Acta Musei Nationalis Pragae, Series B, Historia Naturalis, 50(1994)(1–4): 13–24 issued December 1995

MUSCLE ATTACHMENT AREAS IN THE SILURIAN BELLEROPHONTACEAN GASTROPODS *BELLEROPHON SCABER* (PERNER) AND *BUBOVICUS TARDUS* (BARRANDE IN PERNER)

RADVAN J. HORNÝ
Department of palaeontology, National Museum, 115 79 Praha 1, Czech Republic

Horný, R. J. (1995): Muscle attachment areas in the Silurian bellerophontacean gastropods *Bellerophon scaber* (PERNER) and *Bubovicus tardus* (BARRANDE in PERNER). - Acta Mus. Nat. Pragae, Ser. B, Hist. Nat., 50(1994)(1-4): 13-24. Praha. ISSN 0036-5343

Abstract. Two symmetrical umbilical muscle attachment areas are described on internal moulds of the bellerophontaceans *Bellerophon scaber* (PERNER, 1903) and *Bubovicus tardus* (BARRANDE in PERNER, 1903) from the Silurian of Bohemia. For the first time, myostracum is reported covering the attachment area, continuously increasing throughout the shell ontogeny. Some earlier records of muscle scars are discussed in this connection. Mode of fossilisation and later chemical processes are considered important for the shape and appearance of the preserved muscle attachments.

■ bellerophontacean gastropods, muscle attachment areas, myostracum, Silurian, *Bellerophon, Bubovicus*

Received May 06, 1993

The presence of a pair of retractor muscle scars in the umbilical area of a bellerophontiform shell seems to indicate most reliably its assignment to the real Bellerophontina and, therefore, to the Class Gastropoda. Knight (1947) was the first to describe these scars in *Bellerophon* MONTFORT, 1808 and *Sinuites* KOKEN, 1896, pointing out their systematic importance. According to Peel (1982), scars of this type are frequently found on the internal moulds of Carboniferous species of *Bellerophon* from Ireland and United Kingdom. All other finds are rare and exceptional. To date, retractor muscle insertions have been reported and described in *Sinuites* (Knight 1947, Peel 1980, Runnegar 1981, Horný 1992a,b), *Sylvestrosphaera* PEEL, 1980 (Peel 1980), *Bellerophon* (Knight 1947, Peel 1972, 1982), *Salpingostoma* ROEMER, 1876 (Peel 1972), *Tremanotus* HALL, 1865 (Peel 1972), *Megalomphala* ULRICH in ULRICH et SCOFIELD, 1897 (Peel 1976; 1991b), *Strangulites* HORNÝ, 1962 (Horný 1990a, b), and *Carinaropsis* HALL, 1847 (Peel 1993). Following the previous descriptions of muscle scars in *Sinuites* and *Strangulites* from the Ordovician, the Silurian *Bellerophon* and *Bubovicus* HORNÝ, 1962 are here added to the list of genera with ascertained circumbilical retractor scars from the Barrandian area (Central Bohemia).

Bellerophon scaber (PERNER, 1903) was originally described as *Tremagyrus scaber* PERNER, 1903. *Tremagyrus* PERNER, 1903 was later (Knight et al. 1960) synonymized with *Tremanotus* HALL, 1865, but the type species of *Tremagyrus* was assigned to *Bellerophon* (*Bellerophon*) by Horný in 1963a. It is stratigraphically the oldest representative of *Bellerophon* from the Barrandian area.

Bubovicus, based on *Cymbularia tarda* BARRANDE in PERNER, 1903, is a rare Silurian genus, a member of the Family Bellerophontidae McCOY, 1851. It is related to *Bellerophon* MONTFORT, 1808 from which it distinguishes itself by the laterally compressed, high, moderately phaneromphalous shell with a narrow slit, generating a narrow raised selenizone on a crest-like angulation.

With the exception of a few specimens of *B. scaber* from the Lištice locality near Beroun,

both rare species have been collected to date at only one locality, the Barrande's excavation in a pine-tree wood between the town Loděnice and the village Bubovice (a protected locality "Černidla"). The excavation was situated in a local, about 20 m long, lens-like accumulation of benthic shelly fauna mixed with volcanic material, in a sequence of alternating limestone beds and shales with volcanic admixture, respectively (uppermost Wenlockian; Homerian, Zone Cyrtograptus lundgreni, Sub-zone Testograptus testis). Some museum specimens bear Barrande's handwriting in black ink, indicating the locality (Bubowitz). The exact location of the locality was lost for about a hundred years. It was rediscovered in the 1950s and since that time some more material has been collected, but only from a small old collectors' dump. The fossiliferous lens - or at least its favourably weathered subsurface part - seems to have been totally quarried and exploited.

At present, there are about 40 specimens of both species, including the types, available in the collections of the Department of Palaeontology, National Museum, Prague. More specimens might be still found associated with the samples of other fauna, dispersed in the collections. They are all to some extent fragmentary, either due to short transport before deposition or to not enough care during collection. The carbonatic, seemingly recrystallized, whitish to yellowish shell wall is rather fragile, cracking perpendicularly to the shell surface; it is easily removable from the internal mould by the use of a vibro-tool. Many specimens preserve geopetal calcite fills. This is important for study of the muscle impression structures which cannot be easily observed on the normal coarse, grey-green carbonatic tuffaceous matrix.

Environmental conditions and biology

Both species occur in a shallow marine assemblage. This high-energy environment was strongly influenced by contemporary volcanism. Tuffaceous shales with irregularly bedded limestones containing variable amounts of volcanic products predominate. The fossiliferous lens represented a rapid accumulation of the remains of animals and plants which originally inhabited a variety of environments near the volcanic islands - solid substrata in high-energy conditions to clayey volcanic deposits in local temporary shelters. Fossils are chaotically deposited, often fragmentary, adults with juvenile shells, and mixed with small unsorted shell fragments, tephra, and sharply angulated fragments or even small pebbles of tuffaceous shales. Gastropods predominate, with the variety of shell form indicating variable living conditions: a high percentage of trochiform and lenticular pleurotomariins, bellerophontins, holopeids, platyceratids, oriostomatids, loxonematins, subulitids, and others. Most of the isostrophic shells have either the left or right side filled with matrix and the other side with crystallized calcite, indicating their postmortal position on the bottom. *Cyclotheca* is a characteristic genus, and the problematic *Ceratotheca adunca* (BARRANDE, 1867) belongs to the most frequent fossils. Brachiopods form the second abundant group (e. g. *Leptaena, Pentlandina, Strophonella, Coolinia* and others). Crinoid columnals, tabulate corals, bryozoans, and hyolithids are common, while trilobites are rare and nautiloids, bivalves and other groups occur only sporadically. Algae are common, like *Acanthochonia barrandei* HINDE, 1884 (previously known as *Ischadites*), and *Pachytheca* (see also Kříž 1992).

Bellerophon scaber probably inhabited high energy environment as an active, perhaps semi-infaunal predator. A thick shell, with radial aperture and strong retractor muscle insertions, confirms this presumption. Linsley (1977, 1978), after discussing shell form and rates of locomotion, concluded that *Bellerophon* was a streamlined and quite fast gastropod. According to Peel (1984), the globose, compact shell of *Bellerophon*, with narrow or closed umbilici, may suggest a mobile, infaunal, perhaps predatory habit comparable to some living bullomorphs.

Bubovicus tardus, possessing a laterally compressed, high, phaneromphalous shell with pseudo-tangential aperture could be probably classified as a slower, but still active epibenthic inhabitant following Linsley's scheme, possibly an algal grazer in less dynamic conditions. This presumed mode of life would be in accordance with the thinner shell and much weaker muscle insertions than in *Bellerophon scaber*.

Morphology

Genus *BELLEROPHON* Montfort, 1808

Type species: *Bellerophon vasulites* MONTFORT, 1808; Middle Devonian, Germany.

Bellerophon scaber (PERNER, 1903)

Pl. 1; 2; 3; 4, figs 1-5

1903 *Tremagyrus scaber* PERNER; Perner, Text-figs 91, 92 (pp. 129, 130) (holotype L 5790).
1903 *Cymbularia Bacchus* PERNER; Perner, Pl. 87:20 (paralectotype L 5793); 87:35, Text-figs 107a,f (p. 153) (lectotype L 5792); Text-figs 107b,c,d (p. 153) (paralectotype L 5794); Text-fig. 107e (p. 153) (paralectotype L 30431); unfigured specimen, originally labelled as additional type to Text-fig. 107 (p. 153) (paralectotype L 5795).
1903 *Cymbularia verrucosa* PERNER; Perner, Pl. 87:15-18, Text-figs 106a,b (p. 152) (lectotype L 5791); 87:19 (paralectotype L 5844).
1941 *Tremagyrus scaber* PERNER; Knight, p. 352, Pl. 13:1a,b.
1960 *Tremanotus scaber* (PERNER); Knight et al., Treatise I, 1, p. *I*180.
1963a *Bellerophon* (*B.*) *scaber* (PERNER); Horný, pp. 125, 126, Pl. 37:1-6, Pl. 46:5.

Description. A detailed description was published by Perner (1903), Knight (1941) and Horný (1963a). It should only be added that the species has a radial aperture and that the shells do not show the asymmetry pointed out by Perner (1903). All other additions concern structures connected with the muscle insertions, observed in six specimens: L 30427, L 30428, L 5794, L 5793, L 30429, and L 5795.

Specimen L 30427 (Pl. 1, figs 3-6), an internal mould of a juvenile, has the left side mostly filled with crystallized calcite, the right side with grey-green matrix. Length 13.8 mm; height 10.2 mm.

On the left side, a shallow, narrow circumbilical groove, delimiting the dorsal margin of the muscle attachment area, is located just below the whorl angulation of the internal mould preserved in whitish crystallized calcite. The groove, regularly following the coiling spiral, is transversely asymmetrical, deepest near its addorsal, steepest slope. It is filled with brownish-grey myostracal deposit, observable as a narrow, dark, smooth, flat band, 0.05 - 0.25mm wide (adapically narrowest). The band-like deposit is locally exfoliated and the depth of the groove is thus exposed. Adaperturally, the band widens into a small islet of dark grey myostracum, originally covering the whole insertion plane, and extending down onto the umbilical wall of the whorl. The adapertural margin of the muscle area, where the myostracal deposit was thinnest, is indistinct. The whole observed muscle attachment structure occupies about 310 degrees of a volution, the distance between the anterior margin of the insertion and the aperture being 210-220 degrees, i.e. slightly over a half of a whorl. The surface of the umbilical part of the internal mould near the aperture bears characteristic foliated structure, fading out addorsally and adapically towards a smooth area, about 1 mm long, in front of the muscle impression. A fibrillar structure is preserved on a small area adjacent addorsally to the circumbilical groove. Structures on the right side of the shell are symmetrical but less well preserved.

Specimen L 30428 (Pl. 3, figs 1-3), an internal mould of a not fully mature individual, lacks the apertural part; it is filled with dark grey limestone. Height 13.3 mm.

The left side shows the proximal part of the muscle area with a well exposed addorsal groove. It is mostly empty and longitudinally striated, but with a patch of myostracum distally. Adaperturally, the groove deviates from the isometric spiral, the scar widens addorsaly and the internal mould becomes slightly laterally inflated at its periphery. The adapertural part of the umbilical wall shows foliated structure, gradually fading out and disappearing about 2 mm before the indistinct anterior margin of the muscle attachment area. A straight groove-like repaired injury obliquelly crosses the left dorsolateral area between the dorsal median line and the muscle attachment area interrupting its addorsal ridge. The right side of this specimen was not prepared.

Specimen L 5794 (Pl. 3, fig. 6) is a fragment of a not fully mature individual with damaged apertural part; the right side preserves shell, but the left side exposes the internal mould of whitish coarsely crystallized calcite. The right side is filled with greenish limestone with a volcanic component. Height 13.4 mm. This specimen was figured by Perner (1903, Text-fig. 107c, d).

The adapertural part of the muscle attachment area on the left side is damaged. Central and distal parts are sharply delimited by a 0.2 mm wide circumbilical groove, which deviates adaperturally such that the widened functional attachment area is located on the slightly inflated portion of the lateral side of the internal mould.

Specimen L 5793 (Pl. 3, fig. 5) represents an almost mature, incomplete specimen without aperture; the left side preserves the shell, while the right side exhibits the internal mould of mainly crystallized calcite. Height 15.7 mm. This specimen was figured by Perner (1903, Text-fig. 107b).

The right side shows well developed inflation of the whorl in place of the functional muscle attachment area. The area itself was not prepared in order to preserve the original appearance of the specimen.

Specimen L 30429 (Pl 4, figs 1, 2) is an internal mould of an almost mature individual, filled with greenish limestone with a volcanic component; the spire is partly filled with crystallized calcite. The narrow, 8 mm long slit is well exposed. Length 18.0 mm; height 15.8 mm.

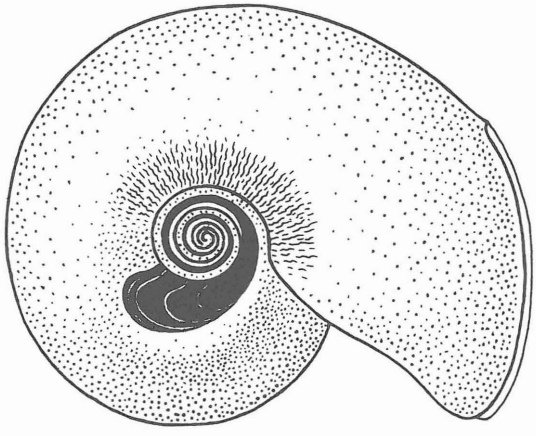
The muscle attachment area on the right side lacks myostracal deposits. The circumbilical groove is best preserved in the adapical part, where it is 0.30 mm wide. The anterior margin is indistinct, distant about 220 - 230 degrees of a volution back from the aperture. The location of the functional part of the muscle scar is indicated by inflation of the internal mould. Foliated structure is visible on the surface of the internal mould near the aperture, locally obliterated by a layer with fibrillar structure. The area immediately adapertural of the muscle insertion area is smooth. The opposite side of the specimen was not prepared to save the patches of shell.

Specimen L 5795 (Pl. 2, figs 1-6; Pl. 3, fig. 4; Pl. 4, figs 3 - 5) represents an internal mould of a mature individual with patches of shell, mostly filled with green-grey limestone with a volcanic component and fragments of fauna. The spire is partly filled with crystallized calcite. Length 24 mm; height 18 mm. This specimen represents an additional specimen to Perner (1903, Text-fig. 107).

The left side in this adult specimen has the best preserved muscle attachment area. The adapertural part is mostly covered with dark grey myostracal deposits, maximum 0.05 mm thick, but these are lost in the narrower adapical part. The circumbilical groove, originally located below the whorl angulation, gradually deviates from its spiral course in a dorsoanterior direction, extending over the inflated area of the whorl. The sharply delimited addorsal margin of the myostracal deposit continues anteriorly to form a convex crescent-like edge locally followed by a thin stria at a distance of about 0.1 mm. After turning adumbilically, down, it extends slightly obliquely over the umbilical wall as a darker grey film disappearing under the unprepared shell wall, towards the median plane of the shell. The surface of the myostracal deposit, originally adherent to the shell wall, is uneven, irregular, locally bearing fibrillar structure; it is without crescentic structures but two short ridges follow the addorsal margin. The deposit is slightly raised above the surrounding surface of the mould; its variable thickness reaching a maximum of about 0.05 mm. An area where the myostracal deposit has exfoliated shows an uneven, rough surface, with one incomplete crescentic structure. This surface seemingly represents a real adhering surface of the muscle attachment. The adapical part of the insertion area, free of deposit, shows the circumbilical groove as well as relics of an extremely thin, grey layer, preserved between the umbilical wall of the mould and the remains of shell; this seemingly represents the abandoned parts of thinner, ontogeneticaly younger myostracal deposit. A smooth area adapertural to the muscle attachment area, about 3 mm long, gradually passes into foliated structure, well developed on the adapertural part of the internal mould. The distance between the anterior margin of the scar and the aperture is about 250 - 260 degrees of a volution. The opposite side of the mould has bilaterally symmetrical, but less well preserved, structures.

Recapitulation

The retractor muscle attachment areas, observed on internal moulds of *Bellerophon scaber,* are located on the umbilical walls, symmetrically on both sides of the shell. The ontogenetically earliest trace of the muscle impressions has been ascertained below the angulation of the second whorl where it is preserved as a shallow groove 0.05 mm wide. Its adapical end is hidden under the shell, too deep to be prepared. It clearly continues to the previous whorl, however, being probably developed since the very beginning of the shell. The longest preserved muscle impression occupies about 310 degrees of a volution; width of the groove increases from 0.05 to 0.25 mm during this distance. In several places, the groove is filled with pigmented myostracum, usually deep brownish and smooth on its observable surface, extending as a thin film onto the umbilical wall towards the median plane of the shell. The groove, corresponding to a narrow addorsal myostracal ridge, is isometric, following the shell spiral coiling. Its transverse section is asymmetric, the addorsal slope being steeper. The surface of the groove is rough, usually bearing irregular spiral structures. Before reaching the adult stage, the muscle attachment area deviates from the isometric spiral; it widens addorsally to the proximity of the umbilical shoulder, and the groove gradually changes into a low, narrow ridge, passing into an adaperturally convex, rounded, crescentic margin irregularly crossing the umbilical wall. The functional muscle attachment area, located on the laterally inflated part of a whorl, seemingly not observable on outer shell surface (probably also mentioned by Peel 1972, p. 413) is covered with a variably thick myostracum (a maximum 0.05 mm). Its lower surface, originally adherent to the shell wall, is uneven, irregular, without crescentic structures, and only slightly raised above the surrounding plane of the internal mould. The upper plane, corresponding to its original surface, is either smooth or rather coarse, irregular, and rarely with crescentic or longitudinally arranged structures. The surface of the internal mould on the umbilical wall is smooth in front of the muscle attachment area; after a distance of about 1–3 mm foliated structure gradually appears which continues to the aperture but which is absent on all other parts of the mould. The smooth area may be obliterated by a thin layer of myostracal deposit. The foliated structure is locally obliterated in some specimens by a layer bearing fibrillar structure, appearing also on the upper (observable) surface of myostracum in specimen L 5795. The distance between the adapertural margin of the muscle attachment area and the aperture changes during ontogeny: in the youngest observed specimen it is 210–220 degrees of a volution, in the almost mature specimen L 30429 it is 220–230 degrees. In the mature specimen L 5795 it is 250–230 degrees. This increase corresponds with the rate of withdrawal of the soft body in the stage of sexual maturity.



Text-fig. 1. Muscle attachment area in *Bellerophon scaber*. Restored after the specimens L 30427 and L 5795. Orig.

Genus *BUBOVICUS* Horný, 1962

Type species: *Cymbularia tarda* PERNER, 1903, Silurian, Bohemia.

Bubovicus tardus (BARRANDE in PERNER, 1903)

Pl. 4, fig. 6; Pl. 5; Pl. 6, figs 1-5

1903 *Cymbularia tarda* BARRANDE; Perner, Pl. 87:32-34, 36, Text-fig. 105c (p. 150) (lectotype L 5787); Text-fig. 105a (p. 150) (paralectotype L 5788); Text-fig. 105b (p. 150) (paralectotype 30424); unfigured paralectotype L 30437.
1936 *Cymbularia impressa* n. sp.; Říha, p. 6, 7, Pl. 1:9, 10 (holotype L 30438).
1962 *Bubovicus tardus* (PERNER); Horný, p. 474.
1963a *Bubovicus tardus* (PERNER); Horný, p. 121, 122, Pl. 37:7, 8, Pl. 38:6, 7.

Description. A detailed description was given by Perner (1903) and Horný (1963a). To the synonomy of this species belongs also *Cymbularia impressa* ŘÍHA, 1936, by error originally reported from the Ordovician strata. A careful study of all available material proved that a weak spiral dorsolateral angulation exists in one specimen only, L 5789, figured by Horný (1963, Pl. 37:7, 8). It probably represents an individual feature, not characteristic for the whole population of the species. The position of the aperture is near to tangential. All other additions concern structures connected with the muscle insertions and were observed in six specimens: L 30432, L 30433, L 30434, L 30435, L 30436, and L 5789.

Specimen L 30432 (Pl. 4, fig. 6; Pl. 6, fig. 1) is an internal mould of a juvenile with patches of shell; the left side was not prepared to preserve the shell. The mould is obliquely filled with crystallized calcite (the right side) and with tuffaceous limestone (the left side). Length 19.4 mm; height 16.2 mm.

The muscle attachment area on the right side is not delimited by a groove but can be observed as a smooth area addorsally adjoining an otherwise coarse surface of the internal mould below the whorl angulation. Weak grooves accompany the addorsal margin. The addorsal circumbilical margin lies just below the umbilical shoulder, without deviation from the coiling spiral in its anterior part. The region between the indistinct, anterior margin of the attachment area and the aperture bears foliated structure which is less well observable in the proximity of the muscle scar. Estimated distance between the anterior margin of the attachment area and aperture is 180 degrees of a volution.

Specimen L 30433 (Pl. 5, fig. 3) is a juvenile with the right side mostly with shell, the left side is preserved as an internal mould filled with greenish tuffaceous limestone. Length 24.0 mm; height 19.0 mm.

The surface of the internal mould on the left side is coarse but with observable structures. The adapical part of the attachment area is delimited addorsaly by an obscure, rounded, low, spiral ridge located more adumbilically below the angulation than in L 30345. The functional part of the attachment area is indistinctly delimited; it is covered with a thin colourless shell layer without details on its surface. The anterior margin is unclear, probably adaperturaly convex; weak foliated structure is developed slightly in front of the margin. The distance between the anterior margin and aperture is estimated to about 180 degrees of a volution.

Specimen L 30434 (Pl. 6, fig. 2) is a weathered internal mould with patches of shell of a juvenile; the left side is partly filled with crystallized calcite while the right side is preserved in grey limestone. Height 14.3 mm. The functional part of the muscle attachment area on the left side is located below the whorl angulation. The addorsal margin is delimited by a circumbilical groove, exposed in the adapical part. Most of the attachment area is covered with a thin layer bearing reflected, transversely oriented, foliated structure on its observable surface. The layer covers the whole exposed umbilical wall, extending to near the median shell plane. The anterior margin of the attachment area is almost indistinct, but is located at about 200 degrees of a volution from the aperture; the area in front of the scar is smooth. The traces of myostracum attached to the area are brown due to higher concentration of limonite.

Specimen L 30435 (Pl. 5, figs 4–6) represents the internal mould of an immature specimen, with small patches of shell. The left side is partly filled with crystallized calcite, the right side with greenish tuffaceous limestone. Length 26.0 mm; height 21 mm.

On the left side, a shallow circumbilical groove is visible below the shoulder in the exposed adapical part; it approaches the whorl angulation adaperturally and fades away in the functional part of the muscle attachment area, the anterior part of which is not clearly delimited. The surface of the area is covered with scattered traces of a thin myostracal layer, locally showing transversely arranged foliated structure on its surface. Below this layer obscure, irregular, fine spiral striae are locally visible. The myostracal layer extends over the umbilical wall, where it is preserved as small islets even in the adapical part, locally with fine and weak fibrillar structure on its surface. In the most adapically exposed part, a short oblique line crosses the circumbilical groove (seemingly not a part of the scar). The whole muscle attachment area is slightly brown coloured, especially the islets of myostracum.

Specimen L 30436 (Pl. 6, figs 3–5) is the internal mould of a mature specimen with patch of shell showing the selenizone on a crest. The left side of the mould is partly filled with crystallized calcite, the right side with greenish tuffaceous limestone. The specimen carries Barrande's inscription in black ink: Bubow. (= loc. Bubovice). Length 26.0 mm; height 23.0 mm.

The muscle attachment area on the left side is well marked by brownish colouration, but rather weakly in terms of relief. The circumbilical ridge is weak, just observable on the addorsal margin of the functional attachment, where it is located well below the whorl angulation. The anterior margin is only slightly marked by the extent of thin myostracal deposit, extending also deeply down onto the umbilical wall. The area in front of the attachment area is smooth over a distance of about 3 mm, after which fine, dense, foliated structure gradually appears. The anterior margin of the attachment area is about 270 degrees of a volution back from the aperture. The umbilical area of the left side is filled with shell.

Specimen L 5789 (Pl. 5, figs 1–2) represents the largest specimen with an observable muscle attachment area. It is an internal mould with a large proportion of preserved shell; the left side with a visible muscle attachment area is partly filled with crystallized calcite, other parts with greenish tuffaceous limestone. Length 28,6 mm; height 26.5 mm. Specimen figured by Horný (1963, Pl. 37, figs 7, 8).

The adapical part of the muscle attachment area is not exposed. The extent of the muscle area is not sharply delimited, but it is observable as a structure deviating from the circumbilical spiral and extending to the shoulder. Rather small islets of very thin myostracal layer remain on its surface; the whole area bears dense, fine transverse foliated structure which continues adaperturally without interruption. The inferred anterior margin is about 270 degrees of a volution back from the aperture.

Recapitulation

Fundamentally, almost all morphological features of *Bubovicus tardus* connected with the muscle attachment are similar to those described in *Bellerophon scaber*, but they are weaker and less well marked. This undoubtedly reflects the different shape of the shell, its thinner wall and assumed different mode of life. In immature specimens, the position of the isometric spiral groove on the upper part of the umbilical wall varies slightly in different specimens but always lies below the umbilical angulation. At maturity, the groove deviates, and the muscle attachment area widens, almost reaching the rounded umbilical shoulder. The functional part of the attachment area is indistinctly delimited, mostly definable only by the extent of rather thin myostracum, either colourless or brownish or grey according to higher content of limonite or carbon. The myostracum covers the whole exposed umbilical wall, extending adumbilically to the proximity of the median shell plane. Its lower surface, originally adherent to the shell wall, is seemingly smooth but often bears the impression of transversely oriented foliated structure from the originally underlying shell layer. The upper plane of the myostracum, corresponding to its original surface, bears weak, irregular, spiral grooves. No inflation of the internal mould connected with the location of the final mature attachment was observed. The surface of the umbilical wall of the internal mould between the attachment

area and the aperture bears fine, dense, transversely oriented, foliated structure, seemingly becoming finer with age, absent on other parts of the internal mould and, in some specimens, probably obliterated with thin myostracal deposit for a short distance (1-3 mm) adapertural to the attachment area. Fibrillar structure is weak and rarely preserved. The distance between the adapertural margin of the muscle attachment area and aperture varies during ontogeny: it is rather small in the juveniles, about 180 degrees but increases to 270 degrees in maturity.

Discussion

Muscle scars in bellerophontacean gastropods have been described previously only on internal moulds. Their preservation and study are, however, influenced by many factors, ranging from the mode of life of the animal, its age, shell composition and structure to the geological processes itself. Finally, we must also take account of the methods of preparation.

Knight (1947) characterized molluscan muscle scars as depressions in the inner layer of the shell. Common features of bellerophontacean muscle scars, as we can observe them on internal moulds (i. e., with opposite relief to the shell interior) are usually raised areas or ridges, or depressed areas and grooves, or, rarely, both possibilities combined. All to date described muscle attachment areas in four specimens of *Bellerophon* (Knight 1947, Peel 1972, 1982) are, as a matter of fact, preserved as depressions associated with raised structures, like ridges, swellings etc. This mode of preservation is also well demonstrated on several specimens of the Bohemian *Bellerophon scaber*. The depressed area located below (adumbilically) the addorsal ridge was originally filled with myostracum. In immature shells, this layer was provided with an asymmetric spiral crest generating a circumbilical groove on the internal mould near the addorsal scar periphery. In maturity, the peripheral crest deviated from the isometric spiral, passing into the thickest addorsal margin of the myostracal deposit. The circumbilical groove on the internal mould is thus gradually replaced by a step or a ridge (or other associated structures observed in the Upper Palaeozoic bellerophonts by Peel 1972, equating with channels or ridges on the shell interior). The myostracum deposit in mature *Bellerophon scaber* is about 0.05 mm thick; it was slightly raised above the shell interior and similarly slightly depressed in the underlying shell. Muscle fibres were thus attached to a slightly raised area and not to myostracum in a depression like in many other molluscs (e.g., bivalves or tergomyans). Evaluation of the implication of these observations and associated shell microstructure in terms of functional anatomy and perhaps even bellerophontacean systematics remains for future study. Characteristic is the transversely striated layer which seemingly served for fixing the myostracum on the shell wall; its presence on the umbilical wall is probably the most important criterion for recognizing bellerophontacean gastropods among the bellerophontiform molluscs in cases when the muscle scars are not observable.

Myostracum in the Bohemian material is often coloured. This could probably be connected with its complex-prismatic structure or organic admixture. Brown colour testifies to a higher content of limonite (originally pyrite) and grey colour to carbon (probably bitumen). Similar dark grey or even black structures have been reported in the Silurian *Archaeopraga pinnaeformis* (PERNER, 1903) (Horný 1963) and are well known in the Ordovician tergomyan *Archaeophiala antiquissima* (HISINGER, 1837). Rosov (1975) reported pigmented calcitic layer covering the surface of the muscle scars in *Nyuella bjalyi* ROSOV, 1975.

Myostracum, reported here in the Silurian species of *Bellerophon* (and *Bubovicus*), was definitely developed also in Carboniferous species of the genus. This is in accordance with the statement of MacClintock (1967, p. 50), that „For each isolated accessory scar in the mollusk shell, there is a lath-shaped blade of shell material starting at the apex of the shell and gradually expanding to the outcrop area on the inner surface of the shell." This can be well demonstrated in a juvenile specimen of *Bellerophon scaber* (L 30427, Pl. 1, figs 3-6), where a narrow band of dark brown myostracum extends and gradually widens adaperturally for a visible distance of almost a whorl.

Preservation of myostracal deposits is rather rare. It could have happened in chemically favourable conditions where the shells were quickly buried in shallow-water deposit and rapid crystallization of calcium carbonate took place. In the majority of cases, the innermost layers of the shell, together with myostracum, were the first to undergo dissolution. Different

phases of this process were described by Horný (1992b) in *Sinuites* from the Ordovician of Bohemia (Horný, however, did not explain the process of destruction of the continuous migration tracks as connected with dissolvement of myostracum). Peel (1991a) suggested that differences in the shape of muscle scars in sinuitids and those in *Bellerophon* may be illusory, since described specimens of the latter genus with muscle scars are of Carboniferous age and therefore significantly younger than the sinuitids (p. 25). The find of muscle attachment scars in a Silurian representative of *Bellerophon*, similar to those in the Carboniferous specimens, cannot help to solve the problem. In my opinion, attachment areas in both of these different, but related, groups of bellerophontaceans are fundamentally similar (see also Peel 1991, p. 25) but selective dissolution of myostracum contributed in their apparent dissimilarity (Horný 1992b, pp. 97, 98; Text-fig. 5, p. 85; Pl. 1, figs 6–11).

The muscle attachment area of *Bellerophon* is principially similar to that of some pleurotomariaceans (see also Peel, 1986). In an undetermined Silurian specimen of „*Euryzone*" sp., labelled as *Pleurotomaria* (*Euryzone*) *consolans* BARR. by Perner, the final attachment area lies at the rounded circumbilical angulation, addorsally accompanied by narrow, raised structures deviating from the isometric spiral (Pl. 6, fig. 6). The distance between the adapertural margin of the muscle attachment area and the aperture is about 180 degrees in this specimen (like in the juveniles of *Bubovicus tardus* or in the Upper Palaeozoic representatives of *Bellerophon*).

The recognition of the muscle attachment area in the Silurian *Bellerophon* offers a possibility for comparison with its Upper Palaeozoic representatives. Unfortunately, our knowledge of this most popular genus is rather poor and we could easily find that we are comparing admittedly related, but different, genera with similar shell morphology, representing a well-tested form that existed for considerable time span, more than 200 million years. The type species, *B. vasulites* from the Middle Devonian of Germany, seems to be not too far morphologically from the Bohemian Silurian species. On the contrary, the Upper Palaeozoic heavy thick-shelled species with wide selenizone could represent another genus. Main differences include the depth of location of the muscle attachment areas within the shell, which is 230 degrees back from the aperture in the Silurian species but about 180 degrees in the Upper Palaeozoic material. The position of the circumbilical groove is below the umbilical shoulder in the Silurian species, but at the shoulder in the Upper Palaeozoic material. Abapertural projecting ridges are not developed in the Silurian material, but are well developed in the Upper Palaeozoic specimens. Associated addorsal structures, almost absent in the Silurian, are well developed in the Upper Palaeozoic material. Some of these characters may be connected with mode of life but, in any case, available data are still too limited to evaluate their possible systematic significance.

Acknowledgements

Professor John S. Peel (University of Uppsala) is thanked for reviewing the manuscript prior to publication. Jiří Kříž and Ladislav Marek kindly extended their material for study.

ÚPONY RETRAKTORŮ U SILURSKÝCH GASTROPODŮ *BELLEROPHON SCABER* (PERNER) A *BUBOVICUS TARDUS* (BARRANDE in PERNER) (SOUHRN)

V práci jsou popsány úpony retraktorů u dvou silurských zástupců podřádu Bellerophontina, *Bellerophon scaber* (PERNER, 1903) a *Bubovicus tardus* (BARRANDE in PERNER, 1903). U rodu *Bellerophon* MONTFORT, 1808 byly dosud známy pouze u jedinců z mladšího paleozoika Velké Británie a Severní Ameriky, u rodu *Bubovicus* HORNÝ, 1962 jsou nově zjištěny. Jsou umístěny na periferii umbilikální oblasti po obou stranách ulity. Poprvé je u těchto gastropodů objeveno myostrakum, pokrývající svalovou inserci a souvisle přirůstající v průběhu ontogeneze. Oba nálezy pocházejí ze svrchnowenlockých mělkovodních tufitických vápenců z odkryvu u silnice mezi Loděnicí a Bubovicemi, ve kterých bylo mimořádně vhodné prostředí pro fosilizaci doposud neznámých struktur.

REFERENCES

Horný, R. J. (1962): New genera of Bohemian Lower Paleozoic Bellerophontina. - Věst. Ústř. Úst. Geol., 37(6): 463- 466.

Horný, R. J.(1963a): Lower Paleozoic Bellerophontina (Gastropoda) of Bohemia. - Sbor. geol. Věd, Paleont., 2: 57-164.

Horný, R. J. (1963b): *Archaeopraga*, a new problematic genus of monoplacophoran molluscs from the Silurian of Bohemia. - J. Paleont., 37(5): 1071-1073.

Horný, R. J. (1990a): Svalové vtisky u *Sinuites* (*Strangulites*) (Mollusca) z českého ordoviku. - Čas. Nár. Muz. Praze, Řada přírodověd., 155(1-4): 109-118.

Horný, R. J. (1990b): Další poznatky o svalových vtiscích u *Sinuites* (*Strangulites*) (Mollusca). - Čas. Nár. Muz. Praze, Řada přírodověd., 156(1-4): 46-48.

Horný, R. J. (1992a): Shell morphology and muscle scars of *Sinuitopsis neglecta* Perner (Mollusca, Monoplacophora). - Čas. Nár. Muz. Praze, Řada přírodověd., 157(1-4): 81- 105.

Horný, R. J. (1992b): Svalové vtisky u rodu *Sinuites* (Mollusca, Gastropoda) z českého spodního ordoviku. - Čas. Nár. Muz. Praze, Řada přírodověd., 158(l-4): 79-100.

Horný, R. J. (1993): Retractor muscle scars in the Bohemian Silurian bellerophontacean gastropods *Bellerophon* and *Bubovicus*; a comparison with the muscle scar patterns in the sinuitids and the cyrtonellid tergomyans. - Paläont. Ges., 63. Jahrestagung, Abstr., Praha. 13, 14 pp.

Knight, J. B. (1941): Paleozoic gastropod genotypes. - Geol. Soc. Am., Spec. Pap., 32: 1-510.

Knight, J. B. (1947): Bellerophont muscle scars. - J. Paleont., 21: 264-267.

Knight, J. B. et al. (1960): Systematic descriptions (Archaeogastropoda), Supplement (Paleozoic and some Mesozoic Caenogastropoda and Opisthobranchia). - In: Moore, R. C. (ed.), Treatise on Invertebrate Paleontology, Part I (Mollusca 1). Geol. Soc. Am. and Univ. of Kansas Press. Lawrence, *I*169-*I*332 pp.

Kříž, J. (1992): Silurian field excursions: Prague Basin (Barrandian), Bohemia. - Nat. Mus. Wales, Geol. Ser., 13 : 1-111.

Linsley, R. M. (1977): Some "laws" of gastropod shell form. - Paleobiology, 3: 196-206.

Linsley, R. M. (1978): Locomotion rates and shell form in the Gastropoda. - Malacologia, l7: 193-206.

MacClintock, C. (1967): Shell structure of patelloid and bellerophontid gastropods (Mollusca). - Peabody Mus. Nat. Hist. Bull., 22: 1-140.

Peel, J. S. (1972): Observations on some Lower Palaeozoic tremanotiform Bellerophontacea (Gastropoda) from North America. - Palaeontology, 15: 412-422.

Peel, J. S. (1976): Musculature and systematic position of *Megalomphala taenia* (Bellerophontacea, Gastropoda) from the Silurian of Gotland. - Bull. geol. Soc. Denmark, 25: 49- 55.

Peel, J. S. (1980): A new Silurian retractile monoplacophoran and the origin of the gastropods. - Proc. Geol. Ass., 91: 91 -97.

Peel, J. S. (1982): Muscle scars in *Bellerophon recticostatus* (Mollusca) from the Carboniferous of Ireland. - J. Paleont., 56: 1307-1310.

Peel, J. S. (1984): Autecology of Silurian gastropods and monoplacophorans. - Spec. Pap. Palaeontology, 32: 165-182.

Peel, J. S. (1986): Muscle scars in *Porcellia* (Gastropoda; Pleurotomariacea) from the Carboniferous of England. - Bull. geol. Soc. Denmark, 35: 53-58.

Peel, J. S. (1991a): The Classes Tergomya and Helcionelloida, and early molluscan evolution. - Bull. Grønlands geol. Unders., 161: 11-65.

Peel, J. S. (1991b): Salpingostomatiform and related bellerophontacean gastropods from Greenland and the Baltic region. - Bull. Grønlands geol. Unders., 161: 67-ll6.

Peel, J. S. (1993): Muscle scars and mode of life of *Carinaropsis* (Bellerophontoidea, Gastropoda) from the Ordovician of Tennessee. - J. Paleont., 67(4): 528-534.

Perner, J. (1903): Gastéropodes, 1. - In: Barrande, J.: Systême silurien du centre de la Bohême, 4. Prague, 164 pp.

Rosov, S. N. (1975): Novyj otrjad monoplakofor. - Paleont. Ž., 1975(1): 41-45.

Runnegar, B. (1981): Muscle scars, shell form and torsion in Cambrian and Ordovician univalved molluscs. - Lethaia, l4: 311-322.

Říha, A. (1936): O nových bellerophontidech z českého paleozoika. - Rozpr. Čes. Akad. Věd Um. (II. Tř.), 46(12): 1-13.

EXPLANATION OF THE PLATES

All specimens are deposited in the collections of the Department of Palaeontology, Museum of Natural History, National Museum, Prague. If not otherwise stated, covered with ammonium chloride sublimate.

PLATE 1

Bellerophon scaber (PERNER, 1903)

1–2. L 5791, adult specimen, dorsal and left umbilical views. Note the thick shell, narrow umbilicus and the periodical increments, otherwise uncommon in this species. × 2.5.
3–6. L 30427, internal mould of an initial part of a juvenile with partly prepared spire to show the narrow circumbilical groove, locally filled with brownish-grey myostracum. 3, 4 – not whitened to show the distinct colouring, 3 – × 3, 4 – × 13; 5 – whitened to show the relief, × 13; 6 – enlarged groove with preserved parts of myostracum, × 20.

PLATE 2

Bellerophon scaber (PERNER, 1903)

1–6. L 5795, adult specimen, mostly internal mould. 1 – left side, × 2.5. 2, 3 – two views of the right muscle attachment area, mostly covered with myostracum, × 10; 4 – right side, × 2.5; 5 – left muscle attachment area, adapically without myostracum but with well exposed groove, × 10; 6 – the same, not whitened to show the dark grey coloured myostracum, × 10.

PLATE 3

Bellerophon scaber (PERNER, 1903)

1–3. L 30428, immature specimen, internal mould with a straight injury in the dorsal region. 1 – dorsolateral, 2; 3 – right umblical views in different light; a smooth area (arrowed in 3) is the place of the muscle attachment. Note the injury crossing the addorsal muscle attachment margin. All × 6.
4. L 5795, internal mould with an inflated whorl above the muscle attachment area (arrowed), × 2.5.
5. L 5793, internal mould of an immature specimen with an inflated whorl above the muscle attachment area (arrowed). × 2.5.
6. L 5794, internal mould with a deep, striated, circumbilical groove and patches of myostracum partly covering the muscle attachment area. × 8.

PLATE 4

Bellerophon scaber (PERNER, 1903)

1,2. L 30429, internal mould of an immature specimen. 1 – right side with a long slit, × 2.5; 2 – umbilical wall near the aperture (arrowed in fig. 1). Lower side of the layer with fibrillar structure which obliterate the internal shell surface with foliated structure. × 35.
3–5. L 5795. 3, internal mould, muscle attachment area mostly with preserved myostracum near the adapertural margin, × 10; 4, the same, enlarged to show the myostracum covered with fibrillar layer on its lower irregular surface (originally adherent to the shell wall), × 35; 5 – umbilical wall between the muscle impression area and the aperture, with an impression of a coarse foliated structure. × 35

Bubovicus tardus (BARRANDE in PERNER, 1903)

6. 30432, right umbilical wall of a juvenile with an impression of foliated structure, × 25.

PLATE 5

Bubovicus tardus (BARRANDE in PERNER, 1903)

1–2. L 5789, a mature specimen with patches of shell. 1 – posterodorsal view; 2 – left umbilical view; the circumbilical ridge is visible at the prepared apical end of the whorl (arrowed). × 2.
3. L 30433, left umbilical view of an internal mould of a juvenile, with a low circumbilical ridge (to the left of the umbilicus). × 2.
4–6. L 30435, left umbilical view of an immature specimen (4, × 2), with a well visible sharp circumbilical groove (5, × 4), and with scattered traces of dark brown myostracum delimiting the muscle attachment area (6, × 4, not whitened).

PLATE 6

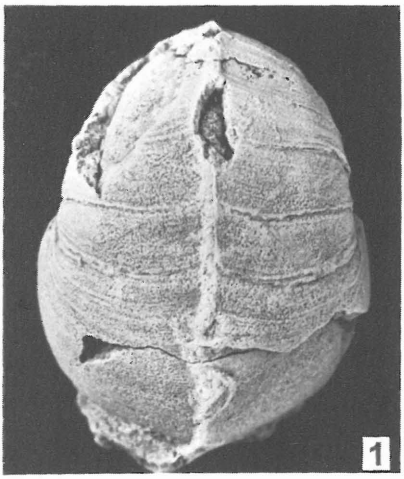
Bubovicus tardus (BARRANDE in PERNER, 1903)

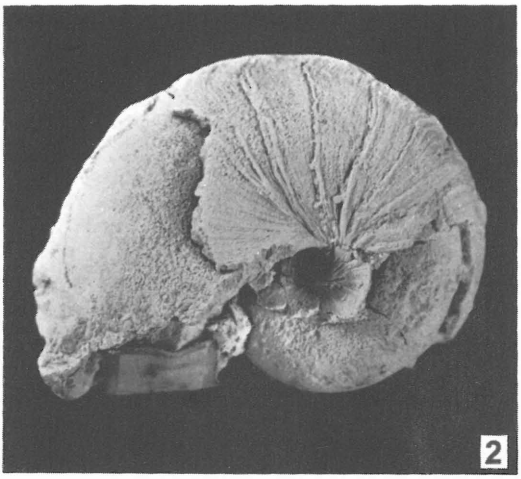
1. L 30432, right umbilical view of a juvenile, internal mould with ill-defined muscle attachment structures (to the left of the umbilicus), × 3.
2. L 30434, umbilical wall of an internal mould of a juvenile with dark patches of myostracum at the attachment area, × 10, not whitened.

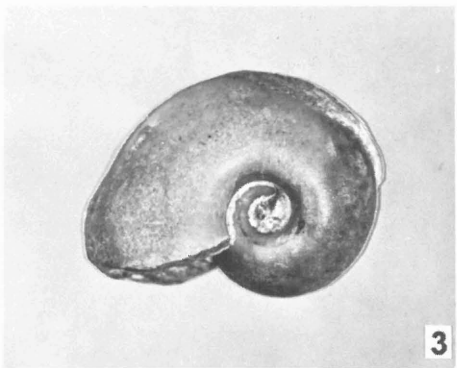
3–5. L 30436, a mature specimen, mostly internal mould, left umbilical view. 3 – × 2; 4 – muscle attachment area, well marked by brownish colouring, × 8, not whitened; 5 – foliated shell structure on the umbilical wall between the anterior margin of the muscle attachment area and the apertural margin, × 25.

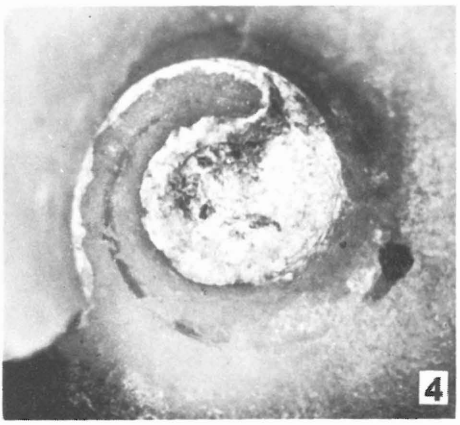
"*Euryzone*" sp., labelled by Perner as *Pleurotomaria* (*Euryzone*) *consolans* BARR.; Silurian, probably Kopanina Formation, Lochkov

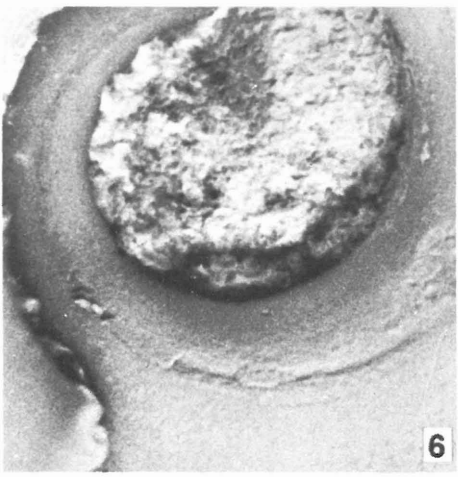
6. L 29618, basal view of an internal mould with preserved muscle attachment macrostructures (to the left of the umbilicus), × 3.

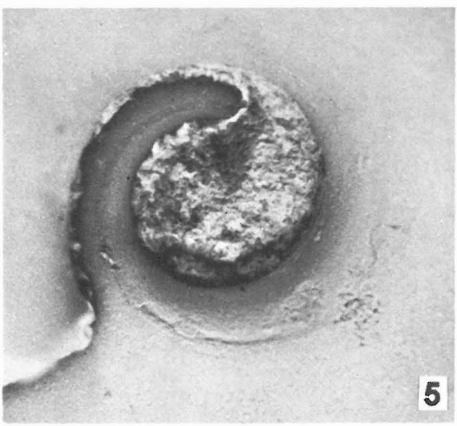

1

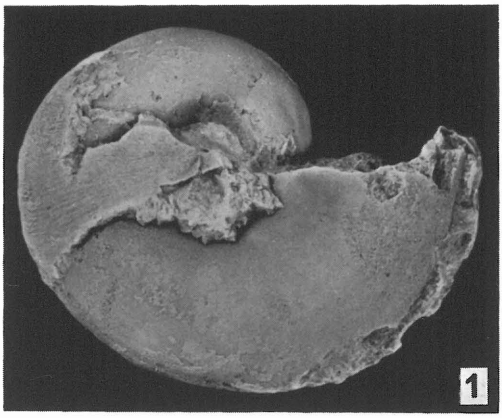

2

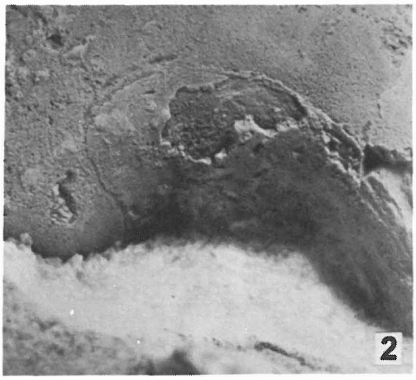

3

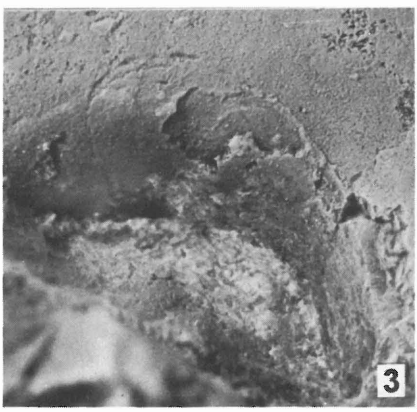

4

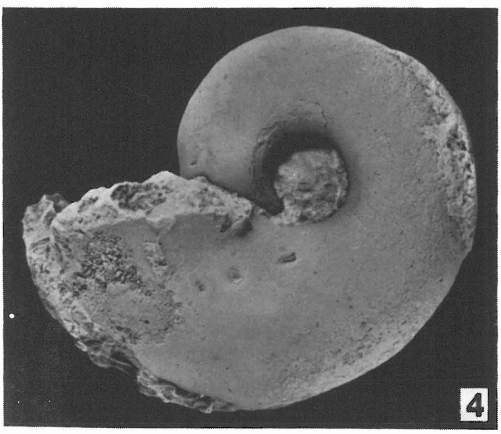

6

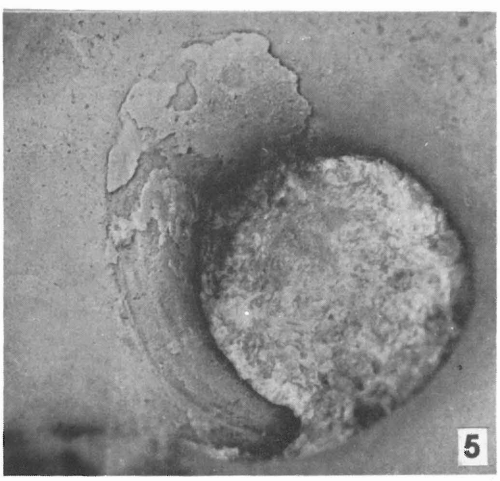

5

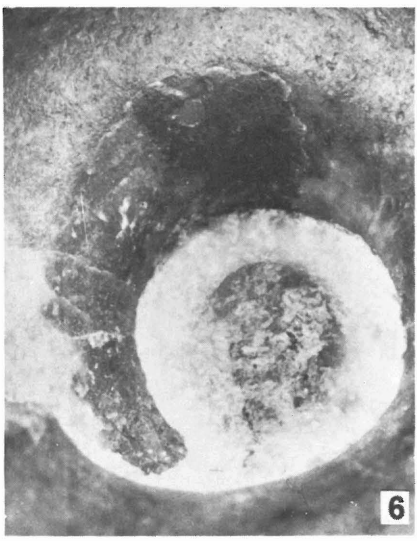

1

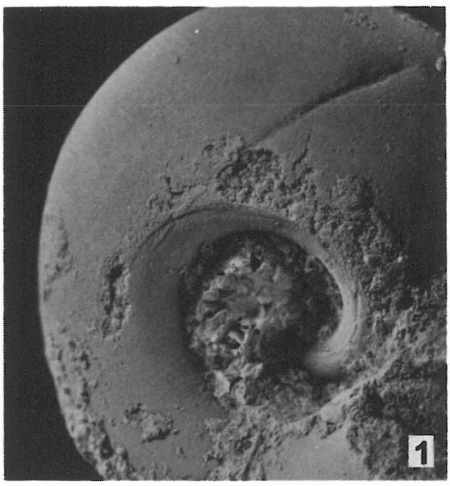

2

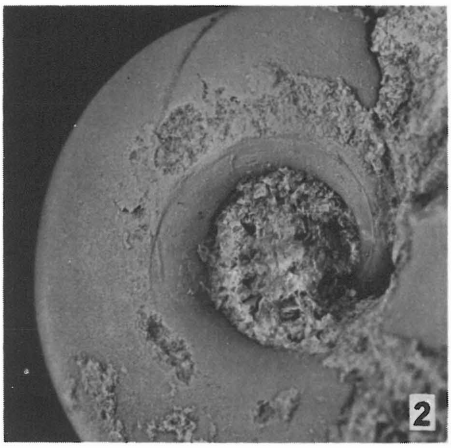

3

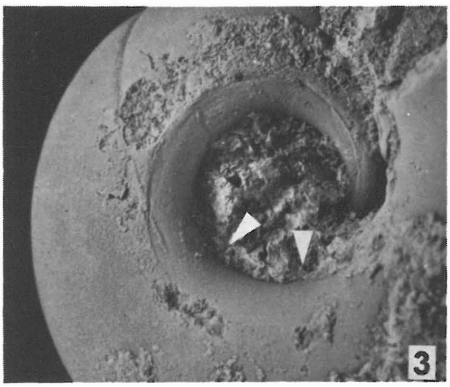

4

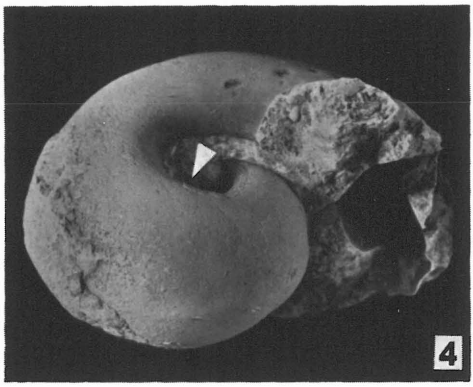

5

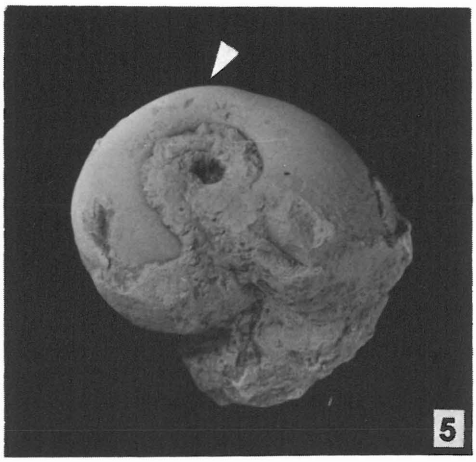

6

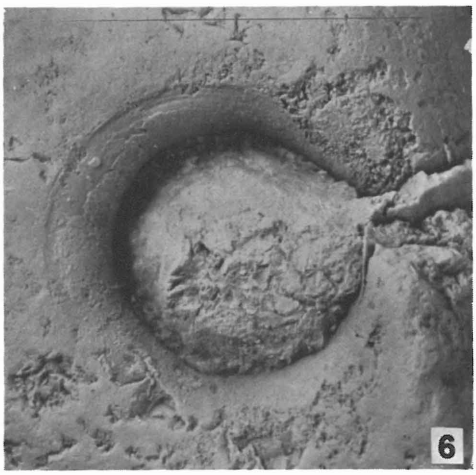

1

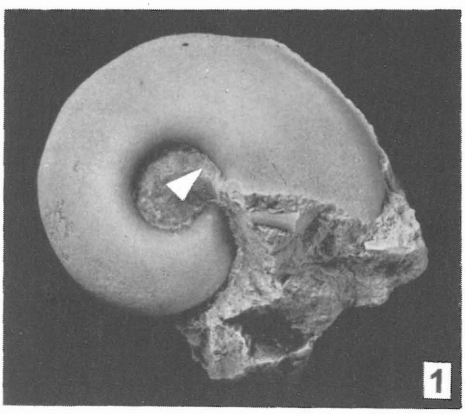

2

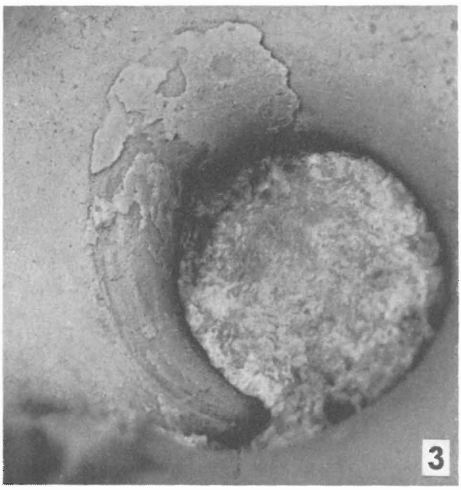

3

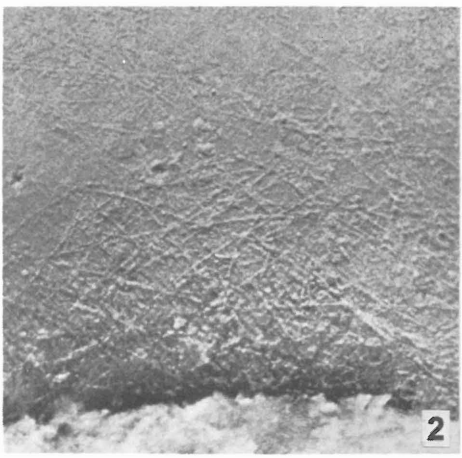

4

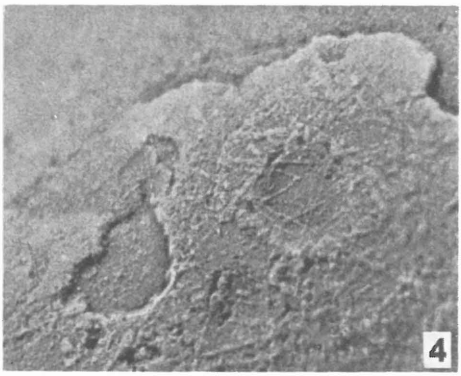

5

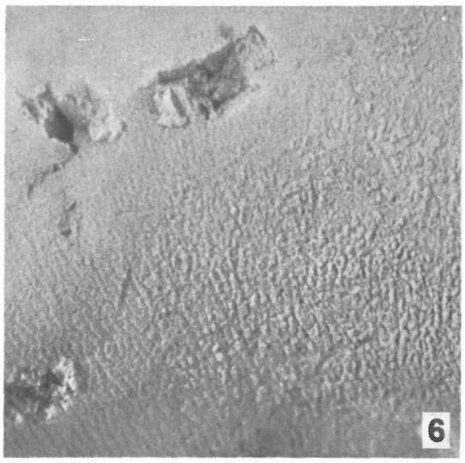

6

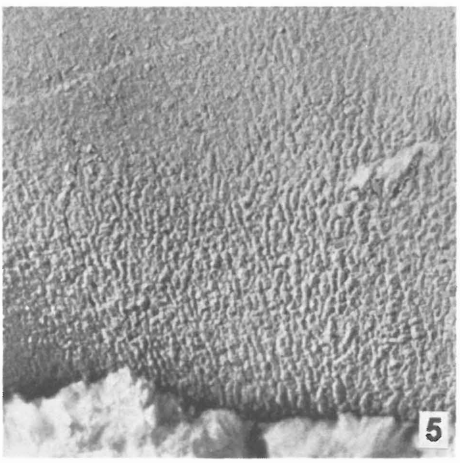

1

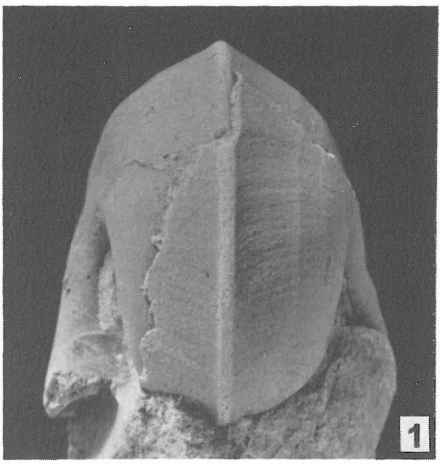

3

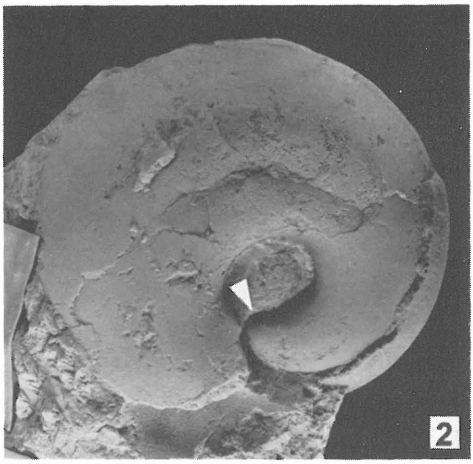

2

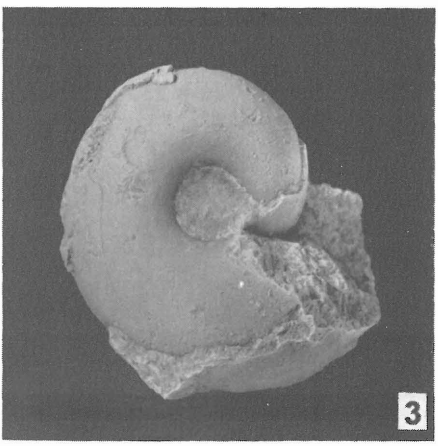

4

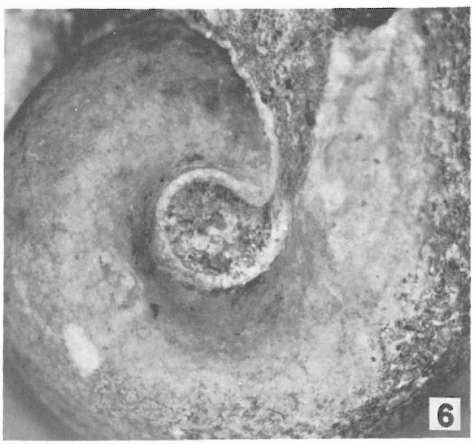

6

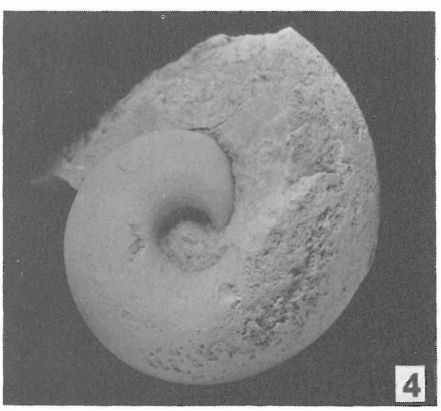

5

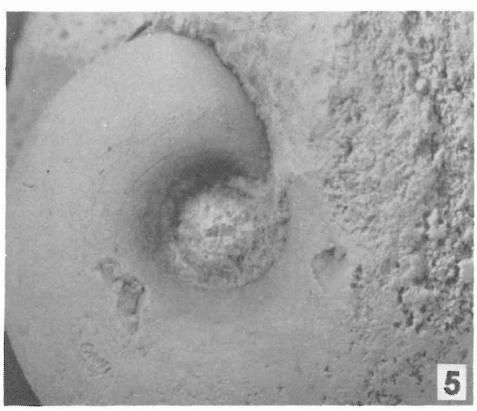

1

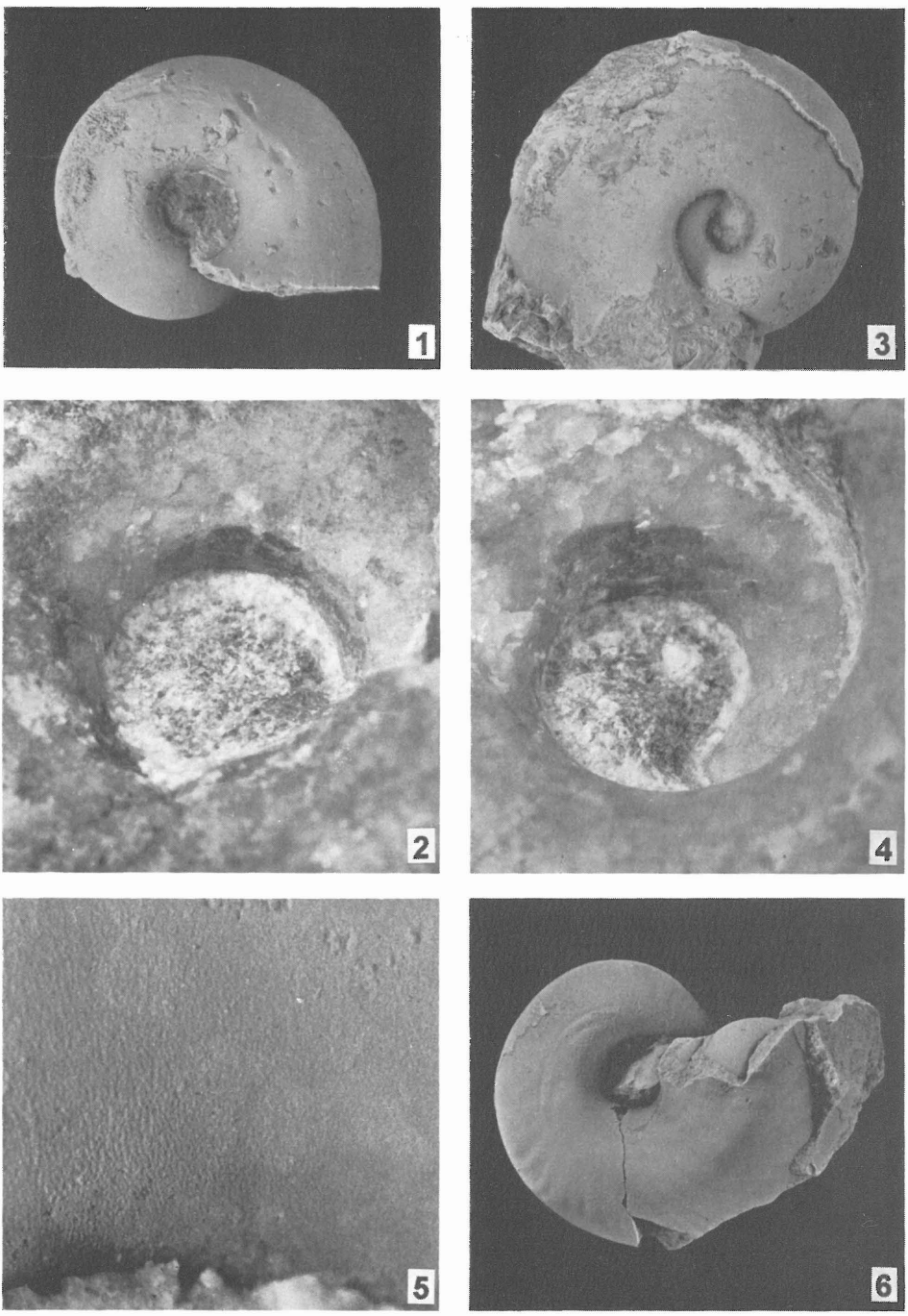

2


3


6


4


5


1
3
2
4
5
6