Unsuccessful predation on Middle Paleozoic plankton: Shell injury and anomalies in Devonian dacryoconarid tentaculites

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Anomalous development of shell ornamentation and repaired shell injury in the Early Devonian dacryoconarid tentaculites are documented and interpreted as either a repaired injury of the shell (evidence of unsuccessful predation obscured by recrystallization), or as a result of an anomalous function of the mantle, caused by injury of the soft body. The manner of shell repair, which resembles the way that some modern marine animals, such as mollusks, repair their shells, is discussed. The issue of phylogenetic affinities of tentaculites has been also outlined. These findings represent the first documentation of unsuccessful predation on the Middle Paleozoic plankton.

Key words: Tentaculitoidea, predation, shell repair, Devonian.

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Introduction

In the last two decades much attention has been paid to predator-prey interactions and to the evolutionary significance of predation itself. Predation has been used to explain many macroevolutionary trends (for reviews see Brett and Walker 2002; Kelley et al. 2003). Despite the importance accorded to predation, the role of predator-prey interactions in evolution remains controversial (e.g., the controversy of two related processes, coevolution and escalation, has been discussed in many papers (e.g., Vermeij 1987; Dietl and Kelley 2002; Dietl 2003)). There is general agreement that an understanding of the macroevolutionary effects of predation requires a knowledge of the predator-prey interactions within the fossil record. Although documentation of ancient predation is difficult, we do have quite a lot of information about the benthic ecosystem, which is reasonably documented. However, there is a lack of documentation of predation in the pelagic ecosystem, particularly in the planktonic realm. There has been only indirect evidence of predation in the planktonic ecosystem during the Paleozoic—demonstrations of antipredatory devices in early phytoplankton, represented by acritarchs (Bengtson 2002) or indirect evidence for predation on graptolites (Underwood 1993).

Vermeij (2002) noted that unsuccessful predation is one of the main reasons why the predation is regarded as an important agency of evolution. According to this author, unsuccessful predation is an extremely common phenomenon, which is directly manifested by repaired injuries. Shell repair has generally been increasing throughout Paleozoic time (Vermeij 2002). During the Phanerozoic, there had been two major increases in predator intensity—the "Middle Paleozoic Marine Revolution" (Signor and Brett 1984) and the "Mesozoic Marine Revolution" (Vermeij 1977). According to the first authors, there is a growing body of evidence that the selective pressure from durophagous predators had, during the Devonian, been markedly increasing. Around the same time, mollusks and other shell-bearing marine animals developed better protective mechanisms such as more spines or more tightly coiled shells (Brett 2003). There is a good evidence for the predation (including unsuccessful predation) on the Devonian benthic organisms as can be inferred from the findings of shells with boreholes and repaired injuries. However, there has been hitherto no evidence for unsuccessful predation in the Devonian planktonic ecosystem. In this short paper, we report an occurrence of anomalous development of shell ornamentation and repaired shell injury on Early Devonian dacryoconarid tentaculites. These shell anomalies are interpreted to be a result of unsuccessful predation on these Middle Paleozoic planktonic organisms.

Institutional abbreviations.—NM, National Musem (Národní muzeum), Prague, Czech Republik; CGU, Czech Geological Survey (Česká geologická služba).

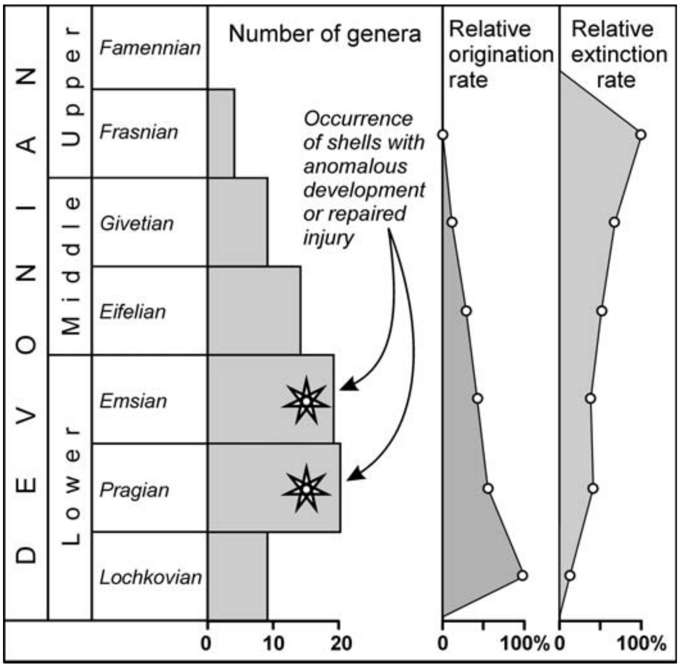

Fig. 1. Diagrams illustrating the total generic diversity of the Order Dacryoconarida and their turnover rates (relative origination and extinction rates). The generic diversity (including the both genera and subgenera) is defined as the number of generic taxa ranging through the time unit, plus half of the number of those confined to the unit or ranging beyond the time unit, but originating or ending within it. Relative turnover rates (origination or extinction) is defined as the total number of generic level taxa originating or going extinct within the time unit, divided by the total generic diversity. Analysis is based on data of Alberti (1993, 1997a, b, 1998, 2000) and Sepkoski (2002).

Devonian zooplankton and dacryoconarid tentaculites

The Devonian period is regarded as a time of major changes in both the terrestrial and marine biospheres, which resulted, among others, in perturbances in the world's planktonic realm (including the early Devonian extinction of graptolites, the appearance of dacryoconarid tentaculites; the Late Devonian decline of acritarchs, and Late Devonian extinction of tentaculites). Nützel and Frýda (2003) documented the macroevolutionary trends in the morphology of planktonic gastropod larvae, towards decreasing proportions of open-coiled protoconchs. According to these authors, this morphological adaptation was in reaction to the increasing activity of Devonian predators. In addition, during the Devonian, some marine invertebrates changed their larval feeding strategy. Frýda (2004) pointed out that the most important post-Cambrian change in larval strategy within the Class Gastropoda (i.e., inception of larval planktotrophy) occurred during the Devonian, and it seems to have been connected with fundamental changes in biogeochemical evolution of the Middle Palaeozoic oceans.

Dacryoconarid tentaculites represent the most typical group of Devonian zooplankton. They appeared in the Lochkovian and during a short time (in the Pragian) they reached a high diversity of about 20 genera and subgenera (Fig. 1), and a cosmopolitan distribution. During the Early and Middle Devonian they were among the most important macrozooplankton. As such, they constituted a large reservoir of available energy within the water column, and thus were one of the major utilizable food sources for pelagic or nektonic predators. Beginning in the middle Early Devonian (Fig. 1), their diversity and relative origination rate started to decline; and their relative extinction rate to increase. Dacryoconarid tentaculites became extinct by the end of the Devonian. It is noteworthy that the time of change in the evolutionary dynamics of dacryoconarid tentaculites (i.e., late Early Devonian) coincides in time with the appearance of the oldest gastropods with planktotrophic development (Frýda 2001; Frýda and Blodgett 2001, 2004). The anomalous shell developments and the repaired injuries in the dacryoconarid shells, documented in this paper, are restricted to the Pragian and Emsian times, as well.

Anomalous shell development and shell injuries

Two different patterns of anomalous shell development were observed in the Early Devonian dacryoconarids. The first comprises shells with an irregular arrangement of the rings (Fig. 2A, B). This type was documented in one specimen of the Pragian *Nowakia* (*Turkestanella*) *acuaria* Richter, 1854, as well as in nine Emsian specimens: *Nowakia cancellata* Richter, 1854 (one specimen); *Homoctenus hanusi* Bouček, 1964 (four specimens); and *Nowakia elegans* Barrande, 1867 (four specimens). Another type of anomalous shell development comprises irregular scars on the shell, documenting the repaired injury. This type was found on the shell of the Emsian *Nowakia elegans* Barrande, 1867 (Figs. 2C, 3). In the latter specimen, the new shell material, repairing the damage, was secreted and attached onto the inner side of the shell. Ornamentation on the newly formed shell differs from the ornamentation terminated by breakage (Figs. 2, 3). Both the regenerated rings and ribs are initially disarranged; however, the arrangement of rings and ribs, typical for this species, was soon restored (Fig. 3).

The present study is based on materials, which comprise samples collected by Pravoslav O. Novák, Bedřich Bouček, and Pavel Lukeš (collections of the National Museum, Prague, Czech Republic, and the private collection of Pavel Lukeš). It is important to mention that each of the above-mentioned scientists had been dealing with tentaculites for a very long time. Among the many thousands of dacryoconarid shells studied, only a few specimens with an anomalous development of shell ornament were found; and just one specimen with an apparent repaired injury. The frequency of shells

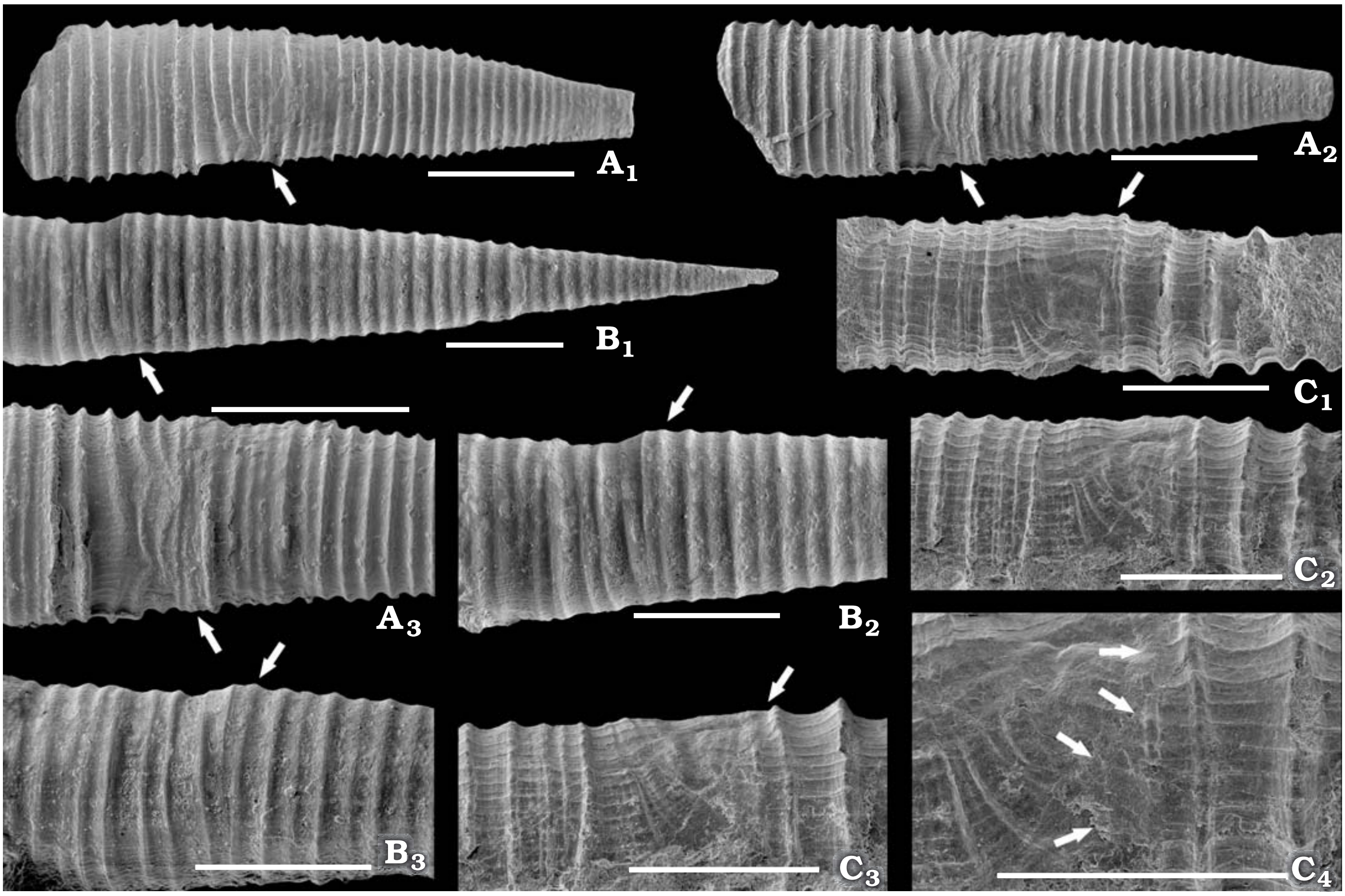

Fig. 2. The shells of the Early Devonian dacryoconarid tentaculites, with anomalous development of the shell ornament or having repaired injuries. **A**. The Emsian *Homoctenus hanusi* Bouček, 1964 (NM L6288) from Daleje-Třebotov Formation, Prague Basin, Holyně locality. Views showing an anomalous development of the shell ornamentation. **B**. The Pragian *Nowakia* (*Turkestanella*) *acuaria* Richter, 1854 (NM L6291) from Praha Formation, Prague Basin, Bráník locality. Views showing the irregular development of the rings. **C**. The Emsian *Nowakia elegans* Barrande, 1867 (CGU PL3970) from the Zlíchov Formation, Prague Basin, Klukovice Locality. Several views demonstrating the damage and the manner of shell repair. All shells illustrated have the same orientation (growth direction is from right to left). Scale bars 1 mm.

bearing traces of repaired injury is less than 0.1%. Therefore, it is obvious that the shells described represent quite a rarity. Nevertheless, it cannot be ruled out that the number of specimens bearing traces of repaired injuries was slightly higher than could be inferred from the above-mentioned data. The dacryoconarid shell with repaired injury described showed a very distinctive deviation from normal shell development (Figs. 2C, 3). However, among some modern invertebrate planktonic animals (such as planktonic gastropod larvae), such distinctive anomalies represent only a small portion of all shells bearing traces of repaired injuries. The vast majority of those showed only slight and weak traces of repaired shell breakage (Fig. 4), which were only observable with use of a SEM. Such indistinct traces cannot be documented in the Devonian dacryoconarids because their shells have been recrystallized, and such fine details were obscured. Therefore, it is plausible that the specimens described here, with anomalous development of the shell ornamentation, in fact may represent shells with repaired injuries, the traces of which were obscured during recrystallization.

Discussion

The newly secreted shell material, repairing damage in the Emsian *Nowakia elegans* (Figs. 2C, 3), is attached on the inner side of the broken shell. This feature resembles the manner with which some modern marine animals, such as mollusks, repair their shells. This same manner of shell repair has been documented in adult benthic mollusks, as well as in planktonic larval shells (e.g., in planktonic gastropod larvae, Fig. 4). Such a similarity may suggest some anatomical as well as phylogenetic affinities. The tentaculites have been assigned to different taxonomic groups. The prevalent opinion on their systematic affinity is that dacryoconarid tentaculites are closely related to molluscs (e.g., Gürich 1896; Fisher 1962; Bouček 1964; Alberti 1975, 1993; Farsan 1994). In molluscs, it is the mantle that is responsible for the secretion of new shell material (similar tissue known as the mantle lobe occurs also in brachiopods). The manner of shell repair, described in the Early Devonian member of the Order

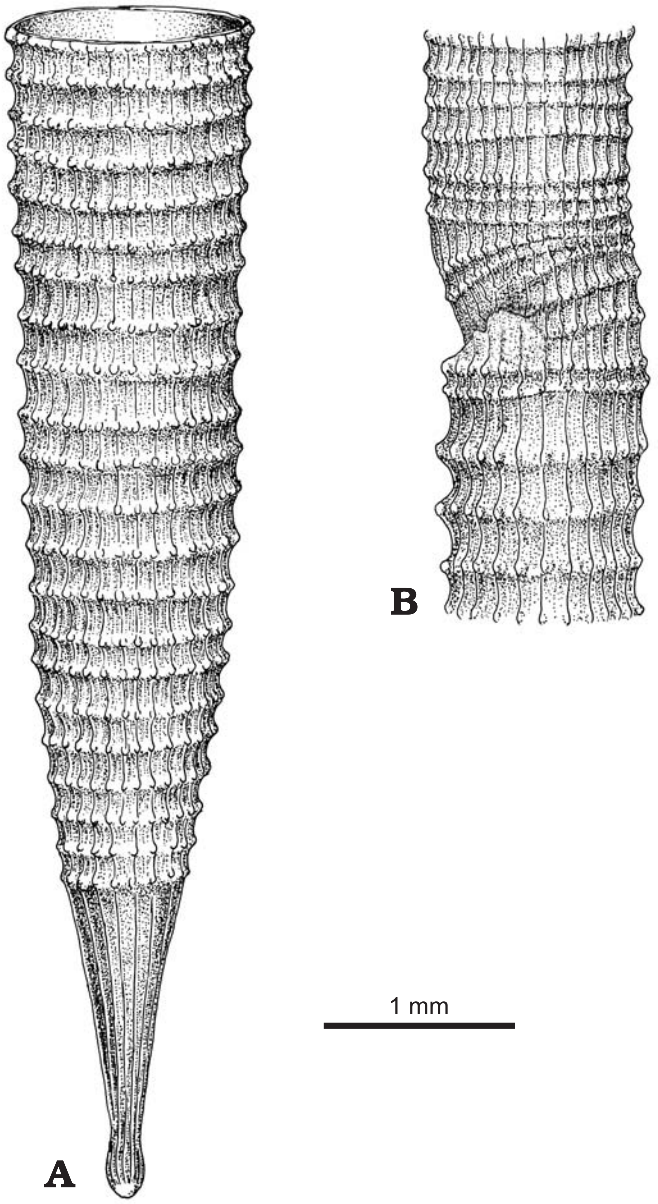

Fig. 3. Reconstructions of the Emsian tentaculite *Nowakia elegans* Barrande, 1867. **A**. Adult shell having normal development. **B**. Reconstruction of the shell figured here as Fig. 2C.

Dacryoconarida Fisher, 1962 could lend support to their molluscan affinity. It is noteworthy that Larsson (1979) described the same method of shell repair in the representatives of the Order Tentaculitida Ljaschenko, 1955. This group is commonly regarded as benthic, and is generally assigned to the same class as dacryoconarids (Tentaculita Bouček, 1964). However, in contrast to the Dacryoconarida, the Silurian representatives of the order Tentaculitida have sometimes been regarded as lophophorates, rather than molluscs (Towe 1978; Lardeux 1969).

Recognition of the causes of shell injury is fundamental, whether made by predators or caused by mechanical damage to the shell by any abiotic process (i.e., by a collision of the shell with any hard object). Several studies on benthic communities (e.g., Vermeij 1982; Feige and Fürsich 1991) have shown that most shell injuries may be attributed to predators, rather than to fragmentation by waves or other mechanical agents. Considering the size of dacryoconarid tentaculites (on average 4 mm long and 1 mm wide, thin-walled cones), their habitat (the open sea), and the tensile properties of water, the possibility of their mechanical damage is very unlike. Some recent experiments on caenogastropod larvae (Hickman 2001) have shown that damage of the planktonic larval shell only occurred when zooplankton predators were present. Similarly Aktürk (1976) and Bé and Spero (1981) suggested that natural predators most commonly caused damage to shells of planktonic organisms, particularly foraminifers.

As mentioned above, the Devonian dacryoconarid tentaculites represented a large reservoir of accessible energy within the water column, and thus were one of the major utilizable sources for pelagic or nektonic predators. Although the identification of the predator is highly speculative, the Devonian sea was undoubtedly fully occupied with potential predators, interested in such a food reservoir. We postulate that attacks by, or contact with the predator (and their victims—dacryoconarid tentaculites) probably occurred with a high frequency. As mentioned above, there are several indirect suggestions for increasing predation activity on the Devonian plankton (e.g., macroevolutionary trends in the morphology of the gastropod larvae, and change in the evolutionary dynamics of dacryoconarids). For all of the above-mentioned factors, we interpret the documented repaired injury of *Nowakia elegans* Barrande, 1867 to be as a result of unsuccessful predation upon this planktonic organism. Regarding those specimens with an anomalous development of their shell ornamentation, parasite infestation (or some disease) could not be excluded. It is obvious, however, that all of the described specimens survived these events. The authors of this paper regard the anomalous development of shell ornamentation as either a repaired injury of the shell (evidence of unsuccessful predation obscured by recrystallization), or as a result of an anomalous function of the mantle, caused by injury of the soft body. Generally, the scarce data about predation upon fossil planktonic organisms is not only a preservation artifact (the lack of traces of weak shell injuries because their erasure during shell recrystallization), but this rarity also may be influenced by the low values in the ratio between unsuccessful and successful predator attacks on small planktonic organisms. According to Vermeij (2002) there is also another possible explanation of the rarity, namely the absence of shell breakers. However, the latter possibility can be ruled because crushing predators (e.g., phylocarid crustaceans, goniatite ammonoids, conodont animals, fish) have been well documented in Devonian.

Taken together it is obvious that documentation of the anomalous development of the shell ornament and repaired injury in the Devonian dacryoconarids is a rarity. This is most probably caused by unsuccessful predation upon these

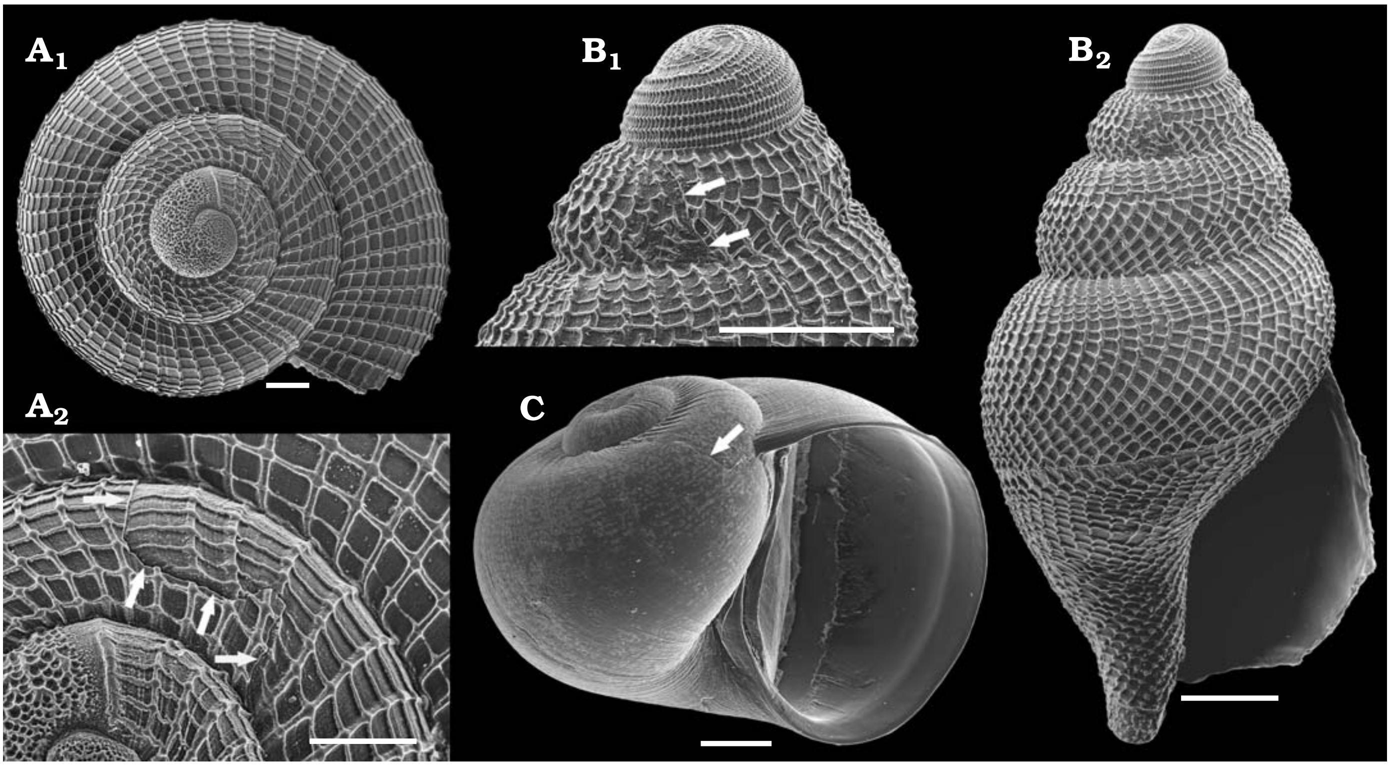

Fig. 4. The shells of the Recent planktonic gastropod larvae bearing traces of repaired injuries. **A**. CGU JF819; A_1, apical view of cypraeid protoconch with repaired apertural margin; A_2, detailed view of specimen A_1. **B**. CGU JF820; B_1, detail of view of turrid protoconch; B_2, lateral view of turrid protoconch. **C**. CGU JF821, naticid protoconch with repaired apertural margin. Damaged apertural margins indicated by white arrows. Scale bars 0.1 mm.

planktonic organisms. Nevertheless, the erroneous attacks on these planktonic organisms cannot be ruled out. If this interpretation is correct, then this is, according to our knowledge, the first documented evidence of unsuccessful predation on Palaeozoic zooplankton.

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References

Aktürk, S.E. 1976. Traumatic variation in the Globorotalia Menardii D'Orbigny group in late Quaternary sediments from the Caribbean. *Journal of Foraminiferal Research* 6 (3): 186–192.

Alberti, G.K.B. 1975. Zur struktur der Gehäusewand von *Styliolina* (Dacryoconarida) aus dem Unter-Devon von Oberfranken. *Senckenbergiana lethaea* 55: 505–511.

Alberti, G.K.B. 1993. Dacryoconariden und homocteniden Tentaculiten des Unter-und Mittel-Devons I. *Courier Forschungsinstitut Senckenberg* 158: 1–230.

Alberti, G.K.B. 1997a. Planktonische Tentaculiten des Devon. I. Homoctenida Boucek 1964 und Dacryoconarida Fisher 1962 aus dem Unterbis Ober-Devon. *Palaeontographica A* 244: 85–142.

Alberti, G.K.B. 1997b. Planktonische Tentaculiten des Devon. II. Dacryoconarida Fisher 1962 aus dem Unter- und Mittel-Devon. *Palaeontographica A* 246: 1–32.

Alberti, G.K.B. 1998. Planktonische Tentakuliten des Devon. III. Dacryoconarida Fischer 1962 aus dem Unter-Devon und oberen Mitteldevon. *Palaeontographica A* 250: 1–46.

Alberti, G.K.B. 2000: Planktonische Tentakuliten des Devon. IV. Dacryoconarida Fisher 1962 aus dem Unter-Devon. *Palaeontographica A* 256: 1–23.

Barrande, J. 1867. *Système Silurien du Centre de la Bohême, 1e partie, vol. 3. Ptéropodes*. 179 pp. Chez l'auteur Paris, Prague.

Bé, A.W.H. and Spero, H.J. 1981. Shell regeneration and biological recovery of planktonic foraminifera after physical injury induced in laboratory culture. *Micropaleontology* 27: 305–316.

Bengtson, S. 2002. Origins and early evolution of predation. *In*: M. Kowalewski and P.H. Kelley (eds.), The Fossil Record of Predation. *Palaeontological Society Special Papers* 8: 289–317.

Bouček, B. 1964. *The Tentaculites from Bohemia. Their Morphology, Taxonomy, Ecology, Phylogeny and Biostratigraphy*. 215 pp. Publishing House of the Czechoslovak Academy of Sciences, Prague.

Brett, C.E. 2003. Durophagous predation on Paleozoic marine benthic assemblages. *In*: P.H. Kelley, M. Kowalewski, and T. Hansen (eds.), *Predator-Prey Interactions in the Fossil Record*, 401–432. Topics in Geobiology, Kluwer Academic/Plenum Publishers, New York.

Brett, C.E. and Walker, S.E. 2002. Predators and predation in Paleozoic marine environments. *In*: M. Kowalewski and P.H. Kelley (eds.), The Fossil Record of Predation. *Palaeontological Society Special Papers* 8: 93–118.

Dietl, G.P. 2003. The escalation hypothesis: One long argument. *Palaios* 18: 83–86.

Dietl, G.P. and Kelley, P.H. 2002. The fossil record of predator-prey arms races: coevolution and escalation hypotheses. *In*: M. Kowalewski and P.H. Kelley (eds.), The Fossil Record of Predation. *Palaeontological Society Special Papers* 8: 353–374.

Farsan, N.M. 1994. Tentaculiten: Ontogenese, Systematik, Phylogenese, Biostratonomic und Morphologie. *Abhandlungen der Senckenbergischen Naturforschcnden Gesellschaft* 547: 1–128.

Feige, A. and Fürsich, F.T. 1991. Taphonomy of the recent molluscs of Bahia la Choya (Gulf of California, Sonora, Mexico). *In*: F.T. Fürsich and K.W. Flessa (eds.), Ecology, Taphonomy, and Paleoecology of Recent and Pleistocene Molluscan Faunas of Bahia la Choya, northern Gulf of California. *Zitteliana* 18: 89–133.

Fisher, D.W. 1962. Small conoidal shells of uncertain affinities. *In*: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology, Part W, Miscellanea*, 98–143. The Geological Society of America and University of Kansas Press, Lawrence, Kansas.

Frýda, J. 2001. Discovery of a larval shell in Middle Paleozoic subulitoidean gastropods with description of two new species from the Early Devonian of Bohemia. *Bulletin of the Czech Geological Survey* 76 (1): 29–37.

Frýda, J. 2004. Phylogeny of Paleozoic gastropods and origin of larval planktotrophy. *In*: F.E. Wells (ed.), *Proceedings of the World Congress of Malacology, Perth 2004, Western Australia*, 42–43. University of Western Australia, Perth.

Frýda, J. and Blodgett, R.B. 2001. The oldest known heterobranch gastropod, *Kuskokwimia* gen. nov., from the Early Devonian of west-central Alaska, with notes on the early phylogeny of higher gastropods. *Bulletin of the Czech Geological Survey* 76 (1): 39–53.

Frýda, J. and 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: 111–132.

Gürich, G. 1896. Das Palaeozoikum im Polnischen Mittelgebirge. *Verhandlungen der Russisch-Kaiserlichen Mineralogischen Gesellschaft zu St. Petersburg* 2 (32): 1–539.

Hickman, C.S. 2001. Evolution and development of gastropod larval shell morphology: experimental evidence for mechanicall defense and repair. *Evolution & Development* 3: 18–23.

Kelley, P.H., Kowalewski, M., and Hansen, T.A. (eds.) 2003. *Predator-Prey Interactions in the Fossils Record*. 464 pp. Kluwer Academic/Plenum Publishers, New York.

Lardeux, H. 1969. Les Tentaculites d'Europe occidentale et d'Afrique du Nord. *Cahiers de Paléontologie*. 239 pp. Editions du Centre National de la Recherche Scientifique, Paris.

Larsson, K. 1979. Silurian tentaculitids from Gotland and Scania. *Fossils and Strata* 11: 1–180.

Nützel, A. and Frýda, J. 2003. Palaeozoic plankton revolution: Evidence from early gastropod ontogeny. *Geology* 31 (9): 829–831.

Richter, R. 1854. Thüringische Tentaculiten. *Deutsche Geologische Gesellschaft* 6 (2): 275–290.

Sepkoski, J.J. Jr. 2002. A compendium of fossil marine animal genera. *Bulletins of American Paleontology*. 363: 1–560.

Signor, P.W. and Brett, C.E. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology* 10: 229–245.

Towe, K.M. 1978. Tentaculites: Evidence for brachiopod affinity? *Science* 201: 26–28.

Underwood, C.J. 1993. The position of graptolites within Lower Palaeozoic planktic ecosystems. *Lethaia* 26: 189–202.

Vermeij, G.J. 1977. The Mesozoic marine revolution: Evidence from snails, predators, and grazers. *Paleobiology* 3: 245–258.

Vermeij, G.J. 1982. Unsuccessful predation and evolution. *American Naturalist* 120: 701–720.

Vermeij, G.J. 1987. *Evolution and Escalation*. 527 pp. Princeton University Press, Princeton, New Jersey.

Vermeij, G.J. 2002. Evolution in the consumer age: predators and the history of life. *In*: M. Kowalewski and P.H. Kelley (eds.), The Fossil Record of Predation. *Palaeontological Society Special Papers* 8: 375–393.