Muscle Scars of the Cambrian Univalved Mollusks and Their Significance for Systematics

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Abstract—Zones of the honeycomb microsculpture have been discovered on the surface of internal moulds of the Cambrian mollusks, i.e., *Bemella communis, B. incomparabilis, Anhuiconus microtuberus* and *Beshtashella tortilis* from the Botomian Stage of South Australia and *Bemella* sp. and *Oelandiella* sp. from the Tommotian Stage of the Siberian Platform. The species represent three families of the Cambrian univalved mollusks: Helcionellidae, Coreospiridae, and Onychochylidae. It is supposed that these zones are the muscle attachment areas, i.e., muscle scars. The significance of this find for the systematics of the Cambrian mollusks is discussed.

The structure of the shell muscles among the Cambrian mollusks has been a stumbling block for malacologists studying the morphology and phylogeny of the most ancient members of the phylum Mollusca. Apart from several dubious finds of the muscle scars among very few forms of the helcionelloideans (Runnegar, 1981; Vassiljeva, 1990; 1998, Geyer, 1994), the reliable position of the muscles within their shells remains unknown, and this fact has been repeatedly noted in the literature (Runnegar and Pojeta, 1974; Pojeta and Runnegar, 1976; Yochelson, 1978; Peel, 1991). This circumstance coincides with the fact that, to date, we have obtained extensive data on the helcionelloid mollusks: about 500 of nominal species are already described (personal estimation). It is really surprising that the shells or internal moulds of helcionelloideans have sometimes perfect preservation even with visible elements of the wall microstructure (Runnegar, 1983; Bengtson *et al.*, 1990; Kouchinsky, 2000) but, at the same time, lack the muscle scars, which can be rather distinctly preserved among some other Cambrian mollusks (bivalves, bellerophontids, etc.).

To explain such a riddle, I speculated (Parkhaev, 2000) that the absence of the muscle scars on the shell of helcionelloideans could have been caused by a specific position of the muscle attachment zone. Probably, the muscles were attached to the shell on the parietal wall in the subapical area. Therefore, it is really difficult to find the scars in this place due to its minor area, not very common preservation, or overlapping by the subsequent whorl (in coiled shells). Recent investigations support this speculation, at least for the spirally coiled forms. Also, the scars of the shell muscles were found on the internal moulds of cap-shaped helcionellids. The result of this study is presented in the paper.

MATERIAL

The extensive collection (about 5000 specimens) from the Lower Cambrian of South Australia (housed at the Paleontological Institute of the Russian Academy of Science, no. 4664) was the basis for the study. Along with excellent preservation, the Early Cambrian fauna of South Australia is extremely diverse taxonomically: here, we have found the members of all the families and subfamilies of the Cambrian mollusks. A total of about 40 species of 27 genera and 10 families/subfamilies were examined. The internal moulds of four species assigned to three genera and three families display the imprints, which with great reliability can be considered to be scars of the shell muscle.

Family Helcionellidae Wenz, 1938

Bemella incomparabilis Parkhaev in Gravestock *et al.*, 2001

The species is a typical member of the genus *Bemella*. It is characterized by moderately high cap-shaped shell with the apex placed above the posterior margin of the aperture (Pl. 3, fig. 3a). The shell length is 2.0–2.5 mm. The surface bears sharp concentric ribs, triangular in cross section. In the microsculptural aspect, the surface of the mould is smooth and only in the apical region a narrow band with specific ornament takes place (Fig. 1c). The band embraces the posterior part of the protoconch (Pl. 3, figs. 3b, 3c) and goes on the lateral surface of the apical area of the definitive shell, where it disappears. The microsculpture of the band is composed of small (~10 μm) polygonal uplifts and thin (~2–3 μm) separating grooves (Pl. 3, fig. 3b). Up to five or six polygonal uplifts fit within the width of the band. Among four specimens of the species, this type of microsculpture was found on two better preserved moulds.

Bemella communis Parkhaev in Gravestock *et al.*, 2001

The shell is cap-shaped, low, and moderately wide. The apex is inclined posteriorly and lies near the posterior margin of the aperture (Pl. 3, figs. 1, 2). The largest
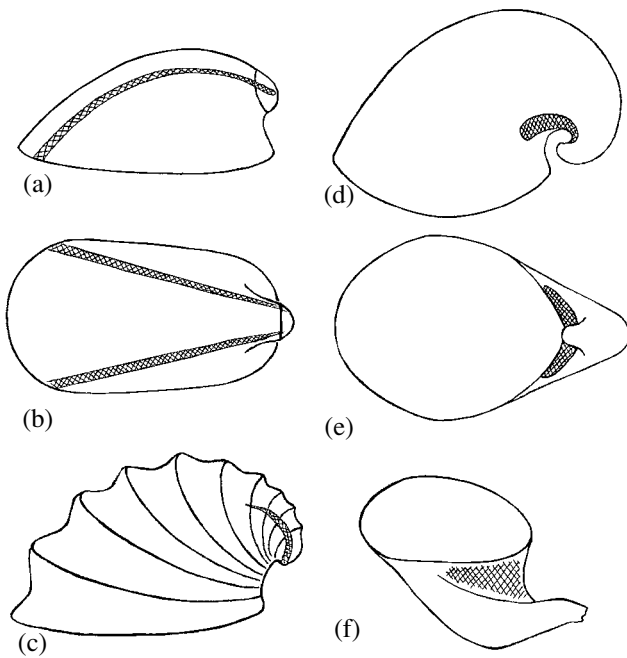
Fig. 1. Localization of zones with honeycomb microsculpture (hatched areas) on the moulds of the mollusks from the Lower Cambrian of South Australia: (a, b) *Bemella communis* Parkhaev: (a) left view; (b) dorsal view; (c) *Bemella incomparabilis* Parkhaev, left view; (d, e) *Anhuiconus microtuberus* Zhou et Xiao: (d) left view; (e) apertural view; (f) *Beshtashella tortilis* Missarzhevsky, apertural view.

elevated balks (2–3 μm wide). Five to six polygons fit within the width of the band. Such a type of the microsculpture is present in different extents on a few dozen moulds among over a hundred of studied specimens.

Family Coreospiridae Knight, 1947

Anhuiconus microtuberus Zhou et Xiao, 1984

The shell of immature specimens is cap-shaped, elongated longitudinally; in adults, it becomes planispirally coiled owing to the posterior bent of the apex. The coiled shell is composed of 0.75–1 whorls or somewhat more (Pl. 4, fig. 1). The largest shell exceeds 3.5 mm in diameter. The exterior of the shell lacks ornamentation. The mould surface sometimes represents faint, smoothed ribs. The microsculpture of the mould is very peculiar. The anterior and lateral sides are finely granulated (diameter of the granules is 4–5 μm); the posterior side of the mould below the apex bears a honeycomb ornament (Figs. 1d, 1e; Pl. 4, figs. 1, 2). This ornament is composed of polygonal depressions (5–7 μm in diameter) and separating balks (2–3 μm wide). The honeycomb microsculpture smoothes out on the lateral sides. Among 15 studied specimens, this type of the microsculpture was observed in three moulds of immature forms.

shell is 2.6 mm long. The anterior and lateral sides of the mould are ornamented by concentric folds, which vary in prominence: some moulds are almost smooth with faint suggestion on the concentric ornament, while others bear regular ribs, even sometimes with sharpen edge. The intergrades are also common. The microsculpture of the mould is finely pitted (Pl. 3, figs. 2b, 2c). The pits are 3–4 μm in diameter; the distance between neighboring pits varies from 4 to 16 μm. (Possibly, the pits on the mould surface are imprints of the fine spiny structures covered the inner surface of the shell. These structures could ensure the better contact between the mollusk mantle and the shell wall.) A pair of narrow bands with honeycomb microsculpture goes from the lateral sides of the protoconch toward the anterolateral margins of the aperture (Figs. 1a, 1b). The microsculpture of the bands is composed (Pl. 3, figs. 1, 2) of polygonal depressions (6–8 μm in diameter) and separating

Family Onychochilidae Koken, 1925

Beshtashella tortilis Missarzhevsky in Missarzhevsky et Mambetov, 1981

The shell is hyperstrophic, sinistral, up to 2.7 mm high, and composed of 1.0–1.5 open coiled whorls (Pl. 4, fig. 4). The teleoconch whorls are elliptical in cross section; their height increase rapidly (2.5–3.0 times per half of the whorl). The umbilical width varies greatly corresponding the extent of tightness of the shells coiling. The surface of the mould is smooth in the microsculptural respect. The umbilical region bears two types of the microsculpture, i.e., pitted and honeycomb. The latter is composed of polygonal depressions (20–25 μm in diameter) and separating balks (4–5 μm wide). Among two dozen specimens being studied, this type of microsculpture is present on seven internal moulds.
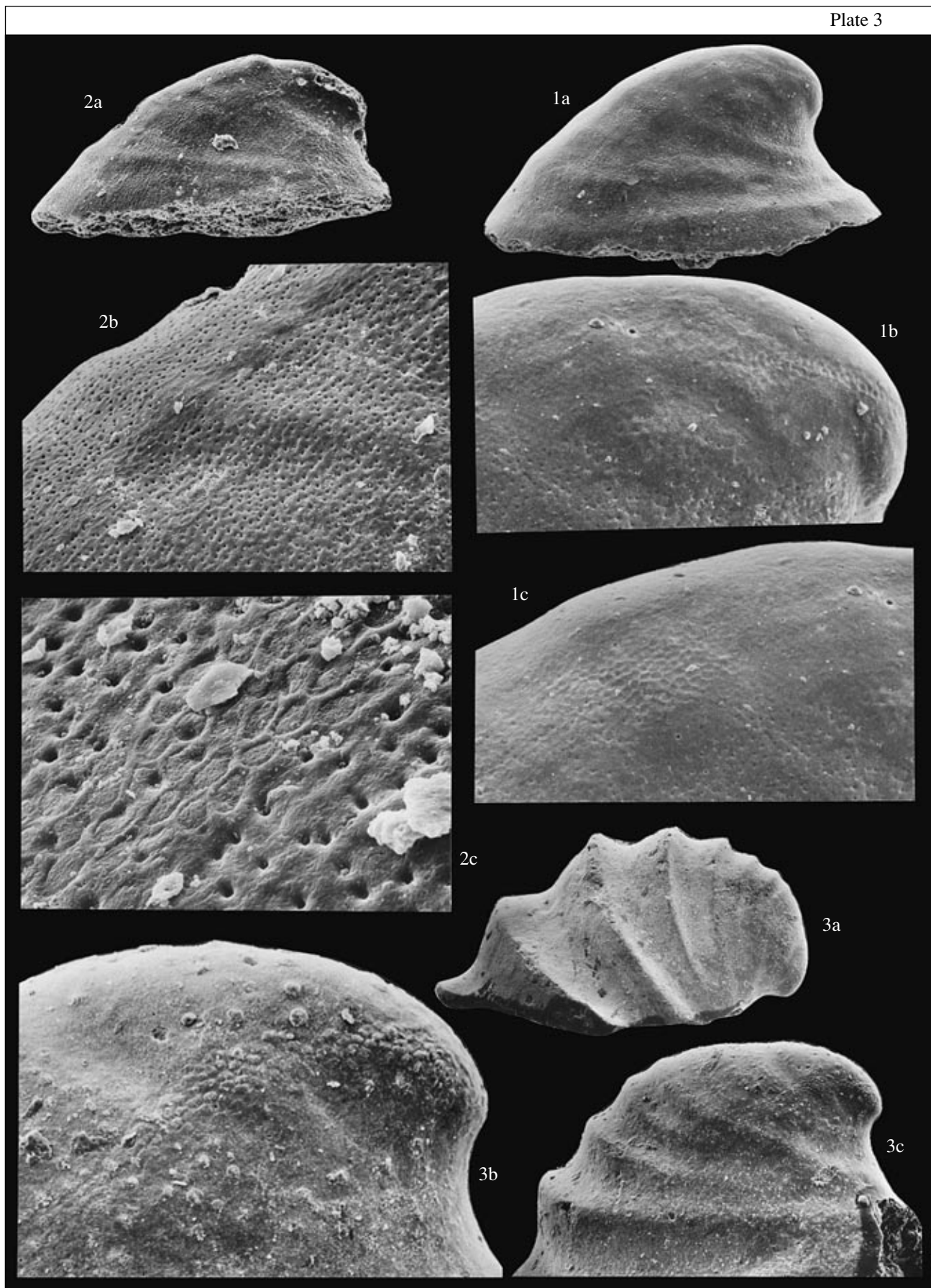
Explanation of Plate 3

All figured specimens came from the Lower Cambrian, Botomian Stage of South Australia.

Figs. 1 and 2. *Bemella communis* Parkhaev in Gravestock *et al.*, 2001; Yorke Peninsula, Curramulka Quarry, Parara Limestone; *Bemella communis* Beds; (1) specimen no. 4664/1271, internal mould: (1a) left view, ×63; (1b) apical area, lateral view, ×185; (1c) fragment of the anterolateral surface, ×185; (2) specimen no. 4664/1262, internal mould: (2a) left view, ×57; (2b) fragment of the anterolateral surface, ×210; (2c) same as previous, ×850.

Fig. 3. *Bemella incomparabilis* Parkhaev in Gravestock *et al.*, 2001; Fleurieu Peninsula, Myponga Beach, Sellick Hill Formation, *Stenotheca drepanoida* Beds; holotype no. 4664/1320, internal mould: (3a) left view, ×28; (3b) apical area, lateral view, ×220; (3c) same as previous, ×61.

Plate 3

Figs. 1 and 2. *Anhuiconus microtuberus* Zhou et Xiao, 1984; Lower Cambrian, Botomian Stage, South Australia, Yorke Peninsula, Parara Limestone: (1) specimen no. 4664/1867, internal mould of adult specimen, ×23; Horse Gully, *Bemella communis* Beds; (2) specimen no. 4664/1738, internal mould of immature specimen, oblique view from the apex; SYC-101 Borehole (167.87 m deep, *Stenotheca drepanoida* Beds), ×220.

Fig. 3. *Oelandiella* sp.; Lower Cambrian, lower part of the Tommotian Stage, Siberian Platform, right bank of the Yenisei River, 6 km downstream of Plakhinskii Island: (3a) left view, ×56; (3b) fragment of the subapical area, ×820.

Fig. 4. *Beshtashella tortilis* Missarzhevsky in Missarzhevsky et Mambetov, 1981, specimen no. 4664/1815; Lower Cambrian, Botomian Stage, South Australia, Yorke Peninsula, Horse Gully, Parara Limestone, *Bemella communis* Beds: (4a) internal mould, ×105; (4b) fragment of the umbilical area, ×290.

Fig. 5. *Bemella* sp.; Lower Cambrian, lower part of the Tommotian Stage, Siberian Platform, right bank of the Yenisei River, 6 km downstream of Plakhinskii Island: (5a) right view, ×65; (5b) fragment of the apical area, ×245; (5c) apex from posterior, ×370.

Fig. 6. *Acroloxus shadini* Kruglov et Starobogatov, 1991; recent, Moscow, Tsaritsino Ponds: (6a) fragment of the internal surface with a part of the muscle scar, ×63; (6b) same as previous, ×370.

DISCUSSION

The description given above shows that the surface of internal moulds has heterogeneous pattern in the studied species: the zones with distinct honeycomb ornamentation occurs against a more or less uniform background. The localization of these zone is very peculiar. In cap-shaped and depressed she is of *Bemella communis*, the bands of honeycomb microsculpture are on the whole lateral sides of the shell (Figs. 1a, 1b). In the similar cap-shaped but higher shell of *B. incomparabilis*, the zone is restricted to the apical area (Fig. 1c). Spirally coiled symmetrical *Anhuiconus microtuberus* bears the honeycomb zone on the subapical area (Figs. 1d, 1e), while sinistral hyperstrophic species *Beshtashella tortilis* displays this zone within the umbilical region of the mould that corresponds the columella of the shell. Thus, the zones of honeycomb microsculpture do occur exactly within those places, where the muscle attachment areas can be expected in accordance with morphofunctional reasons, which, in turn, conforms the shells shape.

In addition to the already discussed material from South Australia, muscle scars were found on mollusks moulds forms from the Tommotian Stage of Siberia. With the kind permission of Dr. D.P. Sipin (Joined Institute of Geology and Geophysics, Novosibirsk), I examined the unpublished material collected on the right bank of the Yenisei River, 6 km downstream of Plakhinskii Island (Korovnikov *et al.*, 2002, section no. 3, beds nos. 6 and 7). As was found out, the internal moulds of *Bemella* sp. (family Helcionellidae) (Pl. 4, fig. 5) and *Oelandiella* sp. (family Coreospiridae) (Pl. 4, fig. 3) also bear the zones with honeycomb microsculpture. It is noteworthy that the position of these zones is absolutely analogous with the Australian forms; i.e., the helcionellids bears the zone on the anterolateral side of the mould (Pl. 4, figs. 5b, 5c), while coreospirids display it on the subapical area (Pl. 4, fig. 3b).

Besides the position itself, the microsculptural morphology also supports the muscular nature of these zones. The similar honeycomb pattern is present on the muscle scars of recent mollusks (Pl. 4, figs. 6a, 6b), and it is almost identical among gastropods and pelecypods as well. It is a relief that is typical for palial myostracum, i.e., the shell layer to which the muscle fibers are attached. The honeycomb ornamentation of the surface of palial myostracum is a result of the microstructure of this part of the shell which is composed of calcareous prisms (Taylor and Kennedy, 1969; Popov, 1977).

In addition to different groups of mollusks, the same relief of the muscle scars is known for inarticulate brachiopods, craniids. Williams and Wright (1970) made a detailed study of the shell microstructure of recent *Crania anomala*. According to their investigation, the muscle scars of brachiopod bear a honeycomb microsculpture composed of polygonal elements (10–12 μm in diameter) divided by narrow borders. The borders can be elevated above the surface of the polygons forming skirting around them (Williams and Wright, 1970, pl. 7, fig. 6), or they can be sunk, surrounding the polygons by narrow grooves (Williams and Wright, 1970, pl. 8, figs. 1, 2). The authors did not explain the nature of positive or negative relief of polygons on the muscle scars and only noted that it was probably connected with configuration of the mantle cells covering the scars surface (Williams and Wright, 1970, p. 28). It is supposed that the cells themselves correspond the polygonal elements, while the intracellular borders correspond the skirting or grooves between the polygons. It is noteworthy that, in spite the microstructural difference between the dorsal and ventral craniid valves (the former is composed of laminar secondary layer, while the latter is made from the primary microcrystal layer), the muscles scars on both valves are identical by its microsculpture (Williams and Wright, 1970, p. 29).

The mollusks have absolutely different type of the shell microstructure compared with brachiopods, but the relief of the muscle scars is very similar in both groups. We can assume that the relief of the scars is not directly connected with the microstructure of the shell wall. Probably, the relief replicates only the structure of the muscular tissue, of which the type of attachment to the shell is possibly identical in different groups of invertebrates.

Thus, with great reliability, we can ascertain that the zones of honeycomb microsculpture found in *Bemella, Anhuiconus, Oelandiella*, and *Beshatshella* are actually the scars of shell muscles.

Plate 4
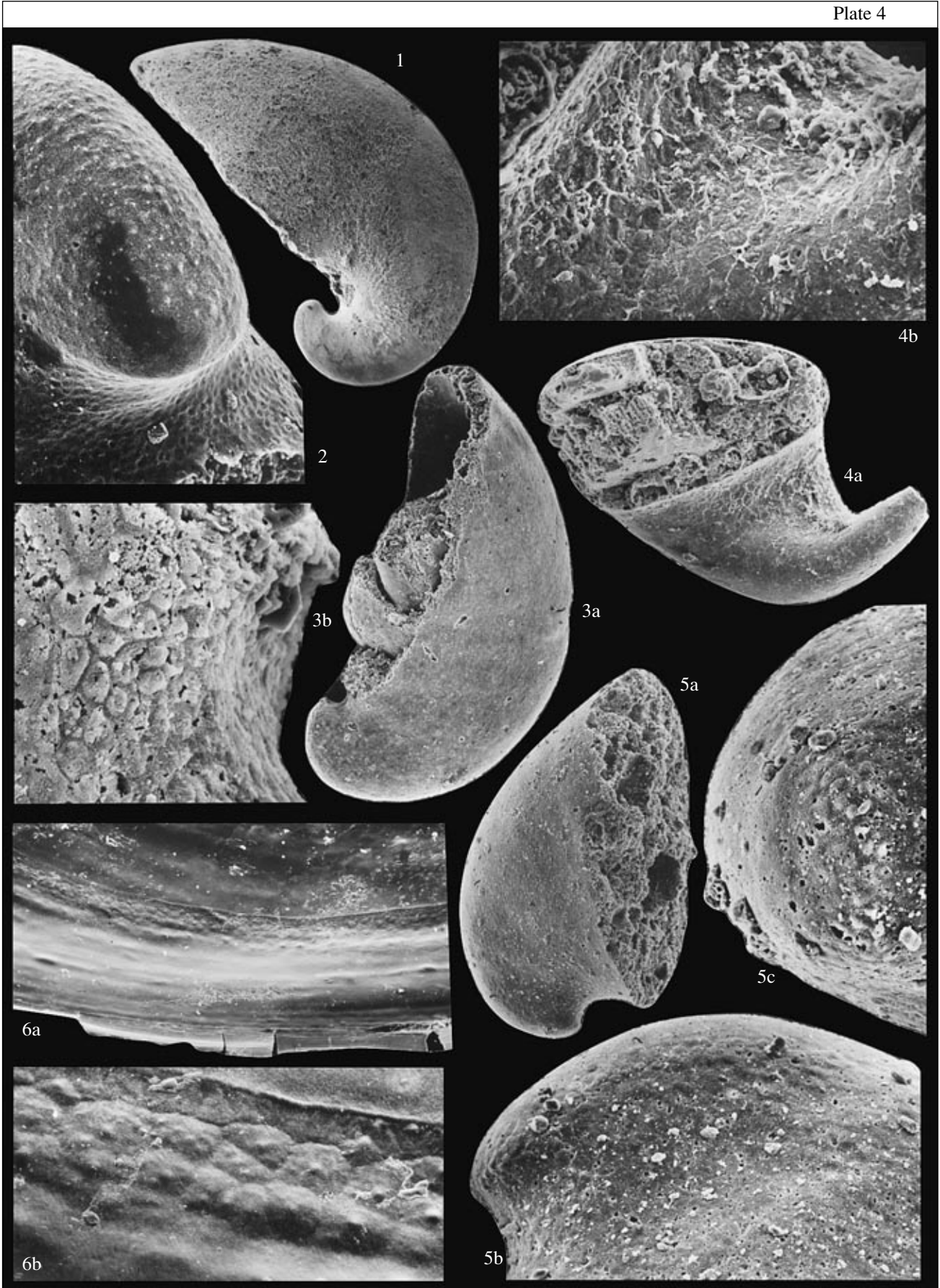
SYSTEMATICAL IMPLICATIONS

In spite the common belief that a find of the muscles scars among the Cambrian mollusks should resolve the problem of their systematic affinity to gastropods or monoplacophorans, the reality is more complicated and not so optimistic. The recent gastropods are extremely variable in the structure of the shell muscles. Forms with multiple muscles scars are present among gastropods showing the similarity with monoplacophorans (Some members of the family Acmaeidae have a horseshoe muscle formed by junction of the left and right juvenile muscles. The muscle is penetrated by large blood sinuses splitting it on several smaller bundles, so the scar gets a multiple pattern). Therefore, a find of the multiple muscle scars on the shells of the Cambrian mollusks would not unambiguously favor their relation to monoplacophorans. The opposite statement is also fair: if the helcionelloids had a single pair of the muscle scars, nobody could be firmly convinced that they are really gastropods, since the several pairs of the scars among recent monoplacophorans could be a result of polymerization of the original single pair, as was already suggested by Starobogatov (1970).

The material studied in the present work allows us to claim the presence of the single pair of shell muscles among the members of the Helcionellidae and single columellar muscle among Coreospiridae and Onychochilidae. It is possible that the single muscle of the coreospirids has originated after the approaching and subsequent merging of the left and right shells muscle during the transformation of the shell from cap-shaped of ancestral Helcionellidae to spirally coiled shell of the descendant Coreospiridae.

As was already mentioned, the data on the structure of the muscular system does not provide evidence for a class assignment of the studied mollusks within the phylum Mollusca. However, the obtained data give important knowledge on the morphology of the helcionelloid mollusks. First, the columellar muscle attachment of the Coreospiridae proves the presence of the endogastric shell (Starobogatov, 1970), once again justifying the assumption about the posteriorly directed apex in helcionelloids (Parkhaev, 2000). Second, the structure of the paired muscle scars in *Bemella* (Figs. 1a, 1b) suggests that, with the shells growth, the muscles grow from the apex toward the anterior margin of the aperture, i.e., from behind to a front but not vice versa as in Patelliformes. This feature adds another difference between the bauplan of the subclasses Cyclobranchia and Archaeobranchia. It is also noteworthy that the muscle scars extend over the lateral surface of the protoconch (Pl. 3, fig. 1b). This fact suggests that larval muscles of *Bemella* correspond to the muscles of the adult mollusk and the larval muscles have been formed already after the torsion. Such a scheme confirms the viewpoint of Bandel (1982) and Haszprunar (1988) that claims that the torsion process is not a result of the muscular activity as have been supposed by

Crofts (1937, 1955) but is a result of the differential growth of the visceral mass.

Nevertheless, the new data on the muscular morphology of the helcionelloideans have some significance for the systematics of the Cambrian mollusks but at lower taxonomic level. The discovered difference in the localization of the muscle attachment areas in the helcionellids and coreospirids is a diagnostic feature for distinction of these families. This feature can be used for family assignment of some cap-like forms, which, earlier, could be regarded as either helcionellids or immature and still uncoiled coreospirids.

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