

THE MIDDLE ORDOVICIAN TERGOMYAN MOLLUSC PYGMAEOCONUS: AN OBLIGATORY EPIBIONT ON HYOLITHIDS

RADVAN J. HORNÝ

Department of Palaeontology, National Museum, Prague, Czech Republic; e-mail: radvan.horny@nm.cz



Horný, R. J. (2006): The Middle Ordovician tergomyan mollusc *Pygmaeoconus*: an obligatory epibiont on hyolithids. – Acta Mus. Nat. Pragae, Ser. B, Hist. Nat., 62 (1–2): 81–95. Praha. ISSN 0036-5343.

Abstract. The Middle Ordovician *Pygmaeoconus porrectus* (BARRANDE in PERNER, 1903) is described as the first known molluscan obligatory epibiont on hyolithids. Its biology is similar to that of the coral *Hyostragulum* and some trepostome bryozoans described by Galle and Parsley (2005). The antero-posterior axis of its cap-shaped shell in the life position was aligned with the longitudinal axis of the hyolithid conch, faced with the anterior side against the current for food and oxygen. Internal moulds bear three to four periodically repeating circular sets of six pairs of discrete pedal muscle scars that relocated by saltation and a pair of cephalic scars. *Pygmaeoconus* is considered a tergomyan mollusc of the family Kirengellidae, subfamily Pygmaeoconinae subfam. n.

■ Mollusca, Hyolithida, Tergomya, Pygmaeoconinae subfam. n., *Pygmaeoconus*, muscle scars, obligatory epibiont, Ordovician.

Received January 30, 2006

Introduction

During the past ten years, three important hyolithid papers appeared devoted to functional morphology (Marek, Parsley, and Galle 1997), hyolithid epibionts (Galle and Parsley 2005), and functional implications of their morphology (Martí Mus and Bergström 2005). A unique find of a specimen of *Pygmaeoconus porrectus* attached to the dorsum of a hyolithid conch contributes to the research of hyolithids and confirms the previous consideration and study.

Pygmaeoconus porrectus (BARRANDE in PERNER, 1903) is a small, cap-shaped Middle Ordovician mollusc relatively common in the Šárka Formation (Darrivillian) and rarely occurring in the Dobrotivá Formation (Dobrotivian) of Bohemia and Spain. The species was distinguished by Barrande (MS) and described and published by Perner (1903, 1911) as *Palaeacmaea porrecta* BARRANDE in PERNER, 1903. Based on this species, Horný (1961) established the new genus *Pygmaeoconus*, originally interpreted as a member of the monoplacophoran family Hypseloconidae KNIGHT, 1956. In his monograph on Czech Lower Palaeozoic Monoplacophora and Patellid Gastropoda (1963), Horný assigned to *Pygmaeoconus*, although tentatively, also the species *Palaeacmaea kettneri* ŘÍHA, 1938. A related species, *Pygmaeoconus gnomicus*, was described from the Middle Ordovician of Spain by Gutiérrez-Marco and Martín-Sánchez (1983). Yochelson (1977) reported *Pygmaeoconus*, albeit with a question, from the Upper Ordovician of Norway (?*Pygmaeoconus compressus* [KOKEN, 1925]). In 1997 Horný distinguished an Upper Ordovician (Berounian) species *Pygmaeoconus krafti* sp. n., locating it, together with the genus *Kornoutella* gen. n., in the family ?Protoconchioididae GEYER, 1994, questionably within the class ?Gastropoda. In the 2002 Catalogue, Horný listed *Pygmaeoconus* as a gastropod within the family ?Archina-cellidae KNIGHT, 1956 or ?Protoconchioididae, containing

P. porrectus, *P. kettneri*, *P. krafti*, and ?*P. latiusculus* (BARRANDE in PERNER, 1903).

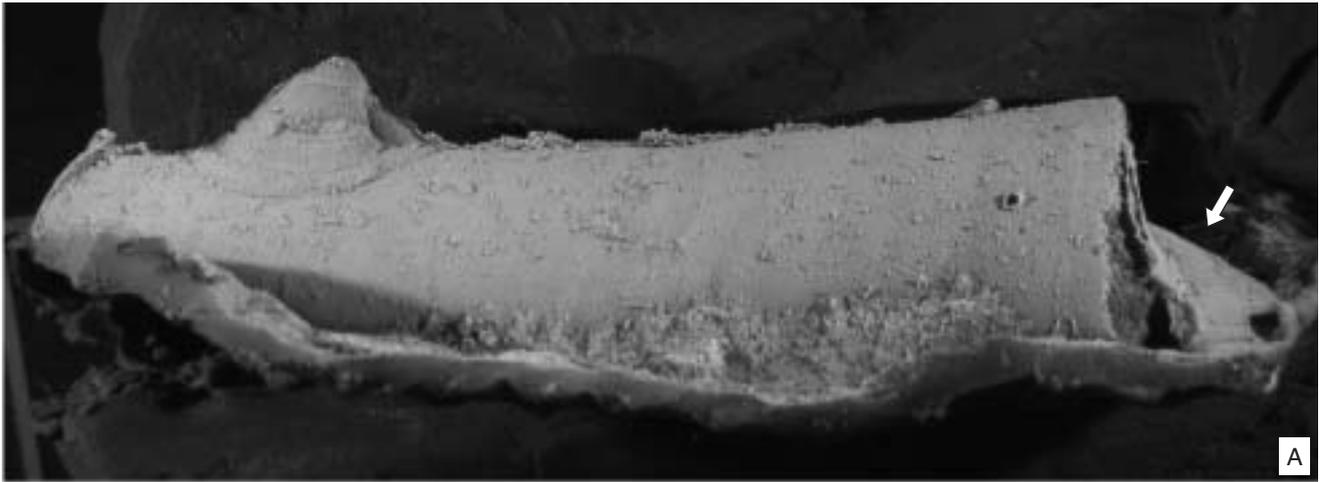
The unique find of a specimen of *P. porrectus* attached to a hyolithid conch comes from the collection of František Hanuš, part of which is deposited in the Department of Palaeontology, National Museum, Prague. It was found at Praha-Šárka at the beginning of the 20th century. Thanks to Hanuš's extraordinary thoroughness and knowledge, the counterpart of the hyolithid was preserved, which enabled the present investigation.

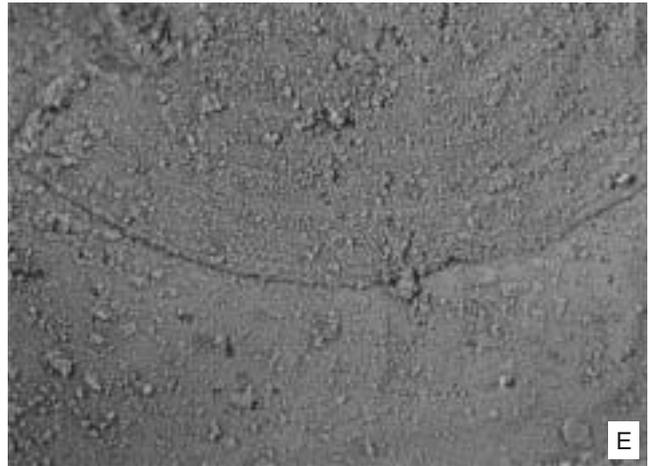
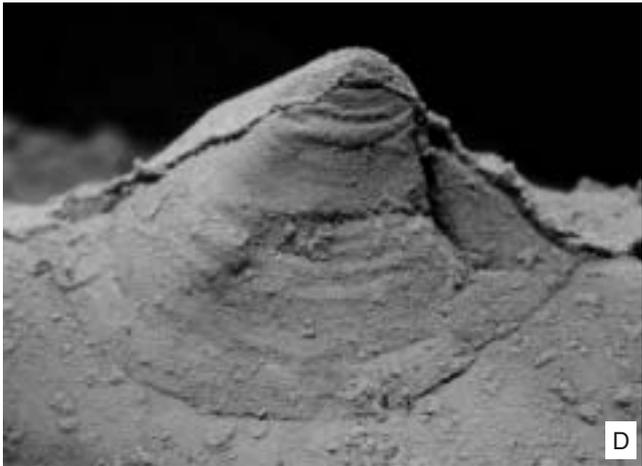
In accordance with the present study, the genus *Pygmaeoconus* is regarded a cyclomyan mollusc, comprising two species in the Ordovician of Bohemia: the Llanvirnian to Dobrotivian *Pygmaeoconus porrectus* and the Berounian *P. krafti*. *P. ? latiusculus* and *P. kettneri* are considered synonymous, representing another, unrelated genus.

Only Bohemian representatives of the species *P. porrectus* were studied for the purpose of this paper. Most of them are deposited in the Museum of Dr. B. Horák at Rokycany (localities Rokycany, Osek, Díly, and Mýto, abbreviation MBHR) and in the National Museum, Prague (localities Osek, Díly, Mýto, Praha-Šárka, abbreviation NM L). Specimens at Rokycany were mostly collected by Jaroslav and Petr Kraft; the majority of those housed in Prague come from the collections of Joachim Barrande, František Hanuš, and Celda Klouček.

Material and methods

All collected specimens (over 120) have been preserved in hard siliceous (probably originally carbonatic) concretions, derived from clayey shales and weathered during the late Cenozoic. Concretions contain taphocoenoses of abundant and often fragmentary benthic fauna. Specimens of *P. porrectus* are mostly preserved as internal moulds, occasionally contained in taphocoenoses between various fossils





Text-fig. 1. *Pygmaeoconus porrectus*, an adult specimen NM L 31987 in life position, attached to the dorsum of a conch of the hyolith *Elegantilites* cf. *euglyphus*; revultex impression. A – right side, $\times 4.8$; B – left side, C – dorsal side with a longitudinal postdiagenetic crack partly filled with revultex, running through the hyolith conch, both $\times 5$. Note the operculum (arrowed), only slightly shifted from its life position. D – right side showing irregular increments and a tight contact with the surface of the hyolith conch. The anterior (right) side is damaged by a crack, $\times 9$. The surface of both the host and the mollusc is slightly weathered and therefore does not show minor details. E – enlarged left anterolateral apertural margin, showing a tight contact with the surface of the hyolith conch, $\times 30$. Dobrotivá Formation, Praha-Šárka, field near the villa. Length of the specimen of *Pygmaeoconus* 7.3 mm.

on the surface of splitted concretions. Only one unique find of a shell attached to a hyolithid conch (*Elegantilites* cf. *euglyphus* [BARRANDE, 1867]) exists (Text-fig. 1), either because the shell fell away after the death, or remained in matrix when the host was collected. Two samples show the shell of *Pygmaeoconus porrectus*, probably coincidentally, in a close proximity to a hyolithid conch *Pauxillites* cf. *pauillus* (NOVÁK, 1891) (Text-figs 2, 3). External surface is observable in counterparts only rarely, being usually neglected by older collectors. The wide space between the internal mould and outer shell surface is either empty or partly filled with soft or dusty limonite; original shell was not observed. These residua were removed by ultrasound and external moulds showing outer shell sculpture were studied on revultex impressions. Photographs of specimens whitened with ammonium chloride sublimate were taken by the Olympus Digital Camera DP 70.

Shell

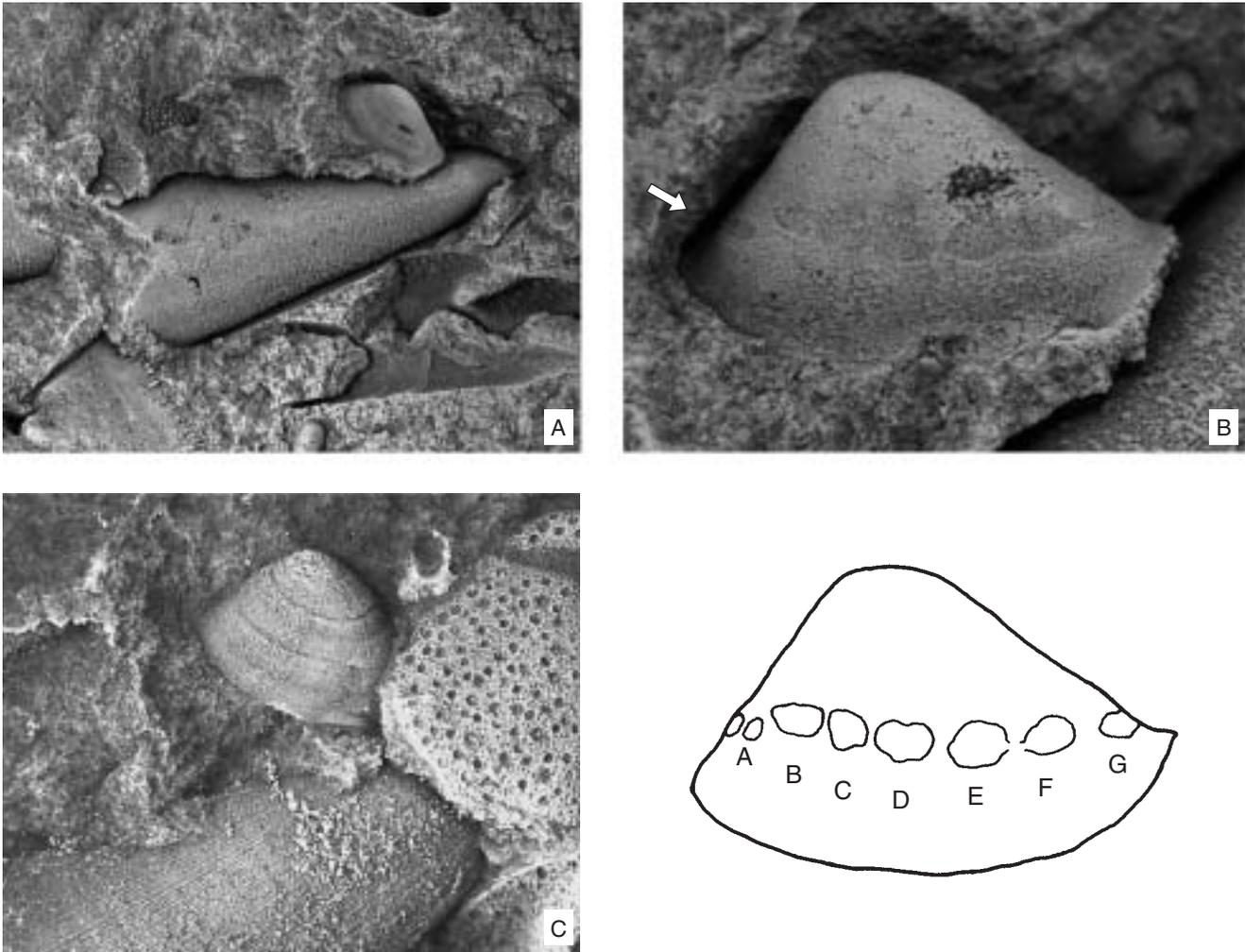
Shell is cap-shaped, rather variable in shape; the variability concerns mutual relationships of height, width, length, and sculpture of the shell surface. The length-width ratio varies between 1.2 and 2.4, as the consequence of sessile life on a more or less limited space of the host surface. (A large variability of width-length ratio was observed by Horný (2005b) in the tryblidiid *Drahomira glaseri* (BARRANDE in PERNER, 1903) that lived on shells of dead orthocones.) The youngest and smallest specimens observed are 1.3 mm long (Text-fig. 4), the oldest and largest 7.5 mm long (Text-fig. 15). The size probably depends on import of nutrients and available space and does not correspond to age; the

largest specimens are not necessarily the oldest. Width of largest specimens varies between 3.0 and 6.3 mm.

The larval shell is hemispherical, with circular aperture, 0.4 mm across (Text-fig. 7B). After settling on the hyolith dorsum, the shell started to increase in one direction, interpreted as posterior (towards the apical part of the host conch). After finishing the growth of the juvenile shell, and obviously after a short period of reduced rate of shell secretion, the shell again began to increase regularly around the whole aperture (Text-figs 9, 17). Two specimens show subsequent rectification of the antero-posterior axis of the adult shell *versus* the axis of the protoconch in the event that the larva settled in a wrong, slightly shifted position (Text-fig. 10). In adult shell, the side interpreted as anterior is always shorter than the posterior one, either more arched or rarely even slightly concave, in such cases with minutely overhanging anterior margin of the juvenile part. The posterior side is usually longer, narrower and less arched; specimens with subcentral apex are rare (Text-fig. 3). The lateral sides are quite steep, variably arched, often to various degree asymmetric (Text-fig. 11).

Shell wall of adults, compared with contemporary epibenthic molluscs of similar size, is strikingly thick, reaching 0.4 mm and being secondarily thickened also in the initial parts of the shell (up to 0.5 mm) (Text-figs 12, 18). Shell wall gradually becomes thin towards the apertural margin, which is sharp and in some specimens more or less flaring. The shell thickness is apparently related to the requirement of a firm anchorage of muscle attachments.

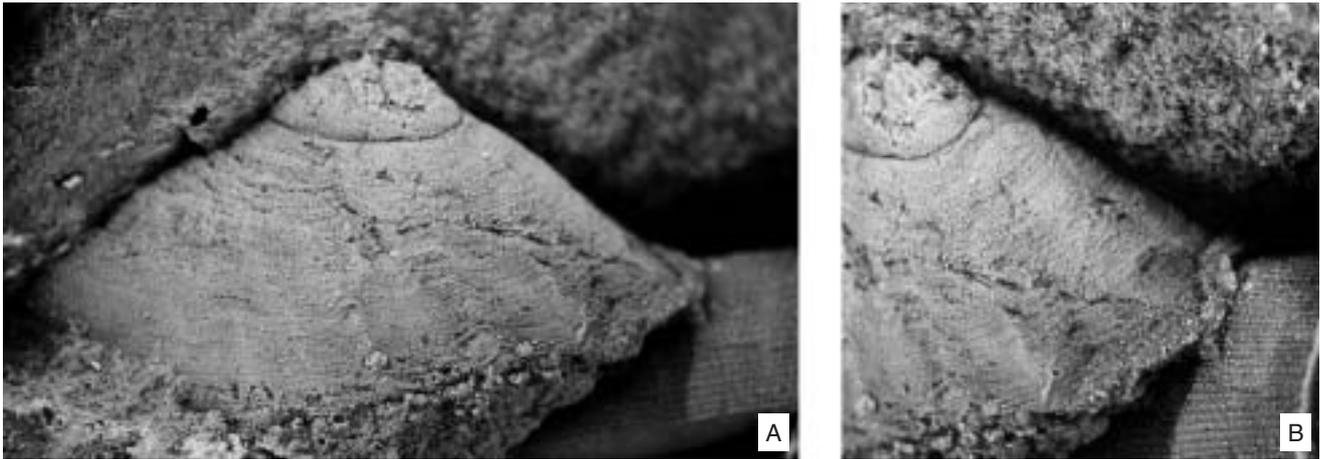
Internal shell surface. The internal shell surface, observable on internal moulds of adult specimens, bears three sets (rarely four in gerontic specimens; Text-fig. 15) of strong muscle scars parallel to the apertural margin. Each



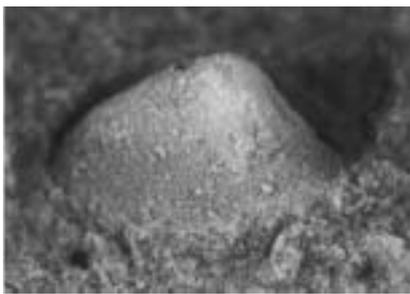
Text-fig. 2. *Pygmaeoconus porrectus*, specimen MBHR 17783a located, perhaps by coincidence, near the conch of *Pauxillites* cf. *pauxillus*; left side. Situation may be also interpreted as early after the death when the anterior part of the shell was probably lifted up from the hyolithid dorsum. **A** – internal mould in a taphocoenose with hyolithids, brachiopods, and trilobites, $\times 5.6$; **B** – enlarged specimen, left side, with partly coalesced scars of pedal retractors and visible cephalic scars (arrowed), $\times 21$; **C** – revulterx impression showing the external surface of the shell with two growth pauses. The posterior part is partially covered by a fragment of a trilobite *Placoparia cambriensis* HICKS, 1875, $\times 10$. The line drawing shows cephalic and pedal muscle scars. Šárka Formation, Osek near Rokycany. Length of the specimen 3.2 mm.

set consists of six pedal retractor scars (B–G), five of them of similar shape and size on each lateral side. The best preserved scars show increments near their adapical margin (Text-fig. 13). The two posterolateral pairs (E, F) consist of discrete, usually irregularly rounded or squared, rarely irregularly coalescent scars (Text-figs 13, 14), the largest 0.4–0.5 mm (sag.) across. The three anterolateral pairs (B–D) contain similar scars but often more or less coalesced (Text-figs 12, 13, 14). The scars of the posterior pair (G) are smaller and may be fused (Text-figs 13, 15). The anterior cephalic scars (A) lie in the frontal gap between the scars of the first pair of the pedal retractors. They probably leave continuous traces through the ontogeny, and are separated by a thin, long, narrow, median ridge. Their active parts are slightly raised and relative to the pedal retractors

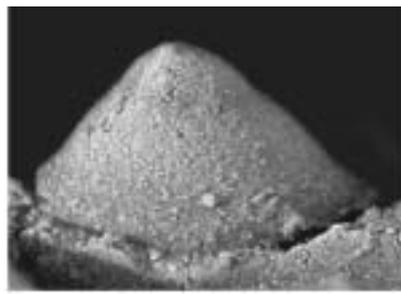
shifted closer to the apertural margin. These cephalic scars have been observed in three specimens (Text-figs 2, 13, 14); however their rather small dimensions and coarse preservation do not allow a detailed study. The abandoned sets with smaller scars are gradually more or less healed with hypostracum. The slightly irregular radial rows of scars are perpendicular (anterolateral) or oblique (posterolateral) to the apertural margin (Text-fig. 15). The growth of muscle attachments was not continuous in the adapertural direction. The attachments clearly migrated by saltation during the ontogeny. These periodically repeated changes strongly influenced the shape of the shell and the arrangement of external growth structures. A remarkable and peculiar character of the pedal muscle scars is that they are not raised above the surface of the internal mould but depressed to a various ex-



Text-fig. 3. *Pygmaeoconus porrectus*, specimen NM L 31981 with subcentral apex, revultex impression with anomalous outer shell sculpture. While the first growth pause is well visible, the remaining intervals of reduced rate of shell secretion are not observable. The surface bears irregular wavy structures. The shell lies close to a conch of a hyolith *Pauxillites cf. pauxillus*. A – left side, B – posterolateral view, both $\times 14.5$. Šárka Formation, Praha-Šárka, the brick-yard. Length of the specimen 6.0 mm.



Text-fig. 4. *Pygmaeoconus porrectus*, specimen NM L 38672, internal mould, right side, $\times 30$; Šárka Formation, Osek near Rokycany. The smallest observed specimen, length 1.3 mm.



Text-fig. 5. *Pygmaeoconus porrectus*, specimen NM L 08269, internal mould; left side, $\times 21$. Paralectotype of Perner 1903. Šárka Formation, Osek near Rokycany. Length 2.1 mm.

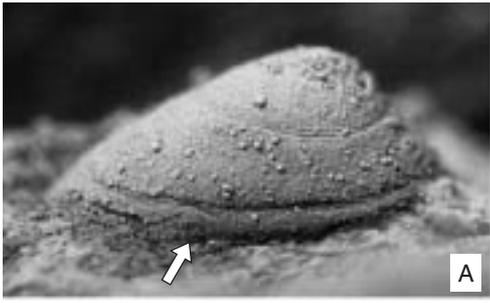


Text-fig. 6. *Pygmaeoconus porrectus*, specimen MBHR 12881, internal mould, right side, $\times 20$; Šárka Formation, Dily near Rokycany. Length 2.3 mm.

tent. The reason for this may be that the muscles transferred to the area of new shell where basal pads of myostracum originated below the attachments. These raised structures may have been more resistant to the *post mortem* diagenetic processes, when the surrounding inner shell surface was to some extent dissolved. Only two specimens have been observed showing flat or slightly raised scars (Text-figs 9, 12). Similar depressed scars were figured by Yochelson (1958) in *Proplina cornutaformis* (WALCOTT, 1879), and figured and discussed by Horný (1991b) in a specimen of *Sinuitopsis neglecta* (BARRANDE in PERNER, 1903) and Horný (2005a) in *Kosovina peeli* HORNÝ, 2005. Geyer (1994) noted that certain hypseloconids also show depressed scars on internal moulds – *?Protoconchioides rasettii* GEYER, 1994, *Kirengella ayaktchica* ROZOV, 1968, and *Lenaella*

octobinaria BJALYI, 1973. However, it should be mentioned that many specimens of *Pygmaeoconus porrectus* show rather poor scars or no scars. The surface of internal moulds is otherwise smooth, rarely with weak and unclear, sparse irregular radial striae (Text-fig. 8).

External shell surface. Outer shell sculpture, previously also unknown, consists of dense (about 20 *per* mm), slightly irregular growth lines the shape of which may have resulted from interaction of the epibiont apertural margin with the host periostracum. In the majority of cases, the growth of this regular microsculpture is periodically interrupted by a short interval of reduced rate of shell secretion manifesting itself by dense increments in a groove around the shell. In specimen MBHR 14464 an irregular stronger flaring brim appears prior to each groove in the anterior and anterolateral



Text-fig. 7. *Pygmaeoconus porrectus*, specimen MBHR 17783b, revultex impression. A – right lateral side with two growth pauses; note the small wave-like irregularity near the apertural margin (arrowed), ×30. B – apical view with mostly exfoliated larval shell, ×30. Šárka Formation, Osek near Rokycany. Length of the specimen 1.7 mm.



Text-fig. 8. *Pygmaeoconus porrectus*, specimen MBHR 13473, posterior side of a revultex impression with three growth pauses, ×26. Note the weak, irregular radial structures. Šárka Formation, Osek near Rokycany. Height of the specimen 2.5 mm.

ral regions (Text-fig. 14). The brim and the consequential segment of dense increments forming a groove characterize the period of transfer of the muscle insertions. This situation (mostly without a brim) repeated always after a period of growth of regular increments (Text-figs 14, 18) when a new, functional set of muscle insertions originated, usually three to four times during the ontogeny.

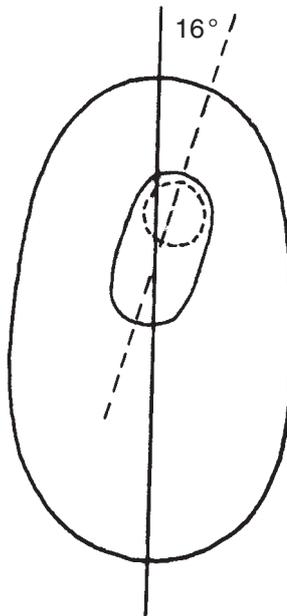
Aperture. The apertural margin is exceedingly thin, adapted to a close contact with the hyolith conch, without emarginations (Text-fig. 1). It is non-planar, with the anterior and posterior parts slightly bent upwards so that the shell resembles a cradle. This specific shape is the most important evidence of epibiotic mode of life on hyolithids in all specimens. It enabled the animal an effective clamping on the hyolithid dorsum, but precluded life on planar, irregular or soft objects. However the degree of curvature is variable, due to various species of hyolithids, their age and the distance of location of the epibiont on the hyolithid conch. Some specimens show a flaring margin; this was also advantageous for the joint with the hyolithid dorsal surface. The apertural margin shows no signs of breakages with an exception of small irregularities or “cross-bedded” structures (Text-figs 17, 18). These wavy or v-shaped structures with rounded centre may have originated when the shell margin grew around small objects adhering to the host periostracum (Text-figs 3, 7, 18). This observation could also contribute to the concept of a sedentary habit of *Pygmaeoconus*.

Mode of life

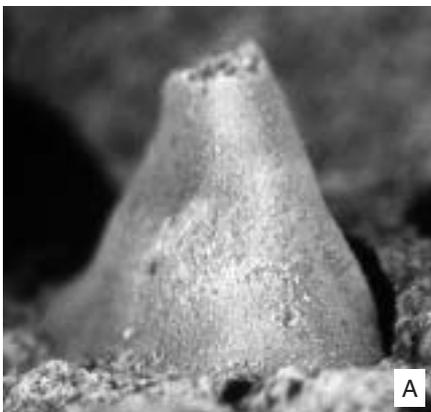
As stated by Havlíček and Vaněk (1990) and especially by Havlíček et al. (1994), the Šárka Formation contains a richly diversified benthic fauna, confined to localities that surround the median graben-like depression of the Pragian basin. This fauna belongs to the *Euorthisina-Placoparia* Community in about B A 3–4 life positions in Boucot’s classification (1975). Most characteristic are trilobites, ostracods, brachiopods, hyolithids, gastropods, cyclomyans, bivalves, calcichordates, graptolites and others. Brachiopods and bivalves are often found with both valves *in situ*. According to Galle and Parsley (2005), hyolithids were the preferred hosts of epibionts, and this feature might have evolved in mutualistic relation to them. The *Pygmaeoconus* larva settled on the hyolithid dorsum, probably attracted by the chemical composition of the host periostracum, similar to larvae of trepostome bryozoans and tabulate corals *Hyostragulum* (Galle and Parsley 2005). An important reason may have been also the stability of the hyolithid conch above the bottom, provided by the pair of helens. The position of the shell of *Pygmaeoconus* approved the longitudinal axis of hyolithid conch, faced against current for food and oxygen (Marek and Galle 1976). The site of settlement was probably not so important as in bryozoan and coral larvae that settled consistently on the juvenile portion of the hyolithid conch. After settling, its shell began to grow in the posterior direction, forming an elongate juvenile shell. After a short period characterized by a reduced rate of growth, the teleoconch began to grow regularly around the apertural margin.



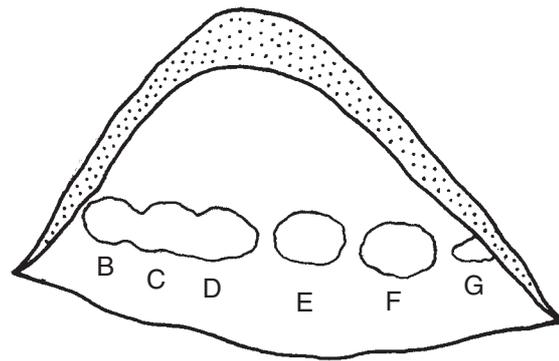
Text-fig. 9. *Pygmaeoconus porrectus*, the lectotype NM L 29379, internal mould. A – right lateral view with weak, flat muscle scars, $\times 16.7$; B – apical view showing the juvenile shell parallel with the teleoconch, narrowed posteriorly, both $\times 16.7$. Šárka Formation, Osek near Rokycany. Length of the specimen 4.5 mm.



Text-fig. 10. *Pygmaeoconus porrectus*, an immature specimen NM L 33503, internal mould, apical view. The initial shell is slightly shifted owing to the antero-posterior axis of the teleoconch and the axis of the hyolith. However this deflection was rectified during the first growth pause. A schematic drawing shows the angle of rectification. Šárka Formation, Osek near Rokycany. Length of the specimen 3.3 mm.



Text-fig. 11. *Pygmaeoconus porrectus*, specimen NM L 05858, internal mould with broken off apex. The specimen is narrow and deformed during growth. A – left lateral view with weak muscle scars, B – posterior view, C – latero-posterior view, all $\times 15$. Šárka Formation, Osek near Rokycany. Length of the specimen 4.2 mm.



Text-fig. 12. *Pygmaeoconus porrectus*, specimen NM L 05877, internal mould, left side. Muscle scars of the third set are irregularly coalesced, flat, bordered with a slightly raised margin. The first and second sets are weak, located in shallow depressions (arrowed). Note the empty space indicating the shell thickness reaching 0.4 mm in this specimen. The line drawing shows shape of the pedal retractor scars. Šárka Formation, Osek near Rokycany. Length of the specimen 6.0 mm.

In case that the antero-posterior axis of the juvenile shell was not parallel to the longitudinal axis of the host, the early stages of the teleoconch rectified the position of the shell to be aligned with its longitudinal axis (Text-fig. 10). Position of *Pygmaeoconus* facing the current and thus accordant to the living position of the host is particularly important for the shell orientation and therefore its systematic position. Apart from this, the living position of *Pygmaeoconus* on the hyolithid dorsum brings an additional argument against the supposed “upside down” position in the Cambrian hyolithid *Guduguwan* KRUSE, 1996 (see Kruse 1996).

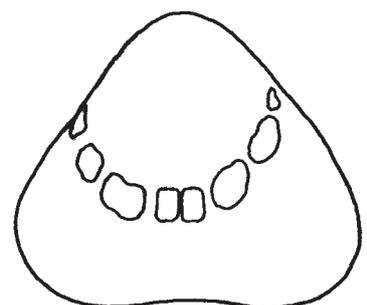
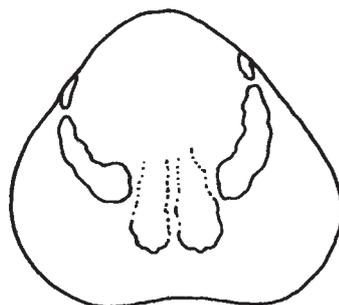
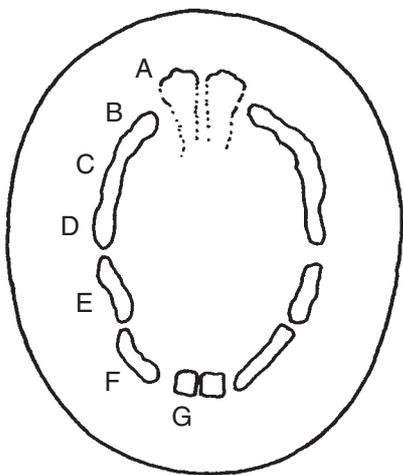
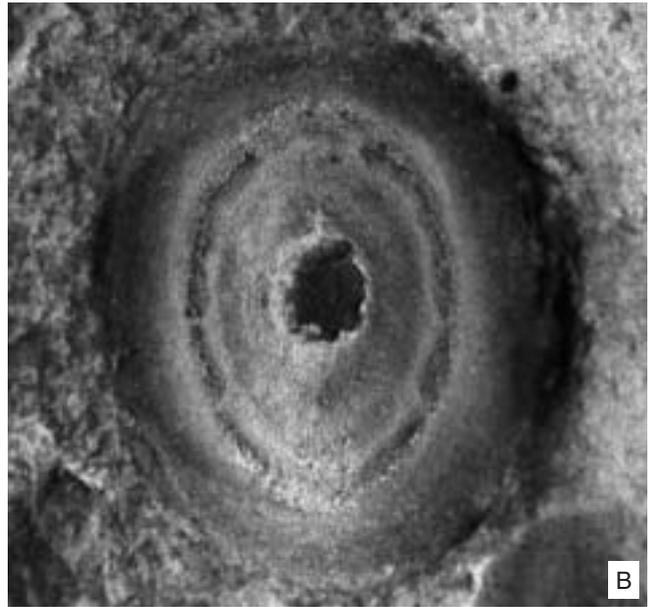
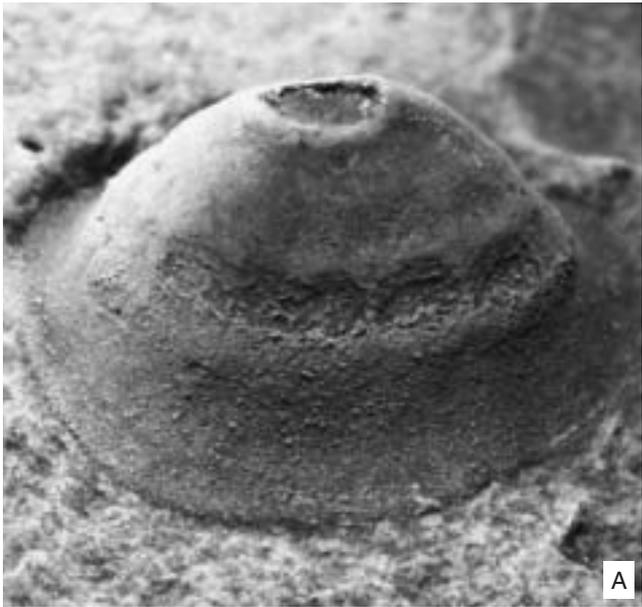
The early teleoconch possessed a set of pedal muscles, disposed parallel to the apertural margin. The first (earliest) set developed early after the beginning of growth of the teleoconch and probably had an identical number of muscle insertions like the sets in adult age (six + 1 on each side). Muscle attachments and slightly widened apertural margin were the precondition to survive the post-settlement mortality. Despite that, the analysis shows that the highest post-settlement mortality took place when the juveniles reached 1.8 mm length, i. e. probably during the first transfer of muscle attachments. Each saltation was accompanied by retardation of growth, perhaps due to the reinforcement of shell and generation of basal muscle pads. Compared with other contemporary molluscs, *Pygmaeoconus porrectus* produced relatively thick and heavy shell, no doubt as a re-

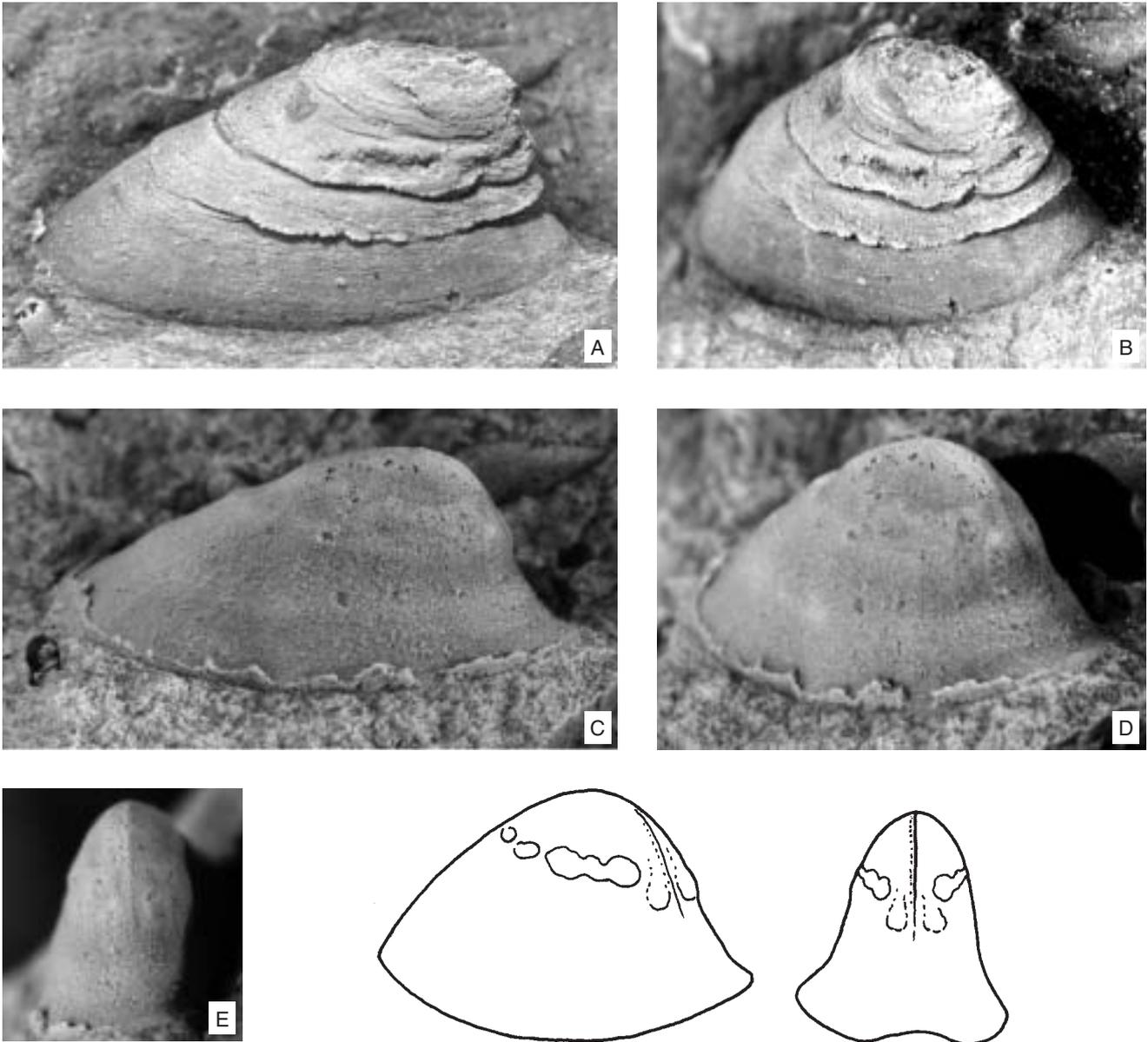
ason for safer position on the exposed hyolithid dorsum. Its weight may have been favourable for the host (see Galle and Parsley 2005). A thin apertural margin copying the arched surface enabled tight contact with the host periostracum all around the shell aperture during various disturbances (storm, attack of predators etc.)

The wide-ranging large shell variability, concerning particularly width/length ratio, is predisposed by the shape of the hyolithid conch. *Pygmaeoconus* probably inhabited variably big and variably wide hyolithid species present in the Šárka and Dobrotivá Formations sea (e.g. *Elegantilites* cf. *euglyphus*), and may have settled on variably old parts of the dorsum. A question is whether it was able to move along the hyolithid conch. However the discrete pedal muscles certainly provided a variable lifting of the shell aperture necessary for water flow through the pallial cavity.

According to the shell morphology, *Pygmaeoconus porrectus* is suspected to have been an obligatory epibiont of hyolithids. No evidence has been uncovered that would indicate a benefit to the host from the epibiont’s presence, but such benefits cannot be ruled out. For instance, it is possible that the epibiont’s weight helped the host to anchor itself more securely (see also Galle and Parsley 2005). *Pygmaeoconus* was a filtrator dependent on oxygen and nutrients, which came from transport by currents, and probably also from disturbed sediments lifted into suspension by feeding

Text-fig. 13. *Pygmaeoconus porrectus*, specimen NM L 31982, internal mould. A – left apico-lateral view with partly coalesced muscle scars of presumed third muscle scar set, $\times 19$. The apical “crater” originated by weathering of partly limonitic matrix. B – apical view showing the oval muscle scar set, apparently interrupted in the anterior part. Individual muscle scars seem to be elongate but this is due to a steep slope of the shell; $\times 17$. C – anterior view with two visible cephalic scars and a low, thin median ridge, running from the apex; $\times 20$. D – posterior side with two smaller, probably coalesced posterior scars, $\times 20$. The line drawings show apical, frontal and posterior views of muscle scars. Šárka Formation, Osek near Rokycany. Length of the specimen 4.1 mm.

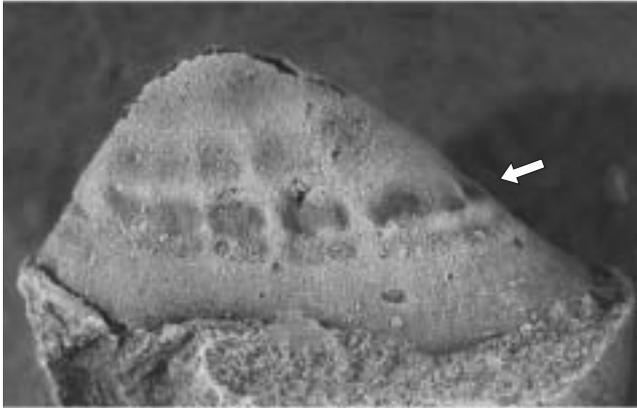




Text-fig. 14. *Pygmaeoconus porrectus*, specimen MBHR 14464; A – right side of a revultex impression demonstrating three growth pauses with preceding brim-like explanations, strongly developed in the anterior and antero-lateral sides but lacking in the posterior one, $\times 13$. B – oblique right anterior view of the revultex impression showing strong brim-like explanations, $\times 13$. C – internal mould, right side, with weak second muscle scar set, $\times 13$; D – internal mould, oblique right latero-anterior view showing a pair of cephalic scars, divided by a narrow ridge, $\times 13$. E – anterior view with a pair of cephalic scars and the median ridge, $\times 13$. The line drawings show right latero-anterior and frontal views of muscle scars. Šárka Formation, Rokycany 2, near the cemetery. Length of the specimen 6.0 mm.

activity of the host (Text-fig. 20). Similar mode of life is expected for the Caradocian (Berounian) species *P. krafti*, which may have lived with bigger hyolithids of the Zahořany Formation, like *Elegantilites elegans* (BARRANDE, 1867). The cradle-like shape of the shell, its thickness, stationary habit, muscle scar pattern, and mode of feeding show that its morphological features were irreversible. The

loss of the host, either by its death or by some accident must have been lethal for the epibiont. Similarly, the survival of larvae unable to locate a hyolithid host is quite improbable. Shells of *Pygmaeoconus porrectus* have not been found in close proximity to various large fragments (e.g. of trilobites), which could have served as a firm substratum for this mollusc.



Text-fig. 15. *Pygmaeoconus porrectus*, specimen NM L 37924, internal mould, left side. Deep, discrete muscle scars of the third muscle set, and weakly marked, incomplete scars of the fourth set. Slightly elongate scars are arranged in radial rows and their number is probably constant in each set. Note the two small posterior scars (arrowed). $\times 10$. Šárka Formation, Mýto near Rokycany. Length of the specimen 7.5 mm.



Text-fig. 16. *Pygmaeoconus porrectus*, specimen MBHR 12488, left side of an internal mould. Two sets of muscle scars (the second and third) are separated by a continuous, rounded "terrace" ridge. The first set was mostly healed with hypostracum (the low depression). $\times 19$. Šárka Formation, Osek near Rokycany. Length of the specimen 3.8 mm.



Text-fig. 17. *Pygmaeoconus porrectus*, specimen MBHR 12123, revultex impression of external surface. A – left side, showing a regularly developed shell surface with four narrow growth pauses; the third one shows wavy disconformities, $\times 13$. B – postero-apical view showing the early stages of shell and a groove separating the juvenile shell from the teleoconch, $\times 15$; C – the same, enlarged apical part showing damaged larval shell, $\times 30$. Šárka Formation, Mýto near Rokycany. Length of the specimen 5.0 mm.

Systematic palaeontology

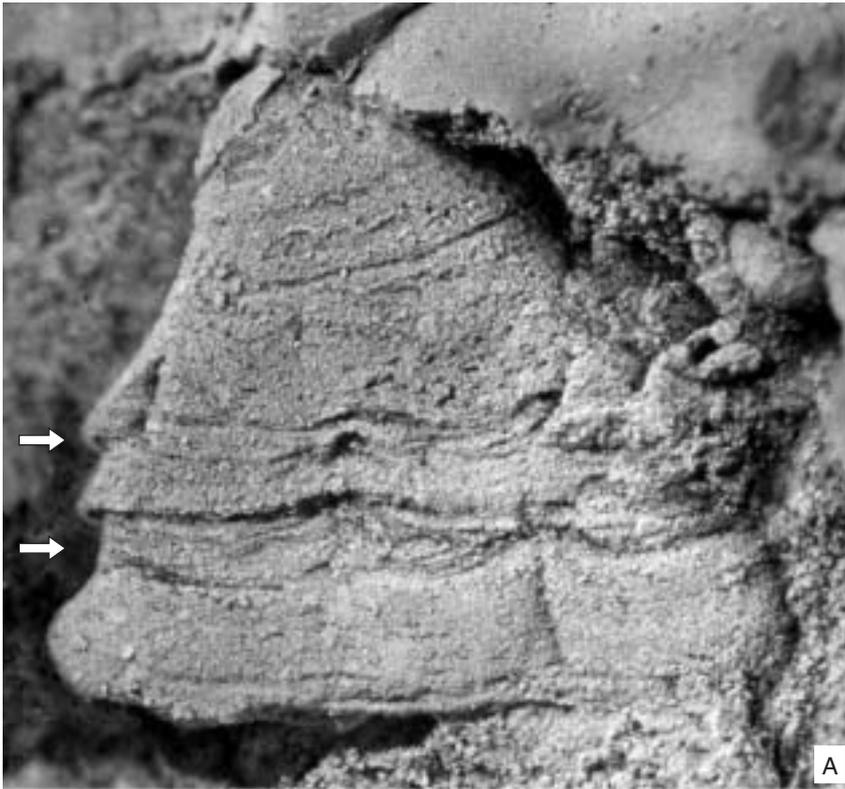
Class **Tergomya** HORNÝ, 1965
 Order **Cyrtonellida** HORNÝ, 1965
 Family **Kirengellidae** STAROBOGATOV, 1970

Subfamily **Pygmaeoconinae** subfam. n.

Diagnosis. Small cap-shaped, thick-shelled cyrtonevellids adapted for stationary life on hyolithid conchs. Apertural margin cradle-like, with lifted anterior and posterior margins to fit with the hyolithid dorsum. A set of discrete muscle scars parallel with the apertural margin relocated by saltation. External surface with crowded thin growth lines

interrupted by periodically repeating intervals of reduced rate of shell secretion corresponding to relocation of muscle attachments.

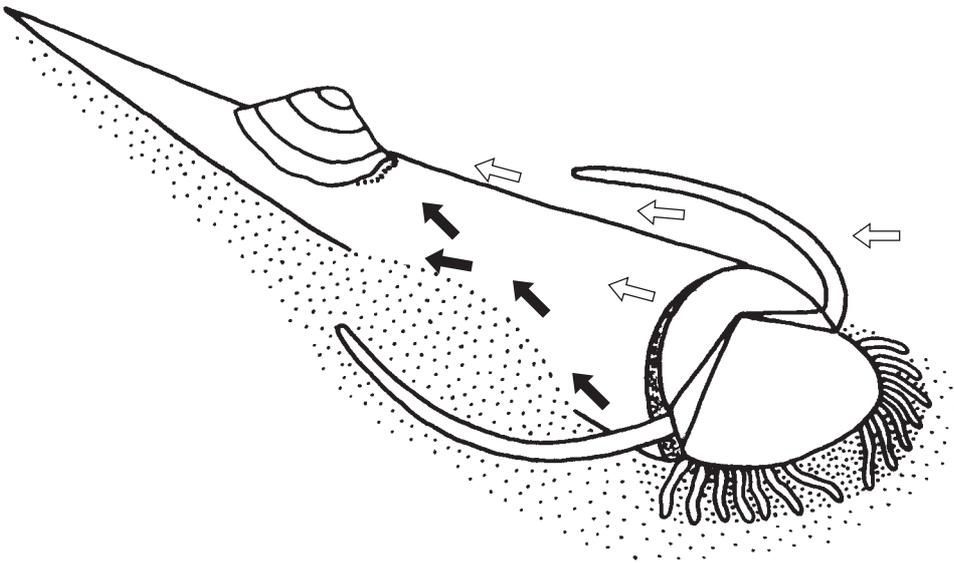
Discussion. The subfamily Pygmaeoconinae is established to embrace highly specialized genus *Pygmaeoconus* adapted to obligatory life on hyolithid conchs. This mode of life caused notable changes of morphology which distinguish this subfamily from all superficially similar kirengellid genera. Higher classification of the subfamily requires better knowledge and detailed study of numerous, mostly imperfectly preserved Middle Cambrian to Lower Ordovician genera, published by Starobogatov 1970, Rozov 1975, Stinchcomb 1986, Webers et al. 1992, Geyer 1994, Stinchcomb and Angeli 2002, among others.



Text-fig. 18. *Pygmaeoconus porrectus*, an immature specimen MBHR 12844, left side. A – revultex impression showing details of external surface. The apex bears a fragment, which may be a slightly displaced residue of juvenile shell. The second transverse groove is thin and simple, the third in the middle part of the shell (arrowed) is doubled (perhaps representing two pauses). Note the thick shell (left) overhanging the anterior margin where new shell grows from below the old shell. The growth pauses are characterized by irregular “cross-bedded” increments, gradually straightening disconformities originated during the transfer of muscle attachments. B – anterolateral view showing thick shell overhanging the cephalic area of the animal, C – internal mould with irregular deep muscle scars, probably of the third transfer phase. Note the empty space after the thick shell wall, reaching here 0.4 mm. All $\times 30$. Šárka Formation, Dily near Rokycany. Length of the specimen 3,8 mm.



Text-fig. 19. *Pygmaeoconus porrectus*, specimen NM L 37500, right side of an internal mould of a narrow, high shell with distinct cradle-like apertural margin. $\times 13$. Šárka Formation, Rokycany, the airport. Length of the specimen 5.5 mm.



Text-fig. 20. *Pygmaeoconus porrectus* in life position on the dorsum of a hyolithid (the hyolithid after Marek, Parsley and Galle 1997). White arrows – the current transporting food and oxygen, black arrows – nutrients from the deposit whirled by the feeding activity of the hyolithid.

Distribution. Middle to Upper Ordovician, peri-Gondwanan Palaeoprovince.

Genus included. *Pygmaeoconus* HORNÝ, 1961; Middle to Upper Ordovician, Bohemia, Spain.

Pygmaeoconus HORNÝ, 1961

Type species: *Palaeacmaea porrecta* BARRANDE in PERNER, 1903. Middle Ordovician Šárka Formation, Bohemia.

Emended diagnosis: Genus of the subfamily Pygmaeoconinae with seven pairs of muscle scars: a pair of anterior scars of cephalic muscles, five lateral paired scars of pedal retractors (three anterior to various extent coalesced), and a posterior pair which may be fused.

Species included: *Pygmaeoconus porrectus* (BARRANDE in PERNER, 1903), *P. gnomicus* GUTIÉRREZ-MARCO et MARTÍN-SÁNCHEZ, 1983, *P. krafti* HORNÝ, 1997.

Notes. *Pygmaeoconus* was originally presented as a genus of the monoplacophoran (in old sense) family Hypseloconidae KNIGHT, 1956 (Horný 1961, 1963). This interpretation was accepted by Yochelson (1977) and later by Gutiérrez-Marco and Martín-Sánchez (1983). In 1997 Horný placed this genus, although questionably, among gastropods, possibly as a member of the family ?Protoconchioididae GEYER, 1994. In 2002 he maintained the interpretation that *Pygmaeoconus* was a gastropod, assigning the genus either to the family ?Archinacellidae KNIGHT, 1956 or ?Protoconchioididae.

In the meantime, monoplacophorans have undergone a basic reorganisation (for details and references see Peel 1991). Peel (1991) transferred Horný's subclass Tergomya to the class level, including orders Tryblidiida LEMCHE, 1957, Cyrtonellida HORNÝ, 1963 and Hypseloconida PEEL, 1991. Although several modifications of this scheme appeared (for a different view and summary see e.g. Harper and Rollins 2000), the adjustment given by Peel (1991) remains still actual and worthwhile to use. The order Tryblidiida encompasses an increasing number of the Cambrian to Recent genera and species [e.g. Wingstrand (1985), Peel (1990), Yu Wen and Yochelson (1999), Horný (2005a, b)]. The orders Cyrtonellida and Hypseloconida, including many Cambrian to Devonian (?Carboniferous) genera and species, may constitute another group of non-torted, primarily exogastric molluscs, the Cyclomya, proposed as a subclass of Monoplacophora by Horný 1965 but not yet accepted (especially Yochelson 1967, 1978, Peel 1991, Geyer 1994). To this group belong, besides the more advanced coiled shells, the majority of various low to high cap-shaped Cambrian and Ordovician molluscs with central or subcentral apex. They were probably slow and less active animals, either filterators or grazers; many of them were reported or described by Starobogatov (1970), Stinchcomb (1986), Webers et al. (1992), Stinchcomb and Angeli (2002), among others.

Pygmaeoconus, despite being one of the best known representatives of the cyclomyans, is too specialized to help much with systematics. The multiple muscle scars may have originated as a consequence of the necessity of tight but individualised attachments, fitted to lift and clamp certain parts of the apertural margin, resembling the hypothetical cap-shaped shell with muscle scars of 'cyclomyan-type' (Peel 1991, p. 22, fig. 16A). Quite unique is the discovery of the location of the anterior side of the animal – thanks to its position on the hyolithid dorsum facing the head of the host. An important character, which may be significant systematically, is the relocation of muscle attachments by saltation, typical for cyrtonellids (Horný 1991a, 1991b, Horný and Peel 1996) and present also in the Lower Ordovician genus *Multifariites* BIALYI, 1873. Classification of *Pygmaeoconus* as a patellostomopod would be rather speculative but we must wait for additional data (for discussions concerning the relationships of Archinacellidae see e.g. Yochelson (1988, 1994) and Peel and Horný (1999)).

Acknowledgements

Financial support from the Ministry of Culture of the Czech Republic, project MK 00002327201, is gratefully acknowledged. Ellis L. Yochelson reviewed the manuscript. Arnošt Galle read the manuscript and made helpful suggestions. Vojtěch Turek read and commented the manuscript. Petr Daneš kindly searched for mistakes in English. A. J. Boucot kindly declassified the draft of the Supplement of the "Evolutionary Paleobiology of Behavior and Coevolution"; Jan Sklenář aided in the preparation of the computer-based photographs. Miroslava Šandová and Martina Korandová loaned the specimens housed in the Museum of

Dr. Bohuslav Horák in Rokycany for study. Vladimír Vonka friendly provided an important specimen found at Mýto near Rokycany. Václav Ziegler helped with preparation of the manuscript.

References

- Boucot, A. J. (1975): Evolution and extinction rate controls. – 425 pp. Elsevier, Amsterdam.
- Galle, A., Parsley, R. L. (2005): Epibiont relationships on hyolithids demonstrated by Ordovician trepostomes (Bryozoa) and Devonian tabulates (Anthozoa). – *Bulletin of Geosciences*, 80 (2): 125–138, 2005.
- Geyer, G. (1994): Middle Cambrian molluscs from Idaho and early conchiferan evolution. *In*: Landing, E. (ed.), *Studies in stratigraphy and paleontology etc.*, New York State Museum Bulletin 481, pp. 380.
- Gutiérrez-Marco, J. C., Martín-Sánchez, J. (1983): Estudio de los monoplacóforos (Mollusca) del Ordovícico de los Montes de Toledo (España central). – *Estudios Geológicos*, 39: 379–385.
- Harper, J. A., Rollins, H. B. (2000): The *Bellerophon* Controversy Revisited. – *American Malacological Bulletin*, 15 (2): 147–156.
- Havlíček, V., Vaněk, J. (1990): Ordovician invertebrate communities in black-shale lithofacies (Prague basin, Czechoslovakia). – *Věstník Ústředního ústavu geologického*, 65 (4): 223–236.
- Havlíček, V., Vaněk, J., and Fatka, O. (1994): Perunica microcontinent in the Ordovician (its position within the Mediterranean Province, series division, benthic and pelagic associations). – *Sborník geologických věd, Geologie*, 46: 23–56.
- Horný, R. J. (1961): New genera of Bohemian Monoplacophora and Patellid Gastropoda. – *Věstník Ústředního ústavu geologického*, 36: 299–302.
- Horný, R. J. (1963): Lower Paleozoic Monoplacophora and Patellid Gastropoda (Mollusca) of Bohemia. – *Sborník Ústředního ústavu geologického, oddíl paleontologický*, 28(1961): 7–83.
- Horný, R. J. (1965a): *Cyrtolites* CONRAD and its position among the Mollusca (Monoplacophora). – *Acta Musei Nationalis Pragae, Series B*, 21 (2): 57–70.
- Horný, R. J. (1965b): On the systematical position of *Cyrtolites* CONRAD, 1838 (Mollusca). – *Časopis Národního muzea v Praze, Řada přírodovědná*, 134: 8–10.
- Horný, R. J. (1991a): Vývoj názorů na klasifikaci cyklomyárních měkkýšů (Mollusca, Monoplacophora). – *Časopis Národního muzea, řada přírodovědná*, 157: 13–32.
- Horný, R. J. (1991b): Shell morphology and muscle scars of *Sinuitopsis neglecta* PERNER (Mollusca, Monoplacophora). – *Časopis Národního muzea, řada Přírodovědná*, 157 (1–4): 81–105.
- Horný, R. J. (1997): New, rare, and better recognized Ordovician Tergomya and Gastropoda (Mollusca) of Bohemia. – *Věstník Českého geologického ústavu*, 73: 223–237.
- Horný, R. J. (2002): Ordovician Tergomya and isostrophic Gastropoda (Mollusca) of Bohemia: Types and referred specimens in the collections of the National Museum, Prague, Czech Republic. – *Acta Musei Nationalis Pragae, Series B, Historia Naturalis*, 57 [2001] (3–4): 69–102.
- Horný, R. J. (2005a): *Kosovina*, a new Silurian tryblidiid genus (Mollusca, Tergomya) from Bohemia (Czech Republic). – *Acta Musei Nationalis Pragae, Series B, Historia Naturalis*, 60 (3–4): 143–148.

- Horný, R. J. (2005b): Muscle scars, systematics and mode of life of the Silurian family Drahomiridae (Mollusca, Tergomya). – *Acta Musei Nationalis Pragae, Series B, Historia Naturalis*, 61 (1–2): 53–76.
- Horný, R. J., Peel, J. S. (1996): *Carcassonnella*, a new Lower Ordovician bellerophonitiform mollusc with dorsally located muscle attachments (Class Tergomya). – *Věstník Českého geologického ústavu* 71 (4): 305–331.
- Knight, J. B., Yochelson, E. L. (1960): Monoplacophora. – In: R. C. Moore (ed.), *Treatise on Invertebrate Paleontology, Part I (Mollusca 1), I77–I84*. – Geological Society of America and University of Kansas Press, Lawrence.
- Kruse, P. D. (1996): Hyolith guts in the Cambrian of Northern Australia turning hyolithomorphs upside down. – *Lethaia* 29: 213–218.
- Marek, L., Galle, A. (1976): The tabulate coral *Hyostragulum*, an epizoan with bearing on hyolithid ecology and systematic. – *Lethaia* 9: 51–64.
- Marek, L., Parsley, R. L., Galle, A. (1997): Functional morphology of hyoliths based on flume studies. – *Věstník Českého geologického ústavu* 72 (4): 351–358.
- Martí Mus, M., Bergström, J. (2005): The morphology of hyolithids and its functional implications. – *Palaeontology*, 48 (6): 1139–1167.
- Peel, J. S. (1990): Morphology and systematic position of *Tryblidium canadense* WHITEAVES, 1884 (Mollusca) from the Silurian of North America. – *Bulletin of the Geological Society of Denmark*, 38: 43–51.
- Peel, J. S. (1991): Functional morphology, evolution and systematics of Early Palaeozoic univalved molluscs. – *The Classes Tergomya and Helcionelloida, and early molluscan evolution*. – *Grønlands Geologiske Undersøgelse, Bulletin* 161: 11–65.
- Peel, J., Horný, R.J. (1999): Muscle scars and systematic position of the Lower Palaeozoic limpets *Archinacella* and *Barrandicella* gen. n. (Mollusca) – *Journal of the Czech Geological Society*, 44 (1–2): 97–115.
- Perner, J. (1903): Gastéropodes. – In: J. Barrande, *Système Silurien du centre de la Bohême*, 4 (1): I–XI, 1–164. Prague.
- Perner, J. (1911): Gastéropodes. – In: J. Barrande, *ibidem*, 4 (3): I–XVII, 1–390. Prague.
- Rozov, S. N. (1975): A new order of the Monoplacophora. – *Paleontological Journal*, 1975 (1): 39–43.
- Starobogatov, Yu. A. (1970): Systematics of Early Paleozoic Monoplacophora. – *Paleontological Journal* 1970, 3: 293–302.
- Stinchcomb, B. L. (1986): New Monoplacophora (Mollusca) from Late Cambrian and Early Ordovician of Missouri. – *Journal of Paleontology*, 60: 606–626.
- Stinchcomb, B. L., Angeli, N. A. (2002): New Cambrian and Lower Ordovician monoplacophorans from the Ozark Uplift, Missouri. – *Journal of Paleontology*, 76 (6): 965–974.
- Webers, G. F., Pojeta, J., Jr., Yochelson, E. L. (1992): Cambrian Mollusca from the Minaret Formation, Ellsworth Mountains, West Antarctic. In: Webers, G. F., Craddock, C., Spletstoesser, J. F. (eds), *Geology and Paleontology of the Ellsworth Mountains*. – Geological Society of America, 170: 181–248.
- Wingstrand, K. G. (1985): On the Anatomy and Relationships of Recent Monoplacophora. – *Galathea Report*, 16: 1–94. Copenhagen.
- Yochelson, E. L. (1958): Some lower Ordovician monoplacophoran molluscs from Missouri. – *Journal of Washington Academy of Sciences*, 48: 8–14.
- Yochelson, E. L. (1977): Monoplacophora (Mollusca) from the Upper Ordovician of Norway. – *Norsk Geologisk Tidsskrift*, 47:312.
- Yochelson, E. L. (1967): Quo vadis, *Bellerophon*? In: Teichert, C. and Yochelson, E. L. (ed.), *Essays in Paleontology and Stratigraphy*, 141–161. Lawrence, University Kansas Press.
- Yochelson, E. L. (1978): An alternative approach to the interpretation of the phylogeny of ancient molusks. – *Malacologia*, 17 (2): 165–191.
- Yochelson, E. L. (1988): A new genus of Patellacea (Gastropoda) from the Middle Ordovician of Utah: the oldest known example of the superfamily. – *Memoires New Mexico Bureau of Mines and Mineral Resources*, 44, 195–200.
- Yochelson, E. L. (1994): *Macroskenella* (Mollusca) from the Middle Ordovician of Wisconsin – a reinterpretation and reassignment. – *Journal of Paleontology*, 68: 1252–1256.
- Yu Wen, Yochelson, E. L. (1999): Some Late Cambrian molluscs from Liaoning Province, China. – *Records of the Western Australian Museum*, 19: 379–389.