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A veliconcha unveiled: observations on the larva and radula of *Conus spurius*, with implications for the origin of molluscivory in *Conus*

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Abstract: The veliconcha larva of the predatory gastropod *Conus spurius* Gmelin, 1791 is described and for the first time illustrated based on material from Sanibel Island, Florida. Hatchling veliconchas were 1470–1570 µm (mean = 1530) long, with first protoconch whorl maximum diameter 670–740 µm (mean = 710), and estimated egg diameter 570 µm. Veliconchas can swim for a few minutes to a few hours before settling. They have well-developed paired velar lobes each 600–700 µm in length, an extensible foot with a distinct metapodium separated from the remainder of the foot by a transverse fold, and operculum. Several early life history traits of *C. spurius*, particularly hatching as large veliconcha larvae with predominantly lecithotrophic, nearly non-planktonic development, closely resemble those of a well-defined clade of *Conus* Linnaeus, 1758 species that prey on other gastropods. They contrast with the majority of species in this hyperdiverse genus, which hatch as much smaller planktonic, obligatory planktotrophic veliger larvae. As adults they comprise a vermivorous feeding guild, preying exclusively or nearly so on polychaete annelids. Limited data suggest that *C. spurius* may share this trait with them but it may also prey on molluscs. Recent molecular phylogenetic trees suggest that the characters “pelagic development” and “non-pelagic development” (or nearly so: <1 day) are distributed independently of phylogeny in the larger clade that includes *C. spurius* and the molluscivorous species. Similarities in veliconcha morphology and developmental mode, adult radular tooth morphometry, phylogenetic position, and earliest fossil records suggest the speculative hypothesis that the monophyletic clade of extant molluscivorous *Conus* species may have evolved in the Miocene from a vermivore or mixed vermivorous-molluscivorous ancestor with these attributes, such as *C. spurius*.

Key words: Conidae, developmental mode, veliconcha, vermivory, food habits

As in many groups of mollusks, different cone snails exhibit distinctive developmental modes, from protracted planktotrophy to lecithotrophic intracapsular development until metamorphosis (Kohn 1961, Kohn and Perron 1994, Kohn 2012, 2014). Duration of the period between hatching and metamorphosis to benthic life varies among species and is directly correlated with egg size and with size at hatching (Perron 1981, Kohn and Perron 1994: Fig. 4.7). Despite the relative ubiquity, shallow-water habits, and broad distribution range of the western Atlantic species *Conus spurius* Gmelin, 1791, there are few published observations of its early development, and neither descriptions nor illustrations of its veliconcha larva. Kesteven (1905, 1912) coined that term (as “veloconch”) to apply to the portion of the gastropod protoconch formed “during the pelagic existence of the embryo, or the equivalent stages in the case of species...which have no planktonic existence...Or more precisely, that portion of the protoconch formed after the flattening out of the primitive shell gland, and before the loss of the velum” (Kesteven 1912: 51). The term veliconcha has been more broadly used by subsequent workers, e.g., Werner (1939, 1955), Penchaszadeh (1988), and the term is applied to bivalve as well as gastropod larvae (e.g., Mackie and Claudi 2010).

This report describes and illustrates for the first time the veliconcha of the venomous gastropod *Conus spurius*, which

is known to prey on polychaete annelids but may also eat other molluscs. *Conus spurius* is the only one of four recognized members of the clade or subgenus *Lindaconus* Petuch, 2002 with available DNA sequence data (Puillandre *et al.* 2015). We briefly compare its veliconcha to similar larvae in related species and raise the question of the possible roles of morphology of the veliconcha, egg masses, and adult radular tooth of this clade in the evolutionary origin of molluscivory in *Conus*.

Roughly 70% of all *Conus* species prey exclusively on worms, predominantly polychaete annelids (Duda *et al.* 2001; see also Puillandre *et al.* 2014). The numerical predominance of this feeding guild, its wide distribution over the phylogenetic tree, and the similarly vermivorous habits of its most likely ancestral taxon, traditionally referred to as the family Turridae, strongly suggest that it is primitive in *Conus* and that the specialist fish- and mollusc-eating guilds are derived. Aman *et al.* (2015) recently described the likely evolutionary transition to piscivory in *Conus*, but the origin of molluscivory in the genus has not previously been explored.

Previous works on egg capsules and larvae of *Conus spurius*

Kohn (2014: 354–355) and Kohn and Perron (1994: Table 2) list works discussing the egg capsules and early developmental stages of *Conus spurius*. D’Asaro (1970) studied the egg capsules of a population of *C. spurius* from Biscayne Bay,

Florida. He counted the number of embryos in each capsule (range = 54–67; mean = 59) but did not describe the embryos or larvae. Bandel (1975) examined the larval shell of *C. spurius* from the Caribbean coast of Colombia; he misidentified his samples of *C. spurius* as *C. largillierti* Kiener, 1847 (Von Cosel and Kohn 2012). The length at settlement indicated by Bandel (*op. cit.*) also differed between the text and the scale in his pl. 20, fig. 4, for the veliconcha of *C. spurius* (as *C. largillierti*). The stated length of 1300 μm is apparently correct, but the length of the larval shell in the illustration based on its scale bar would result in 2100 μm . Bandel (1976: 186–187, fig. 11) described the individual egg capsules of *C. spurius* from Colombia (again, as *C. largillierti*), indicating that “after more than 10 days of development, all 20 to 40 embryos contained within one egg capsule hatch...as veliconcha, being able to crawl and swim.” Penchaszadeh (1984) measured the diameter of uncleaved eggs of *C. spurius* from Golfo Triste, Venezuela, finding a range of 690–710 μm . The veliconchas he observed hatched at the crawling stage, and shell length at hatching was 1200–1300 μm .

MATERIALS AND METHODS

On May 11, 2016, we collected two *Conus spurius* egg masses from a sandy beach off West Gulf Drive on Sanibel Island, Florida. In the laboratory, capsules were immediately examined for the presence of viable eggs and veliconchas, then kept in a saltwater tank. Capsules were opened with a scalpel and contents emptied into sea water in a petri dish. The descriptions and measurements of veliconchas provided here were taken from individuals from the smaller of the two egg masses. Because other individuals from this egg mass hatched in the lab less than a day after the initial isolation of veliconchas for study, we consider that the measurements and morphological attributes described here are equivalent to those “at hatching.”

Images of larval shells were captured under a scanning electron microscope at the Department of Geology, University of Florida, Gainesville. Veliconchas were photographed under a Leica MZ8 dissecting microscope with a Nikon D800 digital single-lens reflex camera coupled by a Leica phototube.

Shell length and maximum diameter (MD) of the first protoconch whorl of 20 veliconchas were measured through a calibrated eyepiece reticle. MDs were measured using the larval shell parameters of Shuto (1974), Hansen (1980), and Jablonski and Lutz (1980), among others. Egg diameter (ED) was estimated from the regression of egg diameter on protoconch MD of 16 *Conus* species calculated by Kohn and Perron (1994: 52, Fig. 4.8).

As an exemplar of adult *Conus spurius* radular teeth we selected a specimen (shell size 54×29 mm) dredged 54 km

west of Tarpon Springs, Florida at 34 m depth, whose teeth, shell, and body were described and illustrated (Kohn 2014: 350; Text-figs. 5.107–5.109). It is preserved in the Florida Museum of Natural History, Gainesville, no. UF 457440.

Voucher specimens of larvae and larval shells are deposited in the Bailey-Matthews National Shell Museum wet collection, nos. BMSM 113208–113210, and at the Florida Museum of Natural History, nos. UF 505176–505178 (shells mounted for SEM scans only).

RESULTS

Egg masses and egg capsules

Capsules from the larger (in number of capsules) of the two egg masses contained 26–57 veliconchas (mean = 35.6, $n = 8$) and from the smaller, 15–45 veliconchas (mean = 31.8, $n = 5$). The former appeared to be at earlier stages of development than those from the smaller egg mass. These values agree with counts by the previous authors indicated above. Opening the egg capsules in a petri dish with sea water prompted a few veliconchas to start swimming; most settled to the bottom in a few hours. Many of the egg capsules contained veliconchas at apparently different stages of development. In 1–2 days other veliconchas from the larger egg mass hatched in the saltwater tank, and settled after swimming for a few hours. Attempts at rearing veliconchas after metamorphosis were not successful.

Larval shell (Fig. 1, A–E)

The shell at hatching is translucent, almost transparent, with about 2 whorls. The aperture is ovoid, with a slight anterior canal and an incipient parietal shield. The only distinct sculptural feature present (visible only under SEM) is a corrugated sutural band resembling “fillet” welding (Fig. 1D, 1E: sb). Shell lengths ranged 1470–1570 μm (mean = 1530 μm , $N = 20$); MD ranged 670–740 μm (mean = 710 μm , $N = 20$).

Bandel (1975) illustrated the shell of the veliconcha from Colombia and indicated protoconch width as 270 μm , much smaller than the maximum diameter found by us (mean = 710 μm). Possibly Bandel measured the first half-whorl of the protoconch instead of the entire first protoconch whorl as used in the present study and defined by the authors cited in the Materials and Methods section above.

Veliconchas (Figs 1, F–H)

The veliconchas have well-developed, functional, paired velar lobes (Fig. 1F, G: vl), each measuring about 600–700 μm in length when fully extended. As in larvae of other *Conus* species, the velar lobes are festooned with pigmented spots of unknown function (Fig. 1G: sp). The foot (Fig. 1G–H: f) is extensible, elongate, well-developed, with a distinct

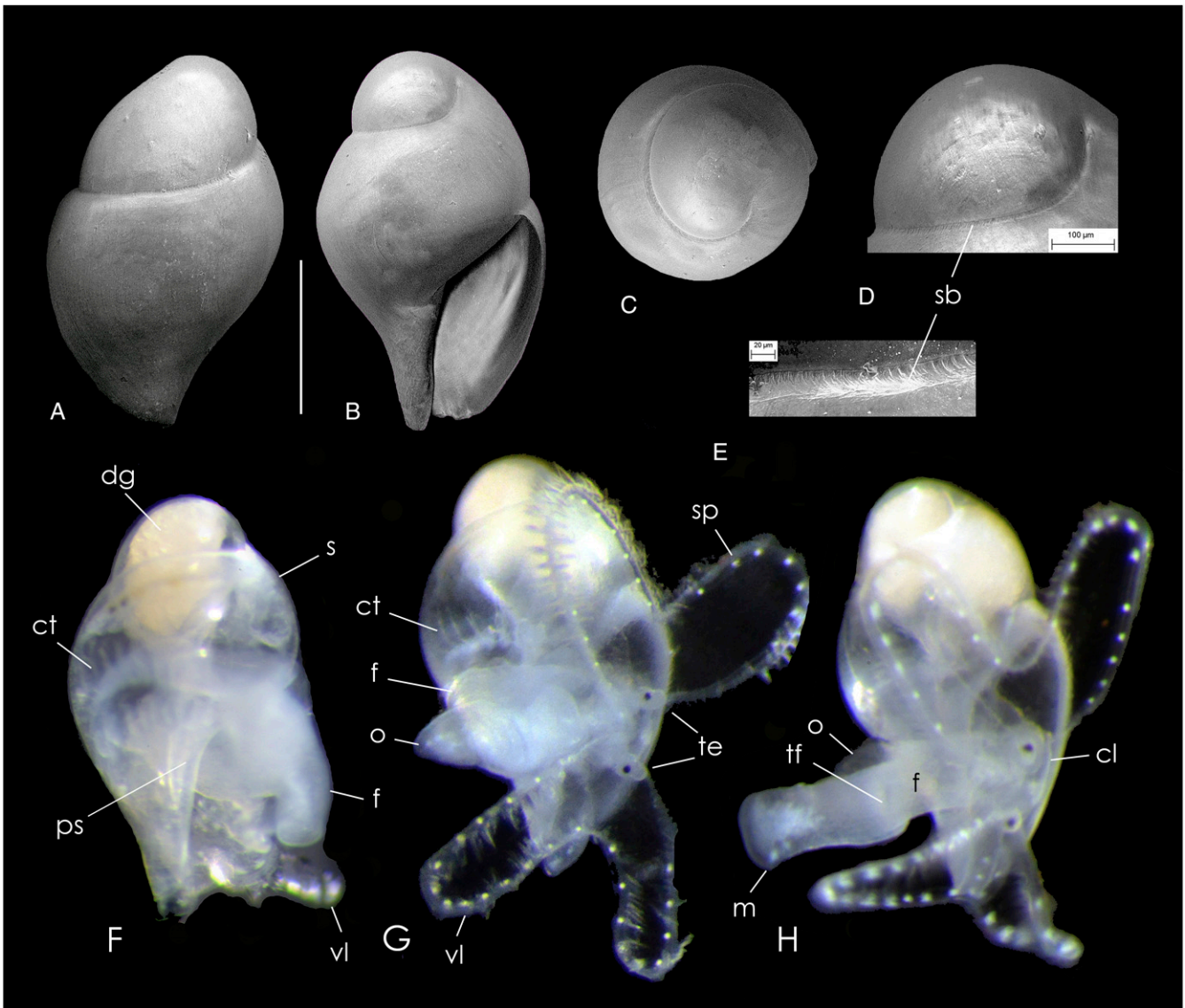


Figure 1. Larval shell and veliconcha of *Conus spurius*. A–E. Scanning electron micrographs of larval shell. A, Abapertural view. B, Apertural view. C, Apical view. D, Detail of the embryonic whorl (first whorl), showing sutural band. E, Detail of the sutural band. F–H. Veliconchas at hatching. F, Veliconcha partially withdrawn into its shell. G, Veliconcha with velar lobes fully expanded. H, Veliconcha with velar lobes expanded and foot extended. Abbreviations: cl, cephalic lobe; ct, ctenidium; dg, digestive land; f, foot; m, metapodium; o, operculum; ps, parietal shell shield; s, shell; sb, sutural band; sp, pigmented spot; te, tentacles with eyes; tf, transversal fold of foot; vm, visceral mass. Scale bar: A–C, F–H = 500 μ m; otherwise indicated on bar.

metapodium (Fig. 1H: m), separated from the remainder of the foot by a transverse fold (Fig. 1H: tf). The foot is capable of withdrawing into the shell by folding transversely (Figs 1G, 1H). The operculum (Fig. 1G–H: o) is ovoid and translucent. The cephalic lobe (Fig. 1H: cl) is not well-developed. An eye spot is present on the median region of each stubby tentacle (Fig. 1G: te). The nearly transparent shell makes it possible to observe the spacious mantle cavity, including the ctenidium

(Fig. 1F, G: ct) and the visceral mass, including the digestive gland (Fig. 1F: dg).

At the hatching stage, the larva is already capable of completely withdrawing into the shell, with the operculum partially sealing the aperture. The visceral mass is visible through the shell as a compact, solid, cream-yellow structure located apically and occupying most of the first whorl of the larval shell.

After removal from the egg capsule, veliconchas showed a range of swimming and crawling behaviors; some were capable of swimming for at least a few hours, some swam less than that, some hovered over the bottom, and others began crawling immediately without undergoing a brief swimming stage. Active ciliary movement on velar lobes upon removal from egg capsules suggests that the larvae probably actively feed on food particles within the capsule. These behaviors and eventually associated morphological variations were not quantified given the variability present within the studied capsules.

Inference of egg size

Uncleaved eggs were not present in the egg capsules examined. However, egg diameter (ED) was estimated from its regression on maximum diameter of the first protoconch whorl (MD). Plotting our mean MD of 710 μm (N=20) on Kohn and Perron's OLS regression indicated egg diameter of 570 μm for the study veliconchas. This estimated value falls outside the range (690–700 μm diameter) obtained by Penchaszadeh (1984) for uncleaved eggs of *Conus spurius* from Golfo Triste, Venezuela. Penchaszadeh (1984) also observed that veliconchas of *C. spurius* hatch as benthic crawlers 1200–1300 μm long, in contrast to 1470–1570 μm (mean=1530 μm) found in the present study.

A possible explanation of these discrepancies with the results from Florida is that the Golfo Triste specimens studied by Penchaszadeh (1984) were trawled at depths of 35–40 m and may be characteristic of the subspecies *Conus s. lorenzianus* Dillwyn, 1817 (Kohn 2014: p. 357). Díaz (1990) noted that in Colombia individuals agreeing with the description of the latter are relatively more common below 30 m.

DISCUSSION

Implications from *Conus spurius* for the possible origin of molluscivory in *Conus*

Several disparate observations, listed below, suggest the hypothesis that the clade comprising the *Conus* species that are specialized predators on other gastropods may have evolved from a vermivorous ancestor with radular teeth and phylogenetic position as well as developmental mode similar to *C. spurius*. Although all intermediate branches are not strongly supported, the current molecular phylogenetic tree of *Conus* species (Puillandre *et al.* 2014) is consistent with the common ancestor of the clades now considered the subgenera *Harmoni-conus* da Motta, 1991 and *Lindaconus* (which includes *C. spurius*) also being ancestral to the monophyletic cluster of clades that include all of the known extant specialized molluscivorous species (*Conus s.s.*, *Leptoconus* Swainson, 1840, *Calibanus* da Motta, 1991, *Darioconus* Iredale, 1930, and *Cylinder* Montfort, 1810) (Puillandre *et al.* 2014: 297, Fig. 2; 2015).

1. Similarity of eggs, egg capsules, and developmental stages of *Conus spurius* to molluscivorous species

Throughout *Conus*, egg size reliably predicts developmental mode including duration of an obligatory planktonic, planktotrophic stage. It also predicts, to some extent, membership in the vermivorous or molluscivorous feeding guild. Eggs ≥ 500 μm in diameter are typically lecithotrophic, hatching as veliconchas with a short or no pelagic stage. These characterize about 30% of known molluscivorous species, but only about 10% in the much larger vermivore guild, whose vast majority lay smaller eggs that hatch as planktonic, planktotrophic veligers with longer durations (Kohn and Perron 1994; summarized here in Fig. 2).

The very large size of the *Conus spurius* egg (reported diameter range = 570–1077 μm ; mean = 780 μm), its developmental mode as described above, and some of the main attributes of veliconcha morphology discussed above closely resemble those of molluscivorous congeners with very short or no pelagic larval stages and lecithotrophic larval development. In addition, *C. spurius* egg masses are of Type II (Kohn and Perron 1994), *i.e.*, most capsules are attached to previously laid capsules rather than directly to the substratum (Type I egg masses). The egg masses of all 14 molluscivorous species that Kohn and Perron (1994) described were of Type II, while almost all other *Conus* egg masses that are known are of Type I (Bandel 1976, Kohn and Perron 1994).

In the four exclusively molluscivorous clades whose eggs and development are best known, the 15 species in the related subgenera *Conus s.s.*, *Calibanus*, *Cylinder*, and *Darioconus* represented in Fig. 2 (Kohn and Perron 1994, Puillandre *et al.* 2014, 2015), mean egg diameter ranged 240–670 μm with mean = 410 μm . For instance, the larval shell of *C. pennaceus* Born, 1778, from Hawaii, with mean egg diameter 490 μm , hatches as a veliconcha with shell about 1250 μm long, similar in size at hatching and number of whorls (about two), to that of *C. spurius* (Kohn 1961: 172, Perron 1981: 32). Morphology and size of velar lobes, head, cephalic tentacles, and eyes in *C. pennaceus*, as inferred and estimated from illustrations in Perron (1981: fig. 5, E, fig. 6, F) also match these attributes of the *C. spurius* veliconcha.

Reduction in the duration or total loss of a pelagic larval stage is known to have occurred *de novo* and independently in many gastropod lineages, including the Conidae (Duda and Palumbi 1999, Kohn 2012, 2014). *Conus spurius* and *C. pennaceus* are widely separated geographically, differ markedly in shell form and feeding biology, but have veliconchas with similar general morphologies (size, number of protoconch whorls, size and shape of velar lobes, and others discussed above). In *C. anemone* Lamarck, 1810 from Australia, the vermivorous species in Fig. 2 with egg size second only to *C. spurius*, the veliconcha is also morphologically very similar to that of *C. spurius*: 1640 μm long at hatching, with smooth, blunt shells

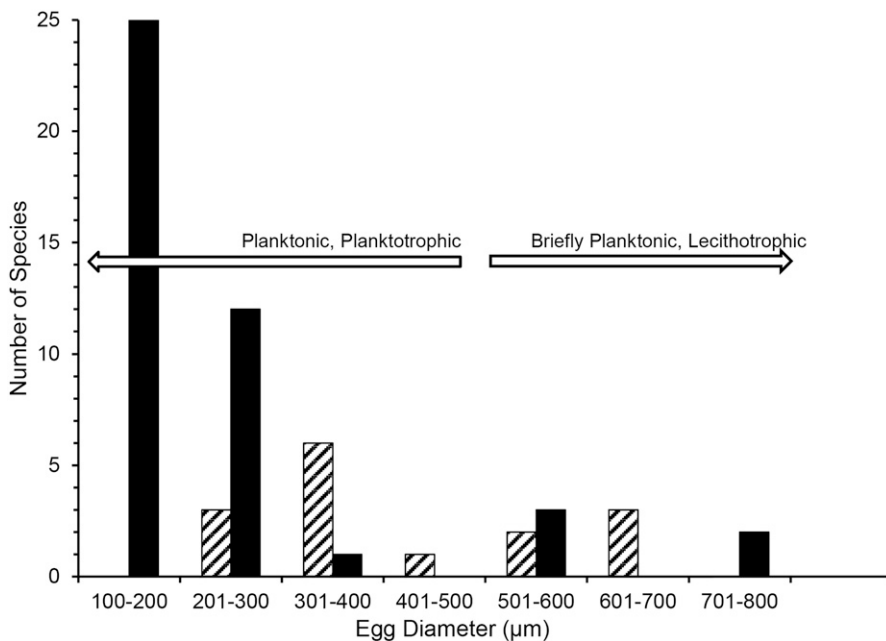


Figure 2. Egg diameters of vermivorous (solid histograms; mean = 244 µm; range 129–780 µm; median = 196 µm; N = 43) and molluscivorous (hatched histograms; mean = 410 µm, range 240–666 µm; median = 338 µm; N = 15) *Conus* species, based mainly on data in Appendix Tables 1 and 2 of Kohn and Perron (1994). Molluscivorous species have very highly significantly larger egg diameters than vermivorous species (Mann-Whitney U test: $U = 79$; $P < 0.0003$). The two vermivorous species with the largest eggs (701–800 µm) are *C. spurius* (including data from the present study) and the Australian *C. anemone* Lamarck, 1810. The graph includes previously unpublished data for the molluscivore *C. bengalensis* (Okutani, 1968) (egg diameter = 400 µm).

spanning two whorls, and similar-sized velar lobes, foot, metapodium, and operculum (Kohn 1993, Kohn and Almasi 1993).

Conus spurius thus shares several reproductive, developmental and early life history characteristics with an Indo-Pacific vermivorous species with unusually large eggs, and with a number of Indo-Pacific molluscivorous congeners. The only other vermivorous species known to have nonplanktonic development (estimated from egg size, 550–600µm) (Fig. 2) are three western Atlantic predators of fireworms, polychaetes of the family Amphinomidae: *C. cedonulli* Linnaeus, 1758, *C. mappa* [Lightfoot], 1786, and *C. pseudaurantius* Vink and von Cosel, 1985 (Kohn and Perron 1994, Kohn 2014). The only western Atlantic molluscivorous species of Conidae is *Conasprella centurio*, with egg diameter 550 µm (Kohn and Perron 1994), in a genus that likely diverged from *Conus s.s.* in the Oligocene Epoch (Duda and Kohn 2005).

2. Several attributes of adult *Conus spurius* radular teeth resemble molluscivorous species more closely than vermivores

All species of Conidae whose feeding biology has been examined are predatory carnivores that swallow prey whole,

usually after envenomating them. While the diet in nature of at least one species includes members of at least four animal phyla and three classes of molluscs (Kohn 1966), most belong to one of three specialized feeding guilds, consuming either worms, mainly polychaete annelids, other gastropods, or fishes (Puillandre *et al.* 2016). The vermivorous guild comprises the majority of all extant *Conus* species and is likely ancestral to the other two (Duda *et al.* 2001).

Unfortunately, the food in nature of *Conus spurius* is virtually unknown. While several studies of its venomous conopeptides state that *C. spurius* is vermivorous (Maillo *et al.* 2002, Rojas *et al.* 2008, Zamora-Bustillos *et al.* 2010), these assertions are undocumented. To our knowledge, in the only well documented case, Kohn (2014) reported extracting remains of a polychaete annelid (family Eunicidae) from the alimentary tract of a preserved specimen from Colombia; he has also heard other anecdotal accounts of vermivory. However, *C. spurius* may well also prey on molluscs in nature. Songdahl (1973) showed that injecting *C. spurius* venom into several gastropods and bivalves in aquaria was toxic,

and also that living molluscs kept in aquaria with *C. spurius* appeared to have been eaten, although he did not observe predation.

Conus spurius radular teeth share several morphological characteristics that are less similar to those of other vermivorous species and more closely resemble those of the molluscivorous species that constitute a monophyletic clade of several subclades now considered subgenera as mentioned above (Puillandre *et al.* 2014, 2015). In particular, the teeth of molluscivorous *Conus* species are typically longer relative to shell length than those of vermivores (Rolán and Raybaudi Massilia 2002). Tooth length:shell length ratios in 11 molluscivorous species had mean = 0.07 and range = 0.03–0.12 (Nishi and Kohn (1999: Table 3) vs. mean ratio = 0.03 and range = 0.02–0.05 in 14 vermivorous species (U-test: $P < 0.001$; data from Kohn *et al.* 1999, Tucker and Tenorio 2013, and Kohn 2014). If *C. spurius* is primarily vermivorous, its tooth (Kohn 2014: Text-fig. 5.109) is the longest relative to shell length (0.05) known in that guild.

In addition, the barb at the tip of the tooth is shorter in relation to tooth length in molluscivores (mean ratio = 0.05; range = 0.03–0.08) than in vermivores (mean ratio = 0.07;

range = 0.03–0.10; U test: $P=0.01$). Finally, the serrations on the teeth of molluscivorous species differ from those of vermivores. The row is generally longer relative to tooth length in molluscivores (mean ratio = 0.63; range = 0.33–0.81) than in vermivores (data from Tucker and Tenorio 2013, and Kohn 2014): (mean ratio = 0.27; range = 0.10–0.52; U test: $P<0.001$). As in tooth length:shell length ratio, *Conus spurius* had the highest serration length:tooth length ratio, 52%, among vermivores. However, the individual denticles that comprise the serration of *C. spurius* resemble the teeth of vermivores in that they are coarser than those of molluscivores (Nishi and Kohn 1999).

Thus tooth form in the molluscivorous *Conus* groups differs substantially from those of the vermivorous majority of species, with vermivory most likely being the ancestral feeding habit of the genus (Duda *et al.* 2001). However, *C. spurius*, with radular teeth closely resembling those of its molluscivorous congeners, may also be capable of eating molluscs, as Songdahl (1973) suggested.

3. Phylogenetic evidence for a most recent common ancestor of *Conus spurius* and the clade of molluscivorous congeners

To estimate the mode of development of the putative common ancestor of *Conus spurius* and, e.g., *C. pennaceus*, we (1) assumed these characters to be discrete, and (2) mapped the observed or predicted modes of development of terminal taxa to a phylogeny of the clade comprising the two species and their nearest likely common ancestor. The recent phylogenetic analyses of the Conidae by Puillandre *et al.* (2014), based on three sequenced mitochondrial genes, indicate that these two species belong to a clade comprising eleven subclades (considered subgenera in Puillandre *et al.* 2014, 2015), represented in those analyses by 38 species. A search for data on the observed or predicted mode of development for these species primarily in the *Conus* Biodiversity Website (Kohn and Anderson 2016) indicated that at least 21 among them have observed or predicted pelagic larval development, 6 have predicted non-pelagic development, and 12 are undetermined.

Mapping the characters “pelagic development” vs. “non-pelagic or nearly non-pelagic (<1 day) development” onto the Puillandre *et al.* (2014) phylogeny for the “*spurius*–*pennaceus*” portion of the tree, pruned to omit additional vermivorous descendant branches (Fig. 3), indicates that distribution of these two characters in the terminal taxa is apparently phylogeny-independent, with only one pair of “sister species” sharing non-pelagic development, and the other five non-pelagic developers randomly distributed in the tree, suggesting that the common ancestor was a pelagic developer. The first published species-level molecular phylogenetic study of *Conus*, based on sequences of the nuclear calmodulin gene (Duda and Palumbi 1999), reached a similar conclusion. Its analysis of 70 species also resulted in well supported clades,

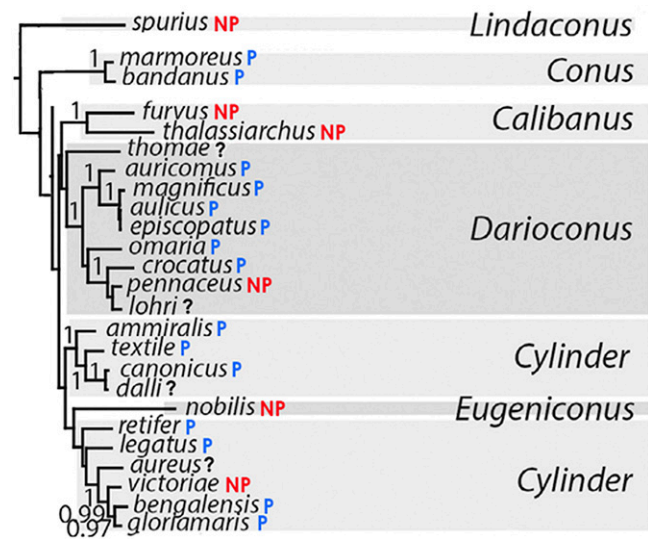


Figure 3. Larval type (pelagic or non-pelagic) mapped on the portion of the Bayesian species-level tree of *Conus* showing the clade containing all known molluscivorous species (modified from Puillandre *et al.* 2014, Fig. 2c). The molecular phylogenetic tree is based on three concatenated mitochondrial genes (CO1, 16S, and 12S), and posterior probabilities (>0.95) are shown for each node. The portion shown illustrates the hypothesized origin of molluscivory in *Conus* (the six known subgenera (*Conus* s.s. to *Cylinder*) from the subgenus *Lindaconus*, of which the likely primarily vermivorous *C. spurius* is the only one of four assigned extant representatives with molecular genetic data (Puillandre *et al.* 2015). Additional clades (subgenera) of vermivorous descendants of *Lindaconus* have been pruned from the tree, including three nodes between *Lindaconus* and the molluscivorous taxa shown that lead to other vermivorous subclades. P, pelagic development; NP, non- or briefly (<1 day) pelagic development; ?, undetermined.

and eight species, each from a different clade of the phylogenetic tree and each from a different ancestor with planktonic larvae, had nonplanktonic development.

4. Fossil record of molluscivorous *Conus* and their hypothesized vermivorous ancestor

Both present knowledge of the fossil record and molecular clock analyses indicate that molluscivory originated only once in *Conus*, most likely in the Middle Miocene, about 11 mya (Duda *et al.* 2001). Duda and Palumbi (1999) also estimated that nonplanktonic development in *Conus* originated at about the same time. The Lower and Upper Miocene records of “*C. spurius* s.l.” from Venezuela reported by Landau *et al.* (2008: App. B) are the earliest of that species or perhaps of an ancestor or close relative.

The results reported here describe the unusual but formerly poorly known early life history of *Conus spurius* and shed some light on the likely origin of molluscivory from

vermivory within the genus *Conus*. However, the evolutionary scenario presented remains very speculative, for several reasons: The most recent species-level phylogenetic trees of *Conus* (Puillandre *et al.* 2014, 2015) include fewer than half of the more than 700 extant species in the genus. More detailed genetic analyses and genomic knowledge, further study of morphology, developmental modes, and feeding biology of *C. spurius*, its closest extant and extinct relatives and other potential ancestors of molluscivorous *Conus* species, and improved knowledge of their fossil record are needed for more convincing phylogenetic character mapping and more confident understanding of how so many closely related species have originated and persisted.

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