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CONCH STRUCTURES, SOFT-TISSUE IMPRINTS AND TAPHONOMY OF THE MIDDLE ORDOVICIAN CEPHALOPOD *TRAGOCERAS FALCATUM* FROM ESTONIA

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Abstract: *Tragoceras falcatum* (Schlotheim, 1820) is a common, loosely coiled estonioceratid (Tarphycerida, Cephalopoda) occurring in the Kunda Regional Stage (early Darriwilian, Middle Ordovician) of Estonia. Although the species is quite well-known, we document some features for the first time. For example, one specimen from the Harku quarry (Estonia) with a phosphatized replacement shell exhibits growth halts (megastriae) on the body chamber. As they are not preserved in smaller specimens, we suggest that these megastriae formed at the approach of maturity, possibly also reflecting sexual dimorphism and cycles of reproduction (iteroparity?). Additionally, the specimen shows minute soft-tissue imprints (drag bands and pseudosutures). These imprints are comparable to patterns in other cephalopods such as ammonoids, bactritids and other nautiloids, but have not yet been reported from Palaeozoic nautiloids. However, they might have been misinterpreted as oncomyarian muscle attachment scars previously. Lastly, we discuss the taphonomy of the specimen, which was encrusted by multiple bryozoan colonies post-mortem. Furthermore, it shows questionable traces of bioerosion.

Key words: Tarphycerida, Estonioceratidae, Darriwilian, megastriae, bryozoa, Baltoscandia

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Introduction

Representatives of the order Tarphycerida were the earliest cephalopods with a coiled conch, a feature that evolved independently multiple times e.g. in modern day *Nautilus* and *Spirula*, but also in many other fossil groups such as ammonoids and lituitids (Dzik 1984, Kröger 2005). Some of the earliest tarphycerids, belonging to the family Estonioceratidae, were not yet fully coiled. They either had gyroconic shells where the whorls do not touch each other, or were only coiled in the early ontogenetic stages, with later stages of the conch diverging (Furnish and Glenister 1964). Estonioceratids are common in the Kunda Stage of Estonia, from which a number of genera and species have been described (King 2014).

Here, we present a remarkable specimen of *Tragoceras falcatum* (Schlotheim, 1820) that was encrusted by a bryozoan colony with another colony on top. Furthermore, we discuss two conspicuous constrictions near the base of the body chamber. Lastly, we describe the clearly visible soft-tissue imprints and discuss their origins.

Material and methods

The specimen was collected from the Harku quarry, near Tallinn, Estonia (lat.: 59.398371 N, long.: 24.563784 E). The locality is well-known for yielding excellent cephalopod remains of the Kunda Regional Stage (early Darriwilian, Middle Ordovician), such as endocerids, actinocerids and tarphycerids, which are commonly phosphatized (e.g. Mutvei 1997a, b, 2002, Kröger 2012). Furthermore, the different localities in Harku Hillock yield abundant benthic organisms and trace fossils. The studied cephalopod specimen is housed in the Institute of Geology at Tallinn University of Technology (Estonia) under the number GIT 819-1 (Text-fig. 1a, d). Further comparative material also originates from the Harku quarry and the nearby locality of Maardu (lat.: 59.4505556 N, long.: 25.0338889 E).

The convex side of the *Tragoceras* conch curvature has long been recognized as the ventral side (e.g. Dewitz 1880, Teichert 1964), which is followed here. Accordingly, the term dorsal refers to the concave side of the curvature,



Text-fig. 1. Megastriae and post mortem epicoles on *Tragoceras falcatum* (Schlotheim, 1820). Arrows and M1–M3 indicate megastriae, bryozoan colonies are indicated by B1 and B2. a: GIT 819-1, left lateral view; b: body chamber of GIT 819-1, dorsal view; c: body chamber of GIT 819-1, left lateral view; d: GIT 819-1, right lateral view; e: PIMUZ 37299, right lateral view; f: detail of the body chamber of GIT 819-1, right lateral view, encrusted by bryozoans; g: bryozoan colony with *Trypanites* borings growing on an older bryozoan crust GIT 819-1. Specimens oriented with aperture downwards. Scale bars 10 mm.

while length, height and width refer to the longitudinal, dorsoventral and lateral axes, respectively.

Institutional abbreviations

GIT – Department of Geology, Tallinn University of Technology, Estonia

TUG – University of Tartu Natural History Museum, Estonia

PIMUZ – Paläontologisches Institut und Museum, University of Zürich, Switzerland

Systematic remarks

Dzik (1984) synonymized a number of loosely coiled estonioceratids, namely *Aserioceras* Stumbur, 1962, *Bentoceras* Stumbur, 1962, *Pycnoceras* Hyatt, 1894 and with reservation *Falcilituites* Remelé, 1886, with *Tragoceras* Remelé, 1890. However, we follow King (2014), who accepted these genera as separate taxa in his review of the Estonioceratidae. Thus, the genus *Tragoceras* has a distinctly curved, slender, slowly expanding conch with a compressed cross section and sutures with broad lateral saddles. Although the genus is fairly common, the apex and juvenile stages of the conch are unknown. Nevertheless, it appears likely that they were tightly coiled (Dzik 1984, King 2014). Also, note that the genus was previously referred to *Planctoceras* Schröder, 1891 on many occasions (e.g. Ulrich et al. 1942, Flower and Kummel 1950, Balashov 1953, Mutvei 1957, 2002, Sweet 1958, Stumbur 1962); however, after Furnish and Glenister (1964) and King (2014), *Tragoceras* has priority and is the valid name for the genus.

According to King (2014), *Tragoceras* contains only the type species, *Tragoceras falcatum* (Schlotheim, 1820) and the species "*T. arciforme*" (Balashov, 1953) is most likely synonymous. However, two additional species have been described which were omitted by King (2014). "*Planctoceras*" *quenstedi* Hyatt, 1894 (Hyatt 1894: 446) was only very briefly mentioned and is probably also synonymous with *T. falcatum*. *T. yichangense* Xu et Lai, 1987 (Xu and Lai 1987: 289, pl. 24, fig. 9) has been described from the Early Ordovician of China, but from the description and figure it is not clear whether the species really belongs to *Tragoceras*. If true, *T. yichangense* would represent the only known *Tragoceras* outside Baltoscandia.

Megastriae

Adult modifications of the body chamber occur in many lineages of Palaeozoic cephalopods and are often caused by a change in growth patterns. In most cases, these involve changes in apical angle, curvature or a contraction or constriction of the aperture (e.g. Stridsberg 1981, Dzik 1984, cf. Bucher et al. 1996, 2003, Urdy et al. 2010). Some more unusual modifications are longitudinal imprints in *Orthoceras* and *Ctenoceras* (e.g. Troedsson 1931, Kröger 2004, Kröger and Isakar 2006), a strongly laterally contracted aperture with a separation of head and hyponome in the Silurian discosorid *Phragmoceras* (e.g. Manda 2008) or lateral outgrowths and visor-like apertures in the Devonian rutoceratids *Ptenoceras* and *Hercoceras* (Turek 2007, 2008).

The preserved part of the body chamber of the herein studied specimen GIT 819-1 is 75 mm long, 23 mm high and 21 mm wide at the base and shows a different modification. The shell is sharply constricted almost immediately adorally to the base of the body chamber, parallel to the growth lines of the shell (Text-fig. 1b, c). Similar constrictions in a specimen of *Tragoceras* were described by Dewitz (1880: 176, pl. 4, fig. 3); however, according to him, the constrictions are only present on the internal mould and were caused by shell thickening. In GIT 819-1, the constrictions are definitely present on the external surface of the shell. On the dorsum, the first constriction can be seen 10 mm from the base of the body chamber. In contrast to Dewitz's (1880) specimen, the constriction is only faintly visible on the internal mould, which is exposed at the left ventrolateral side of the conch. The right ventrolateral side is covered by a bryozoan on the body chamber and thus not visible. Nevertheless, as the constriction is parallel to the growth lines, which slope in an adapertural direction on the dorsum (prorsiradiate), the constriction probably begins very close to the ventral base of the body chamber.

A second constriction (Text-fig. 1b, c) occurs at a distance of 21 mm adorally from the first and is even more pronounced. After both constrictions, the shell expands rapidly in width by about 1 mm, but contracts shortly thereafter, producing a convex outline. Thus, the largest dorsoventral diameter of 25 mm occurs after the second constriction.

Another 21 mm adaperturally from the second constriction at the most anteriorly preserved part of the specimen, there is a third constriction, this time only a shallow constriction (Text-fig. 1b, c), measuring slightly over 23 mm in height.

The constrictions described above resemble growth halts (megastriae) found in certain ammonoids (e.g. Bucher et al. 1996, 2003, Klug et al. 2007). Furthermore, the shell adoral of the constriction is apparently attached to the inside of the shell adapical of the constriction, i.e., the older shell material overlies the more recently formed shell. Thus, we interpret the constrictions as megastriae, representing phases during which the animal stopped growing and later resumed growth. In contrast to ammonoids, however, they appear to be restricted to the adult body chamber in *Tragoceras*. In ammonoids, megastriae are often formed throughout the majority of post-embryonic ontogeny. Thus, they may mark the boundaries between growth phases and therefore are also present on the phragmocone. It is possible that ontogenetically younger constrictions are not visible in our *Tragoceras* specimen because the left side lacks shell remains and the right side is covered by a bryozoan. However, the constrictions mentioned by Dewitz (1880) are also restricted to the body chamber and another specimen illustrated by Schröder (1891: pl. 6, fig. 1a; re-figured by King 2014: fig. 3c) shows two similar constrictions in the adult part of the specimen (although it is not clear from the illustration, where the base of the body chamber is located).

Although *Tragoceras falcatum* is relatively common and several dozens of specimens are deposited at the collections in Tallinn and Tartu, the constrictions are only visible in a limited number of the specimens. This is partly because many of the specimens are broken and only a small part of the conch is preserved. These fragments do not all represent the same ontogenetic stage and the body chamber is not always preserved. Furthermore, the remains are often corroded, making it difficult to discern whether constrictions are present. However, the constrictions are visible in at least one additional specimen, TUG 860-1642 and perhaps also in TUG 1393-57-1, TUG 856-5-2 and GIT 426-125.

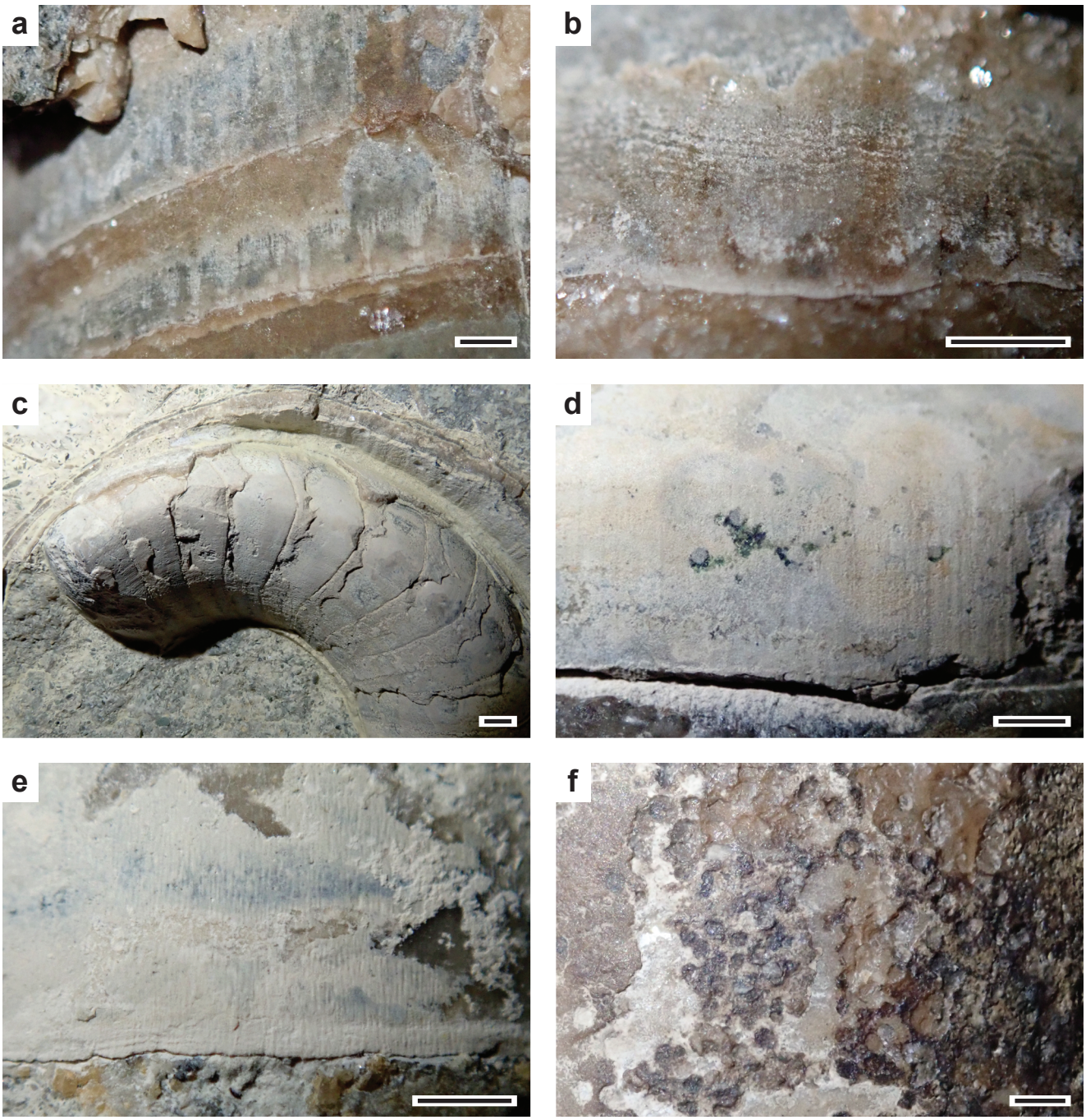
Another well-preserved specimen from Harku (PIMUZ 37299; Text-fig. 1e) shows no sign of any pronounced constrictions, only somewhat irregularly developed growth lines and lirae. These probably represent minor growth cycles or halts, but they did not produce the convex outline as in GIT 819-1. PIMUZ 37299 has a dorsoventral whorl cross section of 20 mm at the base of the body chamber, which only increases to 21 mm over the remaining 90 mm of the body chamber. This corroborates the assumption that the constrictions/megastriae are restricted to the adult body chamber.

As GIT 819-1 is somewhat larger than PIMUZ 37299, this leaves four explanations for the constrictions: 1) the specimens belong to different species; 2) the constrictions represent a pathological condition or reflect other syn vivo-disturbances (injuries, other adverse conditions); 3) PIMUZ 37299 represents an ontogenetically younger stage; 4) the specimens are antidimorphs of one species and thus reflect sexual dimorphism.

We favour explanations 3) or 4), since the constrictions are too regular and occur too commonly to be pathological. It is possible that they belong to different species, but more detailed investigations are needed to confirm this hypothesis. The fact that the difference is confined to the adult stage suggests that ontogeny and sexual dimorphism represent plausible explanations. It is also conceivable – though difficult to test – that the animal ceased growth during phases of reproduction (iteroparity). The number of megastriae would then indicate the number of times that the animal reproduced. By comparison, the iteroparous recent *Nautilus* terminates growth completely at the approach of maturity (Collins and Ward 2010).

Soft-tissue imprints

Soft-tissue imprints from fossil nautiloids are rarely documented and are mostly restricted to muscle attachment scars (e.g. Mutvei 1957, Sweet 1959, King and Evans 2019).



Text-fig. 2. Soft-tissue imprints and traces of bioerosion on Middle Ordovician cephalopods from Estonia. a: GIT 819-1, *Tragoceras falcatum* (Schlotheim, 1820), drag bands; b: GIT 819-1, *T. falcatum*, pseudosutures; c: GIT 819-2, *Estonioceras* sp., drag bands; d: GIT 819-3, cf. *Anthoceras vaginatum* (Schlotheim, 1820), drag bands; e: GIT 819-4, cf. *Orthoceras regulare* Schlotheim, 1820, drag bands; f: Pits on the body chamber of GIT 819-1, *T. falcatum*. Specimens oriented with aperture downwards. Scale bars 1 mm.

These were already described in *Tragoceras falcatum* as "Verwachsungsband" (= adhesion band) by Dewitz (1880) and later by Mutvei (1957) as annular elevation. In *T. falcatum*, the muscle attachment scars are ventromyarian (sensu Sweet 1959). In GIT 819-1, the muscle attachment scars are mostly covered by shell and are thus only partially visible.

Some other imprints are more remarkable. The surface of the internal mould of the phragmocone (where the shell broke off) carries minute, but clearly visible longitudinal markings, so-called "drag bands" (Text-fig. 2a). Similar imprints have been documented by several authors in ammonoids, bactritids and Mesozoic and extant nautilids (Zaborski 1986, Hewitt et al. 1991, Richter 2002, Richter and Fischer 2002, Kröger et al. 2005, Klug et al. 2008, Polizzotto and Landman 2010, Polizzotto et al. 2015). In contrast, they have not yet been described to our knowledge in Palaeozoic nautiloids apart from a few Devonian orthocerids (Kröger et al. 2005). The drag bands are usually interpreted as imprints of muscle fibers of the mantle. The homology of the structures in different groups is not clear and differences exist. In the case of *Tragoceras*, the drag bands are not confined to the mural band but rather continue from one septum to the next.

Further structures are visible in the same specimen, GIT 819-1, namely small undulating transverse lines on the dorsal side of the phragmocone (Text-fig. 2b). As the ventral side of the phragmocone is not exposed, it is not clear, whether these structures are restricted to the dorsum. It is clear that they become weaker towards the flanks and in the other fragment, which exposes the left flank of the phragmocone, they are not visible, although drag bands are clearly discernible in the same position. Nevertheless, the fact that they disappear slightly adorally suggests that these delicate structures might not always be preserved. We interpret these structures as pseudosutures, which are occasionally associated with drag bands but run parallel to the sutures instead of in the direction of growth (Polizzotto et al. 2015). Note that the pseudosutures are distinct from the wrinkle layer ("Runzelschicht") well known in ammonoids and certain nautiloids (e.g. Teichert 1964, Mapes 1979, Kulicki et al. 2001, Korn et al. 2014).

It is interesting to note that the same continuous drag bands occur not only in the closely related *Estonioceras* (GIT 819-2; Text-fig. 2c), but also in endocerids (cf. *Anthoceras vaginatum* (Schlotheim, 1820); GIT 819-3; Text-fig. 2d), both of which also originate from the Harku quarry. We furthermore found drag bands in a stratigraphically slightly younger (Lasnamägi Regional Stage, late Darriwilian, Middle Ordovician) orthocerid (cf. *Orthoceras regulare* Schlotheim, 1820; GIT 819-4; Text-fig. 2e) from the Maardu quarry. In the latter case, the drag bands also occur on the entire free part of the septum. Pseudosutures are not visible in either of the aforementioned specimens. However, the presence or absence of soft-tissue imprints is more likely related to taphonomic processes (e.g. grain size, etc.) rather than phylogeny.

Within the last decade, isolated cases of longitudinal tracks or ridges on the surface of internal moulds of Palaeozoic nautiloid phragmocones have been interpreted as evidence for oncomyarian muscle attachment scars (Evans and King 2012, Mutvei 2013, King and Evans 2019). These structures occur in late Cambrian plectronocerids (King and Evans 2019: 68), Early Ordovician bisonocerids (Evans and King 2012: 25), late Silurian ascocerids (Mutvei 2013: 176) and a number of other specimens of various taxa (see King and Evans 2019: supplementary material). In contrast, the material documented here shows that longitudinal tracks on the phragmocone do not necessarily imply the presence of oncomyarian muscle attachment scars, because they are known to be dorsomyarian in *Orthoceras* and *Anthoceras* and ventromyarian in *Estonioceras* and *Tragoceras* (Mutvei 1957, 2002). In addition, most specimens that have been interpreted previously as oncomyarian based on phragmocone tracks lack actual muscle attachment scars (including the annular elevation) on the body chamber. Thus, the only evidence supporting an oncomyarian condition in these species is the presence of similar longitudinal structures on the body chamber of oncocerids, discosorids and certain ellesmerocerids (e.g. Mutvei 1957, 2002, 2013, Sweet 1959, Kröger 2007, Manda and Turek 2009). In summary, it appears likely that drag bands have been misinterpreted as oncomyarian muscle attachment scars on some occasions and caution is advised when using this character for phylogenetic inferences.

Taphonomy

The shell of GIT 819-1 is thickly encrusted by bryozoans (Text-fig. 1f). Two larger colonies are present which cover the shell over a length of 39 mm and 42 mm respectively, the latter being located more adapically. These occur only on the left side of the conch, thus suggesting that the specimen was deposited with the right side facing the sediment and the bryozoans colonized the shell later. Post-mortem epicoles on cephalopod conchs are well documented throughout the Ordovician (e.g. Davis et al. 1999, Wyse Jackson and Key 2014). In Estonia, encrusting bryozoans on different Ordovician molluscs occur mostly on internal moulds of gastropods and bivalves (own data). This observation can be explained by Calcite Sea conditions, where aragonitic shells dissolved rapidly (Palmer et al. 1988, Palmer and Wilson 2004). Cephalopods with encrusting bryozoans are less common in Estonia, but locally abundant in reef environments such as the Late Ordovician Vasalemma Formation (Kröger and Aubrechtová 2018). Recently, Vinn et al. (2018) described encrusting bryozoans on cryptic surfaces (e.g. cephalopods from the Kunda Regional Stage) and noticed that cephalopods from the Ordovician of Estonia usually show relatively low encrustation densities. Cases of bryoimmuration as recently described by Wilson et al. (2019) are unknown in the Ordovician of Estonia.

Apparently, the large bryozoan colony which is located more adapically (Text-fig. 1d: B1) was later encrusted by another small bryozoan colony (Text-fig. 1g). The small bryozoan colony is hemispherical with a diameter of 6 mm and shows around 20 small circular pits. They are mostly less than 0.5 mm in diameter and likely represent *Trypanites* (e.g. Wyse Jackson and Key 2007), the most abundant bioerosional trace fossil in the Ordovician of Estonia, which often spread on bryozoans (Toom et al. 2019). Clumping behavior is common for macroborers, especially for the trace makers of *Trypanites* (Kobluk and Nemcsok 1981). There are different hypotheses regarding the identity of its producer, however, according to Wyse Jackson and Key (2007), a sessile annelid polychaete worm is the most likely candidate. Further questionable instances of *Trypanites* are visible on the cephalopod shell itself and look very similar to the ones on the bryozoan in Text-fig. 1g.

Distinct from these possible cases of *Trypanites* are some other traces on specimen GIT 819-1. The most adoral part of the body chamber is densely covered by shallow, somewhat irregularly shaped pits, which have a slightly larger diameter than those on the bryozoan (Text-fig. 2f). In many cases, these pits are closer to each other than their own diameter. It is not clear whether the latter pits were produced by boring organisms or diagenetic processes. The latter explanation is supported by the irregular outline and shallow depth of the pits, potentially indicating that the shell was starting to dissolve. However, it is also possible that bacteria or fungi played a role. Thus, at present we leave the questions regarding formation of these structures open.

Similar structures were first described by Girty (1909: 53–54, pl. 6, fig. 6) on a Carboniferous bactritid and by Elias (1958: 50–51, pl. 3, figs 14, 16) on a Carboniferous ammonoid. Based on these findings, the latter author established the new ichnotaxon *Cyclopuncta girtyi* Elias,

1958. Further questionable cases of *Cyclopuncta* were reported on Devonian pseudorthocerids (Niko 1996: 355, fig. 6.2–3). While Girty (1909) considered the punctual traces as an integral part of the shell, Elias (1958) regarded them as having been produced by the attachment of epizoans. In contrast, Hoare et al. (1980) favoured an inorganic origin. The ichnogenus was not accepted by the Treatise (Hantzschel 1962) because the authors considered it as unrecognisable. More recently, Wisshak et al. (2019) classified *Cyclopuncta* within the ichnofamily Planobolidae.

There are differences between our material and the above-described cases of *Cyclopuncta*. Firstly, some of Girty's (1909) original material consists of elevations, rather than depressions. Secondly, *Cyclopuncta* appears to be generally more widely spaced. Nevertheless, the overall appearance is similar. Thus, we refer to the traces as cf. *Cyclopuncta*.

The above suggests that the specimen GIT 819-1 was deposited in a well-oxygenized but low energy environment and was lying on the muddy sea floor for some time after death, allowing bryozoans to use the shell as a substrate. This is in agreement with the slow sedimentation rates proposed by Jaanusson (1972) for the Ordovician of Estonia. Furthermore, the well preserved taphonomic bottom side of the shell suggests that there was limited post-mortem transport, as otherwise the shell would exhibit more characteristic breakage patterns (cf. Wani 2004, Yacobucci 2018).

Conclusions

We describe a specimen of *Tragoceras falcatum* (Schlotheim, 1820) from the Kunda Regional Stage (early Darriwilian, Middle Ordovician) which is unusual in several aspects:

1. The body chamber carries at least two conspicuous constrictions which we interpret as adult growth halts (megastriae), potentially linked to mature growth and possibly reflecting sexual dimorphism since only some specimens show this pattern.

2. The internal mould of the phragmocone exhibits soft-tissue imprints such as drag bands and pseudosutures, which have not been documented before in Palaeozoic nautiloids, although possibly they have been misinterpreted as tracks of oncomyarian muscle scars. We also compare them to other Ordovician cephalopods.

3. The specimen is heavily overgrown by bryozoans, but only on the left side of the conch, which suggests that these are post-mortem encrustations. Further traces of bio(?) erosion (*Trypanites* and cf. *Cyclopuncta*) are also present on the specimen.

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