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A new genus of Late Ordovician–Early Silurian pentameride brachiopods and its phylogenetic relationships

JISUO JIN and LEONID E. POPOV

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Protanastrophia repanda gen. et sp. nov. is a reef-dwelling parastrophinid brachiopod in the Lower Silurian (uppermost Telychian) Attawapiskat Formation of the Hudson Bay region of Canada. It is characterized by a small, quasi-smooth shell with gentle anterior costae, a tendency towards an asymmetrical, sigmoidal anterior commissure, and widely separate, subparallel inner hinge plates. *Protanastrophia* first appeared in the marginal seas of Siberia (Altai, Mongolia) during the Late Ordovician, retaining the primitive character of discrete inner hinge plates in the superfamily Camerelloidea, and preferred a carbonate mound depositional environment. It survived the Late Ordovician mass extinction and subsequently spread to Baltica and Laurentia during Early Silurian (Llandovery) time. Superficially similar asymmetrical shells of *Parastrophina portentosa* occur in the Upper Ordovician carbonate mound facies of Kazakhstan but differ internally from the new genus in having a septum-supported septalium. Phylogenetic analysis indicates that, within the Camerelloidea, asymmetrical shells with a sigmoidal anterior commissure evolved in *Protanastrophia repanda* and *Parastrophina portentosa* independently during the Late Ordovician as a case of homoplasy. The two species belong to separate parastrophinid lineages that evolved in widely separate palaeogeographic regions.

Key words: Brachiopoda, Parastrophinidae, Ordovician, Silurian, Canada, Siberia.

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Introduction

The syntrophiidines constituted a suborder of pentameride brachiopods and underwent two major episodes of diversification during the Early and Middle Ordovician, respectively (Carlson 1996; Harper et al. 2004). The family Parastrophinidae evolved relatively late among the syntrophiidines by late Darriwilian time, characterized by the development of alate plates in their dorsal valves. Parastrophinids survived the Late Ordovician mass extinction event but were rare and low in diversity in the Silurian, and became extinct during the Early Devonian. Despite their nearly cosmopolitan distribution, parastrophinids usually occur only as a minor component of brachiopod faunas in Laurentia (Titus 1986). Notable exceptions include the Trentonian (early Katian) *Parastrophina*-bearing beds in the Ottawa area and the latest Ordovician (Hirnantian) *Parastrophinella reversa* (Billings, 1857) shell beds from the Ellis Bay Formation of Anticosti Island, eastern Canada (Wilson 1914; Jin and Copper 1997, 2000).

In some early studies (Schuchert and Cooper 1932; Amsden and Biernat 1965), there was some confusion about the morphological differences between *Parastrophina* Schuchert and LeVene, 1929 and *Parastrophinella* Schuchert and Cooper, 1931 especially regarding the configuration of the septalium in *Parastrophinella*. The early interpretation of a sessile septalium with subparallel inner hinge plates (= outer plates of old usage) was followed by Amsden and Biernat (1965) in the Treatise on Invertebrate Paleontology and became widely accepted subsequently. Later, Jin and Copper (1997) studied the type species of *Parastrophinella*, *P. reversa* (Billings, 1857), from the type locality of Anticosti Island and showed that its septalium is supported along its entire length by a low median septum, although the septum is buried in shell thickening apically to make the septalium appear sessile.

The early misinterpretation of a sessile septalium with subparallel inner hinge plates led to some misidentifications of *Parastrophinella*. Several Late Ordovician and Early Silurian parastrophinid species with discrete inner hinge plates, which superficially resemble a sessile septalium, were assigned to the genus (Amsden 1968; Rozman 1970a, b, 1981; Rubel 1970; Oradovskaya in Nikolaev et al. 1977; Severgina 1978; Oradovskaya 1983). Most of these taxa were described from the middle Katian (lower Ashgill, Upper Ordovician) of the microplates and island arcs (e.g., Northeast Siberia, Mongolian Altai, and Sayany-Altai of Russia) that probably constituted an active margin of Siberia during the Ordovician. These

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Siberian and Mongolian species exhibit a wide range of variation in external morphology (such as anteriorly developed costae and shell asymmetry), but invariably possess discrete, subparallel inner hinge plates. The forms described by these authors were not assigned to *Anastrophia* Hall, 1867, which has discrete and clearly separated inner hinge plates, because they lack the *Anastrophia*-type, sharply developed costae that extend from the apex to the anterior margin. As a result, after the revised diagnosis of *Parastrophinella* by Jin and Copper (1997), a group of species with relatively weak, anteriorly developed costae and distinctly discrete inner hinge plates were left without a generic assignment.

During recent field work in the Hudson Bay region of Canada, the first author found more material of faintly costate parastrophinid shells, with discrete inner hinge plates, from the Lower Silurian (uppermost Telychian) Attawapiskat Formation. This provided an opportunity to examine this group of parastrophinids in detail. The main objective of this study, therefore, is to evaluate the taxonomic position of these parastrophinids and compare them with similar forms from Siberia, Kazakhstan, and Mongolia reported previously by brachiopod workers of the former USSR.

Institutional abbreviations.—CNIGR, F.N. Tschernyshev Central Geological Scientific Research and Exploration Museum, St. Petersburg, Russia; NMW, National Museum of Wales, Cardiff, UK; ROM, Royal Ontario Museum, Toronto, Canada.

Localities of the Hudson Bay material

A summary of the Palaeozoic Hudson Bay Basin and the Lower Silurian stratigraphy was given recently by Jin (2003, 2005) and will not be repeated here. Suffice it to note that the parastrophinid shells, described in this paper as *Protanastrophia repanda* gen. et sp. nov. (Fig. 1), occur as a relatively minor component of a numerically rich, taxonomically diverse, reef-dwelling brachiopod fauna in the Lower Silurian Attawapiskat Formation. The brachiopod associations are characterized by a high density of individuals and commonly high species diversity, and are dominated variously by pentamerids, gypidulids, leptocoelids, trimerellids, atrypids, and lissatrypids (Jin 2003, 2005). So far, *P. repanda* has been found in three outcrops (AK2, AK4, and AK8) of the Attawapiskat Formation on Akimiski Island of the Hudson Bay region. In the list below, the locality coordinates are given in Universal Transverse Mercator (UTM) grid.

Locality AK2.—Tidal flat outcrop along shoreline at first point southeast of camp site, low-relief reef knob just on northwest side of another knob (AK1). About 1.5 m of section of the Attawapiskat reef exposed along shoreline. AK2a: Collection near southern end of AK2 reef exposure, UTM 17 E0502919, N5883641; a brachiopod cluster dominated by *Pentameroides* Schuchert and Cooper, 1931 and *Gypidula* Hall, 1867. AK2b: Collection from an area of 3 m^2 near AK2c, in central part of AK2 reef exposure, UTM 17 E0502915, N5883664; a brachiopod cluster dominated by relatively small shells. AK2c: Collection from an area about 3 m^2, UTM 17 E0502916, N5883663; a brachiopod cluster dominated by *Gypidula*. AK2-01a: Collection from an area of 3 m^2 area on eastern side of AK2 outcrop, UTM 17 E0502818, N5883943; a brachiopod cluster dominated by *Pentameroides*.

Locality AK4.—Houston Point, a patch reef outcrop on tidal flat immediately northeast of a prominent beach ridge. About 1.5 m of section exposed at low tide and becomes almost completely submerged at high tide. AK4b: Collection from an area of 4 m^2 immediately adjacent to a gravel beach ridge, near south end of AK4 outcrop, UTM 17 E0492180, N5894740; a brachiopod cluster dominated by *Pentameroides*.

Locality AK8.—Shoreline outcrop on east side of Houston Point, with flat-lying shelly wackestone to packstone of inter-reef facies; coral-stromatoporoid biostrome and framestone well developed locally. AK8-01e (AK8e): Collection from an area of 2 m^2, a cluster of mostly hollow shells of *Pentameroides* (with well-preserved juveniles) against a large coral colony, UTM 17 E0492757, N5892783.

Systematic palaeontology

Order Pentamerida Schuchert and Cooper, 1931

Suborder Syntrophiidina Ulrich and Cooper, 1936

Superfamily Camerelloidea Hall and Clarke, 1894

Family Parastrophinidae Ulrich and Cooper, 1938

Genus *Protanastrophia* nov.

Type species: *Protanastrophia repanda* gen et sp. nov. Attawapiskat Formation, Akimiski Island, Hudson Bay region, Nunavut, Canada.

Derivation of the name: Greek, *proto-*, first, early. *Protanastrophia* implies an early form of parastrophinid similar to *Anastrophia*.

Diagnosis.—Small, transversely elliptical to subpentagonal, dorsibiconvex shell, smooth posteriorly, faintly to moderately costate anteromedially; dorsal valve usually larger, deeper, with higher and more prominent umbo than ventral valve. Ventral sulcus and anterior commissure commonly asymmetrical. Ventral median septum short, low; inner hinge plates high, discrete, subparallel to each other; alate plates present.

Other species assigned.—Most species assigned to the new genus were described initially in publications that are not easily accessible. Thus a brief note on each species is provided herein.

Parastrophinella asimmetrica Rozman, 1970a (72, pl. 5: 10–13, text-fig. 20), Upper Ordovician (Katian, Padun Stage), Nalchan Formation, Selenyakh Range, Northeast Siberia,

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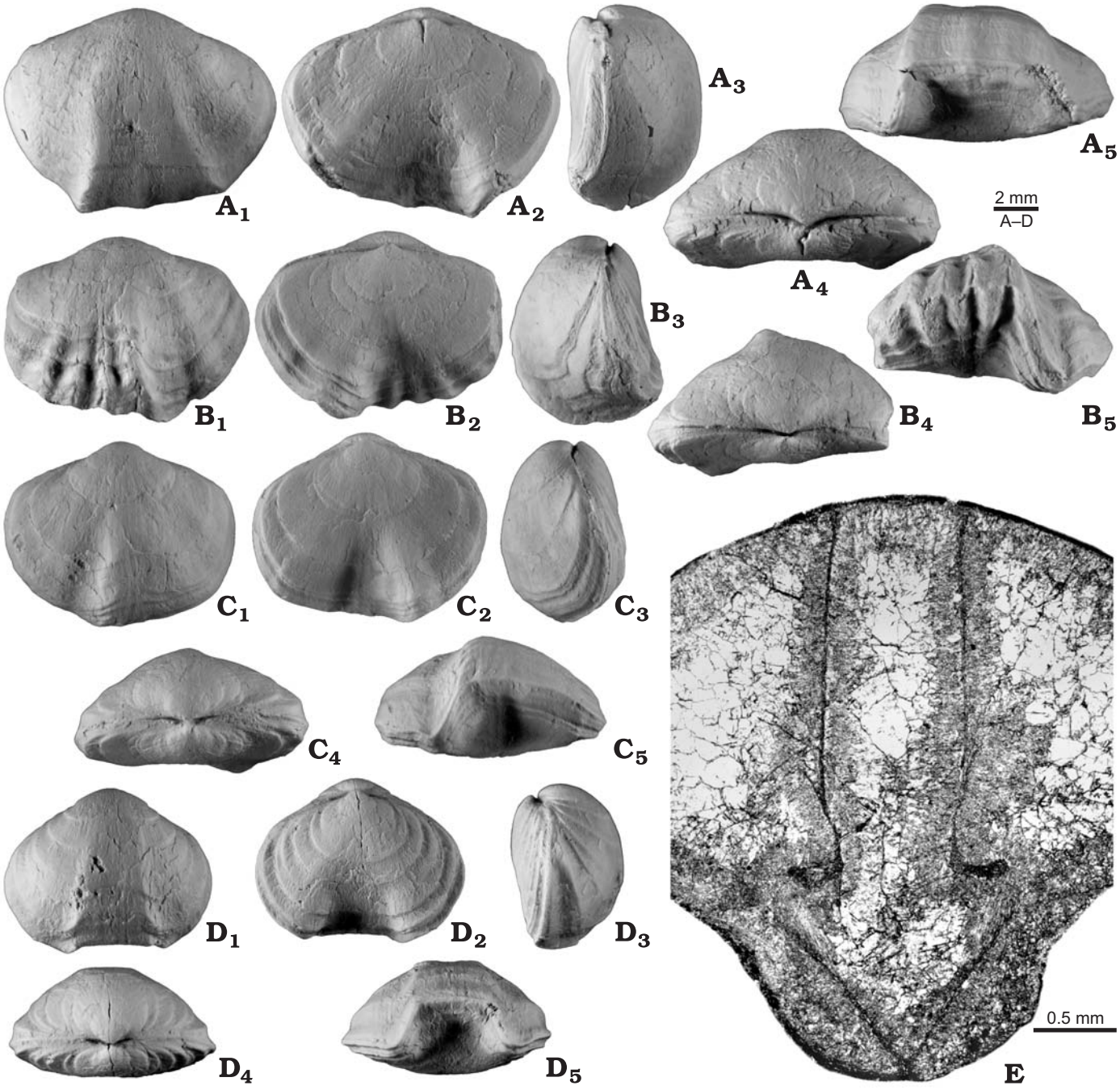

Fig. 1. Pentameride brachiopod *Protanastrophia repanda* gen. et sp. nov.; Attawapiskat Formation, uppermost Telychian, Akimiski Island, Hudson Bay region, Nunavut, Canada. **A**. ROM 57734, holotype, dorsal (A_1), ventral (A_2), lateral (A_3), posterior (A_4), and anterior (A_5) views. **B**. ROM 57735, paratype, dorsal (B_1), ventral (B_2), lateral (B_3), posterior (B_4), and anterior (B_5) views of strongly asymmetrical, anteriorly costate shell. **C**. ROM 57736, paratype, dorsal (C_1), ventral (C_2), lateral (C_3), posterior (C_4), and anterior (C_5) views of asymmetrical shell without costae. **D**. ROM 57737, paratype, dorsal (D_1), ventral (D_2), lateral (D_3), posterior (D_4), and anterior (D_5) views of relatively small, largely symmetrical shell. **E**. ROM 57738, paratype, micrograph of transverse serial section, showing low ventral median septum, broad V-shaped spondylium, smooth alate plates, and discrete inner hinge plates, 0.7 mm from apex (refer to Fig. 3).

Russia. Shell dorsibiconvex, up to 13 mm wide, asymmetrical shell with sigmoidal anterior commissure; ventral sulcus and dorsal fold originating at midlength of mature shells; up to 14 rounded costae in anterior half of shell; discrete, parallel inner hinge plates. Rudimentary strophic shell with a small ventral interarea in this species can be inferred from the transverse serial sections and emended diagnosis of *Parastrophinella* provided by Rozman (1970a).

Parastrophinella distorta Oradovskaya in Nikolaev et al. 1977: 48, pl. 5: 4. Upper Ordovician (Katian, Tirekhtyakh Stage), lower part of Tirekhtyakh Formation, Member N, Northeast Siberia, Russia. Shells up to 15 mm wide, weakly

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dorsibiconvex, strongly asymmetrical shell with sigmoidal anterior commissure; rudimentary, apsacline ventral interarea (Oradovskaya 1983: pl. 9: 2), incipient fold and sulcus originating at 2–3 mm from umbo; up to 24 rounded ribs originating at some distance from umbones of both valves; discrete, subparallel inner hinge plates.

Parastrophinella gracilis Oradovskaya, 1983 (52, pl. 10: 4–7). Upper Ordovician, (Katian, Tirekhtyakh Stage), lower part of Tirekhtyakh Formation, Member Q, Northeast Siberia, Russia. Shells symmetrical, up to 10 mm wide, strongly dorsibiconvex; ventral sulcus and dorsal fold originating at midlength of mature specimens; single low, rounded costa in sulcus and two costae on fold in larger shells; up to two gentle costae on each shell flank in relatively large shells; discrete, subparallel inner hinge plates. Existing descriptions and illustrations make it difficult to determine a strophic or astrophic condition of the shell.

Parastrophinella indistincta Rubel, 1970, Silurian, lower to middle Rhuddanian, Estonia. Shell up to 12 mm long, dorsibiconvex; anterior commissure uniplicate, symmetrical or slightly asymmetrical; ventral sulcus, dorsal fold, and costae developed anteriorly; one or two costae in sulcus, two or three on fold, one to three on each flank; broad spondylium supported by low median septum extending to midlength of valve; parallel inner hinge plates. Strophic or astrophic condition of the shell cannot be determined from available data.

Parastrophinella lepida (Thomas, 1926), St. Clair Limestone, Arkansas, and Clarita Formation (Fitzhugh Member), Wenlock, Oklahoma (see description of Amsden 1968).

Parastrophinella salairica Severgina, 1978 (see also Rozman 1981: 156, pl. 40: 1–10, pl. 41: 1–4, text-figs. 47, 48), Upper Ordovician (Katian), upper Chakyr and lower Dietken regional stages of Salair and Gornyi Altai, southwestern Siberia, Russia; Tsagandel, Sairin, and Uregnur beds of Mongolia. Shells up to 12 mm long, strongly dorsibiconvex; anterior commissure uniplicate, symmetrical or slightly asymmetrical; ventral sulcus and dorsal fold originating at midlength; costae in anterior half of shell, one to five in sulcus, two to six on fold, and three to seven on each flank; narrow spondylium supported by median septum extending to midlength of valve; parallel inner hinge plates. Strophic or astrophic condition of the shell cannot be determined from available data.

Species questionably included.—?*Parastrophinella asimmetrica longiplicata* Rozman, 1981, Upper Ordovician (Katian), middle Tsagandel beds, Mongolia. Known from a single specimen about 10 mm long. Externally similar to *Parastrophinella asimmetrica* but differs in having 18 costae originating in umbonal area. Interior of both valves unknown.

Parastrophinella sp. (Nikiforova, 1978), Silurian (Llandovery), Minkuchar beds, Zeravshan Range, Uzbekistan. Known from one complete shell and three dorsal valves. Smooth, symmetrical, dorsibiconvex shell with ventral sulcus and dorsal fold originating anterior of umbo, subparallel inner hinge plates, and small alate plates.

Occurrences.—Late Ordovician (Ashgill, middle to late Katian)–Early Silurian (Wenlock), North America, Northeast Siberia, Gornyi Altai, Estonia.

Discussion.—The new genus is most similar to *Anastrophia* Hall, 1867 and *Grayina* Boucot, 1975 in having consistently discrete, subparallel inner hinge plates, but the latter two genera of Wenlock–Pragian age have a symmetrical shell with strong costae that extend from the apex to the margin (Havlíček 1990; Carlson 2002). In the new genus, asymmetrical fold and sulcus tend to become common in larger shells (greater than 8 mm long and 10 mm wide). Such shell asymmetry is rare in other genera of the family Parastrophinidae. In all other parastrophinid genera, the inner hinge plates are united basomedially to form a septalium, which may be posteriorly sessile or supported by a median septum along its entire length (Jin and Copper 1997).

Protanastrophia repanda gen. et sp. nov.

Figs. 1–3.

Derivation of the name: Latin *repandus*, curved, deflected, referring to the warped, asymmetrical, anterior shell margin.

Type material: Holotype, ROM 57734 (Fig. 1A) and four figured paratypes, ROM 57735, 57736, 57737, (Fig. 1B–D), and 57738 (the last serially sectioned, see Figs. 1E, 3).

Type locality and type horizon: AK2c is a shoreline outcrop on the north side of Akimiski Island, UTM 17 E0502916, N5883663, Hudson Bay region, Nunavut, Canada.

Type horizon: Attawapiskat Formation (uppermost Telychian, Lower Silurian), UTM 17 E0502916, N5883663, Hudson Bay region, Nunavut, Canada.

Material.—AK2a (5 specimens), AK2b (21), AK2c (21, including illustrated types), AK2-01a (2), AK4b (1), AK8-01e

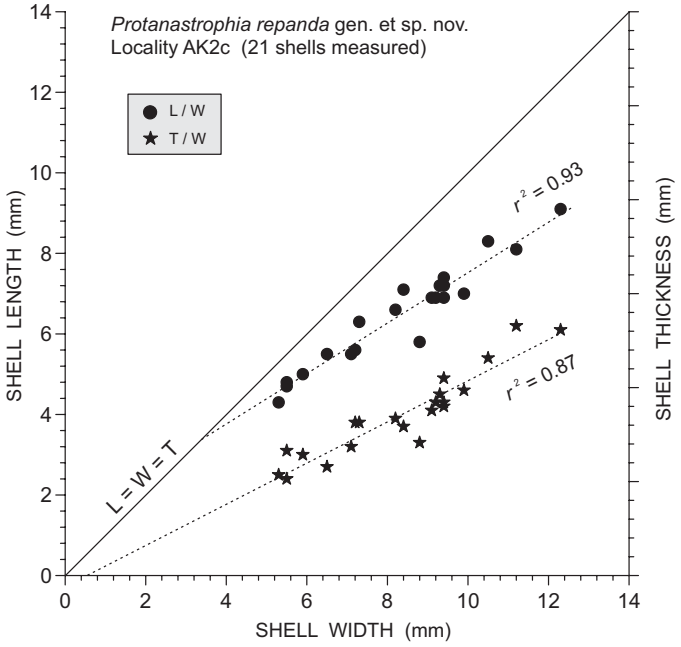

Fig. 2. Shell measurements of *Protanastrophia repanda* gen. et sp. nov. Sample AK2c, Attawapiskat Formation, Akimiski Island, Hudson Bay region, Nunavut, Canada.

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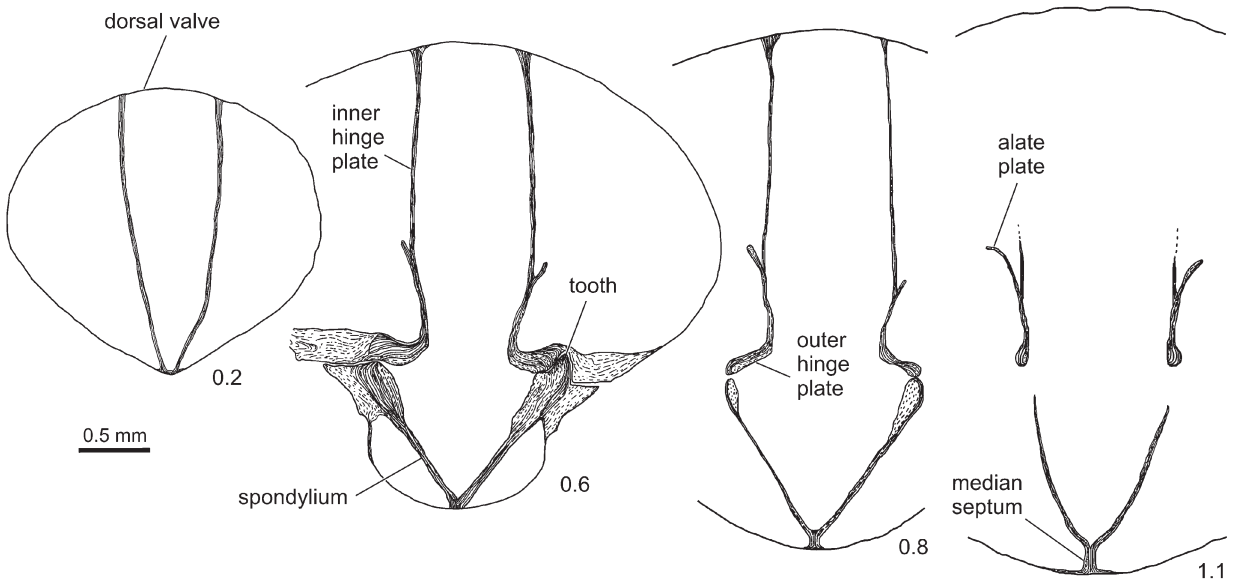

Fig. 3. Sketches of selected serial sections of *Protanastrophia repanda* gen. et sp. nov. ROM 57738, paratype, Attawapiskat Formation, locality AK2c, Akimiski Island, Nunavut, Canada. Numbers denote distance from apex.

(1). All are from the Attawapiskat Formation, uppermost Telychian, Akimiski Island, Hudson Bay region, Canada. Repository: Royal Ontario Museum.

Diagnosis.—Shell small, transversely elliptical to subpentagonal, dorsibiconvex, smooth posteriorly, weakly costate anteromedially; dorsal valve notably larger, deeper, with higher and more prominent umbo than ventral valve. Anterior commissure uniplicate, variably asymmetrical or sigmoidal. Ventral sulcus and dorsal fold developed anteriorly, broad and variously asymmetrical. Ventral median septum short, very low; inner hinge plates high, discrete, subparallel to each other; alate plates well developed.

Description.—Shell small, transversely subelliptical to pentagonal, strongly dorsibiconvex, with average length 6.5 mm, width 8.4 mm, and thickness 4 mm (Fig. 2; Table 1). Hinge line one-third to one-half of shell maximum width; maximum width of shell attained near midlength of shell. Ventral valve weakly convex posteromedially, becoming flattened towards lateral and anterior margins (Fig. 1A–D); ventral umbo low, inconspicuous; sulcus originating near midlength of shell, widening rapidly towards anterior margin, symmetrical in smaller shells, becoming asymmetrical in relatively large forms. Dorsal valve three to four times deeper than ventral, with larger and more convex umbo extending posteriorly beyond that of ventral valve; fold broad, gentle, developed corresponding to sulcus in position and in symmetrical or asymmetrical contours. Posterior and lateral portions of shell surface smooth; anteromedial part of shell varying from smooth, faintly costate, to moderately costate (Fig. 1A_1, B_1, C_1, D_1). Coarse, concentric growth lamellae usually present, best developed at late growth stage.

Table 1. Measurement statistics of 21 shells of *Protanastrophia repanda* gen. et sp. nov. Attawapiskat Formation, locality AK2c, Akimiski Island, Hudson Bay region.

$n = 21$	Length (mm)	Width (mm)	Thickness (mm)
Minimum	4.3	5.3	2.4
Maximum	9.1	12.3	6.2
Mean	6.49	8.35	4.00
Standard deviation	1.27	1.94	1.06

Spondylium broadly triangular in transverse cross section (Figs. 1E and 3), sessile apically, raised slightly above valve floor anteriorly by short, low median septum. Spondylial comb structure (sensu Jin and Copper 2000) not observed. Inner hinge plates slender, high, subparallel to each other along their entire length (except at their apical origin); outer hinge plates rudimentary; alate plates present but not prominent (Fig. 3). Muscle field poorly impressed.

Discussion.—The new species is similar to *Protanastrophia lepida* (Thomas, 1926) in its small, dorsibiconvex shell that is quasi-smooth or has gentle anteromedial costae (see Amsden 1968). *Protanastrophia lepida*, however, tends to have an anteromedially protruding tongue, with a notably higher ventral median septum and more prominent alate plates. The strongly asymmetrical sulcus, which is common in relatively large forms of *P. repanda*, is not obvious in *P. lepida*. The two forms described by Rozman (1970a, 1981) from the Upper Ordovician of Siberia and Mongolia resemble the new species in their asymmetry, but these forms have considerably stronger shell costae.

Genus *Parastrophina* Schuchert and LeVene, 1929

Parastrophina portentosa (Nikitin and Popov in Nikitin et al. 1996)

Figs. 4, 5.

1996 *Parastrophinella portentosa* Nikitin and Popov in Nikitin et al. 1996: 91, figs. 5C, 6A–K.

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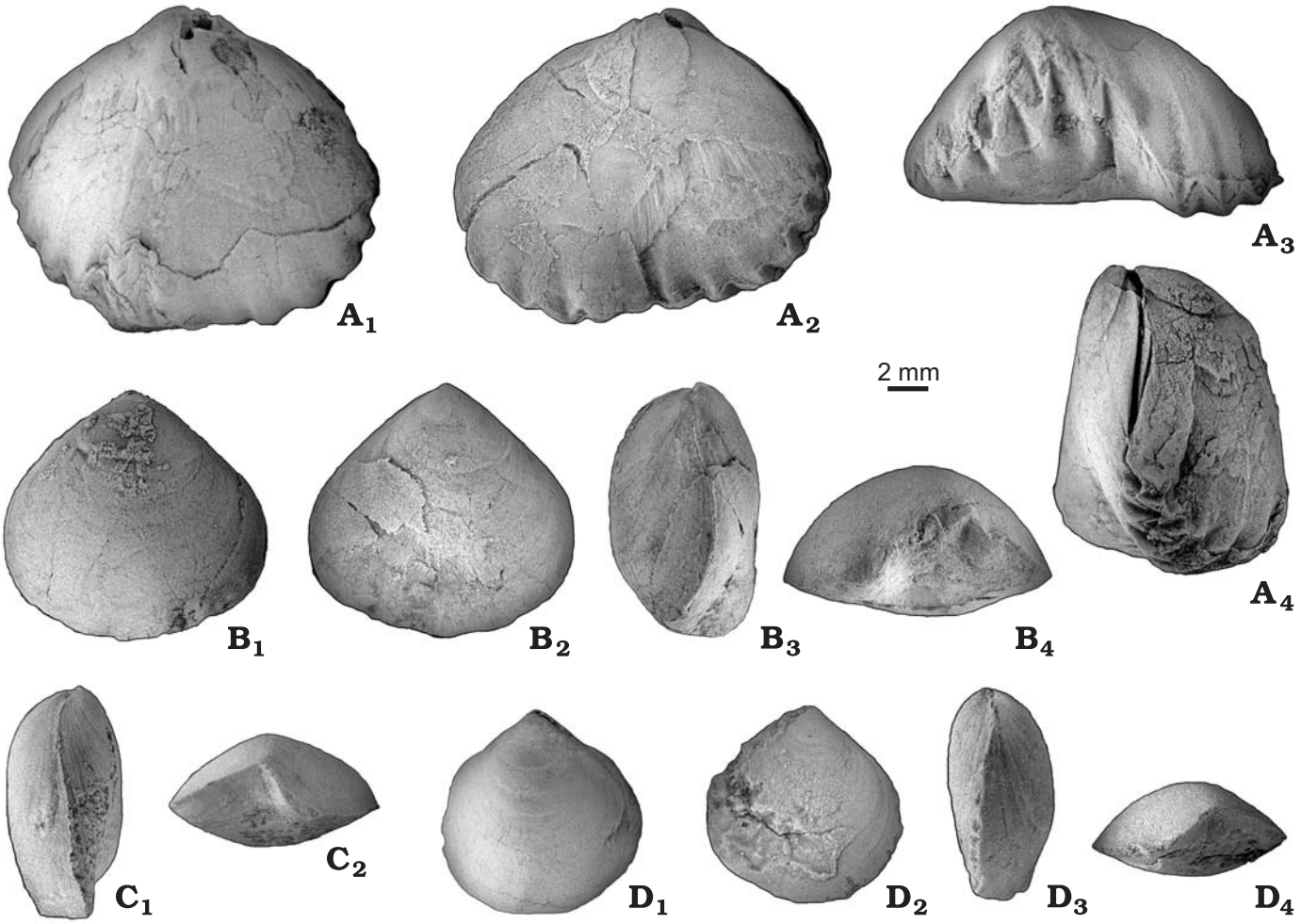

Fig. 4. Pentameride brachiopod *Parastrophina portentosa* (Nikitin and Popov in Nikitin et al. 1996), Upper Ordovician, Dulankara Regional Stage, sample F-1014, Sortan-Manai, northern Betpak-Dala desert, Central Kazakhstan. **A**. NMW 98.28G.351, paratype, dorsal (A_1), ventral (A_2), anterior (A_3), and lateral (A_4) views of asymmetrical shell. **B**. NMW 98.28G.352, paratype, dorsal (B_1), ventral (B_2), lateral (B_3), and anterior (B_4) views. **C**. NMW 98.28G.353, paratype, lateral (C_1) and anterior (C_2) views of smooth, asymmetrical shell. **D**. NMW 98.28G.354, paratype, dorsal (D_1), ventral (D_2), lateral (D_3), and anterior (D_4) views of asymmetrical, juvenile shell.

Type material: Holotype, CNIGR 28/12888, conjoined shell.

Type locality: Sample F-1014, Sortan-Manai, northern Betpak-Dala desert, Central Kazakhstan.

Type horizon: Upper Ordovician, lower Katian, Dulankara Regional Stage.

Material.—Paratypes, NMW 98.351–383, total of 32 complete shells, same locality and stratum.

Diagnosis (emended herein).—Shell subpentagonal, dorsibiconvex, asymmetrical, with sigmoidal anterior commissure; ventral sulcus and dorsal fold originating at 7 mm or more from apex; costae subangular, 5–12 per valve, present in shells larger than 11 mm long. Spondylium V-shaped in transverse cross section, supported by medium septum along its entire length; septalium narrow, usually asymmetrical in cross section, supported by low median septum.

Discussion.—The species was initially thought to have a sessile septalium and assigned to *Parastrophinella* (Nikitin et al. 1996). Subsequent examination of paratypes by detailed serial sectioning shows that the species invariably possesses a low dorsal median septum that supports a septalium. Thus, the species is regarded herein as an aberrant form of *Parastrophina*, characterized by an asymmetrical shell and sigmoidal anterior commissure (Fig. 4), unlike other species of the genus. Its dorsal cardinalia are similar to those of typical *Parastrophina* except for its asymmetrical cross section (Fig. 5). In *Parastrophina iliana* Popov, Cocks, and Nikitin, 2002, from the Upper Ordovician Anderken Formation of the Chu-Ili Range, the adult shells also show a tendency towards an asymmetrical anterior commissure, but their ventral sulcus and dorsal fold are well defined and the anterior commissure retains its uniplicate character.

Cladistic analysis

Outgroup selection and methods.—The morphological evolution of early pentamerides, especially camerelloids, is one of

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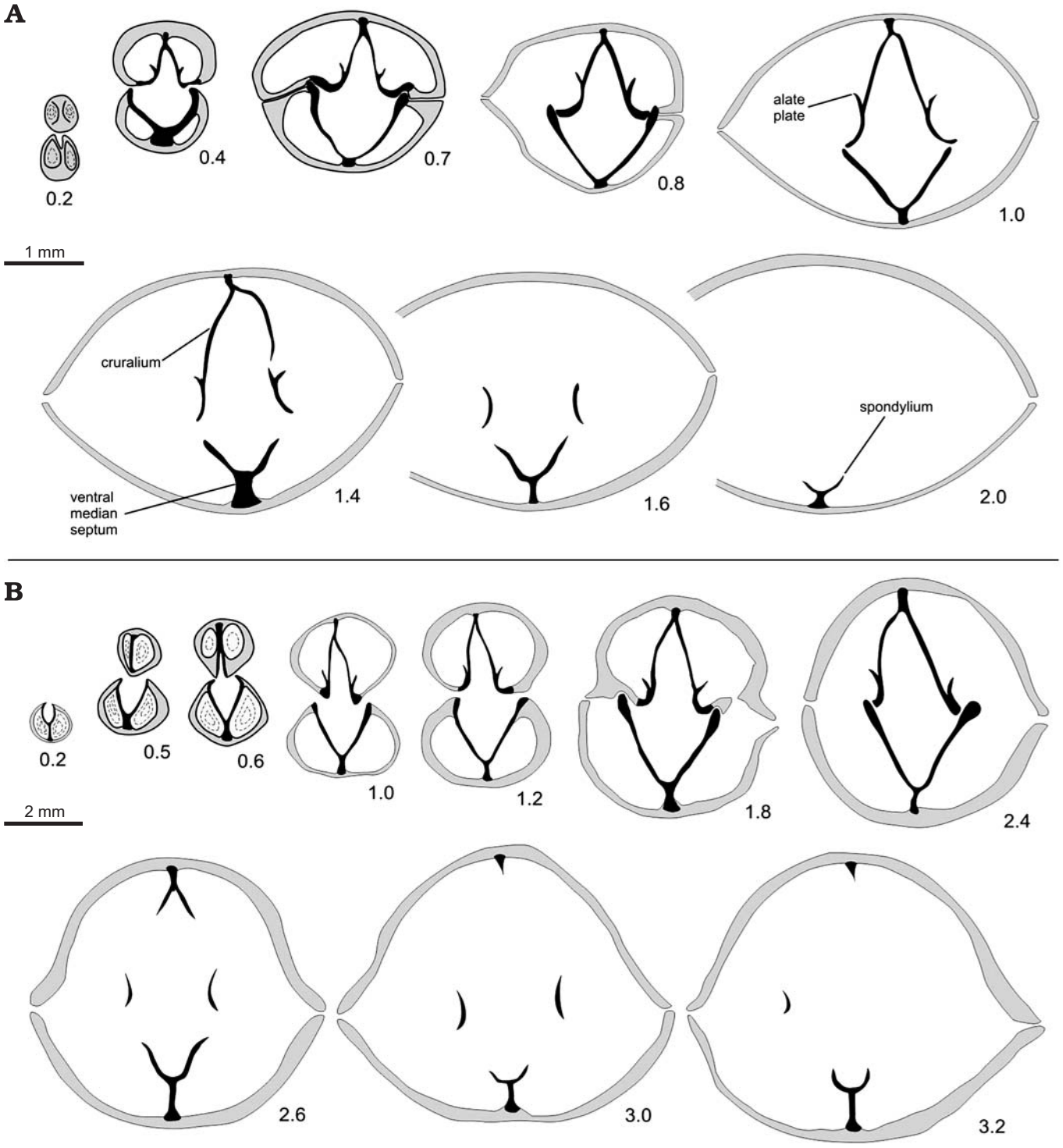

Fig. 5. Transverse serial sections of two paratype specimens of *Parastrophina portentosa* (Nikitin and Popov in Nikitin et al. 1996), Upper Ordovician, Dulankara Regional Stage, sample F-1014, Sortan-Manai, northern Betpak-Dala desert, Central Kazakhstan. **A**. NMW 98.28G.383, juvenile specimen. **B**. NMW 98.28G.377. Numbers indicate distances from apex.

the major features of the Ordovician biodiversification but remains poorly understood and in some cases confusing (Carlson 1993, 1996). In particular, a spondylial structure of pentamerides is thought to have evolved through the merging of discrete dental plates (Carlson 2002). However, *Leioria bentori* Cooper, 1976 from the early Middle Cambrian of the Rift Valley of Israel, one of the earliest known rhynchonelliformean brachiopods, has pentameride features, such as a free spondylium that can merge with the valve floor in the gerontic shells and well-defined brachiophore supports unlike Cambrian orthides, which suggest the species as a member of the ancestral pentameride stock. *Leioria* was assigned by

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Williams and Harper (2000) to the Order Protorthida. Unlike other protorthides, however, *Leioria* has derived cardinalia, with dental sockets and brachiophores, and can be considered within primitive Syntrophiidina as was defined by Carlson (2002). It is thus likely that a free spondylium in pentamerides was a primitive and probably plesiomorphic character shared with protorthides and, in subsequent morphological evolution, it merged with the valve floor to form a sessile spondylium or became supported by a median septum. Moreover, recent study of the ontogeny of *Apomatella* and *Gonambonites* (see Vinn and Rubel 2000; Popov et al. 2007) also shows that spondylium simplex in the early clitambonitides (excluding polytoechioids) formed from a free muscle platform in juveniles. This condition persists in the adult Mid Cambrian *Arctohedra*, that otherwise shows distinct clitambonitide-type cardinalia. Protorthides have very primitive cardinalia devoid of brachiophores or sockets, but possess paired teeth and a free spondylium. For this reason, two protorthide taxa, *Psiloria dayi* Cooper, 1976 with a smooth shell and *Glyptoria gulchensis* Popov and Tikhonov, 1993 with distinct radial ornaments were selected for the present cladistic analysis. The chileides, which probably embrace the most primitive Cambrian rhynchonelliformean brachiopods, were already proven useful for defining a polarity of some basic morphological features (Holmer et al. 1995). Therefore, *Chile mirabilis* Popov and Tikhonov, 1990 was included also in the analysis, as was the early strophomenate *Billingsella aliena* Nikitin, 1956. *Bohemiella romingeri* (Barrande, 1848) and *Wimanella seges* Kruse, 1990 of Mid Cambrian age represent a variety of shell morphotypes within the early orthides.

The main scope of the present study is confined to the family Parastrophinidae, which is considered an advanced group of the Superfamily Camerelloidea (Carlson 1996: 816). To put this study in a broader phylogenetic context, the Late Cambrian *Huenella biplicata* Nikitin, 1956 (family Huenellidae), *Palaeostrophia fibrillosa* Nikitin and Popov, 1983 and the Early Ordovician *Tetralobula peregrina* Popov, Egerquist, and Zuykov, 2005 (family Tetralobulidae) are included in the analysis to cover the basal syntrophiidine stock. *Idiostrophia prima* Popov, Egerquist, and Zuykov, 2005, *Liricamera nevadensis* Cooper, 1956, *Plectocamara*? *extenuata* (Nikitin and Popov, 1984), *Bleshidium patellinum* (Barrande, 1879), and *Schizostrophina margarita* Fu, 1982 were selected as representatives of the families Camerellidae and Parallelelasmatidae.

The core taxa presently considered within the family Parastrophinidae is represented by 19 Ordovician and Silurian species and nine genera (see Appendix 1). A data matrix derived from 48 unordered, unweighted, taxonomically significant characters with 186 character states was analyzed cladistically using the software PAUP 4.0 (Swofford 2002; Appendices 2, 3). A heuristic search resulted in six shortest trees, 439 steps long, with a consistency index of 0.3189, homoplasy index of 0.6811, rescaled consistency index of 0.2069, and retention index 0.6486. A strict consensus tree is shown in Fig. 6 (see also Appendices 1–3).

Character selection.—The number of diagnostic features available for camerelloids is rather limited mainly due to their simple external morphology and inadequate knowledge of their dorsal cardinalia and mantle canal system in most of the taxa. Potentially important differences in the morphology of spondylium, especially its subdivision into spondylium simplex and spondylium duplex, can hardly be applied to the camerelloids unless shell structure and ontogeny are studied and ontogenetic development of the ventral median septum is understood. The spondylium duplex is considered one of the diagnostic characters of the Family Parastrophinidae (Carlson 2002), although this view is not accepted by Sapelnikov (1985) who considered spondylium duplex to be characteristic only of the Pentameridina. In this study, 48 characters are used for the cladistic analysis of a relatively large number of taxa (see Appendix 2).

Results and implications for parastrophinid phylogeny and palaeobiogeography

Results of the present analysis should be viewed as a preliminary attempt to understand the phylogenetic relationships of the taxa within the Superfamily Camerelloidea and, in particular, genera presently included into the family Parastrophinidae. The high level of homoplasy in character transformations resulted in low values of consistency index. This, combined with a limited number of informative features that can be applied to the large number of analyzed taxa, do not allow the cladistic results to be considered as a firm basis for revising the camerelloid systematics. However, the possible plesiomorphic nature of the alate plates in septalium-bearing parastrophinids and their possible secondary loss in the camerellids makes the alate plates a weak basis for defining the Family Parastrophinidae. Results of the analysis also put more weight on the presence of the septalium and the dorsal median septum. As a consequence, genera of the Family Camerellidae appear as a sister stock of early septalium-bearing parastrophinid genera *Eoanastrophia* and *Plectosyntrophia*. Nevertheless, all analyzed camerellid taxa are stratigraphically older, and independent acquisition of the septalium within the group of early camerelloid genera initially lacking the alate plates cannot be excluded from consideration.

The cladogram shows five species of *Protanastrophia* (Fig. 6, node 13) characterized by such a synapomorphic character as shell asymmetry in juveniles. The presence of alate plates and subparallel inner hinge plates seems to be symplesiomorphic at the base of camerelloid clade (node 10). They also constitute a sister group of the Family Parallelelasmatidae, which differs from *Protanastrophia* in the acquisition of an astrophic shell and in the absence (secondary loss) of alate plates.

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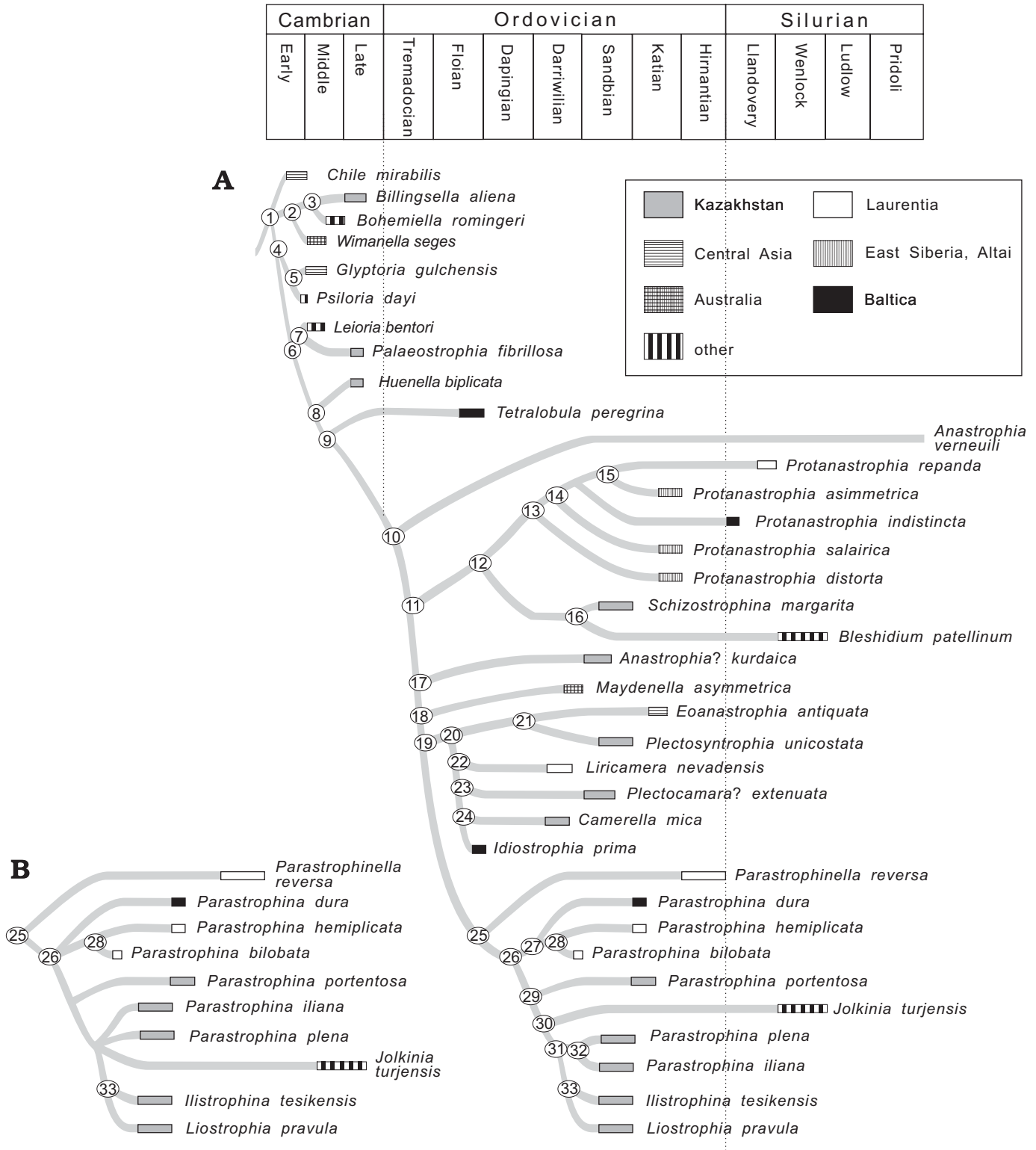

Fig. 6. Stratigraphic ranges and inferred phylogenetic relationships of 19 parastrophinid species and other selected syntrophiidine species based on one of six equally parsimonious cladograms (**A**) and emended topography of the *Parastrophina* cluster shown in strict consensus tree (**B**). Numbered nodes are supported by the character states listed in Appendix 3.

Another outcome of the analysis is that the Silurian genus *Bleshidium*, originally assigned to the Camerellidae (Havlíček and Storch 1990), should be reassigned to the Parallelelasmatidae. The presence of the long, discrete, subparallel inner hinge plates, together with the absence of alate plates, a septalium and a dorsal median septum, is in accordance with the revised diagnosis of the family (Carlson 2002).

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The presence of a septalium and dorsal median septum appears to be synapomorphic feature shared by advanced camerellids and parastrophinids (Fig. 6, node 18), whereas the astrophic shell was acquired by camerellids (Fig. 6, node 23) and advanced parastrophinids (Fig. 6, node 26) independently. The cladistic analysis suggests that the smooth shells of *Liostrophia* Cooper and Kindle, 1936 and *Ilistrophina* Popov, Cocks, and Nikitin, 2002 are the most advanced state of shell morphology within the parastrophinids.

In addition to the paraphyletic nature of the Parastrophinidae, the cladistic analysis shows a clear separation of derived parastrophinids with a septalium from the taxa with discrete inner hinge plates (*Anastrophia*, *Protanastrophia*, and the Parallelelasmatidae), notwithstanding the presence or absence of alate plates. Interestingly, there is a concomitant biogeographical separation between these two groups of parastrophinids.

In Laurentia and peri-Gondwana, parastrophinids with a septalium first appeared near the Mid-Late Ordovician boundary. They coexisted with the family Parallelelasmatidae, a sister group of *Protanastrophia* according to the cladistic analysis of this study. In these palaeogeographic regions, *Anastrophia*? *kurdaica* Sapelnikov and Rukavishnikova, 1975 is the only species known to have discrete inner hinge plates during the Ordovician. In Laurentia, parastrophinids usually constituted an insignificant component of the benthic faunas (Titus 1986) whereas in tropical peri-Gondwana, particularly in North China and the Chu-Ili microplate, they experienced rapid diversification early in the Late Ordovician (Popov et al. 2002; Fu 1982) as a distinct component of the benthic assemblages in the carbonate mound biofacies. Some of these taxa show a tendency towards an asymmetrical shell with a sigmoidal anterior commissure, such as in *Parastrophina portentosa*. In external morphology, *P. portentosa* shows some degree of superficial similarity to *Protanastrophia* gen. nov. and especially to *Protanastrophia repanda* sp. nov., but it differs internally by having a septalium supported by a median septum (Figs. 1, 4, 5). The morphological differences in the dorsal cardinalia of *Parastrophina portentosa* and *Protanastrophia repanda* are shown by the cladistic analysis to be of phylogenetic significance.

The first occurrence of *Parastrophina* in the Oandu Regional Stage (early Katian) of Baltica (Popov et al. 2005) postdates its first occurrence in tropical peri-Gondwana (North China, Chu-Ili) by about one chronostratigraphical stage, suggesting a delayed faunal migration of *Parastrophina* between the two tectonic regions. A probable scenario is that septalium-bearing parastrophinids evolved somewhere in tropical peri-Gondwana and subsequently spread outside Gondwana in two dispersal events, the first being an invasion to Laurentia during the late Darriwilian, and the second to Baltica during the early Katian. A similar migration pattern in Late Ordovician brachiopods was observed also for the trimerellides and early atrypides (Popov et al. 1997, 1999). During the Late Ordovician, *Eoanastrophia* was confined largely to the temperate and high-latitude regions of Gondwana (Mélou 1990; Villas 1985).

The palaeobiogeographic pattern of *Protanastrophia* was remarkably different. All the Late Ordovician occurrences of the genus were confined to the marginal seas of Siberia (Altai-Sayan, Mongolia, and Northeast Siberia), probably the most remote and isolated continent during the Early Palaeozoic (Bassett et al. 2002; Fortey and Cocks 2003). Morphologically, the dorsal cardinalia of *Protanastrophia* were relatively primitive, especially in terms of the widely separated, subparallel inner hinge plates, without any tendency to develop into a septalium. This suggests an early separation of *Protanastrophia* from the main parastrophinid lineage. It is notable that septalium-bearing parastrophinids are absent from Siberia and its adjacent microplates, except for the Altai-Sayan region. Specimens referred by Kulkov and Severgina (1989) to *Parastrophina bilobata* Cooper, 1956 from the Karasinskaya Formation (upper Darriwilian) do not yield adequate information on their cardinalia and thus their parastrophinid affinity is questionable. *Anastrophia* aff. *kurdaica* from the Khankharinslaya Formation (lower Katian) lacks alate plates, which precludes its affinity to the family Parastrophinidae. *Parastrophina orlovensis* Severgina, 1978 and *Eoanastrophia transversa* Severgina, 1978 from the Orlovskaya Formation (upper Katian) may be true septalium-bearing parastrophinids, although their cardinalia remain poorly known.

Despite the incomplete fossil record of Ordovician parastrophinids from Siberia, the predominance of parastrophinids with relatively primitive cardinalia (i.e., widely discrete inner hinge plates) suggests that the Siberian parastrophinids evolved in prolonged palaeogeographic isolation, following an early separation from the main camerelloid stock. Palaeogeographic expansion of *Protanastrophia* towards Laurentia, Siberia and probably terranes of Central Asia in the Llandovery took place under a different palaeogeographic and palaeoenvironmental situation as a result of the Hirnantian mass extinction and the closure of the Iapetus Ocean.

Another outcome of the analysis is a possible link of the early pentamerides to protorthides. *Leioria* and *Palaeostrophia* are placed close to the base of the pentameride clade, whereas *Huenella*, which typifies the family Hunellidae, appears more derived.

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Appendix 1

Taxa used in phylogenetic analysis.

1. *Billingsella aliena* Nikitin, 1956, from the Upper Cambrian, Selety Formation, north-eastern Central Kazakhstan.
2. *Bohemiella romingeri* (Barrande, 1848), Middle Cambrian, Jince Formation, Bohemia.
3. *Chile mirabilis* Popov and Tikhonov, 1990, Lower Cambrian olistholith, Kuchek Alai Range, Kyrgyzstan.
4. *Glyptoria gulchensis* Popov and Tikhonov, 1993, Middle Cambrian olistolith, Arpatektyr Mountain, Kyrgyzstan.
5. *Huenella biplicata* Nikitin, 1956, Upper Cambrian, Selety Formation, north-eastern Central Kazakhstan.
6. *Idiostrophia prima* Popov, Egerquist, and Zuykov, 2005, Lower Ordovician, upper Floian, Billingenian, *Oepikodus evae* Biozone, St. Petersburg region, Russia.
7. *Leioria bentori* Cooper, 1976, Middle Cambrian, Nimra Formation, Timna, Israel.
8. *Palaeostrophia fibrillosa* Nikitin and Popov, 1983; Upper Cambrian, Paibian, Malyi Karatau Range, Kazakhstan.
9. *Plectocamara*? *extenuata* (Nikitin and Popov, 1984); Upper Ordovician, Sandbian, Sargaldak Formation, Kazakhstan. Originally this species was referred to *Eoanastrophia*, however, it shows a sessile septalium with no trace of a dorsal median septum. Alate plates are also absent. Its cardinalia is rather short and do not exceed one-quarter shell length (Nikitin and Popov 1984: text-fig. 34). Shell is definitely astrophic with no trace of a rudimentary ventral interarea.
10. *Psiloria dayi* Cooper, 1976; Lower Cambrian, Burj Limestone, eastern Dead Sea coast, Jordan.
11. *Tetralobula peregrina* Popov, Egerquist and Zuykov, 2005; Lower Ordovician, upper Floian, Billingenian, *Oepikodus evae* Biozone, St. Petersburg region, Russia.
12. *Wimanella seges* Kruse, 1990; Middle Cambrian, Tindall Limestone, Daly Basin, Northern Territory, Australia.
13. *Anastrophia verneuili* (Hall, 1857); Devonian, Lochkovian, lower Heidelberg Group, New York, USA.
14. *Anastrophia*? *kurdaica* (Sapelnikov and Rukavishnikova, 1975); Upper Ordovician, Sandbian, Kendyktas Range, Kazakhstan. The inner hinge plates converge towards the valve floor, but remain separated through the entire length; dorsal median septum absent. Probably an early form of *Anastrophia*. Shell is rudimentary strophic with a very narrow interarea as it can be seen from drawings of transverse serial sections given by Sapelnikov and Rukavishnikova (1975: text-fig. 6).
15. *Bleshidium patellinum* (Barrande, 1879); Silurian, Kopanina Formation, Bohemia.
16. *Camerella mica* Nikitina, Neuman, Popov, and Bassett, in Nikitina et al., 2006; Middle Ordovician, Darriwilian, Uzunbulak Formation, Chu-Ili Mountains, Kazakhstan.
17. *Eoanastrophia antiquata* Nikiforova and Sapelnikov, 1973; Upper Ordovician, Katian, Chashmankolon and Archalyk beds, Zeravshan Range, Uzbekistan. Shell is astrophic with well defined alate plates.
18. *Ilistrophina tesikensis* Popov, Cocks, and Nikitin, 2002; Upper Ordovician, Sandbian, Anderken Formation, Chu-Ili Range, Kazakhstan.
19. *Jolkinia turjensis* (Khodalevich, 1939); Silurian Wenlock, Elkino Beds, Urals, Russia.
20. *Liostrophia pravula* Popov, Cocks, and Nikitin, 2002; Upper Ordovician, Sandbian, Anderken Formation, Chu-Ili Range, Kazakhstan.
21. *Liricamera nevadensis* Cooper, 1956; Middle Ordovician, Darriwilian. Pogonip Group, Nevada, USA.
22. *Maydenella asymmetrica* Laurie, 1991; Middle Ordovician, upper Darriwilian, Cashions Creek Limestone, Tasmania. Rudimentary strophic shell with a very narrow ventral interarea as it was shown in the original description. The inner hinge plates converge onto a low median septum posteriorly. One of the oldest known parastrophinids.
23. *Parastrophina bilobata* Cooper, 1956; Middle Ordovician, uppermost Darriwilian, Pratt Ferry Formation, Alabama, USA. Oldest known species of *Parastrophina*.
24. *Parastrophina hemiplicata* (Hall, 1847), Upper Ordovician, lower Katian (Trentonian), USA, eastern Canada.
25. *Parastrophina iliana* Popov, Cocks, and Nikitin, 2002; Upper Ordovician, Sandbian, Anderken Formation, Chu-Ili Range, Kazakhstan.
26. *Plectosyntrophia unicostata* Popov, Cocks, and Nikitin, 2002; Upper Ordovician, Sandbian, Anderken Formation, Chu-Ili Range, Kazakhstan. Rudimentary strophic shell with a very narrow ventral interarea confirmed by the study of types.
27. *Parastrophina dura* (Oraspõld, 1956); Upper Ordovician, lower Katian, Oanduian, East Baltic.
28. *Parastrophina plena* Sapelnikov and Rukavishnikova, 1975; Upper Ordovician Sandbian, Anderken Formation, Chu-Ili Range, Kazakhstan.
29. *Parastrophinella reversa* (Billings, 1857); Upper Ordovician, Hirnantian, Ellis Bay Formation, Anticosti, Canada.
30. *Schizostrophina margarita* Fu, 1982; Upper Ordovician, Sandbian, Anderken Formation, Chu-Ili Range, Kazakhstan; Jinghe Formation of North China.

31–35. Five species of *Protanastrophia* (*P. repanda*, *P. asimmetrica, P. distorta*, *P. indistincta*, and *P. salairica*); see text for details.

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Appendix 2

Forty-eight diagnostic characters and 186 character states used for cladistic analysis of 36 brachiopod taxa.

1. out1 – shell outline: subcircular (L/W 0.9–1.1) (0), transversely suboval (L/W <0.9) (1), elongate suboval (L/W >1.1) (2), transverse subrectangular to subquadrate (3), transverse semioval (4), elongate subtriangular (5).
2. can – cardinal extremities: obtuse (0), almost right angled (1), evenly rounded (2).
3. pmw – maximum shell width: at hinge line (0), between hinge line and midlength (1) at midlength (2), anterior to midlength (3).
4. prl – profile (sagittal): subequally biconvex (0), dorsibiconvex (1), ventribiconvex (2).
5. hin – hinge: strophic (0), astrophic (1), rudimentary strophic (2). *Remark*: Recent studies revealed that a vestigial ventral interarea (see character 15) and rudimentary strophic hinge line in combination with a palintrope (see character 14) is characteristic of many early pentameridines (Jin et al. 2006; Rong et al. 2007), as well as some camerellids and parastrophinids (Carlson 2002). This condition was also noted by Jaanusson (1971: 36), who pointed out that "topographically anterior margin of these areas situated in front of the main part of the hinge-notch, and, thus, in front of the axis of rotation." It means that these "rudimentary strophic" shells were functionally astrophic.
6. vvp – profile (ventral valve): evenly convex with maximum height at midlength ((0); flattened or gently convex with maximum height at the umbonal area (1); convex with maximum height between the umbo and midlength (2).
7. dvp – profile (dorsal valve): evenly convex (0); convex with maximum height anterior to midlength (1); weakly convex with maximum height anterior to the umbo (2); convex with maximum height between the umbo and midlength (3).
8. asy – asymmetry: absent (0), developed in juveniles (1), developed in adults (2), occasionally developed in adults (3). *Remark*: There are several reasons to assume that asymmetrical or sigmoidal anterior commissure of *Protanastrophia* and some species of *Parastrophina* was genetically controlled. In *Protanastrophia repanda* sp. nov., *Protanastrophia distorta* (Oradovskaya, 1977), and *Parastrophina portentosa* (Nikitin and Popov, 1996), an asymmetrical commissure is evident in the juvenile shells about 4–5 mm long. These taxa also occur together with parastrophinids that have a completely symmetrical shell and anterior commissure in the same clusters and larger pentameridines (e.g., *Pentameroides* and *Gypidula*) that are tightly clustered but do not show any type of consistent asymmetry as in *Protanastrophia*.
9. acm – anterior commissure: rectimarginate (0), uniplicate (1), sigmoidal (2), sulciplicate (3), parasulcate (4).
10. vsl – ventral median sulcus: absent (0), originated in the umbonal area (1), originated posterior to midlength (2), originates at midlength or anterior to midlength (3).
11. vss – ventral sulcus strength: no ventral sulcus (0), weakly defined (1), moderate (2) strongly defined, terminated by tongue (3).
12. dmf – dorsal median fold: absent (0), originated in the umbonal area (1), originated posterior to midlength (2), originates at midlength or anterior to midlength (3).
13. dsl – dorsal sulcus: absent (0), present (1).
14. pal – palintrope; absent (0), present (1).
15. via – ventral interarea, present (0), absent (1), rudimentary (less than half shell width) (2), vestigial (less than quarter shell width) (3).
16. vii – ventral interarea (inclination): strongly apsacline to orthocline (0), apsacline (1), not developed (2).
17. vis – ventral interarea surface: flat (0), curved umbonally flat distally (1), evenly curved, wide (2), evenly curved, narrow (3), absent (4).
18. psd – pseudodeltidium: absent (0), present (1).
19. dpl – divergent dental plates: absent (0), rudimentary (1), well developed (2), no discrete dental plates (3).
20. dia – dorsal interarea: absent (0), rudimentary (1), well developed (2).
21. orc – growth marks: growth lines (0), filae (1), lamellose (2).
22. upf – umbonal perforation of the ventral valve: absent (0), small (1), enlarged by resorption (2).
23. orr – paucicostate radial ornament (variations): absent (0), present only in a fold and sulcus (1), developed in the umbonal area (2), originated posterior to midlength (3), originated at midlength or anterior to midlength (4), other (5). *Remark*: Variably paucicostate radial ornaments are characteristic of many camerelloid taxa. The ribs of some genera (e.g., *Anastrophia*, *Eoanastrophia, Plectosyntrophia*) may originate at the umbo and are homologous with paucicostate ribs of *Parastrophina*, but they do not fit into any formal definition of the feature and are designated as "other".
24. rib – radial ornament: absent (0), capillae (1), fine, multicostellate (2), fine, ramicostellate (3), coarse rounded ribs (4), paucicostate (5), indistinct ribbing anterior to midlength (6).
25. rdn – rib density: smooth (0), sparse (<10 ribs on each valve) (1). average (10–20 on each valve) (2), numerous (20–40 on each valve) (3), very dense (>40 on each valve) (4).
26. nrs – number of ribs in the ventral sulcus: no sulcus (0), no ribs (1), one rib (2), more than one rib (3), other (4).
27. nrf – number of ribs on flanks: no ribs (0), 1–3 (1), more than 3 (2); other (3).
28. nop – notothyrium: absent (0), present, rudimentary, narrow triangular (1), broadly triangular (2).
29. dth – deltidiodont teeth: free (0), confined with a socket (1), distal part projects freely into the interior of dorsal valve (2), no teeth (3), not applicable (4).
30. tes – deltidiodont teeth (shape): not applicable (0), blindly triangular, oblique, curved dorsally (1); large, transverse, anteriorly directed (2); transverse strongly inclined to commissural plane (3). *Remark*: The study of serial sections through the umbonal part of the shell in *Idiostrophia* and various parastrophinids does not confirm resorption of teeth and sockets and in all cases they are considered as deltidiodont (Jaanusson 1971).
31. sst – spondylial structures: absent (0), sessile (1), sessile posteriorly, supported by a septum anteriorly (2), supported by a median septum (3), supported by median septum posteriorly, free anteriorly (4), free (5), free in juveniles, sessile in adults (6).
32. spl – spondylium, length: less then 25% of shell length (0), less than 50% of shell length (1), 50% and more of shell length (2), no spondylium (3).

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33. vms – ventral median septum: less then 25% of shell length (0), less than 50% of shell length (1), 50% and more of shell length (2), absent (3).
34. bsp – brachiophore supports/inner hinge plates: short, divergent (0), long, subparallel, not enclosing adductors (1), long, converging towards bottom (2), forming septalium (3), not developed (4), brachiophores absent (5).
35. op-ip – outer and inner hinge plates: undifferentiated (0), differentiated into outer and inner hinge plates (1), absent (2).
36. hpl – outer hinge plates length (= inner plates): no dorsal cardinalia (0), no brachiophores (1), no differentiated hinge plates (2), longer than inner hinge plates (3); about equal length with inner hinge plates (4), shorter than inner hinge plates (5).
37. spt – septalium: absent (0), sessile septalium (1); septalium supported by septum (2), sessile posteriorly supported by septum anteriorly (3).
38. stl – septalium (shape): absent (0), V-shaped (1), U-shaped (2).
39. dms – dorsal median septum: absent (0), present (1), ridge (2).
40. cru – crura: no dorsal cardinalia (0), absent (1), short (2), long (3).
41. apl – alate plates: absent (0), present (1), no brachiophores (2).
42. soc – sockets: no sockets (0), sockets present (1), hinge-notch (2). *Remark*: Jaanusson (1971) gave a detailed discussion on the difference between conventional sockets of the orthides and the hinge-notch of pentamerides, which will not be repeated here.
43. vmc – ventral muscle canals: pinnate (0), saccate (1), digitate (2).
44. npl – notothyrial platform: absent (0), present, low (1), high, hanging anteriorly (2), other (3).
45. cpr – cardinal process: absent (0), rudimentary (1), simple, ridge-like (2).
46. daf – dorsal adductor field: obscure (0), impressed on valve floor (1), supported by distinct callus of secondary shell (2).
47. asc – adductor scars: median and posterolateral pairs (0), radially arranged (1), quadripartite (2).
48. dsr – socket ridges: absent (0), present, no brachiophores (1), present, transverse, merged with brachiophores (2).

	111111111122222222233333333334444444444 123456789012345678901234567890123456789012345678
Chile mirabilis	10220220000000011100020630303003302000002000010 0
Palaeostrophia fibrillosa	30210210112100012031000001022111300200010221011 0
Tetralobula peregrina	32210200132300012031105144322110300200010221121 0
Anastrophia? kurdaica	02212200123201313030005433212121121500021?00??0
Plectocamara? extenuata	12211030113101124030005433212131220411010 2?30??0
Ilistrophina tesikensis	02211200123201124030000000012120131421131 2?30??0
Liostrophia pravula	02211200121201124030000000012120131421131 2?30??0
Parastrophinella reversa	12212200113201313010003513212131131322121 2?30??0
Parastrophina bilobata	12211000133301134030004513112121131321121 2?30??0
Parastrophina hemiplicata	12211200133301124030004513112131131321121 2?30??0
Parastrophina dura	02211203123201124030004513212132231321121 2?30??0
Parastrophina iliana	02211210223301124030001522012131131322121 2?30??0
Parastrophina plena	02211211323201124030001513212131131321121 2?30??0
Parastrophina portentosa	12211200123201124030002513212121131321121 2?00??0
Parastrophina unicostata	22202230412101313030005423112140031321121 2?00??0
Schizostrophina margarita	5230?200113101??4030204513112121111400020 2?00??0
Protanastrophia repanda	12212031233301313030004513112121211300021 2?00??0
Protanastrophia asimmetrica	12212031232301313030004523112121211300012?00??0
Protanastrophia distorta	12212001212101313030003533212131111300012?00??0
Protanastrophia indistincta	0221?003133301???030004513112131211300021 2?00??0
Protanastrophia salairica	1221?012133301???030004523212131111300031 2?00??0
Eoanastrophia antiquata	022120?021210?323030005433212120031331121 2?301?0
Maydenella asymmetrica	12212203133301313030005433212121131311221 2?30110
Liricamera nevadensis	02222000131301114030005443212121130 53?1202?300?0
Camerella mica	02201000000001124030004520312120233321102?30??0
Idiostrophia prima	52301000000001124030004510312121130421120 2?30??0
Jolkinia turjensis	12211000123 20?124030001513012 13??31321121 2?30??0
Huenella biplicata	41010110313200012032002412 22?1100002002102210110
Billingsella aliena	41120220000010000202115240321203352100112111 2121
Psiloria dayi	31010200122200021032000001020150352100112002011 0
Glyptoria gulchensis	30120010112100011032205323220150352100012002011 0
Leioria bentori	30120200100000012032000001022160300200010 2?10120
Bohemiella romingeri	30120210000010011012105340321303342200012111 2122
Wimanella seges	30120220000010011012100000321303342200112111 1212
Anastrophia verneuili	12212200123201313030004433212121211300021 2?00210
Bleshidium patellinum	1220?230100021??4030003513012131111300020 2?00??0

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Appendix 3

Synapomorphic scheme for internal nodes of the cladogram (Fig. 6A). Paired numbers denote character and character state, respectively (e.g., character 1, state 1 = 1:1)

Node	Character
1	
2	13:1, 21:1, 30:3, 34:4, 36:2, 39:1; 42:1, 43:1, 41:2, 48:2
3	23:5, 25:4, 45:2, 47:2
4	4:1, 7:1, 9;1, 10:1, 11:2,12:1, 19:3, 26:1, 27:2, 31:1, 32:0
5	29:0, 31:5, 34:5, 44:2
6	17:2, 29:2, 35:0, 36:2, 41:0, 42:2, 43:2
7	24:0, 25:0, 27:0
8	2:1, 11:3, 12:2, 23:2, 24:4, 26:2, 33:2
9	2:2, 3:2, 7:0, 10:2, 20:1, 23:4, 25:3, 26:3, 46:2
10	1:1, 5:2, 14:1, 15:3, 17:3, 20:0, 28:1, 31:2, 32:1, 34:1 35:1, 36:3, 40:2, 41:1, 44:0
11	33:1, 46:1
12	10:1; 12:1, 24:5, 25:2, 31:3
13	6:0, 8:1;
14	7:1, 8:2, 10:3, 12:3
15	7:2, 8:1, 9:2 31:2
16	4:0, 17:4, 25:1, 27:1, 41:0
17	23:5, 34:2
18	34:3, 37:1, 38:1, 39:1, 44:3
19	10:1, 37:1
20	6:0, 11:2, 12:1
21	7:3, 9:2, 32:0, 33:0
22	11:1, 15:1, 17:4, 35:0,36:4, 41:0, 46:0
23	5:1, 16:2, 33:2, 40:1
24	4:0, 9:0, 10:0, 11:0, 12:0,23:4,24:5,25:2, 26:0,27:3
25	36:3, 37:1, 38:1, 44:3
26	5:1, 10:2, 16-5:1, 16:2, 17:4
27	23:4
28	10:3, 12:3, 27:1
29	23:2
30	23:1, 27:0
31	1:0, 26:2
32	7:1, 9:2
33	23:0, 24:0, 25:0, 26:2, 31:2, 32:0, 46:3, 40:3

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