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 Céneré 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.


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 Armorican, 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 vanniotti 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 Cénéré Formation. At St Jean-sur-Mayenne, the limestones of the St Cénéré 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 protea (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 Platycceras (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 Platycceras, 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 Platycceras 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 (Jankovsky 2003). Any progress in the taxonomy of the genera Orthonychia and Platycceras, 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 gastropods.

![Figure 1. Muscle scars in the Early Devonian Orthonychia protea (Oehlert, 1883) from Brittany (France).](image-url)
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, Nerrhenidae, 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 platyceratids 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 cyrtoneilloid molluscs. These studies of muscle scars have been focused mainly on “problematic extinct” molluscan taxa like bellerophontiform molluscs (see Wahlmann 1992, Horný 1991, Horný & Peel 1996, Peel 2001 for a review) and they have led to a consensus view that bellerophontiforms 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 bellerophonts (Knight 1952). Nevertheless, not only muscle scars of bellerophontiform 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 anisostrophically-coiled gastropods (e.g., Horný 1995, 2000b, 2004). Platycepidids 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) shows growth lines giving 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 teleconchs 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 teleconchs with an irregular aperture the muscle scar is more laterally situated (Fig. 1G, H, K). In teleconchs 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 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 proteyi

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 undulate (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 calicites 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 Spiniplatyceras 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
increasing predatory “stress” since the Devonian (Signor & Brett 1984, Nützel & Fryda 2003, Berkyvová 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 Brachythiris 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 Devonian 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 Cénéré 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 Dimereocrinites 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
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).
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