

LATEST HELCIONELLOID MOLLUSCS FROM THE LOWER ORDOVICIAN OF KAZAKHSTAN

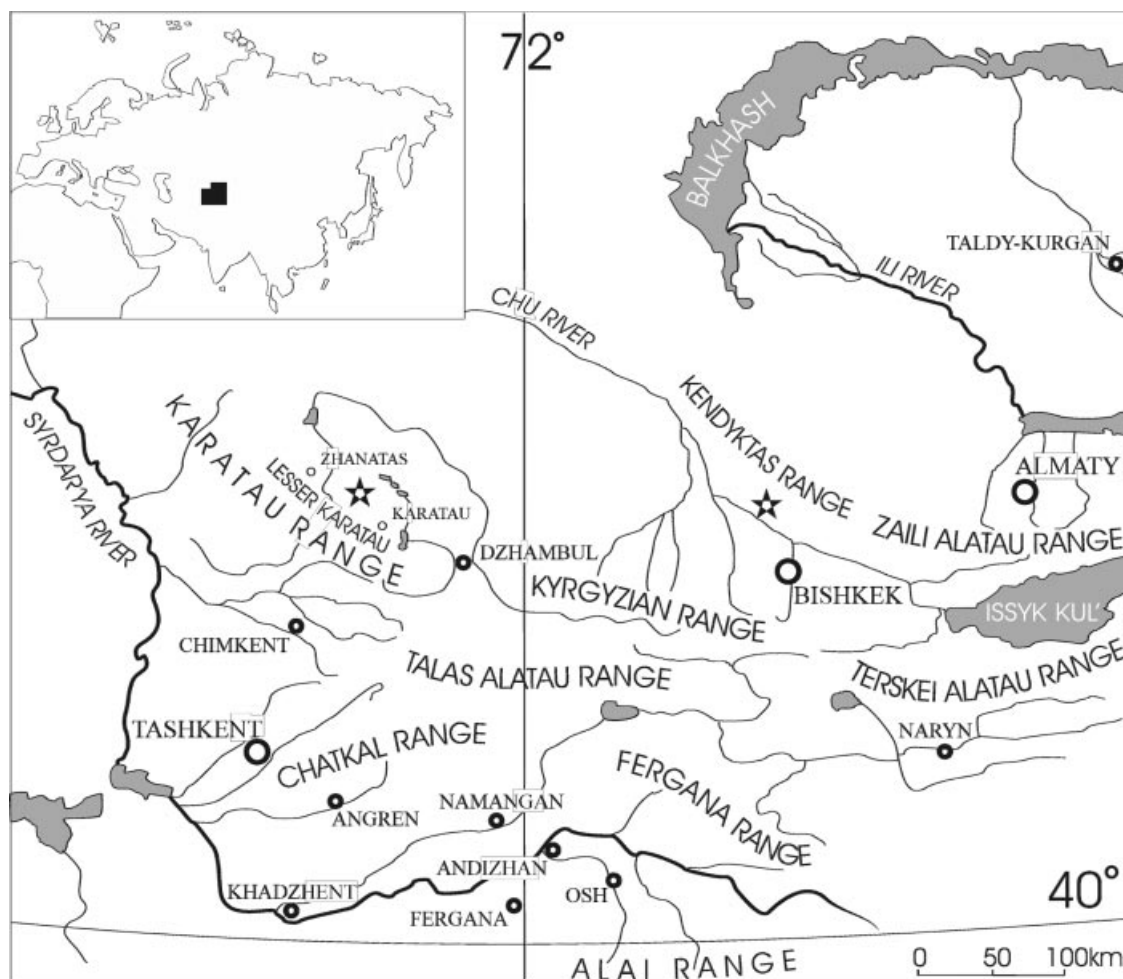
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ABSTRACT. The helcionelloid mollusc *Chuieliella elenae* gen. et sp. nov. is described from the Lower Ordovician of Kazakhstan. It represents the geologically youngest record of a group of mainly bilaterally symmetrical ancient molluscs which originated in the earliest Cambrian, flourished during the early–mid Cambrian and was thought to have become extinct during the late Cambrian. *Chuieliella* is a typical helcionelloid in terms of shell shape, although the comarginal ornamentation characteristic of many helcionelloids is lacking. Interpretation of the raised margin of the aperture adjacent to the earlier coiled whorl as exhalant channels favours reconstruction of helcionelloids as endogastrically coiled, i.e., with the apex posterior.

KEY WORDS: helcionelloid molluscs, late Cambrian, Early Ordovician, Kazakhstan.

MONOPLACOPHORA was informally introduced by Wenz (1940) for a group of Palaeozoic fossil molluscs with a bilaterally symmetrical shell and subsequently formally proposed by Knight (1952) as a class, which he attributed to Wenz as author (Geyer 1994). Although fossil forms have been well described in the literature for more than a century (e.g. Lindström 1884) and the concept as untorted molluscs was well formulated by Knight (1952), it was first with the sensational description of the living *Neopilina galatheae* Lemche, 1957 that the evolutionary significance of the group was fully recognised (Lemche 1957; Lemche and Wingstrand 1959; Wingstrand 1985). Monoplacophora has been generally accepted as a class of Mollusca, but there is controversy concerning its composition, particularly in connection with the Palaeozoic–Triassic Bellerophontoidea and various, mainly Cambrian, coiled microscopic molluscs (summaries in Peel 1991a; Geyer 1994; Runnegar 1996). Several authors have urged that the formal name Monoplacophora be abandoned (Salvini-Plawen 1980; Wingstrand 1985; Peel 1991a, b; Geyer 1994). Peel (1991a, b) recognised two classes of bilaterally symmetrical untorted molluscs to which he gave the names Tergomya and Helcionelloida. The former includes classic monoplacophorans, such as the fossils *Tryblidium* Lindström, 1880, *Pilina* Koken, 1925 and the extant *Neopilina*, which are widespread in the Ordovician and Silurian, but almost unknown between the Devonian and the present day. The Helcionelloida contains more strongly coiled forms such as *Oelandiella* Vostokova, 1962, which appeared in the earliest Cambrian and may have been common in the early–mid Cambrian (Gubanov and Peel 1998, 1999, 2000). The apex in tergomyans is anterior, but Geyer (1986, 1994) and Peel (1991a, b) considered the apex in helcionelloids to be posterior with the shell expanding anteriorly.

Not all Lower Palaeozoic univalved shells assigned to the untorted Tergomya and Helcionelloida are perfectly bilaterally symmetrical (Gubanov and Peel 2000) and not all Lower Palaeozoic molluscs with bilaterally symmetrical shells were untorted (Peel and Horny 1999). Patellogastropods were considered to be the most primitive of all gastropods by Lindberg and Ponder (1996; see also Hedegaard *et al.* 1997). While most authors have suggested that their limpet shells were derived from conispiral ancestors, Haszprunar (1988) proposed that this shell form may have been archetypal for gastropods. While there are a number of gastropod limpets in the Palaeozoic, their relationship to the patellogastropods is tenuous (Peel and Horny 1999). Furthermore, the evolutionary pathway between early gastropods and their untorted ancestors is not well anchored in the geological record; neither is the relationship between tergomyans and helcionelloids. It is certain, however, that the oldest known molluscs were helcionelloids, which appeared with a strongly coiled, not limpet-like, bilaterally symmetrical shell in the latest Precambrian (Khomentovskiy *et al.* 1990; Gubanov and Peel 1999; Gubanov and Peel 2000). In this

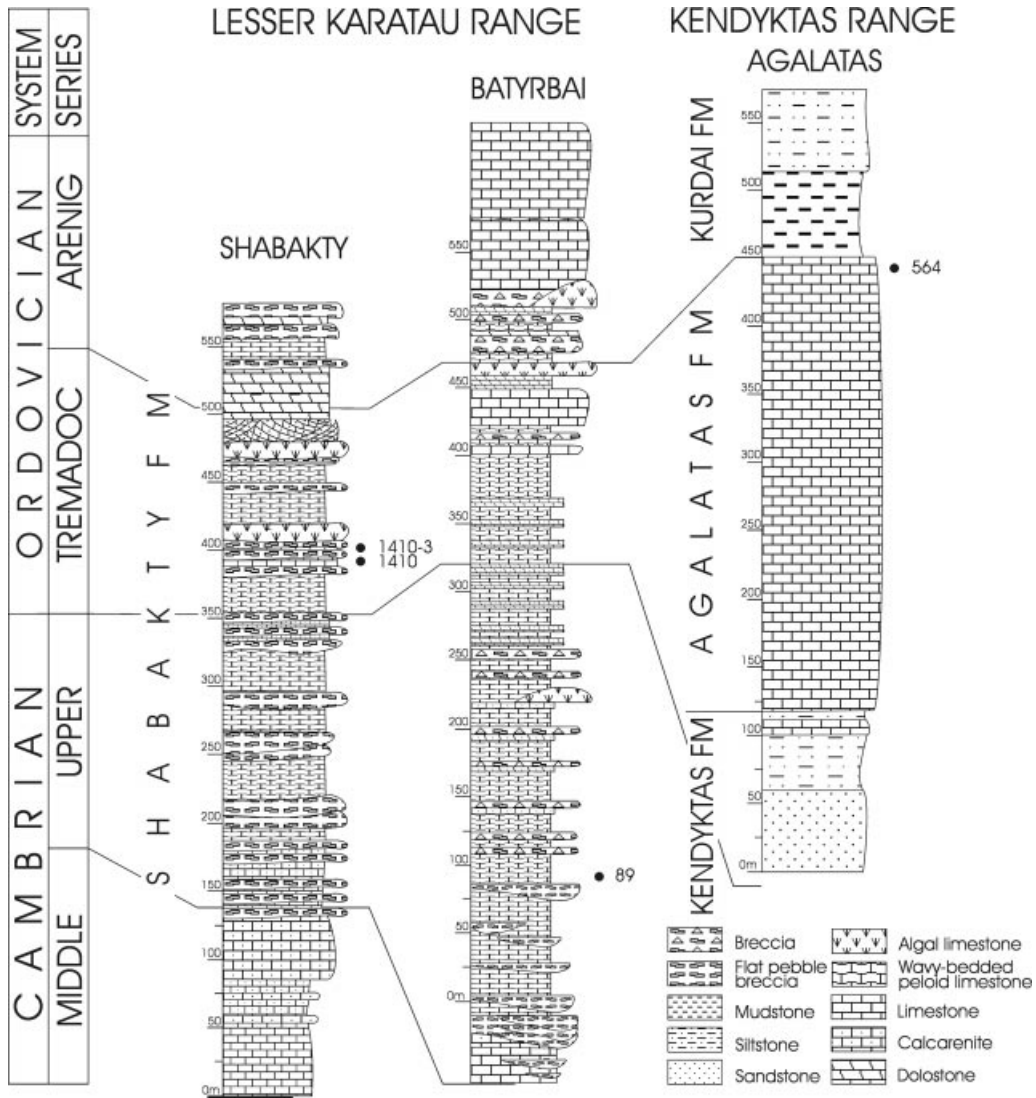


TEXT-FIG. 1. Map of southern Kazakhstan, showing collection localities for *Chuieliella* (stars) in the Lower Ordovician of the Lesser Karatau and Kendyktas.

paper we describe the youngest known descendant of these earliest molluscs from the Lower Ordovician of Kazakhstan.

GEOLOGICAL SETTING

A continuous succession of sedimentary rocks ranging from the upper Proterozoic to the Middle Ordovician is exposed along the Lesser Karatau Range (Abdulin *et al.* 1990; Text-fig. 1) within the northern edge of the Lesser Karatau Anticlinorium in the Kokchetau-Karatau structural zone of Kazakhstan (Nikitin 1972). The well-exposed fossiliferous upper Cambrian–Lower Ordovician carbonate sections in the Lesser Karatau Range comprise one of the most complete Cambrian–Ordovician successions in Asia. Although the global stratotype section of the Cambrian/Ordovician boundary has been chosen by the International Working Group on the Cambrian/Ordovician Boundary in the Green Point section of western Newfoundland (Cooper and Nowlan 1999), the Cambrian–Ordovician succession in Lesser Karatau was a strong candidate to accommodate the global Cambrian/Ordovician boundary



TEXT-FIG. 2. Stratigraphic sections showing the occurrence of *Chuliella* in the Shabakty, Batyrbai and Agalatas sections (after Apollonov *et al.* 1988; Ergaliev 1980; and Popov and Holmer 1994).

(Apollonov *et al.* 1988). The abundant trilobite and conodont fauna (Lisogor 1977; Ergaliev 1980; Apollonov *et al.* 1988) in carbonate sections of the Lesser Karatau, supplemented by graptolites in partly terrigenous sections in the Karatau and Kendyktas ranges, the watershed between Shyderty and Olenty rivers of northern Kazakhstan, and the Baikonur Syncline (Lisogor 1961; Nikitin 1972), allow a proper age determination and correlation with the global chronostratigraphic units (Chugaeva and Apollonov 1982; Shergold 1988; Cooper and Nowlan 1999).

Well-preserved helcionelloid molluscs occur in the Shabakty section (Ergaliev 1980) of the upper Shabakty Formation (Text-fig. 2), dated as early Tremadoc in age according to the decision of the International Working Group on the Cambrian/Ordovician Boundary (Cooper and Nowlan 1999). Very similar, though poorly preserved helcionelloids have been found in the upper Cambrian part of the

Batyrbai section within the *Harpidoides-Platypeltoides* trilobite Zone, which is also dated by conodonts as the *Eoconodontus notchpeakensis* Zone (Apollonov *et al.* 1988).

The upper Tremadoc Agalatas Formation (Nikitin 1972) is exposed along the Kendyktas Range (Text-fig. 1) in the Agalatas Syncline in the Stepnyak-Betpakdala structural zone adjacent to the Kokchetau-Karatau structural zone (Nikitin 1972). The section is situated along the right bank of the Agalatas River (Popov and Holmer 1994). A phosphatized internal mould of a helcionelloid mollusc has been found in the top of the Agalatas Formation just below the boundary with the overlying early Arenig Kurdai Formation (Text-fig. 2).

SYSTEMATIC PALAEOLOGY

The figured material is housed in the Type collection PIN 3811 at the Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya 123, Moscow, and in the Type collection PMU KZ at the Museum of Evolution (Palaeontology section), Uppsala University, Norbyvägen 22, Uppsala, Sweden.

Phylum MOLLUSCA Cuvier, 1797
 Class HELCIONELLOIDA Peel, 1991a
 Order HELCIONELLIDA Geyer, 1994
 Family HELCIONELLIDAE Wenz, 1938
 Genus CHUILIELLA gen. nov.

Derivation of name. From the Chu and Ili rivers, southern Kazakhstan.

Type species. *Chuiliella elenae* sp. nov. from the Shabakty Formation (Lower Ordovician, Tremadoc) of the Lesser Karatau, southern Kazakhstan.

Diagnosis. Small, univalve mollusc with tightly coiled, rapidly expanding shell. The shell surface is smooth with fine striation of growth lines.

Remarks. This new genus resembles the early Cambrian *Oelandiella* and *Latouchella* Cobbold, 1921 and the mid Cambrian *Oelandia* Westergård, 1936 in its general outline, but lacks any comarginal ornamentation such as ribs or plications. It differs from *Oelandiella* and *Latouchella* by its higher degree of whorl expansion.

Chuiliella elenae sp. nov.

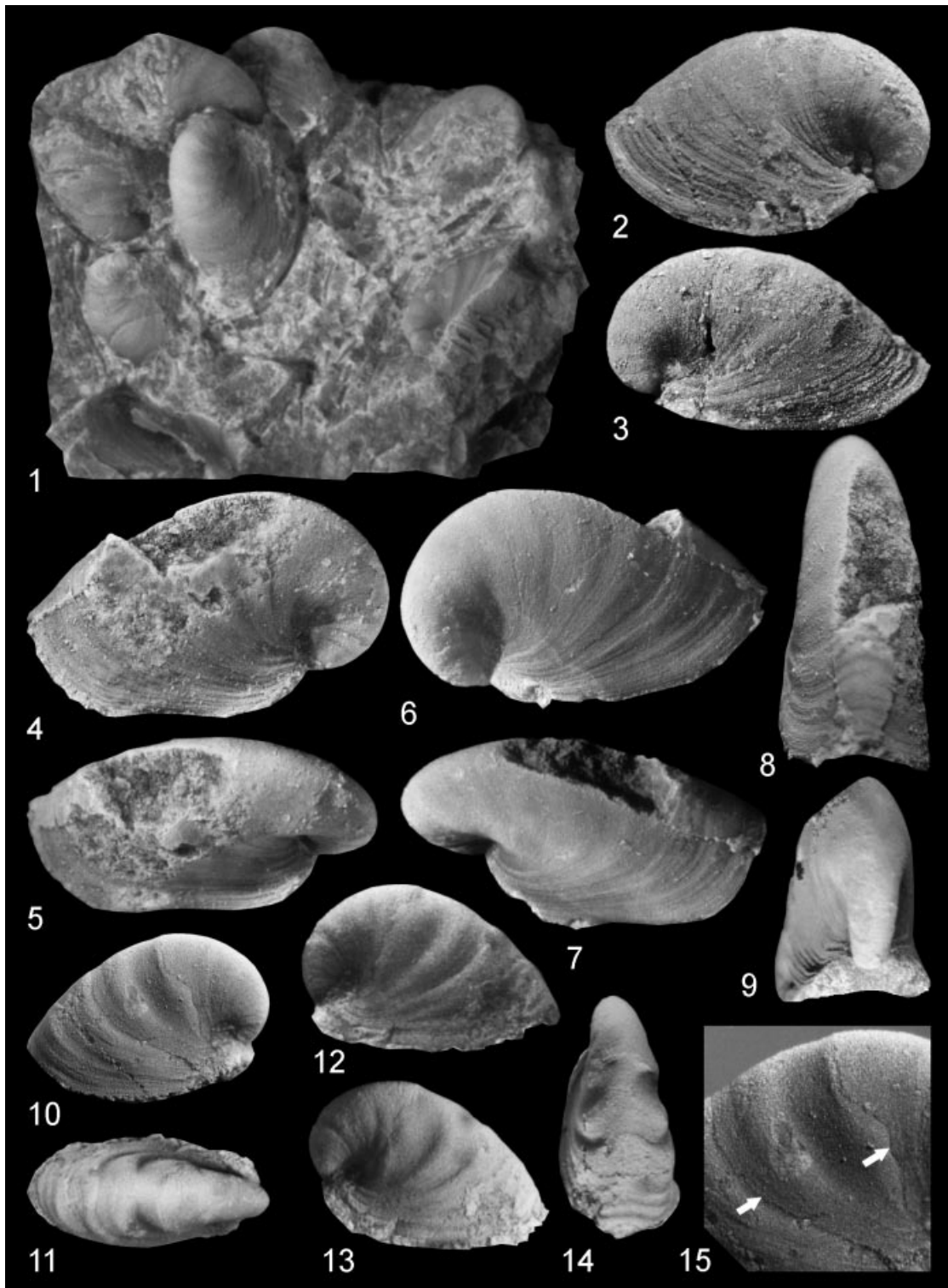
Plate 1; Plate 2, figures 1–8

Derivation of name. In honour of palaeontologist Elena A. Zhegallo, Moscow.

EXPLANATION OF PLATE I

Figs 1–15. *Chuiliella elenae* sp. nov. 1, small slab of limestone with abundant molluscs. 2–3, sample PIN 3811/201. 2, lateral view from the right; 3, lateral view from the left; both $\times 20$. 4–9, holotype PIN 3811/200. 4 lateral view from the right; 5, dorso-lateral view to show concave middle abapertural part of the shell; 6, lateral view from the left; 7, oblique antero-dorsal view; 8, antero-dorsal view to show U-shaped bend of growth lines on the dorsum; 9, posterior view to show lifted up apertural margin; all $\times 20$. 10–15, sample PIN 3811/202. 10, antero-lateral view from the left to show apex overlapped by final whorl; 11, dorsal view; 12, lateral view from the right to show distribution of ribs; 13, Lateral view of right side; 14, antero-dorsal view to show ribs and dorsum slightly shifted left; all $\times 20$; 15, enlarged lateral view; arrows indicate two shell injuries; $\times 30$.

All illustrations are light photographs.



GUBANOV and PEEL, *Chuiliella*

Holotype. PIN 3811/200, from the upper part of the Shabakty Formation (Lower Ordovician), Shabakty, Lesser Karatau Range, southern Kazakhstan.

Material. More than 20 specimens recovered from the very fossiliferous limestone.

Diagnosis. As for the genus. This is the only named species.

Description. The holotype (Pl. 1, figs 4–9) is a laterally compressed, bilaterally symmetrical univalve shell tightly coiled through about one whorl, with a maximum length of 3.1 mm, height of 2.1 mm, and width of 1.1 mm. The aperture is oval with length of 2.3 mm and width of 1.1 mm; the plane of the aperture at its most apical termination is lifted up toward the apex. The final whorl partly overlaps the initial part (Pl. 1, figs 4, 6). The surface of the shell is smooth with frequent fine growth lines, which are slightly convex toward the aperture on the sides. Growth lines on the dorsum show a faint U-shaped sinus, concave towards the aperture (Pl. 1, fig. 8).

Remarks. The smooth unribbed shell of *Chuiliella elenae* differs from the majority of shells of helcionelloid molluscs where strong comarginal ribbing or plication is common. The early Cambrian *Anabarella* Vostokova, 1962 has a smooth shell surface but a more laterally compressed shell form that indicates a semi-infaunal mode of life (Gubanov and Peel 1999). The shell of the young *Chuiliella*, with a relatively wide aperture, is similar in shape to *Oelandiella* and *Latouchella*; it probably reflects a comparable epifaunal mode of life, though adult specimens have rather narrow, laterally compressed shells (Pl. 2, figs 1–4) and probably were able to burrow into sediment. The lack of any coarse sculpture may be an adaptation either to a semi-infaunal mode of life or to life in the high-energy shallow-water environment that existed during the Early Ordovician in southern Kazakhstan (Apollonov *et al.* 1988).

Chuiliella cf. *C. elenae* sp. nov.

Plate 2, figures 9–12

Material. Nine poorly preserved specimens from the Shabakty Formation (upper Cambrian), Batyrbai, Lesser Karatau Range, southern Kazakhstan.

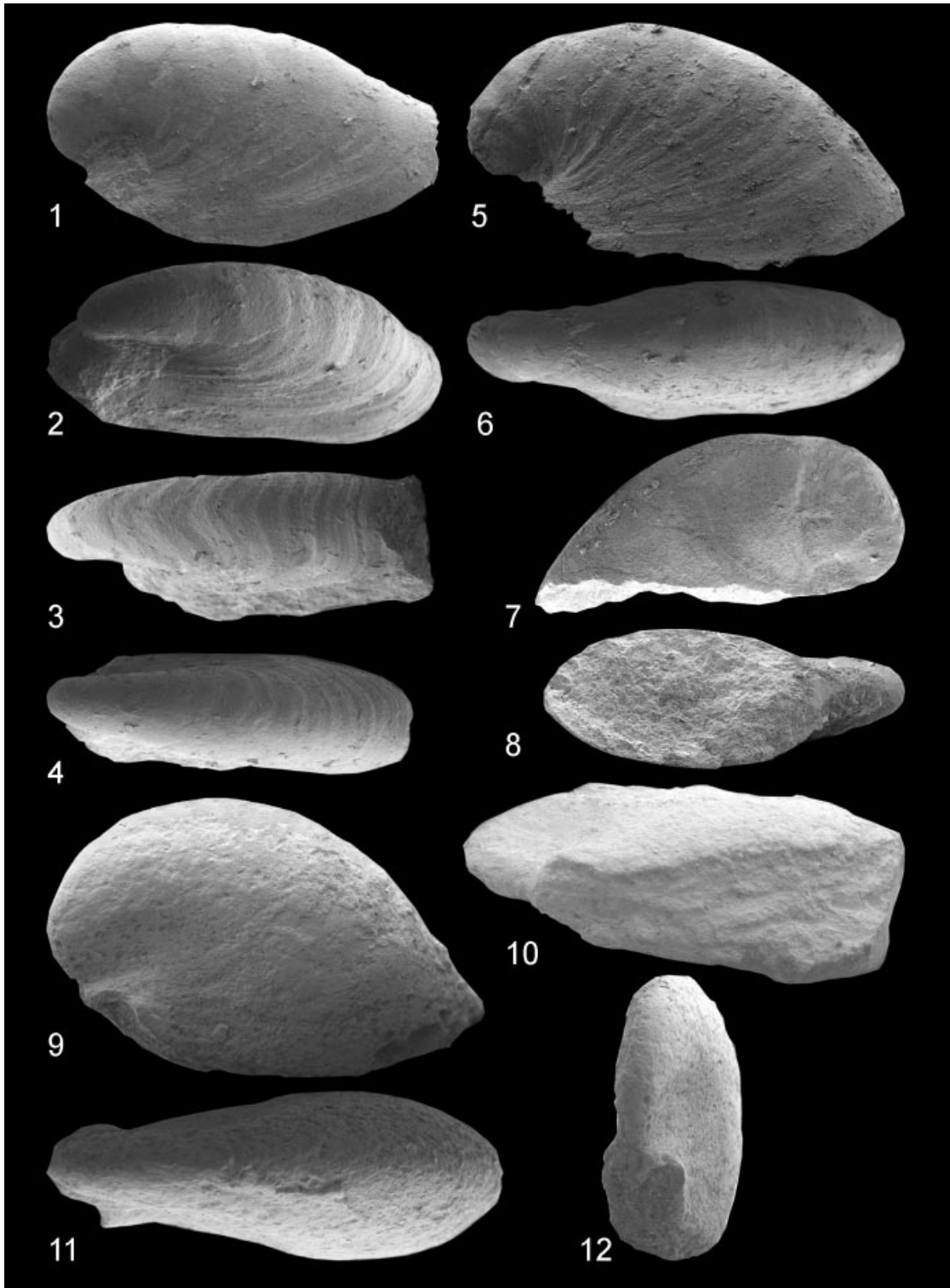
Description. The largest specimen (PMU KZ 1001) from the Batyrbai section has a length of 3.7 mm, height of 2.3 mm and width of 1.4 mm. The surface of the shell is smooth. The aperture expands in the elevated sub-apical part to form two exhalant channels (Pl. 2, figs 9–12) located one on each side; thus the apertural margins are convex in lateral view but become slightly concave adjacent to the umbilici.

Remarks. The aperture in specimens from Batyrbai has similar proportions to that in shells of young *C. elenae* from Shabakty, which is wider than the aperture of adult specimens of *C. elenae*. Documented high variability within and between populations of helcionelloid and other molluscs (cf. Gubanov and Peel

EXPLANATION OF PLATE 2

Figs 1–8. *Chuiliella elenae* sp. nov. 1–4, sample PMU KZ 1002. 1, lateral view to show curved growth lines and lifted up anterior part of the aperture; 2, dorso-lateral view; 3, antero-dorsal view to show U-shaped bend of growth lines on the dorsum; 4, dorsal view to show very elongated shape of the aperture; all $\times 40$. 5–6, sample PMU KZ 1003; 5, lateral view from the left; 6, dorsal view; both $\times 30$; 7–8, PMU KZ 1004; 7, lateral view from the right; 8, apertural view; both $\times 50$.

Figs 9–12. *Chuiliella* cf. *C. elenae*. Sample PMU KZ 1001. 9, lateral view; 10, dorsal view; 11, ventro-lateral view to show the form of the aperture; 12, posterior view to show expanded and lifted posterior part of the aperture; all $\times 25$. All illustrations are scanning electron micrographs.



GUBANOV and PEEL, *Chuiliella*

2000) suggests that the morphological differences between specimens from the Shabakty and Batyrbai sections reflect differences in environment rather than taxonomy, but poor preservation and small sample size preclude positive assignment of the Batyrbai specimens to *C. elenae*. The mollusc-bearing strata of Batyrbai were interpreted as middle–outer shelf in origin by Apollonov *et al.* (1988), in contrast to the inner shelf with thick algal limestone development of Shabakty.

Chuieliella? sp.

Text-figure 3

Material. One phosphatized internal mould (PMU KZ 1005) from the Agalatas Formation (Lower Ordovician), Agalatas, Kendyktas Range, southern Kazakhstan.

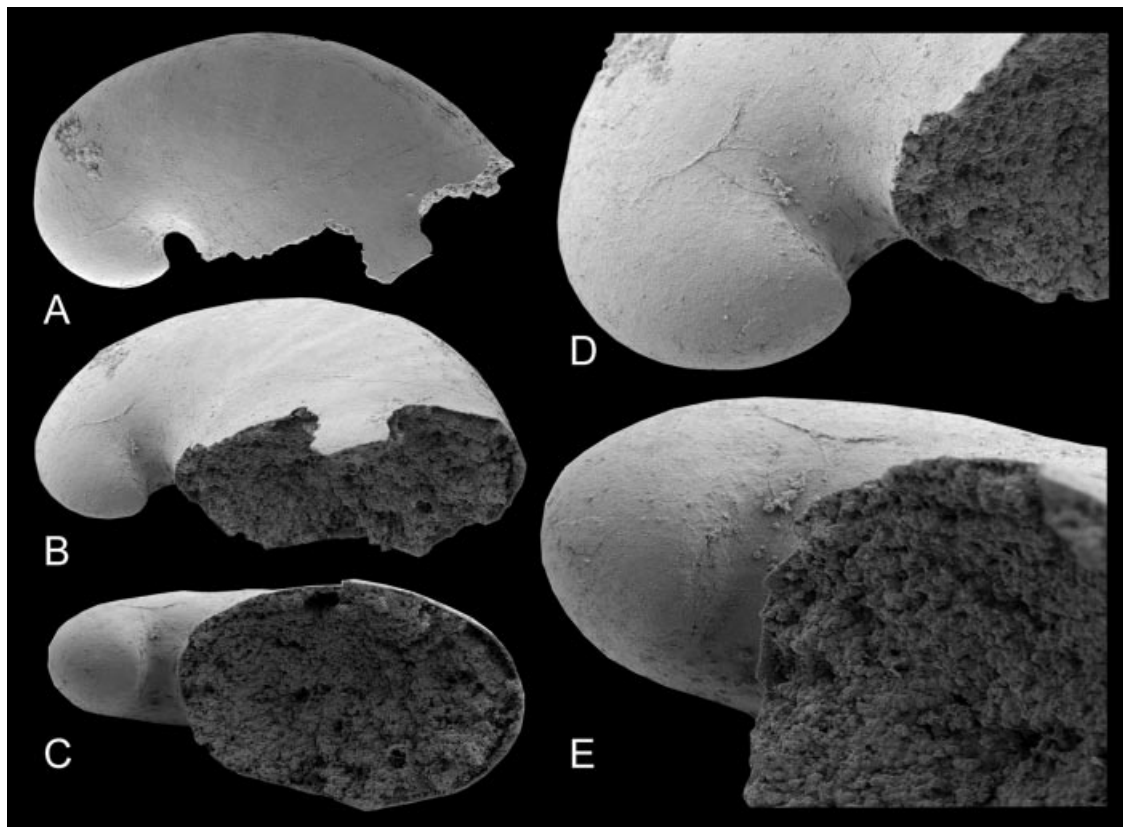
Description. The phosphatized, bilaterally symmetrical internal mould of the single specimen is about 0.8 mm long, 0.4 mm high and 0.35 mm wide. It represents about half a whorl and has a smooth surface. Typical for coiled helcionelloids, the initial part of the specimen has a beak-like shape (Text-fig. 3B, D). The aperture is oval with length: width ratio of about 1.5.

Remarks. Though the sculpture of the inner and outer surfaces of some helcionelloid shells does not always correspond (Runnegar 1985), the transverse plications of the familiar *Oelandiella* are reflected on the internal mould surface as coarse ribs or rugae (Gubanov and Peel 1999, text-figs 4–5). Apparently, the smooth internal mould of the late Tremadoc helcionelloid mollusc described here reflects the smooth unsculptured surface of the original shell that is characteristic of *Chuieliella*. The scarcely visible waving striations on the surface of the latter half of the mould (Text-fig. 3) reflect growth lines rather than a real ornamentation.

GEOLOGICAL RECORD OF HELCIONELLOIDA

The oldest known helcionelloid molluscs, determined as *Oelandiella* sp. and *Archaeospira* sp., have been reported from the Ust'yudoma Formation (Nemakit-Daldynian), 60 m below the boundary with the Pestrosvet Formation (early Tommotian) in south-eastern Siberia (Khomentovsky *et al.* 1990; Khomentovsky and Karlova 1993). *Anabarella* and *Bemella* Missarzhevsky, 1969 appear a little higher in the Tommotian in Siberia (Khomentovsky and Karlova 1993) and Mongolia (Esakova and Zhegallo 1996; Brasier *et al.* 1996). The beginning of the Tommotian is marked by an explosive radiation of helcionelloid molluscs as a result of diversification into new ecological niches (Gubanov and Peel, 1999; Gubanov 2000). One evolutionary-adaptive lineage from *Oelandiella* through *Anabarella* led to the appearance of infaunal genera such as *Watsonella* Grabau, 1900 (Gubanov *et al.* 1999) and, possibly, to the bivalve *Fordilla* Barrande, 1881 (Runnegar and Pojeta 1974). Another, through *Bemella*, led to the epifaunal *Helcionella* Grabau and Shimer, 1909, a typical helcionelloid adapted to a harder substrate (Gubanov in press). There is strong evidence that the highly anisometric, dextrally conspiral *Aldanella* Vostokova, 1962, and possibly also *Pelagiella* Matthew, 1895, is descended from *Oelandiella* where slight asymmetry in both right (dextral) and left (sinistral) directions has been documented (Gubanov and Peel 2000). *Obtusoconus* Yu, 1979 and *Yochelcionella* Runnegar and Pojeta, 1974, which are characterised by a tall conical shape, also appeared in the Tommotian. The late early and mid Cambrian were dominated by *Helcionella*-like molluscs (Runnegar and Jell 1976; MacKinnon 1985; Peel 1991b), many of which have been described as *Latouchella* but lack the main traits of the latter (Gubanov and Peel 1999).

The youngest helcionelloid mollusc noted in print appears to be from the upper Cambrian of the Minaret Formation in the West Antarctica, where two poorly preserved specimens were identified as *Latouchella?* sp. by Webers *et al.* (1992). The main constituent of this Antarctic molluscan fauna is rather diverse, large Tergomya, and it seems that tergomyans and other molluscs largely replaced helcionelloids during the late Cambrian (Stinchcomb 1986; Gubanov 2000). The present records indicate that they survived at least until the Early Ordovician.



TEXT-FIG. 3. A–E, PMU KZ 1005, *Chuliella* sp., phosphatised internal mould. A, lateral view. B, ventro-lateral view. C, apertural view; all $\times 100$. D–E, enlarged part of the internal mould to show beak-like initial part; both $\times 250$. All scanning electron micrographs.

SHELL DAMAGE IN *CHULIELLA*

The smallest available specimen of *Chuliella elenae* has a smooth initial shell, which possesses three pairs of transverse ribs that are restricted to the lateral surfaces. The first pair of ribs has the highest amplitude. Following ribs gradually decrease in height and after the third pair of ribs the shell surface becomes smooth again (Pl. 1, figs 10–13). The ribs on opposite sides of the shell are not completely symmetrical about the median plane, with the smooth dorsum being slightly displaced to the left (Pl. 1, fig. 14). The fact that this first pair of ribs appears immediately after an episode of shell breakage (Pl. 1, fig. 15) indicates that the sculpture is not characteristic of the species but is a result of an injury that probably affected the mantle margin and weakened the animal. The shell damage may have a mechanical origin rather than being the result of failed predation because it is spread along the apertural margin (Savazzi 1991). Such mechanical breakage may be expected in the high-energy shallow water which led to the deposits that characterise these geological sections (Apollonov *et al.* 1988). However, failed predatory attacks may also damage the entire margin of fossil gastropods even though they characteristically involve more penetrative injuries cutting back across several or many growth lines (Ebbestad and Peel 1997; Lindström and Peel 1997). Furthermore, Vermeij (1979, 1982) stressed the minor role of mechanical shell damage when compared with injuries produced by predatory attacks in modern marine gastropods, although the specimens he studied were an order of magnitude larger than the helcionelloids described here. A less pronounced injury occurs a little later in ontogeny, visible as a strongly emphasised growth line (Pl. 1, fig. 15).

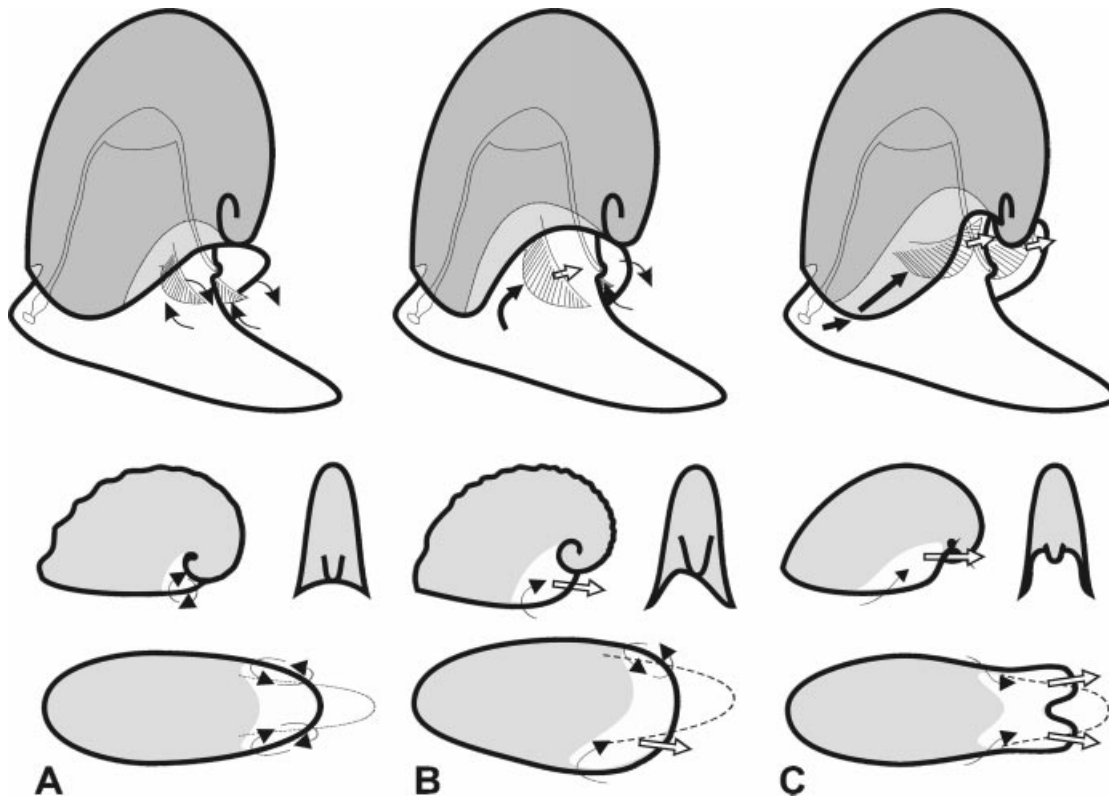
One possible explanation for the unique symmetrical development of the ribs in this specimen of *Chuiiella* is that the injury induced an atavistic pattern of shell growth. While strong comarginal ornamentation is widespread within helcionelloids, only the early Cambrian *Latouchella costata* Cobbold, 1921 displays a pattern with symmetrically placed lateral ribs which do not cross the dorsum (Gubanov and Peel 1998). Marshall *et al.* (1994) estimated that the evolutionary reversal of silenced genes, which are in charge of the appearance of atavistic features, does not exceed 10 myr. This implies that possible intermediates with lateral ribs and a smooth dorsum may have existed during the interval of about 30 myr that separates the early Cambrian *Latouchella* from the Early Ordovician *Chuiiella*. Alternatively, if the estimates of Marshall *et al.* (1994) can be applied at all in an Early Palaeozoic context, it is possible that silenced genes within certain conservative phylogenetic lineages such as the Helcionelloida may be preserved for much longer periods. Equally, however, the reappearance may represent morphological convergence resulting from some unrecognised functional adaptation.

Atavistic growth patterns induced by shell damage have apparently not been reported in molluscs but the explanation is attractive since the characteristic helcionelloid comarginal ribbing appears as a short-time irregularity of shell growth in a mollusc recovering from injury while the overall growth pattern is unchanged. Clearly, with only a single available specimen, no reasonable conclusion can be drawn, but it is important to recognise the role of coincidence and the influence of the viewpoint of the observer on interpretation. Thus, shells of the modern freshwater caenogastropod *Ampullaria* sp. raised in an aquarium with a deficit of calcium carbonate develop a band-like strip of dissolved shell along the median part of the whorl (APG, pers. obs.). With a background in the study of Lower Palaeozoic gastropods, we find it interesting that this strip occurs at the place where remote ancestral pleurotomarioid vetigastropods develop a slit and selenizone in the shell, long hidden and apparently forgotten in the phylogenetic history of gastropods.

MODE OF LIFE AND HYDRODYNAMIC CONTROLS ON MOLLUSCAN SHELL FORM AND ORIENTATION

The explosive evolution of molluscs in the early Cambrian gradually slowed during the later Cambrian such that only minor morphological changes appeared among the latest helcionelloids, although some of these changes may have had important implications for the understanding of molluscan evolution. During its early stages, the evolution of molluscs was manifested by diversification into new habitats and the mastering of new ecological niches (Gubanov and Peel 1999), driven by increasing competition between molluscs as a pioneering group of the Small Shelly Fauna that appeared after the Vendian biotic crisis. The small size of the earliest molluscs apparently reflects the prevalent environment with a lack of benthic vagile fauna and with microscopic, mostly unicellular, planktonic and benthic organisms as the main source of food. The adaptive diversification of the earliest helcionelloids from collecting food on a substrate surface to infaunal deposit feeding seen in the *Oelandiella*–*Watsonella* lineage, and to a grazing on a hard sediment surface in *Helcionella*, has been recently described by Gubanov and Peel (1999). Finds of large helcionelloids in archaeocyathan reefs of late Tommotian age (Dzik 1991; Kruse *et al.* 1995) may suggest carnivorous ‘grazing’ on archaeocyaths and sponges, a life habit capable of supporting molluscs of considerably larger body size.

The Early Ordovician *Chuiiella* has morphological features similar to the early Cambrian epifaunal deposit feeders *Oelandiella* and *Latouchella*, suggesting a similar mode of life. The loss of comarginal rib ornamentation is a possible adaptation to high-energy hydrodynamic conditions. The hydrodynamics of shallow-water environments impose strict constraints on the form and orientation of the mollusc shell (Gubanov 1984, 1985) and promote a hydrodynamically streamlined form, preferably with well-developed bilateral symmetry (Gubanov 1991). Indeed, high-energy hydrodynamic habitats provide a means of evaluating shell/soft body orientation, which is relevant to discussions concerning reconstructions of helcionelloids as exogastric or endogastric (see Peel 1991*a, b* for discussion). All vagile benthic organisms have an oriented movement reaction towards a water stream that is known as a dynamotropism (Gubanov 1991). It gives an advantage to the animal in searching for food and in the remote sensing of potential predators. Water resistance to movement of the animal imposes a strong limitation on the orientation of the



TEXT-FIG. 4. Reconstruction of helcionelloid molluscs. A, *Oelandiella*, juvenile mollusc. B, *Oelandiella*, adult mollusc. C, *Chuieliella*. Turbulent water circulation shown by thin arrows; directed water circulation shown by thick arrows; black and white arrows in C show inhalant and exhalant water streams, respectively. In the middle row all molluscs are shown in lateral and posterior views and in the lower row all are in dorsal view, with the anterior to the left.

helcionelloid shell, with the result that the apex and earlier whorls are oriented behind the animal in an endogastric coil (Gubanov 1985). Forward direction of the apex and earlier whorls (exogastric coiling) is hydrodynamically unstable and requires a permanent effort to maintain balance of the shell. In the case of *Chuieliella*, the apertural channels would open anteriorly in the exogastric orientation, creating additional water resistance (Pl. 1, fig. 9). The orientation of the modern tergomyan *Neopilina* with the apex shifted forward has been a point in a favour of an exogastric interpretation for the earliest molluscs including the coiled helcionelloids (Runnegar and Pojeta 1974). Indeed, for molluscs with a limpet or cone-shaped shell the shell orientation does not provide substantial hydrodynamic advantages, especially in deep-water environment. The principal hydrodynamic requirement for such shells is to keep the aperture parallel to the substrate (Linsley 1977), and the reconstruction of fossil, limpet-like, supposed tergomyan molluscs as exogastric molluscs is convincing. Shells in which the aperture is not planar, and therefore not parallel to the sediment-water interface, are more difficult to interpret since they do not follow Linsley's 'laws' (Linsley 1977).

There is also no large difference in hydrodynamic properties between exogastric or endogastric reconstructions for those bellerophonitoidean and cyrtoneid tergomyan molluscs which have wide, swollen, convolute or involute, rapidly expanding shells. Here, the relatively large distances between muscle attachment points allow easy balancing of the shell whatever reconstruction is favoured. In the case of the strongly coiled and bilaterally compressed helcionelloids, however, exogastric orientation of the shell would be disadvantageous from the point of view of hydrodynamics, and is therefore unlikely to have persisted in a group with a geological history spanning at least 30 myr. The same argument could be

applied to reconstructions of more laterally compressed cyrtoneid tergomyans as exogastric, with the early whorls anterior, advanced largely on the basis of muscle scar patterns (Horny 1965; Horny and Vizcaino 1995). The hydrodynamics of this group in relation to its favoured environments requires further investigation, not least since the ranges of cyrtoneid tergomyans and helcionelloids now overlap, owing to the present description of *Chuiliella* from the Early Ordovician.

RECONSTRUCTION OF WATER CURRENTS IN THE MANTLE CAVITY

The small size of most helcionelloids suggests the presence of an uncomplicated respiratory system composed of primitive gills within the mantle cavity or just mantle folds. Exchange of oxygenated water within the mantle cavity was possibly provided by slight turbulence in the raised posterior part of the aperture (Text-fig. 4A). Increase in size of the mollusc requires development of a considerably larger mantle cavity or increased respiratory efficiency, since the volume of the body increases faster than the surface area. In the case of the early Cambrian *Oelandiella* (Gubanov and Peel 1999, text-fig. 7), increase in the size of the mantle cavity results in asymmetrical widening of the aperture that creates a directed water stream within the mantle cavity (Text-fig. 4B). In high-energy hydrodynamic conditions the departure from bilateral symmetry produced by this asymmetric aperture causes considerable energy drain owing to lost streamlining. The Early Ordovician *Chuiliella* apparently shows new morphological adaptations to this environment. The mantle cavity extends anteriorly (abapically) along both sides of the shell (Text-fig. 4C), and water flow would have been directed from under the lateral part of the apertural margin through the mantle cavity and expelled through two exhalant channels formed by the upwards-deflected posterior apertural margin.

Increase of body size is one of the factors that drove evolution of the respiratory organs in molluscs; a second one is provided by growing competition and predation. More efficient respiration is linked to increasing activity to compete with the many new and rapidly diversifying organisms that appeared during the middle and late Cambrian, and to efforts to escape increasingly abundant predators.

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REFERENCES

- ABDULIN, A. A., APOLLONOV, M. K. and ERGALIEV, G. H. (eds) 1990. *III International Symposium on the Cambrian System, USSR, Novosibirsk, 1990. Field guide, Excursion 2, Kazakh SSR, Maly Karatau*. Alma-Ata, 63 pp.
- APOLLONOV, M. K., CHUGAEVA, M. N., DUBININA, S. V. and ZHEMCHUZHNIKOV, V. G. 1988. Batyrbay section, South Kazakhstan, U. S. S. R. – the potential stratotype for the Cambrian-Ordovician boundary. *Geological Magazine*, **125**, 445–449.
- BARRANDE, J. 1881. *Système silurien du centre de la Bohême, VI*. Bellman, Prague, 226 pp.
- BRASIER, M. D., SHIELDS, G., KULESHOV, V. N. and ZHEGALLO, E. A. 1996. Integrated chemo- and biostratigraphic calibration of early animal evolution: Neoproterozoic–early Cambrian of southwest Mongolia. *Geological Magazine*, **133**, 445–485.
- CHUGAEVA, M. N. and APOLLONOV, M. K. 1982. The Cambrian-Ordovician boundary in the Batyrbaisai section, Malyi Karatau Range, Kazakhstan, USSR. 77–85. In BASSETT, M. G. and DEAN, W. T. (eds). *The Cambrian-Ordovician boundary: sections, fossil distribution, and correlations*. National Museum of Wales, Geological Series, **3**, Cardiff, 227 pp.
- COBBOLD, E. S. 1921. The Cambrian horizons of Comley (Shropshire) and their Brachiopoda, Pteropoda, Gasteropoda and etc. *The Quarterly Journal of the Geological Society of London*, **76**, 325–386.
- COOPER, R. A. and NOWLAN, G. S. 1999. Proposed global stratotype section and point for base of Ordovician System. *Acta Universitatis Carolinae, Geologica*, **43**, 61–64.
- CUVIER, G. 1797. *Tableau élémentaire de l'histoire naturelle des animaux*. Baudouin, Paris, 710 pp.
- DZIK, J. 1991. Is fossil evidence consistent with traditional views of the early metazoan phylogeny? 47–56. In SIMONETTA, A. M. and CONWAY MORRIS, S. (eds). *The early evolution of Metazoa and the significance of problematic taxa*. Cambridge University Press, Cambridge, 296 pp.

- EBBESTAD, J. O. R. and PEEL, J. S. 1997. Attempted predation and shell repair in Middle and Upper Ordovician gastropods from Sweden. *Journal of Paleontology*, **71**, 1007–1019.
- ERGALIEV, G. X. 1980. *Middle and Upper Cambrian trilobites of the Lesser Karatau*. Nauka, Alma-Ata, 210 pp. [In Russian].
- ESAKOVA, N. V. and ZHEGALLO, E. A. 1996. *Biostratigraphy and fauna of the Lower Cambrian of Mongolia*. Nauka, Moscow, 216 pp. [In Russian].
- GEYER, G. 1986. Mittelkambrische Mollusken aus Marokko und Spanien. *Senckenbergiana Lethaea*, **67**, 55–118.
- 1994. Middle Cambrian molluscs from Idaho and early conchiferan evolution. *New York State Museum Bulletin*, **481**, 69–86.
- GRABAU, A. W. 1900. Paleontology of the Cambrian terrains of the Boston Basin. *Boston Society of Natural History, Occasional Paper*, **4** (3), 601–694.
- and SHIMER, H. W. 1909. *North American index fossils. Invertebrates I*. A. P. Seiler and Co., New York, 853 pp.
- GUBANOV, A. P. 1984. Form of the gastropod shell and relation to habitat and mode of life. 53–57. In: *Geological and geophysical study in Siberia*. Institut Geologii i Geofiziki SO AN SSSR, Novosibirsk, 96 pp. [In Russian].
- 1985. Gastropod variations and their dependence on the basin hydrodynamics. *Trudy Instituta Geologii i Geofiziki SO AN SSSR*, **628**, 70–74. [In Russian].
- 1991. The causes and mechanism of morphogenesis. A new method used in the analysis of forms of ancient organisms. 48–53. In KALJO, D., MODZALEVSKAYA, T. and BOGDANOVA, T. (eds). *Major biological events in Earth history*. Institut Geologii, Tallinn, 204 pp. [In Russian].
- 2000. The Early Cambrian molluscan evolution and its palaeogeographic and biostratigraphic implications. *Acta Universitatis Carolinae, Geologica*, **44**, 419–422.
- and PEEL, J. S. 1998. Redescription of the type species of *Latouchella* Cobbold, 1921 (Mollusca) from the Lower Cambrian of Comley (England). *GFF (Geologiska Föreningens i Stockholm Förhandlingar)*, **120**, 17–20.
- 1999. *Oelandiella*, the earliest Cambrian helcionelloid mollusc from Siberia. *Palaeontology*, **42**, 211–222.
- 2000. Cambrian monoplacophoran molluscs (Class Helcionelloida). *American Malacological Bulletin*, **15**, 139–145.
- KOUCHINSKY, A. V. and PEEL, J. S. 1999. The first evolutionary-adaptive lineage within fossil molluscs. *Lethaia*, **32**, 155–157.
- HASZPRUNAR, G. 1988. On the origins and evolution of major gastropod groups, with special reference to the Steptoneura. *Journal of Molluscan Studies*, **54**, 367–441.
- HEDEGAARD, C., LINDBERG, D. R. and BANDEL, K. 1997. Shell microstructure of a Triassic patellogastropod limpet. *Lethaia*, **30**, 331–335.
- HORNY, R. J. 1965. *Cyrtolites* Conrad, 1838 and its position among the Monoplacophora (Mollusca). *Acta Musei Nationalis Pragae*, **21**, 57–70.
- and VIZCAÍNO, D. 1995. *Thoralispira*, a new Lower Ordovician cyrtoneid genus (Mollusca, Tergomya) from the Montagne Noire, southern France. *Bulletin of the Czech Geological Survey*, **72**, 345–349.
- KHOMENTOVSKY, V. V. and KARLOVA, G. A. 1993. Biostratigraphy of the Vendian–Cambrian beds and lower Cambrian boundary in Siberia. *Geological Magazine*, **130**, 29–45.
- VAL'KOV, A. K. and KARLOVA, G. A. 1990. New data on transitional beds in the middle reach of Aldan river. 3–63. In KHOMENTOVSKY, V. V. and GIBSHER, A. S. (eds). *Late Precambrian and Early Palaeozoic in Siberia. Regional stratigraphy*. Institut Geologii i Geofiziki SO AN SSSR, Novosibirsk, 168 pp. [In Russian].
- KNIGHT, J. B. 1952. Primitive fossil gastropods and their bearing on gastropod classification. *Smithsonian Miscellaneous Collections*, **114** (13), 1–55.
- KOKEN, E. 1925. Die Gastropoden des baltischen Untersilurs. *Mémoires de l'Académie des Sciences de Russie, Leningrad*, **37**, 326 pp.
- KRUSE, P. D., ZHURAVLEV, A. Y. and JAMES, N. P. 1995. Primordial metazoan-calcimicrobial reefs: Tommotian (Early Cambrian) of the Siberian Platform. *Palaios*, **10**, 291–321.
- LEMICHE, H. 1957. A new living deep-sea mollusc of the Cambro-Devonian Class Monoplacophora. *Nature*, **179**, 413–416.
- and WINGSTRAND, K. G. 1959. The anatomy of *Neopilina galathea* Lemche, 1957. *Galathea Report*, **3**, 9–71.
- LINDBERG, D. R. and PONDER, W. F. 1996. An evolutionary tree for the Mollusca: branches or roots? 67–75. In TAYLOR, J. (ed.). *Origin and evolutionary radiations of the Mollusca*. Oxford University Press, Oxford, 392 pp.
- LINDSTRÖM, A. and PEEL, J. S. 1997. Failed predation and shell repair in the gastropod *Poleumita* from the Silurian of Gotland, Sweden. *Bulletin of the Czech Geological Survey*, **72**, 115–126.
- LINDSTRÖM, G. 1880. *Fragmenta Silurica*. Samson & Wallin, Stockholm, 64 pp.
- 1884. On the Silurian Gastropoda and Pteropoda of Gotland. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* **19** (6), 250 pp.
- LINSLEY, R. M. 1977. Some 'laws' of gastropod shell form. *Paleobiology*, **3**, 196–206.

- LISOGOR, K. A. 1961. Tremadocian trilobites and their associates in the deposits of the Kendyktas. *Trudy Geologicheskogo Instituta AN SSSR*, **18**, 55–91. [In Russian].
- 1977. Biostratigraphy and trilobites of the Upper Cambrian and Tremadocian in the Malyi Karatau Range (southern Kazakhstan). *Trudy Instituta Geologii i Geofiziki SO AN SSSR*, **313**, 197–265. [In Russian].
- MACKINNON, D. E. 1985. New Zealand late Middle Cambrian molluscs and the origin of Rostroconchia and Bivalvia. *Alcheringa*, **9**, 65–81.
- MARSHALL, C. R., RAFF, E. C. and RAFF, R. A. 1994. Dollo's law and the death and resurrection of genes. *Proceedings of the National Academy of Sciences of the United States of America*, **91**, 12,283–12,287.
- MATTHEW, G. F. 1885. Illustrations of the fauna of the St. John Group continued: on the Conocoryphea, with further remarks on *Paradoxides*. *Transactions of the Royal Society of Canada*, **2** (4), 99–124.
- NIKITIN, I. F. 1972. *Ordovician of Kazakhstan. Part 1. Stratigraphy*. Nauka, Alma-Ata, 242 pp. [In Russian].
- PEEL, J. S. 1991a. Functional morphology of the Class Helcionelloida nov. and the early evolution of the Mollusca. 157–177. In SIMONETTA, A. and CONWAY MORRIS, S. (eds). *The early evolution of Metazoa and the significance of problematic taxa*. Cambridge University Press, Cambridge, 296 pp.
- 1991b. The Classes Tergomya and Helcionelloida, and early molluscan evolution. *Grønlands Geologiske Undersøgelse, Bulletin*, **161**, 11–65.
- and HORNY, R. J. 1999. Muscle scars and systematic position of the Lower Palaeozoic limpets *Archinacella* and *Barrandicella* gen. n. (Mollusca). *Journal of the Czech Geological Society*, **44**, 97–115.
- POPOV, L. and HOLMER, L. E. 1994. Cambrian–Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. *Fossils and Strata*, **35**, 156 pp.
- RUNNEGAR, B. 1985. Shell microstructures of Cambrian molluscs replicated by phosphate. *Alcheringa*, **9**, 245–257.
- 1996. Early evolution of the Mollusca: the fossil record. 77–87. In TAYLOR, J. (ed.). *Origin and evolutionary radiation of the Mollusca*. Oxford University Press, Oxford, 392 pp.
- and JELL, P. A. 1976. Australian Middle Cambrian Molluscs, their bearing on early molluscan evolution. *Alcheringa*, **1**, 109–138.
- and POJETA, J. Jr 1974. Molluscan phylogeny: the paleontological viewpoint. *Science*, **186**, 311–317.
- SALVINI-PLAWEN, L. 1980. A reconstruction of systematics in the Mollusca (phylogeny and higher classification). *Malacologia*, **19**, 249–258.
- SAVAZZI, E. 1991. Constructional morphology of strombid gastropods. *Lethaia*, **24**, 311–331.
- SHERGOLD, J. H. 1988. Review of trilobite biofacies distributions at the Cambrian–Ordovician boundary. *Geological Magazine*, **125**, 363–380.
- STINCHCOMB, B. L. 1986. New Monoplacophora (Mollusca) from Late Cambrian and Early Ordovician of Missouri. *Journal of Paleontology*, **60**, 606–626.
- VERMEIJ, G. J. 1979. Shell architecture and causes of death of Micronesian reef snails. *Evolution*, **33**, 686–696.
- 1982. Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. *Malacologia*, **23**, 1–12.
- VOSTOKOVA, V. A. 1962. Cambrian gastropods from Siberia and Taimyr. *Trudy Nauchno Issledovatel'skogo Instituta Geologii Arktiki*, **28**, 51–74.
- WEBERS, G. F., POJETA, J., Jr and YOCHELSON, E. L. 1992. Cambrian mollusca from the Minaret Formation, Ellsworth Mountains, West Antarctica. *Geological Society of America Memoir*, **170**, 181–248.
- WENZ, W. 1938–1944. Gastropoda. Allgemeiner Teil und Prosobranchia. In SCHINDEWOLF, O. H. (ed.). *Handbuch der Paläozoologie*, **6**, Gebrüder Borntraeger, Berlin, 1639 pp.
- 1940. Ursprung und frühe Stammesgeschichte der Gastropoden. *Archiv für Molluskunde*, **72**, 1–10.
- WESTERGÅRD, A. H. 1936. *Paradoxides Oelandicus* beds of Öland. *Sveriges Geologiska Undersökning, Series C*, **394**, 1–66.
- WINGSTRAND, K. G. 1985. On the anatomy and relationships of Recent Monoplacophora. *Galathaea Report*, **16**, 7–94.
- YU, W. 1979. Earliest Cambrian monoplacophorans and gastropods from western Hubei and their biostratigraphical significance. *Acta Palaeontologica Sinica*, **18**, 233–270.

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