Paleozoic plankton revolution: Evidence from early gastropod ontogeny

Alexander Nützel* Institut für Paläontologie, Universität Erlangen, Loewenichstrasse 28, D-91054 Erlangen, Germany
Jiri Frýda Cesky geologicky ustav, Klarov 3/131, 118 21 Praha 1, Czech Republic

ABSTRACT

A major macroevolutionary trend in gastropod larval shell morphology occurred throughout the middle and late Paleozoic. The majority of Ordovician and Silurian gastropods have openly coiled initial whorls; this morphology was gradually lost. Mesozoic gastropods have exclusively tightly coiled initial whorls. Most protoconchs were formed by planktonic larvae, and this is the first documentation of a supraspecific trend in Paleozoic invertebrate larvae. Open coiling makes shells weak and vulnerable to attack and force. The replacement of weak-shelled plankton by stronger-shelled plankton was probably caused by predatory, selective forces. It coincides with other fundamental changes in plankton communities during the middle and late Paleozoic, including the decline of acritarchs and graptolites. Plankton communities suffered from crises that were probably caused by extrinsic forces. During plankton restructuring in the aftermath, predation could have become an increasingly important selective factor for gastropod larvae.

Keywords: Paleozoic larval shells, gastropods, macroevolution, plankton predation.

INTRODUCTION

The surprising discovery of openly coiled early ontogenetic shells in Paleozoic snails was one of the most important paleontological contributions to the research of the gastropod evolution in the past decades. This feature has been used in phylogenetic analyses and for taxonomic diagnoses (e.g., Dzik, 1994, 1999; Frýda and Manda, 1997; Bandel and Frýda, 1998, 1999; Nützel et al., 2000; Frýda and Heidelberger, 2003). Its paleobiological implications are even more interesting, especially concerning its function and the reason why this openly coiled morphology was lost during the Paleozoic. The quantitative assessment of the openly coiled larval shell morphology shows that its gradual loss represents one of the clearest examples for a macroevolutionary trend, comparable to Vermeijs Mesozoic marine revolution. Since the Jurassic–Cretaceous marine revolution, gastropods representing a wide variety of clades have reacted to increasing selective pressure by durophagous (shell crushing) predators by building stronger external sculptures and narrower apertures bearing dentition (Vermeij, 1977, 1987). Such macroevolutionary changes are probably not constrained by parallel mutations in genomes of separate evolutionary lineages, but by selective forces (Erwin, 2000; Jablonski, 2000). The gradual disappearance of openly coiled gastropod larval shells during the Paleozoic indicates a major change in embryonic and larval shell morphology of this highly diverse marine invertebrate group and represents the first fossil example for a distinct macroevolutionary trend in larval morphology of an invertebrate group. Open coiling makes shells weak and vulnerable to attack and force. The replacement of weak-shelled by stronger-shelled planktonic gastropod larvae was probably caused by predatory, selective forces.

Protoconchs are early ontogenetic gastropod shells that are formed by planktonic larvae and within egg capsules. In well-preserved fossil gastropods, protoconchs may be preserved on the apex of the adult shell. Consequently, gastropod shells reflect ontogenies and life histories to an exceptionally high degree when compared to most other marine invertebrates (Jablonski and Lutz, 1983). Protoconchs can differ considerably from adult shells in shape and ornament and can be used for phylogenetic studies (e.g., Bandel and Frýda, 1999; Nützel et al., 2000) or to infer larval strategies for biogeographic and diversity studies (Jablonski, 1986). When well preserved, it is possible to reconstruct life histories of Paleozoic gastropods. However, preservation of early ontogenetic shells of Paleozoic and early Mesozoic gastropods is rare because protoconchs are small (usually $<$1 mm), delicate, and aragonitic. Consequently, they are commonly removed from the fossil record by taphonomic and diagenetic processes. Despite their comparative rarity, over the past 25 years protoconchs have been increasingly studied and imaged using scanning electron microscopy.

METHODS

We have compiled a database of all published gastropod protoconchs from the Ordovician to the Triassic. In addition, unpublished data were included in the database, which contains 507 species-level taxa with known protoconchs. The protoconchs of just 8% of all described Triassic gastropod species are known and the percentage is even lower for Ordovician to Permian stages, but because the data come from different supraspecific taxa and a wide range of fossil localities representing different stages, sampling can be considered to be essentially random.

Open coiling is used to describe a range of protoconch morphologies in which the interior side of the initial shell tube is disjunct along the coiling axis. Such protoconchs may be umbilicated with a central gap, coiled in a loose spiral, or they may be stretched and tube-like (Fig. 1). Using the present database, the relative occurrence of this conspicuous larval shell morphology can be shown quantitatively through the period 450–200 Ma or approximately the first half of the duration of the class Gastropoda (Fig. 2). Of all described or illustrated Ordovician gastropod species with known protoconchs, 61.0% have an open initial whorl. Ordovician small shelly faunas from different areas of Baltica consist entirely of isolated protoconchs of this type (Bockelie and Yochelson, 1979). Only a few Silurian gastropod protoconchs have been reported (Dzik, 1994; Frýda, 1999) (Fig. 1C), but two largely undescribed small shelly assemblages from Silurian strata of the Prague Basin consist of more than 80% of isolated openly coiled protoconchs (our observation). Of all Devonian protoconchs, 17.4% are openly coiled. This percentage drops further in the Carboniferous (11.7%) and Permian (2.4%). Not a single openly coiled initial whorl has been reported for the Triassic. There is also no report of a post-Triassic protoconch of this form excepting the modern holoplanktic pteropods, which have a stretched protoconch (Bandel and Hemleben, 1995). However, these gastropods are highly derived and have a fossil record only to the early Tertiary. Therefore, their protoconch morphology is not homologous with that of early Paleozoic gastropods, but represents an adaptation to a completely planktonic life cycle. The Caecidae are the only extant benthic gastropods with similar stretched or uncoiled protoconchs, but in contrast to Paleozoic gastropods, their initial whorls are always tightly coiled (Ponder and Keyzer, 1998).

*E-mail: nuetzel@pal.uni-erlangen.de.

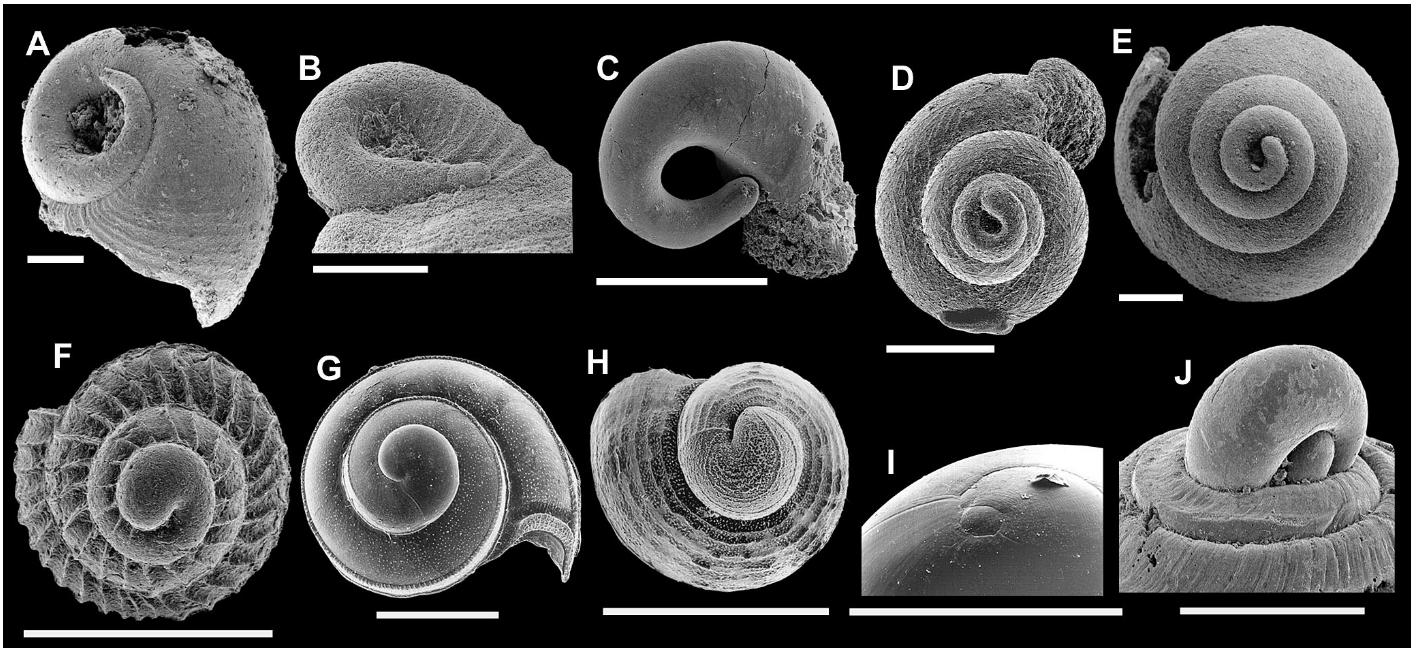

Figure 1. Gastropod initial whorls; scale bars = 0.3 mm. A–E: Ancient type (openly coiled) from Early Devonian (A, E), Late Silurian (C), and Carboniferous (B, D). A is neritimorph, B is limpet-shaped platyceratid, C is isolated larval shell, E is caenogastropod. F–J: Closely coiled initial whorls in four major modern gastropod groups. F is Carboniferous and G is Holocene caenogastropod larval shell. H is Holocene vetigastropod, I is Holocene neritimorph, and J is Pliocene heterostrophic. Sources: A—Fry´da and Manda (1997), B—Bandel and Frýda (1999), C—Fry´da and Blodgett (2001), D, F—Nu¨tzel and Mapes (2001), E—Fry´da (1999), G–J—this study.

DISCUSSION

In contrast to modern gastropods, most early Paleozoic gastropods hatched with a loose initial whorl. The presence of such tube-like protoconchs in most early Paleozoic gastropod groups suggests that this type of protoconch could represent the plesiomorphic state in Gastropoda (Frýda, 1999; Nützel and Mapes, 2001). Few data about the initial whorls of Cambrian univalves are available (Runnegar, 1981, 1983). Some of the oldest putative gastropods such as *Aldanella* have a loosely or openly coiled initial whorl (Runnegar, 1983). However, the phylogenetic relationships of Cambrian univalves to their supposed younger descendants are unresolved (Wagner, 2002). The majority of them are even interpreted to represent untorted molluscs (Peel, 1991). It is currently not possible to correlate the timing of torsion to stages of shell formation (Wanninger et al., 2000); therefore, it is unclear whether openly coiled larval shells were formed by torted or untorted life stages, and it is possible that the larvae of these ancient gastropods were untorted prior to metamorphosis. The initial cap of many of the early Paleozoic gastropods with tube-like protoconchs is ~50–100 μm. In comparison to recent gastropod larval shells, this indicates that they hatched at a small size and that the eggs did not contain much yolk. In gastropods with tightly coiled initial whorls, this size would suggest planktonic and possibly planktotrophic larval development (Jablonski and Lutz, 1983). The only known exception is the planispiral Euomphalidae, which has an initial cap diameter of ~150–200 μm (Nützel, 2002) that indicates lecithotrophic early ontogeny. Therefore, it is likely that the majority of Paleozoic open protoconchs represent shells of planktonic larvae. This is strongly supported by the presence of Ordovician and Silurian small shelly assemblages in which adults are absent and that represent larval shell communities in which metamorphosis was prevented by unfavorable conditions on the bottom (Nützel and Mapes, 2001). In contrast, a gastropod larval shell assemblage from the late Paleozoic (Mississippian) of Arkansas consists largely of specimens with tightly coiled initial whorls (Nützel and Mapes, 2001).

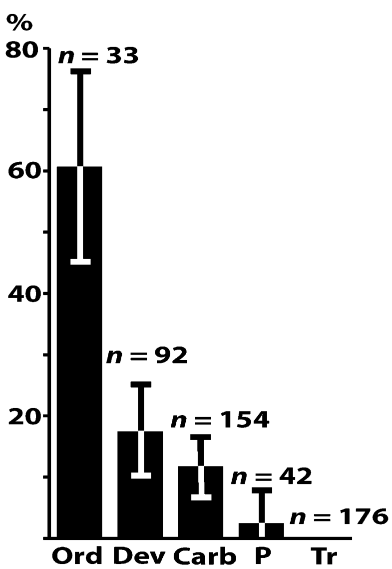

Figure 2. Occurrence of openly coiled initial whorls from Ordovician to Triassic (in percent of published species with known protoconchs). Too few published data are available for Cambrian and Silurian. Ord, Ordovician; Dev, Devonian; Carb, Carboniferous; P, Permian; Tr, Triassic; error bars represent 95% confidence intervals, calculated after Raup (1991) and Kiessling (2002, personal commun.).

Paleozoic gastropods with openly coiled initial whorls show various adult (teleoconch) forms, e.g., naticiform, planispiral, fusiform, and limpet-like. Major extinct Paleozoic clades comprising species with openly coiled protoconchs include the limpet-shaped platyceratids (Bandel and Frýda, 1999) (Fig. 1B) and the planispiral Euomphalidae (Bandel and Frýda, 1998; Nützel, 2002). This morphology is also shown by stem members of extant clades such as the Caenogastropoda (Perunelomorpha) (Frýda, 1999) (Figs. 1D, 1E) and Neritimorpha (Bandel and Frýda, 1999) (Fig. 1A), whereas it is absent in all possible modern descendants of these clades. Openly coiled initial whorls are known from most major Paleozoic gastropod clades excepting the Vetigastropoda, which lack a planktonic larval stage.

One explanation of the lack of this feature in extant gastropods would be that Paleozoic gastropod clades with openly coiled protoconchs became extinct selectively during the Paleozoic and all modern gastropods are exclusively descendants of Paleozoic gastropods that had tightly coiled protoconchs. Another hypothesis would suggest that openly coiled protoconchs were present in the stem lines of most extant gastropod clades, but taxa bearing this feature were differentially lost across major clades. The resolution of the phylogeny of fossil gastropods is not yet good enough to decide which of these hypotheses is closer to the facts. It is possible that both scenarios contributed to produce the lack of openly coiled protoconchs in modern gastropods.

CONCLUSION

Gastropods with openly coiled initial whorls existed for ~250 m.y. (Cambrian to Permian) and dominated faunas for ~100 m.y. in the early Paleozoic (Ordovician—Silurian). The gradual loss of this morphology across distinct high-level clades suggests that a new selective force acted against this morphology. There is a clear analogy with the extremely long-term decrease in openly coiled or umbilicate gastropod teleoconch morphology through the Phanerozoic to Cenozoic (Vermeij, 1987). Such shells are mechanically weaker and more susceptible to successful attack by durophagous predators than the nonumbilicate morphologies that dominate benthic gastropod faunas today. Similarly to the Mesozoic marine revolution, new predators could have emerged, but there is little known about predator and prey relationships involving gastropod larvae even in the recent plankton. Recent planktonic gastropod larval shells commonly have chipped apertures or healed shell fractures, suggesting failed predation attempts (Hickman, 1999). Many recent gastropod larval shells are ornamented and this might represent increased armor to combat predation (Hickman, 1999). Although plausible, predators have yet to be identified. The loss of the openly coiled form in gastropod larval shells is contemporaneous with major changes in world plankton, including the middle to late Paleozoic decline of acritarchs and associated biomarkers (phytoplankton gap) (Moldowan et al., 1996; Riegel, 2001), the Early Devonian extinction of the graptolites (Sepkoski, 1981), and the appearance of dacryoconariid tentaculites. These changes show that the world plankton, including invertebrate larvae, was fundamentally restructured in the middle to late Paleozoic. It is unlikely that gastropod larvae, acritarchs, and graptolites were attacked by the same or similar predators because they are very different in size and ecology. It is probably more realistic that Paleozoic plankton communities suffered from crises caused by extrinsic forces and that during plankton restructuring in the aftermath, predation became an increasingly important selective factor for gastropod larvae.

ACKNOWLEDGMENTS

We thank Jonathan A. Todd (Museum of Natural History, London) for suggestions and critical remarks. Reviews from Geerat J. Vermeij and Alex Cook greatly improved the manuscript. A. Nützel acknowledges support from the Deutsche Forschungsgemeinschaft (NU 96/3-1, 96/6-1). J. Frýda acknowledges support from the Alexander von Humboldt Stiftung and the Grant Agency of the Czech Republic (205/01/0143).

REFERENCES CITED

Bandel, K., and Frýda, J., 1998, Position of the Euomphalidae in the system of the Gastropoda: Senckenbergiana Lethaea, v. 78, p. 103–131.

Bandel, K., and 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, v. 33, p. 219–235.

Bandel, K., and Hemleben, C., 1995, Observations on the ontogeny of thecosomatous pteropods (holoplanktic Gastropoda) in the southern Red Sea and Bermuda: Marine Biology, v. 124, p. 225–243.

Bockelie, T.G., and Yochelson, E.L., 1979, Variation in a species of ''worm'' from the Ordovician of Spitsbergen: Saertrykk av Norsk Polarinstitutt, Skrifter, v. 167, p. 224–237.

Dzik, J., 1994, Evolution of ''small shelly fossils'' assemblages of the early Paleozoic: Acta Palaeontologica Polonica, v. 39, p. 247–131.

Dzik, J., 1999, Evolutionary origin of asymmetry in early metazoan animals, *in* Pályi, et al., eds., Advances in biochirality: Amsterdam, Elsevier, p. 153–190.

Erwin, D.H., 2000, Macroevolution is more than repeated rounds of microevolution: Evolution and Development, v. 2, p. 78–84.

Frýda, J., 1999, Higher classification of Paleozoic gastropods inferred from their early shell ontogeny: Czech Geological Society Journal v. 44, p. 137–154.

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: Czech Geological Survey Bulletin, v. 76, p. 39–54.

Frýda, J., and Heidelberger, D., 2003, Systematic position of Cyrtoneritimorpha within the class Gastropoda with description of two new genera from Siluro-Devonian strata of Central Europe: Bulletin of Geosciences, v. 78, p. 35–59.

Frýda, J., and Manda, S., 1997, A gastropod faunule from the *Monograptus uniformis* graptolite biozone (Early Lochkovian, Early Devonian) in Bohemia: Geologisch-Paläontologisches Institut der Universität Hamburg, Mitteilungen, v. 80, p. 59–121.

Hickman, C.S., 1999, Adaptive function of gastropod larval shell features: Invertebrate Biology, v. 118, p. 346–356.

Jablonski, D., 1986, Larval ecology and macroevolution in marine invertebrates: Bulletin of Marine Science, v. 39, p. 565–587.

Jablonski, D., 2000, Micro- and macroevolution: Scale and hierarchy in evolutionary biology and paleobiology, *in* Erwin, D.H., and Wing, S.L., eds., Deep time: Lawrence, Kansas, The Paleontological Society, p. 15–52.

Jablonski, D., and Lutz, R.A., 1983, Larval ecology of marine benthic invertebrates, paleobiological implications: Biological Reviews, v. 58, p. 21–89.

Moldowan, J.M., Dahl, J., Jacobson, S.R., Huizinga, B.J., Fago, F.J., Shetty, R., Watt, D.S., and Peters, K.E., 1996, Chemostratigraphic reconstruction of biofacies, molecular evidence linking cyst-forming dinoflagellates with pre-Triassic ancestors: Geology, v. 24, p. 159–162.

Nützel, A., 2002, An evaluation of the recently proposed Palaeozoic gastropod subclass Euomphalomorpha: Palaeontology, v. 45, p. 259–266.

Nützel, A., and Mapes, R.H., 2001, Larval and juvenile gastropods from a Mississippian black shale: Paleoecology, and implications for the evolution of the Gastropoda: Lethaia, v. 34, p. 143–162.

Nützel, A., Erwin, D.H., and Mapes, R.H., 2000, Identity and phylogeny of the late Palaeozoic Subulitoidea: Journal of Paleontology, v. 74, p. 575–598.

Peel, J.S., 1991, Functional morphology, evolution and systematics of early Palaeozoic univalved molluscs: Bulletin Grønlands Geolgiske Undersøgelse, v. 161, p. 1–116.

Ponder, W.F., and Keyzer, R.G. de., 1998, Superfamily Risooidea, *in* Beesley, P.L., et al., eds., Mollusca: The southern synthesis, Part B. Fauna of Australia, Volume 5: Melbourne, Australia, CSIRO Publishing, p. 745–766.

Raup, D.M., 1991, The future of analytical paleobiology, *in* Gilinsky, N.L., and Signor, P.W., eds, Analytical paleobiology: Paleontological Society, Short Courses in Paleontology, v. 4, p. 207–216.

Riegel, W., 2001, Phytoplankton development during the late Paleozoic: Terra Nostra, v. 2001, p. 66–72.

Runnegar, B., 1981, Muscle scars, shell form and torsion in Cambrian and Ordovician univalved molluscs: Lethaia, v. 14, p. 311–322.

Runnegar, B., 1983, Molluscan phylogeny revisited: Association of Australasian Palaeontologists Memoires, v. 1, p. 121–144.

Sepkoski, J.J. Jr., 1981, A factor analytic description of the Phanerozoic marine fossil record: Paleobiology, v. 7, p. 36–53.

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

Vermeij, G.J., 1987, Evolution and escalation: An ecological history of life: Princeton, New Jersey, Princeton University Press, 527 p.

Wagner, P.J., 2002, Phylogenetic relationships of the earliest anisotrophically coiled gastropods: Smithsonian Contributions to Paleobiology, v. 88, p. 1–152.

Wanninger, A., Ruthensteiner, B., and Haszprunar, G., 2000, Torsion in *Patella caerula* (Mollusca, Patellogastropoda): Ontogenetic process, timing, and mechanisms: Invertebrate Biology, v. 119, p. 177–187.

Manuscript received 20 February 2003
Revised manuscript received 22 May 2003
Manuscript accepted 25 May 2003

Printed in USA

Geology

Paleozoic plankton revolution: Evidence from early gastropod ontogeny

Alexander Nützel and Jiri Frýda

Geology 2003;31;829-831
doi: 10.1130/G19616.1

Notes