Mystery of naticid predation history solved: Evidence from a "living fossil" species

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ABSTRACT

Observations of living *Cernina fluctuata* (Sowerby), the sole extant species of the Mesozoic and Cenozoic prosobranch gastropod family Ampullospiridae, show that this species is an algal grazer and is not a shell-drilling, predatory naticid gastropod. All Jurassic and Early Cretaceous gastropods previously assigned to Naticidae belong to Ampullospiridae and are now inferred to be herbivores, not shell-drillers. This finding refutes the Triassic origin and favors a Cretaceous origin for naticid drilling predation. A preliminary revision of Cenozoic and Cretaceous species previously assigned to Naticidae suggests that naticids were absent prior to the Cretaceous Campanian and diversified at a modern level in Eocene time. This pattern of naticid diversification from the Late Cretaceous onward coincides roughly with the evidence of naticid predation. The fossil record of naticid drill holes—once of anomalously short duration—now accurately reflects the geologic history of naticid predation activity.

Keywords: Naticidae, living fossils, predation, drill holes, fossil record.

INTRODUCTION

Naticids are predatory prosobranch marine snails that drill characteristically circular, parabolic holes through mollusc shells to consume the soft parts within. The fossil record of naticid drill holes since the middle Cretaceous has been celebrated as a major piece of evidence for the "Mesozoic marine revolution" (Vermeij, 1977). Previous studies have suggested either that naticids initiated drilling predation in the late Early Cretaceous (Taylor et al., 1983), despite having a fossil record in the Jurassic (Tracy et al., 1993), or that they initiated drilling predation (but failed to radiate) in the Late Triassic, on the basis of alleged naticid drill holes in North America (Newton, 1983) and Italy (Fürsich and Jablonski, 1984). The complete absence of naticid drill holes for 120 million years, from the Late Triassic to the late Early Cretaceous, and their near absence (except for one Albian example; see Taylor et al., 1983) for most of the Cretaceous has been a mystery in the history of naticid predation (e.g., Kowalewski et al., 1998). Drill holes first appeared infrequently late in the Cretaceous and significantly increased in the Paleocene and Eocene; after a remarkable decline in the late Eocene, drilling frequencies attained their high modern occurrence levels since the Oligocene but exhibited a slightly fluctuated pattern in the Neogene (Kelley and Hansen, 1993, 1996, 2003; for an exception, see Allmon et al., 1990).

The fossil record has implied that naticid gastropods prior to the late Early Cretaceous all belonged to the almost extinct subfamily Ampullospirinae (here regarded as a family-level taxon). The other naticid subfamilies (Naticinae, Polinicinae, and Sininae) have been recorded since the late Early Cretaceous (Aptian) (Kase, 1984; Tracy et al., 1993). Ampullospirids only became major components of naticid assemblages late in the Cretaceous, and naticids other than ampullospirids radiated at modern levels beginning in the Eocene (Marincovich, 1977). As a result of this fossil record, disagreement about the origin of naticid predation, and interpretation of the mysterious fossil record of drill holes since the middle Cretaceous, primarily centers on whether or not the Ampullospiridae were borers (e.g., Sohl, 1969; Taylor et al., 1980; Fürsich and Jablonski, 1984).

Cernina fluctuata (Sowerby) is the sole living species of Ampullospiridae and has been poorly studied since it was first found >150 yr ago at Mindoro, Philippines. Learning its feeding strategy holds the key to unlocking the mystery of naticid predation history. *Amauropsis* has frequently been cited as another living example of Ampullospiridae, but its naticid affinity is unequivocal, based on radular and egg-mass features (Giglioli, 1955; Marincovich, 1977). Our study of live *C. fluctuata* shows that this snail is an algal grazer and does not belong to the predatory, carnivorous Naticidae. This evidence refutes the presumed Triassic origin of naticid predation and effectively explains the once-mysterious discordance between the fossil record of naticid shells and the fossil record of drill holes.

FEEDING AND ANATOMY OF *CERNINA FLUCTUATA*

Living specimens of *C. fluctuata* were collected on the lower part of a tidal flat on Cuyo Island, Philippines (Fig. 1A). Nocturnal in nature, these snails remain in burrows during daylight hours and emerge at dusk to browse over the substrate. This substrate is composed of coral sand mixed with a large proportion of mud and covered by discontinuous patches of sea grass (*Enhalus acoroides*) and several kinds of macroalgae. Analysis of the animal's alimentary-canal contents showed that the expanded mid-esophagus (esophageal bulb) was filled with large fragments of macroalgae such as *Padina australis* Hauk and *Hypnea* sp. (Fig. 1B). Culturing these snails for three years in an aquarium resulted in their growing quite large (~20% larger in maximum shell diameter) by devouring the macroalga *Undaria pinnatifida*.

Dissection of its soft parts reveals that *C. fluctuata* has anatomical features shared with the freshwater Ampullariidae and the marine Campanilidae (Kase, 1990). The foot of *C. fluctuata* consists of a small, flat, quadrangular propodium and a massive, yet short, metapodium that are separated from each other by an ill-defined fold (Fig. 1A). The wide, flat, bipartite and snoutless head has a mouth at its base that lacks an extensible proboscis (Fig. 1B). In strong contrast, naticids possess anatomical features specialized for drilling predation, including a large plow-like propodium to firmly grasp its molluscan prey, and an accessory boring organ, which is a pad-like structure at the ventral tip of a long, extensible proboscis that contains a radula (Carriker, 1981). Naticid drilling activity is achieved by radular action enhanced by chemical agents released by the tall secretory cells of the accessory boring organ (Carriker, 1981).

The feeding habits and attendant anatomy of *C. fluctuata*, a grazer, are quite distinct from those of the predatory, carnivorous Naticidae, so *Cernina* and all of its relatives in the Ampullospiridae (all of which are inferred to be herbivores) should be removed from the family Naticidae. The lack of available living specimens may have prevented previous researchers from recognizing that the ampullospirid shell is an example of convergence with naticids.

AMPULLOSPIRIDS VS. NATICIDS

Although the supraspecific classification of Ampullospiridae (particularly Mesozoic taxa) has never been thoroughly evaluated (see Ka-
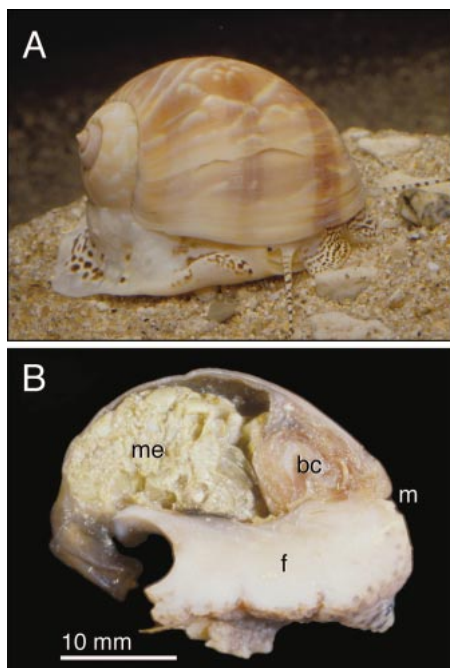
Figure 1. A: A live *Cernina fluctuata* (Sowerby), captured at Cuyo, Philippines, crawling over coral sand in aquarium. Note that small propodium and short metapodium are quite different from those in naticids. B: Sagittal section of animal, showing expanded mid-esophagus (esophageal bulb) filled with large fragments of macroalga *Padina australis* Hauk. Abbreviations: bc—buccal mass; f—foot; m—mouth; me—mid-esophagus.
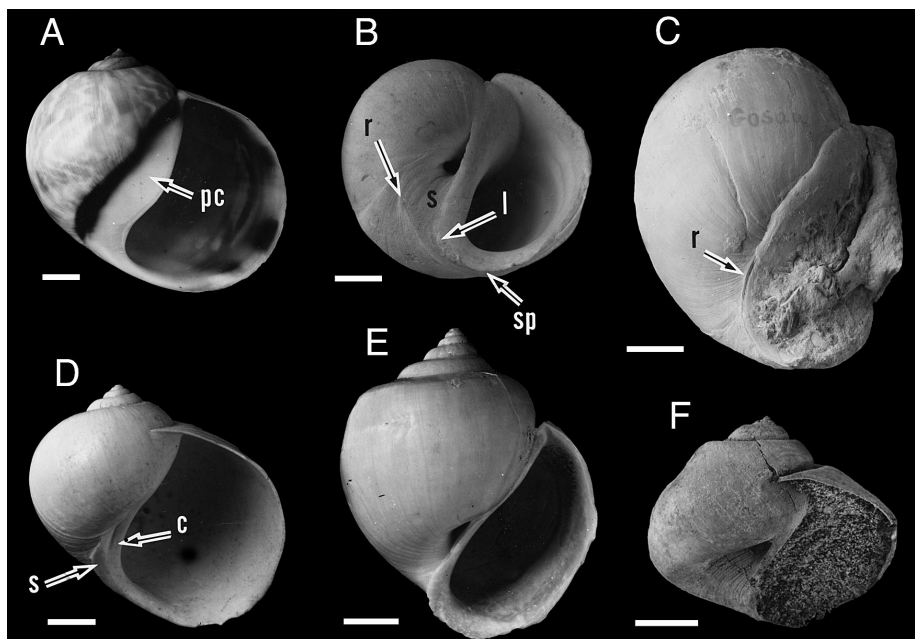

Figure 2. Shells of living and fossil ampullospirids. A: *Cernina fluctuata* (Sowerby), living species from Philippines, showing acuminate and pointed apical whorls and presence of callus (pc) over parietal area. *C. fluctuata* has shell characteristics very similar to those of *Globularia sigaretina* Lamarck (D), except latter species lacks parietal callus. B: Basal view of *Globularia parisiensis* (d'Orbigny) from Eocene of Paris basin, France, with lobe on columella (l) and wide sheath (s) that is surrounded by rim (r) and that begins at anteriormost point (sp) of aperture. C: *Pseudamaura bulbiformis* (Sowerby) from Upper Cretaceous of Gosau district, Germany, is elongate ampullospirid, in which sheath is usually covered by columellar lip. However, rim (r) is exceptionally visible in specimen illustrated here. Oblique apertural view. D: *Globularia sigaretina* Lamarck from Eocene of Paris basin, France. Sheath is incorporated into columellar border. E: *Crommium willemeti* (Deshayes) from Eocene of France. Sheath is enrolled entirely by columellar border. F: *Gyrodes spillmani* Gabb from Maastrichtian of Tennessee. Scale bar represents 10 mm for A and C and 5 mm for B, E, and F.

bat, 1991), paleontologists have long been aware of the differences in shell features between naticids and ampullospirids (e.g., Wrigley, 1946; Sohl, 1960; Marincovich, 1977). In addition to the usually highly elevated, pointed spire and tabulate (sometimes grooved) whorls, ampullospirid shells have distinguishing umbilical features (Fig. 2). The columellar lip is lined abaxially with a feature (sometimes raised above the base) termed a ''sheath'' by Wrigley (1946; s in Fig. 2B). The sheath generally begins from just behind the anteriormost tip of the aperture (sp in Fig. 2B), coils alongside the columellar lip, and is delimited abaxially from the shell base by a rim (r in Fig. 2B) that originates from a somewhat raised bundle of growth lines at the point where the growth lines change curvature from the base to the umbilical area. The anterior tip of the columellar lip often expands abaxially into a round lobe that covers (and may be slightly elevated above) the sheath (l in Fig. 2B); in some taxa (e.g., *Globularia sigaretina* [Eocene]) the columellar lip is entirely incorporated into the sheath (Fig. 2D). Development of the sheath varies among ampullospirid species. Those species with a wide umbilicus have a wide sheath (Fig. 2B), whereas the sheath narrows or becomes indis-

tinct (or absent) in species with a small umbilicus (Fig. 2D) or mostly closed umbilicus (e.g., *Crommium willemeti* [Eocene]; Fig. 2E). The Cretaceous genera *Tylostoma* and *Pseudamaura* most probably represent one end member of a broad spectrum of such variation, where the sheath is only slightly present (Fig. 2C) or is totally absent owing to being covered by the columellar lip. In *Cernina* and *Eocernina*, the columellar lip, parietal area, and sheath are further covered with a thick parietal callus (pc in Fig. 2A).

In contrast, naticids generally are devoid of a sheath and instead develop one or more funicles (plug-like structures growing continuously from the columellar lip and extending spirally into the umbilicus) that partly or wholly fill the umbilical cavity. The size, shape, and position of the funicle(s) differ among naticid species. In *Amauropsis* and *Bulbus*, the columella forms a thin, simple lip without a funicle. Some polinicine naticids, however, possess a sheath-like structure in the umbilicus (e.g., *Polinices flemingianus*), but it differs from the ampullospirid sheath in important ways: the structure starts from behind the anteriormost columellar lip (so that it

starts more adaxially than in ampullospirids), and the columellar lip is simple and never expands onto the sheath.

Protoconch morphology is another shell character that separates the two groups. This distinction is particularly evident in species with a small protoconch, which most probably reflects planktotrophic development. The protoconch in this type of ampullospirid (including *C. fluctuata* and many fossil ampullospirids we examined) consists of 1.2–1.5 helicospiral, smooth, inflated whorls with an almost-smooth protoconch I (Figs. 3B and 3C) nearly identical to that of *Campanile symbolicum* (see Houbrick, 1981), whereas a naticid protoconch consists of 2.2–3.5 whorls with a protoconch I that is coiled almost planispirally and ornamented with granules, often arranged spirally (Fig. 3A; see also Bouchet and Warén, 1993). Owing to this difference, apical whorls are acutely pointed in ampullospirids and obtusely pointed in naticids.

Kowalke and Bandel (1996) proposed the new family Pseudamaurinidae [sic], primarily based on protoconch morphology that differs from naticids, and suggested an affinity with the herbivorous Cerithiimorpha (see also Ban-
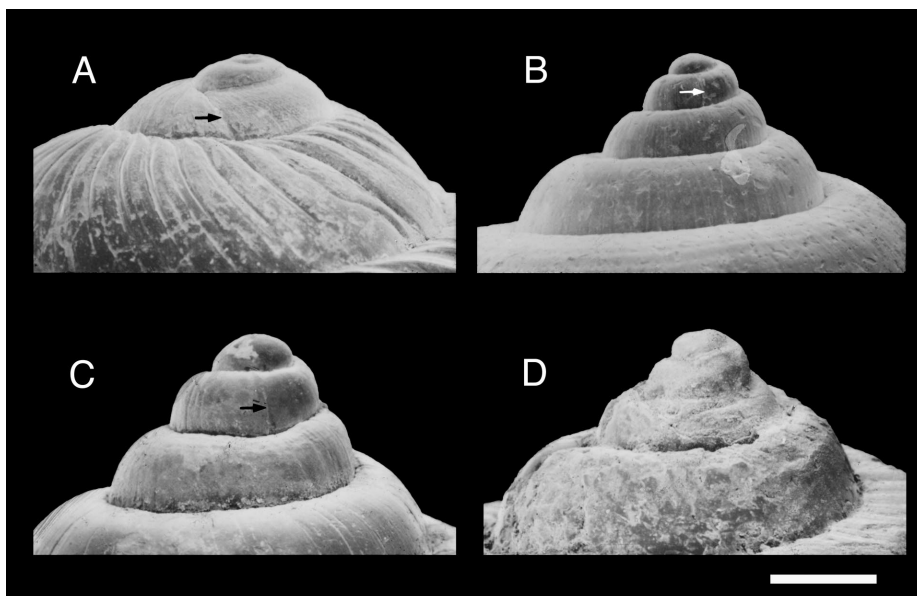
Figure 3. Scanning electron microscope (SEM) micrographs showing apical teleoconch whorls and protoconch of naticid (A) and ampullospirid gastropods (B–D). Scale bar represents 500 μm. **A:** *Natica lurida* (Philippi), living specimen from Philippines, showing planktotrophic protoconch and apical teleoconch whorls typical of naticids. Arrow indicates boundary between teleoconch and protoconch. **B:** *Cernina fluctuata* (Sowerby) from Philippines. Apical teleoconch whorls are distinctly inflated and highly elevated, and protoconch consists of ~1.5 smooth and elevated helicospiral whorls. **C:** *Globularia parisiensis* (d'Orbigny) from Eocene of Paris basin, France, exhibiting apical whorls and protoconch almost identical to those of *C. fluctuata*. **D:** *Gyrodes spillmani* Gabb from Maastrichtian of Tennessee, showing protoconch and apical teleoconch whorls similar to those of ampullospirids.

del, 1999). Unfortunately, this proposal appears to be based on misperceptions. First, the protoconch that ostensibly characterizes the new family was stated to be on the Late Cretaceous *Natica lyrata* (Sowerby), which is a typical ampullospirid. Second, the protoconch morphology does not actually differ from that of *C. fluctuata* and other typical ampullospirids. Bandel (1999) assigned a number of ampullospirid species to the proposed new family.

Gyrodes is a dominant genus in the Late Cretaceous ''naticid'' fauna and has been assigned to the subfamilies Gyroninae (Sohl, 1960; Popenoe et al., 1987) and Ampullospirinae (Marincovich, 1977) (Fig. 2F). Deciding its systematic placement (Ampullospiridae versus Naticidae) primarily centers upon understanding the diversification of naticids in the Cretaceous. Popenoe et al. (1987) viewed the modern naticid *Hypterita helicoides* (Gray) as the sole living species of Gyrodinae, thereby implying a naticid affinity for the subfamily. We differ in thinking that *Gyrodes* belongs in Ampullospiridae, because its shells often have an acute spire and tabulate whorls, which are characteristic of ampullospirids. Popenoe et al. (1987) observed that the Eocene *Gyrodes robustus* Waring is morphologically similar to a species of the ampullospirid *Eocernina* and suggested derivation of the lat-

ter genus from *Gyrodes*. Such a view is clearly supported by the presence on *Gyrodes* of a protoconch and apical teleoconch whorls, which are typical of ampullospirids (Fig. 3D).

On the basis of the aforementioned criteria, we reexamined a total of 394 nominal species of the Cretaceous gastropods previously described as naticids and/or ampullospirids in published monographs. We find that the oldest unequivocal fossil naticids are from the Campanian of the Aachen Cretaceous in northern Europe (*Lunatia stoliczkai* and *L. klipsteini*), the Maastrichtian of India (*Mammila carnatica* and *M. edura*), the Campanian and Maastrichtian of the United States (*Euspira rectilabrum*, *E. obliqua*, *E. dakotensis*, *Polinices kummeli*, and *Banis similformis*), and the Maastrichtian of Chile (*Polinices ganae*), and also that all species older than Campanian are ampullospirids. Even the four species from the Middle Albian Blackdown Greensand of England, which allegedly made the oldest naticid drill holes (Taylor et al., 1983), are ampullospirids. The purported oldest naticid, assigned to *Euspira* sp., is based on a few poorly preserved Aptian specimens from Japan (Kase, 1984; see also Tracy et al., 1993). However, an additional better-preserved specimen reveals that this species belongs in the Ampullospiridae, most probably to *Globularia*, given its narrow sheath. In summary, although some

dubious naticid species in Cretaceous faunas need further assessment (e.g., Popenoe et al., 1987), naticids evidently first appeared in the Campanian.

DISCUSSION AND CONCLUSIONS

The previous theory that naticid drilling predation originated in the Late Triassic (Newton, 1983; Fürsich and Jablonski, 1984) was anomalous, given the absence of evidence for drilling in the Jurassic and early Early Cretaceous, the infrequent occurrence of drill holes during most of the Late Cretaceous, and the overall high frequency of drilling from the Eocene to the present. Late Triassic drill holes were attributed to associated ampullospirid shells in the faunas, because past workers erroneously assigned ampullospirids to the durophagous, predatory family Naticidae. Our research now makes it highly likely that these naticid-like drill holes were produced by other, as yet unknown predators.

Naticiform snails were as common in the Mesozoic as in the Cenozoic (Sohl, 1969; Marincovich, 1977; Taylor et al., 1983), but we assign all Late Triassic to Early Cretaceous taxa (previously regarded as naticids) to the Ampullospiridae. Our new evidence strongly favors a Late Cretaceous origin for naticid drilling predation (Sohl, 1969; Taylor et al., 1983) and is in accord with the once-mysterious lack of naticid drill holes in the Jurassic and early Early Cretaceous. Recently discovered Jurassic predatory drill holes are thought to be the handiwork of organism(s) other than naticids (Harper et al., 1998; Kowalewski et al., 1998).

Our analysis of naticid diversity (defined as the number of naticid species divided by the total number of prosobranch species in local faunas worldwide, as treated in published monographs) from the middle Cretaceous onward sheds new light upon the history of naticid predation: durophagous predatory naticids were absent or, if any, very uncommon and localized prior to the Campanian, but became common and widespread in Campanian and Maastrichtian shallow-marine environments; by Eocene time, such naticids were as common as in modern seas (Fig. 4; see Tables DR1 and DR2[1]). It is interesting to note that increased naticid diversification since the Cretaceous (the Paleocene being an exception) closely coincides with an increase in naticid drill holes, as observed by many workers. Given the excellent correlation between increased naticid diversification and evidence
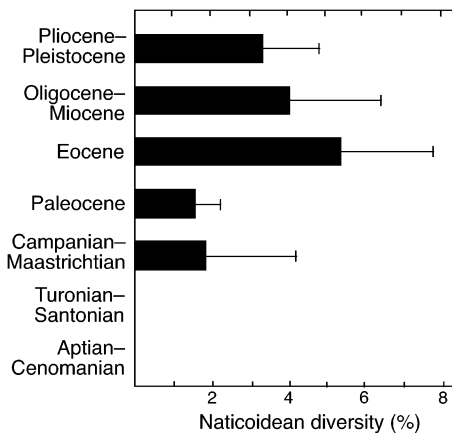
Figure 4. Historical changes in naticid diversity. Each bar represents mean percentage of naticid species divided by total number of prosobranch species in local faunas. Values used are based upon data from published studies of gastropod faunas in local areas, geographic regions, formations, or stratigraphic intervals: 7 for Pliocene–Pleistocene, 16 for Oligocene–Miocene (two studies span Miocene–Pliocene), 7 for Eocene, 6 for Paleocene, 10 for Campanian–Maastrichtian, 3 for Turonian–Santonian, and 8 for Aptian–Cenomanian. Naticid diversity was significantly lower in Cretaceous and Paleocene than in later three age classes (Mann-Whitney's U test, p < 0.05).

for drilling since the later Cretaceous, we suggest that the infrequent pre-Cenozoic evidence of naticid drilling predation is primarily due to the scarcity of naticid species and that the abundance of Cenozoic drilling is due to the radiation of naticids from the Eocene onward.

Naticid-like drill holes in the Late Triassic molluscan fossils of Italy and the Albian Blackdown Greensand of England remain mysterious, given that they are difficult to distinguish from those produced by modern naticids. We cannot identify the culprits responsible for those drill holes and prefer to think that they resulted from predation by organism(s) other than naticids. Similar drill holes have been recorded widely in the Paleozoic and Mesozoic, suggesting the presence of unidentified organisms that practiced predation by means of naticid-like drilling (Ausich and Gurrola, 1979; Smith et al., 1985; Harper et al., 1998; Baumiller et al., 1999). The Albian drill holes could be interpreted as the result of one or more associated muricids because Herbert and Dietl (2002) have shown that some modern muricids produce drill holes undistinguishable from those of naticids.

By excluding ampullospirids from Naticidae, the fossil record of true naticid drill holes realistically reflects changes in naticid predation intensity since the Late Cretaceous. The scenario of marine predation we present here is a rare example of direct paleontological ev-

idence for increased predation pressure on benthic marine assemblages after the middle Cretaceous, as one aspect of the Mesozoic marine revolution.

REFERENCES CITED

Allmon, W.D., Nieh, J.C, and Norris, R.D., 1990, Drilling and pealing of turritelline gastropods since the Late Cretaceous: Palaeontology, v. 33, p. 595–611.

Ausich, W.I., and Gurrola, R.A., 1979, Two boring organisms in a Lower Mississippian community of southern Indiana: Journal of Paleontology, v. 53, p. 335–344.

Bandel, K., 1999, On the origin of the carnivorous gastropod group Naticidae (Mollusca) in the Cretaceous with description of some convergent but unrelated groups: Greifswalder Geowissenschaftliche Beiträge, v. 6, p. 143–175.

Baumiller, T.K., Leighton, L.R., and Thompson, D.L., 1999, Boreholes in Mississippian brachiopods and their implications for Paleozoic gastropod drilling: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 147, p. 283–289.

Bouchet, P., and Warén, A., 1993, Revision of the northeast Atlantic bathyal and abyssal Mesogastropoda: Bolletino Malacologico, Supplemento 3, p. 580–840.

Carriker, M.R., 1981, Shell penetration and feeding by naticacean and muricacean predatory gastropods: A synthesis: Malacologia, v. 20, p. 403–422.

Fürsich, F.T., and Jablonski, D., 1984, Late Triassic naticid drill holes: Carnivorous gastropods gain a major adaptation but fail to radiate: Science, v. 224, p. 78–80.

Giglioli, M.E.C., 1955, The egg masses of the Naticidae (Gastropoda): Journal of Fisheries Research Board of Canada, v. 12, p. 287–327.

Harper, E.M., Forsythe, G.T.W., and Palmer, T., 1998, Taphonomy and the Mesozoic marine revolution: Preservation state masks the importance of boring predators: Palaios, v. 13, p. 352–360.

Herbert, G.S., and Dietl, G.P., 2002, Tests of the escalation hypothesis: The role of multiple predators: Geological Society of America Abstracts with Programs, v. 34, no. 6, p. 538–539.

Houbrick, R.S., 1981, Anatomy, biology and systematics of *Campanile symbolicum* Iredale with reference to adaptive radiation of the Cerithiacea: Malacologia, v. 21, p. 263–289.

Kabat, A.R., 1991, The classification of the Naticidae (Mollusca: Gastropoda): Review and analysis of the supraspecific taxa: Museum of Comparative Zoology Bulletin, v. 152, p. 417–449.

Kase, T., 1984, Early Cretaceous marine and brackish-water Gastropoda from Japan: Tokyo, National Science Museum, 263 p.

Kase, T., 1990, Research report on ecology of a living fossil of extinct naticids, *Globularia fluctuata* (Sowerby) (Gastropoda, Mollusca) in Palawan, the Philippines—II: Tokyo, Journal

of Geography, v. 99, p. 398–401 (in Japanese).

Kelley, P.H., and Hansen, T.A., 1993, Evolution of the naticid gastropod predator-prey system: An evaluation of the hypothesis of escalation: Palaios, v. 8, p. 358–375.

Kelley, P.H., and Hansen, T.A., 1996, Recovery of the naticid gastropod predator-prey system from the Cretaceous-Tertiary and Eocene-Oligocene extinctions, *in* Hart, M.B., ed., Biotic recovery from mass extinction events: Geological Society [London] Special Publication 102, p. 373–386.

Kelley, P.H., and Hansen, T.A., 2003, The fossil record of drilling predation on bivalves and gastropods, *in* Kelley, P.H., et al., eds., Predator-prey interactions in the fossil record: Kluwer Academic/Plenum Press, p. 113–139.

Kowalewski, M., Dulao, A., and Fürsich, F.T., 1998, A fossil record full of holes: The Phanerozoic history of drilling predation: Geology, v. 26, p. 1091–1094.

Kowalke, T., and Bandel, K., 1996, Systematik und paläoökologie der Küstenschnecken der nordalpinen Brandenberg-Gosau (Oberconiac/Untersanton) mit einem vergleich zur Gastropodenfauna des Maastrichts des Trempbeckens (Südpyrenäen, Apnian): Mitteilungen aus der Bayerischen Staatssammlung für Paläontologie und Historische Geologie, v. 36, p. 15–71.

Marincovich, L., Jr., 1977, Cenozoic Naticidae (Mollusca: Gastropoda) of the northeastern Pacific: Bulletins of American Paleontology, v. 70, p. 169–497.

Newton, C.R., 1983, Triassic origin of shell-boring gastropods: Geological Society of America Abstracts with Program, v. 15, p. 652–653.

Popenoe, W.P., Saul, L.R., and Susuki, T., 1987, Gyrodiform gastropods from the Pacific Coast Cretaceous and Paleocene: Journal of Paleontology, v. 61, p. 70–100.

Smith, S.A., Thayer, C.W., and Brett, C.E., 1985, Predation in the Paleozoic: Gastropod-like drill holes in Devonian brachiopods: Science, v. 230, p. 1033–1035.

Sohl, N.F., 1960, Archaeogastropoda, Mesogastropoda and stratigraphy of the Ripley, Owl Creek, and Prairie Bluff Formations: U.S. Geological Survey Professional Paper 331-A, p. 1–151, plates 3–18.

Sohl, N.F., 1969, The fossil record of shell boring by snails: American Zoologist, v. 9, p. 725–734.

Taylor, J.D., Morris, N.J., and Taylor, C.N., 1980, Food specialization and the evolution of predatory prosobranch gastropods: Palaeontology, v. 23, p. 375–409.

Taylor, J.D., Cleevely, R.J., and Morris, N.J., 1983, Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England: Palaeontology, v. 26, p. 521–553.

Tracy, S., Todd, J.A., and Erwin, D.H., 1993, Mollusca: Gastropoda, *in* Benton, M.J., ed., The fossil record 2: London, Chapman and Hall, p. 131–167.

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

Wrigley, A., 1946, English Eocene and Oligocene ampullinids: Proceedings of the Malacological Society of London, v. 27, p. 88–104.