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A new type of entombment of *Peronopsis* (Agnostida) in a hyolithid conch

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Abstract: An enrolled exoskeleton of the holaspide specimen of a tiny agnostid *Peronopsis integra* (BEYRICH, 1845) entombed inside a conch of the hyolithid ?*Buchavalites* sp. is described from the middle Cambrian (Drumian) Jince Formation of the Příbram-Jince Basin (Czech Republic). The agnostid is associated with an ichnofossil of the feeding trace classified as *Arachnostega*-type behaviour. The enrolled attitude of the agnostid exoskeleton suggests that the specimen is a carcass rather than moult. Either the storm disturbance and/or well-protected source of food hypotheses could explain the entombed agnostid. This additional example supports a benthic mode of life in the agnostid *P. integra*. The studied association of feeding tunnels of an unknown *Arachnostega*-strategist and *Peronopsis* preserved inside a hyolithid conch is a case of "frozen" behaviour.

Key Words: Agnostid palaeoecology; trilobites; Drumian; Cambrian; Jince Formation; Barrandian area; Příbram-Jince Basin; Czech Republic.

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Résumé : Un nouveau type d'enfouissement pour *Peronopsis* (Agnostida) dans une coquille d'hyolithide.- Un exosquelette recroquevillé d'un spécimen holaspide d'un petit trilobite agnostide, *Peronopsis integra* (BEYRICH, 1845), a été observé enfoui à l'intérieur de la coquille de l'hyolithide ?*Buchavalites* sp. provenant de la Formation de Jince attribuée au Cambrien moyen (Drumien) du Bassin de Příbram-Jince (République tchèque). L'agnostide est associé à une trace fossile en lien avec une activité d'alimentation, attribuée à un comportement de type *Arachnostega*. La disposition recroquevillée de l'exosquelette de l'agnostide suggère que ce spécimen est une carcasse plutôt qu'une mue. L'hypothèse d'une perturbation causée par une tempête et/ou celle d'une source de nourriture bien abritée permettraient d'expliquer l'agnostide enfoui. Ce nouvel exemple confirme un mode de vie benthique chez l'agnostide *P. integra*. L'association étudiée de terriers alimentaires d'un stratège inconnu de type *Arachnostega* et d'un *Peronopsis* préservé à l'intérieur de la coquille d'un hyolithide est un exemple d'action figée.

Mots-clefs : Paléoécologie des agnostides ; trilobites ; Drumien ; Cambrien ; Formation de Jince ; Aire Barrandienne ; Bassin de Příbram-Jince ; République tchèque.

Introduction

The conchicolous habit (= "the use by other animals of shells as residences after the original builders have died" following VERMEIJ, 1987, p. 240) is very rare in the fossil record. Similarly rare is also inquinalism of invertebrates (e.g., FRAAYE & JÄGER, 1995; BOUCOT & POINAR, 2010; KLOMPMAKER & FRAAIJE, 2012). Possible early Palaeozoic examples have been reported from the Cambrian, Ordovician and Silurian of Laurentia (U.S.A.; e.g., BRANDT, 1993; DAVIS *et al.*, 2001), Baltica (Sweden; e.g., ZWANZIG & LIEBERMANN, 2012) and West Gondwana (Czech Republic and Portugal; e.g., FATKA *et al.*, 2008a; GUTIÉRREZ-MARCO *et al.*, 2009; FATKA & BUDIL, 2014).

The oldest fossils documenting conchicolous habit of an unknown organism were announced

by UNAL and ZINSMEISTER (2006) from the Early Cambrian of California; somewhat younger examples of entombed agnostids and eodiscid trilobites were described from the middle Cambrian of the Burgess Shale, British Columbia (CHATTERTON *et al.*, 2003) and from the Jince Formation of the Czech Republic (FATKA *et al.*, 2009; FATKA & SZABAD, 2011). Other example of a possible conchicolous habit of trilobites preserved inside of large hyolithids was discussed by FATKA *et al.* (2008a) and VALENT *et al.* (2008) based on fossils from the Buchava Formation (Drumian). Clusters of trilobites, preserved prone or partly enrolled, have been described under disarticulated skeletal elements of large trilobites were described from Middle Ordovician sediments of northern Portugal (GUTIÉRREZ-MARCO *et al.*, 2009) and the Czech Republic (FATKA

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& BUDIL, in press). Diverse trilobites entombed inside cephalopod shells are known from the Middle Ordovician of the Czech Republic (FATKA, BUDIL, KRAFT unpublished observation), from the Upper Ordovician of the U.S.A. (e.g., DAVIS *et al.*, 2001), as well as from the Silurian of the U.S.A., the Czech Republic (e.g., DAVIS *et al.*, 2001; BUDIL *et al.*, unpublished observation) and also from Sweden (ZWANZIG & LIEBERMANN, 2012). BRANDT (1993, Fig. 3.6) figured an enrolled trilobite preserved inside a gastropod body chamber from the Upper Ordovician of the U.S.A.

UNAL and ZINSMEISTER (2006) suppose that the hyolith conchs were used as shelters and interpreted these finds as possible evidence of a strategy to avoid predation. CHATTERTON *et al.* (2003), VALENT *et al.* (2008), FATKA *et al.* (2009), GUTIÉRREZ-MARCO *et al.* (2009) and FATKA & SZABAD (2011) speculated that agnostids and some trilobites might have entered diverse empty tubes and other restricted spaces for a specific purpose, most likely to feed (scavenge on remnants of a dead priapulid worm, hyolithid or large trilobite) or to hide. Other possible explanation of arthropods include post-mortem transportation or moulting (e.g., DAVIS *et al.*, 2001; SCHULTZ, 2002; FRAAIJE & PENNINGS, 2006). DAVIS *et al.* (2001) and FATKA *et al.* (2009) documented two rare finds of comparatively small hyolithid conchs containing articulated agnostids in prone attitude from the richly fossiliferous *Paradoxides* (*Paradoxides*) *paradoxissimus gracilis* Trilobite Biozone of the middle Cambrian Jince Formation. The aim of the present contribution is to describe a nearly complete hyolithid conch with an entombed enrolled agnostid; this specimen was recently found by the junior author at the Vystrkov Hill near Jince (see FATKA & SZABAD, 2014, outcrop 6 in Fig. 1). The studied sample is housed in the collections of the Czech Geological Survey, Klárov 3, Praha 1, CZ-118 21, Czech Republic under the designation CW 010. FATKA and SZABAD (2011), ZWANZIG and LIEBERMANN (2012) and FATKA and BUDIL (in press) discussed the feeding, storm disturbance and hiding hypotheses.

Geological setting and fossil association

The fossil comes from an extensive quarry in green, fine-grained greywacke with thin lenses of shale of the middle Cambrian Jince Formation was exploited at the north-eastern slope of Vystrkov Hill near Jince (49°46'45.922"N, 13°58'2.379"E) from 1970 to the 90's. Lower levels of the quarried succession exposed deposits of the *Paradoxides* (*Paradoxides*) *paradoxissimus gracilis* Trilobite Biozone (FATKA & SZABAD, 2014). The associated skeletal fauna has been discussed by FATKA *et al.* (2004, 2009), GEYER *et al.* (2008), and FATKA and SZABAD (2014). It consists of abundant trilobites (e.g., *Conocoryphe*, *Paradoxides*, *Ptychoparia*), agnostids (*Peronopsis*, *Hypagnostus* and *Phalagnostus*), echinoderms (e.g., *Akadocrinus*, *Vyscystis*, *Etocte-*

nocystis, *Stromatocysties*), bivalved arthropods (*Tuzoia*, *Liangshanella* and *Konicekion*) and hyolithids (e.g., *Jincelites*, *Buchavalites*) associated with rare brachiopods, gastropod-like molluscs, fossils distantly resembling *Selkirkia* and ichnofossils.

Stratigraphy and palaeoecology

Occurrence of the zonal paradoxid trilobite *Paradoxides* (*P.*) *paradoxissimus gracilis* and the index agnostid *Hypagnostus parvifrons* makes it possible to correlate a part of the Jince Formation exposed at Vystrkov Hill with middle and higher levels of the Baltic *Paradoxides* (*P.*) *paradoxissimus* Biozone (AXHEIMER & AHLBERG, 2003; HØYBERGET & BRUTON, 2008; WEIDNER & NIELSEN, 2013), as well as with the Caesaraugustian Regional Stage in the West Gondwanan chronostratigraphic sequence (see GEYER *et al.*, 2008; GOZALO *et al.*, 2011). These levels correspond to the Drumian Stage of Cambrian Series 3.

Articulated exoskeletons of the tiny agnostid *Peronopsis integra* are abundant in the higher levels of the *Paradoxides* (*Eccaparadoxides*) *pussillus* Biozone and in particular in the *Paradoxides* (*Paradoxides*) *paradoxissimus gracilis* Biozone of the Jince Formation (see ŠNAJDR, 1958; FATKA *et al.*, 2004). Similarly, conchs of the small to middle-sized hyolithid genus *Buchavalites* MAREK, 1975, have been found in the *Paradoxides* (*Paradoxides*) *paradoxissimus gracilis* Trilobite Biozone (because of poor preservation, these hyolithids were classified as *Orthotheca* sp. A by FATKA *et al.*, 2004, tab. 5).

Palaeoecology of agnostids

Some authors provided arguments for a planktonic habit (e.g., ROBISON, 1972, 1975), while others suggested an epifaunal mode of life (PEK, 1977). However, evidence for a benthic mode of life in adult agnostids is accumulating (e.g., JAGO, 1974; MÜLLER & WALOSSEK, 1987; CHATTERTON, 2001; CHATTERTON *et al.*, 2003; FATKA & SZABAD, 2011; ESTEVE & ZAMORA, 2014).

Palaeoecology of hyolithids

DZIK (1981) favoured a pelagic mode of life for hyolithids, but also pelagic, nektic and benthic habits have been suggested (e.g., FISHER, 1962). Many of authors accepted with a vagrant benthic habit (e.g., DUNCAN, 1957; YOCHELSON, 1957, 1961; MAREK & GALLE, 1976; MAREK & YOCHELSON, 1976; VALENT *et al.*, 2011; MARTÍ MUS *et al.*, 2014). Hyolithids have never been considered as infaunal organisms.

Description

All the specimens are preserved in a small slab of fine shale measuring 22 x 19 mm. The rock surface bears 1) a nearly complete hyolithid conch, 2) an isolated cephalic shield of a small specimen of *Peronopsis integra* (CPer at Fig. 1.B), and 3) one ossicle of indeterminable

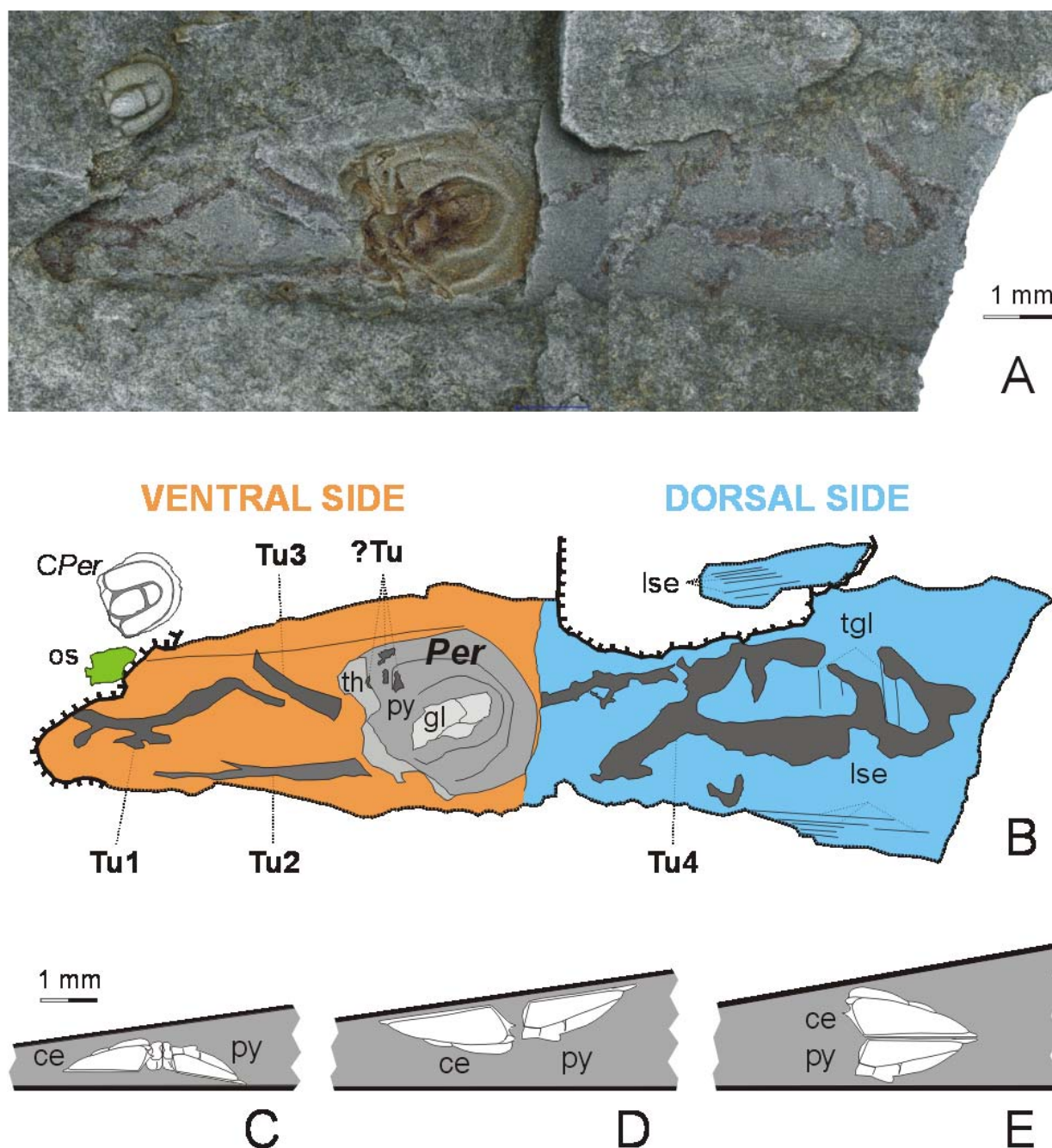


Figure 1: Agnostid inside a hyolithid conch. A – internal mould of conch of ? *Buchavalites* sp. Containing enrolled specimen of *Peronopsis integra* (BEYRICH, 1845), CW 010. Coated by ammonium chloride. B – reconstruction of the conch of ? *Buchavalites* sp. and the specimen of *Peronopsis integra* (BEYRICH, 1845). C – part of conch of *Jincelites vogeli* containing articulated specimen of *Peronopsis integra*, specimen VV 001, modified after FATKA *et al.* (2009, Fig. 3B). D – part of the conch of ? *Buchavalites* sp. containing articulated specimen of *Peronopsis integra*, specimen VV 002, modified after FATKA *et al.* (2009, Fig. 3D). E – part of the conch of ? *Buchavalites* sp. containing articulated specimen of *Peronopsis integra*, specimen CW 010. A, B – dorsal views, C, D, E – lateral views. Tu – feeding tunnels of *Arachnostega*-strategist, ?Tu – irregular holes in right antero-lateral surface of pygidial shield of *Peronopsis integra*, Per – *Peronopsis*, ce – cephalic shield, os – echinoderm plate, gl – glabella, lse – longitudinal sculpture elements, py – pygidial shield, tgl – transverse growth-lines, th – thorax.

echinoderm (os in Fig. 1.B). The preserved part of the hyolithid conch identified as ? *Buchavalites* sp. measures 13.35 mm in length and 3.25 mm in its widest visible part; the apical end of the conch is embedded in the sediment, the apertural part is broken off (Fig. 1.A-B). Estimated length of the complete conch possibly exceeded 23 mm.

Both ventral surface and the visible dorsal surface of the hyolithid conch are slightly compressed but uncrushed. The external surface of the conch is generally smooth; several very fine transverse growth-lines (tgl in Fig. 1.B) and fine narrowly spaced longitudinal sculptural elements (lse in Fig. 1.B) are seen in several areas; no trace of muscle scars is visible.

Within the conch a specimen of *Peronopsis integra* is apparent. The external mould of the agnostid pygidium does not show any traces of crushing or biting on its exoskeletal surface. However, antero-laterally the surface of the pygidial shield bears at least four tiny holes of irregular shape (?*Tu* in Fig. 1.B). The pygidium measures about 2.25 mm in sagittal length and 2.35 mm in maximum width. The axial part of the pygidial shield includes pressed remains of a glabella (*gl* in Fig. 1.B). The external surface of the second thoracic segment (*th* in Fig. 1.B) is preserved at the anterior pygidial margin. The agnostid exoskeleton lies with its pygidial dorsal side directed to the ventrum of the hyolith conch (Fig. 1.E). Tiny remains of the glabella are visible inside the pygidial axis and articulated remains of the second thoracic segment indicates that all these remains belong to a complete enrolled specimen with the dorsal side of the cephalon pointing to the dorsal side of the hyolithid conch (Fig. 1.E). Total length of the articulated prone agnostid is estimated to be about 5 mm.

The generally smooth external surface of the hyolithid conch bears several fine ribbon-like particles of diverse width and length. The presence of three longer ribbon-like elements behind the enrolled agnostid exoskeleton in the very narrow apical portion of the hyolithid conch (*Tu1*, *Tu2* and *Tu3* in Fig. 1.B) excludes the assignment of these particles to agnostid faeces. However, the irregular ribbon-like elements could represent either (1) scattered hyolithid soft parts (e.g., remains of the gut filling), or (2) they could belong to tunnels of a tiny burrow system.

(1) Remains of hyolithid guts have been rarely observed in the early Cambrian of China (LUO *et al.*, 1982), western Nevada (ENGLISH & BABCOCK, 2010) and Canada (BUTTERFIELD, 2003), as well as in the middle Cambrian of the U.S.A. (BABCOCK & ROBISON, 1988) and China (MAO *et al.*, 1992). Recently, DEVAERE *et al.* (2014) summarized all earlier published data on hyolithid guts proving presence of a simple U-shaped tract with straight branches in all hyolithids showing soft-parts.

Diverticulate character combined with diverse width and diagonal course of these elements in the apertural sector of the conch (*Tu1*, *Tu2* and *Tu4* in Fig. 1.B) excludes the interpretation of the ribbon-like particles as hyolithid gut fillings.

(2) FATKA *et al.* (2011, p. 375, Fig. 6) reported a rare occurrence of simple to divergent tunnels (= simply looping or ramifying systems) inside diverse invertebrate skeletons from the Barrandian area, including the middle Cambrian Jince Formation. These tunnels presumably represent early "growth stage" of an organism actively searching for food inside skeletons lying on the seafloor or partly embedded in it. Such tunnelling was proposed for the

Arachnostega-type behaviour (strategy) and is classified as feeding traces of the ichnogenus *Arachnostega* (see BERTLING, 1992; FATKA *et al.*, 2011).

We prefer to ascribe the fine ribbon-like and ramifying tunnels to traces of the *Arachnostega*-type behaviour by an unknown organism (? Errant polychaetes, see BERTLING, 1992, p. 182). The tunnel by burrowing organism fed on decaying soft tissue of the hyolithid; the general arrangement of these tunnels obviously copies the disposition of the gut inside a hyolithid conch (see DEVAERE *et al.*, 2014).

Discussion

Very good, nearly 3D, preservation of the agnostid pygidial shield, associated with parts of the tightly joined second thoracic segment and the remains of the glabella, proves the interpretation that the agnostid is an enrolled carcass rather than a moult. Accordingly, it could be concluded that, when the agnostid entered the hyolithid conch, it was resting on the sea floor. Unfortunately, the incomplete preservation in a very small rock sample makes it impossible to decide if the hyolithid was situated in its usual posture with the ligula resting on the sea floor or upside down. The orientation and disposition of the enrolled agnostid exoskeleton differs from entombed agnostids described earlier (*cf.* Fig. 1.C-E).

Similarly, as in other finds of entombed agnostids and eodiscid trilobites, it is not possible to give the exact reason why *Peronopsis integra* entered the restricted space within the hyolithid conch. However, at least four different hypotheses for an agnostid entering such a specific environment were proposed by CHATTERTON *et al.* (2003) and FATKA *et al.* (2009):

(1) Hiding place. An empty conch provided a hiding place (sheltering) for the small animals during their usual activity;

(2) Disturbance. A hyolithid conch, either with or without the soft tissue, could be an ideal place to survive periods of seafloor disturbance;

(3) Food. A hyolithid conch with decaying soft parts within could provide a well-protected source of food for small benthic scavengers and/or

(4) Moulting in shelter.

(1) Hiding place. Scars attributed to sublethal predation have been only rarely documented in agnostids (BABCOCK, 2003). However, the recently described articulated specimen of *Phalagnostus prantli* with several small scars on the posterior pygidial border (FATKA *et al.*, 2009) documents the presence of potential predators of small benthic animals in the middle Cambrian of the Příbram-Jince Basin (compare HAUG *et al.*, 2012).

Occurrence of potential predators supports the possibility of hiding during usual activity.

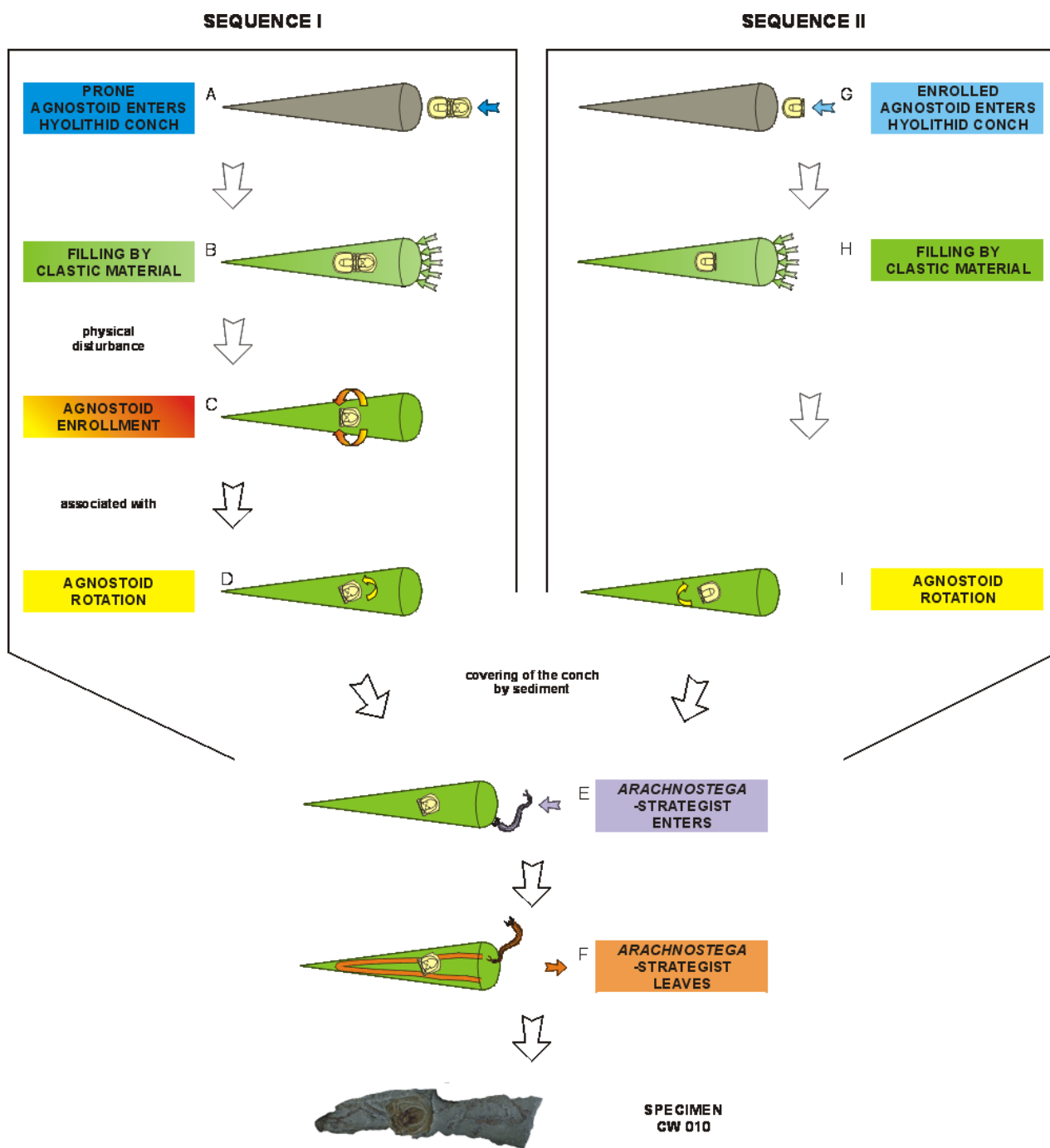


Figure 2: Two simplified sequences leading to possible origin for the association of feeding tunnels produced by *Arachnostega*-strategist and *Peronopsis* inside hyolithid conch.

(2) Disturbance. Entombed specimens of *Peronopsis* supports the earlier speculation that some taxa of small agnostids voluntarily entered empty spaces inside various invertebrate skeletons lying on the bottom (e.g., CHATTERTON *et al.*, 2003; FATKA & SZABAD, 2011). The enrolled attitude of the exoskeleton favours the sea-floor disturbance hypothesis.

(3) Food. Presence of a simply looping to ramifying tunnel system of an *Arachnostega*-strategist proves that the hyolithid conch contained edible soft tissue. The co-occurrence of feeding tunnels and the enrolled agnostid *Peronopsis integra* inside the hyolithid conch makes possible the explanation, that the agnostid was

attracted to feed on the hyolithid carrion inside the conch. Consequently, the hypothesis of a well-protected source of food for small benthic scavengers is suitable.

Four tiny holes visible at the pygidial surface (?Tu in Fig. 1.B) imply that when the producer of the feeding tunnels entered the hyolithid conch, the enrolled agnostid had already been entombed inside this restricted space.

Based on the above discussion, the origin of the described association of the tunnel system of *Arachnostega*-strategist and *Peronopsis* inside a hyolithid could be explained by the following two sequences:

Sequence I

- the agnostid in prone attitude entered the restricted space inside the hyolithid conch lying on the sea bottom to feed or to hide, or both (A in Fig. 2),
- the conch with the entombed prone agnostid was partly and/or completely filled by clastic material (B in Fig. 2). Possibly due to physical disturbance, the conch was partly or completely embedded (C in Fig. 2). This explains the enrollment and the slightly rotated orientation of the agnostid exoskeleton as a protective reaction, which was associated with a slight rotation of the enrolled agnostid (D in Fig. 2),
- Archnostega*-strategist entered the partly to fully embedded conch to feed on soft parts of the hyolithid or agnostid carcasses, or on both (E in Fig. 2),

- the tunnel burrowing organism feeding on soft tissue of the hyolithid carrion possibly used the hyolithid gut to burrow easily through the hyolithid conch (F in Fig. 2).

Sequence II

- agnostid in enrolled attitude entered the restricted space inside the hyolithid conch lying on the sea bottom to feed or to hide or both (G in Fig. 2),
- the conch with entombed agnostid in enrolled attitude was partly and/or completely filled by clastic material (G in Fig. 2),
- agnostid slightly rotated due to partial or complete embedding of the conch (G in Fig. 2).

The rest of this sequence is the same as in the sequence I.

Specimen	Entombed species	Entombed inside	Length of conch	Max width of conch / tube	Width of conch / tube in the place with entombed specimen	Width of entombed specimen	Width of entombed specimen / width of conch or tube
VV 001A, B	<i>Peronopsis integra</i>	Hyolithid conch (<i>Jinzelites</i>)	16 mm	3.9 mm	2.05-3.00 mm	1.65 mm	55-80 %
VV 002A, B	<i>Peronopsis integra</i>	Hyolithid conch (<i>Buchavalites</i>)	23 mm	5.5 mm	1.85-2.05 mm	1.65 mm	80-89 %
CW 010	<i>Peronopsis integra</i>	Hyolithid conch (? <i>Buchavalites</i>)	> 23 mm	> 3.3 mm	2.6 mm	2.3 mm	88 %
ROM 543455	<i>Ptychagnostus preacurrens</i>	Priapulid tube (<i>Selkirkia</i>)	32.9 mm	6.0 mm	5.0-5.3 mm	3.9 mm	76 %
ROM 54344	<i>Pagetia bootes</i>	Priapulid tube (<i>Selkirkia</i>)	> 29 mm	5.7 mm	5.5 mm	?	-
					4.3 mm	3.4 mm	79 %
					3.7 mm	2.8 mm	76 %
ROM 54346	<i>Pagetia bootes</i>	Priapulid tube (<i>Selkirkia</i>)	> 24 mm	5.7 mm	4.4-4.8 mm	2.8 mm	61 %

Table 1: Dimensions of entombed agnostids, eodiscid trilobites, hyolithid conchs and tubes of priapulid worm.

Earlier described entombed specimens of the eodiscid trilobite *Pagetia bootes* as well as the agnostid *Ptychagnostus preacurrens* and *Peronopsis integra* supposedly entered the restricted space inside priapulid worms and hyolithid conchs on its own as part of their normal behaviour (CHATTERTON *et al.*, 2003; FATKA *et al.*, 2009). The width of entombed eodiscid trilobites and agnostids ranges from 1.65 to 3.9 mm and reaches 55-89 % of width of the priapulid tube and hyolithid conch in the place of entombment (Table 1). Width of the *Peronopsis integra* described here fits with the earlier observed range, as it reaches 89 % of the hyolithid width in the place of entombment.

Conclusions

An enrolled agnostid specimen preserved inside a hyolithid conch represents a new type of entombment. The enrolled attitude of this agnostid *Peronopsis* prioritizes the seafloor disturbance hypothesis for explanation of entombment of this specimen. This fits well with the earlier observations that some taxa of small agnostids voluntarily entered empty spaces inside various invertebrate skeletons lying on the bottom (*e.g.*, CHATTERTON *et al.*, 2003; FATKA &

SZABAD, 2011).

The described association of feeding tunnels produced by an *Archnostega*-strategist and *Peronopsis* inside of a hyolithid conch is designated as a case of "frozen" behaviour *sensu* BOUCOT (1990) and BOUCOT and POINAR (2010).

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