Evaluation of character state polarity of *Conus* radular tooth characters

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KEY WORDS: Conoidea, Conidae, *Conus*, radular tooth, character state, polarity, plesiomorphism, apomorphism.

ABSTRACT The character state polarity of fifteen characters of *Conus* radular teeth is evaluated by analysing a large data set (1400 radular teeth from 450 *Conus* populations of specific and subspecific rank) from previously published as well as unpublished results. A selected sample of radular teeth in different developmental stages is employed here to exemplify the characters and the results of the analysis. The selected sample is representative of putative primitive, generalist, vermivorous, molluscivorous and piscivorous type of teeth occurring in species of the genus *Conus* and includes radular teeth information for some species of older and more recent turrids that likely represent out-group and/or sister groups. Based on the state of the characters in putative ancestral species and, where available, on the evidence provided from the intra-specific ontogenetic change observed, plesiomorphy or apomorphy of each character are determined.

RIASSUNTO Viene analizzato lo stato di quindici caratteri del dente radulare del genere *Conus* L. Lo studio di oltre 1400 radule da 450 popolazioni (*species* e *subspecies*) di *Conus* costituisce l'ampia base di dati indispensabile per tale analisi. Per esemplificare i caratteri e riepilogare i risultati di questa analisi, viene utilizzata una selezione di denti radulari in differenti stadi di sviluppo. Il campione è rappresentativo dei diversi tipi morfologici osservati in *Conus* spesso correlabili alle specializzazione trofica specifica e qui classificati come "primitivo", "generalista", "vermivoro", "molluscivoro". Il campione include il dente radulare di alcune specie di turridi, potenziale *out-group* e/o *sister groups* in una analisi cladistica. Lo stato plesiomorfico o apomorfico di ciascun carattere viene infine determinato confrontando lo stato del carattere in specie ritenute ancestrali in base ad altri caratteri morfologici, al *record* fossile dove noto e sull'evidenza fornita dalle modificazioni ontogenetiche osservate a livello intraspecifico.

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INTRODUCTION

Turridae and Conidae, here considered as two distinct groups according to the classic systematic arrangement, are among the richest families in species number, have a relatively high density in the majority of their populations and most species live in shallow water. These attributes offer good opportunities for a systematic study of the radula.

The study of the radular tooth in the venomous genus *Conus* L. started already in the second third of the XIX century, but only in the last third of the XX century it increased notably. In the recent years many studies on *Conus* radular tooth were published.

This was probably due to several factors as, for instance, to an increased interest and knowledge of collectors for this group, to an increased facility to collect material from previously less accessible localities, to the interest of biologists for the intriguing biochemical properties of *Conus* venom. Though a primary aim of some authors has been the potential use of difference in the radular teeth for taxonomic purpose and in species separation, the evolutionary history underlying *Conus* biology may help clarifying the systematic of this large group and understanding functional aspects of the complex mechanisms by which species in this taxonomically difficult genus envenomate their prey, defend from predators and deter competitors.

In the course of previous studies, important differences between juvenile and adult individuals of some *Conus* species were pointed out, thus demonstrating an ontogenetic evolution of the radular tooth and arising a special attention.

A phylogenetic hypothesis is not yet available for *Conus* and molecular data have been assembled only for a limited number of species (DUDA & PALUMBI,1999; ESPIRITU *et al.*, 2001) mostly from a single geographic area (i.e. the Indopacific marine province) and generally for shallow-water species. Thus a phylogenetic scheme for the radular tooth based on qualitative and quantitative characters observed in large series of *Conus* teeth, would be desirable.

References to previous studies on the radular teeth of *Conus* can be found in ROLÁN (1992, 2000) and KOHN, NISHI & PERNET (1999).

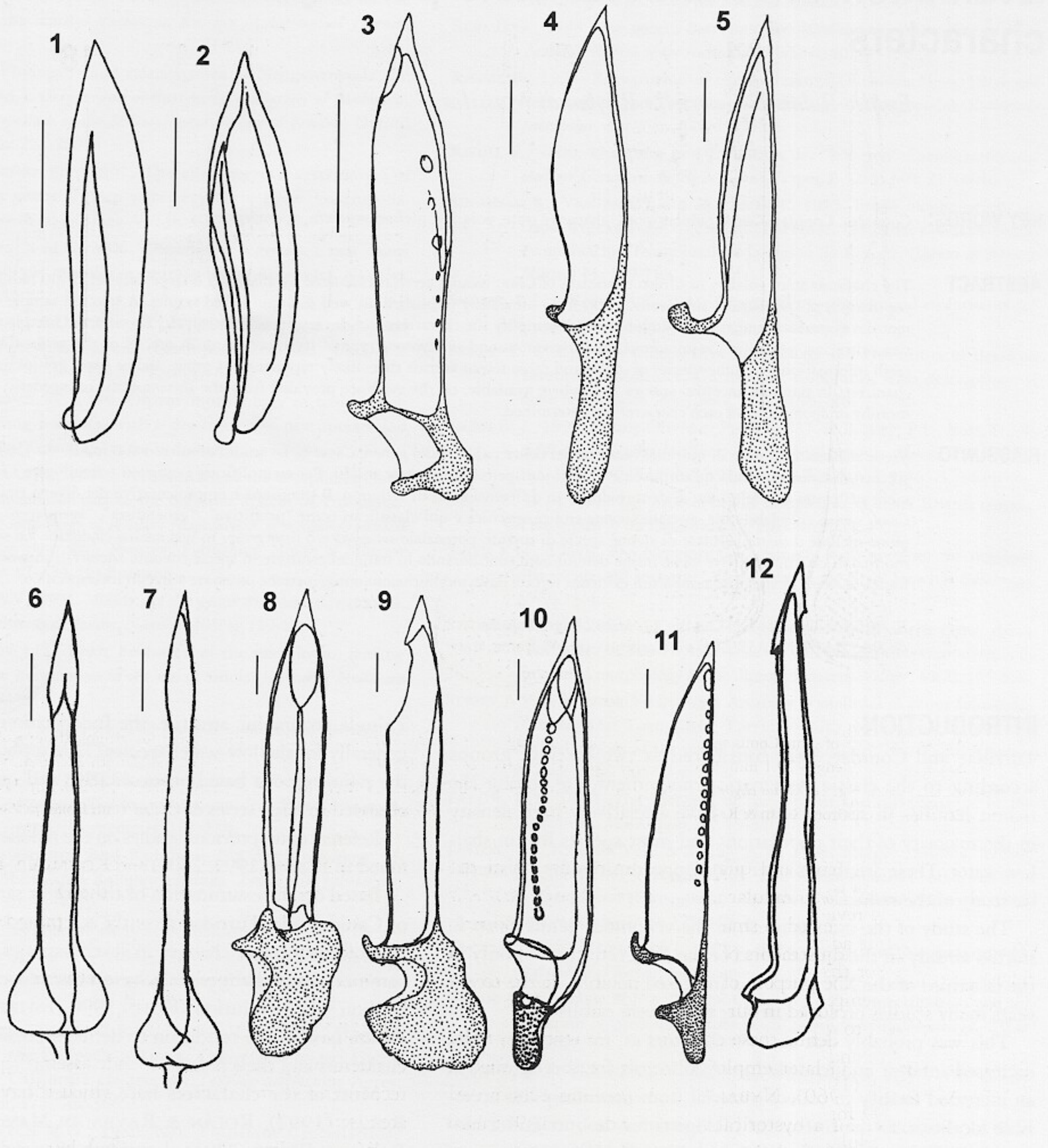
Based on the examination of the largest sample of radular teeth of Conidae and Turridae recently attempted and on the observation of ontogenetic changes in several species, we could infer how some of these changes may have occurred during the about 55 million years evolution (KOHN,1990, ESPIRITU *et al.,* 2001) and we are now in the condition to define a possible state of the main characters and their polarity.

Most of the characters here studied have been discussed in ROLÁN (1992), ROLÁN & RAYBAUDI MASSILIA (1994a) and in ROLÁN & BOYER (2001) along with the study of the ontogeny of *Conus ermineus*.

MATERIAL AND METHODS

The authors studied more than 1400 radulae of *Conus*, collected worldwide from a wide range of depth, including at least 350 species or taxa of specific or sub-specific rank. When different populations of a single species are considered and including information from literature, we have knowledge of the radular tooth morphology of about 450 populations of *Conus*. Additionally, in order to compare putative primitive state of the characters, the radular tooth of 55 species of Turridae were included in this study.

Radular teeth from several growth series of *Conus* species were studied and their ontogenetic change was observed. Though the "ontogenetic rule" is not acceptable as a general rule, it proved to

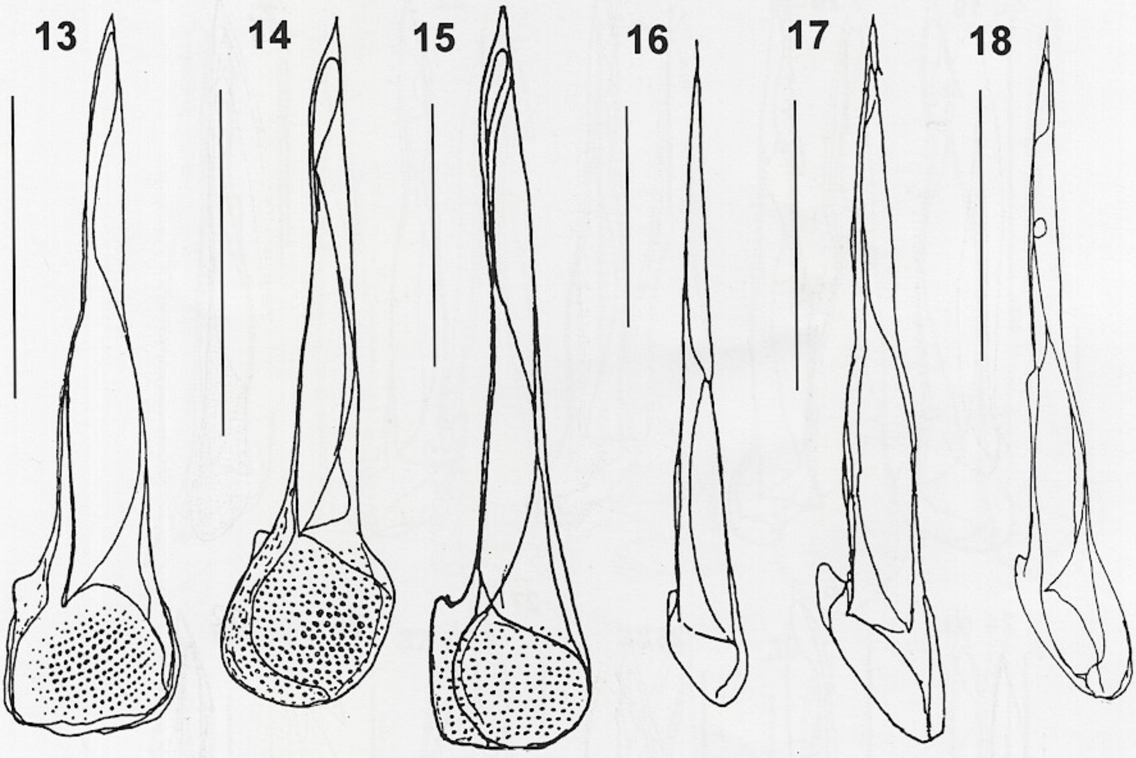


Figs. 1-12. Radular tooth of some Turridae species. Scale bar 0.01 mm. Fig. 1: *Crassispira callosa*, shell length 28.8 mm, Miamia, Ghana (from Fernandes, Rolán & Otero-Schmitt, 1995). Fig. 2. *Crassispira funebralis*, shell length 28.8 mm, Farol das Lagostas, Angola (from Fernandes, Rolán & Otero-Schmitt, 1995). Fig. 3. *Mangelia merlini*, shell length 7.0 mm, P. Cansado, Mauritania (from Rolán & Otero-Schmitt, 1999). Fig. 4. *Mangelia pontyi*, shell length 4.0 mm, Luanda, Angola (from Rolán & Otero-Schmitt, 1999). Fig. 5. *Mangelia albilonga*, shell length 8.0 mm, Luanda, Angola (from Rolán & Otero-Schmitt, 1999). Fig. 6. *Mitrolumna monodi*, shell length 4.2 mm, Dakar, Senegal (from Rolán & Boyer, 2001). Fig. 7. *Mitrolumna saotomensis*, shell length 4.0 mm, São Tomé (from Rolán & Boyer, 2001). Figs. 8-9. *Mangelia congoensis*, shell length 3.0 mm, Luanda, Angola (from Rolán & Otero-Schmitt, 1999). Figs. 10-11. *Mangelia digressa*, shell length 4.1 mm, Luanda, Angola (from Rolán & Otero-Schmitt, 1999). Fig. 12. *Benthofascis* sp. (from Powell, 1966).

be extremely useful to confirm some important trends and to support our determination of characters state polarity.

Thus, starting from the state of the character in putative outgroup and sister-group species of turrids as well as in putative oldest species of *Conus* (according to shell morphology and information on shells from the fossil data in THIELE, 1929-31, PETUCH, 1988, KOHN, 1990) and by analysing either inter-specific variation and intra-specific ontogenetic changes, we selected a set of characters believed to be of essential complementation to other morphological, anatomical and molecular characters for working out a phylogenetic analysis of the genus *Conus*.

Previously published works (ROLAN, 1992, 1993, ROLAN & RAYBAUDI MASSILIA, 1994a, 1994b, and ROLAN & BOYER, 2000) and personal unpublished observations include the wide body of



Figs. 13-18. Radular tooth of some Conus species. Scale bar 0.1 mm. Fig. 13. *Conus trovaoi*, shell length 32.5 mm, Limagens, Angola (from Rolán & Röckel, 2000). Fig. 14. *Conus neoguttatus*, shell length 29.1 mm, Santa Maria, Angola (from Rolán & Röckel, 2000). Fig. 15. *Conus naranjus*, shell length 22.7 mm, Santa Maria, Angola (from Rolán & Röckel, 2000). Fig. 16. *Conus elegans*, shell length 29.2 mm, Aden Gulf, N. Somalia. (from Rolán & Raybaudi Massilia, 1994). Fig. 17. *Conus stocki*, shell length 26.7 mm, Masirah, Oman (from Rolán & Raybaudi Massilia, 1994). Fig. 18. *Conus lizarum*, shell length 20.8 mm, N. Somalia (from Rolán & Raybaudi Massilia, 1994).

information, quantitative and qualitative determination of the several descriptors of *Conus* radular morphology. Though KOHN *et al.* (1999) recently reviewed a small part of our data set and proposed nomenclature adjustments of some terms used, for practical convenience and for the purpose of this paper we prefer to maintain the acronyms employed in our previous works.

The terms used to define these characters were introduced by TROSCHEL (1866), and later employed and increased by BERGH (1895), WARMKE (1960), NYBAKKEN (1970) and others (see KOHN *et al.*, 1999 for a hystorical review). ROLÁN (1992) used some ratios for radular teeth in species separation. KOHN *et al.* (1999) adopted most of these characters translating the terms into English and adding some new ratios. We prefer to maintain our original terms: DR was translated to TL, LC to SL. etc., a change which does not represent an important contribution. Furthermore, we did not employ some of these more recent parameters introduced by KOHN *et al.* (1999) considering that they could be useful only in the concrete case of comparative study of two teeth.

The parameters not adopted in the present work are the following:

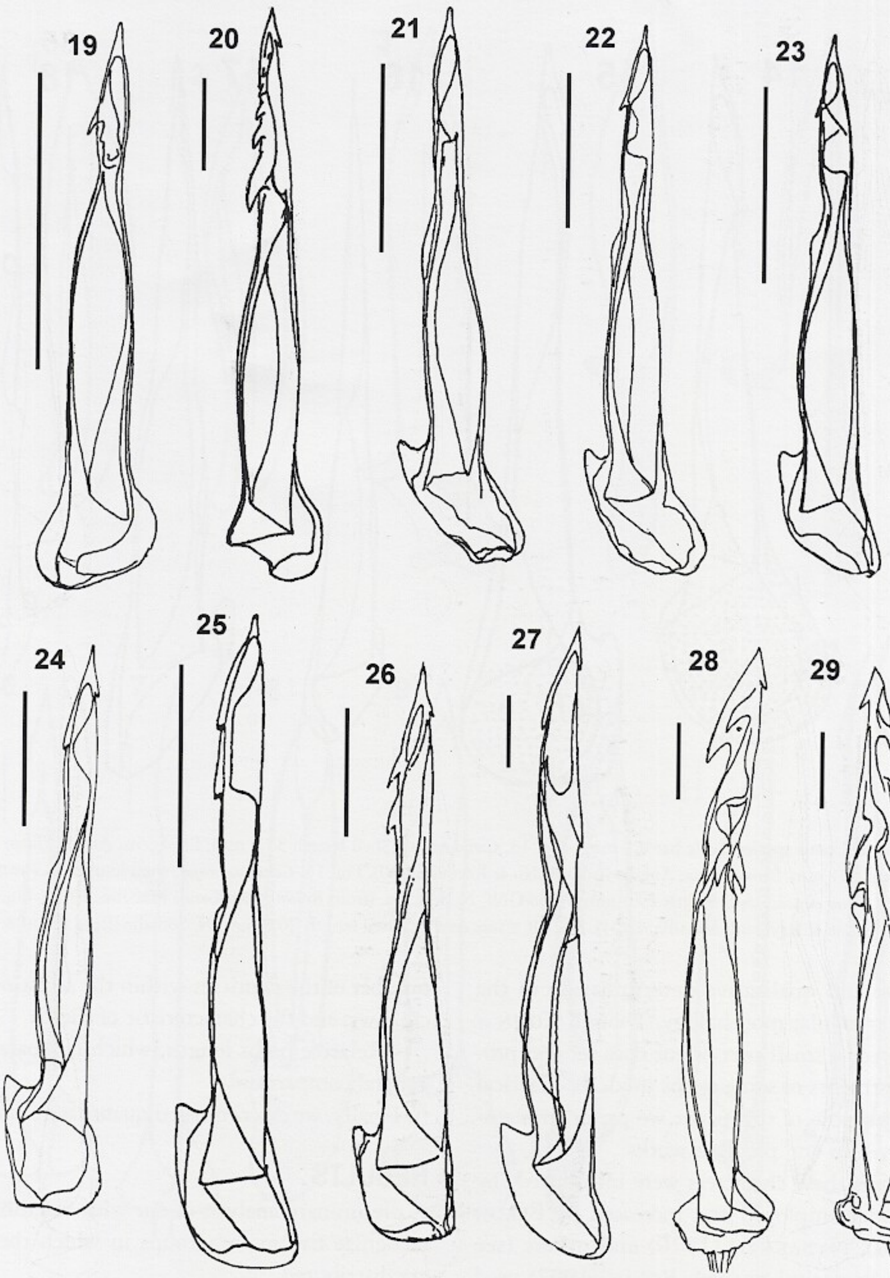
- Length of the adapical opening. This character revealed to be inconsistent, because it changes within a same tooth according to whether the tooth is dry, as that employed for the SEM photographs) or wet, as in the living animal.
- Length of the serration. This is better represented by the number of the denticles within the serration, the number of denticle rows, and the characteristic of the D.
- Relative barbs length, which is a parameter hardly useful for general comparison.

Finally, we discriminated quantitative and qualitative characters.

RESULTS

A preliminary analysis of our wide assemblage of data allowed to recognize five main groups in which the radular teeth of *Conus* are distributed.

We could have coded them by a letter or by an ordinal number, but we prefer to adopt a more descriptive term since the correlation of radular tooth morphology with feeding habits in *Conus* is perhaps one of the few widely accepted concepts concerning *Conus* biology. Exceptions to this correlation do exist however, with the most striking example being represented by *C. geographus*, a well- known fish hunting species, whose radular tooth is typical of molluscovorous species. The "net strategy" of prey capture adopted by *C. geographus* (Olivera, 1997) may help explaining how adaptive or behavioural traits can superimpose to evolutionary traits. Thus, as already explained in ROLAN & RAYBAUDI MASSILIA (1994a, 1994b) besides the terms "vermivorous", "molluscivorous" and "piscivorous" morphological type of radular tooth, we refer to the "generalist" type, because several deep water species for which the prey is still unknown have

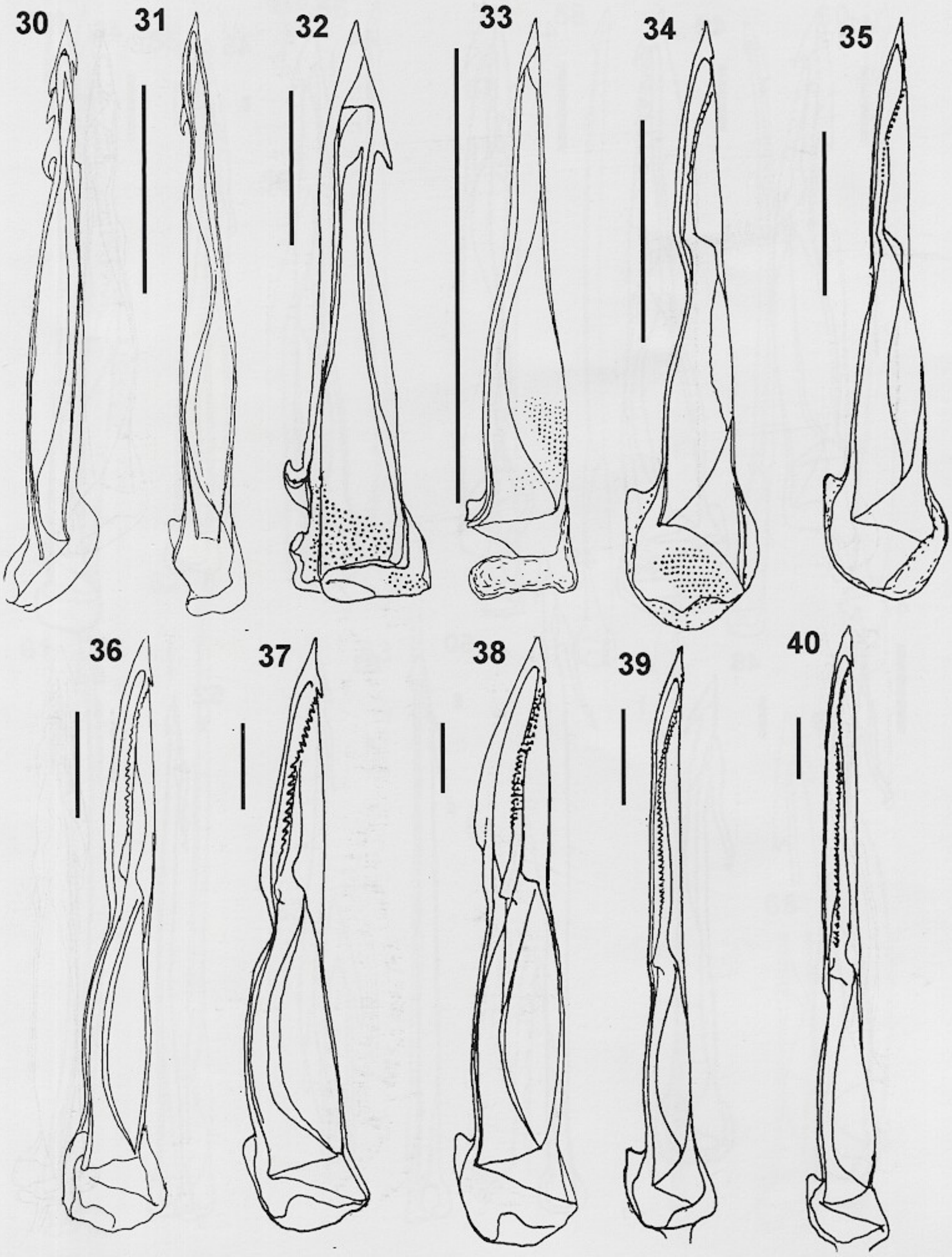


Figs. 19-29. Radular tooth of some Conus species. Scale bar 0.1 mm. Fig. 19. *Conus acutangulus*, shell length 10.0 mm, Hawaii. Fig. 20. *Conus praecellens*, shell length 41.8 mm, Cebu, Philippines. Fig. 21. *Conus jaspideus*, shell length 21.5 mm, Bahamas. Fig. 22. *Conus mindanus*, shell length 26.3 mm, Brazil. Fig. 23. *Conus pealii*, shell length 19.6 mm, Caribbean. Fig. 24. *Conus bozzettii*, shell length 41.8 mm, Cape Ras Hafun, E. Somalia (from Rolán & Raybaudi Massilia, 1994b). Fig. 25. *Conus orbignyi*, shell length 38.0 mm, Philippines (from Rolán & Raybaudi Massilia, 1994b). Fig. 26. *Conus comatosa*, shell length 34.0 mm, Philippines (from Rolán & Raybaudi Massilia, 1994a). Fig. 27. *Conus teramachii*, shell length 67.5 mm, Philippines (from Rolán & Raybaudi Massilia, 1994b).. Figs. 28-29. *Conus californicus*, shell length 28.5 mm, Gulf of California, USA.

teeth similar to *C. californicus*, a well known generalist feeder. The definition "primitive" type of tooth, though on a less concrete ground, may also refer to generalist or vermivore feeders. It has been chosen because this type of tooth reflects the least derived state of the main characters of the radular tooth of *Conus* compared with turrids radular teeth.

Types of teeth

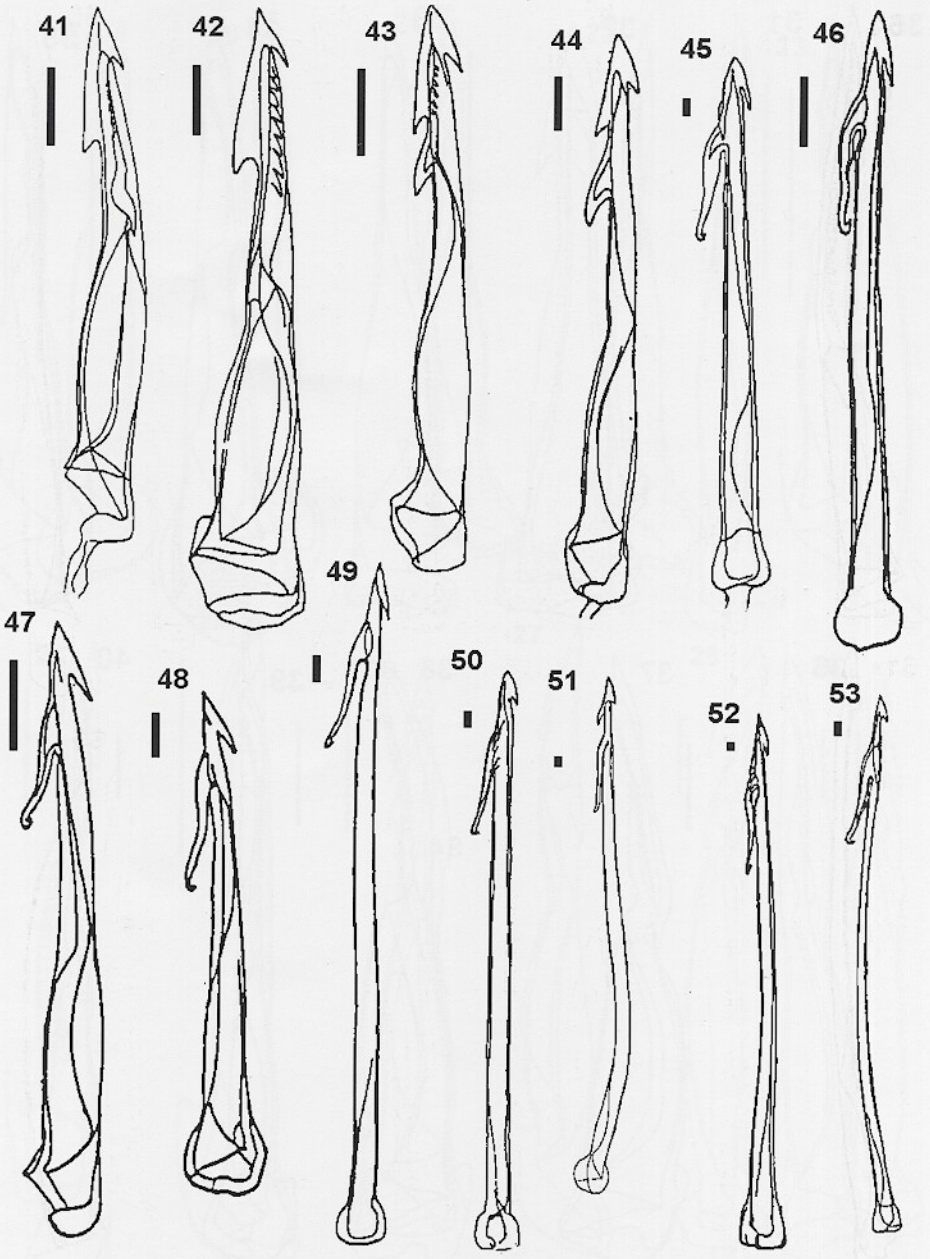
1- Primitive type of tooth: simple, small teeth (lowest relative tooth length) with few characters (absence of barbs or presence of a single barb, a long saw without a serration, a broad and strongly reinforced base, a prominent basal spur and a poorly defined waist). Teeth with the closest similarity to those of



Figures 30-40. Radular tooth of some Conidae and Turridae species. Scale bar 0.1 mm. Figs. 30-31. *Conorbis coromandelicus*, shell length 37.9 mm, Cuddalore, India. Fig. 32. *Genota marchadi*, shell length 34.5 mm, Dakar, Senegal. Fig. 33. *Genota vafra*, shell length 30.0 mm, Farol das Lagosta, Angola. Fig. 34. *Conus naranjus*, shell length 19.1 mm, Angola (from Rolán & Röckel, 1999) Fig. 35. *Conus flavusalbus* shell length 21.9 mm, Baia das Pipas, Angola (from Rolán & Röckel, 1999). Fig. 36. *Conus ventricosus*, shell length 30 mm, Algarve, Portugal. Fig. 37. *Conus miliaris*, shell length 28.7 mm, Queensland, Australia (from Rolán & Raybaudi Massilia, 1994a). Fig. 38. *Conus borgesi*, shell length 26.3 mm, Baia das Gatas, Cape Verde Is. (from Rolán, 1992). Fig. 39. *Conus franciscoi*, shell length 34.4 mm, Chapeu Armado, Angola (from Rolán & Röckel, 1999). Fig. 40. *Conus guinaicus*, shell length 35.3 mm, Dakar, Senegal.

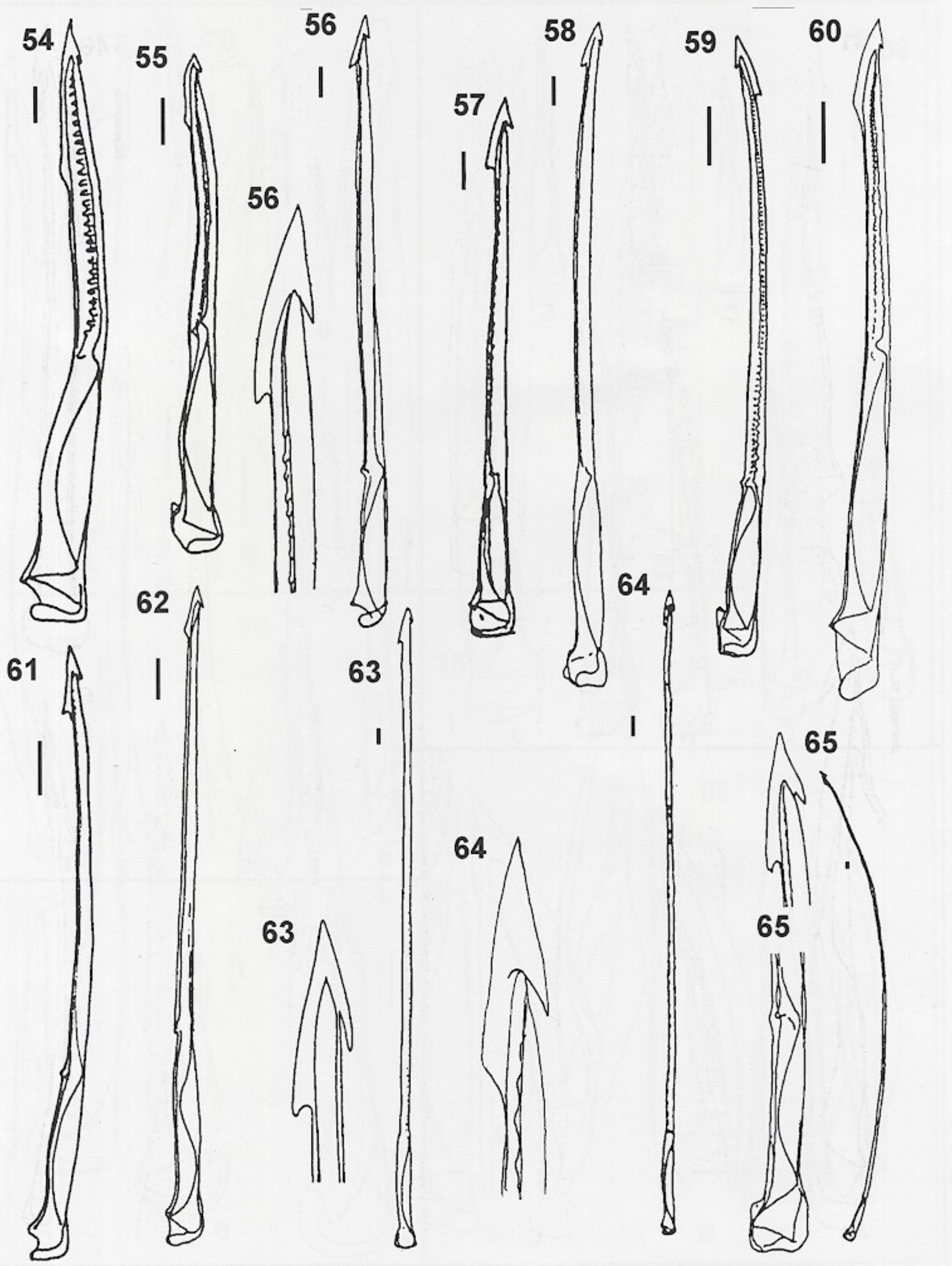
some turrids (Figs. 1-12). Selected examples include *C. trovaoi* (Fig. 13), *C. neoguttatus* (Fig. 14), *C. naranjus* in early post-metamorphic stage (Fig. 15), but also the adult stages of *C. elegans* (Fig. 16), *C. stocki* (Fig. 17), *C. lizarum* (Fig. 18).

2- Generalist type of tooth: more complex than previous teeth, still very short compared to shell length, with several barbs, a well evident waist and an usually obliquely elongated large base. The adapical opening is still wide and a serration is often just sketched. The first group includes *C. acutangulus* (Fig. 19), *C. praecellens* (Fig. 20), *C. jaspideus* (Fig. 21), *C. mindanus* (Fig. 22), *C. pealii* (Fig. 23) and *C. bozzettii* (Fig. 24); A second group includes *C. orbignyi* (Fig. 25), *C. comatosa* (Fig. 26) and *C. teremachii* (Fig. 27) which can be compared with those of *C. californicus* (Figs. 28-29), *Conorbis coromandelicus* (Figs. 30-31), *Genota marchadi* (Fig. 32) and *Genota vafra* (Fig. 33).



Figures 41-53. Radular tooth of some Conus species (from Rolán & Raybaudi Massilia, 1994a, b). Scale bar 0.1 mm. Fig. 41. *Conus friedae*, shell length 40.2 mm, Sri Lanka. Fig. 42. *Conus cordigera*, shell length 35.5 mm, Indonesia. Fig. 43. *Conus salzmanni*, shell length 18.7 mm, Gulf of Aden. Fig. 44. *Conus jickeli*, shell length 39.7 mm, Gulf of Aden. Fig. 45. *Conus julii*, shell length 52.0 mm, Mauritius. Fig. 46. *Conus solomonensis*, shell length 30.0 mm, Guadacanal, Solomon I. Fig. 47. *Conus zapatosensis*, shell length 19.2 mm, Philippines. Fig. 48. *Conus scalptus*, shell length 22.3 mm, Philippines. Fig. 49. *Conus timorensis*, shell length 35.9 mm, Mauritius. Fig. 50. *Conus achatinus*, shell length 47.7 mm, Thailand. Fig. 51. *Conus ermineus*, shell length 60.1 mm, Cape Verde Is. Fig. 52. *Conus striatus*, shell length 83.0 mm, Philippines. Fig. 53. *Conus leehmani*, shell length 55.3 mm, Maldive Is.

3- Vermivorous type of tooth. This is the most frequently observed type of tooth in our analysis: a medium sized tooth (relative tooth length: LC/DR between 27, in the largest teeth, and 120, in the case of the smallest teeth. These numbers can show us the % of the shell length with the ratio 100/(LC:DR). So, in the mentioned cases the extremes represent 3.6% of the shell length, in the largest teeth, up to 0.83%, in the smallest). The width of the tooth (DR/APA) is in the range 8 – 19. Teeth have usually a well defined waist, a single barb opposing a medium sized blade, a denticulate saw (serration), a moderate central cusp and a more or less conspicuous base with a projecting spur. A typical vermivorous tooth is found chiefly in very shallow or moderately shallow water species. Examples of this type are represented by the tooth of adult specimens of *C. naranjus* (Fig. 34) and *C. flavusalbus* (Fig. 35), as well as by less complex teeth with a lower number of denticles (D) within the serration (S); medium sized vermivorous teeth are also those of



Figures 54-65. Radular tooth of some Conus species (from Rolán & Raybaudi Massilia, 1994a, b). Scale bar 0.1 mm. Fig. 54. *Conus carnalis*, shell length 63.0 mm, Angola. Fig. 55. *Conus algoensis simplex*, shell length 55.5 mm, South Africa. Fig. 56. *Conus rubropennatus*, shell length 46.7 mm, Reunion I. Fig. 57. *Conus amadis*, shell length 48.6 mm, India. Fig. 58. *Conus episcopatus*, shell length 34.3 mm, Thailand. Fig. 59. *Conus terebra*, shell length 40.8 mm, Mauritius. Fig. 60. *Conus moreleti*, shell length 50.5 mm, Hawaii. Fig. 61. *Conus pennaceus*, shell length 21.5 mm, Mauritius. Fig. 62. *Conus lischkeanus*, shell length 57.8 mm, Japan. Fig. 63. *Conus paulucciae*, shell length 55.0 mm, Mauritius. Fig. 64. *Conus ammiralis*, shell length 47 mm, Philippines. Fig. 65. *Conus ammiralis pseudocedonulli*, shell length 65.0 mm, Reunión.

C. ventricosus (Fig. 36) and *C. miliaris* (Fig. 37). Larger teeth are those of *C. borgesi* (Fig. 38), which are broad and with several rows of denticles within the serration, while in other species they are elongate as in *C. franciscoi* (Fig. 39) or *C. guinaicus* (Fig. 40).

4- Piscivorous type of tooth. This is a large and elongate tooth (LC/DR between 30 – 8, that is 3.3% to 12.5 % shell length). The width of tooth (DR/APA) ranges from 21 for the wider teeth, to 120 in the largest. These teeth have three barbs B1, B2, B3: showing different directional arrangement in postmetamorphic transitional stages of development, before attaining reproductive maturity, as in the fully adult stage of *C. friedae* (Fig. 41), *C. cordigera* (Fig. 42), *C. salzmanni* (Fig. 43), and *C. jickeli* (Fig. 44); Barbs may be alternately oriented as in the mature stage of *C. julii* (Fig. 45), *C. solomonensis* (Fig. 46), *C. zapatosensis* (Fig. 47), *C. scalptus* (Fig. 48), *C. timorensis* (Fig. 49), *C. achati-*

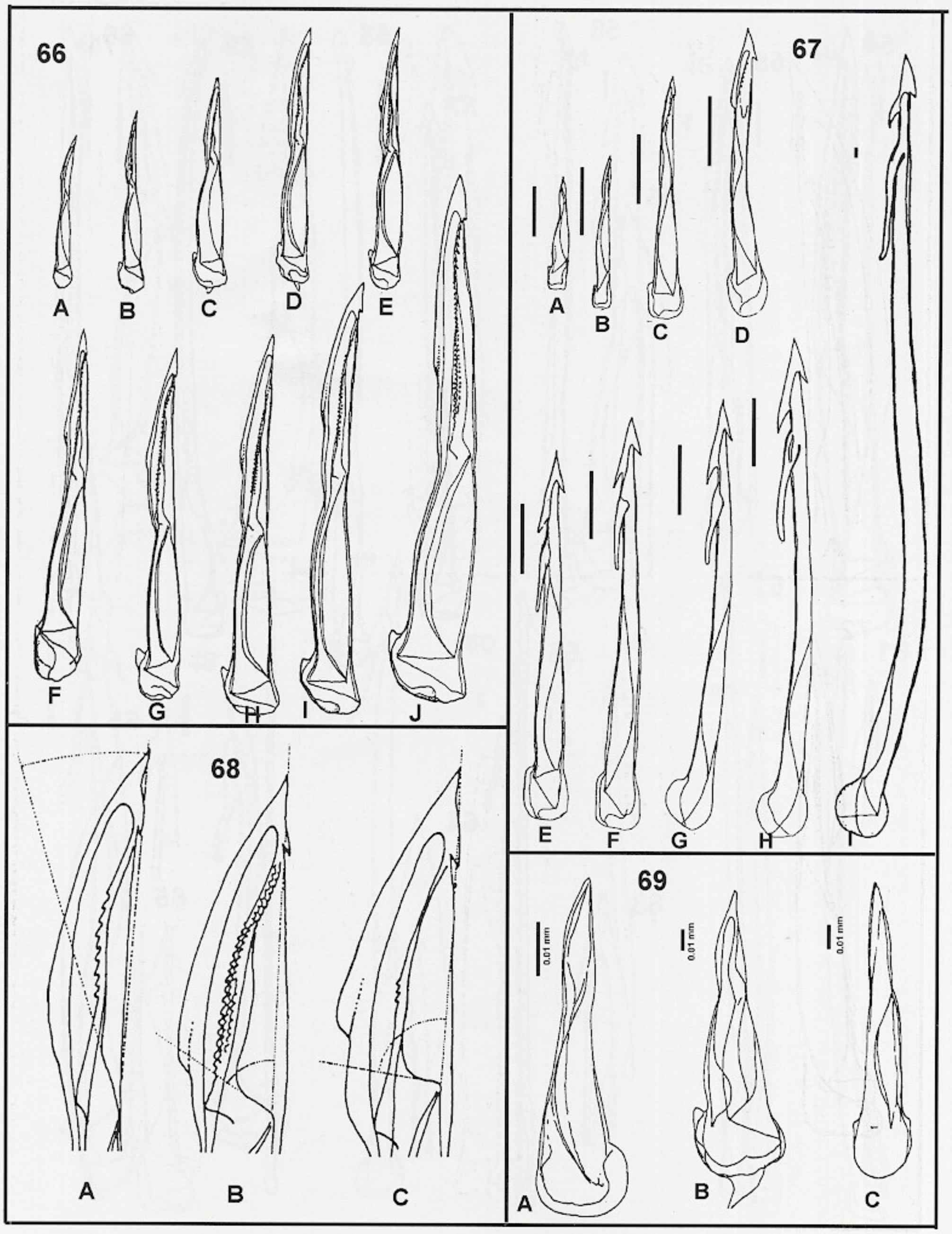


Fig. 66. Growth series of radular teeth from *C. trochulus*, Cape Verde Islands. Shell size of the specimens: A: 14.3 mm. B: 16.8 mm. C: 15.7 mm. D: 17.7 mm. E: 20.1 mm. F: 26.4 mm. G: 31.6 mm. H: 35.3 mm. I: 43.5 mm. J: 52.5 mm. **Fig. 67.** Growth series of radular teeth from *C. ermineus*. Shell size of the specimens: A: 8.0 mm. B: 10.1 mm. C: 13.0 mm. D: 13.0 mm. E: 13.9 mm. F: 12.1 mm. G: 13.4 mm. H: 11.9 mm. I: 60.1 mm. **Fig. 68.** Basal angle of the serration (ABS): A: *C. miruchae*; B: *C. borgesi*; C: *C. navarroi*. **Fig. 69.** Postmetamorphic radular teeth from: A- *C. trochulus, C. diminutus* and *C. curralensis,* Cape Verde Is. Scale bar 0.01 mm.

nus (Fig. 50), and teeth may be more elongate as in *C. ermineus* (Fig. 51), C. *striatus* (Fig. 52) and *C. leehmani* (Fig. 53). Here again, three subgroups may be further splitted upon qualitative (i.e. orientation of barbs) and quantitative parameters.

5- Molluscivorous type of tooth. They are among the largest and narrowest teeth observed (LC/DR ranging from 27 up to 9, corresponding to a relative tooth length between 3.7 and 11% LC). Teeth are very narrow, with DR/APA ranging from 15 to 100 in the most elongate teeth. These teeth have a blade replacing Barb 2, as it is observed in the ontogeny of some species as *C. carnalis* (Fig. 54), *C. algoensis simplex* (Fig. 55) or in fully grown individuals as in *C. rubropennatus* (Fig. 56), *C. amadis* (Fig. 57), *C. episcopatus* (Fig. 58), *C. terebra* (Fig. 59), *C. moreleti* (Fig. 60), *C. pennaceus* (Fig. 61), *C. lischkeanus* (Fig. 62), *C. paulucciae* (Fig. 63), *C. ammiralis* (Fig. 64) and *C. ammiralis pseudocedonulli* (Fig. 65). Some subgroups may be further defined within this type of tooth.

Quantitative characters

The characters which will be commented here are those usually

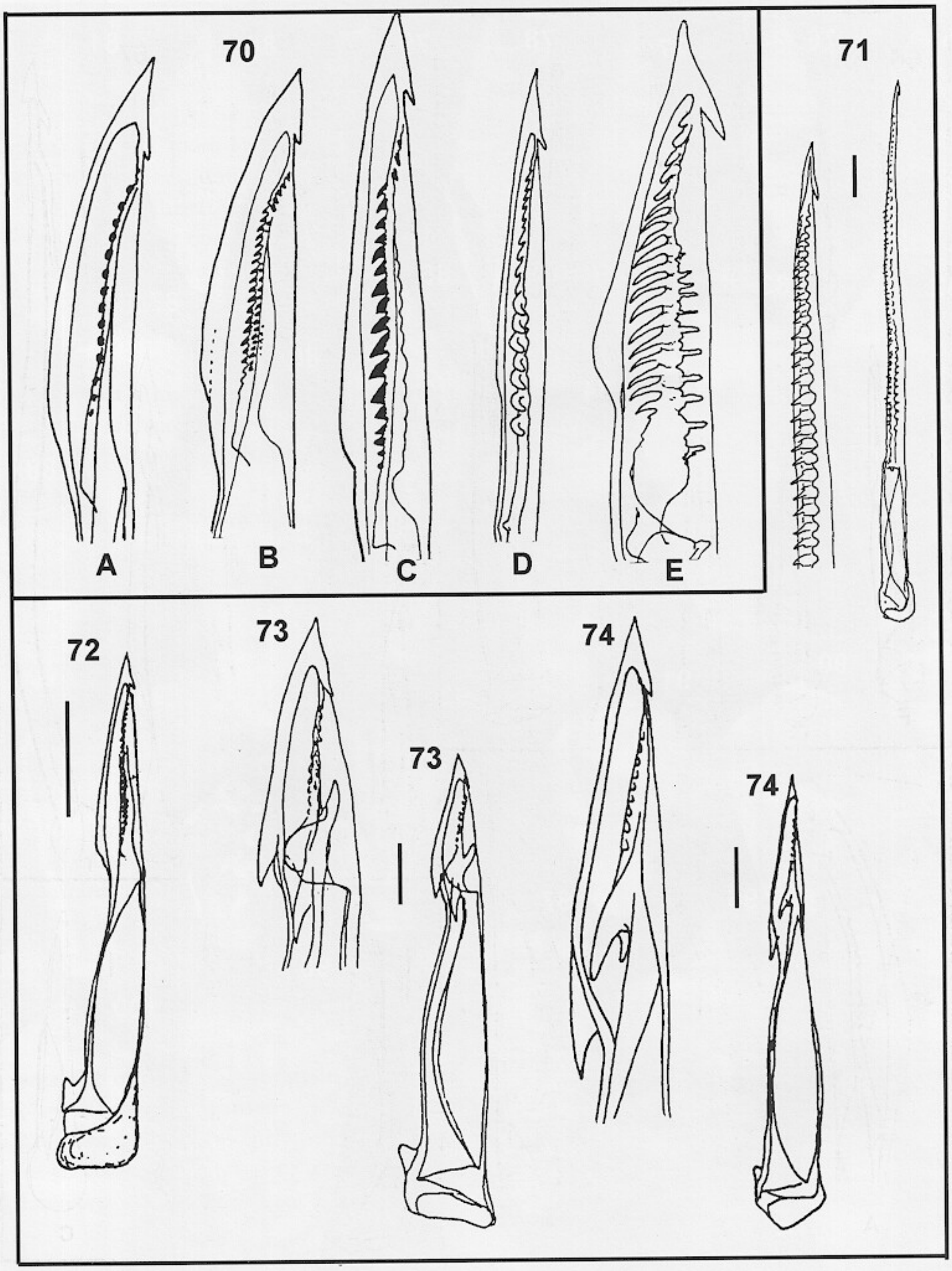


Fig. 70. Shape of the denticles within the serration of the radular tooth: A: *C. miruchae*. B: *C. ateralbus*. C: *C. tabidus*. D: *C. planorbis*. E: *C. miles*. Scale bar 0.1 mm. **Fig. 71.** *C. splendidulus*, shell length 51.0 mm, Little Aden **Fig. 72.** *C. characteristicus*, shell length 17 mm, Thailand **Fig. 73.** *C. duffyi*, shell length 35.0 mm, Los Roques, Venezuela **Fig. 74.** *C. imperialis*, shell length 36.0 mm, Reunion.

employed in the radular studies and illustrated in previous works, for instance, in ROLÁN (1992).

1 Number of teeth within the radula sac (ND)
Counting the total teeth within the radula sac is easy if the animal has been preserved in alcohol and the entire content of radular sac can be studied. This information is not easy to get in those cases in which the radula is studied from dry animals. Though this information is not available for all the species we have examined, the sample is wide enough to allow generalization. This character may be not independent from relative tooth length and a correlating test should be carried out before use for statistical purposes, however we selected it because it may well allow prediction of prey type and envenomation strategy.

For turrids, we have not such a wide body of information on radular teeth, however we could observe that in some species only 7 teeth were present in the radula sac, as in *Mangelia angolensis*; usually the number of teeth was between 26 in *Genota vafra* up to more than 100 teeth, as it observed in some species of *Crassispira* (see FERNANDES, ROLÁN & OTERO-SCHMITT, 1995)

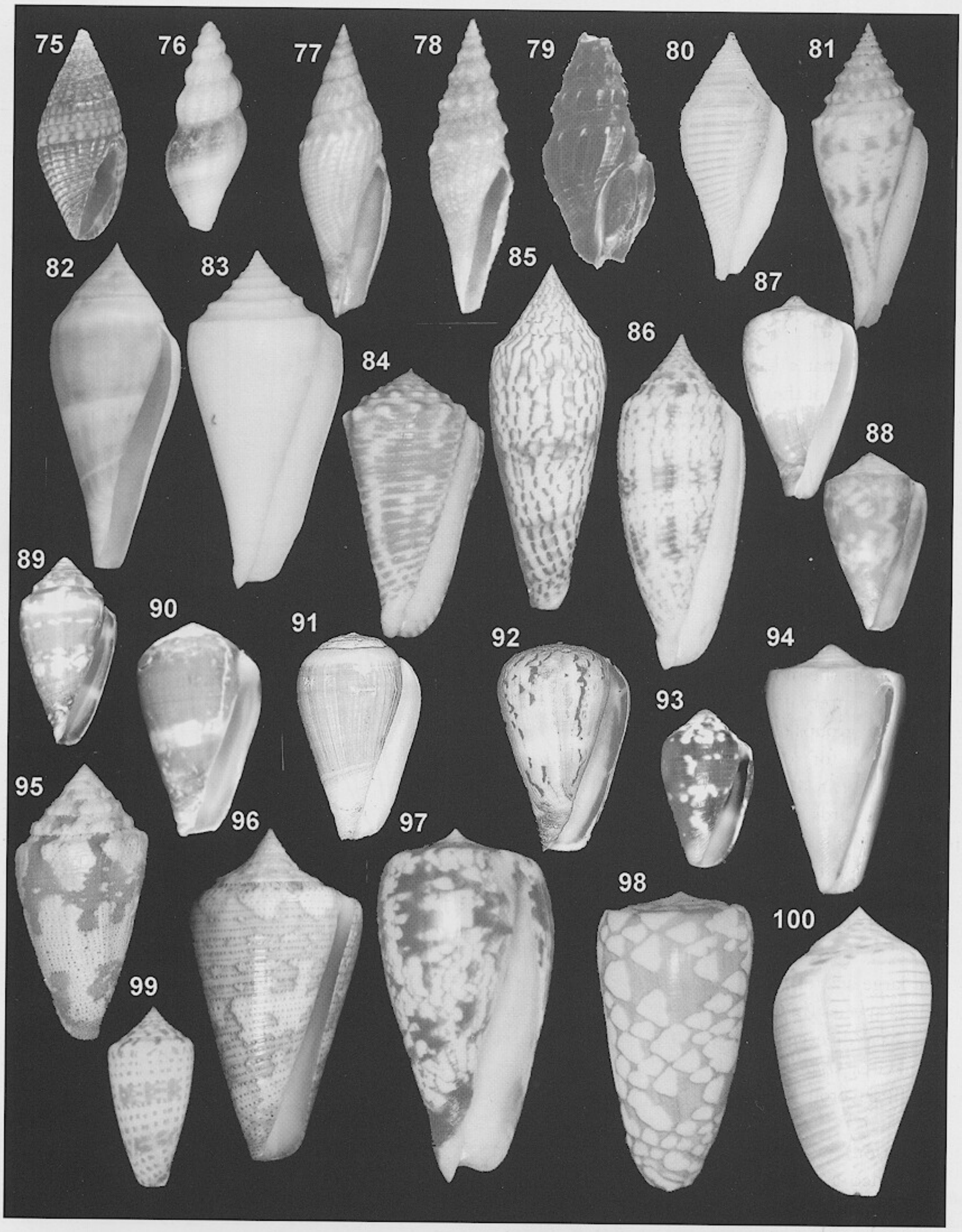


Fig. 75. *Mitrolumna monodi*, 4.4 mm, Cap Vert, Senegal (from Rolán & Boyer, 2000) **Fig. 76.** *Mangelia albilonga*, 8.0 mm, paratype (CER), Buraco, Palmeirinhas, Angola **Fig. 77.** *Genota marchadi*, 34.3 mm, Dakar, Senegal (from Rolán & Raybaudi, 1994b) **Fig. 78.** *Genota mitraeformis*, 49 mm, Gabon (from Rolán & Raybaudi, 1994b) **Fig. 79.** *Crassispira funebralis*, 32 mm, Pointe Noire, Congo **Fig. 80.** *Conorbis coromandelicus*, 40 mm, Coromandel Coast, India (from Röckel, Korn & Kohn, 1995, courtesy ConchBooks, Germany) **Fig. 81.** *Conus orbignyi elokisimenos*, 60 mm, Natal, South Africa (from Rolán & Raybaudi, 1994b) **Fig. 82.** *C. profundorus*, 113 mm, Balut Islands, Philippines (from Rolán & Raybaudi, 1994b) **Fig. 83.** *C. teramachii*, 102.4 mm, Japan (from Rolán & Raybaudi, 1994b) **Fig. 84.** *C. sulcocastaneus*, 51 mm, Punta Engaño, Philippines (from Rolán & Raybaudi, 1994b) **Fig. 85.** *C. ranonganus*, 100 mm, Ranong, Thailand (from Rolán & Raybaudi, 1994b) **Fig. 86.** *C. australis*, 85.7 mm, Taiwan (from Rolán & Raybaudi, 1994b) **Fig. 87.** *C. borgesi*, 26.1 mm, holotype (MNCN), Gatas, Boa Vista, Cape Verde Archipelago **Fig. 88.** *C. curralensis*, 24.8 mm, holotype (MNCN), Curral, Santa Luzia, Cape Verde Archipelago **Fig. 89.** *C. navarroi*, 19 mm, holotype (MNCN), Calhau, São Vicente, Cape Verde Archipelago **Fig. 90.** *C. babaensis*, 25.8 mm, holotype (MNCN), Baia da Baba, Angola (from Rolán & Röckel, 2001) **Fig. 91.** *C. flavusalbus*, 23.7 mm, holotype (MNCN), Baia das Pipas, Angola (from Rolán & Röckel, 2001) **Fig. 92.** *C. trovaoi*, 38 mm, holotype (MNCN), Limagens, Angola (from Rolán & Röckel, 2001) **Fig. 93.** *C. hieroglyphus*, 14 mm, Aruba, Antilles **Fig. 94.** *C. daucus*, 25.5 mm, Los Canarreos, Cuba **Fig. 95.** *C. duffyi*, 40.5 mm, Los Roques Archipelago, Venezuela (from Rolán & Raybaudi, 1994a) **Fig. 96.** *C. cedonulli*, 44.0 mm, St. Vicente, Antilles **Fig. 97.** *C. spectrum*, 69 mm, Gladstone, Queensland, Australia (from Rolán & Raybaudi, 1994b) **Fig. 98.** *C. cordigera*, 40.0 mm, Balabac, Palawan, Philippines (from Rolán & Raybaudi, 1994b) **Fig. 99.** *C. satzmanni*, 27 mm, Little Aden (from Rolán & Raybaudi, 1994b) **Fig. 100.** *C. scalptus*, 28 mm, syntypes (BMNH), locality unknown (from Rolán & Raybaudi, 1994b)

and up to 134 teeth in the radula sac of *Mitrolumna monodi* (see ROLÁN & BOYER, 2001). The primitive type of tooth is generally present in a higher number within the radula sac of vermivorous and generalist species of *Conus*. On the contrary, the molluscivorous and piscivorous types of tooth are usually present in lower number. The lowest observed number of teeth in radula sac was 20 for *Conus regius*, a specialized Amphinomids- hunting species. The highest ND was 130, observed in *C. beilarensis*. Thus, the general trend appear to have been towards a decrease of number, together with an increase of dimensions of the tooth.

Table 1 resumes the state of this character in a selected sample of species for each group.

Therefore, we conclude that a high number of teeth within the radular sac, a shared state of the character in turrids and in the majority of *Conus* species (generalist and vermivorous species) is plesiomorphic.

Conversely, a low number of teeth within the radula sac, a shared state of the character among the most derived type of teeth, i.e. the molluscivorous and the piscivorous type is apomorphic.

2. Relative length of the radular tooth, calculated as the ratio of shell length to DR (LC/DR)

As mentioned above, this character can be transformed in % of the shell length. This is the most important quantitative character because discrete intervals clearly separate at least the three main large trophic groups of *Conus* species.

Table 2 resumes data for some turrids and *Conus* species (most of data are from ROLÁN & RAYBAUDI (1994a, 1994b).

The general trend towards an increase in absolute as well as relative length of the tooth is evident from our sample.

From the analysis of our wide data set, we conclude that small size of the radular tooth, a state of the character shared by turrids, generalist and vermivorous species of *Conus* is plesiomorphic.

Conversely, the large size of radular tooth attained by fewer, extremely specialized species (including species known also from molecular study to have diverged very recently (i.e. *C. consors-C. magus*, *C. purpurascens-C. ermineus*, ESPIRITU *ET AL.*, 2001), i.e. piscivorous and molluscivorous species represent an apomorphy.

3. Presence (and position) or absence of Waist (W)

Waist has been defined as the constriction of the shaft, the columnar body of the radular tooth (NYBAKKEN, 1970). A waist is absent in old turrids and in many species of higher turrids. When present in higher turrids (Conidae *sensu* TAYLOR *et al.*, 1993) (i.e. *Mitrolumna sp.*, (Figs. 6-7) *Lovellona sp., Genota marchadi* (Fig. 32) it is located at the adapical third.

In *Conus* and *Conorbis*, a waist is present in the primitive and generalist type of tooth (as in *Conorbis coromandelicus*, Figs. 30-31), located at the same high position. During the post-metamorphic developmental stages of most vermivorous species, but often even in intra-capsular stages, a waist is initially present at the adapical third of the tooth reaching a central position at full maturity. The waist disappears in the transitional stages of a piscivorous tooth and is practically absent in the molluscivorous type of teeth.

Figs. 66 and 69A illustrate the presence of the waist during the ontogeny of the worm-hunting *C.trochulus*; Its presence in the generalist type of tooth can be observed in Figs. 19-29 and in Figs. 30-31 (*Conorbis coromandelicus*). Fig. 67 demonstrates that a waist is present only in the earliest ontogenetic stages of the fish-hunting *C. ermineus*.

In higher turrids, the presence of a waist can be observed in

Table 1. Average number of teeth in the radular sac for a selected sample of adult specimens from species differing in trophic specialization and geographic distribution

Conidae	shell size in mm (LC)	number of teeth(ND)
Vermivorous type:		
C. arenatus	26.6	22
C. limpusi	35.2	27
C. papuensis	22.9	30
C. daucus	31.3	30
C. borgesi	34.5	32
C. segravei	29.6	35
C. tribblei	54.3	42
C. ventricosus	32.4	47
C. pineaui	24.4	50
C. eburneus	40.3	57
C. bulbus	18.4	63
C. babaensis	24.8	78
C. zebroides	30.8	102
C. belairensis	32.0	122
piscivorous type		
C. salzmanni	18.7	20
C.ermineus	26.0	24
C. striatus	83.0	24
C. julii	52.0	30
C. terminus	55.2	38
C. achatinus	50.5	42
molluscivorous type		
C. lischkeanus	57.8	31
C. quercinus	107.6	40
C. patonganus	44.0	44
C. paulucciae	49.3	74
generalist type		
C. praecellens	41.8	44
C. profundorum	35.5	48
C. pagodus	48.5	71
C. jaspideus	21.5	85
C. deyncerorum	14.1	87

Table 2. Ratio between shell length (LC) and radular tooth length (DR) in several species of the different radular groups of Conidae, showing the % of tooth length with respect to shell length.

Conidae

	LC	DR	100/(LC/DR) = %
vermivorous type			
C. limpusi	32.4	0.66	2.3
C. gondawanensis	18.8	0.36	1.9
C. clarus	31.8	0.50	1.5
C. reductaspiralis	39.8	0.75	1.9
C. ventricosus	29.6	0.61	2.0
C. queenslandis	77.5	0.95	1.2
C. rufimaculosus	36.0	0.80	2.2
C. papuensis	22.9	0.36	1.6
C. wallangra	29.9	0.63	2.1
C. gloriakiensis	64.0	0.83	2.1
C. ritae	18.4	0.50	2.7
C. eburneus	40.3	0.49	1.2
C. pauperculus	16.8	0.37	2.2
C. cuvieri	11.3	0.41	3.6
C. miliaris	10.1	0.24	2.3
C. musicus	19.5	0.45	2.3
C. shikamai	16.7	0.42	2.5
C. characteristicus	25.8	0.58	2.2
C. pulicarius	17.2	0.32	1.8
C. hieroglyphus	18.6	0.39	2.1
C. echinophilus	13.5	0.26	1.9
C. belairensis	32.0	0.31	0.9
C. mercator	32.0	0.77	2.4
C. coffeae	36.5	0.70	1.9
C. fuscolineatus	31.0	0.79	2.5
piscivorous type			
C. sertacinctus	27.6	1.35	4.8
C. scalptus	22.3	1.15	5.1
C. barthelemyi	19.0	1.34	7.0
C. lovellreveei	33.2	1.37	4.1
C. stercusmuscarum	48.9	5.45	11.1
C. solomonensis	30.0	2.50	8.3
C. achatinus	47.7	4.25	8.9
C. mucronatus	26.9	1.11	4.1
C. gubernator	53.7	4.50	8.3
C. monachus	31.8	2.95	9.2
C. julii	52.0	3.00	5.7
C. terminus	55.2	6.12	11.0
C. striatus	62.8	7.20	11.5
molluscivorous type			
C. geographus	67.0	7.80	11.6
C. crocatus	50.2	2.30	4.5
C. paulucciae	55.0	4.55	8.2
C. omaria	57.0	4.60	8.0

	LC	DR	100/(LC/DR) = %
C. victoriae	54.0	4.50	8.3
C. lischkeanus	57.8	2.05	3.5
C. barbieri	26.0	1.91	7.3
C. patonganus	44.0	3.35	7.6
C. acuminatus	35.0	1.20	3.4
C. lividus	45.2	1.87	4.1
C. episcopatus	34.3	2.22	6.4
C. terebra	40.8	1.25	3.1
C. pennaceus	21.5	1.24	5.7
C. eximius	47.5	1.85	3.9
C. nicobaricus	50.7	1.03	2.0
C. quercinus	54.5	1.19	2.1
C. marmoreus	53.0	3.00	5.6
C. splendidulus	50.0	1.33	2.6
C. obscurus	28.1	3.85	13.7
generalist type			
C. vaubani	29.3	0.95	3.2
C. loyaltiensis	22.4	0.60	2.6
C. deyncerorum	15.0	0.28	1.8
C. eugrammatus	24.0	0.49	2.0
C. lizarum	20.8	0.25	1.2
C. pagodus	48.5	0.43	0.9
C. kimioi	14.0	0.26	1.8
C. rutilus	11.8	0.44	3.7
C. profundorum	35.5	0.52	1.4
C. aphroditae	16.1	0.25	1.5
C. orbignyi	38.0	0.32	0.8
C. lucidus	27.0	0.33	1.2
C. jaspideus	21.5	0.30	1.4
C. pealii	16.4	0.25	1.5
C. memiae	25.5	0.55	2.1
C. delesserti	60.6	0.61	1.0
C. bozzettii	41.8	0.42	1.0
C. acutangulus	10.0	0.18	1.8
C. praecellens	41.8	0.63	1.5
C. aff. *vanhingi*	16.7	0.30	1.7
C. stocki	26.8	0.25	0.9
C. longurionis	35.5	0.38	1.0
Conorbis coromandelicus	37.9	0.34	0.9
Turridae			
Genota marchadi	34.3	0.38	1.1
Genota vafra	30.0	0.12	0.4
Mitrolumna monodi	4.2	0.08	1.9
Mitrolumna saotomensis	3.7	0.07	1.9
Mangelia merlini	7.0	0.18	2.6

Genota marchadi (Fig. 32) and in *Mitrolumna* (Figs. 6-7) (see ROLÁN & BOYER, 2001).

Though a character certainly more typical of the tightly coiled *Conus* radular tooth than the turrids tooth, the presence of a waist is a shared character of some higher turrids, of the generalist species of *Conus* and *Conorbis* and of the great majority of vermivorous *Conus*.

We conclude that the presence of a waist is a plesiomorphy. The position of the waist may usefully differentiate the generalist type of tooth and several subgroups of vermivorous. Thus, this character would be better represented by a two state character: presence–absence and a binary state for its position: a) Present and high (about 1/3 radular tooth), b) Present and central (about 1/ 2 of the radula tooth) and –Absent (lost)

Thus, absence of a waist is a plesiomorphy in turrids. Loss of a waist is considered a derived state in *Conus*.

4. Relative length of the apical portion (PA), calculated by its relation with the absolute tooth length (DR/PA)

In the studied turrids, when a waist exists, it is located at the apical third (already mentioned for *Genota* and *Mitrolumna*).

All the vermivorous teeth studied in their ontogeny definitively show a short PA which increases in advanced stages. Examples may be found in ROLÁN (1992) (see Fig. 66), and in NYBAKKEN (1990).

In fish-hunting *Conus*, as *C. ermineus*, as well as in all the piscivorous type of teeth examined, PA is observed to increase since the earliest post-metamorphic stages (ROLÁN & BOYER, 2000) (Fig. 67). PA also increases during the ontogeny of the molluscivorous type of tooth, *C. fergusoni*, *C. pennaceus*, (see NYBAKKEN, 1988).

It is necessary to explain that because of the loss of the waist (W) in adult piscivorous and molluscivorous teeth, PA can be calculated only from the PB crossing point with the shaft, which is evident and marks the boundary between PA and PB.

We conclude that a PA <_ DR is a shared state of the character among higher turrids, and of generalist species and vermivorous species in *Conus* and *Conorbis*; additionally the PA increase is well documented by the ontogenetic change observed in worm-hunting, fish- and mollusc-hunting species of *Conus*.

Thus, we consider PA<1/2 DR a plesiomorphic character. Conversely, the extremely elongated PA observed in the molluscivorous type of tooth is here considered the most derived state of the character.

5. Presence or absence of a blade (F)

In turrids, the presence of a structure similar to a blade is infrequent. However the radular tooth of some species of *Benthofascis* (Fig. 12), *Phenatoma*, *Typhlodaphne*, and *Pontiothauma* (see POWELL, 1966) have a well defined blade.

In the tooth of post-metamorphic juvenile specimens of worm-hunting or fish-hunting *Conus*, there is no evidence of a blade in PA, (Figs. 66, 67 and 69). F is absent in the most primitive vermivorous teeth as *C. trovaoi* (Fig. 13), *C. neoguttatus* (Fig. 14) and *C. naranjus* (Fig. 15).

In mature stages of the vermivorous type of *Conus* tooth, the blade is usually covering most of PA, as it may be observed in *C. ventricosus* (Fig. 36), *C. miliaris* (Fig. 37), *C. borgesi* (Fig. 38). F is variable in size, as can be observed in *C. miruchae*, *C. borgesi* and *C. navarroi* (Fig. 68) or in other species (Fig. 70).

Thus, the presence of a blade is considered a derived state shared by only some turrids and by *Conus*.

6 Relative length of the blade (F) (as % of PA)

In a large number of *Conus* where a short F has been observed in the adult stage, a larger F has been observed during juvenile stages. Examples of the ontogenetic change of F are represented in Fig.66 for *C. trochulus*, a worm-hunting species.

A blade is probably present also in the generalist tooth; however, in this group the blade appears to turn into a barb (B) very rapidly during the ontogeny, therefore it is difficult to observe its transition (Figs. 19-27).

In the molluscivorous type of tooth, F is extremely short and it decreases inversely with tooth length (Figs. 54-65).

In fish-hunting species adopting the hook-and line capture strategy (Olivera, 1997)as in *C. ermineus* (Fig. 67) the gradual shortening of F may be observed during the transition from the vermivorous to the piscivorous tooth, a transition which has been correlated with a switch in the targeted prey from polichaets to fish. During the transitional stages the blade is shorter either in relation to PA and DR.

In the piscivorous tooth of fully adult, fish-hunting individuals, the blade is definitively turned into a barb (B2). Thus, in these teeth a blade is not absent but "shortened" since it has been transformed in an additional barb.

In conclusion: a high value of relative length of the blade is a primitive state of the character in the vermivorous tooth, while a short F is a derived state of the character. Finally, a very short blade changed into a second barb during the transitional stages from the vermivorous to the piscivorous type of tooth demonstrates that a short or transformed F is an apomorphic character shared by species of *Conus* possessing piscivorous and molluscivorous types of tooth. This situation is probably better described by a three.states of the characters.

7. Presence or absence of denticles in serration (D)

Serration is defined as a longitudinal row of denticles extending along or proximally from the adapical opening of the lumen (LOVEN,1847; PEILE, 1939; ROLÁN, 1992; KOHN *et al.*, 1999). When present, one or more rows of denticles may be present

A serration is absent in the radular teeth of almost all the species of the higher turrids examined. An apparently single row of small, rounded denticles was observed only in some species of *Mangelia* (Figs. 3, 10-11) but the interpretation of this imagine is dubious, because they could be nodules or holes.

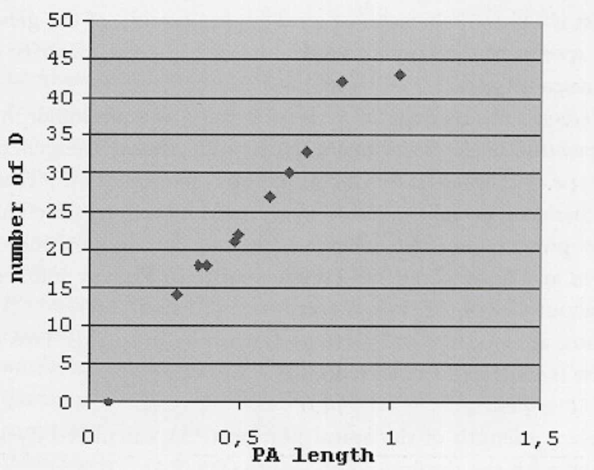
In *Conus*, a serration is present in the mature tooth of one group of generalist species, as *C. acutangulus* (Fig. 19) and *C. praecellens* (Fig. 20), where it consists only of three denticles, early transformed into cusps during the ontogeny. In the primitive type of teeth and during the juvenile stages of the vermivorous teeth, denticles are either absent, as in *C. trochulus*,

Table III A.

Number of denticles in serration (D) (counting only a single row) during the ontogeny of *C. trochulus* from Cape Verde Islands.

Shell	LC in mm	DR	D in S
Fig 69 A	1.39	0.06	0
Fig. 66 A:	14.3	0.29	14
B:	16.8	0.36	18
C:	15.7	0.39	18
D:	17.7	0.48	21
E:	20.1	0.49	22
F:	26.4	0-62	27
G:	31.6	0.66	30
H:	35.3	0.72	33
I:	43.5	0.84	42
J:	52.5	1.03	43

Table III B. Relation of D *vs.* PA, in *C. trochulus*



C. diminutus and *C. curralensis* (Fig. 69), or they are just sketched and rounded in the most simple teeth, as in *C. naranjus* (Fig. 34) or in *C. fuscoflavus* (Fig. 35). Adult individuals of the great majority of worm-hunting *Conus* species have one or more rows of denticles within the radula serration.

Denticles are absent in the early post-metamorphic vermivorous stages of the piscivorous *C. ermineus*; they are present in the transitional stages; then again they are absent i.e. lost completely) in the mature piscivorous tooth (Fig. 67). D are visible in species which retain as adult, an intermediate form of the piscivorous type of tooth, as in *C. cordigera* (Fig. 42) and *C. salzmanni* (Fig. 43).

In the molluscivorous type of tooth the serration is vestigial and the small and rounded denticles are likely non-functional (Figs. 57-60, 64).

We conclude that absence of a serration is a primitive state of the character shared by most turrids and by *Conus* species, during the earlier developmental stages of the generalist, primitive and vermivorous type of tooth The presence of denticles within the serration is here considered a derived state of the character shared by the majority of worm-hunting species of *Conus*. The vestigial presence of a serration in the mollusc-hunting species and the complete loss of D in fish-hunting species are considered as the most derived state of the character.

8 Number of denticles in serration (D)

In the generalist type of *Conus* teeth in which a serration is present, the number of denticles is very low (3-5) (Figs 19-20). In the primitive type of tooth, denticles were observed sometimes, in teeth clearly evolving towards a molluscivorous type, as in *C. carnalis* (Fig. 54) or *C. splendidulus* (Fig. 71).

The ontogeny of a typical worm-hunting species as (for example *C. trochulus*, Fig. 69) shows that in early post-metamorphic stages the saw bears no denticles, or they are few and arranged in a single row, while in the following stages an appreciable number of D increases with shell length. This was similar for other species studied.

The vestigial denticles in the hidden, non-functional serration of the larger molluscivorous teeth are scantly visible, nevertheless their number is enormously increased: the serration of *C. ammiralis pseudocedonulli* (a mollusc-hunting species) (Fig. 65) bears more than 300 denticles. Moreover, the number of denticles correlates directly with an increasing PA, as can be observed in Table III, for *C. trochulus*.

From our results, we conclude that a low number of D is a plesiomorphy shared by a group of *Conus* species with a generalist and primitive type of tooth and by subadult individuals of almost all the worm-hunting *Conus* species examined.

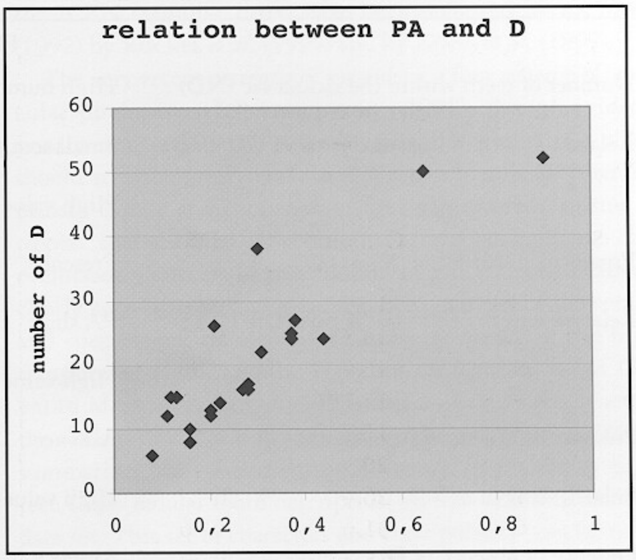
Conversely, the higher number of D shared by adult worm-hunting and mollusc-hunting species of *Conus* is considered a derived character. The loss of a serration is considered an apomorphy peculiar of the adult piscivorous tooth.

9. Number of rows of D

This character is not present in each type of tooth. However, since it is so widely distributed in the main trophic group (worm-hunting species probably approaches >70% of *Conus* species) it is useful to analyse its state for differentiating sub-

Table IV. Relation between PA (relative length in mm) and D in several species.

C. barbieri	26.0	40
C. crocatus	50.2	60
C. lischkeanus	57.8	31
C. lividus	45.2	50
C. acuminatus	35.0	48
C. patonganus	44.0	44
C. paulucciae	49.3	74
C. pennaceus	21.5	43
C. quercinus	39.0	90
C. quercinus	107.6	40
C. terebra	40.8	52
C. victoriae	54.0	50



groups of species with a vermivorous type of tooth).

The ontogenetic change observed in several species (*C. borgesi*, *C. trochulus* in ROLÁN, 1992) show a clear trend towards an increase in number of denticles within a single row, as well as an increase in number of rows.

We thus conclude that, within the vermivorous teeth of *Conus*, a single row of denticles within the serration is a primitive state of the character, while two or more rows represent a derived state.

Qualitative characters

10. Shape of denticles within the serration

This character is not present in turrids and in some generalist teeth, but in at least one large group of species with a generalist type of tooth (*i.e.* species usually assigned to (sub) genus *Conasprella* Iredale) the few denticles D are highly enlarged like in *C. praecellens* (Fig. 20).

In the vermivorous type of tooth and during the developmental stages of post-metamorphic molluscivorous and/or piscivorous teeth, the early appearing denticles in the serration are like small tubercles, as in *C. miruchae* (Fig. 70 A). In most species or in more advanced developmental stages, the denticles often become sharp-pointed, as in *C. ateralbus* (Fig. 70 B) and increase their size, sometimes very evidently, as in *C. tabidus* (Fig. 70 C), sometimes curving, as in *C. planorbis* (Fig. 70 D) and sometimes becoming very elongated as in *C. miles* (Fig. 70 E).

Tubercle-like denticles are thus considered a primitive state of the character, while elongated or pointed is a derived state of the character.

11. Basal angle of the serration (ABS)

The ABS is the angle formed by the basal part of the serration, in the side opposite to the cusp, with the axis of the tooth (Fig. 68) (ROLÁN, 1992 and ROLÁN & RAYBAUDI MASSILIA, 1994a).

In turrids, it is not easy to find a serration and to measure its angle with the tooth axis. In some teeth as in *Genota marchadi* (Fig. 32) a very acute angle can be supposed.

This character is difficult to be interpreted in some generalist teeth as in *C. teremachii* (Fig. 27) or in *C. californicus* (Figs. 28-29). At least in one group of generalist teeth where the few denticles D are highly enlarged as, for example, in *C. acutangulus* (Fig. 19) or in *C. praecellens* (Fig. 20), the ABS can be studied and it is acute. In other teeth, even without a serration, where the ABS can be supposed, as in *C. elegans* (Fig. 16), *C. stocki* (Fig. 17) or *C. lizarum* (Fig. 18) the angle is acute.

As it may be observed in *C. naranjus* (Figs. 15) and in *C. lizarum* (Fig. 18), the is ABS is acute in the primitive, older vermivorous and even in the more derived type of tooth of *C. miruchae* (Fig. 68 A).

In the most derived vermivorous teeth the ABS can reach 60º, like in *C. borgesi* (Fig. 68 B) or near 90º as in *C. navarroi* (Fig. 68 C). This angle increases in the intermediate type of molluscivorous tooth as in *C. carnalis* (Fig. 54) or in *C. moreleti* (Fig. 60). However, this angle can not be evaluated in the larger molluscivorous and piscivorous teeth perhaps because elongation of the teeth makes it very acute.

Thus, in the vermivorous type of tooth an acute ABS is plesiomorphic and increase of the angle is the derived state. The state of the character is less clear in the primitive, generalist or in the molluscivorous and piscivorous type of teeth.

12. Presence or absence of a cusp (C) and its size

A cusp is absent in all the turrid radular teeth known.

In the earlier developmental stages of the post-metamorphic vermivorous type of tooth there is no prominence at the base of the S, (for example in *C. elegans* Fig. 16). In several generalist

Table V. Polarity state of the radular tooth characters studied.

	PLESIOMORPHIC	APOMORPHIC
Number of teeth within the radula sac (ND)	High number of teeth	Low number of teeth
Relative length of the radular tooth (LC/DR)	Small tooth	Large tooth
	High value of ratio	Low value of ratio
Presence or absence of Waist (W)	Presence	Absence
Relative length of the apical part (DR/PA)	PA short	PA large
	High value of ratio	Low value of ratio
Presence or absence of a blade (F)	Absence	Presence
Relative length of F (% of PA)	High value	Low value
Presence or absence of D	Absence	Presence
Number of D	Low number	High number
Number of rows of D	Few rows	More rows
Shape of D	small tubercles	Large, sharp
Basal angle of the serration (ABS)	< 45º	>45º
Presence or absence of a cusp (C)	Presence	Absence or transformation
Presence or absence of a basal spur	Presence	Absence
Width of the base (BA/DR)	Large base High value of ratio	Small base Low value of ratio
Shape of the base (BA)	Rectangular, large, obliquely elongate	Small, rounded

teeth, the cusp is changed early into a barb, as in *C. acutangulus* (Fig. 19) or in *C. praecellens* (Fig. 20). In the more typical vermivorous tooth, the cusp is present and usually small (i.e. in *C. flavusalbus* (Fig. 35), *C. ventricosus* (Fig. 36) and more prominent in other cases, as in *C. characteristicus* (Fig. 72), *C. borgesi* (Fig. 38) or *C. guinaicus* (Fig. 40).

Within a specialized line of vermivorous, (feeding on amphinomid worms) as *C. duffyi* (Fig. 73) and *C. imperialis* (Fig. 74) the prominent cusp is transformed into a barb. Also in the intermediate stage of piscivorous tooth the cusp is changed into a B3, i. e., *C. salzmanni* (Fig. 43) and in *C. jickeli* (Fig. 44) as it is well documented by the ontogenic change observed in *C. ermineus* (Fig. 67).

In the molluscivorous type of tooth, a cusp is always present and relatively prominent with respect to tooth width (Figs. 54-65).

Thus, the presence of a cusp is only evaluable in the primitive and in the vermivorous teeth, where its presence and its more prominent size is considered a derived state.

13. Presence or absence of a basal spur (SP)

Spur is defined as a distally oriented projection from the base of the radular tooth (PEILE, 1939).

A spur (SP) is absent in Drillidae, Clavatulidae and Crassispirinae. A spur is present in most species of higher turrids (Conidae *sensu* TAYLOR *et al.*, 1999), as Mangelinae (Figs. 3-5, 8-11), Clathurellinae and Onopotinae, though barely noticeable in some genera, as *Mitrolumna* (Figs. 6-7), or *Borsonella*, for example.

In *Conus* species, a basal spur (SP) appears in the most primitive type of teeth (Figs. 13-18); it is always present in the vermivorous (Figs. 34-40), and generalist type (Figs. 19-29), while it decreases in size in the large molluscivorous teeth (Figs.

54-65) and is definitively absent (lost) in the piscivorous teeth(Figs. 43-53).

The presence of SP, a shared state of the character of higher turrids, generalist and vermivorous *Conus* radular tooth, is here considered a primitive state of the character, therefore a plesiomorphy in *Conus*. Conversely, a very small sized or barely evident spur as well as the loss of a spur are derived states of the character.

14 Width of the base (BA/DR)
The width of the base has been defined as the ratio of base size on the radular tooth length (ROLÁN, 1992, ROLÁN & RAYBAUDI 1994). It coincides with the English translation of the terms proposed by KOHN *et al.* (1999).

The base is relatively larger in higher turrids teeth (Figs. 3-12), as well as in the primitive type of *Conus* teeth, (Figs. 16-18) in the generalist teeth (Figs. 19-27) and in the earlier developmental stages of the vermivorous teeth (Fig. 13-15, 34-35). BA decreases in the more typical type of vermivorous teeth (Figs. 36-40) and in the molluscivorous type of tooth (Figs. 54-65). Therefore the trend observed for width of the base is its decrease from the more primitive state of the character, shared by the great majority of *Conus* species, towards a derived state, shared by species of *Conus* with a molluscivorous and piscivorous type of teeth.

High values of this ratio are plesiomorphic, smaller ones are apomorphic.

15. Shape of the base (BA)
The base is relatively broad and often heavily reinforced in higher turrids as *Mangelia* (Figs. 3, 8-9), sometimes elongate (Figs. 4-5, 10-11), *Mitrolumna* (Figs. 6-7), *Genota* (Figs. 32-33). Furthermore, in primitive (Figs. 16-18) and older vermivorous (Fig. 13-15) it can be rounded; it is rectangular in some vermivorous lineages (Figs. 36-40). In piscivorous (Figs. 42-53) its shape is relatively small and rounded. In most generalist species (Figs. 19-27) is broad and its shape is obliquely elongated. In the molluscivorous tooth (Figs. 54-65) it is relatively small and rectangular. The shape and size of BA can define some lineage.

Thus, the broad rectangular and obliquely elongated base, a widespread state of the character in higher turrids and generalist, primitive and vermivorous types of *Conus* radular tooth, is a primitive state of the character in *Conus*. Conversely, a smaller and rounded base, a character shared by species of *Conus* with a molluscivorous and piscivorous type of tooth is an apomorphy.

DISCUSSION

Few molluscan groups suffered the difficulty to organize the available information from such a diverse sources as the Conidae. We face the problem raised from a large and taxonomically difficult group, with a rapidly increasingly number of species descriptions, for which an uncontestable stubborness of researchers led to maintain under a single genus as many as probably 750 living species, notwithstanding a stand-by taxa-park including 90 infra-sub-generic validly established names. The historical reasons of such a non-conventional approach (according to the ICZN standing rules) have been reviewed by DA MOTTA (1992) by ROCKEL *et al.* (1995) and by KOHN *et al.* (1999).

The very recent attempt of providing a first scheme of molecular phylogeny (ESPIRITU *ET AL.*, 2001), though evidently poorly resolved at the several nodes determinating clades, should stimulate researchers and it urgently calls for interdisciplinary debate and cooperation. Prey-capture mechanisms and trophic specialization are certainly essential determinants of the evolutionary success of this molluscan group. Both factors are clearly correlated with the sophisticated delivery of the complex and species-specific venom of *Conus*, by means of the highly transformed radular tooth. Thus, we confirm our belief (RAYBAUDI MASSILIA & ROLAN, 1995) that a phylogenetic scheme of the radular tooth will give an important contribution. Table V summarizes our conclusions on character state polarity for fifteen *Conus* radular tooth descriptors, based on the analysis of our data set. This set of characters and their polarity can be used in future for the elaboration of a cladistic analysis in order to compare the results with the molecular phylogenetic scheme (partial) proposed by Espiritu et al.2001.

Previous recent analysis (NISHI & KOHN, 1999, KOHN *et al.*, 1999) reviewed and defined a number of additional characters which may be useful for distinction at the species level and to discriminate subgroups within the five main types of radular tooth.

In the present work the known types of radular teeth have been shown and 15 characters and morphometric parameters employed in previous works to describe the different radula teeth were studied , determining the plesiomorphy or apomorphy of theit state.

As explained under Methods, we have maintained our original terms for the radular characters. Finally, we are more and more convinced that for a complete comparison, the use of camera lucida drawings is more useful than SEM photographs, because the latter may provide a good interpretation of the shape of the tooth, but does not allow to observe structure details which are extremely useful for comparative analysis.

Addendum
Information on the species whose radular teeth are presented with the indication of locality data of collected specimens.

Benthofascis sp. (from POWELL, 1966)
Conorbis coromandelicus E. A. Smith, 1894
Conus achatinus Gmelin, 1791, Thailand
Conus acuminatus Hwass, 1792, Dijbouti
Conus acutangulus Lamarck, 1810, Hawaii
Conus aphrodite Petuch, 1979, Philippines
Conus algoensis simplex Sowerby, 1857, South Africa
Conus amadis Gmelin, 1791, S. India
Conus ammiralis Linnaeus, 1758, Philippines
Conus ammiralis pseudocedonulli Blainville, 1818, Reunion Island

Conus arenatus Hwass, 1792, Comores Islands
Conus ateralbus Kiener, 1845, Cape Verde Archipelago
Conus australis Holten, 1802, Philippines
Conus babaensis Rolán & Röckel, 2001, Angola
Conus barbieri G. Raybaudi Massilia, 1995, Philippines
Conus barthelemyi Bernardi, 1861, Reunion
Conus belairensis Pin & Leung Tack, 1989, Senegal
Conus borgesi Trovão, 1979, Cape Verde Archipelago
Conus bozzettii Lauer, 1991, E. Somalia
Conus bulbus Reeve, 1843, Angola
Conus californicus Reeve, 1844, Gulf of California, USA
Conus carnalis Sowerby, 1879, Angola
Conus cedonulli Linné, 1767, Lesser Antilles
Conus chaldeus Röding, 1798, Pacific
Conus caracteristicus Dillwyn, 1817, Thailand
Conus coffeae Gmelin, 1791, Solomon Islands
Conus comatosa Pilsbry, 1904, Philippines
Conus cordigera Sowerby, 1866, Philippines.
Conus crocatus Lamarck, 1810, Solomon Is.
Conus curralensis Rolán, 1986, Cape Verde Archipelago
Conus cuvieri Crosse, 1858, Red Sea
Conus daucus Hwass, 1792, Brazil
Conus delanoyae Trovão, 1979, Cape Verde Archipelago
Conus delesserti Récluz, 1843, USA
Conus deyncerorum Petuch, 1995, Mexico
Conus diminutus Trovão & Rolán, 1986, Cape Verde Archipelago
Conus duffyi Petuch, 1992, Los Roques, Venezuela
Conus eburneus Hwass, 1792, Thailand
Conus echinophilus (Petuch, 1975), Senegal
Conus elegans Sowerby, 1895, Aden Gulf
Conus episcopatus Da Motta, 1982, Thailand
Conus ermineus Born, 1778, Senegal; Cape Verde Archipelago
Conus eugrammatus Bartsch & Rehder, 1943, Philippines
Conus eximius Reeve, 1849, Philippines
Conus fergusoni Sowerby, 1873, Gulf of California; Ecuador
Conus flavusalbus Rolán & Röckel, 2000, Angola
Conus franciscoi Rolán & Röckel, 2000, Angola
Conus friedae (Da Motta, 1991), Sri Lanka
Conus fuscolineatus Sowerby, 1905, Angola
Conus geographus Linnaeus, 1758, Solomon Islands
Conus gloriakiiensis Kuroda & Ito, 1961, Japan
Conus gondawanensis Röckel & Moolenbeek, 1995, New Caledonia
Conus guinaicus Hwass, 1792, Dakar, Senegal
Conus gubernator Hwass, 1792, Mozambique
Conus hieroglyphus Duclos, 1833, Nethelands Antilles
Conus imperialis Linnaeus, 1758, Reunion Island
Conus infrenatus Reeve, 1848, South Africa
Conus jaspideus Gmelin, 1791, Colombia; Bahamas
Conus jickeli Weinkauff, 1873, Djibouti
Conus julii Liénard, 1870, Reunion Island
Conus kimioi Habe, 1965, Philippines
Conus leehmani Da Motta & Röckel, 1979, Reunion Islands
Conus limpusi Röckel & Korn, 1990, Queensland
Conus lischkeanus Weinkauff, 1875, N. Somalia
Conus lividus Hwass, 1792, Hawaii
Conus lizarum Raybaudi & Da Motta, 1992, N. Somalia
Conus longurionis Kiener, 1845, Philippines
Conus lovellreveei G. Raybaudi Massilia, 1993, India
Conus lucidus Wood, 1828, Panama
Conus marmoreus Linnaeus, 1758, New Caledonia
Conus memiae Habe & Kosuge, 1970, Philippines
Conus mercator Linnaeus, 1758, Senegal
Conus miles Linnaeus, 1758, Reunion Island
Conus miliaris Hwass, 1792, Queensland, Australia.
Conus miruchae Röckel, Rolán & Monteiro, 1980, Cape Verde Archipelago
Conus moreleti Crosse, 1858, Hawaii
Conus monacus Linnaeus, 1758, Solomon Islands
Conus mucronatus Reeve, 1843, Philippines
Conus musicus Hwass, 1792, New Caledonia
Conus naranjus Trovão, 1975, Angola
Conus navarroi Rolán, 1986, Cape Verde Archipelago
Conus neoguttatus Da Motta, 1991, Angola
Conus nicobaricus Hwass, 1792, Philippines
Conus obscurus Sowerby, 1833, Reunion Island
Conus omaria Hwass, 1792, Philippines
Conus orbignyi Audouin, 1831, Philippines
Conus pagodus Kiener, 1845, Philippines
Conus papuensis Coomans & Moolenbeek, 1982, New Guinea
Conus patonganus da Motta, 1982, Thailand
Conus paulucciae Sowerby, 1876, Reunion Island
Conus pauperculus Sowerby I & Sowerby II, 1834, South Africa
Conus pealii Green, 1830, Florida
Conus pennaceus Born, 1778, Hawaii
Conus pineaui Pin, 1989, Senegal
Conus planorbis Born, 1778, Philippines
Conus praecellens A. Adams, 1854, Philippines
Conus profundorum (Kuroda, 1956), New Caledonia
Conus pulicarius Hwass, 1792, Hawaii
Conus queenslandis da Motta, 1984, Australia
Conus quercinus Lightfoot, 1786, Mozambique; Reunion Islands
Conus ranonganus da Motta, 1978. Andaman Sea; Solomon Islands
Conus reductaspiralis Walls, 1979, W. Australia
Conus ritae Petuch, 1995, Honduras
Conus rubropennatus Da Motta, 1982, Reunion Island
Conus rufimaculosus Macpherson, 1959, Queensland

Conus rutilus Menke, 1843, W. Australia
Conus salzmanni Raybaudi Massilia & Rolán, 1995, N. Somalia
Conus scalptus Reeve, 1843, Philippines
Conus segravei Gatliff, 1891, S. Australia
Conus sertacinctus Röckel, 1986, Solomon Islands
Conus shikamai Coomans & Moolenbeek, 1990, Philippines
Conus solomonensis Delsaerdt, 1992, Solomon Islands
Conus spectrum Linné, 1758, Queensland
Conus splendidulus Sowerby, 1833, Yemen
Conus stercusmuscarum Linnaeus, 1758, Solomon Islands
Conus stocki Coomans & Moolenbeek, 1990, Oman
Conus striatus Linnaeus, 1758, Philippines; Reunion Island
Conus sulcocastaneus Kosuge, 1981, Philippines
Conus tabidus Reeve, 1844, Cape Verde Archipelago
Conus teramachii Kuroda, 1956, Philippines
Conus terebra Born, 1778, Philippines
Conus terminus Lamarck, 1810, Reunion Island
Conus timorensis Hwass, 1792, Mauritius
Conus tribblei Walls, 1977, Philippines
Conus trochulus Reeve, 1844, Cape Verde Archipelago
Conus trovaoi Rolán & Röckel, 2000, Angola
Conus aff. vanhyningi Rehder, 1944, Aruba, Antilles
Conus vaubani Röckel & Moolenbeek, 1995, New Caledonia
Conus ventricosus Hwass, 1792, Portugal
Conus venulatus Hwass, 1792, Cape Verde Archipelago
Conus victoriae Reeve, 1843, W. Australia
Conus wallangra Garrard, 1961, W. Australia
Conus zapatosensis Röckel, 1987, Philippines
Conus zebroides Kiener, 1845, Angola
Crassispira callosa (Valenciennes, 1840), Ghana
Crassispira funebralis Fernandes, Rolán & Otero-Schmitt, 1995, Angola
Genota marchadi Pin, 1993, Senegal
Genota vafra Sykes, 1905, Angola
Mangelia albilonga Rolán & Otero-Schmitt, 1999, Angola
Mangelia congoensis Thiele, 1925, Angola
Mangelia digressa Rolán & Otero-Schmitt, 1999, Angola
Mangelia merlini Dautzenberg, 1910, Mauritania
Mangelia pontyi Dautzenberg, 1910, Mauritania
Mitrolumna monodi (Knudsen, 1956), Senegal
Mitrolumna saotomensis Rolán & Boyer, 2001, São Tomé Island

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