

Developmental origins of complex radular characters in the Muricidae: the bifid rachidian edge

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Abstract. Muricid gastropod radulae are more complex than those of most other neogastropods, especially in the number and variety of cusps, denticles, and interlocking mechanisms. How this complexity evolved, however, is unknown. Morphological gaps between higher taxa within the Muricidae are substantial, and there are few unambiguous intermediates. Here, we use developmental data from the Patagonian trophonine muricid *Trophon geversianus* to investigate the evolution of an unusual condition in which there are two marginal cusps at each end of each central rachidian tooth, rather than one or none as in most muricids. *Trophon geversianus* begins ontogeny with one marginal cusp (the inner marginal cusp), but a second (the outer marginal cusp) appears later, arising from separation of the rachidian base edge from the radular membrane rather than through bifurcation or lateral migration of pre-existing cusps. Truncation of development (i.e., paedomorphosis) at this second developmental phase in a trophonine ancestor provides an explanation for the lack of transitional forms between most adult trophonine muricids, which have the plesiomorphic condition of one marginal cusp, and sister group ocenebrine muricids, which have the derived condition of two marginal cusps.

Additional key words: Muricidae, heterochrony, paedomorphosis, ontogeny, radula

Identifying homologous characters across higher taxa with disparate adult features is one of the most challenging steps of phylogeny reconstruction using morphological characters (Oakley & Cunningham 2002; Sereno 2007). The innovations that define new taxa, however, are generally derived through modifications of pre-existing developmental systems, a process that preserves transitional morphologies between ancestral and derived states and thus provides clues to character identity within an ontogeny (Müller & Wagner 1991, 1996; Shubin et al. 1997; Müller & Newman 1999). Previous developmental studies have confirmed that developmental series can be useful for understanding the origins and identities of novel characters over a broad range of taxa (Marden & Kramer 1994; Dehal et al. 2002; Smith 2006; de Lussanet 2011; Heers & Dial 2012; Page 2012).

Application of developmental data to studies of molluscan evolution remains relatively infrequent, but has increased dramatically in recent years,

particularly for the gastropod family Muricidae (Hickman 1980; Fujioka 1984, 1985; Guralnick & Lindberg 1999; Merle 1999; Merle & Houart 2003; Herbert et al. 2007; Pastorino et al. 2007; Pastorino & Penchaszadeh 2009). The radulae (mineralized feeding teeth) of muricids are among the most intricate and structurally complex within the Neogastropoda and are well known for remarkable examples of character convergence (e.g., D'Attilio 1980; Harasewych 1984; Bouchet & Houart 1996; Merle 1999; Herbert et al. 2007). Refining homology assessments for the radula character complex is essential to providing a foundation for future broad-scale, morphology-based and total-evidence phylogenetic analyses of the family, as well as deepening our understanding of general macroevolutionary processes.

The muricid radula is composed of several hundred transverse rows of mineralized teeth, with each row possessing a broad, multi-cusped, rachidian tooth flanked on each side by a single, sickle-shaped lateral tooth. While the lateral teeth are used to scrape and pass flesh to the esophagus, the rachidian tooth of muricids is used as an instrument to

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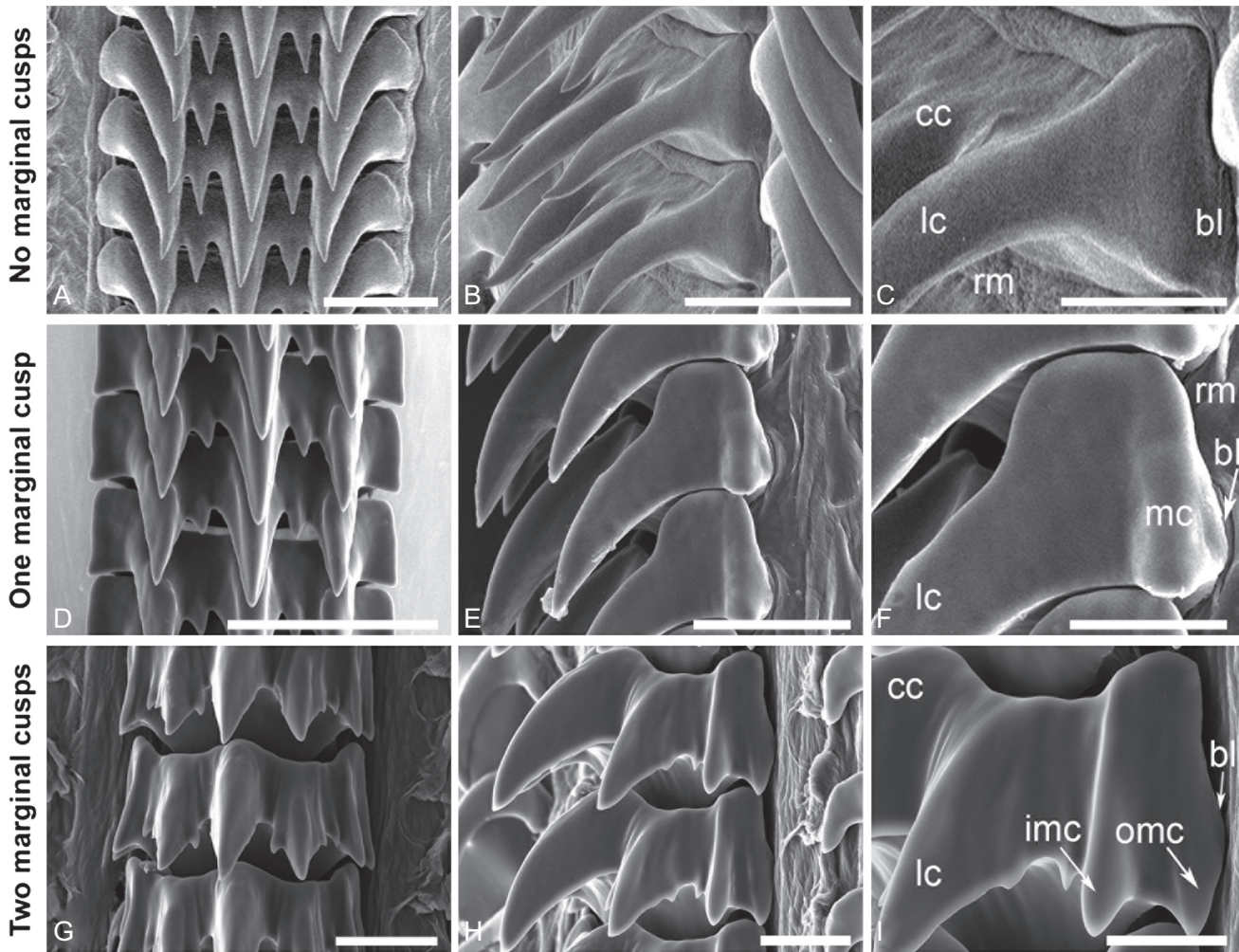


Fig. 1. Muricid rachidia with zero, one, and two marginal cusps. A–C. *Phyllonotus pomum* (Subfamily Muricinae). A. Dorsal view. Scale bar=100 μ m. B. Lateral view of rachidian margin. Scale bar=100 μ m. C. Magnification of marginal area showing basal lobe with no marginal cusps. Scale bar=100 μ m. D–F. *Chicoreus dilectus* (Subfamily Muricinae). D. Dorsal view. Scale bar=100 μ m. E. Lateral view of rachidian margin. Scale bar=50 μ m. F. Magnification of marginal area showing basal lobe accompanied by one marginal cusp. Scale bar=50 μ m. G–I. *Acanthina monodon* (Subfamily Ocenebrinae). G. Dorsal view. Scale bar=10 μ m. H. Lateral view of rachidian margin. Scale bar=10 μ m. I. Magnification of marginal area showing a basal lobe accompanied by two marginal cusps. Scale bar=10 μ m. bl, basal lobe; cc, central cusp; imc, inner marginal cusp; lc, lateral cusp; mc, marginal cusp; omc, outer marginal cusp; rm, radular membrane.

drill holes through the shells of invertebrate prey (Carriker et al. 1974) and is unique among neogastropods in its structural complexity and diversity of form (Ponder 1973; Harasewych 1984). The origins of this diversity and the homology of derived features are largely unknown (Harasewych 1984; Tan 2003; Herbert et al. 2007), despite the traditional emphasis on radular characters in gastropod systematics (e.g., Gray 1854; Troschel 1856–1893; Thiele 1929–1931), and investigators have struggled to translate structural elements of the rachidian teeth into characters and character states for cladistics analyses of the family. Kool's (1993b) phylogenetic

analysis of the muricid subfamily Rapaninae, for example, included just two extreme-multistate characters describing the radula, in part, to avoid spurious homology interpretations. However, Kool's own taxon descriptions suggest that there may be twenty or more independently varying rachidian structural elements available for coding. Similarly, Tan (2003) acknowledged problematic homology interpretations in his coding of rachidian cusps of haustriine and rapanine muricids and suggested that these problems might be resolved through developmental studies.

Except for the central cusp of the muricid rachidian, the homology of all other structural elements

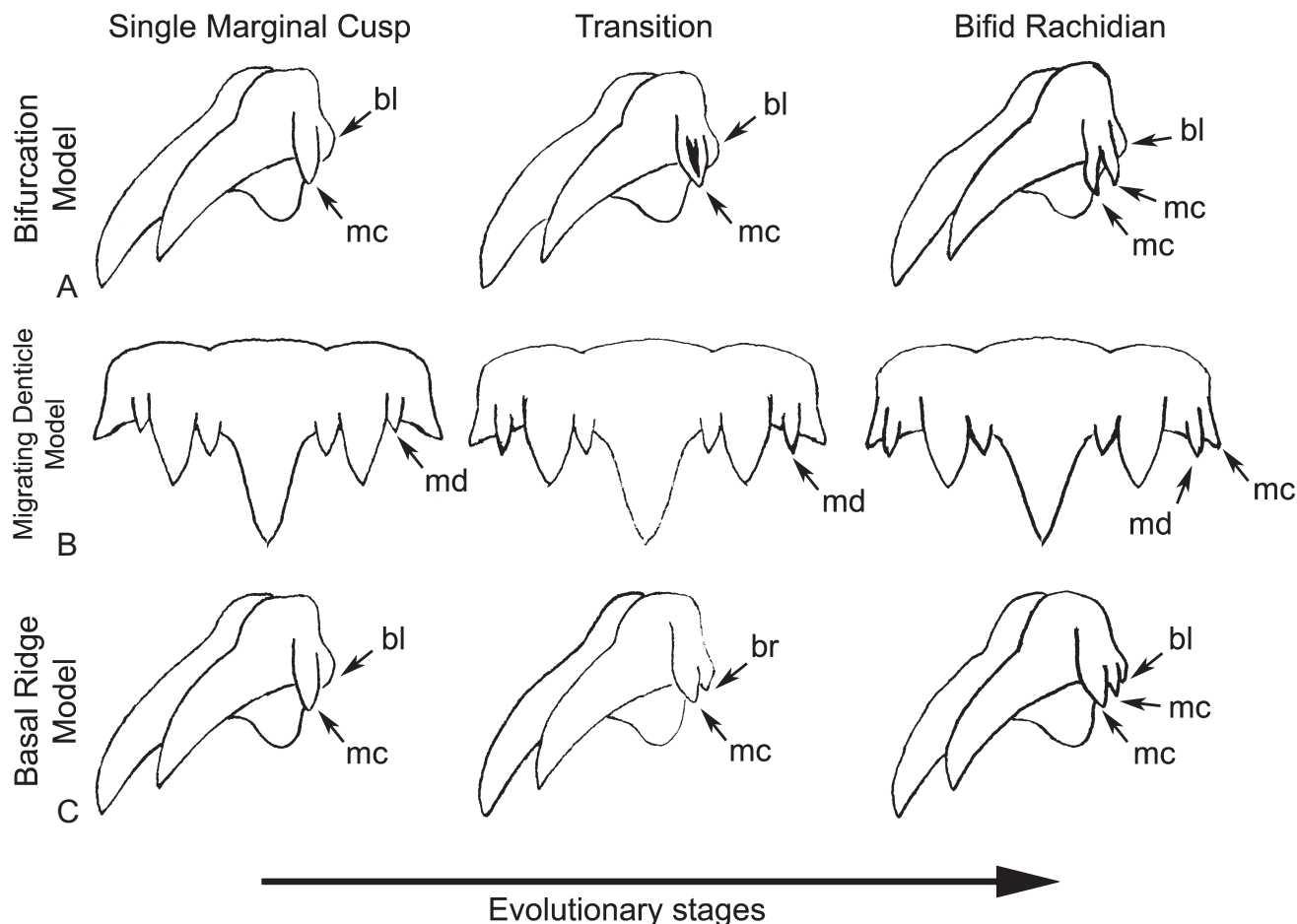


Fig. 2. Three evolutionary models for the origin of a second marginal cusp (bifid condition). Note the different homology interpretations of each model. **A.** Bifurcation model. **B.** Migrating denticle model. **C.** Basal ridge model. Bl, basal lobe; br, basal ridge; mc, marginal cusp; md, marginal denticle.

is uncertain when considered at the scale of the entire family. This study focuses on structures near or at the rachidian lateral margins, which feature lobes and cusps that vary in number, shape, and size. These can be grouped into three general morphotypes: (i) a rounded rachidian basal plate with no marginal cusps at the postero-lateral edges (Fig. 1A–C), (ii) a rounded rachidian basal plate or lobe with one marginal cusp (Fig. 1D–F), and (iii) a basal lobe accompanied by two marginal cusps at the postero-lateral edges (the “bifid” condition) (Fig. 1G–I). Based on comparisons with other neogastropods, the first morphotype is the plesiomorphic condition for the Muricidae. However, the first two morphotypes both occur in multiple subfamilies (e.g., Muricinae, Typhinae, Muricopsinae, Trophoninae, Rapaninae, Ergalataxinae), which points to the likelihood of convergent evolution. In contrast, the bifid condition—the highest degree of rachidian marginal complexity to evolve in the Neogastropoda—reportedly occurs only in species of the

Ocenebrinae (Radwin & D’Attilio 1971, 1976; Kool 1993a,b) and Muricopsinae, although perhaps not in homologous form (Harasewych 1984).

Evolution of a bifid rachidian could have occurred through a variety of pathways, each with its own implications for homology and character coding. Three possible pathways are shown in Fig. 2(A–C). The bifurcation model of Radwin & D’Attilio (1971) proposes that the double marginal cusps of ocenebrine muricids evolved by bifurcation of a single, pre-existing marginal cusp (Fig. 2A). In this model, both of the marginal cusps in the bifid condition would be homologous with the single marginal cusp of other muricids. An alternative hypothesis, the migrating denticle model (Fig. 2B), was described by Wu (1968), who suggested that the inner marginal cusp in ocenebrines is not a true cusp but a wayward marginal denticle that migrated laterally toward the tooth margin and took on a cusp-like size and shape. Some ocenebrine muricids, such as *Chorus giganteus* (LESSON 1829), appear to fit

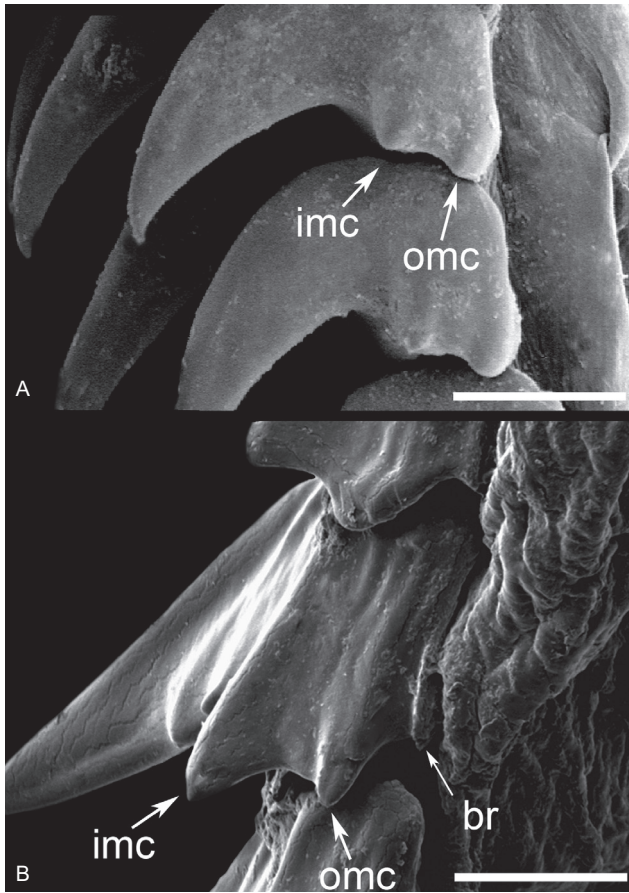


Fig. 3. Examples of variation in the bifid condition within the Ocenebrinae. **A.** The smaller inner marginal cusp and larger outer marginal cusp in *Chorus giganteus*. Scale bar=10 µm. **B.** The inner marginal cusp, outer marginal cusp, and basal ridge resembling a third marginal cusp in *Eupleura tampaensis*. Scale bar=10 µm. br, basal ridge; imc, inner marginal cusp; omc, outer marginal cusp.

Wu's model in having an inner marginal cusp that is small and denticle-like compared to the outermost, larger marginal cusp, and in lacking any feature that could be identified by form or position as a marginal denticle (Fig. 3A). A similar mechanism was proposed by Tan (2003) to account for other novelties of some muricid radula.

A third model, the basal ridge model (Fig. 2C), posits that marginal cusps form from the edge of the rachidian basal plate. This basal plate is often sharp-edged and cusp-like, and, although the base itself is firmly attached to the supporting radular membrane, the cusp-like edge may be free. The complete transformation from basal plate edge to marginal cusp would involve only slight modifications of this initial variation, such as thickening of the base edge into a ridge and extension of the space between the nascent cusp and that attached portion

of the basal plate. This model has not been proposed elsewhere, but is based on published and new scanning electron micrographs showing lateral views of rachidian teeth. In the rapanine *Phycothais reticulata* (QUOY & GAIMARD 1832), the edge of the basal lobe against the radular membrane forms a narrow, short ridge resembling a second marginal cusp (figure 14H of Tan 2003). Similarly, the attached edge of the basal lobe of the ocenebrine *Eupleura tampaensis* (CONRAD 1846) (Fig. 3B) forms a third, but smaller marginal cusp to form a trifid rachidian, a morphology that has not been described previously. Because the basal edge model allows for new marginal cusps to be added repeatedly from similar modification of the basal lobe, it is not possible to differentiate between total and partial/serial homology (see Abouheif 1997) based on cusp morphology alone. It is important to point out that these three models are also not mutually exclusive. The first marginal cusp could evolve from a basal edge, while a second marginal cusp could be added by either bifurcation of that cusp or migration of a denticle to the tooth margin.

As an initial test of these models, we investigated radular development in *Trophon geversianus* (PALLAS 1774), the type species of the type genus of the subfamily Trophoninae (as redefined by Barco et al. 2012). Trophonines are of particular interest because as adults, they lack a bifid rachidian, the plesiomorphic condition for the family (e.g., Harasewych 1984; Pastorino 2005). However, the Trophoninae is firmly established as the sister group to the subfamily Ocenebrinae (Harasewych 1984; Kool 1993a,b; Barco et al. 2010, 2012), in which the bifid condition is a presumed synapomorphy (Radwin & D'Attilio 1976). If the bifid nature of the ocenebrine rachidian evolved through modification of a pre-existing developmental trajectory as expected, then the transition between these subfamily-level character states should be evident within the ontogeny of sister group trophonines. Our data include new scanning electron micrograph views of rachidian from the perspective of the lateral margins over a complete developmental sequence of *T. geversianus*, beginning with intracapsular embryos. This study complements previous work on the development of the rachidian of *T. geversianus* (Herbert et al. 2007), which examined only frontal views of teeth and only the earliest and latest ontogenetic stages rather than a complete developmental sequence.

We show that a bifid rachidian occurs in juveniles of *T. geversianus* between non-bifid embryo and non-bifid adult ontogenetic stages. We use the transitional morphologies between ontogenetic states to

test competing homology models for the origin of the second marginal cusp, and propose a new classification of rachidian structures that will be useful in future efforts aimed at understanding the phylogeny of the Muricidae.

Methods

Material examined

Specimens of *Trophon geversianus* were collected by hand from intertidal rocky shores along the Patagonian Coast from the Rio Negro, Chubut, and Tierra del Fuego provinces, and preserved in 70% ethanol. Shell length of the forty-four specimens chosen for dissection ranged from 1–55 mm, with the smallest shells harvested from egg capsules. Sex determinations for late juveniles and adults were made by visual inspection. For comparisons with rachidia of other muricids, we also dissected an additional twenty specimens representing the following species: *Phyllonotus pomum* (GMELIN 1791), *Chicoreus dilectus* (A. ADAMS 1855), *Acanthina monodon* (PALLAS 1774), *Chorus giganteus*, and *Eupleura tampaensis*.

Radula preparation

Radulae were isolated by dissolving dissected proboscis and buccal mass tissues in a concentrated solution of sodium hypochlorite. Radular ribbons were collected with forceps, washed in distilled water, mounted on stubs with double-sided conductive tape, and coated with Au-Pd for scanning electron microscopy. Radulae of snails collected from egg capsules were recovered by crushing the larval shells in a shallow petri dish filled with a concentrated solution of sodium hypochlorite. For a subset of juvenile and adult snails, radulae were dissected with the odontophore. All radulae were examined with a Philips XL 30 scanning electron microscope at the Museo Argentino de Ciencias Naturales (MACN).

Radular terminology

Radular terminology follows Kool (1993a) and Herbert et al. (2007).

Results

Radular ontogeny of *Trophon geversianus*

Developmental changes of the rachidian of *Trophon geversianus* are illustrated in Fig. 4(A–U). They

progressed gradually through three loosely defined phases. The timing of changes was not synchronized across characters. In the first phase, rachidia of intracapsular embryos 2–3 mm in shell length possessed a narrow, rectangular rather than flat base (Fig. 4B–C) and a short, recurved central cusp (Fig. 4B–C,E–F). Inner lateral denticles were long and not attached at the base to the lateral cusps (Fig. 4A,D). The rachidian margin had broad basal lobes that were thickened at their lateral edges, but attached along their length to the radular membrane (Fig. 4B–C). The posterior corner of each lobe nearest the radular membrane was sometimes rounded, as in the images shown here, or sometimes shaped into a blunt angle (see figure 6B of Herbert et al. 2007). The rachidian possessed a single marginal cusp, which was nearly equal in size to the lateral cusp. On the inner side of this marginal cusp was a single, small marginal denticle.

A second, intermediate phase was characteristic of post-hatching juveniles up to at least 20 mm in shell length. In this phase, rachidia were characterized by a rectangular base proportionally more broad and shallow than in the first stage, with a much longer and straighter central cusp (Fig. 4H,K,N), inner lateral denticles that were $\frac{3}{4}$ of the length of the lateral cusps and shared a common base with the lateral cusps (Fig. 4G,J,M), lateral cusps that projected more strongly from the base, marginal cusps that were shorter than the lateral cusps (Fig. 4H,K,N), and partial to complete loss of the marginal denticle, which had merged into the marginal cusp (Fig. 4I). The rachidian margin had an inner marginal cusp in the position occupied by the marginal cusp of intracapsular embryos as well as a novel feature closer to the base (Fig. 4I,L). In smaller juveniles, this feature was a subtle thickening (ridge) of the rounded basal lobe. In larger juveniles, this feature became an outer marginal cusp that was robust and free from the radular membrane along its lateral edge, and accompanied by a new basal lobe that formed between it and the radular membrane (Fig. 4O). This new basal lobe was thin, flat, and attached to the radular membrane along its entire length.

The third phase was characteristic of the largest specimens observed in this study (>20 mm) and previous studies. The rachidian base was broader than in earlier ontogeny, and intermediate in depth between the rectangular rachidia of ocenebrines and the smallest juveniles of *T. geversianus* and the flat rachidia of muricine muricids (Fig. 4Q,T; see also figure 34 of Kool 1993a; and figure 18 of Pastorino 2005), while the central cusp was long with a broad cusp base (Fig. 4P,S). Intermediate lateral denticles

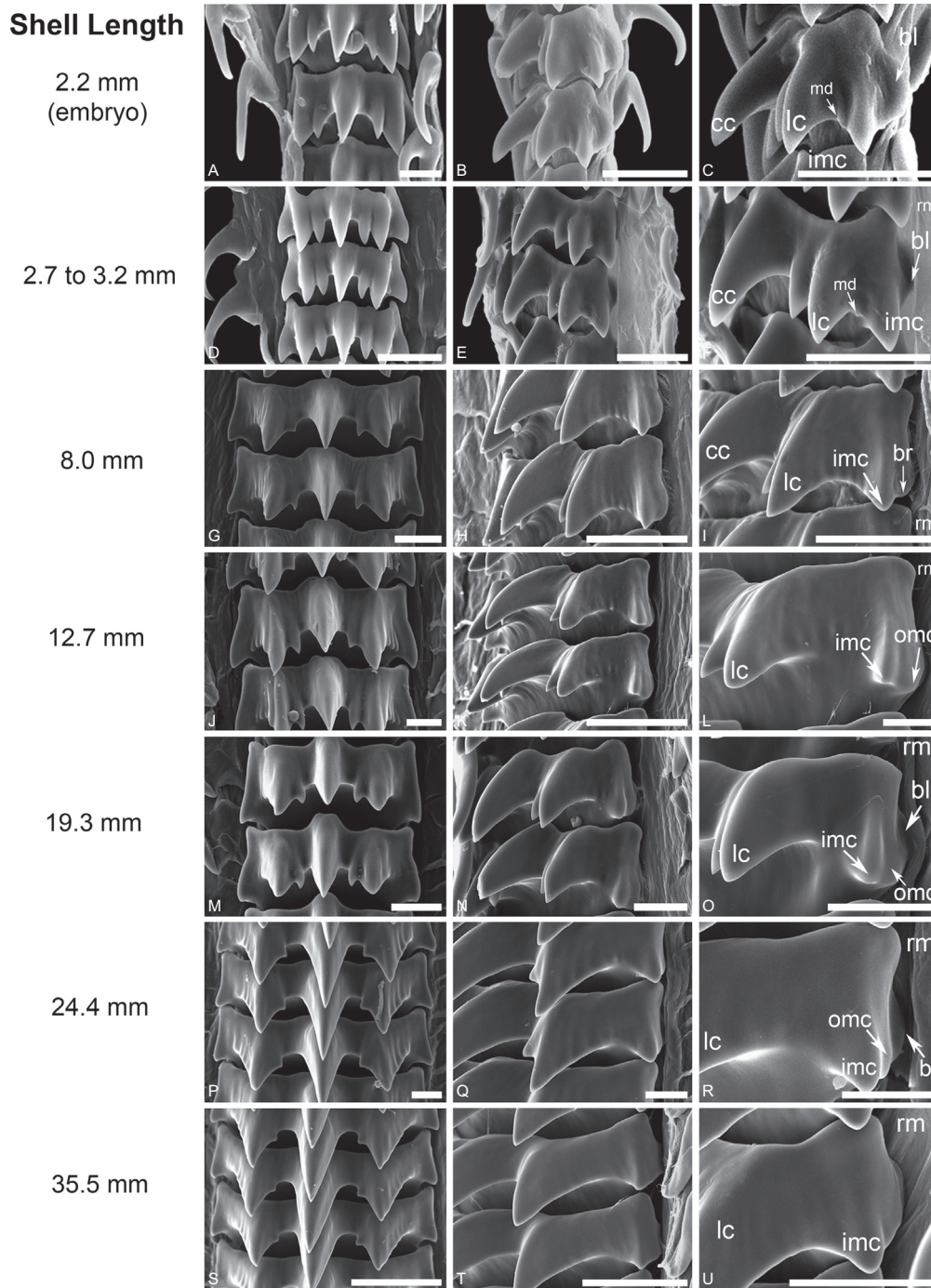


Fig. 4. Dorsal and lateral views of rachidian tooth ontogeny of *Trophon geversianus*. **A–C.** Tooth of an intracapsular embryo from a sealed egg capsule, shell height (SH)=2.2 mm, Puerto Madryn, Argentina. **D.** Tooth of an intracapsular embryo from an open egg capsule, SH=2.9 mm, Puerto Madryn, Argentina. **E.** Tooth of an intracapsular embryo from an open egg capsule, SH=2.7 mm, Puerto Madryn, Argentina. **F.** Tooth of an intracapsular embryo from an open egg capsule, SH=3.2 mm, Puerto Madryn, Argentina. **G–I.** Tooth of a post-hatching juvenile, SH=8.0 mm, Puerto Madryn, Argentina. **J–L.** Tooth of a post-hatching male juvenile, SH=12.7 mm, Puerto Madryn, Argentina. **M–O.** Tooth of an adult female, SH=19.3 mm, Puerto Madryn, Argentina. **P–R.** Tooth of an adult female, SH=24.4 mm, Playas Doradas, Rio Negro, Argentina. **S–U.** Tooth of an adult male, SH=35.5 mm, Tierra del Fuego, Argentina. All specimens collected by GP. Scale bars: A=5 μ m; C–F,J,L=10 μ m; B,G–I,K,M–R=20 μ m; S,T=30 μ m; U=50 μ m. Bl, basal lobe; cc, central cusp; im, inner marginal cusp; lc, lateral cusp; m, marginal cusp; md, marginal denticle; om, outer marginal cusp; rm, radular membrane.

were reduced to small points along the mid-length of the lateral cusps, having been nearly completely absorbed by them (Fig. 4P,S). Lateral cusps were triangular in shape, with a broad base and an outer smooth or serrated edge. Marginal denticles were absent. The tooth's lateral margins each retained a short inner marginal cusp, the tip of which was indistinct and separated from the tooth base in the largest specimens studied (Fig. 4U). The outer marginal cusp varied from a distinct but narrow ridge, completely detached from the tooth base (Fig. 4R) to completely absorbed into the deep tooth margin (Fig. 4U). In all adult individuals studied, a narrow basal lobe was present and adherent to the radular membrane (Fig. 4R).

Discussion

Formation of bifid cusps at the rachidian margins

Individuals of *Trophon geversianus* begin development with a single marginal cusp (the inner marginal cusp), but a second marginal cusp (the outer marginal cusp) begins to form shortly after hatching by a multi-step process that includes deepening of the rachidian base and thickening of the lateral edge of the rachidian basal plate into a rib-like structure. This step is followed by separation of this rib away from the base, formation of a new basal lobe, and modification of the rib-like structure into a pointed cusp. Thus, we accept the basal ridge model and reject other models that predicted that the bifid rachidian was formed by either developmental bifurcation of the inner marginal cusp or lateral migration of a marginal denticle. Developmental work on phylogenetically basal muricids could be used to test whether basal folding explains the evolution of marginal cusps in general, including the first (inner) marginal cusp.

The confirmation of the basal ridge model has implications for the homology of the ocenebrine marginal cusps and character construction and coding in future phylogenetic analyses of the Muricidae. The inner marginal cusp and marginal denticle of the bifid rachidia of juveniles of *T. geversianus* and adults of sister group ocenebrines are probably homologous with morphologically similar structures in muricids that have just a single marginal cusp. The outer marginal cusp in ocenebrines and juveniles of *T. geversianus*, however, is novel and should be coded as a separate character rather than simply as serial repetition of identical units. This is supported by the fact that the inner and outer marginal vary independently in their size and shape and orientation relative to the rachidian base. In muricids

that have a single marginal cusp and an adjacent outer ridge that is more prominent than the basal lobe, the outer ridge could be considered a plesiomorphic state of the outer marginal cusp.

One point of caution, however, is highlighted by the example of *Eupleura tampaensis*, which has developed an additional ridge on the rachidian basal plate that resembles a third marginal cusp (Fig. 3B). Repeated thickening and separation of the basal plate (perhaps three separate times in the lineage leading to *E. tampaensis*) suggests that marginal cusp number is potentially misleading as a systematic character. It also indicates that the unique morphologies of marginal cusps can potentially reveal the number of times marginal cusps have evolved and in which clades. Increased use of developmental data, whenever possible, in assessing homology of rachidian structural elements, along with the use of ontogenetic characters and hierarchical coding in phylogenetic analyses, is recommended as a first step in converting complex radular traits in the Muricidae into phylogenetically informative character data. This recommendation follows an approach already in use for shell characters of the Muricidae and other neogastropods (e.g., Merle 1999; Merle & Houart 2003).

Development and the origin of the Ocenebrinae

Ontogenetic shifts in the morphology of the rachidian teeth of *T. geversianus* bridge several macroevolutionary gaps between the subfamilies Trophoninae and Ocenebrinae. One of these gaps involves the evolution of the rachidian tooth base, which can occur in either a broad, flat form that is the plesiomorphic state for the family or the narrow, rectangular form that is a defining characteristic of the Ocenebrinae (Vokes 1971; Radwin & D'Attilio 1976; Harasewych 1984; Kool 1993a,b) at all ontogenetic stages (Herbert et al. 2007). Although adults of *T. geversianus* exhibit the plesiomorphic condition for the rachidian base (Harasewych 1984), Herbert et al. (2007) found that intracapsular embryos of *T. geversianus* have the derived rectangular base of the Ocenebrinae, which is strongly supported as the sister clade to the Trophoninae by molecular and anatomical cladistic analyses (e.g., Harasewych 1984; Kool 1993a; Claremont et al. 2008; Barco et al. 2010, 2012). Given this phylogenetic context, a reasonable conclusion is that the narrow, rectangular rachidian base of the Ocenebrinae evolved by truncation of a trophonine ontogeny (i.e., paedomorphosis) in which this morphology already occurred (Herbert et al. 2007).

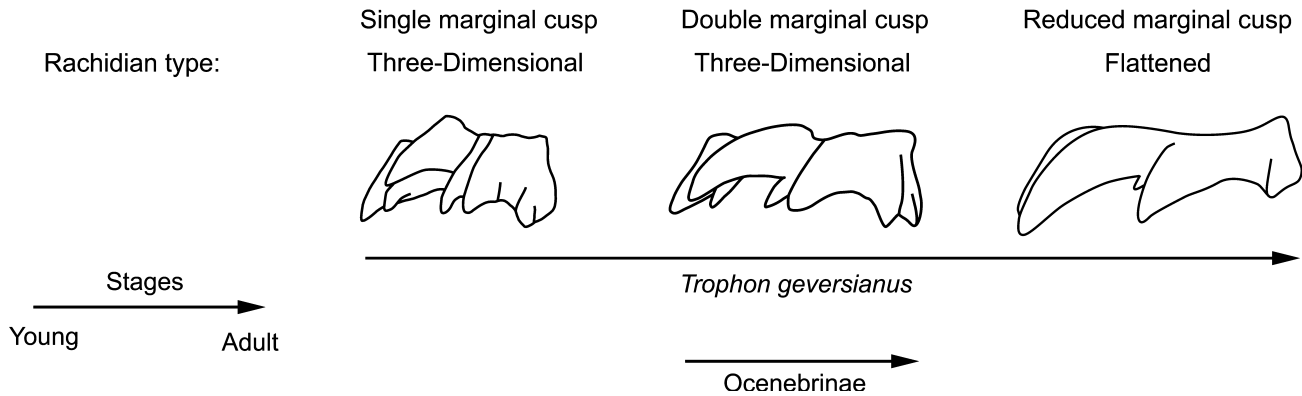


Fig. 5. Evolutionary transformation series for the origin of the Ocenebrinae.

This study supports the generality of pedomorphosis as a mechanism for generating additional ocenebrine innovations beyond a rectangular rachidian base. Unlike embryos and adults of *T. geversianus*, juveniles have short inner lateral denticles that share a common base with the lateral cusps and a second, new cusp (the outer marginal cusp) at the rachidian margin. This intermediate juvenile stage, which was not known previously, results in a completely formed rachidian characteristic of all ocenebrine adults (i.e., narrow, rectangular base; inner lateral denticles appended to lateral cusps; bifid margin). Following the juvenile stage, the rachidian of *T. geversianus* appears to lose the outer marginal cusp it had acquired earlier in ontogeny as it sinks into the rachidian base (see Fujioka 1982, 1984, 1985 for a similar developmental process in rapanine and ergalataxine muricids), although the marginal cusps remain present in a reduced state as indistinct ripples in the rachidian margin.

Many authors have questioned whether the Trophoninae should be retained as a distinct subfamily or synonymized with the Ocenebrinae (Harasewych 1984; Kool 1993a). The developmental data presented here, which show several ocenebrine synapomorphies originating first *within* trophonine ontogeny, could be interpreted as further blurring the morphological distinctions between these higher taxa. We argue instead that our data show the fundamental role of development in the origin of new characters and new higher taxa. Our initial investigations into ocenebrine radular development (Herbert et al. 2007) indicate that ocenebrines undergo minimal change during ontogeny, starting and ending at the same intermediate or juvenile stage of trophonine ontogeny. If the evolutionary transformation series proposed here (Fig. 5) is correct, then evolution of the ocenebrine radula required truncation of *both* ends of the ancestral ontogeny.

Substantial developmental modification itself is, therefore, a possible synapomorphy of the Ocenebrinae. We are currently testing this hypothesis with additional work on ocenebrine ontogeny.

We do not yet know whether similar developmental mechanisms can explain the evolution of other synapomorphies of the Ocenebrinae, including features of shell ornamentation, the operculum, and soft anatomy (e.g., Vokes 1971; Radwin & D'Attilio 1976). If similar developmental modifications affected the shell (i.e., global heterochrony), then the earliest fossil ocenebrines should have adult spiral cord patterns comparable to those exhibited in juveniles of *T. geversianus*. Similarly, if pedomorphosis applies to the evolution of the operculum, then juveniles of *T. geversianus* should have an ocenebrine D-shaped operculum rather than the elongate-oval operculum of adults of *T. geversianus*. Both hypotheses are easily testable with additional data.

Several ocenebrine synapomorphies, however, are traits associated with reproductively mature animals, and, thus, there is potentially no distinct juvenile condition in trophonines for comparison to ocenebrines. These features include penial shape, egg capsule morphology, and whether there is a separate duct in the sole of the foot for the ventral pedal gland (Harasewych 1984; Kool 1993b; Carriker & Gruber 1999). Nonetheless, pedomorphosis can, in theory, explain morphological novelties in these types of features if they can be shown to be compensatory modifications related to detrimental by-products of miniaturization that sometimes accompany developmental truncation (e.g., Hanken 1985; Hanken & Wake 1993). No such evidence is yet available for the evolution of muricid anatomy. However, the extreme variation in body size within mature individuals of *T. geversianus* (specimens from Tierra del Fuego can have three times the shell length of more northern individuals: Pastorino

2005) indicates that future tests of variation and size-compensation in trophonine reproductive traits are possible.

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