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Shell structures in Carboniferous bactritid-like coleoids (Cephalopoda) from South Central USA

HARRY MUTVEI1, ROYAL H. MAPES2 and LARISA A. DOGUZHAEVA1


Abstract: Morphological features of the shell including internal structures of the phragmocones of three different bactritoid cephalopod taxa assigned to the Order Bactritida: Bactrites quadrilineatus, Ctenobactrites lesliensis (L. Carboniferous) and the Order Parabactritida: Rugobactrites jacksboroensis (U. Carboniferous) were studied. The material comes from South Central USA. The features examined include the conch shape, siphuncle shape and ultrastructure of the shell wall, septa, septal neck and the connecting ring. These traits were then compared with Shimanskya postremus from Upper Carboniferous of Texas, which has been originally referred to bactritids and later placed within the coleoids in the Order Spirulida. Based on similarities and differences observed, B. quadrilineatus and C. lesliensis are now also considered being coleoids similar to S. postremus; R. jacksboroensis remains placed in the Order Parabactritida.

Keywords: bactritid-like coleoids; Carboniferous; shell structure; South Central USA.

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Introduction

Some structures of cephalopod shells represent highly conservative evolutionary traits. Such structures include the ultrastructural organization of the shell of the phragmocone and body chamber and the septa, septal necks and the connecting rings of the siphuncle in the phragmocone. Because of the conservative nature of these features, they should be placed at a high level of importance in the classification of the Cephalopoda and that the taxa that exhibit similarities in these traits should be considered as being more closely related to those individuals that do not have similar traits.

Doguzhaeva et al. (1996, 1999, 2010a) found that the shell wall structure in one Upper Carboniferous bactritoid from Texas that was originally identified as Bactrites postremus Miller, 1930, and subsequently by Mapes (1979), differed considerably from that in the Upper Carboniferous Bactrites sp. from the Ural Mountains, Russia (Doguzhaeva 2002). The shell wall in Bactrites sp. from the Ural Mountains consists of a thin outer prismatic layer and a thick inner nacreous layer, similar to the shell wall structure observed in nautiloids and ammonoids. In contrast, B. postremus from the Upper Carboniferous of Texas has two porous and loosely mineralized, prismatic layers of about equal thickness without a nacreous layer. These two layers are separated by a surface covered with parallel ridges that somewhat resemble a finger print pattern. The two loosely mineralized, prismatic layers in B. postremus were interpreted by Doguzhaeva et al. (1999, 2010a) as corresponding to the two prismatic layers in the shell wall of the Recent Spirula (inner and outer plates by Appellöf 1893) and the shell wall structure seen in the Cretaceous spirulids Adygeya Doguzhaeva, 1996 and Naefia Wetzel, 1930. Thus, according to that interpretation, B. postremus must be a coleoid with an internal shell and not a bactritoid. On the basis of its unique shell structure, B. postremus was assigned to the new genus Shimanskya of the new family Shimanskyidea and placed in the Order Spirulida.

With this discovery, the examination of other taxa described as bactritoids seemed warranted to see whether other bactritoid taxa from the Carboniferous have the Shimanskya type of the shell structure or whether they have the typical structure seen in bactritoids, nautiloids and ammonoids.

In order to test other bactritoids for this condition, the Carboniferous bactritoid collection of the second author from the Carboniferous of the Midcontinent of North America was examined, and the most promising specimens were selected for study. Over 10 000 specimens are in this collection, but almost 95% are microscopic bactritellas, and of the larger specimens, most were internal molds without external shell. Of those specimens that retain shell, most are strongly recrystallized shells. Three taxa were eventually isolated as having adequate, although still poorly preserved, shell suitable for this kind of analysis. These taxa are identified by using the terminology of Mapes (1979) as: Bactrites quadrilineatus Girty, 1909 and Ctenobactrites lesliensis Mapes, 1979 from the upper part of
the Lower Carboniferous (Serpukhovian), and *Rugobactrites jacksboroensis* Mapes, 1979 from the upper part of the Upper Carboniferous (Gzhelian). In addition to examining the shell structure, details of the septal structure and siphuncle structure including the septal necks and connecting rings were examined.

**Materials and methods**

The material comprises mainly partial phragmocones and body chambers of *B. quadrilineatus* and *C. lesliensis* from the Lower Carboniferous, and *B. postremus* and *R. jacksboroensis* from the Upper Carboniferous. For comparative purpose *Shimanskyapostremus* was restudied.

The following localities yielded the study material:

*B. quadrilineatus*: Lower Carboniferous – Delaware Creek Member of the Caney Formation in south central Oklahoma. The locality is located approximately 12 km south of Ada, Oklahoma, in the bed of Jack Fork Creek (see Mapes 1979, locality M-1 for details).

*C. lesliensis*: Lower Carboniferous – upper unnamed shale member of the Fayetteville Formation exposed during the construction of Interstate Highway 570 west of the town of West Fork, Arkansas. The exposure is no longer collectable.

*R. jacksboroensis*: Upper Carboniferous – all of the specimens examined are from the Finis Shale Member of the Graham Formation, which is exposed in the northeast, east and southeast of Jacksboro, Jack County, Texas. This taxon was recovered from localities TXV-40 and TXV–56, which are located approximately 7 km southeast of Jacksboro (see Boardman et al. 1994, pp. 94–95 for more locality details).

Additional specimens were recovered at localities BBTXV–82 and BBTXV–86, which are located approximately 15 km east of Jacksboro and 4 km southeast of Jacksboro, respectively (see Boston 1988). Locality BBTXV–89 is a road cut located in eastern Young County that was collected and measured by Boston (1988).

*S. postremus*: Upper Carboniferous – all of the specimens examined are from the Finis Shale Member of the Graham Formation, which is exposed in the northeast, east and southeast of Jacksboro, Jack County, Texas. Seven localities have produced specimens. Localities TXV-30, 34, 36 and 56 are given in Boardman et al. (1994, pp. 94–95). Locality TXV-200 is the Lost Creek emergency spillway located approximately 7 km northeast of Jacksboro (see Rice et al. 1996; Mapes and Mapes 1997 for additional details). For additional details on localities BBTXV 60 and BBTXV–89, see Boston (1988).

The structure of the shell wall and siphuncle was studied in median and transverse sections that were polished with aluminum oxide. The preparations were studied either unetched or etched for 3–8 min with a solution of 1:1 mixture of 25% glutaraldehyde and 1% acetic acid to which alcan blue was added (Mutvei’s solution in Schöne et al. 2005). All preparations of *B. postremus* and *C. lesliensis* were studied with a scanning electron microscope Hitachi 4300 at the same Museum. Analysis on elemental distribution in the shell was made with an energy dispersive apparatus (EDAX). All specimens are reposited at the Ohio University Zoological Collections (OUZC) in Athens, OH.

**Observations on shell structures**

*S. postremus* (Miller, 1930)

Figs. 1–6

*B. postremus* Miller, 1930, pl. 38, fig. 11.

*B. postremus* Mapes, 1979 pl. 21, figs. 13–15; pl. 33, figs. 10–13; pl. 35, figs. 1–3.

*S. postremus*, Doguzhaeva, Mapes and Mutvei, 1999, fig. 1A, B.

*S. postremus*, Doguzhaeva, Mapes and Mutvei, 2010a, figs. 2A, 3A.

**Shell**

The best-preserved material comprises about 40 phragmococon and body chamber fragments. Twenty-five specimens were cut either longitudinally or transversally, and studied with light microscope and SEM.

The conch of *S. postremus* is longiconic with well-spaced septa and orthochoanitic septal necks (Figs. 1A,B, 6A–C). The apical end of the conch is unknown and so far as is known, this cephalopod has no ink, arm hooks or a rostrum. Because of its unusual shell structure, it was placed in the coleoid Order Spirululida because the only members of that coleoid order have a similar shell structure.

**Shell wall in the phragmococone**

The shell wall in the phragmococone is composed of three layers: a thick outer and inner layer separated by a thin intermediate layer.

The outer shell layer (Figs. 1B, 2A,B, 4B, 5) is more crystallized than the inner layer. It is both finely granular and compact (Figs. 4B, 5) or coarsely granular (Fig. 2A,B). The layer probably had a high porosity and high content of organic substance. The high porosity is indicated in a phragmococone in which the outer shell layer is impregnated by high contents of zinc and sulfur, whereas the inner shell layer lacks these elements.

The structure of the inner layer of the shell wall is preserved only in few preparations. The layer consists of narrow, vertical lamellae that are composed of acicular crystallites (Fig. 2C). The crystallites have an oblique orientation to the vertical axis of the lamellae (Fig. 2C). In most preparations, the presence of the vertical lamellae is indicated by indistinct, vertical striations (Figs. 4B, 5).

The intermediate layer that separates the outer and inner shell layers is thin, about one-fifth of the thickness of the inner layer. It is composed of what appears to be a series of frequently parallel calcareous rods (Figs. 1C, 4A,B, 5). In places, the rods have more or less rounded shape in some cross sections suggesting that diagenetic alteration has occurred (Fig. 4B), but in other places the rods have a distinctly angular, sub-triangular shape (Fig. 5). The latter probably represents the most unaltered shape of the rods. The upper surfaces of the rods form distinct, parallel ridges (Figs. 1B,C, 2A,B, 3A–C, 4A) that appear to be somewhat like a fingerprint pattern. The rods sometimes branch forming two distinct and equal in size ridges (Doguzhaeva et al. 1999, Fig. 1B). The rods may have been as porous as the outer shell layer because in places they have acquired similar fine granular and compact structures through diagenetic processes (Fig. 5).
Shell wall in the body chamber
On juvenile specimens, the external surface of the shell is smooth and without growth lines or other ornament. On mature specimens, broad ribs 1–2 mm in breadth are developed which are inclined toward the aperture on the dorsum (Fig. 3A); these ribs are interpreted as a mature modification. The ribs are dark colored, and have a flat upper surface and a slightly convex lower surface. The structure of the ribs is not preserved. The

Fig. 1. *S. postremus*. (OUZC 8576) Longitudinal section of a partial phragmocone showing the concave septa, septal necks and connecting rings, × 2.5. B, C. (OUZC 5977) B. Phragmocone segment in which the outer shell has been removed showing the septal spacing, × 3. C. Enlargement of the intermediate shell layer showing the ridges and valleys that form the fingerprint-like pattern, × 70.
course of the ribs indicates that the shell aperture has a broad dorsal lobe and a shallow ventral sinus.

On the mature body chamber, the outer layer decreases in thickness toward the aperture. As a result, the ribs are situated directly on the upper surface of the intermediate layer (Fig. 3A). The rods in the intermediate layer and the ribs on the shell surface have somewhat different course (Fig. 3A). Close to the shell aperture at presumed or near maturity, the inner layer and outer layers become thinner and the intermediate layer covers the inner surface of the shell wall (Fig. 4C). The rods in this layer on the available specimens appear to have been partly dissolved prior to burial with sediment similar to that in the body chamber filling the cavities left after the solution of the rods (Fig. 4C).

Flexible deformation of the shell wall

In several places on phragmocones and body chambers, the shell surface shows more or less distinct, flexible deformations of the
intermediate layer. Also, as can be seen in a longitudinal section of one phragmocone, the shell wall bends distinctly inwards and forms three depressions of different sizes (Fig. 3C). It is probable that many deformations originated in the body chamber during the lifetime of the animal because they do not affect the septa and the siphuncle. This deformation of the phragmocone indicates that the shell wall has to have been somewhat flexible because of its relatively high organic content, porous mineralized structure and reduced thickness near the aperture.

Septa and septal necks
The length of the mural part of the septum is about of the chamber height. In several phragmocones, the shell wall forms a shallow circular constriction at the mural part of each septum. Median sections show that each septum is composed of 10–20 lamellae parallel to the septal surface (Fig. 6C). Each lamella is composed of acicular crystallites that have a more or less oblique orientation. The lamellae are similar to those in the inner lamellar–prismatic layer of the shell wall, but they are less porous and have uniform breadth and structure. The septa do not show any sign of flexible deformation like that seen in the shell wall. In median and tangential sections, the septal neck is slightly curved toward the siphuncular cavity (Fig. 6A). Its distal portion is somewhat thickened and has a club-like shape. It has the same prismatic–lamellar structure as the septum (Fig. 6A–C), and the lamellae in the septum are directly continuous into the septal neck (Fig. 6C).

Connecting ring
The connecting ring is preserved as a thin, dark layer that originates from the outermost portion of the septal neck (Fig. 6A,B). This layer seems to be composed of hardened (tanned)
organic fibers, similar to the fibrous-organic (chitin) layer of the connecting ring in ammonoids (Mutvei et al. 2005; Mutvei and Dunca 2007; Doguzhaeva et al. 2010b). In higher magnification, it shows a globular structure typical of fossilized organic material. Because the growth lamellae in the distal end of the septal neck terminate without a continuation into the connecting ring, we have to assume that the connecting ring also had a thick, soft, inner fibrous-organic sub-layer that was destroyed by
Fig. 5. *S. postremus*. SEM image. Longitudinal section of the shell wall to show the outer, intermediate and inner shell layers; note that the rods in the intermediate layer, together with the outer layer, have lost their original structure, and that the inner shell layer shows indistinct vertical lamellae of acicular crystallites. Scale bar: 40 μm.

Fig. 6. *S. postremus*. A. (OUZ 5848) Median section of the siphuncle; note the thin connecting ring that is composed of the outer sub-layer whereas the thick, inner sub-layer, has been destroyed by diagenesis, its original position is indicated by X, × 50. B. (OUZ 5849) Septal neck and connecting ring in higher magnification to show the lamellar–prismatic structure of the septal neck; the thick inner sub-layer of the connecting ring is not preserved; its original position is indicated by X, × 100. C. Lamellar–prismatic structure of the septum and septal neck; note that the lamellae in the septum continue into the septal neck, × 150.
diagenesis. Its position during the lifetime of the animal is indicated by the X in Fig. 6A,B. The connecting ring extends adapically to the preceding septal neck and is attached to its inner surface (Fig. 6A).

*C. lesliensis* Mapes, 1979

Figs. 7–11

*C. lesliensis* Mapes, 1979, pl. 34, figs. 9–11.

**Shell**

The studied material comprises five phragmocone fragments. Four were cut longitudinally and studied with light microscope and SEM.

The conch of *C. lesliensis* is longiconic with well-spaced septa and orthochoanitic septal necks. The apical end of the conch is unknown. In so far as is known, this cephalopod is not known to have ink, arm hooks or a rostrum. Taxa belonging to the genus have been recovered in Russia (Shimansky 1968) and in Ohio, USA (Sturgeon et al. 1982). Until the present time, this genus has been thought to be a bactritoid.

**Shell wall structure**

Two structurally different layers can be distinguished in the shell wall. The outer layer is in most parts completely black and silicified, containing 45% silica. The silicified layer does not show any crystalline structure (Fig. 7A,B). It penetrates into the upper portion of the inner shell layer and forms an irregular
boundary between these two layers (Fig. 7A,B). This indicates that the outer layer had high porosity whereas the inner layer was less porous and, therefore, not impregnated by silica. The shell surface shows prominent, broad growth ridges with flat surfaces (Fig. 7A).

The inner layer of the shell wall is composed of acicular crystallites that in most places are arranged in vertical lamellae of variable thickness (Fig. 7B). The orientation of the crystallites is in some lamellae vertical, but in other lamellae more or less oblique to the vertical axis of the lamellae. This layer is not silicified. In places, this layer is divided into two vertical prismatic sections, and it is not clear whether this division is a diagenetic or a biological feature.

The intermediate layer is only exposed on a broken edge of OUZC 5834 in which the shell layers are separated (Fig. 9C). At that place the boundary between the upper and inner layers is exposed showing a thin intermediate layer that is slightly wrinkled, indicating that originally it was probably an organic film. There are no traces of a finger print pattern in association with this presumed organic film.

Flexible deformation of the shell wall
One phragmocone fragment (OUZC 5836), about 30 mm in length and 20 mm in diameter, shows considerable deformation to the conch. As seen in tangential section, the ventral side of the shell wall has two depressions (Fig. 8A). Note that three septa with septal necks and connecting rings in this section are not affected by the deformation of the shell wall. This indicates that the depressions were formed in the living chamber at an earlier growth stage during the lifetime of the animal. On the left lateral side of the same phragmocone, the two depressions increase in depth toward the dorsal side (Fig. 8B). On the external surface of the broken phragmocone, the shell shows some fractures that are due to diagenetic crushing; however, the amount of crushing is not sufficient to account for the size of the depressions in the conch.

Septa and septal necks
The distance between two consecutive septa is equal to about half of the median diameter of the phragmocone. On specimen OUZC 5836, the length of the mural part of the septa is most unusual in that it appears to extend the entire length of the chamber to the next septum (Fig. 9A,B). The septa and septal necks are composed of distinct prismatic lamellae that are parallel to the upper and lower septal surfaces (Fig. 11B). The lamellae are about 8–10 \( \mu \text{m} \) thick and consist of acicular crystallites. The crystallites have a more or less oblique orientation within the lamellae. As in \( S. \ postremus \), the distal end of the septal neck increases somewhat in thickness and has a club-like shape (Fig. 10A,B). Each septal neck consists of about 20 prismatic lamellae (Fig. 11A). In addition to the prismatic lamellae, the outer surface of the septal neck is covered by a porous layer that in higher magnification shows a spherulitic–prismatic structure (Figs. 10B, 11A). This layer is not developed in the other bactritoid-like coleoids described herein.

Connecting ring
As in \( S. \ postremus \), the connecting ring consists of a thin, dark, fibrous-organic sub-layer that emerges from the outer surface of the septal neck (Fig. 10A). This layer is internally covered by a calcareous layer that probably has a diagenetic origin. During the lifetime of the animal, the connecting ring probably also consisted of a thick, inner, fibrous-organic sub-layer that was destroyed by diagenesis. The existence of this sub-layer is indicated by numerous prismatic lamellae at the distal end of the septal neck that terminate without continuation into the connecting ring (Figs. 10B, 11A). The original position of this sub-layer is indicated by X in Figs. 10B and 11A.

\( B. \ quadrilineatus \) Girty

Fig. 12

\( B. \ quadrilineatus \) Girty, 1909 pl. 6, figs. 1–4a
**B. quadrilineatus** Mapes, 1979 pl. 1, figs. 6–9; pl. 2, figs. 7–9; pl. 3, figs. 1–3, 7–11; pl. 4, figs. 10, 12–16; pl. 12, fig. 3.

**Shell**

The material consists of about 20 phragmocone fragments. The conch of *B. quadrilineatus* is longiconic with well-spaced septa and orthochoanitic septal necks. The apical end of the conch is a sub-spherical ball shape without a rostrum. In so far as is known, this cephalopod is no known to have ink, or arm hooks. Taxa belonging to the genus have been recovered worldwide from the Devonian to the Permian and possibility the Triassic. (See Mapes 1979 for an extended discussion.) Until the present time this taxon has been considered to belong in the Order Bactritoidea.

**Shell wall**

The shell wall is recrystallized and its structure cannot, therefore, be observed except in one phragmocone (OUZC 5838) in which the typical intermediate layer is exposed. The outer surface of the inner layer in this specimen retains the impression of strongly inclined ridges that are similar to the finger print pattern seen on the outer surface of the inner layer of *S. postremus* (Fig. 12D).

**Siphuncle and septa**

Distances between the septa are equal to the dorsoventral diameter of the shell. The septal necks have shape similar as those in *S. postremus* and *C. lesliensis*. One specimen (OUZC
5837) has the typical lamellar–prismatic structure of the septal neck preserved (Fig. 12B). The connecting ring is composed of a thin, fibrous-organic layer that emerges from the outer surface of the septal neck. The connecting ring must have been somewhat flexible because in two phragmocones it has been detached from the preceding septal neck and bent, without breaking, into the chamber (Fig. 12A,C). As in other bactritoid-like coleoids, the main, inner sub-layer of the connecting ring is not preserved.

*R. jacksboroensis* Mapes, 1979

Fig. 13

*R. jacksboroensis* Mapes, 1979, pl. 29, figs. 6, 8, 9, 12, 14–17.

**Shell**

The material consists of eight phragmocone fragments. The conch of *R. jacksboroensis* is breviconic with closely spaced septa and cyrtochoanitic septal necks (Fig. 13B,C). The apical end of the conch is unknown and so far as is known it is without a rostrum. Based on the recovered material, this cephalopod is not known to have ink, arm hooks or a rostrum. Taxa belonging to the genus have only been recovered from Carboniferous sediments in Arkansas, Nevada, Texas and Oklahoma in North America (see Mapes 1979 for additional information). Until the present time, this taxon has been considered to belong in the Order Bactritoidea.

**Shell wall**

The shell wall has a similar structure with two layers as that in *S. postremus*. The outer shell layer has been diagenetically altered and has a granular structure (Fig. 13A). The occurrence of the vertical prismatic lamellae in the inner layer is indicated by indistinctly visible, vertical striations (Fig. 13A). The intermediate layer has not been observed. The shell wall shows flexible deformations similar to those in *S. postremus* and *C. lesliensis*.

**Siphuncle**

The septal necks are strongly cyrtochoanitic (Fig. 13C). Both the septa and septal necks are composed of prismatic lamellae that have similar arrangement and structure as those in other bactritoid-like coleoids described herein (Fig. 13C). The connecting rings are not preserved, but based on the configuration of the septal necks, the connecting rings were probably inflated rather than tubular as seen in the other bactritoid-like coleoids described herein.

**Discussion and conclusions**

The intermediate layer in *Shimanskya* has previously been interpreted as the wrinkle layer (Mapes 1979) that covers the inner surface of the body chamber in several nautiloids and ammonoids (Clausen 1968; House 1971; Senior 1971; Kroger

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*Fig. 10. C. lesliensis. A, B (OUZC 5835) Median section showing a septal neck and connecting ring, × 43. B. Distal portion of the septal neck and connecting ring; inner sub-layer of the connecting ring destroyed by diagenesis, but its original position is indicated by X, × 90.*
et al. 2005). The wrinkle layer shows close similarity with the oblique prismatic layer that covers the inner shell surface in many gastropod taxa with narrow shells (Gainey & Wise 1976; Uozumi & Togo 1975; Solem & Lebryk 1976; Bandel 1979a,b). This layer is often composed of oblique tablets that point toward the shell aperture and are arranged in irregular rows, more or less parallel to the apertural margin. Gainey & Wise (1976, p. 412) concluded that this layer and the mantle serve “as a ratcheting mechanism to supply traction for the extension of the mantle when the animal is emerging from within its shell”.

As the oblique prismatic layer in gastropods, the wrinkle layer in nautiloids and ammonoids probably prevented the body from sliding back into the shell when it protruded from the shell aperture (Doguzhaeva & Mutvei 1986, 1996). With the aid of hydrostatic pressure, the body surface was pressed against the wrinkles on the inner surface of the body chamber (Doguzhaeva & Mutvei 1986, Fig. 10E,F), and the layer functioned as a “brake”.

The intermediate layer in Shimanskyia differs from the wrinkle layer in nautiloids and ammonoids in that it only covers the anterior portion of the inner surface of the body chamber, whereas in the posterior portion of the body chamber it is covered by the inner prismatic layer of the shell wall (Fig. 14B,C). As a contrast to the nautiloid and ammonoid wrinkle layer, the intermediate layer is, therefore, embedded between two layers of the shell wall. This indicates that it is not identical with the wrinkle layer in ammonoids and nautiloids and that it had a different function.

S. postremus was originally considered to be a bactritoid until Doguzhaeva et al. (1996, 1999, 2010a) studied the ultrastructure and determined that the outer shell organization was not typical of any described ammonoid, nautiloid or bactritoid. Instead of two prismatic layers separated by a thick nacreous layer as seen in nautiloids and ammonoids (Fig. 14A), the shell wall in Shimanskyia has no nacreous and prismatic layers but is composed of a granular outer layer and a lamellar–prismatic inner layer separated by thin intermediate layer (Fig. 14B). The shell has high content of organic matter and is thought to have been elastic. These features indicate that the shell was internal and covered by soft tissue. This conclusion is in agreement with the findings by Poulíček et al. (1986). These workers found that in molluscan shells that are more or less covered by the mantle fold, the chitin content increases and the degree of calcification decreases (Poulíček et al. 1986, p. 9).

The only close morphological match to Shimanskyia that Doguzhaeva et al. (1999, 2010a) found was with the spirulid coleoids, specifically Spirula, Naefia and Adygeya, which are only found in the Cretaceous and Recent. For that reason and understanding that the basic shell ultrastructure of cephalopods shows little evolution change through time and that major changes in shell structure indicate a high level of systematic importance, they identified Shimanskyia as a coleoid and

Fig. 11. C. leslieiensis. SEM images. A. Median section of the distal end of septal neck to show the lamellar–prismatic inner layer and the spherulitic–prismatic outer layer. B. Lamellar–prismatic layer in the septal neck in higher magnification; note that the lamellae are composed of acicular crystallites. Scale bars: A = 40 μm, B = 10 μm.
reassigned the genus to the Spirulida on the basis of certain similarities in shell ultrastructures. Other researchers on fossil cephalopods have been reluctant to accept this systematic decision of placing Shimanskya in the Spirulida. For instance, Becker, as a personal observation in Warnke et al. (2003, p. 258), rejected the Spirulida systematic assignment of Shimanskya because “... extant Spirula clearly represents the Decabrachia, whereas Palaeozoic forms such as Shimanskya lack clear evidence of diagnostic features and are better assigned to stem-group taxa from which both the Decabrachia and Octobrachia may have been derived”. Fuchs & Warnke (2005, p. 71) accepted the assignment of Shimanskya as a coleoid but did not place it at any specific higher classification level. And, most recently, Kröger et al. (2011, p. 8) have indicated that this taxon

![Fig. 12. B. quadrilineatus. A. (OUZC 5841) Median section of a phragmocone; note that the connecting ring was flexible and has been bent into the chamber, × 16. B. (OUZC 5837) Median section of the septal neck and connecting ring; note that the septal neck has a lamellar–prismatic structure, × 85. C. (OUZC 5842) Median section of a phragmocone showing the flexible bending of the connecting ring, × 25. D. (OUZC 5838) Outer surface of the intermediate layer of the shell wall with parallel rods, × 38.](image-url)
together with Pohlsepia “... should be interpreted as stem group coleoids” that “... requires further morphologic and systematic scrutiny”. Thus, Shimanskya is accepted as a coleoid, but “more morphologic and systematic scrutiny” is required for an accepted placement into the Spirulida.

Evaluation of additional morphological specimens of Shimanskya and three other taxa (C. lesliensis, B. quadrilineatus and R. jacksboroensis) currently assigned to the Bactritoidea provide more morphological data on this problem.

All four taxa (i.e. S. postremus, C. lesliensis, B. quadrilineatus and R. jacksboroensis) have nearly identical shell ultrastructure. In Shimanskya, the outer layer of the shell wall is characterized by high porosity and probably high content of organic matrix. The inner shell layer consists of more or less regularly arranged vertical lamellae composed of acicular crystallites. In the other three genera, the shell is composed of two layers, but recrystallization has destroyed the original fabric except that the outer layer is more loosely organized than the inner layer, which is also the case in Shimanskya. The surface of the inner layer in Shimanskya has more or less parallel flat-topped ridges and grooves on the surface that form a finger-print like pattern. This same structure is present in B. quadrilineatus except in Shimanskya the grooves and ridges are approximately equal in size and in B. quadrilineatus the flat-topped ridges are much wider and the grooves are relatively narrow. Also, in these four genera these two layers are separated by an intermediate organic film layer. The structure of the latter layer has no counterpart in shells of other mollusks. The shell wall in Shimanskya is deformed in places and this indicates that the shell wall must have been somewhat flexible in life. The septa and septal necks
in all four taxa consist of prismatic lamellae. Their connecting rings are composed of a single fibrous-organic layer as that in ammonoids, but only a thin outermost sub-layer is hardened and preserved, whereas the thick inner sub-layer is destroyed by diagenesis.

In terms of overall morphology three of the taxa studied (S. postremus, C. lesliensis, B. quadrilineatus) are longiconic with cyrtochoanitic septal necks. Based on the morphological similarities seen in C. lesliensis and B. quadrilineatus in comparison with S. postremus, it is logical to reassess that these two genera belong to the coleoids and note their possible assignment to the Spirulida with C. lesliensis, oensis.

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