

Mode of life of Early Devonian *Orthonychia protei* (Neritimorpha, Gastropoda) inferred from its post-larval shell ontogeny and muscle scars

JIŘÍ FRÝDA, PATRICK R. RACHEBOEUF & BARBORA FRÝDOVÁ



Rich fossil material of the Early Devonian *Orthonychia protei* (Oehlert, 1883) from the Saint Cénére Formation, Brittany (France) provides a unique chance to analyze the infraspecific variability of muscle scars and post-larval shell morphology. The position of the muscle scar in this species depends on the shape of the teleoconch, which seems to be influenced by its living position upon the crinoid host. Individuals having a teleoconch aperture with a pentagonal outline and five apertural processes probably lived on top of a crinoid calyx and their muscle was attached to the center of their teleoconchs. However, muscle scars are situated more laterally in individuals with irregular teleoconchs lacking apertural processes. The latter group was probably attached to another part of the crinoid body or even to another type of hard substrate. Juvenile post-larval *Orthonychia protei* was a mobile animal, but very early in its ontogeny became adapted to a fixed position on the crinoid body and remained immobile for the majority of its post-larval ontogeny. Long-term coexistence of *Orthonychia protei* with the same crinoid suggests that this species had a long-term advantage from such an ecological strategy. However, the existence of individuals with irregularly shaped teleoconchs suggests that *Orthonychia protei* could also live successfully outside of the digestive openings of crinoids and, thus, use a food source not closely connected with crinoids. This interpretation can be supported by the fact that at least some Silurian and Devonian platyceratids were adapted to living on small firm objects (like empty cephalopod shells) lying on the sediment surface. • Key words: Gastropoda, muscle scars, ontogeny, Orthonychiidae, Early Devonian, W France.

FRÝDA, J., RACHEBOEUF, P.R. & FRÝDOVÁ, B. 2008. Mode of life of Early Devonian *Orthonychia protei* (Neritimorpha, Gastropoda) inferred from its post-larval shell ontogeny and muscle scars. *Bulletin of Geosciences* 83(4), 491–502 (5 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received November 17, 2008; accepted in revised form December 3, 2008; issued December 31, 2008.

Jiří Frýda, Czech Geological Survey, P.O.B. 85, 118 21 Prague 1, and Faculty of Environmental Sciences, CULS, 165 21 Prague 6, Czech Republic; bellerophon@seznam.cz • Patrick R. Racheboeuf, UMR CNRS 6538, Domaines Océaniques, Université de Bretagne Occidentale, Brest, UFR des Sciences et Techniques, 6, avenue Le Gorgeu, C.S. 93837, F-29238 Brest Cedex 3, France; patrick.racheboeuf@univ-brest.fr • Barbora Frýdová, VÚVR v.v.i., Research Institute, Drnovská 507, 161 06 Prague – Ruzyně, Czech Republic; frydova@vuvr.cz

Platyceratid gastropods form one of the most common and easily recognizable groups of Paleozoic gastropods. The oldest members of this group have been recognized in Middle Ordovician strata (Knight *et al.* 1960, Frýda & Rohr 2004); the age of the youngest platyceratids is still a matter of debate (Bandel & Frýda 1999, Bandel 2007). Typical features of platyceratid gastropods are the high morphological variability of their shells and the close ecological connection at least some of them to Paleozoic echinoderms. The first feature makes their species-level taxonomy very difficult. The high morphological variability of platyceratids was recognized by the first researchers on Paleozoic gastropods. In 1890 Charles R. Keyes wrote: “The three hundred species which have been ascribed to *Platyceras* present such a great variety of forms that it is difficult to foresee just how they can be most satisfactorily arranged when they have been carefully

considered anew and in relation to one another” (Keyes 1890, p. 7). Up to now many hundreds of the Paleozoic platyceratid species were established on fossil material from Paleozoic strata of almost all paleocontinents. However, it is almost impossible to make species-level determination for a majority of these taxa without additional data on the region and stratal horizon from which the particular species are derived. Such an unpleasant systematic reality has existed now for slightly more than 100 years. As consequence, the majority of modern researchers have not been determining species-level names for the platyceratid gastropods from newly studied gastropod faunas. As a result, thousands of records of platyceratid gastropods are known from different Paleozoic faunas, but very few are known regarding the environment, as well as about the stratigraphic and geographic ranges of individual species.

The close ecological connection of platyceratid gastropods and echinoderms has been studied since the 19th century. Several different models have been proposed for this interaction (see Rollins & Harper 1988; Baumiller 2002, 2003; Gahn & Baumiller 2003 for a review) and this ecological strategy is the most frequent reason why researchers have been interested in the platyceratids. Another reason why these extinct gastropods are occasionally studied is their still-uncertain phylogenetic position. They were considered to represent the ancestral group of Neritimorpha or Patellogastropoda by Ponder & Lindberg (1997), Bandel (1992), Bandel & Frýda (1999), and most recently by Frýda *et al.* (2008). In addition, data on the protoconch morphology of platyceratid gastropods suggests that they are not a monophyletic group (Frýda 1998a, b, 1999). The recent discovery of soft body parts in presumed platyceratids has also increased interest in this gastropod group (Sutton *et al.* 2006).

The platyceratid gastropods described here come from several localities in the eastern part of the Massif Armoricain, in the Mayenne department, W France. Saint Jean-sur-Mayenne and Saint Germain-le-Fouilloux are famous since Oehlert's work in the late 19th century. Both villages are about 8 km N of Laval. The La Roussière quarry at St Germain is the type locality for many Lower Devonian (Pragian) fossils and this locality also yielded the most important collection known of the crinoid *Thylacocrinus vannioti* Oehlert, 1878. It is now supposed that the quarry, which has yielded a fossilized crinoid meadow exposes the middle part of the Early Devonian Saint Céneré Formation. At St Jean-sur-Mayenne, the limestones of the St Céneré Fm are well exposed in the cliff along the left bank of the Ernée River. The locality La Baconnière is situated about 15 km NW of Laval and is famous for several now-abandoned quarries that have provided paleontologists with very abundant, well-preserved fossils, among which are very numerous gastropods. The best known localities are La Poupardière, and La Jallerie quarries, which are between 1.5 km and 2.5 km S of La Baconnière. The Saint Roch quarry, N of Saint Ouen-des-Toits, is close to the La Jallerie quarry, and situated about 3 km S of La Baconnière. Maps and detailed description of above-mentioned localities can be found in the monographs of Morzadec (1971) and Racheboeuf (1976).

In this short paper we discuss the variability and position of muscle scar attachment of *Orthonychia protei*

(Oehlert, 1883) based upon relatively large samples from the above-mentioned localities. Special attention is paid also to the post-larval shell ontogeny of this species.

Systematic position of *Orthonychia*

The genus *Orthonychia* has posed taxonomical problems since its erection by Hall in 1843. As noted by Knight (1941), Hall used the generic name *Orthonychia* without species name attached to it, referring only to a figure of a specimen. Later in 1859, Hall used the name *Platyceras* (*Orthonychia*) *subrectum* for the same specimen. Knight (1941) mentioned that the latter specific name was the first that was coupled with the genus name *Orthonychia*, and so it can be considered to be its type species on the basis of monotypy. A similar problem is connected with the generic level position. *Orthonychia* has been considered to be a junior synonym of *Platyceras*, or its subgenus, or even a distinct genus (Wenz 1938–1944; Knight *et al.* 1960; Bandel & Frýda 1999; Horný 2000a, 2004). Problems about the position of the genus *Orthonychia* mainly result from the unusual variability of the shell morphology of the species assigned to the genus. In addition, shells of *Orthonychia* are smooth and bear irregular growth lines. As noted by some authors (*e.g.*, Horný 2000a), there are also transitions in general shell shape among species placed in the genera *Orthonychia* and *Platyceras* Conrad, 1840, even though the shells of their type species differ. On the other hand, nobody has performed an analysis of the morphological variability including a significant portion of known species. Some analyses of the morphological variability of a particular species revealed rather low variability (Jankovský 2003). Any progress in the taxonomy of the genera *Orthonychia* and *Platyceras*, either at the species or at the genus level, is impossible without extensive analysis of the morphological variability of known species.

Similar to generic level taxonomy, the higher phylogenetic position of the genus *Orthonychia* is also uncertain. The latter taxon together with all platyceratid gastropods has been considered to form the ancestral or basal group of the Neritimorpha (Bandel 1992, Bandel & Frýda 1999) or Patellogastropoda (Ponder & Lindberg 1997). The first hypothesis was based on a similarity of shell forms of Paleozoic platyceratids to some Triassic neritimorph gas-

Figure 1. Muscle scars in the Early Devonian *Orthonychia protei* (Oehlert, 1883) from Brittany (France). • A, B – holotype of *Acroculia protei* Oehlert, 1883 [= *Orthonychia protei*] figured on pl. XVI, fig. 5 in Oehlert (1883). A – lateral view, × 1, B – apical view, × 1. • C, F, I – *Orthonychia protei* from Saint Germain-le-Fouilloux (8 km N of Laval), topotype specimen A from the same collection as the holotype, C – lateral view, × 1, F – oblique view, × 1, I – apical view, × 1. • D, E – *Orthonychia protei* from Saint Jean-sur-Mayenne (8 km N of Laval), D – apical view, × 1, E – oblique view, × 1. • G, H – *Orthonychia protei* from La Jallerie quarry (about 15 km NW of Laval and 2 km S of La Baconnière), specimen A, coll. De Viennay, G – oblique view, × 1, H – apical view, × 1. • J – *Orthonychia protei* from La Roussière quarry at St Germain-le-Fouilloux (8 km N of Laval), oblique view, × 1.2. • K – *Orthonychia protei* from La Jallerie quarry (about 15 km NW of Laval and 2 km S of La Baconnière), specimen B, coll. De Viennay, oblique view, × 1.



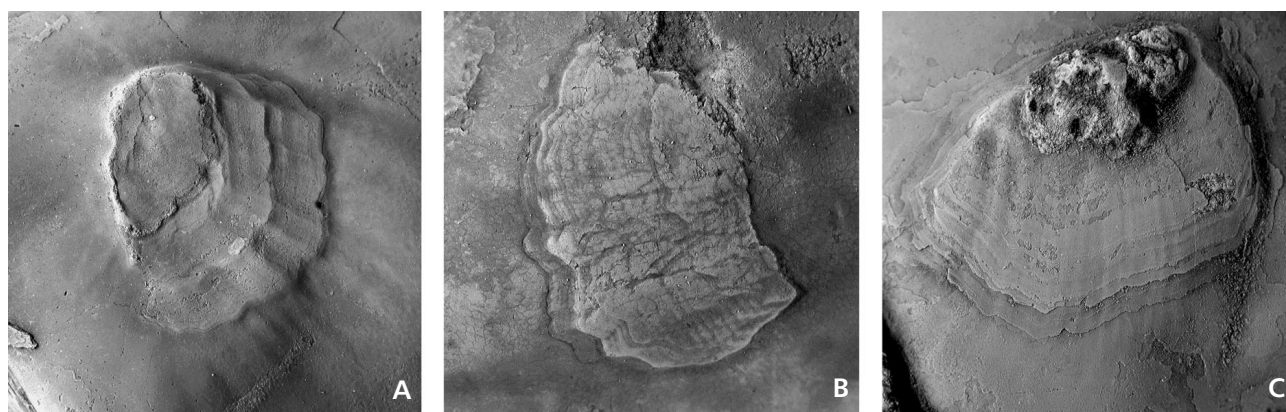


Figure 2. Detailed view of muscle scars in the Early Devonian *Orthonychia protei* (Oehlert, 1883) from Brittany (France). • A – specimen figured on Fig. 1H, $\times 2$. • B – specimen figured in Fig. 1K, $\times 1.8$. • C – specimen figured in Fig. 1J, $\times 2.3$. Note growth lines on surface of muscle scar and abapically oriented traces of muscle activity across muscle scar and surrounding inner shell surface.

tropods. The phylogenetic position of these Triassic taxa within the clade Neritimorpha was documented by the nature of their larval shells (see Bandel 2007). The second interpretation was inferred from their shell structures (Ponder & Lindberg 1997). However, this situation becomes even more complicated by discoveries of protoconchs in presumed Paleozoic neritimorphs. Frýda (1998a, 1999) pointed out that these gastropods have two different larval shells: one closely coiled (but not convolute like post-Paleozoic neritimorph gastropods; e.g., Bandel 2007, Nützel *et al.* 2007), and the other beginning with nearly orthoconic growth followed by an open-coiled, fishhook-like larval shell. The first group includes “Platyceratidae”, Plagiothyridae, Naticopsidae, Nerrenidae, and “Oriostomatoidea” (Yoo 1994, Bandel & Frýda 1999, Bandel & Heidelberger 2001, Nützel *et al.* 2007), and displays a tightly coiled homeostrophic larval shell that is little different from the larval shells of caenogastropods. Frýda (1998b, 1999) named the second protoconch group the Cyrtoneritimorpha (Bouchet *et al.* 2005) and interpreted it as the stem group of the neritimorphs. Later, Bandel & Frýda (1999) included in it two new families (e.g., Vltaviellidae and Orthonychiidae) based on middle and late Paleozoic specimens. However, teleoconchs of the Silurian and Devonian cyrtoneritimorphs led Frýda and Heidelberger (2003; also, Frýda, unpublished data) to question whether cyrtoneritimorphs do form the stem group of neritimorphs. A quite different protoconch morphology in species of *Orthonychia* (see Bandel & Frýda 1999) from the rest of presumed Paleozoic neritimorphs led Bandel & Frýda (1999) to consider a model in which *Orthonychia* and related genera (not *Platyceras*) form an independent phylogenetic lineage of Paleozoic gastropods (family Orthonychiidae). This model was included in the most recent proposal for the classification of the Class Gastropoda (Bouchet *et al.* 2005). However, recent discovery of well-preserved protoconchs in Devonian platyce-

ratids reveals more complicated phylogenetic relationships within this extinct gastropod group (Frýda, unpublished data).

Muscle scars

Muscles attaching a gastropod soft body to its shell usually leave characteristic muscle scars on the inner shell surface (Figs 1 and 2). This morphological feature of fossil gastropods has been the subject of great interest during many of the past decades. Muscle scars are considered to reveal important information on the anatomical organization of the soft body in fossil univalved molluscs. For this reason many researchers have tried to find, describe and interpret the muscle scars in fossil molluscs since Wenz’s (1940) documentation of segmented dorsal muscle scars in the Devonian cyrtoneiloid molluscs. These studies of muscle scars have been focused mainly on “problematic extinct” molluscan taxa like bellerophonitiform molluscs (see Wahlmann 1992, Horný 1991, Horný & Peel 1996, Peel 2001 for a review) and they have led to a consensus view that bellerophonitiforms include both “monoplacophorans” and gastropods (Knight *et al.* 1960; Yochelson 1967; Peel 1991a, b, 2001; Horný 1991; Wahlmann 1992; Horný & Peel 1996), either because of parallel evolution of shell form (Yochelson 1967, Wahlmann 1992) or because gastropods evolved amid untorted bellerophonitiforms (Knight 1952). Nevertheless, not only muscle scars of bellerophonitiform molluscs have been described. During the last few decades muscle scars were documented in another bilaterally-coiled molluscan group, the Porcellioidea (Peel 1986). The latter belongs to gastropods having a nacreous shell and represents an extinct lineage of archaeogastropods originating in the Silurian and becoming extinct in the Cretaceous (Frýda 1997; Frýda & Blodgett 1998, 2004; Kiel & Frýda 2004; Frýda & Farrell 2005). The muscle scars were also

documented in different groups of anisotrophically-coiled gastropods (e.g., Horný 1995, 2000b, 2004). Platyceratids are a gastropod group where the muscle scars were recognized very early (e.g., Oehlert 1883, Keyes 1890), but published studies are based on the description of a single or a few specimens with preserved muscle scars. On-going revision of the large fossil material of Devonian gastropods from Brittany reveals an unusually high number of shells belonging to *Orthonychia protei* (Oehlert, 1883) with a well-preserved muscle scar. This material enables analysis of the infraspecific variability of shape, size and position of the muscle scar.

The muscle in *Orthonychia protei* is attached to the inner shell surface, forming a very shallow depression which is visible as a slightly elevated area (Figs 1 and 2) on a cast of the inner shell surface. The surface of the muscle attachment area (muscle scar) bears growth lines showing clearly asymmetrical growth (Fig. 2). During ontogeny the muscle attachment area has a roughly constant shape and becomes larger by growing in abapical and lateral directions (Fig. 2). On the other hand, the shape of the muscle scar varies among individual specimens from almost isometric polygons to distinctly elongated muscle scars (Fig. 2). Maximum and minimum diameters of muscle scars in all studied specimens ($n = 15$) show statistically significant correlation (Fig. 3A) even though the shape of their muscle scar varies.

The position of the muscle scar on the shell also varies, but some rules controlling its position can be observed. In low teleoconchs with a distinctly pentagonal aperture (as in the holotype of *O. protei*; Fig. 1A–C, F, I), the muscle scar is attached roughly in the center of the flat area forming the inner upper surface of the teleoconch. In teleoconchs with an irregular aperture the muscle scar is more laterally situated (Fig. 1G, H, K). In teleoconchs lacking the flat top, the muscle scar is situated on a lateral side (Fig. 1D, E). The latter position corresponds to a growth stage when the slowly coiled teleoconch stops its coiling and starts to grow only in an abapical direction. However, transitional forms amongst all above-mentioned teleoconch shapes were found in the studied material (more than 50 specimens with a complete teleoconch) (Fig. 1J). Thus, it seems probable that all these shells belong to the same species, *Orthonychia protei*, and their teleoconch shape was influenced by different life positions (see below).

An unusually high number of specimens with well-preserved muscle scars allows analysis of the relationship between size of the muscle attachment area and the inner volume of the teleoconch. Only very simple measurement of both variables was used because not all shell apertures are complete. In addition, some specimens have a partly-preserved shell, which also complicates measurement of inner shell volume. For this reason, we cannot measure

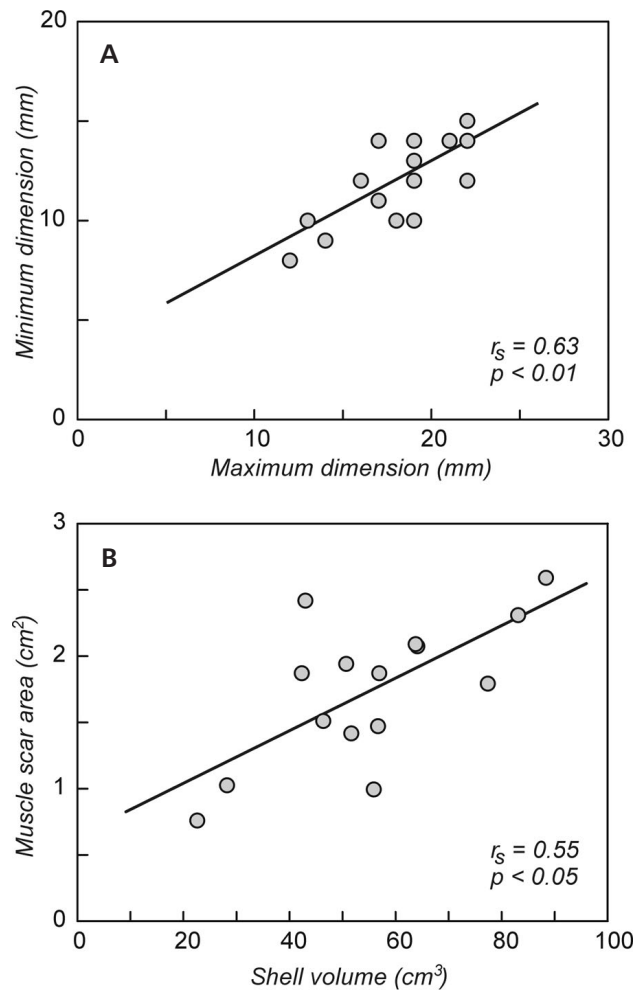


Figure 3. A – bivariate plot showing relationships of maximum and minimum muscle scars diameters in *Orthonychia protei* (Oehlert, 1883) from Brittany (France). Both variables show a statistically significant link ($r_s = 0.63$, $p < 0.01$). B – bivariate plot showing a statistically significant correlation between inner shell volume and size of muscle scar area in the same specimens ($r_s = 0.55$, $p < 0.05$). Because the linearity of the above-mentioned relationships cannot generally be assumed, a non-parametric Spearman's correlation coefficient was used for the correlation analysis.

more exactly the shell inner volume (such as measuring the volume of liquid filling a cast of the inner shell surface), but we simply calculate the volume of a truncated pyramid, cone or prism according to the best fit with the measured teleoconch parameters. The relative error of this approximation is about ten percent. The muscle scar area was determined as the area of a closed polygon fitting in the muscle scar outline. In addition, estimation of this variable is rather approximate. Nevertheless, both of the above-mentioned variables (size of muscle attachment area and inner volume of the teleoconch) show statistically significant correlation (Fig. 3B). This fact suggests that the muscle scar area increased during growth of the entire teleoconch.

Post-larval shell ontogeny of *Orthonychia protei*

The protoconch was not found in any of the studied shells and so it is difficult to determinate the size of the first post-larval whorl. Nevertheless, the most juvenile teleoconch was tightly coiled (Figs 4 and 5). A characteristic feature of the juvenile post-larval shell (*i.e.* juvenile teleoconch) is its rapid whorl expansion. At a size of about 5 mm the maximum diameter of shell aperture approaches the maximum size of the teleoconch. After this ontogenetic stage the whorl expansion rate increases and the teleoconch begins to be limpet-shaped (Fig. 5B). The wide aperture has the shape of a slightly irregular ellipse, but its margin lies in approximately one plane. The growth of the limpet-like teleoconch with a rapidly expanded aperture continues up to a shell size of about 3–4 cm. At this stage the whorl expansion rate starts to decrease and the shell coiling rate approaches an almost zero value. Subsequent teleoconch development is limited to abaxial growth with a very slow whorl expansion (Fig. 5E–G). A rapid change of apertural morphology is a typical feature for this and the end of previous ontogenetic stage. The five roughly equidistant processes start to grow at the apertural margin in a direction perpendicular to the apertural plane (Fig. 5D–G). The length of these apertural processes increases during later ontogeny, reaching a size of about half the maximum diameter of the shell aperture. The processes have rounded margins and their width is about half of their length. Apertural margins between apertural processes become undulose (Fig. 4B, D, H–J). The last growth stage is characterized by very slow whorl expansion, almost no coiling (moderate dextral coiling was recognized in some specimens), and by rapid adapical growth. Because of these growth parameters the adult teleoconch is high and column-like (Fig. 4B, C, J).

Mode of life

The paleoecology of platyceratid gastropods has been discussed for over 100 years (see Rolins & Harper 1988; Baumiller *et al.* 1999; Baumiller 1990, 2002, 2003; and Horný 2000a for a review). Paleozoic platyceratids have frequently been found attached to echinoderms (typically on crinoids and blastoids), often taking a position over the host anus. Such biotic interaction was interpreted as evidence

for a platyceratid predatory, coprophagous, parasitic (kleptoparasitic), or commensal nature. Probably the first interpretation of the platyceratid-crinoid association was published by Austin & Austin (1843–9) who suggested that the crinoids were feeding on those gastropods. The latter interpretation was subsequently rejected by Meek & Worthen (1866, 1868) who suggested that platyceratids were relying upon crinoids for food. The main reason for rejection of the interpretation of platyceratids being crinoid prey was the tight fit between the gastropod aperture and the crinoid calyx. Meek & Worthen (1866, 1868) also noted that the shell aperture in platyceratids conforms to the morphology and ornamentation of the crinoid calyx. Later, Meek & Worthen (1873) and Hinde (1885) described their observations on the consistent placement of the platyceratid shells over the anal opening of the host crinoids. These observations led Hinde (1885) and Keyes (1888, 1890) to interpret platyceratids as coprophagous gastropods feeding on crinoid excrement, an interpretation that was widely accepted for many decades (*e.g.*, Bowsher 1955, Lane 1978, Meyer & Ausich 1983, Boucot 1990).

Modification of the latter idea was published by Lane (1984) who postulated out that platyceratids might be occasional gametophages, feeding on crinoid gametes, arguing that Paleozoic crinoids must have shed their gametes through their anal vent, which was occupied by platyceratid gastropods. On the other hand, Rollins & Brezinski (1988) suggested that platyceratids were mainly detritus feeders. The latter authors, based on their study of serial sections of platyceratid-crinoid couplets, expressed the opinion that the position of the terminus of the crinoid anal tube abuts the gastropod shell and so it is poorly situated for fecal ingestion by gastropods and, for that reason, they suggested that the platyceratids were likely taking advantage of an elevated position above the sediment surface afforded by their placement on the crinoid calyx. Lindström & Peel (2003) expressed the opinion that the habit of some platyceratid gastropods living on echinoderm calices might have provided a refuge from benthic predators.

In this context it is noteworthy that some Devonian and Mississippian platyceratids developed long hollow spines on their external shell surface. In some species of Devonian *Spinipatyceras* Blodgett & Frýda, 1999, these spines can be even longer than the maximum diameter of the adult shell. Such a shell morphology is unknown among Ordovician and Silurian platyceratid species and might suggest that the spines served as a protection for these gastropods against

Figure 4. Early Devonian *Orthonychia protei* (Oehlert, 1883) from Brittany (France). • A–I – specimen from Saint Roch quarry (N of Saint Ouen-des-Toits), about 3 km S of La Baconnière (about 15 km NW of Laval), A – detailed lateral view of shell apex showing tightly coiled juvenile whorls, $\times 1.7$, B – adapical lateral view, $\times 1$, C – right lateral view, $\times 1$, D – detailed view of shell apex, $\times 1.5$, E – apical view, $\times 1$, F – right lateral view, $\times 1$, G – oblique abapical view, $\times 1$, H – detailed apical view showing undulating margin between apertural processes, $\times 2.3$, I – oblique abapical view, $\times 1$; • J – *Orthonychia protei* from Saint Germain-le-Fouilloux (8 km N of Laval), lateral view showing apertural processes, $\times 1.5$.



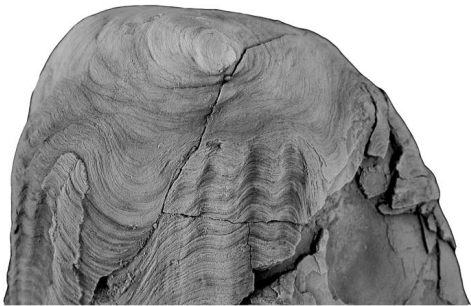
A



B



C



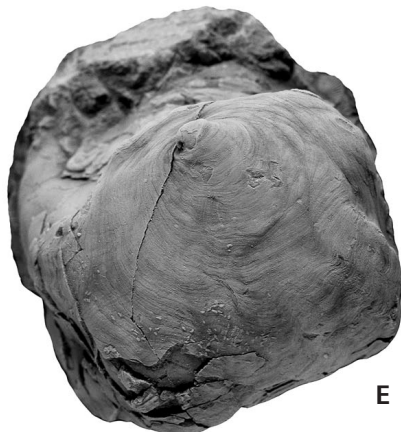
D



E



F



G



H



I



J

increasing predatory “stress” since the Devonian (Signor & Brett 1984, Nützel & Frýda 2003, Berkyová *et al.* 2007, and references herein). Brett *et al.* (2004) suggested that abrupt co-evolution of spinosity in the platyceratids and their crinoid hosts during the Middle Devonian might reflect targeting by newly evolved durophagous fishes at this time.

On the other hand, some recent studies suggest that at least some platyceratids were capable of drilling into their crinoid host to gain access to their soft body. Baumiller (1990, 1993, 1996) and Baumiller & Macurda (1995) studied boreholes in Devonian and Mississippian blastoids and crinoids and interpreted these as the work of platyceratid gastropods. This interpretation was based on several facts: the boreholes in the tegmen of the Mississippian crinoids occur directly beneath the infesting platyceratid shell; the boreholes in different crinoids are similar in their position and morphology; and, in addition, the discovery of numerous examples of boreholes in several blastoid genera (some of which have been found with attached platyceratids) also supported the drilling abilities of platyceratids. Baumiller *et al.* (1999) have gone on to report data on Paleozoic boreholes in Lower Mississippian brachiopods (the spiriferid genera *Brachythyris* and *Spirifer*) and interpreted these also as the result of platyceratid drilling activity. These authors suggested that most boreholes would not have been immediately lethal and that they opened access for the borer to the brachial (food) groove of the brachiopod’s lophophore. This strategy suggests that the platyceratid-brachiopod association is a parasitic interaction. Baumiller *et al.* (1999) concluded that the generally sessile habit of the platyceratids and the low biomass of the brachiopods make it unlikely that these gastropods would become predatory rather than parasitic.

Gahn & Baumiller (2003) recently showed that Middle Devonian camerate crinoids infested by platyceratids are significantly smaller than uninfested crinoids. According to these authors, platyceratids could have functioned as kleptoparasites extracting partially-digested pellets directly from the posterior digestive tract of crinoid through the anus. Baumiller (2003) then quantitatively analyzed this hypothesis using a cost-benefit approach. The results of his analysis suggested that some crinoids were capable of capturing sufficient nutrients to fulfill their metabolic needs as well as those of the infesting platyceratids. He also noted that a parasitic strategy would have provided them with a greater energetic return than a predatory one.

Baird *et al.* (1990) mentioned the rare occurrence of two or more platyceratids on the same crinoid. Such a multi-snail infestation was later analyzed by Baumiller (2002) who concluded that platyceratids settled on crinoids as spat, were not yet strictly coprophagous during life, and benefited from a position over the anal vent.

Important observations were published by Horný (2000a) who demonstrated that several Silurian and Devo-

nian platyceratid species spent their life on small firm objects (like empty cephalopod shells) lying on the sediment surface. Horný concluded that his observations supported the model published earlier by Rollins & Brezinski (1988) and suggested that the platyceratids were mainly detritus feeders.

Conclusions

The morphology of the early post-larval tightly coiled shell in the Early Devonian *Orthonychia protei* (Oehlert, 1883) suggests its ability to be mobile. Rapid whorl expansion during the next ontogenetic stage is connected with the formation of a limpet-shaped shell having an almost planar aperture. This ontogenetic stage is probably linked with an adaptation to being steadily attached to a hard surface, thus, to a mode of life well documented in living patellogastropods. At the same time the planar aperture became more complex and five processes start to grow perpendicular to the apertural plane. Such a type of shell morphology suggests a limited mobility or even immobility. Subsequently, the teleoconch of *Orthonychia protei* started to grow into a high, column-like shell with a slowly expanded aperture bearing five distinct processes (Fig. 5E, F). At this stage the shell of *Orthonychia protei* bears five protruding processes and its active movement was probably impossible. A constant apertural shape during late ontogeny suggests that the shell was for most of the time attached to the same surficial place. Strong muscle growth during the entire post-larval ontogeny probably helped to fix the shell. The morphology of the post-larval shell clearly shows that *Orthonychia protei* spent the vast majority of its post-larval ontogeny as an immobile or almost immobile animal. A teleoconch with a pentagonal apertural outline and five distinct apertural processes (Fig. 5) is the most common teleoconch type in *Orthonychia protei*. We presume that these individuals lived on the top of a crinoid calyx amongst its arms. Even though we did not find any shells of *Orthonychia protei* in situ, we presume such a life position because of the pentagonal symmetry of its aperture. Such a mode of life has been documented for some Mississippian platyceratids with the same apertural shape (*e.g.*, Rollins & Brezinski 1988; Fig. 5I). The relatively large crinoid species, *Thylacocrinus vannioti* Oehlert, 1878, is the only one which is known to occur in all the localities of the Saint Céneré Formation in Brittany from which the studied specimens of *Orthonychia protei* are derived (Le Menn 1974, 1985). In two of the four (St Roch and La Jallerie quarries), another large crinoid occurs together with *T. vannioti*, namely *Dimerocrinites oehlerti* Le Menn, 1980. Shell apertures in *Orthonychia protei* and the calyx diameter of the above-mentioned crinoid species are very similar in size, suggesting that both were probable hosts to *Orthonychia protei*. To the west and

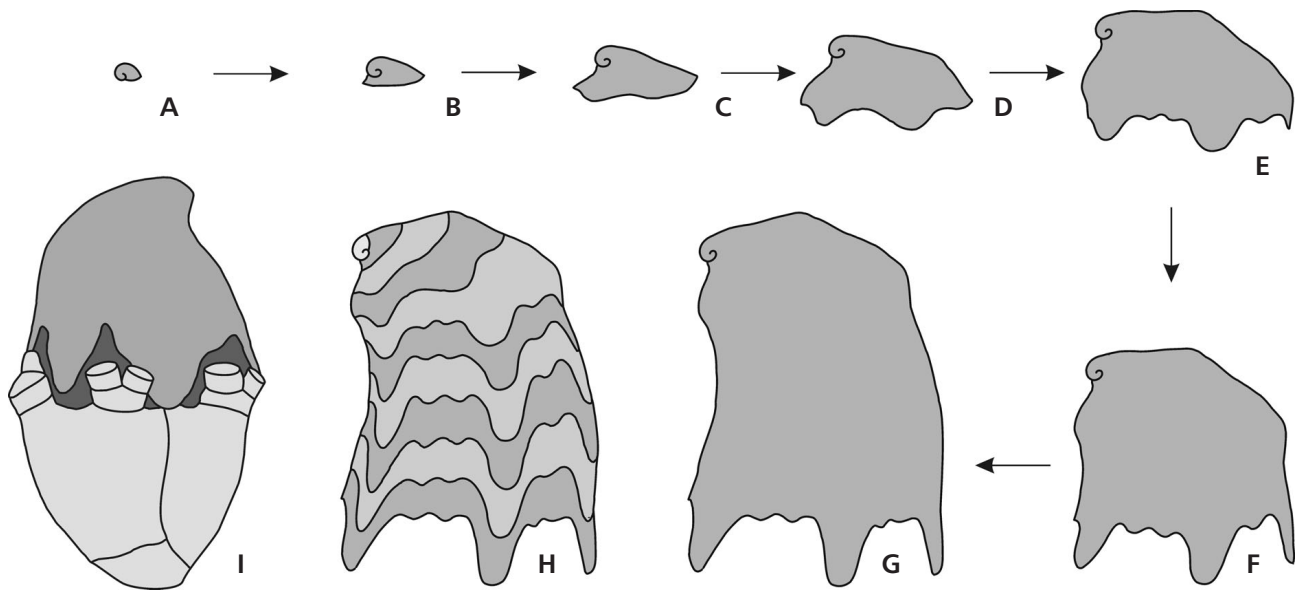


Figure 5. A–H – diagrammatic reconstruction of post-larval shell morphology in *Orthonychia protei* (Oehlert, 1883) from Brittany (France), A – juvenile post-larval stage with tightly coiled shell, B–D – post-larval stage with limpet-shaped shell, E–H – late post-larval, immobile stage, H – diagram showing shell growth lines on adult shell. • I – diagrammatic reconstruction of life position of the Mississippian platyceratid (modified after fig. 3b in Rollins & Brezinski 1988).

outside of Mayenne department, *Orthonychia protei* and *Dimerocrinites oehlerti* occur together in limestones of the Early Devonian Bois-Roux Member, Bois-Roux Formation in the long-time abandoned Bois-Roux, and Izé quarries, NE of Rennes (Renaud, 1930, pp. 253, 254; 1942, pp. 63–66), but both taxa are still unknown from the Rade de Brest area.

The occurrence of less frequent forms of *Orthonychia protei* (with shells lacking a distinct pentagonal aperture and the muscle scar located more laterally) may be explained by the observation already made by Keyes (1889), who reported on the relationship of shell form and convexity of the surface to which the *Platyceras* was attached. He mentioned that shells of *Platyceras equilateratum* Hall “resting on flat crinoidal vaults are very much depressed, the aperture proportionally broader, and the spire more closely coiled; those shells attached laterally to crinoids have a tendency to become more conical, the aperture relatively smaller, the spire entirely free from body whorl, and the apex extended often to a considerable distance beyond the posterior margin of the aperture” (Keyes 1889, p. 333). Thus, intraspecific variability of platyceratid shells might have been influenced by their living position on the crinoid host. Less frequent individuals of *Orthonychia protei* having irregular shells probably did not live amongst crinoid arms, but rather in another position on the crinoid body or even on a different type of hardground. This interpretation may also explain the differing positions of the muscle scar in those individuals.

Taken together, data on post-larval shell ontogeny and nature of muscle scars in *Orthonychia protei* found in the

Early Devonian of Brittany suggest that its mobility was restricted only to the early stages of its post-larval ontogeny. *Orthonychia protei* was immobile for the vast majority of its post-larval ontogeny, living in the same position on the crinoid host. Thus, the mode of life of the Early Devonian *Orthonychia protei* was probably identical to that of some Mississippian platyceratids (e.g., Rollins & Brezinski 1988 and here Fig. 5I). Long-term coexistence of one *Orthonychia protei* individual with the same crinoid animal also testifies against its predation on crinoids. A more probable scenario is that *Orthonychia protei* had an advantage from its elevated position on the crinoid during the greater part of its post-larval ontogeny. Such a living position amongst the crinoid arms (inferred from the pentagonal outline of its aperture) gave it a chance for different ecological strategies, which could include any of the earlier published models on the platyceratid mode of life suggesting a coprophagous, parasitic (kleptoparasitic) or commensal nature. However, the occurrence of irregularly-shaped forms of *Orthonychia protei* provides evidence that this mollusc could also live successfully outside the digestive openings of crinoids. Thus, *Orthonychia protei* could probably have used a food source that was not closely connected with crinoids. This interpretation may be supported by the fact that at least some Silurian and Devonian platyceratids were adapted on living on small firm objects (like empty cephalopod shells) lying on the sediment surface (Horný 2000a). The Early Devonian *Orthonychia protei* probably took advantage of an elevated position above the sediment surface atop crinoids as suggested for other platyceratids by Rollins & Brezinski (1988).

Acknowledgements

This work was supported by grants from the Czech Academy of Science (KJB307020602), the Grant Agency of the Czech Republic (205/08/0062), and the Czech-American Cooperation Programme (Kontakt ME08011). The revision of Lower Devonian gastropods from the Massif Armoricaïn was made possible through an invited professorial position for Jiří Frýda by the Université de Bretagne Occidentale (Brest) in April 2008. The authors thank Robert B. Blodgett (Anchorage) and Štěpán Manda (Prague) for their helpful reviews.

References

- AUSTIN, T. & AUSTIN, T. 1843–9. *Monograph on recent and fossil Crinoidea*. 128 pp. Bristol, London.
- BAIRD, G.C., BRETT, C.E. & TOMLINSON, J.T. 1990. Host-specific acrothoracid barnacles on Middle Devonian platyceratid gastropods. *Historical Biology* 4, 221–244.
- BANDEL, K. 1992. Platyceratidae from the Triassic St. Cassian Formation and the evolutionary history of the Neritimorpha (Gastropoda). *Paläontologische Zeitschrift* 66, 231–240.
- BANDEL, K. 2007. Description and classification of Late Triassic Neritimorpha (Gastropoda, Mollusca) from the St Cassian Formation, Italian Alps. *Bulletin of Geosciences* 82(3), 215–274. DOI 10.3140/bull.geosci.2007.03.215
- BANDEL, K. & FRÝDA, J. 1999. Notes on the evolution and higher classification of the subclass Neritimorpha (Gastropoda) with the description of some new taxa. *Geologica et Palaeontologica* 33, 219–235.
- BANDEL, K. & HEIDELBERGER, D. 2001. The new family Nerheridae (Neritimorpha, Gastropoda) from the Givetian of Germany. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 12, 705–718.
- BAUMILLER, T.K. 1990. Nonpredatory drilling of Mississippian crinoids by platyceratid gastropods. *Palaeontology* 33(3), 743–748.
- BAUMILLER, T.K. 1993. Boreholes in Devonian blastoids and their implications for boring by platyceratids. *Lethaia* 26(1), 41–47. DOI 10.1111/j.1502-3931.1993.tb01508.x
- BAUMILLER, T.K. 1996. Boreholes in the Middle Devonian blastoid *Heteroschisma* and their implications for gastropod drilling. *Palaeogeography, Palaeoclimatology, Paleoecology* 123(1–4), 343–351. DOI 10.1016/0031-0182(95)00124-7
- BAUMILLER, T.K. 2003. Evaluating the interaction between platyceratid gastropods and crinoids: a cost-benefit approach. *Palaeogeography, Palaeoclimatology, Paleoecology*, 201(3–4), 199–209. DOI 10.1016/S0031-0182(03)00625-4
- BAUMILLER, T.K. & MACURDA, D.B. 1995. Borings in Devonian and Mississippian blastoids (Echinodermata). *Journal of Paleontology* 69(6), 1084–1089.
- BAUMILLER, T.K., LEIGHTON, L.R. & THOMPSON, D.L. 1999. Boreholes in Mississippian spiriferid brachiopods and their implications for Paleozoic gastropod drilling. *Palaeogeography, Palaeoclimatology, Paleoecology* 147(3–4), 283–289. DOI 10.1016/S0031-0182(98)00165-5
- BERKYOVA, S., FRÝDA, J. & LUKEŠ, P. 2007. The first documentation of unsuccessful predation on the Middle Paleozoic plankton. *Acta Palaeontologica Polonica* 52(2), 407–412.
- BLODGETT, R.B. & FRÝDA, J. 1999. New Devonian gastropod genera important for paleogeographic reconstructions. *Journal of the Czech Geological Society* 44, 293–308.
- BOUCOT, A.J. 1990. *Evolutionary paleobiology of behaviour and coevolution*. 725 pp. Elsevier, Amsterdam.
- BOUCHET, P., ROCROI, J.P., FRÝDA, J., HAUSDORF, B., PONDER, W., VALDES, A. & WARÉN, A. 2005. Classification and nomenclator of gastropod families. *Malacologia* 47(1–2), 1–368.
- BOWSHER, A.L. 1955. Origin and adaptation of platyceratid gastropods. *University of Kansas, Paleontological Contributions, Mollusca* 5, 1–11.
- BRETT, C.E., GAHN, F.J. & BAUMILLER, T.K. 2004. Platyceratid gastropods as parasites, predators, and prey and their possible effects on echinoderm hosts; collateral damage and targeting. *Geological Society of America Abstracts with Programs* 36(5), 478.
- CONRAD, T.A. 1840. Third Annual Report on the Paleontological Department of the Survey. *New York Geological Survey, Annual Report* 4, 199–207.
- FRÝDA, J. 1997. Oldest representatives of the superfamily Cirroidea (Vetigastropoda) with notes on their early phylogeny. *Journal of Paleontology* 71(5), 839–847.
- FRÝDA, J. 1998a. Did the ancestors of higher gastropods (Neritimorpha, Caenogastropoda, and Heterostrophia) have an uncoiled shell?, 107. In BIELER, R. & MIKKELSEN, P.M. (eds) *Abstracts, World Congress of Malacology*. UNITAS Malacologica, Chicago.
- FRÝDA, J. 1998b. Higher classification of the Paleozoic gastropods inferred from their early shell ontogeny, 108. In BIELER, R. & MIKKELSEN, P.M. (eds) *Abstracts, World Congress of Malacology*. UNITAS Malacologica, Chicago.
- FRÝDA, J. 1999. Higher classification of Paleozoic gastropods inferred from their early shell ontogeny. *Journal of the Czech Geological Society* 44, 137–152.
- FRÝDA, J. & BLODGETT, R.B. 1998. Two new cirroidean genera (Vetigastropoda, Archaeogastropoda) from the Emsian (late Early Devonian) of Alaska with notes on the early phylogeny of Cirroidea. *Journal of Paleontology* 72(2), 265–273.
- FRÝDA, J. & BLODGETT, R.B. 2004. New Emsian (late Early Devonian) gastropods from Limestone Mountain, Medfra B-4 quadrangle, west-central Alaska (Farewell terrane), and their paleobiogeographic affinities and evolutionary significance. *Journal of Paleontology* 78(1), 111–132. DOI 10.1666/0022-3360(2004)078<0111:NELEDG>2.0.CO;2
- FRÝDA, J. & FARRELL, J.R. 2005. Systematic position of two Early Devonian gastropods with sinistrally heterostrophic shells from the Garra Limestone, Larras Lee, New South Wales. *Alcheringa* 29, 229–240. DOI 10.1080/03115510508619303
- FRÝDA, J. & HEIDELBERGER, D. 2003. Systematic position of Cyrtoneritimorpha within class Gastropoda with description

- of two new genera from Siluro-Devonian strata of Central Europe. *Bulletin of Geosciences* 78(1), 35–39.
- FRÝDA, J., NÜTZEL, A. & WAGNER, P.J. 2008. Paleozoic gastropods, 237–268. In PONDER, W. & LINDBERG, D.L. (eds) *Phylogeny and Evolution of the Mollusca*. 466 pp. University of California Press, Berkeley & Los Angeles, California.
- FRÝDA, J. & ROHR, D.M. 2004. Gastropoda, 184–195. In WEBBY, B.D., PARIS, F., DROSER, M.L. & PERCIVAL, I.G. (eds) *The Great Ordovician Biodiversification Event*. 408 pp. Columbia University Press, New York.
- GAHN, F.J. & BAUMILLER, T.K. 2003. Infestation of Middle Devonian (Givetian) camerate crinoids by platyceratid gastropods and its implications for the nature of their biotic interaction. *Lethaia* 36(2), 71–82.
DOI 10.1080/00241160310003072
- HALL, J. 1859. Contributions to the palaeontology of New York; being some of the results of the investigations during the years 1855, 1856, 1857, and 1858. *Twelfth Annual Report of the Regents of the University of the State of New York on the condition of the State Cabinet of Natural History and the Historical and Antiquarian Collection Connected Therewith*, 8–110.
- HINDE, G.J. 1885. Description of a new species of crinoids with articulated spines. *Annals and Magazine of Natural History, 5th series*, 157–173.
- HORNÝ, R. 1964. Svalové vtisky u českých platyceratidních břichonožců (Gastropoda). [Muscle scars in the Bohemian platyceratids (Gastropoda).] *Časopis Národního muzea, Oddíl přírodovědný* 133(2), 88–92.
- HORNÝ, R. 1991. Vývoj názorů na klasifikaci cyklomyárních měkkýšů (Mollusca, Monoplacophora). [Problems of classification of the cyclomyan molluscs (Mollusca, Monoplacophora) – a historical review.] *Časopis Národního muzea, Řada přírodovědná* 157(1–4), 13–32.
- HORNÝ, R.J. 1995. Apertural location of the retractor muscle attachment area in *Oriostoma* (Mollusca, Gastropoda): a consequence of mode of life. *Časopis Národního muzea, Řada přírodovědná* 164(1–4), 39–44.
- HORNÝ, R.J. 2000a. Mode of life of some Silurian and Devonian platyceratids. *Bulletin of the Czech Geological Survey* 75(2), 135–143.
- HORNÝ, R.J. 2000b. *Tachloconcha* gen. n. and *Spirina* Kayser, 1889, two additional Lower Palaeozoic gastropods with preserved retractor muscle attachment areas. *Bulletin of the Czech Geological Survey* 75(4), 415–426.
- HORNÝ, R.J. 2004. The oldest description and illustration of muscle scars in platyceratid gastropods, published by Daniel Oehlert in 1883. *Časopis Národního muzea, Řada přírodovědná* 173(1–4), 59–64.
- HORNÝ, R.J. & PEEL, J.S. 1996. *Carcassonnella*, a new Lower Ordovician bellerophonitiform mollusc with dorsally located retractor muscle attachments (Class Tergomya). *Bulletin of the Czech Geological Survey* 71(4), 305–331.
- JANKOVSKÝ, M. 2003. Shell morphology and palaeoecology of *Praenatica gregaria* Perner, 1903 from the Koněprusy Limestone (Lower Devonian) of Bohemia (Czech Republic). *Bulletin of Geosciences* 78(4), 423–429.
- KEYES, C.R. 1888. On the attachment of *Platyceras* to palaeocrinoids, and its effects in modifying the form of the shell. *Proceedings of the American Philosophical Society, Transactions* 25, 231–243.
- KEYES, C.R. 1889. Variation exhibited by a Carbonic gastropod. *The American Geologist* 3, 330–333.
- KEYES, C.R. 1890. Generic relations of *Platyceras* and *Capulus*. *The American Geologist* 6, 6–9.
- KIEL, S. & FRÝDA, J. 2004. Shell structure of Late Cretaceous *Sensuitrochus ferrerii* (Cirridae, Gastropoda). *Journal of Paleontology* 78(4), 795–797.
DOI 10.1666/0022-3360(2004)078<0795:NILCSF>2.0.CO;2
- KNIGHT, J.B. 1941. Paleozoic gastropod genotypes. *Geological Society, Special Papers* 32, 1–510.
- KNIGHT, J.B. 1952. *Primitive fossil gastropods and their bearing on gastropod classification*. Smithsonian Miscellaneous Collections 117(13). 56 pp. Smithsonian Institution, Washington.
- KNIGHT, J.B., COX, L.R., BATTEN, R.L. & YOCHELSON, E.L. 1960. Systematic descriptions. In MOORE, R.C. (ed.) *Treatise on invertebrate paleontology. Part I. Mollusca 1*. University of Kansas Press, Lawrence, Kansas.
- LANE, N.D. 1978. Mutualistic relations of fossil crinoids, T345–T347. In TEICHERT, C. (ed.) *Treatise on Invertebrate Paleontology, Part T*. Geological Society of America & University of Kansas Press, Lawrence, Kansas.
- LANE, N.D. 1984. Predation and survival among inadunate crinoids. *Paleobiology* 10(4), 453–458.
- LE MENN, J. 1974. Le genre *Thylacocrinus* Oehlert, 1878 (Crinoidea, Camerata). *Annales de la Société Géologique du Nord* 94(3), 97–108.
- LE MENN, J. 1985. Les Crinoïdes du Dévonien inférieur et moyen du Massif Armoricain. *Mémoires de la Société Géologique et Minéralogique de Bretagne* 30, 1–268.
- LINDSTRÖM, A. & PEEL, J.S. 2003. Shell repair and mode of life of *Praenatica gregaria* (Gastropoda) from the Devonian of Bohemia (Czech Republic). *Palaeontology* 46(3), 623–633.
DOI 10.1111/1475-4983.00312
- MEEK, F.B. & WORTHEN, A.H. 1866. Descriptions of invertebrates from the Carboniferous System. *Geological Survey of Illinois 2, Palaeontology*, 143–411.
- MEEK, F.B. & WORTHEN, A.H. 1868. Notes on some points in the structure and habits of the Palaeozoic Crinoidea. *Proceedings of the Academy of Natural Sciences of Philadelphia* 20, 323–334.
- MEEK, F.B. & WORTHEN, A.H. 1873. Descriptions of invertebrates from the Carboniferous System, *Geological Survey of Illinois 5, Palaeontology* 2, 323–619.
- MEYER, D.L. & AUSICH, W.I. 1983. Biotic interactions among Recent and among fossil crinoids, 337–427. In TAVESZ, M.J.S. & MCCALL, P.L. (eds) *Biotic interactions in recent and fossil benthic communities*. Plenum Publishing Corp., New York.
- MORZADEC, P. 1971. Quelques Asteropyginae (Trilobites, Phacopacea) des schistes et calcaires à *Athyris undata* (Dévonien inférieur) du Massif Armoricain. *Palaeontographica A* 138, 166–184.

- NÜTZEL, A. & FRÝDA, J. 2003. Paleozoic plankton revolution: evidence from early gastropod ontogeny. *Geology* 31, 829–831. DOI 10.1130/G19616.1
- NÜTZEL, A., FRÝDA, J., YANCEY, T.E. & ANDERSON, J.R. 2007. Larval shells of Late Palaeozoic naticopsid gastropods (Neritopsoidea: Neritimorpha) with a discussion of the early neritimorph evolution. *Paläontologische Zeitschrift* 81(3), 213–228.
- OEHLERT, D. 1878. Description de deux nouveaux genres de Crinoides du terrain dévonien de la Mayenne. *Bulletin de la Société Géologique de France*, 3^e série 7, 6–10.
- OEHLERT, D. 1883. Description de deux nouvelles espèces d'Acroculia du Dévonien inférieur de la Mayenne. *Bulletin de la Société Géologique de France*, 3^e série 11, 602–609.
- PEEL, J.S. 1986. Muscle scars in *Porcellia* (Gastropoda; Pleurotomariacea) from the Carboniferous of England. *Bulletin of the Geological Society of Denmark* 35(1–2), 53–58.
- PEEL, J.S. 1991a. Functional morphology of the class Helcionelloida nov., and the early evolution of the Mollusca, 157–177. In SIMONETTA, A. & CONWAY, M.S. (eds) *The early evolution of Metazoa and the significance of problematic taxa*. Cambridge University Press & University of Camerino, Cambridge.
- PEEL, J.S. 1991b. The classes Tergomya and Helcionelloida, and early molluscan evolution. *Bulletin Grønlands Geologiske Undersøgelse* 161, 11–65.
- PEEL, J.S. 2001. Musculature and asymmetry in a Carboniferous pseudo-bellerophontoidean gastropod (Mollusca). *Palaeontology* 44(1), 157–166. DOI 10.1111/1475-4983.00175
- PONDER, W.F. & LINDBERG, D.R. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society* 119, 83–265. DOI 10.1111/j.1096-3642.1997.tb00137.x
- RACHEBOEUF, P.R. 1976. Chonetacea (Brachiopodes) du Dévonien inférieur du Bassin de Laval (Massif Armorica). *Palaeontographica A* 152, 14–89.
- RENAUD, A. 1930. Etude de la faune de calcaires dévoniens de bois-Roux. *Bulletin de la Société Géologique et Minéralogique de Bretagne* 9(1928), 141–292.
- RENAUD, A. 1942. Le Dévonien du Synclinorium Médian Brest-Laval. *Mémoires de la Société Géologique et minéralogique de Bretagne* 7(1), 1–184 (Stratigraphie), (2), 1–439 (Paléontologie).
- ROLLINS, H.B. & BREZINSKI, D.K. 1988. Reinterpretation of crinoid platyceratid interaction. *Lethaia* 21(3), 207–217.
- SIGNOR, P.W. & BRETT, C.E. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology* 10, 229–245.
- SUTTON, M.D., BRIGGS, D.E.G., SIVETER, D.J. & SIVETER, D.J. 2006. Fossilized soft tissues in a Silurian platyceratid gastropod. *Proceedings of the Royal Society B: Biological Sciences* 273(1590), 1039–1044.
- WAHLMANN, G.P. 1992. Middle and Upper Ordovician symmetrical univalved mollusks (Monoplacophora and Bellerophonina) of the Cincinnati Arch region. *U.S. Geological Survey Professional Paper* 1066-O, O1–O203.
- WENZ, W. 1938–1944. Gastropoda, 1–1639. In SCHINDEWOLF, O.H. (ed). *Band 6, Teil 1–7, Handbuch der Paläozoologie*. Borntraeger, Berlin.
- WENZ, W. 1940. Ursprung und frühe Stammesgeschichte der Gastropoden. *Archiv für Molluskenkunde* 72, 1–10.
- YOCHELSON, E.L. 1967. Quo Vadis, Bellerophon?, 141–161. In MOORE, R.C. (ed.) *Essays in paleontology and stratigraphy*. University of Kansas Press, Lawrence.
- YOO, E.K. 1994. Early Carboniferous Gastropoda from the Tamworth Belt, New South Wales, Australia. *Records of the Australian Museum* 46, 63–120.