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#### Notes

## Mystery of naticid predation history solved: Evidence from a “living fossil” species: Comment and Reply

### COMMENT

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Kase and Ishikawa (2003) argue that they have solved the “mystery” of naticid predation history. The mystery involves an inconsistency between the Cretaceous onset of abundant naticid-type predatory drill holes and the first appearance of the group in the Jurassic. Kase and Ishikawa’s argument can be summarized as follows: (1) the sole living member of the Ampullospirinae, *Cernina fluctuata*, is a grazer, not a predator; thus (2) ampullospirins are not naticids; (3) “ampullospirids” were the only pre-Cretaceous naticids; and therefore (4) removal of the grazing “Ampullospiridae” from the predatory Naticidae produces a revised Naticidae with a fossil shell record temporally consistent with the drilling fossil record.

We accept Kase and Ishikawa’s claims that *C. fluctuata* is a non-naticid grazer. However, the rest of their argument is based on two critical assumptions: that removal of *C. fluctuata* from the Naticidae justifies removal of the subfamily Ampullospirinae from the Naticidae; and that the feeding strategy of *C. fluctuata* is representative of all “ampullospirids.” We show that these assumptions are flawed and that Kase and Ishikawa’s argument is logically untenable.

Removal of a subfamily from a higher taxon is valid only if the type species for the subfamily can be removed. As *C. fluctuata* is not the name-bearer for the Ampullospirinae, or even its sole living member, its removal from the Naticidae is irrelevant to whether the rest of the subfamily is removed.

Rules of systematic nomenclature aside, Kase and Ishikawa argue for separation of the “Ampullospiridae” based on morphology: ampullospirids differ from naticids in that the former possess an elevated, pointed spire, tabulate whorls, and a columellar sheath. The two groups also can be distinguished by the protoconch: ampullospirids have a smooth protoconch with 1.2–1.5 whorls, whereas naticids have a granular protoconch with 2.2–3.5 whorls. However, these features may be dependent on larval mode, which varies within naticids and ampullospirids. Whereas the protoconch of planktotrophic naticids is large with granules, in non-planktotrophic taxa, the protoconch lacks ornament and the number of whorls decreases (Bandel, 1999). This evidence suggests that non-planktotrophic naticids will have a morphology that corresponds to Kase and Ishikawa’s description of ampullospirid protoconchs.

Shell morphology also is variable: extant naticids may possess high or pointed spires (e.g., *Conuber conicus*), or tabulate whorls (e.g., *Naticarius alapapillonis*). Similarly, taxa designated as ampullospirids may have low spires (e.g., *Gyrodes spillmani*, Fig. 2F of Kase and Ishikawa) and rounded whorls (e.g., *Globularia sigaretina*, Fig. 2D of Kase and Ishikawa). The columellar sheath also is unreliable as a diagnostic characteristic. The presence and size of the sheath is dependent on the size and geometry of the umbilicus and columellar lip, and the presence or absence of a parietal callus. Thus, several ampullospirids lack evidence for a columellar sheath. In short, none of the fea-

tures noted by Kase and Ishikawa reliably distinguish ampullospirids from other naticids. Moreover, even if these features were diagnostic of the “Ampullospiridae,” *Cernina fluctuata*, the exemplar for feeding mode, has a low spire, lacks tabulate whorls, and has a columellar region obscured by a parietal callus, i.e., it does not fit Kase and Ishikawa’s diagnosis for ampullospirids. Given this, how can *C. fluctuata* be representative of the Ampullospiridae?

Even if *C. fluctuata* is an ampullospirid, its feeding strategy cannot be used to infer that of all extinct ampullospirids or to argue that ampullospirins are not naticids. This argument is analogous to suggesting that giant pandas and their close relatives should be removed from the Order Carnivora because pandas are herbivores. Similarly, gastropod clades can include both predators and grazers. Indeed, cowries, a probable sister taxon of naticids (Bandel and Riedel, 1994), are one such example. Vermeij and Lindberg (2000) argued that grazing is most often a derived feeding strategy; it is just as plausible that grazing within the *Cernina* lineage is a recent development as it is that Mesozoic ampullospirins were grazers. Inferring that all ampullospirids, including Mesozoic taxa, were grazers based on a single living species is blind uniformitarianism. Short of radular evidence from the Jurassic, feeding strategy can be hypothesized only by mapping the behavior onto a robust phylogeny.

Finally, we suggest that the “mystery” of naticid predation has been overstated. Examples of Jurassic beveled borings do exist (Harper et al., 1998), consistent with the presence of ampullospirins at that time. However, such borings are rare, which led Fursich and Jablonski (1984) to speculate that naticids had evolved by the Triassic, but had not yet radiated. Although such a hypothesis is feasible, it is based on the assumption that the radiation is dependent on feeding strategy or the drilling habit. Any other synapomorphy could serve as a “key innovation” for naticid diversification. Two alternatives for the paucity of drill holes deserve consideration. First, there may be preservational biases to explain the low incidence of drilling predation in the Jurassic (Harper et al., 1998). Second, drilling predators do not always drill their prey when other means of taking the prey are available. Some naticids are capable of smothering, rather than drilling, their prey (Vermeij, 1980). These alternative attack strategies, the use of which could be determined by the available prey, could bias drilling frequency in the fossil record (Leighton, 2002). The problem of naticid predation has not been solved. The solution will require more detailed morphological and phylogenetic analyses of fossil taxa, as well as further examination of taphonomic conditions, predatory traces, and potential prey in the Mesozoic.

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## REPLY

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We thank Aronowsky and Leighton for the opportunity to further discuss our conclusion that the fossil members of Ampullospiridae were herbivores, based on the discovery of algal feeding in the sole living species, *Cernina fluctuata*, and the complete absence of naticid drill holes in the Jurassic and early Cretaceous. The latter point implies the absence of predatory naticoideans at that time (Kase and Ishikawa, 2003). Aronowsky and Leighton contradicted our interpretation with the following claims: (1) Ampullospiridae and Naticidae are difficult to separate conchologically; (2) *C. fluctuata* is not a representative of Ampullospiridae and it is not even related to fossil ampullospirids; (3) the herbivory of *C. fluctuata* is a feeding strategy only recently developed in the *Cernina* lineage and fossil ampullospirids were carnivores; and (4) the fossil record of naticids and their drill holes is not anomalous. Our reply addresses these four points.

Aronowsky and Leighton have ignored the comprehensive studies on Mesozoic and Cenozoic naticoideans and ampullospirids by previous authors (e.g., Wrigley, 1946; Sohl, 1960; Marinovich, 1977). We remain convinced that *C. fluctuata* is the sole living species of Ampullospiridae, even though it develops a thick parietal callus on the inner lip. A similar parietal callus appeared at times in Mesozoic (e.g., *Globularia hemisphaerica*) and Cenozoic (*Eocernina hannibali*) ampullospirids. There is no difference in shell characters between *C. fluctuata* and *Globularia sigaretina*, aside from the presence of a parietal callus in the former (see Kase and Ishikawa, 2003, Fig. 2, A and D). The conchological characteristics we presented to distinguish Ampullospiridae from Naticoidea apply to typical ampullospirids, because they are based on a wide variety of shell forms. Some end members may lack a given character (e.g., tabulate whorls or a sheath), but they can be identified by a combination of characters. *G. sigaretina* is such an example in that it lacks tabulate whorls, whereas *C. fluctuata* has very weakly tabulate whorls (this structure is difficult to see in apertural view). The sheath can be seen in *C. fluctuata* underneath the transparent callus.

We agree with Aronowsky and Leighton that the features of non-planktotrophic protoconchs usually do not show genealogical relationships among gastropods (e.g., Kano and Kase, 2000). Our discussion was concerned only with the planktotrophic protoconch of naticoidean and ampullospirid shells. Aronowsky and Leighton stated that the non-planktotrophic protoconchs of naticoideans do not differ from the planktotrophic protoconchs of ampullospirids, but this is clearly in error, because the former generally consist only of protoconch I, and the latter consist of protoconchs I and II. Aside from this difference, ampullospirid planktotrophic protoconchs are, as we discussed, more highly elevated than are naticoidean non-planktotrophic protoconchs. Bandel (1999) illustrated the protoconch of a very small shell (1 mm

long) from the Eocene of Damery in the Paris basin, which he identified as the ampullospirid *Crommium* sp. This protoconch is unusual among ampullospirids, but we strongly doubt that this shell was correctly identified. At this classic Eocene site, *Crommium* is represented by *C. acutum* (Lamarck, 1804) (= *C. willemeti*) (P. Lozouet, 2003, personal commun.). We have observed that the protoconch of *C. willemeti* is identical to that of *C. fluctuata* and *Globularia parisiensis*. Protoconch morphology remains a reliable character for separating ampullospirids from naticoideans.

We concur with Aronowsky and Leighton that feeding strategy can be hypothesized only by mapping the behavior onto a robust phylogeny. Although a detailed description of the soft anatomy has not yet been published, we listed several features of the soft body of *C. fluctuata* that are quite different from those of naticoideans. Additional features important in assessing the systematic position of *C. fluctuata* are: (1) a hypoathroid nervous system identical to that of freshwater Ampullariidae, except that the pleural ganglia are separated from the pedal ganglia by short connectives; (2) the long intestine; (3) the open pallial gonoduct in both sexes; (4) the absence of a penis in males; (5) protandrous hermaphroditism (sex change occurs when the shell attains about 50 mm in width); (6) the presence of a receptaculum seminis in the pericardial cavity in females; and (7) ultrastructures of the sperm are the same as in Campanilidae (Kase, 1990; J. Healey, 2003, personal commun.). These features demonstrate that *C. fluctuata* is not related to Naticoidea. A preliminary phylogenetic analysis has shown that freshwater Ampullarioidea (Architaenioglossa), which are macrophagous herbivores like *C. fluctuata*, is the sister taxon of Ampullospiridae. Strong (2003) has shown that carnivory appeared only in a terminal clade (that includes Naticoidea) after the diversification of Littorinidae during the evolution of Caenogastropoda (see Strong, 2003, their Fig. 33). These facts strongly suggest that fossil Ampullospiridae were macrophagous grazers, and there is no basis for assuming they were carnivores.

The complete absence of unequivocal naticoidean drill holes in the Jurassic and early Cretaceous would be anomalous only if fossil ampullospirids were drilling predators. Aronowsky and Leighton viewed this anomaly as resulting from a taphonomic bias, or a non-drilling predatory strategy by ampullospirids. However, our discovery of the feeding method of *C. fluctuata* clearly refutes such views. The most plausible interpretation of the lack of naticid drill holes in the Jurassic and early Cretaceous fossil record was the absence of naticoideans.

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