

Radular morphology of *Conus* (Gastropoda: Caenogastropoda: Conidae) from India

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Abstract

Radular morphologies of 22 species of the genus *Conus* from Indian coastal waters were analyzed by optical and scanning electron microscopy. Although the majority of species in the present study are vermivorous, all three feeding modes known to occur in the genus are represented. Specific radular-tooth structures consistently define feeding modes. Species showing similar feeding modes also show fine differences in radular structures. We propose that these structures will be of value in species identification in cases of ambiguity in other characteristics. Examination of eight discrete radular-tooth components has allowed us to classify the studied species of *Conus* into three groups. We see much greater inter-specific differences amongst vermivorous than amongst molluscivorous and piscivorous species. We have used these differences to provide a formula for species identification. The radular teeth of *Conus araneosus*, *C. augur*, *C. bayani*, *C. biliosus*, *C. hyaena*, *C. lentiginosus*, *C. lorisii*, and *C. malacanus* are illustrated for the first time. In a few cases our study has also enabled the correction of some erroneous descriptions in the literature.

Key words: cone snail, taxonomy, radula, scanning electron microscopy, feeding modes.

Introduction

A need for an unambiguous taxonomic classification of species of *Conus* Linnaeus, 1758 has become highly relevant due to the use of *Conus* venom in neurobiological research and in drug discovery (e.g., Terlau and Olivera 2004). The toxin composition of *Conus* venom is species specific. Similar or nearly identical constituents possibly exhibit distinct biological activities, considered worthy of clinical application (Jones *et al.* 2001; Livett *et al.* 2004), necessitating accurate species identification (Nishi and Kohn 1999). Precise identification of *Conus* species and their feeding habits are also required in molecular studies of evolutionary relationships within this genus (Duda *et al.* 2001). Although molecular markers have started to play an important part (Blaxter 2003, 2004; Hebert *et al.* 2003; Stoeckle 2003), morphology and other biological information continue to be the primary means of identification (Schander and Willassen 2005).

Presently, determination of *Conus* species is based mostly on the morphology and colour of the shell (Kohn *et al.* 1999). Species determination of live cone snails using shell characters poses some difficulties due to regional and intra-specific variation. Moreover, the periostracum is often thick and opaque and covers the whole shell hiding the colour pattern beneath. Although the periostracum can be removed by chemicals such as concentrated KOH, these treatments are likely to affect shell colour patterns and are impractical with live specimens. Also, specimens are often lacking a protoconch and the colour pattern may be faded or completely lost.

Not only are the venom components highly species specific, geographic and age-related variations have also

been reported (e.g. Bingham *et al.* 1996). Thus, even minor imprecision in species identification may have unwarranted consequences, given that it is possible to characterize 100–200 venom peptides from a single specimen (Olivera 2002). In order to circumvent some of these problems, reliable non-shell characters are needed for species identification. The radula is a useful potential source of such characters.

The shapes and structures of molluscan radular teeth are often unique to a species or a genus and these structures have traditionally been one of the most widely used sources of data for studies on molluscan systematics. Some features of the radula have also been used to study higher level molluscan taxonomic relationships (e.g., McLean 1971, Lindberg 1981, Shimek and Kohn 1981). Piele (1939), Azuma (1964), Lim (1969) and Nybakken (1990) have classified *Conus* species into different feeding modes and groups by studying radular structures. Using quantitative and qualitative characters, Nishi and Kohn (1999) established three distinct groups of radular structures in 11 species of molluscivorous *Conus*, proposing that teeth characters are potentially useful in differentiating species. The radular teeth of *Conus* are single structures with many component characters that differ quantitatively and qualitatively among the species (Kohn *et al.* 1999). Earlier work on *Conus* (Troschel 1866; Bergh 1895; Nybakken 1970, 1990; James 1980; Kohn 1959, 1978; Kohn *et al.* 1972, 1999; Rolan and Massilia 1994a, b; Nishi and Kohn 1999; Rolan 2000) described a remarkable range of structures in their radular tooth morphology. There have been a few previous descriptions of radular teeth of *Conus* based on Indian material (Piele 1939; Azuma 1964; Ramu *et al.* 1996; Nishi and Kohn 1999). While it is clear that characters such as the

foot and proboscis colour patterns and colour and the sculptural and shape details of the shell will continue to be the mainstay of identification, the morphology and morphometry of radular teeth will strengthen the accuracy of species identification. With this end in view we provide an analysis of key features of Indian *Conus* radulae that will assist with species identification based on radular teeth characteristics for the cone snails studied. The genus is diverse in Indian waters. Kohn (1978) reported 48 species of *Conus* from India but recently increased the number to 77 (Kohn 2001; Hylleberg and Kilburn 2003).

Materials and methods

Preparation of teeth for optical microscopy. Specimens of 22 species of genus *Conus* were collected from locations in the west and east coasts of India (Table 1). Species were identified from Rockel *et al.* (1995). Radular sacs were removed from the body cavities and stored in 70% ethanol. From each specimen, 1-6 mature radular teeth were taken from the short arm of the radular sac for morphometric analysis. The teeth were cleaned in dilute sodium hypochlorite solution (20%) followed by double distilled water. Cleaning was repeated two or three times until the soft tissues were completely dissolved, leaving the radula intact. The teeth were mounted in water on glass slides and observed under a compound microscope as described by Kohn *et al.* (1999). Tooth lengths were measured with an optical micrometer to the nearest 0.1 mm. The ratio of shell to tooth length was determined as the mean of values for six teeth taken from a single healthy specimen, with several more specimens examined for broad consistency. Illustrations of radular teeth were made using a camera lucida attachment to the microscope. The proportions of component tooth characters were measured in relation to total tooth length (Table 2). Typical radular teeth showing the tooth characters are illustrated in Figure 1. Radular teeth from all 22 species examined are diagrammatically represented in Figure 7 as an aid for species comparison. Specimens of each species reported here are deposited in the Marine Biological Museum of Annamalai University (MBMAU), Tamilnadu, India. Voucher specimens with repository collections and available data are listed in Table 1.

Preparation of teeth for SEM. The radular teeth were dehydrated in increasing concentrations of ethanol from 10% to absolute ethanol and air-dried. The teeth were subsequently fixed, with the help of a sharp tipped needle, on to double sided tape fixed to SEM stubs. The SEM stubs were then coated with gold and observed on a JEOL JSM-840 scanning electron microscope.

Feeding observations. A large aquarium of about 100 liters capacity was set up at the marine research station in Porto Novo. The aquarium had a bottom substrate of sand and was filled with sea water maintained at a temperature of about 22°C. Each feeding sequence was visually observed and notes were taken. *Conus betulinus*, *C. figulinus* and *C. lentiginosus* were seen while devouring their prey, nereid and

unidentified polychaetes. We did not observe an obvious instance of prey paralysis in these cases. *Conus betulinus* took about 90 minutes to engulf a 20 cms long active non-paralysed nereid. *Conus araneosus* was observed to feed on neritid gastropod; indigestible shell pieces permitted subsequent identification. Although actual capture of fish by *Conus achatinus* was never observed, small marine fish introduced into the aquarium disappeared during night hours and pellets of fish scales were found scattered on the bottom substrate.

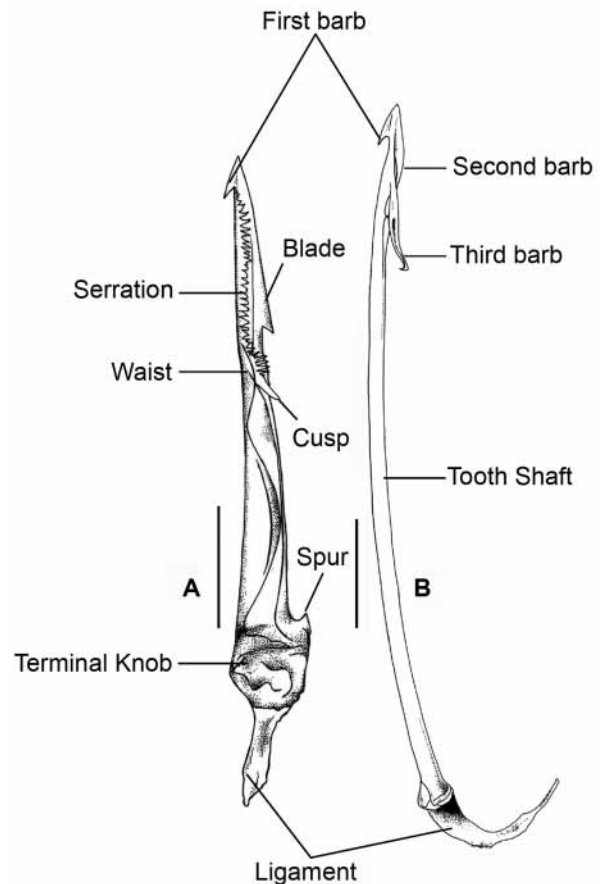


FIGURE 1. Typical radular teeth showing component characters. **A.** *Conus leopardus*. **B.** *C. achatinus*. Scale bars: A = 0.24 mm; B = 1.71 mm.

Results

Description of radular tooth structures.

Conus achatinus Gmelin, 1791

There are three barbs at the tooth apex, two short (Figs 2A; 3A, B, C) and a third which is long with a recurved tip. The long shaft lacks serration and cusp. The shaft ends in an enlarged terminal knob without a spur. Radular teeth of *C. achatinus* resemble those reported for *Conus magus* Linnaeus, 1758, *C. striatus*, *C. catus* Hwass, 1792 and *C. aurisiacus* Linnaeus, 1758 (James 1980). It has been reported that this species feeds on small fishes (Rockel *et al.* 1995). We have also observed *C. achatinus* in our aquarium feeding exclusively on small fish.

TABLE 1. Species included in this study with localities of samples, followed by depth, date of collection, latitude and longitude, voucher number and number of specimens. **MBMAU:** Marine Biological Museum of Annamalai University, Tamilnadu, India. *Minimum depth.

<u>Genus species</u>	<u>Author, date</u>	<u>Locality</u>	<u>Depth*</u> (Meters)	<u>Date of collection</u>	<u>Latitude</u>	<u>Longitude</u>	<u>Voucher number</u>	<u>Number of specimens examined</u>
<i>Conus achatinus</i>	Gmelin, 1791	Colaba Coast, Bombay, India	15	20 Oct. 2003	18° 53' N	72° 48' E	MBMAU101	5
<i>Conus amadis</i>	Gmelin, 1791	Cuddalore, Tamilnadu, India	18	12 Mar. 2004	11° 42' N	79° 48' E	MBMAU104	12
<i>Conus araneosus</i>	Solander [in Lightfoot] 1786	Periyakuppam, Gulf of Mannar, India	20	28 Nov. 2004	11° 29' N	79° 47' E	MBMAU105	16
<i>Conus augur</i>	Hwass [in Bruguière] 1792	Yerwadi, Gulf of Mannar, India	12	20 Mar. 2003	9° 16' N	78° 53' E	MBMAU108	8
<i>Conus bayani</i>	Jousseaume 1872	Cuddalore, Tamilnadu, India	24	8 Dec. 2002	11° 42' N	79° 48' E	MBMAU111	14
<i>Conus betulinus</i>	Linnaeus 1758	Mandapam, Gulf of Mannar, India	30	5 Mar. 2003	9° 17' N	79° 8' E	MBMAU113	18
<i>Conus biliosus</i>	Roding 1798	Keelakarai, Gulf of Mannar, India	25	18 Dec. 2003	9° 14' N	78° 50' E	MBMAU114	9
<i>Conus characteristicus</i>	Fischer 1807	Cuddalore, Tamilnadu, India	20	12 Mar. 2004	11° 42' N	79° 48' E	MBMAU115	6
<i>Conus figulinus</i>	Reeve 1849	Cuddalore, Tamilnadu, India	30	12 Mar. 2004	11° 42' N	79° 48' E	MBMAU123	12
<i>Conus hyaena</i>	Hwass [in Bruguière] 1792	Colaba Coast, Bombay, India	12	8 Nov. 2004	18° 53' N	72° 48' E	MBMAU127	8
<i>Conus inscriptus</i>	Reeve 1843	Palayar, Tamilnadu, India	40	6 Jan. 2003	11° 26' N	79° 59' E	MBMAU129	24
<i>Conus lentiginosus</i>	Reeve 1844	Colaba Coast, Bombay, India	21	8 Nov. 2004	18° 53' N	72° 48' E	MBMAU130	9
<i>Conus leopardus</i>	Röding 1798	Keelakarai, Gulf of Mannar, India	32	20 Mar. 2002	9° 14' N	78° 50' E	MBMAU131	11
<i>Conus loroisii</i>	Kiener 1845	Mandapam, Gulf of Mannar, India	14	27 Feb. 2003	9° 17' N	79° 8' E	MBMAU135	14
<i>Conus malacanus</i>	Hwass [in Bruguière] 1792	Palayar, Tamilnadu, India	42	29 Dec. 2002	11° 26' N	79° 59' E	MBMAU137	8
<i>Conus monile</i>	Hwass [in Bruguière] 1792	Cuddalore, Tamilnadu, India	16	5 Apr. 2004	11° 42' N	79° 48' E	MBMAU142	12
<i>Conus striatus</i>	Linnaeus 1758	Keelakarai, Gulf of Mannar, India	24	15 Dec. 2003	9° 14' N	78° 50' E	MBMAU149	10
<i>Conus terebra</i>	Born 1778	Keelakarai, Gulf of Mannar, India	15	20 Mar. 2002	9° 14' N	78° 50' E	MBMAU152	14
<i>Conus tessulatus</i>	Born 1778	Palayar, Tamilnadu, India	22	6 Jan. 2003	11° 26' N	79° 59' E	MBMAU153	8
<i>Conus textile</i>	Linnaeus 1758	Keelakarai, Gulf of Mannar, India	35	12 Mar. 2003	9° 14' N	78° 50' E	MBMAU154	6
<i>Conus virgo</i>	Linnaeus 1758	Keelakarai, Gulf of Mannar, India	12	20 Mar. 2002	9° 14' N	78° 50' E	MBMAU159	11
<i>Conus zeylanicus</i>	Gmelin 1791	Cuddalore, Tamilnadu, India	22	5 Apr. 2004	11° 42' N	79° 48' E	MBMAU160	15
Total								250

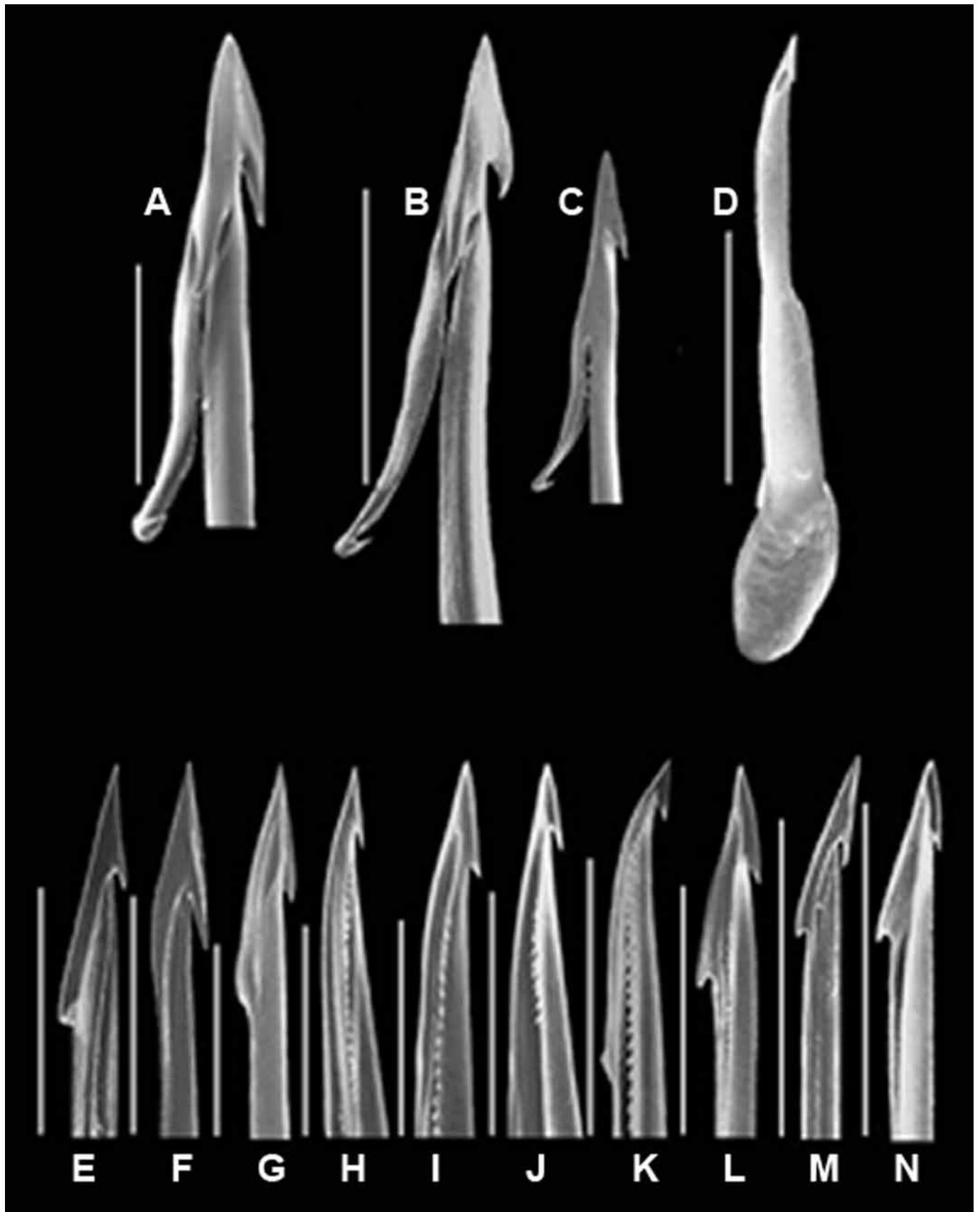


FIGURE 2. Scanning electron micrographs of radular teeth of *Conus* species. **A.** *C. achatinus*. **B.** *C. striatus*. **D.** *C. lentiginosus*. **E.** *C. amadis*. **F.** *C. araneosus*. **G.** *C. biliosus*. **H.** *C. characteristicus*. **I.** *C. inscriptus*. **J.** *C. lorioisii*. **K.** *C. monile*. **L.** *C. terebra*. **M.** *C. textile*. **N.** *C. virgo*. Scale bars: A = 1 mm; B = 2 mm; D = 100 μ m; E = 200 μ m; F = 200 μ m; G = 200 μ m; H = 100 μ m; I = 100 μ m; J = 200 μ m; K = 300 μ m; L = 200 μ m; M = 300 μ m; N = 300 μ m.

TABLE 2. Classification of *Conus* species based on radular teeth characters.

Tooth characters	Group	Species included	Prey species
Three Barbs; third barb with recurved tip; serration, waist, cusp and spur absent.	A	<i>C. achatinus</i> and <i>C. striatus</i>	fishes
One barb and one blade or blade replaced by a second barb, serrations longer terminate in to a prominent cusp, with or without waist, spur absent.	B	<i>C. amadis</i> , <i>C. araneosus</i> and <i>C. textile</i> .	molluscs
One barb and one blade or blade replaced by a second barb, with serration, with or without waist, spur present.	C	<i>C. augur</i> , <i>C. bayani</i> , <i>C. betulinus</i> , <i>C. biliosus</i> , <i>C. characteristicus</i> , <i>C. figulinus</i> , <i>C. hyaena</i> , <i>C. inscriptus</i> , <i>C. lentiginosus</i> , <i>C. leopardus</i> , <i>C. loisii</i> , <i>C. malacanus</i> , <i>C. monile</i> , <i>C. terebra</i> , <i>C. tessulatus</i> , <i>C. virgo</i> and <i>C. zeylanicus</i> .	worms

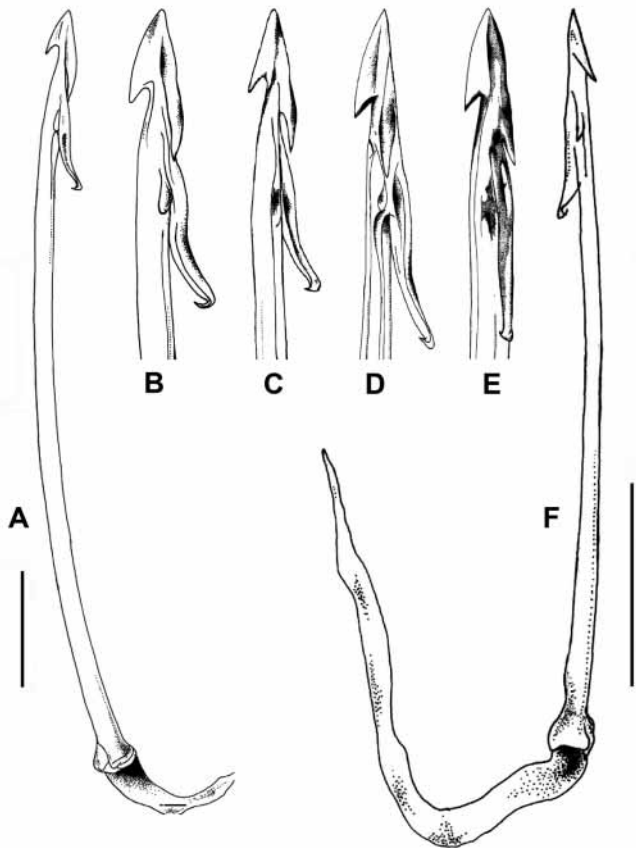


FIGURE 3. Radular teeth of *Conus* species. **A.** *C. achatinus* (entire); **B, C.** *C. achatinus* (apex enlarged). **D, E.** *C. striatus* (apex enlarged). **F.** *C. striatus* (entire). Scale bars: A = 1.71 mm; F = 3.87 mm.

Conus amadis Gmelin, 1791

There is one barb and one blade at the tooth apex (Figs 2E; 4B) with the serration terminating in a cusp. There is a distinct waist distal to the centre of the tooth shaft. The terminal knob lacks a spur. Nishi and Kohn (1999) reported the absence of a spur on the radular teeth of 11 species of molluscivorous species including *Conus araneosus* and *C. textile* (also this study—see below). Lim (1969) and Nybakken (1990) have suggested that *C. amadis* is a molluscivorous species but no direct observations on feeding have been reported.

Conus araneosus Solander [in Lightfoot], 1786

There is one barb and a short blade at the tooth apex (Figs 2F; 4A) with a serration terminating in a cusp just distal to centre of the tooth shaft. A waist is seen distal to the cusp but it is less prominent than in *Conus amadis*. The terminal knob lacks a spur. Our observations are in agreement with earlier observations of Nishi and Kohn (1999). The tooth configurations of *C. amadis* and *C. araneosus* were similar, but the structure of the short blade (Figs 2E, F; 4A, B) distinguishes them. The alimentary track of one specimen was reported to contain remains of columbellid snail, probably *Pyrene testudinaria* Link, 1807 (Kohn 1978). We have observed this species feeding on neritid gastropods.

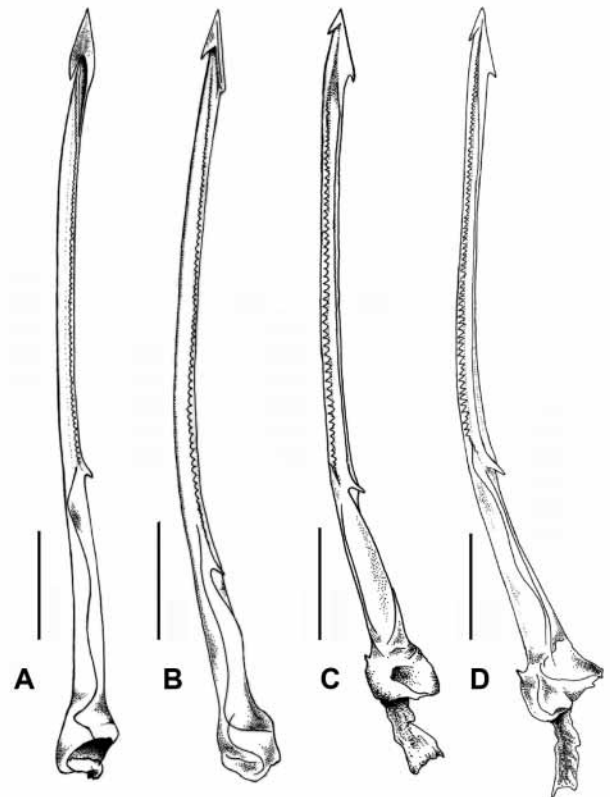


FIGURE 4. Entire radular teeth of *Conus* species. **A.** *C. araneosus*. **B.** *C. amadis*. **C.** *C. terebra*. **D.** *C. virgo*. Scale bars: A = 0.39 mm; B = 0.47 mm; C = 0.37 mm; D = 0.03 mm.

Conus augur Hwass [in Bruguière], 1792

There is one barb and one blade at the tooth apex (Fig. 5A). A distinct waist constricts the tooth at the middle of the shaft. The serration is longer than the blade with prominent

denticles but no cusp. An enlarged terminal knob bears a distinct basal spur. No observations on feeding have been reported.

Conus bayani Jousseaume, 1872

The tooth apex of *Conus bayani* possess one barb and a long blade on the opposite side (Fig. 5B) extending one third of the shaft length. The serration ends in a cusp. The terminal knob bears a sharp spur. No observations on feeding have been reported.

Conus betulinus Linnaeus, 1758

The tooth apex bears a barb and on the opposite side there is a blade that extends posteriorly and is terminated by a barb (Fig. 5C). The anterior part of the tooth is longer than the posterior and has serration. A cusp is absent but a distinct waist and a prominent spur are present on the tooth shaft. Nybakken (1990) included this species in Type 1 of his classification, characterized by a prominent cusp. Our observations of several specimens (Table 1) failed to reveal a cusp in teeth of *C. betulinus*. Kohn (1978) reported that this species feeds on the capitellid polychaete *Dasybranchus caducus* Grube, 1846. We observed this species feeding on nereids.

Conus biliosus Röding, 1798

This species is characterized by the presence of a single barb and a short blade at the apex (Figs 2G; 6H) and there is no serration, waist or cusp. The terminal knob possesses a prominent spur. The tooth morphology of *C. biliosus* was previously not described. Kohn (1978) has reported this species feeds on eunicid and nereid polychaetes.

Conus characteristicus Fischer, 1807

The tooth has one barb and a blade (Figs 2H; 5D) at the apex. A distinct constriction at the mid-point of the shaft forms the waist. The serration terminates at approximately the same place as the blade and a cusp is absent. The terminal knob bears a stout spur. No observations on feeding have been reported.

Conus figulinus Reeve, 1849

There is one barb at the tooth apex and a blade on the opposite side (Fig. 5E). The serration is longer than the blade and terminates at the region of the waist. The terminal knob has a prominent spur. Our observations agree with the illustrations of *Conus figulinus* by Piele (1939). It has been reported that this species feeds on polychaetes (Kohn 1960; Endean and Rudkin 1965). *Conus figulinus* was observed to feed on polychaetes in our aquarium.

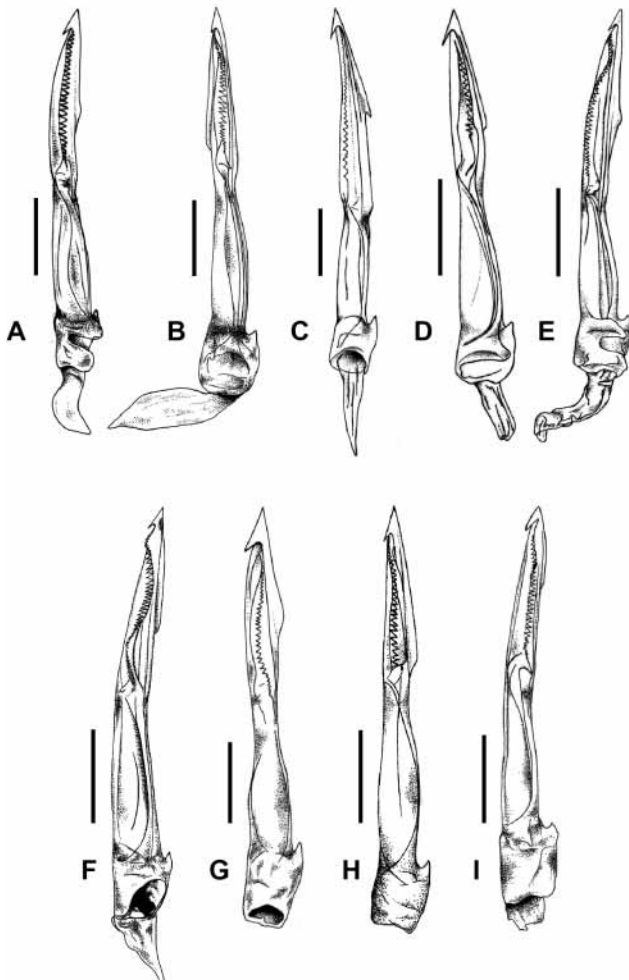


FIGURE 5. Entire radular teeth of *Conus* species. A. *C. augur*. B. *C. bayani*. C. *C. betulinus*. D. *C. characteristicus*. E. *C. figulinus*. F. *C. lorisii*. G. *C. malacanus*. H. *C. hyaena*. I. *C. inscriptus*. Scale bars: A = 0.31 mm; B = 0.13 mm; C = 0.30 mm; D = 0.23 mm; E = 0.23 mm; F = 0.24 mm; G = 0.11 mm; H = 0.13 mm; I = 0.19 mm.

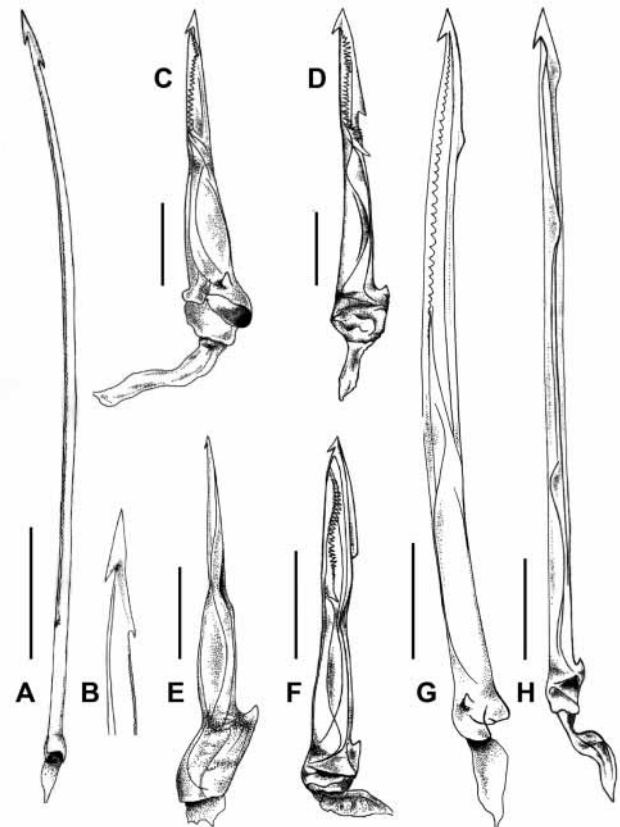


FIGURE 6. Entire radular teeth of *Conus* species. A. *Conus textile*. B. *C. textile* apex enlarged. C. *C. tessulatus*. D. *C. leopardus*. E. *C. lentiginosus*. F. *C. zeylanicus*. G. *C. monile*. H. *C. biliosus*. Scale bars: A = 0.72 mm; C = 0.09 mm; D = 0.24 mm; E = 0.02 mm; F = 0.40 mm; G = 0.05 mm; H = 0.32 mm.

Conus hyaena Hwass [in Bruguière], 1792

Resembles *Conus augur*, *C. characteristicus*, *C. malacanus* and *C. figulinus* in having the anterior armature consist of one barb and one blade (Fig. 5H). The serration terminates at the waist in the middle of the tooth shaft. There is no cusp. The terminal knob bears a prominent spur. The anterior armature in *C. hyaena* resembles that of other vermivorous species in the group; however, the length of the serration and the blade (Table 2; Fig. 7) indicate significant differences among these species. Kohn (1978) reported that this species feeds on errant polychaetes mainly of family Onuphidae but also Eunicidae and Nereidae.

Conus inscriptus Reeve, 1843

A single barb and a short blade are located at the apex (Figs 2I; 5I). The serration terminates in a prominent cusp. There is a distinct waist at the middle of the tooth shaft. The terminal knob bears a short stout spur. Radular tooth morphology of *C. inscriptus* is similar to those of *Conus augur*, *C. characteristicus*, *C. figulinus*, *C. hyaena* and *C. malacanus*. No observations on feeding have been reported.

Conus lentiginosus Reeve, 1844

The tooth apex has one barb and lacks a blade. The tooth shaft lacks serration or cusp (Figs 2D; 6E). The distal half of the shaft is broader than the proximal half. The terminal knob is enlarged and bears a spur. The radular tooth of *C. lentiginosus* resembles that of *C. patricius* Hinds, 1843 as described by Nybakken (1990). This species was observed by us to feed on small polychaete worms.

Conus leopardus Röding, 1798

There is a barb at the tooth apex and on the opposite side a blade that extends posteriorly terminating as a barb (Fig. 6D). The serration terminates in a protruding cusp almost at the middle of the tooth shaft. A distinct waist constricts the tooth just posterior to the middle of the tooth shaft. The enlarged terminal knob bears a short, stout spur. Our observations agree with the descriptions of Piele (1939) and Azuma (1964) of this species. The tooth morphology is indicative of a vermivore species. Kohn (1959) has reported this species feeding on the hemichordate *Ptychodera flava* Eschscholtz, 1825.

Conus lorisii Kiener, 1845

There is one barb and one blade at the tooth apex (Figs 2J; 5F) and a distinct waist is seen at the middle of the tooth shaft. The serration is longer than the blade and terminates at the waist region. There is no cusp; the terminal knob is slightly enlarged and bears a prominent spur. The tooth morphology closely resembles that of *Conus characteristicus*, *C. malacanus* and *C. figulinus*. A difference in blade lengths differentiates the teeth of *C. lorisii* from those of the three species mentioned above (Table 2). *Conus lorisii* is a vermivorous species, feeding on glycerid and capitellid polychaetes (Kohn 1978).

Conus malacanus Hwass [in Bruguière], 1792

There is a barb and a long blade at the apex (Fig. 5G)

and the serration terminates at the waist region, extending almost to the middle of the tooth shaft. The lengths of blade and serration are about the same. The tooth lacks a cusp and the terminal knob possesses a spur. No observations on feeding have been reported.

Conus monile Hwass [in Bruguière], 1792

There is one barb and a short blade at the apex (Figs 2K; 6G), the tooth shaft is slender and long without a cusp or waist. The serration is on the anterior part of the tooth shaft. The shaft is broader at the middle. No observations on feeding have been reported.

Conus striatus Linnaeus, 1758

There are three barbs at the tooth apex (Figs 2B, C; 3D, E, F), of which the third longest barb has a recurved tip. Although the anterior armature resembles that of *C. achatinus*, the other piscivore included in the present study, the first barb in *C. striatus* is relatively larger (9-10 % vs. 4-8 % of tooth length from the apex) than *C. achatinus* (Table 2). The tooth shaft is not serrated. The terminal knob is enlarged, and lacks a basal spur. The tooth morphology of *C. striatus* is similar to that of *C. catus*, *C. magus* and *C. aurisiacus* (James 1980) all of which form one group of piscivorous taxa. However, *C. geographus* Linnaeus, 1758 another piscivorous form, lacks three barbs in its tooth (Halstead 1956). The illustrations of the anterior tooth structure of *C. striatus* by Bergh (1895), Clench and Kondo (1946), Kohn (1956), Azuma (1964), Nybakken (1990) and James (1980) are similar to our material. *Conus striatus* has been reported to feed on fishes and occasionally on molluscs (Kohn 1959).

Conus terebra Born, 1778

Resembling that of *C. virgo* (Fig. 4C, D), the anterior end of the tooth shaft bears two barbs (Fig. 2L). Serration terminates at a prominent cusp distal to the middle of the tooth shaft, just proximal to a distinct waist. The terminal knob is enlarged and possesses a poorly developed short spur. Among the species included in group 'C' of this study (see Discussion), two species, *Conus terebra* and *C. virgo*, possess two barbs at the anterior end of their tooth shaft. Although both the species have similar tooth morphology, the shell: tooth ratio (Table 2) of *C. terebra* is distinctly different from that of *C. virgo*. Piele (1939), Lim (1969) and Rockel *et al.* (1995) have stated that *C. terebra* is vermivorous and it has been reported feeding on terebellids (Kohn and Nybakken 1975; Kohn 1960).

Conus tessulatus Born, 1778

The tooth apex bears a barb and a long blade that terminates at the region of waist. The lengths of blade and serration are nearly equal (Fig. 6C). The tooth shaft constricts about the middle of its length to form a distinct waist and the terminal knob bears a spur. *C. tessulatus* has been reported to feed on nereid and eunicid polychaetes (Endean and Rudkin 1965; Kohn 1968; Reichelt and Kohn 1985).

Conus textile Linnaeus, 1758

Typical of molluscivorous forms with two barbs (Fig. 2M). The width of the shaft is almost uniform from apex to base without any constriction and the serration ends in a short cusp (Fig. 6A, B). Terminal knob is enlarged and lacks a spur. The tooth shaft is relatively long (4.1 mm of tooth length for a shell of 48.1 mm in length) in comparison to that of other molluscivorous species that we have studied. Piele (1939) made a similar observation on *C. textile*. *Conus textile* has been reported to prey on different species of prosobranch gastropods (Cruz *et al.* 1978) including dangerous molluscivorous or piscivorous species of Conidae. This species also feeds on small fishes, worms, dead cephalopods and peeled shrimps (Kohn 1959, 1968, 1983; Kohn and Nybakken 1975; Collins 1987).

Conus virgo Linnaeus, 1758

There are two barbs at the apex (Fig. 2N) and the serration runs along the shaft and ends at the region of waist distal to the middle of the tooth shaft. A prominent cusp is present and the enlarged terminal knob possesses a short spur. Piele (1939) and Azuma (1964) have also observed the presence of a short spur in *C. virgo*. The radular tooth morphology of *C. virgo* (Fig. 4D) resembles that of *C. terebra* (Fig. 4C) except that the tooth is relatively larger in *C. terebra* (Table 2). *Conus virgo* has been reported to feed on terebellids and other polychaetes (Kohn, 1960; Kohn and Nybakken, 1975).

Conus zeylanicus Gmelin, 1791

The anterior end of the tooth shaft possesses a barb and a blade on the opposite side terminated by a barb (Fig. 6F). The tooth shaft constricts at the middle forming a distinct waist, and the serration ends in a cusp while the terminal knob bears a spur. The tooth morphology closely resembles that of *C. inscriptus* except for a slight difference in the length of blade (Figs 5I; 6F). The length of blade in *C. inscriptus* ranges from 18 to 22% whereas in *C. zeylanicus*, the length ranges from 28 to 32% (Table 2). No observations on feeding have been reported.

Characters of Conus radular teeth

The following widely accepted characters of *Conus* radular teeth have been used in the present study to differentiate individual species. By examining the presence and absence of these characters, the species were allocated to three groups, A, B and C. These groups correlate well with the feeding mode of the various species as seen in Table 3. The descriptions below relate to the observations made in this study only.

Barb (B)

Barb is a projection from the shaft with a cutting edge (Fig. 1), extending proximally from the apex, and joining the shaft at an acute angle (Kohn 1999). Most of the *Conus* teeth examined bear one (B₁) or two (B₂) barbs, in a few cases we observed a third barb (B₃).

TABLE 3. Component characters of radular teeth of *Conus* spp. **B₁**. First barb. **B₂**. Second barb. **B₃**. Third barb. **BL**. Blade. **SE**. Serration. **CU**. Cusp. **BS**. Basal spur. **W**. Waist. (+) Presence. (-) Absence.

Species	B ₁	B ₂	B ₃	BL	SE	CU	BS	W
<i>C. achatinus</i>	+	+	+	-	-	-	-	-
<i>C. amadis</i>	+	-	-	+	+	+	-	+
<i>C. araneosus</i>	+	-	-	+	+	+	-	-
<i>C. augur</i>	+	-	-	+	+	-	+	+
<i>C. bayani</i>	+	-	-	+	+	+	+	+
<i>C. betulinus</i>	+	-	-	+	+	-	+	+
<i>C. biliosus</i>	+	-	-	+	-	-	+	-
<i>C. characteristicus</i>	+	-	-	+	+	-	+	+
<i>C. figulinus</i>	+	-	-	+	+	-	+	+
<i>C. hyaena</i>	+	-	-	+	+	-	+	+
<i>C. inscriptus</i>	+	-	-	+	+	+	+	+
<i>C. lentiginosus</i>	+	-	-	-	-	-	+	+
<i>C. leopardus</i>	+	-	-	+	+	+	+	+
<i>C. lorioisii</i>	+	-	-	+	+	-	+	+
<i>C. malacanus</i>	+	-	-	+	+	-	+	+
<i>C. monile</i>	+	-	-	+	+	-	+	-
<i>C. striatus</i>	+	+	+	-	-	-	-	-
<i>C. terebra</i>	+	+	-	-	+	+	+	+
<i>C. tessulatus</i>	+	-	-	+	+	-	+	+
<i>C. textile</i>	+	+	-	-	+	+	-	-
<i>C. virgo</i>	+	+	-	-	+	+	+	+
<i>C. zeylanicus</i>	+	-	-	+	+	+	+	+

First barb (B₁)

The radular teeth of all species have the first barb. Its length ranges from 5 to 10% of tooth length from the apex (Fig. 7; Table 2) except in *C. lentiginosus* where it is 3%.

Second barb (B₂)

Only a small number of species (*Conus terebra*, *C. virgo*, *C. textile*, *C. achatinus* and *C. striatus*) have a second barb. Its length ranges from 8% to 18% of the tooth length from the apex (Fig. 7; Table 2).

Third barb (B₃)

A third barb was observed only in species of group 'A' (see discussion) (*Conus achatinus* and *C. striatus*). In both cases this third barb has a recurved tip directed toward the apex (Fig. 2A–C). The length of the barb in *C. achatinus* ranges from 23 to 27% of the total tooth length from the apex and 28–32% in *C. striatus* (Fig. 7; Table 2).

Blade (BL)

The blade is usually longer than the barbs (B₁, B₂, and B₃). It projects from the shaft and extends proximally from

the apex and terminates bluntly or into a barb (*C. betulinus*, *C. leopardus*) along the shaft. Species in group ‘C’ generally have radular teeth without a blade or with one blade. None of the species in group ‘A’ bears a blade. Species in group ‘B’ such as *C. amadis* and *C. araneosus* have a blade with distinct shapes that differ from each other (Fig. 2E, F). The length of the blade ranges from 10 to 55% of the total tooth length from the apex (Fig. 7; Table 4).

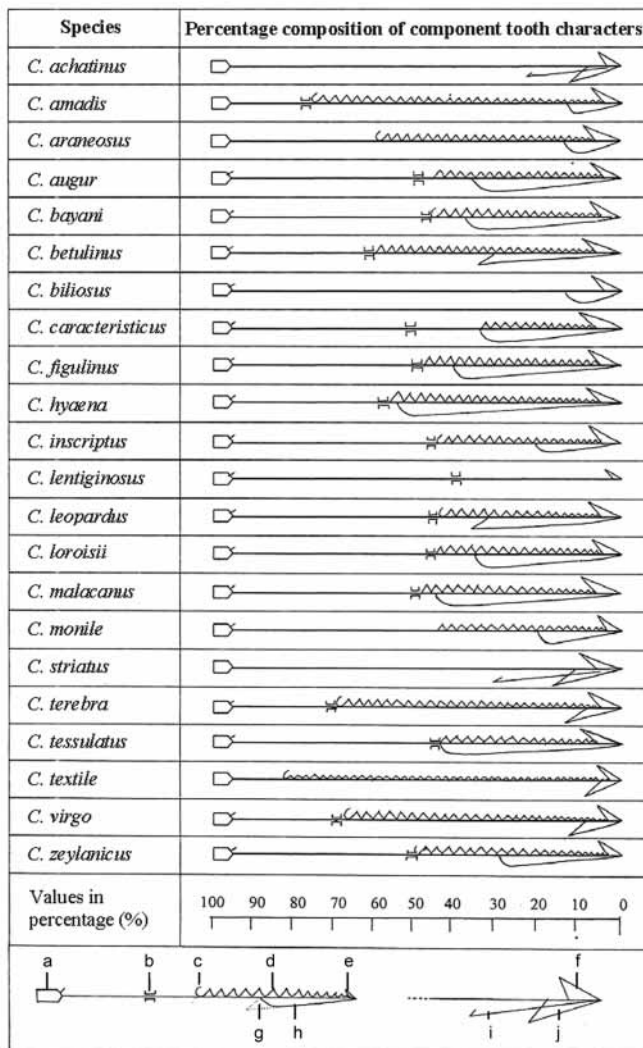


FIGURE 7. Diagrammatic representation of *Conus* spp. radular teeth. **a.** Terminal knob with spur. **b.** Waist. **c.** Cusp. **d.** Serration. **e, f.** First barb. **g.** Blade terminates into barb. **h.** Blade. **i.** Third barb. **j.** Second barb.

Serration (SE)

The serration is a row of denticles that runs longitudinally from the adapical opening nearest to the first barb and terminates in a cusp (*Conus amadis*, *C. araneosus*, *C. bayani*, *C. inscriptus*, *C. leopardus*, *C. terebra*, *C. textile*, *C. virgo* and *C. zeylanicus*), near the middle of the shaft (*Conus augur*) or at the region of waist (*Conus betulinus*, *C. figulinus*, *C. hyæna*, *C. lorisii*, *C. malacanus*, *C. monile* and *C. tessulatus*). The denticles are smaller near the apex and gradually increase in size as the serration extends to the

other end of the shaft. We observed a single row of denticles in all species that possess a serration except in *C. augur* which has two longitudinal rows of denticles comprising its serration. *Conus achatinus*, *C. striatus*, *C. biliosus* and *C. lentiginosus* lack a serration. The length of serration ranges from 32 to 82% of total tooth length from the apex (Fig. 7; Table 2).

Cusp (CU)

The cusp is a hook-like projection directed posteriorly towards the base of the tooth (Fig. 1). It is usually located at the proximal end of the serration. Sometimes a gap is seen between the serration and cusp. The position of cusp along the shaft ranges from 42 to 83% of tooth length from the apex (Fig. 7; Table 2). We observed a prominent cusp in *C. leopardus* (Fig.6G).

Waist (W)

The waist is a well defined point, where the width of the tooth shaft constricts (Azuma 1964; Nybakken 1970; Kohn *et al.* 1999). The length of the waist ranges from 40 to 77% of the tooth length from the apex (Fig.7; Table 2). It is longer in *C. amadis* (77%), *C. terebra* (73%) and *C. virgo* (69%) than the other species that have such a structure. A waist is absent in *C. achatinus*, *C. striatus*, *C. araneosus*, *C. biliosus* and *C. textile*, whose teeth have almost a constant width from apex to base. In *C. monile* the shaft is broader at the middle and lacks a waist.

Basal spur (BS)

Basal spur is the denticle protruding from the terminal knob or base (Fig. 1) (Peile 1939; Kohn *et al.* 1999). All the species we examined in group ‘C’ bear a basal spur (Figs 5A, B, C, D, E, F, G, H, I; 6C, D, E, F, G, H), except two (*C. terebra* and *C. virgo*) where it is less prominent (Fig. 4C, D). Groups ‘A’ and ‘B’ completely lack a basal spur.

Discussion

We have presented a detailed description of the radular tooth structures of twenty two species of Conidae from India, eight of them for the first time. We have also been able to clarify some small errors in literature for six other species, namely *Conus amadis*, *C. betulinus*, *C. inscriptus*, *C. monile*, *C. leopardus* and *C. tessulatus*, illustrating the value of combining both optical and electron microscopy. Preparative artifacts, in particular in small details of structures, can occur in scanning microscopy while it is possible to miss details in optical microscopy due to lack of resolution. Thus, an analysis of specimens with a combined use of these two microscopic methods makes descriptions more reliable than those made with the use of a single method. Although we have presented measurements of six teeth from a single healthy specimen in each species, we have examined for consistency (data not analysed or presented) a number of specimens of each representative species (Table 1).

Table 4. Means and ranges (given in lower rows) for tooth measurements from *Conus* species radulae **A**, **B** and **C**. Refer table 2. **P**. Piscivore, **M**. Molluscivore, **V**. Vermivore, (+). Presence, (-). Absence. Classification of feeding mode is based on observation, ⁺ gut content, *tooth structure.

S.No	Species	Shell length (S _L) (mm)	Tooth length (T _L) (mm)	Shell: tooth ratio (S _L :T _L)	Length of first barb (B ₁) (%)	Length of second barb (B ₂) (%)	Length of third barb (B ₃) (%)	Length of blade (BL) (%)	Length of serration (SE) (%)	Length of cusp (CU) (%)	Length of waist (W) (%)	Group	Feeding mode
1	<i>C. achatinus</i>	58	11.5 (11.0 - 12.0)	5.1 (4.8 - 5.3)	6 (4 - 8)	13 (11 - 15)	25 (23 - 27)	-	-	-	-	A	P
2	<i>C. amadis</i>	100	3.2 (2.6 - 3.8)	32.4 (26.3 - 38.5)	7 (5 - 9)	-	-	12 (10 - 14)	74 (73 - 75)	76 (74 - 78)	77 (75 - 79)	B	M*
3	<i>C. araneosus</i>	95	2.1 (1.5 - 2.7)	49.3 (35.2 - 63.3)	9 (7 - 11)	-	-	11 (9 - 13)	60 (58 - 62)	61 (59 - 63)	-	B	M ⁺
4	<i>C. augur</i>	90	1.6 (1.0 - 2.1)	66.5 (42.9 - 90.0)	7 (5 - 9)	-	-	34 (32 - 36)	45 (43 - 47)	-	48 (46 - 50)	C	V*
5	<i>C. bayani</i>	58	0.5 (0.4 - 0.6)	120.8 (96.7 - 145.0)	7 (5 - 9)	-	-	37 (35 - 39)	41 (39 - 43)	42 (40 - 44)	44 (42 - 46)	C	V*
6	<i>C. betulinus</i>	105	1.4 (1.3 - 1.6)	73.2 (65.6 - 80.8)	9 (7 - 11)	-	-	31 (29 - 33)	56 (54 - 58)	-	58 (56 - 60)	C	V
7	<i>C. biliosus</i>	75	2.4 (1.9 - 2.9)	32.7 (25.9 - 39.5)	6 (4 - 8)	-	-	12 (10 - 14)	-	-	-	C	V
8	<i>C. characteristicus</i>	63	1.0 (0.7 - 1.3)	69.3 (48.5 - 90.0)	10 (8 - 12)	-	-	32 (30 - 34)	32 (30 - 34)	-	50 (48 - 52)	C	V*
9	<i>C. figulinus</i>	79	1.0 (0.8 - 1.2)	82.3 (65.8 - 98.8)	7 (5 - 9)	-	-	40 (38 - 42)	52 (50 - 54)	-	53 (51 - 55)	C	V
10	<i>C. hyaena</i>	60	0.7 (0.4 - 1.0)	105.0 (60.0 - 150.0)	8 (6 - 10)	-	-	54 (52 - 56)	55 (53 - 57)	-	56 (54 - 58)	C	V
11	<i>C. inscriptus</i>	58	0.9 (0.7 - 1.1)	67.8 (52.7 - 82.9)	7 (5 - 9)	-	-	20 (18 - 22)	44 (42 - 46)	45 (43 - 47)	46 (44 - 48)	C	V
12	<i>C. lentiginosus</i>	36	0.3 (0.2 - 0.4)	135.0 (90.0 - 180.0)	3 (2 - 4)	-	-	-	-	-	40 (38 - 42)	C	V
13	<i>C. leopardus</i>	126	1.1 (0.7 - 1.6)	129.4 (78.8 - 180.0)	7 (5 - 9)	-	-	33 (31 - 35)	44 (42 - 46)	45 (43 - 47)	46 (44 - 48)	C	V
14	<i>C. loroisii</i>	75	1.1 (0.8 - 1.4)	73.7 (53.6 - 93.8)	6 (4 - 8)	-	-	35 (33 - 37)	45 (43 - 47)	-	48 (46 - 50)	C	V
15	<i>C. malacanus</i>	50	0.5 (0.4 - 0.6)	104.2 (83.3 - 125.0)	8 (6 - 10)	-	-	43 (41 - 45)	45 (43 - 47)	-	46 (44 - 48)	C	V*
16	<i>C. monile</i>	74	1.0 (0.8 - 1.3)	74.7 (56.9 - 92.5)	5 (3 - 7)	-	-	20 (18 - 22)	43 (41 - 45)	-	-	C	V*
17	<i>C. striatus</i>	80	14.2 (13.3 - 15.1)	5.6 (5.3 - 6.0)	10 (8 - 12)	18 (16 - 20)	30 (28 - 32)	-	-	-	-	A	P
18	<i>C. terebra</i>	82	2.5 (2.1 - 2.8)	34.2 (29.3 - 39.0)	8 (6 - 10)	12 (10 - 14)	-	-	71 (69 - 73)	72 (70 - 74)	73 (71 - 75)	C	V
19	<i>C. tessulatus</i>	55	0.5 (0.4 - 0.6)	114.6 (91.7 - 137.5)	9 (7 - 11)	-	-	42 (40 - 44)	42 (40 - 44)	-	47 (45 - 49)	C	V
20	<i>C. textile</i>	48	4.1 (3.5 - 4.6)	12.1 (10.4 - 13.7)	5 (3 - 7)	8 (6 - 10)	-	-	82 (80 - 84)	83 (81 - 85)	-	B	M
21	<i>C. virgo</i>	115	2.1 (1.7 - 2.4)	57.8 (47.9 - 67.6)	5 (3 - 7)	11 (9 - 13)	-	-	67 (65 - 69)	68 (66 - 70)	69 (67 - 71)	C	V
22	<i>C. zeylanicus</i>	49	1.4 (0.8 - 2.0)	42.9 (24.5 - 61.3)	5 (3 - 7)	-	-	30 (28 - 32)	48 (46 - 50)	49 (47 - 51)	50 (48 - 52)	C	V*

From our studies we find that there are minor errors of description in the extant literature concerning a few species. These include: (1) In their study of the radular teeth of *C. amadis* and *C. monile* Ramu *et al.* (1996) appear to have erred in their description as we found only a single barb and a single blade in both these species. Observations on several specimens showed distinct denticles in *C. amadis* teeth although Ramu *et al.* (1996) stated that these were absent, and we did not observe a spur (that they claim is present) in *C. monile*. We found that the radular teeth of *C. amadis* resembled those of *C. bandanus* and *C. marmoreus* reported by Nishi and Kohn (1999). (2) Piele (1939) had earlier described the radular tooth of *C. inscriptus* as possessing three barbs and Nybakken (1990) included this species in 'Type 4' of his classification (members of this group bear 2 or 3 barbs). Our studies on a large number of *C. inscriptus* specimens are at variance with their observations. Nybakken's description itself relied heavily on Piele's work and is likely a case of a misidentification. While describing the radular teeth of *C. monile*, Nybakken (1990) reported the presence of a prominent 'cusp' but we did not observe any. (3) The radula of *C. tessulatus* is notably different from the teeth of other species included in Group 'C'. Rabensandratana (1973) reported that *C. tessulatus* from Madagascar possessed a radular tooth without a basal spur but we observed a short basal spur. Our description closely matches those of Piele (1939), Azuma (1964) and Nybakken (1990). (4) James (1980) reported the absence of serration in the long shaft of the tooth of *C. textile* whereas Nishi and Kohn (1999) note the presence of serration. Our observations are in agreement with the latter observations and the earlier reports of Halstead (1965), Kohn (1963) and Lim (1969).

Prior literature on radular tooth morphology has classified species only by dietary specialization. The distribution of eight radular tooth characters (Table 4) supported the classification of the 22 species studied into three groups (A, B and C; Table 3) which seem to correlate with their feeding modes. Of the species studied, species in group 'C' are most numerous and possess the most diverse tooth morphology. The tooth structure of *C. lentiginosus* is unique. It shows no resemblance to that of any other species of group 'C' reported here but is included in that group because it has been observed to feed on polychaetes. A summary of distinguishing features of the radular morphologies of the species examined in this study are presented in Table 2 and Figure 7 as an aid to identification. We suggest that similar studies to this on the radular teeth of all species of *Conus* should facilitate species-level identification within the genus.

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