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MORPHOLOGICAL DEVELOPMENT OF THE RADULA OF FOUR SPECIES OF THE NEOGASTROPOD FAMILY MURICIDAE

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ABSTRACT

Radular ontogenies of four species of the neogastropod family Muricidae are described through comparisons of early post-metamorphic and adult developmental stages, with specific focus on the rachidian (central) tooth. The degree of rachidian transformation during ontogeny varies from minor shape change to addition or loss of structural features important for assigning taxa to subfamilies. Changes include: flattening of the rachidian base and a switch from a short, beak-like to a long, flattened central cusp in the rapanine *Stramonita biserialis*; a switch from variable, asymmetric to regular, symmetric expression of inner lateral denticles in the basal muricid *Timbellus phyllopterus*; curvature of the rachidian base at the margins and separation of the pointed base endpoint from the radular membrane to form a marginal cusp in the muricine *Chicoreus dilectus*; and moderate straightening of the rachidian base in the ocenebrine *Vokesinotus perrugatus*. From these observations and previous work, we propose a plesiomorphic developmental sequence for the Muricidae and provide supporting evidence for the developmental origins of novel features of the muricid radula.

Key words: Muricidae, radula, teeth, development, ontogeny.

INTRODUCTION

The gastropod radula is often modified during development, particularly in the number, shape, and size of teeth, cusps, and denticles (e.g., polyplacophora: Minichev & Sirenko, 1975; pulmonates: Sterki, 1893; pulmonates: Kerth, 1979; trochoideans: Warén, 1990; conids: Nybakken, 1990; Nybakken & Perron, 1998; epitoniids: Page & Willan, 1988; atlantid heteropods: Richter, 1961; patellogastropods: Guralnick & Lindberg, 1999). In many of these examples, developmental modifications were found to mirror key evolutionary transitions between higher taxa, suggesting that evolutionary changes in developmental timing (i.e., heterochrony) may be an important mechanism for generating the kinds of morphological novelty studied by systematists.

Heterochronic mechanisms are thought to have been particularly important in the origins of several subfamily-level, radula morphotypes within the neogastropod family Muricidae (Fujioka 1984, 1985; DiSalvo, 1988; Di Salvo & Carriker, 1994; Herbert et al., 2007; Pastorino et al., 2007; Pastorino & Penchaszadeh, 2009; Pio et al., 2014). However, the early ontogenetic stages of the radula are still unknown for most of the nearly 2,000 species currently assigned to the Muricidae, and coverage is uneven at the level of muricid subfamilies. Prior work on muricid radulae has focused mainly on species of the Rapaninae, Ergalataxinae, and Trophoninae. In particular, there are no observations on radular development for any of the putative basal lineages of the family (e.g., *Timbellus* Gregorio, 1885; *Poirieria* Fischer, 1884; *Paziella* Jousseaume, 1880) recognized by

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Merle et al. (2011), although these ontogenies might potentially be useful for understanding whether and how heterochrony (evolutionary changes in developmental timing) contributed to the origin and early morphological diversification of the Muricidae. Here, we present new observations on radular development in four species representing three of the eleven subfamilies of the Muricidae, including one basal member of the family: Rapaninae: *Stramonita biserialis* (Blainville, 1832); Muricinae: *Timbellus phyllopterus* (Lamarck, 1822), *Chicoreus dilectus* (A. Adams, 1855); and Ocenebrinae: *Vokesinotus perrugatus* (Conrad, 1846).

MATERIALS AND METHODS

Species were selected based on availability of early post-metamorphic and adult specimens. Radulae were extracted from adult, alcohol-preserved specimens by dissolving dissected proboscis and buccal mass tissues in a concentrated solution of sodium hypochlorite. Both female and male adult specimens were examined; sex determinations for adults were made by visual inspection. Early post-metamorphic snails were harvested directly from egg capsules deposited by adults for three of the four species studied (*T. phyllopterus, C. dilectus, V. perrugatus*) and opportunistic collection of an early post-metamorphic specimen of *S. biserialis* just after settlement on a natural substrate. None of the juveniles examined had more than a whorl of adult sculpture (Figs. 1–4), indicating recent metamorphosis, and two of the four had little or no adult sculpture (Figs. 3, 4).

Radulae of early juvenile snails were recovered by crushing the shells in a shallow Petri dish filled with a concentrated solution of sodium hypochlorite. In some cases, juvenile radulae were extracted together with the odontophore. Radular ribbons were collected with forceps, washed in distilled-water, mounted on stubs with double-sided conductive tape, air-dried, and coated for scanning electron microscopy with Au-Pd. All radulae were examined using a Scanning Electron Microscope (SEM).

Voucher specimens for juvenile and adult radulae are reposited as collective lots in the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (MACN). These are as follows: *Chicoreus dilectus* (MACN-In 39550); *Stramonita biserialis* (adult only) (MACN-In 39551); *Stramonita biserialis* (juvenile only) (Yale Peabody Museum No. 28490) *Timbellus phyllopterus* (MACN-In 39552); *Vokesinotus perrugatus* (MACN-In 39553).

Abbreviations and Terminology

The terminology used to describe structural elements of the radula follows Radwin & D'Attilio (1976), Kool (1993) and Herbert et al. (2007) and is illustrated in Figures 2–5. b: rachidian base; cc: central cusp; ild: inner lateral denticle; imc: inner marginal cusp; lc: lateral cusp; mc: marginal cusp; md: marginal denticle; old: outer lateral denticle; omc: outer marginal cusp; rm: radular membrane; s: shoulder; sild: serrated inner lateral denticle.

Following Vokes (1971), a "3-D" base is one in which the rachidian base is not flat or straight along its length but has depth due to the appearance of being angled or bent. A bend in the base can occur at the position of each lateral cusp, which gives the base a V-shape, or at the position of each marginal cusp, which produces a broader, U-shaped or "rectangular" rachidian. The distinction between different types of bending points along the rachidian base was not recognized by Vokes (1971) or Herbert et al. (2007).

RESULTS

Subfamily Rapaninae

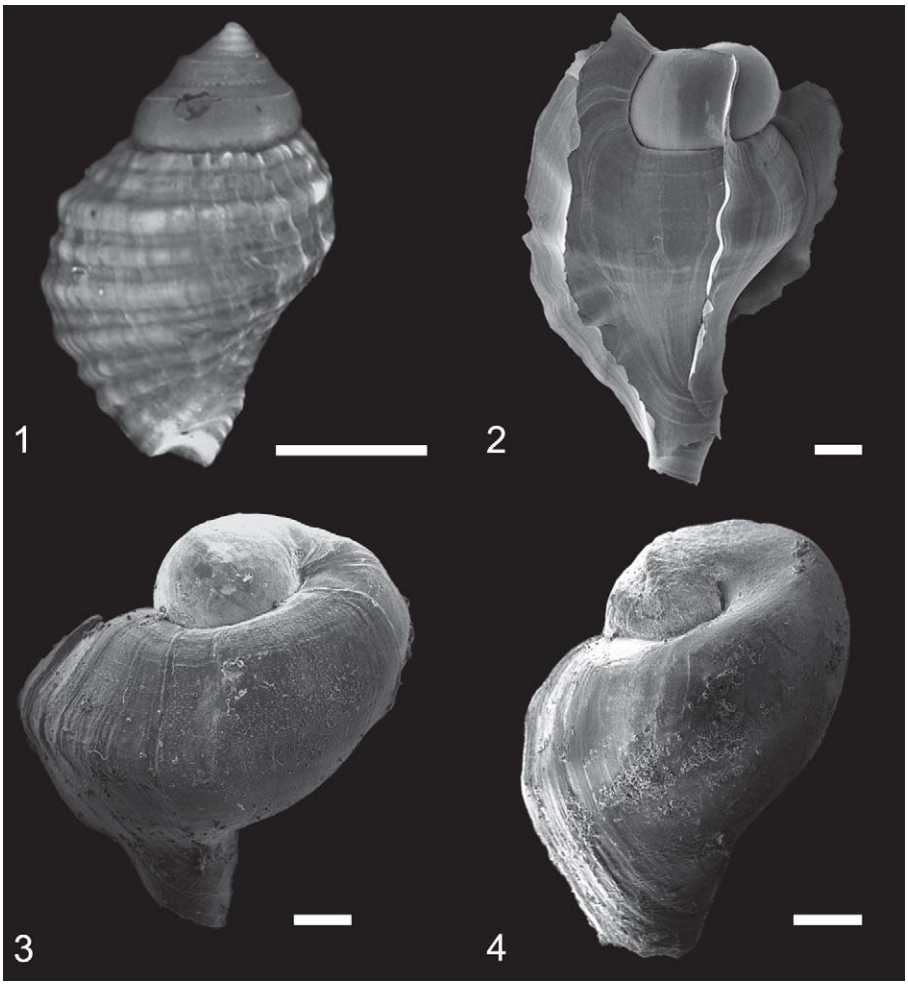
Stramonita biserialis (Blainville, 1832)
(Figs. 1, 5–10)

Material Examined

One early post-metamorphic specimen of *Stramonita biserialis* (Yale Peabody Museum No. 28490) with shell length of roughly 2 mm was collected post-settlement from the carapace of a sea turtle at Costa Careyes, Mexico. Nine adult specimens were collected from boulders in the exposed rocky intertidal around Isla Venado, Gulf of Panama, in August 2005 and January 2006.

Ontogeny

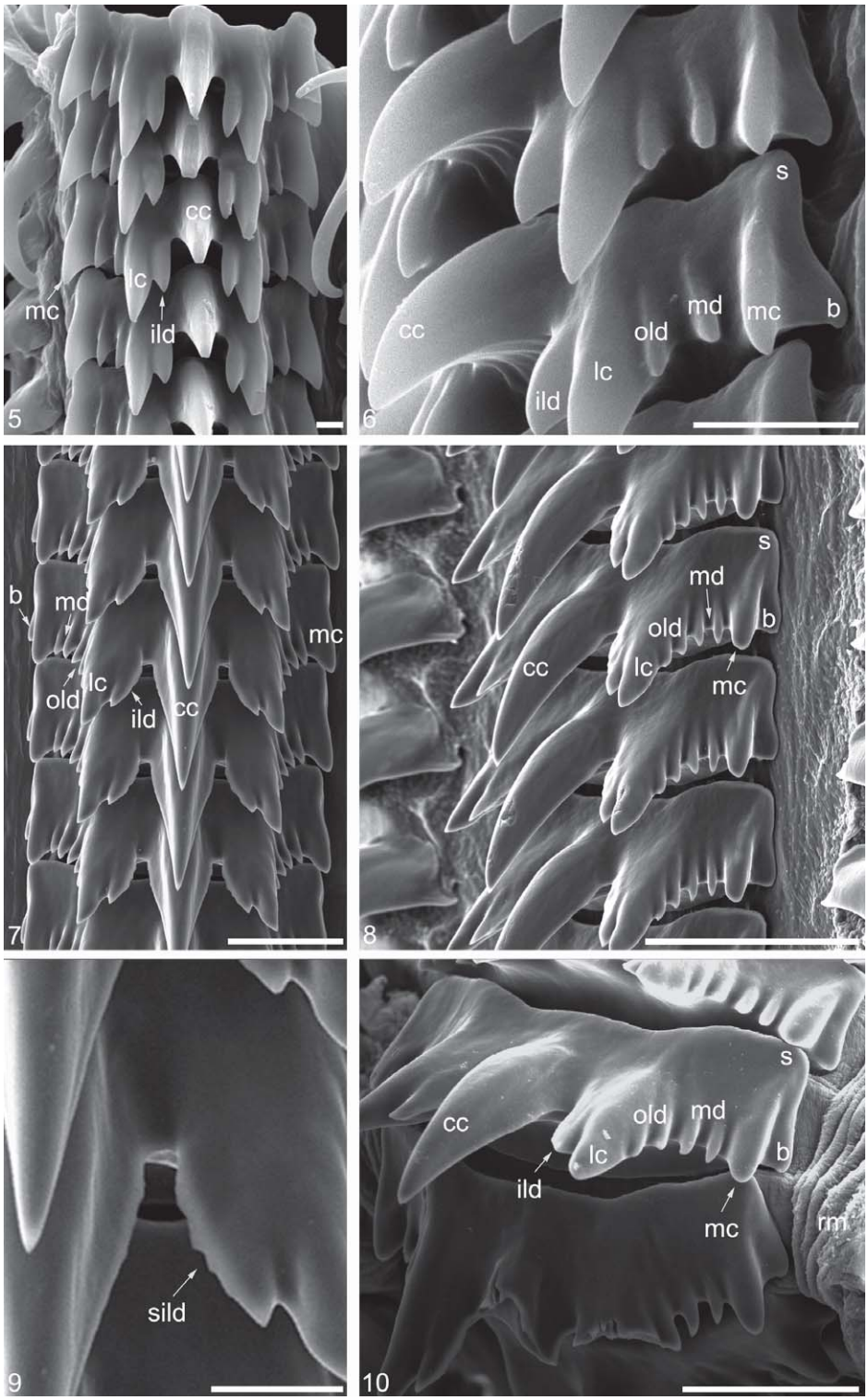
Juvenile teeth (Figs. 5, 6): With V-shaped, 3-D base and narrow, curved, central cusp projecting almost 90° from base. Lateral cusps projecting 45° away from rachidian base, positioned close to central cusp, and sharing



FIGS. 1–4. Dorsal views of juvenile shells. FIG. 1: *Stramonita biserialis*, shell height (SH) = 2.8 mm; FIG. 2: *Timbellus phyllopterus*, SH = 1.5 mm; FIG. 3: *Chicoreus dilectus*, SH = 1.75 mm; FIG. 4: *Vokesinotus perrugatus*, SH = 1.42 mm. Scale bars: Fig. 1 = 1 mm, Figs. 2–4 = 200 µm.

common base with shorter inner lateral denticles. Central and lateral cusps approximately same length. Marginal area with two marginal denticles, including one flanking outer edge of lateral cusp. One marginal cusp, separated from broad, lobe-like extension of rachidian base. Tip of base with prominent, cusp-like end-point. Rachidian base with high, narrow, rounded shoulder.

Adult teeth (Figs. 7–10): With rachidian base slightly bent at lateral cusp position (V-shaped base) and long, straight, triangular central cusp at 45° with rachidian base (Fig. 8). Lateral edges of central cusp near base with subtle serrations. Lateral cusps shorter than central cusp, splayed laterally, and projecting 45° away from rachidian base (co-planar with central cusp). Inner lateral denticle short, strongly serrated along inner edge, splayed laterally, and sharing common base with lateral cusp (Figs. 7, 9). Outer edges of lateral cusps with two or three, small denticles. Marginal area with two marginal denticles (Figs. 8, 10). One marginal cusp separated from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broad, lobe-like extension of rachidian base (Figs. 8, 10). Lobe-like extension shorter, more rounded than in juvenile. Rachidian base with low, broad shoulder.

Remarks

The ontogeny of *S. biserialis* mirrors that of the Chilean rapanine *Concholepas concholepas* (Bruguière, 1789), as described by Herbert et al. (2007). In both species, adult rachidia have typical rapanine features (e.g., flat rachidian base, a central cusp aligned in the same plane as the lateral cusps, and lateral cusps with a broad, flat base: see Kool, 1987, 1993), while early post-metamorphic individuals have a rachidian that fits the generalized morphology of the subfamily Ocenebrinae (e.g., 3-D rachidian base; short, projecting central cusp; and narrow, conical lateral cusps with appended inner lateral denticles).

The 3-D nature of the juvenile rapanine rachidian base is superficially similar to that of juvenile and adult ocenebrines but differs in having a bend or angle at each lateral cusp, which produces a base with a V-shape. In ocenebrines, the rachidian is angled 90° at the position of each inner marginal cusp, producing a broad U-shape, and sometimes has an additional angle in the middle of the rachidan or at the lateral cusp positions (see *V. perrugata* description below). Another feature of juvenile rapanine rachidia that is superficially similar to that of ocenebrines is a rachidian with pseudo-bifid basal margins (appearance of two cusps). In juvenile rapanines we have studied thus far (*C. concholepas*: Herbert et al., 2007, *S. biserialis*: this study), the bifid morphology is formed by one marginal cusp and a cusp-like ridge at the rachidian base end-point that remains attached to the radular membrane along its entire length. In ocenebrines, however, the bifid morphology is formed by two true marginal cusps, both completely separated from the radular membrane by a narrow, lobe-like feature (Herbert et al., 2007; Pio et al., 2014). Rapanines generally do not retain this pseudo-bifid morphology into adulthood (Kool, 1987, 1993; but see Tan, 2003: fig. 16H), as the ridge at the rachidian base edge becomes less cusp-like in larger juveniles and adults (Fujioka, 1984, 1985; Herbert et al., 2007).

Subfamily Muricinae

Timbellus phyllopterus (Lamarck, 1822)
(Figs. 2, 11–16)

Material Examined

Material used includes seven adults (one male and six females) collected from Basse Terre Island, Guadeloupe and ten newly hatched, direct developing juveniles with shell lengths between 1–2 mm. Juveniles were reared from capsules in aquaria as described by Pointier & Lamy (1985).

Ontogeny

Juvenile teeth: With narrow, flat rachidian base and conical central and lateral cusps projecting 45° from base (Figs. 11, 12). Lateral cusps outwardly splayed. Short, conical inner lateral denticle between central and lateral cusps, closer to lateral cusp but not attached to lateral cusp base. Inner lateral denticles sometimes absent or underdeveloped on one side (Fig. 11). Marginal denticles present as indistinct tubercles (Fig. 12: md). Rachidian base with high rounded shoulder and large, outwardly splayed, cusp-like base endpoint (Figs. 12: b).

Adult teeth: With broad, flat rachidian base, and triangular central and lateral cusps projecting almost 90° from base at point of basal attachment but curved distally (Figs. 13–14). Lateral cusps with slight outward curvature, shorter than central cusp, and bending halfway along their length. Narrow inner lateral denticle (Figs. 13, 14: ild) with slight outward curvature, nearly as long as adjacent lateral cusp, equidistant between lateral and central cusps, and free from both. Marginal area

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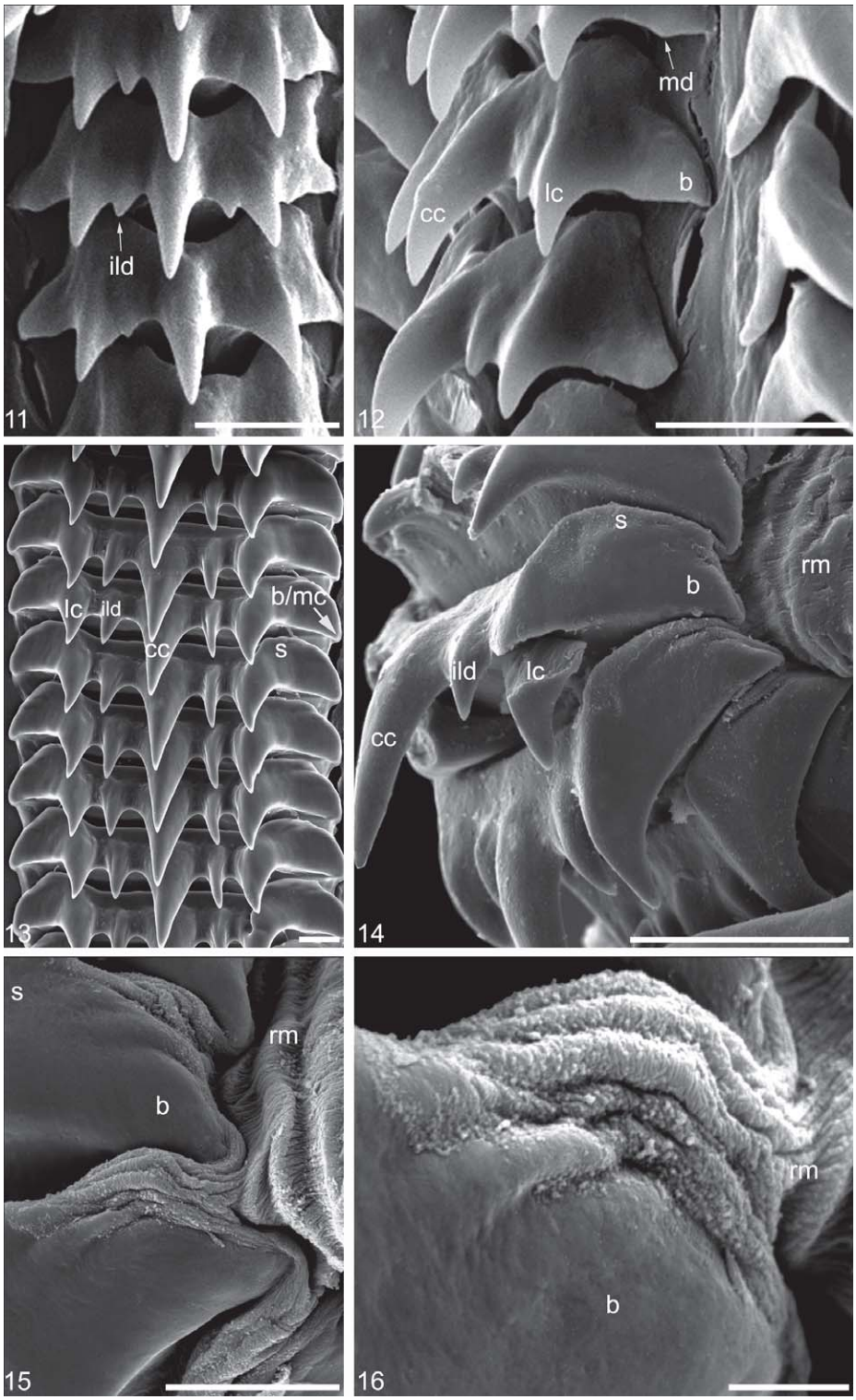
FIGS. 5–10. Dorsal and lateral views of rachidian tooth ontogeny of *Stramonita biserialis*. FIGS. 5, 6: Tooth of a juvenile, shell height (SH) = 2.8 mm; FIGS. 7, 8: Tooth of an adult, SH = 31 mm; FIG. 9: Serrated inner lateral denticles of an adult tooth, SH = 31 mm; FIG. 10: Adult radula over the bending plane of the odontophore, SH= 25 mm. Scale bars: Fig. 5 = 2 µm, Fig. 6 = 5 µm, Fig. 7 = 50 µm, Fig. 8 = 100 µm, Fig. 9 = 10 µm, Fig. 10 = 50 µm; b = base; cc = central cusp; ild = inner lateral denticle; lc = lateral cusp; mc = marginal cusp; md = marginal denticle; old = outer lateral denticle; sild = serrated inner lateral denticle.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broad, flat, with no marginal denticles (Fig. 14). Rachidian base with broad, rounded shoulder and broad, rounded, cusp-like end-point. Outer edge of shoulder with smooth or folded surface (Figs. 15, 16).

Remarks

One of the most notable features of the rachidian teeth of *T. phyllopterus* is ontogenetic change in variability of expression of the inner lateral denticles, which changes from irregular expression in juveniles to regular expression in adults. Rachidia of adults consistently have one inner lateral denticle on each side of the central cusp. In juveniles, however, these structures may be present on both sides of the central cusp as in adults, underdeveloped or absent on just one side (asymmetrical expression), or, less commonly, absent on both sides, all within a single radular ribbon. A second notable feature of the *T. phyllopterus* radula is that there is no clear differentiation between the rachidian base and marginal cusp in either juvenile or adult individuals. Instead, the end of the base is rounded and adherent to the radular membrane along nearly its entire length.

The entire rachidian development of *T. phyllopterus* is remarkably similar to that of *Phyllonotus pomum* (Gmelin, 1791) as described previously by Herbert et al. (2007). Both genera have traditionally been classified as belonging to the Muricinae (Radwin & D'Attilio, 1971, 1976; Ponder & Vokes, 1988; Vokes, 1990, 1992), but morphological and molecular data (Vokes, 1971; Merle, 1999; Barco et al., 2010) suggest that this subfamily is polyphyletic, with *Phyllonotus* Swainson, 1833, belonging to a separate, younger branch (*Hexaplex* group) of true muricines and *Timbellus* Gregorio, 1885, belonging to an as-yet unnamed and much deeper branch.

The fossil record of *Timbellus* Gregorio, 1885, extends back to the Early Paleocene, making it one of the oldest lineages of the Muricidae and one of just three muricid genera to have evolved by that time (Vokes, 1971, 1990, 1992; Garvie, 1991; Merle et al., 2011).

Chicoreus dilectus (A. Adams, 1855)
(Figs. 3, 17–22)

Material Examined

Five juveniles with shell lengths around 1.75 mm were harvested from capsules deposited by adults in laboratory aquaria. Four adults (two males and two females) were collected from sea grass in water 1 m deep in St. Joseph Bay, Florida in June 2007.

Ontogeny

Juvenile teeth (Figs. 17, 18, 21): With narrow, lightly curved rachidian base and long, conical, central and lateral cusps projecting 45° from rachidian base. Lateral cusps slightly splayed, same length as central cusp. Inner lateral denticle conical, thin and shorter than lateral cusps (Fig. 17). No space between inner lateral denticle and adjacent central and lateral cusp. Broad marginal area with one or two low marginal denticles (Figs. 17, 18). Rachidian base with high rounded shoulder and large, outwardly splayed, base point or marginal cusp (Fig. 18) attached over the entirety of its length to radular membrane (Fig. 21). Lobe or extension of rachidian base past marginal cusp absent.

Adult teeth (Figs. 19, 20): With narrow, rectangular rachidian base, long conical lateral cusps, and long, triangular central cusp projecting 45° from rachidian base (Figs. 19, 20). Lateral cusps curving laterally at distal ends, nearly same length as central cusp, with low ripples along the outer edges in the position normally occupied by outer lateral denticles (Figs. 19, 20). Short inner lateral denticle, equidistant between lateral and central cusps, and free from both (Fig. 19). Marginal area short with no marginal denticles and one short, rounded, outwardly splayed marginal cusp (Fig. 20). Marginal cusp free from radular membrane over entire length, separated from membrane by small, lobe-like extension of rachidian base (Figs. 4, 20).

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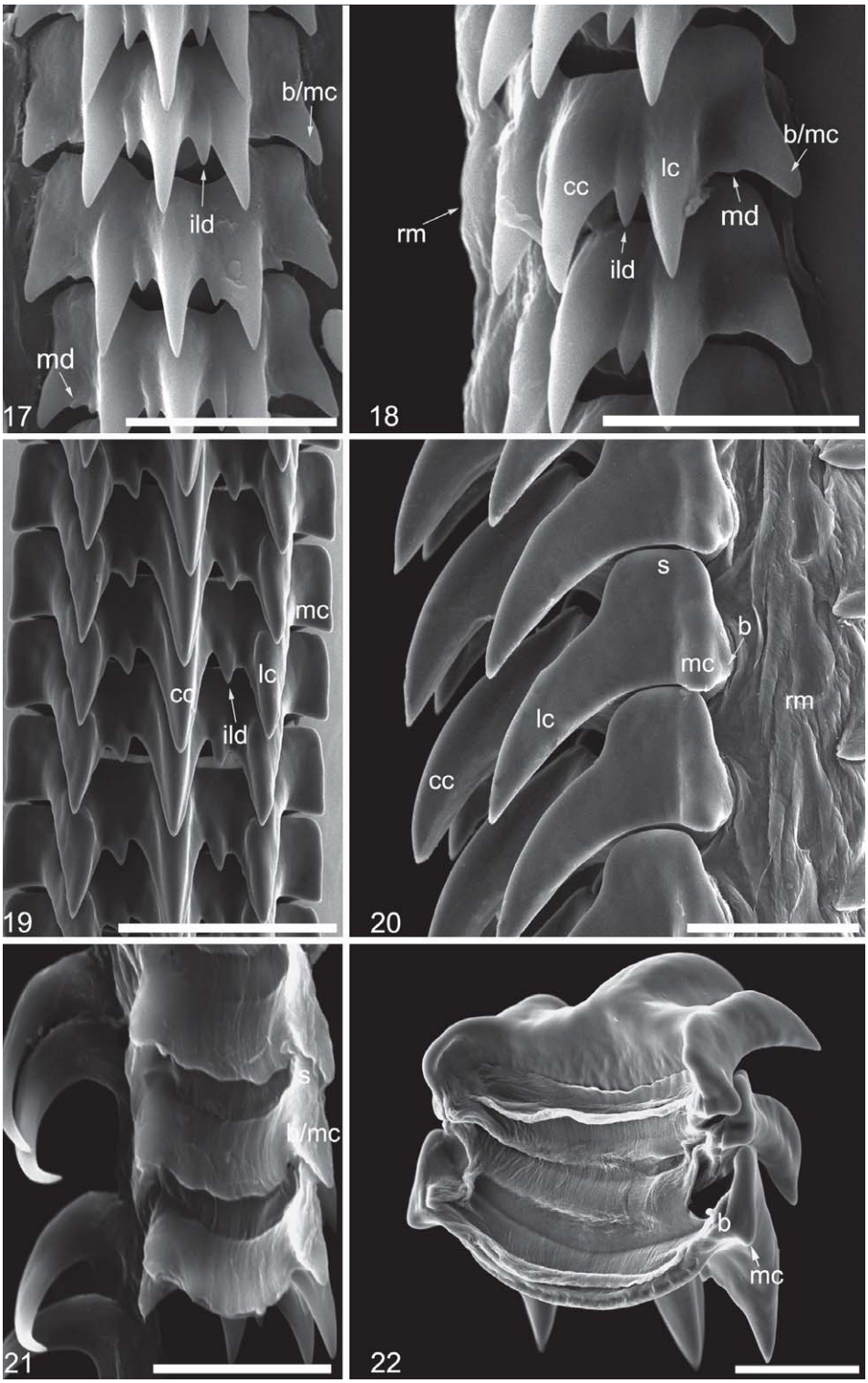
FIGS. 11–16. Dorsal and lateral views of rachidian tooth ontogeny of *Timbellus phyllopterus*. FIGS. 11, 12: Tooth of an intracapsular embryo from a closed egg capsule, SH = 1.5 mm; FIG. 13: Tooth of an adult, SH = 63 mm; FIG. 14: Adult radula over the bending plane of the odontophore, SH = 63; FIG. 15: Marginal area of an adult radula; FIG. 16: Detail of the folded marginal area of an adult radula, SH = 63. Scale bars: Fig. 11 = 5 µm, Fig. 12 = 10 µm, Fig. 13 = 20 µm, Fig. 14 = 50 µm, Fig. 15 = 20 µm, Fig. 16 = 5 µm; b = base; b/mc = base/marginal cusp; cc = central cusp; d = denticle; ild = inner lateral denticle; lc = lateral cusp; md = marginal denticle; rm = radular membrane.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Remarks

The development of *C. dilectus* is distinct from that of other muricines studied thus far. There is no variable or asymmetric expression of inner lateral denticles in *C. dilectus* as in *P. pomum* or *T. phyllopterus*. Additionally, the marginal cusp, which is long and partially adhered to the radular membrane in juvenile *C. dilectus* (Figs. 17, 18, 21: b/mc), is shorter, more rounded distally, and completely separated from the radular membrane in adults (Figs. 17, 18, 22: mc). Separation of the marginal cusp from the membrane in *C. dilectus* is accompanied by bending of each end of the rachidian base at the position of the lateral cusp so that it forms a 3-D, U-shaped structure (Fig. 22). A by-product of these changes is the formation of a new basal lobe (Fig. 20: b), which is merely the portion of the rachidian base that extends past the now more medially located marginal cusp (Fig. 20). In *P. pomum* and *T. phyllopterus*, no separation of the base endpoint from the radular membrane occurs, leaving the rachidian base and marginal cusp as a single, undifferentiated feature as it appears to be in larval *C. dilectus* (Fig. 21).

Chicoreus dilectus is the only muricid reported thus far to have a rectangular rachidian base. This characteristic is not obvious from frontal or side views of the rachidian and is best viewed from the back side of teeth after they have been separated from the odontophore (Fig. 22).

Subfamily Ocenebrinae

Vokesinotus perrugatus (Conrad, 1846)
(Figs. 4, 23–28)

Material Examined

Six juveniles with shell lengths around 1 mm were harvested from capsules deposited by adults in laboratory aquaria. Ten adults (six females and four males) were collected from sea grass in water 1 m deep in St. Joseph Bay, Florida in June 2007 and preserved in ethanol.

Ontogeny

Juvenile teeth (Figs. 23, 24): With narrow, 3-D base and narrow, short central cusp projecting almost 90° from base. Rachidian base bent at center (V-shape) and at base margins (U-shape). Lateral cusps longer than central cusp and projecting 45° away from rachidian base, positioned close to central cusp, and sharing common base with shorter inner lateral denticle (if present) (Fig. 24). Inner lateral denticles weakly and asymmetrically developed, or absent on most teeth (Fig. 23: ild). Marginal area wide with one larger outer lateral denticle (Figs. 23, 24: old) appended to outer edge of lateral cusp, one to two marginal denticles, and two marginal cusps (Fig. 24: imc, omc). Inner marginal cusp longer than outer marginal cusp but similar in thickness (Fig. 24). Rachidian base with narrow, rounded shoulder (Fig. 24: s). Rachidian base extending laterally past outer marginal cusp forming narrow lobe (Fig. 24: b).

Adult teeth (Figs. 25–28): With broad, 3-D base and short, narrow central cusp projecting between 45–75° from base. Rachidian base slightly bent at center, strongly bent at margins. Lateral cusps same length as central cusp and projecting between 20–50° away from rachidian base, positioned close to central cusp, and sharing common base with shorter inner lateral denticle (Fig. 25). Inner lateral denticles present on all teeth (Fig. 25: ild). Marginal area wide with one outer lateral denticle (Figs. 25, 26: old), one or two marginal denticles (Figs. 25, 26: md), and two marginal cusps (Figs. 26, 27: imc, omc). Inner marginal cusp longer, thicker than outer marginal cusp. Rachidian base with low, narrow, rounded shoulder (Figs. 25, 28: s). Rachidian base extending laterally past outer marginal cusp with narrow lobe. Outer edge of lobe forming short, narrow, cusp-like ridge (Fig. 28: b).

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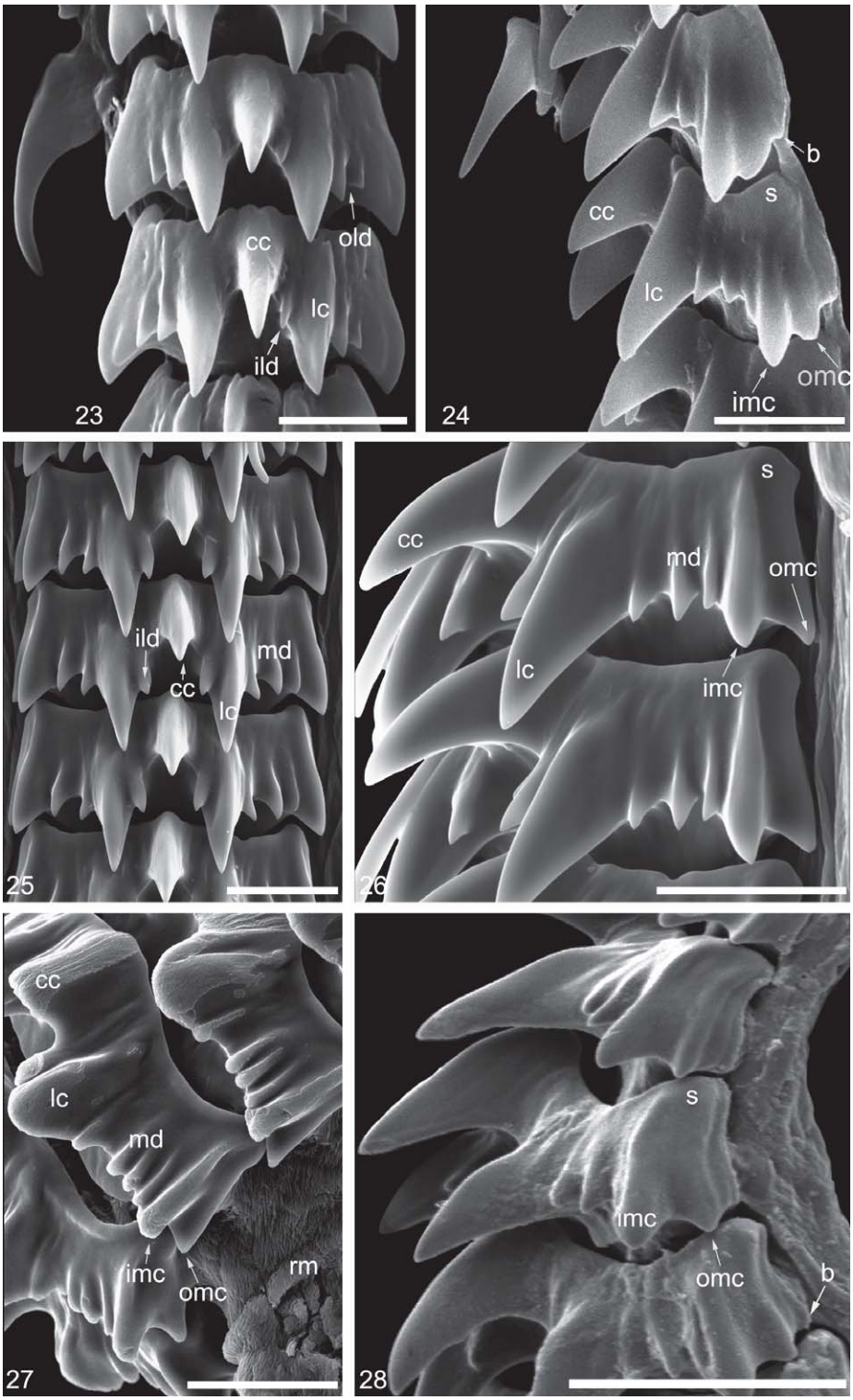
FIGS. 17–22. Dorsal and lateral views of rachidian tooth ontogeny of *Chicoreus dilectus.* FIGS. 17, 18: Tooth of an intracapsular embryo from a closed egg capsule, SH = 1.75 mm; FIGS. 19, 20: Tooth of an adult, SH = 52 mm; FIG. 21: Back view of the radula of an intracapsular embryo from closed egg capsule, SH = 1.75 mm. FIG. 22. Back view of an adult radula, SH = 52 mm. Scale bars: Fig. 17 = 10 µm, Fig. 18 = 100 µm, Fig. 19 = 10 µm, Fig. 20 = 50 µm, Fig. 21 = 10 µm, Fig. 22 = 50 µm; b = base; b/mc = base/marginal cusp; cc = central cusp; ild = inner lateral denticle; mc = marginal cusp; lc = lateral cusp; md = marginal denticle; rm = radular membrane.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Remarks

The rachidian teeth of *V. perrugata* undergo relatively little shape or structural change between the early post-metamorphic and adult ontogenetic stages, which is similar to the development of another ocenebrine *Urosalpinx cinerea* (Say, 1822) (Herbert et al., 2007). Changes in *V. perrugata* are limited to moderate straightening of the center of the rachidian base, widening of the marginal area, and a shift from irregular to consistent, symmetrical expression of inner lateral denticles.

This species has traditionally been assigned to the genus *Urosalpinx*, but the fossil record of *V. perrugata* can be traced back to the Pleistocene species *Vokesinotus griffini* Petuch, 1991, from which it differs only in size (Petuch, 2003, 2013). The fossil record of *Vokesinotus* extends at least into the late Early Miocene and encompasses a genus-level clade represented by several independent lineages during the Pliocene and Early Pleistocene (Petuch, 1997).

DISCUSSION

Inferring the Plesiomorphic Developmental Sequence for the Muricidae

The rachidia of larval and early post-metamorphic muricids differ in predictable ways from those of adults, regardless of subfamily affiliation. Two differences, in particular, stand out. The smallest juveniles just after metamorphosis (< 1 mm shell length) tend to have a narrow rachidian base relative to conspecific adults, and expression of inner lateral denticles is typically irregular and asymmetric in juveniles but regular and symmetric in adults. The pervasiveness of these developmental trends across the Muricidae (Herbert et al., 2007; Pio et al., 2014; Herbert et al., this study), including within a basal lineage of the family – the genus *Timbellus* – suggests that these characteristics were likely part of the plesiomorphic radular ontogeny of the family. Inner lateral denticles are somewhat uncommon in neogastropods outside the Muricidae, but have been observed in species of Marginellidae, Harpidae, Vexillidae and two undescribed species of the Turbinellidae (Y. Kantor & Bruce Marshall, unpublished data) and Costellariidae (Sasha Fedosov, personal communication). In light of the presence of inner lateral denticles in adults of closely related neogastropods, inner lateral denticles were likely present in adults of the earliest progenitors of the Muricidae. We hypothesize that inner lateral denticles are homologous across the Neogastropoda and typical features of late ontogeny.

Another relatively common developmental pattern observed in some muricids is for early juvenile character states to be extended into adulthood. Examples include the relatively narrow, 3-D rachidia of some adult muricopsines and ocenebrines (Herbert et al., 2007), the asymmetric expression of inner lateral denticles in adult typhines and *Vitularia* (Radwin & D'Attilio, 1976; Houart, 1991; Herbert et al., 2007), and the absence of inner lateral denticles in adults of the muricine *Bouchetia vaubanensis* (Houart, 1986) (Houart & Héros, 2008: fig. 9C) and the rapanine *Vexilla vexillum* (Gmelin, 1791) (Kool, 1987: figs. 30–31). We hypothesize that these examples highlight the important role that developmental modification, specifically paedomorphosis, has played in the evolutionary diversification of the Muricidae. More detailed discussions of the role of developmental change in the evolution of the muricid radula can be found in Herbert et al. (2007) and Pio et al. (2014).

Evolution and Function of a 3-D Rachidian

Vokes (1971) was one of the first systematists to recognize that the rachidian base of muricids is either flat or has depth ("3-D"), and that this character might have phylogenetic significance. A 3-D rachidian tooth is present in larval and early post-metamorphic juveniles of the Ocenebrinae, Rapaninae, and Trophoninae and retained into adulthood in the Ocenebrinae (Herbert et al., 2007). It is also present in some adults of species of the Muricopsinae and

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FIGS. 23–28. Dorsal and lateral views of rachidian tooth ontogeny of *Vokesinotus perrugatus*. FIG. 23: Tooth of a hatching specimen, SH = 2.8 mm; FIG. 24: Tooth of a hatching specimen, SH = 1.4 mm; FIGS. 25, 26: Tooth of an adult, SH = 25 mm; FIG. 27: Adult radula over the bending plane of the odontophore, SH = 25 mm; FIG. 28: Cusp-like ridge of rachidian base in adult radula, SH = 32 mm. Scale bars: Fig. 23 = 5 µm, Fig. 24 = 5 µm, Fig. 25 = 20 µm, Fig. 26 = 20 µm, Fig. 27 = 25 µm, Fig. 28 = 25 µm; b = base; bmc = bifid marginal cusp; b/mc = base/marginal cusp; cc = central cusp; ild = inner lateral denticle; lc = lateral cusp; old = outer lateral denticle; rm = radular membrane; tmc = third marginal cusp.

Muricinae (Houart, 1992; Herbert et al., 2007; this study). In most other muricids, including the basal lineage *Timbellus*, the rachidian is flat. This is consistent with Vokes' (1971) propososal that a flat rachidian ("muricine" condition) is the plesiomorphic state for the Muricidae.

What Vokes and others (e.g., Herbert et al., 2007) overlooked, however, is that a 3-D rachidian base can result from a bend or angle at a single point (near the rachidian center), at two points (at each lateral cusp, at each marginal cusp, or at each base margin), or at multiple points. In juvenile rapanines and juvenile and adult ocenebrines studied, the base has a single angle near its center to form a V-shape. A flat rachidian base characterizes many species assigned presently to the subfamily Muricinae, but the rachidian base of *C. dilectus* is bent at two points, once at each base margin, near the position of each lateral cusp. Houart (1992) showed similar 3-D morphology for a juvenile of the muricine *Chicoreus torrefactus* (G. B. Sowerby II, 1841). Ocenebrine rachidia are also bent at each of the margins but at the position of each marginal cusp instead of the base margin. Ocenebrine rachidia may also be bent slightly at the lateral cusp positions.

Herbert et al. (2007) proposed that a 3-D rachidian base could be a functional adaptation that helps the tooth withstand mechanical stresses of predatory drilling, a common mode of attack of muricids in which the radula is used along with chemical secretions of the accessory boring organ to bore a hole through the shells of molluscan or barnacle prey. Herbert et al. (2007) based this hypothesis on the fact that a 3-D rachidian is present early in the ontogeny of the rapanine *Concholepas concholepas* when it employs its radula for mechanical drilling of shelled prey but is lost in ontogeny when juveniles begin to kill prey by other means (e.g., toxins) and use the radula primarily for tearing soft flesh (Herbert et al., 2007, and references therein). Drilling is also the predominant form of attack among small ocenebrines and muricopsines, in which the 3-D adult rachidian morphology is expressed in its most extreme form, while a flat rachidian base is more common in muricids that employ toxins and other modes of attack that do not require similar mechanical stresses on radular teeth (reviewed by Herbert et al., 2007).

Evolutionary Innovation at the Rachidian Base

The number of marginal cusps at the rachidian base endpoints has traditionally been used to delineate muricid subfamilies, but here and in previous work (Pio et al., 2014), we have shown that the number of marginal cusps can increase or decrease during normal development within a single individual. In basal muricids, such as *T. phyllopterus*, the adult rachidian base margin is tapered to a dull point (a pseudo-marginal cusp) that is adherent to the radular membrane along its entire length. In other muricids, including adult *C. dilectus* and *S. biserialis,* however, this base margin is detached from the supporting membrane and occupies a more medial position to form a true marginal cusp. In *C. dilectus*, this detachment occurs during ontogeny, and the developmental continuity between the base endpoint and marginal cusp in this species reveals that they are homologous structures. The part of the base still adherent to the radular membrane expands in some muricids to form what is often described as a distinct character – the basal lobe (see Kool, 1993). Pio et al. (2014) showed that within the development of *Trophon geversianus* (Pallas, 1774), this lobe can also develop into a pointed structure (a pseudo-marginal cusp) and become detached from the membrane during ontogeny to produce a second (outer) marginal cusp behind the first (inner) marginal cusp. In some species of the Ocenebrinae and Muricopsinae, a new lobe forms again behind the second marginal cusp. The outer edge of this new lobe often takes on a ridged or cusp-like appearance, giving the rachidian margins of these ocenebrines and muricopsines a tri-cusped appearance (Herbert et al., 2007; Pio et al., 2014; Herbert, unpublished data).This process of detachment of the rachidian base end-point from the radular membrane provides a mechanistic explanation for the origin of marginal cusps in general, and the repetition of this single mechanism in some lineages up to three times suggests that acquisition of one or more marginal cusps has likely occurred multiple times in the Muricidae via convergent evolution.

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