32: 145–163.
- Bandel, K. 1994. Triassic Euthyneura (Gastropoda) from St. Cassian Formation (Italian Alps) with a discussion on the evolution of the Heterostropha. *Freiberger Forschungshefte* 452: 79–100.
- Bandel, K. and Heidelberger, D. 2002. A Devonian member of the subclass Heterostropha (Gastropoda) with valvatoidean shell shape. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2002 (9): 533–550.
- Bazhenov, M.L., Collins, A.Q., Degtyarev, K.E., Levashova, N.M., Mikolaičuk, A.V., Pavlov, V.E., and Van der Voo, R. 2003. Paleozoic northward drift of the North Tien Shan (Central Asia) as revealed by Ordovician and Carboniferous paleomagnetism. *Tectonophysics* 366: 113–141.
- Byalyj, V.I. [Bályj, V.I.] 1974. Ordovician Monoplacophora, Gastropoda and Cephalopoda [in Russian]. In: L.V. Ogienko, V.I. Bályj, and G.R. Kolosnycyna (eds.), *Biostratigrafiâ kembrijskikh i ordovijskikh otloženij fga Sibirskej platformy*, 53–68. Nedra, Moskva.
- Boucot, A.J. 1975. *Evolution and Extinction Rate Controls*. 427 pp. Elsevier, Amsterdam.
- Boucot, A.J. 1999. Some Wenlock-Gedinnian, chiefly brachiopod dominated, communities of North America. In: A.J. Boucot and J.D. Lawson (eds.), *Paleocommunities: A Case Study from the Silurian and Lower Devonian*, 548–591. Cambridge University Press, Cambridge.
- Bradfield, K.E.S. 1999. Fossil communities of the late Ludlow and early

- Pridoli in Wales and the Welsh Borderland. In: A.J. Boucot and J.D. Lawson (eds.), *Paleocommunities: A Case Study from the Silurian and Lower Devonian*, 370–372. Cambridge University Press, Cambridge.
- Bretsky, P.W. 1970. Upper Ordovician ecology of the Central Appalachians. *Bulletin of the Peabody Museum of Natural History* 30: 1–150.
- Cooper, G.A. 1956. Chazyan and related brachiopods. *Smithsonian Miscellaneous Collections* 127: 1–1245.
- Cuvier, G. 1797. *Tableau élémentaire de l'histoire naturelle des animaux*. 710 pp. Baudouin, Paris.
- De Koninck, L.G. 1883. Faune du calcaire carbonifère de la Belgique, 3^e partie: Gastéropodes (suite en fin). *Annales du Musée Royal d'Histoire de Belgique, Série Paléontologique* 8: 1–240.
- Emig, C.C. 1986. Conditions de fossilisation du genre Lingula (Brachiopoda) et implications paléoécologiques. *Palaeogeography, Palaeoclimatology, Palaeoecology* 53: 245–253.
- Emig, C.C. 1997. Ecology of the inarticulated brachiopods. In: R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology. Part H. Brachiopoda (Revised)*, 473–495. Geological Society of America and University of Kansas Press, Lawrence.
- Fortey, R.A. and Cocks, L.R.M. 2003. Palaeontological evidence bearing on global Ordovician–Silurian continental reconstruction. *Earth Science Reviews* 61: 245–307.
- Frýda, J. 1999. Higher classification of Paleozoic gastropods inferred from their early shell ontogeny. *Journal of the Czech Geological Society* 44: 137–153.
- Frýda, J. and Blodgett, R.B. 2001. The oldest known heterobranch gastropod *Kuskokwimia* gen. nov., from Alaska, with notes on the early phylogeny of higher gastropods. *Bulletin of the Czech Geological Survey* 76: 39–53.
- Frýda, J. and Rohr, D.M. 2004. Gastropods. In: B.D. Webby, F. Paris, M. Droser, and I.G. Percival (eds.), *The Great Ordovician Biodiversification Event*, 184–195. Columbia University Press, New York.
- Frýda, J. and Rohr, D.M. 2006. Shell heterostrophy in Early Ordovician *Macluritella* Kirk, 1927 and its implications for phylogeny and classification of Macluritoidea (Gastropoda). *Journal of Paleontology* 80: 264–271.
- Gorjansky, V.Ju. [Горанский, В.У.] and Popov, L.E. 1985. Morphology, systematic position and origin of the inarticulate brachiopods with carbonate shells. *Paleontologičeskij žurnal* 1985(3): 3–14. [In Russian].
- Gubanov, A.P., Ebbestad, J.O.R., and Bogolepova, O.K. 1999. Microfossil assemblage of the Boda limestone (Upper Ordovician, Sweden). *Acta Universitatis-Carolinae-Geologica* 43: 421–423.
- Hall, J. 1847. *Palaeontology of New-York. Volume I. Containing descriptions of organic remains of the lower division of the New-York System, (equivalent to the Lower Silurian rocks of Europe)*. 338 pp. C. Van Benthuyzen, Albany.
- Havlíček, V. 1982. Lingulacea, Paterinacea, and Siphonotretacea (Brachiopoda) in the Lower Ordovician sequence of Bohemia. *Sborník geologických věd; Paleontologie* 25: 9–82.
- Havlíček, V. 1989. Climatic changes and development of benthic communities through the Mediterranean Ordovician. *Sborník geologických věd Geologie* 44: 79–116.
- Holmer, L.E. and Popov, L.E. 2000. Lingulata. In: R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Revised)*, 30–146. Geological Society of America and University of Kansas Press, Lawrence.
- Holmer, L.E., Koneva, S.P., Popov, L.E., and Zhylkajdarov, A.M. 1996. Lingulate brachiopods and associated conodonts from the Middle Ordovician (Llanvirn) of the Malý Karatau Range, Kazakhstan. *Paläontologisches Zeitschrift* 70: 481–495.
- Horný, R.J. 1997. Ordovician Tergomya and Gastropoda (Mollusca) of the Anti-Atlas (Morocco). *Acta Musei Nationalis Pragae* 53: 37–78.
- Isakar, M., Ebbestad, J.O.R., and Peel, J.S. 1999. Homeomorphic gastropods from the Silurian of Norway, Estonia and Bohemia. *Norsk Geologisk Tidsskrift* 79: 281–288.
- King, W. 1846. Remarks on certain genera belonging to the class Pallio-brachiata. *Annals and Magazine of Natural History, Series 1* 18: 26–42.
- Kiselev, V.V. 1999. U-Pb zircon geochronology of magmatic formations of the Northern Tien Shan [in Russian]. *Izvestiâ Nacionaloj Akademii Nauk Kyrgyzstana* 1999: 21–33.
- Klenina, L.N. 1984. Brachiopods and biostratigraphy of the Middle and Upper Ordovician of the Chingiz-Tarbagatai Meganticlinorium [in Russian]. In: S.M. Bandaletov (ed.), *Brachiopody i biostratigrafija srednego i verhnego ordovika hrebla Čingiz*, 6–125. Nauka, Alma-Ata.
- Knight, J.B. 1941. Paleozoic gastropod genotypes. *Geological Society of America Special Papers* 32: 1–510.
- Koken, E. and Perner, J. 1925. Die Gastropoden des Baltischen Untersilurs. *Mémoires de l' Académie des Sciences de Russie, Série 8, Classe Physico-Mathématique* 37: I–VII+1–326.
- Linsley, R.M. 1977. Some “laws” of gastropod shell form. *Paleobiology* 3: 196–206.
- Massa, D., Havlíček, V., and Bonnefous, J. 1977. Stratigraphic and faunal data on the Ordovician of the Rhadames Basin (Libya and Tunisia). *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* 1: 3–27.
- Menke, C.T. 1828. *Synopsis methodica Molluscorum generum omnium et specierum earum, quae in Museo Menkeano Adservantur*. xii + 91 pp. G. Uslar, Pyrmonti.
- Mergl, M. 2002. Linguliformean and craniiformean brachiopods of the Ordovician Třenice to Dobrotiva formations of Barrandian, Bohemia. *Acta Musei Nationale Prague, series B, Natural History* 58: 1–82.
- Miller, A.K. and Youngquist, W. 1947. Ordovician fossils from the southwestern part of the Canadian arctic archipelago. *Journal of Paleontology* 21: 1–18.
- Misius, P.P. 1986. *Brachiopody ordovika Severnoj Kirgizii*. 254 pp. Ilim, Frunze.
- Mossakovskii, A.A., [Моссаковский, А.А.], Ruzhentsev, S.V. [Ружентьев, С.В.], Samygin, S.G., and Kheraskova, T.N. [Хераскова, Т.Н.] 1993. Geodynamic evolution of the Central-Asia folded belt and history of its development [in Russian]. *Geotektonika* 6: 3–33.
- Nikitin, I.F. 1974. New Middle Ordovician plectambonitaceans (Brachiopoda) from Kazakhstan [in Russian]. *Paleontologičeskij žurnal* 1974 (3): 57–67.
- Percival, I.G., Webby, B.D., and Pickett, J.W. 2001. Ordovician (Bendigonian, Darrielian to Gisbornian) faunas from the northern Molong Volcanic Belt of New South Wales. *Alcheringa* 25: 211–250.
- Perner, J. 1903 Gastéropodes. 1. Texte (Patellidae et Bellerophontidae) et Planches 1 B 89. In: J. Barrande, *Système Silurien du Centre de la Bohême*, 4, I–IX+1–164. Charles Bellman, Prague.
- Pickerill, R.K., Harland, T.L., and Fillion, D. 1984. In situ lingulids from deep water carbonates of the Middle Ordovician Table Head Group of Newfoundland and the Trenton Group of Quebec. *Canadian Journal of Earth Sciences* 21: 194–199.
- Popov, L.E. 1980. New brachiopod species from the Middle Ordovician of the Chu Ili Range [in Russian]. *Ežegodnik Vsesoúzного Paleontologičeskogo Obšestva* 23: 139–158.
- Popov, L.E. 1985. Brachiopods of the Anderken horizon, Chu-Ili Mountains (Kazakhstan) [in Russian]. *Ežegodnik Vsesoúzного Paleontologičeskogo Obšestva* 28: 50–68.
- Popov, L.E., Cocks, L.R.M., and Nikitin, I.F. 2002. Upper Ordovician brachiopods from the Anderken Formation, Kazakhstan: their ecology and systematics. *Bulletin of the British Museum (Natural History), Geology Series* 58: 13–79.
- Popov, L.E., Nikitin, I.F., and Cocks, L.R.M. 2000. Late Ordovician brachiopods from the Otar member of the Chu-Ili Range, south Kazakhstan. *Palaeontology* 43: 833–870.
- Popov, L.E., Nikitin, I.F., and Sokiran, E.V. 1999. The earliest atrypides and athyridides (Brachiopoda) from the Ordovician of Kazakhstan. *Palaeontology* 42: 625–661.
- Raup, S. 1966. Geometric analysis of shell coiling: general problems. *Journal of Paleontology* 40: 1178–1190.
- Rohr, D.M. 1999. Lower Silurian to Lower Devonian gastropod communities. In: A.J. Boucot and J.D. Lawson (eds.), *Paleocommunities: A Case*

- Study from the Silurian and Lower Devonian*, 132–136. Cambridge University Press, Cambridge.
- Rukavishnikova, T.B. [Rukavišnikova, T.B.] 1956. Ordovician brachiopods of the Chu-Ili Range [in Russian]. *Trudy Geologičeskogo Instituta Akademii Nauk SSSR* 1: 105–168.
- Scotese, C.R. and McKerrow, W.S. 1991. Ordovician plate tectonic reconstructions. In: C.R. Barnes and S.H. Williams (eds.), Advances in Ordovician Geology. *Geological Survey of Canada, Paper* 90: 271–282.
- Sengör, A.M.C. and Natal’in, B.A. 1996. Paleotectonics of Asia: fragments of a synthesis. In: A. Yin and M. Harrison (eds.), *The Tectonic Evolution of Asia*, 486–640. Cambridge University Press, Cambridge.
- Sharpe, D. 1853. Notes and a description of the animal remains. In: C. Ribeiro (ed.), On the Carboniferous and Silurian Formations of the neighbourhood of Bussaco in Portugal. *Quarterly Journal of the Geological Society of London* 9: 146–158.
- Torsvik, T.H. 1998. Palaeozoic palaeogeography: A North Atlantic viewpoint. *GFF* 120: 109–118.
- Thiele, J. 1925. Gastropoda der Deutschen Tiefsee-Expedition. II Teil. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer Valdivia. 1898–1899* 17 (2): 35–382.
- Ulrich, E.O. and Scofield, W.H. 1897. The Lower Silurian Gastropoda of Minnesota. The Geology of Minnesota. *Final Report on the geological and natural history survey of Minnesota. Paleontology* 3: 813–1081.
- Vermeij, G.J. 1971. Gastropod evolution and morphological diversity in relation to shell geometry. *Journal of Zoology* 163: 15–23.
- Vostokova, V.A. 1955. Class Gastropoda [in Russian]. In: O.I. Nikiforova (ed.), *Polevoj atlas ordovikskoj i silurijskoj fauny Sibirsкоj platformy*, 82–86. Gosgeoltehizdat, Moskva.
- Vostokova, V.A. 1956. Ordovician gastropods of Chu-ili Range [in Russian]. *Trudy Geologičeskogo Instituta Akademii Nauk SSSR* 1: 70–194.
- Vostokova, V.A. 1962. Ordovician and Silurian gastropods of the Siberian platform [in Russian]. *Trudy Vsesoūzного Naučno-Issledovatel’skogo Geologičeskogo Instituta (VSEGEI) Ministerstva Geologii i Ohrany Nedr SSSR* 75: 1–29.
- Waagen, W. 1885. Salt Range Fossils. I. Productus-Limestone Fossils. *Geological Survey of India, Memoirs, Palaeontologia Indica, Series 13* 4: 729–770.
- Wagner, P.J. 2002. Phylogenetic relationships of the earliest anisostrophically coiled gastropods. *Smithsonian Contributions to Paleobiology* 88: 1–152.
- Webby, B.D., Percival, I.G., Edgecombe, G.D., Cooper, R.A., VandenBerg, A.H.M., Pickett, J.W., Pojeta, J., Playford, G., Winchester-Seeto, T., Young, G.C., Zhen, Y-y., Nicoll, R.S., Ross, J.R.P., and Schallreuter, R. 2000. Ordovician biogeography of Australasia. In: A.J. Wright, G.C. Young, and J.T. Talent (eds.), *Palaeobiogeography of Australasian Faunas and Floras. Memoir of the Association of Australasian Palaeontologists* 23: 63–126.
- Weber, V.N. 1948. Trilobites of the Silurian of the USSR [in Russian]. *Monografii po paleontologii SSSR* 69: 1–111.
- Wenz, W. 1938. Gastropoda, Teil 1, Allgemeiner Teil und Prosobranchia. In: O.H. Schindewolf (ed.), *Handbuch der Palaeozoologie*, 1–240. Gebrüder Borntraeger, Berlin.
- Whitfield, R.P. 1886. Notice of Geological Investigations along the Eastern Shore of Lake Champlain, Conducted by Prof. H.J. Seely and Pres. Ezra Brainerd, of Middlebury College, with Descriptions of the New Fossils Discovered. *Bulletin of the American Museum of Natural History* 1: 24–35.
- Wilde, P. 1991. Oceanography of the Ordovician. In: C.R. Barnes and S.H. Williams (eds.), Advances in Ordovician Geology. *Geological Survey of Canada, Paper* 90: 283–298.
- Xu, H. 1979. Brachiopoda. In: Jin Y., Ye S., Xu H., and Sun D. *Palaeontological Atlas of North-Western China. 1, Qinghai* [in Chinese], 60–112. Geological Publishing House, Beijing.
- Yochelson, E.L. 1963. The Middle Ordovician of the Oslo Region, Norway. 15. Monoplacophora and Gastropoda. *Norsk Geologisk Tidsskrift* 43: 133–213.
- Zhao, X., Coe, R.S., Gilder, S.A., and Frost, G.M. 1996. Palaeomagnetic constraints on the palaeogeography of China: implications for Gondwanaland. *Australian Journal of Earth Sciences* 43: 643–672.
- Zernetskaya, N.V. [Zernetskaâ, N.V.] 1976. Ordovician gastropods of the Molodovsky Horizon of Podoli [in Russian]. In: P.L. Šul’ga (ed.), *Paleontologija i stratigrafiâ verhnego dokembriâ i nižnego paleozoâ ûgo-zapada Vostocno-Evropskoj platformy*, 136–148. Izdatelstvo Naukova Dumka, Kiev.