# Circumbilical retractor muscle attachment areas found in *Tropidodiscus* (Gastropoda, Bellerophontoidea)

## Cirkumbilikální vtisky retraktorů nalezeny u rodu *Tropidodiscus* (Gastropoda, Bellerophontoidea) (Czech summary)

*(6 text-figs)*

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Circumbilical retractor muscle attachment areas have been found in *Tropidodiscus pusillus* (Barrande in Perner, 1903) from the Middle Ordovician (Darriwilian) of the Barrandian Area, Bohemia. The location and shape of the attachment areas confirm that *Tropidodiscus* belongs to bellerophontoidean gastropods. In spite of the fact that the species is very abundant, covering bedding planes and filling concretions in countless masses, only two specimens have been collected showing the muscle scars. This is due both to the small dimensions of the shell and to rather disadvantageous preservation of strongly contracted internal moulds. *Tropidodiscus pusillus* is interpreted as a suprabenthic to epinektic genus living on algal thalli, characteristic for the *Tropidodiscus* Community (Horný 1997d).

*Key words:* Gastropoda, Bellerophontoidea, *Tropidodiscus pusillus*, preservation, circumbilical retractor muscle attachment areas, mode of life, Middle Ordovician, Barrandian Area, Bohemia

## Introduction

During the past ten years, five genera of Ordovician Bellerophontoidean gastropods have been found in the Barrandian Area showing circumbilically positioned retractor muscle areas: *Sinuites* Koken, 1896 (Šárka and Králův Dvůr Formations, Darriwilian and Královdorian), *Strangulites* Horný, 1962 (Králův Dvůr Formation, Královdorian), *Bucanopsina* Horný, 1997 (Letná to Bohdalec Formations, Berounian), *Grandostoma* Horný, 1962 (Zahořany and Bohdalec Formations, Berounian), Králův Dvůr Formation (Královdorian), and *Tritonophon* Öpik, 1953 (Letná to Bohdalec Formations, Berounian), Králův Dvůr Formation (Královdorian) (see Horný 1990, 1991a, 1992, 1996a, 1997a, b, c). Besides these, fossils of two genera of cyrtonellid tergomyans yielded muscle scars, *Sinuitopsis* Perner, 1903 (Letná to Bohdalec Formations, Berounian) and *Cyrtodiscus* (Perner, 1903) (Šárka Formation, Darriwilian) (see Horný 1991b, 1996b). All finds come from weathered siliceous and carbonate concretions, occurring in clayey or silty shales. In the majority of cases, the shell has been dissolved and the muscle scars, preserved on internal moulds, show many details, rarely including even the myostracum deposits.

In spite of a careful study of thousands specimens of *Tropidodicus pusillus*, extending over many years, no scars have been found in this extremely abundant species. An important reason for this unsuccessful investigation is the specific preservation of the internal moulds. Among the Bohemian Ordovician gastropods and cyrtonellid tergomyans, *Tropidodiscus pusillus* was the only species in which the internal moulds in the majority of specimens have strongly reduced in size relative to the external moulds, loosing details on its surface. Another reason is the depth of the location of scars – more than a half whorl back from the apertural margin, where the internal mould is usually fragile and incomplete. Finally, two specimens have been found in the collections of the Museum of Dr. B. Horák at Rokycany which show clear and well defined muscle scars. A few more internal moulds show imperfectly preserved traces which cannot be defined with certainty. The find of circumbilical retractor muscle scars confirms the presumption that the genus *Tropidodiscus* belongs to the bellerophontoidean gastropods. The number of anatomically verified bellerophotoidean gastropods thus increases to thirteen (see Horný 1996a, b).

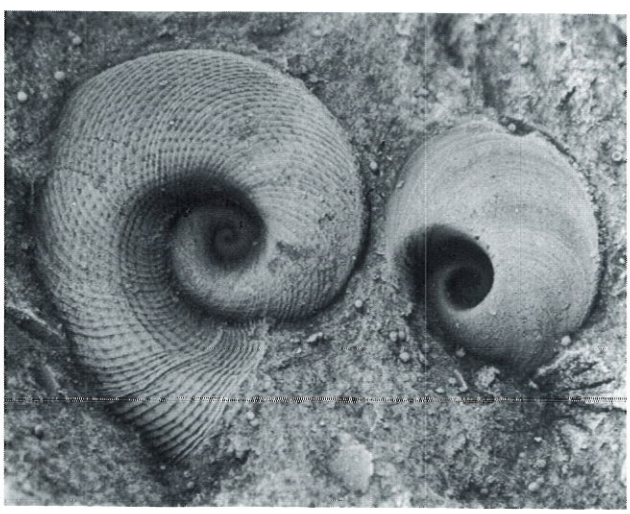

Fig. 1. *Cyrtodiscus nitidus* (Barrande in Perner, 1903), left, a suprabenthic tergomyan, and *Tropidodiscus pusillus* (Barrande in Perner, 1903), an epinectic gastropod. Latex impression, showing an external appearance of the shells. Šárka Formation, Darriwilian; Osek near Rokycany; MBHR 14827. x8.

All studied specimens come from the Middle Ordovician Šárka Formation (Darriwilian), the majority of them from the locality Osek near Rokycany. They are deposited in the Museum of Dr. B. Horák at Rokycany (abbreviation MBHR) and in the Department of Palaeontology, Natural History Museum, National Museum, Prague (abbreviation NM L).

## Descriptive part

### *Retractor muscle attachment areas*

Specimen MBHR 4640, Text-fig. 2A, B; Šárka Formation, Darriwilian, Osek near Rokycany.

Left side of an incomplete, smooth internal mould in a siliceous concretion, filled with many specimens of *T. pusillus*. The adapertural part of the mould is lost; the incomplete adapical part consists of loosely accumulated grains of rock. One and a half of whorls are preserved; maximum diameter is 6.0 mm. The muscle attachment area is located about 200° back from the apertural margin. It lies on the umbilical shoulder, slightly extending over the flat lateral side of the whorl as a slightly depressed, adaperturally widening zone, addorsally bordered with a low but well-defined ridge. Maximum observable length of the area is 0.8 mm, maximum visible width 0.25 mm.

Specimen MBHR 12508, Text-fig. 2C; Šárka Formation, Darriwilian, Osek near Rokycany.

This is the right side of an incomplete internal mould, lacking the anterodorsal part and the initial part of spire, preserved in a siliceous concretion, containing several specimens of *T. pusillus*. Two whorls are preserved, maximum diameter is 5.3 mm. The muscle attachment area is located about 220° back from the apertural margin. It lies on the umbilical shoulder, slightly extending over the flat lateral side of the whorl as a slightly depressed zone, addorsally bordered with a low but well-defined ridge. Maximum observable length of the area is 0.7 mm, maximum visible width 0.2 mm. The surface of the mould is rather coarse, with no details of morphology.

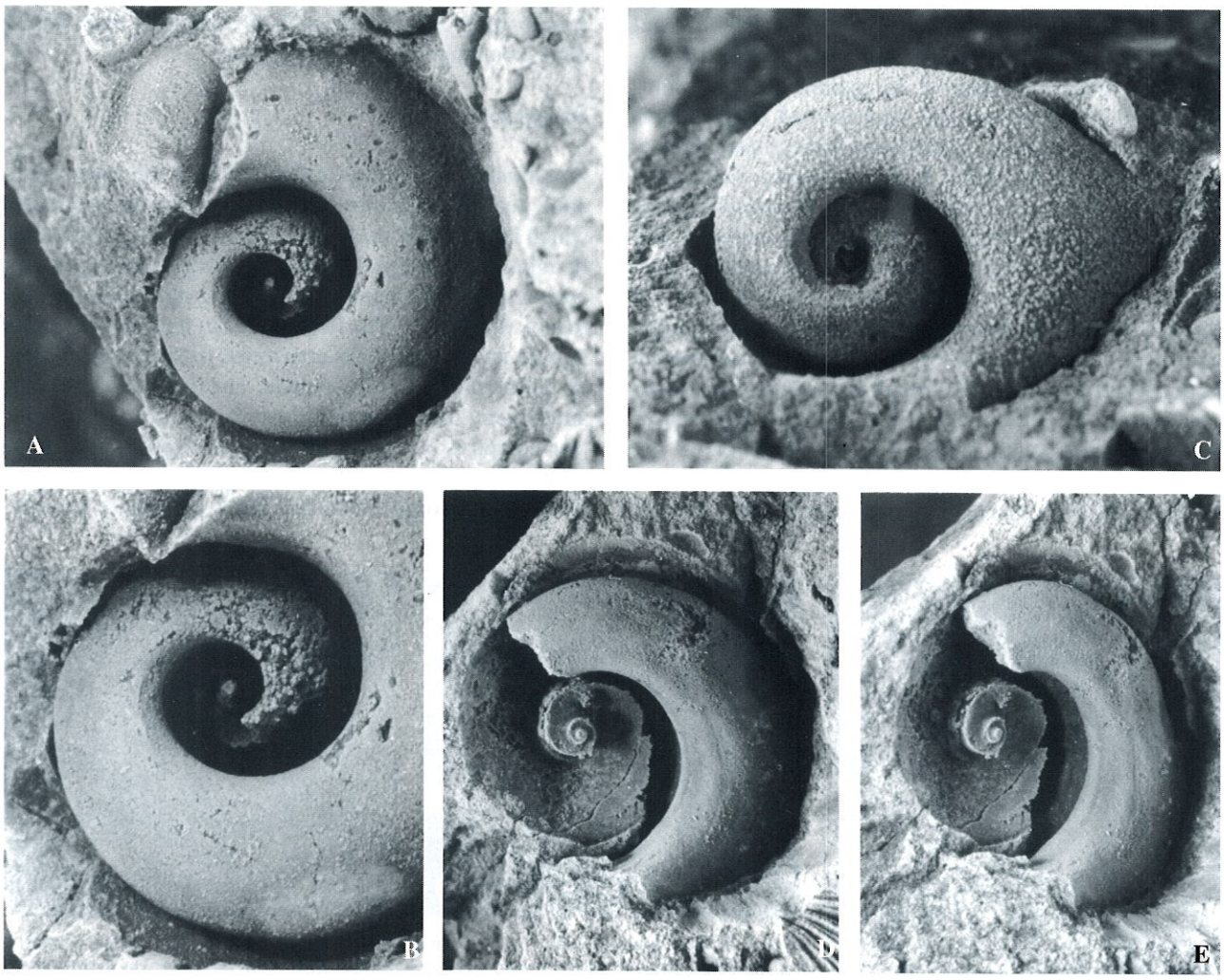


Fig. 2. *Tropidodiscus pusillus*. A, internal mould MBHR 4640 with best preserved muscle scar, x9. B, enlarged, x12. C – internal mould MBHR 12508 with coarse surface and well visible muscle scar, x12. D, E – incomplete internal mould NM L 32638 with spiral grooves on the umbilical slope and above the umbilical shoulder; umbilical and oblique umbilical views, x8. All specimens from the Šárka Formation, Darriwilian; Osek near Rokycany.

### *Spiral structures*

Spiral structures are relatively common, appearing on the internal moulds with a smooth surface. These structures are developed as four narrow, shallow, groove-like depressions, two on each side of the adapertural half of the final whorl, located below and above the umbilical shoulders. They could correspond to low spiral ridges on the shell interior, but the shell is unknown and a chance to observe its internal surface immediately reflected on the internal mould is minimal. An explanation that these depressions, running along the umbilical shoulder, were connected with musculature is not likely, both for functional and morphological reasons. It is most probable that these structures originated during the diagenesis. (Text-fig. 2D, E.)

### *Contraction of the internal mould*

The majority of specimens of *T. pusillus* occurring in siliceous concretions of the Šárka Formation, show a striking disproportion between the outer shell morphology as expressed by the external mould and the internal mould. This phenomenon is less obvious in silty or sandy rocks, where the shape of the internal moulds is closer to the outer shell surface. As observed in specimens from various localities, including Morocco and France, the shell wall in *T. pusillus* is generally thin, on average 0.05 mm–0.15 mm in adult specimens. In many siliceous concretions, where the space between the external and internal moulds in other associated gastropods corresponds to the original shell thickness, it is 2–6 times wider in *T. pusillus*. In these cases, the internal mould is thin and weak, strongly reduced in size, fragile, connected with the surrounding rock through the aperture and through the deep slit. The surface of the external mould is usually clean and smooth, showing fine growth lirae. If not sufficiently weathered, the space between the moulds is filled to different extent with various minerals, usually gypsum, limonite or ankerite, or just with clay. In some cases the cavity is filled with irregular crusts, probably of ankerite. (Text-figs 3, 4.)

The reduction of fine sediment filling within the shell is probably connected with the mode of life (and mode of death) of this gastropod. While the empty shells of epibenthic gastropods laid on the bottom after the death and were gradually filled with sediment, the suprabenthic to epinektic tropidodiscids may have been subject to different processes. Adapted to well-aerated zone, they may have been killed when the storms separated them from algal thalli, and with soft parts deeply retracted, they fell to the ill-aerated bottom. In addition, they were quickly covered with sediment after the storm, and died in masses in rather chaotically accumulated taphocoenoses. Because of the deeply withdrawn, incompletely decayed body, the inside of the shell was only partly filled with sediment near the aperture. After the loss of organic matter, minerals substituting the original carbonates of the shell matrix, larger in volume, probably compressed the residue consisting of fine sediment fractions. The process may have been also predisposed by a specific mineral composition of the shell, probably different from that of other contemporaneous gastropods.

## Discussion

*Tropidodiscus pusillus* is undoubtedly the most abundant peri-Gondwanan bellerophontoidean gastropod which inhabited the aerated zones of the Darriwilian sea. Its minute shells usually occur in chaotic taphocoenoses, concentrated in concretions, known from Bohemia, Morocco, and France. The find of the circumbilical retractor muscle attachment areas confirmed its systematic position within the Class Gastropoda. The depth of the muscle attachment area from the apertural margin is 200–220° [for comparison: *Tritonophon peeli*, Upper Ordovician (Horný 1997) about 200°, *Bucanopsina calypso*, Upper Ordovician (Horný 1997) 210–220°, *Grandostoma bohe-*

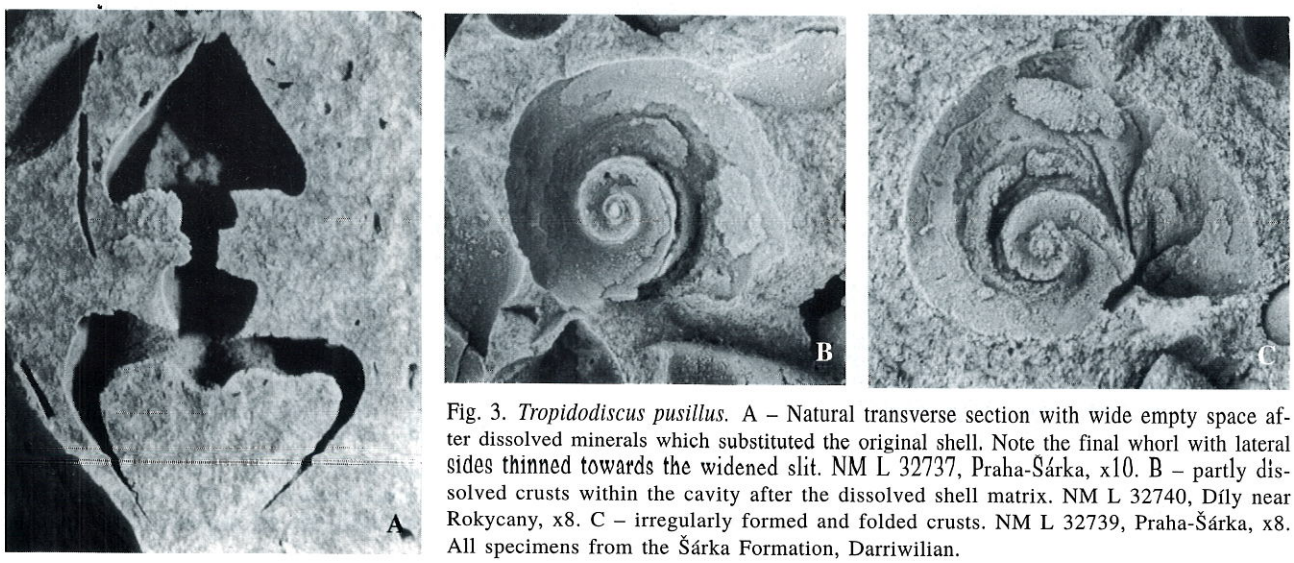


Fig. 3. *Tropidodiscus pusillus*. A – Natural transverse section with wide empty space after dissolved minerals which substituted the original shell. Note the final whorl with lateral sides thinned towards the widened slit. NM L 32737, Praha-Šárka, x10. B – partly dissolved crusts within the cavity after the dissolved shell matrix. NM L 32740, Díly near Rokycany, x8. C – irregularly formed and folded crusts. NM L 32739, Praha-Šárka, x8. All specimens from the Šárka Formation, Darriwilian.

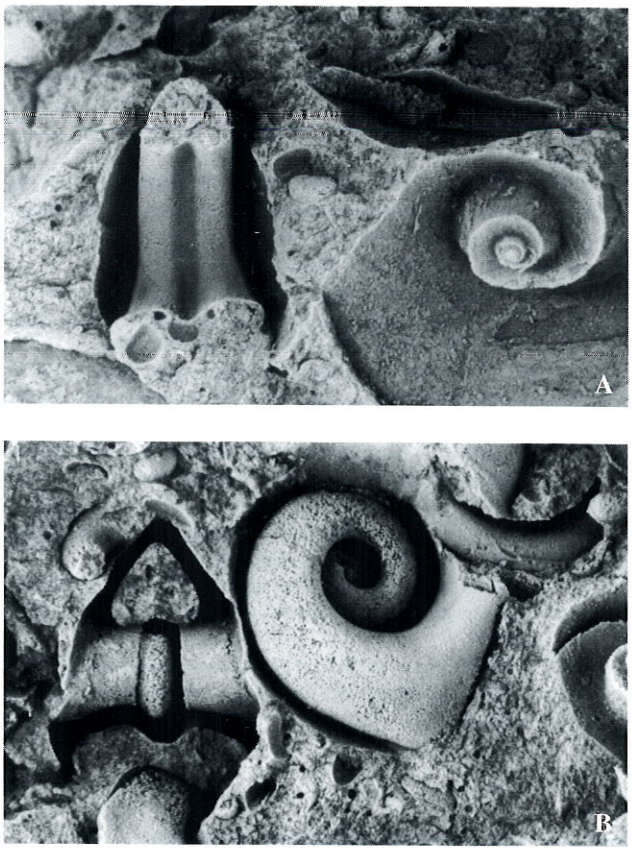


Fig. 4. *Tropidodiscus pusillus.* A – a strongly contracted internal mould surrounded by a wide space after the dissolved shell. MBHR 14717, Šárka Formation, Darriwilian, Osek near Rokycany. x7. B – two internal moulds with a wide space after the dissolved shell. MBHR 14833, Šárka Formation, Darriwilian; Osek near Rokycany. x9.

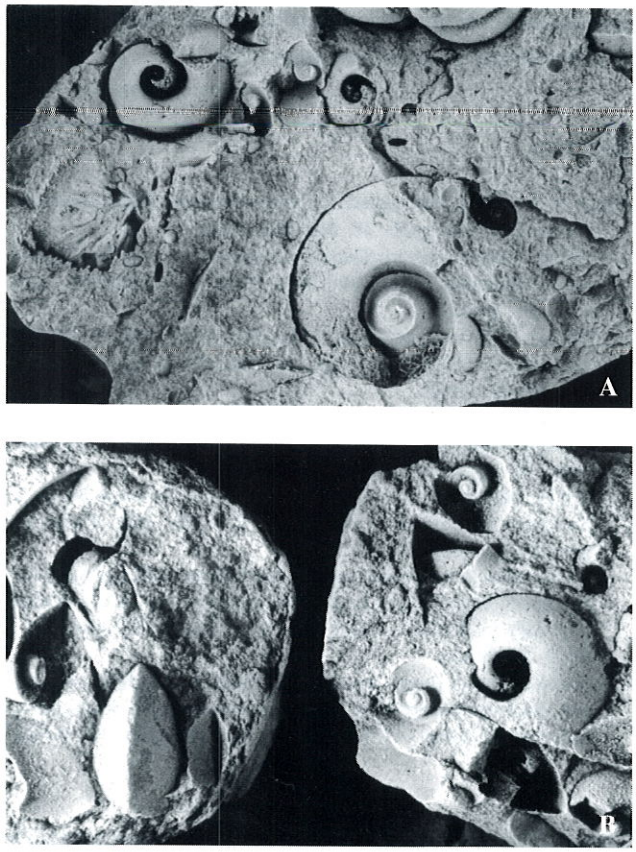


Fig. 5. *Tropidodiscus pusillus.* A – a nodule containing specimen of *Tropidodiscus pusillus* figured in Fig. 2A, B (upper left) with a wide empty space after the dissolved shell, and a specimen of *Lesueurilla prima* (Barrande in Perner, 1903) with a thin empty space, common in other gastropods. MBHR 4640, Šárka Formation, Darriwilian, Osek near Rokycany. x3. B – two parts of a silty nodule with numerous specimens, preserved as uncontracted internal moulds. The specimen near the right margin shows an original thickness of the shell. NM L 32741a, b. Dobrotivá Formation, Darriwilian; Praha-Libeň, Hercovka. x3.

*micum*, Upper Ordovician (Horný 1997) 120°, *Grandostoma grande*, Upper Ordovician (Horný 1997) 180–200°, *Bellerophon scaber*, Silurian (Horný 1995) 210–250°, *Bubovicus tardus*, Silurian (Horný 1995) 180–270°, *Bellerophon recticostatus*, Carboniferous (Peel 1982) 180°]. As the shell was rather thin (on average 0.05–0.2 mm), the muscle attachment areas must have been also shallow.

As suggested by Peel (1977, 1978) for minute *Tropidodiscus* from the Silurian of Nova Scotia, the Darriwilian tropidodiscids, as inferred from their large horizontal distribution and mode of occurrence and preservation, may have been algal dwellers. The lenticular shape of the shell may have been advantageous for life in algal thalli. The restoration of a large *Tropidodiscus* as given by Linsley (1978), based on the Devonian type species, shows a quite different adaptation. The Ordovician tropidodiscids, somewhat similar to *Tritonophon* Öpik, 1953 [by Peel (1978) also listed among the foliage dwellers], have a shell morphology different from the Devonian type which led Horný (1962) to establish *Peruniscus*, as a subgenus of *Tropidodiscus*. The validity of this taxon needs to be justified by further study.

The conclusions made on specific preservation of contracted internal moulds may be useful as a criterion for recognising mass killing events, possibly related to storm activity, within the geological records.

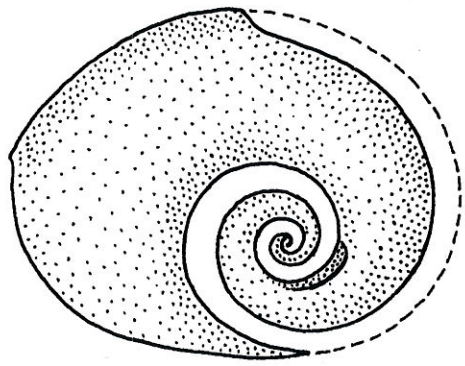

Fig. 6. *Tropidodiscus pusillus.* Schematic drawing showing the gross shell morphology, contraction of the internal mould, and location of the circumbilical muscle attachment area. After specimens NM L 32736 and MBHR 4640. Orig.

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## Cirkumbilikální vtisky retraktorů nalezeny u rodu *Tropidodiscus* (Gastropoda, Bellerophontoidea)

Po mnoha letech pátrání po svalových vtiscích u *Tropidodiscus pusillus* (Barrande in Perner, 1903) ze šáreckého souvrství (střední ordovik, darriwil) byli mezi tisíci exempláři tohoto masově se vyskytujícího bellerofontoidního plže nalezeni dva jedinci se zachovanými svalovými vtisky. Vtisky obou retraktorů jsou v cirkumbilikální pozici, což podle současných názorů potvrzuje, že rod *Tropidodiscus* je plž, patřící k nadčeledi Bellerophontoidea.

Mimořádná vzácnost svalových vtisků je podmíněna zvláštním zachováním vnitřních jader, jejichž objem je vzhledem k ulitě značně redukován. Je vyslovena domněnka, že jedinci druhu *Tropidodiscus pusillus*, kteří pravděpodobně žili epiplanktonně, byli při bouřích separováni od plovoucích řas a klesali ke dnu, kde v prostředí s deficitem kyslíku zahynuli, hluboko zataženi do ulit a překryti sedimentem. Výplň ulity tak obsahovala sediment s vysokým podílem organických látek, po jejichž rozkladu mohlo dojít k redukci výplně, doprovázené rekrystalizací ulity a tím i zvětšení objemu původního karbonátu. Ani původní, ani sekundární minerály se však ve zvětralých konkrecích, použitých ke studiu, nezachovaly. Je pozoruhodné, že ulity ostatních gastropodů, vyskytujících se v tafocenozách, tomuto procesu nepodlehly. Nelze vyloučit, že minerální složení ulit tropidodisků bylo poněkud odlišné.