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New Data on the Morphology of Shell Muscles in Cambrian Helcionelloid Mollusks

P. Yu. Parkhaev

Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia
e-mail: pparkh@paleo.ru

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Abstract—Scars of shell muscles have been discovered on internal molds of helcionelloid mollusks of the family Stenothecidae for the first time. The localization of the scars is similar to that in the family Coreospiridae. Since these two families evolved from the ancestral group independently, similar shell muscle systems of Cambrian helcionelloid mollusks may be explained by parallel development.

Key words: morphology, Cambrian, univalved mollusks, shell muscles.

INTRODUCTION

After a recent publication by this author in which the muscle scars of the Cambrian univalved mollusks were described for the first time (Parkhaev, 2002a), the study of the internal molds of mollusks of this age using SEM was continued in order to yield new data on the morphology of the shell muscle system. In this way, scars of shell muscles have been discovered in molds of helcionelloid mollusks from the family Stenothecidae.

MATERIAL

The material being studied is housed at the Paleontological Institute of the Russian Academy of Sciences (collection nos. 2019, 4368, and 4664).

DISCUSSION

The internal molds of *Anabarella* sp. from the Lower Cambrian of Transbaikal Region (Bystraya Formation, Georgievka Locality) contain a site with cellular microsculpture (Pl. 2, fig. 5) that is similar in appearance to scars of shell muscles that have been described earlier for Cambrian mollusks from the families Helcionellidae, Coreospiridae, and Onychochilidae (Parkhaev, 2002a). The scar is situated in the subapical part of the mold at the boundary between its posterior surface and the roof of the parietal train. The scar consists of polygonal depressions that are 10–12 μm in diameter and thin dividing balks approximately 3 μm wide (Pl. 2, fig. 2). Such a type of microrelief of the internal mold surface is a replica of the prismatic shell layer, i.e., myostracum. The pallial myostracum shows a similar prismatic structure in different groups of mollusks and even in brachiopods (Taylor *et al.*, 1969; 1973; Williams and Wright, 1970; Popov, 1977; Parkhaev, 2002a).

After the above-mentioned scars on the molds of Transbaikalian anabarellas were discovered, I restudied the vast collection of mollusks from the Lower Cambrian of South Australia, in which there are also members of the genus *Anabarella*. The collection contains several hundred differently preserved internal molds and shells of *Anabarella australis* Runnegar, 1990. Thorough investigation of the best preserved internal molds revealed that some specimens bear muscle scars on the subapical surface. The scars are not as distinct as in Transbaikalian anabarellas (the polygonal depressions and dividing balks are not as prominent in relief), have a different shape, and slightly differ in position

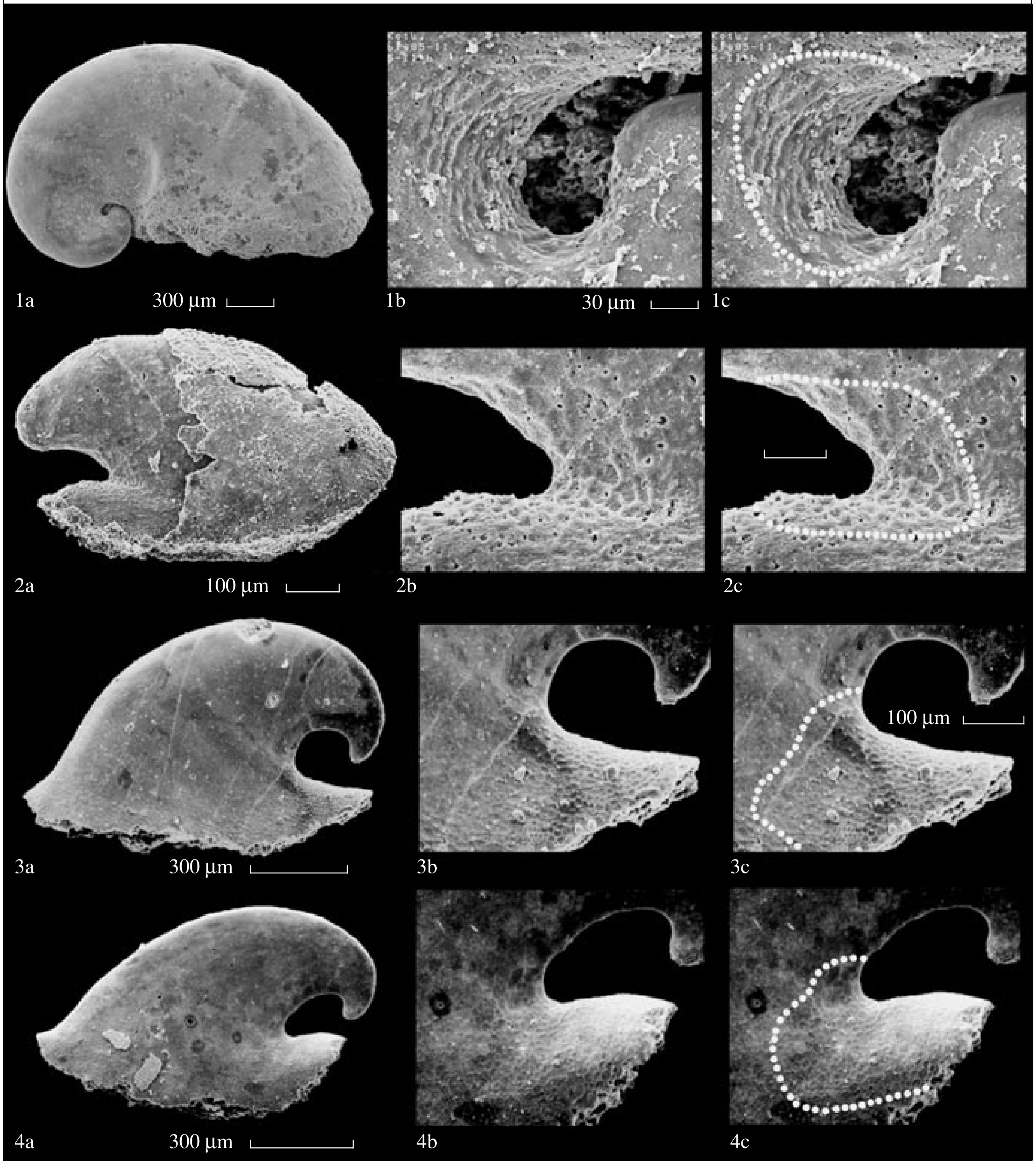
E x p l a n a t i o n o f P l a t e 2

Fig. 1. *Oelandiella korobkovi* Vostokova, 1962; specimen no. 4368/1008, internal mold; Lower Cambrian, lower part of the Tommotian Stage, Siberian Platform, southwestern Anabar Region, Kotuĭ River: (1a) internal mold, right view, ×26; (1b) umbilical area with muscle scar, ×250; (1c) same view, supposed margin of the scar is dotted, ×250.

Fig. 2. *Anabarella* sp.; specimen no. 2019/1036, internal mold; Lower Cambrian, Botoman Stage; Transbaikalia, Chita Region, village of Georgievka: (2a) internal mold, right view, ×95; (2b) subapical area with muscle scar, ×370; (2c) same view, supposed margin of the scar is dotted, ×370.

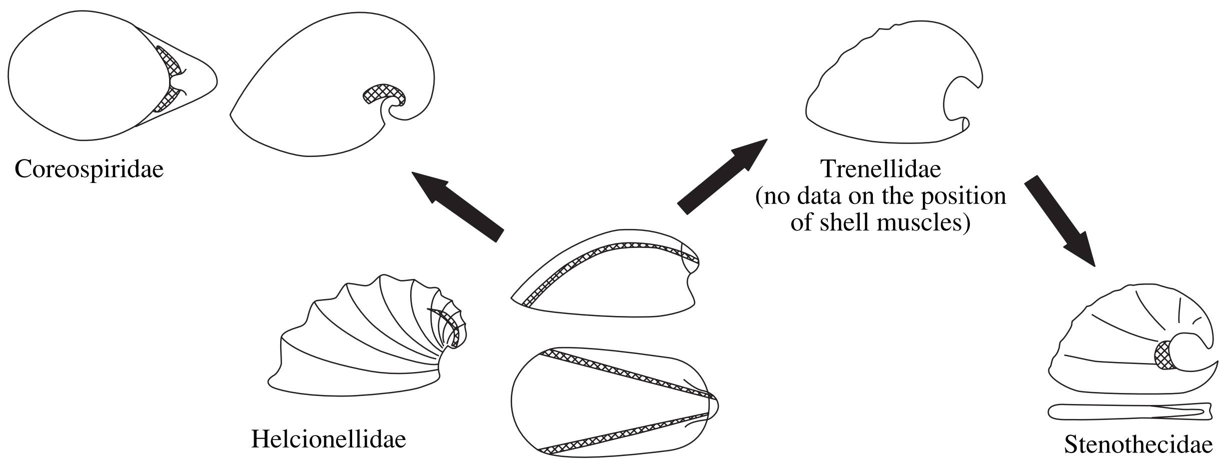
Figs. 3 and 4. *Anabarella australis* Runnegar in Bengtson *et al.*, 1990; Lower Cambrian, Botoman Stage, South Australia, Yorke Peninsula, Parara Limestone; (3) specimen no. 4664/1295, internal mold; Curramulka Quarry: (3a) internal mold, left view, ×57; (3b) subapical area with muscle scar, ×110; (3c) same view, supposed margin of the scar is dotted, ×110; (4) specimen no. 4664/1648, internal mold; SYC-101 Borehole, depth 198.5 m: (4a) internal mold, left view, ×60; (4b) subapical area with muscle scar, ×150; (4c) same view, supposed margin of the scar is dotted, ×150.

Plate 2



(Pl. 2, figs. 2, 3). A major part of the muscle scar in *A. australis* lies on the roof of the parietal train and extends slightly to the posterior surface of the mold. In addition, the scar goes as far as the lateral surfaces of the train. The polygonal depressions are 10–15 μm in diameter, and the width of the balks is about 3–5 μm.

Thus, muscle scars have been found in members of the family Stenothecidae for the first time. It is noteworthy that the position of these scars on the subapical surface of the molds is also typical of another group of Cambrian mollusks, i.e., the family Coreospiridae (Pl. 2, fig. 1).



Changes in the localization of the attachment sites of shell muscles in helcionelloid mollusks that are associated with the morphogenesis of the shell (muscle scars are hatched).

If the phylogenetic development of the Cambrian univalved mollusks that was assumed by the author earlier (Parkhaev, 2002b) is correct, i.e., the families Coreospiridae and Stenothecidae evolved from the ancestral Helcionellidae independently, this is an example of parallel evolution of shell muscles in helcionelloid mollusks.

It is probable that the same localization of the muscle attachment sites in coreospirids and stenothecids was achieved by the general modification of the shell shape in the ancestral helcionellids, which was accompanied by the displacement of the shell muscles from the anterolateral areas to the subapical zone (figure). It is obvious that, in the case of coreospirids, this displacement is a result of spiral coiling of the shell. In stenothecids, the shells of which are strongly laterally compressed, the muscle displacement may be due to this lateral compression. Today, unfortunately, we have no data on the position of the muscle scars in the family Trenellidae, which most probably evolved from Helcionellidae and is ancestral to Stenothecidae (figure).

It is quite possible that trenellids possessed an intermediate morphology in which muscles were located on the lateral surface within the apical part of the shell.

It is noteworthy that the variability in shell structure and the numerous cases of parallel development in shell muscles are fairly common in gastropods. For instance, a horseshoe-shaped shell muscle occurs among different and relatively phylogenetically distant groups of recent gastropods. In general, with slight modifications, it is most typical of members of the primitive subclasses Scutibranchia and Cyclobranchia but also occurs in some groups of Pectinibranchia (Capulidae and Muricidae), Divasibranchia (Siphonariidae), and even in Pulmonata (Acroloxidae and Planorbidae).

All these cases of independent development of the horseshoe-shaped shell muscle are due to similar shell morphogenesis (all the above-mentioned gastropods have shells with a cap-shaped or similar form).

Obviously, the high plasticity of shell morphology and, as a result, the plasticity in the structure of the shell muscles were already present among Cambrian helcionelloid mollusks. Thus, this supplies additional evidence that helcionelloid mollusks belong to gastropods. A further study of the microsculpture and microstructure of the shell of Cambrian univalved mollusks will assist us in reconstructing the major evolutionary changes in the shell muscular system, thus, in turn, providing additional material for the study of the evolution of the earliest gastropods.

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