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Innovation and evolution at the edge: origins and fates of gastropods with a labral tooth

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I combined data from the taxonomy, phylogeny, functional morphology, biogeography, and fossil record of gastropods to probe the origins, distribution, and fates of predatory gastropod clades characterized by the presence of a labral tooth, a downwardly projecting tooth or spine formed at the edge of the outer lip of the shell. A labral tooth occurs in at least 608 species, of which 251 are Recent. Studies of the type and position of the labral tooth, along with other characters, indicate that the labral tooth has evolved independently at least 58 times, beginning in the Campanian epoch of the late Cretaceous. The labral tooth plays a more or less active part in predation on relatively large prey animals that are protected by a hard skeleton. In the Recent fauna, tooth-bearing species are overwhelmingly warm-temperate to tropical in distribution (240 of 251 species; 96%). Within Muricidae (excluding Coralliophilinae), however, there is no discernible latitudinal gradient in the number of tooth-bearing species relative to total regional diversity. First appearances of clades with a labral tooth are overwhelmingly concentrated in the late Oligocene to Pleistocene interval, with the largest number appearing during the early Miocene (12 clades). The temporal pattern differs significantly from that expected on the basis of the number of faunas available per time interval, and is therefore not an artifact of sampling or fossil preservation. The most consistent factor associated with, and permitting the repeated evolution of, the labral tooth is high planktonic primary productivity. Two factors may account for the link between primary productivity and the evolution of labral teeth: (1) the general economic opportunity afforded by ready availability of an access to nutrients, and (2) the greater abundance and sizes range of available suspension-feeding prey animals. Incumbency—the presence of already well-adapted species—often controls evolutionary opportunity. The complementary distributions of major tooth-bearing clades in many parts of the world point to the role of well-adapted incumbents in limiting the adaptive exploration by other clades that could in principle evolve a labral tooth. The elimination of incumbents by extinction, however, does not provide opportunities for other clades to fill the adaptive void.   © 2001 The Linnean Society of London

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INTRODUCTION

Innovation—the origin of new characters—is a recurrent theme in evolution and in human economic history. Despite its great retrospective importance, we still know little about the circumstances surrounding innovation. When, how, and under what circumstances do new characters arise? Which factors determine whether an innovation is a short-lived inconsequential trial balloon or an event with long-range repercussions for diversity and economic structure?

In order to answer these and other questions, we must approach the subject of innovation systematically rather than anecdotally. Most previous studies of innovation have concentrated on those novelties that in

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hindsight have proved to be long-lasting and consequential. For example, so-called key innovations are recognized because they made possible the establishment of new economic entities with disproportionately large effects on other entities (Vermeij, 1999a) or because they led to prodigious diversification in the clades in which they arose (Schaeffer & Hecht, 1965; Heard & Hauser, 1995; Hunter & Jernvall, 1995; Galis & Drucker, 1996). Some innovations are so rare that a systematic study is impractical; there are simply too few instances among which comparisons can be made, with the result that a hypothetical link between an innovation and its effect must remain a 'just-so' scenario that is difficult to evaluate without additional evidence (Lauder, 1981). Maynard Smith & Szathmáry (1999), for example, argue that such far-reaching innovations as the origin of the eukaryotic cell and the

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origin of language were unique events in the history of life.

The study of innovations and their effects therefore requires the identification of characters that arose many times independently. For organisms, this requires skeletal characters preserved in fossils in clades that are well understood phylogenetically and that have a geographically and stratigraphically abundant fossil record. This approach of analysing the origins, distribution, and fates of minor innovations is the one I take in this paper.

The minor innovation I have chosen to analyse is the labral tooth, a downwardly projecting tooth or spine formed at the edge of the outer lip of the shell of many predatory gastropods. For several years, I have been studying the taxonomy, phylogeny, functional morphology, and distribution of labral-tooth-bearing gastropods and their relatives. My purpose here is to present a synthesis of this work, with the ultimate goal of understanding the conditions that favour the origin and spread of evolutionary novelties.

After identifying the clades in which a labral tooth has evolved and discussing the structure and possible functions of the labral tooth, I shall outline the phylogenetic, geographical, ecological, and stratigraphic distribution of the feature; and I shall ask where, when, and in what kinds of environments the labral tooth has arisen. Drawing on evidence concerning other innovations, I shall then assess the generality of the patterns and results obtained in this study.

BACKGROUND AND HYPOTHESES

THE CONDITIONS FOR INNOVATION

Evolutionary innovations in morphology are like technical inventions by humans. They usually improve the effectiveness of some function or open up previously unavailable economic possibilities, and are therefore both predictors and products of economic growth (Mokyr, 1990). Whether an innovation in fact contributes to long-term success depends on the magnitude of the benefits of the innovation to individuals and the more inclusive groups to which those individuals belong, as well as on the responsiveness of the ecosystems in which the innovation arises and of the economic entities with which the bearers of the innovation interact. The question of origin is therefore separate from the question of fate.

Explanations for the time of appearance of evolutionary innovations emphasize either the mechanisms underlying the development and expression of morphology (or technology) or the external conditions that favour the changes in the status quo necessary for innovation. The intrinsic genetic and developmental mechanisms that underlie the emergence of evolutionary novelties include gene duplication, changes in the timing and location of developmental events, and the establishment of partnerships or symbioses among organisms from different phylogenetic backgrounds. Innovations arising from intrinsic breakthroughs in genetic and developmental architecture often enable organisms to compartmentalize functions, carry out multiple functions simultaneously, and free up structures and resources for possible new roles (see e.g. Vermeij, 1973; Kirschner & Gerhart, 1998). Well-known examples include the functional separation between the jaw dentition and the pharyngeal grinding apparatus in cichlid and related labroid fishes (Liem 1973; Galis & Drucker, 1996); the evolution of partnerships such as the eukaryotic cell, algal–fungal associations, mycorrhizae and land plants, and sociality (Margulis, 1981; Buss, 1987; Maynard Smith & Szathmáry, 1999); the evolution of internal fertilization (West-Eberhard, 1983; Vermeij, 1996b); and the production of extra cusps on mammalian teeth (Hunter & Jernvall, 1995; Jernvall, 2000).

In explanations based on external triggers, environmental changes provide opportunities for innovation. Such changes fall into several categories. In established ecosystems, well-adapted incumbent species offer potential resistance both to would-be invaders, which in general are less well adapted to prevailing conditions, and to the evolution of phenotypes that are already represented among incumbents. Opportunities for innovation should therefore increase when incumbents are overexploited or disappear. Under this scenario, it follows that episodes of innovation should be concentrated after large extinction events.

A second view, not necessarily in conflict with the first, is that increases in the availability of raw materials and biologically useful energy provide opportunities for innovation. For example, episodes of large-scale submarine volcanism, which release vast quantities of nutrients, greenhouse gases, and heat, are associated with the evolution of energy-intensive phenotypes and with diversification (Vermeij, 1995, 2001c). Innovation is especially likely when the per-capita energy budget expands, so that new functions can be added and old ones can be enhanced without undue compromise. Expansion under a regime of intense selection due to enemies and allies therefore favours the evolution of phenotypes that confer competitive, defensive, and reproductive benefits.

Mass extinctions often eliminate competitively and defensively sophisticated species (Vermeij, 1987a, 1995, 1999a), so that the post-crisis ecosystem may not necessarily favour energy-intensive innovations, because the survivors exist under conditions in which resources are controlled by relatively unsophisticated organisms. Under this scenario, I would expect innovations to be concentrated during times of general

economic expansion, marked by global warming and plentiful nutrients, and not immediately following mass extinctions.

Intrinsic and extrinsic explanations are not mutually exclusive, but instead emphasize different aspects of the evolution of novelties. If, for example, a symbiosis or novel biochemical pathway requires or leads to a higher energy demand, its origin and ultimate success will depend on the existence of suitable extrinsic conditions of readily available energy that is easily transformed into biological work. The common element of all the hypotheses is that innovations can arise only when circumstances—structural alteration, a new partnership, or environmental change—selects for or makes possible a phenotype that did not previously exist.

First appearance of a trait in the fossil record is not necessarily the same as the origin of that trait. In clades with a prolific fossil record, however, time of appearance and time of origin should approach each other. In the case of Cenozoic gastropods, the record is sufficiently detailed that, for some intervals and in some regions at least, the time of first appearance of a minor innovation like a labral tooth should not lag too far behind the actual time of evolution of the trait. My approach is therefore to determine and interpret patterns of first appearance of the labral tooth in all the clades in which such a tooth evolved.

PREVIOUS WORK

Although evolutionary innovation has been the subject of numerous studies, there have been relatively few attempts systematically to document the times and circumstances of first appearances of these innovations. Bateman & DiMichele (1994) showed that heterospory, the production of two sizes of spores in land plants, arose at least 11 times independently, mainly during two intervals, the Late Devonian to Early Carboniferous and late Cretaceous to early Cenozoic. Plusquellec, Webb & Hoeksema (1999) documented the evolution of mobility in corals, a phenomenon that occurred multiple times during the Paleozoic and later. In their study of innovations among cheilostome bryozoans, Jablonski, Lidgard & Taylor (1997) showed that most of these occurred during the early Cretaceous; but the authors documented only the time a given innovation appeared in the first lineage to acquire it, and not the times when a similar innovation evolved subsequently in other lineages. Poor phylogenetic resolution within the Cheilostomata unfortunately makes such an analysis unfeasible at present.

There are several studies of the timing of major ecological transitions, which are at least in part made possible by morphological or biochemical innovations. Thayer (1983), for example, systematically surveyed animals at the phylum and class level in order to determine when and how often the habit of burrowing into sediments or living beneath the sediment-water boundary evolved from the habit of living at or above the sea bottom. There are similar studies on transitions from the benthos to the plankton (Signor & Vermeij, 1994; Rigby, 1997), between sea and land (Vermeij & Dudley, 2000), and from a surface existence to a rock-boring habit (Vermeij, 1987a). Vermeij & Lindberg (2000) compiled data on the time of origin and evolutionary derivation of marine animals that eat attached multicellular plants, and I did the same for animals that live in and carry with them the shells of molluscs (Vermeij, 1987a).

Finally, several studies equated evolutionary innovation with the appearance of order-level or higher-level taxa. They indicate that such taxa preferentially originated in near-shore as compared to off-shore marine environments, and at equatorial as compared to temperate or polar latitudes (Jablonski & Bottjer, 1990, 1991; Jablonski, 1993). The underlying assumption is that groups of high taxonomic rank originate because of an evolutionary breakthrough, and that all instances of such breakthroughs are reflected at an appropriately high taxonomic rank. In this paper, I examine the appearance of the labral tooth in all clades regardless of taxonomic rank.

As a relatively conspicuous feature of many gastropod shells, the labral tooth has attracted occasional attention from previous authors. Lamy (1931) and Fischer (1939) described the characteristics, mode of formation, and possible functions of the labral tooth in *Leucozonia* and *Chicoreus* respectively. Vignon (1931) provided a partial catalogue of tooth-bearing taxa, and distinguished between a tooth formed at the end of a groove (*dent de sillon*) and a tooth formed at the end of a cord (*dent de cordon*). Vignon's list, however, excluded many taxa with a labral tooth, and included some (such as *Bufonaria echinata*, as *Ranella spinosa*) that lack a tooth. Several authors have referred to the tooth as 'labial', but in the current terminological convention, 'labium' refers to the shell's inner lip (the columellar or axial side of the aperture), whereas 'labrum' denotes the outer lip, or abaxial side of the aperture. Paine (1966) seems to have been the first author to speculate about the functions of the labral tooth on the basis of observations of gastropods feeding in the wild.

Taxonomists have often, but by no means always, noted the presence of a labral tooth or spine. A survey of tooth-bearing species based only on the published taxonomic literature would be seriously incomplete, because labral teeth have often been overlooked or perhaps not thought worth mentioning. For this reason, I have combined a thorough evaluation of the

literature with intensive surveys of thousands of living and fossil gastropod species as represented in museums and in my own collection. This work has resulted in dozens of taxonomic and systematic papers. The present study represents a synthesis and interpretation of my findings.

LABRAL-TOOTH-BEARING CLADES

In order to estimate how many times a given trait has evolved, it is critical to reconstruct the history of evolutionary branching. Detailed phylogenies are not available for many groups of gastropods, and those that are (e.g. Marko & Vermeij, 1999; Haasl, 2000; Vermeij & Carlson, 2000) do not always provide unequivocal results. The approach I take in this paper is to analyse the characters and distribution of tooth-bearing species and their likely relatives. Although these methods often do not involve formal, computer-aided cladistic analyses, they incorporate the main tenets of rigorous phylogenetic inference: evaluation of homology, establishment of scenarios linking ancestors to likely descendants through plausible intermediates, and scrutiny of all observable characters and aspects of distribution.

I have tried to identify all instances of evolution of a labral tooth. Each independent instance represents a clade. I define a clade as an ancestor and all of its descendants. In most cases, all species of a tooth-bearing clade have retained a labral tooth, but some secondary losses are inferred to have occurred in the Pseudolividae, Ancillinae, and perhaps *Panamurex* and the *Microrhytis* clades (see Appendix, notes 9, 29, 40, and 57). The size of a clade is measured as the number of fossil and living species known for that clade. In the clades that contain toothed as well as untoothed species, I have counted only the number of tooth-bearing species. All clades are listed in Table 1 and discussed in detail in the Appendix. The Appendix contains numerous new generic assignments of fossil and living species, and many other previously unpublished data.

My comparative taxonomic and evolutionary studies indicate that a labral tooth occurs in at least 608 species, of which 251 are Recent. These species are distributed among 58 clades (Table 1); that is, I estimate that a labral tooth has evolved independently at least 58 times. These clades range in size from a single species to groups that have been accorded familial or subfamilial taxonomic rank. All belong to the clade of higher Caenogastropoda that Riedel (2000) has called Latrogastropoda. All but one (*Argobuccinum*, in the cassoid family Ranellidae) belong to the monophyletic Neogastropoda. Within Neogastropoda, all clades except *Ancillinae* (in the Olividae) and *Dentimargo idiochila* (in the Marginellidae), which Riedel

(2000) assigns to the major neogastropod clade *Volutina*, are part of the suborder-level clades Muricina and Buccinina in the Muricoidea. Half (29) of the 58 labral-tooth-bearing clades belong to the Muricidae. Detailed arguments for the existence, size composition, distribution, phylogeny, and relationships of labral-tooth-bearing clades appear in the Appendix.

The estimate of 58 clades is subject to some uncertainty. The number could be higher if the labral tooth evolved more than once in the *Ocinebrina* clade (Appendix, note 33) and the Ancillinae (note 57; see also Michaux, 1989, 1991). It may be somewhat lower if Cretaceous clades with a labral tooth are phylogenetically more closely linked than the meagre evidence currently indicates (see notes 1–7, 9, 56, 57).

Some populations are phenotypically polymorphic in the expression of the labral tooth. A labral tooth may be present or absent in *Argobuccinum tumidum*, *A. pustulosum*, *Melongena lainei*, *Iosepha glandiformis*, *Pollia undosa*, *Hexaplex angularis*, *'Ceratostoma' virginiae*, *Ocinebrellus aduncus*, *O. inornatus*, *Nucella canaliculata* var. *compressa*, *'N.' squamosa*, *Hanetia haneti*, *Xanthochorus cassidiformis*, and *X. buxeus*.

STRUCTURE OF THE LABRAL TOOTH

The labral tooth of gastropods forms in at least three distinct ways and at various positions along the shell's outer lip. Details for each clade possessing a labral tooth are given in the Appendix. Here I briefly summarize the main types.

The most common type of labral tooth is formed at the end of an external groove or depression(Fig. 1D–O). Such a tooth evolved in 35 of 58 tooth-bearing clades (60%). This prevalence is especially strong among the 11 clades with ten or more species. Among these, a tooth formed at the end of an external concavity occurs in nine clades (81%). In clades consisting of only one species, this kind of tooth is known in 12 of 23 cases (52%).

Teeth formed at the end of a groove vary widely in their positions along the outer lip. The tooth lies abapical of all sculpture on the last whorl in some Muricidae (e.g. *Mexacanthina*), Nassariidae (*Hebra* clade), Fasciolariidae (*Opeatostoma*), and Buccinidae (*Preangeria*). In other clades, it is almost medial in position, as in some Muricidae (*Murex*, *Hexaplex* clade, and *Muricanthus*) and Buccinidae (*'Buccinum' cinis*, and *Pollia* in the *Cantharus* clade). Usually, the lip as a whole extends to form the tooth, but in two muricid clades (*Inermicosta colorata* and some members of the *Acanthina* clade) only the adaxial (inner) side protrudes, leaving the abaxial part (the side away from the aperture) in the same plane as the rest of the outer lip edge. *Opeatostoma* may be unique in having the

Table 1. Summary of gastropod clades with a labral tooth. Key to abbreviations: Campan, Campanian; Maastr, Maastrichtian; eEo, Early Eocene; mEo, Middle Eocene; lEo, late Eocene; lOligo, late Oligocene; eMio, early Miocene; mMio, middle Miocene; lMio, late Miocene; Pli, Pliocene; ePli, early Pliocene; mPli, middle Pliocene; lPli, late Pliocene; Pleist, Pleistocene; ePleist, early Pleistocene; lPleist, Late Pleistocene; Rec, Recent; c, tooth formed at end of cord; g, tooth formed at end of groove; o, tooth formed otherwise; ?, tooth formed in unknown manner. For Note, see Appendix

Clade	Range	Species		Tooth type	Note
		living	total		
Ranellidae					
Argobuccinum	lPleist-Rec	2	2	g	1
Buccinoidea					
Buccinopsis	Campan–Maastr	0	8	g	2
Odontobasis	Maastr	0	4	g	3
Hydrotribulus	Maastr	0	3	c	4
Fulgerca	Maastr	0	2	c	5
Protobusycon	Maastr	0	2	g	6
Cornulina	eEo–lEo	0	7	g	7
Melongena lainei	eMio	0	1	g	8
Pseudolividae	Campan–Rec	16	110	g	9
Fasciolariidae					
Benimakia	lMio–Rec	3	5	c	10
Dennantia	lEo–ePli	0	5	c	11
Leucozonia	lMio–Rec	5	7	c	12
Opeatostoma	lPleist–Rec	1	1	g	13
Buccinidae					
Phoracanthus	mEo	0	1	g	14
Cominella	Rec	1	1	c	15
Iosepha	lPli–Rec	3	3	o	16
Accidenticulabrum	lMio–ePli	0	2	g	17
Editharus	eEo–lEo	0	9	o	18
Cantharus clade	eMio–Rec	24	31	g	19
Gemophos n.sp.	ePleist	0	1	g	20
Preangeria	eMio–Rec	1	5	g	21
'Buccinum' clade	Rec	1	1	g	22
Janiopsis angulosa	lMio–ePli	0	1	g	23
Nassariidae					
Hebra clade	lMio–Rec	13	15	g	24
Turbinellidae					
Columbarium	Maastr–Rec	12	24	c	25
Ceratoxancus	Rec	3	3	g	26
Muricidae, Muricinae					
Attiliosa gibsonsmithi	lMio	0	1	c	27
Acantholabia	ePli–lPli	0	2	c	28
Panamurex	eMio–mPli	0	6	c	29
Murex	eMio–Rec	27	33	g	30
Hexaplex clade	eMio–Rec	13	14	g	31
Muricanthus	ePli–Rec	3	3	g	32
Muricidae, Ocenebrinae					
Ocenebrina clade	lOlig–Rec	8	23	c	33
Inermicosta colorata	mMio	0	1	g	34
Hadriania	Pli–Rec	1	2	c	35
Jaton decussatus	lPleist–Rec	1	1	c	36
'Ocenebra' katayamai	eMio	0	1	c	37

continued

Table 1—*continued*

Clade	Range	Species		Tooth type	Note
		living	total		
Ocinebrellus	eMio–Rec	2	3	g	38
Muregina lugubris	Rec	1	1	g	39
Microrhytis clade	eMio–Rec	1	10	g	40
Mariasalpinx	lMio	0	1	c	41
Hanetia	Rec	1	1	c	42
Forreria clade	eMio–Rec	1	12	g	43
Acanthina clade	lOlig–Rec	6	27	g	44
Mexacanthina	Pleist–Rec	3	3	g	45
Nucella packi	lOlig	0	1	g	46
Nucella canaliculata	Rec	1	1	c	47
'Nucella' squamosa	Rec	1	1	c	48
Xanthochorus	Pleist–Rec	2	2	g	49
Muricidae, Rapaninae					
Agnewia kempae	lPleist	0	1	c	50
Muricodrupa fenestrata	Rec	1	1	c	51
Acanthais	Rec	1	1	g	52
Mancinella alouina	Pli–Rec	1	1	g	53
Neorapana	eMio–Rec	3	4	g	54
Concholepas	lPli–Rec	1	2	g	55
Olividae					
Ptychosyca	Maastr	0	1	g	56
Ancillinae	Maastr–Rec	86	191	g	57
Marginellidae					
Dentimargo idiochila	Rec	1	1	?	58

labral tooth entirely enveloped by the mantle when the animal is active.

In rare instances, two labral teeth are formed at the outer lip. This is typical for the rapanine muricid *Concholepas*, but in other clades it is a highly exceptional condition that may be related to mantle damage. DeVries (1997) reports an example in the fossil South American muricid *Chorus*, and I have seen one instance in the Californian muricid *Forreria belcheri* (Hinds).

A labral tooth formed as an extension of an external spiral cord or ridge (Fig. 1A–C) occurs in 20 of 58 clades (34%). The tooth varies in position from basal (at the adapical end of the siphonal canal), as in the muricid *Muricodrupa*, to medial as in the fasciolariid *Leucozonia*. Among large clades of ten or more species, a tooth at the end of a cord occurs in only two cases (18%). There are ten cases (44%) among the 23 clades consisting of only one species each.

In three clades, the tooth is formed in unusual ways. The tooth in the buccinids *Iosepha* and *Editharus* forms at the point where the adapical and abapical sectors of the outer lip meet at an angle. It therefore does not correspond to either a cord or a groove on the shell's exterior. A tooth formed in this way has a medial position along the outer lip. The tooth of the marginellid *Dentimargo idiochila* does not correspond to any element of sculpture, and its mode of formation remains uncertain.

Although the ontogeny of labral teeth has not been investigated in all cases, examination of various growth stages indicates that the tooth is often a feature of later growth stages. There is no labral tooth in the immature stages of *Ceratostoma* (Spight & Lyons, 1974), nor in the early growth stages of the muricids *Muregina*, *Ocinebrellus*, *Fenolignum* (*Ocinebrina* clade) and the fasciolariid *Leucozonia*. In many muricids in which shell growth is discontinuous, as indicated by the presence of axial sculpture differentiated into normal ribs and enlarged varices, the tooth evidently forms discontinuously on the adapertural face of each successive varix. This condition is evident in *Ceratostoma* (*Ocinebrina* clade), *Jaton*, the *Pterorytis* clade, *Chicoreus*, *Hexaplex*, *Muricanthus*, *Murex*, and *Panamurex*.

The major clades to which labral-tooth-bearing clades belong are generally characterized by an outer shell lip whose edge is crenulated throughout its length. This is typical of most Muricidae, pisaniine Buccinidae, and Fasciolariidae. The labral tooth there-
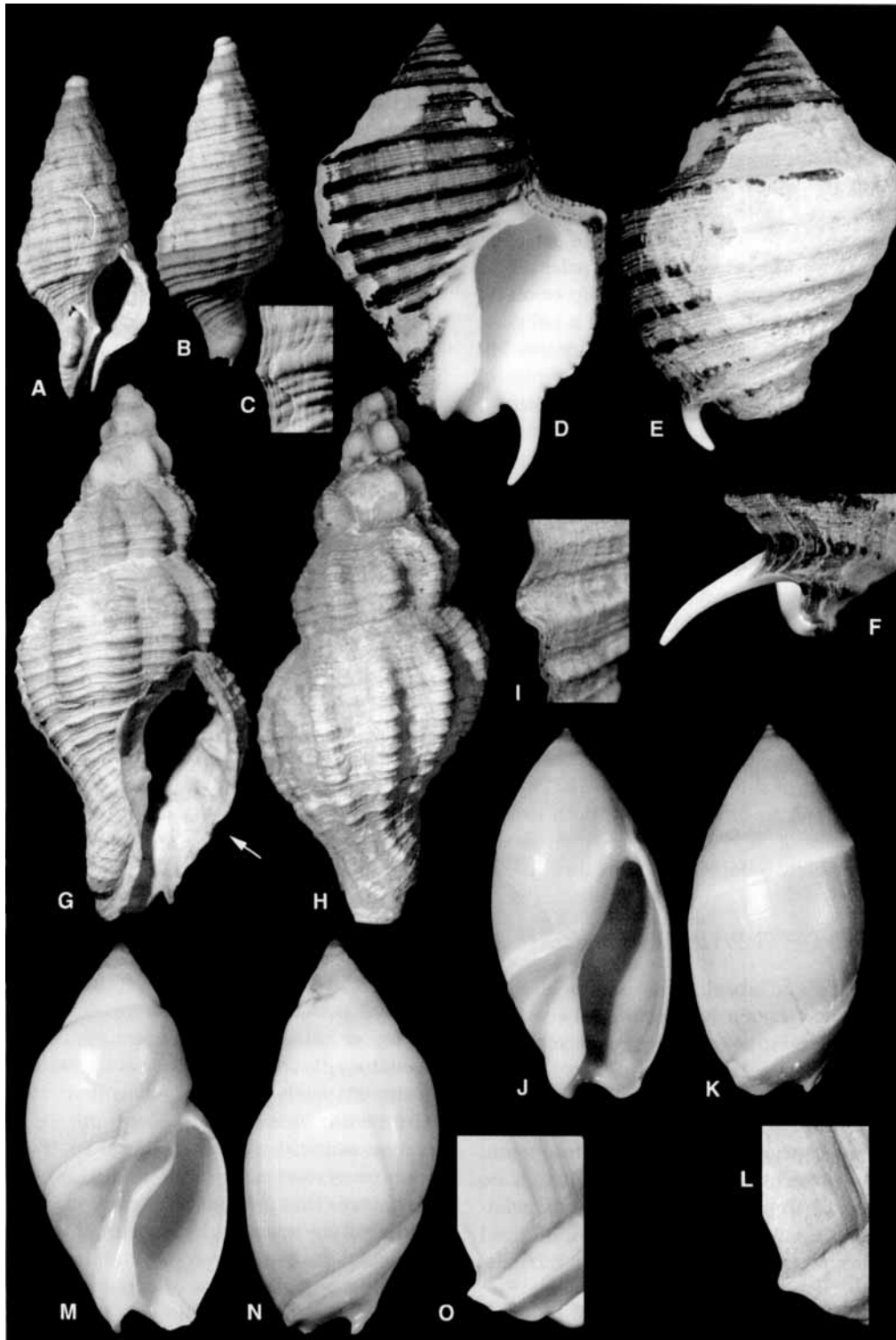
Figure 1. Examples of gastropods with a labral tooth; apertural and dorsal views of all specimens, followed by labral tooth viewed from dorsum. A–C, *Dennantia cingulata* Tate, Balcombe Bay, Fyansford Formation, middle Miocene, Victoria Australia; NMV 304124; height 20.8 mm. D–F, *Opeatostoma pseudodon* (Burrow), Playa Brava, Veragua Province, Panamá; Vermeij collection; height 42.3 mm. G–I, *Janiopsis angulosa* (Brocchi), Orsiano, Pliocene of Italy; IRSNB; height 50.8 mm. J & K, *Baryspira mucronata* (Sowerby), off Omaha Beach, near Leigh, Auckland, New Zealand; Vermeij collection; height 38.8 mm. M–O, *Eburna glabrata* (Linnaeus), El Playon, Paraguaná Peninsula, Falcó Province, Venezuela; Vermeij collection; height 40.9 mm.

fore represents an enlargement of one of the crenulations (see also Vermeij & Kool, 1994). This is not, however, the case in ancilline Olividae, in which the edge of the outer lip is polished and smooth. In Pseudolividae, the abapical sector of the outer lip may be crenulated, with the adapical-most crenulation being enlarged to form the labral tooth, but the lip sector above (adapical to) the tooth is generally smooth.

Several gastropods are characterized by a series of sharp, ventrally or anteriorly projecting prickles or barbs along the whole length of the outer lip or on its abapical sector. The barbs usually occur on a polished edge, and are all found in sand-dwelling species belonging to clades in which a labral tooth is typically not developed. Examples include Cassidae (*Casmaria*, *Phalium*), Strombidae ('*Strombus*' *dentatus* Linnaeus), Nassariidae (*Alectrion*, *Niotha*, *Telasco*, and *Zeuxis*, possibly all belonging to a single derived clade), Mitridae (*Mitra* in the strict sense), Harpidae (some *Harpa*), and Volutidae (two early Miocene species of *Lyria*; see Hoerle & Vokes, 1978; Vokes, 1998). Somewhat similar but finer crenulations ornament the sharp-edged abapical sector of the outer lip in some Conidae (*Conus marmoreus*, *Cylinder textile*, both of Linnaeus), Costellariidae (*Vexillum* in the strict sense), and Pseudolividae (some Eocene species of *Sulcobuccinum*; see Vermeij, 1998a). All these species, except *Lyria* and *Sulcobuccinum*, are known only from the Pliocene to Recent of the Indo-West Pacific region. I do not consider them to have a labral tooth except for the Eocene species of *Sulcobuccinum*, in which the crenations appear below (abapical to) the labral tooth.

FUNCTIONS OF THE LABRAL TOOTH

Every clade in which a labral tooth occurs is characterized by the presence of a siphonal canal or notch, and is known or inferred to be comprised of carnivorous species. No herbivorous, detritivorous, or microphagous gastropods, including those with a well developed siphonal canal (such as many cerithioideans, stromboideans, and cypraeoideans) have a labral tooth. With the possible exception of ancilline olivids, no predatory gastropods that subdue their victims primarily by enveloping them in a large foot have a labral tooth. I include in this group cassids, volutids, harpids, and naticids. Where predation has been observed in Olividae, it is accomplished by envelopment in the foot; but there are no observations on the mode of feeding in ancillines, many of which have a labral tooth. My own attempts to observe the food and feeding of *Baryspira australis* (Sowerby) in northern New Zealand were unsuccessful. I conclude that the labral tooth has functions related to predation, particularly those forms of predation not involving engulfment by a large foot.

The known feeding habits of gastropods possessing a labral tooth involve subduing and often digesting the prey outside the predator's shell. Many muricids drill their shell-bearing prey by making a small, usually circular, usually straight-sided hole through the shell wall of its prey. The aperture and foot of most muricids are too small for this to be accomplished by enveloping the prey in the foot, as is done by shell-drilling naticids and by many other predatory gastropods. Peterson & Black (1995) suggested that the buccinids *Cominella lineolata* (Lamarck), a species without a labral tooth, and *Iosepha tasmanica* Tenison-Woods, a species with a tooth, drill bivalve prey, because they found drilled valves in enclosures containing these two predators; but they did not observe how the drilling was accomplished. Ansell (2000) shows that aggregations of *I. glandiformis* (Reeve) in New Zealand are associated with drilled bivalve prey only when they are accompanied by predatory drilling muricids of the genus *Xymene*. He suspects, as do I, that *Cominella* and *Iosepha* attack prey only by way of the commissure between the valves, and that they do not drill. The muricid *Acanthinucella* in California brings its labral tooth down forcefully on the opercular plates of prey barnacles. Prying apart or shattering these plates greatly speeds up predation when compared to the more standard drilling employed by this gastropod (Sleder, 1981; Perry, 1985).

The labral tooth in several muricids (*Ceratostoma*, *Mexacanthina*, *Chicoreus*, and *Muricanthus*) is associated with the ability of the predator to pry apart barnacle opercular plates or to drill a hole at the junction between valves of a closed prey bivalve (Vermeij, 1978; Kent, 1981; Malusa, 1985; Vermeij *et al.*, 1994). A significant hazard associated with bivalve edge-drilling and with other forms of predation that involve penetration by the predator between prey valves or into the prey's aperture is the loss of the predatory gastropod's proboscis. Radwin & Wells (1968) document such loss and subsequent regeneration in *Stramonita haemastoma floridana* (Conrad), a rapanine muricid without a labral tooth that typically feeds on oysters in the Gulf of Mexico by edge-drilling. Structures that prevent prey-valve closure or complete sealing of the aperture by an operculum could therefore be useful in avoiding injury to the predator and in speeding up the process of subjugating prey. A labral tooth may well function in this way. The short labral tooth of *Neorapana tuberculata* (Sowerby) may function to wedge or push the prey gastropod's operculum aside, as Sleder (1981) has also suggested for *Acanthinucella* preying on littorines.

Kantor & Bouchet (1997) inferred a direct role for the labral tooth in predation in the deep-water Indo-West Pacific turbinellid genus *Ceratoxancus*. They observed that the incidence of repaired breaks, which

were concentrated in the basal sector at the level of the tooth, is conspicuously high (often one to three breaks per individual) within tooth-bearing members of the genus compared to species without a tooth. From this observation they inferred that the outer lip, and especially the labral tooth, may be used forcibly to enter or open the skeletons of prey. Lip breakage related to the forcible opening of bivalves is known in busyconine whelks (Malgalhaes, 1948; Paine, 1962; Kent, 1983; Dietl & Alexander, 1998), the fasciolariid *Fasciolaria* (*Cinctura*) *hunteria* (Perry) (Wells, 1958), and thick-shelled populations of the buccinid *Buccinum undatum* Linnaeus (Nielsen, 1975). The outer lip is strongly convex in all these predators, none of which has a labral tooth.

Edge-drilling and other forms of predation involving penetration through the aperture or between plates or valves occur widely among predatory molluscs that lack a labral tooth. In fact, the presence of a tooth does not guarantee that the tooth plays a direct role in predation. *Mexacanthina angelica* (Oldroyd) feeding on oysters in the northern Gulf of California drill their victims through the centre of the upper valve rather than at the valve edge, and the well developed labral tooth does not appear to have a function in drilling (Vermeij *et al.*, 1994). The rapanine muricid *Neorapana tuberculata* in the northern Gulf of California attacks some limpet-like gastropods at the shell edge (Paine, 1966), and preys on coiled gastropods by way of the aperture, apparently without drilling (Paine, 1966; Vermeij & Carlson, 2000). Species of *Leucozonia* attack barnacles, bivalves, vermetid gastropods, and small mobile gastropods (Ingham & Zischke, 1977; Bandel, 1984), but the method of predation and the possible functions of the labral tooth remain unknown. In *Opeatostoma*, which apparently feeds on polychaetes (Paine, 1966) and barnacles in the wild (Spight, 1976) and on barnacles in the laboratory (Ankel, 1976), the very long, curved labral tooth is conspicuously sharp and unworn at its tip, indicating that it is not used directly to subdue resisting individual prey (Lamy, 1931).

Clades whose members are known to specialize on a diet of worms (polychaetes, hemichordates, and sipunculans), sponges, cnidarians, echinoderms, or ascidians do not develop a labral tooth. Some species with a labral tooth may include polychaetes in a very broad diet (e.g. the buccinids *Pollia fumosa* and *P. undosa* and the fasciolariid *Opeatostoma pseudodon*; see Taylor, 1984; Kohn, Taylor & Wai, 1997), but all species with a labral tooth for which data on diet are available contain at least some prey with an enclosing hard skeleton.

One possible function of the tooth is anchorage or enhanced stability during predation. With the tooth wedged against the prey or against the substratum,

the predator can achieve a certain stability while it thrusts the proboscis into prey at odd angles or positions. This has been suggested for *Ceratostoma foliatum* by Kent (1981), but experimental verification of this effect is required. In support of this idea, it is noteworthy that species of *Mexacanthina* cling very tightly while feeding, whereas they are very loosely attached by the foot when the animal is resting (Vermeij *et al.*, 1994). DeVries (2000) has also suggested that the paired labral teeth of the rapanine muricid *Concholepas concholepas* brace the prey while the predator attacks barnacles, mussels, and ascidians.

Anchorage of the type described above would be useful on hard substrata, but not on sand or mud. Most gastropods with a labral tooth are indeed rock-dwellers, but species of *Murex*, *Columbarium*, the *Hebra* clade of Nassariidae, and the Ancillinae are typically found in sand or mud. I have no idea how the labral tooth might function in these taxa.

In summary, although a great deal remains to be learned about the functions of the labral tooth, a more or less active role in predation seems likely in most instances. In the best investigated case, *Acanthinucella* feeding on barnacles (Perry, 1985), the presence of a labral tooth greatly decreases handling time per prey individual, and therefore the potential risk to the predator of remaining exposed to dangerous situations (see also Vermeij, 1987a, 1993a). Furthermore, the presence of a labral tooth may enable a predator to take a larger range of sizes of prey, including prey that must be subdued and consumed outside the confines of the predator's body.

LABRAL TEETH IN SPACE AND TIME

In order to describe and analyse the geographic and stratigraphic pattern of distribution of clades and species with a labral tooth, I compiled absolute numbers of labral-tooth-bearing species for each of several biogeographically homogeneous Recent faunas and for well-sampled formations representing homogeneous fossil faunas. Within Muricidae, I compiled the number of tooth-bearing species and compared it to the total number of co-occurring species in order to analyse the evolutionary dynamics of species with a labral tooth against that of the more inclusive clade as a whole. In this comparison, I excluded the Coralliophilidae, a derived Middle Eocene to Recent clade of muricids that feed on cnidarians and that lack a labral tooth (see Lozouet & Le Renard 1998, and Riedel, 2000, for history and phylogenetic relationships of Coralliophilidae; Kantor, 1995, for anatomy). I did not perform such comparisons for other more inclusive clades such as the Buccinidae and Fasciolariidae or for higher caenogastropods as a whole because of uncertainties

concerning the scope of the inclusive clades. For example, I might compare the number of tooth-bearing fasciolariids to the total number of species of Fasciolariidae or to its subfamily Peristerniinae (to which all tooth-bearing fasciolariids apparently belong), but there is no consensus at present about which genera and species belong to these taxa. Moreover, Riedel (2000) has argued that fasciolariids are paraphyletic, comprising not only several derived clades but also the stem group of neogastropods that gave rise to Buccinidae and even the small-shelled Columbellidae.

Data on the geographical and stratigraphic distribution of tooth-bearing species come primarily from monographic accounts of faunas, extensively supplemented by taxonomic revisions of individual groups and by my own observations. Absolute numbers of species depend on taxonomic practice and are therefore subject to some uncertainty and possible revision. For example, the muricid faunas of the Mediterranean Pliocene may be taxonomically oversplit; and current understanding of species boundaries within the Ancillinae is rudimentary, with the possibility that sexual dimorphism could account for the co-occurrence of several supposed species in the same subgenus. Unless taxonomists have explicitly revised the interpretations of faunistic monographs, however, I have retained the numbers of species as given in the faunistic monographs and surveys.

GEOGRAPHICAL DISTRIBUTION

Whatever the functions and advantages of a labral tooth may be, they are not uniformly distributed among the world's living predatory gastropod faunas. In terms of absolute numbers, species with a labral tooth are overwhelmingly tropical to warm-temperate in distribution. Of the 251 living species with a labral tooth, 240 (96%) occur in these warmer zones. The only cold-water species with a labral tooth are the ranellids *Argobuccinum pustulosum* in South Africa and *A. tumidum* in New Zealand; the ancillines *Baryspira bathami* (Dell) and *B. southlandica* (Fleming) in New Zealand; and seven muricids: *Ceratostoma burnetti* (Adams and Reeve) and *C. foliatum* (Gmelin) in the northwestern and northeastern Pacific respectively, *Ocinebrellus aduncus* (Sowerby) and *O. inornatus* (Récluz) in the northwestern Pacific, *Acanthina monodon* (Pallas) and *Concholepas concholepas* (Bruguière) in southern South America, and 'Nucella' squamosa (Lamarck) in South Africa. Except for the ancillines and *A. monodon*, these species range into warm-temperate waters. No clade consists exclusively of cold-water species.

The number of muricid species with a labral tooth as a percentage of the total regional muricid fauna does not, however, follow a latitudinal trend. Among muricid faunas of ten or more species, this percentage varies from 0 to 19% in the tropics, 0 to 17% in the warm-temperate zones, and 0 to 18% in the cool-temperate zones (Table 2).

Within climatic zones, there are strong regional differences in the percentage of labral-tooth-bearing species (Table 2). I shall discuss contrasts within the temperate zones, among islands and continental shores, and among tropical continental regions.

Among temperate muricid faunas, those of the northeastern, northwestern, and southeastern Pacific stand out as rich in species with a labral tooth. This richness reflects both a fairly large number of clades and a relatively large number of co-occurring species within clades. By contrast, the muricid faunas of the temperate North Atlantic and southwestern Pacific contain no living species with a labral tooth; and that of southern Africa contains only two species. In the case of the Atlantic, especially the cool-temperate North Atlantic, this absence may simply reflect the small size of the muricid fauna (five or fewer species), but such an artifact cannot explain the absence of tooth-bearing muricids in temperate Australia or New Zealand and their near absence in southern Africa.

It is noteworthy that, whereas muricids with a labral tooth are rare or absent in temperate Australia, New Zealand, and southern Africa, clades with a labral tooth are well represented in these regions. All three regions support a number of tooth-bearing Ancillinae. Tooth-bearing pseudolivids and turbinellids (*Columbarium*) occur in warm-temperate Australia and southern Africa; the ranellid genus *Argobuccinum* occurs in South Africa and New Zealand; and buccinids (*Cominella* and *Iosepha*) have tooth-bearing species in warm-temperate Australia and New Zealand. These clades are generally not represented in Recent temperate Pacific faunas where tooth-bearing muricids are well represented. The chief exception is the pseudolivid genus *Macron*, which is represented by two warm-temperate species in southern California and northwestern Mexico, an area rich in tooth-bearing muricids. Non-muricid tooth-bearing clades are also absent in the temperate North Atlantic.

Another contrast exists between the shores of small oceanic islands and those of continents and large islands. In both the Atlantic and Indo-West Pacific region of the tropics, the incidence of tooth-bearing species is significantly lower on islands than along continental margins. Among Indo-West Pacific muricid faunas with ten or more species, all seven island faunas have lower percentages of tooth-bearers (0–5.6%) than the four faunas from continental and large-island shores (12–19%; see Table 2).

This pattern is not confined to muricids. Ancillines, pseudolivids, turbinellids, the *Hebra* clade of nassariids, and *Cantharus* (in the *Cantharus* clade of

Table 2. Number of muricid species M, number of labral-tooth-bearing muricids M_1, & total number of labral-tooth-bearing gastropods L in space & time

Region, age, & fauna	M	M_1	L
WARM WESTERN ATLANTIC			
Maastrichtian			
Ripley Formation, Tennessee & Mississippi	0	0	10
early Paleocene (Danian)			
Matthews Landing Member, Porters Creek Formation	3	0	2
late Paleocene (Thanetian)			
Bells Landing Member, Tuscahoma Formation	1	0	3
middle Eocene (Lutetian)			
Gosport Sand, Alabama	5	0	3
late Eocene (Priabonian)			
Moodys Branch Formation, Mississippi	6	0	2
early Oligocene (Rupelian)			
Suwannee Limestone, Florida	7	0	0
Red Bluff Formation, Mississippi	9	0	0
late Oligocene (Chattian)			
Tampa Limestone, Florida	12	0	1
Haywood Landing Member, Belgrade Formation	12	2	2
early Miocene (Burdigalian)			
Chipola Formation, Florida	42	3	4
Kirkwood Formation, New Jersey & Delaware	10	2	2
Cantaure Formation, Venezuela	21	4	5
middle Miocene (Langhian)			
Plum Point Member, Calvert Formation	16	0	0
middle Miocene (Serravallian)			
Drum Cliff Member, Choptank Formation	10	1	1
late Miocene (Tortonian)			
Chancellor's Point Member, St. Marys Formation	8	1	1
Cercado Formation, Dominican Republic	20	0	1
Gatun Formation, Panamá	21	2	3
Entreriense Formation, Argentina	18	1	1
early Pliocene			
Yorktown Formation Zone 2, Virginia	10	1	1
Pinecrest bed 7, Florida	46	4	4
Gurabo Formation, Dominican Republic	44	0	2
late Pliocene			
Caloosahatchee Formation, Florida	25	2	2
Moín Formation, Costa Rica	28	0	0
early Pleistocene			
Bermont Formation, Florida	25	0	2
Recent, continental & large-island shores			
Florida	60	0	2
Aruba, Curaçao, & Bonaire	24	0	3
Greater Antilles	49	0	1
Venezuela	45	0	3
Amapa to Alagoas, Brazil	25	0	4
Recent, oceanic island shores			
Fernando de Noronha, Brazil	10	0	1
Trindade, Brazil	7	0	2

Table 2—*continued*

Region, age, & fauna	M	M_1	L
WARM EASTERN PACIFIC			
late Eocene			
Talara Formation, Peru	3	0	3
early Pliocene			
Esmeraldas beds, Onzole Formation, Ecuador	22	2	2
Recent			
northern Gulf of California	50	3	3
Panamá	65	5	6
Galápagos Islands	35	2	4
WARM EASTERN ATLANTIC			
early Paleocene (Danian)			
Calcaire de Mons, Belgium	1	0	7
middle Paleocene (Selandian)			
Lelinge Greensand, Denmark	1	0	3
late Paleocene (Thanetian)			
Paris Basin, France	4	0	4
Ewekoro Formation, Nigeria	1	0	5
early Eocene (Ypresian)			
Gan, southern France	14	0	3
Paris Basin, France	7	0	3
middle Eocene (Lutetian)			
Paris Basin, France	16	0	8
Loire-Inférieure, France	12	0	5
middle Eocene (Bartonian)			
Paris Basin, France	13	0	6
Ameki Formation, Nigeria	3	0	2
late Eocene (Lattorfian)			
northern Germany	18	0	3
early Oligocene (Rupelian)			
Mainz Basin, Germany	14	0	0
Etampes, France	12	0	1
late Oligocene (Chattian)			
northern Germany	18	0	2
Egerian, Hungary	9	0	0
Aquitaine Basin, France	56	0	2
early Miocene (Aquitanian)			
Aquitaine Basin, southwestern France	48	2	4
early Miocene (Burdigalian)			
Aquitaine Basin, France (early)	39	1	3
Miste beds, Aalten Member, Breda Formation	17	0	1
middle Miocene (Langhian)			
Loire Basin, France	26	1	3
Aquitaine Basin, France	23	3	5
late Miocene (Tortonian)			
Montegibbio, Italy	48	3	5
Kostej, Rumania	35	0	2
Pliocene			
Oorderen Member, Lillo Formation, Belgium	5	1	1
Kruisschans Member, Lillo Formation, Belgium	3	1	1
early Pliocene, Malaga	22	3	5
Pliocene, northern Italy	30	4	5

Table 2—*continued*

Region, age, & fauna	M	M_l	L
Recent			
Gabon, tropical West Africa	20	0	2
Angola, subtropical West Africa	25	0	3
Senegal, subtropical West Africa	25	3	4
Western Sahara, warm-temperate Africa	14	1	1
northern Mediterranean sea, warm-temperate	15	1	1
Cape Verde Islands, tropical	8	0	2
St. Helena, warm-temperate	4	0	0
Madeira, warm-temperate	10	1	1
WARM INDO–WEST PACIFIC			
middle Eocene (Lutetian)			
Nanggulan Formation, Java	7	0	4
early Miocene			
Nyalindung beds, Java	7	3	8
Quilon Formation, south India	9	2	3
late Miocene			
various locations, East Borneo	12	3	9
upper Dingle Formation, Panay, Philippines	8	3	5
Recent, continental & high-island shores			
Philippines	138	16	36
North Queensland, Australia	101	12	25
Southern Japan	88	11	16
Eastern Arabian Peninsula	47	9	16
Recent, oceanic-island shores			
Society & Tuamotu Islands	64	2	4
Marquesas Islands	38	0	1
Easter Island	6	0	0
Hawaiian Islands	33	0	0
Henderson Island	21	0	0
Guam, Mariana Islands	45	1	4
Palau Islands	30	2	7
COOL-TEMPERATE NORTHERN HEMISPHERE			
early Miocene			
basal Jewett Sand, California	10	2	2
middle Miocene			
Olcese Sand, California	10	1	1
late Miocene			
Etolon Formation, Kamchatka	11	0	0
Pliocene			
Hokkaido, Japan	10	2	2
Pleistocene			
upper San Pedro beds, California	19	5	7
Recent			
Southern California	46	8	10
Puget Sound, Washington	17	1	1
Hokkaido, Japan	17	3	3
Virginia	5	0	0
Maine	4	0	0
Southern Norway	5	0	0

Table 2—*continued*

Region, age, & fauna	M	M_1	L
TEMPERATE SOUTHERN HEMISPHERE			
late Eocene			
La Meseta Formation, Seymour Island	3	0	0
Kaiatan stage, New Zealand	5	0	2
late Oligocene			
Duntroonian Stage, New Zealand	5	0	4
early Miocene			
Waitakian Stage, New Zealand	9	0	1
Otaian Stage, New Zealand	13	0	4
Altonian Stage, New Zealand	28	0	9
Pliocene			
Mangapanian Stage, New Zealand	14	0	4
Nukumaruan Stage, New Zealand	22	0	6
central Chile	6	5	6
Cape Province, South Africa	8	2	3
Pleistocene			
Castlecliffian Stage, New Zealand	26	0	5
Haweran Stage, New Zealand	29	1	4
Recent			
South Australia	33	0	8
North Island, New Zealand	36	0	7
South Island, New Zealand	26	0	3
central Chile	9	4	4
western Cape Peninsula, South Africa	20	1	10
Golfo de San Matías, Argentina	5	0	0
Kerguelen Island	7	0	0

Sources. Numbers of muricid species were generally taken from Vermeij (1996a) and references therein. Data on other faunas were taken from the following sources:

Warm western Atlantic. Cretaceous: Wade, 1926; Sohl, 1964a. Paleogene: Dockery, 1977, 1998; Palmer & Brann, 1966; Haasl & Hansen, 1996; Mansfield, 1937; Petuch, 1998; MacNeil & Dockery, 1984. Neogene: Campbell, 1993; Petuch, 1993; Ward, 1998. Recent: de Jong & Coomans, 1988; Voskuil, 1991; Houart, 1991; Leal, 1991.

Warm eastern Pacific. Eocene: Olsson, 1928, 1930. Pliocene: Olsson, 1964; Vokes, 1988. Recent: Keen, 1971; Skoglund, 1992.

Warm eastern Atlantic. Paleocene and Eocene: Cossmann, 1897, 1902, 1919, 1923; von Koenen, 1889; Eames, 1957; Glibert, 1973; Ravn, 1939; Adegoke, 1977; Pacaud & Le Renard, 1995; Pacaud & Schnetler, 1999; Merle, 1989. Oligocene: Cossmann, 1893; Baldi, 1973; Kuster-Wendenburg, 1973; R. Janssen, 1979; P. Lozouet, personal communication. Miocene: Böttger, 1902, 1906; Montanaro, 1935; Glibert, 1952; Bellardi, 1882; A. W. Janssen, 1984; P. Lozouet, personal communication. Pliocene: Bellardi, 1873, 1882; D'Ancona, 1871; Marquet, 1993, 1997; Muñiz Solís & Guerra-Merchán, 1994; Lozouet, 1992. Recent: Houart, 1996, 1997; Houart & Abreu, 1994.

Warm Indo-West Pacific. Eocene: Martin, 1914, 1931. Miocene: Martin, 1921; Dey, 1962; Beets, 1941, 1981, 1983a,b, 1984a,c, 1986; Shuto, 1969. Recent: Wilson, 1994; Bosch *et al.*, 1995; Kuroda, Habe & Wai, 1971; Kay, 1979; Rehder, 1980; Tröndle & Houart, 1992; Houart & Tröndle, 1997; Preece, 1995.

Cool-temperate North Pacific. Miocene: Addicott, 1970; Gladenkov & Sinelnikova, 1990. Pleistocene: Grant & Gale, 1931.

Temperate southern hemisphere. Eocene: Maxwell, 1992; Stilwell & Zinsmeister, 1992. Oligocene to Pleistocene: Beu & Maxwell, 1990; Herm, 1969; Kensley & Pether, 1986. Recent: Wilson, 1994; Powell, 1979.

buccinids) are restricted to continental and large-island margins. Many tooth-bearing clades such as *Murex*, *Mancinella alouina*, *Columbarium*, and *Preangeria* are apparently absent even from such island groups as Palau, which lies within 700 km of the more continental coasts of New Guinea, the Philippines, and Indonesia.

Island faunas generally are less diverse than those of continental margins, and species living in sand or mud are especially underrepresented (Kay, 1967; Vermeij, 1987b). It is therefore not surprising that tooth-bearing clades should also be less diverse on islands, especially those like *Murex*, *Columbarium*, and the Ancillinae, which live in sand. Removal of sand-dwelling muricids from the tallies for Indo-West Pacific localities in Table 2 narrows but does not eliminate the difference in the percentage of muricid species with a labral tooth between island and continental faunas.

Islands have probably rarely served as sites for the evolution of a labral tooth. Several endemic tooth-bearing species are known from oceanic islands—*Leucozonia ponderosa* Vermeij & Snyder at Trindade in the South Atlantic, *L. triserialis* (Lamarck) in the Cape Verde Islands, *L. tuberculata* (Broderip) in the Galápagos and Cocos Islands, and *Benimakia marquesana* (A. Adams) from the Marquesas Islands, *Neorapana grandis* (Sowerby) from the Galápagos, *Iosepha norfolkensis* at Norfolk Island—but these species belong to clades whose other members occur on continental margins. These endemics therefore probably represent instances of colonization of a tooth-bearing ancestor, followed by divergence. Only one clade, *'Buccinum' cinis* (Reeve) from the Galápagos and Cocos Islands, is restricted to the shores of oceanic islands and may have evolved its tooth there. Its evolutionary relationships and origins remain unclear, however, and it is equally possible that *'B.' cinis* represents a case of geographical restriction.

Finally, there is a strong regional contrast in the representation of tooth-bearing species among tropical faunas from continental or large-island margins. In the tropical western Atlantic, no living muricid has a labral tooth. In other major clades, tooth-bearers are known only in the fasciolariid genus *Leucozonia* (two allopatric species) and the ancilline genera *Eburna*, *Amalda*, and *Hesperancilla* (six allopatric species). West African shores support tooth-bearing muricid species (*Jaton decussatus*, *Hexaplex angularis*, *Ocinebrina aciculata*) and pseudolivids (*Fulmentum sepimentum*), but no fasciolariids or ancillines. All major tooth-bearing clades except pseudolivids are well represented on continental shores of the Indo-West Pacific. Tooth-bearing muricids, for example, make up 19% of the muricid fauna of the eastern Arabian peninsula, and about 12% of that in the Philippines (Table 2).

Pseudolivids in the Indo–West Pacific are represented only by two deep-water species of *Fusulculus* around New Caledonia (Vermeij & Bouchet, 1998). In the eastern tropical Pacific, there are tooth-bearing muricids (*Muricanthus*, *Neorapana*, *Acanthais*, *Muregina*, and *Pterorytis*), fasciolariids (*Opeatostoma*) and (marginally in the southern Gulf of California) two species of the pseudolivid genus *Macron*.

TEMPORAL DISTRIBUTION OF LABRAL TEETH

Analysis of the temporal distribution of species with a labral tooth entails answering two questions. First, what is the temporal pattern of origination (or at least first appearance) of labral-tooth-bearing clades? Second, what is the temporal pattern of diversity within these clades relative to the diversity of related species that lack a labral tooth?

In order to answer the first question, I have attempted to identify the time of first appearance of each labral-tooth-bearing clade. Details are given in the Appendix; the data are summarized in Table 3 and Figure 2.

Clades with a labral tooth are overwhelmingly post-Eocene in distribution. Of the 58 tooth-bearing clades, 45 (77%) appeared during or after the late Oligocene (Table 3). Among Muricidae, which with 29 tooth-bearing clades account for half the independent acquisitions, none appears before the late Oligocene. When expressed as numbers of first appearances per Myr (Table 3), using the Cenozoic time scale of Berggren *et al.* (1995), appearances of tooth-bearing clades are well above the average for the past 80 Myr (0.6 per Myr) during the early Miocene (1.6 clades per Myr), Pliocene (1.6 per Myr), and Pleistocene (2.3 per Myr), and well below average during the Paleocene, Eocene, and early Oligocene. The overall pattern departs significantly from the null expectation of a constant frequency of appearance through time (*P*<than 0.01, chi-square test).

The predominance of labral teeth formed at the end of a groove or depression has existed since the beginning of labral-tooth evolution. Of 13 clades with origins in the Cretaceous to Eocene interval, eight (62%) have the tooth formed at the end of a groove, compared to only four (31%) in which the tooth is formed at the end of a cord. For the late Oligocene to Recent interval, these numbers are 27 (60%) and 16 (35%) respectively. One Paleogene and two Neogene clades have a tooth formed either as an angular junction of the abapical and adapical sectors of the outer lip or in an unknown manner.

The stratigraphic distribution of species with a labral tooth is given in Table 2, and summarized in Figures 2 and 3. Temporal patterns of distribution are best discussed at the regional level rather than globally,

Table 3. Times of first appearance of labral-tooth-bearing gastropod clades

Time	Number of first appearances	Rate of first appearances (in Myr)
late Cretaceous	9	0.6
early Paleocene	0	0.0
late Paleocene	0	0.0
early Eocene	2	0.33
middle Eocene	1	0.13
late Eocene	1	0.31
early Oligocene	0	0.0
late Oligocene	3	0.62
early Miocene	11	1.6
middle Miocene	1	0.22
late Miocene	7	0.6
Pliocene	6	1.6
Pleistocene	7	2.3
Recent	10	
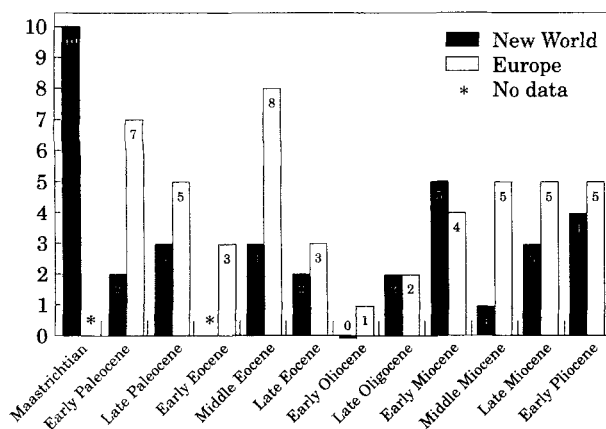
Figure 2. Absolute number of tooth-bearing species through time in the warm-temperate to tropical New World and Europe.
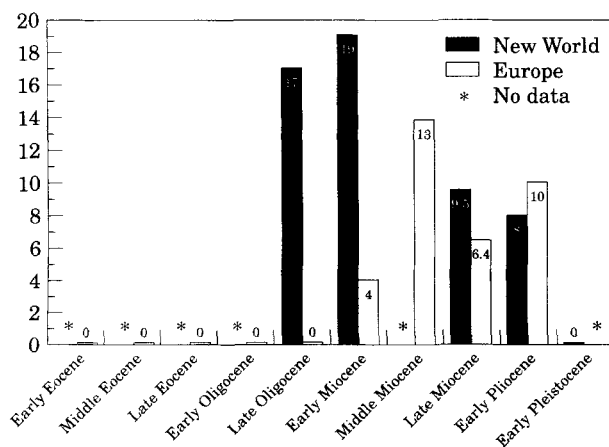
Figure 3. Percentage of tooth-bearing muricids relative to total muricid fauna through time.

because a global account would mask important variation in evolutionary dynamics among biotas from different regions. Moreover, by examining history region by region, we have a greater opportunity to uncover causal connections and circumstances than if we concentrated only on global signals, which often incorporate opposing trends among regions.

Although muricids played no role as labral-tooth-bearers during the early Cenozoic, tooth-bearing species in other clades were relatively diverse then, especially during the Middle Eocene in Europe. The peak in absolute numbers was evidently due to diversification within tooth-bearing clades, which generally originated before the middle Eocene, and not due to the origination of new clades. Absolute numbers in the New World remained lower during the early Cenozoic and had a somewhat broader early to middle Eocene peak.

Following the decline and extinction of most tooth-bearing species during and at the end of the late Eocene, the four early Oligocene (Rupelian) faunas I investigated contained no species with a labral tooth. The recovery in absolute numbers was slow, with the result that a regional maximum in the number of species with a labral tooth was not achieved in Europe until the middle Miocene. The number of species during the Neogene never exceeded five in either the western Atlantic or in Europe, but did exceed this number both in Chile and in the Indo-West Pacific, regions whose Miocene faunas are relatively small as well as only sketchily known.

The limited data in Table 2 indicate that the distributional pattern of muricids with a labral tooth has remained more or less stable in several parts of the world. Where they are sufficiently characterized, the Miocene and Pliocene muricid faunas in California,

western South America, the tropical eastern Pacific, and the continental Indo-West Pacific supported a relatively large number of tooth-bearing species, just as do Recent muricid faunas in those regions. The muricid fauna in New Zealand has never supported a tooth-bearing species except for the brief appearance of *Agnewia kempae* Powell during the Haweran (last interglacial) in northern New Zealand. Similarly, no fossil temperate Australian muricid with a labral tooth is known, indicating that the absence of tooth-bearing muricids there is of long standing.

The exception to this temporal stability occurs in the western Atlantic and to a lesser extent the northeastern Atlantic. From the late Oligocene to the late Pliocene, most muricid faunas in the Atlantic supported at least two species with a labral tooth. As many as four tooth-bearing species occurred in the Cantaure Formation (early Miocene) of Venezuela and the Pinecrest beds (middle Pliocene) of Florida, where they make up 19% and 8.7% of total muricid species diversity respectively. Pleistocene and Recent muricid faunas in the western Atlantic lack tooth-bearing species. Losses of labral-tooth-bearing muricids were smaller but nonetheless notable in western and southern Europe and in South Africa (Table 2). Pliocene levels in the eastern Atlantic were maintained only in Senegal, in tropical West Africa.

Other clades with tooth-bearing members in the western Atlantic have also declined. There are no tropical shallow-water Pseudolividae in the western Atlantic after the Miocene. Ancillinae are not known in Florida after the early Miocene, and have not occurred in the Greater Antilles since the late Pliocene. The group is today confined in the Atlantic to the continental coasts and nearby islands of Central and South America. Only *Leucozonia*, with two Recent allopatric species, has not declined.

If I had tracked the history of only a single major clade of tooth-bearing gastropods through time, I would have arrived at conclusions different from the one indicated by data on all the clades combined. For muricids, I would have concluded that the frequency of labral teeth increased greatly after the early Oligocene, following a very long (65 my) lag since the first appearance of muricids during the Cenomanian stage of the mid-Cretaceous. For pseudolivids, by contrast, a peak in diversity was reached early (during the Paleocene), followed by stepwise declines (Vermeij, 1998b). The complete picture is more complex. The record indicates an early Oligocene trough between a Paleogene peak dominated by pseudolivids and a Neogene peak dominated by muricids or ancillines.

RELIABILITY OF THE PATTERN

Stratigraphic, taxonomic, and phylogenetic uncertainties potentially compromise the reliability of the findings of this study. I shall try to show, however, that the patterns documented in this paper are robust and not likely to be altered greatly by additional information.

Inferences about the times of first appearance, stratigraphic range, diversity, geographic range, and time of extinction of fossil taxa are notoriously affected by sampling and preservation. At the smallest scale of sampling, even those formations that have been intensively studied continue to yield more species as more material becomes available (Jackson *et al.*, 1999). On a larger scale, some time intervals are represented by few or no fossils or by individuals whose preservation is poor. Biologically productive environments are likely to be both over represented and more thoroughly sampled in the fossil record than those in less productive settings. The same is true of times when sea level was high as compared to times of low sea level. Rocky shores, where many labral-tooth-bearing gastropods live, are rarely preserved. Fortunately, most rock-associated tooth-bearing species extend from the intertidal zone to sublittoral habitats, whose faunas are well represented in Cenozoic deposits. At most ten of 251 Recent tooth-bearing gastropod species are strictly confined to intertidal levels.

Several authors have proposed methods for evaluating completeness in the fossil record and for estimating confidence intervals for times of origination and extinction of taxa based on first and last occurrences in the fossil record (Marshall, 1990; Foote, 1997; Foote & Sepkoski, 1999; Wagner, 2000). The assumptions underlying these methods cannot be satisfied by any of the data available for museum collections or the literature, and would likely also be violated in most field situations (see also Budd, Johnson & Stemann, 1996). I have therefore not used these methods.

Instead, I have developed a crude test that evaluates some aspects of bias and sampling, based on the number of geographically and stratigraphically distinct faunas available for each time unit. I divided the last 80 Myr into the following intervals: late Cretaceous, Paleocene and early Eocene, middle and late Eocene, early Oligocene, late Oligocene, early Miocene, middle Miocene, late Miocene, Pliocene, and Pleistocene. For each interval, I counted the total number of distinct faunas from which I extracted data on the potential occurrence of tooth-bearing species. There were 372 such faunas. The null expectation is that the number of first appearances during a given interval is proportional to the number of distinct faunas sampled. I therefore compared the expected number of first appearances of labral-tooth-bearing clades with the number actually observed. For example, the 36 early Miocene faunas comprise 9.7% of the 372 faunas from which I extracted data; I would therefore expect 4.7

clades (9.7% of 48 clades with a fossil record) to show first appearances in the early Miocene. The actual number is 12. Similarly for the middle and late Eocene, the expected number of first appearances, based on 19 middle Eocene and 24 late Eocene faunas, is 11.6% of 48, or 5.6, a number considerably higher than the observed number of two first appearances.

The pattern of observed numbers of first appearance differs significantly from that expected on the basis of the number of faunas examined. This is true when all intervals from the late Cretaceous to the Pleistocene are considered ($P<0.01$, chi-square test) and when only the six post-Eocene intervals were analysed ($P<0.01$, 260 faunas, 35 clades). I conclude that the temporal pattern of appearance of tooth-bearing clades cannot be explained by the number of faunas sampled.

The test described above evaluates only one aspect of sampling and preservational bias. It does not take into account differences in species richness or sampling intensity among faunas, nor does it directly control for the extent of geographic coverage per interval, although the number of faunas per time interval is correlated with areal coverage.

Intervals of time not represented by fossiliferous formations do pose potential problems. In the Indo-West Pacific region, there are very few known Oligocene faunas, and even the very well preserved Miocene and Pliocene molluscs of India, Indonesia, the Philippines, and some western and central Pacific islands are represented by relatively small samples whose stratigraphic position is imprecisely known. The tropical eastern Pacific record is relatively sparse throughout, but is especially poor in the Oligocene. There is essentially no post-Eocene record in West Africa except for a small early to middle Miocene fauna in Angola. In South Africa, there is no pre-Pliocene fauna from the Cenozoic. For all these regions, first appearances of endemic tooth-bearing clades must be cautiously interpreted in the light of these gaps. A more or less continuous Cenozoic record exists in Europe, the Atlantic Coastal Plain, New Zealand, and the North Pacific.

The effect of missing intervals on the findings of this study is relatively small. Thirteen clades have first appearances following geological intervals that are not represented by significant faunas in the regions where the clades appear. Of these first appearances, one is middle Eocene (*Phoracanthus* in Indonesia), one late Eocene (*Dennantia* in Australia), two late Oligocene, eight early Miocene, and one early Pliocene (*Acantholabia* in Florida). Six of the eight early Miocene cases are from the tropical and warm-temperate Indo-West Pacific region including Japan. It is therefore possible that the currently recognized early Miocene peak of first appearances will be pushed back in time, perhaps to the late Oligocene, when more data become

available. I shall argue below that such a backward shift will not materially change the interpretation of the circumstances of the evolution of labral-tooth-bearing clades. It is worth noting that several first appearances are in faunas of very low diversity (50 species or fewer). This is notably the case for *Nucella packi* and the *Acanthina* clade in the late Oligocene, and *'Ocenebra' katayamai* and *Ocinebrellus* in southern Japan in the early Miocene.

How sensitive are inferred patterns of distribution and evolution of labral-tooth-bearing clades to improvements in taxonomic knowledge? My analysis of the number of fossil and living labral-tooth-bearing species described during each twenty-year interval beginning in 1740 indicates that many more tooth-bearing taxa remain to be discovered (Vermeij, 1999c). The most recent twenty-year interval (1980–1999) witnessed the largest number of newly named living species with a tooth and a slight rise in the rate of description of fossil species over previous intervals. By the year 1860, when half the known living species and 13% of fossil species with a tooth had been named, the main features of the spatial and temporal distribution of clades and species with a labral tooth would already have been evident. For example, an early Miocene peak in first appearances was already detectable. Four of the 11 tooth-bearing clades known in 1860 had their earliest known representative recorded from the early Miocene; two each were recorded as appearing in the late Cretaceous and middle Eocene. The only significant departure from the currently recognized pattern was the absence in 1860 of tooth-bearing clades appearing in the Pliocene. By the year 1900, 20 tooth-bearing clades with fossil species were known, whose dates of first appearance as known at that time are as follows: late Cretaceous, six; early, middle, and late Eocene, each one; early Miocene, six; and late Miocene, five. Nine new dates of first appearance including four in previously undescribed single-species clades, became known after 1980: one in the late Oligocene, three in the early Miocene, two in the late Miocene, two in the Pliocene, and one in the early Pleistocene. These new records did not significantly alter the temporal pattern that could have been known had it been looked for in 1980. We can therefore expect the number of clades and species with a labral tooth to grow as taxonomic and phylogenetic knowledge continues to accumulate, but major patterns of distribution in space and time are unlikely to change much with the new discoveries.

THE LABRAL TOOTH AS KEY INNOVATION

In order to show that a given character is a key innovation, three conditions must be satisfied. First,

the character must enable its bearer to occupy environments or pursue ways of life not previously exploited by its ancestors. Second, the species with the key innovation must outnumber those in the sister clade, in which the innovation is absent. Third, diversification should follow immediately upon the origin of the key innovation. Evaluation of the second criterion is often problematic, because it requires precise knowledge of the node at which the clade with the key innovation and its sister clade without the innovation diverge. More often than not, the sister clade will be difficult to differentiate from the plesiomorphic stem group, that is, the clade with the key innovation may bud from the main stem rather than originate as a fork-like dichotomy. The sizes of the two clades are therefore difficult to estimate.

Although sister-group relationships are, for the most part, not well established, the available evidence fails to support the hypothesis that the labral tooth is a key innovation. At least 23 clades (40%) are as small as they can be, consisting of one species each. Of these monospecific clades, 11 are extinct today, and 13 are still living and therefore have the potential to diversify. Among large clades (ten or more species) whose sister-group relationships are more or less well established, only three of six have more species than their sister groups. Thus even among those clades that by virtue of their large size are most likely to be more diverse than their sister clades, there is no indication that the presence of a labral tooth has conferred a macro-evolutionary advantage.

These results accord with expectation. Although the labral tooth probably offers adaptive advantages for individuals, and may expand the trophic breadth of its bearer compared to the condition in which a tooth is lacking, such advantages do not necessarily translate into a higher rate of speciation. Careful surveys of some other innovations, such as image-forming eyes (de Queiroz, 1999) and the assumption of herbivory by marine animals (Vermeij & Lindberg, 2000), have similarly failed to reveal consistent positive effects on diversity. Other innovations, however, do have such effects. Examples include internal fertilization and attendant sexual selection in animals (West-Eberhard, 1983), a fourth cusp (the hypocone) on the primitively three-cusped molar teeth in mammals (Hunter & Jernvall, 1995), and the assumption of herbivory by insects (Mitter, Farrell & Wiegmann, 1988).

The marked concentration of labral-tooth-bearing clades within a single major clade, the Latrogastropoda, may indicate an underlying genetic potential that itself can be interpreted as a key innovation. The evolution of this potential, presumably through modification of genetic regulatory mechanisms, might have occurred only once during the early Cretaceous or even earlier, before the Neogastropoda and Cassoidea diverged from a common latrogastropod ancestor (for phylogeny see Riedel, 2000). The various evolutionary expressions of the tooth, which were especially numerous in three subfamilies (Muricinae, Ocenebrinae, and Rapaninae) of the Muricidae, would still be independent of each other, but they would be rendered more probable by the evolution of a genetic enabling mechanism. That mechanism is a key innovation in the sense that it made possible the evolutionary exploitation of habitats and modes of life which were previously unavailable.

Similar interpretations have been offered for the expression of other innovations. Riedel (2000), for example, suggests that columellar folds in gastropods have evolved many times independently in the Latrogastropoda once the genetic potential underlying such expression was established. A similar genetic potential may explain the repeated evolution of eyes (see de Queiroz, 1999), four-cusped mammalian teeth (Jernvall, 2000), eusociality in snapping shrimps (Duffy, Morrison & Rios, 2000), and probably many other repeatedly evolved morphological, ecological, and behavioral innovations.

The question of when and how the enabling genetic mechanism evolved is thus separate from the question of when and how the realization of this potential came to be. The existence of the potential is a necessary, but not sufficient, condition for the evolutionary manifestation of structures like the labral tooth, columellar folds, or eyes. In fact, many large clades within the Latrogastropoda and even within the Muricidae never evolved a labral tooth (e.g. the muricid subfamilies Typhinae and Muricopsinae). I therefore turn to the question of which circumstances permit or select for the expression of a labral tooth when the genetic potential to make one already exists.

THE CIRCUMSTANCES OF INNOVATION

What do the data on the geographical and temporal origins of gastropod clades with a labral tooth say about the circumstances of minor innovation? I shall argue here that (1) the most consistent factor associated with, and permitting the repeated evolution of, the labral tooth, is high planktonic primary productivity, that is, abundance of an easy access to resources; and (2) the presence of labral-tooth-bearing incumbents may prevent the evolution of a labral tooth in co-occurring or invading clades, but the elimination of incumbents and the process of extinction in general do not stimulate minor innovation as represented by the acquisition of a labral tooth.

High diversity is not itself a factor favourable to the evolution of a labral tooth. As I pointed out in the discussion of the reliability of observed patterns, there

is no tendency for first appearances of tooth-bearing clades to concentrate during times represented by exceptionally diverse faunas. Among fossil molluscan faunas of 400 or more species, the incidence of tooth-bearing species among muricids varies from zero (early and middle Eocene of the Paris Basin, middle Eocene of Gulf Coastal Plain and Italy), to 19% (early Miocene Cantaure Formation of Venezuela). Only where high diversity is associated with high planktonic productivity do the frequency of first appearances and the incidence of tooth-bearing species among muricids achieve high values.

HIGH PLANKTONIC PRODUCTIVITY

In benthic communities, high planktonic productivity is manifested by a large biomass, expressed as both high abundance and large body sizes, of suspension-feeding animals that capture planktonic organisms (Birkeland, 1989). In Cenozoic faunas, the most conspicuous suspension-feeders with a fossil record are bivalves, barnacles, bryozoans, and various groups of endolithic animals. A wealth of evidence indicates that suspension-feeders tend to be large not because they live longer, but because they grow fast (see e.g. Kirby, Soniat & Spero, 1998; Kirby, 2000, 2001). Among endolithic animals, there is a general correlation between planktonic productivity and the density of endolithic traces made by suspension-feeders tunnelling into corals, shells, and rock (Highsmith, 1980). Size and density of suspension-feeders can therefore serve as qualitative indicators of planktonic primary productivity.

Peaks in first appearances of tooth-bearing clades generally correlate with times and occur in places of high productivity, whereas lows coincide with low rates of production, as indicated by suspension-feeders. The late Cretaceous of the Gulf Coastal Plain of the United States seems to have been a time of abundant resources. Large exogyrine and liostreine oysters characterized the suspension-feeding biota of this time and region during the Campanian and Maastrichtian epochs. During this interval, nine clades of tooth-bearing gastropods appeared.

The Paleogene (early Cenozoic), during which few tooth-bearing clades appeared, is generally characterized by small-bodied suspension-feeders. In the southeastern United States, no early Paleocene, middle Eocene, late Eocene, or early Oligocene species of suspension-feeding turritellid gastropods exceeded a height of 68 mm (Allmon, 1996). Large Paleogene turritellids occurred during the late Paleocene Sabinian stage of the southeastern United States (maximum height 110 mm) and the middle Eocene Lutetian stage of Europe (height 1150 mm) (Allmon, 1996; Tracey & Todd, 1996). Suspension-feeding bivalves show comparable size patterns. Most large-bodied Paleocene and Eocene molluscs (height 100 mm or more) were grazing campanilid, neritid, stromboidean, and cypraeoidean gastropods, and a few predatory volutid, mitrid, conid, and *Clavilithes*-group fasciolariid gastropods. Paleocene and Eocene muricids, buccinids, and typical fasciolariids rarely exceeded a height of 50 mm.

A rise in first appearances of tooth-bearing clades beginning during the late Oligocene and continuing into the early Miocene coincides with a marked increase in the size range of suspension-feeding barnacles and bivalves and of such predatory gastropod groups as Muricidae, Buccinidae, Melongenidae, Turbinellidae, tonnoideans, and typical fasciolariids.

The earliest tooth-bearing muricids of the late Oligocene Haywood Landing Member of the Belgrade Formation of North Carolina co-occur with the earliest large balanomorph barnacles (Zullo, 1984, 1992) and with gigantic oysters (Kirby, 2000). Large suspension-feeding scallops (diameter 100 mm or more) appeared during the late Oligocene and increase in size during the early Miocene (Addicott, 1974; Smith, 1991; Waller, 1991). Caribbean reef systems of the late Oligocene and early Miocene are characterized by high abundances of bioeroders and other indicators of high planktonic productivity (Edinger & Risk, 1994). In the temperate western Atlantic, suspension-feeding bivalves and gastropods reached large sizes comparable to those during the late Miocene but not achieved during the intervening middle Miocene (Ward, 1998).

The number of species and first appearances of tooth-bearing clades was also high during the late Miocene and early Pliocene. Large body size characterizes bivalves, barnacles, and suspension-feeding gastropods during these intervals in California (Kirby, 2001), the temperate and tropical western Atlantic (Campbell, 1993; Allmon *et al.*, 1996), the northwestern Pacific, and the Mediterranean region (for a review see Vermeij, 2001c).

The extinctions of the middle and late Pliocene selectively eliminated tooth-bearing gastropods and large-bodied suspension-feeders in some regions but not in others. In the temperate and tropical North Atlantic, severe extinction selectively removed many large barnacles, bivalves, and suspension-feeding gastropods, and is linked to a reduction in body size in many surviving clades (Vermeij, 1989, 2001c; Stanley, 1986; Allmon, 1992; Roopnarine, 1996). During this interval, tooth-bearing muricids disappeared from the western Atlantic, and ancilline olivids became extinct in the eastern Atlantic (Lozouet, 1992). Suspension-feeders remained large from the Pliocene to the Recent in the tropical eastern Pacific, northwestern Pacific, and (perhaps with brief interruptions) the northeastern Pacific, all regions where the magnitude of Pliocene extinction was lower and the number of tooth-bearing clades and species has remained high. In the

southeastern Pacific, a large extinction event eliminated many species during the middle Pliocene, but suspension-feeders remained large, and most clades of tooth-bearers survived, albeit it with fewer species.

Finally, the contrast between islands and continental shores supports the role of productivity in affecting tooth-bearing clades. The waters adjacent to continents and large nearby islands support more tooth-bearing clades and species than do those of most isolated oceanic islands. Planktonic productivity, body size of suspension-feeders, and nutrient concentrations are all higher in coastal waters of continents and large islands than in the oceanic waters around small remote islands (Birkeland, 1989; Vermeij, 1990; Taylor, 1993). The Galápagos Islands are unique among oceanic island groups in harboring a relatively large number of labral-tooth-bearing gastropods (four species in four clades) and in being bathed in cool, productive, upwelling waters.

Two factors may account for the link between primary productivity and the distribution of labral teeth. The first is the general economic opportunity afforded by the ready availability of, and access to, nutrients. Energetically costly but functionally useful innovations of all sorts can arise under such circumstances. The second factor is more specific to labral teeth. If labral teeth speed up predation or expand the size range of available hard-shelled prey, then the greater abundance and larger sizes of suspension-feeders made possible by increased planktonic productivity should be especially favourable to the evolution of features that allow for more effective exploitation of those prey resources.

THE ROLE OF INCUMBENTS

In trying to understand the conditions under which minor innovations such as labral teeth evolved, it is instructive to ask what prevents their evolution. Why, for example, have the Ranellidae—a highly diverse worldwide clade extending back in time to the Aptian stage of the early Cretaceous (Riedel, 1995)—evolved a labral tooth only in one small cool-temperate clade in the southern hemisphere during the Pleistocene, apparently in the absence or near absence of other tooth-bearing gastropods co-occurring on hard substrata? Why have muricids in temperate Australia and New Zealand only once (and then only in a short-lived lineage) produced a labral tooth when muricid clades elsewhere evolved the feature many times? Which factors prevented muricids, whose history dates back to the Cenomanian stage of the middle Cretaceous (Garvie, 1991), from evolving a labral tooth until the late Oligocene?

I suggest that incumbency—the presence of already

Table 4. Pattern of extinction of labral-tooth-bearing gastropods

| Time | Number of clades | |
	total	extinct
end-Cretaceous	9	6
end-Eocene	8	4
end-middle Miocene	18	3
end-Pliocene	26	5

well-adapted species—often controls evolutionary opportunity. Unless circumstances are especially favourable to economic growth, a novice with an as yet very imperfect adaptation is at a distinct disadvantage to a well-adapted incumbent in which a similar feature has been tested for a long time. The complementary distributions of major tooth-bearing clades on hard substrata in the western Atlantic, southern Africa, temperate Australia, New Zealand, and the North Pacific all point to the role of well-adapted incumbents in limiting the adaptive exploration of other clades that could in principle evolve a labral tooth. Only in highly productive sites and times is the conservative role of incumbents relaxed, as during the early Miocene of the western Atlantic and Indo-West Pacific, the early Pliocene of tropical America.

The elimination of incumbents by extinction does not necessarily provide opportunities for other clades to fill the adaptive void. This may be because other disruptions accompany the disappearance of labral-tooth-bearing incumbents.

The major extinction events on the last one hundred million years hit labral-tooth-bearing clades hard and provided very little opportunity for the evolution of functional innovations during the recovery phases immediately following the crises. During this interval, the extinction events of largest magnitude occurred at the Cenomanian–Turonian boundary in the Cretaceous, the Maastrichtian–Danian boundary (end-Cretaceous), the Thanetian–Ypresian boundary (end-Paleocene), the Priabonian–Rupelian boundary (end-Eocene), and to a lesser extent the late middle Miocene and Pliocene. Magnitudes of extinction of labral-tooth-bearing clades (Table 4) were highest at the end of the Cretaceous (67% of clades extinct) and late Pliocene (19% extinct). These figures generally underestimate extinction, because surviving clades often lost many members or became geographically restricted during the crises. This effect is best documented for the late Pliocene, when the *Microrhytis* clade became extinct in the western Atlantic (but survived in the tropical eastern Pacific) and the *Ocinebrina* clade became extinct in the tropical eastern Pacific (but survived in the North Pacific and in Europe). There were also

reductions in the number of species of *Forreria*, *Spinucella*, and the *Acanthina* clade.

Labral-tooth-bearing clades did not appear immediately following extinctions. During the Late Cretaceous, first appearances were in the Campanian stage, more than 10 Myr after the Cenomanian–Turonian crisis. Some tooth-bearing clades may have appeared earlier, but the diverse Turonian and Coniacian assemblages of gastropods from California, in which many higher caenogastropods are represented (Saul & Popenoe, 1993; Saul, 1996), show no evidence of labral teeth or of various other morphological innovations and specializations that became common during the subsequent Campanian and Maastrichtian stages. There is no compelling evidence that labral-tooth-bearing clades evolved during the Paleocene, following the end-Cretaceous extinction, or during the early Oligocene following the end-Eocene crisis. Lag times for the evolution of labral teeth were at least 10 and 7 Myr respectively. The Neogene extinctions were less dramatic and geographically more restricted in their effects. Six tooth-bearing clades are known as fossils only from the Pleistocene, after the Pliocene extinction events. Of these, *Agnewia kempae*, *Jaton decussatus,* and *Argobuccinum* are known only from the last interglacial stage of the late Pleistocene (Haweran stage in New Zealand, Harounian stage in Morocco), and not from the well-sampled early Pleistocene strata in these regions (see Brébion, 1979; Beu & Maxwell, 1990). Two others (*Mexacanthina* and *Opeatostoma*) have a strikingly sparse fossil record, so that I have little confidence in their dates of first appearance. Only *Gemophos* n. sp. from the Bermont Formation of Florida dates from the early Pleistocene and could reasonably be taken as an example (albeit a short-lived one) of an origination stimulated by a prior crisis. A possible second example is *Concholepas*, tooth-bearing members of which appeared during the late Pliocene after a major extinction in Peru during the middle Pliocene (DeVries, 2000). This case is interesting because it represents an instance of evolution of a labral tooth in the presence of tooth-bearing incumbents in other clades in an extremely productive ecosystem.

These data indicate that the elimination of incumbent species is not sufficient as a stimulus for the evolution of minor innovations such as a labral tooth. Additional, new factors must be in place that allow or favour the acquisition of new traits. Although I have identified increased (or high) planktonic productivity as one possible factor, there may be others, including a general warming or the expansion of warm zones, and an overall increase in the area of shallow-water productive habitats. The latter factor may have played a role during the late Oligocene to early Miocene interval, when sea levels rose worldwide and warm regions expanded far north and south. Similar but less dramatic sea-level rises and widening of warm belts took place after the Miocene. Global warming and the widening of warm-climate zones in the early Eocene did not, however, result in a large number of first appearances of tooth-bearing clades.

This argument still does not fully explain why muricids have been so dominant among Neogene clades with a labral tooth and so minor during the Paleogene, when pseudolivids and several other buccinoid clades were prolific. After all, pseudolivids did survive the end-Eocene extinctions and could have rediversified during the Oligocene and early Miocene. Instead, their recovery was slow and resulted in a modest diversity of tooth-bearing species only in highly productive waters (northeastern and southeastern Pacific, and South Africa) or in deep water (see Vermeij, 1998b). Similarly, *Columbarium* persisted through the end-Eocene crisis, but it has since remained restricted to deep water (Darragh, 1969).

The clade replacement in the shallow-water tropics seems to be related to passive shell armour. Pseudolivids and *Columbarium* have a thin, unreinforced outer lip, and their axial sculpture is present mainly in the form of nodes or short spines, if it is present at all. By contrast, most tropical and many temperate muricids have a thickened outer lip and strong external shell sculpture consisting of varices and ribs. The same is true for the *Cantharus* clade, which has been diverse in the Indo-West Pacific since the early Miocene. The armoured Neogene muricids and buccinids should be more resistant to breakage by predators than are pseudolivids and members of other tooth-bearing clades that flourished during the Paleogene and late Cretaceous. In the living biota, these less-armoured groups are confined to deep waters or to latitudes outside the tropics, where selection for armour seems to be less intense (Vermeij, 1978, 1993a).

Morphologically, the evolution of a labral tooth would seem to be a simple matter. The shell-secreting mantle edge must be extended beyond the rest of the lip's edge in order to produce a projection. How this is accomplished mechanically is unknown. Local extension exposes part of the mantle edge, and therefore the animal as a whole, to potential dangers from predators. Unless the process takes place in seclusion while the animal is inactive, the conditions that make the production of a tooth initially possible may therefore indicate either a very strong advantage of having a tooth or an environment in which the usual risks are diminished. A reduction in risk means an increase in opportunity, a circumstance promoting evolutionary exploration of phenotypic combinations that were unachievable because of previous compromises and the selection-induced maintenance of a strict status quo (Vermeij, 1978, 1987a, 1995, 1999a). The protection

provided by a predation-resistant shell may have been necessary as a factor contributing to that opportunity for post-Eocene warm-water gastropods.

The circumstances for minor innovation should be more common and less different from normal conditions than the circumstances of normal major breakthroughs. Moreover, they may be more unusual for the first appearance of a trait than for later instances. If, for example, a novel structure like a labral tooth makes possible predation on larger, more protected prey, then escalation between predators and prey may itself create circumstances that are more favourable to the repeated evolution or retention of that structure. The role of such positive feedback in innovation is important, and has been explored somewhat by economists (Arthur, 1989; Mokyr, 1990), but it remains an underappreciated aspect of biological evolution.

GENERALITY OF THE RESULTS

There are not enough comparative studies of minor innovations to make statements about the generality of the results of this study. Elsewhere, I have summarized evidence that major innovations are concentrated during geological intervals when large land masses began to break up and to drift apart, sea levels and temperatures rose, and the oxygen concentration of the atmosphere increased (Vermeij, 2000a). Noteworthy intervals of innovation include the Vendian to Early Cambrian, Late Cambrian to Middle Ordovician, Silurian to Early Carboniferous, Jurassic to Late Cretaceous, and shorter intervals of the Cenozoic (early Eocene, late Oligocene to early Miocene, and early Pliocene) (see also Vermeij, 1987a, 1995). The geological evidence suggests that primary productivity during these intervals was globally high. As with minor innovations, the rarer major innovations do not immediately follow mass extinctions. Ecological expansions such as transitions between land and sea, invasion of deep sediment layers and the endolithic (within rock) environment, and the occupation of the upper seashore by marine clades similarly are concentrated during times of high productivity and in the presence of intense competition and predation (see also Vermeij & Carlson, 2000; Vermeij & Dudley, 2000). Importantly, and in a striking parallel with growth in the human economy, these innovations and expansions further stimulated productivity and opportunity (see also Vermeij, 1999a).

The study of minor innovations as reported here for labral teeth could be done profitably with many other kinds of fossilizable structures, and would shed further light on the circumstances of evolutionary innovation. Vertebrate teeth, coral and bryozoan colonies, landplant leaf and stem architecture, bivalve sculpture, and many aspects of gastropod shell form offer promising material for the phylogenetic, stratigraphic, ecological, and geographic analyses of new and potentially beneficial traits. It is through this kind of comparative paleobiology that we can expect to arrive at a coherent economic and evolutionary account of the history of life.

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APPENDIX

CLADES OF LABRAL-TOOTH-BEARING GASTROPODS

Abbreviations: CAS, California Academy of Sciences,
San Francisco; IRSNB, Institut Royale des Scieces
Naturelles de Belgique, Brussels; MNHN, Muséum
Nationale d'Histoire Naturelle, Paris; NMV, Na-
turhistorisches Museum Wien, Vienna; UF, Florida Mu-
seum of Natural History, Gainesville.

1. Argobuccinum

The only clade of predatory gastropods outside the Neo-
gastropoda containing species with a labral tooth is the
ranellid genus *Argobuccinum.* In some individuals of
A. pustulosum (Lightfoot) from South Africa and *A.
tumidum* (Dunker) from New Zealand, a small labral
tooth is formed at the end of a groove situated near the
base of the last whorl above the siphonal canal. The two
taxa involved, which are usually considered subspecies
of a single species (*A. pustulosum*), are recorded as
fossils only in the late Pleistocene (Beu, 1976; Kensley
& Pether, 1986). Other Recent species or subspecies
from western South America, Tristan da Cunha, and
the southern Indian Ocean islands of St. Paul and
Amsterdam lack a labral tooth (Smith, 1970; Beu, 1988).
The same is true for the Pliocene South African *A. casus*
Pether and Kensley.

As understood by Smith (1970) and Beu (1985, 1988),
Argobuccinum first appeared during the late Eocene in
the northeastern Pacific as *A. jeffersonense* (Durham)
from the Keasey Formation of Oregon. Other species
assigned to *Argobuccinum* and its probable synonym
Mediargo occur in the Miocene and Pliocene on both
sides of the North Pacific. *Priene*, a Miocene to Recent
genus from western South America, may be derived from
an early northern-hemisphere stock of *Argobuccinum*
(Beu, 1988). The Pliocene to Recent *A. pustulosum* group
may represent a quite recent trans-equatorial invasion
of *Argobuccinum* to the southern hemisphere (Smith,
1970; Beu, 1985, 1988). According to Beu (1988), *Ar-
gobuccinum* is itself derived from *Ameranella*, a Pa-
leogene group from Atlantic and Pacific North America.
None of these fossil forms has a labral tooth.

2. Buccinopsis

Nine described species and subspecies from the late
Cretaceous (Campanian and Maastrichtian) belong to
the genus *Buccinopsis*. Eight of these are known from
the Campanian and Maastrichtian of the southeastern
United States (Sohl, 1964a), and one has been described
from the Maastrichtian of Kamchatka in eastern Russia
(Blank, 1980). *Buccinopsis* is characterized by the pres-
ence of a short labral tooth situated at the end of a basal
groove. Blank (1980) did not mention a tooth in his
Buccinopsis crassa kamtchatica, but I have included
this Russian taxon as a tooth-bearer because of Blank's
assignment of it to *Buccinopsis*.

Allmon (1990) considered *Buccinopsis* to be the oldest
member of the *Bullia* group, which is typically placed
in the nassariid subfamily Dorsaninae (see Cernohorsky,
1984). The presence of a terminal (abapical) columellar
fold, indeterminate growth, and absence of a parietal
rib or tooth support this assignment. No other dorsanine,
however, has a labral tooth, and no pre-Pliocene dor-
sanines reach the large size (almost 100 mm high) of
some *Buccinopsis crassa* (Wade). Sohl (1964a), Blank
(1980), and Bandel (1993) assign *Buccinopsis* to the
Buccinidae, broadly defined. This is also the placement
advocated by Haasl (2000), who on the basis of his
morphology-based phylogeny excludes *Buccinopsis* from
the Nassariidae.

3. Odontobasis

The late Cretaceous genus *Odontobasis* consists of five
species, two from the Gulf Coastal Plain, two from the
Western Interior Seaway, and one from the Koryak
Highlands of Kamchatka (see Meek, 1876; Sohl, 1964b;

Blank, 1980). At least the four American species have a labral tooth, which is situated at the end of a basal groove. Blank (1980) did not mention a tooth when he described *Odontobasis constricta korjakensis*, but I shall assume that this Russian species likewise has a tooth. Wade (1917) considered *Odontobasis* to be closely related to *Buccinopsis*. *Odontobasis* differs from that genus by having two or three columellar folds instead of only one basal fold. Allmon (1990) did not include *Odontobasis* along with *Buccinopsis* in the *Bullia* group of dorsanine nassariids. I tentatively regard the acquisition of the tooth in *Odontobasis* as independent of that in *Buccinopsis*. Further comparative work is needed to resolve the taxonomy and phylogeny of these groups.

4. Hydrotribulus

Sohl (1964a) recognizes three species of *Hydrotribulus* from the Maastrichtian (late Cretaceous) of the Gulf Coastal Plain of the United States. At least one of these, *H. nodosus* Wade, appears to have a labral tooth at the end of a cord (Vermeij, 1998a). When he introduced the genus, Wade (1916) assigned *Hydrotribulus* to the Buccinidae. Sohl (1964a) included it in the Pseudolivinae, but I excluded it from that group (Vermeij, 1998a, as Pseudolividae) because the labral tooth of *Hydrotribulus* is situated at the end of a cord instead of a groove. *Hydrotribulus* has a distinct parietal tooth at the adapical end of the inner lip, a feature unknown in any Cretaceous or Paleogene pseudolivid. Resolution of the position of *Hydrotribulus* must await phylogenetic analysis of the complex neogastropod radiation of the late Cretaceous.

5. Fulgerca

The two Maastrichtian (late Cretaceous) species of the enigmatic high-spired genus *Fulgerca* from the Gulf Coastal Plain of the United States have a small labral tooth at the end of the basal fasciolar band. Although Wade (1926) and Sohl (1964a,b) regarded the genus as pseudolivine, I removed it from that group (Vermeij, 1998a) on the basis of the mode of formation of the basal labral tooth.

6. Protobusycon

Still another late Cretaceous (Maastrichtian) neogastropod with a labral tooth is *Protobusycon*. Two stratigraphically separated species from the Ripley Formation of Tennessee and Mississippi in the Gulf Coastal Plain, *T. cretaceum* (Wade) and *P. binodosum* Sohl, have the tooth formed at the end of a deep groove situated just adapical to the long siphonal canal. Groups to which this genus has been assigned include Melongenidae (Wade, 1917; Sohl, 1964a; Saul, 1996), Turbinellidae (Bandel, 1993), and Ficidae (Riedel, 1994). The absence of columellar folds and the presence of a parietal swelling in *P. cretaceum* (USNM 32897) persuade me that none of these assignments is likely to be correct. It is possible that *Protobusycon* belongs to the same clade as *Cornulina* and related Paleogene taxa (Note 7). There is a significant stratigraphic gap between the youngest species of *Protobusycon* with a labral tooth (late Maastrichtian) and the oldest *Cornulina* with such

a tooth (early Eocene). Saul (1996) assigned *P. judithae* Saul from the Paleocene of California to *Protobusycon*. Like late Paleocene members of the *Cornulina* group from Europe and West Africa, this species apparently lacks a labral tooth. I therefore consider the acquisition of a labral tooth in *Cornulina* to have been independent of that in *Protobusycon*.

7. Cornulina clade

The *Cornulina* clade is a late Paleocene to latest Eocene group of gastropods usually assigned to the Melongenidae. At least some species have a basal groove, which in well preserved shells can be seen to end in a small labral tooth on the abapical half of the outer lip. I have confirmed the presence of a labral tooth in *C. armigera* (Conrad) from the Gosport Sand (middle Eocene) of Alabama, *C. minax* (Solander) from the Bartonian (late middle Eocene) of the Paris and Hampshire Basins of Europe, and *C. praecursor* (Cossmann) from the early Eocene (Ypresian) of the Paris Basin. A basal spiral groove has been described for *C. dalli* (Harris), *C. dalli cetaria* Palmer, and *C. louisianae* Palmer, all from the late Eocene (Jackson stage) of the Gulf Coastal Plain; and *C. minax dockeryi* Garvie from the early middle Eocene of Texas. There is also a basal spiral groove in *Mazzalina (Pineda) heilpriniana pyrobola* Gardner from the early Eocene of Texas, and *Cornulina (Revilla) lita* Gardner from the ?Paleocene of Tamaulipas, Mexico. I cannot tell if these species have a labral tooth. The evolution of the tooth of *Cornulina* appears to be independent of, and later than, that in *Protobusycon* (Note 6; see also Vermeij, 1998a).

8. Melogena lainei

The large early Eocene (Aquitanian to early Burdigalian) *Melongena lainei* (Basterot) from southern Europe has a sharply crenulated, abapically convex outer lip, which in some specimens bears a labral tooth situated at the end of a groove. The groove is located above (adapical to) the row of basal spines that characterizes the external sculpture of *M. lainei* and most other species of *Melongena*. Earlier species of *Melongena* such as *M. laxecarinata* (Bellardi) from the early Oligocene of southern Europe, *M. crassicornuta* (Conrad) from the early Oligocene of Mississippi, *M. basilica* (Bellardi) from the late Oligocene of southern Europe, and *M. sculpturata* (Dall) from the late Oligocene of Florida, apparently lack a labral tooth. The lineage of *M. lainei*, which has a relatively narrow aperture, evidently does not extend beyond the early Miocene. More typical *Melongena*, including *M. cornuta* (Agassiz) from the early to middle Miocene of Europe and many early Miocene to Recent species in tropical America also do not develop a labral tooth, and have a relatively broader aperture. I have not examined fossil melongenids of late Oligocene to Pliocene age from the Indo–West Pacific region, as reviewed by Vredenburg (1924). No Recent Indo–West Pacific members of the Melongenidae have a labral tooth. The entire family requires taxonomic revision and a phylogenetic analysis (see also Vermeij & Wesselingh, in prep.).

9. Pseudolividae

This late Cretaceous (Campanian) to Recent clade is characterized by a variably developed labral tooth situated on the abapical sector of the outer lip, usually at the end of a deep groove or less commonly (in the genera *Benthobia* and *Fusulculus*) a scar-like zone. The tooth is secondarily absent in the eastern Pacific Recent genus *Triumphis*. Kantor (1991) has characterized the group anatomically, and showed that the plesiomorphic genus *Benthobia* has several characters thought to be primitive among neogastropods. My genus-level revision (1998a) and synthesis (Vermeij, 1998b), together with emendations and species-level revisions of many Cretaceous and Paleocene taxa (Pacaud, 1998; Pacaud & Schnetler, 1999; Pacaud & Tracey, 2000), indicate that the family comprises 16 living and 94 fossil species. Genera with a tooth are *Fulmentum* (Recent, temperate and tropical West Africa), *Hubachia* (Paleocene, Colombia), *Fusulculus* (late Cretaceous to Eocene, North America and Europe; Recent, Indo–Pacific), *Luizia* (early Miocene to Recent, West Africa), *Macron* (early Miocene of Venezuela, middle Miocene to Recent of the northeastern Pacific), *Naudoliva* (?late Miocene of Trinidad, Recent of southern Africa), *Pseudoliva* (early Miocene to Recent, West Africa), *Sulcobuccinum* (Campanian to late Eocene), *Sulcoliva* (Eocene, Peru), *Testallium* (early Miocene to late Pliocene, western South America), and *Zemira* (late Eocene to Recent, Australia). I agree with Pacaud (1998) and Pacaud & Schnetler (1999) that several species I had assigned to *Sulcobuccinum* (Vermeij, 1998a) in fact belong to *Fusulculus*; but I am not convinced that the genera *Buccinorbis*, *Calorebama*, *Pegocomptus*, and *Popenoeum* are distinct from *Sulcobuccinum*, nor that any Paleogene species should be assigned to *Pseudoliva* as Pacaud (1998), and Pacaud & Schnetler (1999) maintain. Neogene *Pseudoliva* differs from Paleogene *Sulcobuccinum* in several respects, so that I maintain the view (Vermeij, 1998a) that the latter genus represents a plesiomorphic group, which gave rise to several derived taxa including *Pseudoliva*. It may turn out that *Buccinorbis*, *Calorebama*, *Pegocomptus*, and *Popenoeum* should be recognized as distinct clades, but the characters said to distinguish these taxa from each other and from *Sulcobuccinum* are both too variable and too inconsistent to warrant such taxonomic distinction (Vermeij, 1998a).

The genus *Fusulculus* exhibits a more or less juvenilized appearance and consists of small to minute species. Whether these characteristics are derived or primitive remains uncertain, but at least one species (*F. alienopriscus* Pacaud & Tracey) from the early Eocene London Clay Formation of England has a multispiral protoconch indicating planktotrophic development, a condition that is likely to be plesiomorphic for the family (see Pacaud & Tracey, 2000). The anatomically plesiomorphic *Benthobia* also has a planktotrophic larval stage (Bouchet & Warén, 1985; Kantor, 1991).

I interpret the labral tooth of pseudolivids as having arisen only once, but there is room for reasonable argument on this point. Campanian and Maastrichtian pseudolivids belong to *Fusulculus* and *Sulcobuccinum*. The former genus, characterized by a slender, relatively high-spired shell, has a weakly developed, sometimes obsolete tooth. Riedel (2000) considers the Pseudolividae

to be polyphyletic, apparently because *Benthobia* (together perhaps with *Fusulculus*) and *Macron* may belong to other clades (F. Riedel, pers. comm., March, 2000). The planktotrophic larva of *Benthobia* and the globular shell of the adult of this deep-sea genus cause Riedel to question the assignment of *Benthobia* to the Pseudolividae. I am inclined to agree with Kantor (1991) that *Benthobia* represents a highly plesiomorphic pseudolivid, but more data are needed to resolve its phylogenetic relationships. The buccinid-type radula of *Macron* indicates to Riedel that *Macron*, probably together with the toothless *Triumphis*, belongs to the Buccinidae rather than to the Pseudolividae (for further discussion see Vermeij, 1998a). The shells of *Macron* and *Triumphis* are not easily connected through intermediate morphologies to other buccinids, whereas they closely resemble other pseudolivids in details of sculpture. Data confirming the radular characters of *Macron* and *Triumphis* are needed to determine the phylogenetic position of these genera. If *Macron* is indeed a buccinid, it would represent an independent early Miocene acquisition of a labral tooth.

10. Benimakia

Benimakia was distinguished as a distinct genus of Fasciolariidae by Habe (1958) on the basis of its radula (Habe's pl. 3, fig. 11). Habe (1958) noted that the posterior margin of the marginal teeth has seven cusps, of which the outermost one is remote from the others. The shell morphology of *Benimakia* is also distinctive. Although previous authors (Dunker, 1860; Reeve, 1847; Habe, 1958; Wilson, 1994) did not mention a labral tooth in the species they treated, it is nonetheless a prominent feature on the outer lip. The tooth is formed as an extension of a prominent central cord at the adapical end of the basal constriction of the last whorl. Below the tooth, there is a prominent abapical sinus. The spire is high (0.40–0.50 total shell height) and marked by distinct sutures. Six to seven (rarely eight) axial ribs per whorl line up in straight rows across the sutures. These are crossed by low, indistinct cords, which do not nodulate the ribs. Five or six cords ornament the siphonal canal, which lacks the axial ribs. The outer lip on the central sector is crenulated and planar; above it is a well-defined adapical sinus. The inner (adaxial) side of the outer lip bears smooth, long lirae. Two to five weak columellar folds are situated adapical to the siphonal canal. There is no umbilical slit.

The type species, *Turbinella rhodostoma* (Dunker), was described from southern Japan. I have seen possibly conspecific material from Palau (my collection), Zanzibar (ANSP), northwestern Madagascar (ANSP), and the Gulf of Oman (M. A. Snyder collection). Other very similar species of *Benimakia* include *B. lanceolata* (Reeve) from the Philippines, Solomon Islands, and Maldive Islands; *B. marquesana* (A. Adams) from the Marquesas Islands. A probable fossil member is *Latirus bandongensis* Martin from the Miocene of Java. An even earlier, somewhat divergent species, *Fusus angsananus* Martin, from the Nyalindung beds (early Miocene) of Java, may also belong to *Benimakia*. It differs from other species by having 12 axial ribs per whorl, but there is a distinct labral tooth.

I also provisionally assign two large Recent species,

B. nodata (Gmelin) and *B. robillardi* (Tapparone-Cane-fri) to *Benimakia*. They differ from typical *Benimakia* in being substantially larger (more than 100 mm high as compared to 45 mm for the largest *B. lanceolata*), in having the large node-like axial ribs not lined up in straight rows across the sutures, and in having a broad lobe projecting downward just adapical of the upper end of the basal constriction instead of a labral tooth. *B. nodata* occurs widely in the Pacific from the Philippines and Micronesia to Hawaii, Ducie, and Henderson Island in the Pitcairn Group in eastern Polynesia, and in the Pleistocene of the New Hebrides (Abrard, 1946; Paulay, 1990; other distributional data from USNM). *B. robillardi* is a distinctive Indian Ocean species differing from *B. nodata* by having three keel-like cords on the siphonal canal instead of low indistinct cords. The early Miocene *B. njalindungensis* (Martin), described by Martin (1921) as a *Lathyrus*, is very similar to *B. nodata* but much smaller.

As an exclusively Indo-West Pacific group, *Benimakia* is biogeographically distinct from other fasciolariids with a labral tooth. *Benimakia* may have differentiated from a species of the circumtropical genus *Polygona*, which has a planar to convex outer lip with smooth lirae and without a labral tooth. The acquisition of the labral tooth in typical *Benimakia* occurred by early Miocene time and was independent of the evolution of the labral tooth in *Dennantia*, *Leucozonia*, and *Opeatostoma* (see Notes 11–13).

11. Dennantia (Fig. 1A–C)

Tate (1888) named *Dennantia* on the basis of fusiform shells with dominantly spiral sculpture and the presence of a labral tooth at the end of a cord situated above the basal constriction of the last whorl. He included *Fusus ino* Tenison-Woods (type species) and *Dennantia cingulata* Tate, both from the middle Miocene Fyansford Formation of Victoria, Australia. T. Darragh (pers. comm., November, 1998) also includes *Peristernia aldingensis* Tate from the late Eocene of Victoria, a species with well-developed axial sculpture, and three species from the Fyansford Formation described by Tate (1888) as *Leucozonia micronema*, *L. staminea*, and *L. tumida*, in *Dennantia*. The last three species are probably variants of a single species, which by page priority should bear the name *Dennantia micronema*. Darragh (1985) gives the stratigraphic range of *Dennantia* as late Eocene to Pliocene.

Previous authors have considered *Dennantia* to be closely related to *Buccinulum*, which they place either in the Buccinulidae (Powell, 1929) or Buccinidae (Wenz, 1938–1944; Glibert, 1963). From my examination of specimens of *D. ino* (NMV 304126 and 304127), *D. cingulata* (NMV 304124), and *D. micronema* (NMV 304125), I conclude that *Dennantia* belongs to the Fasciolariidae. This assignment is supported by the presence of an adapical sinus on the outer lip, and by the indeterminate growth of the shell, as indicated by the absence of a unique modification of the outer lip. No living fasciolariid has determinate growth, whereas this condition typifies *Buccinulum* and many related buccinoids. Further work is needed to establish the number of species and the phylogenetic relationships of *Dennantia*, but I provisionally consider the evolution of the

labral tooth in this genus as separate from that in other fasciolariids.

12. Leucozonia

Seven species of the late Miocene to Recent fasciolariid genus *Leucozonia* are characterized by the presence of a well-developed, medially situated labral tooth, which is formed as an extension of a cord located well above the basal constriction of the last whorl (Vermeij, 1997; Vermeij & Snyder in prep.). These are *L. nassa* (Gmelin) from the western Atlantic (possibly a complex of two or three species), *L. leucozonalis* (Lamarck) from the northwestern Caribbean, *L. ponderosa* Vermeij & Snyder from the South Atlantic island of Trindade, *L. triserialis* (Lamarck) from the Cape Verde Islands in the eastern Atlantic, *L. tuberculata* (Broderip) from the Cocos and Galápagos Islands, *L. rhomboidea* (Gabb) and *L. striatula* Vermeij from the late Miocene to early Pliocene of the Dominican Republic. The distinctively beaded spiral ridge on the inner (adaxial) side of the outer lip separates *Leucozonia* from other fasciolariids with a labral tooth. This character, together with the existence of three Recent species of *Leucozonia* without a labral tooth, indicates that the tooth in *Leucozonia* evolved independently from that in other fasciolariids.

The early Miocene *Mazzalina costata* Dall from the Chipola Formation of Florida lacks a labral tooth but may be close to the ancestry of *Leucozonia*, with which it shares the presence of beaded lirae. Vermeij and Snyder (in prep.) will propose a new genus for this species. The Indo–West Pacific genera *Latirus* (in the narrow sense, having beaded lirae and with the axial ribs connecting two spiral rows of nodes on the last whorl) and *Latirolagena* are also closely related to *Leucozonia* (see also Bullock, 1974) and lack a labral tooth. All these genera may form a Neogene clade, in which a labral tooth evolved in tropical America no later than the late Miocene.

13. Opeatostoma (Fig. 1D–F)

Berry (1958) named *Opeatostoma* as a monotypic genus for *Buccinum pseudodon* Burrow, a species long mistakenly assigned to *Leucozonia*. This highly unusual eastern Pacific species has the longest known labral tooth of any gastropod. A specimen in my collection from Playa Brava, Panamá, measuring 42.3 mm in length, has a long, curved labral tooth 12.3 mm long. The tooth is unusual for at least three reasons other than its length. First, as pointed out by Lamy (1931), the tooth is always sharp, and thus never worn from use, at the tip. Second, it is entirely smooth, indicating that it is covered by an extension of the mantle in life. Third, it is separated from the adapical sector of the outer lip by a deep sinus, which therefore exaggerates the tooth's length. The tooth lies at the end of a basal groove, a mode of formation not otherwise known in the Fasciolariidae. The phylogenetically isolated position of *Opeatostoma* is underscored by a number of unusual shell characters, including the absence of basal constriction of the last whorl, absence of axial sculpture, and an unusually deep adapical sinus on the outer lip. I have seen Pleistocene specimens from Oaxaca, Mexico,

and La Punta, Ecuador (CAS). The only published reference to fossil material I have been able to find is Hoffstetter's (1954) report of subfossil specimens, which he called *Macron cingulatus* (Lamarck), from the Santa Elena peninsula of Ecuador.

14. Phoracanthus

In the middle Eocene Nanggulan Formation of Java, Indonesia, Martin (1914) described a peculiar species of *Siphonalia*, for which he and Cossmann erected the new subgenus *Phoracanthus*. *S. (P.) ickei* is characterized by a sharp labral tooth situated at the end of a furrow. This furrow is abapical in position, but there are three shallower grooves abapical to it. The species lacks lirae on the inner side of the outer lip, as well as a parietal tooth and columellar folds. Its assignment to the Buccinidae in the broad sense therefore seems well founded, but whether and how it is related to such Neogene genera as *Siphonalia*, *Kelletia*, and *Siphonofusus* remains unclear. *Phoracanthus* is the only labral-tooth-bearing clade with a middle Eocene first appearance. This date cannot be taken too seriously, however, because the early Eocene is evidently not represented by fossiliferous strata in Indonesia.

15. Cominella

The buccinid genus *Cominella* in the strict sense as used by Ponder (1968) and Beu & Maxwell (1990) occurs in temperate Australia and New Zealand. In the western Australian *C. acutinodosa* (Reeve), a small labral tooth is formed at the end of a cord situated slightly abapical to the middle of the last whorl (Vermeij, 1998a, 1999b). In other species of Cominella I have examined, the outer lip is ventrally strongly convex but lacks a labral tooth. Beu & Maxwell (1990) record *Cominella* in New Zealand from the early Miocene (Altonian, = Burdigalian) to the Recent. In Australia it may already have existed by the late Eocene (Tate, 1888; Darragh, 1970).

16. Iosepha

The high-spired buccinid genus *Iosepha* (often misspelled *Josepha*) is known from the late Eocene of the Antarctic Peninsula (Stilwell & Zinsmeister, 1992) and from the late Oligocene (Duntroonian) to Recent of New Zealand, as well as in the Recent fauna of Australia (see Ponder, 1968; Beu & Maxwell, 1990). The Recent southern Australian *I. tasmanica* Tenison-Woods, type of the genus, has a small, medially situated labral tooth, which is formed at a point where the adapical and abapical sectors of the outer lip meet (Vermeij, 1998a, 1999b). A similar projection is found in populations of *I. glandiformis* (Reeve) from northern New Zealand, but it is absent in populations I have examined from the South Island. Iredale's (1940) description of *Cominista norfolkensis*, a species endemic to Norfolk Island that Ponder (1968) assigns to *Iosepha*, indicates that this form may also have a similarly formed labral projection. Other New Zealand species of *Iosepha* I have examined—*I. quoyana* (A. Adams) and *I. virgata* (H. & A. Adams)—have a ventrally convex outer lip but lack a distinct angular projection or tooth. *I. glandiformis* is

known from Pliocene (Nukumaruan) strata in New Zealand (Beu & Maxwell, 1990).

17. Accidenticulabrum

The buccinid genus *Accidenticulabrum* comprises two species, *A. sangiranensis* (Martin) and *A. javanum* (Martin), respectively from the Pliocene and late Miocene of Indonesia. This genus, which I first named *Denticulabrum* (Vermeij, 1999b) which had to be renamed *Accidenticulabrum* because of homonymy (Vermeij, 2000a), has a small labral tooth near the base, formed at the end of a groove (Vermeij, 1999b). The group seems on morphological grounds to be most closely related to *Cominella*, but differs from that genus and from related taxa such as *Iosepha* by having determinate growth (a unique adult outer lip, externally thickened and adapically extended). The tooth is in any case formed differently from the teeth in *Cominella* and *Iosepha* (see Notes 15 and 16).

18. Editharus

Editharus is a distinctive group of ten species of pisaniine buccinids collectively ranging from the early to late Eocene of Europe. It is characterized by a medially situated labral tooth, which is formed where the adapical and abapical sectors of the outer lip meet at an angle (Vermeij, 2001a). In most pisaniines, the edge of the outer lip is convex when viewed from the apertural side, but in *Editharus* the evenly convex profile is replaced by an angular projection. In a comparative study of Paleogene pisaniines, I concluded that *Editharus* may be derived from *Endopachychilus* (late Paleocene to late Eocene), a group resembling *Editharus* in having a determinate outer lip and in features of external and apertural sculpture. Neither genus seems to have left Neogene descendants.

19. Cantharus clade

Three genus-level taxa – *Cantharus*, *Cancellopollia*, and *Pollia*—comprise an early Miocene to Recent clade of 31 fossil and living species belonging to the buccinid subfamily Pisaniinae. With the exception of the Recent West African *Pollia vermeuleni* Knudsen, all species occur in the Indo-West Pacific region. The labral tooth is formed at the end of a groove, which is situated at a nearly medial position in *Pollia* and *Cancellopollia* and a more basal position (but still adapical to at least three spiral cords) in *Cantharus* (see Vermeij & Bouchet, 1998). The tooth is obsolete in the two deep-water species of *Cancellopollia* and in such species of *Pollia* as *P. mollis* (Gould), *P. subcostata* (Krauss), and *P. subrubiginosa* (Smith). In *P. undosa* (Linnaeus), type species of *Pollia*, the tooth is absent in some individuals and populations. The earliest species I have found with a labral tooth in this clade is *Pollia njalindungensis* (Martin) from the early Miocene of Java. It is possible that some late Oligocene species named by Vredenburg (1923) from India and Burma also have a labral tooth, but I have not examined these species, and I cannot tell from the figures or descriptions whether they have a tooth.

The *Cantharus* clade as defined here is part of a larger clade of cantharoid pisaniines that can be traced back to

the early Cretaceous, and which also includes *Editharus* (Note 18), *Gemophos* (Note 20), and *Preangeria* (Note 21), among others. The *Cantharus* clade typically has a parietal rib at the adapical end of the inner lip, unlike most Cretaceous to Eocene and some Neogene and Recent cantharoids (Vermeij, in review). The position of the labral tooth in the *Cantharus* clade differs from that in the other cantharoids and therefore likely evolved independently.

The evolutionary origin of the *Cantharus* clade remains obscure. Species morphologically similar to *Pollia* but lacking the medial labral tooth occur in the Oligocene and Miocene of Europe, in the late Oligocene to Recent of tropical America, and in the Indo–West Pacific. Research in progress indicates that American species of *Gemophos* and related genera with a parietal tooth or rib evolved the latter feature independently of that in the Old World *Cantharus* clade. The most likely sister group of the *Cantharus* clade therefore consists of a small number of Indo–West Pacific species, which belong to *Prodotia* and to *Pollia* in the broad sense.

20. *Gemophos* n. sp.

In striking contrast to the Indo-West Pacific, where 31 species in the *Cantharus* clade have a more or less well developed labral tooth, only one American cantharoid pisaniine buccinid has such a tooth. This species, from the Bermont Formation (early Pleistocene) of Florida, is an undescribed species of the genus *Gemophos*, a late Miocene to Recent group of approximately 16 species from tropical America and one from West Africa. The position of the tooth in the new species is more basal than that in any member of the *Cantharus* clade, although it has a similar mode of formation at the end of a spiral groove.

Vermeij & Bouchet (1998) noted the presence of a labral tooth at the end of a cord in one individual each of three closely related Recent tropical eastern Pacific species that they assigned to *Muricantharus*, but which I here assign to its subjective senior synonym, the pisaniine genus *Hesperisternia*. I observed the tooth in the holotype of *H. panamica* (Hertlein & Strong) (CAS 065978), the holotype of *H. shaskyi* (Berry) (CAS 043930), and a specimen of *H. rehderi* (Berry) (USNM 753042). My examination of 13 additional lots of *H. panamica*, five lots of *H. shaskyi*, and two lots of *H. rehderi* at LACM and SBMNH failed to yield any additional examples, nor have I observed a labral tooth in any other fossil or living species of *Hesperisternia*, a late Oligocene to Recent genus occurring on both coasts of tropical America. I have not included *Hesperisternia* as a labral-tooth-bearing taxon, because the available evidence indicates that the tooth is an inconsistent and rare feature.

21. *Preangeria*

Five described species, collectively ranging from the early Miocene to the Recent in the central Indo–West Pacific region, comprise the highly distinctive buccinid genus *Preangeria*. The group is characterized by a well-developed basal labral tooth, which is located at the end of a groove immediately above the siphonal canal.

Although Beets (1984b) assigned *Preangeria* to the muricid genus *Taurasia*, radular morphology and various shell characters indicate that *Preangeria* is a pisaniine buccinid (Vermeij, 1998d). The position of the labral tooth differs from that in other pisaniines, and thus implies that the tooth of *Preangeria* arose independently from that in other pisaniines. The phylogenetic relationship of *Preangeria* to other buccinids, however, needs further clarification.

22. *'Buccinum' cinis*

The unusual buccinid *'Buccinum' cinis* (Reeve) from the Galápagos Islands and Isla del Coco in the eastern tropical Pacific has a medially situated, small but distinct labral tooth at the end of a groove. Although this species was tentatively assigned to *Caducifer (Monostiolum)* or to *Engina* in the broad sense (Keen, 1971; Cernohorsky, 1975), it belongs to neither of these groups. In common with a few other very peculiar eastern Pacific species, *'B.' cinis* has no known fossil record, and appears not to be closely related to any other species. Keen's (1971) record from Mexico appears to be in error and evidently refers to a true *Monostiolum*.

23. *Janiopsis angulosa* (Fig. 1G–I)

Janiopsis is a taxon of late Paleocene to Pliocene and perhaps Recent pisaniine buccinids. Of the species I have examined, only the type species, *J. angulosa* (Brocchi), has a labral tooth, which is formed medially at the end of a distinct groove (Vermeij, 1998d). This species is known from the late Miocene and Pliocene of the Mediterranean region. Although the tooth forms as in *'Buccinum' cinis* (Note 22) and the *Cantharus* clade (Note 19), unpublished phylogenetic analyses place *Janiopsis* quite far from these and other labral-tooth-bearing pisaniines.

24. *Hebra* clade

A very small, blunt labral tooth occurs at the end of a narrow basal groove below all external sculpture in at least 15 late Miocene to Recent species of Nassariidae from the Indo–West Pacific region (Vermeij 1999b). This tiny tooth is at the abapical end of the terminal outer-lip varix. Cernohorsky (1984) assigned these species to *Hebra* and *Nassarius (Niotha)*. The species of *'Niotha'* strongly resemble *Hebra* not only in the presence of the labral tooth but also in spiral sculpture, which consists of a few prominent, often strongly beaded or spinose cords. I suspect strongly that this group of species comprises a subclade (Vermeij, 1999b) within a larger derived clade of Indo–West Pacific nassariids (Haasl, 2000). It is remarkable that a tooth has not evolved in any other Nassariidae, which is represented by hundreds of fossil and living species from the late Oligocene to the Recent in all tropical to cool-temperate seas (see Cernohorsky, 1984).

The time of appearance of the *Hebra* clade is in doubt. The probable earliest species, *Hebra junghuhni* (Martin), comes from a Miocene locality in Java whose precise location and age are unknown (Cernohorsky, 1984). The two known specimens are juvenile, and their assignment to *Hebra* is uncertain (see Cernohorsky,

1984). I tentatively consider the *Hebra* clade as having appeared during the late Miocene, but definite members are known only from the Pliocene onward.

Many Indo–West Pacific nassariids that have been assigned to such taxa as *Alectrion*, *Nassarius*, *Niotha*, *Telasco*, and *Zeuxis* (Cernohorsky, 1984) have several sharp spines or denticles along part or all of the edge of the outer lip. In *Nassarius* (*Zeuxis*) *olivaceus* (Bruguière), type of *Zeuxis*, and in the very similar *N. (Z.) micans* (A. Adams), one of the denticles near the abapical end is typically larger than the others, and therefore resembles a labral tooth. I have not counted these species as having a labral tooth.

25. Columbarium

As restricted by Darragh (1969), *Columbarium* is characterized by a fusiform shell, very long anterior siphonal canal, raised erect inner lip, rounded aperture, scaly or spinose spiral keels, and a small labral tooth formed as an extension of the most abapical keel. I know of 24 species and subspecies, collectively ranging from the late Cretaceous (Maastrichtian) to the Recent (see Darragh, 1969, 1987). Species in the Recent fauna occur in deep waters around the fringes of the tropical Indo–West Pacific region, especially around Japan, Taiwan, Australia, and southern Africa. During the Paleocene, the genus was also represented in Europe and the southeastern United States. The earliest species from which a labral tooth has been definitively reported is *C. rugatoides* Darragh from the Pebble Point Formation (late Paleocene) of Australia (see Darragh, 1997). My examination of *C. heberti* (Briart & Cornet) from the Calcaire de Mons (early Paleocene) of Belgium (IRSNB 5453) failed to confirm the presence of a labral tooth, but I have not examined Maastrichtian material of this species (see Darragh, 1969). I tentatively consider the Maastrichtian rather than the late Paleocene as the time of first appearance of the labral tooth in *Columbarium*.

26. Ceratoxancus

Kantor & Bouchet (1997) have comprehensively reviewed the six known Recent species of this Indo–West Pacific genus of ptychatractine turbinellid gastropods. A labral tooth formed at the end of a groove on the base occurs in *C. teramachii* Kuroda (type of the genus), *C. elongatus* Sakurai, and *C. leios* Kantor & Bouchet. The tooth in *C. teramachii* can be very long; a specimen at MNHN 28.8 mm long has a 4.2 mm long spine, separated from the adapical sector of the outer lip by a deep sinus. Anatomically, *Ceratoxancus* is very similar to *Latiromitra*, a Pliocene to Recent genus from the tropical Atlantic and Indo-West Pacific (Bouchet & Kantor, 2000). It is likely that *Ceratoxancus* is derived as a Pacific group within *Latiromitra*. The absence of fossils is surprising given that deep-water groups such as this are well represented in the Neogene Indo–West Pacific fossil record. For this reason I suspect that the labral tooth of some species of *Ceratoxancus* is geologically recent in origin, probably post-Pliocene.

27. Attiliosa gibsonsmithi

The early Oligocene to Recent taxon *Attiliosa* comprises a possibly heterogeneous group of plesiomorphic muricine muricids characterized by a fusiform, axially ribbed shell, by denticles on the inner side of the outer lip, basal ridges on the inner lip, and the absence of a parietal rib at the adapical end of the inner lip. Vokes (1999) has comprehensively reviewed the species of *Attiliosa*. One species (*A. gibsonsmithi* Vokes) in the typical group of *Attiliosa* (Vokes's Group 2), known from the Mataruca Member of the Caujarao Formation (late Miocene) of Venezuela, has a labral tooth formed at the end of a spiral cord on the upper end of the basal sector of the last whorl. Members of Vokes's Group 2 extend back to the early Oligocene.

I tentatively interpret the labral tooth of *Attiliosa gibsonsmithi* as having been derived independently from that in *Panamurex* (see Note 29). Vokes (1999) maintains that *A. gibsonsmithi* may have descended from European species resembling the late Oligocene to early Miocene *A. sacyi* (Cossmann & Peyrot) and *A. villai* (Michelotti). All three species lack spines on the axial ribs. The labral-tooth-bearing species of *Panamurex* generally have spines on the varices, a condition perhaps inherited from spiny Oligocene ancestors.

28. Acantholabia

The muricine muricid genus *Acantholabia* consists of two species from Florida, *A. sarasotaensis* Petuch from the middle Pinecrest Beds (mid-Pliocene) and *A. floridana* Olsson & Harbison from the Caloosahatcheee Formation (late Pliocene). Both species are characterized by a large, bifid or trifid labral tooth formed continuously at the growing end of a very broad spiral cord situated above the concave base of the last whorl.

Vokes (1992b) is probably correct in suggesting that *Acantholabia* is derived from *Calotrophon*, a New World genus without a labral tooth. Like *Acantholabia*, typical *Calotrophon* (late Miocene to Recent) is characterized by axial ribs not differentiated into varices and lacking spines. The two genera also have in common indeterminate growth, a smooth inner lip, and the absence of a parietal tooth or rib. *Calotrophon* itself probably arose during or after the early Miocene from ancestors resembling the early Miocene Floridian *Panamurex mauryae* (Vokes), which like *Calotrophon* lacks varices, spines, and a labral tooth. Like other species of *Panamurex* and *Attiliosa*, however, *P. mauryae* has ridges on the abapical sector of the inner lip. The loss of these ridges therefore sets *Calotrophon* and *Acantholabia* apart from *Panamurex* and *Attiliosa*. Species of *Attiliosa* and *Panamurex* in which a labral tooth occurs (see Notes 27 and 29) differ from *Acantholabia* in that the tooth forms discontinuously, at the apertural edge of each successive axial rib, instead of continuously as in *Acantholabia*. The available evidence therefore supports the interpretation that the tooth of *Acantholabia* evolved independently from that in *Panamurex* and *Attiliosa*.

29. Panamurex

The name *Panamurex* has been used for an early Oligocene to Recent group of small, plesiomorphic muricines characterized by indeterminate growth, undifferentiated axial ribs, ridges on the abapical sector of the inner lip, and the absence of a parietal rib at the adapical end of the inner lip. The typical group of *Panamurex*, comprising five species collectively ranging

from the early Miocene to the middle Pliocene, is char-
acterized by a labral tooth formed discontinuously as
an extension of a spiral cord on the adapertural side of
successive axial ribs (Vokes, 1992b). The tooth-bearing
cord is separated from the concave base of the last whorl
by a smaller cord, and is therefore not homologous to
the tooth-bearing cord of *Acantholabia* (see Note 28).
Tooth-bearing species of *Panamurex* are *P. alaquaensis*
(Mansfield) and *A. clarksvillensis* (Mansfield) from the
middle Pliocene of Florida, *P. gatunensis* (Brown &
Pilsbry) (type of the genus) from the Gatun Formation
(late Miocene) of Panamá, *P. laccapoia* (Gardner) from
the Chipola Formation (early Miocene) of Florida, and
P. rutschi (Vokes) from the Punta Gavilan Formation
(early Pliocene) of Venezuela (see Vokes, 1992b). A likely
sixth species is a small muricid described as *Steph-
anosalpinx candelabra* by Petuch (1988b) from the Chop-
tank Formation (middle Miocene) of Maryland. My
examination of the single known specimen (UF 21452)
indicates that this species differs from typical *Pana-
murex* by having the tooth situated on a cord just above
the concave base instead of one cord removed from it.
It also has more numerous cords on the last whorl, and
the inner side of the outer lip is smooth instead of
ridged or denticulate. It is possible that the specimen
in question is juvenile. G. Herbert (pers. comm., March,
2000) considers *S. candelabra* a species of *Panamurex*,
a group to which Petuch (1988b) did not originally
compare his species.

Panamurex and *Attiliosa* may have shared a common
ancestor in the early Oligocene and have been derived
from ancestors assigned to *Poirieria*, which lack inner-
lip ridges (Vokes, 1992b). Most tooth-bearing species of
Panamurex, including *P. candelabra*, have a row of
spines on the axial ribs at the shoulder angulation, and
differ in this respect from the tooth-bearing *Attiliosa
gibsonsmithi* (Note 27). I therefore consider the ac-
quisition of the tooth in *Panamurex* to be independent
of that in *Attiliosa*.

30. Murex

All species of *Murex*, as restricted by Ponder and Vokes
(1988), have a labral tooth situated slightly below the
middle of the outer lip at the end of a groove. The 33
species collectively range from the early Miocene to the
Recent, and are all from the tropical Indo–West Pacific
region to warm-temperate Japan (Ponder & Vokes, 1988;
Nakagawa, 1998). *Murex* is characterized by a highly
elongate, usually spinose siphonal canal; three varices
per whorl at later growth stages, all with three or more
simple (that is, unbranched) spines; a smooth-edged
inner lip; and the absence of a parietal rib at the adapical
end of the inner lip. The species tend to live in sandy
or muddy environments.

Murex is one of several muricine taxa with a greatly
elongated, narrowly open siphonal canal. Genus-level
taxa of this kind include the multivaricate *Bolinus* (late
Oligocene to Recent, eastern Atlantic) and the tri-
varicate *Siratus* (early Oligocene to Recent, western
Atlantic, and Recent, Indo–West Pacific), *Vokesimurex*
(early Miocene to Recent, tropical America and Indo–
West Pacific), *Promurex* (late Oligocene to Pliocene of
Europe, Pliocene to Recent of the Indo–West Pacific),

and *Haustellum* (Recent of the Indo–West Pacific, pos-
sibly late Miocene to early Pliocene of the western
Atlantic) (see Ponder & Vokes, 1988; Vokes, 1990;
Petuch, 1994; Houart, 1999). *Murex* shares with early
members of *Siratus* and *Promurex* the absence of a
parietal tooth at the adapical end of the inner lip, as
well as the presence of spines on the main part of the
last whorl and the siphonal canal. Spines on the canal
also occur in many species of *Vokesimurex*. Ponder &
Vokes (1988) suggested that *Murex* is derived from *Pro-
murex*, which in turn may have been derived from a
stem-group *Bolinus*. Given that *Murex* is restricted to
the Indo–West Pacific region, it is reasonable that its
sister group also originated there. The sister group
of *Murex* may comprise Indo–West Pacific species of
Promurex, *Vokesimurex*, and *Haustellum*. The species-
level taxonomy of Ponder & Vokes (1988) and Houart
(1999) indicates that this sister group contains at least
33 species, making *Murex* and its sister group of ap-
proximately equal diversity. The entire long-canal group
of muricines apparently originated in the Americas dur-
ing or before the early Oligocene, and spread to the
eastern Atlantic by the late Oligocene before invading
the Indo–West Pacific.

31. Hexaplex clade

Two muricine genera in the Recent fauna of the Indo–
West Pacific collectively comprising 13 species, are char-
acterized by a medially situated labral tooth at the end
of a groove. As restricted by Houart (1992), *Chicoreus*
in the strict sense comprises seven Recent Indo–West
Pacific species, typified by the widespread *C. ramosus*
(Linnaeus), the largest known muricid (height 327 mm;
see Houart, 1992). One species, *C. asianus* Kuroda, is
also known as a Pliocene fossil. *Hexaplex*, as restricted
here, consists of at least nine species, of which six in
the Indo–West Pacific have a labral tooth: the Recent
H. bozzadamii Franchi from Somalia, *H. cichoreum*
(Gmelin) (the large and elaborately spinose type species)
from Indonesia and the Philippines, *H. conatus*
(McMichael) from northwestern Australia, *H. ku-
esterianus* (Tapparone-Canefri) from the northwestern
Indian Ocean, and *H. rileyi* (d'Attilio & Myers) from the
Persian Gulf; and the early to late Miocene *H. junghuhni*
(Martin) from Java. *H. angularis* (Lamarck) from the
early Pleistocene to Recent of West Africa (Rosso, 1974;
Brébion, 1979) sometimes also has a labral tooth (Hou-
art, 1996). Morphologically similar species of *Hexaplex*
without a labral tooth include the Recent *H. stainforthi*
(Reeve) from northwestern Australia and the Miocene *H.
ardjunoi* (Beets) and *H. grooti* (Jenkins) from Indonesia.
These species are also very similar to members of the
early Miocene to Recent Mediterranean and West Af-
rican genus *Trunculariopsis*, all of whose species lack a
labral tooth.

The labral tooth of *Chicoreus* and *Hexaplex* appears
to be homologous, both in position and form. It is situated
at the end of a deep spiral groove, which separates the
two abapical primary spines of the last whorl from the
three (sometimes four) adapical primary spines. The
tooth is the adapical member of a pair of crenulations
at the edge of the outer lip at this position.

The homologous labral tooth and many other sim-
ilarities in sculpture between *Hexaplex* and *Chicoreus*

indicate that these two taxa, in their restricted sense, comprise a single clade in which the labral tooth evolved once. Both taxa are characterized by a smooth-edged inner lip, absence of an adapical notch on the outer lip, similar number of foliose (branched) primary spines on the varices, and the presence of two or three spines on the siphonal canal. *Chicoreus* differs from *Hexaplex* only by the expression of axial sculpture. There are usually three varices on the last whorl in *Chicoreus*, although *C. bundharmai* Houart and some *C. virgineus* (Röding) have four; and adjacent varices are separated by one to three axial nodes. *Hexaplex* has five to nine varices and generally lacks intervarical nodes, although the latter are sometimes expressed in *H. grooti*. The single origin of the labral tooth and the much earlier appearance of the tooth in *Hexaplex* (early Miocene) than in *Chicoreus* (Pliocene) would require that the tooth arose in a multivaricate ancestor resembling *H. junghuhni*, and that the trivaricate condition of *Chicoreus* is a derived character state in this clade. Evidence from the ontogeny of axial sculpture supports this interpretation. In most trivaricate muricines and ocenebrines, the early whorls of the teleoconch bear six or more axial ribs or lamellae that are not differentiated into varices and intervarical nodes. Differentiation into three varices and one or more intervarical ribs or nodes occurs on later whorls (see e.g. Vokes, 1968; Ponder & Vokes, 1988; Houart, 1996; Vermeij & Vokes, 1997; Vermeij & Houart, 1999). In *Pterorytis (Microrhytis)* (see Note 39) the multivaricate condition has been neotenically retained in the adult.

An alternative hypothesis, implicitly favoured by most previous authors as reflected in their taxonomy of the group (Vokes, 1967, 1990; Merle, 1989, 1994; Houart, 1992), is that the trivaricate condition of *Chicoreus* in the strict sense is inherited from trivaricate muricines without a labral tooth. These toothless trivaricate forms belong to such taxa as *Pterymarchia, Pterynotus, Chicomurex, Naquetia, Chicopinnatus, Rhizophorimurex*, and *Triplex*. The last three taxa, along with *Chicoreus* in the narrowest sense, are usually considered subgenera of a broadly defined genus *Chicoreus* (Houart, 1992). The trivaricate *Siratus* is typically also included in this broad concept of *Chicoreus*, but seems more appropriately to be placed among the long-canal muricines related to *Murex* (30). Species of *Chicoreus* in the broad sense extend back to the late Oligocene. If developed, spines in this group are branched. Trivaricate muricids without spines or with simple, unbranched spines first appeared during the early Paleocene, and have been assigned to *Pterynotus* (Vokes, 1992b). If tooth-bearing *Chicoreus* is derived from *Triplex* or some other trivaricate muricine, then its labral tooth evolved independently of that of *Hexaplex*.

Because of uncertainties about phylogenetic relationships among toothless species of *Hexaplex, Triplex*, and related taxa, delineation of the sister group of the tooth-bearing *Hexaplex* clade is difficult. Aperture size in the *Hexaplex* clade is relatively large, in contrast to that of nearly all Indo–West Pacific species of *Triplex, Rhizophorimurex*, and related taxa classified by Houart (1992) in *Chicoreus* in the broad sense. This makes me suspect that the sister group of the tooth-bearing *Hexaplex* clade may consist only of species of *Hexaplex* without a labral tooth.

32. *Muricanthus*

Three living species of *Muricanthus*—*M. nigritus* (Philippi) from northwestern Mexico, *M. ambiguus* (Reeve) with a broad tropical eastern Pacific distribution, and *M. radix* (Gmelin) from the Gulf of Panamá—have a short labral tooth. One of these species, *M. ambiguus*, is also known from the Esmeraldas beds of the Onzole Formation (early Pliocene) of Ecuador (Vokes, 1988). As in *Hexaplex* and *Chicoreus* (Note 31), the labral tooth of *Muricanthus* is situated medially at the end of a spiral groove. Two primary spines lie abapical to it, as in *Hexaplex* and *Chicoreus*, and five to six primary spines are situated adapical to it, including one or two spines near the suture. Unlike the tooth of *Hexaplex* and *Chicoreus*, that of *Muricanthus* is the central member of a group of three crenulations on the edge of the outer lip; in the former, it is the abapical member of a pair of crenulations.

Vokes (1992a) suggested that *Muricanthus* of the eastern Pacific evolved from an eastern Atlantic ancestor similar to or identical with the Pleistocene to Recent West African *Hexaplex angularis*, a species which sometimes has a labral tooth (see Note 31). According to this interpretation, the labral tooth of *Muricanthus* would have been inherited from that in the *Hexaplex* clade. Differences in the formation of the labral tooth and other features of morphology, however, support the alternative interpretation that the labral tooth of *Muricanthus* evolved independently of that in *Hexaplex* and *Chicoreus*. In *Muricanthus*, the outer lip forms an adapical notch where it joins the preceding whorl. This notch, which corresponds to a sutural spine, is absent in *Hexaplex* and *Chicoreus*, as well as in such related taxa as *Trunculariopsis* and *Triplex*, in which a labral tooth is absent.

The likely sister group of *Muricanthus* is a clade of four species that I would assign to *Muricanthus* in the broad sense: *M. fulvescens* (Sowerby) from the middle Pliocene to Recent of the southeastern United States, *M. princeps* (Broderip) from the eastern Pacific, *M. hertweckorum* Petuch from the middle Pliocene Pinecrest beds of Florida and the early Pliocene Esmeraldas beds of Ecuador (Vokes, 1988), and *M. jameshoubricki* Petuch from the uppermost Pinecrest or lowermost Caloosahatchee Formation of Florida. These species lack a labral tooth, but resemble tooth-bearing *Muricanthus* in having a smooth, adherent inner lip.

M. hertweckorum has a sutural spine, as do tooth-bearing species of *Muricanthus*, but it lacks the latter's adapical notch. The adapical notch of *Muricanthus* is convergent with that of the American muricine genus *Phyllonotus*, and may be associated with the ability of muricids of these two genera to crawl on or burrow partially into sand. The *M. fulvescens* clade appears today to be restricted to hard substrata. Vokes (1968, 1990) may be correct in suggesting that the *M. fulvescens* clade is derived from an invader related to *Trunculariopsis duplex* (Röding) from West Africa.

33. *Ocinebrina* clade

Many ocenebrine muricids have a labral tooth situated at the end of a spiral cord on the abapical sector of the last whorl. The earliest of these are two species from the

Haywood Landing Member of the Belgrade Formation of North Carolina, which appears to be of Chattian (late Oligocene) age (Denison *et al.*, 1993). These are *Fenolignum umbilicatum* Vermeij & Vokes and *Pteropurpura* (*Odontopurpura*) *festivoidea* (Vokes) (see Vermeij & Vokes, 1997). Species of *Ocinebrina* with a labral tooth include *O. avitensis* (Cossmann & Peyrot) from the earliest Miocene (Aquitanian) of France, *O. francesae* Gibson-Smith & Gibson-Smith in Vermeij & Vokes from the Cantaure Formation (early Miocene: Burdigalian) of Venezuela, *O. bicaudata* (Borson) from the middle Miocene (Langhian) of southern Europe, *O. concerpta* (Bellardi) and *O. scalaris* (Brocchi) from the Pliocene of Italy, and the Recent type species, *O. aciculata* (Lamarck) from the Recent fauna of western Europe, the Mediterranean, and northwestern Africa. All members of the genus *Ceratostoma* – 11 North Pacific species (early Miocene to Recent) and one from the Pliocene of Ecuador—have a well developed tooth or spine (for species accounts see Vermeij & Vokes, 1997; Amano & Vermeij, 1998b; Ozawa, Tanaka & Tomida, 1998). I initially interpreted the labral tooth of *Ceratostoma* as arising from a groove near the base of the last whorl, because the abaxial face of the tooth consistently bears a groove (Vermeij & Vokes, 1997; Vermeij, 1998c; Amano & Vermeij, 1998b). Closer examination, however, reveals that the tooth forms discontinuously on the adapertural faces of successive varices as an extension of a minor cord (Marko & Vermeij, 1999). Finally, two species of *Kestocenebra* collectively ranging from the Aquitanian to Tortonian (early to late Miocene) in Europe have a labral tooth formed at the end of a prominent cord located above the base (Vermeij, 1998c).

In order to ascertain how often the labral tooth in these genera arose independently, Marko & Vermeij (1999) conducted phylogenetic analyses of partial DNA sequences of two mitochondrial genes, 18S rRNA and cytochrome oxidase I, in several eastern Pacific species. The topology of the resulting phylogenetic trees depends strongly on the choice of outgroups and on assumptions about whether the labral tooth, once evolved, can be lost subsequently. When the tree is rooted with eastern Pacific rapanine muricid outgroups (*Plicopurpura* and *Stramonita*), there is a basal node separating the South African '*Nucella*' *dubia* (Krauss) from all eastern Pacific ocenebrines investigated: *Ceratostoma foliatum* (Gmelin), several species of *Nucella* (without labral tooth), *Acanthina unicornis* (Bruguière), three species of *Acanthinucella* (with tooth), *Ocinebrina circumtexta* (Stearns) (without tooth), and two species of *Mexacanthina*. The eastern Pacific clade consists of two subclades, one consisting of *Acanthina* + *Acanthinucella* (see Note 44), the other consisting of *Ceratostoma* and its sister group *Ocinebrina* + *Nucella* + *Mexacanthina*. Strictly interpreted, this evolutionary tree implies that a labral tooth evolved three times among the taxa considered: once in *Ceratostoma* (at the end of a cord), and twice at the end of a groove (in *Acanthina* + *Acanthinucella* and in *Mexacanthina*). The node connecting the *Acanthina* clade to the large *Ceratostoma* clade may represent a condition in which the ancestor to these clades lacked a labral tooth. With the tree rooted in the *Acanthina* clade, the three acquisitions are retained, although in this case *Mexacanthina* (tooth

formed at groove) and *Ceratostoma* (tooth formed at cord) form sister groups, which together are sister to the clade *Ocinebrina* + *Nucella*. In a rooting with toothless eastern Pacific *Ocinebrina*, *Nucella* forms a sister group to a clade including *Mexacanthina*, *Ceratostoma*, *Acanthina* + *Acanthinucella*, and the South African '*Nucella*' *dubia*. An interpretation of this tree allows the labral tooth to have evolved three times among the taxa studied, and a potential fourth time if tooth-bearing Atlantic *Ocinebrina* gave rise to the toothless eastern Pacific members of that genus.

The stratigraphic and geographical data provided by the fossil record can inform scenarios for the evolution of ocenebrines and their characteristics. The earliest definite species in the *Ocinebrina* group are of early Oligocene age from Europe (Marko & Vermeij, 1999; Vermeij & Houart, 1999). It was not until the late Oligocene when the first labral tooth, formed at the end of a cord, appeared in the North American *Fenolignum* and *Odontopurpura*. Tooth-bearing *Ocinebrina* appeared in Europe during the earliest Miocene. There is an excellent record of Oligocene ocenebrines and other muricids in Europe, where diversity of muricids was consistently higher than in eastern North America (Vermeij, 1996a; see also Table 2). The literal reading of the fossil record, which indicates a western Atlantic first appearance of a cord-based tooth among ocenebrines during the late Oligocene, may therefore reflect reality. The identity and characters of the ancestor of tooth-bearing ocenebrines of the *Fenolignum–Odontopurpura–Ocinebrina–Ceratostoma* clade remain unknown, however.

The most plausible scenario, consistent with the molecular data and the fossil record, is that a toothless ocenebrine stem group gave rise in the Atlantic during the late Oligocene to a clade (the *Ocinebrina* clade) in which the tooth forms at the end of a cord. The tooth-bearing *Ocinebrina* clade spread eastward across the Atlantic to Europe and westward to the eastern Pacific during the earliest Miocene. The stem group without a labral tooth also spread to the eastern Pacific, perhaps by several routes, where it gave rise to clades in which the tooth forms at the end of a groove. According to this scenario, the labral tooth of *Ocinebrina*, *Fenolignum*, *Odontopurpura*, *Kestocenebra*, and *Ceratostoma* evolved only once. Under this hypothesis, I predict that there is less divergence between *Ceratostoma* and tooth-bearing species of *Ocinebrina* than there is between *Ceratostoma* and toothless eastern Pacific *Ocinebrina*. How tooth-bearing Atlantic *Ocinebrina* are related to Atlantic species of that genus and of other ocenebrine genera without a tooth (*Africanella*, *Inermicosta*, *Heteropurpura*, *Vaughtia*, and many species of *Hadriania*, *Jaton*, and *Ocinebrina*) remains to be determined. As discussed further in Note 36, the labral tooth of *Jaton decussatus*, which forms at the end of a cord in a position homologous to that in the *Ocinebrina* clade, evidently evolved independently. The same is true for two species of *Hadriania* (see Note 35) and for *Inermicosta colorata* (Note 34).

The hypothesis that a cord-associated tooth evolved only once in the *Ocinebrina* clade contrasts with Amano & Vermeij's (1998b) earlier hypothesis that *Ceratostoma* (here interpreted as a member of the *Ocinebrina* clade)

arose from an Atlantic ancestor similar to or identical with *Microrhytis*. This latter hypothesis was based on the assertion that *Ceratostoma*'s tooth forms at the end of a groove, as it does in *Microrhytis*. Amano & Vermeij (1998b) argued that the tooth of *Ceratostoma* evolved in a trivaricate ancestor. The hypothesis I favour here is that the trivaricate condition of *Ceratostoma* evolved independently of that in *Microrhytis*. It is also possible that *Ceratostoma* evolved its tooth from a trivaricate ancestor that, unlike *Microrhytis*, lacked a tooth. Appropriate trivaricate ocenebrines are known from the late Oligocene of North Carolina (*Argyrobessa kellumi* (Richards)) and Europe (species of *Inermicosta* and *Jaton*) (see Vermeij & Vokes, 1997; Vermeij & Houart, 1996, 1999).

The scope of the sister group of the *Ocinebrina* clade is uncertain. It may comprise most fossil and living northern-hemisphere ocenebrines apart from *Acanthinucella* and *Nucella*, or it may be a much more restricted group. Resolution must await further comparative studies of anatomy and DNA sequences and additional fossil discoveries.

34. Inermicosta colorata

The small ocenebrine muricid *Inermicosta colorata* (Degrange-Touzin) from the middle Miocene (Langhian) of southwestern France has a blunt labral tooth formed at the end of a basal groove (Vermeij & Houart, 1999). The tooth is unusual in that, as in some members of the *Acanthina* clade, it affects only the adaxial (inner) side of the outer lip, leaving the abaxial or outer margin unaffected. The specimen I have seen at MNHN from Orthez has seven rounded axial ribs extending abapically to the siphonal canal, which is ventrally open. There is a very slight parietal thickening at the adapical end of the inner lip. Vermeij & Houart (1999) assigned this species to *Inermicosta* with some hesitation. The living type species of that genus, *I. inermicosta* (Vokes) from tropical West Africa, has three varices, adjacent ones separated by an intervarical node, and a ventrally sealed canal. Neither it nor several late Oligocene and early Miocene species assigned tentatively by Vermeij & Houart (1999) to *Inermicosta* has a labral tooth. I provisionally consider the acquisition of the tooth in *I. colorata* to be independent of that in other ocenebrines. Further study may reveal additional tooth-bearing ocenebrines in Europe and may clarify the interrelationships of *I. colorata* and the numerous other Miocene and Pliocene species that previous authors have dumped in such genera as *Ocenebra*, *Ocinebrina*, *Hadriania*, and *Urosalpinx*.

35. Hadriania

In the Pliocene (Astian) of Italy, *Hadriania funiculosa* (Bronn) has a small but distinct labral tooth formed at the end of a cord. My examination of specimens at IRSNB shows that the species otherwise closely resembles the Recent Mediterranean type species of *Hadriania*, *H. provencalis* (Risso), which lacks a labral tooth. Both species have a relatively high spire, a single terminal varix, a ventrally sealed canal, and a deep adapical notch on the outer lip. Earlier (Oligocene and Miocene)

species of *Hadriania* resemble *H. provencalis* in lacking a labral tooth.

A second possible tooth-bearing species of *Hadriania* is the small warm-temperate South African muricid usually known as *Ocenebra sperata* (Cossmann). Like European *Hadriania*, this species has a high spire and deep adapical notch, but it differs in having the siphonal canal ventrally open instead of sealed. The cord-based tooth of *O. sperata* and *H. funiculosa* is here interpreted as having arisen only once from a tooth-less species of *Hadriania*.

36. Jaton decussatus

A labral tooth situated at the end of a cord just above the basal constriction of the last whorl characterizes *Jaton decussatus* (Gmelin), an ocenebrine muricid known from the late Pleistocene and Recent of West Africa (Vermeij & Houart, 1996). The position of the tooth is similar to that in *Ocinebrina*, and the ventrally sealed siphonal canal further indicates that *Jaton* is a likely member of the *Ocinebrina* clade. The fossil record, however, indicates that the tooth of *J. decussatus* evolved independently from that in other members of the *Ocinebrina* clade. *Jaton*, which is characterized by a trivaricate last whorl and by a unique pattern of two divergent upper spiral cords on each intervarical node, can be traced back to the late Oligocene of southwestern France, but only *J. decussatus*, which first appears in the Harounian stage (late Pleistocene) of Morocco (Brébion, 1979) has a labral tooth (Vermeij & Houart, 1996).

37. 'Ocenebra' katayamai

An unresolved problem in the taxonomy and phylogeny of ocenebrine muricids is the position of the Japanese *Ocenebra katayamai*, described by Matsubara (1996) from the early Miocene Yotsuyaku Formation. Though not recognized in Matsubara's original description, *O. katayamai* has a small labral tooth at the end of a cord (Amano & Vermeij, 1998a). Unlike the condition in the *Ocinebrina* clade, the siphonal canal is ventrally open instead of sealed. Axial sculpture is not differentiated into varices, a condition also found in *Ocinebrina* and various other plesiomorphic ocenebrines. I provisionally consider the tooth of *O. katayamai* as having evolved independently from that in other ocenebrines. *Ocinebrellus* (Note 38), also known from the early Miocene of Japan, has a labral tooth formed at the end of a groove. *Ocenebra* is a European genus known from the Miocene to the Recent, characterized by the absence of a labral tooth.

38. Ocinebrellus

The genus *Ocinebrellus* consists of six species collectively ranging from the late early Miocene to the Recent in the northwestern Pacific. Three species—*O. aduncus* (Sowerby) from the Pliocene to Recent, *O. inornatus* (Récluz) from the late Miocene to Recent, and *O. nagaokai* Matsubara & Amano from the late early Miocene—have a short labral tooth formed at the end of a groove situated below all primary cords. The tooth occurs only during later growth stages, and is not developed

in some populations of *O. aduncus* and *O. inornatus* (see Amano & Vermeij, 1998a). Three other species—*O. lumarius* (Yokoyama) from the Pleistocene and Recent, *O. ogasawarai* Amano & Vermeij from the Pliocene, and *O. protoaduncus* (Hatai & Kotaka) from the late middle Miocene, lack a labral tooth (Amano & Vermeij, 1998a). That this absence of a tooth represents a secondary loss is suggested by the observation that the oldest species of *Ocinebrellus*, *O. nagaokai*, has a labral tooth and is morphologically intermediate between (and could be ancestral to) the later *O. aduncus* and *O. inornatus* stocks (Matsubara & Amano, 2000). Both of the latter stocks comprise species with and without a labral tooth.

The origins of *Ocinebrellus* remain obscure. The earliest species, *O. nagaokai*, occurred in a warm, shallow-water environment and therefore likely reached Japan from the south and west rather than from the east across the North Pacific. The position and mode of formation of the labral tooth in *Ocinebrellus* are like those in the *Microrhytis* clade, from which *Ocinebrellus* differs by having a multivaricate or simply axially ribbed shell instead of a primitively trivaricate one, and by lacking the adapical keel connecting adjacent varices. If the *Microrhytis* clade was already present in southern Europe during the early Miocene, for which no evidence exists at present, *Ocinebrellus* could be derived from an eastward-migrating member of that mainly tropical American clade.

It is perhaps more likely, however, that *Ocinebrellus* is derived from a more plesiomorphic ocenebrine such as *Pterynopsis* that lacked a labral tooth. In that case, the tooth would have evolved independently of that in the *Microrhytis* clade. *Pterynopsis* occurred in the late Oligocene of both northern and southern Europe and persisted in Europe until the Pliocene (see Vokes, 1972; Lozouet, 1999).

39. Muregina

As I understand the group at present, *Muregina* consists of three ocenebrine muricid species: *M. ecuadoria* (Olsson) from the Esmeraldas beds (Pliocene) of Ecuador and *M. kuscheli* (Fleming) from the early Miocene of Chile, both without a labral tooth, and the Recent tropical eastern Pacific *M. lugubris* (Broderip), which has a labral tooth formed at the end of a groove (Vermeij, 1998c). This record indicates that the acquisition of the tooth occurred independently from that in other ocenebrines. With its undifferentiated axial sculpture, *Muregina* resembles *Ocinebrellus*, but the pattern of its spiral sculpture is different. Given the geographic disparity between *Ocinebrellus* and *Muregina*, and the absence in older species of *Muregina* of a labral tooth, I suggest that the tooth of *Muregina* and *Ocinebrellus* arose independently.

40. Microrhytis clade

Many varix-bearing ocenebrine muricids have a sharp labral tooth formed discontinuously on the adapertural faces of successive varices at the end of an abapical groove or depression. These include four species of *Microrhytis*, collectively ranging from the early Miocene (Burdigalian) to late Miocene of tropical America; and three species of *Pterorytis*, two collectively from the late

Miocene to late Pliocene of the eastern United States and one Recent species from the tropical eastern Pacific (Vermeij & Vokes, 1997). The Pliocene South African *Namamurex odontostoma* Carrington and Kensley also belongs in this group. *Murex genei* Bellardi and Michelotti from the middle Miocene of southern Europe, previously assigned to *Ceratostoma* (Vermeij, 1998c; Amano & Vermeij, 1998b), has the tooth formed at the end of a groove, and may therefore instead belong to *Microrhytis*. This may also be the case with *Murex virginiae* Maury, an early Miocene species from the Chipola Formation of Florida, which was also previously assigned to *Ceratostoma* (Vermeij & Vokes, 1997; Amano & Vermeij, 1998b). Species of *Microrhytis* and *Namamurex* have three varices on the last whorl and one intervarical node between adjacent varices, whereas *Pterorytis* has four to nine varices without intervening nodes. All members of the group are united by the presence of a strong continuous keel connecting adjacent varices at the shoulder angulation, and by lamellar axial ornamentation on the early teleoconch whorls. These features are absent in trivaricate species of *Ceratostoma* and *Jaton*, in which the labral tooth forms at the end of a cord, as well as in most other ocenebrine genera.

The taxon most similar to the *Microrhytis* clade is *Pterynopsis*, whose nine species collectively range from the late Oligocene to the middle Pliocene in Europe (see Vokes, 1972; Lozouet, 1999). Most species of *Pterynopsis* have three varices on the last whorl and a distinct almost keel-like shoulder angulation. Spiral sculpture is subdued, as in most species of the *Microrhytis* clade, but there is no labral tooth. The early teleoconch whorls are sculptured with axial lamellae (see A. W. Janssen, 1984). I suggest that *Pterynopsis* may be the stem group of the *Microrhytis* clade. Whether the labral tooth of *Microrhytis* evolved in the eastern or western Atlantic is not clear. If the proposed sister-group relationship is correct, however, westward invasion from Europe to North America no later than the early Miocene (Burdigalian) would be required. Additional fossil discoveries may shed further light on evolutionary events in this group of ocenebrines.

Montanaro (1935) described a labral tooth in the late Miocene (Tortonian) species he identified as *Ocenebra (Pterorytis) jani* (Döderlein) from Montegibbio, in northern Italy. This species, which also occurs in the Italian Pliocene, was validly introduced as *Murex jani* Döderlein by Bellardi (1873). Vokes (1971) and Chirli (2000) assign it to the muricine genus *Dermomurex*. There is no compelling evidence for a labral tooth in this species, either in the figures of Montanaro (1935) and Chirli (2000) or in Chirli's detailed description. I therefore reject Montanaro's assertion that *Murex jani* has a labral tooth, and I accept assignment of the species to *Dermomurex*.

41. Mariasalpinx

As noted by Petuch (1988a) in his original description of *Mariasalpinx emilyae* from the St. Marys Formation (late Miocene: Tortonian) of Maryland, this species is characterized by the presence of a blunt labral tooth at the end of a thick, enlarged spiral cord situated just above the basal constriction of the last whorl. The ten axial ribs of the last whorl end abapically at this cord.

Petuch (1988a) may be correct in regarding *Mariasalpinx* as a short-lived, tooth-bearing derivative of *Urosalpinx*, a member of a diverse eastern North American clade that may itself be derived from a toothless clade of *Ocinebrina*. Petuch (1993) mentions a second, undescribed species from the slightly older Little Cove Point Member of the St. Marys Formation. Although some specimens of this form in the collections of the Florida Museum of Natural History have an enlarged cord, there is no strong evidence of a labral tooth in this second species (G. Herbert, pers. comm., February, 2000).

43. Hanetia

Costa (1993) reports that the Recent Brazilian ocenebrine muricid *Hanetia haneti* (Petit de la Saussaye) sometimes has a small labral tooth at the end of a basal spiral cord. Vokes (1989) argued that *Hanetia* is a synonym of *Urosalpinx*, typified by the toothless eastern North American *U. cinereus* (Say). *H. haneti* and the late Miocene *Urosalpinx denticulatus* Vokes, a species without a labral tooth from the Dominican Republic, differ from typical *Urosalpinx* by having large denticles on the inner side of the outer lip. If Vokes's (1989) interpretation of *H. haneti* is correct, the labral tooth of that species evolved independently from that in other ocenebrines.

43. Forreria clade

Forreria is a highly distinctive lineage of muricids from the northeastern Pacific, characterized by adapically spinose, angular axial ribs that weaken toward the base and that often terminate at a deep spiral groove, at the end of which is situated a labral tooth. The tooth forms discontinuously on the adapertural edge of each successive rib. Because the group has not previously been examined critically as a whole, the number of distinct species remains uncertain. Based on my examination of specimens, I recognize the following species: *F. belcheri* (Hinds) (type of the genus), Pleistocene and Recent of southern California; *F. belcheri avita* (Nomland), Etchegoin Formation, Pliocene of California; *F. cancellaroides* (Arnold), early and middle Miocene of California; *F. carisaensis* (Anderson), late Miocene Santa Margarita Formation, California; *F. coalingensis* (Arnold), Etchegoin Formation; *F. emersoni* Addicott, basal Jewett Sand (early Miocene), California; *F. gabbiana* (Anderson), Temblor Formation and upper Olcese Sand (middle Miocene), California; *F. magister* (Nomland), Jacalitos Formation (latest Miocene), California; *F. milicentana* (Loel & Corey), Vaqueros Formation and Jewett Sand (early Miocene), California; and *F. wrighti* (Jordan & Hertlein), lower Almejas Formation (middle Miocene), Baja California. Addicott (1970) considered *F. gabbiana* and *F. milicentana* to belong to *Ocenebra* because of the supposed absence of a labral tooth and accompanying groove and, in the case of *F. milicentana*, because of the unusually well developed spiral sculpture. My examination of the type specimens, however, reveals that both species have a labral tooth at the end of a groove. Neither these two species nor any other species of *Forreria* have the closed siphonal canal and terminal

adult varix that are characteristic of *Ocenebra* and *Ocinebrina*.

Arnold (1907) proposed *Purpura vaquerosensis* for a large (more than 100 mm) gastropod from the 'Vaqueros' stage (early Miocene or latest Oligocene) of California, characterized by a row of shoulder knobs or spines and a constricted base. Loel & Corey (1932) considered it a species of *Rapana*, a middle Miocene to Recent genus of muricids from the western Pacific and Indian Oceans. Although this assignment is unjustified, they were correct in suggesting that *Rapana imperialis* Hertlein & Jordan from the Isidro Formation of Baja California (upper 'Vaqueros' stage) is a spinose form of this species. Although none of the specimens I examined has an intact outer lip, the shells of both forms have a basal groove that probably ended at the lip in a labral tooth. The adaperturally hollowed curved spines of the *imperialis* form bear considerable similarity to the adaperturally concave axial ribs and shoulder spines of *Forreria*, but the area between the suture and the spines is much broader in *P. vaquerosensis* than in *Forreria*. I am inclined to the view that the labral tooth of *Forreria* and that of *P. vaquerosensis* represents a single evolutionary acquisition.

Hertlein & Jordan (1927) introduced the name *Thais wittichi* for a peculiar muricid from the San Ignacio Formation (middle to late middle Miocene) of Baja California. It is characterized by six to seven abaperturally excavated axial ribs extending abapically to the siphonal canal. At the upper end of the basal constriction of the last whorl is a groove, which ends on the lip in a labral tooth, not mentioned in the original description. The species differs from most members of *Forreria* by having eight denticles on the adaxial side of the outer lip, and by having a corresponding number of distinct spiral cords. Although it may well represent an independent acquisition of the labral tooth, I tentatively regard *T. wittichi* as part of the *Forreria* complex.

Forreria closely resembles *Austrotrophon*, an early Miocene to Recent group co-occurring with *Forreria* in the temperate northeastern Pacific. *Austrotrophon* differs from *Forreria* mainly by lacking a labral tooth and the corresponding groove. Citing the lateral position of the nucleus of the operculum, McLean (1996) assigned both *Forreria* and *Austrotrophon* to the Ocenebrinae. D'Asaro (1991) and Kool (1993) also pointed to similarities of egg-capsule and anatomical features of *Forreria* to those of other ocenebrines, and further pointed to the close similarity in these traits with the South American tooth-bearing genus *Chorus*. It is therefore possible that *Forreria* and *Chorus* both came from a tooth-bearing ancestor. DeVries (1997) and I, however, hold that the acquisition of the tooth is independent in the two genera. *Chorus* appears to be derived from an ancestor similar to *Herminespina katzi*, the earliest known member of the *Acanthina* clade (see Note 44). Although *H. katzi* has axial sculpture, its axial elements are very low, broad waves rather than lamellar ribs. *Forreria* might be derived from an *Austrotrophon*-like ancestor, which like *Forreria* and *Austrotrophon* would have had well-developed, adaperturally reflected axial lamellae. This ancestor, in turn, might well be related to the morphologically similar southern-hemisphere genus *Trophon*, many species of which also have adaperturally

reflected axial sculpture. Whichever of these two scenarios is correct, the origin of *Forreria* is connected with the northward invasion of a South American stock near the beginning of the Miocene. Similar transequatorial northward invasions evidently explain the appearance of *Acanthinucella* in the *Acanthina* clade (Note 44) and probably that of *Nucella* and several other taxa (see also Marko & Vermeij, 1999).

Austrotrophon and the very similar genus *Zacatrophon* together likely comprise the sister group of *Forreria*. Both genera in the toothless sister group occur on the warm-temperate coasts of California and subtropical northwestern Mexico. Together they comprise eight fossil and living species.

44. *Acanthina* clade

As interpreted here, the *Acanthina* clade consists of five named genera of ocenebrine muricids characterized by dominantly spiral sculpture, a relatively short and broadly open siphonal canal, and a labral tooth formed at the end of a groove that lies near the base above at least one spiral cord. These genera are *Acanthina* (middle Miocene to Recent, western South America and the Falkland Islands, two living and at least four fossil species), *Acanthinucella* (late Miocene to Recent, warm-temperate northeastern Pacific, three living and two described fossil species), *Herminespina* (late Oligocene to late Pliocene, western South America, four species), and *Spinucella* (early Miocene to late Pleistocene, seven European and North African species and one Pliocene South African species) (see Vermeij, 1993b; DeVries, 1997; DeVries & Vermeij, 1997; Marko & Vermeij, 1999), and *Chorus* (late Miocene to Recent, western South America, one living and five fossil species). In *Acanthina* and in the late Miocene *Chorus frassinettii* DeVries, the labral tooth is confined to the adaxial (inner) side of the outer lip, leaving the abaxial or outer margin unaffected. In other members of this clade, the tooth forms in the more usual way, involving the outer lip as a whole (Vermeij, 1993b; DeVries, 1997).

Support for the existence of a monophyletic clade comprising *Acanthina* and *Acanthinucella* comes from a phylogenetic analysis of two mitochondrial gene sequences in eastern Pacific ocenebrines (Marko & Vermeij, 1999). *Acanthina unicornis* (Bruguière) from central Chile consistently formed a clade with the three living Californian species of *Acanthinucella* in analyses that also included species of *Nucella*, *Mexacanthina*, *Ceratostoma*, *Ocinebrina circumtexta* (Stearns), and the South African 'Nucella' *dubia* (Krauss).

The fossil genus *Herminespina* is morphologically very similar to *Acanthina* and *Acanthinucella* and can be interpreted as both the stem group and sister group of *Acanthina*, *Acanthinucella*, and *Chorus* (see also DeVries & Vermeij, 1997). *Herminespina* differs from the other genera by having more or less well-developed, rounded axial ribs. We did not include the living *Chorus giganteus* (Lesson) in our molecular analysis, but fossil evidence indicates that *Chorus* may have been derived from an early member of the *Acanthina* clade. DeVries (pers. comm., November, 1999) has found middle Miocene fossils in Peru that morphologically link *Chorus*, which lacks axial sculpture and which has a long siphonal canal, with the late Oligocene to early middle

Miocene *Herminespina katzi* (Fleming in Watters & Fleming), the earliest known member of the *Acanthina* clade, in which axial sculpture is very weakly expressed as low rounded waves. D'Asaro (1991) and Kool (1993) suggested that *Chorus* very closely resembles the northeastern Pacific *Forreria belcheri* (Hinds) in anatomy and in the morphology of its egg capsules (see also Gallardo, 1981). These similarities together with the long siphonal canal of both genera, may be correlated with the sandy and muddy bottom that both inhabit, in contrast to the rocky-shore habitats of *Acanthina* and *Acanthinucella*. As discussed further in Note 43, I interpret the acquisition of the labral tooth in *Forreria* as independent of that in *Chorus* and other members of the *Acanthina* clade.

The fossil eastern Atlantic genus *Spinucella* resembles the eastern Pacific members of the *Acanthina* clade in the position of the labral tooth, and like *Herminespina* is characterized by axial sculpture. Its axial elements, which in the Pliocene South African *S. praecingulata* (Haughton) appear only in young stages of growth, vary from high ribs in *S. angulata* (Dujardin) from the middle Miocene of France to low, tightly packed riblets whose strength is similar to that of the spiral cords, as in *S. tetragona* (Sowerby) and its subspecies *S. t. alveolata* (Sowerby) from the Pliocene of the North Sea basin. Although *Spinucella* in the eastern Atlantic is geographically well separated from the eastern Pacific members of the *Acanthina* clade, the morphological similarities between *Spinucella* and *Herminespina* point to common ancestry. The labral tooth, which is at a homologous position in the two genera, would therefore have evolved only once, probably in the southern temperate zone.

In Marko & Vermeij's (1999) phylogenetic analyses (for discussion see Notes 33 and 43), the *Acanthina* clade is inferred either to be the sister group of all other eastern Pacific ocenebrines sampled (*Nucella*, *Ceratostoma*, *Mexacanthina*, and *Ocinebrina circumtexta*) or the sister group of the South African 'Nucella' *dubia*. We did not sample other southern-hemisphere ocenebrines, so that the precise scope of the sister group of the *Acanthina* clade remains unclear. A reasonable hypothesis is that the *Acanthina* clade is derived from a southern-hemisphere stem group without a labral tooth. This same stem group would have given rise to the genera *Lepsiella* in New Zealand and Australia, *Trochia* in South Africa, and *Nucella* in the northern hemisphere.

45. *Mexacanthina*

Marko & Vermeij (1999) showed that *Mexacanthina*, a clade of two described and one undescribed species from the Pleistocene and Recent coasts of northwestern Mexico, evolved a sharp labral tooth independently of that in the morphologically superficially similar *Acanthina* clade. The tooth is formed at the end of a depression situated below all spiral cords on the last whorl, a position relatively lower than that in the *Acanthina* clade. Phylogenetic analyses of eastern Pacific ocenebrines in which the trees are rooted with rapanine muricids indicate a sister-group relationship between *Mexacanthina* and *Nucella*. In trees rooted with the

Acanthina clade and in which rapanines were not included, *Mexacanthina* is the sister group of *Ceratostoma*. Rooted with *Ocinebrina circumtexta*, the tree implies that *Mexacanthina* is derived from *Nucella*. On morphological grounds, a relationship between *Nucella* and *Mexacanthina* seems far more plausible than that between *Ceratostoma* and *Mexacanthina*. Like *Nucella* and the *Acanthina* clade, *Mexacanthina* lacks the varices that characterize *Ceratostoma*, and has a short, widely open siphonal canal instead of a narrow, long, ventrally sealed canal.

Species of *Mexacanthina* inhabit intertidal rocky shores, habitats not conducive to fossilization. The time of appearance of *Mexacanthina* therefore cannot be estimated with any degree of precision. *Mexacanthina angelica* (Oldroyd) and the type species, *M. lugubris* (Sowerby), are known from Pleistocene deposits in northwestern Mexico as well as from the living fauna.

46. Nucella packi

Nucella packi (Clark) from the San Ramon Sandstone (late Oligocene) of northern California has a labral tooth at the end of a spiral groove near the base of the last whorl (Amano, Vermeij & Narita, 1993; Collins *et al.*, 1996; Marko & Vermeij, 1999). I consider the acquisition of the tooth as being independent of that in the *Acanthina* clade and in *Mexacanthina* (see Notes 44 and 45). The tooth in *N. packi* is also formed differently from that in *N. canaliculata* (Note 47), in which it forms at the end of a cord. In *N. packi*, the tooth has a basal position, whereas in the *Acanthina* clade it lies above at least one basal cord. In its basal position, the tooth of *N. packi* resembles that of *Mexacanthina*, but the sculpture of *N. packi* (closely packed spiral cords and no axial ribs or nodes) contrasts strongly with that of *Mexacanthina*, in which the four to five broad rounded cords on the last whorl form distinct nodes where they cross well-defined ribs.

Marko & Vermeij (1999) argued that *N. packi* is best interpreted as a tooth-bearing member of *Nucella*, whose other species (early Miocene to Recent) generally lack a tooth (but see Note 47). *N. packi* is morphologically very similar to the next oldest species, *N. tokudai* (Yokoyama) from the early to middle Miocene of the northeastern Pacific and the early middle Miocene of northeastern Asia (see Amano *et al.*, 1993). I tentatively interpret *N. packi* to be an early tooth-bearing derivative of a toothless clade, which arrived in the northeastern Pacific from the southern hemisphere during late Oligocene time. The toothless species of *Nucella* would then collectively comprise the sister group of *N. packi*.

47. Nucella canaliculata

Nucella canaliculata (Duclos), a northeastern Pacific late Miocene to Recent species, normally lacks a labral tooth; but populations in central California, which Dall (1915) distinguished as the variety *compressa*, have a small tooth at the end of a cord near the base (Collins *et al.*, 1996). I have seen toothed specimens only from the Recent fauna near Monterey, where they occupy wave-exposed high-intertidal rocky-shore habitats.

48. 'Nucella' squamosa

Some individuals of 'Nucella' squamosa (Lamarck), a Recent rocky-shore species from South Africa, have a labral tooth formed at the end of a basal cord. I have seen such examples from False Bay, Cape Province. The affinities of 'N.' squamosa remain unclear. The species is not a member of the *Nucella* clade (Collins *et al.*, 1996; Marko & Vermeij, 1999), but its relationship to *Spinucella* (a fossil eastern Atlantic genus in the *Acanthina* clade; see Note 44) is problematic. Because the tooth of 'N.' squamosa is formed differently from that in *Spinucella*, I consider its acquisition to be separate in the two taxa.

49. Xanthochorus

The temperate western South American genus *Xanthochorus* comprises two or three living species and a number of late Miocene to Recent undescribed fossil species. In *X. cassidiformis* (de Blainville), the type species of the genus, there is often a broad, low labral tooth formed at the end of a concavity situated below all sculpture on the last whorl. A similar tooth is sometimes present but less conspicuous in *X. buxeus* (Broderip). Herm (1969) reports *X. buxeus* from the Pleistocene of Chile. T. DeVries (pers. comm., June, 2000) has collected fossil *Xanthochorus* from late Miocene and Pliocene strata in southern Peru. These species evidently lack a labral tooth, and resemble *Trophon* in sculpture. They differ from *Chorus* both in sculpture (presence of axial sculpture) and in the style of preservation of the outer shell layer. The radula of *X. cassidiformis*, however, resembles that of *Chorus giganteus* (Lesson) (G. Herbert, pers. comm., June, 2000). Based on DeVries's unpublished work, I am inclined to consider the evolution of the labral tooth in some individuals of *Xanthochorus* as independent of that in the *Acanthina* clade, which includes *Chorus*.

50. Agnewia kempae

The rapanine genus *Agnewia* is represented by two species, *A. tritoniformis* (de Blainville) from southern Australia and northern New Zealand, which lacks a labral tooth, and the labral-tooth-bearing *A. kempae* Powell from northern New Zealand. The tooth in *A. kempae*, not mentioned by Powell (1934) in his original description, is formed at the end of a basal cord (Beu & Maxwell, 1990). *A. kempae* is confined to the Haweran stage (late Pleistocene). The genus *Agnewia* is a member of the ergalataxine subclade of the muricid subfamily Rapaninae (see Vermeij & Carlson, 2000).

51. Muricodrupa fenestrata

The common high intertidal *Muricodrupa fenestrata* (de Blainville) from the tropical Indo-West Pacific has a tiny labral tooth formed at the end of a cord situated at the upper end of the short siphonal canal, below all external sculpture on the last whorl. This admittedly very small feature does not occur in the other lower intertidal and subtidal species of the genus, such as *M. fiscella* (Gmelin), *M. jacobsoni* Emerson and D'Attilio, and the Plio-Pleistocene *M. schroederi* (Wissema) (see also Vermeij & Carlson, 2000). *Muricodrupa* is part of the large

Indo–Pacific ergalataxine radiation within the Rapaninae (Vermeij & Carlson, 2000).

52. Acanthais

Vermeij & Kool (1994) proposed the genus *Acanthais* for a common Recent tropical eastern Pacific high intertidal rapanine muricid, *A. brevidentata* (Wood). This species is characterized by the presence of denticles on the inner side of the outer lip, a broad low columellar fold, and a small but sharp labral tooth situated at the end of a groove that lies below all primary spiral cords. Several species of *Stramonita* resemble *Acanthais* in having denticles on the inner side of the outer lip. These species, which extend back to the early Miocene of Venezuela (see Vermeij, 2001b), lack a labral tooth, but are likely to be similar to the ancestor of *Acanthais*. *Acanthais*, *Stramonita*, and several other early Miocene to Recent tropical genera comprise the *Thais* clade of Rapaninae (Vermeij & Carlson, 2000).

53. Mancinella alouina

The Pliocene to Recent Indo–West Pacific rapanine genus *Mancinella* is a member of the *Thais* clade (Vermeij & Carlson, 2000). Apparently only one species, *M. alouina* (Röding), has a labral tooth, which is formed at the end of a groove between the fourth and fifth primary spiral cords on the last whorl (Vermeij, 1998c). This position differs from that in other members of the *Thais* clade (*Acanthais* and *Neorapana*; see Notes 52 and 54), in which the tooth-bearing groove lies below all primary cords. This fact, together with the observation that only one species of *Mancinella* has a labral tooth, leads me to conclude that the labral tooth of *Mancinella* evolved independently of that in other members of the *Thais* clade (see also Vermeij, 1998c; Vermeij & Carlson, 2000).

54. Neorapana

In the Recent fauna, *Neorapana* is represented by three allopatric species in the tropical eastern Pacific, *N. grandis* (Sowerby) from the Galápagos Islands, *N. muricata* (Broderip) from Central America (type species), and *N. tuberculata* (Sowerby) from Mexico. The fossil record of the genus in the eastern Pacific extends back to the Pliocene. The only other described species is *N. rotundata* Gibson-Smith, Gibson-Smith, and Vermeij from the Cantaure Formation (early Miocene: Burdigalian) of Venezuela (see Gibson-Smith, Gibson-Smith & Vermeij, 1997). All these species have a labral tooth situated at the end of a basal groove. *Neorapana* is a member of the *Thais* clade of Rapaninae (Vermeij & Carlson, 2000), in which the labral tooth evolved independently from that in other members of that clade (*Acanthais* and *Mancinella*; see also Gibson-Smith *et al.*, 1997; Vermeij, 1998c; Notes 53 and 52).

55. Concholepas

The bizarre, limpet-like genus *Concholepas* is represented by a reasonably continuous series of rapanine muricid species from the late early Miocene to the Recent in western South America (DeVries, 1995, 2000). From its first appearance (as *C. unguis* DeVries) to the late Pliocene, *Concholepas* lacked a labral tooth. During the late Pliocene, following a large extinction event that eliminated some 80% of species, including warm-water taxa, the species *C. camerata* DeVries evolved paired basal teeth, which form at the ends of basal interspaces between cords. Similar teeth occur in *C. concholepas* (Bruguière), which succeeded *C. camerata* during the early Pleistocene and lives today on the coasts of Peru and Chile (see Vermeij, 1998c; DeVries, 1995, 2000). *C. concholepas* has also been recorded from the late Pleistocene of the west coast of South Africa (Kensley, 1985). The excellent fossil record, together with a phylogenetic analysis of the Rapaninae (Vermeij & Carlson, 2000), indicates that the labral tooth of *Concholepas* evolved independently of that in other clades.

56. Ptychosyca

The enigmatic olivid-like genus *Ptychosyca* is represented by one described species from the Maastrichtian (late Cretaceous) of the Gulf Coastal Plain. Its labral tooth is situated at the upper end of the siphonal canal at the end of a broad groove. Pending phylogenetic analysis, I tentatively consider *Ptychosyca* as a distinct taxon. I excluded it from the Pseudolividae (Vermeij, 1998a), where Sohl (1964a) had provisionally assigned it.

57. Ancillinae

The largest clade of gastropods with a labral tooth is contained in the olivid subfamily Ancillinae. I know of at least 191 species with a labral tooth, which is formed at the end of a basal groove (the so-called ancillid groove). At least 86 of these species are living. Genus- or subgenus-level taxa in which a tooth occurs include *Alocospira*, *Amalda*, *Ancilla*, *Ancillopsis*, *Baryspira* (Fig. 1J–L), *Eburna* (Fig. 1M–O), *Gracilispira*, *Hesperancilla*, *Mundaspira*, *Sparella*, *Sparellina*, and *Spinaspira* (see Chavan & Fischer, 1939; Chavan, 1965; Kilburn, 1981, 1993; Kilburn & Bouchet, 1988; Ninomiya, 1990; Bouchet & Kilburn, 1991; Lozouet, 1992; Vermeij, 1998a). An additional 109 species lack a labral tooth. The absence of a labral tooth characterizes *Ancillarina*, *Ancillina*, *Ancillista*, *Ancillus* (= *Gracilancilla* and *Turrancilla*), *Anolacia*, *Chilotygma*, *Entomoliva*, *Eoancilla*, *Exiquaspira*, *Javancilla*, *Micrancilla*, *Olivula*, and *Tanimasanoria*; some species of *Ancillopsis* and *Sparella* also lack a tooth (see also Ninomiya, 1988; Kase, 1990, 1992; Maxwell, 1992; Davoli, 1989).

Conclusions about the origin of the Ancillinae and of phylogeny within the group must be interpreted with caution in view of the many uncertainties concerning the taxonomy and relationships of the nominal genera and subgenera. Riedel (2000) regards the Ancillinae as the stem group of olivids and as the probable sister group of the Olivinae + Olivellinae. The earliest species belonging to *Eoancilla* (or *Ancillus* or *Turrancilla*, depending on one's predilection) and of *Tanimasanoria*, are of Campanian to Maastrichtian (late Cretaceous) age. These forms lack a labral tooth. The absence of a tooth and the restricted development of secondary callus deposits on the shell's spire of these genera (Sohl, 1964a; Kase, 1990) indicate plesiomorphic character states compared to most later species. In his phylogenetic analysis

based on shell characters, with special reference to species from New Zealand, Michaux (1989, 1991) concluded that *Turrancilla* (= *Ancillus*), a probably paraphyletic genus lacking a tooth, gave rise to *Ancillista* (also without a tooth) and to a group comprising *Alocospira* and *Amalda* (the latter including *Baryspira*, *Gracilispira*, and *Spinaspira*). All these taxa collectively form a sister group to *Ancilla* (including *Chilotygma*, *Javancilla*, *Sparella*, *Sparellina*, and *Eburna*). This phylogeny would imply that the labral tooth arose twice, in the *Alocospira–Amalda* clade and in the *Ancilla* clade (Michaux, 1989, 1991; see also Kilburn, 1981). The tooth of *Ancilla* would then have arisen after the Eocene, with the middle Eocene genus *Javancilla* serving as stem group (Kilburn, 1981). The tooth in the *Alocospira–Amalda* clade would have arisen either in the latest Cretaceous or earliest Paleocene. Early species with a tooth include *Amalda vetusta* (Forbes) from the Maastrichtian of India and Pakistan, *A. milthersi* (Ravn) from the Paleocene of Denmark, and '*Ancilla*' *mediavia* (Harris) from the Matthews Landing Member of the Porters Creek Formation (early Paleocene: Danian) of Alabama (see Harris, 1899; Chavan, 1965).

As is true in other gastropods in which the outer shell surface is covered with an extension of the foot or mantle, details of external callus vary considerably even within species. Characters distinguishing genera often concern such details and may not be reliable in phylogenetic analyses. I have therefore taken the very conservative position that the labral tooth in the Ancillinae evolved only once.

Ancillines are sand-dwellers. The living species show a markedly relictual distribution with large concentrations of species in such traditional refugial areas as Australia, New Caledonia, southern Japan, southern Africa, the western Indian Ocean, and the mainland Caribbean coast of Central and South America. There are, however, no living ancillines in the tropical eastern Pacific, another area well known as a geographical refuge. Species without a tooth make their last appearance in the eastern Pacific during the Oligocene.

58. *Dentimargo idiochila*

Schwengel (1943) described *Marginella idiochila* on the basis of several very small, biconic specimens characterized by the presence of a distinct labral tooth located about 2/3 the distance from the suture to the abapical end of the last whorl. There is no external shell sculpture, so that the mode of formation of the tooth cannot be determined. In Coovert and Coovert's (1995) classification, this species fits best in the Eocene to Recent genus *Dentimargo*, a taxon that may well require subdivision. *D. idiochila* appears to be the only species, among some 483 living species of the family (Coovert & Coovert, 1995) with a labral tooth. It occurs mainly in southeastern Florida. I am unaware of any fossil species with a labral tooth, despite a very prolific fossil record.