

## SNAIL SPEARS AND SCIMITARS: A CHARACTER ANALYSIS OF *CONUS* RADULAR TEETH

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### ABSTRACT

Knowledge of the attributes of the venom-injecting radular teeth of *Conus* can enhance understanding of the functional biology of feeding and the systematics of this large and taxonomically difficult genus of gastropods. We define and provide a scheme for coding the states of *Conus* radular tooth characters, in order to facilitate their use in taxonomic and phylogenetic studies. To exemplify these characters, we describe and illustrate teeth of putatively primitive species and of species representing generalized, vermivorous, molluscivorous and piscivorous feeding groups within the genus. We define and address the intraspecific and interspecific variation of ten presence-absence characters and 15 continuous characters, of which at least five and ten, respectively, are present in most species. Some continuous characters are bimodally distributed among the species sampled. If this distribution still obtains when additional species are examined, these characters could also be coded unambiguously as having two states. We also review the several previously proposed classification schemes of *Conus* radular teeth and of species according to tooth characters. As Troschel suggested in 1866, a tooth length:width ratio greater than or less than 20 separates the genus into two distinct species groups, now known to comprise the molluscivorous and piscivorous species in the former, and vermivorous and generalized species in the latter. Important subsidiary characters are the number of barbs, presence/absence of blade, cusp, and spur, length of serrations, relative width of base, and tooth length:shell length ratio.

### INTRODUCTION

The radula provides taxonomically useful characters in many groups of gastropod molluscs. In the past this has not been true in *Conus*, whose species have been distinguished almost exclusively, but often with considerable uncertainty, on shell characters (Röckel, Korn & Kohn,

1995). Species in this taxonomically challenging genus have unusually large, complex, varied and highly specialized radular teeth, but these have not been employed seriously and recently as sources of taxonomic characters. Each radular row consists of one pair of hollow, harpoon-like marginal teeth, and each tooth functions independently. In predation, one tooth is held within the tip of the long, tubular proboscis. Increased hydrostatic pressure in the proboscis propels the tooth, which simultaneously penetrates the prey's body wall, catches and holds the victim, and delivers a potent neurotoxin into the wound, paralyzing the prey which is then swallowed whole. The tooth thus functions as a combination hypodermic needle and harpoon; the muscular proboscis is analogous to the hypodermic syringe and also to the harpoon line. In most cases the prey is pulled into the expanded rhynchodeum or proboscis sheath by contraction of the proboscis, and swallowed whole (Kohn, 1998). Most *Conus* species are predators on polychaete annelids. A few of these also prey on worms of other phyla, mainly enteropneusts and echiurans. Two smaller groups of *Conus* species prey exclusively on other gastropods and on fishes. These dietary specializations likely played an important role in the rapid evolutionary diversification of this unusually large genus (Kohn, 1990). Here we examine the hypothesis that the characteristics of *Conus* radular teeth, the structural basis of the conotoxin delivery system used to overcome prey, can provide additional characters of use in differentiating species and thus in enhancing the presently limited base of taxonomic information.

As discussed more fully in the next section, Quoy and Gaimard (1834) first described *Conus* radular teeth, and numerous subsequent studies have demonstrated a remarkable range of diversity of teeth among species (Lovén, 1847; Troschel, 1866; Bergh, 1895; Nybakken, 1970; James, 1980; Rolán and Raybaudi

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Massilia, 1994). A number of authors (Peile, 1939; Azuma, 1964; Lim, 1969; and Nybakken, 1990) have categorized different tooth types and used this information for grouping different *Conus* species according to tooth type. No one, however, has provided a descriptive character analysis with evaluation of intra- and inter-specific variability of traits. In addition, *Conus* radular tooth characters have not been coded suitably for use in phylogenetic analysis, although this has been done for general tooth type in the related family Turridae (Shimek & Kohn, 1981) and for the Superfamily Conoidea as a whole (Taylor, Kantor & Sysoev, 1993).

These deficiencies and the paucity of existing objective taxonomic characters are primary reasons to learn more about comparative morphology and morphometry of *Conus* radular teeth. Two prerequisites to the use of characters in taxonomic analysis are 1) a clear description of character states (and a system for coding them) and 2) estimates of the range of variation in characters within and among individuals and within and among species. We address the first of these in this report. We describe radular tooth attributes, indicate those characters likely to be most informative taxonomically, and illustrate the range of variation in these characters among diverse species groups in this very large genus. The accompanying paper (Nishi & Kohn, 1999) examines the second, with emphasis on one species group within *Conus*, and tests the effectiveness of radular tooth characters in distinguishing similar species. We hope that these results will 1) improve species-level systematic knowledge by expanding the set of available taxonomic characters, 2) add characters that will help generate the first objective phylogenetic hypotheses for this unusually species-rich genus, a major evolutionary radiation of marine animals, and 3) advance understanding of functional morphology of the radular teeth as the delivery system for the potent contotoxin venoms used by these snails to overcome and paralyze their prey.

#### HISTORICAL PERSPECTIVE: PRIOR COMPARATIVE STUDIES AND CLASSIFICATIONS OF *CONUS* RADULAR TOOTH TYPES

Quoy and Gaimard (1834) gave the first, brief description of *Conus* teeth, perhaps based on anatomical studies by H. de Blainville (Appel, 1975). After noting the oppositely oriented directions of the teeth in the two branches of

the radular sac (see Kohn, 1998), they correctly hypothesised the function of the teeth but not how it was carried out (p. 81): 'Il n'est pas plus facile de se rendre compte de la manière dont l'animal se sert de ces aiguillons, qui, par leur forme en harpon, doivent le plus souvent rester dans le corps où ils s'implantent.' Following Quoy and Gaimard, Lovén (1847: 196) described the teeth of an unidentified *Conus* species in Swedish, illustrated the tooth of an undetermined species, and added an accurate and concise Latin diagnosis: 'aculeus e lamina tenui convolutus, cui insidet interne crista per dimidiam partem anteriorem denticulata, capitulo subhamato, apice perforato.' He also correctly proposed that the teeth function in envenomation of prey: 'Af denna egna form skulle jag vilja förmoda, att de äro giftorganer' (op. cit., p. 186). ['I would presume that these are venomous structures.']

The most thorough comparative morphological investigations of the radular teeth of *Conus* are still those made later in the 19th century by Troschel (1866) and Bergh (1895). In his monumental monograph on gastropod radular teeth, Troschel (1866) described those of 11 determined species of *Conus* in detail, established the terminology of their component parts, and included morphometric data on their proportions. Troschel included species now known to represent the vermivorous, molluscivorous and piscivorous feeding groups. He clearly described, accurately illustrated, and identified most of the major features of the teeth, including apex, adapical opening, barbs, blade, serration, external fold, cusp, and spur. In a major general comparative anatomical treatment of *Conus*, Bergh (1895) gave the most detailed description of the radular teeth heretofore published, including an account of their synthesis within the radular sac. He described and provided detailed line drawings of the teeth of 31 species, but he did not group them according to tooth characters.

Three major studies have attempted to subdivide the genus *Conus* into 6-12 species groups according to radular tooth form (Tables 1-4). Only the first of these (Troschel, 1866), provided a dichotomous key to the teeth that divided the 11 species he studied among seven groups. The primary criterion was tooth length:width ratio (>20 vs. <20) and presence or absence of a spur. (Descriptive terms are defined in the next section.) The presence or absence of barb(s), blade, serration, and cusp served as subsidiary criteria (Table 1). Most subsequent authors eschewed keys, although in

**Table 1.** Troschel's (1866) key to eleven species of *Conus* based on radular tooth characters. Feeding types are identified from subsequent studies as follows: M, Molluscivores; P, Piscivores; V, Vermivores.

Tooth Type	Feeding Type
I. Tooth >20 times as long as wide; base lacking a spur	
A. With a blade	
a. Cusp within the distal 2/3 of the tooth ( <i>C. marmoreus</i> , <i>C. araneosus</i> )	M
b. Cusp within the proximal 1/3 of the tooth ( <i>C. furvus</i> )	M(?)
B. With barbs but no blade ( <i>C. geographus</i> , <i>C. canonicus</i> , <i>C. textile</i> )	M + P
II. Tooth <20 times as long as wide; base with a spur	
A. Without barbs or cusp	
a. Without serration ( <i>C. ebraeus</i> )	V
b. With serration ( <i>C. ventricosus</i> )	V
B. With barb, blade, and cusp	
a. Cusp distal to center of the tooth ( <i>C. pulicarius</i> )	V
b. Cusp at or proximal to center of the tooth ( <i>C. mus</i> , <i>C. planorbis</i> )	V

For names of authors of species not otherwise mentioned in the text, see Röckel et al. (1995).

their briefer discussions of far more species, Peile (1939) divided 88 species among twelve groups, and Nybakken (1990) apportioned 100 species among six groups. In both cases, keys could be constructed from the characters they used (Tables 2, 3). Unfortunately each of these three schemes is based on different character sets, and they are only partially reconcilable with each other.

Peile's (1939) groups are rather crudely delineated. He included a partial key, based on Troschel's but limited to four groups (Table 2). These contain 27 species with serrate teeth, but the key does not clearly distinguish them from some of the species he assigned to groups outside the key. Virtually translating Peile (1939) into Japanese, Azuma (1964) classified *Conus* radular teeth into nine groups, most identical to those of Peile, and indicated examples of each (Table 2). Warmke (1960) also published a key to *Conus* radular teeth, but it is only partly dichotomous and is restricted to the seven Caribbean species she considered.

Following Kohn's (1959) characterization of the three main functional feeding groups of specialist Indo-Pacific species, Endean and Rudkin (1965) first related radular tooth form to the type of prey known to be utilized by members of these groups. Prey type can thus be indicated for the species groups of both earlier and later authors (Tables 1-3). Endean and Rudkin (1965) based their system of five groups on that of Peile (1939). They identified two types of piscivorous teeth, equivalent to Peile's (1939) first two groups (Table 2), and two types of molluscivorous teeth, by subdividing Peile's third group. In both molluscivorous groups, the

teeth are also elongate and minutely serrate with slightly enlarged bases, and a cusp on the proximal half. In the first group, including *C. textile* Linnaeus, *C. aulicus* Linnaeus and others, the cusp is close to the base and there are two barbs (Nishi and Kohn, 1999). In the second group, represented by *C. marmoreus*, the cusp is located more centrally on the shaft, and there is one barb and one blade (see Fig. 7). Endean and Rudkin lumped all of the vermivorous species, including *C. lividus*, *C. virgo*, *C. distans*, *C. quercinus* and others, in their final group, with short or long shafts, a prominent base usually with a spur, and a cusp (Table 4; see also Fig. 6).

Barnard (1958) illustrated and briefly described the radular teeth of several South African species, including proportional serration lengths. According to Endean and Rudkin's (1965) criteria, these probably include both vermivorous and molluscivorous species. Van Mol, Tursch and Kempf (1967) illustrated the radular teeth of six Brazilian species of *Conus*, all likely in the vermivorous group according to the same criteria. Lim (1969) listed 36 vermivorous, 9 molluscivorous and 10 piscivorous species from the Indo-Pacific region, based on both Endean and Rudkin's (1965) tooth character scheme and on diet data. In a detailed systematic study of west American *Conus*, Nybakken (1970a) described and illustrated the teeth of the 28 species known from this region. The tooth morphology of the five species with known diets (Nybakken, 1967, 1968, 1970b) also conform with the above criteria for the three functional feeding groups. Bandel (1984) described the radular teeth of five Caribbean

**Table 2.** Peile's (1939) and Azuma's (1964) groups of *Conus* species based on radular tooth characters. Feeding groups are identified from subsequent studies, as in Table 1.

Peile (1939): Criteria	Group*	Species Included	Azuma (1964): Criteria	Group	Species Included	Feeding Type
Tooth long, with relatively small base; with 2 bars; serration ~ tooth length	(1)	<i>geographus, cuvieri, with deshayesii, gilchristi, tulipa</i>	Tooth long, spear-shaped; one barb	1	<i>geographus</i>	P
with 3 bars; no serration	(2)	<i>monachus, catus, purpurascens, striatus, testudinarius, etc.</i>	with barb with recurved tip	2	<i>monachus, catus, striatus, fulmen, obscurus</i>	P
with 2 bars; cusp in proximal part; finely serrate	(3)	<i>textile, aulicus, canonicus, omaria, marmoreus</i>	Tooth with a small cusp in proximal part	3	<i>textile, profundorum</i>	M
Tooth with a larger base and a spur; with long shaft; weak serration; well developed spur	(4)	<i>virgo, terebra, princeps</i>	Tooth with serration; with a well-developed spur	4	<i>virgo, vexillum, lividus</i>	V
with moderately long shaft; strong serration; without spur	(5)	<i>vexillum, ermineus, monile, rattus, striatellus, cernicus, maldivus, etc.</i>				V
without serration; with minute cusp	(6)	<i>lividus, flavidus, quercinus</i>				V
without barb, blade or serration	(7)	<i>ebraeus, chaldaeus</i>	Tooth with a central waist	5	<i>ebraeus, chaldaeus, betulinus</i>	V
with barb and blade; without serration	(8)	<i>agassizi, puncticulatus</i>				V
Teeth <20 times as long as wide; serration shorter than blade; without barb	A i (9)	<i>tessulatus, ventricosus, miliaris, etc.</i>	serration shorter than blade; without barb	6Aa	<i>tessulatus, capitanelus, etc.</i>	V
serration shorter than blade; with a barb	A ii (10)	<i>arenatus, pulicarius, zeylanicus</i>	serration shorter than blade; with a barb	6Ab	<i>sieboldi, praececellens, etc.</i>	V
serration longer than blade; without barb	Bi (11)	<i>miles, incarnatus, figulinus, nux, etc.</i>	serration longer than blade; without barb	6Ba	<i>miles, capitaneus, etc.</i>	V
serration longer than blade; with a barb	B ii (12)	<i>litteratus, leopardus</i>	serration longer than blade; with a barb	6Bb	<i>litteratus, leopardus</i>	V

\* Groups were not numbered by Peile (1939); they are numbered here to facilitate comparison with Azuma's (1964) groups. For names of authors of species not otherwise mentioned in the text, see Röckel et al. (1995).

**Table 3.** Nybakken's (1990) groups of *Conus* species based on radular tooth characters related to Piele's (1939) groupings (see Table 2).

Criteria	Group	Species Included	Equivalent Peile Group
Waist central; tip with one barb and either one blade or a second barb; serration present, usually terminating in a cusp; base slightly enlarged, with a spur	1	22 vermivorous species	(5), (7), (9), (10), (11), (12), in part
Waist proximal to center of shaft, with longer serration and more prominent cusp than Group 1	1a	6 vermivorous species	(4), (6), (9), in part
With or without a waist; with two barbs and no blade; with long serration; without a spur	1b	5 molluscivorous species + 9 with unknown diets	(3)
Shaft very elongate; with three barbs, the third with a recurved tip; without waist or serration	2	8 piscivorous species	(2)
With a waist; with four barbs; without a cusp; base with spur	3	3 vermivorous species + 5 with unknown diets	none
With a prominent waist distal to center of shaft; with two or three barbs; without blade, serration or cusp; base with a large spur	4	2 vermivorous species + 4 with unknown diets	none

species of *Conus*, illustrated them as well as teeth of some species from other regions, and reviewed knowledge to that date of the relationship of tooth form to prey type. Rolán (1990) described and illustrated the radular teeth of 18 newly described species from the Cape Verde Islands. More recently, Rolán and Raybaudi Massilia (1994) concisely and quantitatively described and illustrated radular teeth of 127 species, most of which had not been previously described or figured, from various world regions.

Following description of the feeding mechanism and mode of radular tooth function in *Conus* (Kohn, 1956), Kohn, Nybakken and Van Mol (1972) elucidated the functional morphology of the tooth based on the first application of scanning electron microscopy to the problem and on the tooth of *C. imperialis* as an exemplar. More recently, Rolán (1986) and Nybakken (1990; Nybakken and Perron, 1988) have related ontogenetic change in *Conus* radular tooth morphology to change in diet during postmetamorphic life history.

The third major classification scheme (Nybakken, 1990) produced six groups comprising 100 species according to both radular tooth form and dietary type (Table 3), as well as 10 species

with unique tooth types. All of the latter were vermivores or generalists. Nybakken (1990) used the presence and position of a waist as his primary criterion, and he did not use tooth length as a character at all, so the species composition of his groups differs substantially from the keys and groupings of prior authors (Table 4).

#### GENERAL MORPHOLOGY AND TERMINOLOGY OF THE *CONUS* RADULAR TOOTH

Here we summarize the taxonomically most informative descriptors of the *Conus* radular tooth. Each is defined, and the authors who first introduced it and who first used the English term are cited. More or less complete terminologies in other languages are given by Quoy and Gaimard (1834) in French, Lovén (1847) in Swedish, Troschel (1866) and Bergh (1895) in German, Azuma (1964) in Japanese, and Rolán (1990) in Spanish. In the earliest account, Quoy and Gaimard (1834: 80) described the teeth as 'crochets cornés, un peu friables, en form d'hameçons à une ou deux denteleures, variants selon les espèces,' and as noted above referred

**Table 4.** Summary of proposed classification schemes of *Conus* radular teeth and of species according to radular teeth characters. P/A = presence or absence; n.q. = not quantified.

Author	Date	Primary Discriminant	Subsidiary Discriminants	No. of Groups	No. of Species	Key to Groups?	Designators of Groups
Troschel	1866	Tooth length $>/\leq 20x$ width	P/A of barbs, blades, cusp, serration	7	11	yes	Iaa-IIbB
Peile	1939	Tooth length (n.q.), base large/small	P/A of barbs, blade, spur, cusp; P/A, length of serration	12	88	partial	1 <sup>st</sup> -3 <sup>rd</sup> major groups; Ai-Bii within 3 <sup>rd</sup> group
Warmke	1960	P/A of barb, blade, serration	Serration length, tooth length, spur	4	7	yes	1, II-IV
Azuma	1964	Tooth length (n.q.)	P/A of barb, cusp, spur, waist; length of serration	9	32	no	1-5, 6Aa-6Bb
Endean & Rudkin	1965	Tooth length (n.q.)	Diet; P/A of barb, blade, serration, spur; P/A, position of cusp	5	18	no	none
Nybakken	1990	P/A, position of waist	Tooth length (n.q.); P/A of barbs, blade, cusp, serration, spur	6	100	no	1, 1a-1c, 2-4

to them as 'aiguillons' (stings). Lovén (1847) used 'nål' (needle), and Adams (in Adams and Reeve, 1848) appears to be the first to have referred to the teeth of *Conus* in English and the first to attribute human injury to them: 'At the little island of Mayo, one of the Moluccas, near Ternate, Sir Edward Belcher [Captain of H.M.S. Samarang] was bitten by one of the Cones [*C. aulicus*], which suddenly exerted its proboscis as he took it out of the water with his hand and he compared the pain experienced to that produced by the burning of phosphorus under the skin. The instrument which inflicted the wound, in this instance, was probably the tongue, which in these mollusks is long, and armed with two ranges of sharp-pointed teeth.' In German, Troschel (1866) used the term 'Pfeilzahn' (arrow-tooth), and Bergh (1895), 'Zahnplatte' (tooth plate) and 'Giftzahn' (poison tooth). Azuma (1964) used the term 'shizetsu,' and Rolán (1990), 'diente.'

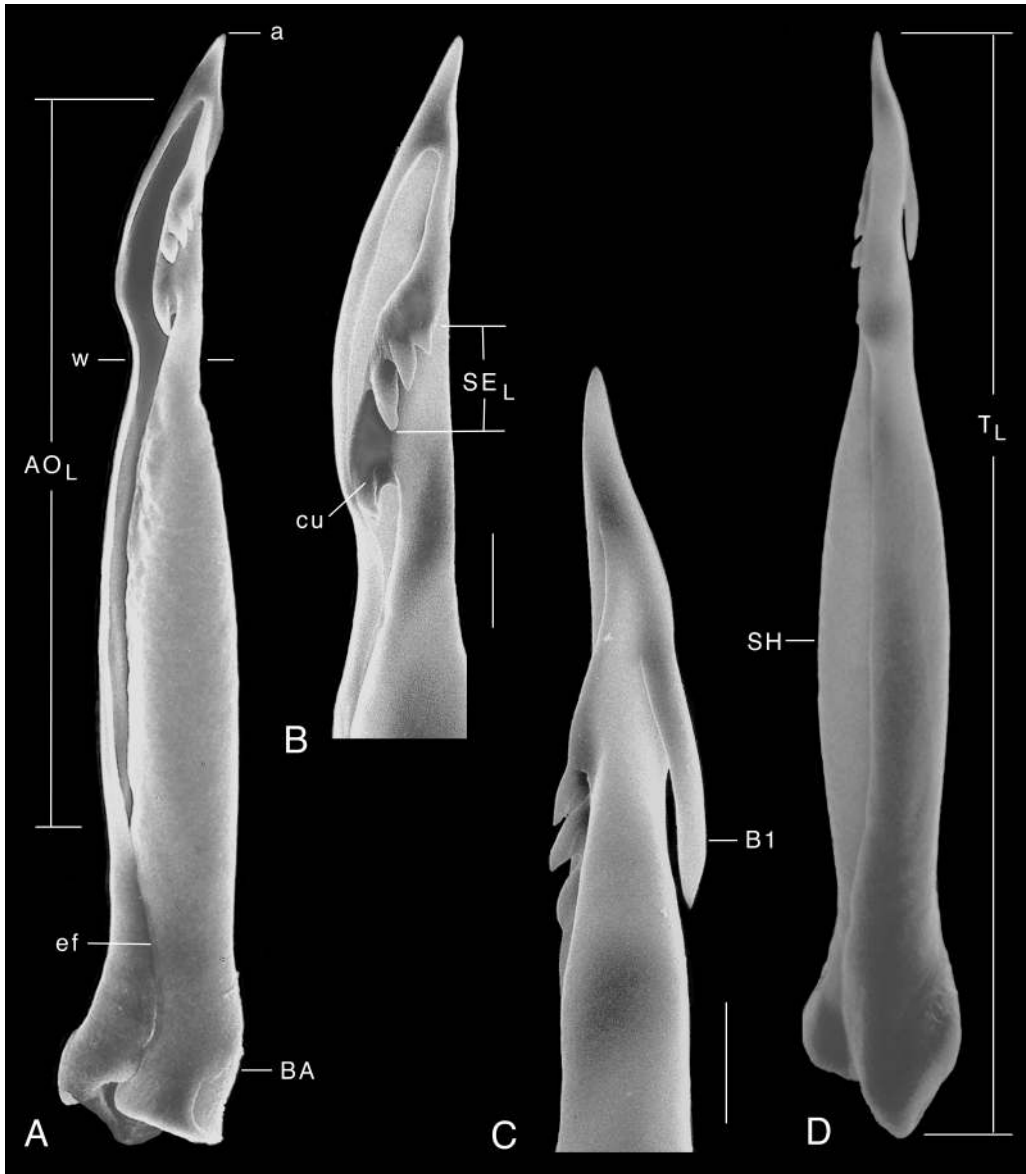
In this section, we first list terms that characterize the tooth as a whole, followed by those that apply to features ordered from distal to proximal ends of the tooth. The designators of attributes used as taxonomic characters are also defined. One or two capital letters, or capital

letters followed by a subscript if necessary for clarity, designate these structures and their measured absolute lengths or widths. Lower case letters designate other structures, including those treated as presence-absence characters.

Several prior authors have published labeled drawings of either generalized or exemplary *Conus* radular teeth to indicate their components (Warmke, 1960; Nybakken, 1970a, 1990; Kohn, Nybakken and Van Mol, 1972; Rolán and Raybaudi Massilia, 1994). In lieu of another such diagram, we label each feature defined below at least once in Figs. 1-7. The following features appear to be universal, that is they are present in all *Conus* species we have examined:

**Tooth length ( $T_L$ ).** The absolute length of the tooth measured along the tooth from apex to base (Fig. 1D). For curved teeth, we also measured  $ST_L$ , the straight-line distance between its apex and base, and calculated curvature (q.v. below) as  $T_i/ST_L$ . As a measure of tooth length relative to body size (shell length,  $S_L$ ) we use  $T_i/S_L$ .

**Apex (a).** Distal point (Peile, 1939) or tip (Endean and Rudkin, 1965) of the tooth (Fig. 1A) (Troschel, 1866: 'Spitze'), designated **a**



**Figure 1.** *Conus acutangulus*, radular teeth. **A**, Entire tooth, oriented with distal end up; length 0.21 mm. **B**, Detail of apex of tooth showing distal part of adapical opening, serration of three denticles, and cusp. **C**, Detail of apex of a tooth turned to show barb; denticles are visible on the left. **D**, Entire tooth oriented as in **C**, to show shape of shaft and form of base; length 0.21 mm. Abbreviations: **a**, apex; **AO<sub>L</sub>**, length of adapical opening; **B1**, barb; **BA**, base; **cu**, cusp; **ef**, external fold; **SE<sub>L</sub>**, length of serration; **SH**, shaft; **T<sub>L</sub>**, tooth length; **w**, waist. Scale bars in **B** and **C**: 0.01 mm. Specimen 17 × 8 mm, from Hansa Bay, Papua New Guinea.

following Rolán and Raybaudi Massilia (1994). *Adapical opening* (**AO**). Exit route of venom from the lumen of the radular tooth into the victim (Troschel, 1866: 'Spaltöffnung;' Kohn, Nybakken and Van Mol, 1972). **AO<sub>L</sub>** is the

proximal-distal length of the adapical opening (Fig. 1A), and its relative length is **AO<sub>L</sub>/T<sub>L</sub>**. *Shaft* (**SH**). The columnar portion of the tooth between its apex and base (Quoy and Gaimard, 1834: 'langue;' Bergh, 1895: 'Röhre;' Peile,

1939) (Fig. 1D). The shaft is tubular, consisting of a rolled sheet of chitin, often of 2-3 whorls, and a central lumen (Bergh, 1895: 'Höhle'). Venom flows through the lumen into the victim when the tooth is deployed. The measure of



shaft width (**SH<sub>w</sub>**) is taken where it is maximal. **External fold (ef)**. Outer whorl of the rolled sheet, its edge visible along the shaft (Troschel, 1866: 'äussere freie Rand;' Kohn, Nybakken and Van Mol, 1972) (Fig. 1A).

**Base (BA)**. Proximal end of the tooth, often expanded laterally in a flange and reinforced by thickening (Lovén, 1847: 'ansvällda basalände;' Peile, 1939). The base (Fig. 1A) bears the basal opening of the lumen. The width of the base is designated **BA<sub>w</sub>**. This is the only character used here that is also used by Taylor *et al.* (1993); however, they code it as a binary character with states 0 = large base and 1 = thin small base. To quantify base width relative to tooth length and width, we calculated **BA<sub>w</sub>/T<sub>L</sub>** and **SH<sub>w</sub>/BA<sub>w</sub>**, respectively. Together, these provide measures of general tooth thickness or robustness and the inverse of enlargement of the base relative to the shaft.

**Basal opening (bo)**. Large, proximally or partly laterally directed opening of the lumen on the base (Fig. 2A), through which venom flows into the lumen of the tooth from the proboscis (Kohn, Nybakken and Van Mol, 1972).

**Ligament (l)**. A band of tissue connecting the base of the tooth to the radular sheath (Fig. 5C) (Quoy and Gaimard, 1834: 'pédicule filamenteux;' Lovén, 1846: 'tungbandet'). It probably functions in moving the tooth into the short or storage arm of the radular sac as in Turridae (Shimek, 1975) but has no active role in venom injection.

The following structures and attributes are present in the teeth of some species but absent in others:

**Curvature (T<sub>L</sub>/ST<sub>L</sub>)**. The ratio of tooth length as measured along a curved tooth (**T<sub>L</sub>**) (Bergh, 1895: 'mitunter etwas gebogene Röhren'), to the straight line distance between its apex and base (**ST<sub>L</sub>**). Because most *Conus* radular teeth are straight (**T<sub>L</sub>/ST<sub>L</sub>**=1.0), we place curvature in this group of characters. The longest *Conus* teeth are often curved, at least when preserved specimens from within the radular sac are examined. It is likely that these teeth, whose length may exceed 10% that of the shell (see below), must be flexible enough to curve to

**Figure 2.** *Conus australis*, radular teeth. A, Entire tooth; length 0.61 mm. B, Detail of apex of tooth showing distal part of adapical opening, serration, blade, and cusp. C, Detail of base of tooth, showing spur. Abbreviations: BL<sub>L</sub>, length of blade; bo, basal opening; sp, spur. Scale bars in B and C: 0.1 mm. Specimen 52 × 20 mm, from S. China Sea, Hong Kong, 21°00.3'N, 115°17.8'E, in 126m.



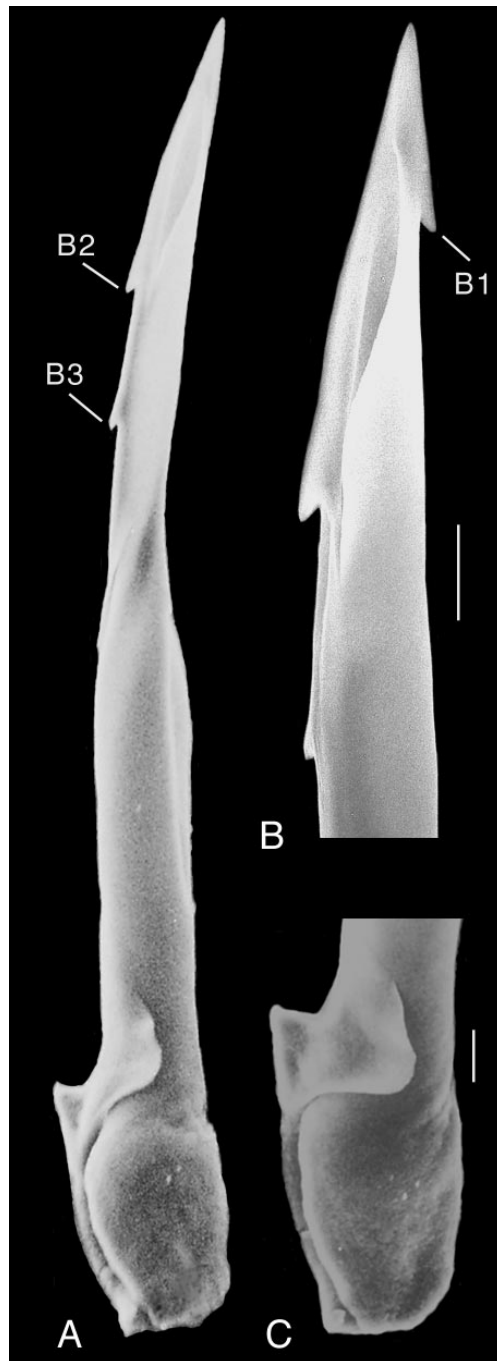
varying extents during movement of the radular sac and other organs in activities such as extension from and retraction into the shell, feeding and swallowing. Thus large absolute measurements of curvature may be artifactual.

**Barb (B).** Projection from the shaft with a cutting edge, extending proximally from the apex, and joining the shaft at an acute angle (Figs. 1C; 3A, B; 4B, C) (Quoy and Gaimard, 1834: 'dentelure;' Troschel, 1866: 'Widerhaken.' Most *Conus* teeth bear one or two barbs (Figs. 1, 2, 5–7), but the range in number is 0–5 (Figs. 3, 4). **B<sub>1L</sub>**, **B<sub>2L</sub>**, etc. indicate the length of each barb parallel to the shaft from the apex to its proximal extremity. Relative barb length was calculated as **B<sub>nL</sub>/T<sub>L</sub>**.

**Blade (BL).** Projection from the shaft with a cutting edge extending proximally from the apex, and joining the shaft at an obtuse angle (Figs. 2B, 7B) (Bergh, 1895: 'Schneiderrand;' Peile, 1939). Typically each tooth bears 0 or 1 blade. The blade if present is usually longer than the barbs and opposite the first barb. **BL<sub>L</sub>** (Fig. 2B) indicates the length of the blade parallel to the shaft from the apex to its proximal extremity. Relative blade length was calculated as **BL<sub>L</sub>/T<sub>L</sub>**.

**Serration (SE).** One or more longitudinal rows of two or more proximally directed denticles extending along or proximally from the adapical opening of the lumen (Lovén, 1847: 'rad af tagger;' Peile, 1939), sometimes terminating in a projection, the cusp. If present, serration typically extends along the side of the adapical opening nearest the first barb and more or less opposite the blade. It ranges from a short group of three large, exposed denticles in *C. acutangulus* (Fig. 1B) to a very long row of minute, obscure denticles mainly hidden by the external fold within the lumen of the tooth in *C. marmoreus* and *C. bandanus* (Fig. 7C). **SE<sub>L</sub>** indicates the length of the serration (Fig. 1B), and **SE<sub>L</sub>/T<sub>L</sub>**, its length relative to that of the tooth. In the species described here, the serration is either present and continuous to about the level of the proximal end of the blade or waist, or it is absent. In some other species it is interrupted centrally (Nishi and Kohn, 1999).

**Cusp (cu).** Short projection extending proximally from the shaft, usually approximately half way along its length, sometimes at the proximal end of the serration (Figs. 1B, 7A) (Troschel 1866: 'mittlere Widerhaken;' Peile, 1939). Peile



**Figure 3.** *Conus orbigny*, radular teeth. A, Entire tooth; length 0.32 mm. B, Detail of apex of tooth showing adapical opening and all three barbs. C, Detail of base of tooth showing full extent of spur. Abbreviations: **B<sub>1</sub>**, first barb; **B<sub>2</sub>**, second barb; **B<sub>3</sub>**, third barb. Scale bars in B and C: 0.01 mm. Specimen 44 × 15 mm, from S. China Sea, Hong Kong, 21°18.3'N, 114°48.1'E, in 90 m.

(1939) used the term spur for both cusp and basal spur.

**Waist (W).** A narrow or constricted portion of the shaft (Fig. 1A) (Azuma, 1964; Nybakken, 1970). The waist may be a well-defined point

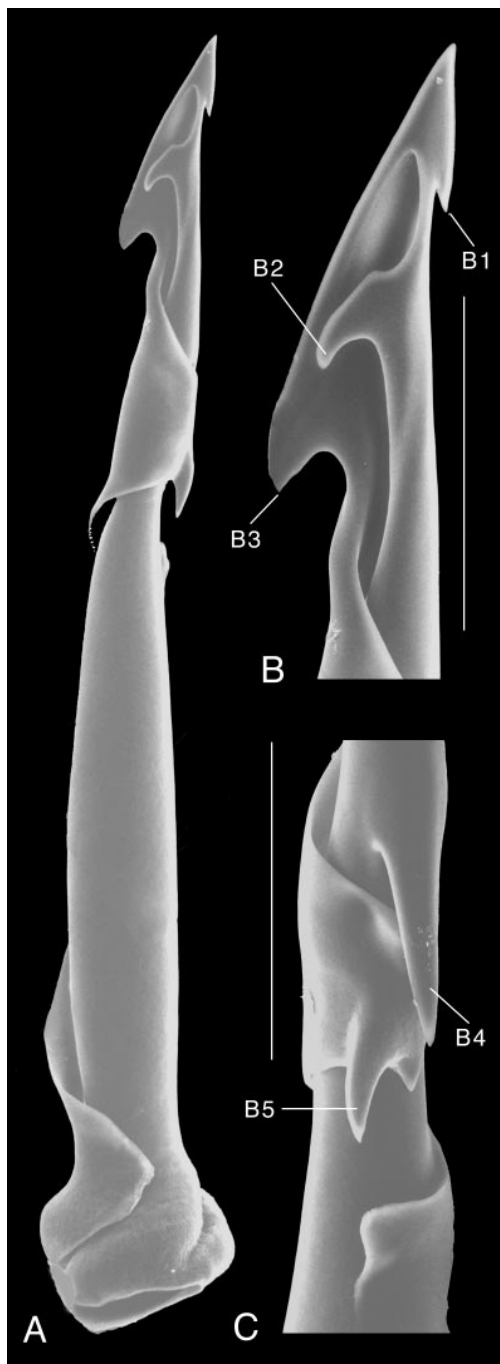
but in most species the width of the shaft changes gradually and the waist is not sharply demarcated. If the waist is well defined, its width is designated  $W_w$ . The length of the distal portion of the tooth ( $W_l$ ) is its length from apex to waist, or the line segment  $aW$ . This is identical to the 'part proximal to apex' or PA of Rolán and Raybaudi Massilia (1994). Its length relative to the tooth is calculated as  $W_l/T_L$ , and its width relative to the base, as  $W_l/BA_w$ .

**Spur (sp).** A distally oriented tooth-like projection from the base (Troschel, 1866: 'Zahn'; Peile, 1939), the spur (Figs. 2C, 3C, 5C, 6A, C) is usually aligned with the blade or second barb. It presumably functions with the flange of the base to permit the lip of the proboscis to grasp the base firmly during feeding, and thus to prevent its premature loss from the proboscis.

#### MATERIALS AND METHODS

To appreciate the range of variation in radular tooth form and specific characters among *Conus* species, we selected representatives of putatively primitive species and species from several functional feeding groups for morphometric analysis and representation by scanning electron microscopy. We supplemented this set with data on more extreme variants from a preliminary survey of radular characters of 118 mainly Indo-Pacific *Conus* species (database available from the first author) and from Rolán and Raybaudi Massilia (1994).

**Preparation of teeth.** Specimens of *Conus* were fixed in formalin and preserved in ethanol (70%, with 5% glycerine). The sizes of specimens whose teeth are illustrated are given as shell length  $\times$  maximum diameter. Radular teeth were dissected from the radular caecum (Taylor, Kantor & Sysoev, 1993), also called the short or proximal arm of the radular sac (Kohn, Nybakken & Van Mol, 1970), and cleaned briefly in dilute sodium hypochlorite. For morphometric analysis, teeth were mounted unstained on slides and examined with a Normarski differential interference microscope. For scanning electron microscopy, teeth were dehydrated through increasing concentrations to absolute ethanol, transferred to hexamethyldisilazane for 15 min, then air-dried, mounted on stubs with double-sided tape, and sputter-coated with gold-palladium. They were examined with a JEOL JSM-35 scanning electron microscope.



**Figure 4.** *Conus californicus*, radular teeth. A. Entire tooth; length 0.96 mm. B. Detail of apex of tooth showing adapical opening and first three barbs. C. Detail proximal to B, showing fourth and fifth barbs. Abbreviations: **B1**, first barb; **B2**, second barb; **B3**, third barb; **B4**, fourth barb; **B5**, fifth barb. Scale bars in B and C: 0.1 mm. Specimen 19  $\times$  12 mm, from Dike Rocks, La Jolla, California.

*Orientation of teeth.* *Conus* radular teeth are complex in three dimensions, bilaterally asymmetrical and, because they are paired marginal teeth, left- and right-handed. Thus a conventional orientation is desirable for illustrative representation and for descriptive terminology. Here we adopt the conventions of Rolán and Raybaudi Massilia (1994), who

represent teeth with the apex up and adapical barb (**B1**), blade (**BL**) and spur (**sp**) visible, and with blade (**BL**) and spur (**sp**) to the observer's left side. We illustrate radular tooth characters in scanning electron micrographs (SEM), usually following this convention, with **B1** extended to the right. In this orientation the adapical opening (**AO**) and serration (**SE**) are also usually visible, and the blade and spur, if present, are opposite the first barb, i.e. extending to the left. However, in this orientation the widest part of the base often extends toward the viewer, so its maximal width is not apparent. Thus the actual ratio  $BA_w/T_L$  is often greater than would be measured from the SEM's.

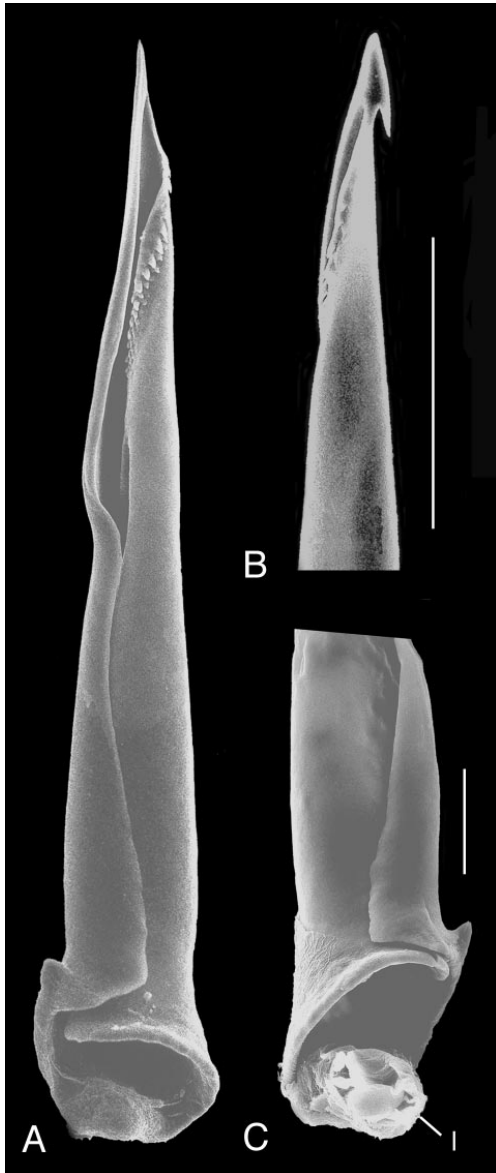
### RESULTS: CHARACTERISTICS OF RADULAR TEETH OF SELECTED SPECIES

Tables 5 and 6 summarize the states of the continuous and two-state characters, respectively, including estimates of intraspecific variation in the former.

*Putatively primitive species groups.* Some workers (e.g. Thiele, 1931) refer these species to the subgenera *Asprella* Schauffuss and *Conasprella* Thiele. They share a number of shell characteristics with the likely ancestors of *Conus* in the traditional family Turridae (Kohn, 1990). In particular, their shells are thin and have high spires and narrow apertures. Their radula teeth are thus of interest as possible sources of plesiomorphic characters and states.

#### *Conus acutangulus* Lamarck

*Conus acutangulus* is traditionally assigned to the subgenus *Conasprella* (e.g. Marsh and Rippingale, 1974), sometimes raised to genus level (e.g. Kira, 1965). The length of the radular tooth is less than 2.0% that of the shell (Table 5) (1.8% acc. Rolán and Raybaudi Massilia (1994). A short row of three large denticles occurs along the edge of the adapical opening on the side opposite the external fold (Fig. 1A,B). Proximal to the row of denticles is a cusp, a barblike structure whose tip lies within the adapical opening rather than projecting outward from the shaft (Fig. 1B). This arrangement resembles that of *C. imperialis* Linnaeus (Kohn, Nybakken and Van Mol, 1972), although in the latter the denticles are much smaller and more numerous. We regard the larger structures of *C. acutangulus* as denticles comprising serration rather than barbs because they originate along the adapical opening rather than at the apex of the tooth. The serration extends for about 7% of the tooth length. A single true barb with an elongate free end extends from the apex to about 18% of  $T_L$ , or about to the level of the third denticle, but not in the same plane



**Figure 5.** *Conus eburneus*, radular teeth. A. Entire tooth; length 0.56 mm. B. Detail of apex of tooth showing adapical opening and barb. C. Detail of base, showing spur, basal opening, and remnant of ligament (**l**). Scale bar in C: 0.1 mm. Specimen 49 × 30 mm, from Monigondon Reef, Philippines, in 4-15 m.

**Table 5.** Matrix of quantitative characters of *Conus* radular teeth. N = number of specimens examined. Ranges are given in parentheses.

Character No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Character Description	Adapical															
Character No.	Shell length	Tooth shell length	Barb1 length	Barb2 length	Barb3 length	Barb4 length	Barb5 length	Blade length	Opening length	Serration length	Waist length	Shaft length	Base length	Waist length	Shaft length	Curvature
Character Designation	$S_L$	$T_L/S_L$	$B1_L/T_L$	$B2_L/T_L$	$B3_L/T_L$	$B4_L/T_L$	$B5_L/T_L$	$BL_L/T_L$	$AO_L/T_L$	$SE_L/T_L$	$W_L/T_L$	$SH_L/T_L$	$BA_W/T_L$	$W_W/SH_W$	$SH_W/BA_W$	$T_L/ST_L$
Species	N															
<i>C. acutangulus</i>	1	23.5	0.016	0.18					0.66	0.068	0.30	0.14	0.26	0.35	0.53	1.00
<i>C. australis</i>	2	50.5 (49.0–52.0)	0.012 (0.058–0.064)	0.061				0.23 (0.21–0.25)	0.45	0.29 (0.29–0.30)	0.46 (0.46–0.46)	0.11 (0.10–0.11)	0.22 (0.21–0.23)	0.65 (0.60–0.70)	0.50 (0.46–0.55)	<1.01
<i>C. orbigny</i>	1	43.5	0.007	0.083	0.21	0.30			0.14		0.41	0.094	0.17	0.50	0.57	<1.01
<i>C. californicus</i>	2	16.7 (14.3–19.0)	0.050 (0.049–0.051)	0.068 (0.063–0.072)	0.12 (0.12–0.13)	0.31 (0.30–0.31)	0.34 (0.34–0.34)		0.23		0.36 (0.35–0.38)	0.12 (0.12–0.13)	0.26 (0.23–0.28)	0.30 (0.26–0.33)	0.49 (0.46–0.51)	1.00
<i>C. eburneus</i>	3	48.0 (45.2–50.9)	0.011 (0.010–0.011)	0.070 (0.061–0.075)				0.38 (0.375–0.383)	0.35 (0.34–0.35)	0.20 (0.199–0.203)	0.43 (0.43–0.44)	0.16 (0.15–0.19)	0.22 (0.19–0.25)	0.50 (0.47–0.53)	0.73 (0.66–0.78)	1.00
<i>C. abbreviatus</i>	3	30.6 (21.1–31.2)	0.021 (0.019–0.021)	0.080 (0.070–0.096)				0.38 (0.34–0.42)	0.078	0.26 (0.21–0.30)	0.46 (0.42–0.48)	0.12 (0.12–0.15)	0.21 (0.18–0.25)	0.55 (0.47–0.55)	0.63 (0.61–0.66)	1.00
<i>C. marmoreus</i>	15	54.8 (33.3–80.0)	0.033 (0.029–0.038)	0.074 (0.065–0.093)				0.13 (0.11–0.15)	0.061	0.46 (0.41–0.50)		0.049 (0.038–0.076)	0.11 (0.08–0.13)	0.45 (0.39–0.65)	1.06 (1.03–1.11)	
<i>C. catus</i>	4	32.0 (26.0–36.0)	0.082 (0.071–0.099)	0.12 (0.10–0.13)	0.18 (0.17–0.19)	0.35 (0.33–0.38)			0.16			0.047 (0.042–0.053)	0.094 (0.090–0.100)	0.50 (0.45–0.54)	1.05 (1.04–1.06)	
Known range	in	genus	.01–.14	.03–.18	.05–.28	.18–.35	.31	.34	.09–.45	(.08–.66)	.07–.81	.30–.71	.02–.16	.30–.65	.45–.73	1.00–1.06

**Table 6.** Matrix of two-state characters of *Conus* radular teeth for the species discussed in this report. +, present; -, absent. Characters designated by lower-case letters are two-state characters only. Those designated by capital letters are also measured as quantitative characters (See text and Table 4).

Character No.	1	2	3	4	5	6	7	8	9	10
Character	Barb 1	Barb 2	Barb 3	Barb 4	Barb 5	Blade	Serration	Cusp	Waist	Spur
Species	<b>B1</b>	<b>B2</b>	<b>B3</b>	<b>B4</b>	<b>B5</b>	<b>BL</b>	<b>SE</b>	<b>cu</b>	<b>W</b>	<b>sp</b>
<i>C. acutangulus</i>	+	-	-	-	-	-	+	+	+	-
<i>C. australis</i>	+	-	-	-	-	+	+	+	-	+
<i>C. orbigny</i>	+	+	+	-	-	-	-	-	+	+
<i>C. californicus</i>	+	+	+	+	+	-	-	-	+	-
<i>C. eburneus</i>	+	-	-	-	-	-	-	-	-	+
<i>C. abbreviatus</i>	+	-	-	-	-	+	+	-	+	+
<i>C. marmoreus</i>	+	-	-	-	-	+	+	+	-	-
<i>C. catus</i>	+	+	+	-	-	-	-	-	-	-

(Fig. 1C,D). The waist of the *C. acutangulus* tooth is pronounced and located about 30% from the tip (Fig. 1A,D).

A striking feature of the *Conus acutangulus* tooth is that from the base the external fold is appressed to the shaft for only about the proximal 30% of its length. It then diverges distally to leave a long and rather broad adapical opening (Fig. 1A). When viewed with **B<sub>1</sub>** to the right and **SE** to the left, the shaft is markedly biconvex in outline, with a second waist just distal to the base (Fig. 1D). The tooth length is about 7 times maximum shaft width, shaft width/base width is ~0.53 (Table 5), and the minimum, i.e. waist width/base width, is ~0.18. The base is broad, ~18% of **T<sub>L</sub>** as measured on SEMs (Fig. 1A,D), but about 25% measured on specimens mounted on slides; the latter are most likely to orient with the broadest dimension parallel to the slide.

#### *Conus australis* Holten

*Conus australis* is traditionally assigned to the subgenus *Asprella* (e.g. Marsh and Rippingale, 1974), sometimes raised to genus level (e.g. Kira, 1965). The *C. australis* radular tooth (Fig. 2A) is about 1.2% as long as the shell (Table 5). A single barb extends from the tip to about 6% of total tooth length, terminating distal to the distal end of the serration. The serration consists of a row of about 12-14 rather large denticles and terminates some distance distal to a prominent cusp within the lumen (Fig. 2B). A long but narrow blade extends from the tip to 20-25% of the tooth length (Table 5). The tooth is about 10 times as long as wide (Table 5).

As in *C. acutangulus*, the external fold diverges from the shaft along much (about 60-65%) of its length, leaving a gap continuous with the apical opening. However, the external fold is appressed at the waist (Fig. 2A). Also as in *C. acutangulus*, there is a second waist just distal to the base. The base itself is not broad (maximum **SH<sub>w</sub>/BA<sub>w</sub>**~0.5; **BA<sub>w</sub>/T<sub>L</sub>**~ 0.2), is rather elongate, and bears a spur about 15% from the proximal end of the tooth (Fig. 2C).

#### *Conus orbigny* Audouin

*Conus orbigny* is traditionally assigned to the subgenus (e.g. Marsh and Rippingale, 1974) or genus (Kira, 1960) *Asprella*. The tooth (Fig. 3A) is extremely small, less than 1% of shell length. It has three barbs, extending respectively about 8%, 21%, and 30% proximally from the tip (Table 5). The first barb is opposite the other two, which are almost in line with each other and with the spur (Fig. 3B). The radular teeth of *C. saecularis* Melvill and *C. comatosa* Pilsbry, illustrated but not discussed by Rolán and Raybaudi Massilia (1994: Figs. 90, 91) are similar with respect to the number and arrangement of barbs and other features. Unlike *C. acutangulus* and *C. australis*, the external fold is appressed to the shaft, so the adapical opening is considerably shorter than in those species. There is no serration. The waist is less pronounced than in the other two species, about 50% of shaft width. The form of the base is similar to that of *C. australis*, being narrow (**SH<sub>w</sub>/BA<sub>w</sub>**~0.57; **BA<sub>w</sub>/T<sub>L</sub>**~0.17), elongate, and bearing a prominent spur (Fig. 3A,C).

*Generalist feeders.* In this section we discuss two species known to feed on an array of prey organisms that is unusually diverse for the genus. Kohn (1966) described the diet of *Conus californicus* as including 8 species each of gastropods, bivalves, and polychaetes, and one each of cephalopods, amphipods and fish. Its diet remains the most catholic of any known *Conus* species. While dietarily less diverse, *C. eburneus* is unusual in preying mainly on polychaetes like most other *Conus* species but also on fishes (Kohn and Nybakken, 1975).

#### *Conus californicus* Reeve

Piele (1939), Hanna (1963), and Nybakken (1970a) have illustrated and very briefly described the radular tooth of *Conus californicus*, generally regarded as unusual for the genus. Five barbs varying widely in



**Figure 6.** *Conus abbreviatus*, radular teeth. A and B. Entire teeth of the same individual shown at different magnifications; length 0.65 mm. The blade is oriented toward the viewer in A and toward the left in B. C. Detail of base, showing spur. Scale bar C = 0.1 mm. Specimen 31 × 20 mm, from Makapuu Point, Oahu, Hawaii.

shape are present, of which only the first and last are aligned (Fig. 4A). The adapical opening extends from distal to B1 to proximal to B3 (Figs. 4A,B). Although there is no serration, the large B2 occupies its usual place and may be homologous as a single very large denticle. B3 is opposite B1, in the position that B2 or a blade occupies in most *Conus* species (Fig. 4B). The tips of B4 and B5 are about one-third of the tooth length from the apex (Fig. 4C). The external fold also spirals about the long axis of the tooth more than in most species. The tooth lacks both cusp and spur. Nybakken (1970) described the base as 'large and rectangular.' The tooth length is about 5% that of the shell and the tooth is about 8 times as long as wide (Table 4).

#### *Conus eburneus* Hwass

The *Conus eburneus* radular tooth (Fig. 5) is small (about 1% of shell length) and robust (about 6 times as long as wide), bears a single barb extending about 7% of the tooth length (Fig. 5B), a weak blade on the opposite side extending 38% of the tooth length, and a complex serration of large denticles that is shorter than the blade (Fig. 5A; Table 5). No cusp is present at the proximal end of the serration. The adapical opening is broad and extends about 1/3 of the tooth length (Table 4), that is longer than in most species but shorter than in *C. acutangulus* and *C. australis*. The basal opening is broad and directed terminally, and a spur is present (Fig. 5C).

*Vermivorous feeders.* Most *Conus* species whose diets have been studied are more specialized predators on one of three main prey types: worms, mainly polychaetes, other gastropods, and fishes (Kohn, 1959). About 75% of Indo-Pacific species for which food in nature is known (N=58) are predators exclusively or predominantly of polychaetes. A few also include enteropneusts and echiurans in the diet, but no species of *Conus* have been reported to eat members of other worm phyla such as Sipuncula and Nemertea (Kohn and Nybakken, 1975; Reichelt and Kohn, 1985; Kohn, unpub. observations). Radular tooth form varies more among species of vermivores than in other *Conus* feeding groups. While several attributes of the teeth of vermivorous species likely relate to the particular polychaetes consumed, neither descriptive-correlative nor experimental studies

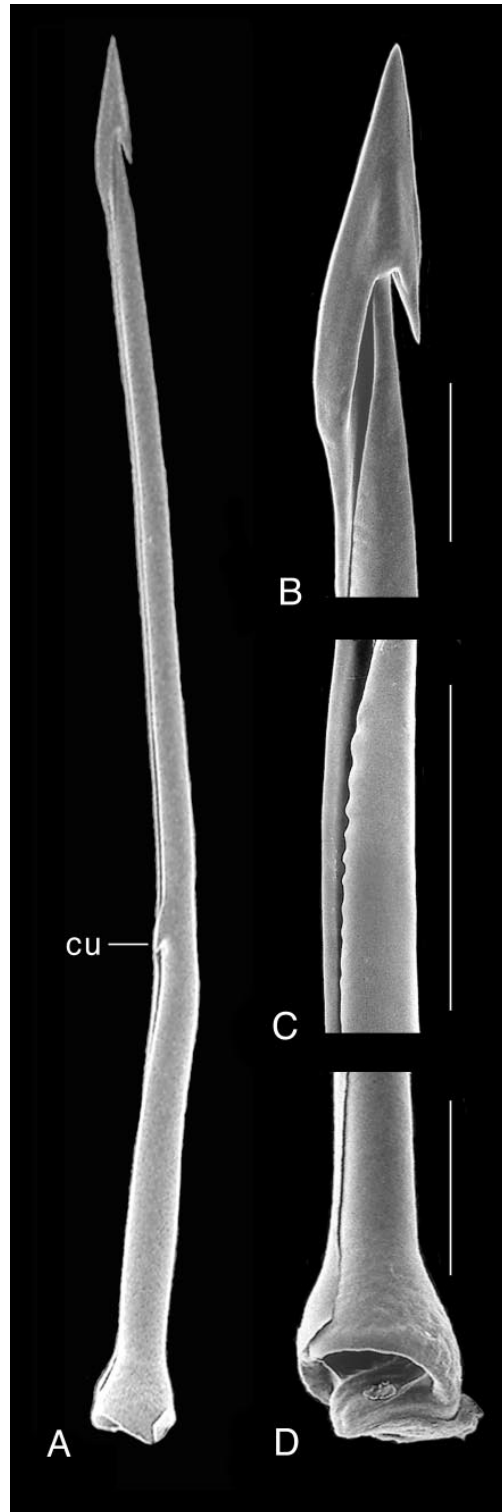
**Figure 7.** *Conus marmoreus* and *C. bandanus*, radular teeth. A. *C. marmoreus*, entire tooth; length 2.50 mm. B. *C. marmoreus*, detail of apex, showing barb to right, blade to left, and adapical opening in center. C. *C. bandanus*, detail of distal portion of serration, showing proximal end of adapical opening at top. D. *C. bandanus*, detail of base, showing basal opening. Scale bars in B, C and D: 0.1 mm. Tooth length in C and D, 1.51 mm. Specimen of *C. marmoreus* 80 × 43 mm, from lagoon, Majuro Atoll, Marshall Islands. Specimen of *C. bandanus* from Barking Sands, Oahu, Hawaii.

of this have yet been made. In general, the prey is impaled by the barb(s) at the apex of the radular tooth and venom is injected, the proboscis lip firmly grips the base of the tooth, and the proboscis shortens, drawing the worm into the expanded rhynchodeum (Kohn, 1998 and unpub. obs.). An early detailed functional morphological analysis (Kohn, Nybakken and Van Mol, 1972) described the radular tooth of *C. imperialis*, a trophically specialized vermivore whose robust and complex tooth is used to prey primarily on polychaetes of the family Amphinomidae (Kohn, 1959). Here our example is a simpler tooth but one whose basic features are common to most vermivorous *Conus* species.

#### *Conus abbreviatus* Reeve

A species endemic to Hawaii, *Conus abbreviatus* is traditionally placed in the subgenus *Virroconus* (Marsh and Rippingale, 1974). Its radular tooth (Fig. 6), about 2% as long as the shell, was also briefly described and illustrated by James (1980) and Rolán and Raybaudi Massilia (1994); the latter authors call it 'a typical vermivorous tooth.' The tooth is about 8 times as long as wide, and has a single barb (Fig. 6A) extending about 7% of the tooth length from the tip, and a narrow, obscure blade extending about 38% of tooth length (Table 5). The blade ends just distal to the waist of the tooth and projects toward the observer in Fig. 6A and to the left in Fig. 6B. The serration consists of a row of about 12 large denticles (not all visible in Fig. 6B) extending about 1/4 of the tooth length; the serration does not terminate in a cusp. The thickened base bears a spur (Fig. 6C), and the basal opening is directed terminally. The general similarity of this tooth and that of *C. eburneus* (Fig. 5, Table 5) suggests that the latter species is primarily also vermivorous, also supported by data on its diet in nature (Kohn & Nybakken, 1975).

*Molluscivorous feeders.* About 15% of Indo-Pacific *Conus* species for which food in nature is known are predators on other gastropods, pre-



dominantly other prosobranchs and sometimes including congeners, but not conspecifics (Lim, 1969; Kohn and Nybakken, 1975; Reichelt and Kohn, 1985; Kohn, unpub. obs.). Tooth function in molluscivorous species typically differs somewhat from that in vermivores. The latter use only one tooth to envenomate a prey organism. Molluscivores may use several (up to six observed in *C. textile*) in a single feeding episode, with the base of each tooth being freed from the proboscis and left in the body of the prey like a hollow arrow. The proboscis is then withdrawn, the rhynchodeum expanded into the aperture of the victim's shell and its body swallowed (Kohn, unpub. obs.).

#### *Conus marmoreus* Linnaeus

*Conus marmoreus* is the type species of the genus *Conus* (Kohn, 1992). Its radular tooth is about 3% as long as the shell, comparable to the vermivorous species described above, but considerably shorter than the teeth of other molluscivorous species (Nishi and Kohn, 1999). As in most molluscivores the tooth is very narrow—about 20 times as long as wide—curved, and rather simple, with one barb extending about 7% of the tooth length and one narrow blade about twice as long (Table 4, Figs. 7A,B). The serration extends for nearly half of the tooth length, terminating at the prominent cusp (Fig. 7A), but most of its many very fine and closely spaced denticles appear to be hidden under the external fold. They are visible with transmitted light but not in SEMs. Some of the more widely spaced distal denticles are visible just proximal to the adapical opening in *C. marmoreus* (Fig. 7A) and in the very closely related *C. bandanus*, whose radular tooth is almost identical to that of *C. marmoreus* (Fig. 7C). The *C. marmoreus* tooth lacks a definite waist. Its maximum base width is about twice the shaft width (Table 5) and is about 10% of tooth length measured from specimens mounted on slides, although it appears narrower when oriented as in Fig. 6A. In general the base of the teeth of molluscivorous species is narrower than in vermivorous species (Table 5; Nishi and Kohn, 1999).

*Piscivorous feeders.* About 10% of Indo-Pacific *Conus* species for which food in nature is known prey exclusively on fishes (Kohn, 1956; Kohn and Nybakken, 1975; Kohn, unpub. obs.). The mode of tooth function varies among piscivorous species. Several, including *C. striatus* Linnaeus and *C. catus*, discussed below, employ the tooth as a combined hypodermic needle and harpoon as in vermivorous species, impaling the prey, paralyzing it, and pulling it into the expanded rhynchodeum by contraction of the proboscis (Kohn, 1956). Others, e.g. *C. geographus* Linnaeus, engulf the prey prior to envenomation (Johnson and Stablum, 1971).

#### *Conus catus* Hwass

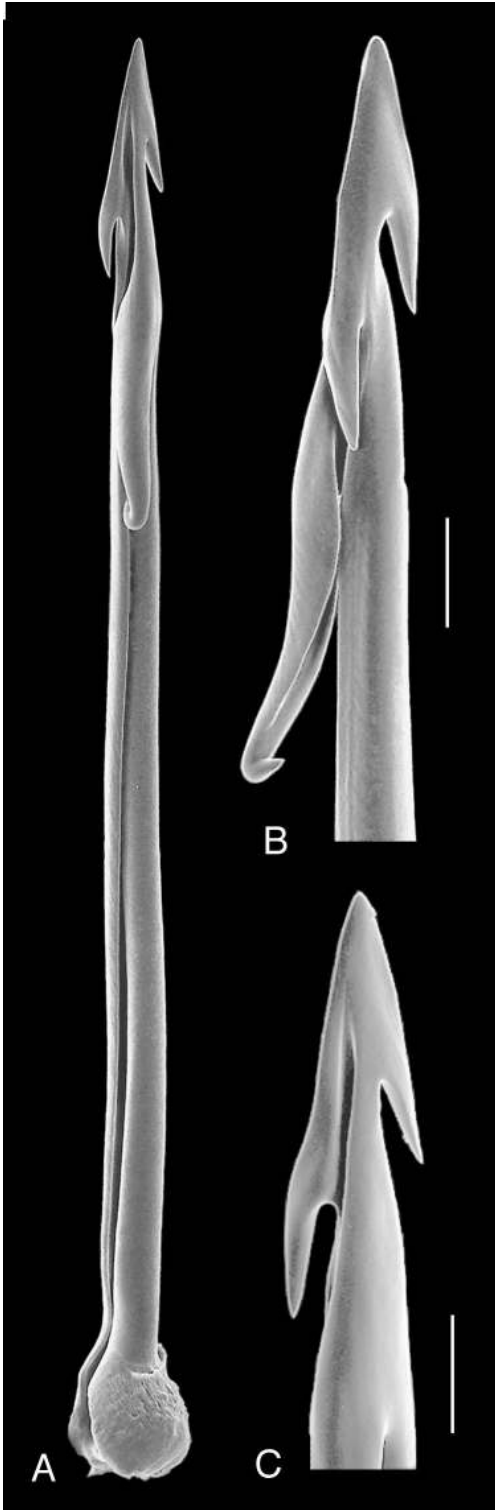
One of the smallest piscivorous species in the genus, *Conus catus* usually attains a maximum shell length of less than 50mm. It is traditionally assigned to the subgenus *Chelyconus* (Kira, 1965; Marsh and Rippingale, 1974). Radular teeth of piscivorous species are generally larger relative to body size than those of the other trophic groups; that of *C. catus* is about 8% of  $S_L$  and is elongate, about 20 times as long as wide. The tooth is equipped with three barbs, extending from the tip about 12%, 18% and 35% of tooth length (Table 5, Fig. 8). The proximal end of the largest barb is recurved as a hook (Fig. 8). The tooth lacks blade, serration, cusp and waist. Its maximum base width is about twice the shaft width and is about 9% of tooth length, similar to that of *C. marmoreus* (Fig. 7). In general the bases of the teeth of piscivorous species resemble those of molluscivores in being narrower and simpler than in vermivorous species (Kohn, unpub. obs.).

### STRUCTURAL CHARACTERS OF *CONUS* RADULAR TEETH AND THEIR CODING

*Continuous characters.* Although Table 5 lists 15 continuous radular tooth characters, for most *Conus* species the maximum is about 10, because the teeth of few species have more than two barbs and because two characters are not independent of others. The reasons for including the latter are given below. All characters except No. 15 are rendered as ratios of the smaller to larger measurement, and are thus coded as decimal fractions with a range of 0-1. Following character No. 1, the ratio of tooth length to shell length, the next 11 attributes are measured parallel to the long axis of the tooth, with tooth length as the denominator. Character No. 15 measures curvature, with absolute tooth as the numerator, so its minimum value is 1.0, for straight teeth. Table 5 also indicates all mean parameter values and their ranges in the rather small samples of the species considered in this report, as well as the range of values currently known for the genus as a whole, based on our preliminary survey of 118 species.

1. Relative tooth length. ( $T_L/S_L$ ). This character indicates the ratio of absolute tooth length to shell length, a commonly used measure of body size. Its range in the species studied here was about 1-8%. From our survey of 118 Indo-Pacific species, *C. leopardus* (Röding) and *C. orbigny* have the smallest tooth relative to body size (0.7%), and *C. geographus* Linnaeus (13%) and *C. obscurus* Sowerby (14%) have the largest.





**Figure 8.** *Conus catus*, radular teeth. A. Entire tooth, showing first barb to right, second barb to left, and third barb facing observer; length 2.0 mm. B. Detail of apex, showing recurved hook on third barb. C. Detail of apex oriented to show first and second barb and adapical opening. Scale bars in B and C: 0.1 mm. Specimen in A and B from Fort Kamehameha Reef, Oahu, Hawaii. Specimen in C 36 × 22 mm, from Milolii, Kauai, Hawaii.

2. Relative first barb length. ( $B1_i/T_L$ ). This is the length of  $B1$  from the tip of the tooth, measured parallel to the long axis of the tooth, to  $B1$ 's most proximal extent, divided by  $T_L$ . Except for the unusually long barb (18% of tooth length) of *C. acutangulus*, it ranged from 3% in *C. ammiralis* Linnaeus, *C. canonicus* Hwass and *C. textile* Linnaeus to 12% in *C. catus*, *C. striolatus* Kiener, and *C. thalassiarchus* Sowerby.

3. Relative second barb length. ( $B2_i/T_L$ ). Measured as in Character No. 2, it ranged from 12% in *C. californicus* to 21% in *C. orbigny*. In molluscivorous species with a second barb (unlike *C. marmoreus*), it is usually shorter (e.g., 5-6% in *C. textile*, *C. ammiralis*, and *C. canonicus*; Nishi and Kohn, 1999), and it is very long (28%) in *C. planorbis* Born.

4. Relative third barb length. ( $B3_i/T_L$ ). Also measured as in Character No. 2, it ranged from 18% in *C. californicus* to 35% in *C. catus*. The only other species with a third barb that we have observed is *C. orbigny*, where it extends 30% of tooth length (Table 4).

5. Relative fourth barb length. ( $B4_i/T_L$ ). Also measured as in Character No. 2, this character occurred only in *C. californicus* (31%) of the species studied. To our knowledge, no other species of *Conus* has a fourth barb.

6. Relative fifth barb length. ( $B5_i/T_L$ ). Also measured as in Character No. 2, this character occurred only in *C. californicus* (34%) of the species studied, and to our knowledge no other species of *Conus* has a fifth barb.

7. Relative blade length. ( $BL_i/T_L$ ). Also measured as in Character No. 2, this character occurred in four of the eight species studied; it ranged from 13% in *C. marmoreus* to 38% in *C. abbreviatus*. The longest blade we have seen extends 45% of tooth length in *C. characteristicus* Fischer, and the shortest is only 9%, in *C. furvus*. Rolán and Raybaudi Massilia (1994) also reported that the blade of *C. bruuni* Powell is 9% of tooth length.

8. Relative length of adapical opening. ( $AO_i/T_L$ ). Always present, the adapical open-

ing ranged in length relative to the tooth in the species studied from 8% in *C. abbreviatus* to 66% in the unusually openly coiled tooth of *C. acutangulus*. This is similar to the teeth of many turrids (Taylor, Kantor and Sysoev, 1993) and may be a primitive character state.  $\mathbf{AO}_L$  usually cannot be measured accurately on slide-mounted teeth examined with transmitted light. For this reason we measured it only on SEM's, and this usually resulted in only a single measurement for each species.

9. Relative length of serration. ( $\mathbf{SE}_L/\mathbf{T}_L$ ). Five of the species described here have serrated teeth, although as noted above it is possible that the second barb of *C. californicus* is homologous with the serration rather than with the second barb of other species. Among the species studied,  $\mathbf{SE}_L/\mathbf{T}_L$  ranged from 7% in *C. acutangulus* to 46% in *C. marmoreus*. In other molluscivorous species it is much longer (to 81% in *C. textile*) but the denticles are very fine (Nishi and Kohn, 1999).

10. Relative length of waist. ( $\mathbf{W}_L/\mathbf{T}_L$ ). In teeth with a definite constriction,  $\mathbf{W}_L$  corresponds with the 'anterior part' (PA) of Rolán and Raybaudi Massilia (1994), and they reported its value for about 30 species. The teeth of six of the species studied here have waists, the exceptions being those of the molluscivorous and piscivorous species. In those with waists,  $\mathbf{W}_L/\mathbf{T}_L$  ranged from 30% in *C. acutangulus* to 46% in *C. australis* and *C. abbreviatus*. The largest reported value is 71%, for *C. bruuni* (Rolán and Raybaudi Massilia, 1994), and all other values they reported were greater than 30%.

11. Relative width of shaft. ( $\mathbf{SH}_w/\mathbf{T}_L$ ). This measure of overall tooth stoutness was generally considerably lower in the specialized piscivorous and molluscivorous species than in the others, i.e., longer teeth are generally narrower, and it is probably bimodally distributed. It was 5% in *C. catus* and *C. marmoreus* and is similar or even less (2.3% in *C. textile*) in other members of their trophic types. It ranged from 9% to 16% in the other species studied, with *C. eburneus* the most robust.

12. Relative width of base. ( $\mathbf{BA}_w/\mathbf{T}_L$ ). This also estimates overall tooth stoutness, based on base width rather than shaft diameter. Like  $\mathbf{SH}_w/\mathbf{T}_L$ , it is generally considerably lower in the specialized piscivorous and molluscivorous species (4-9% in 90% of species) than in the others (10-27% in 87% of species) and is probably bimodally distributed in the genus.

13. Relative width of waist to shaft. ( $\mathbf{W}_w/\mathbf{SH}_w$ ). This measure of minimum to maxi-

mum shaft width indicates the relative prominence of the waist, when one is present. In the six species with a definite waist, its value ranged from 30% in *C. californicus* to 65% in *C. australis*. All other species we examined had values intermediate between these extremes.

14. Relative width of shaft to base. ( $\mathbf{SH}_w/\mathbf{BA}_w$ ). This inverse measure of maximum base width relative to maximum shaft diameter was also low in some molluscivorous species (45-48% in *C. bandanus*, *C. marmoreus*, and *C. araneosus* [Lightfoot]) as well as in *C. californicus* (49%) and the three putatively primitive species (50-57%). *C. eburneus* and other molluscivores (*C. omaria* Hwass, *C. pennaceus* Born) had the highest shaft-to-base ratio (73%).  $\mathbf{SH}_w/\mathbf{BA}_w$  is often underestimated from the SEM's in this report, as most are not oriented so as to show the maximal extent of base width. Because Character Nos. 11 and 12 relate shaft diameter and base width to tooth length, and because Character No. 14 relates shaft diameter to base width, only two of these three characters are logically independent. We include all three because while No. 11 distinguished several species in this study, we found No. 12 a more effective species-level discriminator within the molluscivorous group (Nishi and Kohn, 1999).

15. Curvature. ( $\mathbf{T}_L/\mathbf{ST}_L$ ). This measure of the absolute length of the tooth relative to the straight-line distance between its extremities may be an artifact of preservation when it is very large (see above). It is generally correlated with both absolute and relative tooth length.  $\mathbf{T}_L/\mathbf{ST}_L$  exceeded 1.0 only in the two longest teeth studied here, *C. marmoreus* (1.06) and *C. catus* (1.05). The teeth of other molluscivorous species are similarly curved (Nishi and Kohn, 1999). Curvature in the two other species discussed here that appear to be curved, *C. australis* (Fig. 2), and *C. orbigny* (Fig. 3) was less than 1%.

*Discrete characters.* Radular teeth of all *Conus* species share certain qualitative features. The tooth is a sheet of chitin formed as a rolled-up, hardened shaft, differentiated to form a broadened, thickened base at the proximal end and a sharply pointed distal apex. All have a basal opening through which venom enters, and an adapical opening through which the venom is injected into the body of the prey. The following characters do not occur in the teeth of all species. For those whose teeth we describe in this report, they are coded as present (+) or absent (-) in Table 6.

1-5. Barbs. (**B1-B5**). Most *Conus* species, including all described in this report, have at least one barb near the apex of the tooth. However some barbless teeth occur in the vermivorous trophic group, for example *C. ebraeus* Linnaeus (Troschel, 1866; Nybakken, 1990). The maximum number of barbs in any species of *Conus* is five, known only in the 'unique type' of tooth (Nybakken, 1990) of *C. californicus*. Considering each barb as a presence-absence character gives five two-state barb characters.

6. Blade. (**BL**). *Conus* teeth have no or one blade, a long cutting edge that contrasts with the barbs by making an obtuse rather than an acute angle with the shaft.

7. Serration. (**SE**). If present, serration extends from the adapical opening to the blade or waist. Because it may be interrupted, as in some molluscivorous species (Nishi and Kohn, 1999), one could also consider serration a three-state character, present and continuous, present and discontinuous, or absent.

8. Cusp (**cu**). If present, the cusp is usually at the proximal end of the serration, although there may be a gap between the two (Fig. 2).

9. Waist. (**W**) A waist is present if the shaft of the tooth is constricted at one point (or occasionally at two, in which case the waist is the more distal). It is absent if the shaft is uniform in width throughout.

10. Spur. (**sp**) A spur is present if the distal portion of the base bears a distally oriented tooth-like projection. It is absent if the distal portion of the base is smoothly rounded.

## DISCUSSION

The genus *Conus* has radiated remarkably since its early Eocene origin to its modern status as perhaps the largest genus of marine invertebrates (Kohn, 1990; Röckel *et al.*, 1995). While this has made *Conus* an attractive subject for comparative studies of ecology, development, and biochemistry (Kohn, 1998), inferences from such studies remain limited by persistent species-level taxonomic confusion and the lack of a phylogenetic framework. If an objective phylogenetic hypothesis for the genus is to be advanced in the future, clearly defined characters and a coding system for their states are prerequisites.

Here we have taken steps in those directions by initiating comparative morphological and morphometric analyses of an easily accessible and potentially useful but heretofore under-

utilized character set, the radular teeth, using a sample of seven species to represent the wide range of variation present in the genus. We have sought to expand the set of available objective taxonomic characters and to code their states so that they can be of use in distinguishing very similar species (Nishi and Kohn, 1999) and contribute to generating the first objective phylogenetic hypothesis for this unusually species-rich genus.

Although the *Conus* radular tooth is a single structure, it has several semiautonomous components that differ qualitatively and vary widely quantitatively among species (Tables 5, 6). The tooth thus has some properties of structures with independent elements (Vermeij, 1974). This plasticity likely enables the components to evolve independently to some extent, thus enhancing the scope for evolutionary diversification and facilitating their potential utility for phylogenetic analysis.

Prior workers back to Troschel (1866) have identified sets of salient features of *Conus* radular teeth, including both continuous and discrete characters, and we have largely maintained their usage. Troschel (1866) used one character of each type for his primary division of the 11 species he considered into those with long, narrow teeth (length > 20X width, and without a spur on the base), and relatively shorter, broader teeth (length ≤ 20X width, with a spur). Twentieth-century studies (Endean and Rudkin, 1965; Nybakken, 1990) showed that this effectively divided the genus into functional feeding types, the first group containing specialized molluscivorous and piscivorous species, and the second, vermivorous and generalist predators. Subsequent studies, including Rolán and Raybaudi Massilia (1994), the results reported here, and Nishi and Kohn (1999) have greatly expanded the number of species examined, and they show that although continuous, Troschel's primary character essentially represents a fixed difference and thus remains a useful and valid discriminant. His primary presence-absence character, the spur, is indeed absent from the very long teeth of molluscivores and piscivores, but it is not present in all of the vermivorous species with shorter teeth. Subsequent to Troschel, the several attempts to group *Conus* species according to radular tooth characters have been inconsistent in their use of characters and states, in whether or not they included keys, in the sets of species they considered, and in the systems used to designate groups (Tables 2, 3, 6).

We (and Rolán and Raybaudi Massilia, 1994)

have begun to determine radular tooth morphometric characters of many species of *Conus*. Our database, available electronically from the first author, presently comprises 118 mainly Indo-Pacific species or about 35% of that region's species and less than 25% of the extant species in the genus (Röckel *et al.*, 1995). It has provided the summaries of ranges for values given in the last row of Table 5. In addition to Troschel's (1866) tooth length/width character (equivalent to our Character No. 11, relative width of shaft or  $SH_w/T_L$ ), some other characters are strongly bimodally distributed in this sample. These include No. 1, relative tooth length ( $T_L/S_L$ ), and No. 12, relative width of base ( $BA_w/T_L$ ). If the pattern of bimodality persists when more species are sampled, it may be possible to code these unambiguously as two-state characters and avoid the problems inherent in coding continuous variables for objective phylogenetic analysis (e.g. Strait, Moniz and Strait, 1996).

More thorough studies of radular teeth of more species and the use of these, other morphological, and molecular character sets to generate phylogenetic hypotheses are needed to clarify the classification of the genus *Conus* into species groups. At present, we believe that little is to be gained from a more detailed attempt to organize species according to their radular tooth characters alone. Only with multiple datasets can we assess the utility of tooth characters in improving understanding of the phylogeny of *Conus* and the evolution of its structurally and functionally specialized radula.

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